# THE SYSTEMATICS OF THE CRABS OF THE FAMILY VARUNINDAE (BRACHYURA, DECAPODA)

**NG NGAN KEE**

***(B. Sc., NUS)***

**NATIONAL UNIVERSITY OF SINGAPORE**

**2006**

# THE SYSTEMATICS OF THE CRABS OF THE FAMILY VARUNINDAE (BRACHYURA, DECAPODA)

**NG NGAN KEE**

***(B. Sc., NUS)***

**A THESIS SUBMITTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY**

**DEPARTMENT OF BIOLOGICAL SCIENCES**
**NATIONAL UNIVERSITY OF SINGAPORE**

**2006**

## ACKNOWLEDGEMENTS

I would like to thank my supervisor, Professor Peter K.L Ng for his tremendous patience, exhaustive guidance, and his invaluable discussion about the topic.

Thanks are also due to Professor Peter K.L Ng for his research grants (RP960314 to Dr. P.K.L. Ng); National Science and Technology Board (now A*STAR), NUS Research Project grants, Lady McNecice for financial support to attend conferences and visit to overseas museums.

My deepest gratitude to all the guys and gals (past and present) in the Systematics and Ecology Laboratory, who had been, and still are, putting up with my nuisances and nonsense and for their wonderful help (Dr. Darren Yeo, Dr. Tan Swee Hee, Dr. Tan Heok Hui, Dr. Leong Tzi Ming, Dr. Daisy Wowor; Miss Joelle Lai, Miss Zeehan Jaafar, Mr. Tran Anh Duc; Mr. Rubeun Gopalasamy, M. Norman Lim; Mr. Jose Christopher E. Mendoza. Particularly, Dr. Darren Yeo and Dr. Tan Swee Hee for laboriously going through my thesis despite their heavy workloads, Mr. Tran Anh Duc and Mr. Mendoza with the photography of the specimens. Dr. Tohru Naruse for his help with scanning the figures needed in this report.

My sincere thanks to the following colleagues for their guidance and discussion, and their help with loan of specimens from their respective museums and institutions, their hospitality when I was visiting their museums:

**A) East Asia**

**Professor Yang Siliang** (Beijing National History Museum, Beijing, People's Republic of China); **Professor Dai Ai-Yun (deceased), Dr. Chen Guoxiao, Dr. Li Shuqiang (**Institute of Zoology, The Chinese Academy of Sciences, Beijing, People's Republic of China); **Professor Liu Ruiyu, Professor Chen Huilian (deceased), Dr. Li Xinzheng, Dr. Yu Haiyan (**Institute of Oceanography, The Chinese Academy of Sciences,

Qingdao, People's Republic of China); **Dr. Fang Xiaohua (**Xiamen Institute of Oceanology, Xiamen, People's Republic of China).

**Dr. Jeng Meng-Shiou (**Institute of Zoology, Academia Sinica, Nankang, Taiwan); **Dr. Wang Chia-Hsiang (**National Taiwan Museum, Taipei, Taiwan; **Dr. Ho Ping-Ho (**National Museum of Marine Sciences and Oceanology, Taiwan); **Dr. Lee Kuan-Xin (**Pei Kuan Museum, Hua-Lian, I-Lan county, Taiwan); **Professor Yu Hsiang-Ping, Professor Chan Tin-Yam (**National Taiwan Oceanography University, Keelung, Taiwan); **Dr. Shih Hsi-Te (**National Chung Hsing University, Taichung, Taiwan); **Dr. Huang Jung-Fu (**National Kaoshiung University of Management and Technology, Kaohsiung, Taiwan); Dr. Liu Hung-Chang **(**Institute of Zoology, Academia Sinica, Nankang, Taiwan).

**Dr. Tomuyuki Komai (**Natural History Museum & Institute, Chiba, Japan); **Dr. Junji Okuno** (Coastal Branch of Natural History Museum & Institute, Chiba, Japan); **Dr. M. Takeda (**National Museum of Science and Technology, Tokyo Japan); **Professor S. Shokita, Dr. Yukio Nakasone, Dr. Tohru Naruse (**Department of Marine Sciences and Chemistry, University of Ryukyus, Okinawa, Japan); **Dr. K. Muraoka** (Kanagawa Prefectural Natural History Museum, Kanagawa, Japan).

**B) South East Asia**

**Dr. Daisy Wowor (**Museum Zoologicum Bogoriense, Research Center for Biology, Indonesian Institute of Sciences, Cibinong, Indonesia).

**BMRI (**Marine Research Institute, Universiti Malaysia Sabah, and Sabah Museum, Malaysia)**; SMUM (**Sabah Museum, Universiti Malaysia, Malaysia).

.

**Professor Phaibul Naiyanetr (**Department of Biology, Chulalongkhorn University, Bangkok, Thailand).

**Ms. Marivene Manuel (**National Museum, Manila, Philippines); **Dr. Lawrence Liao and his students (**University of San Carolos, Cebu City, Philippines).

**Mrs. Yang Chang Man, Mr. Yeo Keng Loo (deceased), Ms. Lua Hui Kheng, Mr. Kelvin Lim, Ms. Greasi Simon (**Zoological Reference Collection, Raffles Museum of Biological Research, National University of Singapore, Republic of Singapore)

**C) Australia and New Zealand**

**Dr. Diana Jones, Ms. Melissa Hewitt (**Western Australian Museum, Perth, Australia); **Dr. Peter Davie** Queensland Museum, Brisbane, Australia); **Dr. Shane Ahyong** (National Institute of Water and Atmospheric Research, (NIWA), Wellington, New Zealand)

**Assoc. Professor Colin McLay (**School of Biological Sciences, Canterbury University, Canterbury, New Zealand).

**D) India**

**Professor Antony Fernando; Professor A. Ajamal Khan; Professor T. Kundapundi; Dr. Olivia Fernando; Dr. S. Ravichandran** (Centre of Advanced Study in Marine Biology, Annamalai University, Porto Novo, India).

**E) Europe**

**Professor Dr. Daniele Guinot, Dr. Alain Crosnier, Dr. Nguyen Ngoc-Ho and Mr. Regis Cleva** (Muséum National d'Histoire Naturelle , Paris, France).

**Professor Lipke B. Holthius, Dr. Charles Fransen** (Nationaal Natuurhistorisch Museum [formerly Rijksmuseum van Natuurlijke Historie], Leiden, The Netherlands); **Dr. Dirk Plavoet** Zöologisch Museum Amsterdam, Universiteit van Amsterdam, Amsterdam, The Netherlands).

**Professor Micheal Türkay, Dr. Micheal Apel and his team (**Senckenberg Natural History Museum, Frankfurt am Main, Germany); **Professor Dr. Angelika Brandt**

**(**Biozentrum Grindel und Zoologisches Museum (formally Zoological Institute and Museum), Universität Hamburg, Hamburg, Germany); **Dr. Oliver Charles Coleman (**Museum für Naturkunde, Humbolt-Universität zu Berlin, Berlin, Germany). **ZSM (**Zoolog. Staatssammlung Münich, Münich, Germany).

**Dr. Paul F. Clark (**Natural History Museum, London, United Kingdom); **Dr. Ray Ingle (**Natural History Museum, London, United Kingdom).

**Dr. Peter Dworschak (**Naturhistorisches Museum in Wien, Vienna, Austria).

**Curator** (Zoological Museum, University of Copenhagen, Copenhagen, Denmark).

**Dr. Ambros Haeggi** and **Dr. Urs Wüest** (Naturhistorisches Museum Basel, Basel, Switzerland).

**<u>South Africa</u>**

**Ms Liz Hoenson, (**South African Museum, Cape Town, South Africa).

**<u>United States of America</u>**

**Dr. Raymond Manning (deceased), Dr. Rafeal Lemaitre and Dr. Chris Tudge (**United States National Museum of Natural History, Smithsonian Institution, Washington D.C., United States of America); **Dr. Patsy A. McLaughlin** (Shannon Point Marine Station, Washington State, United States of America). **Mr. George Holm** (Northwest Shell Club, Seattle, United States of America).

**<u>Others</u>**

I would also like to thank the staff members of Department of Biological Sciences, National University of Singapore, for their help and support throughout the candidature period.

My sincere thanks to everyone who has contributed to make this study possible.

My family members (Mama, Lao-Pa, Erjie, Sanjie), my cousins, uncles and aunties and all my friends for standing behind me all these years, especially the past one year during my personal crisis.

## TABLE OF CONTENTS

## LIST OF TABLES

## SUMMARY


Crabs of the family Varunidae are a large group of primarily marine and freshwater crabs that occur in tropical to temperate seas worldwide. Currently, there are 19 known genera with over 100 known species, many of which are of commercial, economic, medical and scientific importance. Varunid crabs also have one of the most diverse habitat ranges, from freshwater to marine, and occurring in caves and high mountains to the deep sea and hydrothermal vents. The last comprehensive review of this family was done more than a hundred years ago by Alcock (1900), and many modern workers still follow the system in which the varunid crabs are regarded as a subfamily of the Grapsidae. In recent years, however, some molecular and larval studies have argued for the recognition of these grapsoid subfamilies as full families. The present study reviews and revises all the genera and species now regarded as members of the Varunidae to ascertain if the grouping is natural. Its status as a distinct family is also assessed and its relationship with other taxon examined. A cladistic analysis, using adult morphological characters, was conducted to examine these relationships. The study uses traditional characters as well as a variety of new sexual and non-sexual features which throw new light on how these taxon are identified and classified.

The Varunidae is here shown to be a monophyletic taxa. Within the Grapsoidea, where the Varunidae belongs, the study also recognizes five other families: Grapsidae *sensu stricto*, Sesarmidae, Gercarcinidae, Plagusiidae and Glyptograpsidae. The two recognized subfamilies in the Varunidae are redefined (notably the Cyclograpsinae), and two new subfamilies are established – Gaeticinae and Thalassograpsinae. One enigmatic Indo-West Pacific genus associated with hydrothermal vents, *Xenograpsus*, is shown to be unrelated to varunids despite superficial similarities, and is transferred to a new family, Xenograpsidae. One genus, *Gnathograpsus*, long synonymised under *Ptychognathus*, is resurrected. A total of 13 new genera and eight new species are also described in this study. All the species, genera and subfamilies are diagnosed and/or described, and keys are provided.

## DISCLAIMER

**THIS REPORT IS NOT TO BE CONSIDERED AS PUBLISHED WORK.**

**ALL THE NEW NAMES USED IN THIS THESIS HAVE TO BE VALIDATED IN FORMAL PUBLICATIONS.**

# INTRODUCTION

The crabs of the superfamily Grapsoidea MacLeay, 1838, form a large group of primarily inter-tidal crabs that occur in tropical to temperate seas worldwide. While many burrow into soft sediments, others live in crevices and under stones on rocky shores. Traditionally, this taxon was regarded just as a family (Grapsidae) with four subfamilies - Grapsinae MacLeay, 1838, Varuninae Alcock, 1900, Sesarminae Dana, 1852, and Plagusiinae 1852, Dana (see Crosnier, 1965). In recent years, this group has been receiving considerable attention with regards to their alpha taxonomy as well as phylogeny after reappraisals of their larval, genetic and adult morphology. These studies point to the need for a more radical re-evaluation of the Grapsidae and Grapsoidea; and the current consensus is that the traditional subfamilies should be regarded as distinct families instead, i.e Grapsidae sensu stricto, Varunidae, Sesarmidae and Plagusiidae (see Schubart *et al.,* 1999; Ng *et al.*, 2001; Martin & Davies, 2001).

The Varunidae was established as a subfamily in 1900 by Alcock (see also later) for a group of crabs that were found to be straddling between freshwater rivers and coastal areas. It currently comprises 19 known genera with over 100 known species, many of which are of commercial, economic and scientific importance. Crabs from this family are known for their abilities to live in both freshwater and marine environments. The adults are usually found along the banks of the streams, hidden under rocks or pebbles, or burrow into the banks of rivers and shorelines. Almost all adults have to migrate to brackish waters or the open sea for spawning. The larvae of these crabs are salinity-dependent, and for the freshwater species, the juveniles will migrate back to this habitat when they metamorphose or are sexually mature.

## A. Importance of varunid crabs:

Varunid crabs are important commercially, scientifically and medically *Eriocheir sinensis*, *E. japonica*, *Platyeriocheir formosa*, *Varuna litterata*, *V. yui* and *Metaplax gocongensis* etc. are considered by Asians as delicacies. The most commercially valuable is certainly *Eriocheir sinensis* (Chinese mitten crabs or Chinese Hairy crab) – a species which has long been acclaimed by East Asians as a delicacy due to its supposedly unique flavor (Ng, 1998; Peng, 1986; Zhao, 1988; Lai *et al*., 1992). Traditionally, Chinese mitten crabs have been harvested near the coast during their annual migration from freshwater rivers to the coastal areas for spawning. Due to increased demand and a decrease in supply, the species has been widely cultured for the last 70 years in almost every part of China (Y. Cai & A. Dai, pers. comm.; Du, 1982; Zhao, 1986). *Platyeriocheir formosa* is also widely harvested in Taiwan for food (Ho, 1996; Hung & Yu, 1996; Yu *et al*., 1996; Jeng, 1997; Jeng & Ng, 1998; Chen, 1998), while the smaller *Eriocheir japonica* is collected in many places as well (Ng, 1998; Kobayashi & Matuura, 1991; Kobayashi *et al.*, 1997). *Varuna litterata* and *V. yui*, although not as popular as *Eriocheir*, is still sold in many East and South East Asian markets at a relatively high price when they are available (Ng, 1998; pers. observ.). Interestingly, the supply of *Varuna* is somewhat sporadic as nobody has been able to culture the crab commercially. As for *Metaplax gocongensis*, the newly molted crabs are collected in large number on the fifth day of the fifth month of the lunar year in south Vietnam, for making a special traditional regional dish named 'mam cong lot' (salty molted-crab). The carapace, abdomen, stomach and gills are discarded, and the rest of the crab is preserved in saltwater. This special dish is highly regarded by old people of the Gocong Province and some gourmets in Ho Chi Minh City. Residents still living in Gocong Province still make this salty 'mam cong lot' every year for gifts. This dish is also sold to passengers on the ferry-boat in Myloi of Gocong Province (Davie & Nguyen, 2002).

This family of crabs also contains one species which is on the world's list of 100 most invasive aquatic invertebrates (Lowe *et al*., 2004), viz. *Eriocheir sinensis*. Other invasive species also include *Hemigrapsus penicillatus*, *Hemigrapsus takanoi*, *H. sanguineus*, *Cyclograpsus integer* and *Cyclograpsus punctatus*. *Eriocheir sinensis* was introduced (probably accidentally through ballast water) into Europe (Panning, 1933; Christiansen, 1969) in the 1920s, and has spread throughout northern Europe. It has reached the north parts of Norway (Christiansen, 1973), and down south to Portugal (Cabral & Costa, 1999). The species has entered Britain (Ingle, 1980; Clark, 1984) and it is now creating problems in the Thames River (P.F. Clark, pers. comm.). It has also been reported to be found on the Serbian part of the Danube River (Paunoic *et al.*, 2004). It entered North America (Nepszy & Leach, 1973; Cohen & Carlton, 1997) in the 1970s and its population has increased along the coast of San Francisco (R.B. Doran & G. Miller, pers. comm.). The crab is still spreading. Two specimens of *Eriocheir sinensis* were recently reported from Tokyo Bay, Japan in 2004 (S. Kobayashi, pers. comm.). In February 2006, the Japanese government established the 'Invasive Alien Species Act' and free trading and incubation of *E. sinensis* is strictly restricted as from February 2006. The Invasive Alien Act is an "Act for preventing adverse effects on ecosystems caused by invasive alien species", and is targeted at *E. sinensis* and its sister species, *E. hepuensis*. Recently, *E. hepuensis* has been found in Kuwait (M. Apel, pers. comm.). *Hemigrapsus penicillatus* was introduced to the coast of France in 1996 (Noel, 1997) and has been in the Netherlands since then (Faase, *et al*., 2002). *Hemigrapsus sanguineus* has been reported from the east coast of America (Schubart, 2002) and in Europe (Breton *et al.,* 2002).

Due to their ability to tolerate variable salinities, live out of water for long periods of time and/or require very little water, several species (adults and larvae) in this family viz. *Eriocheir sinensis*, *Gaetice depressus*, *Chasmagnathus convexus* etc. have been extensively used as experimental animals for various physiology, toxicology and heavy metal studies (e.g. Sullivan, 1977; Péqueux & Gilles, 1981; Péqueux *et al.*, 1984; Gilles, 1996; Zhao *et al.*, 1997; Gimenez & Anger, 2001; Kopin *et al.*, 2001; Rainbow & Black, 2001; Rodríguez *et al.*, 2001; Luquet *et al.*, 2002; Weihrauch1 *et al.,* 2003; Mo *et al.*, 2003; Genovese *et al.*, 2004).

The carapace of several species is also quite colorful and/or distinctive, and combined with their generally docile behaviour, they can make good aquarium pets. For example, *Gaetice depressus* (Gistel, 1835) is becoming very popular in some East Asian countries because of its highly variable colour patterns (Figure 1A) on the carapace (The Straits Times, 2003). *Chasmagnathus convexus* De Haan, 1835 (Figure 1B) is so docile that they can be kept by children as pets, and is often offered for sale in Hong Kong pet shops (P.K.L. Ng, pers. comm.).

As varunid crabs predominantly live in freshwater or waters with low salinity, they are an important intermediate host for *Paragonimus westermanii* (Kerbert, 1878) or the human lung fluke. This disease is very prevalent in Asia, especially in East Asia like China (Zhong *et al.*, 1981; Xu, 1991; Yu *et al.*, 1994; Yu, 1996; Chui *et al.*, 2001), Korea (Shin & Joo, 1990; Im *et al.*, 1997), Japan (Mukae *et al.*, 2001; Nakamura-Uchiyama *et al.*, 2002), Laos, Philippines, India, Sri Lanka, Taiwan (Davies *et al.*, 1994; WHO, 1995), Thailand (Johnson & Johnson, 1983), and Viet-Nam (Tran Thi, 1997). *Paragonimus westermanii* is also prevalent in regions where people consume half-raw or uncooked freshwater crabs living in Central-West Africa, South America (for example Ecuador, Perù, Venezuela) (WHO, 1995; Vélez *et al.*, 2002).

As a family, varunids, as they are known now, probably have the most diverse habitat range, from freshwater to marine, from shallow waters to the deep sea, with a good number living in extreme environments. For example, *Varuna litterata* is the most naturally widespread species of varunid, ranging from Africa to across the West Pacific. *Parapyxidognathus deianera* is found in mangrove areas, while all *Pyxidognathus* species are known from freshwater or near-mangrove sites. *Pseudograpsus crassus* has been reported to be found from mountains some 708m in altitude (Tesch, 1918); crabs from the genus *Orcovita* are all found in anchialine caves (Ng & Tomascik, 1994); all *Euchirograpsus* species live in the deep sea of between 200-290 meters (Crosnier, 2001); crabs from the genus *Xenograpsus,* are all associated with shallow-water hydrothermal vents (Jeng *et al.*, 2004) with even one species occurring in deeper water (McLay, 2006). Crabs from the genus *Scutumara* and some species of *Pseudograpsus* live among intertidal coral sand and loose rubble (Ng *et al.*, 2001), while several species of *Acmaeopleura* even form symbiotic associations with tube worms and thalassinid shrimps (Itani, 2000, 2002, 2003; Itani *et al.*, 2002, 2005).

It is interesting to note that in general, there are very few specimens of many of the species known from this family in museum collections, except for commercially important ones like *Eriocheir* or common intertidal ones like *Hemigrapsus* and *Varuna*. For many species, only the type specimens are available. This can be easily explained by the fact that not many carcinologists know where to look for the crabs since their habitats are so specialized and the crabs often have very cryptic habits (e.g. *Pseudograpsus setosus*, see Ng *et al.*, 2002).

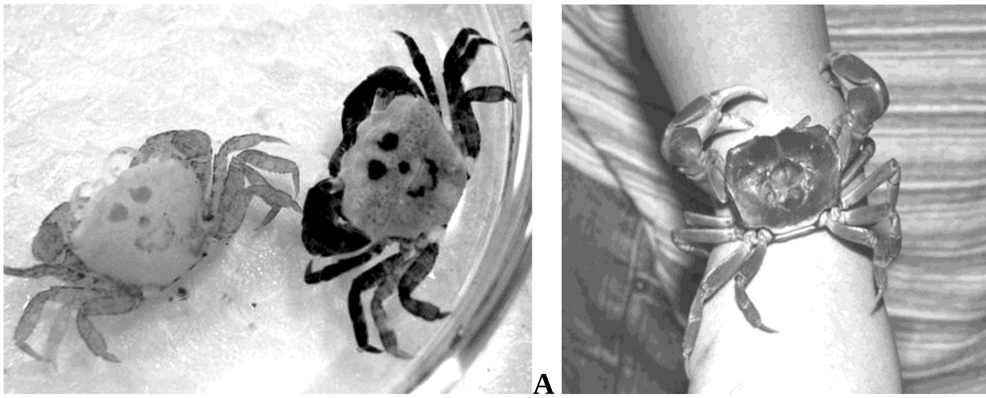



Figure 1. Photographs of *Gaetice depressus* (Gistel, 1835). A) showing highly variable coloration, and *Chasmagnathus convexus* De Haan, 1835; B) showing the docile nature of the crab.

Many genera of varunid crabs, notably *Helice* and *Cyclograpsus*, also communicate via sound (Sakai *et al.*, 2006). This is done by rubbing the stridulatory granules on the suborbital ridge against the inner margin of the merus of the cheliped. Many species also exhibit interesting behaviour like swarming of young crabs as seen in the megalops of *Varuna litterata* in Fiji (Ryan & Choy, 1990) and Taiwan (M.S. Jeng, pers. comm.) and the mass migrations of adults to the sea for spawning, for example, *Pseudograpsus setosus* (Ng *et al.,* 2002; K.X. Lee, pers. comm.), *Platyeriocheir formosa* (T.Y. Chan, pers. comm.; Ho, 1996; Hung & Yu, 1996; Yu *et al.*, 1996; Jeng, 1997; Jeng & Ng, 1998; Chen, 1998), and *Eriocheir sinenis* (Y. Cai, A.Y. Dai & R.Y. Liu, pers. comm.; Du, 1982, Zhao, 1986; Dai *et al.,* 1991; Guo *et al.,* 1997).

Many species of this family also have the potential to be excellent bioindicators. For example, the presence of *Ptychognathus barbatus* and *Hemigrapsus penicillatus* indicates that the habitat has been adversely affected, as there are usually no other crustaceans present in the same area (R.Y. Liu, S.H. Ko, pers. comm.; unpublished data). As for *Scutumara*, crabs from this genus are usually associated with pristine beaches with clean coral sand (pers. observ.).

## B. Systematics Review and Brief Historical Account

The last comprehensive review of the Varunidae was done over 100 years ago by Alcock (1900). Modern workers still follow the system in which the varunid crabs are regarded merely as a subfamily within the Grapsidae. The weight of accumulating evidence suggests, however, that this classification is not parsimonious and it should be recognized as a full family instead. The family Varunidae has a long and complex history, and it seems pertinent to give a brief historical account of the family.

The first classification system of this group was provided by De Haan (1833). He divided the subgenus 'Grapsi' into two smaller subgroups based on the form of the third maxillipeds. The first subgroup included the genera *Grapsus, Trichopus* (now *Varuna*), and *Eriocheir*. The second subgroup contained *Platynotus, Brachynotus*, *Goniopsis* and *Pachysoma* (now *Sesarma* or *Chiromantes*). In De Haan's classification, the second subgroup had contained part of H. Milne Edward's Cyclograpsi (i.e. *Platynotus* and *Brachynotus*). De Haan had placed *Helice* and *Chasmagnathus* in the subgenera *Ocypode* (see later).

In his monograph, Dana (1852) established the Grapsoidea, and divided it into five families, viz. Goneplacidae (sic Gonoplacidae), Macrophthalmidae, Gercarcinidae, Pinnotheridae, Mictyridae (sic Myctridae) and Grapsidae. He noted that genera like *Helice* and *Chasmagnathus* possessed the characters of the *Sesarma*, and included them into his subfamily Sesarminae but he had classifiedd *Sesarma*, *Sarmatium* together with the common character '*Articulus maxillipedis externi 3tius apice rotundatus*'; and he placed *Cyclograpsus*, *Chasmagnathus* and *Helice* into one group with the common character '*Articulus maxillipedis externi 3tius apice truncatus scepeque excavatus*' (Dana, 1852: 133).

Dana (1852: 309) stated that he did not agree with De Haan's 'Grapsi' classification as De Haan had neglected the important distinction based on 'the male verges' or the male mouthpart. He further added that Randall (1839), also had a 'somewhat similar subdivision' (Dana, 1852: 329), but stressed that Randall had retained *Grapsus* under De Haan's *Goniopsis* group, and called it *Pachygrapsus*. Dana felt that it was not a valid grouping just based on the form of the third maxillipeds. Thus, he (1852) re-divided the genus *Grapsus* into *Grapsus* and *Goniopsis*, noting that the *Goniopsis* was not the same as De Haan's *Goniopsis* or Randall's *Pachygrapsus*. Dana (1852: 331) also regarded the *Gnathochasmus* of MacLeay (1838) and *Cyclograpsus* of H. Milne Edwards (1837) to be identical, and gave the group a distinct name calling it *Hemigrapsus*. In his subsequent definition of the Grapsinae, Dana used gape size of the third maxillipeds as a key character, and he further divided the Grapsinae into two smaller groups, the first group included *Pseudograpsus*, *Heterograpsus*, *Eriocheir*, *Platynotus* and *Trichopus* (or De Haan's *Varuna*); and the second *Cyrtograpsus*, *Grapsus*, *Goniopsus*, *Planes* and *Hemigrapsus* (which also consists of part of De Haan's *Grapsus* and part of H. Milne Edwards's (1834) Cyclograpsi).

Two years later, H. Milne Edwards (1853: 163) established Varunacaea and Cyclograpsacaea as two 'satellite' tribes, under the 'Principal group of Grapsaceae, which was in turn placed under the 'Deuxième Tribu Principale' – Grapsinae. He had also recognized the possible existence of a very distinct group of *Varuna*-related crabs within the Grapsinaea; and thus established the satellite tribe, Varunacaea, which included *Varuna*, *Eriocheir* and *Utica*. In Cyclograpsacea, H. Milne Edwards included *Pseudograpsus*, *Heterograpsus* (now in two genera, *Brachynotus* and *Hemigrapsus*), *Paragrapsus*, *Cyclograpsus*, *Chasmagnathus* and *Platynotus* (currently *Gaetice*).

Although there was no mention of the 'oblique setose piliferous ridge across the external maxillipeds', Haswell (1882), in his Catalogue of the Australian Stalked and Sessile Eyed Crustacea, had placed the genus *Paragrapsus* in the subfamily Sesarminae together with *Cyclograpsus*, *Helice* and *Chasmagnathus*, because *Paragrapsus* has 'Orbits and submarginal grooves as in *Cyclograpsus* …. Legs as in *Cyclograpsus*.' He further commented that 'This genus is scarcely distinct from *Chasmagnathus*' (Haswell, 1882: 104). Examination of this genus by recent workers has confirmed its placement in the Cyclograpsinae (Campbell & Griffin, 1966).

The next major breakthrough was the review by Alcock (1900). Based on his study of the Indian specimens, Alcock (1900: 288) divided the family Grapsidae into four distinct subfamilies (1900: 288) viz. Grapsinae, Varuninae, Sesarmine and Plagusiinae. His subfamily Varuninae is made up of all the Varunacea of H. Milne Edwards (1853), and part of the Cyclograpsacea (above). According to Alcock (1900), the subfamily Sesarminae is made up of Sesarmacea and part Cyclograpsacea, with the front strongly deflexed, the lower border of the orbit commonly runs downwards towards the angle of the buccal cavern: the external maxillipeds leave a wide rhomboidal gap between them, an oblique hairy crest transverses them from a point near the antero-external angle of the ischium to a point near the antero-internal angle of the merus, their palp articulates either at the summit or near the antero-external angle of the merus, and their exognath is slender and either partly or almost entirely concealed. The male abdomen either fills or does not quite fill all the space between the last pair of ambulatory legs. The antennal flagella conditions are variable, with a strong emphasis on the oblique crest on the maxiilipeds. He included *Sesarma, Sarmatium, Metasesarma, Clistocoeloma* and *Metaplax* in his diagnosis stating that *Metaplax* has the oblique piliferous ridge across the merus and ischium of the external maxillipeds, the side walls of the body are vertical and like the pterygostomian regions, ornamented in the usual manner of what he defined as sesarmine crabs.

The subfamily Varuninae was made up of all the Varunacea of H. Milne Edwards (1853), and part of Cyclograpsacea of H. Milnes Edward (1853), and part of Grapsinae of Dana (1852). Alcock redefined the Varuninae as having the "front moderately or little deflexed, sometimes subliminar: the suborbital crest, which supplements the defective lower border of the orbit, is rather distant from the orbit and usually runs nearly in a line with the anterior border of the epistome: antennal flagellum usually of good length: the external maxillipeds do not often gape widely, though usually there is something of a gap, they are not transversed by any oblique hairy crest, their palp articulates with the middle of the anterior border of the merus, and their exognath is generally broad and is exposed throughout. The male abdomen, though not narrow, rarely covers all the space between the last pair of ambulatory legs". Alcock (1900) had only included *Varuna*, *Ptychognathus* and *Pyxidognathus* in his account.

Interestingly, Kossmann placed *Cyclograpsus* and *Chasmagnathus* into one new subfamily, Helicinae (1877: 57) on the basis of the morphology of the antennae. Unfortunately, the form of the antennae from the various species of this subfamily does not support his separation, and his subfamily was ignored by later workers.

In her studies of 'The Danish Expedition to Siam' materials, Rathbun (1909, 1910), placed *Camptandrium palucdicola* Rathbun, 1909, into subfamily Varuninae, but her inclusion was not accepted until Balss (1957) (see below). Tesch (1918) followed Alcock's (1900) and Borradaile's (1898) classification of the subfamily Varuninae, but stressed that Borradaile's key are not reliable (Tesch, 1918: 70, footnotes). Tesch further included *Ptychognathus*, *Pyxidognathus*, *Acmeopleura*, *Planes*, *Varuna*, *Baruna*, *Pseudograpsus (*part of Dana's, and = *Brachynotus*), *Utica*, *Brachynotus, Eriocheir*, *Perigrapsus* (now *Cardisoma carnifex*) and *Gaetice* in the subfamily Varuninae.

In the same year, Rathbun (1918) transferred *Cyrtograpsus*, *Glytograpsus* Smith, 1870 and *Platychirograpsus* into the subfamily Varuninae, and established a new genus *Tetragrapsus* for *Brachynotus* (*Heterograpsus*) *jouji* Rathbun, 1893. She did not justify her inclusion of the three genera in the Varuninae. The classification system has been rather stable after Tesch (1918), as most workers have considered the subfamily Sesarminae to contain the genera *Sesarma s. l.*, *Sarmatium*, *Aratus*, *Holometopus* (now *Chiromantes*), *Metasesarma*, *Metagrapsus, Cyclograpsus*, *Chasmagnathus*, *Helice*, *Metaplax* and *Paragrapsus*.

Balss (1922), in his review of Asian decapods, followed Tesch's (1918) classification. In his later study (Balss, 1957) on the systematics of the decapods, he agreed with the subfamily Varuninae classification. However, he noted that in all members of the Sesarminae, the male abdomen either filled the sternum completely or nearly so at the fourth ambulatory legs (Balss, 1957: 1669), although he did not comment further. In addition, he included *Cyrtograpsus*, *Euchirograpsus*, *Glyptograpsus* and *Platychirograpsus* in the Varuninae.

Crosnier (1965) moved *Planes* and *Ilyograpsus* back to the Grapsinae, but did not elaborate further. At his time, the subfamily Varuninae had the following genera: *Acmeopleura, Brachynotus, Cyrtograpsus, Eriocheir, Euchirograpsus, Gaetice, Glyptograpsus, Platychirograpsus, Pseudograpus, Ptychognathus, Pyxidognathus, Utica* and *Varuna*. And it was readily accepted by fellow carcinologists. Sakai (1976) later established a new genus, *Neoeriocheir*, for *Eriocheir leptognathus* Rathbun, 1914, but did not comment on the grouping of the subfamily.

Guinot (1979), in her extensive studies on the position of the male gonopores, stated there was a need to check the types of all the species of the subfamily Varuninae. However, her comments were not acknowledged until Davie (2002). In Guinot & Bouchard's (1998) study on the abdominal holding systems of brachyuran crabs, they again indicated that Varuninae and Sesarminae are paraphyletic, and should be reviewed. Similarly, Guinot (1979) also indicated that both *Metaplax* and *Cyclograpsus* should be transferred to Varuninae. Guinot & Bouchard's (1998) work on the locking buttons of the sternum of Brachyura also indicated likewise. A recent DNA study by Schubart *et al.* (2000) suggested that *Helice, Chasmagnathus, Cyclograpsus* and *Metaplax* are not sesarmines but closer to varunines. While Ng *et al.* (2001) acknowledged Schubart *et al.* (2000) report by placing these four genera in the subfamily Varuninae, they tentatively disagreed with the proposal to recognize Sesarminae and Varuninae as separate families, stating they preferred to be conservative while waiting for the morphological studies to be completed. Schubart *et al.* (2000) proposal was readily accepted by Martin & Davies (2001) but they did not provide any comment on the status of the families. Guinot's statement was finally formalized when Davie (2002) resurrected the subfamily Cyclograpsinae H. Milne Edwards, 1853, even though he did not provide any detailed appraisal of the family Varuninae.

While there is not much change within the Varunidae, grapsoid systematics, however, continues to be in a state of flux. This is especially so in the last few years, with an overwhelming increase in the number of scientists using molecular biology to solve confusing taxonomic problems (e.g. Richardson *et al.*, 1986; Hewitt, 1986; Hillis & Moritz, 1990; Ferrarris & Palumbi, 1996) in systematic biology. This technique has been applied to crustacean studies (e.g. Keenan *et al.*, 1995; Kitaura *et al.*, 1998, Schubart, 2000, 2002, 2006). Molecular biology techniques have provided a supposed simple and direct way of determining the genetic relationships of species, and even the extent of differentiation, as well as the phylo-geographic relationships among populations of widely distributed species. It is supposed to help resolve some of the more problematic genera as molecular characters/results could be used as additional evidence to support the separation or synonymy of difficult species. However, the two genes, 16s and COI, used in most molecular biology techniques thus far, have not been able to resolve many of the complicated species-complex problems. Sternberg & Cumberlidge (1998) and Schubart *et al.* (2000) have shown that the Grapsinae and the Sesarminae (sensu stricto) are monophyletic lineages, and they went so far as to recognise both subfamilies as families within the superfamily Grapsoidea but this move was not widely accepted until recently.

Rice's (1980) study on the classification system of brachyuran crabs based on larval characters has shown that it has an important bearing on modern classification system. Larval characters can be used as a key character if adults are difficult to separate. In recent years, the study by Schubart & Cuesta (1999) on 40 different grapsid crabs larval forms, which is only a small portion of the entire grapsid family (ca. 20%), remains inconclusive. Nevertheless, they transferred several genera from the subfamily Sesarminae to Varuninae. Schubart *et al.* (2000a) using DNA sequences of the mitochrondrial large subunit ribosomal RNA (16s rRNA) and zoeal morphology (see Schubart & Cuesta, 1999), transferred several genera previously placed in the subfamily Sesarminae (i.e. H*elice, Helograpsus, Paragrapsus* and *Metaplax*) into the subfamily Varuninae. In addition, they have also raised all the subfamilies to the family level (Schubart *et. al.*, 2000a) without consideration of the adult characters.

The three genera, previously under H. Milne Edwards' (1853) Cyclograpsaceae viz. *Cyclograpsus*, *Helice* and *Chasmagnathus* have been misplaced in the subfamily Sesarminae by Dana (1852), due to the presence of 'piliferous oblique crest and the setose pterygostome' has been shown by other workers on the form of the orbital ridge, the position of the genital openings and abdominal locking mechanism respectively (Crosnier, 1965; Guinot, 1979; Guinot & Bouchard, 1998) that they should be placed with the varunines instead of the sesarmines. In any case, these genera have a strongly developed, typically stridulatory, sub-orbital crest that is relatively straight. The sub-orbital crest (infra-orbital ridge), which also extends across the lateral branchial region, is also very similar to Varuninae, and this supports a alleged sister-group relationship corroborating the results of Schubart *et al.* (2000a) and Kitaura *et al.* (2002) (see section on subfamily Cyclograpsinae). Recent larval and molecular evidences (Schubart & Cuesta, 1998; Schubart *et al.*, 2000a; Kitaura *et al.*, 2002) have supported the position of *Cyclograpsus*, *Helice*, *Chasmagnathus, Paragrapsus* and *Helograpsus* in the Varuninae. As such, these genera are here transferred from the Sesarmidae to the Varunidae, but they are distinct from the usual varunine crabs in several features, justifying Davie's (2002) placement of these genera into their own subfamily. Two names are available for the taxa concerned: Cyclograpsacea H. Milne Edwards, 1853, and Helicinae Kossmann, 1877. Since, H. Milne Edwards' name is the oldest, 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.

Recent publications on the larval morphology and 16s rRNA has more or less supported the classification system based on adult morphology. In Schubart *et al.*'s (2000a) publication of the phylogeny of the American Grapsoidea, his 16s rRNA tree (Schubart *et al.*, 2000a: Fig. 1) have showed very clearly the distinct clades which correspond to the various subfamilies viz. the Grapsinae clade with *Planes*, *Goniopsus, Geograpus, Grapsus, Pachygrapsus* and *Leptograpus* clustering in one clade, while the rest of the subfamilies come out in another clade. Interestingly, *Gercarcinus + Cardisoma* and *Percnon* come out in their own distinct clades. Again it is to be expected, as the morphology of the *Gercarcinus and Cardisoma* is very different from the rest of the grapsid crabs. *Percnon,* although has been placed under the subfamily Plagusiinae with *Plagusia*, comes out on its own. This is also to be expected as the overall morphology of *Percnon* is very different from those of *Plagusia* and *Euchirograpsus* (see chapter on Plagusiidae). The sesarmine subfamily with *Sesarma, Metopaulias, Armases* and *Aratus* grouped as one clade but is flanked by both the *Platychirograpsus + Glyptograpsus* on the top, and *Euchirograpsus + Plagusia* on the bottom, indicating that the sesarmine crabs are a very good clade. The messy part is the presence of *Cyclograpsus* and *Chasmagnathus* within the varunine subfamily. Again, it is to be expected because both *Cyclograpsus* and *Chasmagnathus* have been originally grouped together with *Varuna* and *Eriocheir* and not with the *Sesarma* sensus lato (H. Milne Edwards, 1853). Even with Dana's (1852) definition of Sesarminae, *Cyclograpsus*, *Chasmagnathus* and *Helice* were grouped together under the subfamily Sesarminae, and strongly indicated that H. Milne Edwards and Dana had both already recognized the very close affinities of *Cyclograpsus* and *Chasmagnathus*, whether or not the infamous 'piliferous setose ridge across the maxillipeds' is present or not in these two genera (see section on Cyclograpsinae).

Schubart *et al.* (2000a) had raised all the subfamilies in the Grapsoidea to family level based solely on molecular data, and sometimes including larval data (Cuesta *et al*, 2001 etc.). However, it is not sufficient, and it must be considered in the context of previous workers who have indicated and made similar proposals based on adult morphology (Dana, 1852; H. Milne Edwards, 1853; Guinot, 1979 etc.). In any case, it is very impractical to be using larval and molecular data for identification in the laboratory, as it is expensive and tedious. It is impossible to use these two characters in the field. Furthermore, the use of 16s rRNA, COI or microsatellites, or a combination of two or three genes does not present the entire genome, and therefore, does not fully elucidate the differences or similarities between the various taxon. The expression of these few genes may not even have the same outcome. As such, it also makes good sense to carefully consider what the morphological characters are telling us, i.e. after all the genes have been more or less fully expressed. The molecular data, like the gastric mill data (Yang, 1986; Abele & Felgenhauer, 1986; Felgenhauer & Abele, 1989), position of the genital openings (Guinot, 1978), and the locking mechanism of the abdomen (Guinot & Bouchard, 1998), are some of many characters that can be utilized to demonstrate the phylogenetic relationships of these animals.

Davie (2002) took the conservative approach of treating the Grapsinae, Sesarminae, Cyclograpsinae and Varuninae as subfamilies of the Grapsidae. However, it seems increasingly clear that at least some of these subfamilies deserve family distinction. The Glyptograpsidae Schubart, Cuesta & Felder, 2002, appears to have closest affiliations with the Varunidae than to any other grapsoid group, and hence there is a need to re-appraise this family as well. Schubart *et al.* (2001) have made a compelling case using DNA, larval and adult morphological characters to justify their family, and at the moment, we have no reason to doubt their arguments. It is here regarded as a subfamily of Varunidae. As discussed, Schubart *et al.* (1999) recognized the Varunidae as a full family, and this new status has been widely accepted (Martin & Davies, 2001). In this study, the family Varunidae is recognized and includes four subfamilies viz. Varuninae, Cyclograpsinae as well as two new ones for the genera *Gaetice* and *Thalassograpsus*, respectively. One "varunid" genus, *Xenograpsus*, is removed to its own family. These taxon are redefined by adult morphological characters. Similarly, the Grapsidae, Glyptograpsidae and the Sesarmidae are also recognized as separate families.

### C. Aims and Objectives of the present study

By using a combination of predominantly molecular and larval techniques, traditional taxonomy based solely on adult crab morphology has been challenged. The superfamily Grapsoidea now comprises the Gecarcinidae, Glyptograpsidae, Grapsidae, Plagusiidae, Sesarmidae, and Varunidae (Schubart *et al.*, 2000a; Schubart & Ng, 2000; Karasawa & Kato, 2001; Ng *et al.*, 2001; Martin & Davies, 2001). More revision at the family level may be necessary before the systematics of the Grapsoidea can be considered stable.

The present thesis focuses primarily on the challenges and problems within the Varunidae, and its supposed relationships with other taxa. As such, the aims and objectives of this dissertation are as follows:

1. To review the current morphological characters used in the taxonomy of this family, and to uncover new sexual and non-sexual characters which can be used for improving their taxonomy,
2. To re-appraise the taxonomy of the family Varunidae and establish a new family, Xenograpsidae,
3. To document and describe new species, genera and subfamilies discovered,
4. To provide diagnostic keys for the identification of the various subfamilies, genera and species,
5. To investigate the phylogenetic relationships of the various generic groups within the subfamilies and families, and
6. To review the adaptations of these animals for living in freshwater and terrestrial habitats.

## MATERIALS AND METHODS

Specimens examined were from the following museums:-

| Acronym | Organization |
|---|---|
| **ASIZ** | Institute of Zoology, Academia Sinica, Nankang, Taiwan |
| **BMRI** | Marine Research Institute, Universiti Malaysia Sabah, Malaysia |
| **BNHM** | Beijing National History Museum, Beijing, People's Republic of China |
| **CBM** | Natural History Museum & Institute, Chiba, Japan |
| **CMNH** | Coastal Branch of Chiba Museum of Natural History, Japan |
| **CUB** | Department of Biology, Chulalongkhorn University, Bangkok, Thailand |
| **CUC** | School of Biological Sciences, Canterbury University, Canterbury, New Zealand |
| **IZAS** | Institute of Zoology, The Chinese Academy of Sciences, Beijing, People's Republic of China |
| **KPMNH** | Kanagawa Prefectural Museum of Natural History, Kanagawa, Japan |
| **MNB** | Museum für Naturkunde, Humbolt-Universität zu Berlin, Berlin, Germany |
| **MNHN** | Muséum National d'Histoire Naturelle , Paris, France |
| **MZB** | Museum Zoologicum Bogoriense, Research Center for Biology, Indonesian Institute of Sciences, Cibinong, Indonesia |
| **NHM** | Natural History Museum, London, United Kingdom. |
| **NHMW** | Naturhistorisches Museum in Wien, Vienna, Austria |
| **NIWA** | National Institute of Water and Atmospheric Research, New Zealand; |
| **NKUMT** | National Kaoshiung University of Management and Technology, Kaohsiung, Taiwan |
| **NMB** | Naturhistorisches Museum Basel, Basel, Switzerland |
| **NMCR** | National Museum, Manila, Philippines |

| | |
|---|---|
| **NMMBA** | National Museum of Marine Biology and Aquarium, Kenting, Taiwan |
| **USNM** | Smithsonian Institution, United States National Museum of Natural History, Washington D.C., United States of America |
| **NMNS** | National Museum of Natural Sciences, Taichung, Taiwan |
| **NSMT** | National Museum of Science and Technology, Tokyo, Japan |
| **NTOU** | National Taiwan Oceanography University, Keelung, Taiwan |
| **PKM** | Pei Kuan Museum, Hua-Lian, I-Lan county, Taiwan |
| **QIH** | Institute of Oceanography, The Chinese Academy of Sciences, Qingdao, Shangdong Province, People’s Republic of China |
| **QMW** | Queensland Msueum, Brisbane, Australia |
| **RMNH** | Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands. |
| **SFM** | Research Institute and Natural History Museum, Senkenberg, Frankfurt am Main, Germany |
| **SAM** | South African Museum, Cape Town, South Africa |
| **SMUM** | Sabah Museum, Universiti Malaysia |
| **TMCD** | National Taiwan Museum, Taipei, Taiwan |
| **URJ** | Department of Marine Sciences and Chemistry, University of Ryukyus, Okinawa, Japan |
| **USCC** | University of San Carolos, Cebu City, Philippines |
| **WAM** | Western Australian Museum, Perth, Australia |
| **XIO** | Xiamen Institute of Oceanology, Xiamen, Fujian Province, People’s Republic of China |
| **ZIM** | Biozentrum Grindel und Zoologisches Museum (formally Zoological Institute and Museum), Universität Hamburg, Hamburg, Germany |
| **ZMA** | Zöologisch Museum Amsterdam, Universiteit van Amsterdam, Amsterdam, The Netherlands |
| **ZMK** | Zoological Museum, University of Copenhagen, Copenhagen, Denmark |

| | |
|---|---|
| **ZRC** | Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore, Singapore |
| **ZSM** | Zöologisch Staatssammlung Münich, Münich, Germany |

Measurements provided are of the carapace width and length, respectively. The abbreviations M, P, and D refer to the meri, propodi, and dactyli of the ambulatory legs, respectively; while the number preceding it refers to the respective leg; G1 and G2 are used for the male first and second pleopods, respectively; coll. – collector; don. – donated by; km – kilometer; mm – millimeter; MA – million years ago. The term physiognomy is used to describe the thickness of the cephalothorac when view from the lateral side. The term pulvinus is defined as a cushionlike swelling at the base of the cheliped fingers. The term anchialine is used in the sense of Holthuis (1973) where 'anchialine' comes from the Greek word, 'anchialos', near the sea. These caves are usually found along the coasts, containing a mixture of freshwater and brackish water, with no surface connection with the sea but fluctuates with the tides. They occur in many parts of the world, and often contain highly specialized and endemic faunas.

In addition to the old museum material, fresh specimens collected from Japan, Taiwan, Hong Kong, People's Republic of China, Indonesia, Thailand, Vietnam, India, Sri Lanka, South Africa, United States of America, New Zealand and Australia, were utilized in this study. The specimens were obtained mainly by turning over rocks or by dredges by gill nets. Some of the specimens were also purchased from local markets where they were sold as food. All fresh specimens were preserved in 70-95% alcohol for a few days, before transferring to new 70% alcohol for long-term storage.

All species described under the family Varunidae were examined as far as possible. In addition, specimens from other allied families were also examined for comparative purposes. Examination of specimens was in most cases carried out using a Nikon SMZ-10 stero-microscope and drawings were made with the help of a camera lucida mounted on the same microscope. Photographs were usually taken of fresh specimens when possible (for live colour notes) with a Nikon 995 digital camera.

Most of the taxonomic characters used in this study have been utilized in past works (see Ng, 1998). The second male gonopods (G2) of this group of animals are very similar in their morphologies, and are not very useful as one of the diagnostic characters. There are many new diagnostic characters discovered during the course of this work. These new characters are: (1) form of the orbit of the eye; (2) mobility of the basal article of the antenna; (3) presence or absence of a medial vertical groove on thoracic sternites 5, 6 and 7; (4) absence/presence and form of the short, setae on the dactyli of the ambulatory legs; and (5) position of the male gonopore (sensu Guinot, 1978).

All morphometric measurements are made with a pair of dial Vernier-callipers, up to 0.05mm accuracy. Only smaller ones (observed under a stereomicroscope) are measured with a stage micrometer up to 0.01mm accuracy.

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* were 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 and 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 Mr Bayes 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 2000 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 5th character and transversions were weighed three times transitions. Confidence values for the proposed groups within the inferred trees were calculated with the nonparametric bootstrap method (2000 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.

The six available families will be dealt with, with details in the family Varunidae including establishment of two new subfamilies, and the new family established in this present study. At the family and subfamily level, in the listing of synonyms, a simple key will be provided, followed by the list of synonyms, the type genus, diagnosis and ending with the remarks. At the generic level, the synonyms are listed first, followed by the type species, diagnosis of the genus, and ending in remarks. A key will also be provided to the different species in each treated genus (unless it is monotypic). At the species level, the list of synonyms will be provided first, followed by materials, diagnosis, size, colour, habitat, remarks and known distribution. Either a line drawing and/or a photograph of the taxon will be included.

A phylogenetic analysis was also carried out to investigate the relationship of the different taxa.

The vernacular names of some Malay geographic terms commonly used in the text are as follows: Kg. – Kampong/Kampung (village); P. – Palau (island); Sg. – Sungei (river/stream); Tg. – Tanjong/Tanjung (cape).

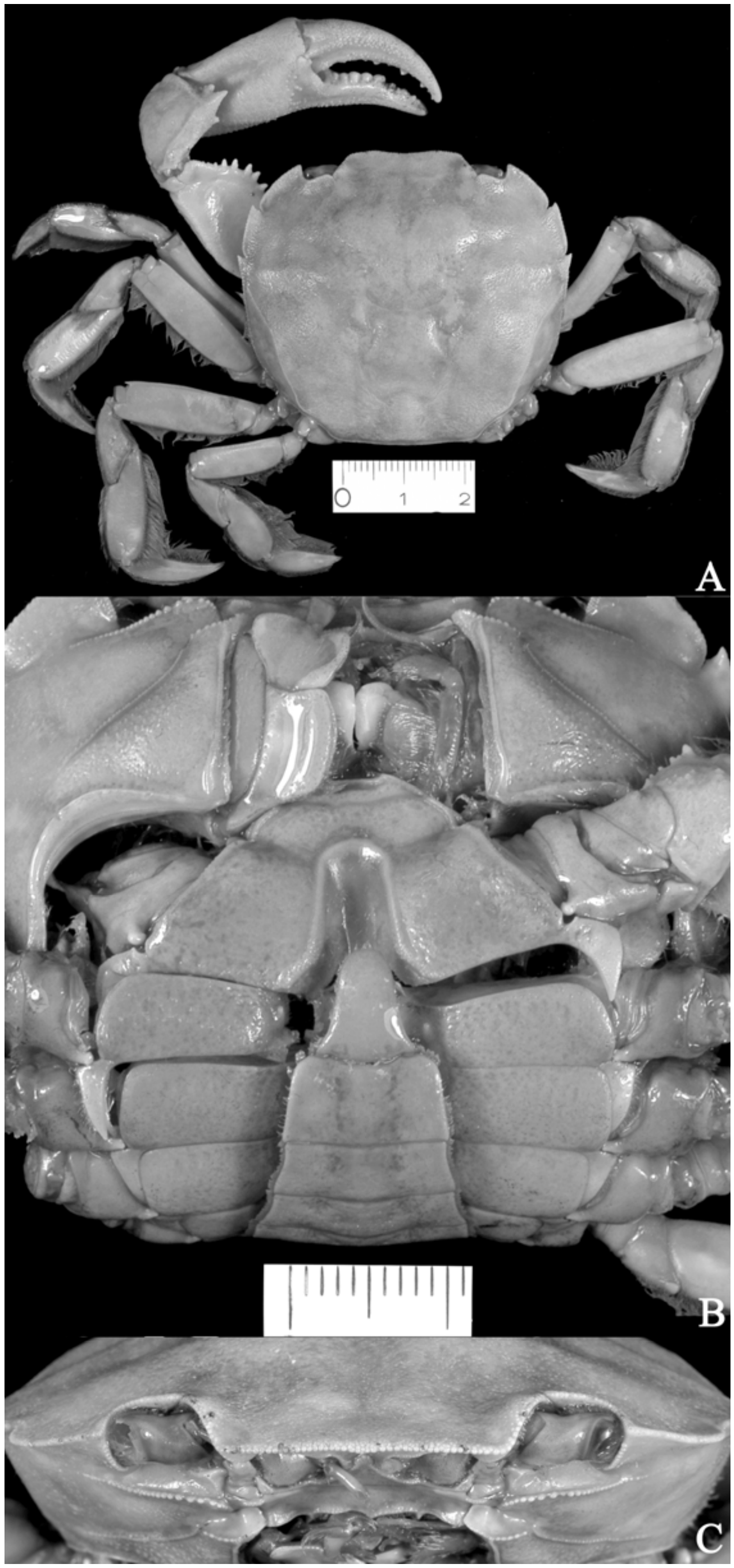



Figure 2. Photographs of typical varunid crab (*Varuna litterata* Fabricius, 1798). A) dorsal view; B) ventral view; C) frontal view.

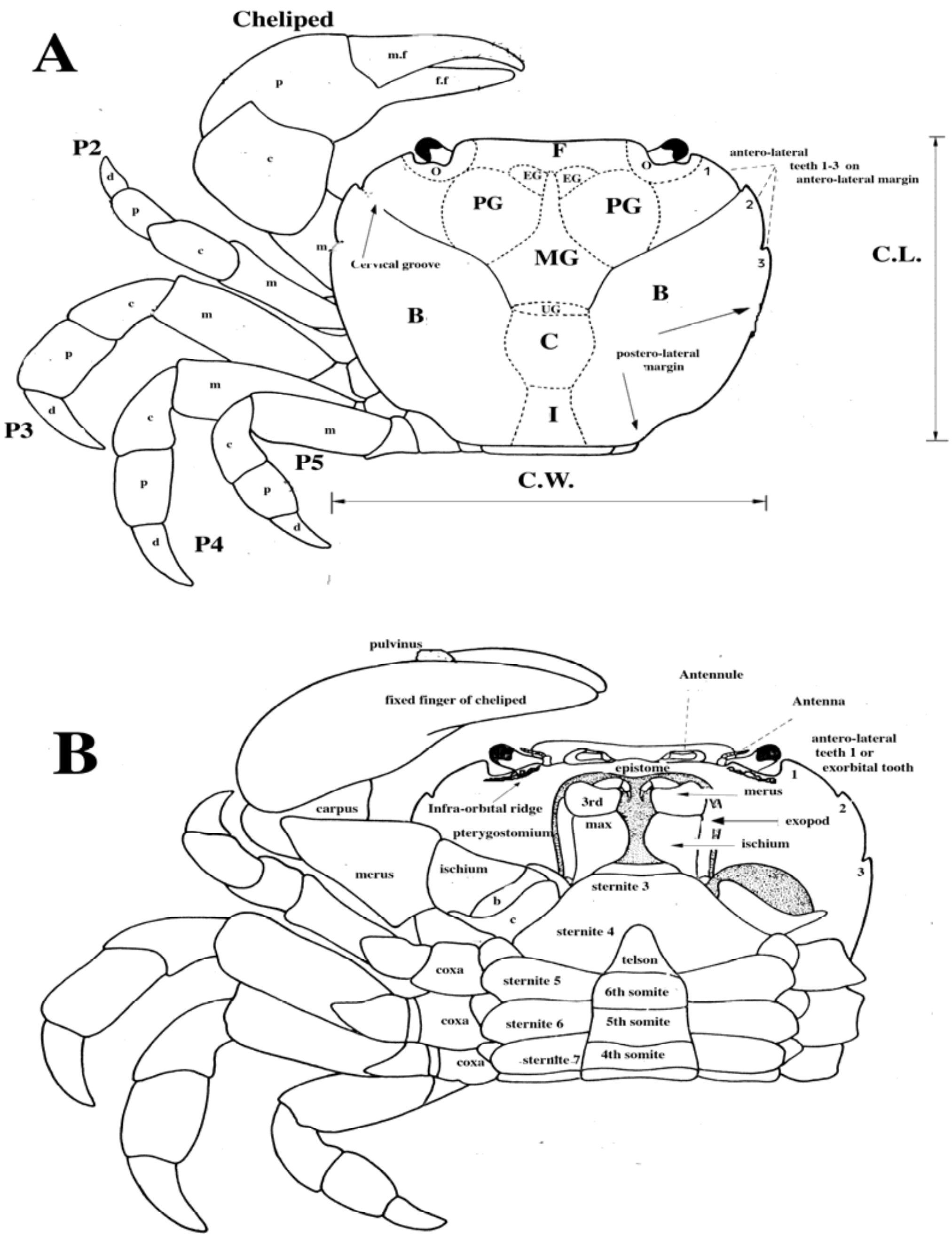



Figure 3. Schematic diagram of a varunid crab. A) dorsal view (C.L.=Carapace Length; C.W.=Carapace Width; F=frontal region; EG=epi-gastric region; O=orbital region; PG=proto-gastric region; MG=meso-gastric region; UG=uro-gastric region; C=cardiac region; I=intestinal region; B=branchial region; P2=second ambulatory leg; P3=third ambulatory leg; P4=fourth ambulatory leg; P5=fifth ambulatory leg; m=merus; c=carpus; p=propodus; d=dactylus; m.f.=movable finger; f.f.=fixed finger); B) ventral view (b=basis; c=coxa; 6$^{th}$ somite=sixth abdominal somite; 5$^{th}$ smomite= fifth abdominal somite; 4$^{th}$ somite= fourth abdominal somite) (After Crosnier, 1965).

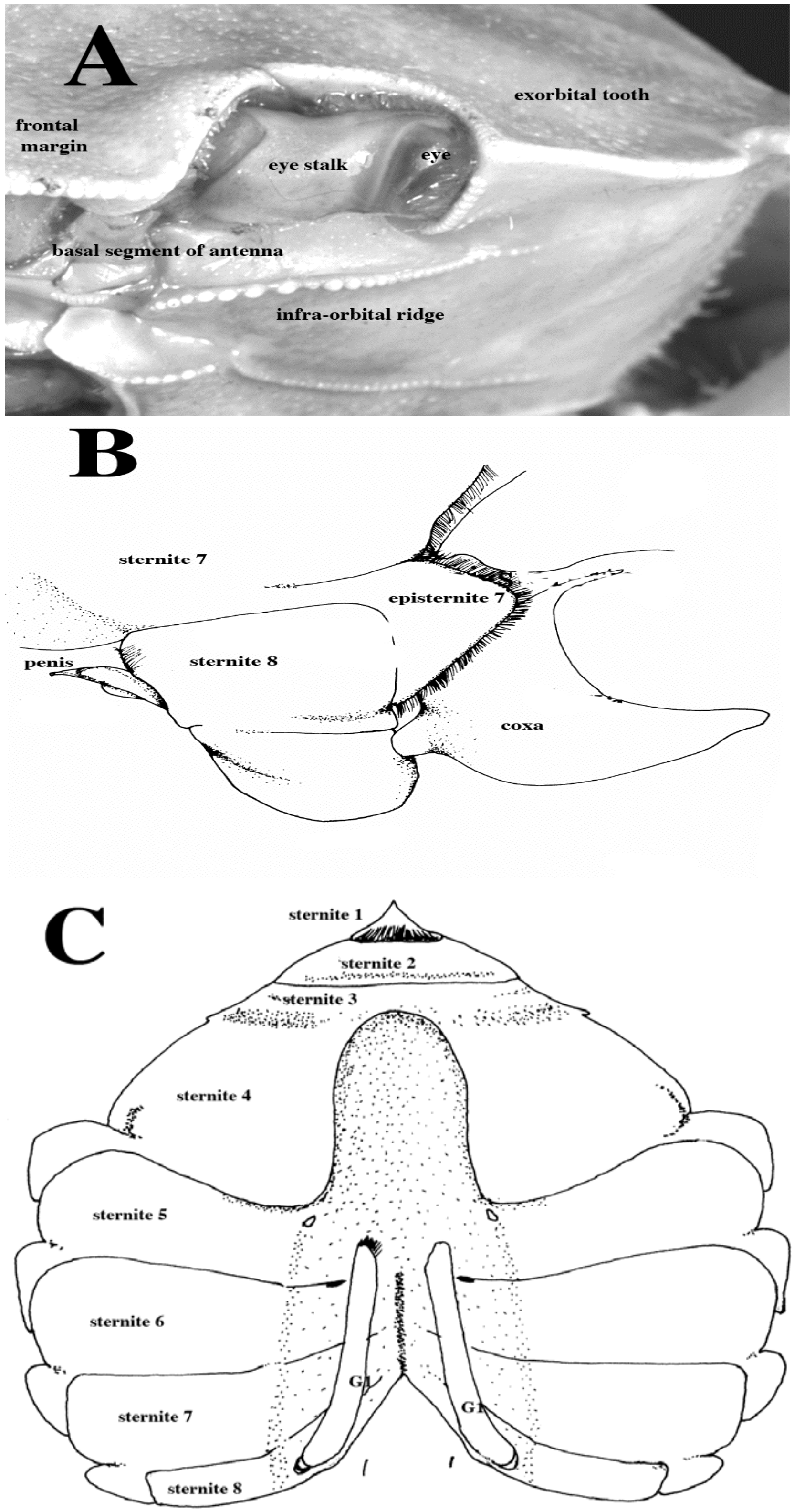



Figure 4. A) Orbit and basal segment of the antenna; B) Position of the male gonopore (sensu Guinot, 1978). C) Medial vertical groove on sternites 5,6 and 7 (G1=first male gonophore).

# TAXONOMY

## Family VARUNIDAE H. Milne Edwards, 1853

Varunacea H. Milne Edwards, 1853: 125.

Cyclograpsacea H. Milne Edwards, 1853: 191.

Pseudograpsinae Kossmann, 1877: 57.

Helicinae Kossmann, 1877: 57.

Varuninae Alcock, 1900: 288; 400.

**Diagnosis.**— Carapace usually quadrate; surface smooth, punctate; with fine posterolateral striations; usually glabrous; regions usually not well-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; sometimes with only trace of a single epibranchial tooth, usually with two and more teeth including exorbital tooth. Orbit a deep sunken cavity, almost complete; lower margin of exorbital tooth extending medially as a ridge to form a 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, which may or may not be stridulatory. Basal antennal article immobile, locked against the inner orbital tooth laterally. Interantennular septum in form of narrow keel, clasped by incision in lower frontal margin. Pterygostome with simple lateral groove, but without supplementary grooves. Third maxilliped with merus and ishium subrectangular, inner margins meeting medially,  leaving a small rhomboidal gape when closed; anteriorly reaching as far as epistome, completely closing buccal cavity; surface granular, without deep grooves and without oblique setose crest extending across outer distal corner of ischium; exopod of third maxilliped normal, not swollen or unusually enlarged. Chelipeds robust, swollen, row of granules near posterior margin of cheliped; fingers sometimes armed with subapical brush of setae; carpus unarmed with inner margin rounded, without spine. Ambulatory legs flattened; meri anteriorly with bluntly rounded keel, with broad thick subdistal lobe; dactyli short, broad. Chelae and legs usually unarmed, lacking setae, or bristles. Male abdomen with seven movable segments including telson. Male gonopore separated from the coxa of fifth ambulatory leg by an elongation of episternite 7 meeting thoracic sternite 8. Female gonopore operculate, usually circular in shape.

**Type subfamily.**— Varuninae H. Milne Edwards, 1853, by original designation.

**Remarks.**— The study of this group of crustaceans began when De Haan (1833) divided the currently extant Grapsoidea into two groups, the *Ocypus* group and *Grapsus* group. In the *Ocypus* group, the fourth article of the outer (or third) maxilliped articulates with the outer angle of the third article, and the genera included were *Scopimera*, *Myctiris*, *Gelasimus*, *Macrophthalmus*, *Cleistostoma*, *Cardisoma*, *Chasmagnathus*, *Helice*, *Uca*, *Ocypoda* and *Acantopus* (now part of the genus *Plagusia*). In the *Grapsus* group, this article articulates with the middle of the apical margin of the third maxilliped, and the genera included were *Gercarcinus*, *Philyra*, *Plagusia*, *Grapsus*, *Trichopus*, *Eriocheir*, *Pachysoma*, *Goniopsis*, *Platynotus*, *Brachynotus*, *Nautilograpsus* and *Cyclograpsus*. He also further divided the *Grapsus* group into two smaller subgroups according to the form of the third maxilliped. In the first subgroup, *Grapsus*, this article is scarcely longer than broad, and contained the genera *Grapsus* and *Trichopus* (now synonymized under *Varuna*). In the second subgroup, *Goniopsus*, this segment is oblong or as long as the second article, and contains the genera *Platynotus* (= now *Gaetice*), *Brachynotus*, *Goniopsis* and *Pachysoma* (= *Sesarma* and/or *Chiromantes*). It is obvious that this character used by De Haan is not suitable because the classification he derived was too simplistic and general. He had not taken into account many external key characters in his report. For example, De Haan’s *Goniopsis* subgroup that contained *Platynotus* and *Brachynotus*, was later placed by H. Milne Edward in his Cyclograpsi group. The genera *Helice* and *Chasmagnathus* had been previously placed under the subgroup *Ocypus* group by De Haan (1833) but they are so different from all the taxa now in the genus *Ocypode* in their external morphology (see below on Remarks on Cyclograpsinae). De Haan’s classification system was also rather “odd”, as it can be seen from his description of *Eriocheir japonicus* De Haan, 1835. He placed this species under the first subgroup, *Grapsus*, with the generic name, *Grapsus* (*Eriocheir*). It is noteworthy to note that in De

Haan's 1841 publication, "Decas Septima", he had even included the genera *Pinnotheres* and *Hymensosoma* in his *Grapsus* group as he had defined it. These genera are today in Pinnotheridae and Hymenosomatidae respectively.

In 1837, Henri Milne Edwards established the 'famille Catométopes', and the 'tribu des Grapsoïden' with five other 'tribes' including Thelpheusiens, Gécarcinens, Pinnothériens, Ocypodiens and Gonoplaciens. In addition to creating the six tribes, H. Milne Edwards also created several genera to accommodate the new species he was describing (see below). Under the Tribe Grapsoïden, he had included the genera *Sesarma* Say, 1819, *Cyclograpsus* H. Milne Edwards, 1837, *Grapsus* Lamarck, 1801, *Nautilograpsus* H. Milne Edwards, 1837 (now *Planes* Bowdich, 1825), *Pseudograpsus* H. Milne Edwards, 1837, *Plagusia* Latreille, 1804, and *Varuna* H. Milne Edwards, 1830. In the same report, H. Milne Edwards further subdivided the genus, *Cyclograpsus* into two smaller groups based on several characters like the form of the carapace, eyes, chelae and ambulatory legs. One of the groups contains *Cyclograpsus sexdentatus* H. Milne Edwards, 1837, from New Zealand, *C. crenulatus* H. Milne Edwards, 1837, also from New Zealand, and *C. octodentatus* H. Milne Edwards, 1837, while the other groups contain the other *Cyclograpsus* species, and some of the *Paragrapsus* species we recognize today (see below on remarks in subfamily Cyclograpsinae).

Dana (1852) was the first person to state that he did not agree with De Haan's classification as he felt that De Haan had neglected many of the important distinctions except the male verges (mouthparts). In his comments on the Grapsidae, Dana further added that Randall (1839) had also independently derived a somewhat similar subdivision as De Haan's. Dana (1852) also regarded *Gnathochasmus* of MacLeay (1838) and *Cyclograpsus* of H. Milne Edwards (1837) to be identical. Dana argued that De Haan's (1833) *Grapsus* group could have constituted part of H. Milne Edwards' Cyclograpsi as the forms of the outer or third maxillipeds are different. Dana added that two *Cyclograpsus* species viz. *C. sexdentatus* and *C. crenulatus* (which belonged to Milne Edwards' Cyclograpsi) do not have the typical characters of a Cyclograpsi, and should be grouped together because they both do not have the third article of the third maxilliped crossed by an oblique piliferous crest. He called this the *Hemigrapsus* group and also included De Haan's Grapsi, but he did not elaborate further.

In the same report, Dana established the Superfamily Grapsoidea, which corresponded to H. Milne Edwards' Catometopa but without the freshwater crabs or H. Milne Edwards' 'tribu des Thelpheusiens'. In this superfamily, there are six families viz. Gonoplacidae, Macrophthalmidae, Grapsidae, Gercarindae, Pinnotheridae and Myctiridae. The latter five families are morphologically very similar to each other. The Goneplacidae (sic for Gonoplacidae) on the other hand, is very different in having cancroid third maxillipeds even though it has similar carapace form. Within his family Grapsidae, he established the three subfamilies, Grapsinae, Sesarminae and Plagusiinae. In his subsequent definition of his subfamily Grapsinae, Dana (1852) regarded as key characters the following: "Antennae internae fronte tectae. Articulus maxillipedis externi 3tius costâ obliquâ in 2dum productâ non ornatus" [Antennae hidden by front, third maxilliped articulate]. Within the Grapsinae, he had two smaller groupings. The first with the character "Maxillipedes externi vix hiantes" [external maxilliped's gap narrow in shape] in which he included the genera *Pseudograpsus*, *Heterograpsus*, *Eriocheir*, *Platynotus* and *Trichopus* (= *Varuna*). The second group, in which he included the genera *Grapsus*, *Goniopsus*, *Planes*, *Hemigrapsus* and *Cyrtograpsus*, he defined with the character "Maxillipedes externi rhomboidice hiantes" [external maxilliped's gap widely rhomboidal in shape]. The genus *Hemigrapsus*, as defined by Dana, is made up of De Haan's *Grapsus* and part of H. Milne Edwards's Cyclograpsi. The other genera, *Cyclograpsus*, *Helice* and *Chasmagnathus*, were grouped together under the Sesarminae on the basis of the form of the third maxillipeds (see below remarks on subfamily Cyclograpsinae).

Two years later, Henri Milne Edwards (1853) established Varunacea as a 'satellite tribe' under the 'Premier Agèle Principal Grapsaceae', which was in turn, placed under the 'Deuxième Tribu Principale' of the Grapsinae. Henri Milne Edwards had provided a good definition for the Grapsaceae; he included the genera *Goniopsis* De Haan, 1933, *Metopograpsus* H. Milne Edwards, 1853, *Grapsus* Lamarck, 1801, *Leptograpsus* H. Milne Edwards, 1853, *Nautilograpsus* (now *Planes*) and *Euchirograpsus* H. Milne Edwards, 1853, in it. It is interesting to note that since its establishment, the genus *Euchirograpsus* has always been treated as a grapsid crab until Balss (1957) transferred the genus to the subfamily Varuninae (see later). In his brief discussion of the

Grapsinae, H. Milne Edwards (1853) recognized the possible existence of a very distinct group of *Varuna*-related crabs within the Grapsinae, and thus, he established the 'satellite tribe', Varunacea, that only included *Varuna* H. Milne Edwards, 1830, *Eriocheir* De Haan, 1835, and *Utica* White, 1847. These three genera were different from the other Grapsaceae taxa in that the front is facing forwards, the ambulatory legs are broad with the margins setose, the last pair of ambulatory legs are modified for swimming, and the third maxillipeds are small or not gaping when closed. In the same publication, H. Milne Edwards (1853) also established Cyclograpsacea (see below on remarks under subfamily Cyclograpsinae). The main characters he used were the almost oval-shaped carapace, the smooth form of the carapace, and the short, stout and almost glabrous ambulatory legs. The Cyclograpsacea had originally included the following genera *Pseudograpsus* H. Milne Edwards, 1837; *Heterograpsus* Lucas, 1846 (= *Brachynotus* or *Hemigrapsus*); *Paragrapsus* H. Milne Edwards, 1853; *Cyclograpsus* H. Milne Edwards, 1837; *Chasmagnathus* De Haan, 1833; *Platynotus* De Haan, 1835 (or *Gaetice*), *Helice* De Haan, 1833, and *Metaplax* H. Milne Edwards, 1852.

The classification systems provided by Dana (1852), and H. Milne Edwards (1853) are similar in the following a) both systems recognized that there is one group of crabs that contained *Grapsus* and its closely allied genera, and another group that of crabs that contained *Sesarma* and its closely allied genera; (b) both systems acknowledged that *Varuna* and its closely allied genera are different from *Grapsus* and its closely allied genera, and *Sesarma* and its closely allied genera. In H. Milne Edwards's classification, he recognized this group, and created a taxon, Varunacea, to accommodate them. In Dana's classification, he merely conceded the presence of these two groups but did not name them or elaborate further. These two classification systems were accepted, and remained unchallenged for many years despite the tremendous number of new taxa which have been named by carcinologists over that period. Dana (1852), and H. Milne Edward (1853) were reviewed and followed by Kingsley (1880) and Miers (1886).

Alcock (1900), in his study of the Indian carcinological fauna, realized that the two systems were inadequate in that it was unable to accommodate the many newly described taxa described in the following years. In particular, the number of species allied to *Varuna* had increased remarkably. Alcock modified the classification systems of H. Milne Edwards' and Dana's, dividing the family Grapsidae into four distinct subfamilies, viz. the Grapsinae, Varuninae, Sesarminae and Plagusiinae. The subfamily Varuninae consisted of all the Varunacea as defined by H. Milne Edwards (1853), part of the Cyclograpsacea of H. Milne Edwards (1853), and part of the Grapsinae sensu Dana (1852). Alcock re-defined the subfamily Varuninae as having the front moderately or slightly deflexed; the infra-orbital crest supplements the lower border of the orbit, and usually runs nearly in a line with the anterior border of the epistome; the antennal flagellum is usually of a good length; the external maxillipeds do not often gape widely (although there is usually a gap, the merus and ischium are not transverse by any oblique setose crest); the palp articulates with the middle of the anterior border of the merus; and the exognath is generally broad and is exposed throughout. The male abdomen, which is not narrow, rarely covers all the space between the last pair of ambulatory legs. With this definition, Alcock included only the genera *Varuna*, *Ptychognathus*, and *Pyxidognathus* in his subfamily. Alcock (1900: 289) also transferred the other genera of H. Milnes Edwards's (1853) Cyclograpsacea and all of H. Milne Edwards' (1853) Sesarmacea into his subfamily Sesarminae (also see remarks under subfamily Cyclograpsinae). Alcock's classification was followed closely by Borradaile's (1907).

Tesch (1918) followed Alcock's (1900) and Borradaile's (1907) classification of the subfamily Varuninae. He further added that the carapace of crabs from the subfamily Varuninae is somewhat vaulted, and mostly with arched lateral margins, the front is not strongly deflexed, the gap between the external maxilliped is rarely wide, and the chelae of male are very often covered with setae. He included *Ptychognathus*, *Pyxidognathus*, *Acmaeopleura*, *Planes*, *Varuna*, *Baruna*, *Pseudograpsus* (which was part of Dana's *Hemigrapsus*), *Utica, Brachynotus, Eriocheir, Perigrapsus* (now *Cardisoma carnifex*) and *Gaetice* in this subfamily. The genus *Acmeopleura* Stimpson, 1858, was included in the Varuninae by Tesch (1918: 106) as he argued that the carapace is subcircular, unarmed at the margins and resembling that of *Cyclograpsus*. In addition, *Acmaeopleura parvula* also has some setae on the chelipeds. *Utica* was included as the shape of the carapace and front closely resembled *Ptychognathus* (Tesch, 1918: 95). He did not, however, state why he had included *Planes, Baruna,* and

*Perigrapsus* in the subfamily as well. In the same year, Rathbun (1918) transferred *Cyrtograpsus*, *Glyptograpsus* and *Platychirograpsus* into the Varuninae, and created a new genus *Tetragrapsus* for *Brachynotus* (*Heterograpsus*) *jouyi* Rathbun, 1893. She also did not offer any note or explanation to her inclusion of these three genera in the subfamily Varuninae. The subfamily Varuninae, as defined by Tesch (1918) and Rathbun (1918), contained 16 genera. Balss (1922) also followed Tesch's (1918) classification very closely. However, in his later study on the systematics of the decapods, he also included *Euchirograpsus* in the Varuninae (Balss, 1957: 1669). Since then, many of the genera have been retained in the subfamily Varuninae. In later years, some of the genera have been removed by various authors to other subfamilies, while many genera have also been created to accommodate the new species that were discovered between 1922 and 2000 (see below on the remarks on the subfamilies Varuninae and Cyclograpsinae).

The studies that have been carried out by previous workers from H. Milne Edwards (1853); Dana (1852); Alcock (1900); Rathbun (1918); Tesch (1918) and Balss (1922 & 1957), were based entirely on adult morphology. Their studies have shown that the classification system for the family Grapsidae has been relatively quite stable, with four distinct groups viz. a) the *Grapsus*-group with *Grapsus*, *Pachygrapsus* and *Goniopsus* (i.e. subfamily Grapsinae); b) the *Varuna*-group with *Varuna*, *Ptychognathus*, *Pseudograpsus*, *Eriocheir* and 12 other genera (subfamily Varuninae); c) the *Sesarma*-group containing the genus *Sesarma* and 15 closely allied genera (subfamily Sesarminae); and d) the *Plagusia*-group with the genus *Plagusia*, *Percnon* (subfamily Plagusiinae). The subfamily Varuninae was widely accepted, although there were questions about the relatedness of the each taxa and even the placement of these taxon in the varunine subfamily and its natural grouping (Crosnier, 1965; Guinot, 1979; Davie & Nguyen, 2002).

Crosnier (1965) commented that *Varuna*, *Ptychognathus* and *Pseudograpsus* are very close to each other, and that their distinctive characters appear rather artificial. In her study on the position of the male gonopores, Guinot (1979) stated that the position of the gonopores of the various genera are distinctly different, and indicated that there was a need to check the types of all the species of the Varuninae and Sesarminae to ascertain their affinities. Based on molecular data, Schubart *et al.* (2000, 2001, 2002) suggested that *Helice, Cyclograpsus* and *Metaplax* are more closely affiliated to Varuninae, and should be transferred to Varuninae. Likewise, larval morphology studies by Cuesta and co-workers (Cuesta, 1999; Cuesta *et al*., 2000; Cuesta *et al.*, 2001) have given a similar prognosis. Davie (2002, see below on remarks on subfamily Cyclograpsinae) resurrected the cyclograpsine subfamily, but he did not do a full reappraisal of the cyclograpsines. The gastric mill studies by Yang (1986) had also indicated that there is a need to review the subfamilies Macrophthalminae (especially the genus *Uca*), Sesarminae (particularly the genera *Metaplax*, *Helice* and *Chasmagnathus*), and Varuninae. Preliminary studies on two gastric mill ossciles, urocardiac ossicle and zygocardiac ossicle of the genera *Gaetice*, *Euchirograpsus* and other varunine species have indicated that Varuninae is distinctly paraphyletic (in collaboration with S. L. Yang, unpubl.). Guinot & Bouchard's (1998) indicated that the Varuninae and the Sesarminae are paraphyletic and should be revised. Davie (2002) resurrected the subfamily Cyclograpsinae, and the three genera *Cyclograpsus*, *Helice* and *Chasmagnathus* have been transferred to the subfamily Cyclograpsinae (see below for the remarks for the subfamily).

The use of larval characters for the brachyuran classification in the past 20 years has been increasingly useful in providing an insight into the phylogeny of crustaceans (Cuesta, 1999, P.F. Clark, pers. comm.). Larval characters have been used as one of the key characters if the adults are difficult to separate by external morphology (Ng *et al*., 1998). Rice (1980) first proposed the large-scale use of larval characters for crustacean classification, stating that the adult morphology could not resolve the origin of the true crabs, and there were numerous problems with the various classifications provided by earlier workers (Rice, 1980). Based on his extensive studies on the crustacean larvae, Rice (1980) proposed that the division of Brachyura into three main divisions, viz. Dromiacea, Archaeobrachyura and Higher Brachyura, the latter most being where grapsid crabs belong. In Rice's (1980) classification, the families Grapsidae, Mictyridae, Gecarcinidae, Ocypodidae, Pinnotheridae, Hymenosomatidae, Leucosiidae and Matuninae (Calappidae) all fall under the second Brachyrhynchan group under the Catometopa. Within the family Grapsidae, Rice (1980) recognized three distinct smaller groups. The first and second groups correspond to Dana's Grapsinae and Plagusiinae, respectively. The third group consists of Sesarmine and Varuninae. Although Rice did not distinguish the two subfamilies, he stated that *Hemigrapsus, Cyclograpsus, Chasmagnathus, Helice* and *Eriocheir* share similar larval characters; while S*esarma, Metasesarma, Aratus* and *Chiromantes* shared a separate suite of characters. Rice added that *Gaetice depressus* and *Acmaeopleura parvula* are intermediate between the sesarmine and varunine crabs. He further speculated that the grapsine crabs are the most evolved of all the grapsid crabs (Rice, 1983). The larval studies carried out by Schubart & Cuesta (1999); Schubart, Cuesta & Diesel (2002), on more than 40 different species of grapsoid crabs are not entirely conclusive, although their results have an important bearing on the modern classification system. It must be noted that the use of larval characters also present numerous problems. The availability of gravid female crab specimens for obtaining the larval specimens, the sparse knowledge associated with their collection, and their close similarity are just a few of the problems associated with using these characters (sensu Rice, 1980) for taxonomy. It is also very difficult to identify larval specimens that are collected from the wild.

The use of molecular techniques on grapsoid crabs was first started by Schubart *et al.* (1999) and later expanded by Schubart *et al.* (2000). The use of 16s rRNS, 18S rRNA and COI has been shown to be useful in elucidating the phylogenetic relationships of closely-allied species, cryptic species and possibly provide a simple and direct way of determining the genetic relationships of species, and the extent of differentiation, as well as the phylo-geographic relationships among populations of widely distributed species. It has also helped to resolve some of the more problematic genera as molecular characters/results could be used as additional evidence to support the separation or synonymy of difficult species (e.g. see Kitaura *et al*., 1998). It must be noted that molecular data, although a powerful tool, have been shown to be inadequate in solving some of the more challenging taxonomic problems. For example, the recent DNA studies on *Eriocheir, Platyeriocheir* and *Neoeriocheir* conducted by numerous workers (Chu *et al.*, 2003; Tang *et al.*, 2003, 2004) have yet to solve the “identity crisis” of *Eriocheir sinensis* and its relationship to *Neoeriocheir* and *Platyeriocheir.* Morphological examination of the specimens from the three genera has shown that they are three distinct genera (see below).

The combination of these two techniques has shown to be useful for many of the difficult crustacean taxon. These publications have more or less supported the classification system based on adult morphology that have been suggested or proposed by earlier workers. In Schubart *et al.*'s (2000: Fig. 1) publication of the phylogeny of the American Grapsoidea, his 16s rRNA tree showed very clearly the distinct clades which have corresponded to the various subfamilies proposed by Dana (1852), H. Milne Edwards (1853) and Alcock (1900), i.e. the Grapsinae clade (consisting of *Planes, Goniopsus, Geograpus, Grapsus, Pachygrapsus* and *Leptograpsus*), while the rest of the subfamilies cluster in another clade. It is interesting to note that the *Gercarcinus* and *Cardisoma* came out in one clade. This is expected as the morphologies of *Gercarcinus* and *Cardisoma* are very different from the rest of the grapsoids. However, *Percnon*, which is placed in the subfamily Plagusiinae with *Plagusia*, comes out in its own clade. This is also to be expected as the detailed morphology of *Percnon* is rather different from *Plagusia* and *Euchirograpsus* (see Davie, 2002). The Sesarminae, with the genera *Sesarma*, *Metopaulias*, *Armases* and *Aratus* are all grouped into one single clade. Both the *Platychirograpsus+Glyptograpsus*, and *Euchirograpsus+Plagusia* clades came out as two separate, distinct clades. The sesarmine clade came out between the *Platychiropgrapus+Glyptograpsus* clade and *Euchirgrapsus+Plagusia* clade. This strongly indicates that the sesarmine crabs form a very good clade (see Schubart *et al*., 2000). It is interesting to note that *Cyclograpsus* and *Chasmagnathus* emerged within the varunine clade. This observation is to be expected because both *Cyclograpsus* and *Chasmagnathus* have been originally grouped together with *Varuna* and *Eriocheir* by H. Milne Edwards (1853) but not with the *Sesarma* sensu lato (see H. Milne Edwards, 1853). Even with Dana's definition of the Sesarminae, *Cyclograpsus*, *Chasmagnathus* and *Helice* were grouped together as one distinct group within the subfamily Sesarminae (see Dana, 1852). This strongly indicated that both H. Milne Edwards (1853) and Dana (1852) have already recognized the very close affinities of *Cyclograpsus* and *Chasmagnathus* with the subfamily Varuninae despite the presence of the 'piliferous setose ridge across the maxilliped' in these two genera (see below on remarks on Cyclograpsinae).

The phylogenetic tree generated by Schubart *et al.* (2000) is very similar to the classification systems of Dana (1852) and H. Milne Edwards (1853). On the basis of the molecular and larval data, Schubart *et al.* (2000a) raised all the four subfamilies of Dana's to family level (see Schubart *et al.*, 2000; Cuesta *et al.*, 2001). Based on differences in the larval forms, molecular differences and adult morphology data, Schubart *et al.* (2002) established the family Glyptograpsidae for the genera *Platychiropgrapus* and *Glyptograpsus*. The classification system of Schubart *et al.* (2000, 2002) has been widely accepted (Martin & Davies, 2001; Ng *et al.*, 2001; Davie, 2002; McLaughlin *et al.*, 2005).

Based on the problems associated with larval data and molecular data, it is obvious that both molecular data and larval data do not provide sufficient evidence to resolve difficult taxa, and therefore, they are not suitable to be used without substantial adult morphological characters at the subfamilial and familial levels. The basis of systematics should be based on external morphological characters of adult specimens as these characters are the most obvious and easiest to use. It is very impractical to be using larval and molecular data for identification in the field or in the laboratory. The use of 16s rRNA or COI or micro-satellites or a combination of two or three genes does not present the entire genome, and therefore, does not fully elucidate the differences or similarities between the various taxonomic groups. The expression of these few genes may not even have the same outcome. The current knowledge on genetic expression and functional genomics has yet to be fully understood, and it is inappropriate to base our conclusions on just two or three genes. As such, the more logical and practical approach is to use the characters after all the genes have been more or less fully expressed i.e. the adult morphological characters. Other external morphological characters like the position of the genital opening (Guinot, 1978), the locking mechanism of the on the sternal plates (Guinot & Bouchard, 1998), and internal morphological characters gastric mill data (Yang, 1986; Abele & Felgenhauer, 1986; Felgenhauer & Abele, 1989), are few of the many characters that can be utilized to demonstrate the phylogenetic relationships of these animals.

In this report, I follow the classification system of Schubart *et al.* (2000), in which I recognize the family Varunidae, currently consisting of 27 genera and 140 species. I also recognize the subfamily Cyclograpsinae (see Davie, 2002) for the group of crabs consisting of the genera *Cyclograpsus*, *Paragrapsus*, *Metaplax*, *Helice* and its closely-allied genera, *Chasmagnathus*, *Paragrapsus* and *Helograpsus*, which have been misplaced in the family Sesarmidae (see below). I have examined each genus now placed in the family Varunidae sensu lato and subfamily Cyclograpsinae sensu lato. Based on external adult morphological characters, two genera, *Gaetice* and *Setostoma*, new genus, that exhibit filter feeding habits, have to be removed and placed in their own subfamily Gaeticinae (see below). The genus *Thalassograpsus*, which is distinctly different in the form of the carapace and third maxillipeds, will be placed in its new subfamily Thalassograpsinae in this study. Overall, I have divided the family Varunidae into four subfamilies viz. Varuninae; Cyclograpsinae; Gaeticinae and Thalassograpsinae. The genus *Xenograpsus*, originally placed in the Varuninae, has been shown in this study to be very different from the rest of the family, and has been transferred to its own new family Xenograpsidae (see below). I recognize the families Grapsidae, Sesarmidae, Gercarcinide, Plagusidae and Glyptograpsidae. The representative genera from these families and subfamilies have been included in this report as they have been used for comparative purposes.

**Key to subfamilies in Varunidae**

1a. Carapace rounded to quadrangular in shape. Pterygostome with complex reticulations of setae; presence of a deep vertical groove parallel to buccal cavity; presence of an oblique setose crest across merus of third maxilliped. -------------------- --------------------------------------------------------------------------- **Cyclograpsinae**

1b. . Carapace quadrate or quadrangular in shape. Pterygostome without any complex reticulations of setae; without deep vertical groove parallel to buccal cavity or oblique setose crest across merus of third maxilliped. ------------------------------ **2**

2a. Orbits of the eyes open laterally. Third maxilliped leaving a narrow elongated gape when closed. Palp of third maxilliped very elongated, armed with a brush of very long setae that rests on sternal plastron; sternal plastron with a deep medial groove to receive setae of the third maxillipeds. --------------------- **Gaeticinae, new subfamily**

2b. Orbits of the eyes nearly closed. Third maxilliped leaving either no gape or small rhomboidal gape when closed. Palp of third maxilliped short, without long setae, sternal plastron without medial groove. --------------------------------------------------- **3**

3a. Antennal flagellum long. Third maxilliped moderately gaping when closed, merus of third maxilliped with antero-external angle strongly produced and auriculate; exopod of third maxilliped narrow or greatly widened and broader than ischium, with long flagellum. ------------------------------------------------------------------------ **Varuninae**

3b. Antennal flagellum short. Third maxilliped without any gap when closed, merus of third maxilliped with very small antero-external angle, exopod of third maxilliped narrow, never broader than ischium, with short flagellum. ------------------------------- ------------------------------------------------------ **Thalassograpsinae, new subfamily**

## Subfamily Varuninae H. Milne Edwards, 1853

Varunaceae H. Milne Edwards, 1853: 191.

Varuninae – Alcock, 1900: 288; Rathbun, 1918: 260; Tesch, 1918: 82; Sakai, 1939: 647, 658; 1965: 195; 1976: 637; Gamô, 1958: 373; 1960: 373; Edmondson, 1959: 176; Crosnier, 1965: 33; Kim, 1973: 461; Sakai, 1976: 637; Terada, 1981: 66; Kim & Chang, 1985: 41; Dai *et al.*, 1986: 467; Depledge, 1989: 253; Kim & Hwang, 1990: 793; 1995: 411; Dai & Yang, 1991: 514; Ng *et al.*, 1999: 154; Ng & Ng, 2002: 663.

**Diagnosis.**— Carapace quadrate or quadrangular in shape, with lateral margins convex to subparallel; regions often discernible; dorsal surface usually glabrous, physiognomy sometimes flat to deeply vaulted or very convex; anterolateral margins entire or with one, two or four teeth or notches including exorbital tooth. Front deflexed; broad, less than half maximum carapace breadth. Orbits open laterally; sub-orbital crest more or less straight, typically long, extending to a short distance across lateral branchial region, not stridulatory; pterygostomial grooves opening into anterolateral corner of buccal cavity; pterygostome, subbranchial, sub-hepatic regions glabrous; pterygostome without a deep vertical groove placed subparallel to buccal cavity. Third maxilliped without oblique setose crest extending across merus, outer distal corner of ischium; with small rhomboidal gape when closed; reaching forward to margin of epistome to completely close buccal cavity anteriorly; exopod normal, narrow; flagella of maxilliped exopods not especially elongated, not noticeably protruding from behind third maxilliped. Endostome smooth, more or less medially prominent. Chelipeds usually symmetrical, large in adult males. Ambulatory legs flattened, oval in cross section, typically more or less narrow, not markedly dorso-ventrally flattened; posterodistal margin of meri not armed with spines; propodi, dactyli not armed with strong black bristles. Male abdomen with seven moveable segments (six abdominal somites plus telson). Male gonopore is located a distance from coxa, embedded within sternite 8. G1 usually long and narrow; G2 small. Female gonopore operculate, usually circular in shape.

**Type Genus.** — *Varuna* H. Milne Edwards, 1830.

**Remarks.**— Since the history of this subfamily has been treated earlier, and hence, it will not be treated further here. Most of the genera in the Varunidae have basically remained unchanged until recently, when Schubart *et al.* (2002) established the new family Glyptograpsidae for two genera, *Glyptograpsus* and *Platychirograpsus*.

There are a few taxa whose classification within the Varunidae that have been somewhat confused, particularly at the subfamilial level, and they are discussed below.

*Ilyograpsus paludicola* (Rathbun, 1909) (originally in the genus *Camptandrium* Stimpson, 1858, which is now a member of the Camptandriidae Stimpson, 1859) was originally placed under the subfamily Varuninae by Rathbun (1918), and later moved to Grapsinae by Crosnier (1965). Fukuda (1978) proposed that *I. paludicola* should belong to the Ocypodidae; and more precisely, in the subfamily Macrophthalminae, as indicated by Cuesta (1999). On the other hand, preliminary larval analyses suggested that the Ocypodidae sensu lato may be paraphyletic and that the Macrophthalminae could be instead, assigned to the Grapsoidea (Flores *et al.*, 2003) and be recognized as a family (Kitaura *et al.*, 2002).

The genus *Euchirograpsus* H. Milne Edwards, 1853, has been moved from the subfamily Grapsinae to subfamily Varuninae by Balss (1957). Molecular data from Schubart *et al.* (2000) had proposed the placement of *Euchirograpsus* into the family Plagusiidae, and Schubart *et al.* (2000) and Schubart & Ng (2000) had raised the subfamily Plagusiinae to family level. This placement has been accepted widely (see Martin & Davies, 2001; Ng *et al.*, 2001; Davie, 2002) although this taxonomy has not been substantiated by any published morphological data. In this study, morphological examination of the five species of *Euchirograpsus* supports Schubart *et al.*'s (2000) proposals. The key morphological characters are the presence of the cleft in the front to receive the antenna, male abdominal segments of either 3-5 fused or 3-6 fused, and the third maxilliped with a very reduced exopod and lacking a flagellum (see Table 6).

The genus *Planes* Bowdich, 1825, was included in the subfamily Varuninae by Tesch (1819). Crosnier (1965) moved *Planes* back to Grapsinae. In his remarks, he commented that even though *Planes* may superficially look like a varunine crab it should be placed in the Grapsinae. Close examination of *Planes* specimens in the current study support's Crosnier's prognosis (1965). The genus *Perigrapsus* Heller, 1862, has been shown to be a junior synonym of *Cardisoma carnifex* (see Türkay, 1974), i.e. a member of the Gercarcinidae (Türkay, 1974; Ng & Guinot, 2002). The genus *Baruna* has been shown to belong to the family Camptandriidae (see Harminto & Ng, 1991). The genus *Gaetice* was included into the Varuninae by Tesch (1918), but is transferred to its own subfamily in this report (see below).

The species *Cyclograpsus octodentatus* H. Milne Edwards, 1837, was transferred by Griffin (1969) to the genus *Leptograpsodes* Montgomery, 1931 (now Grapsidae sensu stricto). The genus *Brachygrapsus* was established by Kingsley (1880) for *Brachygrapsus laevis* Kingsley, 1880, from Port Philip, Victoria, Australia. *Brachygrapsus laevis* has been shown to be a junior synonym of *Litocheira bispinosa* Kinahan, 1856. Türkay (1975) transferred *Brachygrapsus laevis* to the family Goneplacidae.

A comment on one very perplexing species is needed. Holmes (1900) described a new genus and new species, *Grapsodius eximius* from San Diego in California, U.S.A. The description was based on a small male specimen that was in poor condition in the museum and there was no field data with it. Holmes (1900) did not provide any figure, although his description of the genus and species was relatively long. Rathbun (1918) cited his taxon verbatim but she accepted his identification, although retaining it in the Grapsinae. The species has never been seen again. The types are apparently no longer extant and it is a problem taxon (Schubart *et al.*, 1999). Holme's description is troubling, as it cannot be assigned to any known taxon from that area – in particular, his description of the swollen orbit is unusual. Schubart *et al.* (1999) speculated it might be an aberrant specimen of *Pachygrapsus* or *Plane*s (both Grapsidae sensu stricto). From his description, it may also be an aberrant *Grapsus*. Certainly Holme's description of the legs being spinous suggests against it being a varunid as defined here. As such, it is excluded from this thesis.

All the remaining genera that currently recognized in the subfamily Varuninae will be treated below.

The genus *Cyrtograpsus* Dana, 1852, was placed under Grapsinae by Dana (1852). Rathbun (1918: 225) transferred the genus to the subfamily Varuninae based on the form of the carapace, third maxillipeds and male abdomen. The most confusing and problematic genus is *Hemigrapsus* Dan, 1852. Dana (1852) established *Hemigrapsus* for a group of H. Milne Edwards's 'Cyclograpsi crabs' (*C. sexdentatus* and *C. crenulatus*) that did not possess the 'piliferous oblique crest and the setose pterygostome' that defined members of the subfamily Sesarminae. Dana did not want to use *Gnathochasmus* MacLeay, 1838 (Dana, 1852: 331) even though *Gnathochasmus* is a junior synonym of *Cyclograpsus* H. Milne Edwards, 1837 (Ng & Ahyong, 2001). The subfamily Varuninae has remained basically unchanged from the years 1922 to 2000 except for the addition of several new genera: *Parapyxidognathus* Ward, 1941; *Neoeriocheir* Sakai, 1976; *Xenograpsus* Takeda & Kurata, 1977; *Scutumara* Ng & Nakasone, 1993; *Orcovita* Ng & Tomascik, 1994, and *Platyeriocheir* Ng, Guo & Ng, 1999. Most recently, the genus *Noarograpsus* Ng, Manual & Ng, 2006, was established for an unusual Philippine species previously referred to *Hemigrapsus*.

In this report, all the problematic and complex genera within the subfamily Varuninae will be treated. Genera like *Ptychognathus* Stimpson, 1858; *Utica* White, 1947; *Pseudograpsus* H. Milne Edwards, 1837; *Cyrtograpsus* Dana, 1852, and *Hemigrapsus* Dana, 1852, are completely revised.

The subfamily Varuninae, as redefined in this thesis, now comprises 33 genera of which 13 are new. Each genus will be treated below.

**Key to genera in Varuninae**

1a. Carapace distinctly rounded or subquadragular in shape. ---------------------------- **2**

1b. Carapace distinctly quadrate in shape. ------------------------------------------------ **6**

2a. Anterolateral margin with two teeth including exorbital tooth. --------------------- **3**

2b. Anterolateral margin with two or more teeth (lobes) including exorbital tooth. -- **5**

3a. Carapace surface setose, regions not defined. Exopod of third maxilliped narrower then ischium. Ambulatory legs glabrous. -------------------------- ***Acmaeopleura***

3b. Carapace surface glabrous, regions not well-defined. Exopod of third maxilliped broader than ischium. Ambulatory legs setose. -------------------------------------- **4**

4a. Expod of third maxilliped broad, flat. Ambulatory legs very broad and short, sparsely covered with long and short setae. ----------------------- ***Cebuanograpsus***

4b. Expod of third maxilliped broad, convex. Ambulatory legs proportionately shorter, more laterally compressed than those in *Cebuanograpsus*; densely setose with long setae. ------------------------------------------------------------------ ***Ptychognathus***

5a. Anterolateral margin with two to three teeth (including exorbital tooth). Exopod of third maxilliped broad, flat. Ambulatory legs very long, slender, setose.. --- ***Orcovita***

5b. Anterolateral margin with three teeth (including exorbital tooth). Exopod of third maxilliped broad, convex. Ambulatory legs broad, short, glabrous. ---------------------- ------------------------------------------------------------------------------ ***Pyxidognathus***

6a. Anterolateral margin with two or three lobes including exorbital lobe. -------------- **7**

6b. Anterolateral margin with three or more teeth including exorbital tooth. -------- **8**

7a. Carapace with two lobes including exorbital lobe; broad as long; surface punctate, Outer surface of cheliped with a tuft of short setae. Ambulatory legs short, very sparingly setose. ---------------------------------------------------------- ***Quadragrapsus***

7b. Carapace with three lobes including exorbital lobe; slightly longer than broad; surface smooth. Outer surface of cheliped usually without tuft of setae. Ambulatory leg broad, glabrous. -------------------------------------------------------- ***Scutumara***

8a. Anterolateral margin of carapace with four or more teeth including exorbital tooth. ---------------------------------------------------------------------------------------------- **9**

8b. Anterolateral margin of carapace with three teeth including exorbital tooth. ------ **16**

9a. Carapace with five anterolateral teeth including exorbital tooth; fourth anterolateral tooth largest and broadest. ------------------------------------------------- ***Cyrtograpsus***

9b. Carapace with four anterolateral teeth including exorbital tooth, with exorbital tooth very small or very broad. ------------------------------------------------------------ **10**

10a. Carapace surface pilose and thin, texture papery thin, frontal region produced, carapace regions not well defined. ----------------------------------- ***Papyrograpsus***

10b. Carapace surface glabrous or punctate, texture thick, smooth, frontal region not produced, carapace regions well defined. ---------------------------------------- **11**

11a. Carapace with lateral margins almost parallel. -------------------------------- **12**

11b. Carapace with lateral margins subparallel. -------------------------------------- **13**

12a. Carapace with exorbital tooth smallest, regions not defined, surface glabrous. Exopod of third maxilliped broader than ischium, convex. Outer surface of cheliped with a tuft of setae. Ambulatory legs broad, short, setose. ----------------- ***Abakos***

12b. Carapace with exorbital tooth broad, regions well defined, surface smooth. Exopod of third maxilliped narrower than ischium, flat. Inner surface of cheliped with a tuft of setae. Ambulatory legs broad, long, sparingly setose. --------------- ***Tetragrapsus***

13a. Carapace physiognomy broad. Frontal margin of carapace lobulated. Cheliped setose. ------------------------------------------------------------------------------ **14**

13b. Carapace physiognomy narrow. Frontal margin of carapace straight. Cheliped glabrous or setose. --------------------------------------------------------------- **15**

14a. Frontal margin of carapace with four distinct lobes or teeth. Cheliped with outer and inner surfaces densely setose. Ambulatory legs all densely setose. ------------------ ---------------------------------------------------------------------------------- ***Eriocheir***

14b. Frontal margin of carapace slightly bilobed; anterolateral margin of carapace widest after fourth anterolateral tooth. Chela with base of fingers setose. Ambulatory legs slightly setose. ------------------------------------------------- ***Austrograpsus***

15a. Cheliped with inner and outer surfaces glabrous. ------------------ ***Patagograpsus***

15b. Chela with inner surface densely setose. ------------------------------ ***Neoeriocheir***

15c. Cheliped with inner surface densely setose. --------------------------- ***Platyeriocheir***

16a. Carapace surface pilose or granulated. ------------------------------------------- **17**

16b. Carapace surface glabrous and smooth. ---------------------------------------- **19**

17a. Carapace surface pilose, covered with dense short bristle-like setae. Ambulatory legs densely setose. --------------------------------------------------- ***Hirtograpsus***

17b. Carapace surface punctate, with prominent granulated ridges. Front slightly produced. Ambulatory legs sparingly setose. -------------------------------- **18**

18a. Carapace with granulated ridges demarking the different regions. ---------------------
--------------------------------------------------------------------------------- ***Noarograpsus***

18b. Carapace with a single raised, granulated, setose horizontal ridge on branchial region. ----------------------------------------------------------------------------- ***Utica***

19a. Carapace physiognomy broad. Anterolateral teeth of carapace broad, blunt. **-- 20**

19b. Carapace physiognomy narrow. Anterolateral teeth of carapace acute, sharp. **-- 21**

20a. Exopod of third maxiliped broader than ischium, convex. Ambulatory legs short and broad, very sparingly setose. ------------------------------------- ***Gnathograpsus***

20b. Exopod of third maxilliped narrower than ischium, flat. Ambulatory legs broad and long, densely covered with bristle-like setae. -------------------------- ***Pseudograpsus***

21a. Exopod of third maxilliped as broad as or broader than ischium. ------------- **22**

21b. Exopod of third maxilliped narrower than ischium. ----------------------------- **25**

22a. Exopod of third maxilliped as broad as ischium, flat. ------------------------------ **23**

22b. Exopod of third maxilliped broader than ischium, convex. ------- ***Mitragrapsus***

23a. Posterior margin of propodus of ambulatory legs with numerous spines. -------------
-------------------------------------------------------------------- ***Parapyxidognathus***

23b. Posterior margin of propodus of ambulatory legs without spines. ----------------- **24**

24a. Male abdomen triangular in shape; distal margin of male telson convex in shape. Chelipeds with fingers longer than palm. --------------------------- ***Neoptychognathus***

24b. Male abdomen narrowly triangular in shape; distal margin of male telson concave in shape. Chelipeds with fingers as long as palm. --------------------------- ***Cognatus***

25a. Posterolateral margins of carapace almost parallel. --------------------------- **26**

25b. Posterolateral margins of carapace distinctly converging. --------------------- **29**

26a. Ischium of third maxilliped as broad as long. Absence of pulvinus but presence of setae on cheliped. --------------------------------------------------------------------- **27**

26b. Ischium of third maxilliped longer than broad. Presence of pulvinus and/or soft setae on either outer or inner surfaces of chelipeds. -------------------- ***Hemigrapsus***

27a. Frontal margin of carapace bilobed. Cheliped with a tuft of setae on inner surface of cheliped. Ambulatory legs glabrous. ----------------------------------- ***Pseudogaetice***

27b. Frontal margin of carapace straight. Cheliped with a tuft of short setae on outer surface. Ambulatory legs setose. ---------------------------------------------------- **28**

28. Carapace with a granulated ridge at by the third anterolateral tooth. Exopd of third maxilliped less than one-third width of ischium. ------------------------- ***Asiagrapsus***

28b. Carapace without granulated ridge at by the third anterolateral tooth. Exopd of third maxilliped about one-half width of ischium. ------------------------- ***Pseudoutica***

29a. Anterolateral teeth very acute and sharp. Cheliped with pulvinus present at base of fingers. Ambulatory legs glabrous. ------------------------------------- ***Brachynotus***

29b. Anterolateral teeth broad and sharp. Cheliped without pulvinus at base of fingers. Ambulatory legs long, setose. --------------------------------------------------- **30**

30a. Cheliped with setae on the outer and inner surfaces. Ambulatory legs moderately setose. -------------------------------------------------------------------- ***Tanyograpsus***

30b. Cheliped glabrous on inner and outer surfaces. Ambulatory legs densely setose. ----------------------------------------------------------------------------------------- ***Varuna***

Table 1. List of distinguishing characters of the four varunid subfamilies: Varuninae, Cyclograpsinae, Gaeticinae and Thalassograpsinae within the family Varunidae.

| Subfamily / Characters | Gaeticenae | Cyclograpsinae | Thalassograpsinae | Varuninae |
|---|---|---|---|---|
| **Eye Orbit** | Open laterally | Open laterally | Open laterally | Open laterally |
| **Front cleft to receive antennues** | No | No | No | No |
| **Basal article of antenna** | Mobile | Mobile | Mobile | Mobile |
| **Suborbital crest form** | Straight | Small granules | Small granules | Small granules |
| **Suborbital crest** | Non-stridulatory | Stridulatory | Non-stridulatory | Non-stridulatory |
| **Pterygostomial groove** | Present, but not opening to anterolateral corner | Present but shallow | Absent | Absent |
| **Pterygostomial region-reticulted setae** | Absent | Absent | Absent | Absent |
| **Third maxilliped- gape** | Narrow elongated gap | Narrow rhomboidal gap | Almost no gap | Small rhomboidal gap |
| **Third maxilliped-no of suclcus on merus** | One | One | One | One |
| **Third maxilliped-no of suclcus on ischium** | One | One | One | One |

| | | | | |
|---|---|---|---|---|
| **Third maxilliped- oblique setose crest** | Absent | Present | Absent | Absent |
| **Third maxilliped- reaching epistome** | Yes | No | No | No |
| **Third maxilliped- closing entire cavity** | Yes | No | No | No |
| **Third maxilliped- palp** | Very long | Normal length | Very short | Normal length |
| **Third maxilliped- length of plap when folded** | Reaching abdomen when folded | Not reaching abdomen when folded | Not reaching abdomen when folded | Not reaching abdomen when folded |
| **Articulation of third maxilliped** | Nearly vertical | Nearly vertical | Horizontal | Nearly vertical |
| **Sternite 3/4 with depressed sulcus** | No | No | No | no |
| **Sternite 3/4 suture** | Visible | Visible | Not visible | Visible |
| **Medial groove reaching anterior margin of sternite 3** | No | No | No | No |
| **Abdomen- segments** | 3-6 fused | 7 free segments | 7 free segments | 7 free segments |

| | | | | |
|---|---|---|---|---|
| **Position of male gonopore** | Gonopore embedded in sternite 8, no contact with coxa of fifth ambulatory leg and thoracic sternite 7 | Gonopore embedded in sternite 8, no contact with coxa of fifth ambulatory leg and thoracic sternite 7 | Gonopore embedded in sternite 8, no contact with coxa of fifth ambulatory leg and thoracic sternite 7 | Gonopore embedded in sternite 8, no contact with coxa of fifth ambulatory leg and thoracic sternite 7 |
| **Presence of mobile setae on dactylus of ambulatory legs** | No | No | No | No |
| **Presence of spines on ambulatory dactyli** | No | No | Small, chitinous spines | No |
| **Ambulatory legs- longest** | Second pair | Second pair | Second pair | Second pair |

## Genus *Acmaeopleura* Stimpson, 1858

*Acmaeopleura* Stimpson, 1858: 105; 1907: 130, pl. 11, fig. 4; Sakai, 1934: 324, pl. 17, fig. 2; 1935: 231, pl. 62, fig. 4; 1939: 662, pl. 75, fig. 4; 1965: 195, pl. 91, fig. 5; 1976: 643, pl. 220, fig. 2; Kim, 1973: 461; Fukui *et al.*, 1989: 229, figs. 17, 18; Jeng *et al.*, 1998: 123; Ng *et al.*, 2001: 44.

**Type species.**— *Acmaeopleura parvula* Stimpson, 1858, by monotypy.

**Gender.**— Feminine.

**Diagnosis.**— Carapace rounded, broader than long; dorsal surface setose, punctate; regions not well defined, convex. Frontal margin slightly convex, straight. Anterolateral margin subcristate with two teeth including exorbital tooth, first very broad; second tooth lobe-like. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped short, stout, closed with a small, distinct rhomboidal gape when closed; palp short, with short setae; exopod with short flagellum. Epistome broad, flat, posterior margin entire. Inner surface of chela with granules; outer surface of pollex and manus with tufts of long, stiff setae, a patch of short stiff setae near posterior margin of manus; fingers as long as palm. Ambulatory legs with short setae, dactylus stout. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular, with all segments freely moveable (six somites plus telson).

**Remarks.**— *Acmaeopleura* is here restricted to two species, viz. *A. parvula* Stimpson, 1858, and *A. rotunda* Rathbun, 1909. Based on the present study of *A. parvula* and Rathbun's description of *A. rotunda*, both appear to be free-living, intertidal species that possess normal mouthparts for omnivorous feeding.

Three species originally described as *Acmaeopleura* species (*A. balssi* Shen, 1932, *A. depressa* Sakai, 1965, and *A. toriumii* Takada, 1971) have different forms of the palps of the third maxillipeds, anterior segments of the thoracic sternum, male abdomens and feeding habits. These characters warrant the removal of these three to a new genus, and their transfer to a new subfamily, Gaeticinae (see remarks for the subfamily). The key differences of *Acmaeopleura* and the new genus, *Setostoma*, are listed in Table 5.

It is interesting to note that many pinnotherid crabs are very similar to this genus in their adult morphologically and habits. It is possible that these two taxa are convergent in their evolution. Larval and DNA studies on pinnotherid crabs by J. Cuesta and C.D. Schubart (pers. comm.) has shown that some pinnotherid crabs (notably members of the subfamily Astheognathinae) are, in fact, are very closely affiliated to varunid crabs in the subfamily Gaeticinae (see later). As such, it will be worthwhile for future workers to re-examine the family Pinnotheridae in even more detail to check this connection.

**Key to the species in *Acmaeopleura***

1a. Carapace subquadrangular. Anterolateral with only one tooth. Ambulatory legs setose. ------------------------------------------------------------------------ ***A. parvula***

1b. Carapace subcircular. Anterolateral margin with two teeth including ex-orbital tooth Ambulatory legs glabrous. ---------------------------------------------------- ***A. rotunda***

### *Acmaeopleura parvula* Stimpson, 1858

(Figure 5A-I)

*Acmaeopleura parvula* Stimpson, 1858: 105; 1907: 130, pl. 11, fig. 4; Sakai, 1934: 324, pl. 17, fig. 2; 1935: 231, pl. 62, fig. 4; 1939: 662, pl. 75, fig. 4; 1965: 195, pl. 91, fig. 5; 1976: 643, pl. 220, fig. 2; Kim, 1973: 462, text-fig. 199, pl. 91, fig. 152; Fukui, Wada & Wang, 1989: 229, figs. 17, 18; Jeng *et al.*, 1998: 123; Ng *et al.*, 2001: 44.

**Material examined.**— **Neotype –** 1 male (9.2mm x 7.4mm), 1 female (9.6mm x 7.4mm), (Chiba-ZC1032), Japan, no collection date. **– Others – Japan** –4 males (9.3-12.3mm x 8.3-10.2mm), 1 female (13.5mm x 10.7mm), (MNHN-B-11164), Tokyo area, Japan, coll. Harmond, 1906; 1 male (7.1mm x 5.9mm) (SFM-22491), Manazumi, Kanagawa, Honshu, Japan, coll. H. Suzuki, no collection date; 1 male (15.5mm x 12.2mm) (SFM-22490), Muroni, Hakata, Fukuoka, Kyushu, Japan, coll. K. Sakai, 1978; 1 male (17.4mm x 16.1mm), 2 females (ovigerous) (17.5-18.0mm x 16.1-16.5mm) (SFM-22493), Manzuru, Kanagawa, Honshu, Japan, leg H. Suzuki, 28 Feb. 1978; 4 males (6.8-13.0mm x 5.4-10.5mm) (SFM-no cat. number), Manazuru, Kanagawa-ku, Honshu, Japan, coll. H. Suzuki, 5 Apr. 1960; 1 male (17.7mm x 13.7mm), 2 females (10.7-11.4mm x 8.5-8.9mm) (NSMT-Cr-6681), Ogasawara Islands, coll. Apr. 1968; 2 females (9.5-11.2mm x 8.0-9.5mm) (RNHN-D-26507), Sagami Bay, Kanagawa Prefecture, Japan, coll. H. Suzuki, 5 Sep. 1968; 1 male (21.4mm x 18.3mm), 1 female (15.8mm x 13.4mm) (SFM-7658), Manazuru, Japan, coll. T. Watanabe; 4 males (13.7-16.6mm x 11.1-13.1mm), 3 females (9.6-11.8mm x 7.5-9.5mm) (SFM-5506), Sakurajima, Japan; 1 male (7.1mm x 5.9mm) (SFM-22491), Manazuru, Kanagawa, Honshu, Japan, coll. H. Suzuki; 2 males (7.6-11.3mm x 5.8-9.4mm), 4 females (10.2-11.8mm x 8.1-9.3mm), (SFM-6907), Manazuru, Japan, leg. 5 Oct. 1971. – **Taiwan** – 1 female (13.6mm x 10.5mm) (TMCD-2513), Ba-Dou-Zhi, Keelung, Taiwan, coll. C.H. Wang, 12 Apr. 1989; 1 male (8.4mm x 6.2mm) (TMCD-2525), Hsin-Gang, Tou-Cheng, I-Lan County, Taiwan, coll. C.H. Wang, 13 Apr. 1989; 1 female (7.3mm x 5.3mm) (TMCD-2547), Xiao-Hsiang-Lan, Fu-Lung, Taipei County, Taiwan, coll. C.H. Wang, 20 Apr. 1989; 1 male (11.2mm x 9.1mm) (AZIS-71691), He-Mei, Taiwan, coll. M.S. Jeng, 4 Nov. 1997; 1 male (11.2mm x 9.1mm) (ASIZ-71691), He-Mei, Taiwan, coll. M.S. Jeng, 4 Nov. 1997.

**Diagnosis.**— Carapace almost subcircular, dorsal surface convex, punctate, regions not defined. Anterolateral margins, subcristate with two teeth including exorbital tooth.

Third maxilliped very broad; ischium, merus broad, exopod very narrow. Cheliped large, with a tuft of long soft setae on outer surface of immovable finger. Ambulatory legs short, slender, covered with short setae. G1 long, slender, almost straight, distal end slightly bilobed. Female gonopore operculate, circular in shape.

**Colour.**— The colour of fresh specimens is dark cream to light reddish brown, and all preserved specimens examined are all light brown in colour.

**Size.** — The largest male specimen examined is 21.4mm x 18.3mm (SFM-7658), and largest female examined is 15.8mm x 13.4mm) (SFM-7658).

**Habitat.**— *A. parvula* can be found under rocks or vegetation, along the river banks (pers. observ.).

**Remarks.**— Superfically, *Acmaeopleura parvula* looks very much like *Cyclograpsus* senus lato. However, the third maxilliped lacks the pilifereous setose ridge across the merus and ischium, and the pterygostome is not reticulated with setae. The overall physiognomy of the carapace is also not as high as those in the genus *Cyclograpsus*. This species is rarely collected.

This species is free-living and is not found in close association with any organism.

**Distribution.**— Taiwan, China, Japan.

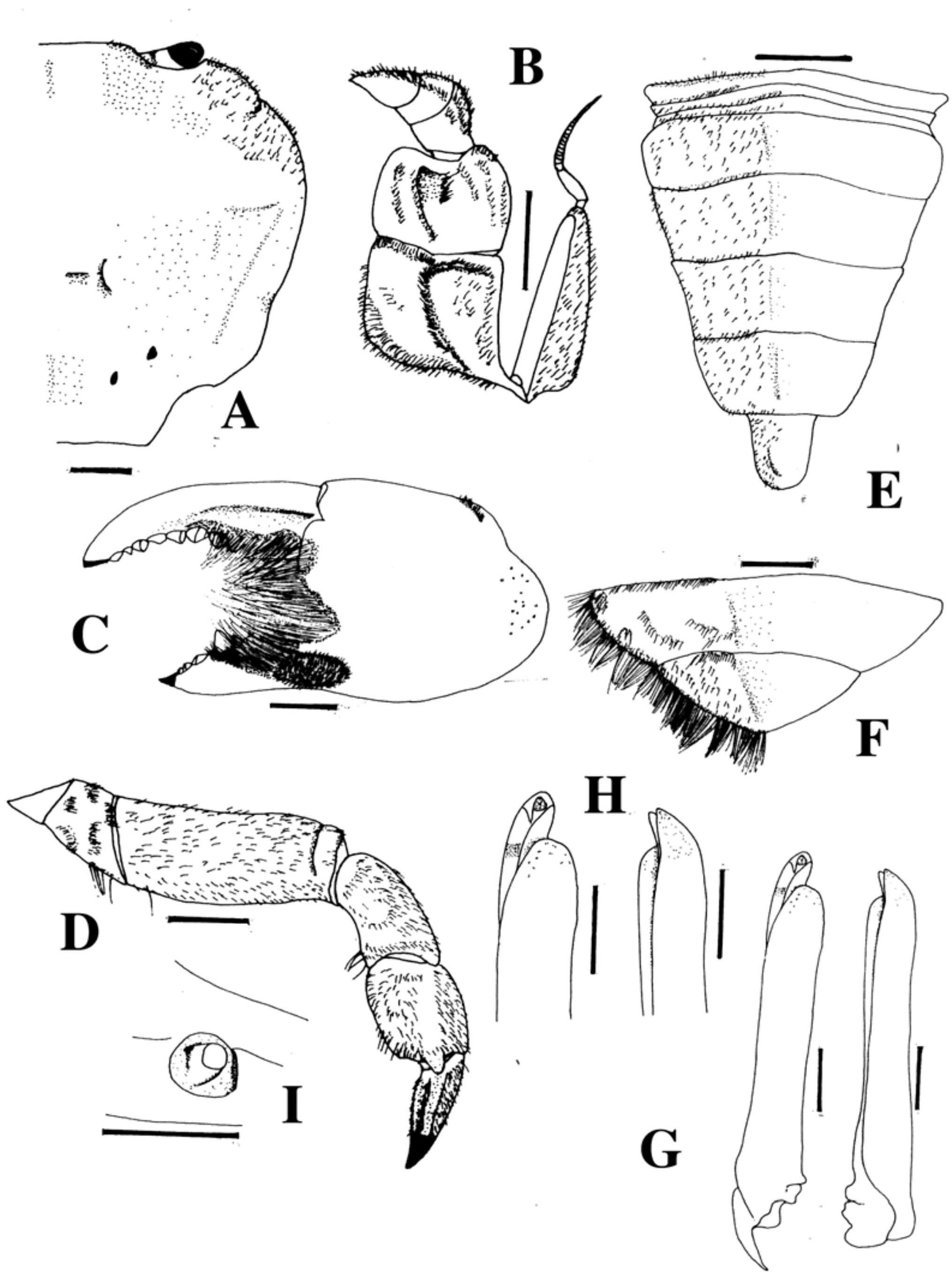



Figure 5. *Acmaeopleura parvula* Stimpson, 1858, male, 8.4mm x 6.2mm (TMCD-2525), female (7.3mm x 5.3mm) (TMCD-2547). A) carapace; B) third maxilliped; C) outer surface of male chelilped; D) last ambulatory leg; E) male abdomen; F) sixth abdominal somite and telson of female abdomen; G) G1; H) tips of G1, and I) female gonopore. (Scale=1.0mm).

## *Acmaeopleura rotunda* Rathbun, 1909

*Acmaeopleura rotunda* Rathbun, 1909: 109; Naiyanetr, 1998: 102.

**Material examined.**— No material examined. Rathbun (1909) only had one small specimen.

**Diagnosis.**— Carapace almost subcircular, dorsal surface convex, punctate, regions not defined. Anterolateral margins with only exorbital tooth. Third maxilliped very broad; ischium, merus broad, exopod very narrow. Cheliped large, with a tuft of long soft setae on outer surface of immovable finger. Ambulatory legs narrow, slender, unarmed. (Modified from Rathbun, 1909).

**Colour.**— The colour of fresh and preserved specimens have not been documented.

**Size.** — The only known specimen is a male 2mm x 1.7mm (Rathbun, 1909). The female is not known.

**Habitat.**— *A. routunda* can be found in mud, about 35m in depth (Rathbun, 1909).

**Remarks.**— This species has been described by Rathbun based one small male specimen, and was never reported again. The description given was very brief, and there was no figure provided. The validity of this species could possibly only be ascertained if fresh material were collected from the type locality. Based on the description provided by Rathbun (1909), the species could be a megalopa of any grapsid crab. It could even be a pinnotherid - *Pinnotheres kutensis* Rathbun, 1909, which was also found in that area. Considering how different they are and on the assumption that Rathbun would know better, I reluctantly retain this species in this genus until fresh material can be examined.

**Distribution.**— Koh Kut (Thailand) only.

### Genus *Brachynotus* De Haan, 1833

*Goneplax* – Risso, 1827: 13 (not *Goneplax* Leach, 1814)

*Brachynotus* De Haan, 1833**:** 5,7; Monod, 1933: 219, fig. 7; Bouvier, 1940: fig. 184A; Forest & Guinot,, 1956: 41; Monod, 1956: 428, figs. 589-592; Forest, 1957: 505, figs 2, 4, 6, 8, 10, 12, 14; Holthuis & Gottlieb, 1958: 102; Forest & Gantes, 1960: 354, fig. 2; Holthuis, 1961: 59; Lewinsohn & Holthuis, 1964: 60; Bacescu, 1967: 321, fig. 7, 10a, c, d, 11a-c, 12a, 14g, h, 136, 137a-b, 138a; Geldiay & Kocatas, 1968: 5, figs. 1, 2b, d, f, pl. figs. 2-3; 1972: 13, 14, 17, 29; Zariquiey Alvarez, 1968: 5, figs. 142a-c, 143a, 144; 431, figs. 142d, e, 143b-d, 145; Stevcic, 1969: 132; 1971: 528, 530; 1973: 115, 116; Kocatas, 1971: 31, pl. 5, fig. 2; Geldiay & Kocatas, 1972: 13, 14, 15; Koukouras, 1973: 762; Georgiadis & Georgiadis, 1974: 242, 246, figs. 5-7; Kattoulas & Koukouras, 1975: 301; Froglia, 1976: 172, fig. 2; Pastore, 1976: 106, 108, 113; Ramadan & Dowidar, 1976: 133; Froglia & Manning, 1978: 691; Manning & Holthuis, 1981: 247; Ates, 1999: 116; Cuesta *et al.*, 2000: 207; Cuesta *et al.*, 2001: 903, figure 3; Schubart *et al..*, 2001: 41; Schubart *et al.*, 2002: 39; McLay & Schubart, 2004: 695.

*Heterograpsus* Lucas 1846: 194; H. Milne Edwards, 1853: 192; Miers, 1876: 37; Kingsley, 1880: 207; Lenz, 1901: 472.

*Shurebus* Verany 1846: 7.

*Hemigrapsus* – Dana, 1852: 348, pl. 22, fig. 2 (part); Filhol, 1885: 388 (not *Hemigrapsus* Dana, 1852).

**Type species.** — *Goneplax sexdentatus* Risso, 1827, by subsequent monotypy. *Heterograpsus sexdentatus* Lucas, 1846 is a subjective junior synonym of *Goneplax sexdentatus* Risso, 1827).

**Gender**.— Masculine.

**Diagnosis.** — Carapace quadrangular, broader than long; dorsal surface punctate; regions well defined, flat. Frontal margin sinuous or bilobed. Anterolateral margin with three teeth including exorbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Inner surface of chela with granules; outer surface of pollex and manus without setae; fingers as long as palm, base of fingers with a distinct pulvinus. Ambulatory legs with short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular with all segments freely moveable (six somites plus telson). G1 slender, narrow. Female gonopore operculate, rounded.

**Remarks.**— There has always been a lot of confusion between the genera *Brachynotus* De Haan, 1833, *Heterograpsus* Risso, 1849, and *Hemigrapsus* Dana, 1852. McLay & Schubart (2004) have given a detailed historical account of these genera. There is no need for me to elaborate further in this report.

*Brachynotus* is distinctly different from *Hemigrapsus* in the following features a) anterolateral teeth more acute and sharp (vs. broader and blunt teetth in *Hemigrapsus*); b) infra-obital ridge of male and female specimens with numerous isomorphic granules (vs. presence of isomorphic and heteromorphic granules in *Hemigrapsus*); c) absence of setae on the surfaces of the chelipeds (vs. usually presence of setae on chelipeds surfaces in *Hemigrapsus* except *H. sexdentatus*); d) presence of a distinct pulvinus at the base of the cheliped fingers (vs. absence of pulvinus or presence of only a small indistinct pulvinus in adult material of *Hemigrapsus*); e) cheliped fingers usually gaping when closed (vs. non gaping when closed in *Hemigrapsus*); f) fingers of chelipeds usually very long and slender (vs. short fingers in *Hemigrapsus*); g) propodus of last ambulatory leg slender and narrow (vs. broader and stotuter propodus in *Hemigrapsus*); h) posterior margin of propodus of ambulatory legs with a angular protusion towards proximal end (vs. absence of such protusion in *Hemigrapsus*); i) G1 very long and slender (vs. long and stout in *Hemigrapsus*), and j) female gonopore usually flat and small (vs. large and protruding in *Hemigrapsus*). Molecular and larval data have supported the distinction of *Brachynotus* from *Hemigrapsus* (Schubart *et al.*, 2000, 2001). The genus is restricted to the Mediterranean Sea, the Atlantic coast of northern Africa and southern Europe.

Schubart *et al.* (2001) questioned the validity of *Brachynotus gemmmellari* (Rizza, 1839), stating that the 16s rRNA of *B. gemmellari* and *B. sexdentatus* are identical in the studied region of the 16s rRNA gene. However, there are distinct morphological differences between the two species, and the characters listed by Froglia & Manning (1978) work well even for specimens that are of very small size. This indicates that the characters are very stable, and they are not affected by age or size. As such, perhaps the gene region that has been studied could not elucidate the differences between the two species.

Risso (1827) described *Goneplax sexdentatus* from specimens collected from Nice in Europe. De Haan (1833) probably realized that *G. sexdentatus* is not a *Goneplax* Leach, 1814. In his monograph, he transferred *Goneplax sexdentatus* to his genus *Brachynotus* De Haan, 1833, and designated this taxon as its type species. Separately, Lucas (1846) established the genus *Heterograpsus* for his *Heterograpsus sexdentatus* species which he described from Algeria.

Independently, H. Milne Edwards (1837) described a new species *Cyclograpsus sexdentatus* from New Zealand. He was apparently not aware of Risso's name. When Dana (1852) established the genus *Hemigrapsus* for H. Milne Edwards' cyclograpsines, Dana transferred *Cyclograpsus sexdentatus* to the genus *Hemigrapsus* since it does not have the 'oblique piliferous crest across the merus of the third maxillipeds. Henri Milne Edwards (1853) synonymised Dana's *Hemigrapsus* under *Heterograpsus*, he also probably realized that Lucas' species has the same name as his *Heterograpsus sexdentatus*, and so he changed the name of Lucas' species to *Heterograpsus lucasi*, to retain '*Heterograpsus sexdentatus*' for his New Zealand species. Hilgendorf (1881) was the first to realize that *Brachynotus sexdentatus* and *Heterograpsus lucasii* are the same species. Since *Brachynotus* is the older available name, Hilgendorf (1882) synyomised *Heterograpsus* under *Brachynotus*. Hilgendorf (1882) also assigned a new name, *Heterograpsus edwardsii*, for H. Milne Edwards' species from New Zealand.

Rathbun had also recognized that the two genera, *Brachynotus* and *Hemigrapsus* are distinctly different. She resurrected *Hemigrapsus* Dana, 1852, and designated *Hemigrapsus crassimanus* Dana, 1852, as the type species (Rathbun, 1900, 1931). She was apparently not aware of the study done by Hilgendorf (1882), as she designated *B. lucasi* as the type species for the genus *Brachynotus*. In doing so, she created confusion over the correct name for the New Zealand species which were being identified as "*Hemigrapsus edwardsii*".

McLay & Schubart (2004) correctly synonymized *Brachynotus edwardsii* Hilgendorf, 1882, under *B. sexdentatus* (presently regarded here as a valid species of *Hemigrapsus*). Since the New Zealand species clearly belongs to *Hemigrapsus*, the issue of homonymy is not applicable since *Brachynotus* and *Hemigrapsus* are now regarded as separate genera. The original name *Hemigrapsus sexdentatus* H. Milne Edwards, 1837, is thus now valid. *Hemigrapsus sexdentatus* is also a New Zealand/Australian species, while *B. sexdentatus* is a Mediterranean species. Both the *H. sexdentatus* and *B. sexdentatus* are morphologically distinct and they fit into the definitions of *Hemigrapsus* and *Brachynotus* respectively, very well.

As currently defined, there are four species in this genus, viz. *Brachynotus sexdentatus* (type species), *B. foresti* Zariquiey Alvarez, 1968, *B. gemmellari* (Rizza, 1839), and *B. atlanticus* Forest, 1957.

**Key to species in *Brachynotus***

1a. Chelipeds with fingers shorter than palm. **------------------------------------------- 2**

1b. Chelipeds with fingers longer than palm. **-------------------------------------------- 3**

2a. Base of cheliped fingers without distinct pulvinus. Infra-orbital ridge with two distinct granules below orbit. **---------------------------------------------- *B. atlanticus***

2b. Base of cheliped fingers with distinct pulvinus. Infra-orbital ridge with three distinct granules below orbit. **--------------------------------------------------- *B. sexdentatus***

3a. Chelipeds with propodus short and flat, distal end of anterior margin of propodous with small broad spine. **----------------------------------------------------- *B. gemellari***

3b. Chelipeds with propodus very short and flat, distal end of anterior margin with short acute spine. **----------------------------------------------------------------------- *B. foresti***

**Brachynotus sexdentatus (Risso, 1927)**

(Figure 6)

*Goneplax* s*exdentatu*s – Risso, 1827: 13 (not *Goneplax* Leach, 1814)

*Brachynotus sexdentatus* – De Haan, 1833**:** 5,7; Monod, 1933: 219, fig. 7; Bouvier, 1940: fig. 184A; Forest & Guinot,, 1956: 41; Monod, 1956: 428, figs. 589-592; Forest, 1957: 505, figs 2, 4, 6, 8, 10, 12, 14; Holthuis & Gottlieb, 1958: 102; Forest & Gantes, 1960: 354, fig. 2; Holthuis, 1961: 59; Lewinsohn & Holthuis, 1964: 60; Bacescu, 1967: 321, fig. 7, 10a, c, d, 11a-c, 12a, 14g, h, 136, 137a-b, 138a; Geldiay & Kocatas, 1968: 5, figs. 1, 2b, d, f, pl. figs. 2-3; 1972: 13, 14, 17, 29; Zariquiey Alvarez, 1968: 5, figs. 142a-c, 143a, 144; 431, figs. 142d, e, 143b-d, 145; Stevcic, 1969: 132; 1971: 528, 530; 1973: 115, 116; Kocatas, 1971: 31, pl. 5, fig. 2; Geldiay & Kocatas, 1972: 13, 14, 15; Koukouras, 1973: 762; Georgiadis & Georgiadis, 1974: 242, 246, figs. 5-7; Kattoulas & Koukouras, 1975: 301; Froglia, 1976: 172, fig. 2; Pastore, 1976: 106, 108, 113; Ramadan & Dowidar, 1976: 133; Froglia & Manning, 1978: 691; Manning & Holthuis, 1981: 247; Ates, 1999: 116; Cuesta *et al.*, 2000: 207; Cuesta *et al.*, 2001: 903, figure 3; Schubart *et al..*, 2001: 41; Schubart *et al.*, 2002: 39; McLay & Schubart, 2004: 695.

*Heterograpsus sexdentatus* **–** Lucas 1846: 194; H. Milne Edwards, 1853: 192; Miers, 1876: 37; Kingsley, 1880: 207; Lenz, 1901: 472.

*Hemigrapsus sexdentatus* – Dana, 1852: 348, pl. 22, fig. 2 (part); Filhol, 1885: 388 (not *Hemigrapsus* Dana, 1852).

*Brachynotus sexdentatus* – Lewinsohn & Holthuis, 1964: 60; Bacescu, 1967: 321, figs. 7, 10a, c, d,

**Material examined.**— 1 male, 1 female (small, dry, mounted on board) (MNHN-MBP-3347), Mediterranean, coll. A. Milne-Edwards, 1903; 1 male, 1 female (mounted on board ventral side up) (MNHN-3508) coll. J. Steward, det. Filhol, no collection date; 6 males (3.5-5.9mm x 2.5-4.9mm), 6 females (3.4-6.1mm x 2.4-4.8mm) (MNHN-MPB-8839), Golf de Ceabe, coll. Fauna de Yeoiner, Sep. 1892; 1 male (13.0mm x 10.7mm) (RMNH), Barcelona, coll. de Man, no collection date; 12 males (12.2-16.6mm x 10.0-13.4mm), 4 females (11.0-14.0mm x 8.4-11.0mm), 2 females (ovigerous) (11.2-11.4mm x 8.9-9.6mm) (RMNH-D142558), Zoology Station, Napels, Italy, coll. May 1959; 20 males (6.8-13.8mm x 5.5-10.4mm), 9 females (7.5-13.8mm x 5.7-10.2mm) (RMNH-D11067), Havan von Barcelona, Spain, coll. R. Zariguiey Alvarez, Nov1955; 1 male (18.1mm x 14.9mm) (RMNH-D10545), Haven von

Barcelona, Spain, coll. R. Zarigueiy Alvarez, May 1955; 2 males (12.0-13.4mm x 9.8-10.6mm), 5 females (11.3-13.2mm x 9.0-10.3mm) (RMNH-D1252), Stiges Province, Barcelona, Spain, coll. P Antiga, no collection date; 7 males (9.1-15.8mm x 7.4-12.5mm), 1 female (13.5mm x 10.4mm), 9 females (ovigerous) (13.0-15.5mm x 10.6-12.5mm) (RMNH-D11528), Havan von Barcelona, Spain, coll. R. Z. Alvarez, 24 May 1957; 3 males (7.9-11.2mm x 6.3-8.9mm), 1 female (8.6mm x 7.1mm) (RMNH-D10240), Tel Aviv, Israel, coll. Jos Carssin, 11 May 1929; 2 males (5.8-8.7mm x 5.2-7.1mm), 2 females (4.3-5.9mm x 3.9-4.8mm), (SFM-no cat. number.), Limcki Canal, Lastrien, Yugoslavia, coll. M. Turkay, 11 Sep. 1974; 1 female (11.3mm x 9.0mm) (SFM-12979), Lanuder, Venice, Itlay, coll. A. Allspach, 20 Jul. 1984; 1 male (8.9mm x 7.3mm), 2 females (3.0-4.7mm x 2.5-3.8mm) (SFM-14018), Luiski canal, Rovini, Yugoslavia, coll. 12 Sep. 1985; 1 male (13.1mm x 10.4mm), 2 females (9.7-10.8mm x 8.1-8.6mm) (SFM-13191), 5km south of Sosospol, Bulgaria, coll. V. Gohler, 13-20 May 1982; 1 male (5.9mm x 4.6mm), 1 female (7.4mm x 5.9mm), 1 female (ovigerous) (10.5mm x 8.4mm) (SFM-12091), Limski South, Yugoslavia, coll. 10 Sep.1983; 1 male (14.5mm x 10.8mm), 1 female (13.2mm x 10.3mm) (USNM-152256), Trapani canal mouth, Mediterranean Sea, Sicily, Italy, coll. Luiciotta, 16 Jun.1974; 3 males (11.3-16.0mm x 9.4-13.1mm), 1 female (13.8mm x 10.9mm), 1 female (ovigerous) (16.2mm x 12.8mm), (USNM-152255), Trapani canal mouth, Sicily, Italy, coll. Luiciotta, 16 Jun. 1974; 1 male (10.2mm x 8.2mm), 1 female (11.2mm x 8.8mm), 1 female (ovigerous) (9.6mm x 7.9mm), (USNM-258092), Salammbo, Tunisia, Mediterranean Sea, coll. R. B. Manning *et al.,* 7 Aug. 1973; 6 males (9.8-13.8mm x 8.1-11.0mm), 4 females (7.5-12.1mm x 5.9-9.2mm) (USNM-152257), East sewall, Trapani Habour, Sciliy, Italy, coll. Luiciotta, 19 Jun. 1974; 2 males (15.0-15.9mm x 11.8-12.6mm), 2 females (11.9-12.6mm x 9.3-9.7mm) (USNM-171475), south edge of habour, canal mouth, Trapani, Sicily, Italy, coll. R.B. Manning, 17 Jun. 1974; 1 male (14.2mm x 11.0mm), 1 female (ovigerous) (13.9mm x 10.9mm) (USNM-123244), Port of Bacelona, Spain, coll. R. Zariquiey, Jul. 1957; 4 males (6.7-8.5mm x 4.9-6.8mm), 1 male (8.8mm x 6.8mm), 1 female (ovigerous) (8.1mm x 6.4mm) (USNM-170885), outside northern Punic Port, Salamanbo, Tunisia, coll. R. B. Manning, 15 May 1973; 2 males (15.7-18.0mm x 12.4-14.1mm), 1 female (ovigerous) (13.8mm x 11.1mm) (USNM-265741), Lac de Biban, Tunisia, coll. C. Forglia & Jeddi, no collection date; 1 female (ovigerous) (12.4mm x 9.8mm) (USNM-258090), canal leading from south Punic Port, Salammbo, Tunisia, coll. R. B. Manning *et al.,* 16 Jul. 1973; 12 males (7.5-12.5mm x 6.0-9.7mm), 2 females (6.5-10.0mm x 5.5-8.1mm) (USNM-265735), La Marsa Corniche, Tunisia, coll. R. B. Manning *et al*., 6 Sep. 1973; 10 males (4.4-12.6mm x 3.5-10.1mm), 2 females (6.2-10.5mm x 5.6-8.1mm), 2 females (ovigerous) (10.0-13.0mm x 8.0-9.6mm) (USNM-258087), south of Punic Port, Salammbo, Tunisia, coll. L. B Holthuis & R.B. Manning, 6 Oct. 1972.

**Diagnosis.**— Carapace distinctly quadrangular, dorsal surface sculptured, flat, punctate, regions well-defined. Frontal margin bilobed. Infra-orbital ridge with three distinct granules and other smaller granules. Anterolateral margins with three distinct teeth including exorbital tooth. Third maxilliped broad, ischium, merus broad, exopod very narrow. Fingers of cheliped short, broad, without any setae, base of fingers with distinct pulvinus. Ambulatory legs short, slender, covered with short setae. G1 long, slender. Female gonopore large, operculate, circular in shape.

**Colour.**— The colour of fresh specimens is unknown but all preserved specimen are brown in colour.

**Size.**— The largest male specimen examined is 18.1mm x 14.9mm (RMNH-D10545), and largest female specimen examined is 16.2mm x 12.8mm (USNM-152255).

**Habitat.**— The animals can be found under rocks, boulders, on the rocky reef, on sand and mud flats, near river mouth. They are rarely found outside the inter-tidal zone (Froglia & Manning, 1978).

**Remarks.**— This species has a long taxonomic history (see above; McLay & Schubart, 2004). Its taxonomy was stabilized by Froglia & Manning (1978) who restricted it to the Mediterranean Sea. Forest (1957) synonymized the Mediterranean species, *Brachynotus lucasi*, under *B. sexdentatus*.

**Distribution.**— Mediterranean Sea.

Figure 6. *Brachynotus sexdentatus* (Risso, 1827), male, 13.4mm x 10.6mm (RMNH-D1252). Dorsal view.

## *Brachynotus atlanticus* Forest, 1957

*Brachynotus sexdentatus* – Monod, 1933: 219, fig. 7; Bouvier, 1940: fig. 184A; Sourie, 1954: 295, 304, 308 (not *Brachynotus sexdentatus* (Risso, 1827)).

*Brachynotus sexdentatus* spp *lucasi* H. Milne Edwards, 1853 – Monod, 1956: 428, figs. 589-592 (not *Brachynotus lucasi* H. Milne Edwards, 1853).

*Brachynotus atlanticus* Forest, 1957: 505, figs. 2, 4, 6, 8, 10, 12, 14; Forest & Gantes, 1960: 354, fig. 2; Manning & Holthuis, 1981: 247; Schubart *et al.*, 2001: 41; Schubart *et al.*, 2002: 39.

**Material examined.— Lectotype** – 1 male, 2 females (MNHN), Cansado Bay, Atlantic coast of Sahara, coll. Gruvel, 1908. – **Others** – 1 male (7.3mm x 6.0mm) (RMNH-D36294), South Spain, coll. 30 Oct.1974; 1 male (5.7mm x 4.8mm) (RMNH-D36345), Algarve Province, South Portugal, coll. 3 Nov.1974; 3 males (4.5-6.5mm x 3.5-5.5mm) (RMNH-D36343), 22 km north of Rabat, Morroco, coll. 19 Oct. 1974; 11 males (3.3-6.8mm x 2.8-5.5mm), 5 females (5.2-9.5mm x 4.1-7.5mm) (RMNH-D36344), 23 km from Rabat, Morroco, doll. 20 Oct. 1974; 9 males (4.9-9.7mm x 3.9-6.9mm), 4 females (4.9-9.1mm x 3.9-7.1mm), 5 females (ovigerous) (6.5-8.3mm x 5.0-6.6mm) (SFM-8033), Jugoslawioen, leg. Z. Stevcic, 25 May 1970; 2 males (8.5-9.0mm x 7.2-7.4mm), 1 female (10.0mm x 7.9mm), 1 female (ovigerous) (7.5mm x 6.1mm) (SFM-17258), San Pernando, Apain, leg. J.E. Gracia-Raso, 19 Oct. 1984; 1 male (7.8mm x 6.4mm) (USNM-205564), Bay of Cadiz, Sapia, North Atlantic Ocean, coll. L.B. Holthuis, 30 Oct. 1974; 7 males (3.8-7.0mm x 3.5-5.8mm), 5 females (4.1-5.6mm x 3.1-4.6mm) (USNM-205562), 16km south of Rabat, Temara, Morroco, North Atlantic Sea, coll. L.B. Holthuis, 21 Oct. 1974; 70 males (6.4-10.8mm x 5.1-8.6mm) 51 females (5.0-11.0mm x 4.1-8.98mm) (USNM-258364), Albufira, Algarve, Portugal, North Atlantic Ocean, no collection date; 1 male (8.7mm x 7.0mm) (USNM-258358), Bay of Cadize, Bajo de Las Casbezuela; Spain, North Atlantic Ocean, coll. 29 Oct. 1974; 75 males (3.9-12.5mm x 3.2-8.3mm) 36 females (4.1-10.1mm x 3.2-8.1mm) (USNM-251836), Puerto Santa Maria, Bay of Casize, Spain, North Atlantic Ocean, coll. 26 Oct. 1974.

**Diagnosis.**— Carapace distinctly quadrangular, dorsal surface sculptured, flat, punctate, regions not well-defined. Frontal margin bilobed. Infra-orbital ridge with two distinct granules and other smaller granules. Anterolateral margins with three teeth including exorbital tooth. Third maxilliped broad, ischium, merus broad, exopod very narrow.

Fingers of cheliped short, broad, without any setae base of fingers with very small or almost no pulvinus. Ambulatory legs short, slender, covered with short setae. G1 long, slender. Female gonopore operculate, slightly protruding, circular in shape.

**Colour.**— The colour of fresh specimens is specimens unknown but all preserved specimens examined are dark cream colour.

**Size.**— The largest male specimen examined is 12.5mm x 3.2-8.3mm (USNM-251836), and largest female examined is 10.1mm x 8.1mm (USNM-251836).

**Habitat.**— *B. atlanticus* can be found under rocks or muddy vegetation, along the banks of the river (Manning & Holthuis, 1981).

**Remarks.**— *Brachynotus atlanticus* is very closely related to *B. foresti*, but can be easily distinguished from *B. foresti* by the following characters a) a less prominently sculptured carapace; b) relatively shorter fingers (vs. longer fingers in *B. foresti*); c) presence of ridges on the fingers of carapace (vs. absence of ridges in *B. foresti*); and d) presence of a very small indistinct pulvinus or sometimes absent (vs. presence of a distinct pulvinus in *B. foresti*).

Little is known about the ecology of this species.

**Distribution.**— Atlantic coast of Northern Africa to southern Europe.

### *Brachynotus foresti* Zariquiey Alvarez, 1968

(Figure 7A-C)

*Brachynotus sexdentatus* – Holthuis & Gottlieb, 1958: 102; Holthuis, 1961: 59; Lewinsohn & Holthuis, 1964: 60.

*Brachynotus foresti* Zariquiey Alvarez, 1968: 431, figs. 142d,e, 143b-d, 145; Kocatas, 1971: 31, pl. 5 fig. 2; Georgiadis & Georgiadis, 1974: fig. 5; Kattoulas & Koukouras, 1975: 301; Froglia, 1976: 172, fig. 2; Froglia & Manning, 1978: 692; Schubart *et al.,* 2001: 41; McLay & Schubart, 2004: 695.

**Material examined.**— 1 male (9.1mm x 7.4mm), 1 female (ovigerous) (13.4mm x 9.5mm) (MNHN-MPB-12529), Izmir, coll. Kocatas, no collection date; 1 male (14.9mm x 12.3mm), 1 female (9.8mm x 8.0mm), 1 female (ovigerous) (12.2mm x 9.5mm) (MNHN-B-12734), Porto Cesaro, Halie, det. Forest, Oct. 1966; 2 males (10.3-14.2mm x 8.5-11.5mm) (RMNH-D23795), Izmiz, Turkey, coll. A. Kocatas, 22 Jun. 1967; 1 male (5.2mm x 4.3mm) (RMNH-D18869), Haifu, Israel, coll. 15 Oct. 1956, Costa; 1 male (8.1mm x 6.2mm) (RMNH-D18860), Northwest Israel, coll. L.B. Holthuis, 30 Apr. 1962; 1 male (14.3mm x 11.7mm) (RMNH-D37916), Lonic Sea, Greece, coll. R. Afes, 18 Jun. 1987; 2 males (8.7-12.7mm x 7.3-10.0mm), (SFM-4116), Jordan, coll. Zoological Expedition, 12 Sep. 1952; 2 males (10.7-11.5mm x 8.7-9.3mm) (SFM-7487), Thermuillos Gulf, Greece, coll. Koukouras, 13 Jun. 1971; 3 males (7.2-13.8mm x 6.0-11.3mm), 3 females (8.8-11.9mm x 7.0-9.5mm), 1 female (ovigerous) (9.7mm x 7.8mm) (SFM-8032), Foca, Bay of Izmir, Turkey, leg. Kocatas, 15 Jun. 1970; 1 male (12.0-12.8mm x 9.6-10.5mm), 1 female (ovigerous) (11.0mm x 8.6mm) (USNM-171473), 2km west of Houmt Soule, Djerba, Tunisia, North Africa, coll. R.B. Manning, 7 Jun. 1973; 1 female (10.0mm x 7.8mm) (USNM-190887), Gabes Port, Tunisia, Mediterranean Sea, coll. R.B. Manning, 5 Jun. 1973; 12 males (3.8-10.7mm x 3.1-8.4mm), 3 females (6.2-9.8mm x 4.9-7.7mm), 1 female (ovigerous) (9.1mm x 7.0mm) (USNM-170891), in front of Hotel Sidi Saad, Zarzis, Tunisia, coll. R.B. Manning, 25 Aug. 1973; 2 males (12.0-13.0mm x 9.5-10.7mm) (USNM-190890), Tunisia, coll. R.B. Manning *et al.,* 14 May 1973; 1 female (7.2mm x 5.2mm) (USNM-170889), Gerra, Mediterranean Sea, coll. R.B. Manning *et al.*, 10 May 1974; 1 male (9.3mm x 7.0mm), 3 females (9.7-10.5mm x 7.7-8.1mm) (USNM-170892), Disco Beach, Fal Conssa, Anion, Adriatic Sea, Italy, coll. C. Froglia, 11 May 1973; 1 male (7.6mm x 5.5mm), 1 female (5.0mm x 4.0mm) (USNM-258360), North West of mouth of Rio Jara beach, 8km north of Tarifa, Tarifa, Rio Jara, Spain, coll. 27 Oct. 1974; 3 males (9.8-12.3mm x 7.8-9.8mm) (USNM-170888), 2km from Houmt Souk, on road to Bordj Djillidi, Djerbo Island, Tunisia, coll. R.B. Manning *et al.*, 23 Aug. 1963.

**Diagnosis.**— Carapace distinctly quadrangular, dorsal surface sculptured, flat, punctate, regions not well-defined. Frontal margin bilobe. Infra-orbital ridge with two distinct granules and other smaller granules. Anterolateral margins with three teeth including exorbital tooth. Third maxilliped broad, ischium, merus broad, exopod very narrow. Fingers of cheliped long, slender, without setae, base of fingers with distinct pulvinus. Ambulatory legs short, slender, covered with short setae. G1 long, slender. Female gonopore operculate, small, flat, circular in shape.

**Colour.**— The colour of fresh specimens is unknown but all preserved specimens examined are dark cream in colour.

**Size.** — The largest male specimen examined is 14.9mm x 12.3mm (MNHN-B-12734), and the largest female specimen examined is 13.4mm x 9.5mm (MNHN-MPB-12529).

**Habitat.**— It can be found under rocks or sandy/muddy bottom (Frogila & Manning, 1978).

**Remarks.**— *Brachynotus foresti* is very closely related to *B. atlanticus* but it can be distinguished from *B. atlanticus* by the various morphological characters (see remarks under *B. atlanticus*). Schubart *et al.* (2001) has also showed that *B. foresti* and *B. altlanticus* are clearly genetically distant.

I have not been able to locate the type specimen of Zariquiey Alvarez, which are presumably somewhere in Spain. However, I have examined the specimens used by Froglia & Manning (1978) for their revision.

**Distribution.**— Mediterranean Sea only.

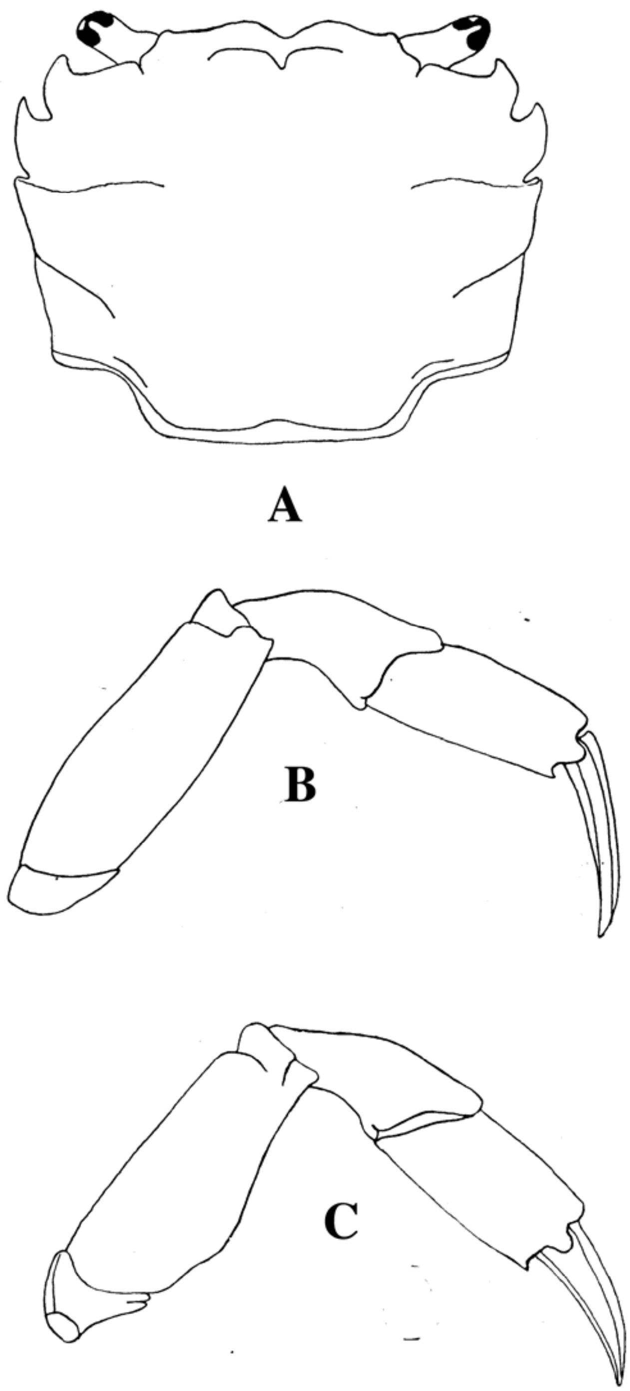



Figure 7. *Brachynotus foresti* Zariquiey Alvarez, 1968. A) dorsal view; B) fourth ambulatory leg; C) fifth ambulatory leg. (After Froglia & Manning, 1978)

### *Brachynotus gemmellari* (Rizza, 1839)

(Figure 8A-C)

*Cleistotoma gemmellari* Rizza, 1839: 372.

*Brachynotus sexdentatus* – Forest & Guinot,, 1956: 41; Bacescu, 1967: 321; Geldiay & Kocatas, 1968: 5; Kotacatas, 1971: 30; Geldiay & Kocatas, 1972: 13, 14, 15.

*Brachynotus foresti* – Pastore, 1976: 113 (not *Bachynotus foresti* Zariquiey Alvarez, 1968).

*Brachynotus gemmellari* – Froglia & Manning, 1978; 695; McLay & Schubart, 2001: 695.

**Material examined.**— **Neotype** – 1 male (18.2mm x 15.0mm) (RMNH-D31719), Gulf di Man Predonca, Italy, Adriatic Sea, coll. C. Forglia, 1 Aug. 1974. – **Others** – 1 female (10.0mm x 7.8mm) (USNM-170887), Gabes Port, Tunisia, Mediterranean Sea, coll. R. B. Manning *et al.*, 5 Jun. 1975; 1 female (6.9mm x 5.5mm) (USNM-205774), Mazara del Vallo, Sicily, Italy, Mediterranean Sea, coll. R. B. Manning & C. Froglia, 30 Aug. 1985; 2 males (10.5-16.2mm x 8.4-13.2mm) (USNM-171474), northern Punic Port, Salammbo, Tunisia, North Africa, coll. R. B. Manning, 25 Apr. 1974; 3 males (8.5-15.8mm x 7.0-12.8mm), 3 males (11.2-12.3mm x 9.0-9.7mm) (USNM-237570), Golfo Di Catania, North Atlantic Ocean, coll. 29 May 1988; 2 males (11.0-14.5mm x 9.0-11.6mm), 1 female (13.4mm x 11.0mm) (USNM-172093), 3m off Aneona, Italy, Adriatic Sea, Mediterranean Sea, coll. C. Forglia & R.B. Manning, 3 Jul. 1963; 1 male (14.2mm x 11.6mm), 1 female (ovigerous) (13.6mm x 11.5mm) (USNM-172094), Ancona, Italy, Adriatic Sea, Mediterranean Sea, coll. C. Forglia & R. B. Manning, 26 Jun. 1973; 5 males (10.0-15.2mm x 8.3-12.8mm), 2 females (9.2-10.0mm x 7.6-7.8mm), 1 female (ovigerous) (11.4mm x 9.4mm) (USNM-152254), Strasino, Adriatic Sea, Mediterranean Sea, coll. C. Froglia, 20 Jul. 1973; 1 male (11.0mm x 8.7mm) (USNM-170884), off Gabes & Zarat, Gulf of Gabes, Tunisia, coll. M. Jeddi, 27 Jun. 1973.

**Diagnosis.**— Carapace distinctly quadrangular, dorsal surface sculptured, flat, punctate, regions not well-defined. Frontal margin sinuous. Infra-orbital ridge with two distinct granules and smaller granules. Anterolateral margins with three teeth including orbital tooth. Third maxilliped broad, ischium, merus broad, exopod very narrow. Fingers of cheliped long, narrow, without any setae, base of fingers with very distinct pulvinus. Ambulatory legs short, slender, covered with short setae. G1 long, slender. Female gonopore operculate, flat, small circular in shape.

**Colour.**— The colour of fresh specimens is cream to light brown in colour (C. Froglia, pers. comm.), and the preserved specimens examined are light brown in colour.

**Size.**— The largest male specimen examined is 18.2mm x 15.0mm (neotype), and largest female examined is 13.6mm x 11.5mm (USNM-172094).

**Habitat.**— *B. gemmellari* can be found under rocks or muddy vegetation, along the banks of the river (Frogila & Manning, 1978).

**Remarks.**— This species was synonmized under *B. sexdentatus* by Forest & Guinot (1956) but was resurrected by Froglia & Manning (1978). I have examined specimens of this species and support its unique identity. This species can be easily discerned from *B. sexdentatus* by the following characters: a) proportionately broader carapace (vs. a narrower carapace in *B. sexdentatus*); b) an infra-orbital ridge with two distinct teeth plus smaller teeth (vs. three distinct teeth plus smaller teeth on the infra-orbital ridge in *B. sexdentatus*); c) the relatively longer fingers of the cheliped (vs. short fingers in *B. sexdentatus*), d) the ambulatory legs are proportionately longer than *B. sexdentatus*; e) the G1 is longer and more slender than in *B. sexdentatus*; and f) the female gonopore is small and flat (vs. large and protruding in *B. sexdentatus*).

Schubart *et al.* (2001) has also shown that *B. gemmellari* is very closely related to *B. sexdentatus*, and they suggested possible recent separation or continuing gene flow between the two species (Schubart *et al*., 2001: 41), but the based on the morphological differences, it would be more likely to be the former species.

**Distribution.**— Mediterranean Sea only.

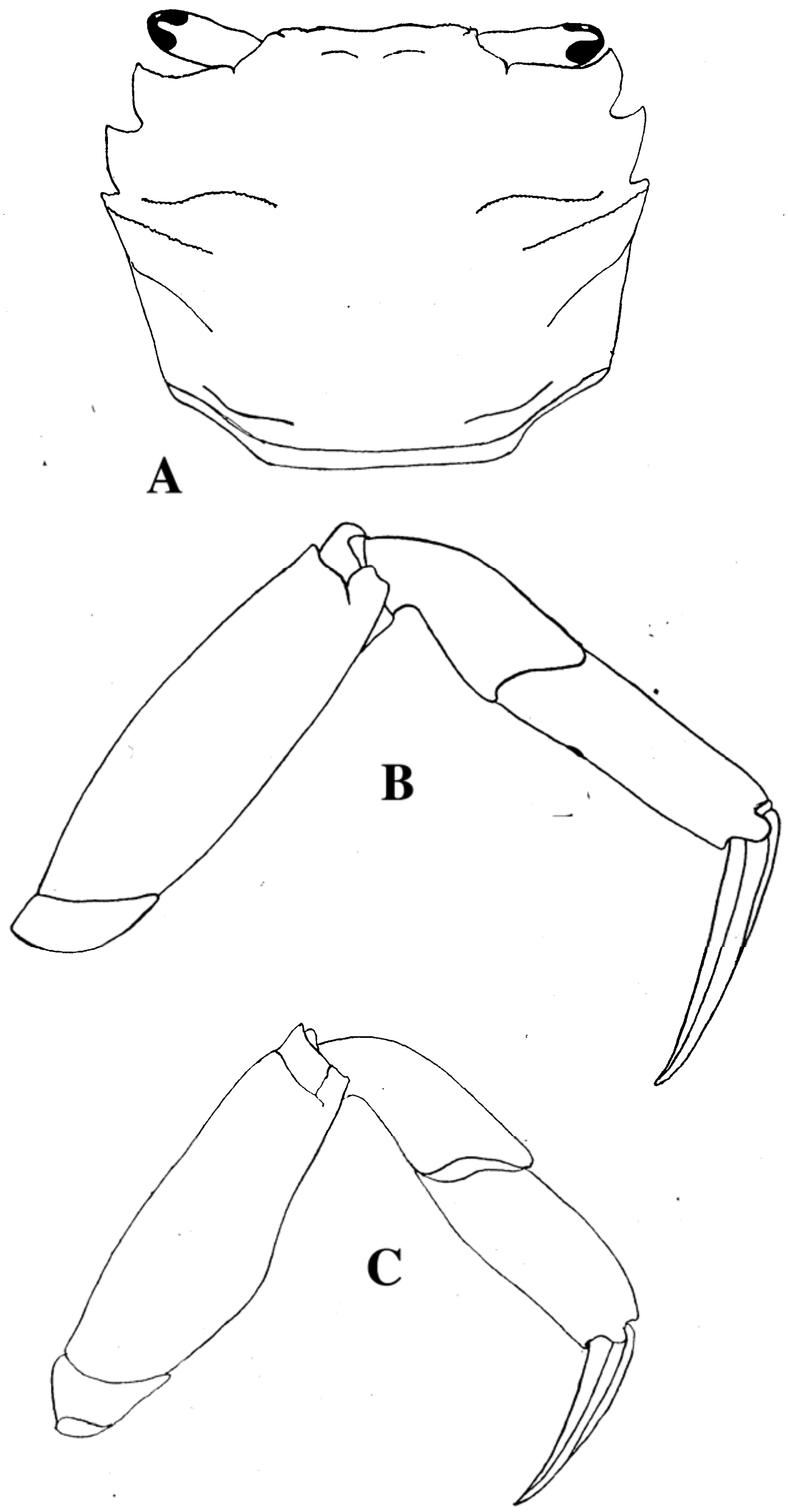



Figure 8. *Brachynotus gemmellari* Rizza, 1839. A) dorsal view; B) fourth ambulatory leg; C) fifth ambulatory leg. (After Froglia & Manning, 1978).

## Genus *Cebuanograpsus*, new genus

**Diagnosis.**— Carapace quadrangular, broader than long; dorsal surface smooth, glabrous; regions not well defined, convex, epigastric cristae low. Frontal margin slightly convex, almost straight. Anterolateral margin finely subcristate with two teeth including exorbital tooth; exorbital tooth distinct, very broad; second tooth lobe like. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Antennules broad. Eyes well-developed, cornea pigmented. Orbits small, eyes completely filling orbit. Third maxilliped short, stout, with exopod very broad, convex, as wide or slightly wider than ishcium; antero-external angle of merus strongly auriculiform. Epistome broad, flat, posterior margin entire. Chela glabrous, fingers as long as palm. Ambulatory legs with short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular, all segments freely movable (six somites plus telson). G1 long, slender. G2 very short.

**Gender.**— Masculine.

**Etymology.**— ‘Cebuano’ is the local dialect spoken on Cebu Municipality in Philippines, and it is used as an adverb with ‘grapsus’.

**Type species.**— *Cebuanograpsus matutinaoensis*, new species, by monotypy.

**Remarks.**— This monotypic genus is closely allied to the genera *Ptychognathus* Stimpson, 1858, and *Orcovita* Ng & Tomascik, 1994. It is very similar to *Ptychognathus* in the form of the third maxilliped, particularly in the broad and convex exopod of the third maxilliped as well as the flat and broad ambulatory legs. However, *Cebuanograpsus* is very different from *Ptychognathus* in the following features: a) the anterolateral margin of carapace is subcristate (vs. cristate in *Ptychognathus*); b) the anterolateral margin of carapace is slightly convex (vs. non-convex in *Ptychognathus*); c) the posterolateral margin of carapace distinctly converging (vs. subparallel in

*Ptychognathus*), and d) the chelipeds are without any setae on the fingers (vs. usually a tuft of soft setae at the base of the fingers in *Ptychognathus*).

*Cebuanograpsus* new genus, is also very similar to *Orcovita* in the form of the carapace, and chelipeds but differs in the following: a) the pigments in the eyes are not reduced (vs. very reduced in *Orcovita*); b) the absence of a pulvinus at the base of the fingers (vs. presence of pulvinus in some species of *Orcovita*); c) the ambulatory legs are broad and stout (vs. very long and slender in *Orcovita*); d) the G1 is broad and long (vs. long and narrow in *Orcovita*), and e) they are found by the river mouths (vs. found in anchialine caves in *Orcovita*).

***Cebuanograpsus matutinaoensis*, new species**

(Figure 9)

**Material examined.**— **Holotype** – 1 male (15.5mm x 12.3mm) (NMPM-uncatalogued), Kawasan Fall, Matutinao Rivermouth, Matutinao, Cebu Island, Philippines, coll. P.K.L. Ng, 25 Nov. 2001. – **Paratypes** – 4 males (11.0-14.6mm x 9.1-11.4mm) (ZRC-uncatalogued), Kawasan Fall, Matutinao Rivermouth, Matutinao, Cebu Island, Philippines, coll. H.C. Liu *et al*., 2 Mar. 2002.

**Diagnosis.**— Carapace quadrangular, overall dorsal surface smooth, glabrous, slightly convex, regions not well-defined. Anterolateral margin finely subcristate with two teeth slightly indicated, external orbital tooth distinct, very broad; second tooth lobiform. Third maxilliped short, stout, very broad; ischium, merus broad, exopod, as wide or slightly wider than ischium. Chela entirely glabrous, fingers as long as palm. Ambulatory legs broad with setae. Male abdomen broadly triangular with all segments freely moveable (six somites plus telson). G1 long, slender. G2 very short.

**Colour.**— The colour of fresh specimens is greenish-brown, and all preserved specimens examined are light brown in colour.

**Size.**— The largest male specimens examined is 15.5mm x 12.3mm (holotype), and the largest female specimen size is not known since only males specimens have been collected.

**Habitat.**— It can be found  under pebbles at the freshwater river mouth along the coast (P.K.L. Ng, pers. comm.).

**Etymology.—** The species is named after its type locality, Matutinao River, Matutinao, Cebu Island, Philippines.

**Remarks.**— So far, only male specimens have been found. I have provided a diagnosis for this species as I am still trying to locate female specimen for the manuscript preparation.

Matutinao, the type locality, is a freshwater river that opens to the sea. There are three cascades of waterfall upstream called the Kawasan Falls. Here, the rare species, *Pseudograpsus crassus* has also been found. At mid-stream, *Ptychognathus riedelii* and *P. pilipes* (both species have been transferred to the genus, *Ganthograpsus*, see below), and sometimes, *Utica gracilipes*, are present. Towards the rivermouth along the banks, where there is tidal influence, *Pyxidognathus granulosus* is common in the rock crevices. At the river mouth, during the low tide, under rocks and pebbles, *Ptychognathus ishii*, *Mitragnathus altimanus* (previously *Ptychognathus*, see below), *Neoptychognathus guijulugani* (previously *Ptychognathus*, see below), and *Gnathograpsus pilosus* (previously *Ptychognathus*, see below) have been found.

**Distribution.**— Philippines (Cebu Island) only.

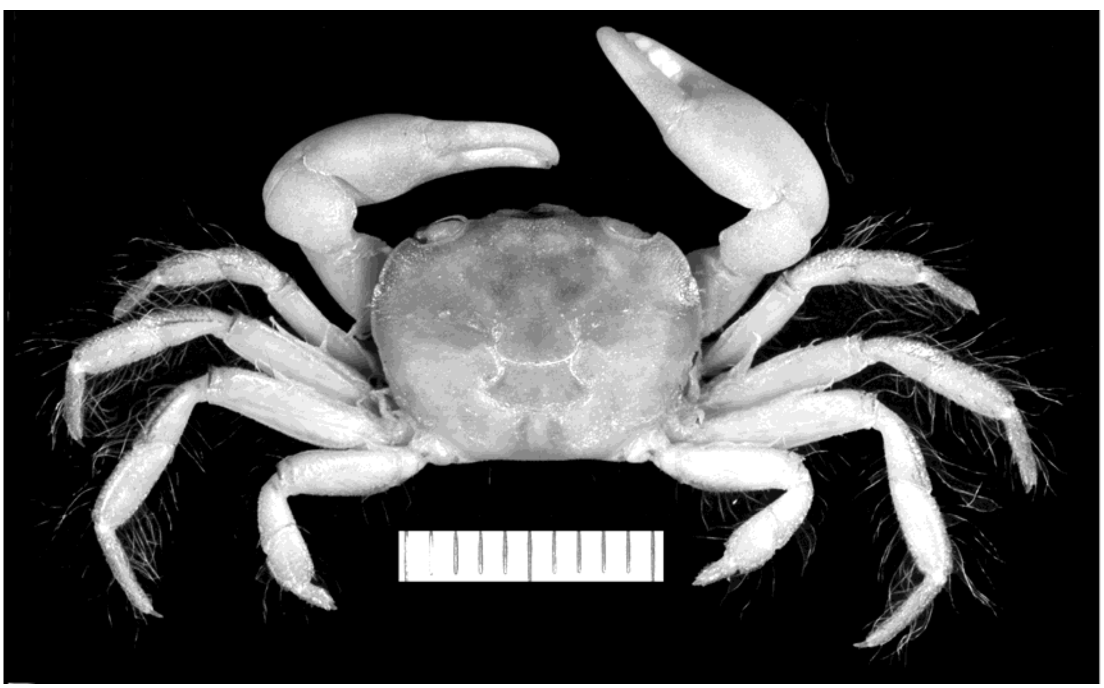


Figure 9. Photograph of *Cebuanograpsus matutinaoensis*, new species, holotype, (14.6mm x 11.4mm) (ZRC-uncatalogued). Dorsal view.

## Genus *Cyrtograpsus* Dana, 1852

*Cyrtograpsus* Dana, 1852: 288; Dana, 1852: 247, 260; Rathbun, 1914: 121; Rathbun, 1918: 260; Garth, 1957: 57; Scelzo & Lichstschein de Bastida, 1979: 103; Spivak, 1999: 249; Spivak & Cuesta, 2000: 29; Schubart *et al*., 2000: 179; Spivak *et al.*, 2003: 212.

**Type species.**— *Cyrtograpsus angulatus* Dana, 1852, by monotypy

**Gender.**— Masculine.

**Diagnosis.**— Carapace quadrangular in shape, broader than long; dorsal surface uneven, punctate; regions well defined, convex, overall margins subcristate, vaulted slightly upwards. Frontal margin produced, convex, bilobed. Anterolateral margin subcristate with four teeth including exorbital tooth. Carapace widest at fourth tooth position. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Cheliped large, symmetrical, glabrous, fingers as long as palm. Ambulatory legs with short setae, stout dactyli. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular, with all segments freely moveable (six somites plus telson).

**Remarks.**— This genus is found only in South America. There were originally three species in this genus viz. *C. angulatus* Dana, 1852, *C. affinis* Dana, 1852, and *C. altimanus* Rathbun, 1914. However, Spivak & Schubart (2003) synonymised *C. altimanus* under *C. affinis*. I concur with Spivak & Schubart (2003). *C. affinis* is so morphologically different from *C. angulatus* that it will be transeferred to its own new genus, *Patagograpsus*, in this report (see below). *Cyrtograpsus* is here regarded as monotypic. As such, two new monotypic genera have been created from *Cyrtograpsus* Dana, 1852.

### *Cyrtograpsus angulatus* Dana, 1852

(Figure 10A-B)

*Cyrtograpsus angulatus* Dana, 1852: 250; 1852: 352; 1855: pl. 22, fig. 6a-e (atlas); Rathbun, 1918: 260; Garth, 1957: 57; Spivak, 1999: 249; Spivak & Cuesta, 2000: 29; Schubart *et al.*, 2000: 179; Spivak *et al.*, 2003: 212.

*Cyrtograpsus cirripes* Smith, 1869: 11, pl. 1 fig. 3.

**Material examined.**— **Lectotype –** 1 male (USNM-2346), Rio Negro, Argentina, coll. J.D. Dana, U.S. Exploring Expedition, no collection date. – **Paralectotype** – 1 male, 2 females (USNM-2346), Rio Negro, Argentina, coll. J.D. Dana, U.S. Exploring Expedition, no collection date. – **Others** – 4 males (14.0-39.3mm x 12.4-34.2mm), 1 female (ovigerous) (11.9mm x 11.0mm) (NMB-610b), Camarores, Patagoriey, coll. Riedtmann, 1909; 1 male (36.8mm x 32.0mm) (NMB-no cat. number), Rio Grarde de Ful, coll. F. Muller, 1887; 1 female (36.7mm x 341.7mm) (USNM-56709), Pocitos Monterrideo, Uruguay, coll. H. M. Smith, 27 Nov. 1922; 1 male (28.1mm x 24.2mm), 1 female (34.1mm x 28.0mm) (USNM-256484), Rio Grande Estuary, Brazil, coll. L. Chaos, 16 Jun. 1980; 5 males (13.0-23.7mm x 11.4-20.2mm) (USNM-70920), I none river, near San Carlos, Uruguay, coll. N. L. Schmit, 5 Dec. 1959; 17 males (7.3-22.3mm x 7.2-19.0mm) 10 females (12.3-17.9mm x 10.3-15.7mm) (USNM-70917), Peurto La Paloma, Uruguay, coll. N.L. Schdmit, 6 Dec. 1925; 2 males (13.6-17.8mm x 11.6-14.7mm), 1 female (13.8mm x 11.6mm) (USNM-90924), Barro del Santa Lucia, Urugau, coll. N.R. Schmitt, 25 Nov. 1925; 1 female (22.8mm x 19.4mm) (USNM-48318), Monterideo, coll. Bisego, 1892; 6 males (19.2-31.2mm x 16.6-28.3mm), 6 females (19.0-25.1mm x 15.9-21.0mm) (USNM-99855), Punta Carretas rocky coast, Rio del la Plata, Montrvideo, Uruguay, coll. C.S. Carbonell, 1955; 4 males (18.4-24.7mm x 15.1-21.1mm), 1 female (21.1mm x 17.8mm) (USNM-18624), San Lorenzo Island, Peru-Ames; 4 males (6.8-12.3mm x 5.9-10.7mm), 15 females (6.5-20.3mm x 5.5-16.8mm) (USNM-7093), Barro del Santa Lucia, Uruguay, coll. N.L. Schmitt, 25 Nov. 1922; 7 males (15.4-47.4mm x 13.3-41.7mm), 1 female (18.8mm x 15.6mm), 4 females (ovigerous) (27.1-34.4mm x 23.5-30.6mm), (USNM-173577), South Atlantic Ocean, Brazil, Rio Grande de Sal Lagon des Patos, coll. C.E. Bembenuti, & A.B. Willimans, 1979.

**Diagnosis.**— Carapace quadrangular in shape, broader than long; dorsal surface uneven, punctate; regions well defined, convex, margins subcristate, vaulted slightly upwards. Frontal margin produced, convex, bilobed. Anterolateral margin subcristate with four teeth including exorbital tooth. Carapace widest at fourth tooth position, fourth teeth largest, broadest. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped short, stout, with a small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Chelipeds large, symmetrical, glabrous, fingers as long as palm. Ambulatory legs with short setae, stout dactyli. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular, with all segments freely moveable (six somites plus telson); telson very broad, enlarged. G1 very thick, broad. Female gonopore operculate, oval in shape.

**Colour.**— The colour of fresh specimens is unknown but all preserved specimens are brown in colour.

**Size.**— The largest male specimen examined is 47.4mm x 41.7mm (USNM-173577), and the largest female is 34.4mm x 30.6mm (USNM-173577).

**Habitat.**— *C. angulatus* can be found in coastal lagoons (C.D. Schubart, pers. comm.).

**Remarks.**— Certain aspects of this species' biology is known, specifically the reproductive biology and recruitment (Amestoy, 1985; Petriella & Boschi, 1997; Bas & Spivak, 2000; Luppi *et al.*, 2002; Greco & Rodríguez, 2003). It is regarded as a common species in South America.

**Distribution.**— Southwestern America only.

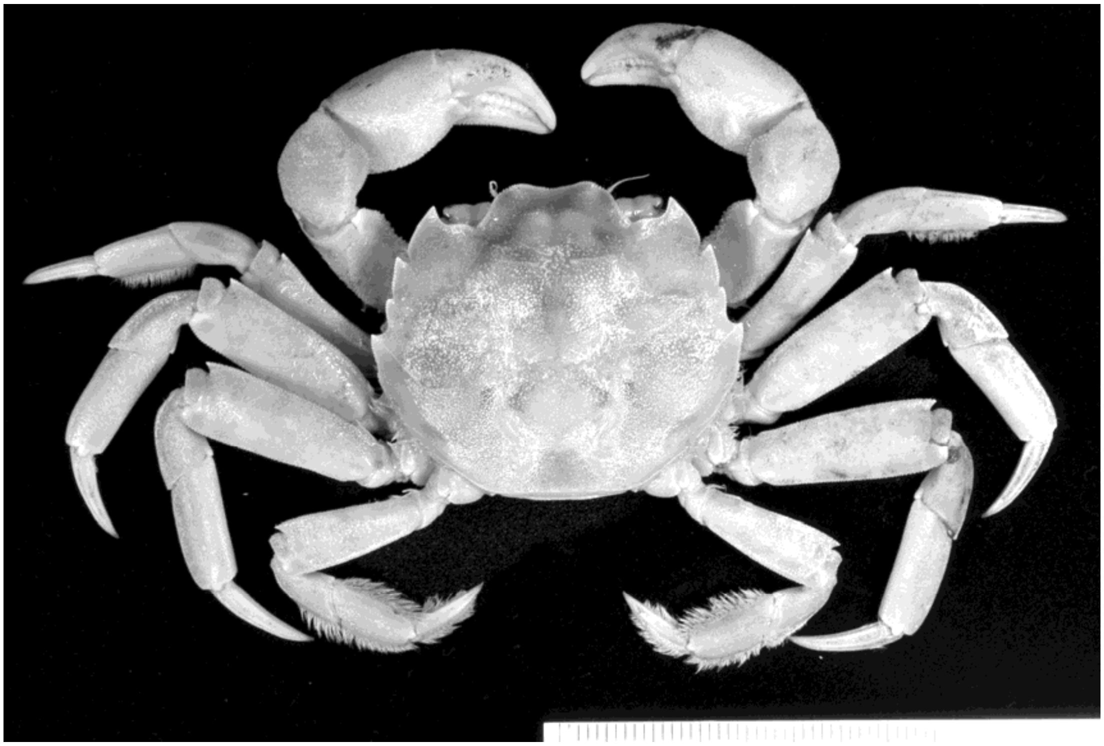


Figure 10. *Crytograpsus angulatus* Dana, 1852, male, 47.4mm x 41.7mm (USNM-173577). Dorsal view.

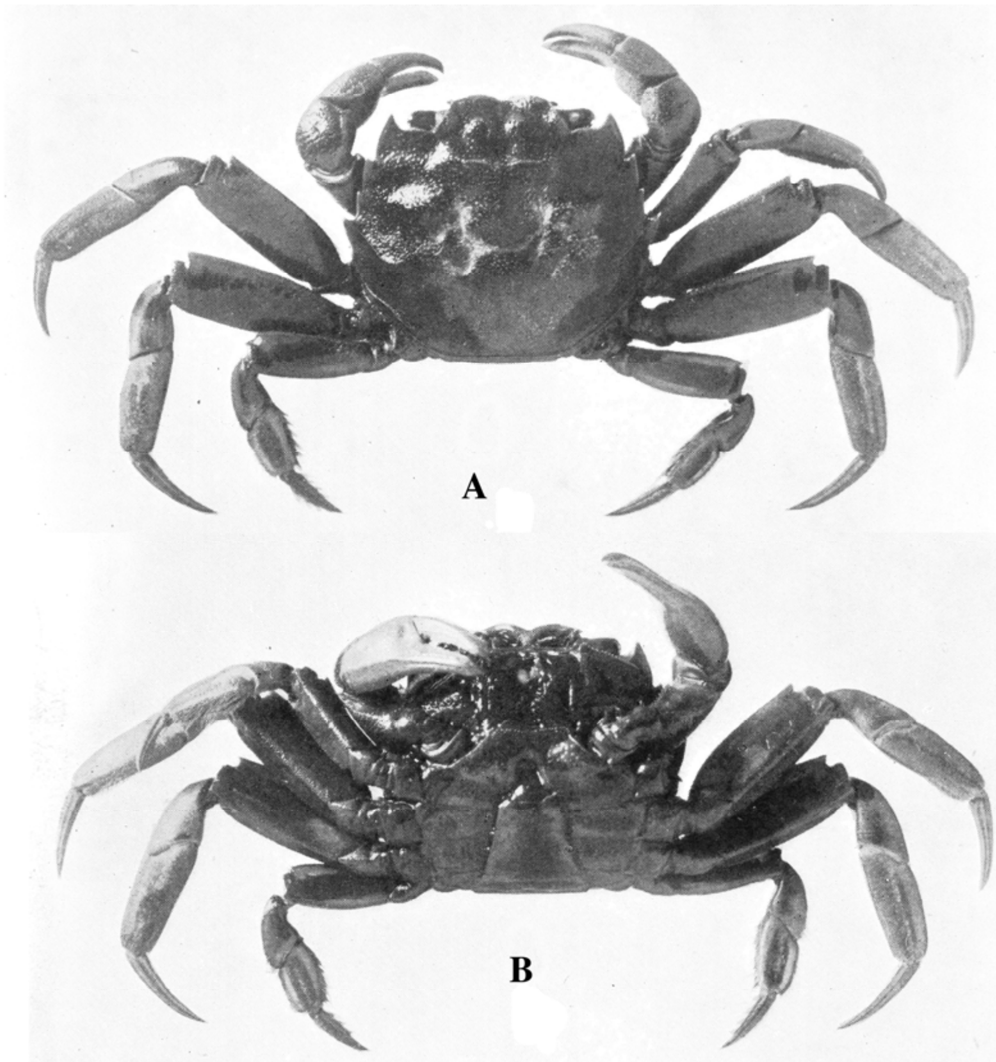



Figure 11. *Crytograpsus angulatus* Dana, 1852. A) dorsal view; B) ventral view (after Rathbun, 1918)

## Genus *Patagograpsus,* new genus

*Cyrtograpsus* Dana, 1852: 288; 1852: 247, 260; Rathbun, 1914: 121; Rathbun, 1918: 260; Boschi, 1964, 57, pls. 3 fig. 16; Scelzo & Lichstschein de Bastida, 1979: 103; Boschi *et al.*, 1992: 77, fig. 87; Melo, 1996: 472, 1 fig.; Spivak & Schubart, 2003: 212.

**Type species.**— *Hemigrapsus affinis*, Dana, 1852, by present designation

**Gender.**— Masculine.

**Diagnosis.**— Carapace quadrangular in shape, broader than long; dorsal surface uneven, punctate; regions well defined, convex, overall margins subcristate, vaulted slightly upwards. Frontal margin produced, convex, strtaight. Anterolateral margin subcristate with four teeth including exorbital tooth. Carapace widest at junction between second and third teeth. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped short, stout, with small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Cheliped large, symmetrical, glabrous, fingers as long as palm. Ambulatory legs with short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular, with all segments freely moveable (six somites plus telson); telson very elongated.

**Etymology.**— ‘Patago’ is the short form of Patagonia since this species is only found in that region, and ‘grapsus’ to indicate that it is still phylogentically linked to the Grapsidae until proven otherwise.

**Remarks.**— This genus is found only in South America. There is only one species in this genus i.e. *C. affinis* Dana, 1852. *Cyrtograpsus altimanus* Rathbun, 1914, has been shown by Spivak & Schubart (2003) to be merely an ecomorphorhic form of *C. affinis* (see below).

The new genus is very different from *Cyrtograpsus* in the following features, viz. a) carapace with frontal margin produced and straight (vs. less produced and bilobed in *Cyrtograpsus*); b) the fourth tooth is the smallest (vs. the largest in *Cyrtograpsus*); c) the third maxilliped is proportionately broader and stouter (vs. more slender and longer in *Cyrtograpsus*); d) the widest part of carapace is between the second and third anterolateral teeth (vs. the widest regions is at the fourth tooth in *Cyrtograpsus*); e) the G1 is very slender (vs. stout *Cyrtograpsus*), and f) the female gonopore is very narrowly rounded (vs. broadly rounded *Cyrtograpsus*).

### *Patagograpsus affinis* (Dana, 1852), new combination

(Figure 12A-C)

*Hemigrapsus affinis* Dana, 1852: 250; 1852: 350; 1855: pl. 22, fig. 5 (atlas); Rathbun, 1918: 264, pl. 67.

*Cyrtograpsus affinis* – Boschi, 1964, 57, pls. 3, 16; Boschi *et al.*, 1992: 77, fig. 87; Melo, 1996: 472, 1 fig; Spivak & Schubart, 2003: 212.

*Cyrtograpsus altimanus* Rathbun, 1914: 121, pl. 4; Rathbun, 1918: 262, pl. 66; Vinuesa, 2005: 15.

**Material examined.**— ***Cyrtograpsus affinis* – Neotype –** 1 male (11.4mm x 10.0mm), (USNM-123623), River Davia, Comodoro, Argentina, coll. Feb. 1916. – **Others** – 3 males (12.8-14.1mm x 11.4-13.4mm) (USNM-123625), Pto. San Antonio, Argentina, coll. Mackiinlay, no collection date; 1 male (11.4mm x 10.0mm), 1 female (ovigerous) (12.7mm x 11.2mm) (USNM-123623), River Davia, Comodoro, Argentina, coll. Feb. 1916; 1 male (12.3mm x 11.3mm), 1 female (12.4mm x 11.3mm) (USNM-123624), Argentina, no other information; 1 female (ovigerous) (4.7mm x 4.4mm) (USNM-123630), south of Mar. de Plata, Argentina, coll. ATARI, Feb. 1924; 1 male (11.3mm x 10.7mm), 2 females (ovigerous) (11.2-12.4mm x 10.3-12.0mm) (USNM-123628), Miramar, Argentina, coll. L. Bernasconi, Apr. 1922; 1 male (11.5mm x 10.2mm) (USNM-71209), Barvo del Santa Lucia, Urugauy, coll. N.L. Schmitt, 25 Nov. 1925. – ***Cyrtograpsus altimanus* – Paratypes** – 2 males (13.6-19.9mm x 12.5-17.7mm) (USNM-22835), San Matias Bay, Patagonia, coll. Hassler Expedition. – **Others** – 3 males (11.5-13.5mm x 10.6-12.0mm) (USNM-229983), Punta Tator, Chunut, Argentina, coll. A.B. William, Apr. 1988; 8 males (4.5-8.5mm x 4.0-7.8mm) (USNM-229984), Punta Melo, Chuhut, Argentina, coll. A.B. Williams, 18 Jun. 1985.

**Diagnosis.**— Carapace squarish in shape, overall dorsal surface, punctate, only very slightly convex, regions well-defined. Anterolateral margins with four teeth including exorbital tooth. Third maxilliped very broad; ischium, merus broad, exopod narrow. Ambulatory legs also slender, long thick setae on anterior, posterior surfaces of carpus, propodus. G1 long, slender, distal margin narrowly rounded, sloping shoulder shaped when viewed laterally, short, chitinuous prominence, slightly curved dorsally outwards with subdistal lobe. Female gonopore small with oval operculum.

**Colour.**— The colour of fresh specimens is unknown, and all preserved specimens examined are brown in colour.

**Size.**— The largest male specimen examined is 14.1mm x 13.4mm (USNM-123625), and the largest female examined is 12.7mm x 11.2mm (USNM-12362).

**Habitat.**— This species is found along the coastal area, in intertidal pools, but Rathbun reported that the specimens were collected from depths of 19-95 metres (Rathbun, 1914). Spivak & Schubart (2003) also reported that the young crabs are subtidal.

**Remarks.**— The type locality of *C. altimanus* and *C. affinis* are both from Patagonia (Dana, 1852; Rathbun, 1914). Dana (1852) described *C. affinis* under the name *Hemigrapsus affinis* based on specimens from Patagonia. Rathbun (1914) described the same species under the name *C. altimanus*. Boschi (1964) was the first to transfer *H. affinis* to *Cyrtograpsus*. There is very little known about the biology of *C. affinis*.

Examination of *C. altimanus* and *C. affinis* specimens in USMN's collection in 2002 has showed that there are very few substantial morphological differences between the two species. However, both species are distinctly different from *Cyrtograpsus* sensu stricto. A recent study by Spivak & Schubart (2003) has further supported my observation. Spivak & Schubart (2003) reported that *C. affinis* tends to be smaller than the other two species of the genus and seems to be restricted to subtidal habitats. However, their morphometric comparisons suggested that the existence of a continuous gradient rather than discrete differences between specimens of *C. affinis* and *C. altimanus*. Morphometric differences were as common among subtidal samples as between subtidal and intertidal samples. Likewise, the comparison of mitochondrial DNA sequences (16s rRNA) did not reveal any diagnostic differences between the two putative species (Spivak & Schubart, 2003), suggesting that *C. altimanus* and *C. affinis* are the same, they are possibly the two forms represent a single species with a high ecological and phenotypic plasticity (see Spivak & Schubart, 2003).

**Distribution.**— Eastern Pacific and Western Atlantic, Brazil, Argentina (Pantagonia).

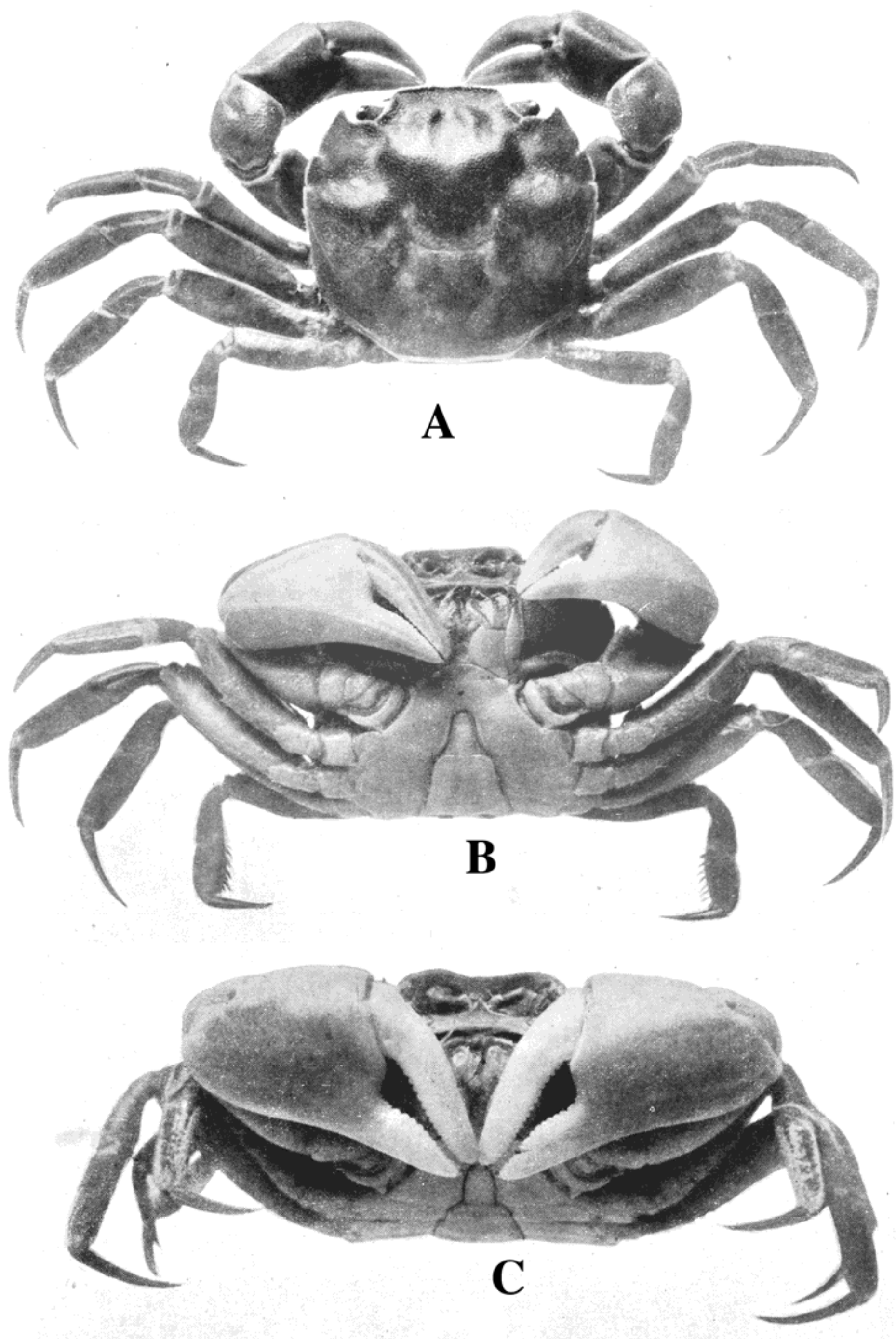



Figure 12. *Patagograpsus affinis* (Dana, 1852). A) dorsal view; B) ventral view; C) frontal view (after Rathbun, 1918).

### Genus *Eriocheir* De Haan, 1835

*Grapus (Eriocheir)* De Haan, 1835: 32.

*Eriochirus* – H. Milne-Edwards, 1853: 176 (wrong spelling).

*Eriocheir* – Kingsley, 1880: 210; Doflein, 1902: 665; Parisi, 1918: 102; Balss, 1912: 152; Kemp, 1918: 231; Tesch, 1918: 107, Schellenberg, 1928: 140, text-fig. 110; Shen, 1932: 172, text-figs. 108, 110, pl. 8, fig. 5; Peters & Panning, 1933: 1-180; Sakai, 1939: 667, pl. 109, fig. 1; Shen & Dai, 1964: 127; Christiansen, 1969: 1; Kim, 1973: 465, fig. 202; Lepzy & Leach, 1973: 1909; Ingle, 1980: 123, fig. 76, pl. 24b; Clark, 1984: 111, pl. 1; Hwang & Mizue, 1985: 12; Gu, 1986: 268; Dai *et al.*, 1986: 523; Yu & Ho 1986: 116; Dai, 1988: 22; Adema, 1991: 201, fig. 79; Dai & Yang, 1991: 523; Dai, 1991: 61; Lai & Lu, 1992: 23; Hong *et al.*, 1993: 10, pls. A & F; Chan *et al.*, 1995: 301, fig. 3B; Ng *et al.*, 1998: 493; Ng *et al.* 1999: 154; Sun *et al.*, 2003: 592; Chu *et al.*, 2003: 738; Tang *et al.*, 2003: 309; Tang *et al.*, 2004: 255; Chan *et al.*, 2005: 457; Komai *et al*., 2006: 1.

**Diagnosis.** — Carapace rectangular, broader than long; dorsal surface glabrous, punctate; regions very well defined, convex. Epigastric and protogastric cristae present. Frontal margin granulated with four teeth. Anterolateral margin subcristate with four teeth Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped broad, ischium and merus broad. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire with lobulations at the lateral ends. Inner and outer surfaces of pollex and manus with thick tufts of long, soft setae, fingers as long as palm. Ambulatory legs slender, long, with short setae, stout dactyli. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial groove. Male abdomen broadly triangular with all segments freely moveable (six somites plus telson). G1 long, slender. Female gonopore operculate, rounded.

**Type species.**— *Eriocheir japonica* De Haan, 1835. De Haan (1835) described *E. japonica* and *E. penicillata* but *E. penicillata* was transferred to *Heterograpus* by Ortmann (1894) (presently in *Hemigrapsus*, see later). Gender is feminine.

**Remarks.**— A short diagnosis of the genus *Eriocheir* is provided since Guo *et al.* (1997) have already provided a good description of the genus.

Currently, there are four valid species in this genus viz. *E. japonica* De Haan, 1835, *E. sinensis* H. Milne Edwards, 1853, *E. hepuensis* Dai, 1991, and *Eriocheir ogasawaraensis* Komai *et al.*, 2006. The taxonomy of this genus has been a subject of some debate in the last decade, and its current status is rather confusing (see Chu *et al.* 2003; Tang *et al.*, 2003; Chan *et al.*, 2005). Komai *et al.* (2006) has well summarized the recent arguments on the taxonomy of the genus and how we should treat the taxa once referred to as *Eriocheir*.

The disagreements were first addressed to the ranking of the taxa, *Eriocheir hepuensis*, first described by Dai (1991) as a subspecies of *E. japonica*. Based on morphometric and allozyme analyses, Li *et al.* (1993) concluded that these three taxa of *E. japonica*, *E. sinensis* and *E. hepuensis* belong to a single species. On the other hand, based on morphological comparisons, Guo *et al.* (1997) recognized the three species as distinct species. A RAPD analysis (Lu *et al.*, 2000) showed that there is low genetic differentiation between the three species, possibly due to hybridization and artificial transplantation in aquaculture. Tang *et al.* (2003) conducted a molecular phylogenetic analysis of the complete sequences of the nuclear DNA internal transcribed spacer (ITS) and portions of the mitochondrial genome corresponding to the Cytochrome Oxidase I (COI), supported the low genetic differentiation between the three species and claimed that the three species could be ranked at most as subspecies of a single species, *E. japonica*. Chu *et al.* (2003) remarked that there are a few constant differences distinguishing the three taxa, although they supported that the three taxa are genetically very similar based on DNA sequence analysis of mitochondrial 16s rRNA, COI and the first internal transcribed spacer of nuclear rRNA.

Tang *et al.* (2003) claimed that they discovered a specimen of *Eriocheir* from Zhujiang, which matched the original descriptions of *E. recta* by Stimpson (1858) and *E. formosa* by Chan *et al.* (1995), with supporting molecular evidence that confirmed their con-specificity. Tang *et al.* (2004) formally designated their Zhujiang specimen, as the neotype of *E. recta*, even though Chan *et al.* (1995) had already valid designated a neotype for this species. This publication by Tang *et al.* (2004) subsequently caused some nomenclatural confusion with regards to *E. recta* Stimpson, 1858. Chan *et al.* (1995) first showed that a species occurring in the eastern part of Taiwan, first identified with *E. recta* by Sakai (1939), does not represent the true *E. recta*. They described *E. formosa* for the population in the eastern part of Taiwan. They also designated a neotype for *E. recta*, a specimen of *E. japonica* collected nearby Zhujiang, China, close to Macau, the original type locality of *E. recta*. Effectively this made *E. recta* as a junior synonym of *E. japonica*. However, Tang *et al.* (2003, 2004) argued that the name *E. recta* should be revived and that *E. formosa* should be synonymized with it. Finally, Chan *et al.* (2005) published a rebuttal to the action of Tang *et al.* (2004), in which they discussed that the action by Chan *et al.* (1995) is fully justified. The entire twisted history of this confusion has been presented in detail by Chan *et al.* (2005).

The generic assignment of the two described species, *E. leptognathus* Rathbun, 1913, and *E. formosa* Chan *et al.*, 1995, has also been a subject of some disagreement. Sakai (1983) established a new genus *Neoeriocheir* to accommodate *E. leptognathus* based mainly on the difference in the structure of the third maxilliped. Subsequent authors (Dai *et al.*, 1984; Dai & Yang, 1991; Chan *et al.*, 1995) did not consider *Neoeriocheir* as a valid genus. Ng *et al.* (1999) revived *Neoeriocheir* for *E. leptognathus*, and further established a new genus *Platyeriocheir* for *E. formosa*. They provided evidence derived from both larval and adult morphology. The generic classification by Ng *et al.* (1999) has not been accepted by Tang *et al.* (2003) and Chu *et al.* (2003), as they argue that *E. leptognathus*, *E. formosa* and the other three taxa form a clade, and as the genetic differentiation among the two species, *E. leptognathus* and *E. formosa*, and the other three taxa is low, such that the separation at the genus level is not fully warranted.

The present study, however, maintains the stand of Guo *et al.* (1996) in regarding *E. japonica*, *E. sinensis* and *E. hepuensis* as distinct species, as some of the differentiating characters proposed by them, including the physiognomy of the carapace, the development of the fourth anterolateral tooth on the carapace, and the stoutness/slenderness of the ambulatory legs, all work. Therefore, I follow Guo *et al.* (1996) in treating the three taxa as full species. I fully concur Chan *et al.* (2005)

regarding the nomenclature of *E. recta* and *E. formosa*. The action by Chan *et al.* (1995) is valid without doubt, fulfilling the all provisions of the current code (ICZN, 1999). As Chan *et al.* (2005) noted, Stimpson (1858, 1907) clearly mentioned in his descriptions of *E. recta* that the indistinctly four-lobed front and the presence of a rudimentary fourth anterolateral tooth on the carapace. In *E. formosa*, the front is truncate and straight, and the fourth anterolateral tooth is completely absent. There is no doubt that *E. recta* and *E. formosa* are the same species. Tang *et al.*'s (2004) strange proposal must be rejected. Although Ng *et al.* (1999) claimed that *Eriocheir* senu lato was heterogeneous recent genetic studies support the monophyly of the assemblage including *E. leptognathus*, *E. formosa*, and the three closely related taxa *E. japonica*, *E. sinensis*, and *E. hepuensis* (Tang *et al.*, 2003; Chu *et al.*, 2003). The genetic relationship proposed by Tang *et al.* (2003) and Chu *et al.* (2003) is as provide below (Figure 13).

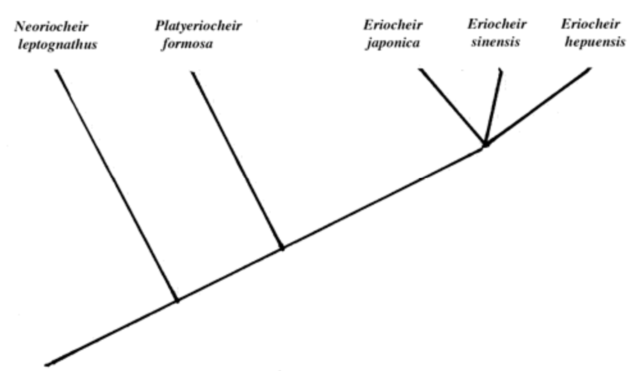



Figure 13. Genetic relationships of *Eriocheir* as proposed by Tang *et al.* (2003) and Chu *et al.* (2003).

However, my recent molecular data (on-going study with G.W. Xu) has shown that the five species all cluster in one clade, but the three species of *Eriocheir* viz. *E. sinensis*, *E. japonica* and *E. hepuensis* split along into a separate lineage, indicating that they are all good species! This phylogenetic pattern does not contradict the generic classification proposed by Ng *et al.* (1999). My cladistics study based on 46 adult morphological characters on *Eriocheir*, *Neoeriocheir* and *Platyeriocheir* have further shown that *Neoeriocheir* and *Platyeriocheir* are distinct genera (see Appendix I). Within the genus *Eriocheir*, the four species are distinctly separated into different lineages (see below).

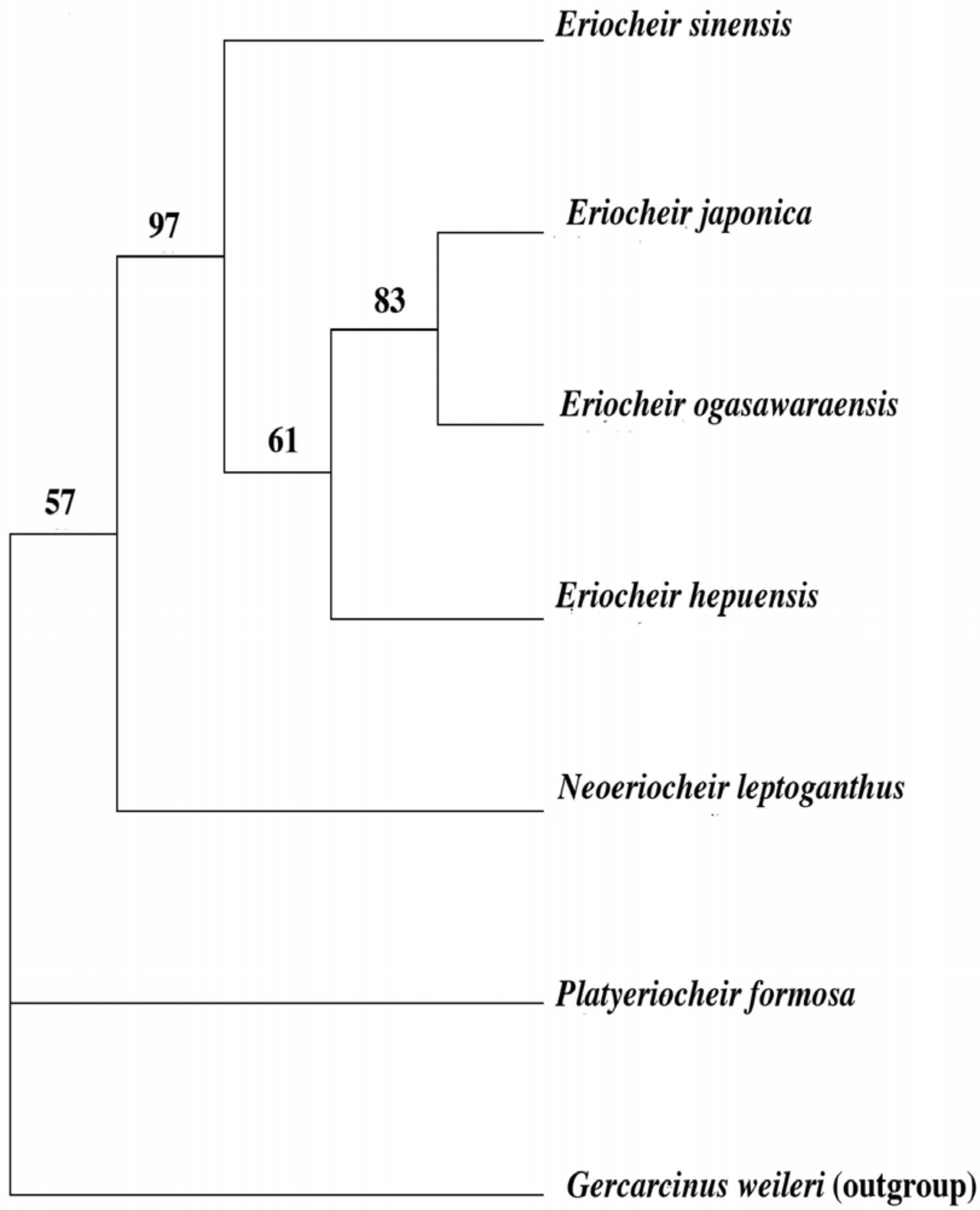



Figure. 14. Strict consensus tree with bootstrap values for the four species of *Eriocheir* viz. *E. sinensis*, *E. hepuensis*, *E. japonica* and *E. ogasawaraensis*; *Neoeriocheir leptognathus*; *Platyeriocheir formosa* and *Gercarcinus weileri* (outgroup), based on 46 adult morphological characters.

**Key to species in *Eriocheir***

1a. Carapace with frontal margin with two inner lobes and two outer sharper teeth. --- **2**

1b. Carapace with frontal margin with four sharp lobes. --------------------------------- **3**

2a. Anterolateral margin with four distinct teeth, fourth tooth distinct. --- ***E. japonica***

2b. Anteroateral margin with four distinct teeth, fourth tooth not distinct. ------------------ -------------------------------------------------------------------- ***E. ogasawaraensis***

3a. Propodus of last ambulatory very long, slender.---------------------------- ***E. sinensis***

3b. Propodus of last ambulatory legs relatively broader, shorter. ------------ ***E. hepuensis***

## *Eriocheir japonica* De Haan, 1835

(Figures 15, 16A-I)

*Grapsus* (*Eriocheir*) *japonicus* De Haan, 1835: 59, pl. 17.

*Eriocheir japonica* – Sakai, 1939: 667, pl. 76: 1; Chang, 1963: 6; Chang, 1965: 60; Sakai, 1976: 646, pl. 221; Dai *et al.*, 1986: 476, fig. 268: 1, pl. 67: 2; Dai & Yang, 1991: 522, fig. 268: 1, pl. 67: 2; Yamaguchi & Baba, 1993: 460, fig. 176; Jeng, Chan *et al.*, 1994: 98; Chan *et al.* 1995: 301, figs. 1A, 2C, 3C; Guo *et al.*, 1997: 460, figs. 5, 6c, 6f, 7c; Ho & Hung, 1997: 87; Ng *et al.*, 1998: 493; Jeng *et al.*, 1998: 69; Ng *et al.*, 1999: 154; Ng *et al.*, 2001: 44; Sun *et al.* , 2003: 592; Chu *et al.* , 2003: 738; Tang *et al.*, 2003: 309; Tang *et al.*, 2004: 255; Chan, Ng & Ng, 2005: 457.

*Eriochirus rectus* Stimpson, 1858: 103.

*Eriocheir japonicus* – Ortmann, 1894: 716; Rathbun, 1902: 24; Brashnikov, 1907:53; Stimpson, 1907: 124; Kemp, 1918: 231; Parisi, 1918: 101; Tesch, 1918: 107; Maki & Tsuchiya, 1923: 100; Sakai, 1935: 227, Pl. 63, Fig. 1; 1939: 667, Pl. 76; Horikawa, 1940: 29; Hoestlandt,1948: 8-9, fig. 6; Lin, 1949: 10; Lin, 1949: 29; Wu *et al.*, 1962: 208; Shen & Dai, 1964: 128, 1 fig.; Kim, 1973: 467, fig. 203, pl. 93, fig. 155; Sakai, 1976; 646-647. Pl. 221; Kobjakova 1976: 56, Fig. 115; Wang & Chen, 1981: 156; Miyake, 1983: 174; Su & Lue, 1984: 63, 67, fig. 16; Dai *et al.* 1986: 476, fig. 268 (1); Fukui *et al.*, 1989: 229; Dai & Yang 1991: 522, fig. 268, pl. 67(2); Shih, Lue & Wang, 1991: 142; Wu, 1992: 110; Li *et al.* 1993: 111; Hong *et al.* 1993: 10, pls. A & F; Yamaguchi & Holthuis 1993: 460, Fig. 176A-E; Wang & Liu, 1996b: 80.

*Etiocheir japonicus* – Jeng *et al*., 1996: 100; Jeng *et al*., 1998: 123 (wrong spelling).

**Material examined.**— (In addition to materials examined in Guo *et al.*, 1997). – **Paralectotypes -** 1 male (RMNH-D1618), Japan, no collection date; 1 female (RMNH-D113), Japan, no collection date; 1 male (RMNH-D114), Japan, no collection date; mouthparts only (RMNH-D42175), Japan, no collection date. — **Paratypes**: 3 males, 3 females (RMNH-D421738, Japan, no collection date; 1 male, 3 females (RMNH-D42174), Japan, no collection date; 1 male (RMNH-D41845), Japan, no collection date; 1 male (RMNH-D25142), Kyushu, Japan, coll. 8 Sep. 1986; 1 male (NMHN-3386S), no other data. – **Others** – **China** – 2 males (ASIZ-02596), Tumenjiang, Juling Province, coll. Jun. 1958; 2 females (AZIS-no cat. number), Yangsicun, Putong, coll. Y. Sakama, 22 Jul. 1938; 1 male (BNHM-no cat. number), Tongtoudao, Zhejiang Province, coll. S.L. Yang & X.M. Sun, 28 Sep. 1996. – **Hong Kong** – 1 male (ASIZ-C02658), Hong Kong; 1 male, 1 female (ZRC 1997.568), Hoi Sing Wan, New Territories, Hong Kong, coll. D. Dudgeon, Mar. 1983; 2 females (ZRC 1997.569), New Territories, Hong Kong, coll. D. Dudgeon, no collection date. – **Japan** – 1 male (53.5mm x 52.0mm) (USNM-229722), Katsuura-gawa, Tokushiora, Japan, coll. K. Sakai, 30 Aug. 1986; 1 male (47.5mm x 43.3mm) (USNM-229723), Katsuura-gawa, Tokushima, Japan, coll. 30 Aug. 1986; 1 male (68.3mm x 63.6mm), 1 female (66.1mm x 61.4mm) (USNM-54520), Oshoro, Hikkaido, Japan, coll. Jul. 1908; 1 male (4.6mm x 41.2mm), 2 females (55.3-57.0mm x 51.7-53.4mm) (USNM-20177), Hakodate, Japan, coll. US Fish Commission, Steamer Albatross 189, 19 Sep. 1896; 2 males (31.4-40.7mm x 28.6-37.5mm), 2 females (31.0-38.1mm x 28.6-35.6mm) (USNM-44579), Sapporo, Japan, coll. 1906; 1 female (ovigerous) (57.3mm x 51.9mm) (USNM-3389), Yokohama, Japan, coll. Tuscarora; 2 males (19.6-33.6mm x 18.1-30.0mm) (USNM-62885), Sasakawa canal, Japan, coll. A.S. Pearse, 21 Jun. 1929; 1 male (74.9mm x 67.3mm) (USNM-54188), Keelung, Taiwan, coll. M. Oshima, 18 Jan. 1916; 1 male (48.3mm x 43.7mm) (USNM-26241), Chikago river, Kurume, Chikago, Japan, coll. Gordon. & Myder, 1900; 1 male (11.1mm x 10.3mm) (USNM-62884), Odashinden, Wakamtsu village, Japan; 1 male (14.7mm x 13.0mm), 1 female (12.0mm x 11.1mm) (USNM-4591), Gojukaku, Kameda Gor., Hokkaido, coll. Imperial Museum Tokyo, 2 Aug. 1878; 1 male (66.4mm x 58.1mm) (USNM-18824), Ohogawa, Ryukyus, Jaoan, coll. Sakamoto, no collection date; 1 female (ovigerous) (63.3mm x 58.6mm) (USNM-26240), Same, Rikuoku, Japan, coll. Gordan & Snyder, 1900; 1 female (30.0mm x 26.6mm) (ZRC-no cat number), Taiho River, Okinawa, Japan, coll. 31 May 1998; 2 carapaces, 1 male, 2 females (ZIM-K-3781), Nagasaki; 5 males, 3 female (ZRC 1997.562), Kagoshima Prefecture, Japan, coll. T. Kishino, 25 Jan. 1996; 2 males, 2 females (ZRC 1997.563), Kagoshima Prefecture, coll. H. Suzuki, 12 Jan. 1996; 3 males (ZRC 1997.564), Kagoshima Prefecture, coll. H. Suzuki, 20 Dec. 1985; 3 males (ZRC 1997.565), Kagoshima Prefecture, coll. H. Suzuki, 16 Dec. 1995; 1 male (ZRC 1997.566), Kagoshima Prefecture, coll. H. Suzuki, 4 Jun. 1987; 1 female (ZRC 1997.567), Kagoshima Prefecture, Japan, coll. H. Suzuki, 31 Jan. 1996. – **Korea** – 1 male, 1 female (ASIZ-02659), northern region of South Korea, coll. summer 1958; 1 male (11.6mm x 10.3mm) (USNM-18428), Gensen, Korea, coll. 1932. – **Taiwan** – 1 male (21.6mm x 20.3mm), 1 female (39.2mm x 36.0mm) (USNM-266669), Loo Choo Island, Taiwan; 1 male (45.7mm x 42.8mm), 1 female (55.9mm x 51.2mm) (USNM-255609), Ali Liao, Taipei, Formosa, coll. 29 Dec. 1961; 4 males (39.5-51.8mm x 36.8-47.6mm), 2 females (43.5-46.7mm x 39.5-43.5mm) (USNM-123471), Ping Lin, Taipei County, Formosa, coll. 25 Nov. 1961; 1 male (74.3mm 68.4mm) (USNM-123468), Ping Lin, Taipei County, Formosa, coll. 18 Sep. 1961; 2 females (48.9-53.4mm x 44.8-49.9mm) (USNM-123468), Ping Lin, Taipei County, Formosa, coll. 18 Sep. 1961; 1 male (44.7mm x 41.5mm), 1 female (50.5mm x 46.7mm) (USNM-123470), Tu Shue Chi, I-Lan County, Formosa, coll. 26 Nov. 1961; 2 males (33.4-35.0mm x 31.4-31.8mm), 4 females (32.2-38.3mm x 29.5-36.0mm) (USNM-103778), Bank of Touchen river, Hsinchu, Hsinchu County, Taiwan, coll. R.E. Kutz; 2 males (43.5-44.0mm x 40.5-40.9mm), 2 females (47.3-48.5mm x 44.4-44.0mm) (USNM-123469), Wu-Ku-Keng, Taipei County, Formosa, coll. 19 Nov. 1961; 5 males (33.3-41.0mm x 31.6-38.3mm), 1 female (29.8mm x 27.6mm) (USNM-106151), Hsinchu market, Hsinchu, Hsinchu County, Formosa, no date; 3 males (35.5-45.8mm x 33.4-42.3mm), 2 females (30.7-37.4mm x 28.1-35.1mm) (USNM-123463), Hisnchu market, Hsinchu, Hsinchu County, Formosa, coll. 12 Sep. 1959; 2 males (53.8-60.3mm x 49.9-54.4mm), 6 females (46.6-59.8mm x 44.0-55.2mm), (NTOU-uncatalogued) Taiwan; 1 male (49.6mm x 46.0mm) (NTOU-uncatalogued), 1 female (57.5mm x 53.3mm), Zhu-Bei, Coll. H.P. Yu, 18 Sep. 1982; 1 male (63.3mm x 59.4mm) (NTOU), Ta-Du-Xi rivermouth, Taichung County, coll. Y.S. Chen, 5 Feb. 1993; 1 male (77.0mm x 68.0mm) (NTOU-uncatalogued), Luo-Dung, I-Lan County, coll. S.Y. Shy & H.Z. Lai, 10 Feb. 1986; 1 male (ZRC 1997.589), I-Lan County, eastern Taiwan, coll. J.J. Huang, 23 Nov. 1983; 1 female (ZRC 1997.590), I-Lan County, Taiwan, coll. L.F. Chen, 26 Nov. 1983; 2 males, 2 females (ZRC 1997.591), Taipei, Taiwan, coll. X.P. Yu, 6 Jun. 1982; 2 males (ZRC 1997.592), Taipei, Taiwan, coll. J.F. Huang, 5 Jun. 1988.

**Diagnosis.**— Carapace rectangular, overall dorsal surface only very slightly convex, regions well-defined, Frontal margin with two inner lobes, two outer sharp teeth. Anterolateral margins with four teeth including exorbital tooth. Third maxilliped very broad; ischium, merus broad, exopod narrow. Ambulatory legs also slender, long, long thick setae on anterior, posterior surfaces of carpi, propodi. G1 long, slender, distal margin narrowly rounded, slopping shoulder shaped when viewed laterally, short, chitinuous prominence, slightly curved dorsally outwards with subdistal lobe. Female gonopore operculate, bluntly triangular in shape, prominent, slightly concave dorsally.

**Colour.**— The colour of fresh specimens is greenish-brown in colour (S. Kobayashi, pers. comm.), and all preserved specimens examined are brown in colour.

**Size.**— The largest male specimen examined is 77.0mm x 68.0mm (NTOU-uncatalogued), and the largest female examined is 66.1mm x 61.4mm (USNM-54520).

**Habitat.**— It can be found in freshwater streams (T.Y. Chan, S. Kobayashi & S.L. Yang, pers. comm.).

**Remarks.**— The taxonomy of mitten crabs (*Eriocheir*) native to East Asia has been problematic and controversial. In the most recent taxonomic revision of the mitten crabs, *Eriocheir*, sensu stricto , is regarded to comprise the species *E. japonica*, *E. sinensis,* and *E. hepuensis,* but this classification scheme has not been widely accepted by other taxonomists. The genetic differences among populations of *Eriocheir* sensu stricto throughout most of its geographical range using mitochondrial Cytochrome *b* and Cytochrome *c* Oxidase I gene sequences has been studied by many workers (Chu *et al.*, 2003, Tang *et al*., 2004). Their results show that *E. hepuensis* is not genetically distinct from *E. japonica* in China and Taiwan and thus should not be considered a separate species. However, preliminary phylogenetic analysis indicates that *E. japonica* (including *E. hepuensis*) in the above region is more closely related to *E. japonica* in Okinawa than to *E. japonica* in Japan, or *E. sinensis*. The genetic divergences among geographical populations of *E. japonica* are high (3-5%), while those among *E. sinensis* populations are much lower (<0.5%). In almost all analyses, *E. japonica* populations constitute a paraphyletic assemblage so that its species status as currently defined to include crabs from outside Japan is debatable. To conclude, new study on *Eriocheir* taxonomy using nuclear DNA markers are needed to resolve this controversy (in prep.).

**Distribution.**— Taiwan, South-eastern China and Japan.

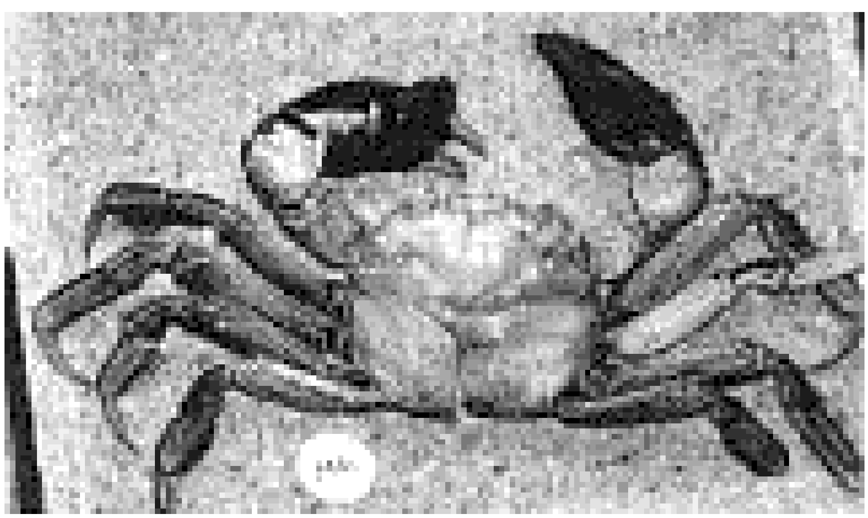


Figure 15. *Eriocheir japonica* (de Haan,1835), lectotype, male, (MNHN-3382). Dorsal view. (After Guo *et al*., 1997).

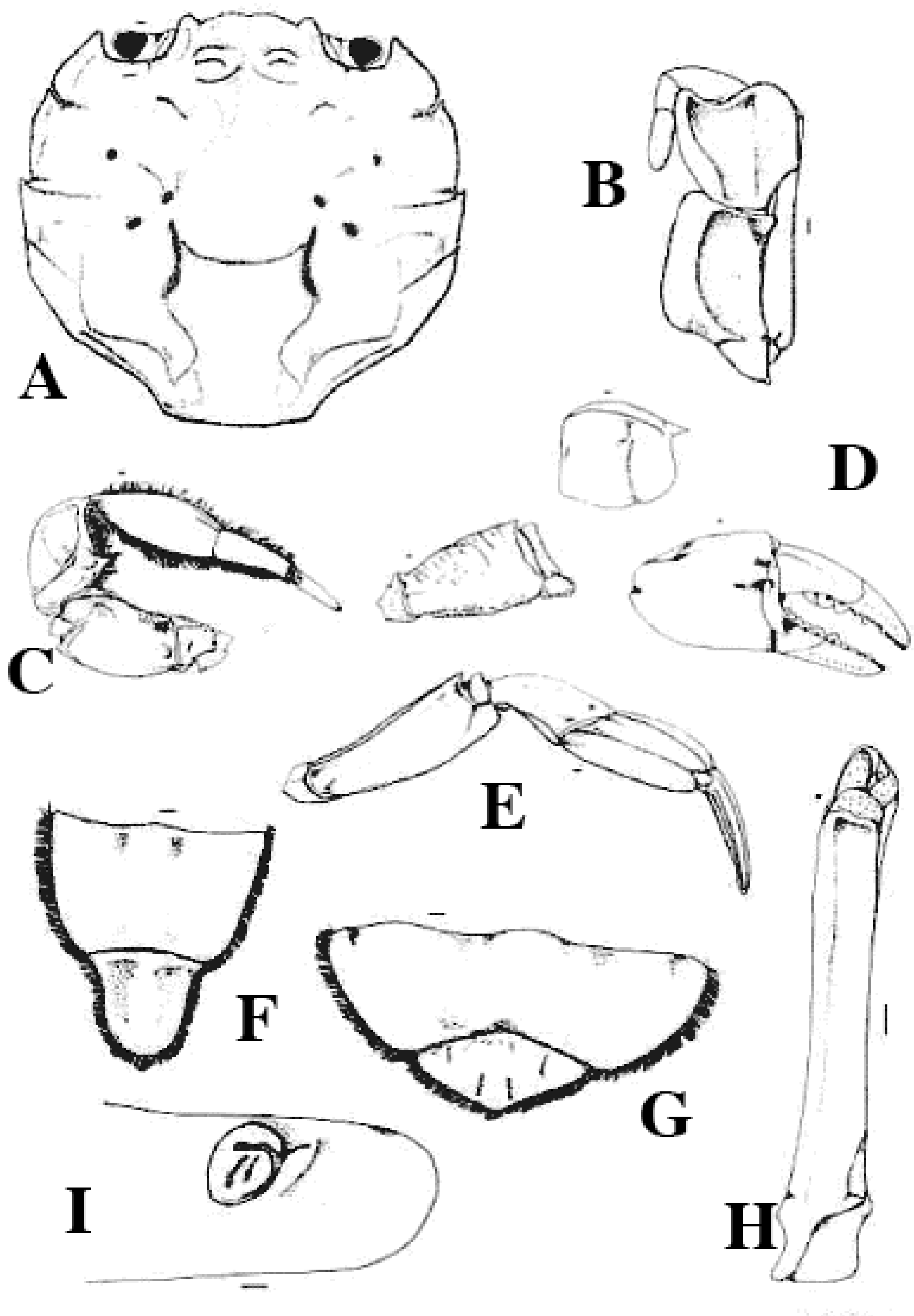



Figure 16. *Eriocheir japonica* (De Haan, 1835), male, 71.8mm x 65.6mm (ZRC 1997.565), female, 58.0mm x 49.0mm (ZRC 1997.565). A) carapace; B) third maxilliped; C) anterior view of chela; D) dorsal view of chele (shaved); E) last ambulatory leg; F) male abdomen (part); G) female abdomen (part); H) G1; I) female gonopore. (After Guo *et al*., 1997).

### *Eriocheir sinensis* H. Milne Edwards, 1853

(Figures 17A-B; 18; 19A-I; 20A-F)

*Eriocheir sinensis* H. Milne Edwards, 1853 Pl. 67(3); fig. 68(2); Kingsley, 1880: 210; Doflein, 1902: 665; Parisi, 1918: 102; Balss, 1912: 152; Kemp, 1918: 231; Tesch, 1918: 107, Schellenberg, 1928: 140, Text-fig. 110; Shen, 1932: 172, Text-fig. 108, 110, pl. 8, Fig. 5; Peters & Panning, 1933: 1-180; Sakai, 1939: 667, pl. 109, Fig. 1; Shen & Dai, 1964: 127; Christiansen, 1969: 1; Kim, 1973: 465, text-fig. 202, pl. 40, fig. 154; Lapezy & Leach, 1973: 1909; Ingle & Andrews, 1976: 638; Ingle, 1980: 123, fig. 76, pl. 24b; Clark, 1984: 111; Hwang & Mizue, 1985: 12; Gu, 1986: 268; Dai *et al.*, 1986: 523; Yu & Ho, 1986: 116; Türkay, 1987: 38; Dai, 1988: 22; Adema, 1991: 201, fig. 79; Dai & Yang, 1991: 523; Dai, 1991: Lai & Lu, 1992: 23; Hong *et al.* 1993: 10, pls. A & F; Chan *et al.*, 1995: 301, fig. 3B; Ng *et al.*, 1998: 493; Ng *et al.*, 1999: 154; Sun *et al.* , 2003: 592; Chu *et al.*, 2003: 738; Tang *et al.*, 2003: 309; Tang *et al.*, 2004: 255; Chan *et al.*, 2005: 457.

*Eriochirus sinensis* – H. Milne Edwards 1853: 176 (wrong spelling).

*Eriocheir sinensis* form *rotundifrons* Panning, 1938: 109, Fig 5; Adema, 1991: 201, Fig. 79.

*E. sinensis* form *acutifrons* Panning, 1938: 109, Fig 6; Adema, 1991: 201, Fig. 79.

*E. sinensis* form *trilobata* Panning, 1938: 110, Fig 7; Adema, 1991: 201, Fig. 79.

*E. sinensis* form *rostrata* Panning, 1933: 53, Fig 22B; 1938: 110, Fig. 8; Adema, 1991: 201, Fig. 79.

**Material examined.**— In addition to the specimens listed in Guo *et al.*, 1997. – **Lectotype** – 1 female (66.0 mm x 57.0mm) (MNHN: B3383S), Macao, China, coll. M. Callery, no date. – **Others** – **Belgium** – 1 specimen mounted on board (ZI-12423); 1 specimen mounted on board (ZI-12452); 1 specimen mounted on board (ZI-12453); 1 female (ovigerous) (RMNH-D2919), Jantvliet, coll. May 1935. – **China** – 1 male (53.0mm x 51.0mm), 1 female (ovigerous) (57.0mm x 53.0mm) (SFM-13231), Shanghai, China, leg. H.L. Chen, 4 Aug. 1984; 1 male, 9 females (ASIZ-02616), Yingkou, Liaoling Province, coll. 20 Aug. 1931; 1 male (ASIZ-02629), Yingkou, Liaoling Province, coll. 6 Jun. 1950; 2 males, 2 females (ASIZ-02628), Fengcheng, Liaoling Province, coll. 15 Sep. 1975; 2 males, 1 female (ASIZ-02590), Shanhaiguan, Hebei Province, coll. 14 Jun. 1929; 14 males, 7 females (ASIZ-02617), Shanhaiguan, Hebei Province, coll. 8 Aug. 1930; 2 females (ASIZ-02611), Qinghuangdao, Hebei Province, coll. 27 Jun. 1930; 8 males, 8 females (ASIZ-02626), Beidaihe, Hebei Province, coll. 4 Jun. 1929; 1 female (ASIZ-02572), Beidaihe, Hebei Province, coll. 24 Jun. 1930; 3 females (ASIZ-02625), Beidaihe, Hebei

Province, coll. 6 May 1950; 2 males (ASIZ-uncatalogued), Baiyangdian, Heibei Province, coll. 1957. 3 males, 1 female (ASIZ-02618), Baiyangdian, Hebei Province, coll. 13 May 1957; 1 female (ASIZ-02598), Beitang, Hebei Province, coll. 2 Apr. 1930; 2 males (ASIZ-02581), Xinzheng, Hebei Province, coll. 20 Jun. 1930; 1 male (ASIZ-02576), Liangminzhuang, Hebei Province, coll. 8 May 1932; 1 male, 1 female (ASIZ-02605), Beitang, Hebei Province, coll. 12 Jun. 1930; 1 male, 2 females (ASIZ-2597), Xinzheng, Hebei Province, coll. 12 May 1957; 5 females (ASIZ-02599), Yanghekou, Hebei Province, coll. 18 Jun. 1931; 14 females (ASIZ-02619), Xigu, Hebei Province, coll. 21 Apr. 1930; 1 male, 6 females (ASIZ-02622), Xigu, Hebei Province, coll. 25 Apr. 1930; 2 males, 4 females (ASIZ-02600), Xigu, Hebei Province, coll. 21 Apr. 1930; 1 male, 1 female (ASIZ-02604), Changzhou, Hebei Province, coll. 19 Aug. 1929; 3 males (ASIZ-02607), Sahe, Hebei Province, coll. 1 Jun. 1926; 1 male, 2 females (ASIZ-02578), Qinghuangdao, Hebei Province, coll. 26 Jul. 1930; 7 males, 7 females (ASIZ-02614), Tongzhou, Hebei Province, coll. 7 Apr. 1930; 1 female (ASIZ-02639), Beijing, coll. 16 Oct. 1930; 1 female (ASIZ-02637), Beijing, coll. 21 Sep. 1928; 15 males, 6 females (ASIZ-no cat. number), Beijing market, coll. 1957; 2 males, 1 female (BNHM-J58-0065), Tianjing; 2 females (ASIZ-02577), Longmen, Shangdong Province, coll. 20 May 1930; 1 female (ASIZ-02588), Yantai, Shangdong Province; 1 male (ASIZ-02589), Yantai, Shangdong Province, coll. 30 May 1930; 2 males, 1 female (ASIZ-uncatalogued), Yantai, Shangdong Province, coll. 1969; 2 males, 1 female (ASIZ-02627), Shangdong Province, coll. 12 Apr. 1975; 1 female (ASIZ-02579), Magongdao, Shangdong Province, coll. 19 May 1931; 2 females (ASIZ-02624), Nanjing, Jiangsu Province, coll. Nov. 1928; 2 males, 1 female (ASIZ-uncatalogued), Nanjing, Jiangsu Province;123 males, 124 females (ZRC 1997.558), Haimen, Jiangsu Province, coll. Nov. 1995; 5 males, 5 females (ZRC 1997.559), Haimen, Jiangsu Province, coll. Oct. 1996; 2 males, 3 females (ASIZ-02575), Wuxi, Jiangsu Province, coll. 29 Apr. 1973; 1 male (ASIZ-02634), Shanghai; 1 male, 1 female (ZIM-K-24729), Shanghai, coll. 1928; 10 males, 8 females (ZIM-K-24843), Shanghai; 1 male, 1 female (ASIZ-02595), Qingtiansien, Zhejiang Province, coll. 8/1978; 3 males (ASIZ-02608), Lisuisien, Zhejiang Province, coll. May 1972; 1 male (ASIZ-02585), Santou, Zhejiang Province, coll. Jul. 1955; 1 male, 1 female (ASIZ-02602), Wenzhou, Zhejiang Province, coll. 20 Sep. 1929; 1 male, 1 female (ZIM-K-3910), Futschau, coll. 13 Jun. 1903; 3 males, 3 females (ZIM-K-3904), Futschau, coll. 31 May 1904; 2 females (ASIZ-02633), Jimei, Fujian Province, coll. 1975; 1 male, 1 female (ASIZ-02631), Longhai, Fujian Province, coll. 5 Mar. 1974; 1 male (ZIM-K-3911), Fo-Kien, coll. 9 Sep. 1904; 1 female (ASIZ-02586), Sapeyan, coll. 11 May 1930; 2 males, 1 female (ASIZ-02636), Xinhouzheng, coll. 13 Jun. 1930; 1 male (ASIZ-uncatalogued), Yantai, Zhihuan, coll. 22 Oct. 1934; 1 male (ASIZ-02593), coll. 21 May 1958; 2 males (ASIZ-02572), Dingxinsien, coll. 17 May 1930; 3 males, 1 female (ASIZ- 14106), Baiyangdian, Baxian, coll. 14 May 1957; 17 males, 3 females (ASIZ-06382), Tongzhou, coll. 8 Apr. 1929; 2 males (ASIZ-02580), Hekai, coll. May 1937; 1

male, 1 female (ASIZ-uncatalogued), no other data; 3 males (ASIZ-uncatalogued), no other data; 1 male (BNHM-J58-0068); 1 female (BNHM-J58-0067); 1 male (BNHM-J58-0064); 1 male, 1 female (BNHM-J58-0066); 1 female (BNHM-J58-0174), coll. 1958; 2 males, 1 female (ZIM-K-3900), Kiautschau, coll. 23 Mar. 1910; 1 female (ZIM-K-24728), Woosung, coll. 1846; 1 male (ZIM-K-3825). – **Korea** – 2 males, 3 females (ASIZ-02615), Jizhou, Korea, coll. 18 Jun. 1930. – **France –** 1 specimen, dry mounted on board (MNHN-3384S); 1 specimen, dry mounted on board (MNHN-3388S); 1 male, 1 female (MNHN-MPB12573), Escaut, no collection date; 1 male (MNHN-B12575), aquarium in Paris, coll. Oct. 1939; 1 female (MNHN B12576), coll. 1939; 1 female (MNHN-MPB-12577), Provenaut des coures d'eau d' Allenmague, coll. 1938; 1 male, 1 female (MNHN-MPB12578), Escaut, no collection date; 2 males (MNHN-MPB12580); 1 male, 2 females (MNHN-MPB12581), Escaut, no collection date; 1 male, 1 female (MNHN-B12583), RatheNov. seer Havel, Allemague, coll. Nov. 1938; 2 specimens, mounted on board dry (MNHN-B10982S), no other data; 1 specimen, dry mounted (MNHN-3387S), no other data. – **England** – 5 males, 2 females (LNHM-uncatalogued), Lots Road, Chelsea, London, England, coll. B.D. Smith & C. Bryne, Nov. 1996. – **Germany –** 1 female (66.0mm x 60.0mm) (SFM-9789), Rheine, Germany, leg. A. Lelek, 5 Dec. 1981; 4 males (41.0-45.0mm x 38.0-43.0mm), 1 female (44.0mm x 41.0mm) (SFM-21973), Rheineland, Germany, coll. R. Pelz, July 1982; 1 male (ZIM-K-24477) (paratype of *E. sinensis* form *rotundifrons*), Hamburg, coll. 14 Mar. 1933; 1 male (ZIM-K-25230) (holotype of *E. sinensis* form rotundifrons), Calbe, coll. 3 Mar. 1935; 1 female (ZIM-K-24470) (paratype of *E. sinensis* form acutifrons), Hafen, Hamburg, 27 May 1933; 1 male (ZIM-K-25236) (holotype of *E. sinensis* form acutifrons), Elbe, coll. 21 Jul. 1935; 1 female (ZIM-K-24475) (paratype of *E. sinensis* form *acutifrons*), Hafen, Hamburg, coll. 9 Mar. 1933; 1 male (ZIM-K-25262) (paratype of *E. sinensis* form *acutifrons*), Elbe, coll. 29 Oct. 1936; 1 male (ZIM-K-24241) (paratype of *E. sinensis* form *trilobata*), Elbe coll. 22 May1936; 1 male (ZIM-K-24471) (paratype of *E. sinensis* form *trilobata*, Koln, coll. 7 Jan. 1933; 1 male (ZIM-K-25232) (paratype of *E. sinensis* form *trilobata* ) Hamburg, coll. 17 Jul. 1935; 1 male (ZIM-K-24473) (paratype of *E. sinensis* form *trilobata*) , Hamburg, coll. 20 Jul. 1933; 1 female (ZIM-K-24847) (paratype of *E. sinensis* form *trilobata*), Brunsbuttel, coll. 27 Jan. 1934; 1 male (ZIM-K-25235) (paratype of *E. sinensis* form *trilobata*), Elbe; 2 females (ZIM-K-25231) (paratypes of *E. sinensis* form *trilobata*), Havel; 1 female (ZIM-K-25238) (holotype of *E. sinensis* form *trilobata*), Unterelbe, coll. 1935; 1 male, 1 female (ZIM-K-24476) (paratype of *E. sinensis* form *rostrata*), Kohlbrand, coll. 7 Jan. 1933; 1 male (ZIM-K-25229) (paratype of *E. sinensis* form rostrata), Elbe, coll. 3 Jul. 1935; 1 male (ZIM-K-25242) (paratype of *E. sinensis* form rostrata), Finkenwarder; 1 male (ZIM-K-25501) (paratype of *E. sinensis* form rostrata), Michealisschlesse, coll. 23 May 1938; 1 male (ZIM-K-25240) (paratype of *E. sinensis* form rostrata), Hafen, Hamburg, coll. 10 Jul. 1936; 1 female (ZIM-K-24510) (*E. sinensis*, Panning's (1938) unnamed variety a), Elbe; 1 female (ZIM-K-

25234) (*E. sinensis*, Panning's (1938) unnamed variety b), Zollenspieker, coll. 19 Sep. 1933; 1 female (ZIM-K-25237) (*E. sinensis*, Panning's (1938) unnamed variety b), Elbe, Germany, coll. 19 Jul. 1935; 1 male (ZIM-K-25243) (*E. sinensis*, Panning's (1938) unnamed variety b), Finkenwarder, Hamburg, coll. 18 Jun. 1936; 1 specimen (MNHN-B12574), Elbe, pris de Wittenberg, coll. 1930; 1 male (ZIM-K-20719), Weser, no collection date; 1 female (ovigerous) (ZIM-K-22689), Norderelbe, coll. 13 Oct. 1924; 1 female (ZIM-K-25336), Elbe, coll. 1 Sep. 1937; 1 female (ZIM-K-22574), Elbe, coll. 15 Sep. 1931; 1 female (ZIM-K-24490), Norderelbe; 1 male (ZIM-K-7869), Unterelbe, coll. 19 Oct. 1924; 1 female (newly moulted) (ZIM-K-12865), Wittensee, coll. 11 Oct. 1927; 1 female (ZIM-K-7971), Unterelbe, coll. 7 Oct. 1924; 3 females, 2 males (ZIM-K-24480), Elbe; 1 female (ZIM-K-7824), Brunsbuttel, coll. 3 Dec. 1924; 1 male (ZIM-K-24845), Mit Renerat, coll. 26 Oct. 1932; 1 male (ZIM-uncatalogued), Bille Kanal, Hamburg, coll. 17 Aug. 1957; 3 females (ZIM-K-24241), Elbwatt; 2 males (ZIM-K-37553), Elbe, no collection date; 1 male (ZIM-K-33364), Oberelbe, coll. 1932; 2 males, 2 females (ZIM-K-24480), Elbe; 2 females (ZIM-K-24846), Elbe, coll. 27 Jan. 1934; 1 male (ZIM-K-22689), Elbe, coll. 28 Sep. 1931; 1 male (ZIM-uncatalogued); 2 specimens, mounted on board, covered with barnacles (ZIM-uncatalogued); 8 females, all covered with barnacles (ZIM-K-24501), Cuxhaven; 4 males, 2 females (ZIM-K-24484); 2 males (ZIM-K-37478), Unterelbe, coll. 1977; 38 males, 23 females (ZIM-K-24504), Hove, no collection date; 1 male, 1 female (ZIM-K-37479), Unterelbe, coll. 1978; 16 males, 22 females (ZIM-K-24490), Elbe; 1 male, 1 female (ovigerous) (SM-10955), Nordsee, Medemmnne 10.17m dept, coll. F.V. Sendenborg, 14 Dec. 1982. – **The Netherlands -** 1 female (ovigerous) (RMNH-D4721), Nord Breveland, coll. 29 Mar. 1963; 1 female (ovigerous) (RMNH-D24720), Oasterzscelde, coll. 8 Jul. 1961; 1 male (RMNH-D37185), Tussen Katwijken Noordwijk, coll. 13 Dec. 1958; 2 males (RMNH-D1819), Leiden, coll. 1935; 1 male (RMNH-D3307), Leiden, coll. 8 Oct. 1940; 1 male (RMNH-D29622), Stomuruk, coll. 4 Oct. 1973; 1 female (ovigerous) (RMNH-D3293), coll. 12 Apr. 1940; 1 male (RMNH-D4478), coll. 13 Aug. 1944; 1 female (ovigerous) (RMNH-D24722), Schouwen, Zealand, coll. 26 Feb. 1962; 1 male (RMNH-D3405), Rypwedering, coll. 1941; 1 male, 1 female (RMNH-D34689), Roclo Faazensiren, coll. 3 Oct. 1981; 1 male (RMNH-D10311), Ringvaart Haarlemmermeerpolder, coll. 15 Nov. 1940; 1 male (RMNH-D3918), Leiden, coll. 29 Sep. 1938; 1 male (RMNH-D4132), Zwette Scharnegoutum, coll. 15 Oct. 1943; 1 male (RMNH-D4133), Scharnegoutum, coll. 15 Oct. 1943; 2 females (RMNH-D3205), Leiden, coll. 22 Nov. 1938; 1 male (RMNH-D3140), Leiden, coll. 1936; 1 male, covered with barnacles (RMNH-D29626), Den Helder, coll. 26 May 1987; 1 male (RMNH-D10312), Reins Henderik Kanaal, coll. 27 Sep. 1955; 1 male, 1 female (RMNH-D2825), Oijde Bifdtzijt, Friesland, coll. 27 Sep. 1932; 1 female (ovigerous) (RMNH-D21348), Scheueningen-naozd, coll. 30 Apr. 1941; 1 male (RMNH-D3126), Leiden, coll. 1936; 1 male (RMNH-D2824), Stezyensas, coll. 13 Aug. 1932; 4 males (RMNH-D36306), Nauecha Noord, coll. 5 Jul. 1985; 1

female (RMNH-D3715), Leiden, coll. 28 Aug. 1943; 1 female (RMNH-D3206), Leiden, coll. 15 Nov. 1938; 1 male (RMNH-D10310), Zoutkamp, Gzoningen Province, coll. 4 Feb. 1932; 1 female (RMNH-D31716), Brezum, Gzoningen, coll. Dec. 1959; 1 male (RMNH-D3714), Scharisshoot, Voozhart, coll. 10 Aug. 1943; 1 female (ovigerous) (RMNH-D32940), Gzenelingen, coll. 26 May 1966; 1 male (RMNH-D3165), Niewkoop, coll. 1936; 1 male (RMNH-D3766), Leiden, coll. 17 Oct. 1943; 1 female (RMNH-D8490), Leiden, coll. 19 Jul. 1952; 1 male (RMNH-D8491), Fegefen Limburg, coll. 4 Aug. 1952; 1 male (RMNH-D3716), Leiden, coll. 28 Sep. 1943; 1 female, ovigerous (RMNH-D32941), Strand-Westduin, 28 Apr. 1962; 1 male (RMNH-D8492), Geneente Wassenawe, 17 Jul. 1962; 1 female, ovigerous (RMNH-D23265), Rockanje, Voorne, Luid-Holland, 6 Jan. 1967; 1 female (RMNH-D3307), Warmord Tb Sveuleborn, 27 Sep. 1940; 1 male (RMNH-D35191), Nymegen, Getalezland, 14 Aug. 1981; 1 female (RMNH-D2500),.Leiden, Nederlands, 1 Nov. 1936; 1 male (RMNH-D35187), Amsterdam, 9 Sep. 1981; 1 female, ovigerous (RMNH-D11345), Noordwykaan Lee, Zuid-Holland, 7 Apr. 1957; 2 males (RMNH-D3717), Leiden, Nederlands, 1 Oct. 1943; 2 males (RMNH-D3768), Leiden, no date; 1 male (RMNH-D3769), Leiden, 5 Nov. 1942; 2 females (RMNH-D16015), Tussen Nazdwrijken, 5 Mar. 1961; only carapace (RMNH-D5325), De Kwak, Voozne, Putten, 10 Jul. 1947; 1 male, 2 females, (RMNH-D3765), Oegstqeist, Oct. 1943; 1 male (RMNH-D2443), de Waal, 1936; 1 male (RMNH-D3306), Leiden, Nederlands, 1939-1940, 4 males (RMNH-D1572), Gwingen, no collection date; 1 male (RMNH-D34690), Fjobbemeee, Zultewaemond, 5 Oct. 1981; 1 male (RMNH-D35191), Maas-Waal Kanaal, 31 Aug. 1981; 1 male (RMNH-D2929), no location, no collection date; 1 male (RMNH-D2527), Brentsche A by de Passt, 20 Oct. 1933; 7 males (RMNH-D2885), Groningen, 17 Sep. 1933; 4 carapaces, 2 female and 1 male abdomens (RMNH-D10248), no location, 10 Sep. 1954; 2 males (RMNH-D36013), Nymegen Waal Centraale, 10 Sep. 1954; 2 females (RMNH-D24723), Naard Brabant, 16 Sep. 1965; 2 males (RMNH-D24724), Naard Brabant, coll. 14 Jan. 1960; 1 male (RMNH-D35931), Nymegen, Getdesland, coll. 26 May 1981; 1 female (left side broken) (RMNH-D4134), coll. 7 May 1944; 1 female (RMNH-D3705), Haven, Leeland, coll. 14 Jun. 1943; 2 males (RMNH-D2528), Paterwoldschemeer, coll. 9 May 1934; 1 female (RMNH-D27189), Warmond, coll. 21 Jul. 1971; 2 males, 1 female (RMNH-D10676), Stzyensas Beyeslad, coll. 29 Apr. 1956; 1 female (RMNH-D24718), Noord Bieshosch, coll. 12 Jul. 1966; 1 female (RMNH-D24719), Sleauuryk, coll. 3 Jul. 1959; 1 male (RMNH-D23962), Moerdyk, N. Brabant, coll. 23 May 1960; 1 male (RMNH-D23963), St Marie aan Schelde, Leeland, coll. 1 Apr. 1960; 1 male (RMNH-D23964), St. Philipsland, coll. 19 Feb. 1962; 16 males, 4 females (barrel 1), 38 males, 44 females (barrel 2) (RMNH-uncatalogued), northern Holland, coll. 5 Apr. 1985; 1 male (RMNH-D45215), northern Holland, coll. 5 Sept.1980; 1 female, carapace covered with barnacles (RMNH-D45191), coll. 15 Jun. 1939 ; 1 specimen (only carapace) (RMNH-D45193), coll. 21 Apr. 1955 ; 1 specimen (only broken carapace) (RMNH-D45194), coll. 23 Mar. 1941; 1 specimen (only carapace) (RMNH-D46866), coll. 6 May 1948; 1 specimen (only carapace) (RMNH-D45199), coll. 11 Jan. 1981; 2 legs and 1 carapace (RMNH-D45196), northern Holland, coll. May-Jul. 1949; 1 specimen (broken carapace) (RMNH-D46867), coll. 23 Mar. 1941; 1 specimen (only carapace) (RMNH-D45195), coll. 4 Apr. 1941; 1 specimen (only carapace) (RMNH-D45204), northern Holland, coll. 1 May 1936; 1 female (RMNH-D46864), Delfgauwse weg Delft, Nov. 1941; 1 male (RMNH-D45206), Zuid-Holland, 10 Aug. 1961; 1 male (RMNH-D5645), Zuid-Holland, coll. Oct. 1935; 1 female (RMNH-D45216), coll. summer of 1940; only 3 fragments (RMNH-D45200), coll. 15 Jul. 1944; only 2 chelipeds (RMNH-D45205), coll. 3 Apr. 1938; 1 specimen (only carapace) (RMNH-D45202), coll. 22 May 1937; 1 female (RMNH-D45212), coll. 8 Sep. 1951; 1 female (RMNH-D45209), coll. 26 Mar. 1961; 1 specimen (only carapace) (RMNH-D45207), coll. 5 Mar. 1944; 1 specimen (only carapace and abdomen) (RMNH-D45204), Den Helder, northern Holland, coll. 1 May 1936; 1 female (RMNH-D45198), coll. Mar. 1942; 1 male (RMNH-D5644), Leiden, coll. 17 Oct. 1940; 1 mounted specimen (RMNH-D45208, coll. 4 Apr. 1969;  1 mounted specimen (RMNH-D45201), Noord-Brabant, coll. 25 Jul. 1953; 2 males, 4 females (RMNH-D33082), northern Holland, coll. 29 Aug. 1980;  1 male (RMNH-D45211), coll.  Nov. 1944; 1 female (RMNH-D45192), coll. 17 Apr. 1947; 1 female (RMNH-D5643), coll. Jun. 1936; 1 female (RMNH-D45213), Gelerland, coll. 1 Apr. 1982; 2 carapaces and 3 legs (RMNH-D45214), coll. 30 Apr. 1951. – **Norway** – 1 female (ZMO-F21015), Visterflo, Rolvsoy Ostofold, coll. D. Anderson, Sep. 1989; 1 male (ZMO-F17280), Arisholmen ved Krakeroy Hvaler Kommune, coll. O. Magussen, 11 Dec. 1976; 2 males, 2 females (ZMO-F4319), Elben nedenfor Freiburg, coll. Nov. 1929.

**Diagnosis.**— Carapace rectangular, overall dorsal surface only very convex, regions well-defined. Frontal margin with four strong, sharp teeth. Anterolateral margins with four teeth including exorbital tooth. Third maxilliped very broad; ischium, merus broad, exopod narrow. Ambulatory legs also slender, long, long thick setae on anterior, posterior surfaces of carpi, propodi. G1 long, slender, distal margin narrowly rounded, slopping shoulder shaped when viewed laterally, short, chitinuous prominence, slightly curved dorsally outwards with subdistal lobe. Female gonopore operculate, bluntly triangular in shape, prominent, slightly concave dorsally.

**Colour.**— The colour of fresh specimens is greenish brown in colour (pers. observ.), and all preserved specimens examined are brown in colour.

**Size.**— The largest male specimen documented was 76mm x 72mm (Zhao *et al.*, 1988), and the largest female documented is 67mm x 65mm (Zhao *et al.*, 1988).

**Habitat.**— It can be found in along the banks in freshwater streams, but they migrate down streams to the coastal area for spawning (Zhao *et al.,* 1988; Guo *et al,* 1997) .

**Remarks.**— Milne Edwards (1853) briefly described *E. sinensis* without specifically stating how many specimens he had available. He, however, provided a somewhat schematic figure of a female specimen. In the MNHN is a dried female specimen labeled as "type" which agrees well with H. Milne Edward's figure (including size). As it was possible that H. Milne Edwards had additional material when he described this species, which may not now be extant or has been misplaced, Guo *et al*. (1997) designated a lectotype to stabilize the taxonomy of this species.

The exact provenance of H. Milne Edward's specimen cannot be ascertained. It is known that the collector, M. Callery obtained specimens from around Guangzhou in southern China (see Ng & Dudgeon, 1992), but being a major trading centre then, he could also have obtained specimens from more northern localities. The high food value of *E. sinensis* would probably have resulted in many specimens being sent throughout China even at that time. The area around Guangzhou, from our data, has only one species, *E. hepuensis*, although it is not very common there. In any case, the lectotype of *E. sinensis* is clearly identical to specimens from northern China and not with *E. hepuensis*.

Panning (1938) recognized six forms of *E. sinensis* in his study of the German *E. sinensis*, but provided names to only four of them, viz. *E. sinensis* form *rotundifrons*, *E. sinensis* form *acutifrons*, *E. sinensis* form *trilobata* and *E. sinensis* form *rostrata*. For these four names, descriptions were provided and holotypes and paratypes were designated. His names are therefore nomenclaturally available, and under the current ICZN (1985) rules, Panning's forms can be regarded as valid taxa. There was thus a necessity to examine Panning's (1938) "forms" and see if any of them might be *E. hepuensis*. This is because while it is generally accepted that it was *E. sinensis* which entered Europe, there is every possibility that *E. hepuensis* might also have been introduced and the various forms might be *E. hepuensis* or even the result of hybridization between the two species.

Examination of all of Panning's (1938) specimens shows that they are *E. sinensis* as presently defined. The differences which led Panning (1938) to recognize several forms are entirely in the form of the frontal margin. The examination of these specimens shows that the observed differences are all results of damage and/or anomalous regeneration. We will now comment with each of his forms individually:

*Eriocheir sinensis* form *trilobata* Panning, 1938, is supposedly characterized by its frontal margin having only three blunt teeth. The type shows a distinct uneven thickening of frontal margin on the median tooth when compared to the lateral teeth. This suggests that the median part of the margin (with two teeth) had been damaged and the single median resultant tooth is the consequence of re-growth.

*Eriocheir sinensis* form *rotundifrons* Panning, 1938, is characterized by its wide elliptical frontal margin without any sharp teeth. Examination of the frontal margins of the syntypes showed that there are rudimentary bumps separated by a slight groove in the center and asymmetrical thickening along the frontal margin respectively. This again, is almost certainly the result of post-injury re-growth.

*Eriocheir sinensis* form *acutifrons* Panning, 1938, is characterized by the frontal margin narrowing to a single sharp tooth which is slightly bent downwards at the middle. In all the syntypes examined, the distances between the outer orbital teeth and the 'median frontal tooth' are unequal. The marginal thickening on the frontal tooth is also distinctly asymmetrical. These observations again indicate possible anomalous re-growth.

*Eriocheir sinensis* form *rostrata* Panning, 1933, has the most peculiar frontal features. The frontal margin is almost straight with two distinct outer orbital teeth. Beneath this margin, there is an unevenly depressed pentagonal outgrowth bearing two minute sharp teeth. Examination of the syntypes revealed that there are numerous compression lines between the frontal margin and the protogastric cristae. Obviously, the frontal margins of these specimens had been "squashed" and severely damaged, possibly shortly after post-moult, and the unusual resultant margin was probably the result of uneven growth and repair.

There are two other forms that Panning referred to as "varieties" without giving any formal names. One variety (Variety A) with only one specimen (ZIM-K-24510) has a higher frontal margin with six small teeth. When viewed dorsally, the three teeth on the left are higher and wider than the three on the right, with the teeth all pointing in different directions. The second variety (Variety B) (three specimens, ZIM-K-25234; ZIM-K-25237; ZIM-K-25243) have virtually no teeth on the frontal margin but numerous small bumps are irregularly spaced along the frontal margin. The asymmetry of the frontal margins in both these "varieties" and unevenness in the thickening of the margins are clear indications of anomalous growth after injuries.

Panning (1938) noted that only 26 specimens belonged to the above-mentioned six forms, out of some 45,000 crabs he examined. This occurrence, at only 0.056%, is extremely small. As I have noted, all the various different frontal characters are clearly the result of damage and subsequent repair. Most of the 26 specimens are juveniles with only three specimens (K-24510, variety A; K24847 and K25238, *E. sinensis* form *trilobata*) being sub-adult in sizes. Examination of these specimens show that other than in the anomalous frontal margin features, there are no other characters which can separate them from typical *E. sinensis*. All the adult specimens of mitten crabs I have examined from Europe correspond very well with what is defined as *E. sinensis* here.

Interestingly, about one year after his 1938 paper, Panning stated that "... Now the mitten crab again has its original form without any deviation from the Chinese specimens brought to me recently from Shanghai ..." (Panning, 1939: 111). I have yet to find any of his six forms as yet nor have there been any reports of these after Panning (1938).

This is a commercially valuable species. It has been considered to be a delicacy by East Asians due to its unique flavor. As such, the mass culture of this species started in 1970s (Peng, 1986; Zhao *et al.*, 1988; Li *et al.*, 1993; Y. Cai, pers. comm.). These crabs have been brought from all over in China for aquaculture ventures, including to Guangzhou (Guo *et al.*, 1997), and Korea (S.H. Ko, pers. comm.).

Li *et al.* (1993) argued that *E. sinensis* is also known in Europe and North America due to "... its strong dispersal ability conflicts with supposedly restricted distributions of *E. sinensis* and *E. japonica*" (p. 113). Their argument for the supposedly “strong dispersal abilities” of the larvae of *Eriocheir* is wrong. The presence of *E. sinensis* in Europe is through human intervention (albeit accidentally) (Panning, 1939, Christiansen, 1969), as is believed to be its occurrence in North America (Nepszy & Leach, 1976; Cohen & Carlton, 1997). Panning (1939) mentioned that "Their presence in Germany was probably made possible by larvae brought to Germany on commercial vessels. When the ships happened to fill their ballast water tanks in central or north Chinese ports during the larvae's spawning time, the 1.7mm to 5mm larvae of the mitten crab would, of course, get into the tanks, and again when the tanks were emptied in the German port, the young mitten crabs ... would, of course, get into one of the German rivers emptying into the North Sea" (pp. 363). The introduction of the mitten crabs into the San Francisco Bay of North America was probably similar - "... when the empty ships leave ports in Europe and Asia, ballast water is pumped into them for stability in crossing. This ballast water, which is said to contain some larval stage of the mitten crab, is then pumped back out when they are filled with cargo in the ports of San Francisco Bay" (R.B. Donor & G. Miller, pers. comm.).

In any case, crab larval dispersion is often closely associated with currents of a region. In fact, the notion that larvae are totally at the mercy of currents alone is now generally acknowledged to be simplistic. Studies have shown that larvae are able to adjust their behaviour and depth of occurrence to ensure they return to or near where they hatched (e.g. Cronin & Forward, 1982, 1986; Forward, 1987, 1989 etc.).

Li *et al.*’s (1993) study requires further comment. Their morphological data of 15 character sets based on actual structural differences in the frontal teeth, epibranchial teeth, protogastric crests and male first gonopod were summarized by Principal Component Analysis into a graph. It grouped *E. sinensis* and *E. japonica* into two discrete sets. The morphological data of the "*E japonica hepuensis*" population, however, straddled the *E. sinensis* and *E. japonica* sets. On the basis of this overlap, as well as literature stating that "... the frontal teeth changes with growth of the carapace", Li *et al*. (p. 113) argued that the different populations of *E. sinensis*, *E. japonica* and "*E. japonica hepuensis*" only represented ecophenotypes and are probably conspecific. However, this is not enough to show that the two species are actually conspecific (see Guo *et al*., 1997).

The morphological characters used at present for distinguishing *E. sinensis* and *E. hepuensis* are very consistent. The morphological characters utilized by Li *et al.* (1993) viz. structures of the frontal teeth (acuity and sharpness of the frontal teeth, and depth of the median cleft), epibranchial teeth (strength of the fourth tooth), protogastric crests (height) and the first male gonopod (meristic data from the distal part), represent only part of a suite of morphological differences that distinguish the species. There are other more clear-cut and useful characters like physiognomy (thickness) of the carapace, strength of the epigastric crests, proportions and degree of setation of the various articles of the ambulatory legs and chelipeds, proportions of the overall male gonopod (not just the distal part), structure of the male and female abdomens, female gonopore form, which they did not consider. The statistical analysis (using SAS program) of all these characters on 247 specimens of *E. sinensis*, and 101 specimens of *E. hepuensis* show conclusively that the two species can be segregated easily with the above-mentioned characters (Guo *et al*., 1997: Table 1). Another important point to note here is that morphological analyses of this nature should be carried out using adults. Studies on juveniles of the various *Eriocheir* species show that some of the characters (notably the frontal and epibranchial teeth) are more variable when the specimens are small. My studies have also found that whilst there are certainly ontogenic morphological changes which are allometric, they nevertheless usually occur within fixed ranges. As noted earlier, the variation has even led to the assignment of names to aberrant juveniles of *E. sinensis* in Europe by Panning (1938)! As such, we are still able to separate most of the smaller or sub-adult specimens using the characters specified earlier. The more juvenile specimens pose more problems for identification than the adults but the characters noted above work in almost all cases. In a few cases where some of the characters are not reliable, we are usually able to ascertain that it was because of physical damage, post-damage growth or prior injury.

The data were also grouped into a Principal Component Analysis graph (Graph 1) (see below, Guo *et al.*, 1997) for both sexes in the present study. There is little overlap between the two groups which clearly showed that they are not ecophenotypes and are definitely not ecospecific. The overlap could be due to occasional and accidental mix-up of specimens or from physical damage. I have examined six specimens Lianhuashan, Guangzhou, China (three males, three females), a loan from Dr. Shen Qi, South China Sea Institute of Oceanography, the Chinese Academy of Sciences, which are very likely the preserved specimens from Li *et al.*'s (1993) studies. They were clearly *E. hepuensis*.

There are possibilities that there are already feral populations of *E. sinensis* in southern China due to the current extensive culture of the species. Therefore, the Lianhuasan population could possibly be *E. sinensis*, a mixture of *E. sinensis* sensu stricto and *E. japonica hepuensis*, or even hybrids of the two. In fact, Li *et al.* (1993) commented that genetic variation was greatest for LHS (Lianhuasan), indicating the gene pool may have been "enriched" through seed crabs releases over many years (Li *et al.*, 1993: 113) and "... seed crabs releases have successfully enhanced mitten crab catches in the Zhujiang River ..." (Li *et al*., 1993:114).

Li *et al.* (1993) also cited literature (Peng, 1986; Zhao *et al.*, 1988) stating that *E. japonica* had been successfully hybridized with *E. sinensis* and the resulting animals closely resemble the Zhujiang Mitten Crabs. Existing literature records and large numbers of specimens we have examined of these two species do not support the contention that they can hybridize naturally. There have not been any reports of intermediates or possible hybrids of *E. sinensis* and *E. japonica* in the wild. Zhao (1988) cited Peng's results but no experimental details or results like the ability of the offspring from these hybridizations to perpetuate successfully were given or observed such events in the wild. Peng's (1986) results are also very difficult to interpret. He stated "... according to initial studies, the 'Zhujiang mitten crab' is the offspring of the *E. sinensis* in the Zhujiang river, but not a new species... "(Peng, 1986: 19), but he provided no details, data or any analysis to justify this statement.

The other key characters that can be used to distinguish the three species of *Eriocheir* are listed in Table 2 (see below).

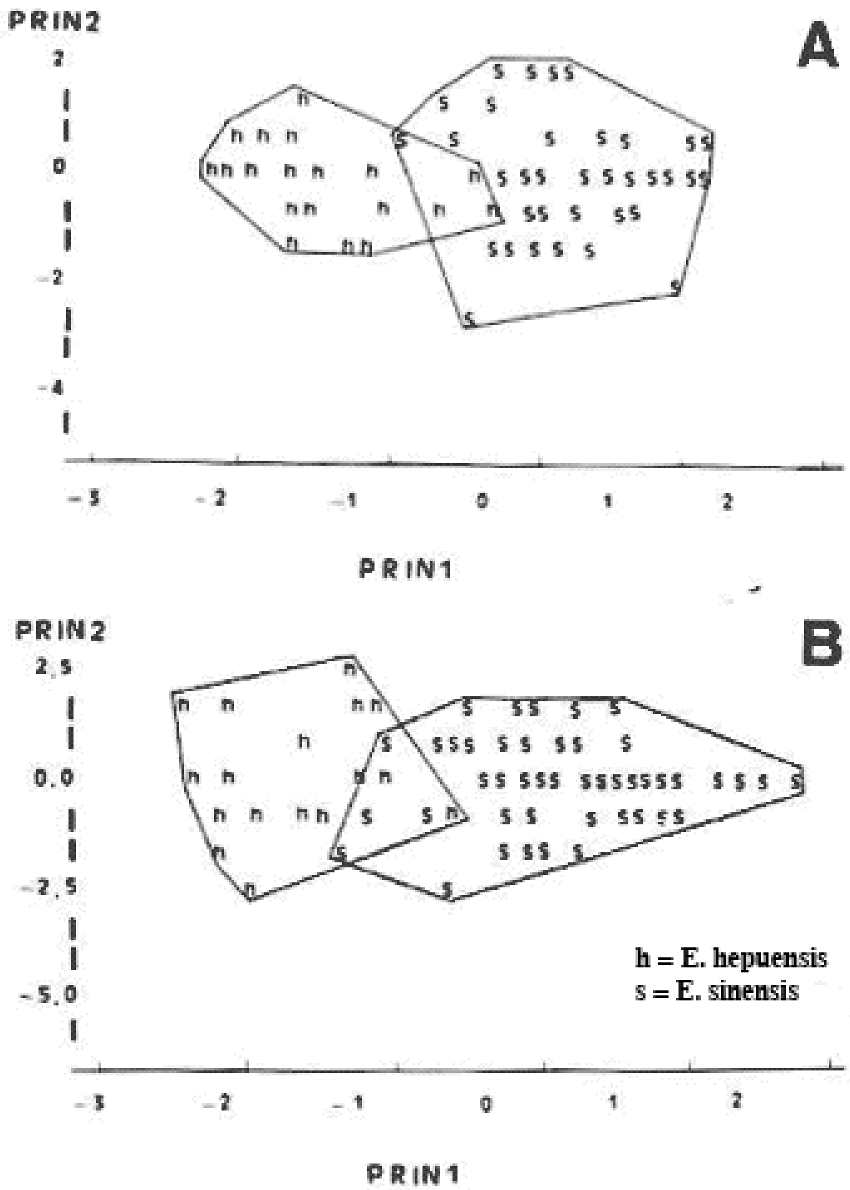



Figure 17. PCA of *Eriocheir sinensis* H. Milne Edwards, 1853, and *Eriocheir hepuensis* Dai, 1991. A) female specimens, and B) male specimens. (After Guo *et al.,* 1997)

**Distribution.**— Naturally, this species is distributed in the river systems along the coastline of northeastern China, Korea. However, it has been introduced into Europe and North America (Guo *et al.,* 1997). Currently, in Europe, it can be found as far south as Portugal, and as far north as Norway. The preliminary COI studies have shown that the current population in Europe was a one-time introduction from northeastern China, but there could have also been a recent introduction from southeastern China. In contrast to the current belief that the population in North America was a one-time introduction from Europe, COI studies have shown that the source of introduction was very likely from mid-western China (G.W. Xu, pers. comm.).

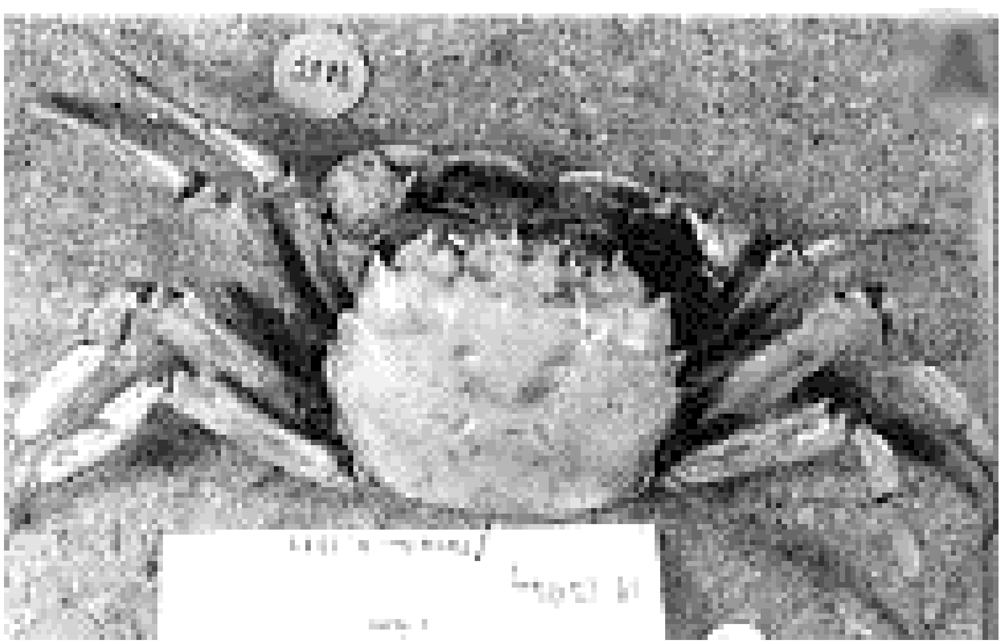


Figure 18. *Eriocheir sinensis* H. Milne Edwards, 1854, lectotype, female (MNHN- B33835). Dorsal view. (After Guo *et al.*, 1997)

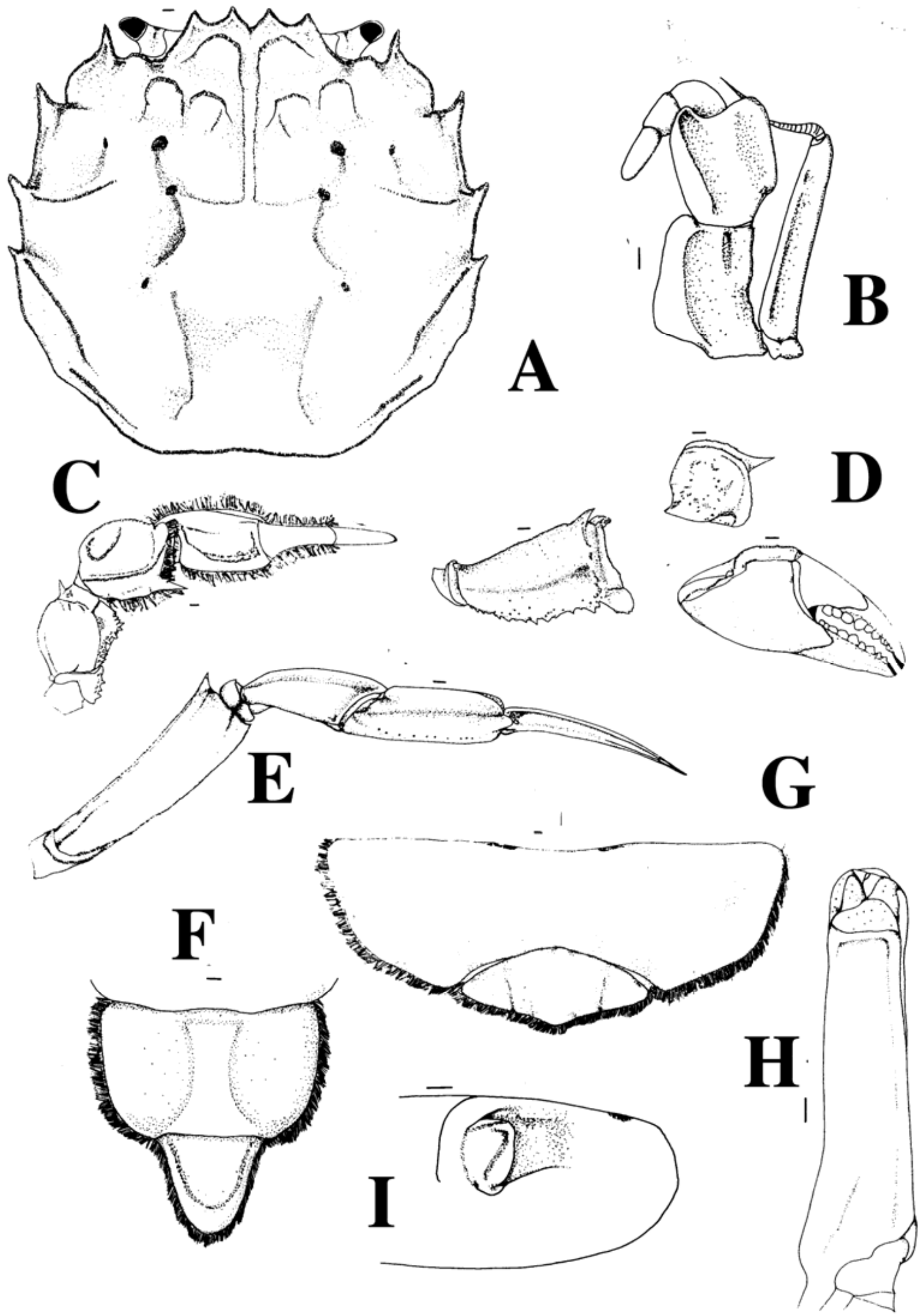



Figure 19. *Eriocheir sinensis* H. Milne Edwards, 1853, male, 53.0mm x 51.0mm (ZRC 1997.558); female, 57.0mm x 53.0mm (ZRC 1997.559). A) carapace; B) third maxilliped; C) dorsal view of cheliped; D) frontal view of cheliped; E) last ambulatory leg; F) male abdomen (part); G) female abdomen (part); H) G1; I) female gonopore. (Scale=1.0mm).

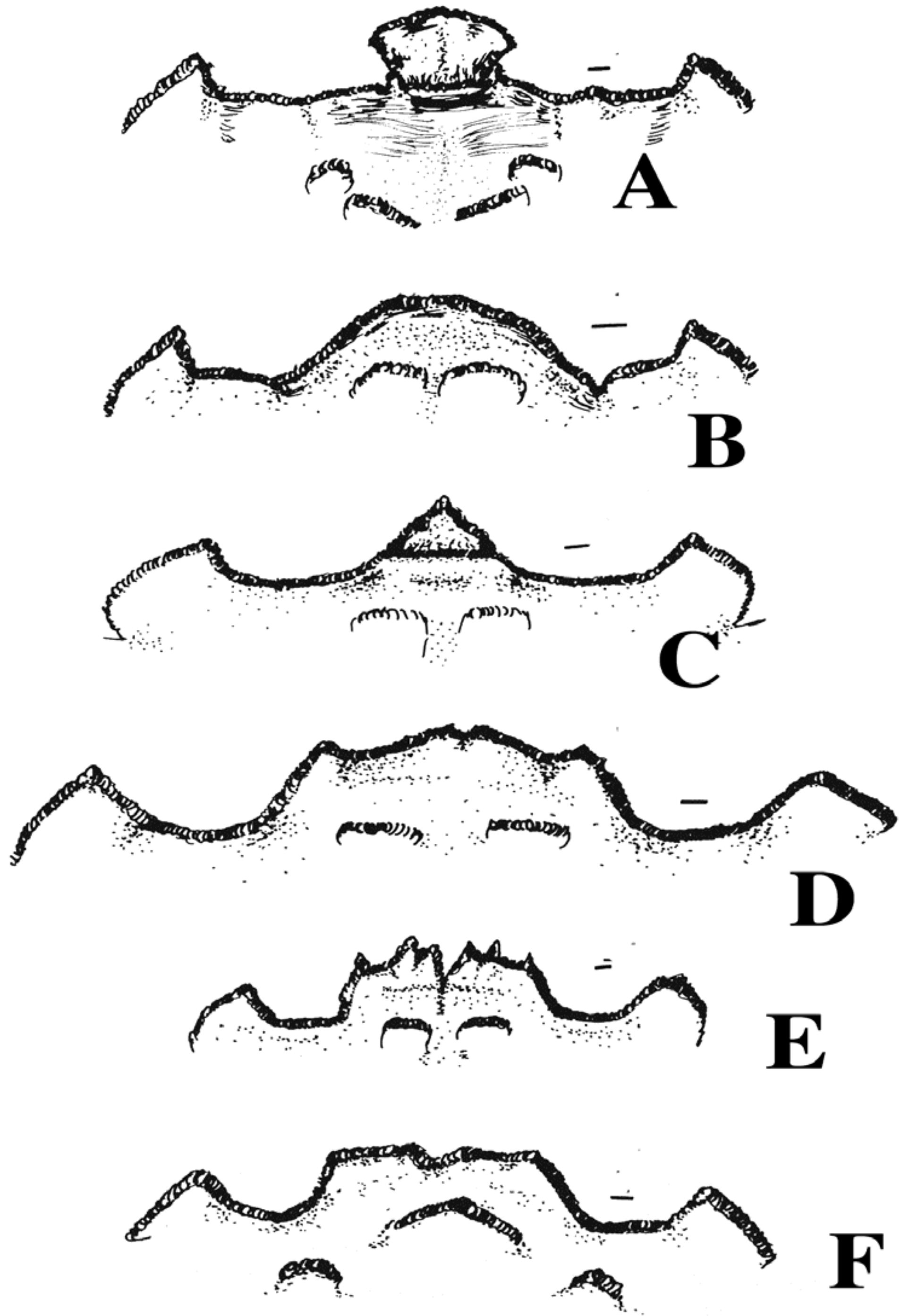



Figure 20. *Eriocheir sinensis* H. Milne Edwards, 1853. Different forms. A) *Eriocheir sinensis* form *rostrata* Panning, 1933; B) *Eriocheir sinensis* form *rotundifrons* Panning, 1938; C) *Eriocheir sinensis* form *acutifrons* Panning, 1938; D) *Eriocheir sinensis* form *trilobata* Panning, 1938) E) *Eriocheir sinensis* variety A (ZIM-K-24510); F) *Eriocheir sinensis* variety B (ZIM-K-25234). (After Guo *et al.*, 1997).

## *Eriocheir hepuensis* Dai, 1991

(Figures 21; 22A-H)

*Eriocheir hepuensis* – Guo *et al*., 1997: 460; Ng *et al*., 1998: 493; Ng *et al*., 1999: 154; Sun *et al*., 2003: 592; Chu *et al*., 2003: 738; Tang *et al*., 2003: 309; Tang *et al*., 2004: 255; Chan *et al*., 2005: 457.

*Eriocheir japonica hepuensis* Dai, 1991: 61, figs 1-11; Dai, 1993: 17.

*Eriocheir sinensis* – Chan, Hung & Yu, 1995: 301 (part), Fig. 3D.

**Material examined.**— In addition to the specimens listed in Guo *et al.,* 1997. – **Holotype** – 1 male (70.2mm x 63.0mm) (ASIZ-GX899024A), Hepu, Guangxi Province, southern China, coll. 18 Nov. 1989. – **Paratypes** – 1 female (68.1mm x 62.7mm) (ASIZ-GX899024B), same data as holotype. – 2 males, 2 female, coll. 20 Dec. 1995; 2 males, 1 female (ASIZ-02662), Hepu, Guangxi Province, China, coll. 19 Nov. 1989; 10 males, 10 females (ASIZ-no cat. number), Gongguan, Guangxi Province, coll. 18 Nov. 1989; 10 males, 10 females (ASIZ-no cat. number), Changluo, Guangxi Province, coll. 19 Nov. 1989. – **Others - CHINA -** 2 males, 5 females (ASIZ-00293), Mawei, Fuzhou, Fujian Province, coll. 14 Oct. 1975; 3 males, 2 females (ASIZ-8514), Fuzhou, Fujian Province; 1 male, 1 female (ASIZ-02587), Haimen, Zhejiang Province, coll. 15 Jul. 1962; 1 male (ASIZ-02641), Guangdong Province, no collection date; 3 males, 1 female (ASIZ-02657), Hepu, Guangxi Province, no collection date; 1 male, 1 female (ASIZ-02664), Beihai, Guangxi Province, coll. Oct. 1978; 3 females (ASIZ-02623), Shantou, Guangdong Province, coll. 19 Mar. 1956; 1 male, 2 females (ASIZ-no cat. number), Hepu, Guangxi Province, coll. Apr. 1989; 1 male, 1 female (ASIZ-02635), Tongtoudao, Zhejiang Province, coll. 2 Jul. 1962; 1 male, 1 female (ASIZ-02663), Beihai, Guangxi Province, coll. Oct. 1978; 1 female (ASIZ-02574), Fujian Province, coll. Aug. 1932; 1 female (ASIZ-02592), Putuo, Zhejiang Province, coll. Jul. 1955; 9 males, 11 females (ASIZ-02570), Xiamen, Fujian Province, coll. Aug. 1928; 1 male, 2 females (BNHM uncatalogued), Chongwen, Fujian Province, coll. S.L. Yang, 20 Nov. 1996; 1 male, 1 female (BNHM-uncatalogued), Nan'ao, Guangdong Province, coll. S.L. Yang, 21 Aug. 1996; 2 males, 2 females (BNHM-J96145), Fuzhou city, Fujian Province, coll. 5 Sep. 1984; 6 males, 4 females (BNHM-J96-141), Nanning, Guangxi Province, coll. 13 Nov. 1994; 1 female (BNHM-J96-002), Tongtou, Zhejinag Province, coll. S.L. Yang & X.M. Sun, 28 Sep. 1996; 6 males, 3 females (BNHM-J580068), Hepu, Guangxi Province; 2 males (BNHM-no cat. number), Tongxing, Guangxi Province, coll. S. L. Yang, 24 Mar. 1992; 16 males, 21 females (ZRC-uncatalogued), Hepu, Guangxi Province, coll. 20 Dec. 1995; 12 males, 9 females (ASIZ-no cat. number), Hepu, Guangxi Province, coll. Nov. 1993; 2 males, 2 females (ASIZ-no cat. number), Hepu, Guangxi Province; 12 males, 11 females (ASIZ-uncatalogued), Hepu, Guangxi Province, coll. 17 Mar. 1992; 5 males, 5 females (ASIZ-no cat. number), Changle, Guangxi Province, coll. 18 Nov. 1989; 14 females (ASIZ-no cat. number), Gongguan, Guangxi Province, coll. 18 Nov. 1989; 4 males, 3 females (ASIZ-no cat. number), Hepu, Guangxi Province, coll. 26 Oct. 1993; 1 male, 4 females (ASIZ-no cat. number), Hepu, Guangxi Province, coll. 19 Nov. 1989; 3 females (BNHM-no cat. number), coll. Guangxi Fisheries Institute, 18 Nov. 1994; 7 males, 4 females (ASIZ-no cat. number), 16 males, 13 females (ASIZ-no cat. number), Hepu, Guangxi Province, coll. Nov. 1994; 28 males, 1 female (ASIZ-no cat. number), Gongguan, Hepu, Guangxi Province; 58 males, 43 females (ZRC 1997.560), Hepu, Guangxi Province, coll. 10 Dec. 1995; 5 males, 5 females (ZRC 1997.561), Hepu, Guangxi Province, coll. Oct. 1996; 3 males, 3 females (SCSIO-uncatalogued), Lianhuashan,Guangzhou, China, no collection date.

**Diagnosis.**— Carapace rectangular, overall dorsal surface convex, regions well-defined. Frontal margin with four sharp teeth. Anterolateral margins with four teeth including exorbital tooth. Third maxilliped very broad; ischium, merus broad, exopod narrow. Ambulatory legs also slender, long, long thick setae on anterior, posterior surfaces of carpi, propodi. G1 long, slender, distal margin narrowly rounded, sloping shoulder shaped when viewed laterally, short, chitinuous prominence, slightly curved dorsally outwards with subdistal lobe. Female gonopore operculate, bluntly triangular in shape, prominent, slightly concave dorsally.

**Colour.**— The colour of fresh specimens is greenish brown to dark brown in colour, and all the preserved specimens examined are brown in colour. Fishermen from the type locality of this species can recognize two fresh colour forms. The dark green-colour form purportedly comes from across the border in northern Vietnam, while the brownish-colour form is from southern China.

**Size.**— The largest male specimen examined is 70.2mm x 63.0mm (holotype), and the largest female specimen examined is 68.1mm x 62.7mm (paratype).

**Habitat.**— It can be found  along the banks in freshwater streams, but they migrate down streams to the coastal area for spawning (A. Dai., pers. comm.).

**Remarks.**— The morphological differences between *E. sinensis* and *E. hepuensis* summarized in Table 1.

There are no detailed reports or studies to show the actual distribution of the three species. Our examination of the available but limited specimens have so far indicated that *E. sinensis* is found mainly in northeastern China while *E. hepuensis* is in southern China and *E. japonica* mostly in southeastern China and west coast of Taiwan. However, no wild hybrids or intermediate forms have been reported or found among these specimens examined.

This species is commonly found along the southwestern coast of China. My examination of numerous '*E. japonica*' specimens collected between 1930-1970 from southern China especially in locations like Fujian Province and Guangzhou Province has shown that many of these "*E. japonica*" specimens are actually *E. hepuensis*, indicating that *E. hepuensis* already existed in this area well before the introduction of *E. sinensis* in 1973.

Studies on larval development (Ng *et al.*, 1998) have shown that the temperature requirement for growth of *E. hepuensis* is very different from that of *Eriocher sinensis*. The growth rate of *E. hepuensis* is the highest when the water temperature is between 23-28˚C (unpublished data).

In early 2006, *E. hepuensis* has been spotted in the wild in one of the rivers in Kuwait, and the author has examined photographs of these specimens (M. Apel, pers. comm.).

**Distribution.**— Southern China, Kuwait.

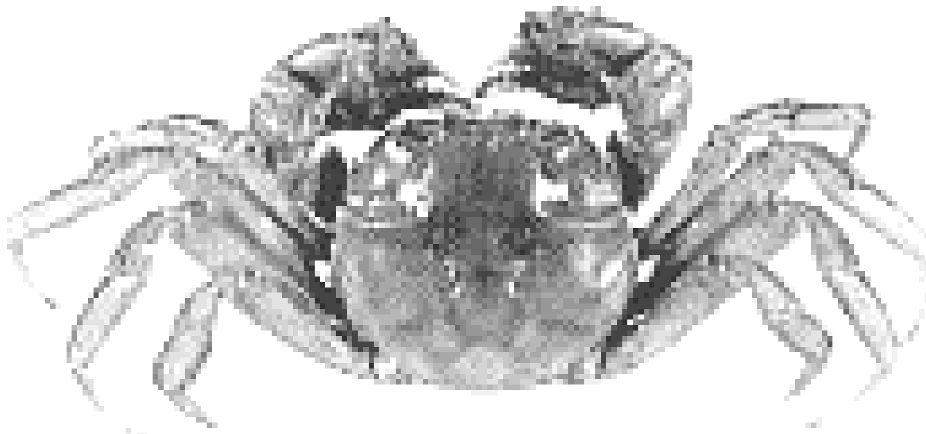


Figure 21. *Eriocheir hepuensis* Dai, 1993, male, holotype, 70.2mm x 63.0mm (ASIZ-GX899024A). Dorsal view (After Guo *et al.*, 1997).

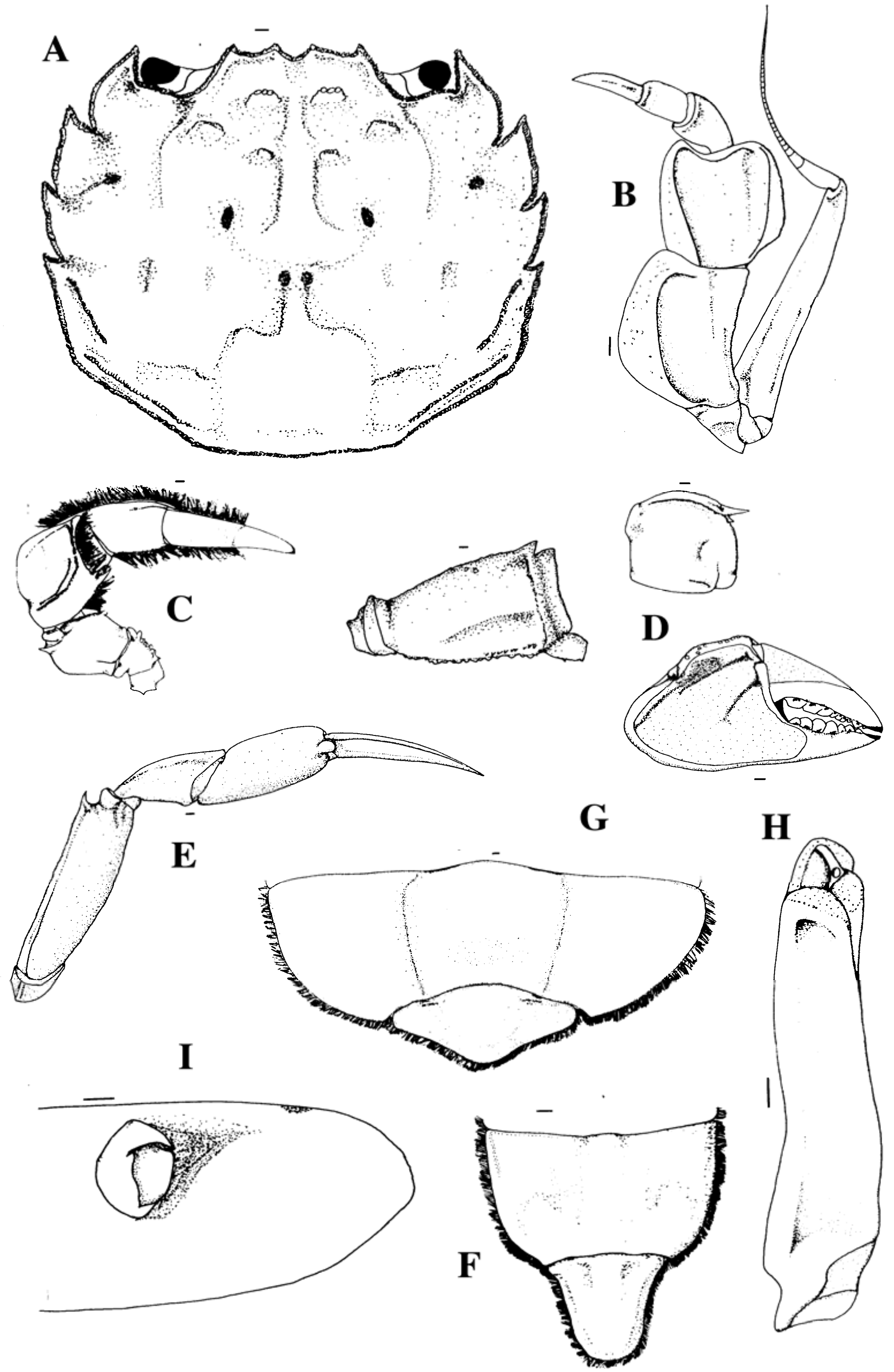



Figure 22. *Eriocheir hepuensis* Dai, 1993, male, holotype, 70.2mm x 63.0mm (ASIZ-GX899024A); female, paratype, 68.1mm x 62.7mm (ASIZ-GX899024B). A) carapace; B) third maxilliped; C) dorsal view of chela; D) frontal view of chela; E) last ambulatory leg; F) male abdomen (part); G) female abdomen (part); H) G1; I) female gonopore. (Scale=1.0mm).

## *Eriocheir ogasawaraensis* Komai, in Komai, Yamasaki, Kobayashi, Yamamoto & Watanabe, 2006

(Figures 23A-F; 24A-G)

*Eriocheir ogasawaraensis* Komai, in Komai, Yamasaki, Kobayashi, Yamamoto & Watanabe, 2006: 1.

*Eriocheir japonica* – Miyake, 1970: 1982: 174 (part); Takeda & Miyake, 1976: 112; Muraoka, 1998: 52 (not *Eriocheir japonica* De Haan, 1835).

**Material examined.**— 1 male (70.5 mm x 60.5mm), 1 female (ovigerous) (90.2mm x 76.2mm), (NTOU-uncatalogued), same data as CBM-ZC8504); 1 female (80.7mm x 68.8mm), (NTOU-uncatalogued), Okumura River, Chichi-jima Island, Japan; 1 male (37.0mm x 32.0mm) (SFM-20421), Ogasawara Islands, Japan, leg. Okamura, 1971.

**Diagnosis.**— Carapace rectangular, overall dorsal surface only very slightly convex, regions well-defined. Anterolateral margins with three teeth including exorbital tooth. Third maxilliped very broad; ischium, merus broad, exopod narrow. Chelipeds setose. Ambulatory legs also slender, long thick setae on anterior, posterior surface of carpus, propodus. G1 relatively slender, ventral surface shallowly sulcate medially; lateral surface with distinct concavity proximal to base of terminal process; terminal process short, rounded, with dense, short, stiff setae obscuring subterminal lobe and distal chitinous prominence; lateral surface of terminal process deeply concave; disto-lateral margin shallowly concave; distal chitinous prominence very short; genital pore subterminal. Female gonopore conspicuous, subconical operculum directed mesially, basally demarcated by broad chitinous suture.

**Colour.**— The colour of fresh specimens is dark brown, with occasional dark purple tinge (Komai *et al*., 2006), and all preserved specimens examined are dark brown in colour.

**Size.**— This species is a relatively large animal. The largest male specimen recorded is 90.2 mm x 76.2mm, and the largest female reported is 95.9mm x 81.0mm in female (see Komai *et al.*, 2006).

**Habitat.**— Young crabs were found to grow in the underwater environment in the freshwater streams or lakes and migrate downstream to the tidal area after attaining maturity. They often appear in the terrestrial environment when migrating seaward. Adult crabs are found in rather wide range of habitats, from estuarine river mouth to the open sea and coastal area (see Komai *et al.*, 2006)

**Remarks.**— This species is only reported from Ogasawara Islands, Japan. *Eriocheir ogasawaraensis* closely resembles *E. japonica* but it can be discerned from the latter in having a) a relatively broader carapace (vs. less broad carapace in *E. japonica*); b) absence of the fourth anterolateral tooth on the carapace (vs. presence of fourth teeth in *E. japonica*); c) relatively large size of reproductive individuals (vs. smaller size in *E. japonica*), and d) relatively large chela without any setae on the ventral surface in both adult males and adult females (vs. presence of setae in *E. japonica*). A detailed description and discussion of the taxa has been provided by Komai *et al.* (2006).

**Distribution.**— Japan (Ogasawara Islands) only

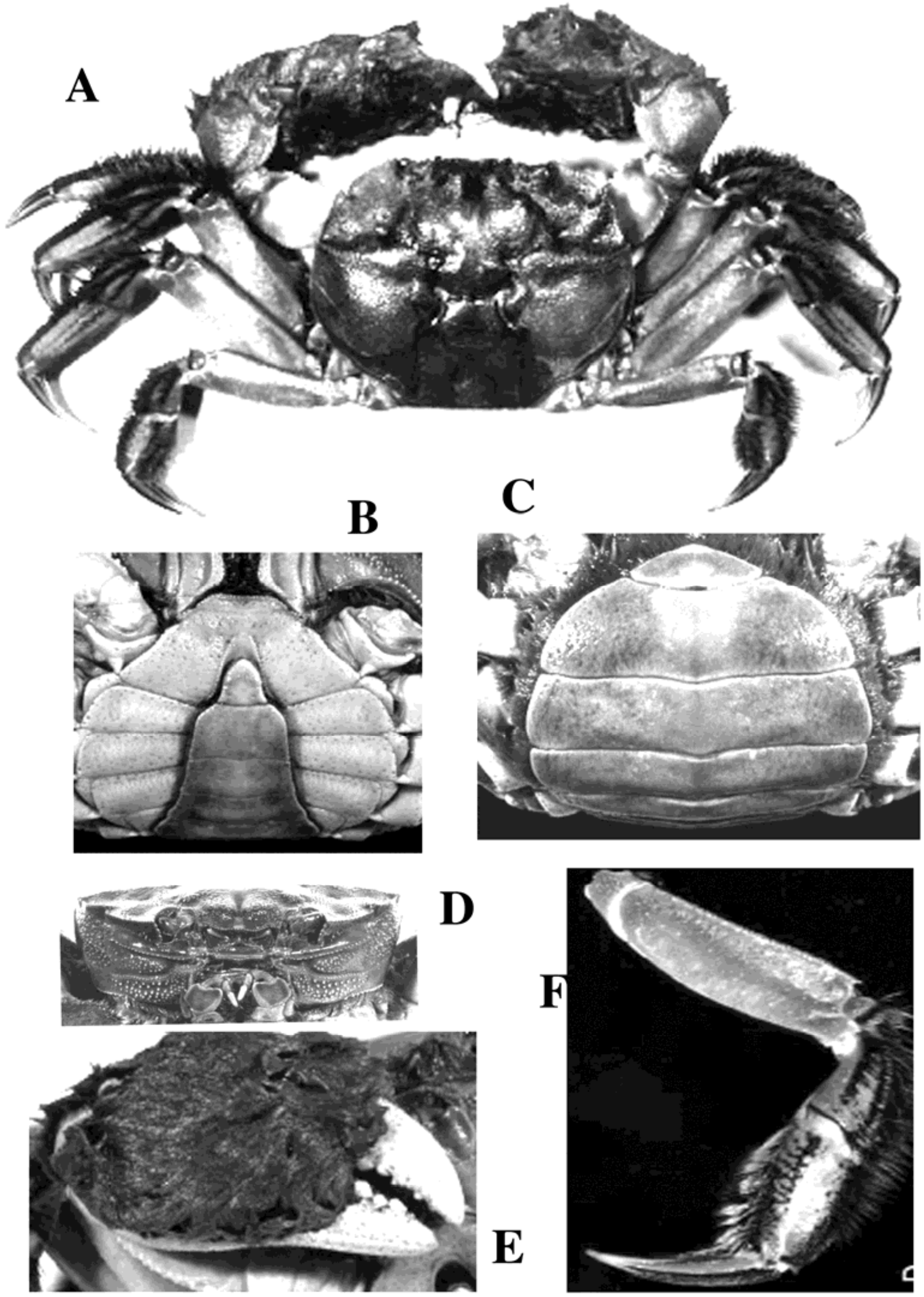



Figure 23. *Eriocheir ogasawaraensis* Komai 2006, male, 70.5 mm x 60.5mm (NTOU-uncatalogued); 1 female, ovigerous, 90.2mm x 76.2mm (NTOU-uncatalogued,; A) dorsal view; B) ventral male of male; C) ventral view of female; D) frontal view of male; E) frontal view of male cheliped; F) fourth ambulatory of male. (After Komai *et al.*, 2006).

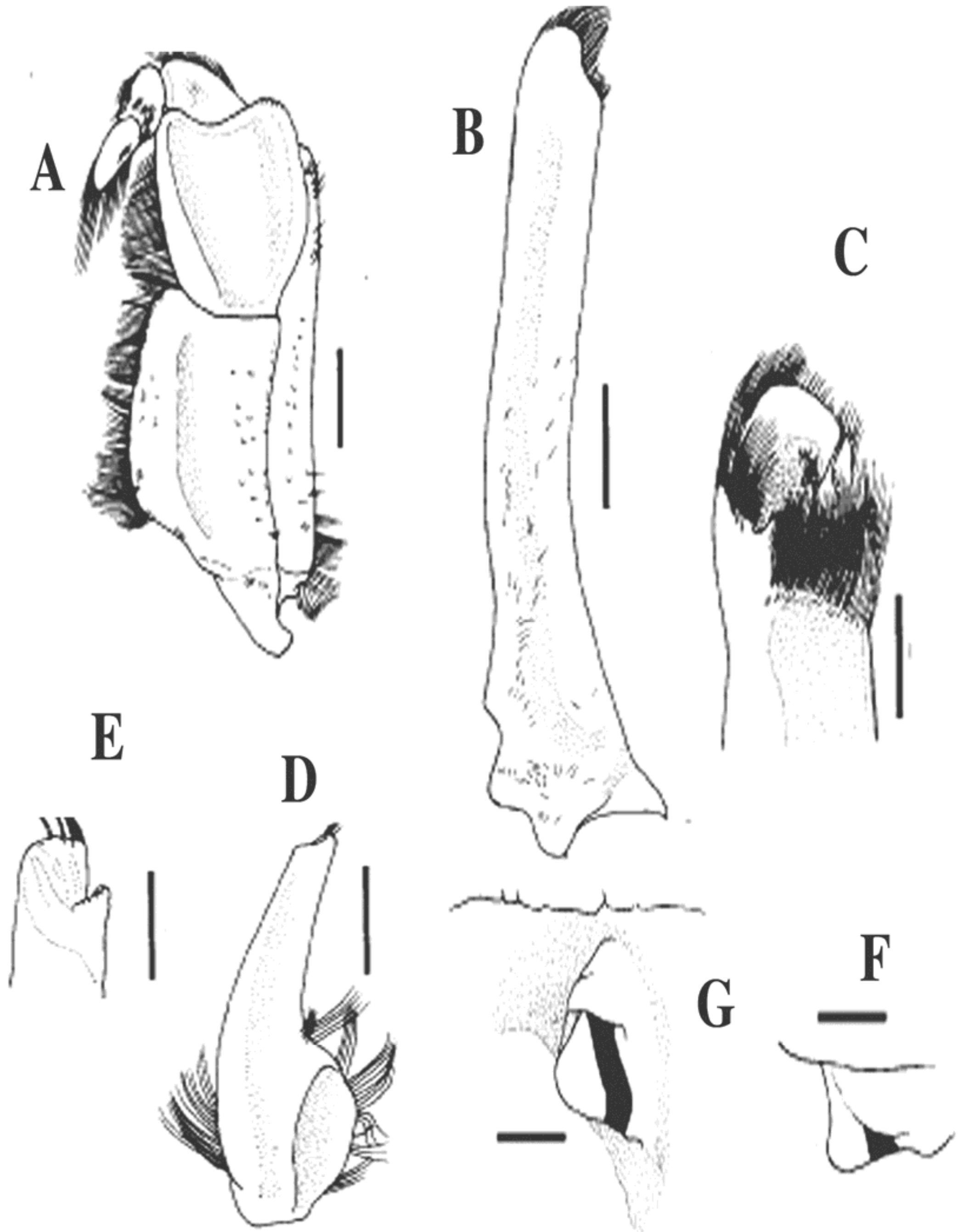



Figure 24. *Eriocheir ogasawaraensis* Komai, 2006, male, 70.5 mm x 60.5mm (NTOU-uncatalogued); 1 female, ovigerous, 90.2mm x 76.2mm (NTOU-uncatalogued,; A) third maxilliped; B) G1; C) tip of G1; D) G2; E) tip of G2; F) female gonopore; G) detailed female gonopore. (Scale=1.0mm). (After Komai *et al.*, 2006).

## Genus *Hemigrapsus* Dana, 1852

*Hemigrapsus* – Dana, 1852: 348; 1852: 247, 250; Rathbun, 1903: 839; 1918: 264; 1929: 87; Tesch, 1918: 105 (footnote); 1929: 87; Yokoya, 1928: 780, text-fig. 8; Sakai, 1936: 228; 1939: 647; 1965: 198; 1976: 630, pl. 222: 2, 649; Horikawa, 1940: 29; Lin, 1949: 29; Edmondson, 1959: 181; Wu *et al.*, 1962: 20; Creel, 1964: 236; Kim, 1973: 471; Miyake, 1983: 175; Dai *et al.*, 1986: 478, fig. 269: 2–3, pl. 67: 5; Fukui *et al*., 1989: 229; Dai & Yang, 1991: 525, fig. 269: 2–3, pl. 67: 5; Manuel *et al.*, 1991: 91; Shih *et al.*, 1991: 142; Wang & Liu, 1996a: 112, figs. 142, 143; Wang & Liu, 1996b: 84; Wang & Liu, 1996c: 227; Ho & Hung, 1997: 91; Jeng *et al.*, 1998: 58; Jeng *et al.*, 1998: 123; Ng *et al.*, 2001: 45, 53; McLay & Schubart, 2004: 695; Asakura & Watanabe, 2005: 279; Asakura, 2006: 33

*Lobograpsus* A. Milne Edwards, 1869: 173.

**Type species.**— *Hemigrapsus crassimanus* Dana, 1852, designation by Rathbun (1918).

**Gender.**— Masculine.

**Diagnosis.**— Carapace quadrangular, broader than long; dorsal surface punctate; regions well defined, convex. Frontal margin slightly convex, straight to bilobed. Anterolateral margin subcristate with three teeth including exorbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod narrow with short flagellum. Epistome broad, flat, posterior margin entire. Inner surface of chela with granules; sometimes a patch of soft, short setae on inner surface or outer surface or both; sometimes chela glabrous, with pulvinus at base of fingers. Ambulatory legs with or without short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen narrowly triangular with all segments freely moveable (six somites plus telson). G1 usually long, stout. Female gonopore operculate, circular in shape.

**Remarks.**— The genus, *Hemigrapsus* was established by Dana (1852) to include part of H. Milne Edwards's (1837) *Cyclograpsus.* It also contains part of De Haan's (1833) *Grapsus* (Dana, 1852: 348) (see above Remarks on family Varunidae).

The type species, *H. crassimanus*, was described by Dana in 1852 based on several specimens that were supposedly collected from the Sandwich Islands, which is today known as Hawaii. There is no other specimen or report on *H. crassimanus* since its original description. Rathbun (1918) designated *H. crassimanus* Dana, 1852, to be the type species of the genus *Hemigrapsus* without any discussion. She had not indicated if she had seen Dana's specimens or re-appraised the genus.

Dana's (1852) specimens are no longer extant except for four juvenile female specimens of *Hemigrapsus crassimanus* (USNM-2400) in the Smithsonian Institution (C.D. Schubart, pers. comm.). I could not examine these specimens in person as they had been loaned out to C. D. Schubart who did not make them available to me for this study. The lot is labeled as syntypes, but there is no other information on these four specimens. It seems likely that these four specimens are indeed the type specimens of Dana as they match his measurements and figures reasonably well. Even if they are, female specimens of *Hemigrapsus* are all very similar each other, rendering them almost useless for modern taxonomic studies. Thus, the true identity of this species cannot be ascertained as fresh material cannot be obtained from the Hawaii islands. Edmondson, who had numerous publications on the crustacean fauna of Hawaii, had never seen *Hemigrapsus crassimanus*. He had merely cited Dana's publications in his 1959's publication, but he had not seen or collected any *H. crassimanus* in Hawaii himself. Dr. L. Eldredge's recent publications on the faunistic studies of Hawaii have not reported any *H. crassimanus* as well. I have tried to obtain specimens from Hawaii Islands many times through my friends, through my supervisor's colleagues in Hawaii or when my supervisor and colleagues go to Hawaii for field trips, they had searched through Hawaii with Eldredge and colleagues from the Bishop Museum as well as Fish and Wildlife Service. They have never seen the species or for that matter, any *Hemigrapsus* species from there. Discussions with the staff in Hawaii, notably with L. Eldredge, indicate that Dana's record of *H. crassimanus* from the islands is almost certainly erroneous. Considering the habits and habitat preferred by *Hemigrapsus* species, it is extremely unlikely that any species was missed through decades of intensive collections, notably by C. H. Edmondson. It would not be the only erroneous record. Dana's expedition took him through many areas, including along the east coast of the U.S. mainland where *Hemigrapsus* species abound. There is precedence. Just recently Emparanza *et al*. (2007) showed that the enigmatic spider crab *Acanthocyclus simplex* Dana, 1852, a species never seen since it was described, again ostensibly from Hawaii, was almost certainly actually a junior synonym of *A. sexdentatus* H. Milne Edwards from Chile! Again, the species has caused a good deal of confusion as members of this genus are typical shallow water crabs associated with algae and easily encountered wherever they are actually present (Emparanza *et al*., 2007).

It is probable that *H. crassimanus* never existed in Hawaii. The *H. crassimanus* specimens examined by Dana are likely to have been collected from mainland United States, and somehow got mixed up with his Hawaiian collections. Also, the *H. crassimanus* species he examined is 6.75 lines in carapace length and 6.25 lines in carapace length (Dana, 1852), which is relatively small, and it is possible that it is only a juvenile specimen of *H. oregonensis* or *H. nudus,* both these species being very common along the east coast.

Dana (1852) provided a fairly detailed description of a male, and provided figures of the overall animal, third maxillipeds, an ambulatory leg and the male abdomen. He did not state the total number of male or female specimens he examined. Based on Dana's descriptions and figures, *H. crassimanus* is very closely allied to *H. oregonensis* (Dana, 1852) in having a defined carapace with three broad anterolateral teeth; a narrow male abdomen, as well as possessing stout and broad ambulatory legs, especially if the specimens have lost their setae. In fact, juvenile specimens of *H. oregonensis* fit Dana's description and figures very well!

In order to preserve the stability of the genus, it is important that the identity of *H. crassimanus* be resolved. However, this can only be done until I have a chance to see the female gonopore structure of the four contentious specimens in question. Currently, these four specimens are on loan to Dr. C.D. Schubart who has provided me with a photograph of one of the syntype specimen (see below). If they are really "unidentifiable" and useless for modern taxonomic studies, then an application will need to be made to the International Commission for Zoological Nomenclature to have the type material suppressed. In such a case, the most parsimonious solution may well be to select the holotype of *H. oregonensis* Dana, 1852, and make it the simultaneous neotype of *H. crassimanus* Dana, 1852. As both *H. crassimanus* and *H. oregonensis* were published by Dana (1852) in the same publication, the first reviser has the right to select the name to have precedence; which logically should be *H. crassimanus* Dana, 1852, as it is the type species of the genus.

One species, *Hemigrapsus affinis* Dana, 1852, has been transferred to *Cyrtograpsus* Dana, 1852, by Boschi (1964). *Hemigrapsus lobulatus* Manuel, Gonzales & Basmayor, 1991, was recently referred to its own genus, *Noarograpsus*, by Ng *et al.* (2006). *Hemigrapsus sinensis* Rathbun, 1929, *Hemigrapsus longitarsis* (Miers, 1879), and *Hemigrapsus spinosus* (H. Milne Edwards, 1853) have been separated into their own genera in this report (see below).

With the current restricted definition of *Hemigrapsus*, there are now 10 species in this genus viz. *H. crassimanus* Dana, 1852 (type species); *H. oregonensis* Dana, 1852; *H. sexdentatus* (Risso, 1827); *H. crenulatus* (H. Milne Edwards, 1837); *H. pallipes* (H. Milne Edwards, 1837); *H. nudus* (Dana, 1852); *H. penicillatus* de Haan, 1835; *H. sanguineus* (de Haan, 1835); *H. takanoi* Asakura & Watanabe, 2005, and *H. estellinensis* Creel, 1964.

**Key to species in *Hemigrapsus***

1a. Carapace high. Anterolateral teeth wide. Chela surface glabrous. -------------- **2**

1b. Carapace low. Anterolateral teeth acute. Chela surface setose. ----------------- **5**

2a. Chelae surface smooth, without any ridge. ----------------------------------------- **3**

2b. Chelae with four ridges on outer surface of cheliped. ------------------ ***H. pallipes***

3a. Chelipeds with distinct pulvinus at base of fingers. ------------------------------- **4**

3b. Chelipeds without pulvinus, no setae on inner surface (Dana's drawing). -------------- ------------------------------------------------------------------------------- ***H. crassimanus***

4a. Infra orbital ridge of male with three rounded granules followed by numerous smaller rounded granules. ---------------------------------------------- ***H. sexdentatus***

4b. Infra orbital ridge of male with five to six striated granules and three smaller striated granules. ---------------------------------------------------------------- ***H. sanguineus***

5a. Chelipeds with short, soft setae on inner and outer surfaces. ----------------------- **6**

5b. Chelipeds with short, soft setae on inner surface only. ------------------------------ **7**

6a. Infra-orbital ridge of male with raised elongated tubercules with rounded granules medially, followed by two smaller tubercules. ----------------------- ***H. takanoi***

6b. Infra-orbital ridge of male with raised elongated tubercules with rounded granules proximally, followed by three smaller tubercules. ----------------- ***H. penicillatus***

7a. Infra-orbital ridge of male with three to four granules. Ambulatory legs setose. --- **8**

7b. Infra-orbital ridge of male with more than five granules. Ambulatory legs glabrous. - ------------------------------------------------------------------------------------------- **9**

8a. Ambulatory legs densely setose. Granules on infra-orbital ridge of male elongated. ------------------------------------------------------------------------------ ***H. oregonensis***

8b. Ambulatory legs less densely setose. Granules on infra-orbital ridge of male dentiform. ---------------------------------------------------------------------- ***H. crenulatus***

9a. Infra-orbital ridge of male with five or six slightly elongated smooth granules. ------------------------------------------------------------------------------------- ***H. estelleinensis***

9b. Infra-orbital ridge of male with 15 isomorphic round granules. --------- ***H. nudus***

## *Hemigrapsus crassimanus* Dana, 1852

(Figure 25)

*Hemigrapsus crassimanus* Dana, 1852: 250; 1852: 349, pl. 22, fig. 4; Rathbun, 1903: 839; Rathbun, 1918: 264; Tesch, 1918: 105 (footnote); Rathbun, 1929: 87; Edmondson, 1959: 181; McLay & Schubart, 2004: 695.

**Material examined.**— **Syntypes** – 4 females (USNM), supposedly Hawaii, no collection date.

**Diagnosis.**— Carapace subquadrate, broader than long, surface covered with fine granules and spots. Anterolateral margin with three teeth including orbital tooth. Infraorbital ridge with three or four elongated tubercules with small granules before and after, female with numerous isomorphic granules. Chelipeds large in male, a patch of short, soft setae on the inner surface of chelipeds, absent in females. Ambulatory legs setose, short, flat, with a small subdistal spine on anterior margin of merus. G1 stout. Female gonopore operculate, with circular in shape.

**Colour.**— Not known.

**Size.**— Not known.

**Habitat.**— Not known.

**Remarks.**— The problems with this species and *H. oregonensis* Dana, 1852, have been discussed in detail earlier under the genus.

**Distribution.**— Hawaii with doubt (See Emparanza *et al*., 2007)

Figure 25. *Hemigrapsus crassimanus* Dana, 1852, female, syntype (Courtesy of C.D. Schubart).

***Hemigrapsus oregonensis* (Dana, 1852)**

(Figures 26A-C; 27A-H)

*Pseudograpsus oregonensis* Dana, 1852: 248; 1852: 334; 1855: 20, fig. 6a-b (atlas).

*Hemigrapsus oregonensis* – Rathbun, 1900: 587; 1918: 270, pl. 70.

*Brachynotus oregonensis* – Holmes, 1900: 82.

**Material examined.**— ***Hemigrapsus oregonensis*** – **Holotype** – 1 male (25.0mm x 22.0mm) (USNM-2333), Puget Sound, Washington State, USA, coll. J.D. Dana, U.S. Exploration Expedition. – **Others** – 1 male (RMNH-D199), California, coll. Dana, 1878; 8 males (12.5-26.3mm x 10.2-22.0mm), 2 females (13.1-16.5mm x 11.1-13.7mm) (RMNH-uncat.), west coast bay, Roche Harbour, San Juan Island, Washington State, U.S.A., coll. L.B. Holthuis, 4 Aug. 1960; 8 males (12.1-22.7mm x 10.3-19.6mm), 7 females (14.2-18.4mm x 12.0-15.3mm) (RMNH-D15642), west coast bay, Roche Harbour, San Juan Island, Washington State, U.S.A., coll. L.B. Holthuis, 7 Aug. 1960; 1 male (14.6mm x 12.7mm), 1 female (ovigerous) (13.3mm x 11.8mm) (RMNH-D24286), Neah Bay, 5 mile east of Cape Flattory, Juan de Fuca Strait, Washington State, U.S,A,, coll. P.A. McLaughlin, 4 Jun. 1964; 1 female (15.8mm x 13.2mm) (RMNH-D24285), San Juan County, San Juan Island, Washington State, U.S.A., coll. P.A. McLaughlin, Aug. 1961; 4 males (9.9-19.6mm x 8.2-17.3mm), 4 females (11.6-15.9mm x 10.0-13.7mm) (RMNH-D24284), Monteret Bay, California, U.S.A., coll. P.A. McLauglin, 1 Jun. 1965; 1 female (ovigerous) (10.2mm x 9.1mm) (RMNH-D9743), Gulf of California, Mexico, coll. H. ten Kate, 1883; 1 female (14.1mm x 12.5mm) (RMNH-D-9742), Guaymas, Gulf of California, Mexico, under stones, coll. M. Cardenas, 20 May 1945; 2 males (13.1-15.4mm x 11.3-13.2mm), 1 female (13.4mm x 11.0mm) (RMNH-D9741), Mitchell Bay, northwest coast of San Juan Island, Washington State, U.S.A., under stones, coll. L.B. Holthuis, 25 Jul. 1952; 4 males (6.8-21.4mm x 5.8-18.3mm) (RMNH-D9740), Culvers Point, near Friday Habour, San Juan Island, Washington State, U.S.A., coll. L.B. Holthuis, 22 Jul. 1952; 4 males (14.1-18.1mm x 12.2-15.8mm) (RMNH-D7479), Gonalex Point, Victoria, British Columbia, Canada, coll. L.B. Holthuis, 5 Aug. 1947.

**Diagnosis.**— Carapace subquadrate, broader than long, surface covered with fine granules and spots. Anterolateral margin with three teeth including orbital tooth. Infraorbital ridge with three or four elongated tubercules with small granules before and after, female with numerous isomorphic granules. Chelipeds large in male, a patch of short, soft setae on the inner surface of chelipeds, absent in females. Ambulatory legs setose, short, flat, with a small subdistal spine on anterior margin of merus. G1 stout. Female gonopore operculate, circular in shape.

**Colour.**— The colour of live specimens can vary from dull grey to dark purplish spots on brown carapace (P.A. McLaughlin, pers. comm.), and all preserved specimens examined were brown in colour.

**Size.**— The largest male specimen examined is 26.3mm x 22.0mm (RMNH-uncatalogued) and largest female examined is 18.4mm x 15.3mm (RMNH-D15642).

**Habitat.**— It can be found on open mud flats, algal mats and eelgrass beds, in bays and estuaries and on open beaches where there is plenty of fine sediment (P.A. McLaughlin, pers. comm.).

**Remarks.**— *Hemigrapsus oregonensis* is very similar to *H. pencillatus* and *H. takanoi* in overall morphology, but it can be easily differentiated from the latter two species by a) having a carapace with different regions well-defined (vs. carapace with different regions less defined in *H. pencillatus* and *H. takanoi*); b) the broad anterolateral teeth on the carapace (vs. acute anterolateral teeth in in *H. pencillatus* and *H. takanoi*); c) the presence of setae only on the inner surface of the chelipeds in males (vs. setae present on outer and inner surfaces in *H. penicillatus* and *H. takanoi* in males); d) the vaulted anterolateral margin (vs. a non-vaulted anterolateral margin in *H. pencillatus* and *H. takanoi*), and e) the absence of purple coloured spots in fresh specimens (vs. presence of purple spots in *H. pencillatus* and *H. takanoi*).

*Hemigrapsus oregonensis* apparently prefers areas with fine sediments, unlike most of its congeners. This species has never been reported outside North America.

**Distribution.**— West coast of United States of America (Resurrection Bay, Alaska to Bahia de Todos Santos, Baja California) and Mexico.

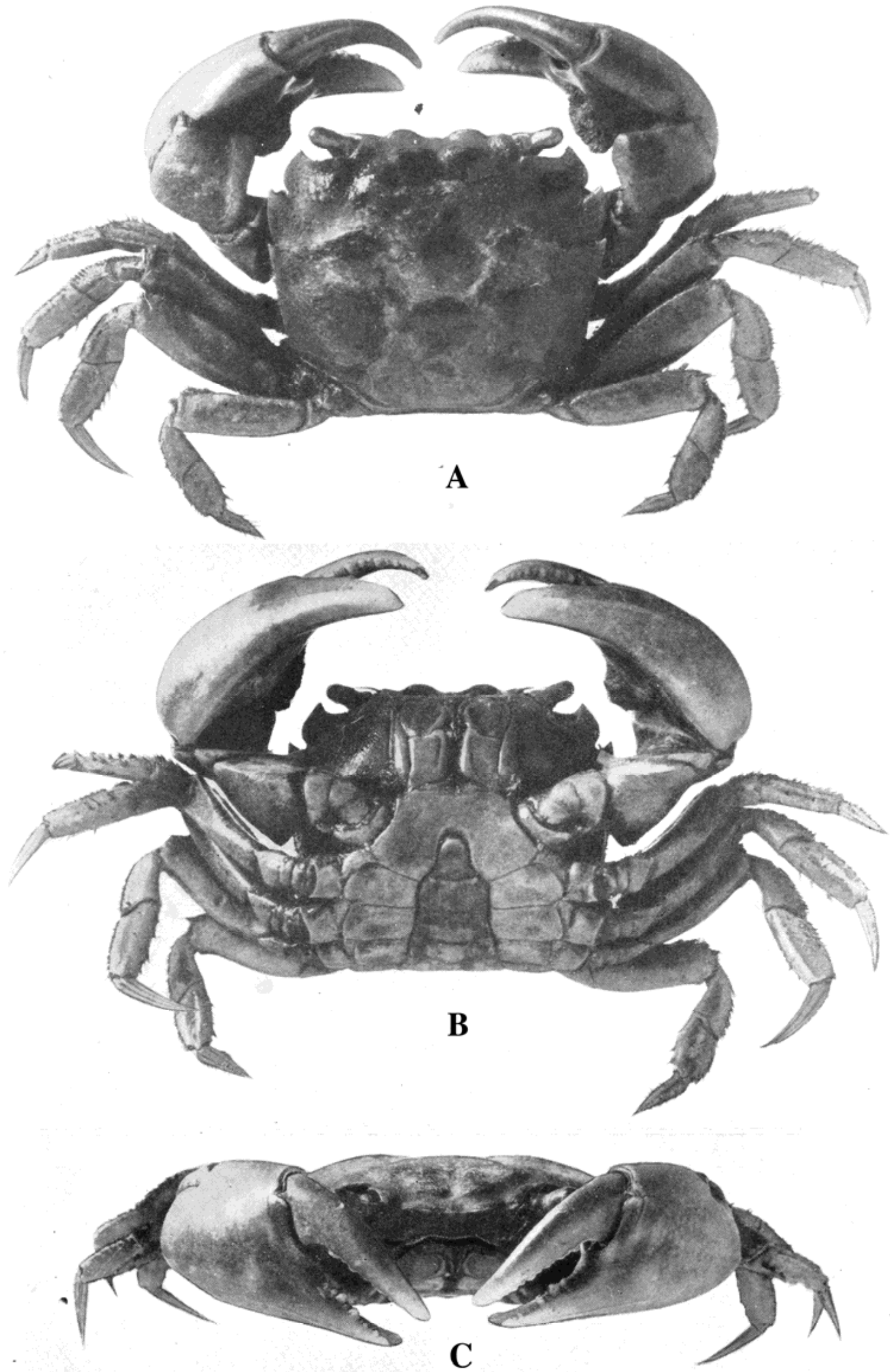



Figure 26. *Hemigrapsus oregonensis* Dana, 1852. A) dorsal view; B) ventral view; C) frontal view. (After Rathbun, 1918).

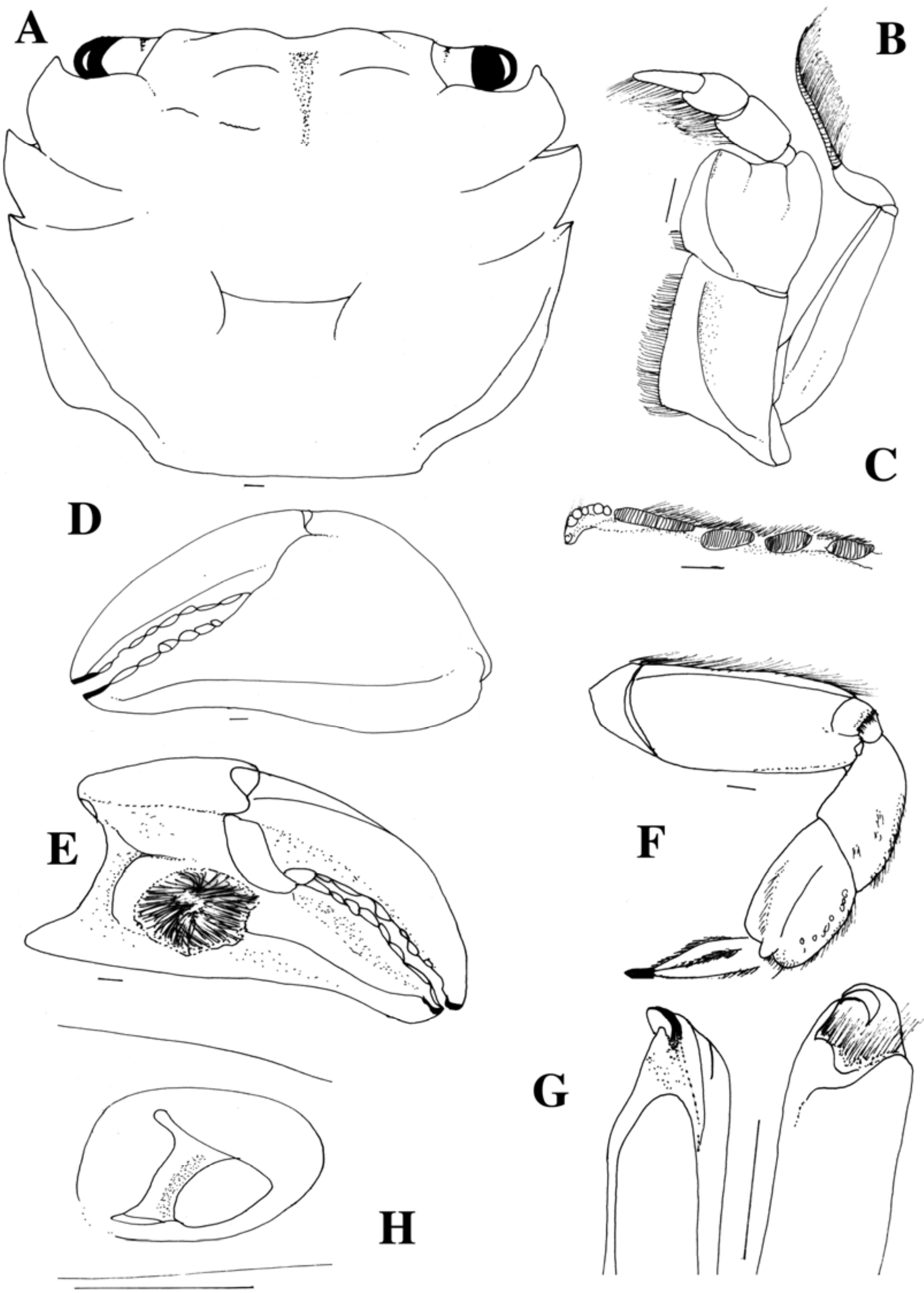



Figure 27. *Hemigrapsus oregonensis* Dana, 1852, male (26.3mm x 22.0mm); female (16.5mm x 13.7mm) (RMNH-uncat.), A) carapace; B) third maxilliped; C) infra-orbital ridge; D) outer view of chela; E) inner view of chela; F) last ambulatory leg; G) G1; H) female gonopore. (Scale=1.0mm).

### *Hemigrapsus crenulatus* (H. Milne Edwards, 1837)

(Figure 28A-B)

*Cyclograpsus crenulatus* H. Milne Edwards, 1837: 80; 1838: 15.

*Heterograpsus crenulatus* – H. Milne Edwards, 1853, 193; Miers, 1876b: 100; Kingsley, 1880: 208; Filhol, 1885: 389; 1886: 500; de Man, 1891: 53. Thomson, 1912: 225; Thomson & Anderton, 1921: 120; Oliver, 1923: 496.

*Brachynotus crenulatus* – Balss, 1930: 195.

*Hemigrapsus crenulatus* – Dana, 1852: 349; 1855: pl. 22, fig. 3 (atlas); Rathbun, 1898: 567; 1910: 589; 1918: 266; Chilton & Bennett, 1929: 731; Bennett, 1930: 255; Porter, 1936a: 150; 1936b: 336; 1937: 20; Richardson, 1949: 29; Garth, 1957: 100; Dell, 1963: 60; Wood, 1963: 1; Bennett, 1964: 100; Batham, 1965: 215; Garth, Haig & Yaldwyn, 1967: 169; Dell, 1968: 13; Wood: 1968: 89; Wear, 1970: 3; Hayward, 1974: 159; Knox *et al.*, 1977: 50; Knox & Bolton, 1978: 111; Knot & Fenwick, 1978: 10; Knox *et al.*, 1978: 100; Knox, 1983: 100; Wear & Felder, 1985: 80; McLay, 1988: 286.

*Lobograpsus crenulatus* – A. Milne Edwards, 1869: 173.

*Trichodactylus granarius* Nicolet, 1849: 151; altas, pl. 2, fig. 3 (wrong citation).

*Trichodactylus granulatus* H. Milne Edwards, 1853: 216 (wrong citations)

*Heterograpsus barbimanus* Heller, 1865: 53, pl. 4 fig. 5; Cano, 1889: 99, 243.

*Heterograpsus sanguineus* Lenz, 1902: 765.

*Heterograpsus barbigerus* Heller, 1862: 522.

**Material examined.**— **Neotype** – 1 male (22.1mm x 19.5mm) (RMNH-D1218), New Zealand, coll. H. Suter, 1894. – **Others** – 1 male (19.1mm x 16.9mm) (RMNH-D2043), New Zealand, coll. H. Milne Edwards, 1878; 1 female (33.1mm x 27.9mm) (RMNH-2023), New Zealand, coll. 1 Apr. 1909.

**Diagnosis.**— Carapace subquadrate, broader than long, surface covered with fine granules, regions well defined. Anterolateral margin slightly curved upwards with three teeth including exorbital tooth. Infraorbital ridge with three or four dentiform granules, female with 15 isomorphic granules. Chelipeds large in male, inner surface of cheliped densely setose, absent in females. Ambulatory legs short, flat, with a small subdistal spine on anterior margin of merus. G1 long, slender. Female gonopore operculate, circular in shape.

**Colour.**— The colour of this species can vary from greenish-yellow to brown, covered with white patches and red purplish spots (C. McLay, pers. comm.). All preserved specimens examined are brown in colour.

**Size.**— The largest male specimen reported is 37.5mm x 32.1mm (McLay, 1988), and the largest female examined is 33.1mm x 27.0mm (RMNH-2023).

**Habitat.**— It can be found on mud flats and sand flats, but it may also occur under boulders on the rocky shore inter-tidal area, usually in sheltered areas (C. McLay, pers. comm.).

**Remarks.**— This species was established by H. Milne Edwards (1837) for a specimen for from an unknown locality. The type material should be kept in MNHN, Paris. I have tried to look for the specimens on two separate occasions but I could not find them. They are almost certainly lost. However, the species is certainly from New Zealand or Chile, and the specimens has been referred to this species by various authors (see synmnonmy), I have no reason to disagree with this. This species is apparently very commonly found along the coast of New Zealand (McLay, 1988), and in Chile (Garth, 1957). As H. Milne Edwards (1837) did not state where his specimens came from. There is no way to ascertain the type locality. It is likely that the specimens that H. Milne Edwards examined are from New Zealand since most of his specimens in his 1837 publication were from New Zealand and Australia. To stabilize the taxonomy of this species, I hereby designate a male specimen designated a male specimen, 22.1mm x 19.5mm (RMNH-D1218), collected from New Zealand by H. Suter, 1894, as the noetype for this species.

The biology of this species has been studied in detail (see McLay, 1988).

It is a pity that I only have examined the specimens collected from New Zealand. Attempts to obtain specimens from Chile have proved to be futile. It is interesting to note that the distribution of this species is disjointed, with one population occurring in New Zealand, and the other occurring in Chile. Studies carried out by Bruce (2002) on the tectonic evolution of New Zealand, West Antarctica and Chile on the South Pacific rim on the 500 million year active margin has also shed some interesting facts about these three regions (see Bruce, 2002).

**Distribution.**— New Zealand and Chile.

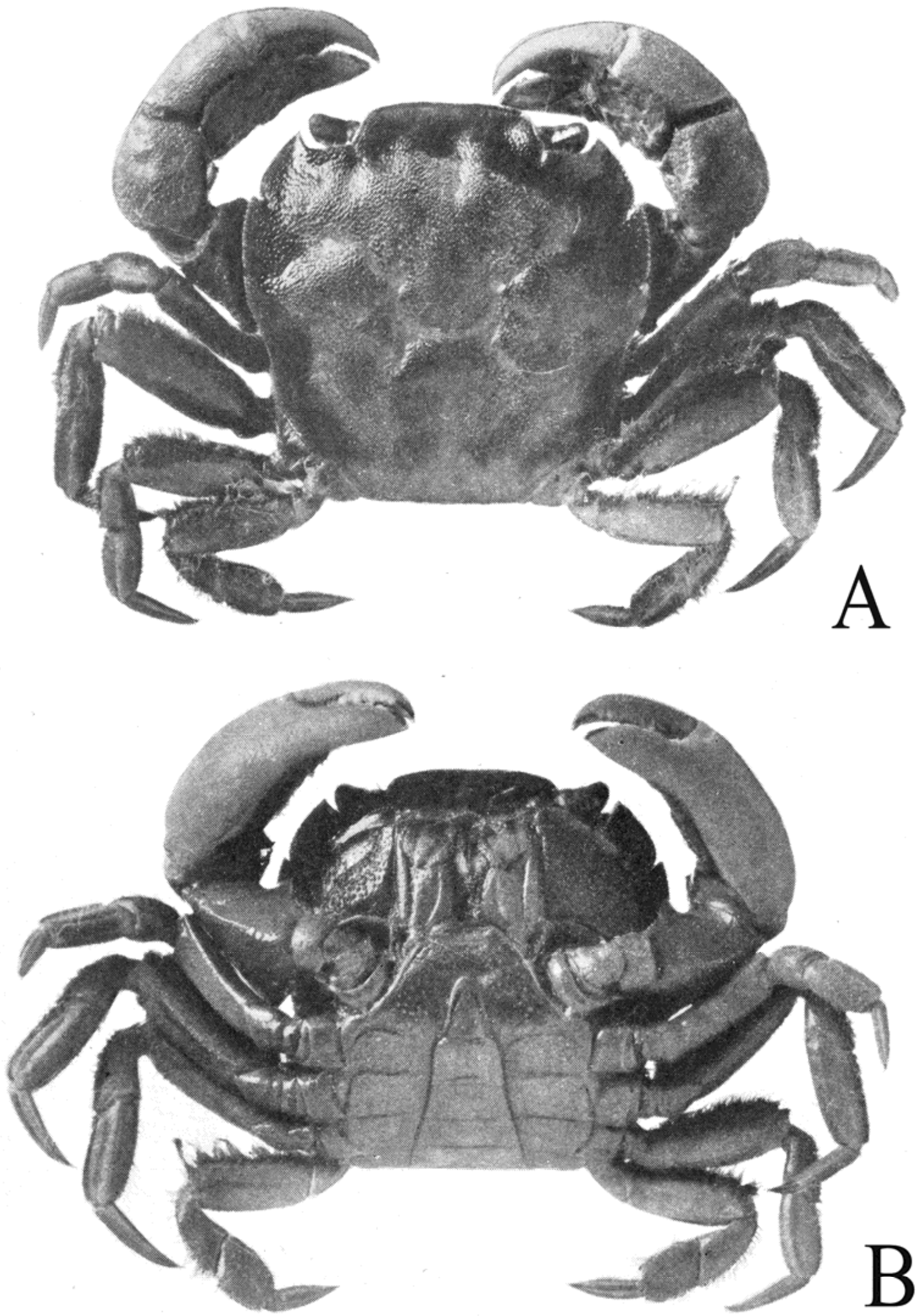



Figure 28. *Hemigrapsus crenulatus* (H. Milne Edwards, 1837). A) dorsal view; B) ventral view. (After Rathbun, 1918).

## *Hemigrapsus penicillatus* (De Haan, 1835)

(Figures 29; 30A-J)

*Grapsus (Eriocheir) penicillatus* De Haan, 1835: 60, pl. 11: 5.

*Heterograpsus penicillatus* – Stimpson, 1858: 104; de Man, 1879: 71; Kingsley, 1880: 209; Ortmann, 1894: 714; Parisi, 1918: 101.

*Brachynotus* (*Heterograpsus*) *penicillatus* – Miers, 1886: 264.

*Brachynotus penicillatus* – Koelbel, 1898: 570, pl. 1, fig. 5-6; Stimpson, 1907: 126; Tesch, 1918: 104; Balss, 1922: 150.

*Hemigrapsus penicillatus* – Horikawa, 1940: 29; Lin, 1949: 29; Sakai, 1936: 228, pl. 62, fig. 1; Sakai, 1939; Sakai, 1940; 1965: 198, pl. 94, fig. 3; 1976: 650, pl. 222: 2; Kamita, 1941: 204, text-fig. 113a,b; Kim, 1973: 473, text-fig. 207, pl. 42, fig. 159; Miyake, 1983: 175; Ogura & Kish, 1985: 377; Dai *et al.*, 1986: 478, fig. 269: 2–3, pl. 67: 5; Okumoto & Kurihara, 1978a: 81; 1987b: 123; Fukui *et al.*, 1989: 229; Okumoto & Kurihara, 1989: 195; Dai & Yang, 1991: 525, fig. 269: 2–3, pl. 67: 5; Shih *et al.*, 1991: 142; Yamaguchi & Baba, 1993: 468, fig. 178; Hsueh, 1996; Wang & Liu, 1996a: 112, figs. 142, 143; Wang & Liu, 1996b: 84; Wang & Liu, 1996c: 227; Fransen *et al.*, 1997: 124; Ho & Hung, 1997: 91; Noël *et al.*, 1997: 741; Takano *et al.*, 1997: 111; d'Udekcem d'Acoz, 1998: 45; 1999: 88; Gollasch, 1999: 359; Jeng *et al.*, 1998: 58; Jeng *et al.*, 1998: 123; Wang & Liu, 1998; Chou *et al.*, 1999; Vincent & Noël, 1999: 19; 2002: 71; Nijland, 2000: 316; 2003: 72; Nijland & Beckman, 2000: 169; Ng *et al.*, 2001: 45, 53; d'Udekcem d'Acoz & Brenton, 2002: 101; d'Udekcem d'Acoz & Faasse, 2002; Akiwa, 2003: 1; Dumoulin, 2004: 5.

*Hemigrapsus penicilletus* – Wu *et al.*, 1962: 20 (wrong spelling)

*Hemigrapsus brevidigitatus* Yokoya, 1928: 780, text-fig. 8.

**Material examined.**— **Lectotypes** – 1 male (18.0mm x 17.0mm) (RMNH-200), Japan, coll. P.F. von Siebold, 1823-1829. – **Paralectotypes** – 1 male (18.1mm x 16.8mm) (RMNH-coln-200), coll. P.F. von Siebold, no collection date; 1 male (13.4mm x 12.2mm) (RMHR-coln-201), Japan, coll. P.F. von Siebold, no collection date; 5 males (16.5-19.6mm x 14.4-16.8mm), 2 females (13.7-15.0mm x 12.2-13.0mm), (RMNH-coln-164), no collection date; 2 males (16.3-20.2mm x 14.6-17.2mm), 3 females (14.3-18.2mm x 12.6-16.7mm) (RMNH-coln-203), Japan, no collection date. – **Others** – **China** – 26 males (11.8-17.8mm x 10.8-15.2mm), 15 females (ovigerous) (13.2-17.7mm x 11.7-16.2mm) (QIH-C02780), Dengshan. Shangdong Province, coll. 24 May 1930; 14 males (19.7-20.0mm x 18.5-17.9mm), 6 females (11.6-16.3mm x 10.2-14.9mm), 1 female (ovigerous) (16.3mm x 14.1mm), (QIH-no cat. number) Dingzhijaing river, Shangdong Province, 21 May 1931; 20 males (10.2-20.0mm x 9.5x 17.5mm), 6 females (12.6-14.9mm x 11.2-13.2mm) (QIH-C02830), Yandai, Shangdong Province, coll. 19 Apr. 1936; 16 males (12.3-27.5mm x 11.0-14.6mm), (ASIZ-no cat. number), Xingjiangkou, coll. 31 May 1931; 1 male (10.8mm x 9,7mm), 2 females (ovigerous) (10.6-13.2mm x 9.1-11.5mm) (ASIZ-no cat. number), Fangcheng, Guangxi Province, 29 Mar. 1992. – **France** – 1 male (12.5mm x 11.3mm), 1 female (10.8mm x 9.8mm) (RMNH-47349), Maritime Estuarary, coll. P. Noel, 9 May 1996**. – Japan** – 1 male (33.8mm x 27.9mm) (SFM-ex-T. Sakai collection), Hokaido, Japan, coll. 1 Aug. 1965; 1 male (22.4mm x 19.2mm) (SFM-ex. T. Sakai collection), Japan; 1 male (18.3mm x 16.0mm) (SFM-7638), Sagami Bay, Japan, coll. T. Sakai, no collection date; 1 male (26.9mm x 23.2mm) (SFM-22467), Mitsuishi, Naruto, Tokushima, Shikoku, Japan, coll. B. & H. Hayashi, 5 May 1987. – **Korea** – 2 males (10.1-13.5mm x 9.1-12.4mm), 3 females (8.7-20.1mm x 8.0-17.2mm) (RMNH-39238), Asan Bay, Southwest of Seoul, South Korea, coll. E. Swennen, 9 Sep. 1989; 1 male (11.4mm x 10.4mm) (RMNH-D39227), Kang-Wha, Heung-Wang River, mudflat, coll. C. Swennen, 6 Sep. 1989. – **Taiwan** – 2 males (11.0- 21.6mm x 10.0-18.6mm mm) (NTOU-uncatalogued), Tam-Hai, Taipei County, coll. 21 Nov. 1985; 2 males (17.4-18.0mm x 15.8-15.6mm) (NTOU-no cat. number), Taixi-Hsiang, Yunlin County, coll. 22 Apr. 1988; 6 males (12.7-17.5mm x 11.2-14.8mm) , 11 females (9.5-13.5mm x 8-11.4mm) (NTOU-no cat. number), Mashakou, Tainan County, coll. J.F. Huang, 1 Dec. 1988; 2 males (18.0-18.1mm x 15.9-16.0mm) (NTOU-no cat. number), Taixi village, Yunlin County, coll.  J.F. Huang, 22 Apr. 1988; 3 males (9.8-23.5mm x 8.7-20.0mm), 1 male (15.5mm x 14.1mm) (NTOU-no cat. number), He-Mei, Taipei County, coll. H.Z. Lai, 1 Dec. 1988; 1 male (13.3-15.5mm x 11.3-13.2mm) (NTOU-no cat. number), Lin-bian, Pingtung County, coll. J.F. Huang, 9 Feb. 1989; 2 males (16.5-22.2mm x 14.4-19.0mm), (NTOU-no cat. number), Kunyu river, Tainan County, coll. J.J. Huang, no collection date; 1 male (11.3mm x 10.1mm) (NTOU-no cat. number), Wu-chi, Taichung County, coll. J.F. Huang, 24 Apr. 1988; 1 male (12.8mm x 11.3mm), 1 female (10.7mm x 9.4mm) (NTOU-no cat. number), Tangang, coll. J.F. Huang, no collection date; 3 males (9.2-16.0mm x 7.8-13.9mm), 3 females (10.6-14.3mm x 9.0-12.1mm) (TMCD-2606), Gaomaei, Taichung County, coll. C.H. Wang, 5 Jan. 1990; 1 male (22.6mm x 19.7mm), 2 females (15.7-21.5mm x 13.5-18.0mm) (TMCD-1510), Baodouzhi, Keelung, coll. C.H. Wang, 12 Apr. 1989; 1 male (9.2mm x 8.2mm) (TMCD-2341), Yangshan Jinmen, coll. L.R. Tung, 30 Jan. 1988; 1 male (21.4mm 18.5mm) (TMCD-2198), Hemei, Fulong, Taipei County, coll. C.H. Wang, 8 Jun. 1986; 6 males (9.3-13.8mm x 8.3-11.7mm) (TMCD-2537), Santiaolun, Yunlin County, coll. C.H. Wang, 18 Oct. 1987; 1 male (12.3mm x 10.9mm) (TMCD-2751), Taixi, Yunlin, coll. C.H. Wang, 27 Nov. 1991; 1 female (20.5mm x 17.5mm)

(TMCD-2205), Zhuyuen, Tansui, Taipei County, coll. 21 Aug. 1986; 1 male (18.5mm x 16.0mm), 1 female (14.6mm x 12.4mm) (TMCD-2336), Jincheng, Jinmen, coll. L.R. Tung, 29 Jan. 1988; 2 males (23.1-31.6mm x 20.3-26.7mm), 1 female (30.8mm x 27.8mm) (TMCD-2189), Xingang, Toucheng, I-Lan, coll. C.H. Wang, 15 May 1986; 3 males (11.8-22.2mm x 10.8-19.3mm), 2 females (13.5-25.6mm x 11.8-21.7mm) (TMCD-2705), De-Zhi-Kou, Zhu-An bridge, I-Lan County, coll. C.H. Wang, 20 Mar. 1991.

**Diagnosis.**— Carapace subquadrate, broader than long, surface pitted, anterior region granulated, front broad, anterior margin concave medially. Anterolateral margin with three sharp teeth including orbital tooth. Infraorbital ridge with six to seven inner granules and three smaller prominences. Chelipeds large in male, with tuft of setae on inner and outer surfaces of chelipeds. Ambulatory legs short, with a small subdistal spine on anterior margin of merus. G1 long, slender, length to width ratio 8.5, with a semicircular distal chitinous process slightly curved dorsally outwards. Female gonopore circular with oval-shaped operculum.

**Colour.**— The colour of fresh specimens is dark brown (C.H. Wang, pers. comm.), and all preserved specimens examined are brown or dark brown in colour.

**Size.**— The largest male specimen examined is 31.6mm x 26.7mm (TMCD-2189), and largest female specimen examined is 30.8mm x 27.8mm (TMCD-2189).

**Habitat.**— It can be found under rocks on sandy or muddy substrates, usually very close to the river mouth.

**Remarks.**— This species was first described by De Haan (1835) based on specimens collected from Japan. The lectotypes and paralectotypes for *H. penicillatus* have been chosen by Yamaguchi (1993). Interestingly, Asakura & Watanabe (2005) have separated a new species, *H. takanoi* from *H. penicillatus*, based on the presence of dark spots on the different parts of the crab. However, workers studying the ecology of *H. penicillatus* (Ogura & Kish, 1985; Okumoto & Kurihara, 1987a & 1987b; Okumoto & Kurihara, 1989; Akiwa, 2003) has already recognized the possibility of two sibling species (Knowlton, 1986, 1993). It must be noted that they also state that the colour is only useful when the specimens are freshly collected or freshly preserved. Asakura & Watanabe (2005) reported that *H. takanoi* has apparently spread to Europe but it has been recognized as *H. penicillatus* (Noël *et al.*, 1997; d'Udekcem d'Acoz, 1998 & 1999; Gollasch, 1999; Vincent & Noël, 1999 & 2002; Nijland, 2000; Nijland & Beckman, 2000; d'Udekcem d'Acoz & Brenton, 2002; d'Udekcem d'Acoz & Faasse, 2002; Nijland, 2003; Dumoulin, 2004).

The recognition of *H. takanoi* has created problems for all old records of *H. penicillatus*. So far, I have not seen any *H. takanoi* specimens in my re-examination of the specimens collected from China and Taiwan.

**Distribution.**— Taiwan, China, Korea, Japan. The species has been introduced into southern France (Noel, 1998).

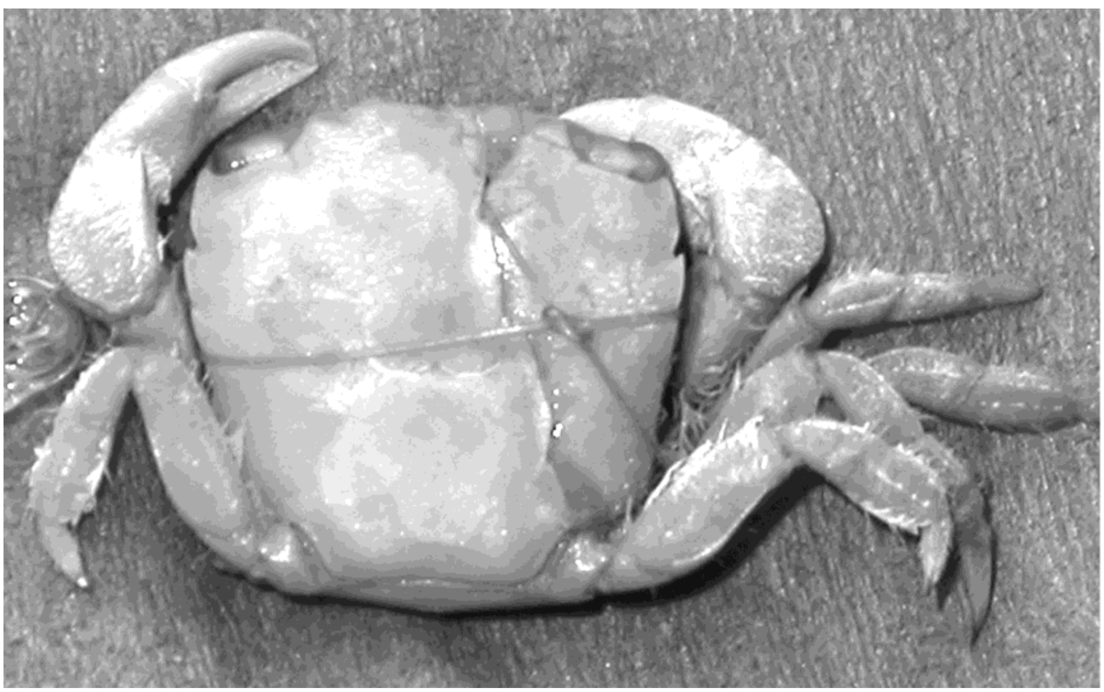


Figure 29. *Hemigrapsus penicillatus* De Haan, 1835, male, lectotype, 18.0mm x 17.0mm (RMNH-200). Dorsal view.

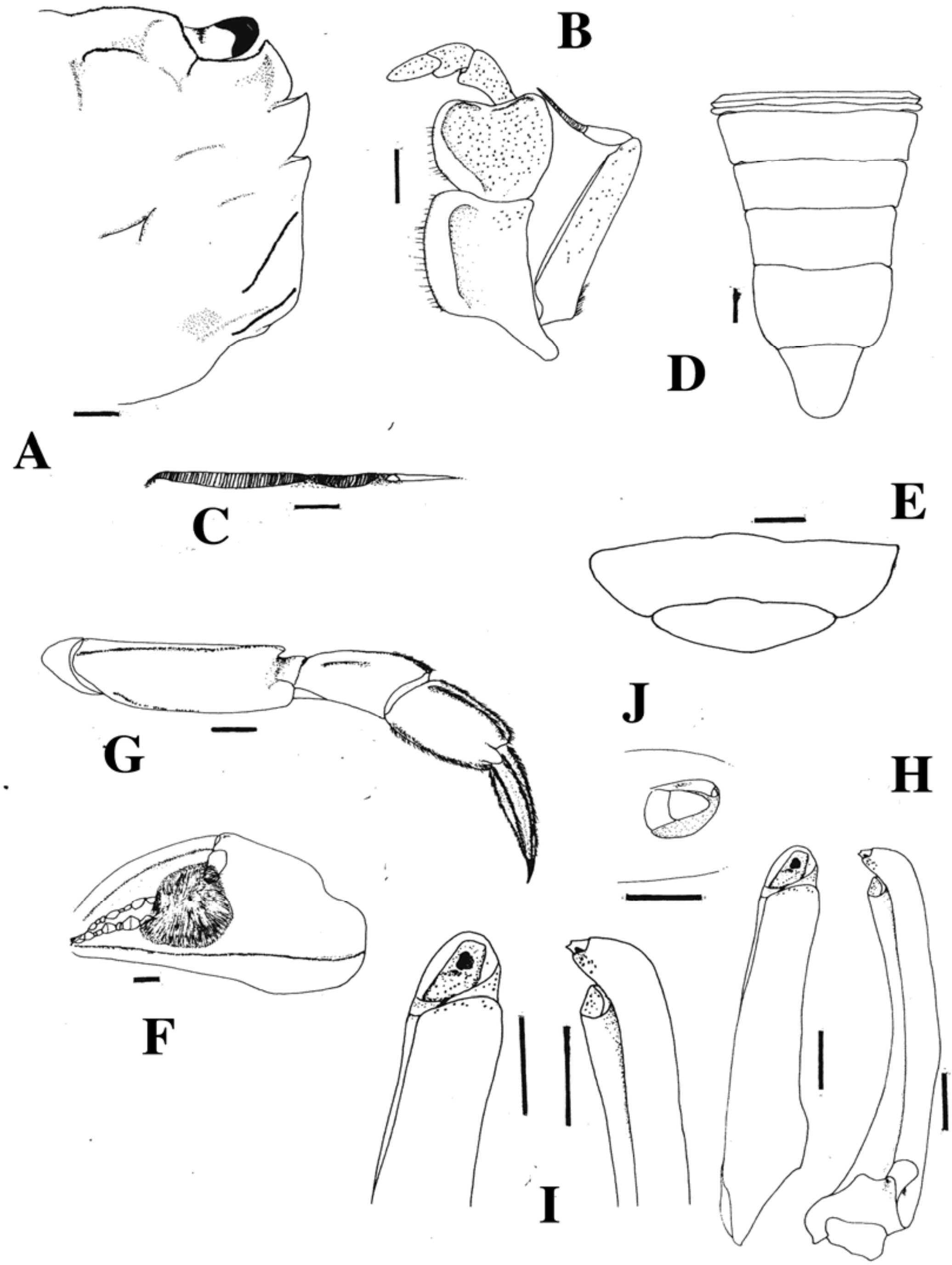



Figure 30. *Hemigrapsus penicillatus* De Haan, 1835. male, 17.8mm x 15.2mm, female 17.7mm x 16.2mm (QIH-C02780). A) carapace; B) third maxilliped; C) infra-orbital ridge; anterior view of cheliped; D) male abdomen; E) female abdomen (part); F) dorsal view of cheliped; G) last ambulatory leg; H) G1; I) distal end of G1; J) female gonopore. (Scale=1.0mm).

## *Hemigrapsus takanoi* Asakura & Watanabe, 2005

(Figures 31A-B; 32A-D)

*Hemigrapsus takanoi* Asakura & Watanabe, 2005: 279; Asakura, 2006: 33.

*Hemigrapsus penicillatus* – Horikawa, 1940: 29 (not *Hemigrapsus penicillatus* (De Haan, 1835).

*Heterograpsus penicillatus* – Stimpson, 1858: 104; de Man, 1879: 71; Kingsley, 1880: 209; Ortmann, 1894: 714 [part].

*Brachynotus* (*Heterograpsus*) *penicillatus* – Miers, 1886: 264.

*Brachynotus penicillatus* – Koelbel, 1898: 570, pl. 1, fig. 5-6; Stimpson, 1907: 126.

*Hemigrapsus penicilletus* – Wu *et al.*, 1962: 20 (wrong spelling).

**Material examined.**— **Paratypes** – 1 male (21.2mm x 17.9mm), 6 females (15.3-17.3mm x 13.8-15.3mm) (ZRC-uncatalogued), Kasai Rinkai Park, Tokyo, coll. W.M. Mingkid, 10 May 2005.

**Diagnosis.**— Carapace subquadrate, broader than long, surface pitted, anterior region granulated, front broad, anterior margin almost straight. Anterolateral margin with three sharp teeth including orbital tooth. Infraorbital ridge with six or seven inner granules, and three smaller prominences. Chelipeds large in male, with tuft of setae on inner, outer surfaces of chelipeds. Ambulatory legs short, with a small subdistal spine on anterior margin of merus. G1 long, slender, length to width ratio 8.5, with a semicircular distal chitinous process slightly curved dorsally outwards. Female gonopore circular with oval-shaped operculum.

**Colour.**— The colour of fresh specimens can vary from grey to green or brown with dark brown or purple spots (A. Asakura, pers. comm.), and the preserved specimens examined are brown or dark brown.

**Size.**— The largest male specimen examined is 22.5mm x 19.8mm (Asakura & Watanabe, 2005), and largest female specimen examined is 17.3mm x 15.3mm (ZRC-uncatalogued).

**Habitat.**— It can be found under rocks on sandy or muddy substrates, usually very near river mouth (A. Asakura, pers. comm.).

**Remarks.**— According to Asakura & Watanabe (2005), this species is very similar to *Hemigrapsus penicillatus* superficially with the presence of spots on the mandible, ventral side of the cephalothorax and abdomen, the diameter of the hair patch on the chela and the morphology of the male first pleopod. Further studies by Mingkid *et al.* (2006) on the male gonopods have supported that *H. takanoi* is a good species. In the same year, Asasukra (2006) validated the Japanese vernacular name for *H. takanoi*, and provided four strong supporting evidences viz. a) the statistical analysis of the first male gonopods and the length to width ratio of sixth abdominal somites; b) the colour forms and distribution of the spots on the various parts of the animals; c) the crutch size and egg size of the two species with *H. penicillatus* having a smaller egg size, and d) the distribution of the two species, with *H. takanoi* in shallow bays and H. *penicillatus* can be found in deeper waters. In the same paper, Asakura cited the gel electrophoresis analysis of two different forms of *H. penicillatus* on 10 different loci by Takano *et al.* (1997). Takano *et al*. (1997) report strongly indicated that there are two different species of *H. penicillatus*. Sakai (2007) has suggested otherwise, he stated that there is no morphological difference on the first male gonopods between *H. penicillatus* and *H. takanoi*. He synonymized *H. takanoi* under *H. penicillatus*. Sakai did not compare other adult morphological characters or provide any additional evidence to support his synonymy.

In addition to the characters cited by Asakura & Watanabe (2005), my examination of *H. penicillatus* and *H. takanoi* specimens (sent to me by the courtesy of Dr. A. Asakura) has shown that *H. takanoi* can be distinguished from *H. penicillatus* by the following additional characters viz. a) the forms of the infra-orbital ridge (see figure 32 below); b) the ischium of third maxillipeds is broad (vs. narrow in *H. penicillatus*); c) presence of several small granules on the inner surface of cheliped (vs. absence of granules in *H. penicillatus*; d) the sixth abdominal somite is narrow (vs. broad in *H. penicillatus*); and e) the telson is broadly triangular in shape (vs. narrowly triangular in *H. penicillatus*).

**Distribution.**— Japan and Europe.

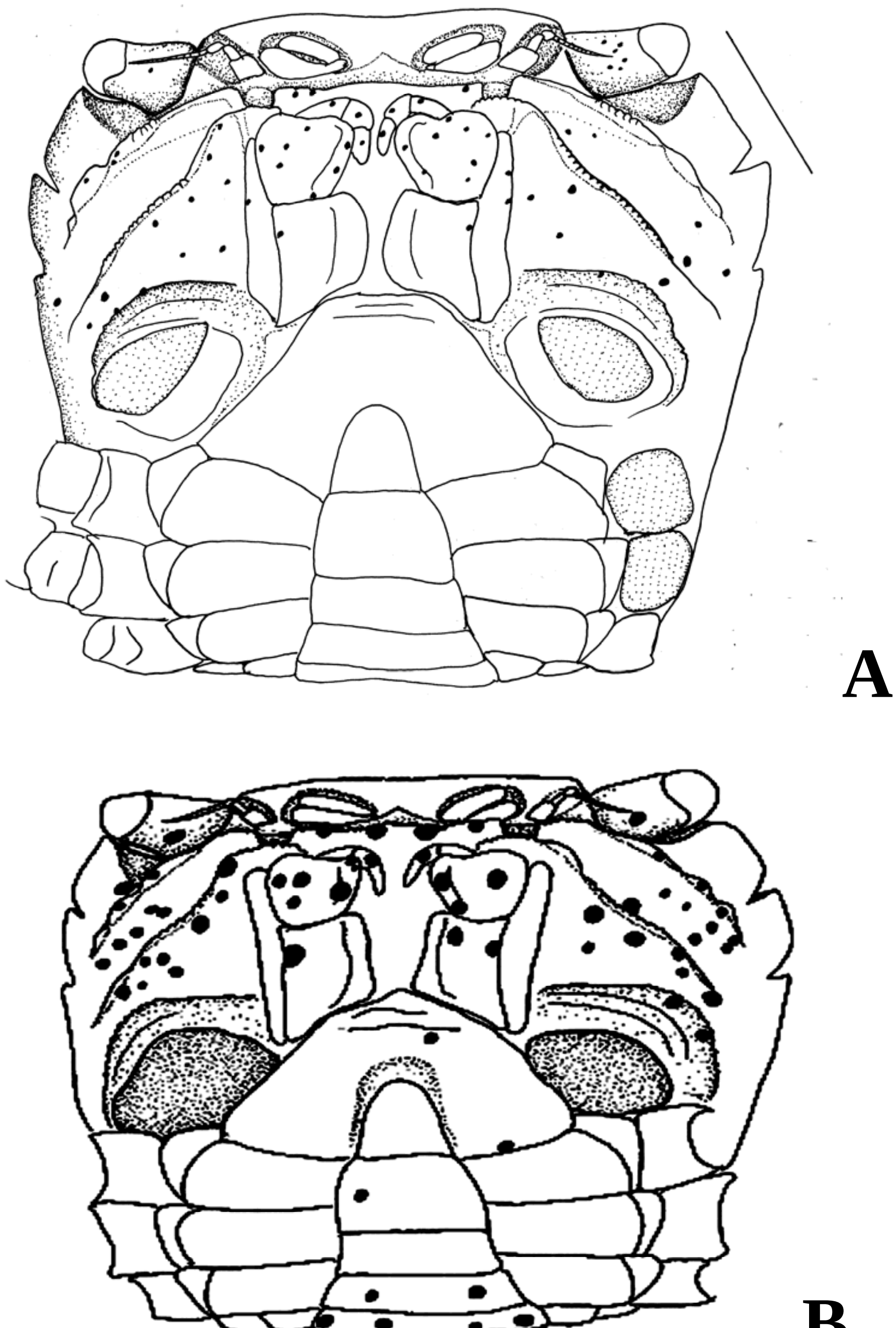



Figure 31. Ventral views. A) *Hemigrapsus takanoi* Asakura & Watanabe, 2005; B) *Hemigrapsus penicillatus* De Haan (1835) (After Asakura & Watanabe, 2005).

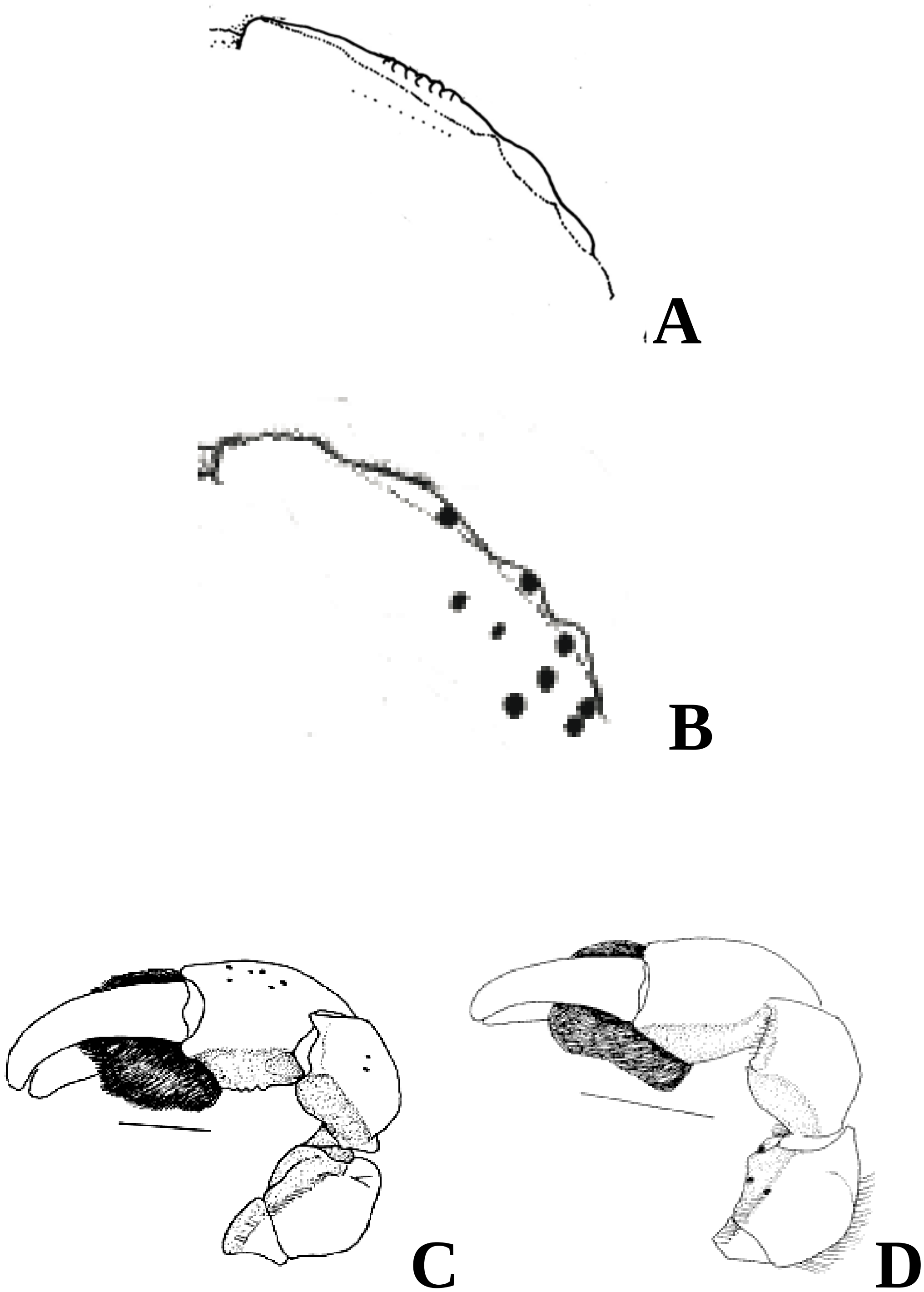



Figure 32. A) Infra-orbital ridge of *Hemigrapsus takanoi*; B) Infra-orbital ridge of *Hemigrapsus penicillatus;* C) dorsal view of chela of *Hemigrapsus takanoi*; D) dorsal view of chela of *Hemigrapsus penicillatus* (After Asakura & Watanabe, 2005).

### ***Hemigrapsus estellinensis* Creel, 1964**

(Figure 33)

*Hemigrapsus estellinensis* Creel, 1964: 236.

**Material examined.**— **Holotype** – 1 male (17.4mm x 15.4mm) (USNM-107855), Estelline Salt Spring, 1/2 mile North East of Estelline, Hall County, Texas State, USA, coll. G.C. Greel *et al.*, 18 Feb. 1962. – **Paratypes** – 3 males (14.8-17.0mm x 12.4-15.1mm), 5 females (14.7-16.9mm x 12.3-13.7mm), 3 females (ovigerous) (14.5-16.0mm x 12.5-13.6mm) (USNM-107856), Estelline Salt Spring, 1/2 mile North East of Estelline, Hall County, Texas State, USA, coll. G. C. Creel *et al.*, 18 Feb. 1962.

**Diagnosis.**— Carapace subquadrate, broader than long, surface covered with fine granules and spots. Anterolateral margin with three teeth including orbital tooth. Infraorbital ridge with five/six inner smooth tubercules, 20-27 isomorphic granules in female. Chelipeds large in male, a tuft of soft, short setae setae on the inner surface of chelipeds, absent in females. Ambulatory legs short, flat, with a small subdistal spine on anterior margin of merus. G1 stout. Female gonopore operculate, circular in shape.

**Colour.**— The colour of live specimens is grey green (Creel, 1964), but all preserved specimens examined are light to dark cream in colour.

**Size.**— The largest male specimen examined is 17.4mm x15.4mm (USNM-107855), and the largest female specimen examined is 16.0mm x 13.6mm (USNM-107856).

**Habitat.**— It can be found inside caves, in salt springs (Creel, 1964).

**Remarks.**— This species is very similar to *Hemigrapsus oregonensis* superficially, and many workers believe that this species is a very odd specimen of *Hemigrapsus oregonensis*, but *H. estellinensis* is different from *H. oregonensis* in the following a) in the form of the carapace less defined (vs. well defined in *H. oregonensis*); b) carapace surface covered with granules and spots (vs. smooth surface in *H. oregonenis*); c) infra-orbital ridge 5-6 rounded granules (vs. 3-4 large granules in *H. oregonensis*); d) short ambulatory legs (vs. longer and more slender ambulatory legs in *H. oregonensis*).

The species is very similar to *H. nudus* in the form of the legs but it does not have any pulvinus present at the base of the chela fingers.

This species is endemic to the U.S. It was discovered only at one location, Estelline Salt Springs in Estelline, Hall County in Texas. Estelline Salt Springs is a group of brine springs less than a mile east of Estelline at the Childress County line in east central Hall County (at 34°33' N, 100°25' W). These springs have been used by servicemen stationed at Childress during World War II. In 1964 the United States Corps of Engineers built a dike around the springs to stop the flow and prevent the salt from entering the river. Since then the springwater has apparently grown more saline. This crab was known to live only at these springs, but may not have survived since the springs have been confined (Brune, 1981).

**Distribution.**— Only reported from one locality in United States of America (Estelline, Hall County, Texas State).

Figure 33. *Hemigrapsus estellinensis* Creel, 1964, male, holotype, 17.4mm x 15.4mm (USNM-107855). Dorsal view.

## *Hemigrapsus sanguineus* (De Haan, 1835)

(Figure 34A-J)

*Grapsus* (*Grapsus*) *sanguineus* De Haan, 1835: 58, pl. 16, fig. 3.

*Hemigrapsus maculatus* H. Milne Edwards, 1853: 193.

*Heterograpsus sanguineus* – Ortmann, 1894: 714; Parisi, 1918: 151.

*Brachynotus sanguineus* – Tesch, 1918: 105; Balss, 1922: 151.

*Hemigrapsus sanguineus* – Rathbun, 1902: 191; Shen, 1932: 159, text-fig 102, 103, pl. 7, fig. 1; Sakai, 1935: 230, pl. 61, fig. 1; 1939: 672, pl. 74: 1; Sakai, 1976: 650, pl. 222: 1; Horikawa, 1940: 29; Lin, 1949: 29; Shen & Dai, 1964: 126; Kim, 1973: 472, text-fig. 206, pl. 42, fig. 158; Miyake, 1983: 175; Dai *et al.*, 1986: 478, fig. 269: 1, pl. 67: 4; Fukui *et al.*, 1989: 229; Dai & Yang, 1991: 524, fig. 269: 1, pl. 67: 4; Shih *et al.*, 1991: 142; Yamaguchi & Baba, 1993: 466, fig. 177; Jeng *et al.*, 1996: 100; Wang & Liu, 1996a: 111, fig. 140, 141; Wang & Liu, 1996b: 82; Fransen *et al.*, 1997: 124; Ho & Hung, 1997: 89; Jeng *et al.*, 1998: 57; Jeng *et al.*, 1998: 123; Ng *et al.*, 2001: 45.

**Material examined.**— **Lectotype** – 1 male (28.0mm x 26.0mm) (RMNH-no cat. number), Japan, coll. Ph. F. von Siebold, 1823-1829. – **Paralectotype** – 1 female (19.7mm x 17.5mm) (RMNH-no cat. number), Japan, coll. Ph. F. von Siebold, 1823-1829. – **Others** – **China** – 1 male (25.6mm x 22.6mm), 1 female (ovigerous) (21.0mm x 18.0mm) (SFM-13229), Chang Sandao, China, coll. Wang, 15 Jun. 1951; 5 females (13.8-21.8mm x 12.2-19.5mm), 1 female (ovigerous) (17.2mm x 15.2mm) (USNM-55714), Peitaiho, North China, coll. A. Sowerby, Aug. 1921; 1 male (24.9mm x 22.0mm) (USNM-59230), Tsingdao, North China, coll. C.J. Urita, 1924. – **Taiwan** – 3 males (10.0-24.0mm x 9.0-20.5mm), 2 females (10.5-24.0mm x 9.2-22.6mm) (NTOU-no cat. number), He-Mei Bridge no. 1, Taiepi County, coll. Z.H. Pang & J.F. Huang, 1 Dec. 1988; 2 males (21.4-31.4mm x 19.0-27.0mm), 1 female (24.8mm x 22.0mm), (IZAS-71695), Ho-Mei, Taipei County, coll. M.S. Jeng, 4 Nov. 1997; 1 male (23.0mm x 19.5mm), 1 female (26.4mm x 22.8mm) (TMCD-2114), Fu-Lung, Taipei County, coll. C.H. Wang, 23 Nov. 1985; 1 female (24.4mm x 20.7mm) (TMCD-2239), Qijing, Kaohsiung, coll. J.C. Lin, 24 Feb. 1987; 2 males (10.8-13.6mm x 9.5-11.4mm), 2 females (14 (28.5mm x 24.8mm) (TMCD/CHCD-48), Hsiangshan, coll. H.C. Liu; 3 males (23.3-31.0mm x 21.2-21.2mm), 1 female (22.2mm x 18.7mm) (NTOU-no cat. number), Tanhai, Taipei County, coll. J.F. Huang, 24 Nov. 1985. – **Japan –** 1 female (ovigerous) (24.6mm x 21.3mm) (MNHN-B1283), Tokyo, Japan, coll. J. Harmand, 1906; 1 male (28.8mm x 25.8mm), 4 females (19.6-

24.2mm x 18.9-21.3mm) (MNHN-B12841), Japan, coll. 5 Aug. 1897; 1 male (30.1mm x 26.2mm) (SFM-7654), Sagami Bay, Japan; 3 males (21.5-27.6mm x 18.7-25.2mm), 1 female (22.1mm x 18.7mm) (SFM-7653), Manszaru, Japan, coll. T. Watabe; 1 male (30.4mm x 27.0mm) (SFM-7655), Sagami Bay, Japan, coll. T. Sakai; 2 males (32.6-42.5mm x 28.8-36.5mm), (SFM-7757), Sagami Bay, Japan, coll.. T. Sskai; 1 male (26.8mm x 24.1mm) (SFM-ex T. Sakai collection), Nagashima, coll. Nov. 1963; 2 males (24.9-25.0mm x 22.5-23.0mm) (USNM-54508), Oshoro, Hokkaido, Japan, coll. M. Saki, Jul. 1915; 1 male (28.8mm x 25.1mm) (USNM-26239), Tokyo, Japan, coll. Garden & Sayder, 1900**. – Korea** – 4 males (17.0-23.7mm x 14.8-20.8mm), 2 females (8.6-10.0mm x 7.5-8.5mm) (USNM-12427), Fusan, Korea, coll. P.Z. Zouy, Jul. 1886. – **North America** – 1 male (27.6mm x 24.6mm), 1 female (16.8mm x 14.5mm) (USNM-259798), Oak Beack, Long Island, New York, North Atlantic Ocean, U.S.A., coll. A. Teros, Jul. 1993; 1 female (ovigerous) (35.0mm x 30.5mm) (USNM-239221), Townsend, Cape May County, New Jersey, North Atlantic Ocean, U.S.A., coll. J.J. Mcdermott, 24 Sep. 1988.

**Diagnosis.**— Carapace subquadrate, slightly broader than long, surface covered with fine granules and spots. Anterolateral margin with threeteeth including orbital tooth. Infraorbital ridge with five/six inner striated granules, and three smaller prominences. Chelipeds large in male, without setae but a small pulvinus is present at base of fingers, absent in females. Ambulatory legs short, flat, with a small subdistal spine on anterior margin of merus. G1 stout, length to width ratio 8.5, distal process with a V-shaped notch. Female gonopore operculate, circular in shape.

**Colour.**— The colour of fresh specimens is brown with dark purplish spots on carapace (Wang & Liu, 1996), and all preserved specimens examined are brown in colour.

**Size.**— The largest male specimen examined is 31.4 x 27.0mm (IZAS-71695), and the largest female is 26.4mm x 22.8mm (TMCD-2114).

**Habitat.**— It can be found under rocks on sandy and/or mudflats near river mouth (Wang & Liu, 1996; S.H. Ko, pers. comm.).

**Remarks.**— Male specimens can be easily distinguished from *H. penicillatus* and *H. takanoi* by a) the presence of a pulvinus at the base of the chelipeds (vs. absence in *H. penicillatus* and *H. takanoi*), and b) the absence of setae on the surfaces of the chelipeds in adults (vs. presence of setae in *H. penicillatus* and *H. taknoi*).

This species is very similar to *H. nudus* found along the coast of North America, in having a glabrous chelipeds, and presence of a pulvinus at the base of the cheliped fingers. *Hemigrapsus sanguineus* can be easily distinguished from *H. nudus* by a) the form of the male infra-orbital ridge, which has five or six inner striated, granules, and three smaller prominences (vs. 15 isomorphic granules in *H. nudus*); b) the female has more than 25 isomorphic granules on the infra-orbital ridge (vs. 15 isomorphic granules in *H. nudus*); c) the absence of a small tuft of setae on the inner surface of cheliped in adults (vs. presence of setae in *H. nudus*); and d) the ambulatory legs are proportionately more slender and narrower (vs. stouter and broader legs in *H. nudus*).

**Distribution.**— Taiwan, China, Korea, Japan, Shahhalin Islands, and recently, it has been reported from the west coast of United States of America (Schubart, 2000), and in Europe (Breton *et al.*, 2002).

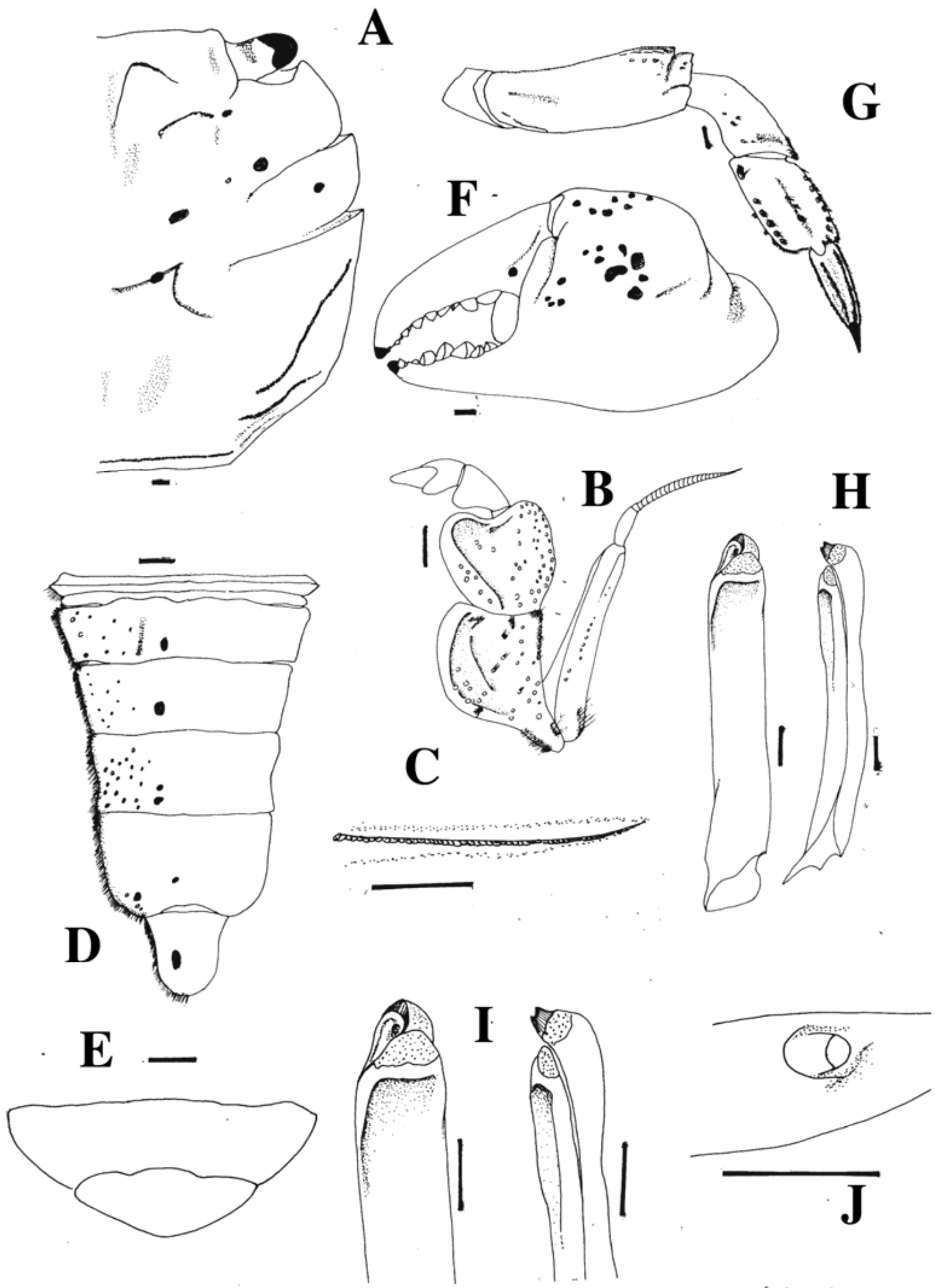



Figure 34. *Hemigrapsus sanguineus* De Haan, 1835, male 24.0mm x 20.5mm, female 24.0mm x 22.6mm (NTOU-no cat. number). A) carapace; B) third maxilliped; C) infra-orbital ridge; anterior view of cheliped; D) male abdomen; E) female abdomen (part); F) dorsal view of cheliped; G) last ambulatory leg; H) G1; I) distal end of G1; J) female gonopore. (Scale=1.0mm).

## *Hemigrapsus nudus* (Dana, 1852)

(Figures 35A-C; 36A-F)

*Pseudograpsus nudus* Dana, 1852: 249; 1852: 335; 1855: pl. 20, fig. 7a-e (atlas).

*Hemigrapsus nudus* – Rathbun, 1900: 587; 1918: 267, pl. 69.

*Brachynotus nudus* – Holmes, 1900: 81; Tesch, 1918: 105.

*Heterograpsus nudus* – Stimpson, 1858: 104.

*Cyclograpsus marmoratus* White, 1847: 41 (nomen nudum).

*Heterograpsus marmoratus* H. Milne Edwards, 1853: 193.

**Material examined.**— **Holotype** – 1 carapace (35.0mm x 30.2mm) (USNM-2331), Puget Sound, U.S. Exploration Expedition, coll. J.D. Dana. – **Paratype** – 1 female (25.5mm x 22.6mm), (USNM-2331), Puget Sound, U.S. Exploration Expedition, coll. J.D. Dana. – **Others** – **Canada** – 1 male (22.2mm x 19.4mm), 1 female (16.0mm x 14.0mm), 2 females (ovigerous) (11.4-11.8mm x 9.4-9.9mm) (RMNH-no cat. number), Gonzalet Point, Victoria B.C., Canada, coll. L.B. Holthuis, 5 Aug. 1947. – **United States of America** – 4 males (17.7-30.8mm x 16.2-27.5mm), 1 female (20.8-18.0mm) (MNHN-B12832), San Fransciso; 1 male (42.1mm x 36.0mm) (RMNH-no cat. number), Monterey Harbour, California, coll. P.A. McLaughlin, 1 Jun. 1965; 3 males (13.2-17.3mm x 11.9-15.1mm), 1 female (14.5mm x 13.2mm), 1 female (ovigerous) (15.4mm x 13.5mm) (RMNH-D23014), Neag Bay, 5 mile from Cape Flattery, ingoing Juan de Fuca Strait, Washingon State, U.S.A., coll. P.A. McLaughlin, 4 Jul. 1969; 1 female (26.1mm x 22.1mm) (RMMHN-7477), Pacific coast by San Pedro, Los Angeles, U.S.A., coll. L.B. Hothius, 13 Aug. 1947; 3 males (15.1-24.5mm x 13.2-20.8mm), 1 female (24.5mm x 21.0mm) (RMNH-B18725), Roche Habour, 0-1.0m depth, San Juan Island, Washington State, U.S.A., coll. L.B. Holthuis, 4 Sep. 1953.

**Diagnosis.**— Carapace subquadrate, slightly broader than long, surface covered with fine granules and spots. Anterolateral margin with three teeth including orbital tooth. Infraorbital ridge with 15 isomorphic granules in male and 20 in female. Chelipeds large in male, inner surface with a patch of soft, short setae in addition to a small pulvinus at base of fingers, absent in females. Ambulatory legs very short, short, flat, without subdistal spine on anterior margin of merus. G1 stout, slender. Female gonopore operculate, circular in shape.

**Colour.**— The colour of fresh material can vary from different shades of red to purple with dark purplish or red spots on carapace and white chela (P.A. McLaughlin, pers. comm.), and all preserved specimens examined are brown in colour.

**Size.**— The largest male specimen examined is 42.1mmx 36.0mm (RMNH-no cat. number), and largest female examined is 24.5mm x 21.0mm (RMNH-B18725).

**Habitat.**— It can be found under rocks along the inter-tidal shore (P.A. McLaughlin, pers. comm.).

**Remarks.**— This species is very similar to *H. sanguineus* as both have a small pulvinus at the base of the fingers, but they can be easily identified due to the following features a) presence of setae on the inner surface of the cheliped (vs. absence of setae in *H. sanguineus*); b) the ambulatory legs are extremely short and broad (vs. longer and narrower legs in *H. sanguineus*); c) the legs are glabrous (vs. presence of some setae in *H. sanguineus*); d) the G1 is very short (vs. much longer G1 *H. sanguineus*), and e) the female gonopore is slightly raised (vs. flat *H. sanguineus*).

**Distribution.**— United States of America (Yakobi Island, Alaska to Bahia de Tortuga) and Mexico. This species is uncommon below central California.

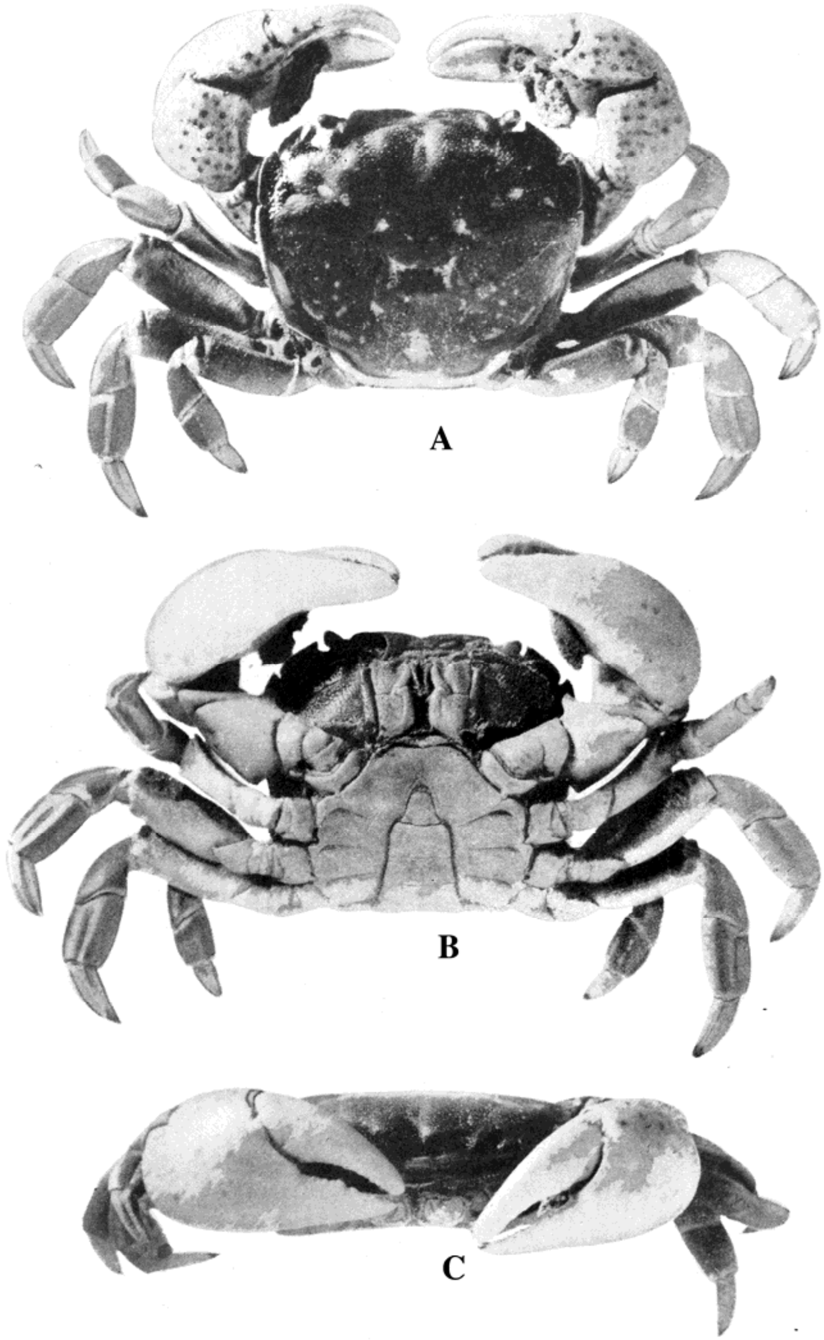



Figure 35. *Hemigrapsus nudus* (Dana, 1852), A) dorsal view; B) ventral view; C) frontal view. (After Rathbun, 1918).

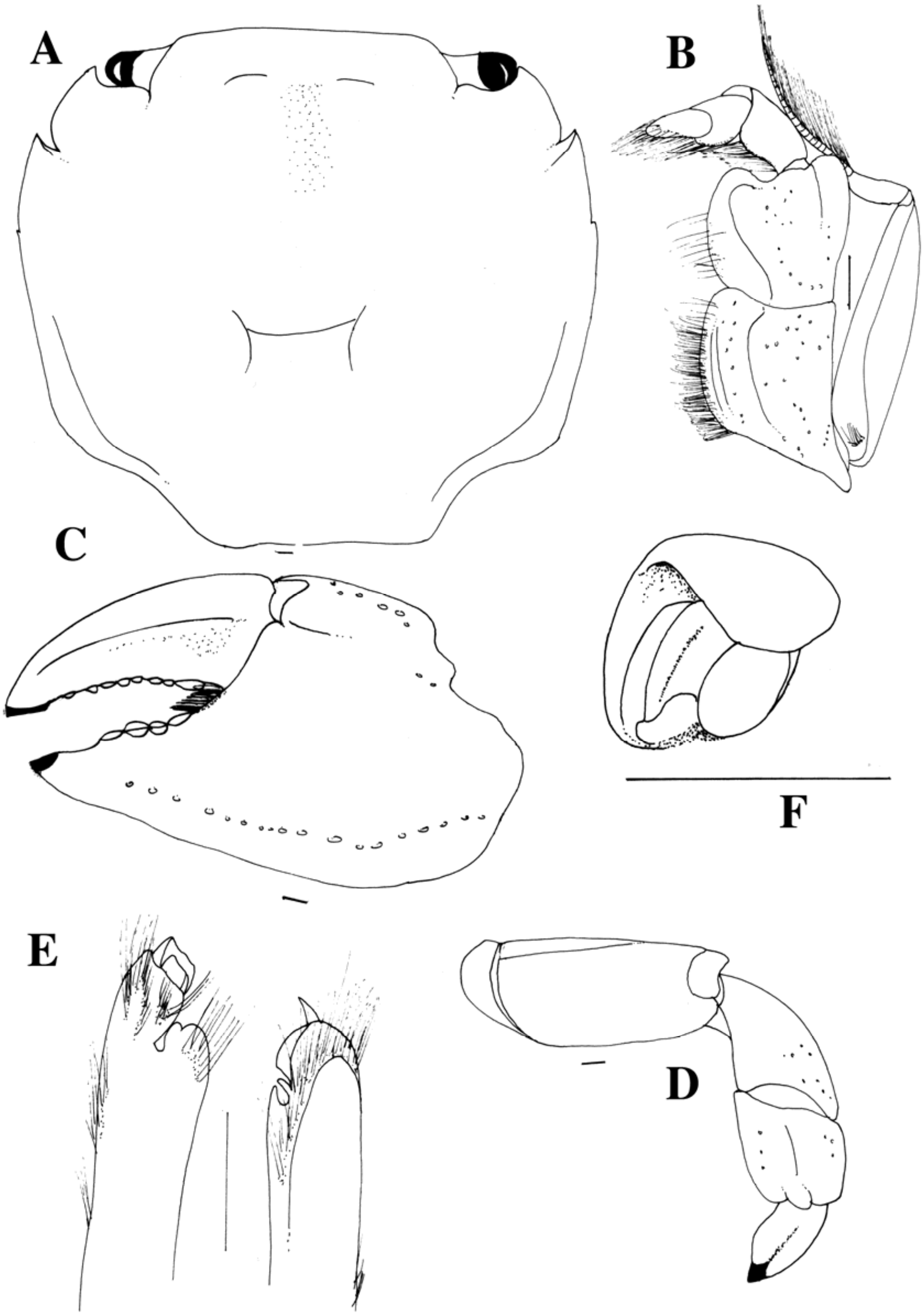



Figure 36. *Hemigrapsus nudus* Dana, 1852, male (24.5mm x 20.8mm); female (24.5mm x 21.0mm) (RMNH-B18725). A) carapace; B) third maxilliped; C) outer view of chela; D) last ambulatory leg; E) distal ends of G1; F) female gonopore. (Scale=1.0mm).

## *Hemigrapsus pallipes* (Latreille, 1817)

*Grapsus pallipes* Latreille, 1817: 431.

*Pseuodograpsus pallipes* – H. Milne Edwards, 1837: 82.

*Heterograpsus pallipes* – H. Milne Edwards, 1853: 194; Haswell, 1882: 100.

**Material examined.**— No specimen examined.

**Diagnosis.**— Carapace subquadrate, slightly broader than long, surface covered with fine granules and spots, front straight. Anterolateral margin with three teeth including orbital tooth. Infraorbital ridge unknown. Chelipeds large in male, glabrous, outer surface of cheliped with four prominent longitudinal crests. Ambulatory legs short, flat, with a small subdistal spine on anterior margin of merus. (Modified from Tesch, 1918).

**Colour.**— The colour of fresh specimens and preserved specimens have not been documented.

**Size.**— The largest male and female specimens have not been documented.

**Habitat.**— The habitat of this species has not been documented.

**Remarks.**— The identity of this species is uncertain, as the description provided by Latreille (1819), H. Milne Edwards (1837, 1853) were all too brief. Their descriptions of the species can refer to either members of *Pseudograpsus* or *Hemigrapsus*.

I have tried to look for the specimens in the MNHN, Paris on two occasions but I was not able to locate the specimens. Since it was collected from Australia, I have tried asking my collaborators from Australia about this species and they are not able to provide any information regarding it. Based on the descriptions provided, this species may prove to be *Hemigrapsus sexdentatus* H. Milne Edwards, 1835.

**Distribution.**— Supposedly Australia only.

## ***Hemigrapsus sexdentatus* (H. Milne Edwards, 1837)**

(Figure 37A-C)

*Cyclograpsus sexdentatus* H. Milne Edwards, 1837: 79; White, 1843: 266.

*Hemigrapsus sexdentatus* – Dana, 1852: 348, pl. 22, fig. 2; Filhol, 1885: 388; Chilton & Bennett, 1929: 764; Graham, 1939: 429; Powell, 1947: 40, fig. 193; Richardson, 1949a: 34, fig. 15; Trevarthen & Kulka, 1950: 54; Wood, 1963: 9; Bennett, 1964: 82, figs. 94, 137, 138; McLay & Schubart, 2004*: 695*.

*Heterograpsus sexdentatus* – H. Milne Edwards, 1853: 192; Miers, 1876: 37; Kingsley, 1880: 207; Lenz, 1901: 472; Hutton, 1904: 249; Thomson, 1905: 546: 1913: 237; Thomson & Anderton, 1921: 100, two figs.; Oliver, 1923: 542; Knox & Kilner, 1973: 353.

*Brachynotus edwardsii* Hilgendorf, 1882: 70; Miers, 1886: 264.

*Hemigrapsus edwardsii* – Richardson, 1949b: 130; Batham, 1956: 458; Knox, 1969: 547; 1975: 384; 1983: 66; Baker, 1971: 297; Knox & Bolton, 1978: 74; Roper *et al.*, 1983: 270; Gunson, 1983: 55, one colour fig.; Denny & Schiel, 2001: 927.

*Hemigrapsus edwardsi* – Batham, 1958: 652; Dell, 1963: 53, 1 fig.; 1968: 227; Wear, 1965: 16, text-fig 6G; Morton & Miller, 1968: 89, pl. 23, 1; Leslie, 1968: 90, fig 82; Wood, 1968: 93; Williams, 1969: 215; Wear, 1970: 14, figs. 27-33; Hicks, 1973: 1; Morton, 1973: 118; Miller & Batt, 1973: 73, fig. 89; Kitching & Lockwood, 1974: 131; Bedford & Leader, 1977: 341; 1978: 147; Marsden & Fenwick, 1978: 11; Marsden, 1981: 24; Westerkov & Probert, 1981: 128; Jones, 1983: 92; Naylor & Williams, 1984: 81; Pellegrino, 1984: 251; Wear & Fielder, 1985: 68, figs. 177, 178; Powell, 1987: 36, fig. 193; McLay, 1988: 280, fig. 62; Feldmann & McLay, 1993: 447; McLay & McQueen, 1995: 49; Gill, 1998: 41, fig. 193; Poinar & Brockerhoff, 2001: 149.

*Brachynotus sexdentatus* – Lewinsohn & Holthuis, 1964: 60; Bacescu, 1967: 321, fig. 7, 10A, C-D, 11A-C, 12A, 14G,H, 136, 137A, B, 138A; Stevcic, 1969: 132; 1971: 528, 530; 1973: 115, 116; Koukouras, 1973: 762; Cuesta *et al.*, 2000: 207; Cuesta *et al.*, 2001: 903, fig. 3; Schubart *et al.*, 2001: 41.

**Material examined.— Lectotype** – 1 male (34.4mm x 29.4mm) (MNHN-B-3509), New Zealand, no collection date. – **Others** – 30 females (10.0-24.8mm x 8.6-22.5mm) (MNHN-B12834), Detroit de Cook, New Zealand, coll. Filhad, no collection date; 3 males (13.9-18.0mm x 11.4-16.8mm), 3 females (13.5-15.0mm x 10.9-12.0mm) (MNHM-D21496), Camanrque, coll.

26 Mar. 1976; 2 males (9.3-11.5mm x 7.7-8.9mm), 1 female (11.0mm x 8.7mm), (MNHN-MPB-12527), Rade d'Algar, coll. Lucus, det Bouvier, no collection date; 18 males (9.6-34.8mm x 8.8-30.2mm), 15 females (19.1-34.0mm x 16.5-30.3mm), 1 female (ovigerous) (21.3mm x 19.0mm) (MNHN-MBP-no cat. number), Detroity der Cook, New Zealand, coll. M.H. Filhol, no collection date; 2 males (21.9-28.7mm x 19.5-24.9mm), 3 males (25.7-40.0mm x 22.6-34.4mm) (SFM-11195), Point Howard, Wellington Habour, New Zealand, coll. J.C. Yaldwyn, 28 Nov. 1983; 7 males (19.9-25.3mm x 18.0-27.7mm), 4 females (17.1-21.5mm x 15.9-19.6mm), 2 females (ovigerous) (16.7-20.5mm x 14.8-18.8mm) (SFM-11194), Petone Beach, Wellington Habour, New Zealand, coll. J.C. Yaldwyn, 28 Nov. 1983.

**Diagnosis.**— Carapace distinctly quadrangular, dorsal surface punctate, regions well-defined. Frontal margin straight. Infra-orbital ridge with three distinct granules and smaller granules. Anterolateral margins with three teeth including exorbital tooth. Third maxilliped broad, ischium, merus broad, exopod very narrow. Fingers of cheliped short, thin, without any setae base of fingers with distinct pulvinus. Ambulatory legs short, slender, covered with short setae. G1 long, slender. Female gonopore large, operculate, circular in shape.

**Colour.**— There seems to be two colour forms for the fresh specimens. It can be either a grey or cream-coloured background with markings of light or dark chestnut-red, or dark purple, sometimes almost purplish black with their legs banded (McLay, 1988). All preserved specimens examined are brown in colour. Colour of small crabs variable.

**Size.**— The largest male specimen reported is 57mm x 47mm and largest female specimen reported is 44mm x 38mm in size (McLay, 1988).

**Habitat.**— It can be found under rocks, boulders, on the rocky reef, on sand and mud flats, near river mouth. They are rarely found outside the intertidal zone (McLay, 1988)

**Remarks.**— This species has a long history (see McLay & Schubart, 2004). In their recent publication, McLay & Schubart (2004) synyomized *Brachynotus edwardsii* (Hilgendorf, 1882) from New Zealand with *Hemigrapsus sexdentatus* H. Milne

Edwards, 1837. They have given a very good account of this species with the selection of a neotype, and hence it will not be treated further here.

**Distributions.**— New Zealand only.

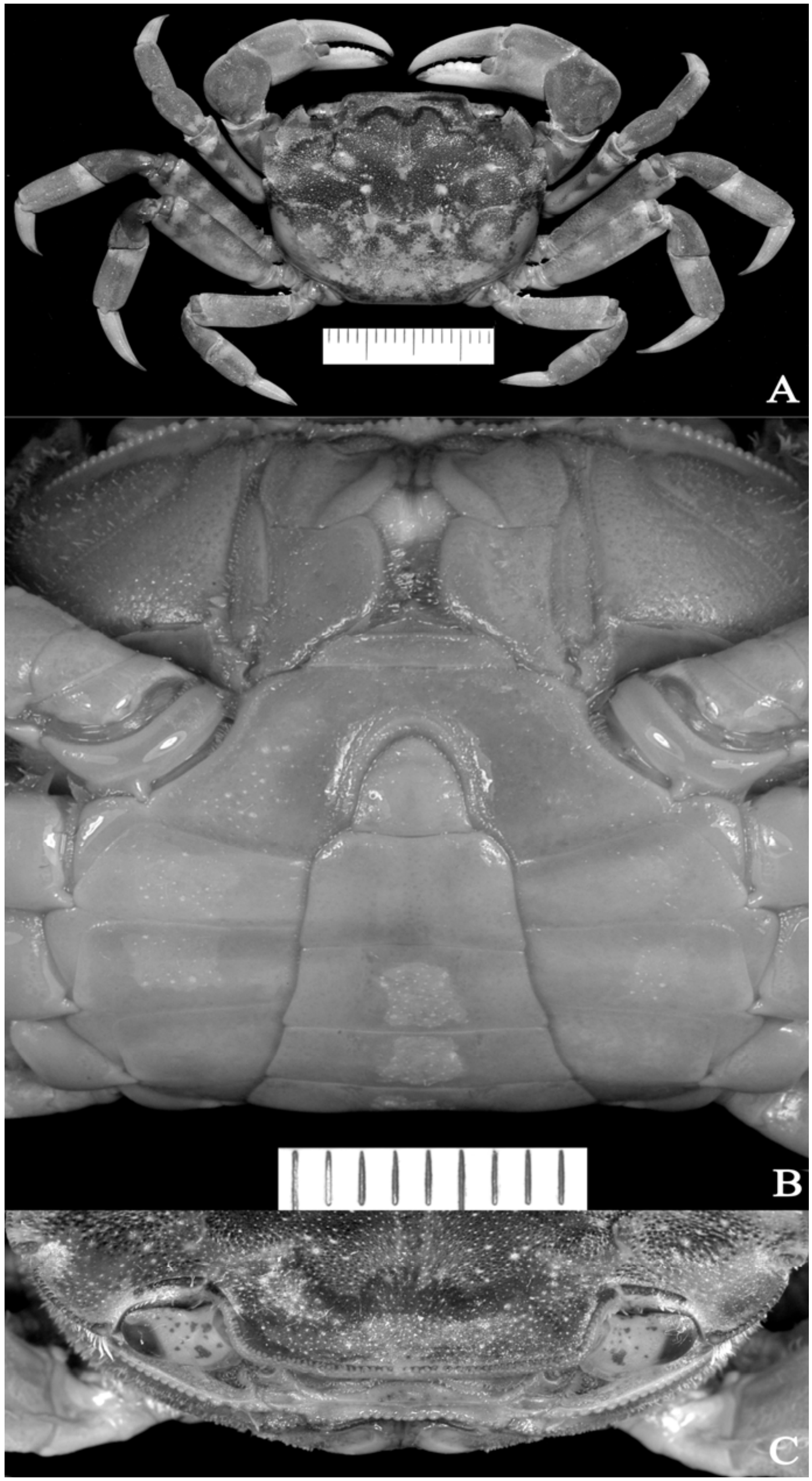



Figure 37. *Hemigrapsus sexdentatus* (H. Milne Edwards, 1837), male 11.5mm x 8.9mm), (MNHN-MPB-12527), A) dorsal view; B) ventral view; C) frontal view.

## Genus *Austrograpsus*, new genus

*Heterograpsus* – H. Milne Edwards, 1853: 194; A. Milne-Edwards, 1874: 82; Kingsley, 1880: 210; de Man, 1891: 56, pl. 4, fig. 15; Ortmann, 1894: 715 (not *Heterograpsus* Lucas, 1849).

*Eriocheir* – Hale, 1927a: 184; 1927b: 312 (not *Eriocheir* De Haan, 1835).

*Brachynotus* –Tweedie, 1942: 57; Griffin, 1969: 88; Griffin, 1969b: 329; Davie, 2002b: 228 (not *Brachynotus* De Haan, 1833).

**Diagnosis.**— Carapace quadrangular, slightly broader than long, surface flat, lateral margins slightly upturned; surface with distinct regions; protogastric, branchial and mesogastric regions. Frontal margin wider than carapace, produced with two lobes, slightly sinuous. Anterolateral margin with four teeth including orbital tooth, three teeth behind orbital tooth closer to each other, second tooth smallest, widest breath of carapace behind last anterolateral tooth. Infra-orbital ridge with numerous rounded granules. Cornea is typically black, but with a white spot (even in preserved specimens). Antennules large; antenna filling entire orbital hiatus. Epistome entire, with lobulations laterally. Third maxilliped very slender, ischium long, narrow; merus relatively broad, gaping. Chelipeds smooth and large, close with a very small gape, setose at the base of fingers. Ambulatory legs glabrous, relatively long, slender. Male abdomen narrow, slender with all segments freely moveable (six somites plus telson).

**Type species.**— *Heterograpsus spinosus* H. Milne Edwards, 1853, by current designation.

**Gender**.— Masculine.

**Etymology.**— ‘Austro’ is the short form of Australia since this species is only found in Australia, and ‘grapsus’ to indicate that it is still phylogentically linked to the Grapsidae.

**Remarks**.— The type species was originally placed in *Heterograpsus*, and later transferred to *Eriocheir* by Hale (1927a, 1927b). Finally, Tweedie (1942) transferred it to *Brachynotus* based probably on the form of the anterolateral teeth and ambulatory legs. However, it is distinctly different from *Brachynotus* and *Hemigrapsus* in the following characters viz. a) the four teeth on anterolateral margin are arranged such that the last three teeth are almost fused, and further away from the orbital tooth (vs. almost equally spaced in *Brachynotus*, and *Hemigrapsus*); b) the widest part of the carapace is at the position of the fourth anterolateral tooth (vs. second anterolateral tooth in *Brachynotus* and *Hemigrapsus*); c) the presence of the white spot on the cornea (vs. absence of the white spot in *Brachynotus* and *Hemigrapsus*); d) the infra-orbital ridge possessing numerous isomorphic granules (vs. presence of heteromorphic granules in *Brachynotus* and *Hemigrapsus*); e) the chela is stout and long (vs. small and stout in *Brachynotus* and *Hemigrapsus*); f) the absence of setae and a pulvinus at the base of the cheliped fingers (vs. presence of setae on the fingers in *Hemigrapsus* and presence of a pulvinus in *Brachynotus*); g) the propodus of the ambulatory legs is proportionately longer and more slender (vs. short and stout in *Brachynotus* and *Hemigrapsus*); h) the merus of the last ambulatory leg has the posterior margin distinctly convex near the proximal end (vs. with a straight margin in *Brachynotus* and *Hemigrapsus*); i) the male abdomen is relatively more slender and narrow (vs. broader in *Brachynotus* and *Hemigrapsus*); j) the G1 is slender (vs. stout G1 in *Brachynotus* and *Hemigrapsus*); and k) the female gonopore is oval in shape and distinctly protruding (vs. round and slightly protruding in *Brachynotus* and *Hemigrapsus*).

The morphology of the carapace of *Austrograpsus* superficially resembles a goneplacid crab, but then again, the family Goneplacidae has been a convenient “dumping ground” for many crabs and is itself in need of a revision. As I understand it, *Austrograpsus* is most closely related to the varunids in habits and morphology and is therefore retained there. Likewise, there are doubts about *Brachynotus* (see above). There is a possibility that *Austrograpsus* (and possibly *Brachynotus* and *Cyrtograpsus* too!) belongs to a separate subfamily within the Varunidae, but there are insufficient grounds to do so at the moment. Although there are numerous characters that strongly suggested the possible placement of this genus in a new subfamily but this genus still retains the characters of a) having the carapace quadrangular in shape; orbits of the eye open laterally; b) third maxillipeds close with a small rhomboid-shaped gap; c) articulation of third maxilliped nearly vertical; d) absence of the oblique setose crest across meri of third maxillipeds, e) absence of complex reticulated setae on the pterygostome, and f) the male gonopore is embedded in sternite 8, no contact with coxa of fifth ambulatory leg and thoracic sternite 7

It is interesting to note that the form of the carapace of *Austrograpsus*, particularly the fourth anterolateral tooth being the largest tooth, and the widest region of the carapace, being at the position of the fourth tooth, is very similar to the genus *Cyrtograpsus* found in South America. However, the two species are distinctly different in the following a) the carapace the form of the third maxillipeds; that of *Austrograpsus* being more slender (vs. broader in *Cyrtograpsus*), and b) the male abdomen is relatively more narrow (vs. broader in *Cyrtograpsus*).

So far, there is only one species in this genus, *Austrograpsus spinosus* (H. Milne Edwards, 1853).

### *Austrograpsus spinosus* (H. Milne Edwards, 1853), new combination

(Figure 38)

*Heterograpsus spinosus* H. Milne Edwards, 1853: 194; A. Milne-Edwards, 1874: 82; Kingsley, 1880: 210; de Man, 1891: 56, pl. 4, fig. 15; Ortmann, 1894: 715.

*Eriocheir spinosus* – Hale, 1927a: 184; 1927b: 312.

*Brachynotus spinosus* –Tweedie, 1942: 16; Griffin, 1969a: 88; Griffin, 1969b: 329; Davie, 2002b: 100.

**Material examined.**— **Lectotype** – 1 male (13.1mm x 11.8mm), 1 female (10.9mm x 9.8mm) (MNHN-MPB-12538), Port Philip Victoria, Australia, leg. Australia Museum, no date. – **Others** – 1 male (14.4mm x 12.6mm) (QM-W12468), Port Victoria, South Australia, coll. P. Davie, 18 Nov. 1983; 1 male (11.6mm x 10.0mm), 1 female (ovigerous) (16.0mm x 13.3mm) (SFM-7305), South West Australia, ex-HMS, leg. D Griffin, no collection date; 5 males (8.4-11.8mm x 7.5-10.0mm), 2 females (10.8-11.2mm x 9.0-10.0mm), 9 females (ovigerous) (9.5-14.9mm x 8.0-12.4mm) (USNM-113547), Howden, northwest bay, South East Tasmania, Australia, coll. D.J.G. Griffin, 10 Nov. 1965; 2 males (14.5-15.3mm x 12.6-13.1mm), 2 females (15.2-17.1mm x 13.1-13.2mm), 2 females (ovigerous) (14.2-16.0mm x 12.8-13.3mm) (USNM-64689), Beaumaris, Port Philip, Victoria, Australia, coll. Mel Hard, Jan. 1926; 5 males (9.8-12.1mm x 8.6-11.2mm), 5 females (12.4-15.2mm x 10.1-12.4mm) plus numerous specimens (USNM-64707), shore at Bellerive, Derwent River, Tasmania, coll. Jul. 1926.

**Diagnosis.**— Carapace subquadrate, slightly broader than long, surface flat, regions well defined. Frontal region granulated, frontal margin produced, bilobed. Anterolateral margin with four teeth including orbital tooth, three teeth behind orbital tooth closer to each other, second tooth smallest, widest breath of carapace behind last anterolateral tooth. Infra-orbital ridge with numerous rounded granules. Cornea is typically black, but with a white spot. Chelipeds normal in male, surfaces smooth with setae at base of fingers, setae absent in females. Ambulatory legs short, very flat, with a small subdistal spine on anterior margin of merus. G1 stout. Female gonopore operculate, oval in shape.

**Colour.**— The colour of fresh specimens is dull green or brown in colour, sometimes with white markings (Tweedie, 1942), all preserved specimens examined are brown in colour.

**Size.**— The largest male specimen examined is 15.3mm x 13.1mm (USNM-64689), and the largest female examined is 16.0mm x 13.3mm (USNM-113547).

**Habitat.**— It can be found  in the inter-tidal area, rocky, muddy and sandy shore or under small stones or driftwood (P. Davie, pers. comm.)

**Remarks.**— Examination of the species has shown that it is an unusual varunid, in the form of the carapace in having the broadest region of the carapace at the position of the fourth anterolateral tooth, and the largest anterolateral tooth is the fourth tooth (see above). There is the possibility that *Austrograpsus spinosus* and *Cyrtograpsus angulatus* could have come from the same ancestral form and have been separated by the vicariance events (see above, and see Discussion below). This species is found only in Tasmania, and nearby areas, suggesting that it is very likely a coldwater species.

**Distribution.**— Australia only.

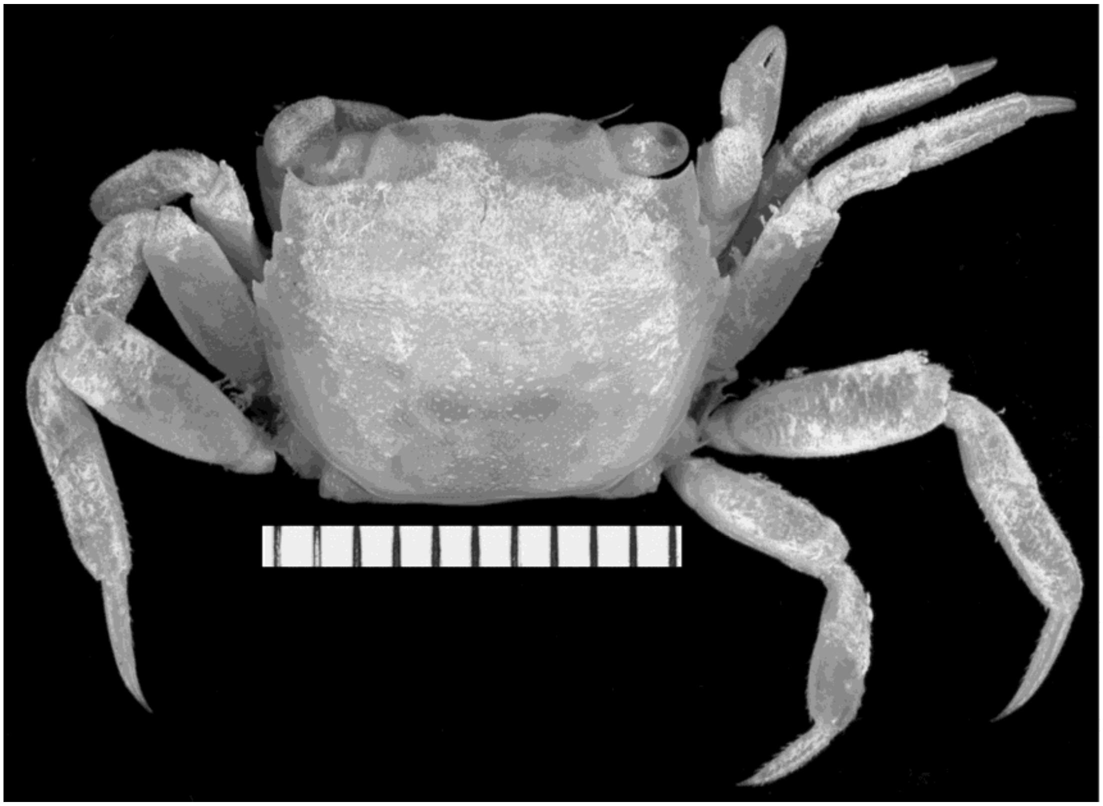


Figure 38. *Austrograpsus spinosus* (H. Milne Edwards, 1853), male, 14.4mm x 12.6mm (QM-W12468), Dorsal view.

## Genus *Asiagrapsus*, new genus

*Hemigrapsus* – Dana, 1852: 250; 1852: 350; 1855: pl. 22, fig. 5; Rathbun, 1918: 264; Rathbun, 1929: 89, pl. 14, fig. 46-47; Shen, 1935: 25, text-fig. 5-6; Shen & Dai, 1964: 126; Kim, 1973: 475; Dai *et al.*, 1986: 479, text-fig. 4, pl.67, fig. 6; Dai & Yang, 1991: 526, text-fig. 269 (part).

**Diagnosis.**— Carapace quadranular, only very slightly broader than long, gently convex, lateral margins slightly upturned; surface with distinct regions; protogastric, branchial, mesogastric regions elevated, surface granulated and setose. Frontal margin about half as wide as carapace, very convex with two lobes, slightly sinuous. Anterolateral margin with three teeth including external orbital tooth. Antennules large; antenna filling entire orbital hiatus. Epistome entire, with lobulations laterally. Third maxilliped slender, ischium long, narrow; merus relatively broad, gaping. Granules present on dorsal margin of chela; fingers of cheliped closing without a gape; densely setose only on outer surface of cheliped. Ambulatory legs slighty setose, relatively long, slender. Male abdomen narrow, slender, with all segments freely moveable (six somites plus telson). G1 long, slender. Female gonopore operculate, circular in shape.

**Type species.**— *Hemigrapsus sinensis* Rathbun, 1929, by current designation.

**Gender.**— Masculine.

**Etymology.— '**Asia' is used since it is found in east Asia, 'Grapsus' is to show its close phylogenetic link to the grapsid crabs.

**Remarks**.— *Hemigrapsus sinensis* Rathbun, 1929, was originally placed in *Hemigrapsus* (type species *H. crassimanus* Dana, 1852). The description provided by Rathbun (1929) on this species was very brief and the photograph provided was also not very clear. Furthermore, the descriptions provided by Rathbun was based on a juvenile female specimen, which render it almost useless since all the females in the genus

*Hemigrapsus* senu lato are very similar to each other. In the same report, Rathbun gave a very short comparison between this species and *Hemigrapsus penicillatus* (De Haan, 1835) and *Pseudograpsus pallipes* (H. Milne Edwards, 1837), but the comparison did not provide any insight into the identity of *H. sinensis*. Subsequently, Shen (1935) provided a detailed description of the male and females specimens, and showed that this is a valid taxa. I have checked the specimens that were examined by Shen in 1996 and 1999 which are housed in the Institute of Zoology, The Chinese Academy of Sciences, Beijing, and these specimens are the same as the holotype specimen which I had examined in the USNM.

The genus is different from *Hemigrapsus* in the following characters viz. a) possessing a granulated and setose carapace surface (vs. smooth surface in *Hemigrapsus*); b) the orbit is very oblique (vs. normal, straight orbit in *Hemigrapsus*); c) the presence of setae only on the outer surface of the chellipeds (vs. presence of setae on the outer and inner surfaces of the chelipeds in *Hemigrapsus*), and d) the presence of three longitudinal rows of granules on the upper outer surface of chelipeds (vs. absent in *Hemigrapsus*).

It is distinctly different from *Brachynotus* in having a) a granulated and setose carapace (vs. smooth and not defined carapace in *Brachynotus*); b) broad anterolateral teeth (vs. narrow anterolateral teeth in *Brachynotus*); c) absence of a pulvinus at the base of the fingers (vs. presence of pulvinus in *Brachynotus*), and d) presence a tuft of setae on the outer surface of the chelipeds (vs. absent in *Brachynotus*).

*Asiagrapsus* is different from *Pseudograpsus* in the following characters viz. a) having a granulated and setose carapace (vs. smooth surface in *Pseudograpsus*); b) proportionately narrow male abdomen (vs. broader male abdomen in *Pseudograpsus*), and c) the very small size when mature, male is 11.1mm x 9.5mm (SFM-ex. T. Sakai collection), female is 12.0mm x 10.1mm (holotype) (vs. large size in *Pseudograpsus*, mature male is 46.0mm x 40.0mm, mature female is 35.0mm x 31.5mm) (SFM-5317).

*Asiagrapsus* is also very similar to *Noarograpsus* in the form of the carapace but it can be discerned by the following characters viz. a) the carapace being distinctly broader than long (vs. only slightly broader than long in *Noarograpsus*); b) presence of granules and setae on the carapace (vs. presence of only granules on the carapace in *Noarograpsus*); c) the granules are present throughout the carapace (vs. granules are present only at distinct regions on the carapace in *Noarograpsus*); d) presence of setae only on the outer surface of the chelipeds (vs. presence of setae on the inner surface of the chelipeds in *Noarograpsus*), and e) the presence of three longitudinal rows of granules on the upper outer surface of chelipeds (vs. absent in *Noarograpsus*).

The genus *Asiagrapsus* is similar to *Ptychognathus* sensu lato in having a tuft of setae on the outer surface of the chelipeds and its small size, but it is distinctly different from *Ptychognathus* sensu lato by the following characters viz. a) the carapace is more rounded (vs. distinctly quadrangular in *Ptychognathus*); b) the granulated and setose carapace surface (vs. smooth carapace surface in *Ptychognathus*); c) the relatively narrow exopod of the third maxilliped (vs. large and convex exopods of the third maxillipeds in *Ptychognathus*), and d) the broader male abdomen (vs. a narrower male abdomen).

*Asiagrapsus* is similar to *Pyxidognathus* in having the sculptured carapace but is different in having a) a flat carapace (vs. very convex carapace in *Pyxidognathus*); b) a narrow ischium of the third maxilliped (vs. broader ischium in *Pyxidognathus*), and c) the absence of spines on the posterior margins of the merus of the ambulatory legs (vs. presence of such spines in *Pyxidognathus*).

### *Asiagrapsus sinensis* (Rathbun, 1929), new combination

(Figures 39; 40A-I)

*Hemigrapsus sinensis* Rathbun, 1929: 89, pl. 14, fig. 46-47; Shen, 1935: 25, text-fig. 5-6; Shen & Dai, 1964: 126; Sakai, 1955: 112; 1976: 651, pl. 222, fig. 309; Kim, 1973: 476, text-fig. 207 pl. 43, fig. 161; Dai *et al.*, 1986: 479, text-fig. 4, pl.67, fig. 6; Dai & Yang, 1991: 526, text-fig. 269.

**Material examined.**— **Holotype** – 1 female (12.0mm x 10.1mm) (USNM-61877), Santu, Fukien Province, China, coll. S.L. Light, Sep. 1923. – **Paratype** – 1 female (10.4mm x 8.8mm) (USNM-61877), Santu, Fukien Province, China, coll. S.L. Light, Sep. 1923. – **Others** – **China** – 1 male (6.3mm x 5.4mm), 1 female (5.8mm x 4.9mm) (ASIZ-uncatalogued), Qingdao, China, coll. 25 May 1977; 1 male (7.2-9.6mm x 6.1-8.5mm) (ASIZ-02439), no other information; 6 males (4.3-7.2mm x 3.7-6.1mm) (ASIZ-no cat. number), Qingdao, China, coll. Oct. 1931; 1 female (ovigerous) (6.9mm x 5.8mm) (ASIZ-02440), no other information; 5 females (7.9-9.0mm x 6.7-8.0mm), (ASIZ-C02438), Zhanjiaodong, Qingdao, China, no other information; 1 male (5.9mm x 5.1mm), 4 females (ovigerous) (4.5-7.3mm x 3.7-5.8mm), (ASIZ-C2437), Longmen, Tuozhou, Guangxi, China, coll. 28 Mar. 1981; 1 female (9.6mm x 8.0mm) (BNHM-J88-134), Fuqing habour, Fujian, China, coll. 13 Apr. 1976; 1 male (6.8mm x 6.0mm) (BNHM-J95-066), Xiajia, Dalian, coll. 16 Jul. 1995; 2 males (8.3-9.3mm x 7.2-8.0mm), 4 females (5.7-6.5mm x 4.9-5.5mm), 1 female (ovigerous) (10.0mm x 8.3mm) (BNHM-J81-0021), Qingdao, China, coll. 25 May 1977. – **Japan** – 3 males (5.5-6.6mm x 4.9-5.9mm), 8 females (5.0-11.8mm x 4.5-10.0mm) (RMNH-no cat. number), Aziike Bay, Mizhuho, northwest of Simabra, Kyushu, Japan, coll. T. Sakai & L.B. Holthuis, 8 Sep. 1968; 5 males (7.2-10.0mm x 6.3-8.0mm), 8 females (5.4-7.2mm x 4.1-6.3mm) (SFM-ex. T. Sakai collection), Japan, coll. 14 Aug. 1962; 1 male (11.1mm x 9.5mm), 1 female (10.4mm x 9.2mm) (SFM-ex. T. Sakai collection), no other data.

**Diagnosis.**— Carapace subquadrate, slightly broader than long, surface granulated, setose. Anterolateral margin with four teeth including orbital tooth. Infraorbital ridge very strongly oblique, with six or seven granules, a gap, and ending with four or five small granules. Chelipeds large in male, with a patch of setae only on outer surface of chelipeds, absent in females. Ambulatory legs short, flat, with a small subdistal spine on anterior margin of merus. G1 stout, distal process distinctly lower than apical process. Female gonopore operculate, with circular in shape.

**Colour.**— The colour of fresh material has not been documented but all the preserved specimens examined are light brown in colour.

**Size.**— This species is very small size animal, the largest male specimen examined is 11.1mm x 9.5mm (SFM-ex. T. Sakai collections), and mm 10.4mm x 9.2mm (SFM-ex. T. Sakai collections).

**Habitat.**— It can be found under rocks on sandy and/or mudflats (S.H. Fang, pers. comm.).

**Remarks.**— There is very little information on the biology of this species, and seems to be rather rare as there are very few specimens in museums. I have gone to the type locality and its surrounding area to collect fresh materials but without much success. The local villagers and fishermen told me that this species used to be very abundant, but the population declined since the 1970s.

**Distribution.**— East coast of China, Japan, and Korea.

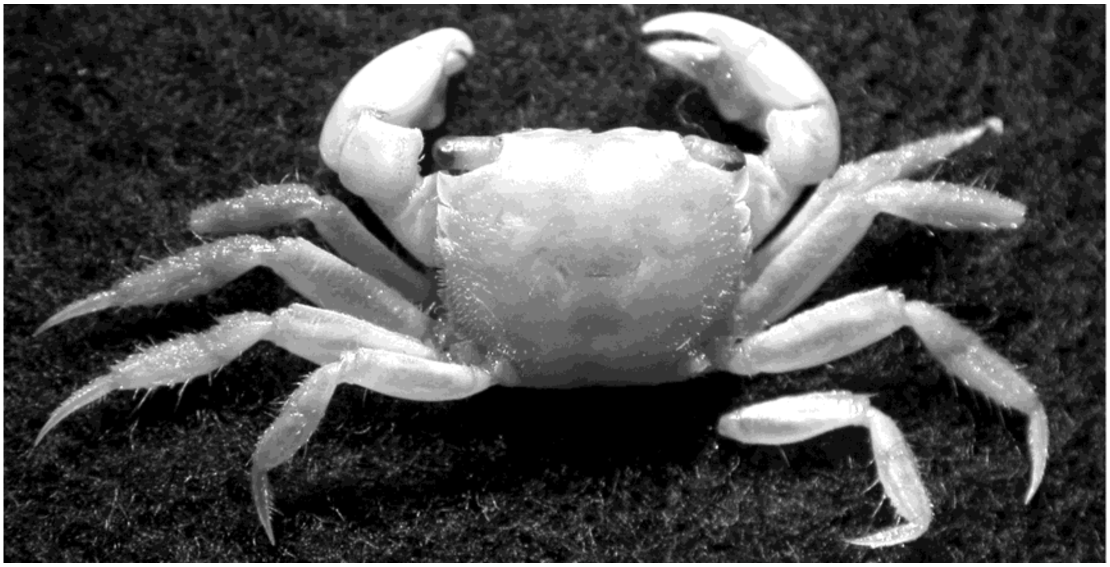


Figure 39. *Asiagrapsus sinensis* (Rathbun, 1929), female, holotype, 12.0mm x 10.1mm (USNM-61877). Dorsal view.

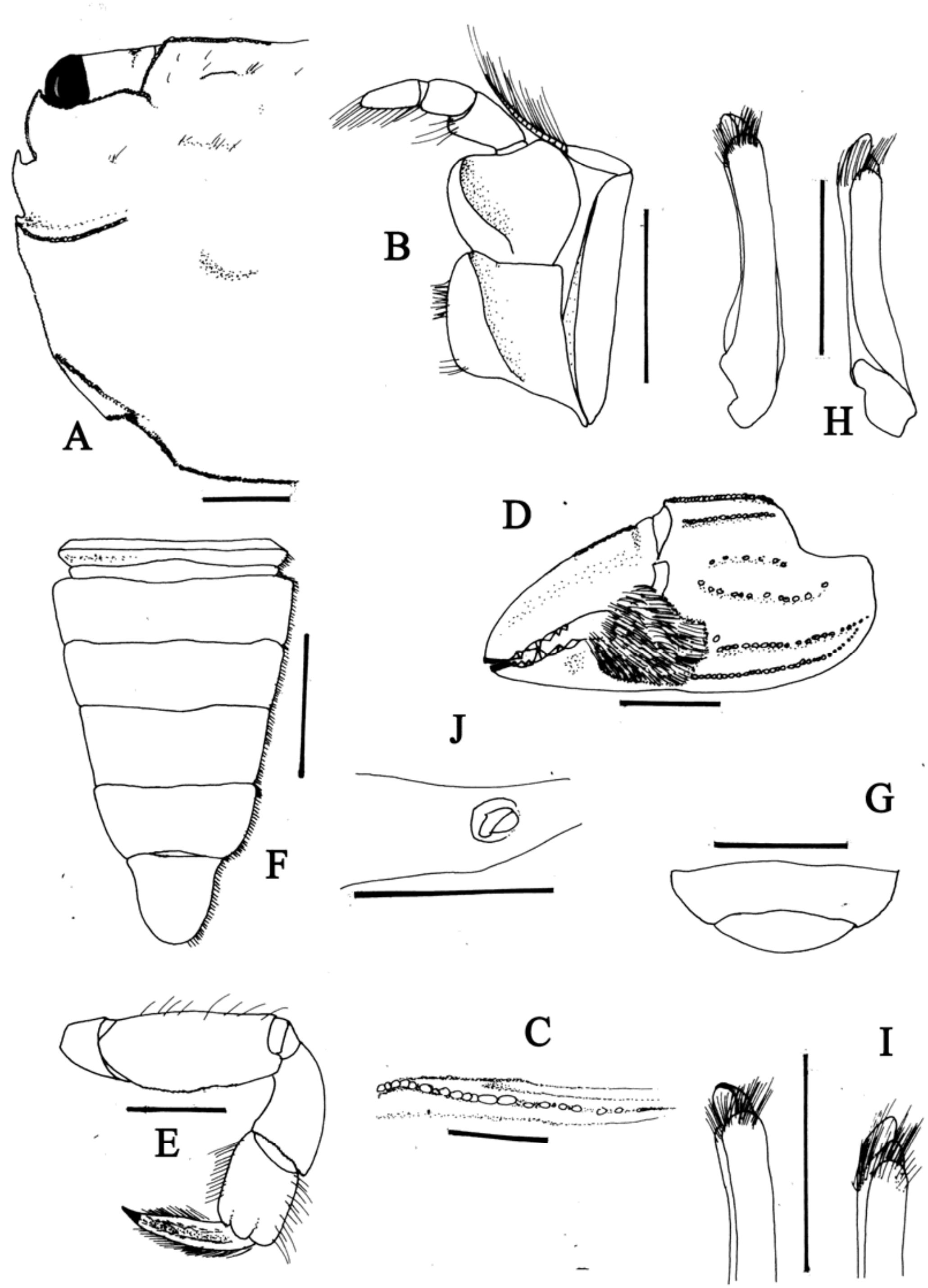



Figure 27. *Asiagrapsus sinensis* (Rathbun, 1929), male, 6.3mm x 5.4mm, female, 5.8mm x 4.9mm. (ASIZ-uncatalogued). A) male carapace; B) third maxilliped; C) infra-orbital ridge; D) frontal view of cheliped; E) last ambulatory leg; F) male abdomen; G) female abdomen (part); H) G1; I) tips of G1; J) female gonopore. (Scale=1.0mm).

## Genus *Papyrograpsus,* new genus

*Heterograpsus* – Ortmann, 1894: 715 (not *Heterograpsus* Lucas, 1846).

*Eriocheir* – Rathbun, 1919: 593, pl. 23 (not *Eriocheir* De Haan, 1835).

*Brachynotus* – Balss, 1922: 151 (not *Bachynotus* De Haan, 1933)

*Hemigrapsus* – Dana, 1852: 250; 1852: 350; 1855: pl. 22, fig. 5; Rathbun, 1918: 264; Shen, 1932: 168, text-fig. 106, pl. 7, fig. 3; Sakai, 1939: 674, pl. 75, fig. 2; 1976: 651, text-fig. 357; Shen & Dai, 1964: 127; Kim, 1973: 475; Dai *et al.*, 1986: 480; Dai & Yang, 1991: 526, text-fig. 270, fig. 1-2; Guo *et al*, 1997: 451 (not *Hemigrapsus* Dana, 1852).

**Type species.**— *Heterograpsus longitaris* Miers, 1879, by present designation.

**Gender**.— Masculine.

**Diagnosis.**— Carapace squarish in shape, as broad as wide; dorsal surface setose, pilose, regions not very well defined, slightly convex. Frontal margin very produced forward, straight. Anterolateral margin subcristate with four teeth including orbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, slightly convex at branchial region, distinctly subparallel. Orbits small, eyes not completely filling orbit. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Inner surface of chela with granules; Chelipeds small, outer surface of cheliped with four rows of granules, manus with tuft of setae, on outer and inner surface, abscent in female. Ambulatory legs with setose, dactylus very long, longer than propodus, recurved. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular, with all segments freely moveable (six somites plus telson).

**Etymology.**— "Papyro' is the Greek term for 'paper', alluring to the very thin carapace, like crisp paper, of the crab after preservation. It is used as an adjective with 'Grapsus', indicating its phylogentical link to the ‘Grapsus’. Interestingly, all the specimens I have examined from the different lost have this papery thin carapace.

**Remarks.**— This species was originally placed in *Heterograpsus* by Miers (1879). Rathbun described the same species under a different name, *Eriocheir misakiensis* in 1919.

The genus is different from *Hemigrapsus* by the following characters viz. a) the carapace dorsal surface is pilose (vs. smooth surface in *Hemigrapsus*); b) the carapace is distinctly squarish in shape (vs. quadrangular in shape in *Hemigrapsus*); c) the ischium of the third maxilliped as broad as wide (vs. slender and narrow in *Hemigrapsus*); d) the presence of four longitudinal rows of granules on the outer outer surface of the chelipeds (vs. absent in *Hemigrapsus*), and e) the dactyli of the ambulatory legs is much longer than propodus (vs. shorter dactyli in *Hemigrapsus*).

It is different from *Brachynotus* in having viz. a) a pilose and not defined carapace surface (vs. smooth and defined carapace in *Brachynotus*); b) the carapace is distinctly squarish in shape (vs. quadrangular in *Brachynotus*); c) the very broad anterolateral teeth (vs. acute anterolateral teeth in *Brachynotus*); d) the absence of a pulvinus at the base of the fingers (vs. presence of pulvinus in *Brachynotus*); e) the presence a tuft of setae on the outer and inner surfaces of the chelipeds (vs. absence in *Brachynotus*), and f) the dactylus of ambulatory legs being much longer than the propodus (vs. relatively shorter dactylus in *Brachynotus*).

The genus is different from a *Pseudograpsus* in the following characters viz. a) pilose carapace surface (vs. smooth surface in *Pseudograpsus*); b) the carapace being distinctly squarish in shape (vs. quadrangular in *Pseudograpsus*); c) the presence of soft setae on the outer surface of chelipeds (vs. long, stiff setae in *Pseudograpsus setosus*, and glabrous in *Pseudograpsus crassus*); d) the narrow male abdomen (vs. broader male abdomen in *Pseudograpsus*), and e) the dactyli of ambulatory legs being much longer than propodi (vs. proportionately shorter dactyli in *Pseudograpsus*).

The genus is very similar to *Noarograpsus* in the form of the carapace but it can be discerned by the following characters viz. a) the carapace being distinctly as broad as wide (vs. only slightly broader than long in *Noarograpsus*); b) the pilose carapace surface (vs. granulated carapace in *Noarograpsus*); c) the presence of setae only on the outer surface of the chellipeds (vs. presence of setae on the inner surface of the chelipeds in *Noarograpsus*); d) the presence of four longitudinal rows of granules on the outer surface of chelipeds (vs. absent in *Noarograpsus*), and e) the dactyli of ambulatory legs is much longer than the propodi (vs. proportionately shorter dactyli in *Noarograpsus*).

The new genus is different from *Ptychognathus* sensu lato in the following characters viz. a) carapace is squarish (vs. distinctly quadrangular in *Ptychognathus*); b) the pilose, and setose carapace surface (vs. smooth carapace surface in *Ptychogtathus*); c) the narrow exopod of the third maxilliped (vs. large and convex exopod of the third maxilliped in *Ptychognathus*); d) the broader male abdomen (vs. a narrower male abdomen), and e) the dactyli of ambulatory legs being much longer than the propodi (vs. proportionately shorter dactyli in *Ptychognathus*).

The new genus is similar to *Pyxidognathus* in having the sculptured carapace but it is different in having a) a flat carapace (vs. very convex in *Pyxidognathus*); b) the presence of setae on the outer and inner surfaces of chelipeds (vs. absence of setae in *Pyxidognathus*); c) the absence of spines on the posterior margins of the merus of the ambulatory legs (vs. presence of spines in *Pyxidognathus*), and d) the dactyli of the ambulatory legs is much longer than the propodi (vs. proportionately shorter dactyli in *Pyxidognathus*).

### *Papyrograpsus longitaris* (Miers, 1879), new combination

(Figures 41; 42A-I)

*Heterograpsus longitarsis* Miers, 1879: 37, pl. 2 fig. 3; Ortmann, 1894: 715.

*Brachynotus longitarsis* – Balss, 1922: 151.

*Hemigrapsus longitaris* – Shen, 1932: 168, text-fig. 106, pl. 7, fig. 3; Sakai, 1939: 674, pl. 75, fig. 2; 1976: 651, text-fig. 357; Shen & Dai, 1964: 127; Kim, 1973: 475, text-fig. 208, pl. 94, fig. 160; Dai *et al.*, 1986: 480; Dai & Yang, 1991: 526, text-fig. 270, fig. 1-2; Guo *et al.*, 1997: 451.

*Eriocheir misakiensis* Rathbun, 1919: 593, pl. 23.

**Material examined.**— **China** – 1 male (6.5mm x 6.4mm), 1 female (8.4mm x 8.4mm) (ASIZ-no cat. number), Yandai, Shangdong Province, coll. 13 Apr. 1936; 1 female (11.2mm x 11.0mm) (ASIZ-no cat. number), Tong Yu Tang, Dalian, coll. 12 Jul. 1992; 1 female (5.4mm x 5.2mm) (BNHM-J96-149), Long Yu Tang, Dalian, coll. 27 Jul. 1995; 2 females (8.8-14.0mm x 8.5-13.0mm (QIH-no cat. number), no locality, coll. 27 Oct. 1958; 2 females (9.9-11.2mm x 9.7-10.4mm), (QIH-no cat. number), Yandai, Shangdong Province, coll. 16 Jan. 1948; 1 male (11.8mm x 11.5mm), 1 female (10.8mm x 10.5mm) (QIH-no cat. number), Qingdao, Shangdong Province, coll. 27 Nov. 1958; 1 female (9.1mm x 8.8mm) (QIH-no cat. number), K292, no collection data; 1 male (13.2mm x 13.0mm), 8 females (8.5-18.3mm x 8.3-13.2mm) (QIH-no cat. number), K334a, no collection date. – **Japan** – 8 females (7.5-10.2mm x 5.8-8.9mm) (SFM-ex. T. Sakai collections), Japan, coll. T. Sakai, no collection date; 1 female (13.2mm x 12.5mm), 1 female (ovigerous) (14.4mm x 13.9mm) (SFM-ex. T. Sakai collection), Japan, no collection date.

**Diagnosis.**— Carapace squarish in shape, as broad as wide, surface pilose, setose. Anterolateral margin with four teeth including orbital tooth. Frontal margin very produced forward, straight. Infraorbital ridge with four to six smooth tubercules. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Chelipeds small, inner surface of chela with granules, outer surface of cheliped with four rows of granules, manus with tuft of setae, on outer and inner surface, absent in female. Ambulatory legs short, flat, setose, with a small subdistal spine on anterior margin of merus, dactylus very long, much longer than propodus. Male abdomen broadly triangular with all segments freely moveable (six somites plus telson). G1 stout, distal process with a V-shaped notch. Female gonopore operculate, circular in shape.

**Colour.**— The colour fresh specimens has not been documented but all the preserved specimens examined are all light brown in colour, the specimens examined are all very soft and papery to touch.

**Size.**— The largest male specimen examined is 13.2mm x 13.0mm (QIH-no cat. number), and the largest female specimen examined is 18.3mm x 13.2mm (QIH-no cat. number).

**Habitat.**— It can be found under rocks on sandy and/or mudflats near river mouths (H.L. Chen, pers. comm.).

**Remarks.**— The species is very distinctly different from species in *Hemigrapsus* sensu lato in that the carapace of all the preserved specimens are very thin and fragile, like crisp-paper. They are not commonly found, and there are very few specimens available in the various museums. There is very little information of the biology of this species.

Miers (1879) has provided a detailed description and figures that leave no doubt about its identity. In the year 2000, I have tried to loan the type specimens, which should be kept in the British Museum, for examination. The curator has not been able to locate the specimens, it is not lost but probably misplaced (M. Lowe, pers. comm.). Since the curator is still in the process of locating the type materials, I will not designate any neotype or lectotype in this report.

**Distribution.**— Taiwan, China, Japan, Korea.

Figure 41. *Papyrograpsus longitaris* (Miers, 1879), male (AMNH) (Courtesy of Peter K.L.Ng)

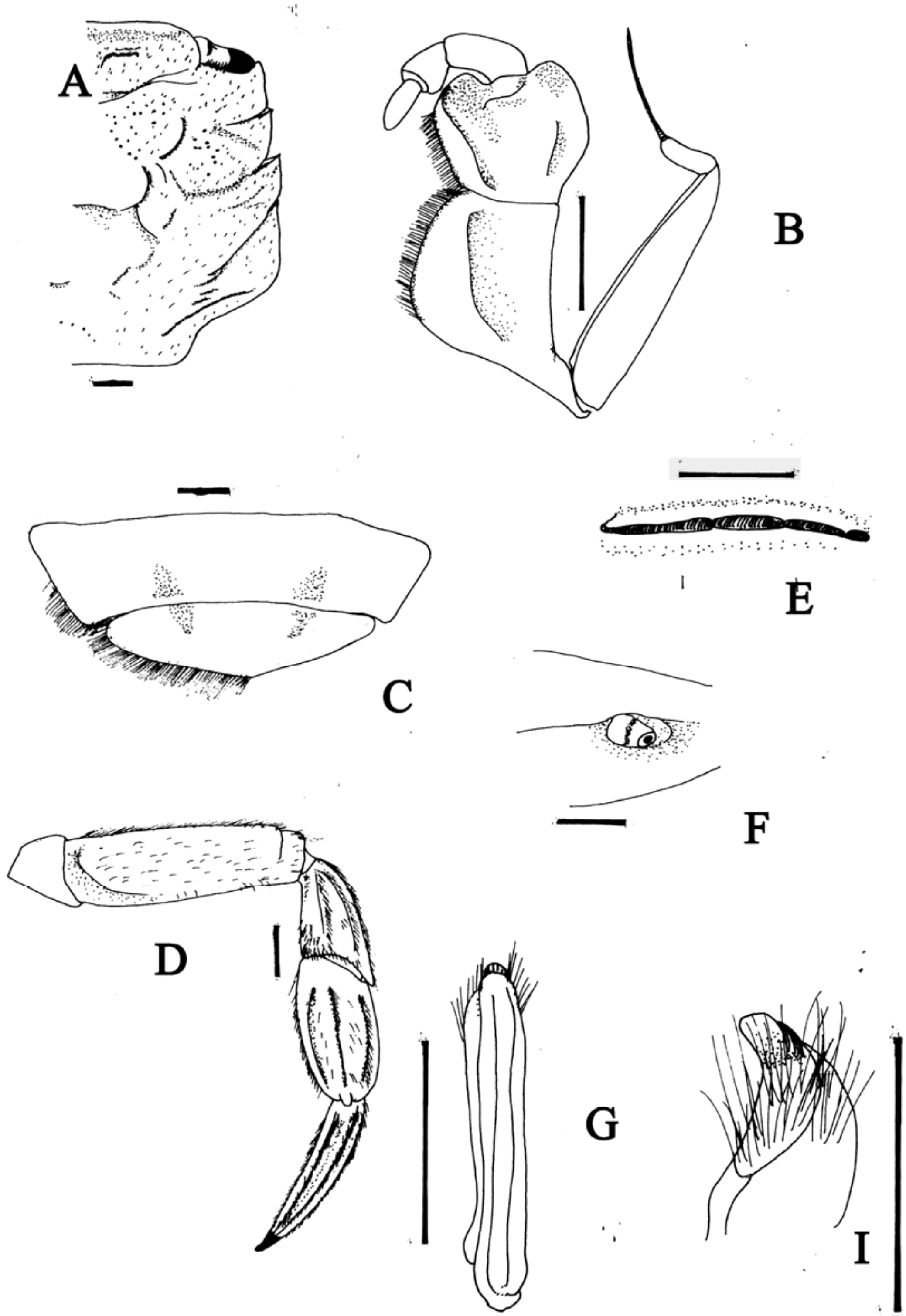



Figure 42. *Papyrograpsus longitaris* (Miers, 1879), male, 6.5mm x 6.4mm, 1 female, 8.4mm x 8.4mm (ASIZ-no cat. number). A) male carapace; B) third maxilliped; C) female abdomen; D) male last ambulatory leg; E) male infra-orbital ridge; F) female gonopore;G) G1; I) tip of G1. (Scale=1.0mm).

## *Noarograpsus* Ng, Manuel & Ng, 2006

*Hemigrapsus* – Manuel, Gonzales & Basmayor, 1991: 91 (not *Hemigrapsus* Dana, 1852).
*Noarograpsus* Ng, Manuel & Ng, 2006: 49.

**Diagnosis.**— Carapace subcircular, slightly broader than long, gently convex, lateral margins slightly upturned; surface with distinct regions; protogastric, branchial and mesogastric regions elevated, each region with numerous clumps of granules of different sizes; cardiac region with a single high, granulated crista. Frontal margin ca. half as wide as carapace, very convex with two lobes, slightly sinuous. Anterolateral margin with three teeth including external orbital tooth. Antennules large; antenna filling entire orbital hiatus. Epistome entire, with lobulations laterally. Third maxilliped slender, ischium long, narrow; merus relatively broad, gaping. Granules present on dorsal margin of chela; fingers of cheliped closing without a gape; densely setose on inner surface. Ambulatory legs glabrous, relatively long, slender. Male abdomen narrow, slender, with all segments freely moveable (six somites plus telson).

**Type species.**— *Hemigrapsus lobulatus* Manuel, Gonzales & Basmayor, 1991, by original designation.

**Gender.**— Masculine.

**Remarks**.— This species was originally placed in *Hemigrapsus* Dana, 1852, but detailed comparisons of *Hemigrapsus lobulatus* with recognized *Hemigrapsus* species showed that this species is different from *Hemigrapsus* sensu stricto or its allies in the following a) in having a distinctly granulated surface with the regions well demarcated (vs. relatively smooth dorsal carapace surface in which the regions are not well demarcated in *Hemigrapsus*); b) the frontal margin is very convex and sinuous (vs. almost straight in *Hemigrapsus*), and c) the inner margins of the third maxilliped close with a small but distinct rhomboidal gap (vs. a even smaller gap in *Hemigrapsus*).

*Hemigrapsus lobulatus* also bears a superficial resemblance to species of *Brachynotus* De Haan, 1835, but is different in a) having a distinctly granulated regions on dorsal carapace (vs. relatively smooth dorsal carapace surface in which the regions are not clearly demarcated in *Brachynotus*); b) a carapace which is slightly broader than long, subcircular (vs. distinctly broader than long, quadrangular in *Brachynotus*), and c) the absence of a pulvinus and setae on the outer surface of the male chela (vs. having both a pulvinus, a small pulvinus at the base of dactylus, and setae on the outer surface of the male chela in *Brachynotus*).

*Hemigrapsus lobulatus* is also similar to species of *Pseudograpsus* H. Milne Edwards, 1837 but it is different in the following features a) carapace slightly broader than long (vs. length and width are sub-equal or with either width or length slightly greater than the other in *Pseudograpsus*); b) the dorsal carapace surface is very granulated with distinct inter-regional grooves (vs. distinctly smoother carapace with less well defined grooves in *Pseudograpsus*); c) the more inflated dorsal carapace with epigastric cristae (vs. the flattened dorsal carapace surface without epigastric cristae in *Pseudograpsus*); d) having a prominently produced front (vs. not well produced front in *Pseudograpsus*); e) the fingers of adult male chela close with no gap or very small gap (vs. distinct gap in *Pseudograpsus*); f) all the ambulatory leg surfaces and margins are glabrous (vs. setose in *Pseudograpsus*); g) the male abdomen is proportionately narrow and more slender (vs. broader male abdomen in *Pseudograpsus*); h) the presence of rounded granules on the dorsal margins of the chela (vs. smooth in *Pseudograpsus*); and i) the lateral margins of the third thoracic sternite are granulated (vs. smooth in *Pseudograpsus*).

*Hemigrapsus lobulatus* is actually closer to species of *Scutumara* Ng & Nakasone, 1993. Nevertheless, *Noarograpsus* is different in the following features a) dorsal surface of the carapace being granulated with clearly demarcated inter-regional grooves (vs. smooth surface without discernible grooves in *Scutumara*); b) the carapace is relatively more inflated with the dorsal surface more prominently convex; the front is more strongly produced; the presence of strong, granulated cristae on the gastric, hepatic, branchial, cardiac and intestinal regions (vs. flat, smooth, front not produced, without distinct cristae on the various regions in *Pseudograpsus*); c) the proportionately more slender third maxilliped (vs. stout in *Pseudograpsus*); d) the presence of short, soft setae on the inner surfaces of the chela (vs. absent in *Pseudograpsus*); e) the presence of rounded granules on the dorsal margins of the chelae (vs. absence in *Pseudograpsus*); f) the granulated lateral margins of the third thoracic sternite (vs. smooth in *Pseudograpsus*); and g) the relatively larger penis (vs. small, slender penis in *Pseudograpsus*).

This species also resembles members of *Pyxidognathus*, especially the type species *P. granulosus* A. Milne-Edwards, 1879. However, *Hemigrapsus lobulatus* can be separated by the following features a) its relatively less convex dorsal carapace surface (vs. very swollen carapace in *Pyxidognathus*, the front view of *Pyxidognathus* appearing almost semi-globular); b) the exopod of the third maxilliped is long and slender, being more slender that the ischium (vs. stout and broad exopod, broader and stouter than ischium in *Pyxidognathus*); c) the chelipeds of males are densely setose on the inner surfaces (vs. glabrous); and d) the absence of spines on the posterior margins of the merus of the ambulatory legs (vs. presence of 1-3 short spines in *Pyxidognathus*) (see Tesch, 1918).

These differences are significant enough at the generic level, and that Ng *et al*. (2006) placed *Hemigrapsus lobulatus* in its own monotypic genus, *Noarograpsus*.

## *Noarograpsus lobulatus* (Manuel, Gonzales & Basmayor, 1991)

(Figures 43A-D; 44A-M; 45A-G)

*Hemigrapsus lobulatus* Manuel, Gonzales & Basmayor, 1991: 91, pl. 3.

*Noarograpsus lobulatus* – Ng *et al.*, 2006: 49.

**Materials.**— **Holotype** – 1 male (8.5mm x 7.5mm) (NMCR-6383), Natuanan Cove, Tabaco, Albay, Philippines, coll. P.C. Gonzales, 23 Aug. 1979. – **Paratypes** – 1 male (7.5mm x 7.0mm) (NMCR-9838), Natuanan Cove, Tabaco, Albay, Philippines, coll. P.C. Gonzales, 7 Jun. 1979; 1 female (7.5mm x 7.0mm) (ZRC 2001.2353), Natuanan Cove, Tabaco, Albay, Philippines, coll. P.C. Gonzales, 7 Jun. 1979 – **Others** – 1 male (7.8mm x 7.2mm) (NMCR-5674), Natuanan Cove, Tabaco, Albay, Philippines, coll. P.C. Gonzales, 7 May 1979; 1 male (7.5mm x 7.0mm) (ZRC 2001.2352), Natuanan Cove, Tabaco, Albay, Philippines, coll. P.C. Gonzales, 7 May 1979; 1 male (6.5mm x 5.5 mm) (NMCR-9830), Natuanan Cove, Tabaco, Albay, Philippines, coll. P.C. Gonzales, 7 May 1979; 1 male (8.5mm x 7.5 mm) (NMCR-9836), Natuanan Cove, Tabaco, Albay, Philippines, coll. P. C. Gonzales, 8 May 1979; 1 male (7.0mm x 6.5mm) (NMCR-9839), Natuanan Cove, Tabaco, Albay, Philippines, coll. P.C. Gonzales, 2 May 1979; 3 males 4 females (ZRC-uncatalogued), Albay, Philippines, coll. A. Deismos, Aug. 2005.

**Diagnosis.**—. Carapace slightly broader than long; dorsal surface granulated, glabrous; regions well defined, strongly convex transversely and longitudinally; each region elevated, with numerous granules, forming clumps of different sizes. Frontal margin very convex, divided into two lobes, median two lobes separated by a wide sinus, lateral lobes not clearly visible dorsally, slightly deflexed downwards; lateral edges appear confluent with supraorbital margin from dorsal view, but not confluent from frontal view; inner edges of smooth, entire supraorbital margins strongly deflexed downwards, more than outer edges of front, forming slight crimp at junction between frontal and supraorbital margins. Infraorbital margin not distinctly cristate, slightly raised; granulated. Anterolateral margin with three distinct anterolateral teeth, including orbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, appearing almost straight, distinctly converging. Third maxilliped with foliaceous merus, merus slightly longer than broad’ ischium longer than broad; exopod with obtuse. Male chelipeds small, subequal; surfaces finely granulated, with short, soft setae on inner surface; dorsal surface of chela granulated; inner surface densely setose. Fingers distinctly longer than palm; dorsal surface of pollex with granules; cutting edge of both fingers with numerous denticles, ending in recurved, sharp tips. Ambulatory legs long, slender, glabrous, all segments smooth, without spines or setae. Male abdomen narrow, triangular with all segments freely moveable (six somites plus telson), telson subrectangular. G1 relatively slender, weakly curving outwards. Female gonopore operculate, subcircular in shape.

**Remarks.** — *Noarograpsus lobulatus* was collected with the fiddler crab *Uca lactea* (De Haan, 1835) (Ocypodidae), which is usually found in the intertidal sandy-muddy flats with constant water movement (Wang & Liu 1996), and there is no contact with any visible freshwater source (P.C. Gonzales, pers. comm.). So far *N. lobulatus* has only been collected by sieving through the sandy-muddy substrate of the type locality. The biology of this crab is unknown. This species like to occupy the softest part of the mudflats and they burrow very quickly into the mudflat once they are startled or frightened.

**Distribution.** — Known only from Philippines (Natunawan Cove, Tabaco, Albay).

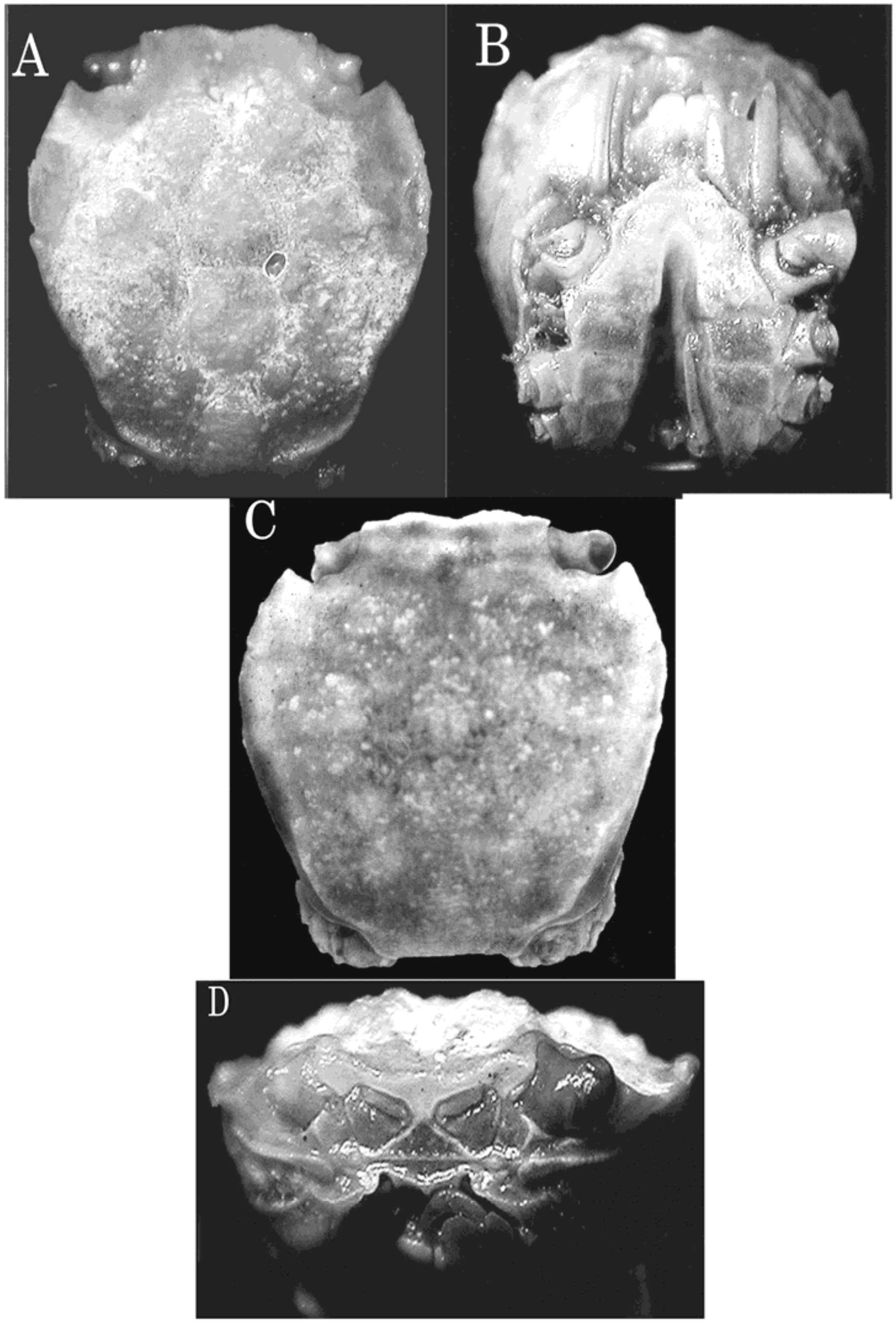



Figure 43. *Noarograpsus lobulatus* (Manuel, Gonzales & Basmayor, 1991), male paratype, 7.8mm x 7.2mm (ZRC 2001.2352); female, paratype, 7.5mm x 7.0mm (ZRC 2001.2353). A) male carapace; B) male ventral view; C) female carapace; D) male frontal view.

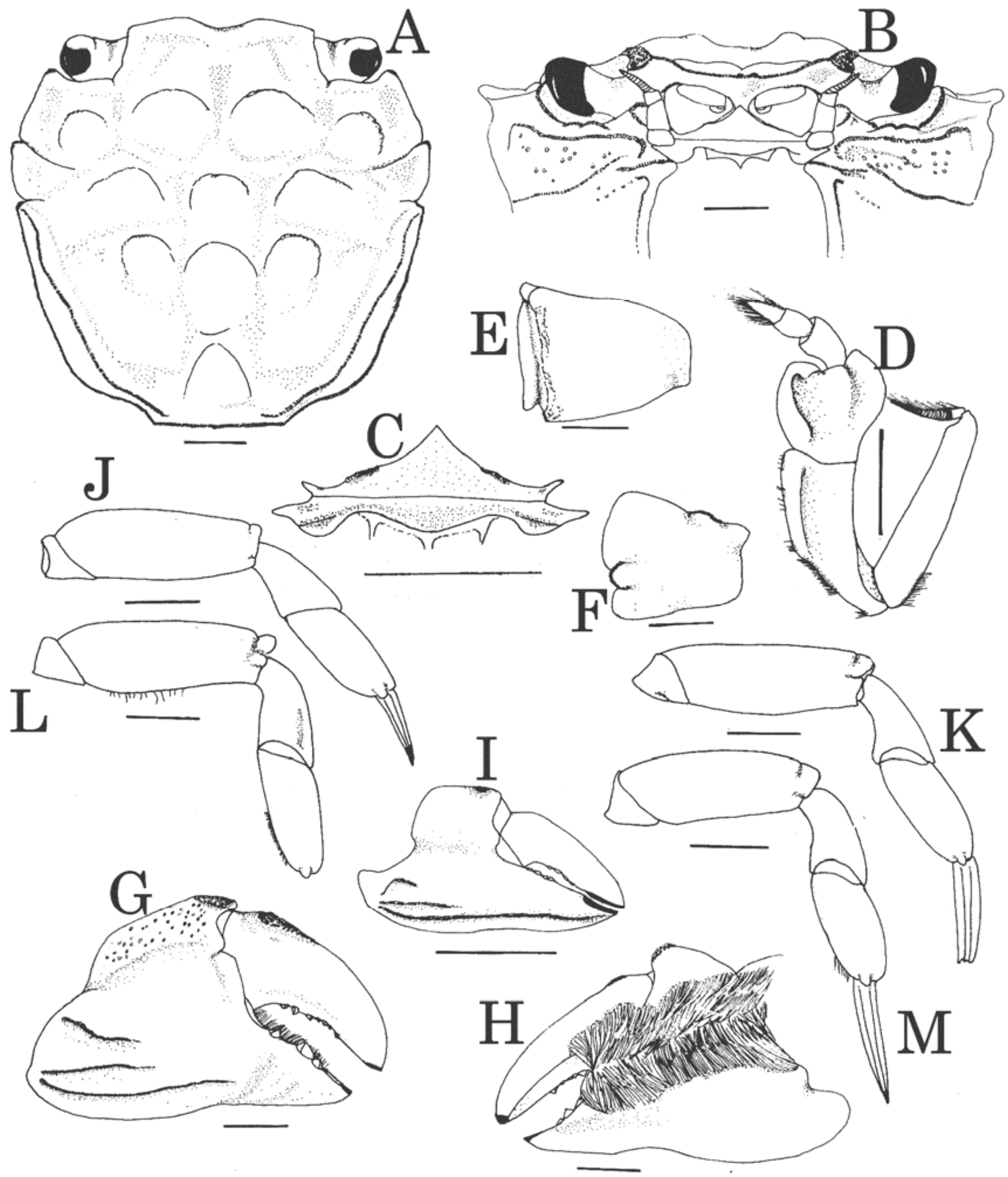



Figure 44. *Noarograpsus lobulatus* (Manuel, Gonzales & Basmayor, 1991), male paratype, 7.8mm x 7.2mm (ZRC 2001.2352); female, paratype, 7.5mm x 7.0mm (ZRC 2001.2353). A) carapace; B) frontal view; C) epistome; D) third maxilliped; E) dorsal view of merus of male chela; F) dorsal view of carpus of male chela; G) outer view of male cheliped; H) inner view of male cheliped; I) dorsal view of female cheliped; J) right first ambulatory leg; K) right second ambulatory leg with broken dactylus; L) right third ambulatory leg with missing dactylus; M) right fourth ambulatory leg. (Scale=1.0mm).

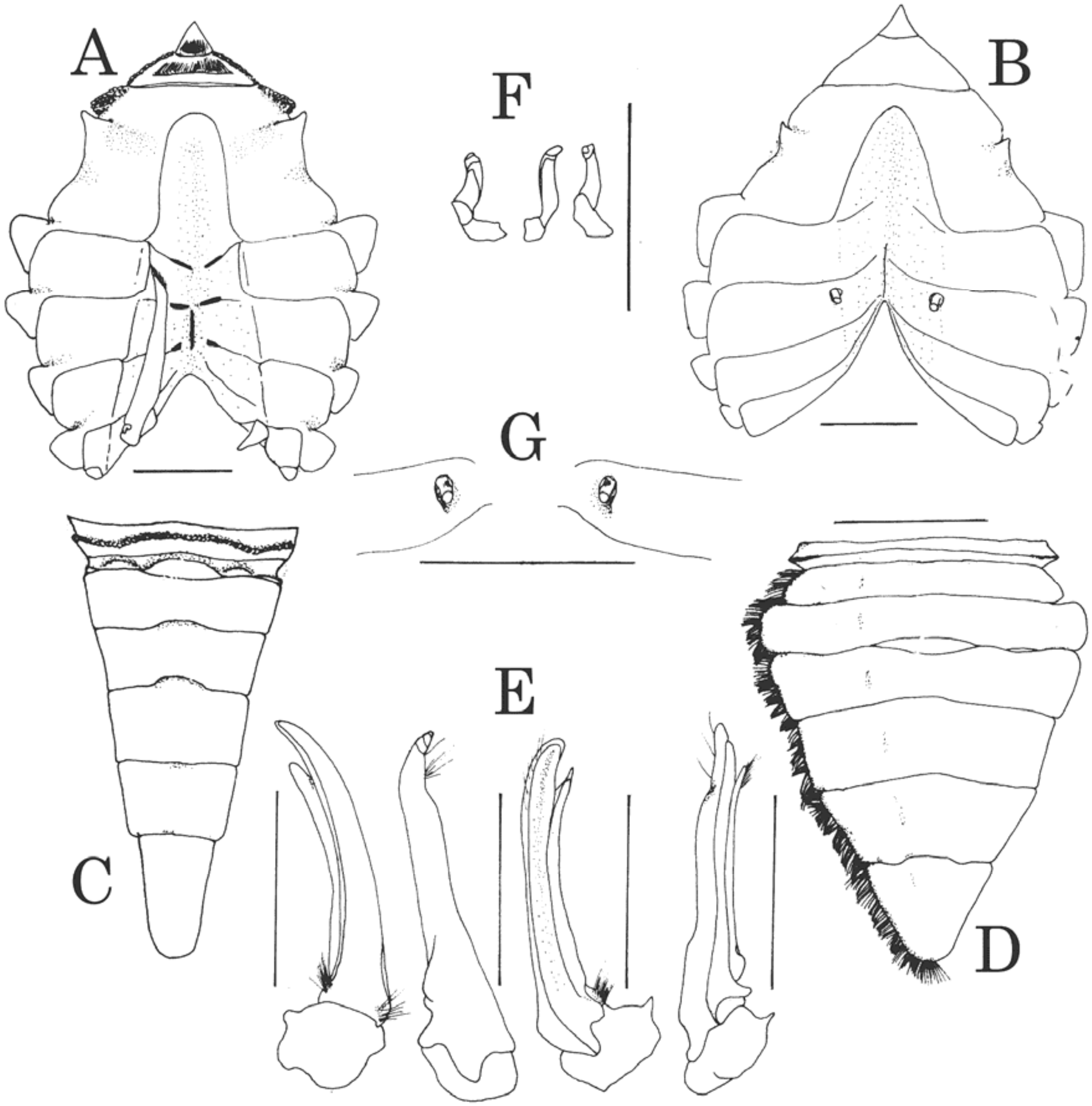



Figure 45. *Noarograpsus lobulatus* (Manuel, Gonzales & Basmayor, 1991), male, paratype, 7.8mm x 7.2mm (ZRC 2001.2352); female, paratype, 7.5mm x 7.0mm (ZRC 2001.2353). A) male thoracic sternum; B) female thoracic sternum; C) male abdomen; D) female abdomen; E) different views of G1 (setae denuded); F) different views of G2; G) Female gonopore. (Scales=1.0mm).

### Genus *Neoeriocheir* Sakai, 1983

*Eriocheir* – De Haan, 1835: 32; Rathbun, 1914: 353; Kemp, 1918: 232; Tesch, 1918: 107; Balss, 1922: 152; Urita, 1926: 433; Sakai, 1939: 671; 1976: 649; Shen & Dai, 1964: 128 (not *Eriochier* H. Milne Edwards, 1853).

*Neoeriocheir* Sakai, 1983: 19, pls. III, VIII; Ng, Guo & Ng, 1999: 154.

**Type species.**— *Eriocheir leptognathus* Rathbun, 1913, by original designation.

**Gender.**— Masculine.

**Diagnosis.**— Carapace quadrate; epigastric, protogastric cristae very low to almost indiscernible; frontal margin very low, lobes faint, appearing almost straight; anterolateral margin with three teeth; posterior margin of epistome entire, lateral parts without lobes or clefts. Merus of third maxilliped slender; dactylus twice as long as propodus; exopod not reaching middle of merus. Outer surface of chelae smooth, glabrous; inner surface covered with dense, soft, long setae. Suture between sternites two and three distinctly convex toward abdomen; lateral margins of sternites 3 and 4 almost entire, no clear notch demarcating edge of suture; longitudinal median groove between sternites five and six narrow; space on sternite eight very narrow throughout length. G1 short, stout. Operculum of female gonopore crenulated, margins setose.

**Remarks.**— Sakai (1983) noted that *E. leptognathus* differed from its congeners in several important characters and referred it to a new genus, *Neoeriocheir*. Subsequent workers, however, have not used this classification (e.g., Dai *et al.*, 1984; Dai & Yang, 1991; Chan *et al.*, 1995; Kim & Hwang, 1995), preferring to retain *E. leptognathus* in *Eriocheir* instead. Chan *et al*. (1995) commented that they could discern no good reasons for recognizing *Neoeriocheir* as a valid genus, and regarded it as a junior synonym of *Eriocheir*. Ng *et al.* (1999) revived *Neoeriocheir* for *E. leptognathus*, and also established a new genus *Platyeriocheir* for *E. formosa* Chan, Hung & Yu, 1995; providing evidence derived from both larval and adult morphology. The generic classification by Ng *et al.* (1999) has not been accepted by Tang *et al.* (2003) and Chu *et al.* (2003), as they argue that *E. leptognathus*, *E. formosa* and the other three taxa form a clade and as the genetic differentiation among the two species, *E. leptognathus* and *E. formosa*, and the other three taxa is so low that the separation at genus level is not fully warranted. However, based on DNA sequence analysis of mitochondrial 16s rRNA, cytochrome c oxidase I, and the first internal transcribed spacer of nuclear rRNA, Chu *et al.*, 2003 also showed that the three *Eriocheir*, sensu stricto, species are genetically similar, and *E. leptognathus* the most distantly related taxon within the group. With the recent analysis on the nuclear DNA, it is very likely that *N. leptognathus* is the ancestral of these few species (J.W. Xu, pers. comm.). In the most recent review of the state of the genus *Eriocheir* and its allies, Komai *et al.* (2006) concurred with the arguments of Ng *et al.* (1999) and recognized all three genera.

The main difference between *N. leptognathus* and all other species of *Eriocheir* was in the form of the third maxilliped. In *N. leptognathus*, the ischium and merus of the third maxilliped are long and narrow. In all other species of *Eriocheir*, however, these segments are short and wide. A detailed comparison of all known taxa of *Eriocheir* (Ng *et al.*, 1999) showed a number of key differences between *N. leptognathus* and the other species. These include differences in characters of the carapace, third maxilliped, anterior thoracic sternites, chelipeds, ambulatory legs, G1 and female gonopore (Table 3). These substantial differences are sufficient to warrant the recognition of *Neoeriocheir* as a valid genus. It is important to note that all the characters listed in Table 3 for *Eriocheir sinensis* also valid for *E. japonica* and *E. hepuensis* (i.e., members of the genus *Eriocheir* sensu stricto).

Comments on characters having generic significance seem pertinent. The carapace in *N. leptognathus* is smooth, with very low epigastric and protogastric cristae (in smaller specimens, these cristae are almost indiscernible). The frontal margins of *Eriocheir* sensu stricto are very distinctly quadrilobe or quadridentate, while the frontal margin lobes of *Neoeriocheir* are so strongly reduced that the frontal margin appears straight.

All species of *Eriocheir* sensu stricto have four teeth along the anterolateral margin but *N. leptognathus* only has three. The presence of long soft setae only on the inner surfaces of the chelae is distinctive for *N. leptognathus*. In species of *Eriocheir* sensu stricto , these setae are present both on the inner and outer surfaces of the chelae. The very differently structured posterior margin of the epistome is a key character. In *N. leptognathus*, the lateral parts are continuous and entire, with only the median lobe present. In species of *Eriocheir* sensu stricto, the lateral part of the posterior margin of the epistome has two distinct clefts, and the margin is tri-lobed. The longitudinal median groove between the fifth and sixth thoracic sternites in *N. leptognathus* is narrow, while in species of *Eriocheir* sensu stricto, this groove is broad. The G1 of *N. leptognathus* is short and thick, with the distal end notably different from those of species of *Eriocheir*.

In addition, there are some general characters which can also differentiate *Neoeriocheir* from known species of *Eriocheir* sensu stricto. The cornea of *N. leptognathus* is smaller than that of *Eriocheir*, and the basal part of the eye-stalk is narrower. The ambulatory legs of *N. leptognathus* are also proportionately longer and more slender than those of *Eriocheir* sensu stricto.

Sakai (1983) used the colour as well as the small size of *N. leptognathus* to justify its placement in its own genus. Colour characters, however, while occasionally useful at the species level, are unlikely to be significant when genera are considered. Neither is size, but marked size differences are sometimes an indication that generic assignments may be incorrect. All known species of *Eriocheir* sensu stricto are relatively large crabs, reaching maturity at carapace lengths of at least 45mm. In contrast, the smallest ovigerous *N. leptognathus* examined was only 10mm in carapace length, the largest mature, non-ovigerous female only 21mm, and the largest mature male was only 20mm. These sizes are less than half those of mature *Eriocheir*.

Comparisons of larval (including megalopal) characters strongly support the recognition of *Neoeriocheir* as a distinct genus. Larval stages have been described for *E. hepuensis* (see Li *et al.*, 1992; Ng *et al.*, 1998), *E. sinensis* (see Liang *et al.*, 1974; Kim and Hwang, 1995; Montti *et al.*, 1996), *E. japonica* (see Morita, 1974; Lai *et al.*, 1986; Kim and Hwang, 1990), and *E. formosa* (as *E. rectus* Stimpson, 1853, cf. Shy and Yu, 1992), while Kim and Hwang (1995) listed the zoeal features of *N. leptognathus*. The main differences are in the absence or presence of first zoeal abdominal somite knobs, the antennular setation, the antennal type and the coxal endite of the maxillule and maxilla (Table 3).

The larval ecology of *N. leptognathus* is strikingly different from that of other species of *Eriocheir*. The fifth zoeal stage and the megalopal stage of species of *Eriocheir* sensu stricto migrate upstream from brackish to freshwater habitats (Zhao *et al.*, 1988; Xu, 1994; Shy & Yu, 1992; Chan *et al.*, 1995). Such behaviour is basically not known for *N. leptognathus*. Instead, both the adults and larvae of *N. leptognathus* remain in coastal areas (Kamita, 1938; A.Y. Dai, pers. comm.). The only exception was the record of a small male found in a fresh-water habitat (Kamita, 1926; Kamita, 1938).

## *Neoeriocheir leptognathus* (Rathbun, 1914)

(Figures 46; 47A-H)

*Eriocheir leptognathus* Rathbun, 1914: 353, figs. 1A-G; 2A; Kemp, 1918: 232; Tesch, 1918: 433; Balss, 1922: 152; Urita, 1926: 433; Sakai, 1933: 106; Karmita, 1938: 383, fig. 2D; Shen & Dai, 1964: 128; Kim, 1973: 470, text-fig. 204, pl. 41, fig. 157; Dai *et al.*, 1986: 475, text-fig. 267; Dai & Yang, 1991: 521, text-fig. 267.

*Utica sinensis* Parisi, 1918: 102, text-fig. 3, pl. 8, fig. 1.

*Eriocheir rectus* – Shen, 1932: 11, fig. 6 (not Stimpson, 1858).

*Neoeriocheir leptognathus* – Sakai, 1976: 671, pl. 109, fig. 2; Ng *et al*, 1999:154.

**Material examined.**— (In addition to the specimens listed in Ng *et al.*, 1999) – **China** – 1 female (11.8mm x 10.8mm) (USNM-64950), Amoy, China, coll. C.J. Shen, Nov. Nov. 1928; 6 males (10.6-15.0mm x 10.0-13.3mm), 7 females (10.0-13.2mm x 8.5-12.0mm) (USNM-58733), Foochow, China, coll. C.R. Kellogg; 2 males (8.5-14.2mm x7.5-12.8mm), 2 females (8.6-9.2mm x 8.2-8.5mm) (USNM-61904), Wendao, Zhejiang Province, China, coll. H.W. Wu; 3 males (9.8-12.3mm x 8.4-11.1mm), 7 females (6.2-15.3mm x 5.7-14.6mm) (USNM) Muiwha, near Foochow, Fijian Province, China, coll. Aug. 1923; 1 female (5.8mm x 4.2mm) (QIH-no-cat. number), Sanyang Beach, 30-50m, mudflat, coll. Feb. 1981; 1 male (13.0mm x 11.5mm) (QIH-no cat. number), coll. 11 Jun. 1957. – **Japan** – 1 female (ovigerous) (24.5mm x 21.5mm), Japan, no collection date; 2 males (18.6-21.2mm x 17.1-17.5mm), 3 females (17.2-20.5mm x 15.5-18.0mm) (SFM-ex. T. Sakai collections), South of Togashima, Japan, coll. H. Ikeda, 6 Jun. 1979.

**Diagnosis.**— Carapace rectangular, overall dorsal surface only very slightly convex, regions well-defined. Anterolateral margins with four teeth including orbital tooth. Third maxilliped very broad; ischium, merus broad, exopod narrow. Chela with setae on the inner surface of the chelipeds. Ambulatory legs also slender, long, long thick setae on anterior, posterior surfaces of carpus, propodus. G1 long, slender, distal margin narrowly rounded, slopping shoulder shaped when viewed laterally, short, chitinuous prominence, slightly curved dorsally outwards with subdistal lobe. Female gonopore with operculum, bluntly triangular in shape, prominent, slightly concave dorsally.

**Colour.**— The colour of fresh specimens is greenish brown (Dai & Yang, 1991) in colour, and all preserved specimens examined are brown in colour.

**Size.**— This species is generally smaller than *Eriocheir* sensu lato, the largest male examined is only 21.2mm x 17.5mm (SFM-ex. T. Sakai collections), while the largest female specimen examined is 24.5mm x 21.5mm (SFM-ex. T. Sakai collections).

**Habitat.**— Both the adults and larvae are found along the coastal waters (S.L. Yang, pers. comm.).

**Remarks.**— Detailed descriptions and figures of this species have been provided by Ng *et al.* (1999) and there is no need to elaborate here.

**Distribution.**— North China, west coast of Korea (Yellow Sea) and Japan (Saga, mouth of Shioda river).

Figure 46. *Neoeriocheir leptognathus* (Rathbun, 1914); male, 13.0mm x 11.5mm (QIH-no-cat. number). Dorsal view.

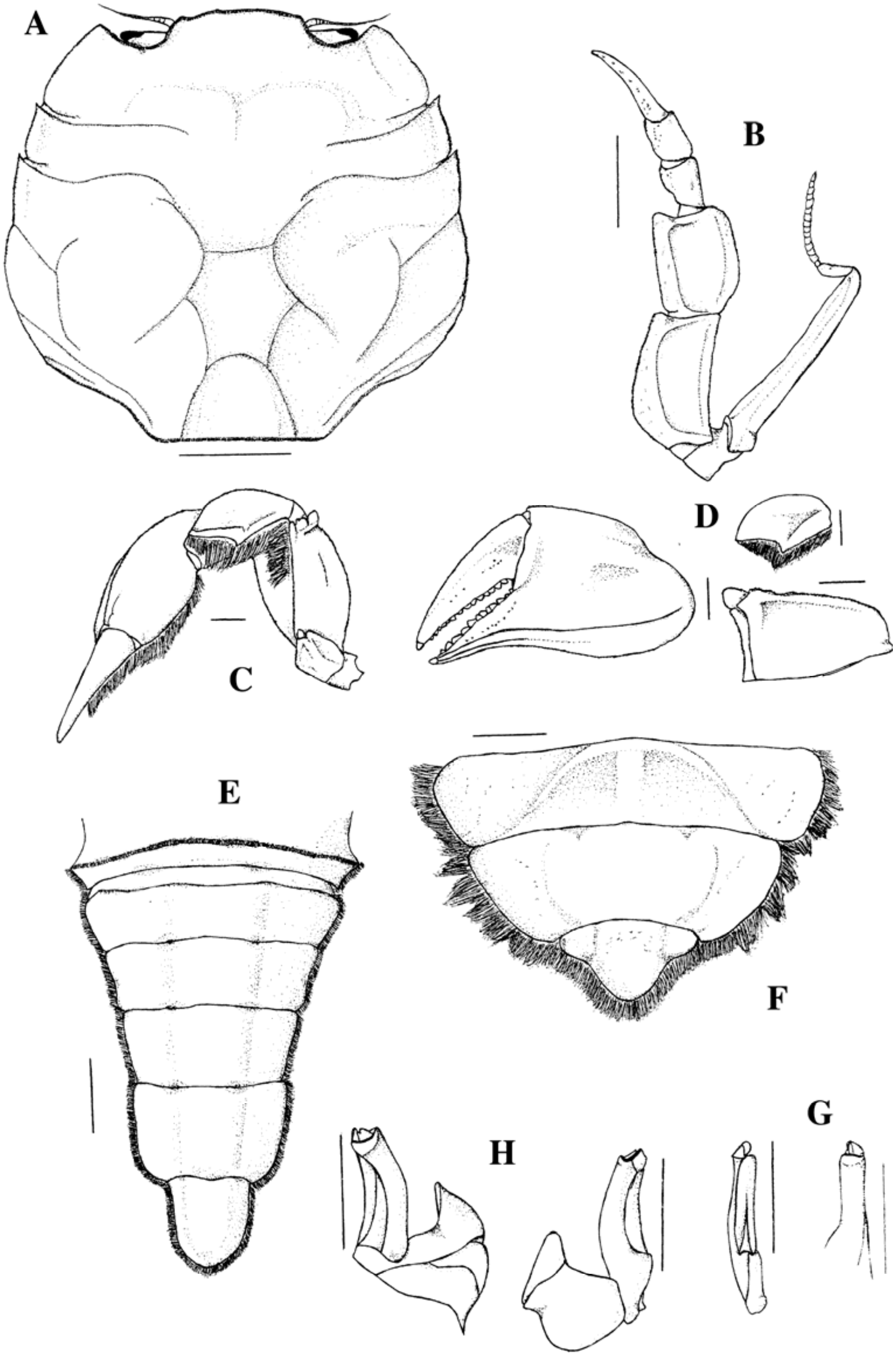



Figure 47. *Neoeriocheir leptognathus* (Rathbun, 1914); male, 13.0mm x 11.5mm, female, 5.8mm x 4.2mm (QIH-no-cat. number). A) carapace; B) third maxilliped; C) dorsal view of cheliped; D) outer view of cheliped; E) male abdomen; F) female abdomen (part); G) G1; H) G2. (Scale=1.0mm.).

## Genus *Orcovita* Ng & Tomascik, 1994

*Orcovita* Ng & Tomascik, 1994: 939; 1996: 109; Ng *et al.*, 2002: Ng & Ng, 2002: 663; Naruse & Tamura, 2006: 147.

**Type species.**— *Orcovita saltatrix* Ng & Tomascik, 1994, by original designation.

**Gender.**— Masculine.

**Diagnosis.**— Carapace rectangular to subrectanglar, distinctly broader than long; dorsal surfaces relatively smooth; regions poorly defined; epigastric cristae low; postorbital cristae sometimes not discernable. External orbital angle very broad, outer margin long with one low epibranchial tooth; frontal median triangle present formed by three granuliform ridges. Antennal segments entering orbital hiatus. Antennules broad. Eyes well-developed, cornea pigmented. Third maxilliped with very broad, stout exopod, as wide as or slightly wider than ishcium; anteroexternal angle of merus strongly auriculiform. Chelipeds relatively long, pulvinus with setose base present at the base of fingers of both male chelae, pulvinus present in female but small. Ambulatory legs subcylindrical in cross-section, segments long and slender, segments long, slender; dorsal and ventral margins gently serrated in first ambulatory merus, progressively less serrated from first to third ambulatory merus, appearing rough to uneven in fourth ambulatory merus. Male abdomen with all segments freely moveable (six somites plus telson); not retained by a 'bouton-pression' (cf. Guinot & Bouchard, 1998), with only a sternal ridge surrounding telson, telson of male abdomen short. G1 relatively short, stout, tip truncate from lateral view. G2 very short, no distal segment present. Female gonopore operculate, triangular in shape.

**Remarks.**— The genus *Orcovita* Ng & Tomascik, 1994, has been described and discussed in detail (Ng & Tomascik, 1994; Ng *et al.*, 1996, Ng *et al.*, 2002), and there is no need to treat it further here.

There are currently six species of the anchialine varunine crab in the genus *Orcovita* Ng & Tomascik, 1994, all known thus far from the Pacific viz. *O. saltatrix* Ng & Tomascik, 1994 (type species), from Indonesia; *O. angulatus* Ng, Guinot & Iliffe, 1996 from the Philippines; *O. fictilia* Ng, Guinot & Iliffe, 1996 from the Philippines; *O. gracilipes* Ng, Guinot & Iliffe, 1996 from Niue; *O. mollitia* Ng, Guinot & Iliffe, 1996 from Guam, and *O. mcneiceae* Ng & Ng, 2002 from the Loyalty Islands. There is a new species, *Orcovita miruku*, recently described from Okinawa, Japan (Naruse & Tamura, 2006).

The genus is most closely related to *Ptychognathus* sensu lato in the form of the broad exopod of the third maxilliped. It can be easily distinguishable from *Ptychognathus* sensu lato by the following features a) the ovate carapace shape (vs. subquadrate to quadrate carapace shape in *Ptychognathus*); b) lack of epigastric crsitae (vs. presence of a small epigastric cristae), and c) the long and slender ambulatory legs (vs. short and broad ambulatory legs in *Ptychognathus*).

*Orcovita* is also very similar to *Acmaeopleura* Stimpson, 1858, in having a broad, almost rounded carapace. It is different from *Acmaeopleura* in having a) glabrous carapace (vs. setose carapace in *Acmaeopleura*); b) a broad exopod of the third maxilliped (vs. narrow exopod in *Acmaeopleura*), and c) very long and slender ambulatory legs (vs. broad and stout legs in *Acmaeopleura*).

It is interesting to note that all the species in this genus have a) reduced cornea; b) a reduction in pigmentation in the eyes; c) long sensory setae on the ambulatory legs, and d) very long and slender ambulatory legs. These are clearly adaptations to living in caves. This is the only genus in the family Varunidae that is truly anchaline in nature. The other probable cave or anchaline species is *Hemigrapsus estellinensis* Creel, 1964, described from Texas, United States of America (see above).

There are reasons to suspect that this genus could be one of the ancestral taxon of grapsid crabs that is present today. As supported by Iliffe's studies on the Caribbean cave crustaceans (1987; 1992; 2004), they have shown that more than 250 new species of marine animals, mainly crustaceans, living in the caves on islands in the Atlantic, Caribbean and Indo-Pacific are endemic, and very primitive 'living' fossils. However, the morphology of these animals strongly suggests that they have entered caves secondarily or later. This fact is supported by the position of this genus after performing the cladistic analysis. This genus comes out together with *Ptychognathus* and *Cebuanograpsus*, suggesting that they are not of very ancient lineage.

Table 4. Length to width ratios of various ambulatory segments of *Orcovita* species [modified from Ng *et al.* (1996) and Ng & Ng, 2002].

| | Third merus | Third propodus | Third dactylus | Fourth merus | Fourth propodus | Fourth dactylus |
|---|---|---|---|---|---|---|
| *O. angulatus* | 5.4 | 5.4 | 16.1 | 4.6 | 3.7 | 6.6 |
| *O. fictilia* | 5.3 | 4.2 | 9.1 | 4.2-4.4 | 2.6-3.0 | 6.2-6.9 |
| *O. gracilipes* | 5.7 | 5.1 | 10.8 | 4.7 | 3.2 | 5.9 |
| *O. mcneiceae* | 5.2 | 5.4 | 9.8 | 5.2 | 3.2 | 4.9 |
| *O. mollitia* | 5.7 | 5.2 | 12.9 | 4.2-4.7 | 2.8-3.2 | 7.6 |
| *O. saltatrix* | 5.8 | 4.3 | 7.8 | 4.4 | 3.1 | 5.5 |
| *O. miruku* | 4.1 | 3.7 | 9.3 | 6.1 | 2.6 | 6.3 |

**Key to species in *Orcovita***

1a. Carapace subrectangular. Merus of third ambulatory leg very short, broad (length to width ratio 4.1). --------------------------------------------------------------- ***O. miruku***

1b. Carapace subrectangular. Merus of third ambulatory leg very long, slender (length to width ratio > 5.0). ----------------------------------------------------------------------- **2**

2a. Propodus of third ambulatory legs short, broad (length to width ratio ca. 4.2). ----- **3**

2b. Prododus of third ambulatory legs long, slender (length to width ratio ca. 5.2-5.4). - **6**

3a. Dactylus of third ambulatory leg shorter and broader (length to width ratio 7.8). ----- ---------------------------------------------------------------------------------- ***O. saltatrix***

3b. Dactylus of third ambulatory leg slightly longer and more slender (length to width ratio ≥ 9.0). ----------------------------------------------------------------------- **4**

4a. Length to width ratio of dactylus of third ambulatory leg ca. 9.1. ------ ***O. fictilia***

4b. Length to width ratio of dactylus of third ambulatory leg ca. 9.8. ---- ***O. mcneiceae***

5a. Length to width ratio of dactylus of third ambulatory leg ca. 10.8. ----- ***O. gracilipes***

5b. Length to width ratio of dactylus of third ambulatory legs > 12.0. ----------------- **6**

6a. Length to width ratio of dactylus of third ambulatory leg ca. 12.9. ------- ***O. mollitia***

6b. Length to width ratio of dactylus of third ambulatory leg ca. 16.1. ---- ***O. angulatus***

### *Orcovita saltatrix* Ng & Tomascik, 1994

(Figure 48A-I)

*Orcovita saltatrix* Ng & Tomascik, 1994: 940; Ng *et al.,* 1996: 109; Fransen *et al.*, 1997: 126; Ng & Ng, 2002: 663; Naruse & Tamura, 2006: 147.

**Materials examined.—** (In addition to the specimens listed in Ng *et al.,* 1996 and Ng & Ng, 2002) – **Holotype** – 1 male (19.0mm x 14.0mm) (MZB-no cat. number), 11m depth, Kakaban, Indonesia, coll. T. Tomascik, 27 Sep. 1993. – **Paratypes** – 1 male (16.8mm x 12.8mm), 1 female (19.2mm x 14.8mm) (MNHN-B22891), 10m depth, Kakaban, Indonesia, coll. T. Tomascik, 29 Sep. 1993.

**Diagnosis.**— Carapace subrectangular, distinctly broader than long (width to length ratio ca. 1.4), dorsal surface smooth, regions poorly defined; frontal margin gently sinuous, strongly deflexed, Anterolateral margins with two indistinct teeth including orbital tooth. Third maxilliped with very broad, stout exopod, as wide as or slightly narrower than ischium, ischium stout; merus broad. Male chelae swollen, subequal; fingers slightly shorter than palm; inner part of cutting edges of fingers with small pulvinus, base and adjacent areas setose. Female chelae similar to those of males but smaller, no setae. Ambulatory legs subcylindrical in cross section, all segments long, slender; second ambulatory leg longest; surface smooth. Anterior, dorsal margin of merus with blunt subdistal tooth; outer surface of carpus with short setae, anterior and posterior margins of propodus with long and short setae respectively; dactylus tapering to slender, acute tip. Dactylus rectangular in cross section, posterior margin comb-like in first three pereiopods. Third merus long, slender (length to width ratio 5.8), third propodus long, slender (length to width ratio 4.3); third dactylus long, slender (length to width ratio 7.8); fourth merus long, slender (length to width ratio 4.4); fourth propodus long (length to width ratio 3.1); fourth dactylus long, slender (length to width ratio 5.5). Male abdomen narrowly triangular with all segments freely moveable (six somites plus telson); lateral margins covered with short, dense setae; telson broadly triangular, lateral margins weakly concave, distal margin rounded. Female abdomen similar to that of male, very broad. G1 slender, gently curving outwards, setose. G2 short, small. Female gonopore operculate, raised, convex, broadly triangular in shape.

**Colour.**— The colour of fresh specimens is greyish-brown to dark grey (Ng & Tomascik, 1994), and the colour of all preserved specimens examined is a dark cream throughout.

**Size.**— The largest male specimen examined is 19.0mm x 14.0mm (holotype), while the largest female examined is 19.2mm x 14.8mm (MNHN-B22891).

**Habitat.**— It was found in an anchialine lake (Ng & Tomascik, 1994).

**Remarks.**— The species has not been reported since its description.

**Distribution.**— Indonesia (Kakaban) only.

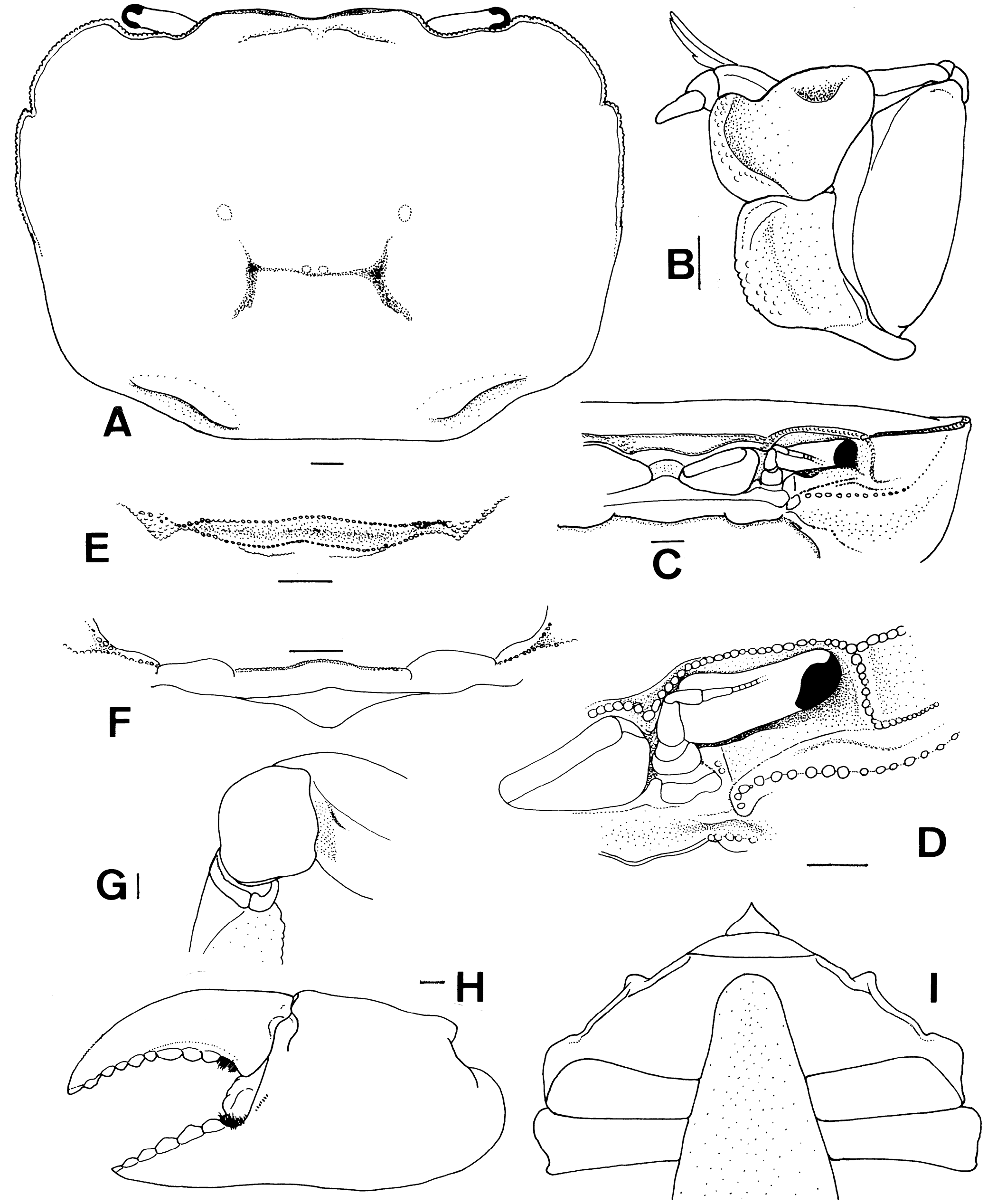



Figure 48. *Orcovita saltatrix* Ng & Tomascik, 1994, male holotype, 19.0mm x 14.0mm (MZB). A) carapace; B) third maxilliped; C) frontal view of carapace; D) antennae, antennules and orbits; E) frontal median triangle; F) posterior margin of epistome; G) distal part of merus, proximal part of chea; H) left chela; I) anterior thoracic sternites. (Scale=1.0mm). (After Ng & & Tomascik, 1994).

## ***Orcovita gracilipes* Ng, Guinot & Iliffe, 1996**

(Figure 49A-G)

*Orcovita gracilipes* Ng, Guinot & Iliffe, 1996: 117; Ng & Ng, 2002: 663; Naruse & Tamura, 2006: 147.

**Material examined.— (**In addition to the specimens listed in Ng *et al.,* 1996; Ng & Ng 2002) – **Holotype** – 1 male (18.4mm x 12.9mm) (MNHN B-22892), station 88-006, Viakona Chasm, Niue, (with a plastic bottle baited with fish and left overnight at 13m depth), coll. T. Illiffe, 6 Feb. 1988. – **Paratypes** – 3 males (11.8-16.1mm x 8.7-10.5mm), 1 female (15.4mm x 11.1mm), 1 female (ovigerous) (17.3mm x 12.6mm) (MNHN B-22893), station 88-006, Viakona Chasm, Niue, (with a plastic bottle baited with fish and left overnight at 13m depth), coll. T. Illiffe, 6 Feb. 1988.

**Diagnosis.—** Carapace subrectangular, distinctly broader than long (width to length ratio ca. 1.4), dorsal surface smooth, regions poorly defined; frontal margin gently sinuous, strongly deflexed, Anterolateral margins with two indistinct teeth including orbital tooth. Third maxilliped with very broad, stout exopod, as wide as or slightly narrower than ischium, ischium stout; merus broad. Male chelae swollen, subequal; fingers slightly shorter than palm; inner part of cutting edges of fingers with small pulvinus, base and adjacent areas setose. Female chelae similar to those of males but smaller, no setae. Ambulatory legs subcylindrical in cross section, all segments long, slender; second ambulatory leg longest; surface smooth. Anterior, dorsal margin of merus with blunt subdistal tooth; outer surface of carpus with short setae, anterior and posterior margins of propodus with long and short setae respectively; dactylus tapering to slender, acute tip. Dactylus rectangular in cross section, posterior margin comb-like in first three pereiopods. Third merus long, slender (length to width ratio 5.7), third propodus long, slender (length to width ratio 5.1); third dactylus long, slender (length to width ratio 10.8); fourth merus long, slender (length to width ratio 4.7); fourth propodus long (length to width ratio 3.2); fourth dactylus long, slender (length to width ratio 5.9). Male abdomen narrowly triangular with all segments freely moveable (six somites plus telson); lateral margins covered with short, dense setae; telson broadly triangular, lateral margins weakly concave, distal margin rounded. Female abdomen similar to that of male, very broad. G1 slender, gently curving outwards. G2 short, small. Female gonopore operculate, raised, convex, broadly triangular in shape.

**Colour.**— The colour fresh specimens has not been documented, and the colour of all preserved specimens examined is a dark cream throughout.

**Size.**— The largest male specimen examined is 18.4mm x 12.9mm (holotype), and the largest female examined is 17.3mm x 12.6mm (MNHN-B-22893).

**Habitat.**— It was found  in anchaline caves (Ng *et al.,* 1996).

**Remarks.**— This species is found only in Niue.

**Distribution.**— Niue only.

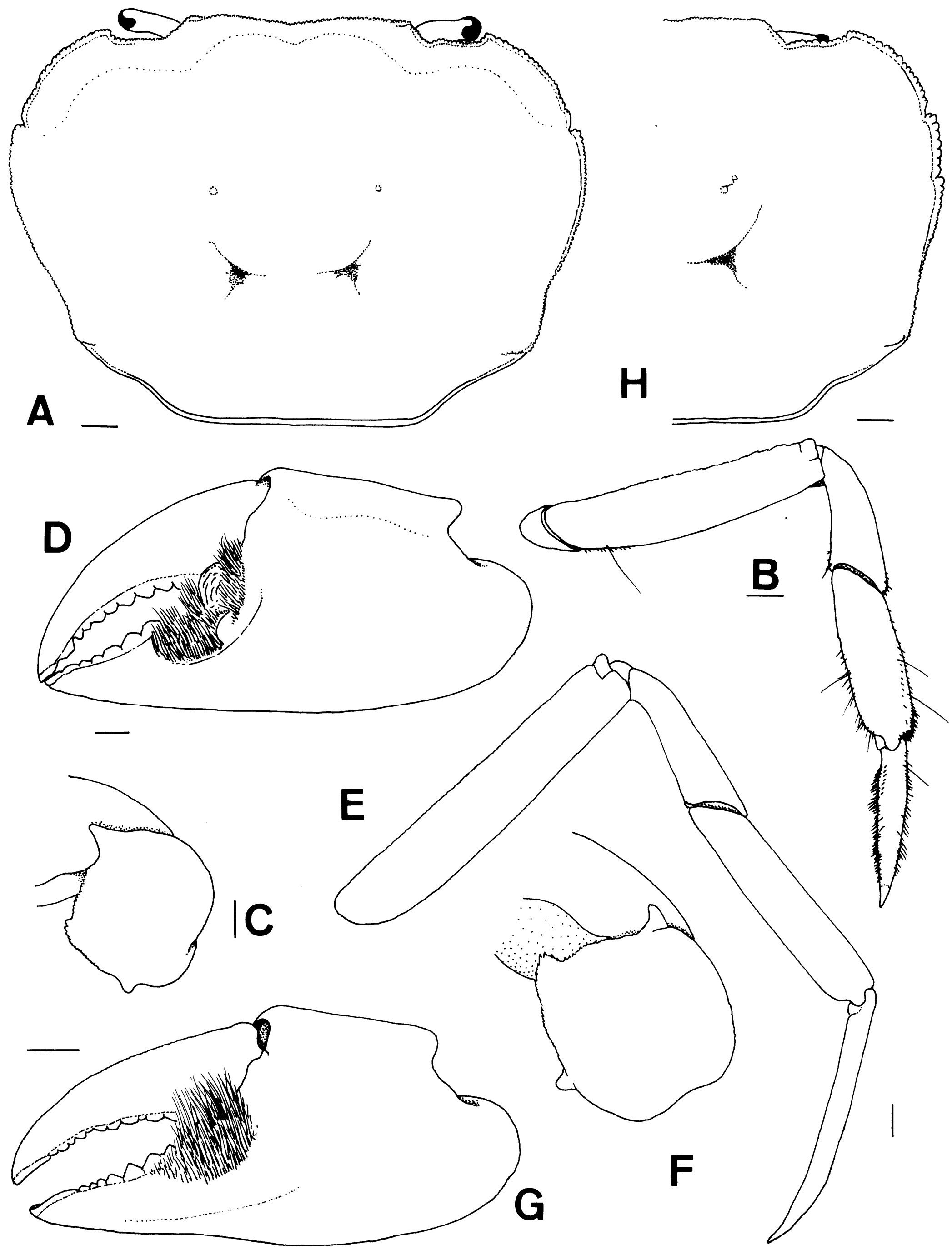



Figure 49. *Orcovita gracilipes* Ng *et al.*, 1996, male holotype, 18.4mm x 12.9mm (MNHN B-22892); female, paratype, 16.8mm x 12.2mm (NNM). A) male carapace; B) fourth ambulatory leg; C) male carpus and proximal part of right chela; D) male left chela; E) third ambulatory leg; F) female carpus and proximal part of right chela; G) female left chela. (Scale=1.0mm). (After Ng *et al.*, 1996).

## *Orcovita mollitia* Ng, Guinot & Illiffe, 1996

(Figure 50A-J)

*Orcovita mollitia* Ng, Guinot & Iliffe, 1996: 121; Ng & Ng, 2002: 663; Naruse & Tamura, 2006: 147.

**Material examined.— (**In addition to the specimens listed in Ng & Ng, 2002) **– Holotype** – 1 male (12.6mm x 9.6mm) (MNHN B-22895), station 85-015, Faifai Beach Cave, Guam, (with plastic bottle trap baited with crab parts and left overnight in 3m water depth), coll. T. M. Illiffe, 27-28 Jan. 1985**. – Paratypes** – 5 males (7.1-10.8mm x 5.4-7.9mm), 4 females (8.6-9.8mm x 6.5-7.0mm) (MNHN B-22896), station 85-015, Faifai Beach Cave, Guam, (with plastic bottle trap baited with crab parts and left overnight in 3m water depth), coll. T. M. Illiffe, 27-28 Jan. 1985. – **Others** – 1 male (14.9mm x 10.9mm) (USNM-364310c), station 85-009, Marbo Cave, in cave pool, Guam, in 0.5m water depth (with plastic bottle trap baited with hermit crab and left overnight in 3m water depth), coll. T.M Illiffe, 20 Jan. 1985; 7 males, 2 females (ZRC 2001.1143), "Hawaiian Rock Quarry", Guam, freshwater pool, 1m depth, ca. 200 m from sea, coll. P. K. L. Ng & C.-H. Wang, 19 Apr. 2000; 1 female (ZRC 2001.1144), Pagat Cave, Guam, in freshwater pool, among rubble, coll. G. Paulay, 30 Jun. 1994; 1 juvenile. (ZRC 2001.1145), freshwater cave, Anderson Air force Base, station TB-7, Guam, coll. 4 Dec. 1992.

**Diagnosis.—** Carapace subrectangular, distinctly broader than long (width to length ratio ca. 1.3-1.4), dorsal surface smooth, regions poorly defined; frontal margin gently sinuous, strongly deflexed, Anterolateral margins with one indistinct tooth including orbital tooth. Third maxilliped with very broad, stout exopod, as wide as or slightly narrower than ischium, ischium stout; merus broad. Male chelae swollen, subequal; fingers slightly shorter than palm; inner part of cutting edges of fingers with small pulvinus, base and adjacent areas setose. Female chelae similar to those of males but smaller, no setae. Ambulatory legs subcylindrical in cross section, all segments long, slender; second ambulatory leg longest; surface smooth. Anterior, dorsal margin of merus with blunt subdistal tooth; outer surface of carpus with short setae, anterior and posterior margins of propodus with long and short setae respectively; dactylus tapering to slender, acute tip. Dactylus rectangular in cross section, posterior margin comb-like in first three pereiopods. Third merus long, slender (length to width ratio 5.7), third propodus long, slender (length to width ratio 5.2); third dactylus long, slender (length to width ratio 12.9); fourth merus long, slender (length to width ratio 4.2-4.7); fourth propodus long (length to width ratio 2.8-3.2); fourth dactylus long, slender (length to width ratio 7.6). Male abdomen narrowly triangular with all segments freely moveable (six somites plus telson); lateral margins covered with short, dense setae; telson, lateral margins weakly concave, distal margin rounded. Female abdomen similar to that of male, very broad. G1 slender, gently curving outwards. G2 short, small. Female gonopore operculate, raised, convex, triangular in shape.

**Colour.**— The fresh specimens are dark cream to pale cream in colour (Ng *et al.*, 1996), and the colour of all preserved specimens examined is a dark cream throughout.

**Size.**— The largest male specimen examined is 14.9mm x 10.9mm (USNM-364310c), and the largest female is 9.8mm x 7.0mm (MNHN B-22896).

**Habitat.**— They are found in anchialine caves.

**Remarks.**— This species is uncommon even in its type locality.

**Distribution.**— Guam only.

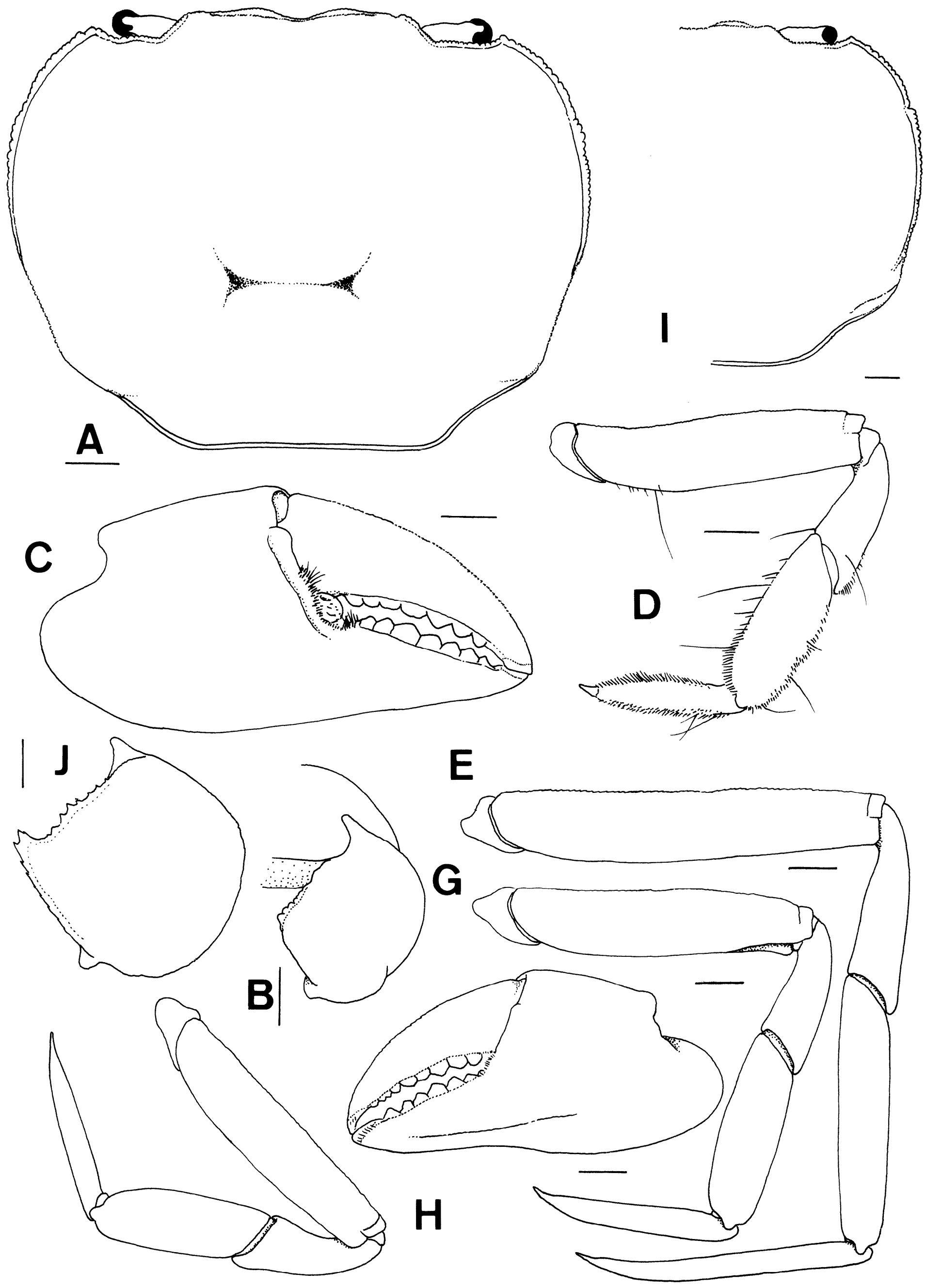



Figure 50. *Orcovita moillitia* Ng, *et al.,* 1996, male, holotype, 12.6mm x 9.6mm (MNHN B-22895); female, paratype, 12.9mm x 9,6mm, (ZRC 1996.98). A) male carapace; B) male carpus and proximal part of chela; C) right chela; D, G) fourth ambulatory leg; E) third ambulatory leg; H) left chela; I) female carapace; J) female carpus and proximal part of chela. (Scale=1.0mm). (After Ng *et al*., 1996).

## *Orcovita fictilia* Ng, Guinot & Iliffe, 1996

(Figure 51A-G)

*Orcovita fictilia* Ng, Guinot & Iliffe, 1996: 124; Ng & Ng, 2002: 663; Naruse & Tamura, 2006: 147.

**Materials examined.— (**In addition to the specimens listed in Ng & Ng, 2002) **– Holotype** – 1 male (21.5mm x 15.3mm) (NMM-no cat. number), station PH 1, Hinaggdanan Cave, -3m, Binag-Dauis, Panglao Island, Bohol, Philippines, coll. B. Sket, 2 Jan. 1995. — **Paratypes** – 1 male (18.8mm x 13.0mm), 2 females (15.8-16.4mm x 11.8-11.8mm) (MNHN-B22897), Hinaggdanan Cave, -0.5m, Binag-Dauis, Panglao Island, Bohol, Philippines, coll. B. Sket, 20 Jan. 1995; 11 malez (largest 17.2mm x 12.3mm) (ZRC 1996.102), station PH 1, Hinaggdanan Cave, -3m, Binag-Dauis, Panglao Island, Bohol, Philippines, coll. B. Sket, 2 Jan. 1995; 1 female (15.0mm x 11.0mm) (NMM-no cat. number), station PH 1, Hinaggdanan Cave, -3m, Binag-Dauis, Panglao Island, Bohol, Philippines, coll. B. Sket, 2 Jan. 1995; 1 male (18.0mm x 13.0mm), 2 females (largest 18.7mm x 14.0mm) (ZRC-uncatalogued), no other data; 1 female (17.0 x 13.0mm) (USNM-364310a), station 85-61, Cansista Cave, Panglao Island, Bohol, Philippines, (with plastic bottle trap left overnight in 1m water depth), coll. T.M. Illiffe, 2 Apr. 1985.

**Diagnosis.**— Carapace subrectangular, distinctly broader than long (width to length ratio ca. 1.5), dorsal surface smooth, regions poorly defined; frontal margin gently sinuous, strongly deflexed, Anterolateral margins with two indistinct teeth including orbital tooth. Third maxilliped with very broad, stout exopod, as wide as or slightly narrower than ischium, ischium stout; merus broad. Male chelae swollen, subequal; fingers slightly shorter than palm; inner part of cutting edges of fingers with small pulvinus, base and adjacent areas setose. Female chelae similar to those of males but smaller, no setae. Ambulatory legs subcylindrical in cross section, all segments long, slender; second ambulatory leg longest; surface smooth. Anterior, dorsal margin of merus with blunt subdistal tooth; outer surface of carpus with short setae, anterior and posterior margins of propodus with long and short setae respectively; dactylus tapering to slender, acute tip. Dactylus rectangular in cross section, posterior margin comb-like in first three pereiopods. Third merus long, slender (length to width ratio 5.3), third propodus long, slender (length to width ratio 4.2); third dactylus long, slender (length to width ratio 9.1); fourth merus long, slender (length to width ratio 4.2-4.4); fourth propodus long (length to width ratio 2.6-3.0); fourth dactylus long, slender (length to width ratio 6.2-6.9). Male abdomen narrowly triangular with all segments freely moveable (six somites plus telson); lateral margins covered with short, dense setae; telson broadly triangular, lateral margins weakly concave, distal margin rounded. Female abdomen similar to that of male, very broad. G1 slender, gently curving outwards, subdistal lobe densely setose. G2 short, small. Female gonopore operculate, raised, convex, triangular in shape.

**Colour.**— The colour fresh specimens has not been documented, and the colour of all preserved specimens examined is a dark cream throughout.

**Size.**— The largest male specimen examined is 21.5mm x 15.3mm (holotype), and the largest female examined is 18.7mm x 14.0mm (ZRC-uncatalogued).

**Habitat.**— It can be found  insides caves and chasms.

**Remarks.**— This species is common in the caves of Panglao and nearby islands.

**Distribution.—** Phlilppines (Panglao) only.

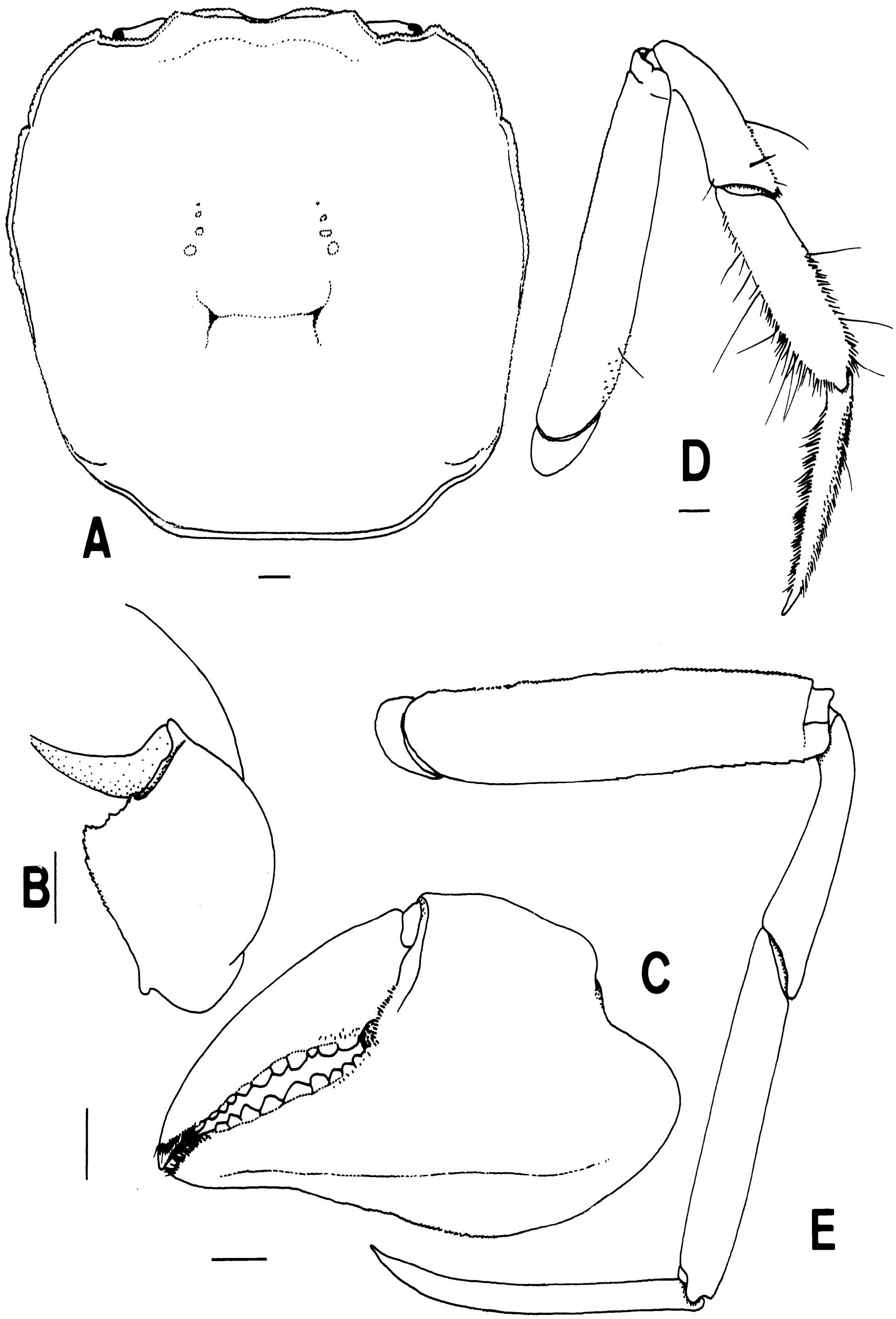



Figure 51. *Orcovita fictilia* Ng *et al.*, 1996, male, holotype, 21.5mm x 15.3mm (NMM-no cat. number); male, paratype, (ZRC 1996.103); female, paratype; 18.7mm x 14.0mm). A) holotype hmale carapace; B) paratype male carapace; C) carpus and proximal part of chela; D, E) right chela; F) left chela; G) holotype abdomen. (Scale=1.0mm). (After Ng *et al.*, 1996).

## *Orcovita angulata* Ng, Guinot & Illiffe, 1996

(Figure 52A-E)

*Orcovita angulata* Ng, Guinot & Illiffe, 1996: 129; Ng & Ng, 2002: 663; Naruse & Tamura, 2006: 147.

**Materials examined.— Holotype** – 1 female (16.7mm x 13.0mm) (USNM-364310b), station 85-65, Raft Cave, Koron Island, Philippines, with a dipnet from the water surface, from a floating log, coll. T. Illiffe, 28 Mar. 1985.

**Diagnosis.**— Carapace subrectangular, distinctly broader than long (width to length ratio ca. 1.3), dorsal surface smooth, regions poorly defined; frontal margin gently sinuous, strongly deflexed, Anterolateral margins with two indistinct teeth including orbital tooth. Third maxilliped with very broad, stout exopod, as wide as or slightly narrower than ischium, ischium stout; merus broad. Male chelae swollen, subequal; fingers slightly shorter than palm; inner part of cutting edges of fingers with small pulvinus, base and adjacent areas setose. Female chelae similar to those of males but smaller, no setae. Ambulatory legs subcylindrical in cross section, all segments long, slender; second ambulatory leg longest; surface smooth. Anterior, dorsal margin of merus with blunt subdistal tooth; outer surface of carpus with short setae, anterior and posterior margins of propodus with long and short setae respectively; dactylus tapering to slender, acute tip. Dactylus rectangular in cross section, posterior margin comb-like in first three pereiopods. Third merus long, slender (length to width ratio 5.4), third propodus long, slender (length to width ratio 5.4); third dactylus long, slender (length to width ratio 16.1); fourth merus long, slender (length to width ratio 4.6); fourth propodus long (length to width ratio 3.7); fourth dactylus long, slender (length to width ratio 6.6). Male abdomen narrowly triangular with all segments freely moveable (six somites plus telson); lateral margins covered with short, dense setae; telson broadly triangular, lateral margins weakly concave, distal margin rounded. Female abdomen similar to that of male, very broad. G1unknown. Female gonopore operculate, raised, convex, broadly triangular in shape.

**Colour.**— The colour fresh specimens has not been documented, and the colour of all preserved specimens examined is a dark cream throughout.

**Size.**— The size of largest male specimen is not known as there is no male specimen reported, and the largest female examined is 16.7 mm x 13.0mm (holotype).

**Habitat.**— It was found  in anchialine caves.

**Remarks.**— So far, no male specimen of this species had been reported.

**Distribution.** — Philippines (Koron) only.

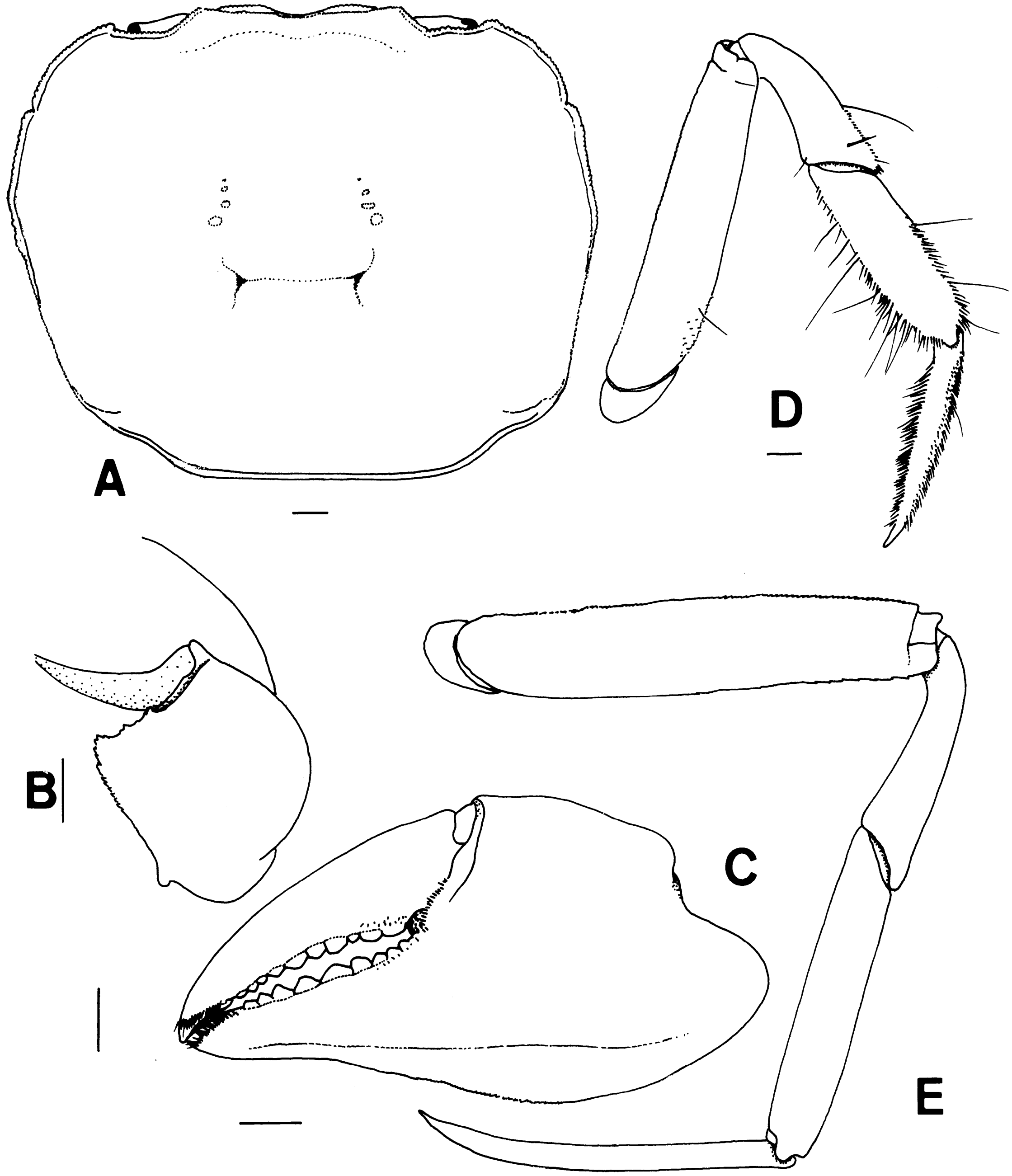



Figure 52. *Orcovita angulata* Ng *et al*., 1996, female, holotype, 16.7mm x 13.0mm (USNM-364310b). A) carapace; B) carpus and proximal part of chela; C) left chela; D) fourth ambulatory leg; E) third ambulatory leg. (Scale=1.0mm). (After Ng *et al*., 1996).

## *Orcovita mcneiceae* Ng & Ng, 2002

(Figures 53; 54A-M)

*Orcovita mcneiceae* Ng & Ng, 2002: 663; Naruse & Tamura, 2006: 147.

**Materials examined.— Holotype** — 1 male (17.0mm x 12.6 mm) (MNHN B-27951), Pueugoni Cave, Lifou Island, Loyalty Islands, coll. 29 Oct. 2000; — **Paratype** – 1 female (15.8mm x 11.8 mm) (MNHN B-27951), Pueugoni Cave, Lifou Island, Loyalty Islands, coll. 29 Oct. 2000; 1 female (16.6mm x 12.5 mm) (MNHN B-27710), Emi, region at entrance of Niri Cave, Mare Island, Loyalty Islands, coll. N. Baillon, 15 Jul. 1988; 1 female (13.5mm x 10.2 mm) (ZRC 2001.1149), Luengoni Cave, Lifou Island, Loyalty Islands, coll. 18 Aug. 1993.

**Diagnosis.—** Carapace subrectangular, distinctly broader than long (width to length ratio ca. 1.3), dorsal surface smooth, regions poorly defined; frontal margin gently sinuous, strongly deflexed. Anterolateral margins with two including orbital tooth. Third maxilliped with very broad, stout exopod, as wide as or slightly narrower than ischium, ischium stout (length to width ratio 2.9); merus broad (length to width ratio ca. 0.7). Male chelae swollen, subequal; fingers slightly shorter than palm; inner part of cutting edges of fingers with small pulvinus, base and adjacent areas setose. Female chelae similar to those of males but smaller, no setae. Ambulatory legs subcylindrical in cross section, all segments long, slender; second ambulatory leg longest; surface smooth. Anterior, dorsal margin of merus with blunt subdistal tooth; outer surface of carpus with short setae, anterior and posterior margins of propodus with long and short setae respectively; dactylus tapering to slender, acute tip. Dactylus rectangular in cross section, posterior margin comb-like in first three pereiopods. Third merus long, slender (length to width ratio 5.2), third propodus long, slender (length to width ratio 5.4); third dactylus long, slender (length to width ratio 10.8); fourth merus long, slender (length to width ratio 5.2); fourth propodus long (length to width ratio 3.2); fourth dactylus long, slender (length to width ratio 5.8). Male abdomen narrowly triangular with all segments freely moveable (six somites plus telson); lateral margins covered with short, dense setae; telson broadly triangular, lateral margins weakly concave, distal margin rounded. Female abdomen similar to that of male, very broad. G1 slender, gently curving outwards, reaching to anterior margin of sternite 5. G2 short, small. Female gonopore operculate, raised, convex, broadly triangular in shape.

**Colour.**— The colour fresh specimens has not been documented, and the colour of all preserved specimens examined is light cream throughout.

**Size.**— The largest male specimen examined is s 17.0mm x 12.6 mm (holotype), and the largest female specimen is 16.6mm x 12.5mm (MNHN B-27710).

**Habitat.**— It was found in anchialine caves.

**Remarks.**— In the form of the carapace, *O. mcneiceae* Ng & Ng 2002, most closely resembles *O. saltatrix* from Kakaban Island (Indonesia), but can easily be separated by its differences ambulatory leg proportions, especially in the longer dactylus (Table 4).

The relatively long ambulatory legs of *O. mcneiceae* resembles those of *O. gracilipes* from Niue, but this species can be separated by the following a) presence of only one distinct tooth on the anterolateral margin of the carapace (vs. two teeth in *O. gracilipes*); b) male cheliped with long setae without swelling among the setae (vs. chela with short soft setae with distinct swelling among the setae in *O. gracilipes*); c) female chelipeds without any setae (vs. presence of short soft setae in *O. gracilipes*); d) tip of G1 more triangular in shape (vs. more stout and rectangular in *O. gracilipes*); e) female gonopore raised, broadly triangular in shape (vs. flattened, circular in shape in *O. gracilipes*), and f) differences in the proportions of the ambulatory legs, especially the shorter dactylus (see Table 4).

The relatively longer ambulatory legs, in particular the dactyli, easily distinguish *O. mcneiceae* from the remaining three species (Table 4). The species is also different from *O. fictilia* in having a distinct tooth on the anterolateral margin (vs. tooth absent in *O. fictilia*), and by the absence of setae on the tip of the fingers of the chela (vs. present in *O. fictilia*). It can be separated from *O. mollitia* in having a large, distinct tooth on the anterolateral margin (vs. with small, indistinct tooth in *O. mollitia*), and the pulvinus of the cheliped being slightly setose (vs. glabrous in *O. mollitia*). It can be separated from *O. angulatus* by the presence of a rounded junction between the anterolateral and posterolateral margin of the carapace (vs. angular in *O. angulatus*), and the absence of setae at the tip of the cheliped (vs. present in *O. angulatus*).

**Distribution.**— Loyalty Islands only.

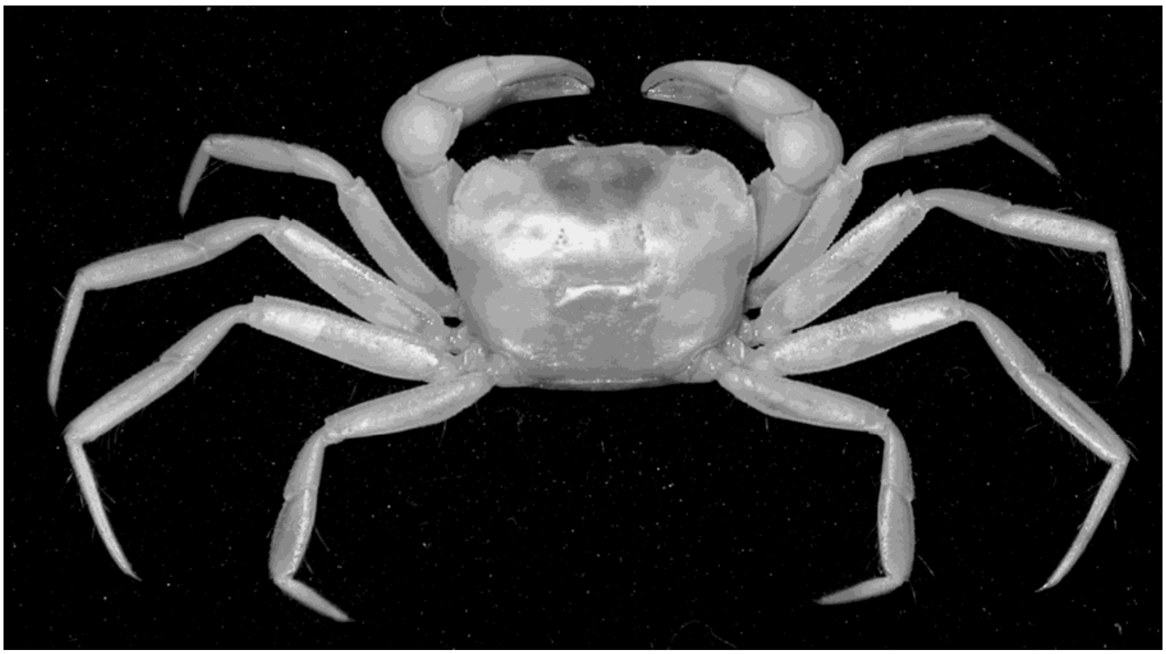


Figure 53. *Orcovita mcneiceae* Ng & Ng, 2002, male, holotype, 17.0mm x 12.6 mm (MNHN B-27951). Dorsal view.

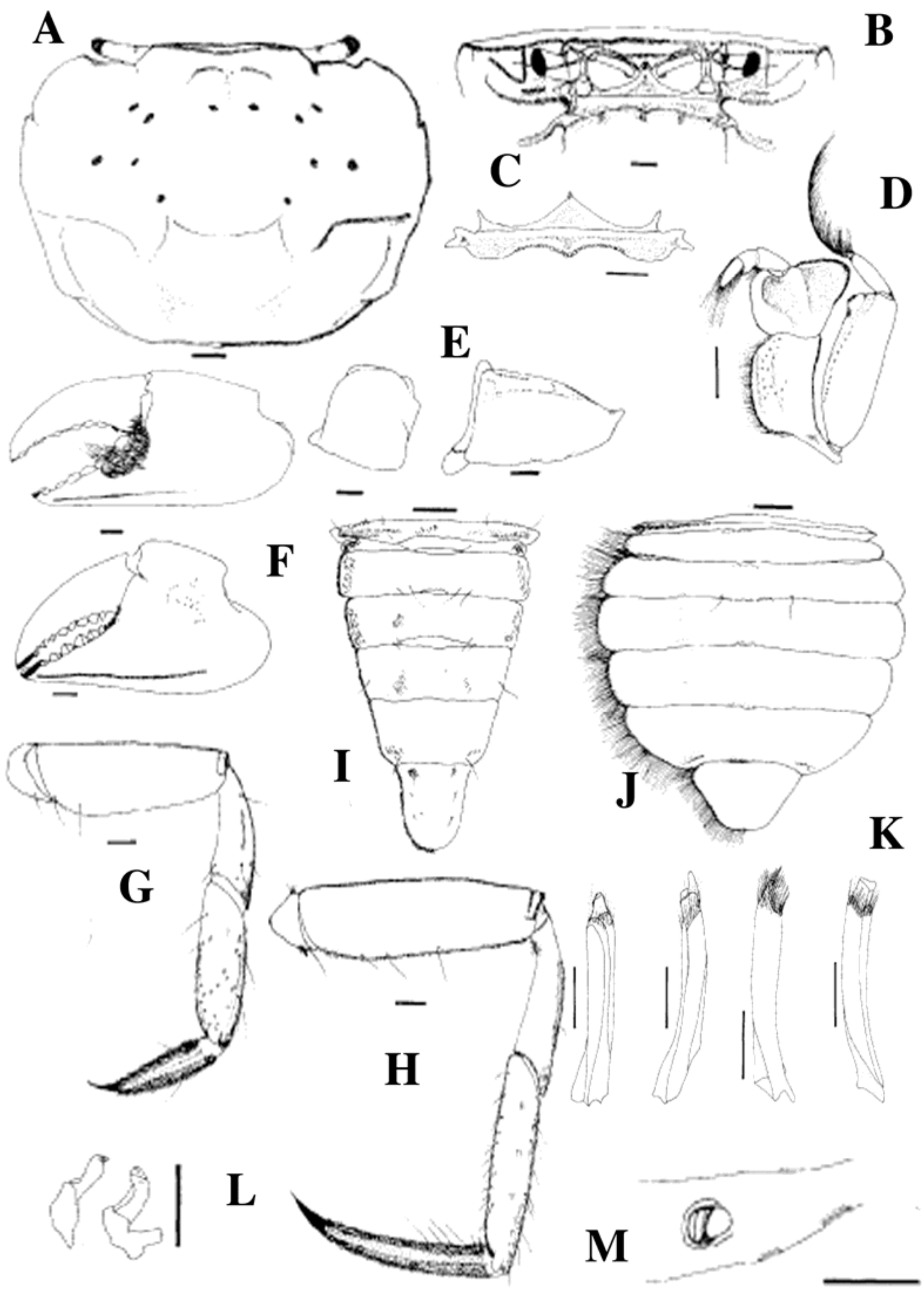



Figure 54. *Orcovita mcneiceae* Ng & Ng, 2002, male, holotype, 17.0mm x 12.6 mm (MNHN B-27951); female, paratype, 15:8 x11:8 mm (MNHN B-27951); A) carapace; B) frontal view; C) eipstome; D) third maxilliped; E) frontal view of male chela; F) frontal view of female cheliped; G) male fourth ambulatory leg; H) male third ambulatory leg; I) male abdomen; J) female abdomen; K) different views of G1; L) different views of G2; M) female gonopore. (Scale=1.0mm).

## *Orcovita miruku* Naruse & Tamura, 2006

(Figures 55; 56A-I)

*Orcovita miruku* Naruse & Tamura, 2006: 147.

**Materials examined.**— **Holotype** – 1 male (18.4mm x 15.0mm) (RUMF-ZC-33), an anchialine pool in a limestone cave (24°34'31.4"N, 124°18'6.8"E), Yoshino, Ishigaki Island, coll. H. Nakai, 22 Jan. 2005.

**Diagnosis.**— Carapace subrectangular, distinctly broader than long (width to length ratio ca. 1.2), dorsal surface smooth, regions poorly defined; frontal margin gently sinuous, strongly deflexed, Anterolateral margins with three teeth including orbital tooth. Third maxilliped stout, exopod, about 0.6 times as broad as ischium. Male chelae swollen, equal, fingers slightly shorter than palm; inner part of cutting edges of fingers. Ambulatory legs subcylindrical in cross section, all segments long, slender; third ambulatory leg longest; surface smooth. Anterior, dorsal margin of merus with blunt subdistal tooth; outer surface of carpus with short setae, anterior and posterior margins of propodus with long and short setae respectively; dactylus tapering to slender, acute tip. Dactylus rectangular in cross section, posterior margin comb-like in first three pereiopods. Third merus long, slender (length to width ratio 4.1), third propodus long, slender (length to width ratio 3.7); third dactylus long, slender (length to width ratio 9.3); fourth merus long, slender (length to width ratio 6.1); fourth propodus long (length to width ratio 2.6); fourth dactylus long, slender (length to width ratio 6.3). Male abdomen narrowly triangular with all segments freely moveable (six somites plus telson); lateral margins covered with short, dense setae; telson broadly triangular, lateral margins weakly concave, distal margin rounded. Female abdomen similar to that of male, very broad. G1 slender, gently curving outwards, subdistal part of dorsal surface with wide slit, forming lobe-like structure, distal part to subdistal lobe with strong setae; G2 short, distal end bilobed.

**Colour.**— *Orcovita miruku* has the body and appendages colour typically associated with cave dwelling animals. (Naruse & Tamura, 2006).

**Size.**— The only male specimen is 18.4mm x 15mm (Naruse & Tamura, 2006). So far, no female specimen has been collected.

**Habitat.**— It was found in anchialine caves (Naruse & Tamura, 2006).

**Remarks.**— From the description, *Orcovita miruku* Naruse & Tamura, 2006, is remarkably different from the known *Orcovita* species in having two anterolateral teeth behind external orbital angle, a relatively convex dorsal surface, and a proportionately less broad carapace. *Orcovita angulata* may be allied with *O. miruku* by the shape of the anterolatetal margin of the carapace. However, *O. miruku* is easily differentiated from *O. angulata* by the fore-mentioned characters and the other characters listed in Table 3 above. So far, only the male specimen has been discovered.

**Distribution.**— Known only from Ishigaki Island, Yaeyama Group, southern Ryukyu Islands, Japan (Naruse & Tamura, 2006).

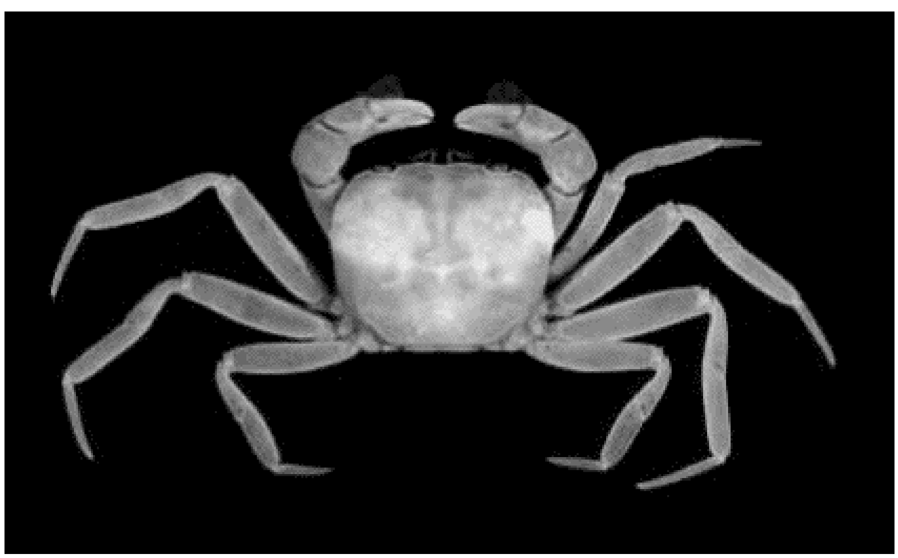


Figure 55. *Orcovita miruku* Naruse & Tamura, 2006, male, holotype, 18.4mm x 15.0mm (RUMF-ZC-33). Dorsal view. (After Naruse & Tamura, 2006).

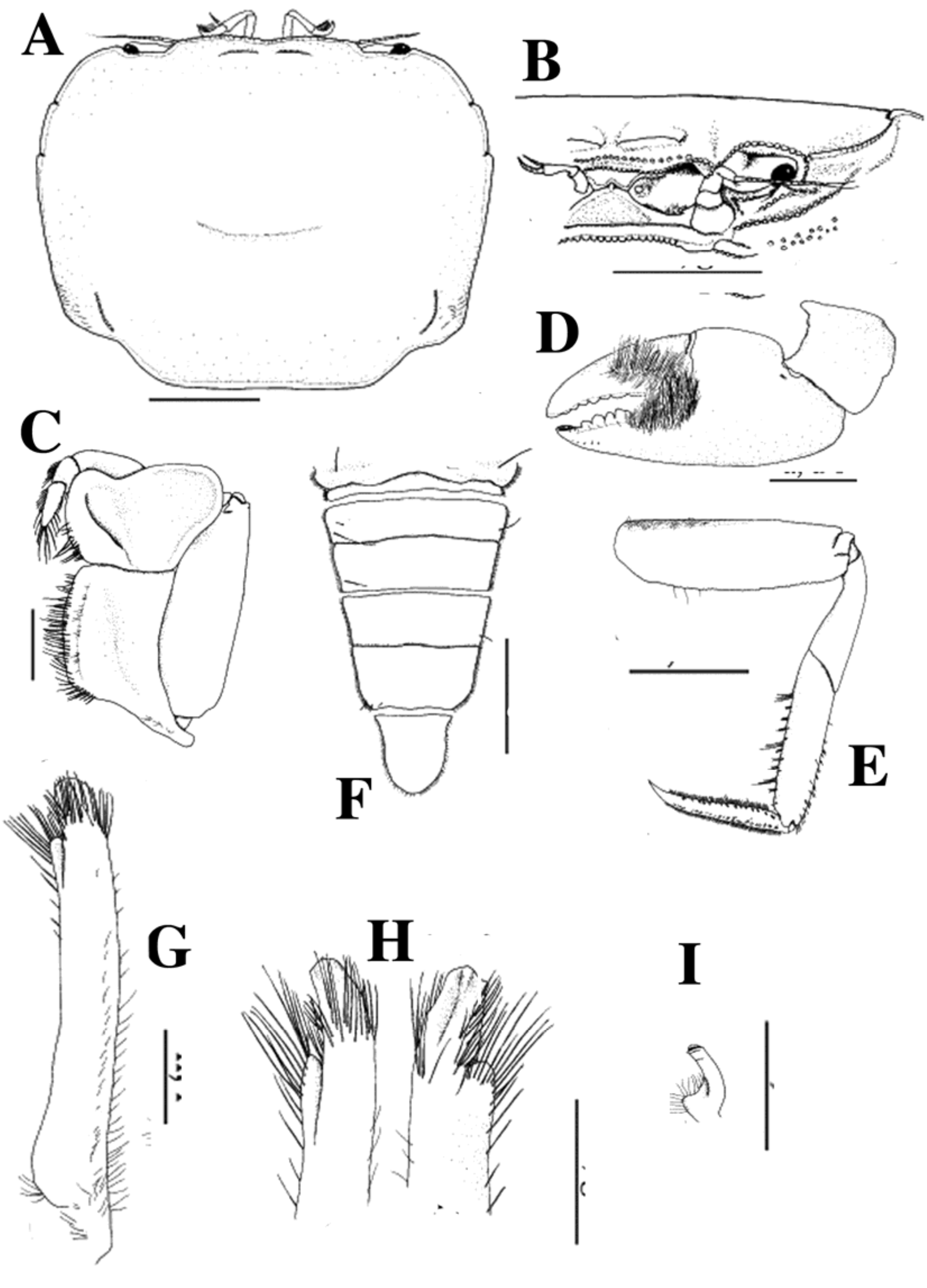



Figure 56. *Orcovita miruku* Naruse & Tamura, 2006; male, holotype, 18.4mm x 15.0mm (RUMF-ZC-33). A) carapace; B) frontal view; C) third maxilliped; D) frontal view of cheliped; E) last ambulatory leg; F) male abdomen; G) G1; H) different view of tip of G1; I) G2. (Scale=1.0mm). (After Naruse & Tamura, 2006).

## *Parapyxidognathus* Ward, 1941

*Parapyxidognathus* Ward, 1941: 15; Balss, 1957: 1668; Takeda & Iwasaki, 1983: 87; Fukui *et al*., 1989: 229; Ng *et al*., 2001: 46.

**Type species.**— *Pyxidognathus deianira* de Man, 1888, by original designation.

**Gender.**— Masculine.

**Diagnosis.**— Carapace quadrangular, distintly broader than long; dorsal surface setose, punctate; regions not well defined, convex. Frontal margin slightly convex, straight. Anterolateral margin subcristate with three teeth including orbital tooth distinct. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Inner surface of chela with granules; outer surface of pollex and manus with tufts of long, stiff setae, a patch of short soft setae near posterior margin of manus; fingers as long as palm. Ambulatory legs with short setae, stout dactylus, posterior margins of propodus with spines. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular, with seven moveable segments (six somites plus telson).

**Remarks.** — Ward (1941) established the genus, *Parapyxidognathus* on the basis of the following features: a) carapace is comparatively broader (vs. narrower in *Pyxidognathus*); b) the front is not produced (vs. distinctly produced in *Pyxidognathus*); c) the exopod of the third maxillipeds is very much broader (vs. less broad in *Pyxidognathus*); d) chela is subequal (vs. equal chelae in *Pyxidognathus*), and e) the ambulatory legs are more longer and slender (vs. shorter and broader legs in *Pyxidognathus*).

When Ward established the *Parapyxidognathus* in 1941, he had only included *Pyxidognathus deianira* in that genus. I found that the morphology of *Pyxidognathus fluviatilus* Alcock, 1900, is quite different from that of *Pyxidognathus* sensu stricto , and should in fact be better referred to *Parapyxidognathus* instead. *Pyxidognathus fluviatilus* (Alcock, 1900), is formally transferred from *Pyxidognathus* to *Parapyxidognathus* in this study (see below).

*Parapyxidognathus* is also related to *Ptychognathus*, but it can be easily discerned by a) the carapace is very much broader than long (vs. carapace not as broad in *Ptychognathus*); b) the absence of a very broad and convex exopod of the third maxillipeds in *Ptychognathus*), and c) the presence of two or more small sharp spines on the posterior margins of the propodi of the ambulatory legs (vs. absence of spines in *Ptychognathus*).

Currently, there are two species in this genus, *Parapyxidognathus deianira* (de Man, 1888) and *P. fluviatilis* (Alcock, 1900).

**Key to species in *Parapyxidognathus***

1a. Carapace with anterolateral teeth acute, narrow. Chelipeds glabrous. -- ***P. fluviatilis***

1b. Carapace with anterolateral teeth relatively broader, wide. Chelipeds with a tuft of long soft setae on outer surface. ---------------------------------------------- ***P. deianira***

## *Parapyxidognathus deianira* (de Man, 1888)

(Figures 57; 58A-I )

*Parapyxidognathus deianira* – Ward, 1941: 15; Balss, 1957: 1668; Takeda & Iwasaki, 1983: 87; Fukui *et al*., 1989: 229; Ng *et al*., 2001: 46.

*Pyxidognathus deianira* de Man, 1888: 148, pl. 10, figs. 4-6; Alcock, 1900: 407; Tesch, 1918: 173, pl. 11, fig. 3; Dai & Song, 1977: 367, pl. 1-2, fig. 3; Dai *et al*., 1986: 471; Dai & Yang, 1991: 517; Naiyanetr, 1998: 103.

**Materials examined.**— **Lectotype** – 1 male (8.0mm x 5.8mm) (MNHN-B13227), from Kemp, Calcutta Museum, no collection date. – **Paratype** – 1 female (9.7mm x 7.9mm) (MNHN-B13227), from Kemp, Calcutta Museum, no collection date. – **Others** – **Indonesia** – 1 male (12.4mm x 9.6mm) (QM-W24121), Maranti river, estuary, Timika, Iran Jaya, Indonesia, no collection date; 1 female (12.1mm x 9.1mm) (QM-W24919), Ajkwa river, estuary, near Timika, southern Iran Jaya, Indonesia coll. 5 Jul. 1998; 1 male (9.8mm x 5.3mm) (QM-W24920), Ajkwa river estuary, Timika, Iran Jaya, Indonesia, 19 Mar. 1998; 1 male (10.8mm x 7.9mm) (QM-W24927), Kamora river, near Timika, southern Iran Jaya, Indonesia, no collection date; 1 male (15.5mm x 9.0mm) (QM-W24923), Main Ajkwa estuary near Timika, south Iran Jaya, Indonesia, coll. 25 Feb. 1998; 1 female (8.4mm x 6.0mm) (QM-W24926), Kamora river system, near Timika, southern Iran Jaya, Indonesia, coll. 20 Mar. 1998; 1 female (6.0mm x 4.4mm) (QM-W24928), Kamora river system near Timika, southern Iran Jaya, Indonesia, coll. 22 May 1998. – **Taiwan** – 10 males (8.8-14.6 x 6.3-11.5mm), 2 females (9.0-10.0 x 6.8-8.0mm) (TMCD-no cat. number), Lin-Bien estuary, Pingtung County, coll. H.C. Liu, 14 Dec. 1999.

**Diagnosis.**— Carapace quadrilateral, surface slightly setose; frontal margin nearly straight. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, meri with antero-external angle broad, exopod very broad, broader than ischium. Cheliped asymmetrical in males, fingers with a tuft of long setae at base of outer surface, absent in female. Ambulatory legs short, flat, densely setose; merus with a sharp subdistal spine on anterior margin, one or more sharp spines on posterior margins of merus. G1 flat, stout, length to width ratio 6.9, with two lobes at subdistal end. Female gonopore operculate, small, circular in shape with a circular operculum.

**Colour.**— The colour of fresh specimens is dark brown or black in colour (H.C. Liu, pers. comm.), and all preserved specimens examined are dark brown in colour.

**Size.**— The largest male specimen examined is 14.6mm x 11.5mm (TMCD-no cat. number), and largest female specimen examined is 10.0mm x 8.0mm (TMCD-no cat. number).

**Habitat.**— It can be found on mud flats, mangroves, brackish waters, muddy river mouths (H.C. Liu, pers. comm.).

**Remarks.**— Besides the morphological differences listed remarks for the genus *Parapyxidognathus* and *Ptychognathus* (see above), there is a additional difference between this species and *Ptychognathus* senu. lato. This species is found in very muddy habitats (vs. *Ptychognathus* species are found under pebbles and habitats with small stones).

The type specimens should be housed in the Natural History Museum in Calcutta, India. However, I have failed to loan out the specimens as they have not response to me or my colleagues with regards the whereabouts of the specimens. As such, to stabilize the taxonomy, I have selected a male specimen, 8.0mm x 5.8mm (MNHN-B13227), which was given by Kemp from Calcutta to MNHN, as the lectotype of the species.

**Distribution.**— Taiwan, China, Java, Sabah, Mergui Archepelago.

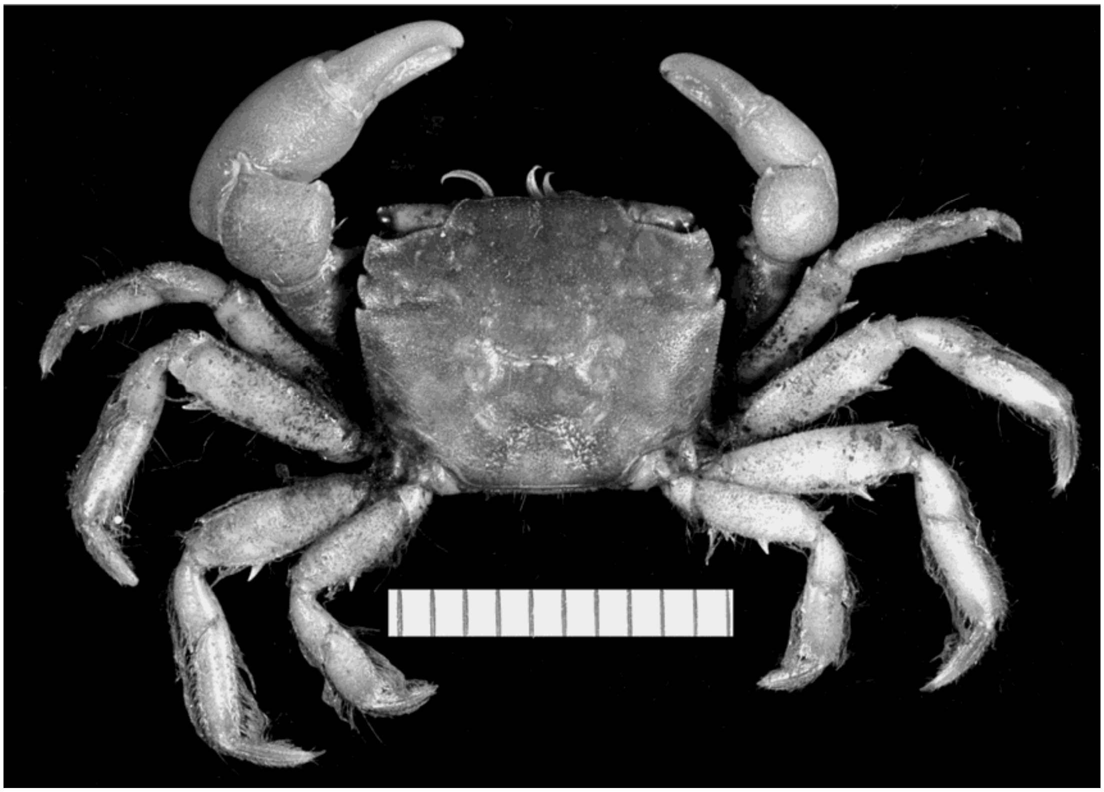


Figure 57. *Paraypyxidognathus deianira* de Man, 1888, male, 12.4mm x 9.6mm, (QM-W24121). Dorsal view.

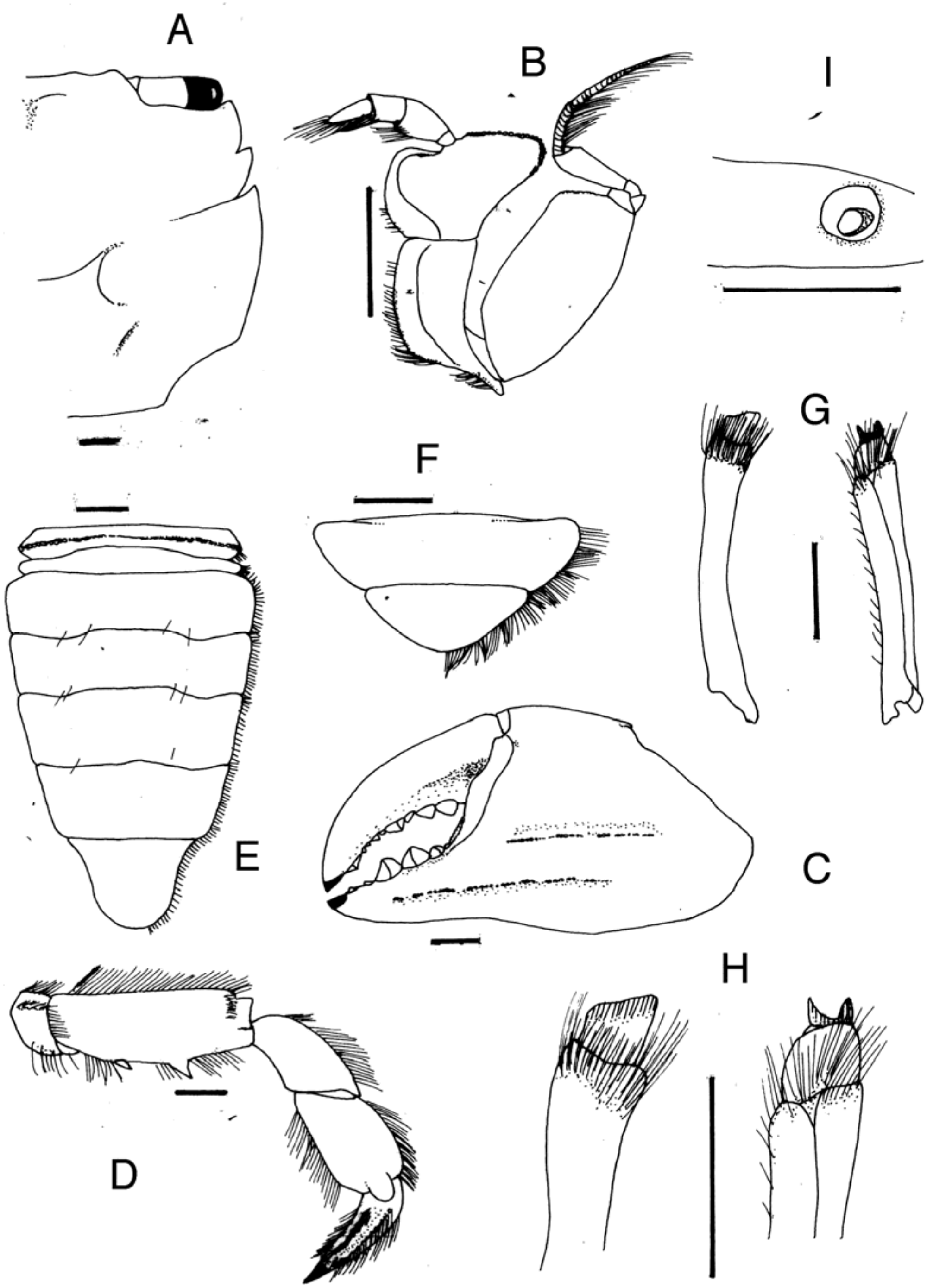



Figure 58. *Paraypyxidognathus deianira* de Man, 1888, 1 male, .6 x 11.5mm (TMCD-no cat. number); female, 10.0 x 8.0mm (TMCD-no cat. number). A) carapace; B) third maxilliped; C) frontal view of cheliped; D) last ambulatory leg; E) male abdomen; F) sixth abdominal segment and telson of female abdomen; G) different views of G1; H) detailed views of tips of G1; I) female gonopore. (Scale=1.0mm).

### *Parapyxidognathus fluviatilis* (Alcock, 1900), new combination

(Figure 59A-C)

*Pyxidognathus fluviatilis* Alcock, 1900: 408; 1902: pl. LXVL, fig. 3, 3a.

**Materials examined.— Neotype** – 1 male (23.3mm x 18.8mm) (ZRC-uncatalogued/NHH9905), tributary of Bagirathi River, north of Ganges River, West Bengal, India, coll. H.H. Ng, 24 Jan. 1999. – **Others** – 1 male (22.8mm x 19.2mm), 1 female (20.9mm x 16.8mm) (ZMA-no cat. number), Khuben Bereden Bergalen, Bengal; Fish Port, coll. de Man, Oct. 1912.

**Diagnosis.—** Carapace quadragular, dorsal surface smooth, flat. Front broad, anterior margin straight. Anterolateral margin subcristate with three teeth including the orbital tooth. Third maxillipeds close with a narrow gap, merus with antero-external angle broad, exopod very broad, broader than ischium. Cheliped asymmetrical in males, large, fingers glabrous. Ambulatory legs long, flat, margins densely setose, posterior margin of merus with numerous small spines, one strong spine near distal end. Male abdomen narrowly triangular with all segments freely moveable (six somites plus telson), in shape, distal margin of telson convex in shape. G1 slender. Female gonopore with rounded operculum, protruding.

**Colour.—** The colour of fresh specimens is mottled dark green (Alcock, 1900), all preserved specimens are brown in colour.

**Size.—** The largest male specimen examined is 22.8mm x 19.2mm (ZMA-no cat. number), and the largest female specimen examined is 20.9mm x 16.8mm (ZMA-no cat. number).

**Habitat.—** Unknown.

**Remarks.**— The species is rare, as it has not been collected since the first report, until 1999, when the third specimens was collected from India. (see above). This species is found in a very large freshwater river, with very fine, grey-coloured sand with pieces of deadwood at the bottom. The river also a species of freshwater sole, and other fishes not associated with estuary habitat.

This species is distinctly different from *P. granulosus* in the following: a) the carapace physiognomy is not high (vs. very high in *P. granulosus*); b) the carapace is quadrate in shape (vs. subquadrate in *P. granulosus*); c) the dorsal carapace surface is glabrous (vs. granulated in *P. granulosus*); ); d) the anterolateral teeth are acute and strong (vs. blunt and weak in *P. granulosus*), and e) the strongest spines on the posterior margins of the propodus of the ambulatory legs are found near the distal end (vs. nearer to the proximal end in *P. granulosus*). Hence, it is being transferred out from the genus *Pyxidognathus*.

The species is actually closest to *Parapyxidognathus deianira* but can be distinguished in a) the dorsal carapace surface is glabrous (vs. slightly setose, punctate in *P. deianira*); b) the anterolateral teeth are more acute, longer and narrow (vs. broader in *P. deianira*); c) the outer surface of the chela is glabrous (vs. presence of a tuft of long soft setae on the outer surface in *P. deianira*); c) the ambulatory legs are sparingly setose (vs. densely setose in *P. deianira*), and d) the strongest spines on the posterior margins of the propodus of the ambulatory legs are found near the distal end (vs. nearer to the proximal end in *P. deianira*).

**Distribution.**— India only.

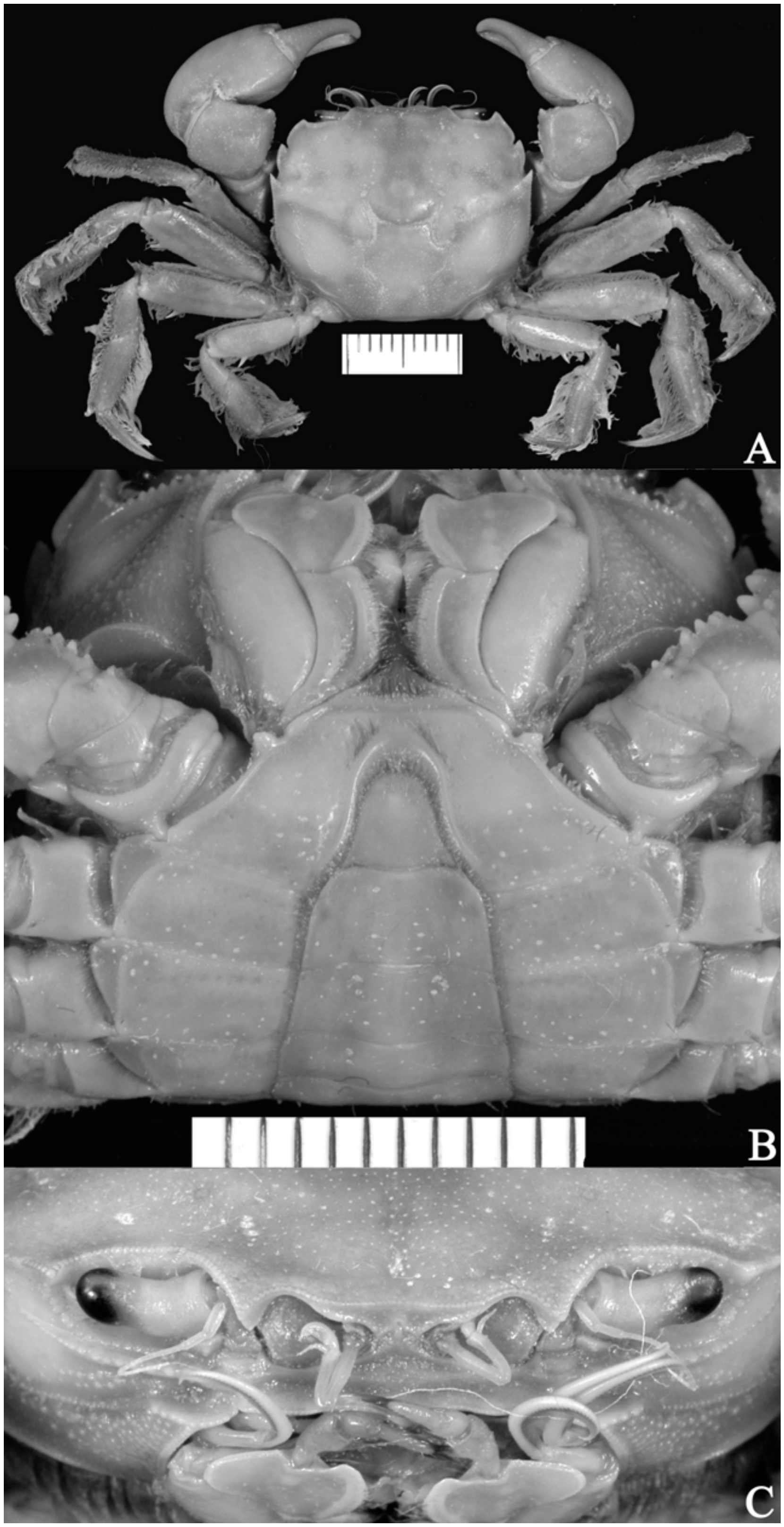



Figure 59. *Parapyxidognathus fluviatilis* Alcock, 1900, male, neotype, 23.3mm x 18.8mm (ZRC-uncatalogued/NHH9905). A) dorsal view; B) ventral view; C) frontal view.

## Genus *Platyeriocheir* Ng, Guo & Ng, 1999

*Platyeriocheir* Ng, Guo & Ng, 1999: 154; Chan, Ng & Ng, 2005: 457.

*Eriocheir* – Sakai, 1939: 669, pl. 109: 3; Horikawa, 1940: 29; Lin, 1949: 29; Sakai, 1976: 647, fig. 355a, c; Dai *et al.*, 1986: 476, fig. 267: 2, pl. 67: 1; Dai & Yang, 1991: 522, fig. 267: 2, pl. 67: 1; Hung *et al.*, 1992: 9; Huang, 1994: 597; Chan *et al.*, 1995: 301. Sun *et al.*, 2003: 592; Chu *et al.*, 2003: 738; Tang *et al.*, 2003: 309; Tang *et al.*, 2004: 255.

**Type species.**— *Eriocheir formosa* Chan, Hung & Yu, 1995, by original designation.

**Gender.**— Feminine.

**Diagnosis.**— Carapace quadrangular, slightly broader than long, flat, depressed; frontal margin straight; dorsal surface sooth, well defined, protogastric cristae low. Anterolateral margin with three teeth including orbital tooth, posterolateral margin smoothly granulated. Chela symmetrical, large in male, outer surface with a tuft of thick setae, tip of dactylus spoon-shaped. Propodus of last short, wide, covered with setae. Lateral margins of first to third thoracic sternites gently serrated. Male abdomen triangular with all segments freely moveable (six somites plus telson). G1 short, stout. Female gonopore with chitinous operculum.

**Remarks.**— *Platyeriocheir* is distinctly different from *Eriocheir* senu stricto in the form of the carapace, third maxillipeds, endostome, chelipeds, and ambulatory legs. These generic differences are tabulated in Table 2 (see above). This genus has only been recorded from Taiwan.

## *Platyeriocheir formosa* (Chan, Hung & Yu, 1995)

(Figures 60; 61A-G)

*Eriocheir rectus* Stimpson, 1858: 103, Sakai, 1938b; Sakai, 1940; Sakai, 1939: 669, pl. 109: 3; Horikawa, 1940: 29; Lin, 1949: 29; Sakai, 1976: 647, fig. 355a, c; Dai *et al*., 1986: 476, fig. 267: 2, pl. 67: 1; Dai & Yang, 1991: 522, fig. 267: 2, pl. 67: 1; Hung *et al*., 1992: 9; Huang, 1994: 597; Sun *et al*., 2003: 592; Chu *et al*., 2003: 738; Tang *et al*., 2003: 309; Tang *et al*., 2004: 255.

*Eriocheir formosa* Chan, Hung & Yu, 1995: 306, figs. 1B, 2A, B, 3A;Yu *et al*., 1996: 15; Jeng, 1997: 18; Jeng, 1998: 84.

*Platyeriocheir formosa* – Ng, Guo & Ng, 1999: 165, figs. 3A–G, 4A–E, 5E, J, 6C; Ng *et al*., 2001: 46; Chan *et al*., 2005: 457.

**Materials examined.**— (In addition the specimens listed in Ng *et al.,* 1999). **– Holotype** – 1 male (60.0mm x 57.0mm) (NTOU-uncatalogued), Nan'ao south stream, I-Lan County, coll. M.S. Hung, 1991. – **Paratypes** – 3 females (ovigerous) (51.9-53.4mm x 48.8-51.2mm) (NTOU-uncatalogued), Taipei County, Bei-Guan, coll. S.Y. Shy & M.S. Hung, 7 Oct. 1991; 4 males (30.2-36.3 x 29.2-34.2mm), 4 females (27.5-36.4 x 26.1-34.6mm) (NTOU-uncatalogued), Nan'ao river, I-Lan County, coll. M.S. Hung, 1993; 1 male (38.0mm x 36.0mm) (SFM-8053), Taiwan, leg. T. Sakai, Nov. 1932.

**Diagnosis.**— Carapace rectangular, overall dorsal surface smooth and very flat, regions well-defined. Anterolateral margins with three teeth including orbital tooth. Third maxilliped very broad; ischium, merus broad, exopod narrow. Cheliped with a tuft of long setae on inner surface of fingers. Ambulatory legs also slender, long, long thick setae on anterior, posterior surfaces of carpus, propodus. G1 long, slender, with chitinuous prominence, slightly curved dorsally outwards with sub distal lobe. Female gonopore operculate, circular in shape.

**Colour.**— The colour of fresh specimens is greenish brown in colour, setae are black (T.Y. Chan, pers. comm.), and all preserves specimens examined are brown in colour.

**Size.**— The largest male specimen examined is 60.9mm x 57.0mm (holotype), while the largest female examined is 53.4mm x 51.2mm (paratypes).

**Habitat.**— It can be found in freshwater rivers, and in the deep region along the coastline during the spawning (Shy & Yu, 1992; T.Y. Chan, pers. comm.).

**Remarks.**— Until 1995, only two species of mitten crabs were recognized from Taiwan viz. *Eriocheir japonica* and *E. recta.* Both species have a very distinct distribution on the island with minimal overlap. *Eriocheir japonica is* found mainly in western Taiwan, while *E. recta* is distributed in eastern Taiwan (Hung, 1993; Chan *et al.,* 1995).

Chan *et al.* (1995) argued, however, that the Taiwanese specimens were not *E. recta,* and synonymized this species with *E. japonica.* They selected a neotype for *E. recta* Stimpson, 1858. They subsequently established a new name, *E. formosa,* for the Taiwanese species previously known as *E. rectus.* Chan *et al.* (1995) gave a concise diagnosis and commented on the differences between *E. formosa* and the other species *of Eriocheir,* including *N. leptognathus.* Detailed comparison of all known species of *Eriocheir* showed a number of differences between *P. formosa* and the other species. These differences are mainly in the carapace, thoracic sternites, chelipeds, ambulatory legs, G1 and female gonopore.

It is interesting to note that Chan *et al.* (1995) had allied *P. formosa* with *Neoeriocheir leptognathus* (as *E. leptognathus),* based on the straight frontal margin and presence of three anterolateral teeth, while citing differences between the two taxa in their maxilliped and sizes. There are also differences in the forms of the eye-stalks, epi-gastic cristae, thoracic sternites, chelae, ambulatory legs, G1, and female gonopore.

The larval ecology of this species is similar to *Eriocheir,* zoeal stage and megalopae migrate upstream to freshwater.

**Distribution.**— Taiwan (River systems of eastern Taiwan, from Hua-Lian County to Pingtung County).

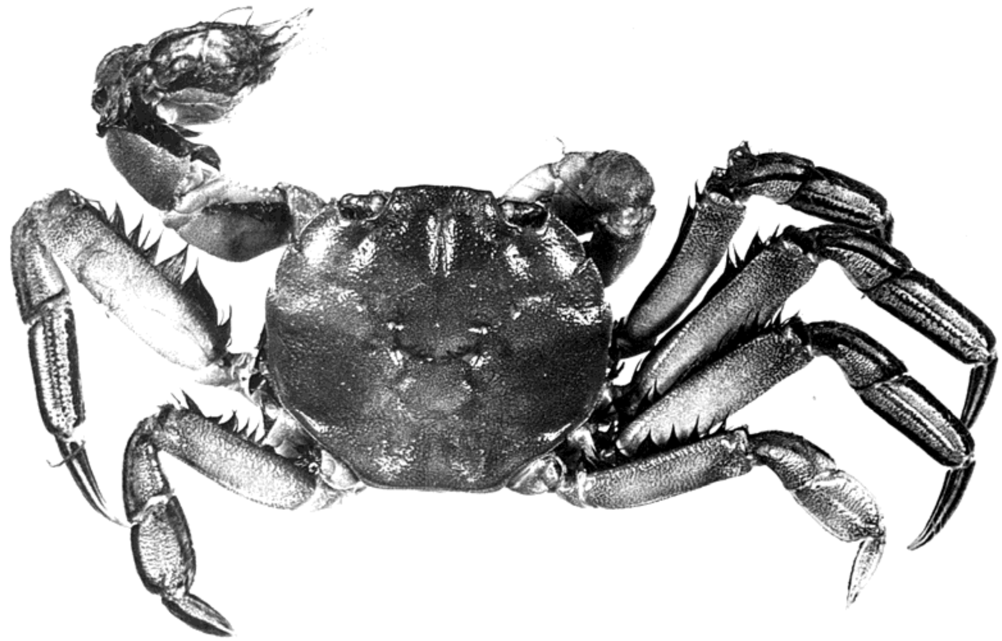


Figure 60. A) *Platyeriocheir formosa* (Chan, Hung & Yu, 1995), male, 58.4mm x 54.8 mm (ZRC 1997.594).

.

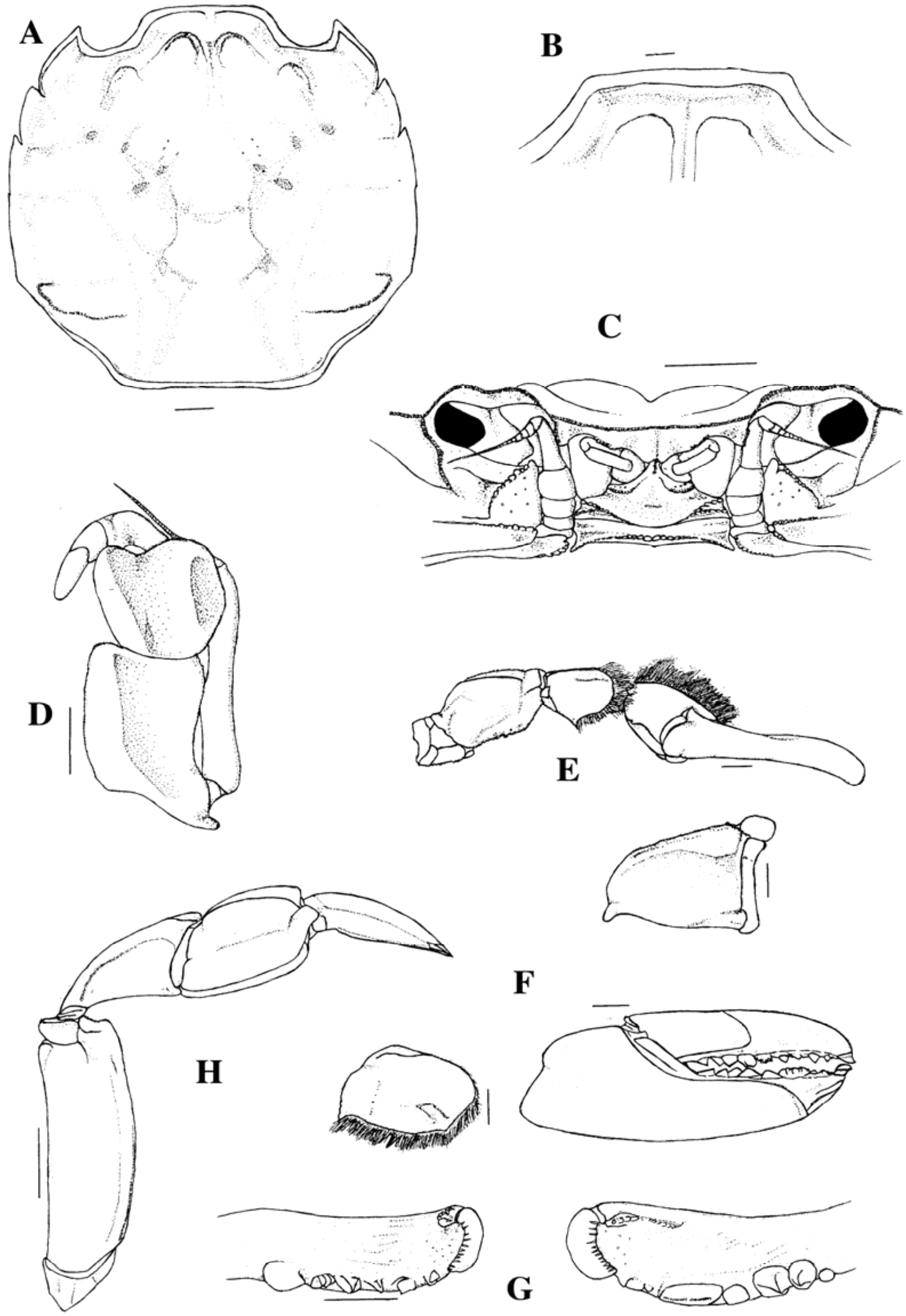



Figure 61. *Platyeriocheir formosa* (Chan, Hung & Yu, 1995), male, holotype (60.0mm x 57.0mm) (NTOU-uncatalogued). A) carapace; B) frontal margin; C) frontal view; D) third maxilliped; E) dorsal view of chela; F) frontal view of chela; G) inner surfaces of chelipeds; H) last ambulatory leg. (Scale=1.0mm).

### Genus *Pseudograpsus* H. Milne Edwards, 1837

*Pseudograpsus* H. Milne Edwards, 1837: 81; Dana, 1852: 248; Tesch, 1918: 97; Balss, 1922: 157; 5Sakai, 1939: 665; Crosnier, 1965: 39; Sakai, 1976: 645; Ng *et al.,* 2000: 759.

**Type species.**— *Grapsus penicilliger* Latreille, 1817, designation by Holthuis (1977).

**Gender.**— Masculine.

**Diagnosis.**— Carapace quadrangular, broader than long; dorsal surface setose, punctate; regions not well defined, physiognomy thick, convex. Frontal margin slightly convex, almost straight. Anterolateral margin subcristate with three teeth including orbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped with foliaceous merus, broader than long; anterolateral angle strongly produced, auriculiform; distal margin distinctly bilobed, outer lobe larger, base with small median cleft. Ischium longer than broad, sulcus not discernible. Small, distinct rhomboidal gape formed when third maxillipeds closed. Exopod with obtuse, blunt inner subdistal angle, flagellum prominent, longer than width of merus. Epistome broad, flat, posterior margin entire. Chelae with inner surface of chela with granules; outer surface of pollex and manus with or without setae. Ambulatory legs with short setae, stout dactyli. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular with all segments freely moveable (six somites plus telson). G1 long, slender. Female gonopore operculate, circular in shape.

**Remarks.**— H. Milne Edwards (1837: 81) named two species as belonging to the genus, *P. pencilliger* (Latreille, 1817), and *P. pallipes* H. Milne Edwards, 1837. No type species was designated. Holthuis (1977) was the first to validly select *Cancer penicilliger* Latreille, 1817, as the type species (see also Ng & Nakasone, 1993: 2). *Cancer penicilliger* was later synonymized under *Pseudograpsus barbatus* (see Ng *et* *al.*, 2002) since *P. barbatus* is a much older name. The genus *Pseudograpsus* has long history of association with *Hemigrapsus* and *Brachynotus* (see above, Tesch, 1918; McLay & Schubart, 2004). Balss (1934) synonymised *P. erythraeus* Kossmann, 1894, under *P. elongathus*. Ng & Nakasone (1993) removed *P. laniger,* and placed it in their new genus *Scutumara* Ng & Nakasone, 1993, with a comment that the genus *Pseudograpsus* needs to be revised.

The genus currently comprises of five species viz. *P. setosus* (Fabricius, 1778) (type species)*; P. crassus* A. Milne-Edwards, 1868*, P. albus* Stimpson, 1858, *P. elongatus* A. Milne-Edwards, 1873, and *P. intermedius* Chhapager, 1955. The genus can be easily divided into two distinct groups based on the adult size of the animals. The first group comprises of the 'large-sized' species of *P. setosus* and *P. crassus*, and the second group are made up of the 'small-sized' species viz. *P. intermedius*, *P. elongatus* and *P. albus*.

The morphology of the 'small-sized' species is distinctly different from the 'large-size' species in the overall forms of the carapace, chelipeds, ambulatory legs and reproductive structures. These differences suggest that their retention in *Pseudograpsus* sensu stricto is not parsimonious. However, each of these three small-size species is also very markedly different from each other in many ways, so much so that to place all three in one genus is just not possible. New genera have been established to accommodate each of them (see below for details).

The genus *Pseudograpsus* now comprises of only the two 'large-sized' species, *P. setosus* Fabricius, 1798, and *P. crassus* A. Milne-Edwards, 1868.

**Key to species in *Pseudograpsus***

1a. Carapace quadrangular glabrous. Cheliped glabrous. ------------------- ***P. crassus***

1b. Carapace quadrangular. Chelipeds with long stiff, black setae on outer surface. ------ ---------------------------------------------------------------------------------- ***P. setosus***

## ***Pseudograpsus setosus*** **(Fabricius, 1778)**

(Figures 62A-C; 63A-O)

"*Cancer barbatus*" Rumphius, 1705: 26, pl. 10, fig. 2; Petiver, 1713: pl. 4, fig. 6.

*Cancer setosus* Fabricius, 1798: 339; Latreille, 1803: 372;

*Grapsus penicilliger* – Latreille: 1817a: 431; Latreille, 1817b: 16, pl. 12, fig. 1; Latreile, 1825: 148; Lamarck, 1818: 249; Desmarest, 1825: 130, pl. 15, fig. 1.

*Cancer penicilliger* – Henschel, 1833: 204.

*Pseudograpsus penicilliger* – H. Milne Edwards, 1837: 82; Lucas, 1840: 71, pl. 3, fig. 3; Holthuis, 1977: 162.

*Eriocheir ? penicilliger* – De Haan, 1835: 31.

*Pseudograpsus barbatus* H. Milne Edwards, 1853: 191; Heller, 1865: 52; de Man, 1902a: 99, 103; de Man, 1902b: 506.

*Pseudograpsus setosus* – Kingsley, 1880: 205; de Man, 1892: 317; Tesch 1918: Holthuis, 1959: 116; Ng & Nakasone, 1993: 2.Ng *et al.*, 2001: 46; Ng *et al.*, 2002: 760, figs. 1–4.

**Materials examined.— Neotype** – 1 male (40.0mm x 35.3 mm) (RMNH-D-191), Ambon, coll. Ludeking, 1864**. – Others –Asia –**1 male (ZMA-no cat. number), no collection data; 1 male (29.6mm x 23.0 mm) (dried, damaged) (MNHN-B-13213), Acas 'd' Asie, coll. Geiche. – **Indonesia –** 2 males (MZB-CRU-1448), Sungei (River) Ilgamung, Desa (Village) Persiapan Air Mancur, Taman (Recreation Park) Wisata Tuti Adagae, Kec. (County) Perwakilan Alor Timur (East), coll. S. Hartini, 17 Apr. 1997; 2 females (MZB-CRU-1449), Desa (Village) Kamot, Kec. (County) Perwakilan Alor Timur (East), Palau (Island) Alor, coll. S. Hartini, 17 Apr. 1997; 1 male (NMB-712a), River Toebah, Ceram, coll. L.F. de Beaufort, 1920; 1 female (19.7mm x 19.3mm) (RMNH-D-2550), River Wukuz by Sikka, Flores, coll. J.G. de Man, 26 Apr. 1930; 11 males (29.8-46.0mm x 25.6-40.0mm), 2 females (34.0-35.0mm x 29.9-31.5mm) (SFM-5317), Ambon, coll. Hitubei Alang, 1890; 2 males (SFM-365), Tubrina, coll. 1891; 1 male (36.7mm x 31.6mm), 1 female (32.2mm x 30.2mm) (SFM-5317), Ambon, no collection date; 1 male (SFM-5325), Ternate, det. de Man, 1902; 1 male (20.8mm x 17.9mm) (SFM-5325), Ternate, det de Man, 1902;; 2 males (12.1-30.0mm x 11.0-27.1mm), 2 females (16.2mm x 14.6-14.9mm) (ZMA no cat. number), River by Bombamg, Flores, coll. M. Weber, 1889; 2 males (ZMA-no cat. number) River Toebah, West Ceram, Feb. 1910; 2 males (32.1-38.8mm x 28.8-33.6mm) (ZMA-no cat. number), River Toebah, coll. W. Ceram, Feb. 1910.1 male (33.8mm x 29.5mm)

(ZMA-no cat. number), no collection data. **– New Guinea** – 2 males (12.0-12.6mm x 9.5-10.3mm) (SFM-7107), New Guina, no collection date. **– Taiwan –** 2 males (IZAS-72487), Geng-Fang River, I-Lan County, coll. K.X. Lee, 29 Apr. 2000; 1 male (NTOU-uncatalogued), Tahsi, I-Lan County, coll. K.X. Lee, Sep. 2000; 1 female (TMCD-uncatalogued), Chang-Yuen, Taitung County, coll. J.H. Lee, 28 Aug. 2000; 1 male, 1 female (ZRC 2000.2230), Tahsi River, I-Lan County, Taiwan, coll. M.S. Jeng, 24 Nov. 1997; 2 males (37.3-39.5mm x 32.8-34.5mm), (IZAS-72487), Geng-Fang River, I-Lan County, coll. K.X. Lee, 29 Apr. 2000; 1 male (NTOU-uncatalogued), Tai-Shi, I-Lan County, coll. K.X. Lee, Sep. 2000; 1 female (TMCD-uncatalogued), Chang-Yuen, Taitung County, coll. J.-H. Lee, 28 Aug. 2000; 1 male, 1 female (ZRC 2000.2230), Tai-Shi River, I-Lan County, Taiwan, coll. M.-S. Jeng, 24 Nov. Nov. 1997; 2 males (27.5-32.0mm x 24.8-28.4mm) (ZRC-uncatalogued), Gengfang River, I-Lan County, coll. K.-X. Lee, Aug. 2000.

**Diagnosis.—** Carapace quadrangular, slightly broader than long; dorsal surface glabrous; regions defined, convex. Frontal margin slightly convex, divided into four indistinct lobes. Anterolateral margin subcristate with three teeth, including external orbital tooth, external orbital tooth most distinct, very broad; second tooth smaller in size, third tooth smallest. Posterolateral margins not sharply demarcated from anterolateral margin, almost straight, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped with foliaceous merus, broader than long; anterolateral angle strongly produced, auriculiform; distal margin distinctly bilobed, outer lobe larger, base with small median cleft. Ischium longer than broad, sulcus not discernible. Small, distinct rhomboidal gape formed when third maxilliped closed. Exopod with obtuse, blunt inner subdistal angle, flagellum prominent, longer than width of merus. Epistome broad, flat, posterior margin entire. Male chelae equal to subequal, inner surfaces glabrous; merus without spines, dorsal surface highly setose; carpus without spines or teeth; outer surface of fingers with tufts of long, stiff black setae. Fingers slightly shorter than palm; cutting edges of both fingers with numerous teeth, finger tips recurved, sharp, hoofed-shaped. Female chelae similar but smaller to those of male, without setae. Ambulatory legs with second pair longest. Merus of all ambulatory legs with long, soft setae; anterior margin with blunt subdistal tooth; outer surface of carpus with short setae, anterior and posterior margins of propodus with short setae. Male abdomen narrowly triangular with all segments freely moveable (six somites plus telson), lateral margins highly setose; female abdomen similar, very broad. G1 slender, gently curving outwards, terminal lobe elongate, slightly curved; genital opening lateral to base of terminal lobe; subterminal lobe pectinated, rounded, densely setose. G2 short, small. Female gonopore operculate, slightly convex, circular.

**Colour. —** The colour of fresh specimens is uniform dark to chocolate brown, with setae on male chelae black in colour (K.X. Lee, pers. comm.), and all preserved specimens examined are brown in colour.

**Size.**— This species is very large in size, the largest male specimen examined is 46.0mm x 40.0mm (SFM-5317), and the largest female specimen examined is 35.0mm x 31.5mm (SFM-5317).

**Habitat.**— In Taiwan, mountain streams at about 300m above sea level. Individuals migrate downstream to the river mouth in March and April, and in June and July, they may be found in the sea itself (Ng *et al.*, 2002).

**Remarks.**— This species was first reported by Rumphius as "*Cancer barbatus*" (1705: pl. 10, No. 2) on the basis of specimen(s) from the Indonesian island of Ambon. The description was very brief but a clear figure was provided. The name "*Cancer barbatus*", however, has no nomenclatural validity as it was a pre-Linnaean name. Fabricius (1798: 339) subsequently described *Cancer setosus* on the basis of an unspecified number of specimens from "Tranquebariae" (India) in the collection of Daldorff. His description, however, is very brief and not very informative: "C. thorace utrinque bidentato, tarsis hirtis. Habitat Tranquebariae Dom Daldorff. Carpus paruum, laeniu sculum margine utrinque acuto, bidentato. Orbita aculorum haud eleuata. Chela breues, inermes pilosae. Pendum tarsis hirti". There was no mention of Rumphius. or his specimens. Latreille (1803: 372) subsequently referred to *Cancer setosus* under a vernacular name, "Crabe Soyeux" (or 'Silk Crab' in English). Latreille (1817a: 431) subsequently named a new species, *Cancer penicilliger*, referring to it in the text under the vernacular name, "Grapse Porte-Pinceau" ('Porte-Pinceau' means 'unstable brush' in English). In describing this species, Latreille (1817a: 431) referred to Rumphius's plate and figure in his text but did not indicate clearly that he had specimens on hand.

Henri Milne Edwards (1837) transferred *Cancer penicilliger* Latreille, 1817, to a new genus, *Pseudograpsus*, together with a new species, *P. pallipes.* However, in a footnote (H. Milne Edwards, 1837: 82), he questioned the validity of *C. penicilliger*, commenting that it was probably synonymous with *Cancer setosus* Fabricius, 1798. From his text, it was clear that he examined at least one specimen in the collection of the Paris Museum. Subsequently, H. Milne Edwards (1853: 191) synonymised *Cancer setosus* Fabricius, 1798, and *Cancer penicilliger* Latreille, 1817, under "*Pseudodgrapsus barbatus* (Rumphius, 1705)". However, since "*Cancer barbatus* Rumphius, 1705" is not a valid name (being pre-Linnaean), H. Milne Edwards (1853) was actually the first author to validate the name "*P. barbatus*" (see also Tesch, 1918). This makes *Pseudograpsus barbatus* H. Milne Edwards, 1853, a junior synonym of both *Cancer setosus* Fabricius, 1798, and *Cancer penicilliger* Latreille, 1817. These three names have since been regarded as subjective synonyms, with *Pseudograpsus setosus* (Fabricius, 1798) being the oldest available name.

In describing *Pseudograpsus*, H. Milne Edwards (1837: 81) named two species as belonging to the genus, *P. pencilliger* (Latreille, 1817) and *P. pallipes* H. Milne Edwards, 1837. No type species was designated. Holthuis (1977: 162) was the first to validly select *Cancer penicilliger* Latreille, 1817, as the type species (see also Ng & Nakasone, 1993: 2).

The type specimens of *Cancer setosus* are no longer extant. Zimsen (1964: 650) notes that there are only dried remains of the specimen labeled as this species in the Copenhagen Museum. We have on hand, a photograph taken in the late 1960s of these remains which show only a few badly broken up pieces of legs. These remains have since been re-hydrated and the third author examined this material in late 1999. This material is in such poor condition, that it is effectively useless, and one cannot even discern the genus they belong to. The type for *Cancer setosus* should be regarded as lost. There was no mention of specimens in Latreille's (1817) original description of *Cancer penicilliger*, but as he referred to Rumphius (1705) book, Rumphius' material from Ambon must be regarded as types. Henri Milne Edwards (1837: 82) noted the presence of specimen(s) in the collections of the Paris Museum. The first author managed to find a single dried damaged male specimen in the MHNH (B-13213), supposedly from "Acas d'Asie" labeled as *Pseudograpsus setosus*, and this may have been the specimen H. Milne Edwards (1837, 1853) (and possibly even Latreille, 1817) based his report. In any case, it should not be regarded as one of Latreille's (1817) types, since he did not mention any specimens other than those of Rumphius. There are no other specimens in the MNHN. The MNHN specimen could also have been obtained well after the time of Latreille and/or Henri Milne Edwards (D. Guinot, pers. comm.). It is possible that the label presently associated with this MNHN specimen, *P. setosus,* was changed by a later worker and it was originally named *C. penicilliger*, but this is pure speculation. Similarly, H. Milne Edwards (1853), in ascribing *Cancer barbatus* to Rumphius (1705), effectively makes all of Rumphius' Ambonese material types as well. Of course, Rumphius' (1705) material is now lost.

It is most unfortunate that the type of *Cancer setosus* Fabricius, 1798, is no longer available as the original description was too poor to be certain if it is actually the same species as *C. penicilliger* Latreille, 1817, and *Pseudograpsus barbatus* H. Milne Edwards, 1853. Rumphius' (1705) material is also no longer extant. In the descriptions provided by Rumphius (1702: 26, pl. 10, fig. 2), Fabricius (1798: 339), Latreille (1817a: 431), the type of setae present on the chelae was not mentioned. Based on their brief descriptions, these authors could be referring to many species of the different genera like *Neoptychognathus* nov. gen (see below) [e.g. *N. barbatus* (A. Milne-Edwards, 1873), *N. easteranus* (Rathbun, 1907), and *N. johannae* (Rathbun, 1914)]; or *Mitragrapsus* [e.g. *M. altimanus* (Rathbun, 1914)]; or *Hemigrapsus* Dana, 1852 (e.g. *H. penicillatus* (De Haan, 1835) and *H. crassimanus* Dana, 1852); or *Asiagrapsus* nov. gen (see below) [e.g. *A. sinensis* Rathbun, 1929)]; or *Parapyxidognathus* A. Milne-Edwards 1879 (e.g. *P. deianira* de Man, 1888); or even a very young *Eriocheir* (De Haan, 1835) as each of these species has a tuft of long setae present on their chelae! The presence of long setae on the outer surface of the male chelae is the most prominent feature of *P. setosus*. This could have led to De Haan's speculative placement of this species in the genus, *Eriocheir* (De Haan, 1835: 31). However, it must be noted that the setae present on the chelae of *P. setosus* are stiff, whiles those present on *Eriocheir* are soft. Interestingly, the vernacular name of this species, "Cattam Gigi Boeloe" (Rumphius, 1705) which means bearded crab in the native language, is still in use today by natives in Ambon and surrounding areas (D. Wowor, pers. comm.). Since *C.*

*penicilliger* Latreille, 1817, is the type species of *Pseudograpsus* H. Milne Edwards, 1837, and all three names are now generally regarded as subjective synonyms, it seems best to select a neotype that keeps the status quo, and the application to the International Commission of Zoological Nomenclature had been submitted ((see Ng & Ng, in press).

In addition, it must be noted that there is no further report of *Cancer setosus* from Tranquebar after Fabricius (1798) report. I visited India in March 2001, in an attempt to collect fresh specimens from Tranquebar, Tamil Nadu State (India), as well as a visit to the local museum (University Museum, Annamalai University) to find specimens of this species but the attempt has failed. Local scientists working on the fauna of Tranquebar have never seen or collected *Cancer setosus*. On the other hand, *Ptychognathus altimanus* (Rathbun, 1914), which closely resembles *P. setosus*, has been quite frequently collected. There is no record of this species from the Andaman and Nicobar islands as well (Sethuramalingam & Khan, 1991; O.F. Fernando & A.F. Fernando, pers. comm.). In addition, all the records of *P. setosus* shown that they are collected from islands, for example Ambon, Ceram, Flores, and Taiwan, but not from any continent. Thus, there is this possibility that Fabricius' specimens are not *Cancer setosus*!

**Distribution.**— Southeastern India, Nicobars, Indonesia and Taiwan. *Pseudograpsus setosus* was previously known from southern India, Nicobars, as well as the islands of Ambon, Timor, Flores and Ternate in Indonesia (Fabricius, 1798; Heller, 1865; de Man, 1892; Tesch, 1918; Holthuis, 1978). The present discovery of *P. setosus* from Taiwan is very interesting as it extends its known range considerably and into northern temperate waters for the first time. In Taiwan, it is known from the northeast and eastern parts of the island but there have been reliable reports that it also occurs in the southeast (H.P. Ho, pers. comm.). All known records are, however, eastern, its distribution being similar to the better known varunine crab, *Platyeriocheir formosa* Chan, Hung & Yu, 1998 (see Ng *et al.,* 1999).

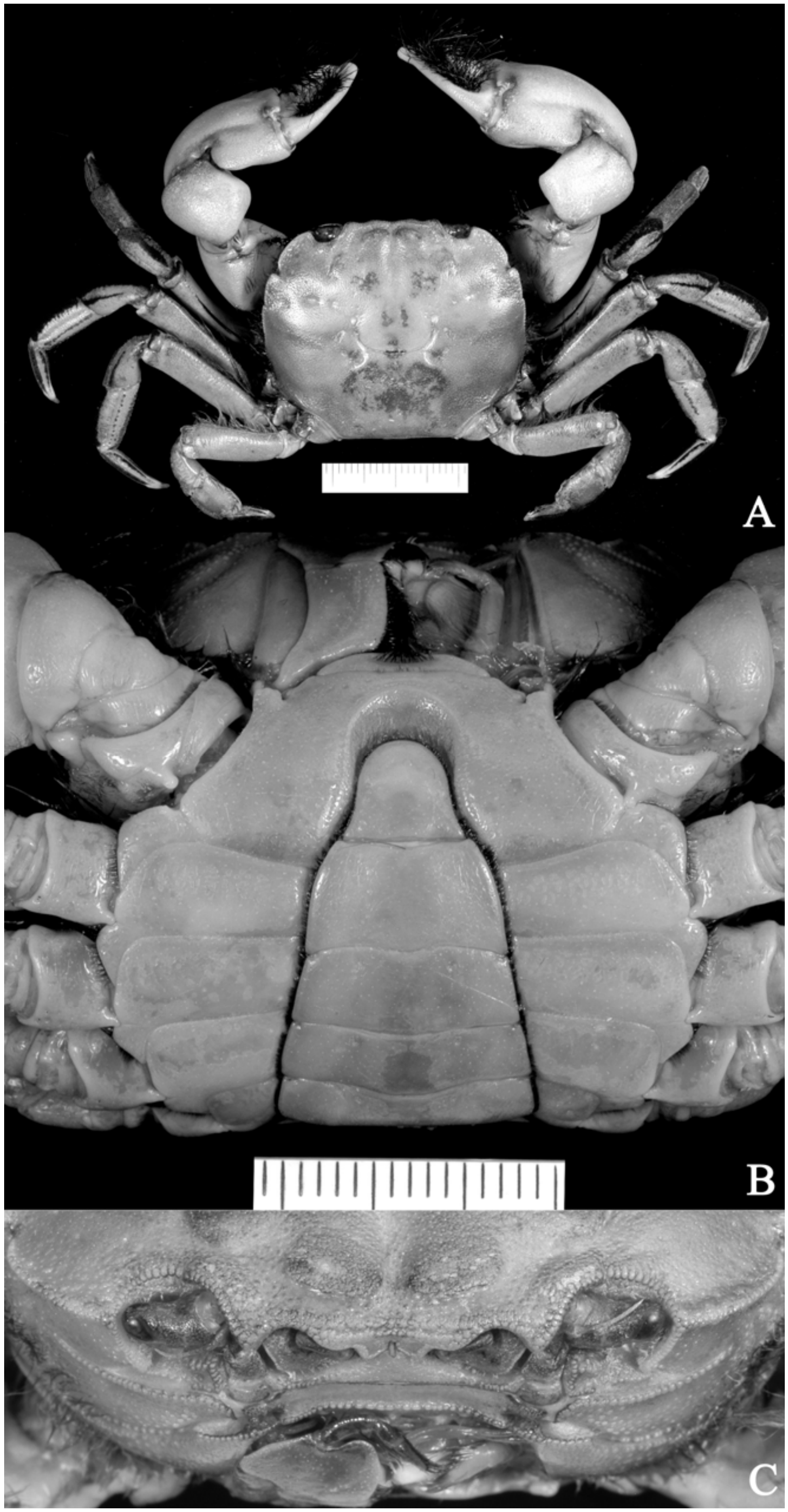



Figure 62. *Pseudograpsus setosus* (Fabricius, 1778), male, 39.5mm x 34.5mm (IZAS-72487) A) dorsal view; B) ventral view; C) frontal view.

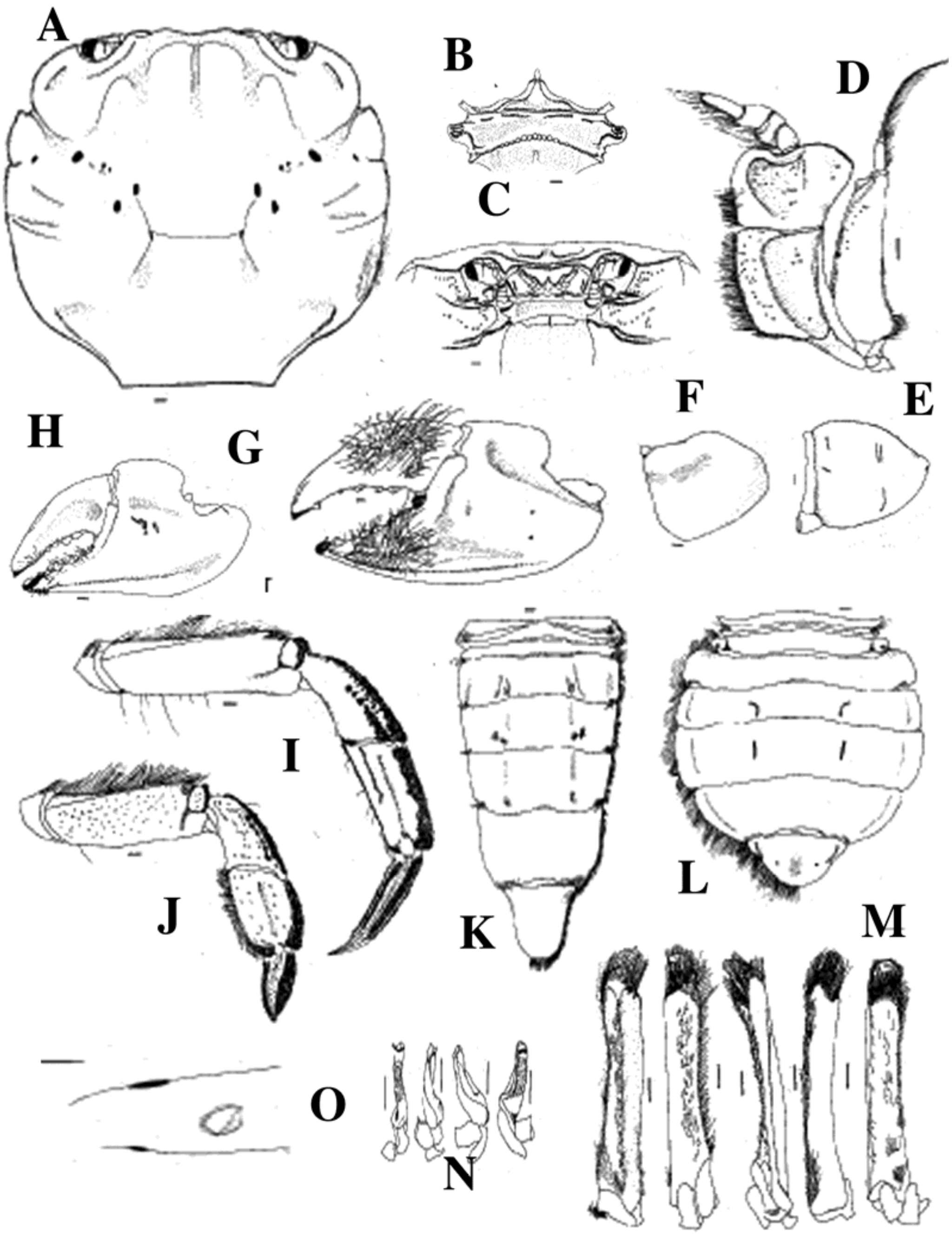



Figure 63. *Pseudograpsus setosus* (Fabricius, 1778), male, 39.5mm x 34.5mm (IZAS-72487), female, 35.0mm x 31.5mm (SFM-5317). A) carapace; B) epistome; C) frontal view; D) third maxilliped; E) merus of chela; F) carpus of chela; G) outer view of male cheliped; H) outer view of) female abdomen; M) different views of G1; N) different views of G2; O) female gonopore. (Scale=1.0mm).

## *Pseudograpsus crassus* A. Milne-Edwards, 1868

(Figure 64; 65A-F)

*Pseudograpsus crassus* A. Milne-Edwards, 1868: 176; Tesch, 1918: 98; Balss, 1922: 152; Ward, 1941: 1104; Yamaguchi & Baba, 1993: 459, fig. 175; Cai & Ng, 2001: 665; Ng *et al.,* 2002: 761.

**Materials examined.——** **Lectotype** – 1 female mounted on board (dry) (MNHN-3623), Manado, Celebes [Sulawesi] coll. M. Reidel, no collection date. – **Paralectotype** – 1 female mounted on board (dry) (MNHN-3623), Manado, Celebes [Sulawesi] coll. M. Reidel, no collection date; 1 female, cracked carapace, mounted on board (dry) (MNHN-3625), Manado, Celebes [Sulawesi], coll. M. Riedel, no collection date. – **Others** – **Indonesia** – 2 males (35.5-40.6mm x 30.7-35.7mm) (NMB-619d), Flores, Indonesia, coll. Wirz, 1931; 4 males (42.8-45.4mm x 37.4-40.0mm) (NMB-619e), Loko Jengo-Bach, Zentralsumba, bei Loko Jengo, coll. E. Sutter, 24 Sep. 1949; 1 male (35.5mm x 31.8mm), 1 female (36.4mm x 32.3mm) (NMB-619a), Tomohon, Celebes [Sulawesi], coll. D.P.F. Sarasin, no collection date; 3 males (28.7-38.9mm x 25.8-33.6mm), 1 female (26.2mm x 23.5mm) (NMB-619c), River Toebah, Ceram, coll. D.L.F. de Beaufort, Nov. 1910;1 male (36.3 x 31.3 mm), 1 female (36.4 x 31.5 mm) (NMB-619a) Jomohon, Celebes, 24 Apr. 1894; 3 males (34.4-39.8mm x 30.0-34.7mm), (RMNH-D40840), Beo Kara Kelong, Talaut Island, Indonesia, coll. Snellius Expedition I, Jun. 1930; 1 male (36.4mm x 31.3mm) (RMNH-D2181), Station 131, Kazukelong, coll. Siboga Expedition, 1899-1900; 1 male (37.2mm x 33.5mm) (RMNH-D35934), Ake Ibu, northewest Halmahera, Indonesia, coll. F.G. Rozendaad; 2 males (40.5-41mm x 35.4-36.0mm) (RNHM-D31607), Lokojeno Beek bij Lokogengo, Central Sumba, Indonesia, coll. E. Sutterr, 24 Sep. 1949; 2 females (22.3-26.3mm x 21.5-24.4mm) (SFM-5306), Sumbava Bima, coll. S. Elbert, 12 Dec. 1909; 1 male (40.5mm x 35.0mm), 1 female (ovigerous) (39.1mm x 34.0mm) (SFM-5305), Halmahera, coll. S. Kukenthal, 1894; 1 male (32.5mm x 28.6mm) (SFM-5309), Halmahera, coll. S. Kukenthal, det de Man, 1902; 1 male (38.6mm x 32.3mm) (SFM-5326), Halmahera, det. De Haan, no collection date; 1 male (22.4mm x 10.2mm) (ZMA-no catalogue no.), Narga Bai, Flores, coll. H. Heberbeg, 1889; 27 males (10.3-41.1mm x 9.3-35.4mm), 6 females (21.0-29.0mm x 19.2-25.9mm) (ZMA-no cat. number), River Toebah, coll. W. Ceram, Feb. 1910; 5 males (35.2-41.7mm x 32.0-36.4mm), 2 females (30.0-34.4mm x 26.8-30.6mm) (ZMA-no cat. number), Station 131, coll. Siboga Expedition. – **Philippines** – 1 male (42.6 x

36.3 mm) (USNM-93152), Siaton River, Siaton Municipality, Province of Negros Oriental, Negros, Philippines, coll. D. V. Hart, no collection date.

**Diagnosis.—** Carapace quadrangular, slightly broader than long; dorsal surface glabrous; regions defined, convex. Frontal margin slightly convex, divided into four indistinct lobes. Anterolateral margin subcristate with three teeth, including external orbital tooth, external orbital tooth most distinct, very broad; second tooth smaller in size, third tooth smallest. Posterolateral margins not sharply demarcated from anterolateral margin, almost straight, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped with foliaceous merus, broader than long; anterolateral angle strongly produced, auriculiform; distal margin distinctly bilobed, outer lobe larger, base with small median cleft. Ischium longer than broad, sulcus not discernible. Small, distinct rhomboidal gape formed when third maxilliped closed. Exopod with obtuse, blunt inner subdistal angle, flagellum prominent, longer than width of merus. Epistome broad, flat, posterior margin entire. Male chelae equal to subequal, inner surfaces glabrous; merus without spines, dorsal surface highly setose; carpus without spines or teeth; outer surface of fingers glabrous. Fingers slightly shorter than palm; cutting edges of both fingers with numerous teeth, finger tips recurved, sharp, hoofed-shaped. Female chelae similar but smaller to those of male, without setae. Ambulatory legs with second pair longest. Merus of all ambulatory legs with long, soft setae; anterior margin with blunt subdistal tooth; outer surface of carpus with short setae, anterior and posterior margins of propodus with short setae. Male abdomen narrowly triangular with all segments freely moveable (six somites plus telson). G1 slender, gently curving outwards. G2 short, small. Female gonopore operculate, circular in shape.

**Colour.—** The colour of fresh specimens is a uniform dark to chocolate brown (H.T. Shih, pers. comm.), and the colour of all preserved specimens examined is dark brown in colour.

**Size.**— This species is very large in size, the largest male specimen examined is 45.4mm x 40.0mm) (NMB-619e), and the largest female specimen examined is 39.1mm x 34.0mm) (SFM-5305).

**Habitat.**— It can be found in fast flowing mountain streams at about 400m above sea level in Philippines (H.T. Shih, pers. comm.), but de Man has reported this species to be found at an altitude of 800m above sea level (Tesch, 1918, Balss, 1922). It is interesting to note that specimens of this species can also be found in the freshwater streams very close to the coastal area (P.K.L. Ng, pers. comm.).

**Remarks.**— This species is very similar to *P. setosus*, but it can be easily distinguished from *P. setosus* by the following characters viz. a) the anterolateral margin is more vaulted (vs. less vaulted in *P. setosus*); b) the third anterolateral tooth is blunt (vs. acute in *P. setosus*); c) the pterygostomial region is glabrous (vs. setose in *P. setosus*); d) the distal dorsal margin of the merus of the third maxlliped is less foliose; e) the absence of a row of grannules just above the moulting suture (vs. presence of granules in *P. setosus*); f) the dorsal surface of the merus of the chelae is prominently glabrous (vs. setose in *P. setosus*); g) the chelae of males is glabrous on the outer surface of the pollex and manus (vs. presence of long stiff black setae in *P. setosus*); h) the propodus of the ambulatory legs is densely fringed with short soft setae (vs. slightly fringed with long soft setae in *P. setosus*); i) a relatively more slender merus of the last ambulatory leg with a length to width ratio of 4.3 (vs. a stouter merus, length to width ratio 3.2 in *P. setosus*); i) a slender propodus of the last ambuatory leg with a length to width ratio of 2.0 (vs. a stouter propodus, length to width ratio 1.7 in *P. setosus*); j) a relatively G1 long and slender (vs. short and stout in *P. setosus*); and k) presence of a long apical process on the G1 (vs. absence of a long apical process on the G1 in *P. setosus*).

Preliminary DNA analysis of *P. setosus* and *P. crassus* carried out by H.T. Shih (as part of another study not associated with the present dissertation) has shown that they belong to the same clade or same genus but there are distinct differences in the number of base-pairs in the 16s and COI sequences. The biology of this species is unknown. There is no report on the larval study of this genus. It is possible that this species behaves in the same manner as its congener, *Pseduograpsus setosus* in its spawning behaviour, but this is purely speculation until more studies is done.

**Distribution.**— Indonesia (Celebes, Sulawesi), Philippines.

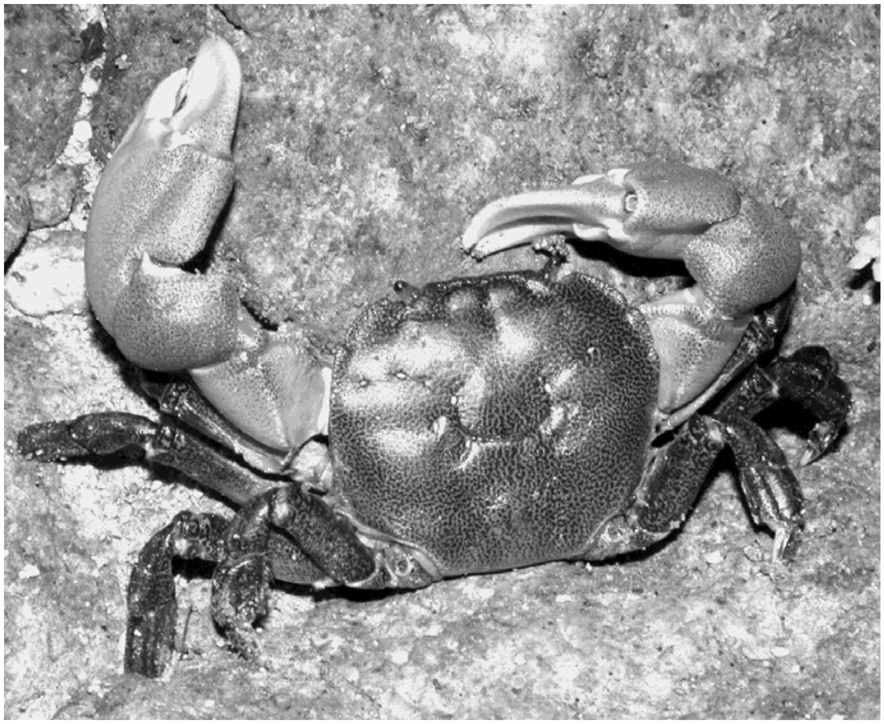


Figure 64. *Pseudograpsus crassus* A. Milne-Edwards, 1868 (courtesy of Dr. H.T. Shih).

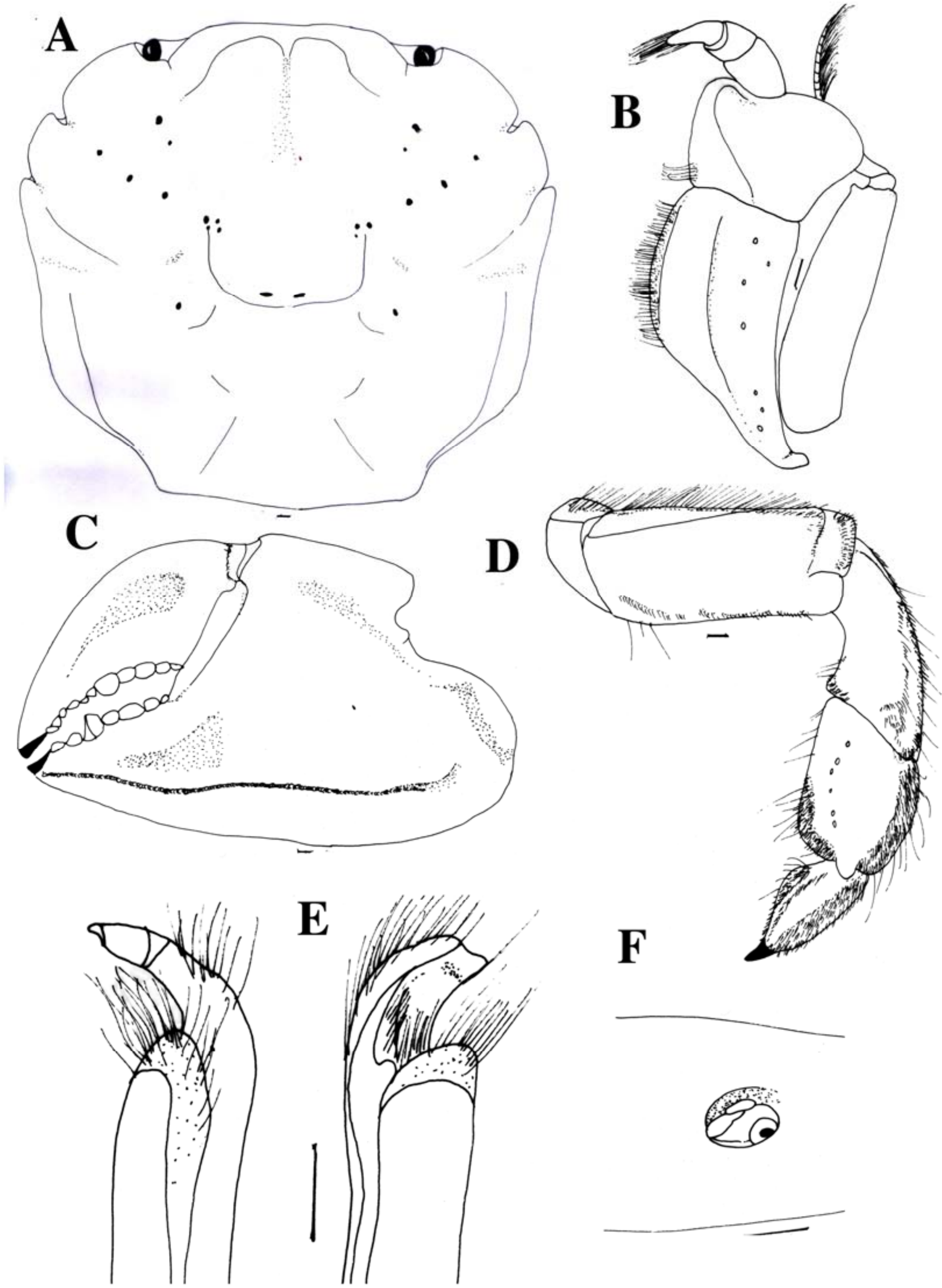



Figure 65. *Pseudograpsus crassus* A. Milne-Edwards, 1868, male (42.6 x 36.3 mm) (USNM-93152), female, 35.0mm x 31.5mm (SFM-5317). A) carapace; B) third maxilliped; C) outer view of male cheliped; D) last ambulatory leg; E) different views of G1; F) female gonopore. (Scale=1.0mm).

### Genus *Hirtograpsus*, new genus

*Pseudograpsus* H. Milne Edwards, 1837: 81; Chhapager, 1955: 257; Chhapager, 1957: 519; Hashmi, 1964: 452; Tirmizi & Ghani, 1996: 170, fig. 65 (not *Pseudograpsus* H. Milne Edwards, 1837).

**Type species.**— *Pseudograpsus intermedius* Chhapager, 1955, by present designation.

**Gender.**— Masculine.

**Diagnosis.**— Carapace squarish in shape, dorsal surface covered with short brown setae; regions well defined, convex. Frontal margin slightly convex, straight. Anterolateral margin subcristate with three teeth including first orbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly subparallel Orbits small, eyes completely filling orbit. Third maxillipeds short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Inner surface of chela with granules; setose. Ambulatory legs with short setae, stout dactyli. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen triangular in shape with seven moveable segments (six somites plus telson).

**Etymology.**— ‘Hirtus’ is the Greek word for hairy, alluring to the setose carapace, and it is used a prefix with ‘grapsus’ to indicate its lineage to the Grapsoidea.

**Remarks.**— The new genus, *Hirtograpsus*, is different from *Pseudograpsus* in the following characters: a) the almost squarish shape of the carapace (vs. subquadrate in *Pseudograpsus*); b) the carapace is densely setose (vs. glabrous in *Pseudograpsus*); c) presence of soft setae on the outer surface of chelipeds (vs. glabrous or presence of long stiff black setae in *Pseudograpsus*); d) the longer and more slender ambulatory legs (vs.

broader, stouter ambulatory legs in *Pseudograpsus*), and e) the fingers are shorter than the palm of the chela (vs. fingers as long as the palm in *Pseudograpsus*).

With regards to the carapace shape, the new genus is also similar to *Quadragrapsus*, new genus, but differs in the following features: a) possessing a setose carapace (vs. glabrous carapace in *Quadragrapsus*); b) the palm of the chelipeds being longer than fingers (vs. palm as long as fingers in *Quadragrapsus*); c) the relatively more slender and longer ambulatory legs (vs. broader and stouter ambulatory legs in *Quadragrapsus*), and d) the setose ambulatory legs (vs. glabrous in *Quadragrapsus*).

The new genus is also different from the *Tanyograpsus*, new genus, in the following characters: a) having a setose carapace (vs. with a glabrous carapace in *Tanyograpsus*); b) having a squarish carapace (vs. subquadrate carapace in *Tanyograpsus*), and c) a proportionately broader and stouter ambulatory legs (vs. longer and slender ambulatory legs in *Tanyograpsus*).

### *Hirtograpsus intermedius* (Chhapager, 1955), new combination

(Figure 66A-D)

*Pseudograpsus intermedius* Chhapager, 1955: 257; 1955: 257; Chhapager, 1957: 519; Hashmi, 1964: 452; Tirmizi & Ghani, 1996: 170, fig. 65; Chakraborty *et al.*, 2002: 1392; Khan *et al.*, 2005: 1319.

**Materials examined.**— 1 male (11.3mm x 10.4mm, 1 female (10.3mm x 9.1mm) (RMNH-D30417), Kali River, India, coll. U.S. Kakati, 1974-1975.

**Diagnosis.—** Carapace almost squarish in shape, slightly broader than long; dorsal surface covered with short brown setae, regions not well defined, convex. Frontal margin slightly convex, slightly bilobed. Anterolateral margin subcristate with three teeth, including orbital tooth, external orbital tooth most distinct, very broad; second tooth smaller in size, third tooth smallest. Posterolateral margins not sharply demarcated from anterolateral margin, almost straight, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped with foliaceous merus, broader than long; anterolateral angle produced, auriculiform; distal margin distinctly bilobed, outer lobe larger, base with small median cleft. Ischium longer than broad, sulcus not discernible. Small, distinct rhomboidal gape formed when closed. Exopod with obtuse, blunt inner subdistal angle, flagellum prominent, longer than width of merus. Epistome broad, flat, posterior margin entire. Male chelae equal to subequal, inner surfaces glabrous; merus without spines, dorsal surface highly setose; carpus without spines or teeth; outer surface of fingers with tufts of long, soft setae. Fingers slightly shorter than palm; cutting edges of both fingers with numerous teeth, finger tips recurved, sharp, hooved. Female chelae similar but smaller to those of male, without setae. Ambulatory legs with second pair longest. Merus of all ambulatory legs with long, soft setae; anterior margin with blunt subdistal tooth; outer surface of carpus with short setae, anterior and posterior margins of propodus with short setae. Male abdomen narrowly triangular with all segments freely moveable (six somites plus telson), lateral margins highly setose; female abdomen similar, very broad. G1 stout, gently curving outwards, terminal lobe elongate, slightly curved. G2 short, small. Female gonopore operculate, circular.

**Colour**.— The colour of fresh specimens is uniform chestnut brown with black setae (Chhapager, 1955), the colour of the preserved specimen examined is brown (RMNH-D30417) in colour.

**Habitat.**— It can be found in burrows in mud flats (Tirmizi & Ghani, 1996).

**Remarks.**— This species is very different from the its congeners. It is found in mangroves while its congeners are found usually in freshwater streams.

This species is very distinct from *Pseudograpsus* sensu stricto in the following characters: a) the carapace is covered with short, brown bristle-like setae (vs. glabrous carapace in *P. crassus* and *P. setosus*); b) the carapace is only slightly broader than long (vs. distinctly borader than long in *P. crassus* and *P. setosus*); c) the chelipeds are long and slender (vs. short and stout in *P. crassus* and *P. setosus*); d) the outer surface of the chelipeds have a tuft of long soft setae (vs. either no setae in *P. crassus* or long stiff setae in *P. setosus*); and e) the ambulatory legs are proportionately broad and stout (vs. longer and more slender legs in *P. crassus* and *P. setosus*).

I have been trying to locate the type materials of Chhapager (1955) but I have not been successful. It could be either in Calcutta Natural History Museum or in Bombay Natural History Society. Numerous checks with Calcutta Natural History Museum have been unsuccessful, and I have yet to hear from the Bombay Natural History Society with regards to the materials.

**Distribution.**— Southeastern India, Pakistan.

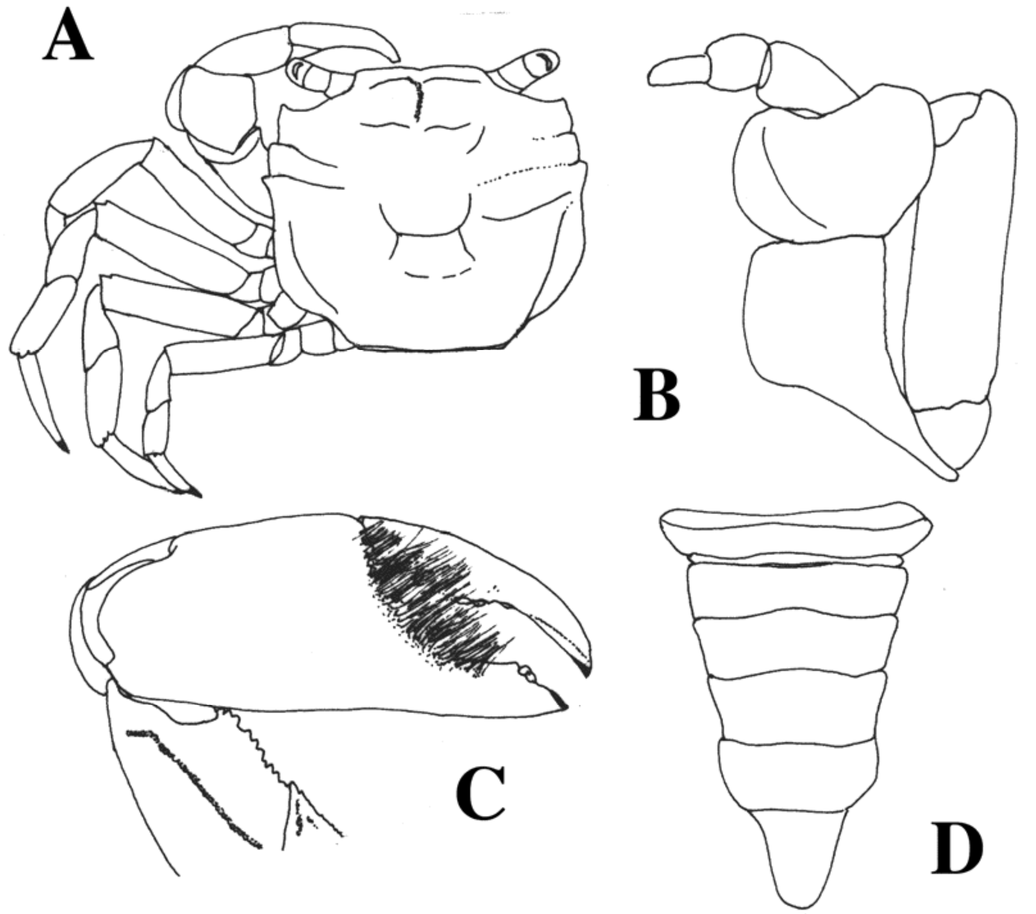



Figure 66. *Hirtugrapsus intermedius* Chhapager, 1955. A) dorsal view; B) third maxilliped; C) frontal view of cheliped; D) male abdomen. (After Tirmizi & Ghani, 1996).

## Genus *Tanyograpsus*, new genus

*Pseuduograpsus* H. Milne Edwards, 1837: 81; Kossmann, 1894: 55; Balss, 1934: 524; Barnard, 1950: 817; Monod, 1956: 423, fig. 578; Crosnier, 1965: 39, figs 47, 49-51; Hartoll, 1975: 305; Vannini & Valmori, 1981: 57; Vine, 1986:100; Nagai & Nomura, 1988: 39; Dahdouh-Guebas, 1994: 1; Ng *et al.*, 2002: 1 (not *Pseudograpsus* H. Milne Edwards, 1853).

**Type species.**— *Pseudograpsus elongatus* A. Milne-Edwards, 1873, by monotypy.

**Gender.**— Masculine.

**Diagnosis.**— Carapace quadrangular, distinctly broader than long; dorsal surface punctate; regions not well defined, slightly convex. Frontal margin slightly convex, bilobed. Anterolateral margin subcristate with three teeth including orbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Inner surface of chela with granules; presence of setae on fingers, fingers as long as palm. Ambulatory legs with short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular, with seven moveable segments (six somites plus telson).

**Etymology.**— "Tanyo' is the Greek word for 'stretch out', alluring to the long slender ambulatory legs of the specimens when they are stretched out for examination.

**Remarks.**— The new genus is different from *Pseudograpsus* in the following characters a) small size species, largest gravid female is only about 15mm on carapace length (vs. large size species in *Pseudograpsus*, the smallest gravid female is about 36mm in carapace length); b) the carapace has the posterolateral margin distinctly converging (vs. almost subparallel in *Pseudograpsus*); c) the presence of three sharp teeth on the anterolateral margin (vs. three blunt teeth in *Pseudograpsus*); d) having a narrow triangular male abdomen (vs. a broad triangular abdomen in *Pseudograpsus*); e) the presence of soft setae on the chelipeds (vs. absence or presence of short stiff black setae in *Pseudograpsus*), and f) the ambulatory legs with long, soft setae (vs. short, stiff setae in *Pseudograpsus*). In addition, while the type species is a wholly marine species, adult members of *Pseudograpsus* are freshwater taxa.

The new genus is also different from *Scutumara* in the following features: a) broader carapace (vs. longer carapace in *Scutumara*); b) the presence of three anterolateral teeth including orbital tooth (vs. with two anterolateral lobe including orbital lobe in *Scutumara*); c) the front is not very produced (vs. very produced in *Scutumara*); and d) the ambulatory legs are setose (vs. glabrous legs in *Scutumara)*.

There is only one species in this genus, *T. elongatus* (A. Milne-Edwards, 1873).

## *Tanyograpsus elongatus* (A. Milne-Edwards, 1873), new combination

(Figure 67A-B)

*Heterograpsus elongatus* A. Milne-Edwards, 1873: 317, pl. 17, fig. 5, 5a-c; Monod, 1956: 423, fig. 578; Crosnier, 1965: 39, figs 47, 49-51; Hartoll, 1975: 305; Vannini & Valmori, 1981: 57; Vine, 1986:100; Nagai & Nomura, 1988: 39; Dahdouh-Guebas, 1994: 1; Fransen *et al.*, 1997: 127; Ng *et al.*, 2002: 1.

*Pseudograpsus erythraeus* Kossmann, 1894: 55; Balss, 1934: 524; Barnard, 1950: 817.

**Materials examined.— *Pseudograpsus elongatus*** – **Lectotype** – 1 male (7.0mm x 6.5mm) (RMNH-D197), New Caledonia, coll. A. Milne-Edwards, 1879. – **Others** – **Australia** – 1 male (9.3mm x 8.5mm) (QM-W16814), Harmer Creek, Queensland, coll. P. Davie & J. short, 31 Oct. 1990; 5 males (5.3-7.7mm x 4.7-6.7mm) (QM-W14795), Dalrymble Point, Port Denison, northeast Queensland, coll. P. Davie & J. Short, 21 Mar. 1987;1 female (9.6mm x 7.4mm) (QM-W18219), Starcke river mouth, Queensland, Australia, coll. P. Davie & J. Short, 13 Nov. 1992. – **Japan** – 1 male (7.2mm x 6.2mm) (SFM-ex. T. Sakai collections), Okinawa, coll. K. Takashi, May 1975; 12 males (3.7-7.5mm x 3.4-6.8mm), 13 females (4.7-7.5mm x 4.0-6.8mm), 1 female (ovigerous) (4.9mm x 4.2mm) (SFM-7676), Ishigaki Island, Okinawa leg. T. Sakai. – **Seychelles** – 1 male (6.7mm x 6.5mm) (ZRC 1972.8.21.1), Male, Seychelles, coll. R. Sérene, May 1972; 6 males (6.8-9.1mm x 6.5-8.3mm), 3 females (6.7-9.5mm x 6.2-8.2mm), 1 female (ovigerous) (6.5mm x 5.9mm) (MNHN-B14043), Seychelles, coll. M. Lantz, 1715-1878; 1 male (8.7mm x 7.9mm), 1 female (ovigerous) (6.5mm x 6.0mm) (MNHN-B-14042), Seychelles, coll. Lantz. – **Sudan** – 1 female (ovigerous) (7.9mm x 7.2mm) (SFM-17279), Sudan, coll. A. Allaspech & M. Turekay, 3 Mar. 1987. – **Unknown locality** – 1 male (7.0mm x 6.2mm) (MNHN-b-214), no other data. 2 males (5.7mm x 7.2mm), 2 females (5.7-6.8mm x 5.4-6.4mm) (RMNH-D-24826), Ahiad Bay, Entdenir, Dahlaka Archipel, coll. 29 Mar. 1962. – ***Pseudograpsus erythreus*** – **Lectotype** – 1 male (10.2mm x 9.2mm) (SFM-9716), Rotes Meir, 1674-25, leg. R. Kossmann, no collection date.

**Diagnosis**.— Carapace quadrangular, broader than long; dorsal surface smooth, glabrous; regions well defined, slightly convex. Frontal margin slightly bilobed. Anterolateral margin with three teeth, including orbital tooth. Third maxilliped with foliaceous merus, broader than long; anterolateral angle strongly produced, auriculiform. Small, distinct rhomboidal gape formed when third maxilliped closed. Chelipeds equal to subequal, inner surfaces smooth, glabrous; outer surface of pollex, manus with tufts of long, soft setae. Ambulatory legs slender, flat, dorsal margins covered with short dense setae. G1 slender, gently curving outwards, terminal lobe elongate, slightly curved. Female gonopore slightly convex, operculum circular in shape.

**Colour.—** The colour of fresh specimens is greenish-brown (P. Davie, pers. comm.), but all preserved materials are light brown to brown in colour.

**Habitat.**— They are found living under rock and pebbles along the coast (Crosnier, 1965).

**Remarks.**— The species is interesting as the it is the next most wide-ranging species after *Varuna litterata*.

**Distribution.**— Africa (Indian Ocean side like Kenya, Sommalia, Tanzania, Sudan), Seychelles, Northern Australia, Japan (Okinawa) and New Caledonia.

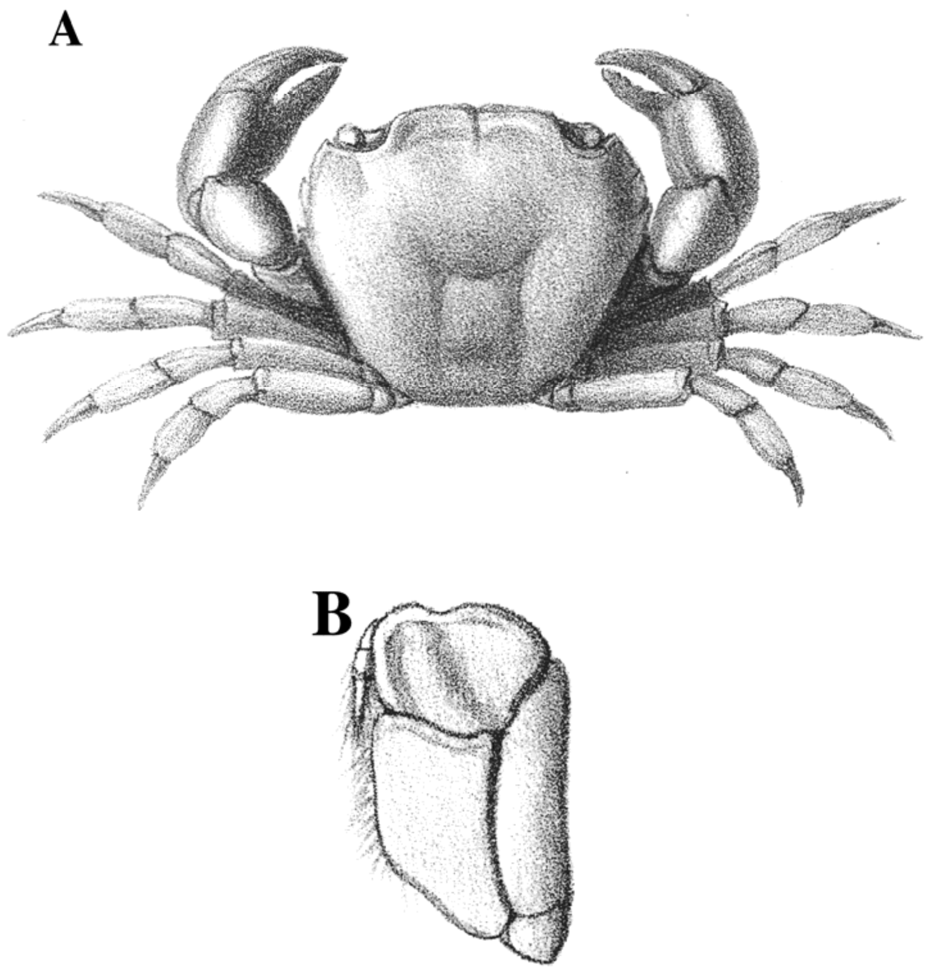



Figure 67. *Tanyograpsus elongatus* (A. Milne-Edwards, 1873). A) dorsal view; B) third maxilliped. (After A. Milne-Edwards, 1873).

## Genus *Quadragrapsus*, new genus

*Pseudograpsus* H. Milne Edwards, 1837: 81 (not *Pseudograpsus* H. Milne Edwards, 1853)
*Pachystomum* Nauck, 1880: 30 (preoccupied name); Miers, 1886: 262.

**Type species.** — *Pseudograpsus albus* Stimpson, 1858, by present designation.

**Gender.** — Masculine.

**Diagnosis.**— Carapace roundly square in shape.very slightly broader than long; dorsal surface glabrous; regions not well defined, convex. Frontal margin slightly convex, straight. Anterolateral margin with two lobes instead of teeth. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly subparallel. Orbits small, eyes completely filling orbit. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Inner surface of chela with granules; long soft setae present on fingers; fingers as long as palm. Ambulatory legs galbrous, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular, with seven moveable segments (six somites plus telson).

**Etymology.**— 'Quadra' is the Latin word for squarish, alluring to the square carapace of the species, it is used as an adverb, with 'grapsus', indicating its lineage to grapsoid crabs.

**Remarks.**— In addition to its small size, the new genus is distinctly different from *Pseudograpsus* in the following characters: a) possession of a squarish carapace (vs. subquadrate in *Pseuograpsus*); b) the presence of two lobes along the anterolateral margin (vs. three distinct anterolateral teeth including the orbital tooth in *Pseudograpsus*); c) the presence of single tuft short soft setae on the fingers of the chelae (vs. numerous tufts of long stiff setae in *Pseudograpsus*); and d) being a generally smaller species, maturing at about 9.8mm x 7.3 mm [ZRC 2000.0529] (vs. larger adult size being mature at about 38.5mm x 34.9 mm in *Pseudograpsus*). In addition, it is a wholly marine genus unlike *Pseudograpsus* which lives primarily in freshwater.

The new genus is different from *Ptychognathus* sensu lato by the following characters viz. a) a narrow expod of the third maxilliped (vs. a broad and convex exopod in *Ptychognathus*); b) the carapace is smooth and glabrous (vs. demarked in *Ptychognathus*); c) the glabrous ambulatory legs (vs.setose to densely setose legs in *Ptychoganthus*), and d) the male abdomen is relatively broader (vs. narrow in *Ptychognathus*).

The new genus is different from *Scutumara* in having a) a broader carapace (vs. longer carapace in *Scutumara*); b) the front not been produced (vs. strongly produced front in *Scutumara*), and c) the merus of the third maxilliped is less foliose (vs. very broad merus in *Scutumara*).

*Quadragrapsus*, new genus, differs from *Tanyograpsus*, new genus, in the following features: a) possessing narrower carapace (vs. wider carapace in *Tanyograpsus*); b) the palm as long as fingers (vs. palm of the chelipeds being longer than fingers in *Tanyograpsus*); c) the broader and stouter ambulatory legs (vs. relatively more slender and longer ambulatory legs in *Tanyograpsus*), and d) the glabrous ambulatory legs (vs. setose in *Tanyograpsus*).

*Quadragrapsus*, new genus, differs from *Hirtograpsus*, new genus, in the following features: a) possessing a glabrous carapace (vs. setose carapace in *Hirtograpsus*); b) the palm as long as fingers (vs. palm of the chelipeds being longer than fingers in *Hirtograpsus*); c) the broader and stouter ambulatory legs (vs. relatively more slender and longer ambulatory legs in *Hirtograpsus*), and d) the glabrous ambulatory legs (vs. setose in *Hirtograpsus*).

Based on the gastric mill structures, Nauck (1880) established a new genus and new species, *Pachystomum philipinense* for specimens that were collected from Philippines. Miers (1886: 262) stated that the descriptions provided by Nauck (1880) on the genus *Pachystomum* Nauck, 1880, is too brief be allied to any distinctive genera, and hence, he synonymized *Coelochirus* under the genus *Pseudograpsus* (Miers, 1886: 262).

de Man examined the specimens of *Pachystomum philippinense*, and synonymized *Pachystomum philipinense* under *Pseudograpsus albus* Stimpson, 1858, on the basis of external adult morphology, stating that the two species are identical (de Man, 1887: 719 and de Man, 1888: 149). I believe that Nauck probably did not compare his specimens against Stimpson's species as his entire monograph was on the internal anatomy, on different forms of the gastric mills found in different crustaceans. Nauck's action provided an additional evidence to remove this species to a new genus, as the gastric mill structures are distinctly different from those of *Pseudograpsus*. The original name provided by Nauck, *Pachystomum* would be ideal for the new genus but the name '*Pachystomum'* is pre-occupied by the name of a lichen, *Platystomum pachystomum* (Ellis & Everh) (see Garrill & Kirk, 2000). A new name, *Quadragrapsus*, therefore needs to be established in this dissertation for *Pseudograpsus albus*.

## *Quadragrapsus albus* (Stimpson, 1858), new combination

(Figure 68A-G)

*Pseudograpsus albus* Stimpson, 1858: 104; A. Milne-Edwards, 1873: 314, pl. 18, fig. 2, 2a; Nauck, 1880: 719; Miers, 1885: 202; 1886: 262; de Man, 1888: 382; 1889: 440; 1895: 111; Stimpson, 1907: 127; Rathbun, 1907: 32; 1918: 99; Tesch, 1918: 99; Balss, 1938: 79; Sakai, 1939: 666; Guinot, 1962: 241, fig. 15a-b; Crosnier, 1965: 42, figs. 48, 52-54; Chen, 1980: 141, pl. 4, 7, fig. 24; Suzuki, 1985: 57 Ng *et al.*, 2001: 46; Ng *et al.*, 2002.

*Pachystomum philipinense* Nauck, 1880: 30

**Materials examined.**— ***Pseudograpsus albus* – Neotype** – 1 male (9.1mm x 8.9mm), (SFM-00297), Modoki, coll. Y. Watanabe, Jul. 1949. – ***Pachystomum philipinense* – Neotype** – 1 male (9.0mm x 8.3mm) (ZRC 1970.1.7.7), Ilo-Ilo, Philippines, coll. R. Sérene, 1965. – **Others** – **Australia** – 1 male (10.0mm x 9.0mm) (WAM-845891), Horsburgh Island, Cocos Keeling Island, coll. D.S. Johnson, 7 Feb. 1989.– **Hawaii** – 2 males (9.8-10.6 x 8.8-9.5 mm), 2 females (8.0-9.2mm x 7.1-8.0 mm) (ZRC 2000.0529), Canton Island, Hawaii, coll. O. Degener, Apr. 1951. – **Indonesia** – 1 male (9.5mm x 8.8mm) (ZMA-De-103.165), station 172, coll. Siboga Expedition, 1899/1900; 1 female (9.5mm x 8.5mm) (ZMA-De-103.165), Tanab, Djampea, station 64, coll. Siboga Expedition, 1899/1900; 1 male (9.0mm x 8.0mm) (ZMA-De-103-614), Fiji, coll. de Man, May 1858. – **Japan** – 3 males (8.7-9.1mm x 7.8-8.9mm), 1 female (9.2mm x 8.4mm) (SFM-00297), Modoki, coll. Y. Watanabe, Jul. 1949; 4 (6.5-7.8mm x 6.2-7.0mm), 1 female (7.8mm x 7.0mm) (SFM-ex. T. Sakai collections), no collection data; 1 male (7.2mm x 6.8mm) (SFM-ex. T. Sakai collections), no collection data; 1 male (8.8mm x 8.0mm) (SFM-ex. T. Sakai collections), Hachijo-jima, Japan, coll. T. Sakai, no collection date. – **Madagascar** – 1 male (9.3mm x 8.2mm) (MNHN-B13211), Fort Danghin, Madagascar, coll. A. Crosnier, no collection date; 1 male (5.0mm x 4.5mm), 1 female (7.3mm x 6.4mm), 1 female (ovigerous) (MNHN-B-13210), Fort Danphin, Madagascar, coll. A. Crosiner, no collection date.– **Mauritius** – 1 male (8.1mm x 7.9mm), 1 female (7.9mm x 7.0mm), (RNHM-D-17043), Pointe aux Sables, Port Louie, Mauritius, coll. 23 Mar. 1960. – **Oceania** – 1 male (4.5mm x 4.2mm) (USNM-33187), Takakara Island, Paremotus outer reef, coll. 12 Oct. 1899; 1 female (ovigerous) (7.8mm x 6.7mm) (USNM-22832), Society Islands, no collection date; 1 female (9.1mm x 8.0mm) (ovigerous) (USNM-56737), Fanning Island, Oceanica, (from Bishop Museum), coll. C.H. Edmondson, 1922; 2 males (5.1-5.8mm x 4.4-5.1mm), 2 females (5.7-6.1mm x 5.0-5.7mm), 1 female (ovigerous) (6.9mm x 6.1mm) (USNM-uncatalogued), Takoke

Island, Razoia Atoll, Tuamotu Islands, coll. J.P.E. Morrison, 22 Jul. 1952; 1 male (9.9mm x 9.1mm), 1 female (8.2mm x 7.3mm) (USNM-81732), Society Island, Oceanica, coll. A. Garrett, no collection date; 1 female (7.1mm x 6.5mm) (NHMN-B-13209), New Caledonia, coll. A. Milne-Edwards, no collection date; 1 male (12.4mm x 10.8mm) (MNHN-B13212), New Caledonia, coll. A. Milne-Edwards, no collection date; 1 male (8.1mm x 7.4mm), 1 female (7.8mm x 6.7mm) (RHNM-D-9599), Takoke Island, Razoia Atoll, Tuamotu Islands, coll. J.P.E. Morrison, 22 Jul. 1952. – **Philippines** – 2 males (5.8-6.3mm x 5.4-5.6mm), 1 female (7.0mm x 6.5mm) (ZRC 1970.1.21.15-17), Guimaras Island, near Ilo-Ilo, Philippines, coll. R. Sérene, 1963. – **Taiwan** – 2 males (8.4-10.1mm x 7.8-9.0 mm), 2 females (ovigerous) (8.4-9.6mm x 7.3-8.5 mm) (ZRC 2000.2231), Hou-Wan, Kenting, Pingtung County, coll. H.C. Liu & N.K. Ng, 14 Sep. 1999. – **No locality data** – 1 female (10.3mm x 9.4mm) 1 female (ovigerous) (9.1mm x 8.0mm) (RNHM-D-1213), no collection data; 2 males (7.9-10.7mm x 6.99.3mm), 2 females (6.5-8.3mm x 5.7-7.5mm) (SFM-5315), No collection data; 2 females (9.1-10.3mm x 8.0-9.4mm) (RMNH-no cat. number), no collection data.

**Diagnosis.**— Carapace quadrangular, dorsal surface flattened, smooth, glabrous. Frontal margin slightly convex, divided into four indistinct lobes, epigastric cristae not discernible. Anterolateral margin with two very blunt teeth, including orbital tooth. Third maxillipeds close small, distinct rhomboidal gap; exopod broad. Chelipeds equal to subequal, inner surfaces smooth, glabrous; outer surface of pollex, manus with tufts of soft, long setae. Ambulatory legs slender, flat, glabrous. G1 slender, gently curving outwards, terminal lobe elongate, slightly curved. Female gonopore with operculum slightly convex, circular.

**Colour.**— The colour of fresh specimens is cream-coloured with light brown spots or bands (pers. observ.), and all preserved specimens examined are overall cream coloured.

**Size.**— This species is small in size, largest male specimen examined is 10.1mm x 9.0mm (ZRC 2000.2231), and largest female specimen is 10.3mm x 9.4mm (RMNH-no cat. number).

**Habitat.**— It can be found under coral rocks on rocky shores (pers. observ.).

**Remarks.**— The species can be commonly found along beaches.

Preliminary examination on the gastric mills of *Q. albus* showed that they match the descriptions and figures provided by Nauck (1880). This further supported de Man's decision to synonymize the two species. The original specimen used by Stimpson (1858), which was collected around Japan (Kakisima) is lost (Evan, 1967; Deiss & Manning, 1981). Likewise for Nauck's specimens (see below for comments under *Ptychognathus pilipes*). Thus to stabilize the taxonomy, I have selected two neotypes, namely one for *Pseudograpsus albus*, a male specimen (9.1mm x 8.9mm, SFM-00297) collected from Japan; and one for *Pachystomum philipinense*, a male (9.0mm x 8.3mm, ZRC 1970.1.7.7) collected from Ilo-ilo, Philippines.

**Distribution.**— Taiwan, China, Japan, Philippines, New Caledonia, Fuji Islands, Tuamotu Island, India and Madagascar.

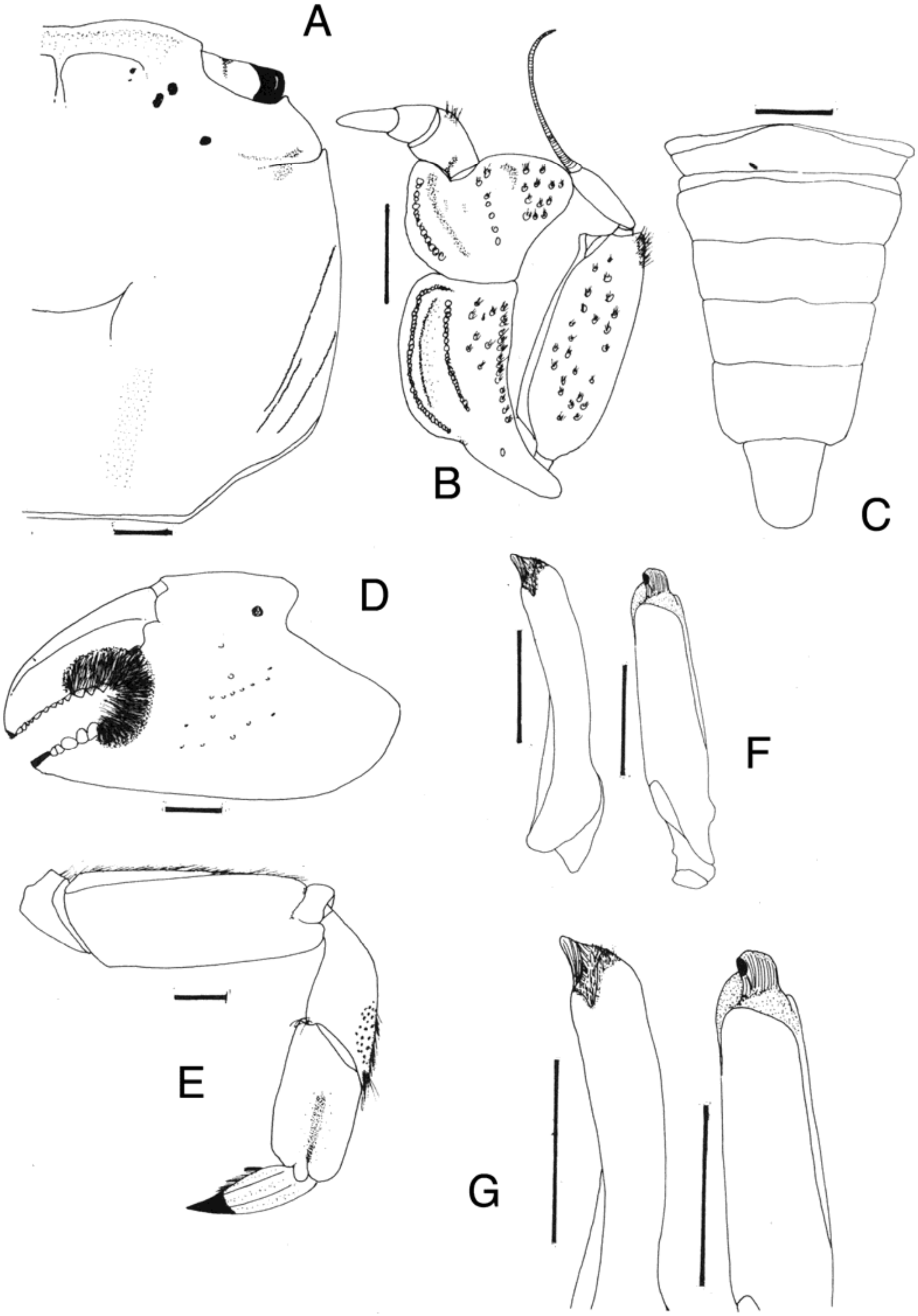



Figure 68. *Quadragrapsus albus* Stimpson, 1858, male, 10.6 x 9.5 mm (ZRC 2000.0529). A) carapace; B) third maxilliped; C) male abdomen; D) male cheliped; E) last ambulatory leg; F) G1; G) distal end of G1. (Scale=1.0mm).

## Genus *Ptychognathus* Stimpson, 1858

*Ptychognathus* Stimpson, 1858: 104; de Man, 1887: 719; de Man, 1895: 90; Alcock, 1900: 402; Stimpson, 1907: 129, pl. 7, fig. 5, 5a; Rathbun, 1914: 69; Tesch, 1918: 85; Sakai, 1939: 647, 658; 1955: 112; Ooishi, 1970: 95, pl. 16, fig. 10; 1976: 639, pl. 219, fig. 14; Crosnier, 1965: 37 (part); 1975: 735; Dai *et al.*, 1986: 467 (part); Dai & Yang, 1991: 515 (part).

**Type species.**— *Ptychognathus glaber* Stimpson, 1858, by monotypy.

**Gender.**— Masculine.

**Diagnosis**.— Carapace quadrangular, slightly broader than long; dorsal surface glabrous, punctate; regions not well defined, flat. Frontal margin slightly convex, usually straight. Anterolateral margin subcristate with two teeth including orbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped short, stout, with small, distinct rhomboidal gape when closed, palp short, with short setae; exopod with short flagellum. Epistome broad, flat, posterior margin entire. Chela with or without setae, fingers as long as palm. Ambulatory legs with short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular, with seven moveable segments (six somites plus telson).

**Remarks.**— The genus, *Ptychognathus* is one of the largest in the family Varunidae, with currently 24 included species, viz. *P. glaber* Stimpson, 1858 (type species); *P. pusillus* Heller, 1865; *P. pilipes* (A. Milne-Edwards, 1868); *P. riedelii* (A. Milne-Edwards, 1868); *P. barbatus* (A. Milne-Edwards, 1873); *P. intermedius* de Man, 1879; *P. dentatus* de Man, 1892; *P. pilosus* de Man, 1892; *P. spinicarpus* Ortmann, 1894; *P. polleni* de Man, 1895; *P. affinis* de Man, 1895; *P. onyx* Alcock, 1900; *P. easteranus* Rathbun, 1907; *P. altimanus* (Rathbun, 1914); *P. johannae* Rathbun, 1914; *P. guijulugani* Rathbun, 1914; *P. demani* Roux, 1917; *P. crassimanus* Finnegan, 1931; *P.*

*ishii* Sakai, 1939; *P. takahashii* Sakai, 1939; *P. hachijoensis* Sakai, 1955, *P. capillidigitalis* Takeda, 1984, *P. andamanensis* Pretzmann, 1984, and *P. insolitus* Osawa & Ng, 2006, and a few more species in the process of being described by the current author (manuscript currently in preparation).

Stimpson (1858) established the genus, *Ptychognathus,* with a very clear description with its members having a flat carapace, front continuously horizontal, anterolateral margin with one acute protrusion, the legs are flat, the male abdomen narrow. These characters ally it with the genus *Platygrapsus* Stimpson, 1858 (now *Gaetice* Gistel, 1835, and *Pseudograpsus* H. Milne Edwards, 1853). The most important character that distinguishes this genus from *Gaetice* and *Pseudograpsus* is the form of the third maxilliped. Stimpson defined the third maxilliped as "exognatho amplissimo, quam ischio non angustior; mero quam ischio breviore sed duplo latiore", i.e. the third maxilliped has a very broad exopod, and a very long and narrow ischium (vs. narrow exopod and broad ischium of the third maxillipeds in *Gaetice* and *Pseudograpsus*). In addition, there are additional characters which distinguish *Ptychognathus* senu stricto from the genus *Gaetice* (see below), and *Pseudograpsus* (see above).

Ten years later, A. Milne-Edwards (1868) established *Gnathograpsus* for two species, *G. riedelii* and *G. pilipes*. Members of the genus *Gnathograpsus* are very similar to those in *Pseudograpsus* sensu stricto, in the form of the carapace, male abdomen and ambulatory legs. It also has the broad exopod and narrow ischium of the third maxillipeds. In 1873, A. Milne-Edwards described *Gnathograpsus barbatus* from New Caledonia, stating that this species is very similar to *Hemigrapsus* in its external morphology except for the exopod of the third maxilliped which is very broad, and the ischium of the third maxillipeds is very narrow and slender. Nevertheless, A. Milne-Edwards (1873) placed this species under the genus *Gnathograpsus*.

In 1880, Nauck established a new genus and species, *Coelochirus crinipes*, based on the gastric mill morphology. Nauck did not justify his actions with external morphological characters, but solely depended on the gastric mill morphology. There were not even any figures of the taxon. De Man (1887: 719; 1888: 149, footnote) was the first to regard *Ptychognathus* and *Gnathognathus* as identical, based on the forms of the ‘external foot-jaw’ or third maxillipeds, and synonymized *Gnathognathus* under *Ptychognathus*. At the same time, de Man also synonymized *Coelochirus* under *Ptychognathus* on the basis of the form of the third maxillipeds and other external features. As a result, subsequent workers (de Man, 1892; Alcock, 1900; Rathbun, 1918; Tesch, 1918; Sakai, 1939 etc.) used the form of the third maxillipeds as one of the key character for the genus *Ptychognathus*. Consequently, many new species with a broad exopod of the third maxilliped were placed under *Ptychognathus*.

Nonetheless, it must be noted that the 24 species of *Ptychognathus* recognized are variable in their carapace forms and ambulatory legs characters, and yet they are all placed together the same genus as they share the similar form of the third maxillipeds. Detailed morphological examination of these 24 species showed that they can in fact be divided into five distinct genera based on the forms of their carapace, ambulatory legs, male abdomen, and the detailed structure of the third maxilliped, whether the outer surface of the exopod of the third maxilliped is convex or flat, and whether the ischium is as broad or narrower than the width of the exopod.

*Ptychognathus* Stimpson, 1858, sensu stricto comprises of *P. glaber, P. ishii*, *P. hachijoensis* and *P. andamanensis*. Three new species are described here under this redefined genus. All of these species have only one anterolateral tooth after the orbital tooth, and their morphological descriptions precisely fit the generic description provided by Stimpson (1858) (see below).

*Mitragrapsus*, new genus, is here established for *P. spinicarpsus*, *P. onyx*, *P. polleni, P. affinis*, *P. altimanu*s and *P. dentatus*. All these species, in addition to the broad and swollen exopods of the third maxillipeds, have two anterolateral teeth after the orbital tooth. Furthermore, they are very ‘*Varuna*-like’ in their overall external morphology. Rathbun had placed them all under the genus *Varuna* (see Rathbun, 1914), but Tesch (1918) transferred them back to the genus *Ptychognathus* on basis of their very convex, broad exopod, very foliaceous merus and very narrow ischium of the third maxilliped.

*Gnathograpsus* A. Milne-Edwards, 1868, is resurrected as a separate genus for *P. pilipes, P. riedelii, P. demani, P. pilosa* and *P. intermedius.* Besides having the characteristic broad, and swollen exopod, and two teeth on the anterolateral margin after the orbital tooth, all these species have very thick carapace physiognomies, i.e. a body form very similar to species in *Pseudograpsus*. In addition, all these species are all relatively large in adult size (ovigerous female carapace width larger than 35 mm).

*Neoptychognathus*, new genus, is established for *P. barbatus, P. pusillus, P. easteranous, P. johanne, P. guijulugani* and *P. crassimanus.* These species have two teeth on the anterolateral margin after the orbital tooth, are small in size (ovigerous female with carapace width not more than 20mm), and are found along the coast by the river mouths.

*Cognatus*, new genus, is established for a very common Indo-West Pacific species that has long being misidentified as *Ptychognathus barbatus*. It is actually an undescribed species, and is different from the 'real' *P. barbatus* in the form of the carapace, third maxillipeds and telson. Not withstanding, many of the identified '*P. barbatus*' specimens also show some variations in their morphology, but they all fall under this group

*Abakos*, new genus, is established for a rather unusual species, *P. takahashii*. This is the only species in *Ptychognathus* s. lato with three anterolateral teeth after the very small orbital tooth. The anterolateral angle of merus of the third maxilliped is very broad, and chela are not as robust as those in *Ptychognathus*.

It is interesting to note that in terms of external morphology, the four genera *Ptychognathus* sensu stricto, *Neoptychognathus*, new genus, *Cognatus*, new genus and *Abakos*, new genus, are more closely allied to each other than to *Gnathograpsus* and *Mitragrapsus*, new genus. The affinities of these genera with other varunid taxa are now being tested using molecular techniques (as part of an ongoing study with Dr. C.D Schubart not connected with the present dissertation). It is also interesting to note that there are habitat preferences in the members of these six genera. Species from

*Ptychognathus* sensu stricto and *Cognatus* are found along coastal areas hiding under rocks and pebbles, and there is usually a freshwater stream or aquifer nearby. Species from *Gnathograpsus* and *Mitragrapsus* are found usually in the freshwater streams under rocks and pebbles, and they are rarely found in the brackish water areas unless they are spawning (0 ppt salinity, pers. observ.). Crabs from *Neoptychognathus* are found usually by the river mouths, under rocks and stones; but they can wander into the wholly freshwater areas occasionally. As for members of *Abakos* there is no report on its preferred habitats, and several attempts to collect the fresh specimens at the type locality have not been unfruitful.

It is noteworthy that the name, *Ptychognathus* Stimpson, 1858, was actually used by Owen (1860) to name a group of Lower Triassic therapsid reptiles from South Africa. This taxa has been now been moved to its own genus, *Lystrosaurus* Cope, 1870 (see Colbert, 1974). In any case, *Ptychognathus* Stimpson, 1858, is the older name.

As it currently defined, the genus *Ptychognathus* now comprises of only *Ptychognathus glaber* Stimpson, 1858 (type species); *Ptychognathus ishii* Sakai, 1939; *Ptychognathus hachijoensis* Sakai, 1955, and *Ptychognathus andamanensis* Pretzmann, 1984, with three new species described in this dissertation (see below).

**Key to species in *Ptychognathus***

1a. Carapace subquatdrate, anterolateral margin with a faint lobe after orbital tooth. ------------------------------------------------------------------------------------------------ ***P. hachijoensis***

1b. Carapace subquadrate, anterolateral margin with a distinct tooth after orbital tooth. ---------------------------------------------------------------------------------------------------- **2**

2a. Carapace surface covered with short, bristle-like setae. ----------- ***P. andamanensis***

1b. Carapace surface glabrous. ------------------------------------------------------------- **3**

3a. Exopod of third maxilliped as broad as ischium. Chela glabrous or setose. ----- **4**

3b. Exopod of third maxilliped broader than ischium. Chela setose. ------------------- **5**

4a. Exopod of third maxilliped convex. Outer surface of chela glabrous. ---- ***P. glaber***

4b. Exopod of third maxilliped flat. Outer surface of chela setose. -- ***P. fukukawanensis***

5a. Outer surface of chela with setae at base of pollex, exopod slightly broader than ischium. --------------------------------------------------------------- ***P. pseudoishii***

5b. Outer surface of chela with setae at base of pollex, exopod distinctly broader than ischium. --------------------------------------------------------------------------- **6**

6a. Exopod 1.3 times broader than ischium, the dactylus of the third ambulatory leg is broader (length to width ratio 4.9). ----------------------------- ***P. kukukawanensis***

6b. Exopod 1.4 times broader than ischium, the dactylus of the third ambulatory leg is narrower (length to width ratio 5.4). ------------------------------------------ ***P. ishii***

## *Ptychognathus glaber* Stimpson, 1858

(Figure 69)

*Ptychognathus glaber* Stimpson, 1858: 104; 1907: 129, pl. 17, figs. 5, 5a; de Man, 1902: 324, pl. 19, fig. 11; Tesch, 1918: 87; Sakai, 1939: 660, pl. 108, fig. 3, 1955: 112; Ooishi, 1970: 95, pl. 16, fig. 10; Sakai, 1976: 639, pl. 219, fig. 14.

**Materials examined.**— **Neotype** – 1 male (20.5mm x 16.0mm (NSMT-Cr), freshwater river, Chichijima island, Bonin Islands, coll. H. Suzuki, Mar. 1972. – **Others** – **Indonesia** – 1 male (12.5mm x 9.8mm) (ZMA- no cat. no), Flores, river by Bombang, Indonesia, coll. M. Weber, 1888/1889. – **Philippines** – 2 males (16.0-17.5mm x 13.2-13.9mm), 1 female (10.3mm x 8.3mm) (RMNH-35278), Joroan River, Albay Province, Luzon, Philippines, coll. B. Gindelbergez, 10 Jul. 1981. **– Japan** – 1 male (4.9mm x 4.3mm) (SFM-22488), Naka domain, Okinawa Island, Ryukyus, Japan, coll. R. Higa, Aug. 1983; 1 female (ovigerous) (6.5mm x 5.6mm) (SFM-7095), coll. R. Serène, 4 Apr. 1963; 1 female (10.6mm x 8.5mm) (SFM-22487), Ngo, Okinawa Island, Ryukyus, Japan, coll. R. Higa, Aug. 1983; 37 males (7.1-14.0mm x 6.2-11.8mm), 8 females (8.2-11.1mm x 7.0-9.4mm) (SFM-22489), Naka domain, Okinawa Island, Ryukyus, Japan, coll. R. Higa, Aug. 1983. – **Taiwan** – 6 males (6.5-10.3mm x 5.9-8.8mm), 2 females (8.6-13.7mm x 7.2-12.0mm), 2 females (ovigerous) (6.7-7.1mm x 6.0-6.2mm), (NMMBA), Laiching Bay, Lanyu Island, coll. H.P. Ho, 19 Apr. 2002.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth, very flat. Front broad, anterior margin straight. Anterolateral margin with two teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod convex, broad, as broad as ischium. Cheliped symmetrical in males, fingers glabrous. Ambulatory legs short, flat, margins slightly setose. G1 long, slender. Female gonopore opperculate, small.

**Colour.**— The colour fresh specimens has not been reported, and the colour of all preserved specimens examined is light brownish in colour.

**Size.**— The largest male specimen examined is 17.5mm x 13.9mm (RMNH-35278), while the largest female specimen examined is 13.7mm x 12.0mm (NMMBA-uncatalogued).

**Habitat.**— It is found under small rocks and pebbles along river banks and the river mouth (Stimpson, 1858).

**Remarks.**— Together with the description of the genus, *Ptychognathus*, Stimpson also described *Ptychognathus glaber* from Port Llyod at Bonin Islands. The crabs were dug out from the sand/gravel along the banks in the esturary (Stimpson, 1858). In his subsequent publication, Stimpson (1907) translated his description; he also figured the overall carapace and the mouthparts. It is a pity that all of Stimpson specimens are no longer extant due to The Great Chicago Fire in 1871 (Evan, 1967; Deiss & Manning, 1981). Sakai, in his description of *Ptychognathus ishii*, he had examined three male and two female specimens collected from Bonin Island, but he did not designated any neotype for *P. glaber* (Sakai, 1939).

Currently, there is no type specimen designated for this species. Although Stimpson (1907) has provided a good description and has a relatively good figure, it would be advisable for a type specimen to be designated if materials are available. This action will stabilize the taxonomy of this genus and will be particularly useful pertaining to the stability of two very closely allied genera, *Orcovita* and *Cebuanograpsus* (see above).

**Distribution.**— Japan, Philippines, Taiwan.

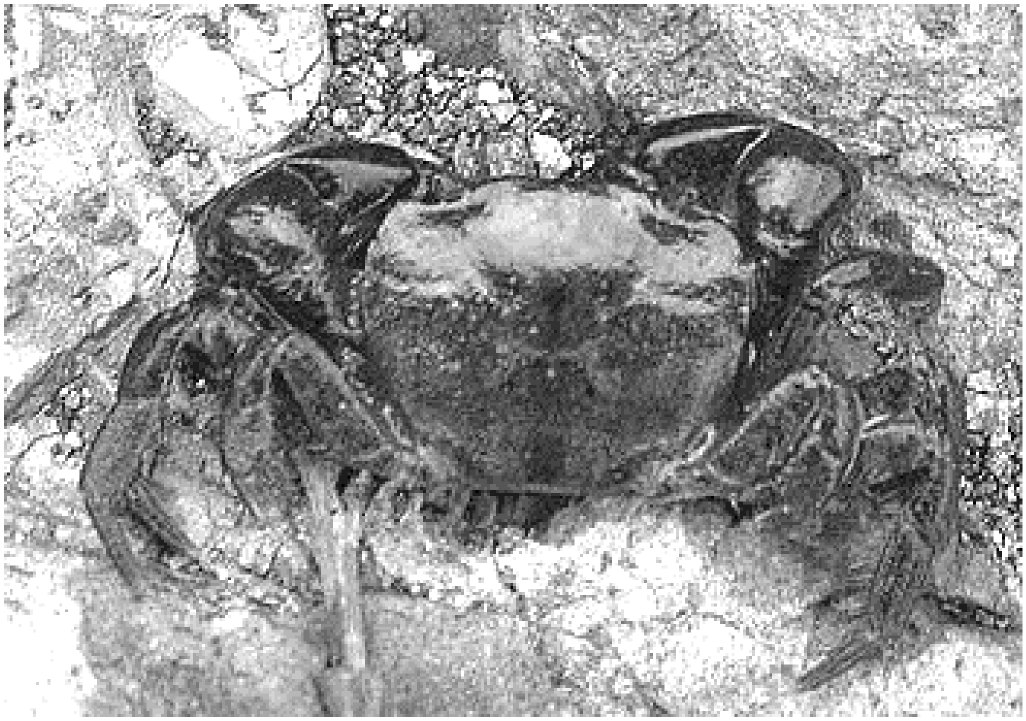


Figure 69. *Ptychognathus glaber* Stimpsin, 1858 (source: ebikaniyado.hp.infoseek.co.jp/kani/kani03.html), specimen collected from Ogasawara Island, Jan. 2006.

## ***Ptychognathus andamanensis* (Pretzmann, 1984)**

(Figures 70; 71A-D)

*Ptychognathus glaber andamanensis* Pretzmann, 1984: 141, figs. 9-12.

**Materials examined.— Holotype** – 1 male (4.2mm x 3.5mm) (NHMW-Nr.4118), June Creek, Corbyns Love, South Andaman, coll. F. Starmühlner, Dec. 1976.

**Diagnosis.—** Carapace subquadrate, dorsal surface setose, flat. Front broad, anterior margin slightly concave medially. Anterolateral margin with two teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod flat, broad, as broad as ischium. Cheliped symmetrical in males, fingers setose on outer surface of pollex, manus. Ambulatory legs long, flat, margins setose. Telson broadly triangular with all segments freely moveable (six somites plus telson). G1 long.

**Colour.—** The colour fresh specimens has not been documented, and the colour of the holotype specimen examined is brownish in colour (NHMW-Nr.4118).

**Size.—** This is a very small-size species, the only male specimen examined being 4.2mm x 3.5mm (holotype) in size. Female specimens are not known.

**Habitat.—** It is found under small rocks and pebbles along river banks and the river mouth (Pretzmann, 1984).

**Remarks.—** The description provided by Pretzmann (1984) is very brief, but he had provided several good photographs of the specimen. Examination of the type specimen has shown that this a valid species, in that it is different from *Ptychognathus glaber* in having the following characters viz. a) setose carapace (vs. glabrous carapace in *P. glaber*); b) the outer surface of the chela is setose (vs. glabrous in *P. glaber*), and c) the surface of the exopod of the third maxilliped is flat (vs. broad in *P. glaber*).

This species has not been collected after its description.

**Distribution.**— Indian Ocean (Andaman Islands) only.

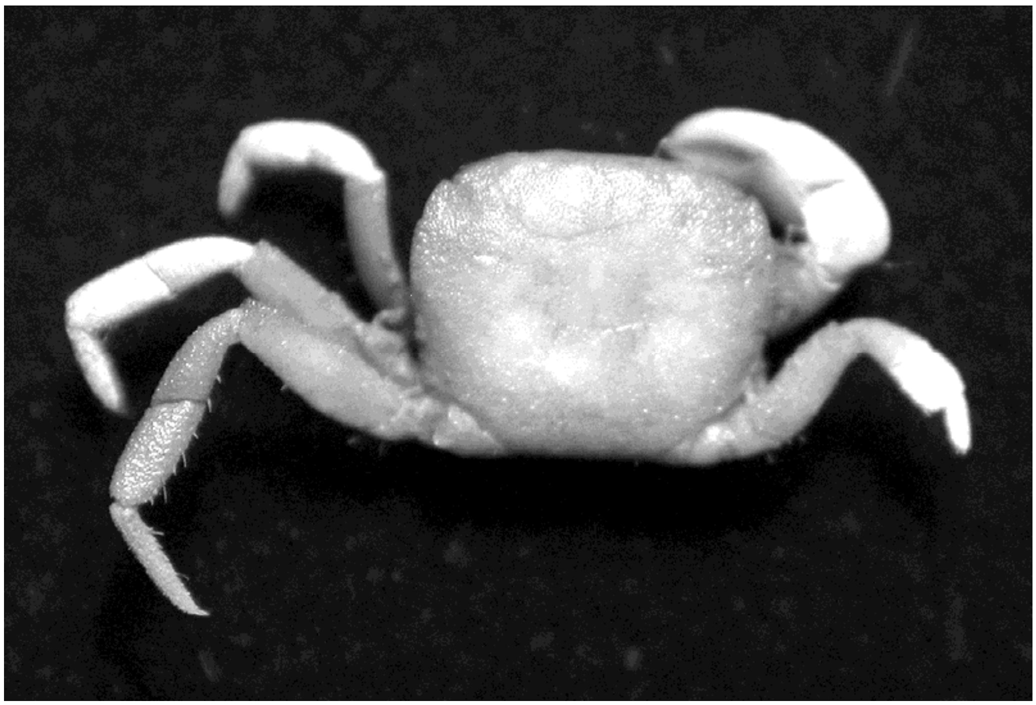


Figure 70. *Ptychognathus andamanensis (*Pretzmann, 1984), male, holotype, 4.2mm x 3.5mm (NHMW-Nr.4118). Dorsal view.

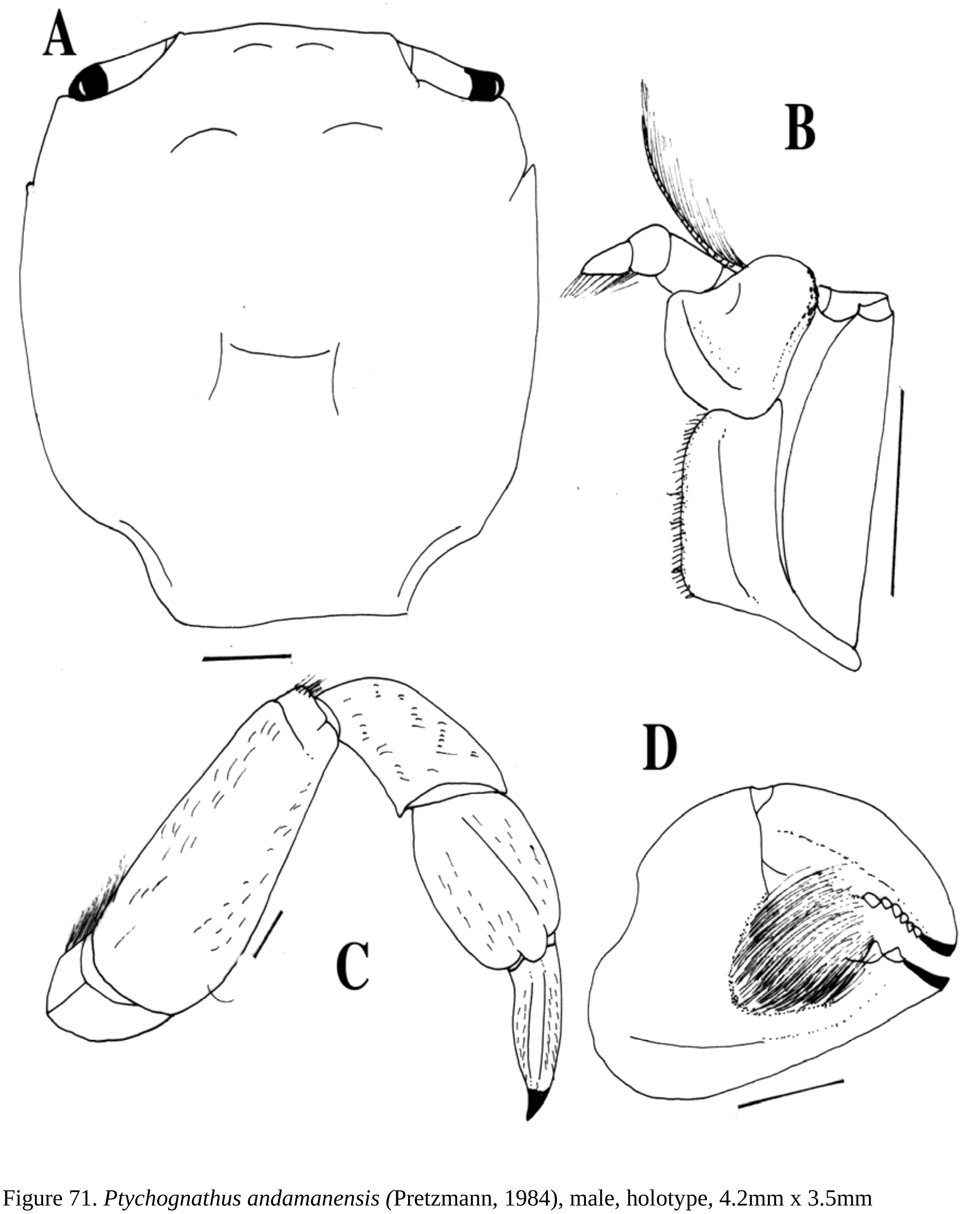



Figure 71. *Ptychognathus andamanensis (*Pretzmann, 1984), male, holotype, 4.2mm x 3.5mm (NHMW-Nr.4118). A) carapace; B) third maxilliped; C) last ambulatory leg; D) outer view of chela. (Scale=1.0mm).

**Ptychognathus ishii Sakai, 1939**

(Figure 72A-G)

*Ptychognathus ishii* Sakai, 1939: 660, text- fig. 114a-c; Horikawa, 1940: 29; Lin, 1949: 29; Sakai, 1976: 639, text-fig. 349a-b, pl. 219, fig. 3; Ng *et al.*, 2001: 46.

**Materials examined.**— **Neotype –** 1 male (12.5mm x 9.5mm) (TMCD-2534), Hsiao-Xiang-Lan, Fu-Lung; Taipei county, Taiwan, coll. C.H. Wang, 21 Apr. 1989. – **Others** – **Japan** – 18 males (7.6-10.1mm x 6.2-7.8mm), 7 females (ovigerous) (7.9-9.9mm x 6.4-7.8mm) (NSMT-CR-9591), Kawanai-gawa, Amamio Shima, Japan, coll. M. Takeda, 15 Jul. 1988; 30 males (5.0-10.2mm x 4.0-7.7mm), 9 females (5.8-11.6mm x 4.5-9.2mm), 1 female (ovigerous) (9.0mm x 7.1mm) (RU-no cat. number), upstream of Benoki river, Okinawa Island, Ryukyus, Japan, no collection date; 8 males (7.5-10.7mm x 6.2-8.5mm) (RU-no cat. number), Benoki river, Okinawa Island, The Ryukyus, Japan, coll. 8 Jul. 1990; 14 males (3.3-10.0mm x 2.8-9.1mm) (RU-no cat. number), Fukukawa river, Junigami village, Okinawa Island, The Ryukyus, Japan, coll. 6 Aug. 1990; 8 males (6.7-9.6mm x 5.0-7.8mm), 5 males (7.1-8.8mm x 5.7-7.5mm) (RU-no cat. number), upstream of Benoki river, Okinawa Island, The Ryukyus, Japan, coll. 28 Jul. 1987; 1 male (9.5mm x 7.5mm) 1 female (7.5mm x 6.4mm) (SFM-24719), Amani, Kagoshima, Japan, coll. K. Sakai, 20 Jul. 1966; 2 males (9.2-9.4mm x 8.4-8.8mm), 1 female (7.3mm x 6.3mm) (SFM-24718, ex-T. Sakai collections), Japan, don. K. Sakai, no collection date; 1 male (8.2mm x 7.0mm) (SFM-ex. T. Sakai collections), Japan, no collection date; 2 males (11.8-12.7mm x 9.4-10.3mm) (SFM-ex. T. Sakai colelctions), Japan, no collection date; 3 males (7.6-8.9mm x 7.0mm), Japan, no collection date; 1 male (11.0mm x 8.9mm) (SFM-ex. T. Sakai collections), Japan, coll. 31 Jul. 1973. – **Taiwan** – 7 males (6.0-9.8mm x 5.0-8.0mm), 1 female (10.0mm x 8.2mm) (TMCD-2534), Hsiao-Xiang-Lan, Fu-Lung; Taipei county, Taiwan, coll. C.H. Wang, 21 Apr. 1989.

**qDiagnosis.**— Carapace subquadrate, dorsal surface smooth, flat, epigastric cristae very weak, barely visible. Front broad, anterior margin slightly concave medially. Anterolateral margin with two teeth including the orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very broad, 2.1 times broader than ischium. Cheliped symmetrical in males, fingers with a tuft of long setae on outer surface extending to base of palm, absent in female. Ambulatory short, flat, densely setose. Male abdomen triangular in shape with all segments freely moveable (six somites plus telson), distal margin of telson convex in shape. G1 long. Female gonopore operculate, rounded.

**Colour.**— The colour of fresh specimens is light brown to dark brown (Y. Nakasone, pers. comm.), and all preserved specimens examined are light brown in colour.

**Size.**— This is a small-sized species. The largest male specimen examined is 12.5mm x 9.5mm (TMCD-2534), and the largest female specimen examined is 11.6mm x 9.2mm (RU-no cat. number).

**Habitat.**— It can be found under rocks and pebbles in freshwater streams (Y. Nakasone, pers. comm.).

**Remarks.**— Sakai's descriptions of *P. ishii* was based on a single specimen collected southern Taiwan (1939). His descriptions were very brief and his figures rather simple. In his original description, he compared between *P. glaber* and *P. ishii*. However, the description of *P. glaber* given by Stimpson (1860) was also very brief. From the description, the main character which differentiated *P. ishii* from *P. glaber* is the presence of a tuft of soft setae on the base of the outer surface in *P. ishii* while the chela of *P. glaber* is glabrous. The examination of *P. glaber* specimens from Luzon, Phillippines (RMNH-D-35278) showed that *P. ishii* can also be separated from *P. glaber* by the following characters viz. a) the ischium of the third maxilliped is less slender, length to width ratio 2.3 (vs. more slender, length to width ratio 2.6 in *P. glaber*); b) the merus of the last ambulatory leg is stouter, length to width ratio 2.7 than (vs. more slender, length to width ratio 3.0 in *P. glaber*); c) the carpus of the last ambulatory leg is stouter, length to width ratio 1.8 (vs. more slender carpus of the last ambulatory legs, length to width ratio 2.2 in *P. glaber*), and d) the telson is almost equal in length and width, length to width ratio 1.0 while (vs. more slender telson in *P. glaber*, length to width ratio 1.3).

I cannot locate the type specimen of *P. ishii*. It is probably lost. Sakai (1939) established this species based on specimens collected from southern Taiwan, but my attempts to collect fresh specimens from the type locality have been futile. I have, thus, designated one male specimens (12.5mm x 9.5mm, TMCD-2534) collected from Hsiao-Xiang-Lan, Fu-Lung; Taipei county, Taiwan as the neotype.

The species usually occurs in small numbers where they have been found, and are extremely sensitive to impact to the coastal area (Y. Nakasone, pers. comm.).

**Distribution.**— Taiwan, Japan, Philippines and Guam.

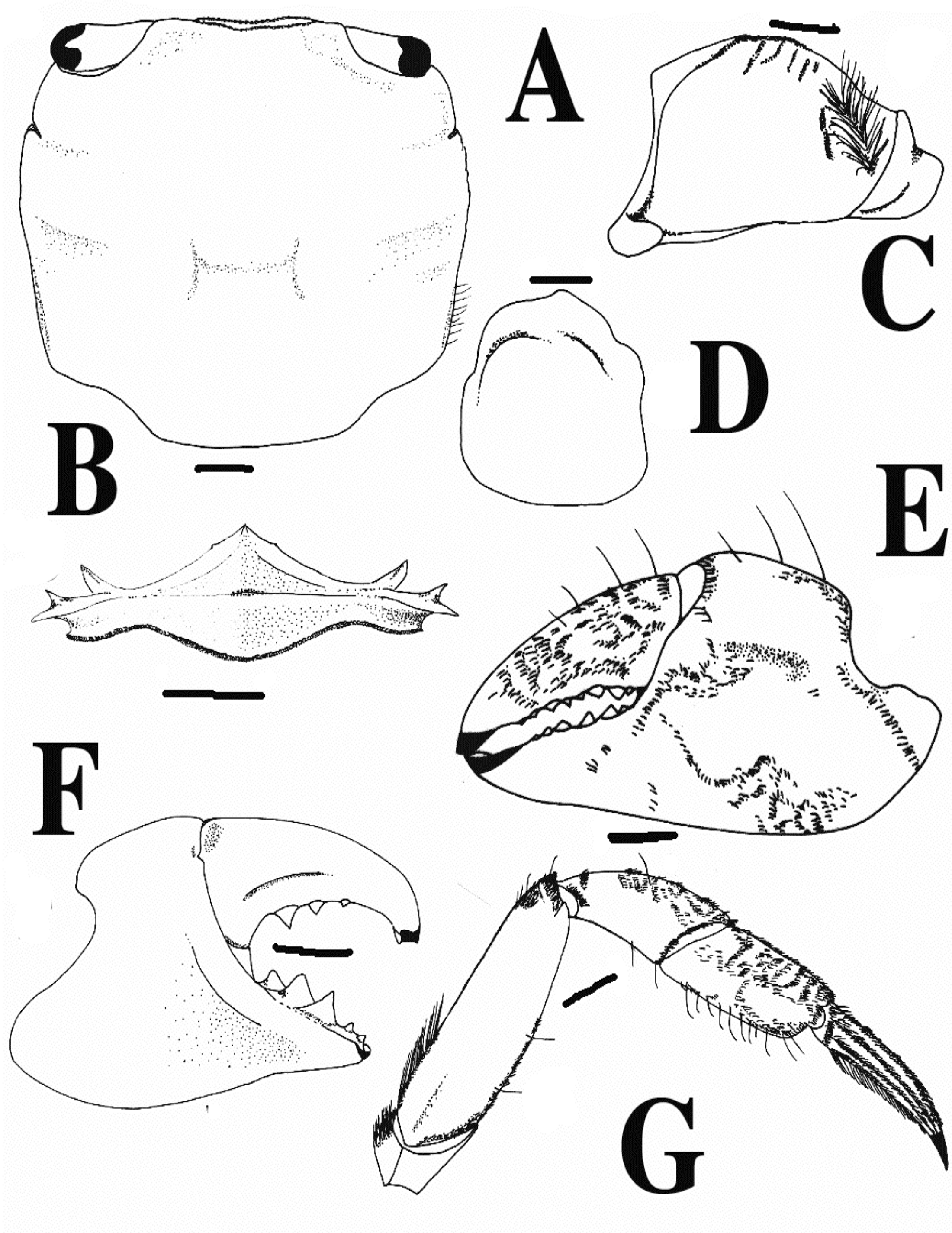



Figure 72. *Ptychognathus ishii* Sakai, 1939, male, 10.7mm x 8.5mm, (RU-no cat. number). A) carapace; B) epistome; C) merus of chela D) carpus of male chela; E) female chela; F) male chela; G) last ambulatory leg. (Scale=1.0mm).

## *Ptychognathus hachijyoensis* Sakai, 1955

(Figure 73A-F)

*Ptychognathus hachijyoensis* Sakai, 1955: 199; Sakai, 1976: 640, text-fig. 349c-d; Fukui *et al.*, 1989: 229, figs. 15, 16; Ng *et al.*, 2001: 46.

**Materials examined.**— **Neotype** – 1 male (13.1mm x 10.7mm) (CMNH-ZC-00428), Ara-ike, Hachijo-jima, Island, Izu Island, Japan, coll. J. Okuno & K. Tanaka, 1 Sep. 1994. – **Others** – 2 males (5.0-8.1mm x 4.5-6.5mm), 2 females (5.0mm x 4.5mm), 1 juvenile. (2.0mm x 1.5mm) (MHNM-B-13221), leg T. Sakai, no collection date; 1 male, 1 female (TMCD-uncatalogued), He-Mei, Taipei County, Taiwan, coll. 20 Nov. 1988; 1 male, 6 females (TMCD-uncatalogued), Patoutzi, Keelung City, Taiwan, 20 Nov. 1988.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth, flat, epigastric cristae strong. Front broad, anterior margin slightly concave medially. Anterolateral margin with single orbital tooth, followed by a faint lobe. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very broad, broader than ischium. Cheliped symmetrical in males, fingers with a tuft of long setae on outer surface restricted at the base of fingers, absent in female. Ambulatory short, flat, densely setose. Male abdomen triangular in shape with all segments freely moveable (six somites plus telson), distal margin of telson convex in shape.

**Colour.**— The colour of fresh specimens is overall light brown with dark brown spots (C.H. Wang, pers. comm.), and all preserved specimens examined are brown in colour.

**Size.**— This is a small-sized species, the largest male specimen examined is 8.1mm x 6.5mm (MHNM-B-13221), and the largest female specimen examined is 5.0mm x 4.5mm (MHNM-B-13221).

**Habitat.**— It can be found under rocks and pebbles, along the river banks (Fukui *et al.* (1989).

**Remarks.**— This species has been first reported from Taiwan by Fukui *et al.*, (1989). This species is not commonly seen.

The location of the type specimen of this species is not known. I have checked the Kanagawa Prefecture Museum of Natural History of Natural History (Dr. M. Muraoka); Natural History Museum & Institute, Chiba (Dr. T. Komai); Coastal Branch of Natural History Museum & Institute, Chiba (Dr. J. Okuno); National Museum of Science and Technology, Tokyo (Dr. M. Takeda), and even the Senckenberg Natural History Museum, Frankfurt am Main (Dr. M. Türkay) for the location of the specimen but it has been fruitless. As such, to stabilize the taxonomy, I have designated a male specimen, 13.1mm x 10.7mm (CMNH-ZC-00428) from collected Ara-ike, Hachijo-jima, Island, Izu Island, Japan as the neotype.

**Distribution.**— Taiwan, Japan.

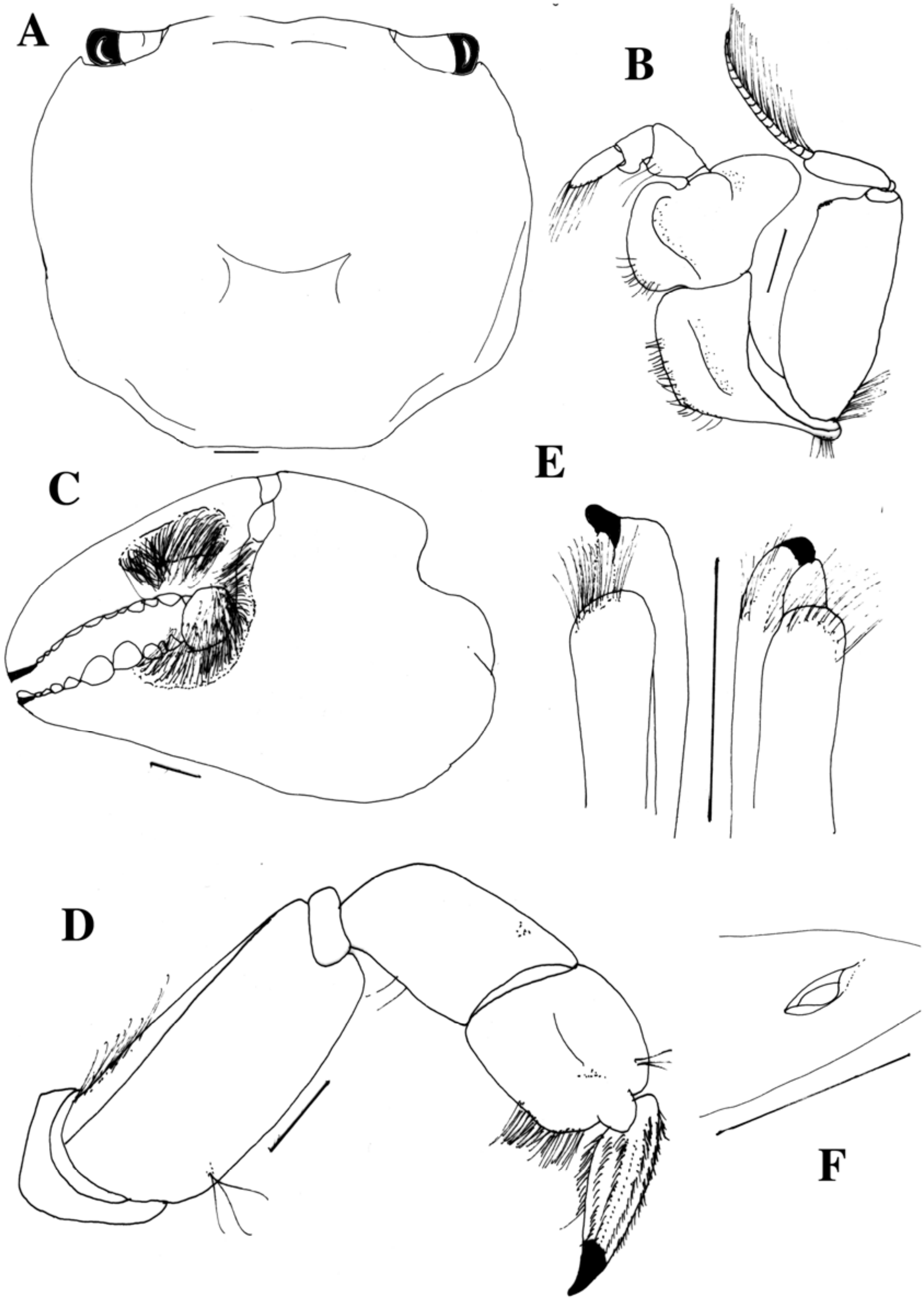



Figure 73. *Ptychognathus hachijyoensis* Sakai, 1955, male, neotype, 13.1mm x 10.7mm (CMNH-ZC-00428), female, 5.0mm x 4.5mm (MHNM-B-13221). A) carapace; B) third maxilliped; C) outer view of chela; D) last ambulatory leg; E) distal ends of G1; F) female gonopore. (Scale=1.0mm).

### *Ptychognathus fukukawanensis*, new species

(Figure 74A-E)

**Materials examined.**— **Holotype** – 1 male (6.4mm x 5.3mm) (RU-no cat. number) Fukukawa River, Kunigami Village, Okinawa Island, Japan, coll. Y. Nakasone, 6 Aug. 1990. – **Paratypes –** 2 males (5.0-5.4mm x 4.0-4.4mm), 3 females (4.4-6.4mm x 3.5-5.2mm) (RU & ZRC-uncatalogued), Fukukawa River, Kunigami Village, Okinawa Island, Japan, coll. Y. Nakasone, 6 Aug. 1990.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth and flat. Front broad, anterior margin slightly concave medially. Anterolateral margin with two teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very broad, as broad as ischium. Cheliped symmetrical in males, fingers setae on outer surface. Ambulatory legs short, flat, margins setose. Male abdomen narrow with all segments freely moveable (six somites plus telson). G1 broad, Female gonopore operculate, rounded.

**Etymology.**— The species  is named after its type locality, Fukukawa River, in Kunigani village on Okinawa Island, Japan.

**Colour.**— The colour fresh specimens is brownish in colour (Y. Nakasone, pers. comm.), and the colour of all preserved specimens examined is brownish in colour.

**Size.**— The largest male specimen examined is 6.4mm x 5.3mm (holotype) while the largest female specimen examined is 6.4mm x 5.2mm (ZRC-uncatalogued).

**Habitat.**— It is found under small rocks and pebbles along river banks, and river mouths (Y. Nakasone, pers. comm.).

**Remarks.**— The descriptions given by Sakai (1955, 1976) of *P. hachijyoensis* were very brief, and his figures are too simplified. The new species closely resembles *P.*

*hachijyoensis* Sakai, 1955, in the form of the carapace. However, when compared with the descriptions, and diagrams given by Sakai (1955, 1976), the new species can be distinguished from *P. hachijyoensis* by the following characters viz. a) the absence of an anterolateral tooth (vs. presence of a vestigal incision behind the external oribtal tooth in *P. hachijyoensis*); b) the exopod of the third maxilliped is as broad as the ischium ((vs. exopod distinctly broader than ischium in *P. hachijyoensis* (cf. Sakai, 976: 640, text-fig. 349c-d); c) the tuft of long soft setae extends from the outer proximal margin of the manus to almost reaching the posterior margin of the manus (vs. the tuft of hair at the outer proximal margin which does not extend onto the palm in *P. hachijyoensis*), and  d) the cheliped of the new species is longer than broad, length to width ratio 2.1 (vs. broader than long cheliped of *P. hachijyoensis*, length to width ratio 1.6 in *P. hachijyoensis*).

**Distribution.**— Japan (Okinawa only).

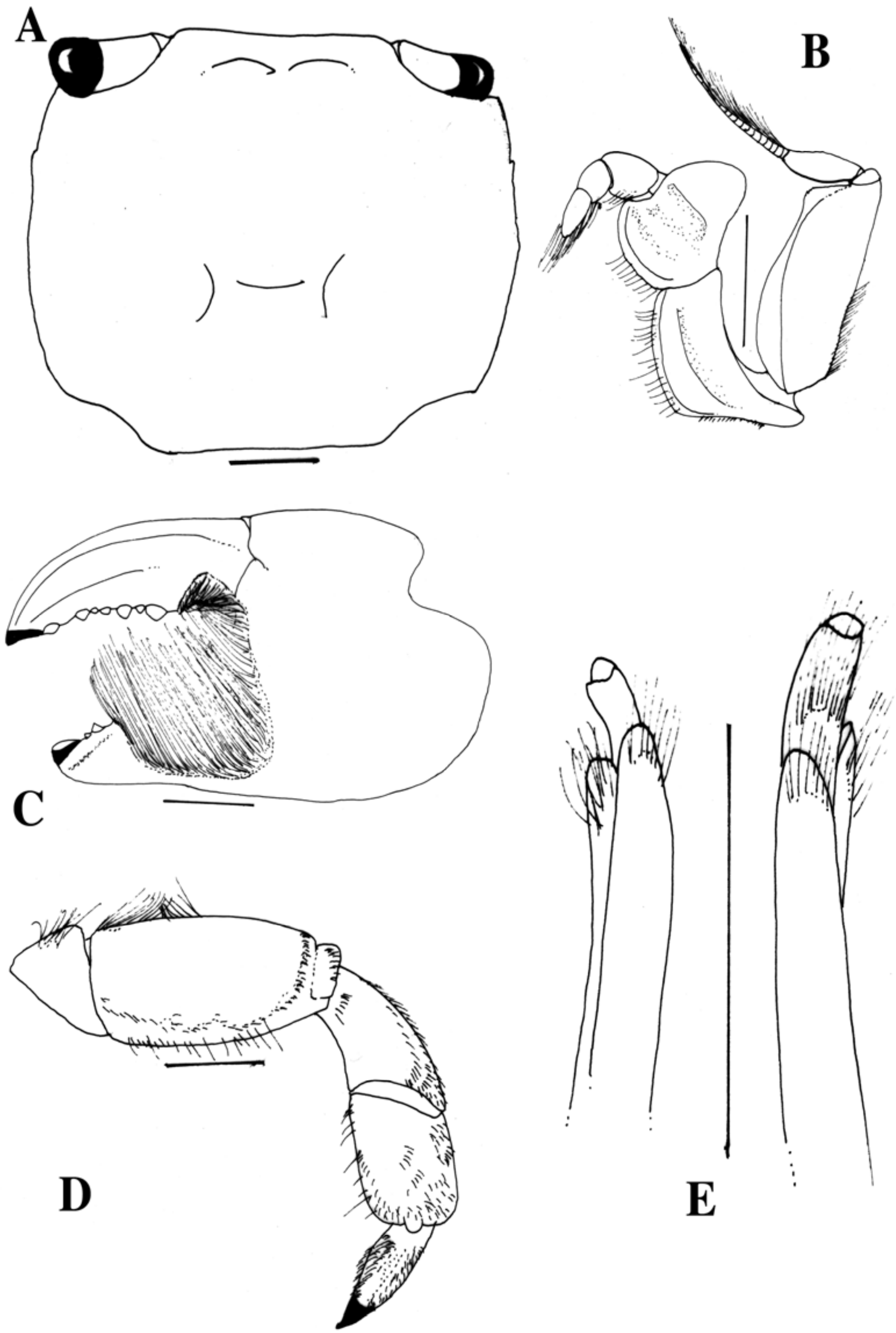



Figure 74. *Ptychognathus fukukawanensis*, new species, male, paratype (5.4mm x 4.4mm), female (6.4mm x 5.2mm) (RU & ZRC-uncatalogued). A) carapace; B) third maxilliped; C) outer view of chela D) last ambulatory leg; E) distal ends of G1. (Scale=1.0mm).

***Ptychognathus kukukawaensis*, new species**

(Figure 75A-I)

**Materials examined.— Holotype** – 1 male (11.0mm x 8.6mm) (RU-uncatalogued), Kukukawa River, Kunigami Village, Okinawa, coll. Y. Nakasone, 6 Aug. 1990. – **Paratypes -** 13 males (5.5-10.4mm x 4.3-8.8mm), 3 females (3.1-7.5mm x 2.3-5.8mm) (RU-uncatalogued), Kukukawa River, Kunigami Village, Okinawa, coll. Y. Nakasone, 6 Aug. 1990.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth and flat. Front broad, anterior margin slightly concave medially. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod broad, 1.4 times broader than ischium. Cheliped granulated, symmetrical in males, fingers setose on proximal region of pollex only. Ambulatory legs short, flat, margins setose. Male abdomen triangular in shape with all segments freely moveable (six somites plus telson)Telson broadly triangular. G1 long. Female gonopore operculate, rounded.

**Etymology.—** The new species  is named after its type locality, Kukukawa River in Kunigami Village, Okinawa Island, Japan.

**Colour.**— The colour of fresh specimens is light brown (Y. Nakasone, pers. comm.), and the colour of all preserved specimens examined is brownish in colour (RU-no cat. number).

**Size.**— The largest male specimen examined is 11.0mm x 8.6mm (holotype), while the largest female specimen examined is 10.4mm x 8.8mm (paratype).

**Habitat.**— It is found under small rocks and pebbles along river banks and river mouth (Y. Nakasone, pers. comm.).

**Remarks.**— The new species is very similar to *P. ishii*, but it is possible to differentiate it by the following characters viz. a) the distinctly longer ischium of the third maxillped, length to width ratio ca. 2.6 (vs. shorter ischium, length to width ratio 2.3 in *P. ishii*); b) the longer merus of the third maxilliped, length to width ratio 2.3 (vs. the broader merus, length to width ratio 2.1 in *P. ishii*); c) the more slender exopod of the third maxilliped, length to width ratio ca. 2.3 (vs. the stouter exopod, length to width ratio 2.1 in *P. ishii*); d) the longer merus of the third ambulatory leg, length to width ratio 3.8 (vs. the shorter merus, length to width ratio 3.3 in *P. ishii*); e) the stouter merus of the last ambulatory leg, length to width ratio 2.5 (vs. the longer merus, length to width ratio 2.7 in *P. ishii*); f) the slightly longer carpus of the last ambulatory, length to width ratio 2.0 (vs. the stouter carpus, length to width ratio 1.8 in *P. ishii*); g) the dactylus of the third ambulatory leg is shorter, length to width ratio 4.9 (vs. longer dactylus, length to width ratio 5.4 in *P. ishii*), and h) the more slender G1, length to width ratio 7.3 (vs. stouter G1, length to width ratio 6.5 in *P. ishii*).

**Distribution.**— Japan (Okinawa) only.

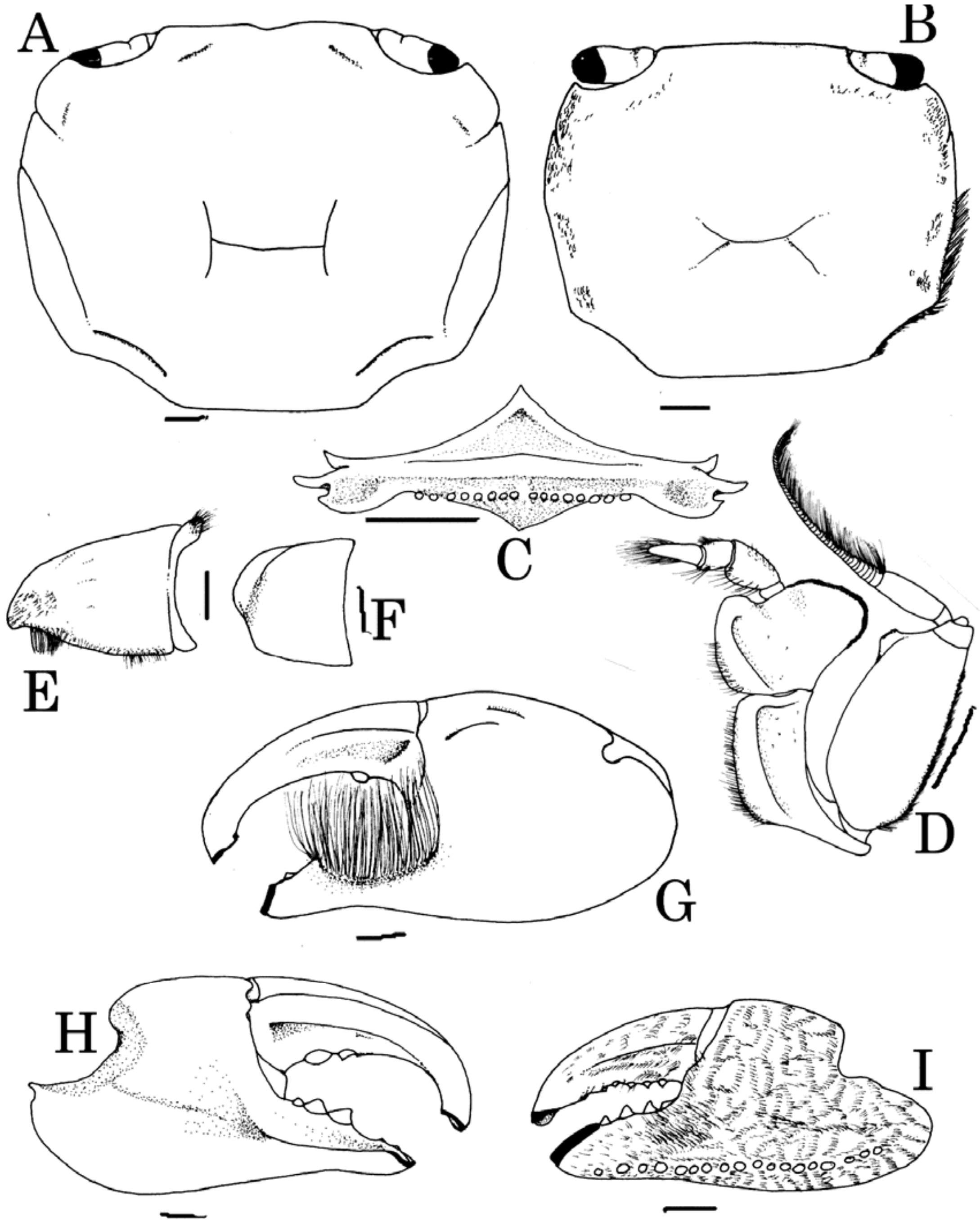



Figure 75. *Ptychognathus kukukawaensis,* new species, male, holotype, 11.0mm x 8.6mm (RU-uncatalogued); female, 7.5mm x 5.8mm (RU-uncatalogued). A) male carapace; B) female carapace; C) epistome; D) third maxilliped; E) merus of chela; F) carpus of chela; G) outer surface of male cheliped; H) inner surface of male cheliped; I) female cheliped. (Scale=1.0mm).

## *Ptychognathus pseudoishii*, new species

(Figure 76A-I)

**Materials examined.**— **Holotype** – 1 male (9.0mm x 7.1mm) (RU-no cat. number), Benoki, Okinawa Island, The Ryukyus, Japan, coll. Y. Nakasone, 28 Jul. 1987. – **Paratypes** – 4 males (8.1-8.8mm x 6.6-7.1mm) 4 females (7.4-9.0mm x 6.2-7.4mm), Benoki, Okinawa Island, The Ryukyus, Japan, coll. Y. Nakasone, 28 Jul. 1987.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth and flat. Front broad, anterior margin slightly concave medially. Anterolateral margin with two teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod 1.1 times broader than ischium. Cheliped symmetrical in males, fingers with distal region of manus setose. Ambulatory legs short, flat, margins setose. Telson broadly triangular with all segments freely moveable (six somites plus telson). G1 long. Female gonopore operculate, roundish in shape.

**Etymology.**— 'Pseudo' is the Latin word for 'false' alluring to the fact that this species has always been mistaken as *P. ishii*.

**Colour.**— The colour of fresh specimens is light brown (Y. Nakasone, pers. comm.), and the colour of all preserved specimens examined is brownish in colour.

**Size.**— The largest male specimen examined is 9.0mm x 7.1mm (holotype) while the largest female specimen examined is 9.0mm x 7.4mm (paratype).

**Habitat.**— This species is found under small rocks and pebbles along river banks and river mouth (Y. Nakasone, pers. comm.).

**Remarks.**— The new species is very similar to *P. ishii* and *P. glaber*. However, it can be differentiated from *P. ishii* by the following characters viz. a) a very narrow exopod, length to width ratio 2.6 (vs. broader exopod, length to width ratio 2.1 in *P. ishii*); b) the exopod is slightly broader than ischium in the third maxilliped, ratio of exopod to ischium 1.1 (vs. exopod distinctly broader than ischium, ratio of exopod to ischium 1.3 in *P. ishii*); c) the very broad merus of the last ambulatory leg, length to width ratio 2.2 compared to a much longer merus (length to width ratio 2.7) in *P. ishii*, and d) the male abdomen is more elongated (overall length to width ratio 1.8) compared to *P. ishii* (overall length to width ratio 1.6).

The new species is very similar to *P. glaber*. However, it can be differentiated from *P. glaber* (RMNH-D35278) by the following characters viz. a) the ischium of the third maxilliped is stouter, length to width ratio 2.2, (vs. narrower, length to width ratio 2.6 in *P. glaber*); b) the exopod is very broad, length to width ratio 2.6 (vs. narrower exopod, length to width ratio 2.1 in *P.glaber*); c) the exopod is only slightly broader than ischium, ratio of exopod to ischium 1.1 (vs. very much broader exopod, ratio of exopod to ischium 1.4 in *P. glaber*); d) the merus of the last ambulatory leg is stouter, length to width ratio 2.2 (vs. narrower merus of the last ambulatory leg, length to width ratio 3.0 in *P. glaber*); e) the carpus of the last ambulatory is more slender, length to width ratio 1.8than (vs. more slender, length to width ratio 2.2 in *P. glaber*); f) the propodus of the last ambulatory is slightly more slender, length to width ratio 1.2 (vs. slightly more slender, length to width ratio 1.3 in *P. glaber*), and g) telson is broader, length to width ratio 1.1) than (vs. more slender telson, length to width ratio 1.3 in *P. glaber*).

**Distribution.**— Japan (Okinawa) only.

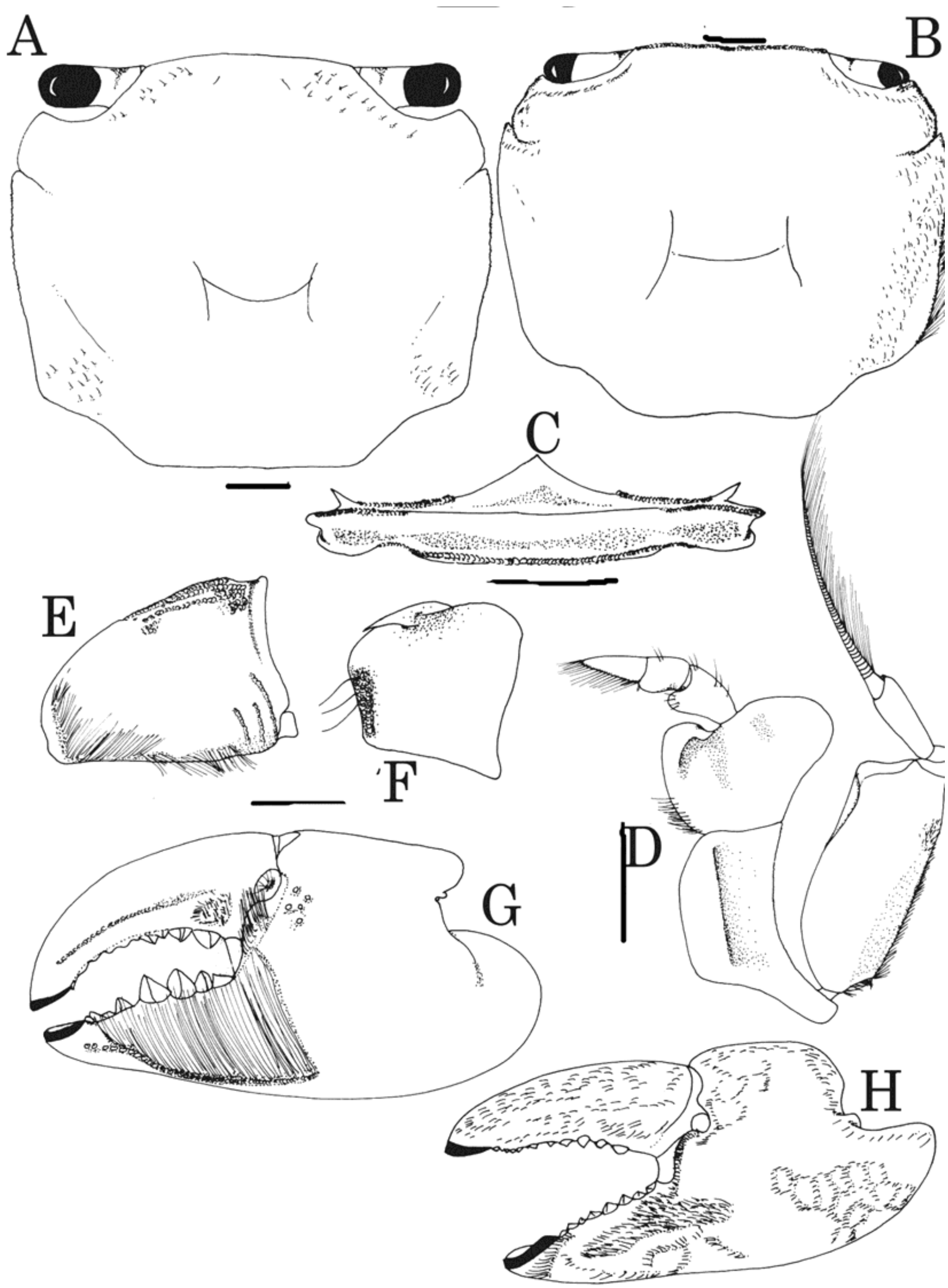



Figure 76. *Ptychognathus pseuoishii*, new species, male, holotype, 9.0mm x 7.1mm; female, paratype, 9.0mm x 7.4mm (RU-no cat. number). A) male carapace; B) female carapace; C) epistome; D) third maxilliped; E) merus of chela; F) carpus of chela; G) male cheliped; H) female cheliped (Scale=1.0mm).

## Genus *Gnathograpsus* A. Milne-Edwards, 1868

*Gnathograpsus* A. Milne-Edwards, 1868: 180.

*Ptychognathus* – Miers, 1886: 262; de Man, 1887: 719; de Man, 1895: 90; Alcock, 1900: 402; Stimpson, 1907: 129, pl. 7, fig. 5, 5a; Rathbun, 1914: 69; Tesch, 1918: 85; Sakai, 1939: 647, 658; Crosnier, 1965: 37 (not *Ptychognathus* Stimpson, 1858)

*Coelochirus* Nauck, 1880: 66; de Man, 1887: 719; de Man, 1888: 149.

**Type species.**— *Gnathognathus pilipes* A. Milne-Edwards, 1868, by current designation.

**Gender.**— Masculine.

**Diagnosis**.— Carapace quadrangular, slightly broader than long; dorsal surface glabrous, punctate; regions not well defined, flat, epigastric cristae not distinct, overall carapace physiognomy thick. Frontal margin slightly convex, usually straight. Anterolateral margin subcristate with two teeth including orbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, subparallel. Orbits small, eyes completely filling orbit. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Chela large, inner surface of chela with granules; outer surface of pollex and manus with or without tufts of setae; fingers as long as palm. Ambulatory legs with short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular in shape, with seven moveable segments (six somites plus telson).

**Remarks.**— This genus is distinctly from *Ptychognathus* sensu stricto by the following features a) having two teeth on the anterolateral margin after the orbital tooth (vs. one tooth in *Ptychognathus*), b) all the listed species in this genus have very thick carapace physiognomy, similar to that of *Pseudograpsus* (vs. thinner carapace thickness in

*Ptychognathus*); c) these species are all large in adult size (vs. small-size species in *Ptychognathus*); d) male abdomen is broader than those of *Ptychognathus*), and e) the G1 is long and slender (vs. stout and short in *Ptychognathus*), and f) the female gonopore are circular and slightly protruding (vs. in slightly elliptical and flat *Ptychognathus*).

Nauck (1880) based on gastric mills morphology, established *Coelochirus crinipes* for the currently known *Ptychognathus pilipes*. His work suggested that the gastic mill is apparently very different from *Ptychognathus* sensu lato. This supports the establishment of the new genus for this group of crabs. As such, two names, *Gnathograpsus* A. Milne-Edwards, 1868, and *Coelochirus* Nauck, 1880, are available for the new genus. *Gnathograpsus* was established by A. Milne-Edwards, 1868 for *G. riedelii* and *G. pilipes*. Both *G. riedelii* and *G. pilipes* are put together in this same small group; this name was synonymised by de Man in 1883. *Gnathograpsus* is the older of the two available names, and hence, the generic name '*Gnathograpsus*' is resurrected for this new grouping.

The six species that are included in the new grouping are *Ptychognathus pilipes* (A. Milne-Edwards, 1868) (type species); *Ptychognathus riedelii* (A. Milne-Edwards, 1868); *Ptychognathus intermedius* de Man, 1879; *Ptychognathus pilosus* de Man, 1892; *Ptychognathus demani* Roux, 1917; and a new species *Gnathograpsus setocarpus* (see below)

**Key to species in *Gnathograpsus***

1a. Carapace subquadrate. Chelipeds glabrous. ---------------------------------------- **2**

1b. Carapace subquadrate. Chelipeds setose. -------------------------------------------- **3**

2a. Outer surface of chela smooth. Exopod of third maxilliped 1.1 times broader than ischium. ----------------------------------------------------------------------- ***G. pilipes***

2b. Outer surface of chela with flat round granules. Exopod of third maxilliped 1.7 times broader than ischium. -------------------------------------------- ***G. intermedius***

3a. Outer surface of chela with no setae on surface except on tips of pollex. - **4**

3b. Outer surface of chela with setae on surface except on tips of pollex. ------- **5**

4a. Exopod of third maxilliped 2.1 times broader than ischium. Outer distal posterior of carpus of chela with tuft of setae. ---------------------------------- ***G. setocarpus***

4b. Exopod of third maxilliped 2.0 times broader than ischium. Outer distal posterior of carpus of chela without a tuft of setae. --------------------------------- ***G. riedelii***

5a. Outer surface of chela with tuft of setae on the fingers as well as on the tip of pollex. Exopod of third maxilliped 2.2 times broader than ischium. ------------- ***G. pilosus***

5b. Outer surface of chela with tuft of long stiff setae mixed with soft short setae on fingers, not on tips of pollex, exopod of third maxilliped as broad as ischium. --------- -------------------------------------------------------------------------------- ***G. demani***

### *Gnathograpsus pilipes* A. Milne-Edwards, 1868

(Figures 77A-C; 78A-D)

*Gnathograpsus pilipes* A. Milne-Edwards, 1868: 184, pl. 27, figs. 6-10; Miers, 1886: 262; de Man, 1888: 149; Tesch, 1918: 88.

*Coelochirus crinipes* Nauck, 1880: 30; de Man, 1888: 149.

**Materials examined.**— ***Gnathograpsus pilipes*** – **Lectotype** – 1 male (9.7mm x 9.1mm) (ZMA-no cat. number), Rio Koiminus, Timor, Indonesia, coll. M. Weber, 1888/1889. – ***Coelochirus crinipes*** **– Neotype** – 1 male (27.2mm x 23.4mm) (ZRC-uncatalogued), Kawasan Fall, Matutinao River, Cebu Island, Philippines, coll. Cai *et al.,* 20 Dec. 2000. – **Others** – **Philippines** – 1 male (40.0mm x 34.0mm) (MNHN-3396), Iles Philippines, coll. Mr. Parte; 1 female (27.9mm x 25.5mm) (MNHN-3396), Iles Philippines coll. Mr. Parte; 1 female (MNHN-3399), 1 male (MNHN-3397), 2 females (MNHN-3398), 1 female (MNHN-3400), Philippines, coll. Mr Parte; 2 males (35.5-36.3mm x 31.0-32.5mm) (MNHN-3626), Iles Philippines, coll. Mr. Parte; 2 males (22.4-24.0mm x 20.0-22.6mm), 2 females (26.2-28.7mm x 23.2-26.0mm) (USNM-44661), Malaga River, Leyte, Philippines, coll. US Fisheries Buearu, 30 Jul. 1909; 14 males (7.3-27.6mm x 6.6-24.1mm), 1 female (18.8mm x 16.5mm) (ZRC-uncatalogued), Inambacan River, Antequerra, Bohol Island, Philippines, coll. P.K.L. Ng, 27 Nov. 2001; 1 female (25.0mm x 21.8mm) (ZRC-uncatalogued), Ginatilan, Cebu Island, Philippines, coll. H.C. Liu *et al.,* 2 Dec. 2001; 9 males (23.0-27.2mm x 21.0-23.4mm) (ZRC-uncatalogued), Kawasan Fall, Matutinao River, Cebu Island, Philippines, coll. Cai *et al.,* 20 Dec. 2000.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth, flat, thick. Front broad, anterior margin slightly concave medially. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, slender and narrow, merus with antero-external angle broad, exopod very broad, convex, 1.1 times broader than ischium. Chelipeds large, symmetrical in males, fingers glabrous. Ambulatory legs short, flat, margins with dense, long setae. Telson triangular in shape. G1 slender. Female gonopore with operculum circular in shape.

**Colour.**— The colour of fresh specimens can be in different shade of brown and green (H.C. Liu, pers. comm.), all preserved specimens examined are brownish in colour.

**Size.**— The largest male specimen examined is 40.0mm x 34.0mm (MNHN-3396), while the largest female specimen examined is 28.7mm x 26.0mm (USNM-44661).

**Habitat.**— It is found under small rocks and pebbles in the freshwater river beds (Y. Cai & H.C. Liu, pers. comm.).

**Remarks.**— Alphonse Milne-Edwards (1868) described this species from Celebes. Many years later, Nauck (1880) established a new genus and species, *Coelochirus crinipes,* for this same species based solely on the differences in the gastric mill morphology. de Man (1888: 149) synonymized *Coelochirus crinipes* under *Ptychognathus pilipes* (A. Milne-Edwards, 1868) on basis of external adult morphology (see above).

The type specimens of Nauck's (1880) study are currently supposedly to be in the Forschungsinstituts und Naturmuseums Senckenberg. The author had tried to look for the specimen in the Zoological Museum of Göttingen University collections which has been transferred to Forschungsinstituts und Naturmuseums Senckenberg since 1985, but to no avail. A second check with the curator (A. Allaspach, pers. comm.) has also failed to locate the specimens. Likewise, two checks with the curator of Berlin Museum have also been futile (O. Coleman, pers. comm.).

Miers (1886: 262) synonymized *Gnathograpsus pilipes* under the genus *Ptychognathus* Stimpson, 1858, stating that the exopods of third maxillipeds are similar. He further stated that the descriptions provided by Nauck (1880) on the genus *Coelochirus* Nauck, 1880, is too brief be allied to any distinctive genera, and hence, he synonymized *Coelochirus* under the genus *Pseudograpsus* (Miers, 1886: 262)

A preliminary examination of two gastric mills of *G. pilipes* has shown that their structures do concur with the descriptions and figures provided by Nauck (1880). A more detailed study on the gastric mills will need to be carried to ascertain the true identity of *Coelochirus crinipes.* Based on the available evidence, we have no reason to doubt that *Coelochirus crinipes* is a junior synonym of *Gnathograpsus pilipes*. To secure the taxonomy for this species, a neotype for *Coelochirus crinipes* Nauck, 1880, is selected from the lot of from 9 males collected from Kawasan Fall, Matutinao River, Cebu Island, Philippines, since Nauck's specimens came from Philippines too. This specimen will be deposited in the ZRC.

**Distribution.**— Philippines and Indonesia only.

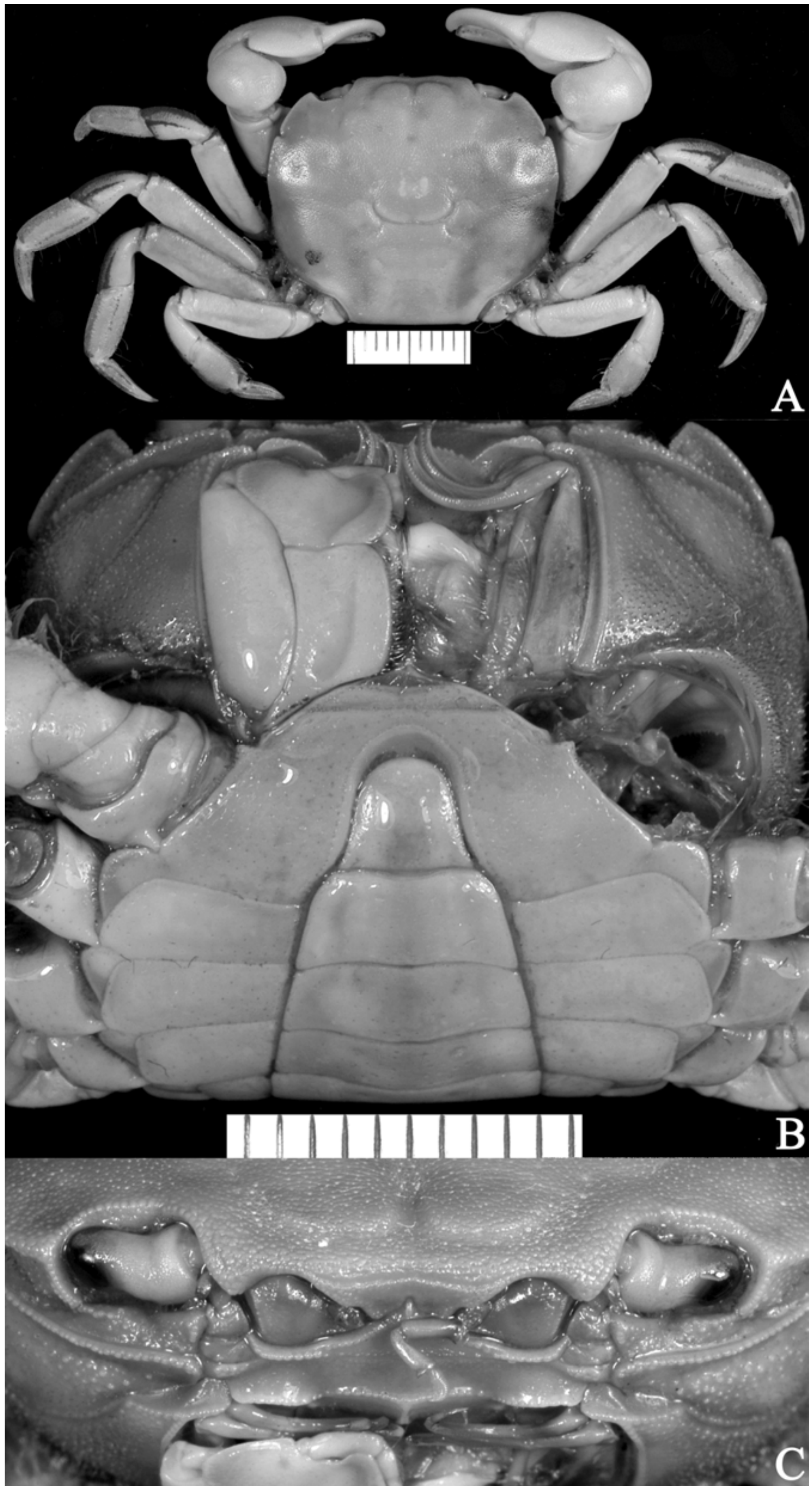



Figure 77. *Gnathograpsus pilipes* A. Milne-Edwards, 1868, male, 27.2 mm x 23.4mm (ZRC-uncatalogued). A) dorsal view; B) ventral view; C) frontal view.

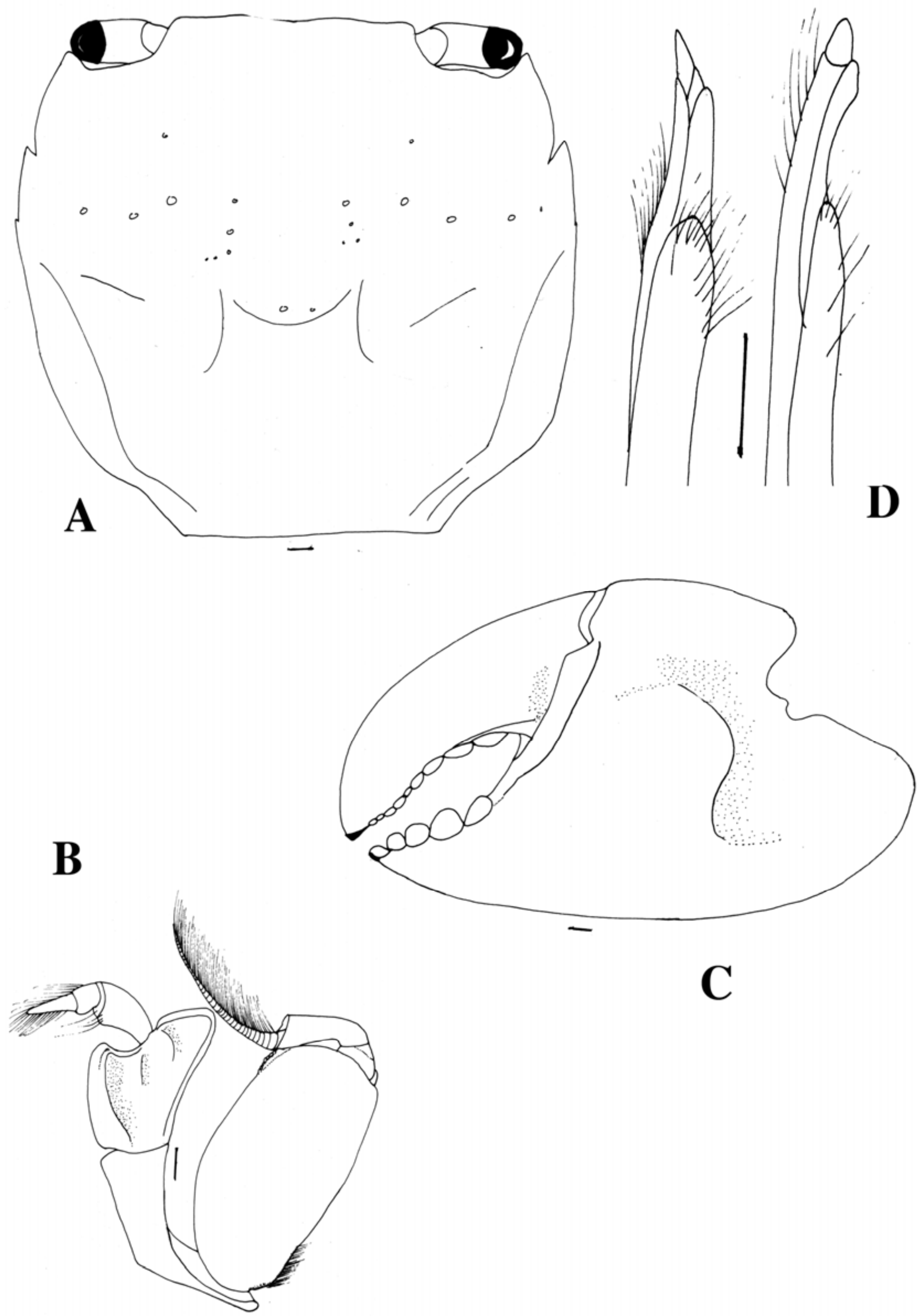



Figure 78. *Gnathograpsus palipes* A. Milne-Edwards, 1868, male, 27.2 mm x 23.4mm (ZRC-uncatalogued) A) carapace; B) third maxilliped; C) outer view of chela; D) distal end of G1. (Scale=1.0mm).

## *Gnathograpsus riedelii* (A. Milne-Edwards, 1868)

(Figures 79A-B; 80A-D)

*Gnathograpsus riedelii* A. Milne-Edwards, 1868: 182, pl. 27, figs. 1-5 (part); Tesch, 1918: 87; Cai & Ng, 2001: 686, Fig. 16.

*Ptychognathus andamanica* Alcock, 1900: 404, 1902: pl. LXV, figs. 3, 3a.

**Materials examined.— Lectotype** – 1 male (23.2mm x 20.4mm) (MNHN-3402), Iles Celebes, Indonesia, coll. M Riedel, no collection date. – **Paralectotype** – 2 males, 1 female (MNHN-3627, dry specimen), Iles Celebes, Indonesia, coll. M. Riedel, no collection date. – **Others** – **Indonesia** – 4 males (14.0-24.2mm x 13.0-11.3mm), 1 female (21.2mm x 20.9mm) (NMB-622c), Baaguia, Ost (East) Timor, Indonesia, coll. D.A. Buhler, Aug. 1935; 6 males (17.6-24.0mm x 16.4-20.8mm), (RMNH-2076), Rosenbeng, Celebes, Indonesia, coll. 18 Apr. 1878; 13 males (21.5-27.2mm x 18.7-22.0mm), 6 females (18.7-20.1mm x 15.8-18.0) (ZMA-no catalogue no.), River Toebah, foreas Tomas, bovenstream, coll. W. Cerem, 27 Feb. 1910; 1 male (26.5mm x 24.4mm) (ZRC-uncatalogued), Telaga River, Bali Island, Indonesia, coll. D. Chia & C.P. How; 1 male (30.0mm x 26.6mm), 1 female (30.1mm x 26.5mm) (ZRC 1965.7.27.159-160), Baguia, Portugese Timor, Indonesia, coll. A. Buhler; 3 females (7.8-20.5mm x 6.9-18.1mm) (ZMA-no cat. number), river Ba by Endeh, Flores, Indonesia, no collection date. – **New Guinea** – 5 males (9.4-21.1mm x 8.5-19.0mm), 1 female (15.5mm x 13.8mm) (RMNH-29297), Manainoemi river, New Guinea, coll. L.B. Holthuis, 21 Feb. 1955; 1 male (11.5mm x 10.3mm),; 2 males (20.9-22.0mm x 18.7-19.4mm), 1 female (17.2mm x 15.2mm) (SFM-7293), Manalnoenu, New Guinea, coll. L.B. Holthuis, 21 Feb. 1955. – **Philippines** – 1 female (ovigerous) (17.1mm x 15.4mm) (ZRC-uncatalogued), Ginatilan, Cebu Island, Philippines, coll. P.K.L. Ng *et al.*, 27 Nov. 2001; 1 female (19.5mm x 17.1mm), 5 females (ovigerous) (19.1-23.3mm x 16.9-19.8mm) (ZRC-uncatalogued), Kawasan Fall, Cebu Island, Philippines, coll. H.C. Liu, *et al.*, 2-3 Dec. 2001; 4 males (18.6-24.6mm x 16.7-21.7mm), 1 female (21.1mm x 18.5mm) (ZRC-uncatalogued), Kawasan Fall, Matutinao River, Cebu Island, Philippines, coll. H.C. Liu, 4 Dec. 2001; 4 males (8.5-13.0mm x 7.8-11.8mm), 2 females (9.7-10.5mm x 8.7-9.8mm) (ZRC-uncatalogued), Inambacan River, Antequerra, Bohol Island, Philippines, coll. P.K.L. Ng, 27 Nov. 2001.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth and flat. Front broad, anterior margin slightly concave medially. Anterolateral margin with three teeth including orbital tooth. Third maxilliped very narrow and thin, close with a small gap, merus with antero-external angle broad, exopod very broad, 2.0 times broader than ischium. Chelipeds large, symmetrical in males, fingers with a small tuft of setae at tips of pollex. Ambulatory legs short, flat, margins setose. Telson triangular. G1 long. Female gonopore with operculum circular in shape.

**Colour.**— The colour of fresh specimens are brownish green to dark brown (P.K.L. Ng pers. comm.), all preserved specimens examined are dark brown in colour.

**Size.**— The largest male specimen examined is 30.0mm x 26.6mm (ZRC 1965.7.27.159-160), while the largest female specimen examined is 23.3mm x 19.8mm (ZRC uncatalogued).

**Habitat.**— It is found under small rocks and pebbles along river bed in freshwater streams (P.K.L. Ng, pers. comm.).

**Remarks.**— Alphonse Milne-Edwards (1868), de Man (1892), and Holthuis (1978) have all discussed the differences between *G. riedelii* and *G. pilipes* in details like the forms of the carapaces and ambulatory legs. In addition to these characters, *G. riedelii* is different from *G. pilipes* in the structure of the third maxilliped, particularly, the very broad exopod of the third maxilliped, which is 2.0 times broader than ischium (vs. 1.1. times broader in *G. pilipes*), and the presence of the setae on the tips of the fixed fingers (vs. the absence of setae in *G. pilipes*).

The type specimen of *P. andmanica* has been reported to be kept in The Natural History Museum, Calcutta. Attempts to borrow the specimens or examine the specimens (through friends and colleagues who visits the museum) have been unsuccessful. There is  still no response on the whereabouts of  the specimen. Based on the descriptions and figures provided by Alcock (1900, 1902), and my examination of juvenile specimens of *G. riedelii*, I believe that *P. andamanica* is young specimen of *P. reidelii.* Thus, I synonmize *P. andamanica* under *G. riedelii* in this report.

Alphonse Milne Edwards had only syntypes in the MNHN, I hereby choose a male specimen, 23.2mm x 20.4mm (MNHN-3402) collected from Celebes [Sulawesi], Indonesia by M. Riedel, by as the lectotype. The rest of A. Milne-Edwards specimens, comprising of two males and one female (MNHN-3627, dry specimen), collected from Celebes [Sulawesi], Indonesia are designated as paralectotypes.

**Distribution.**— Indonesia and Philippines only.

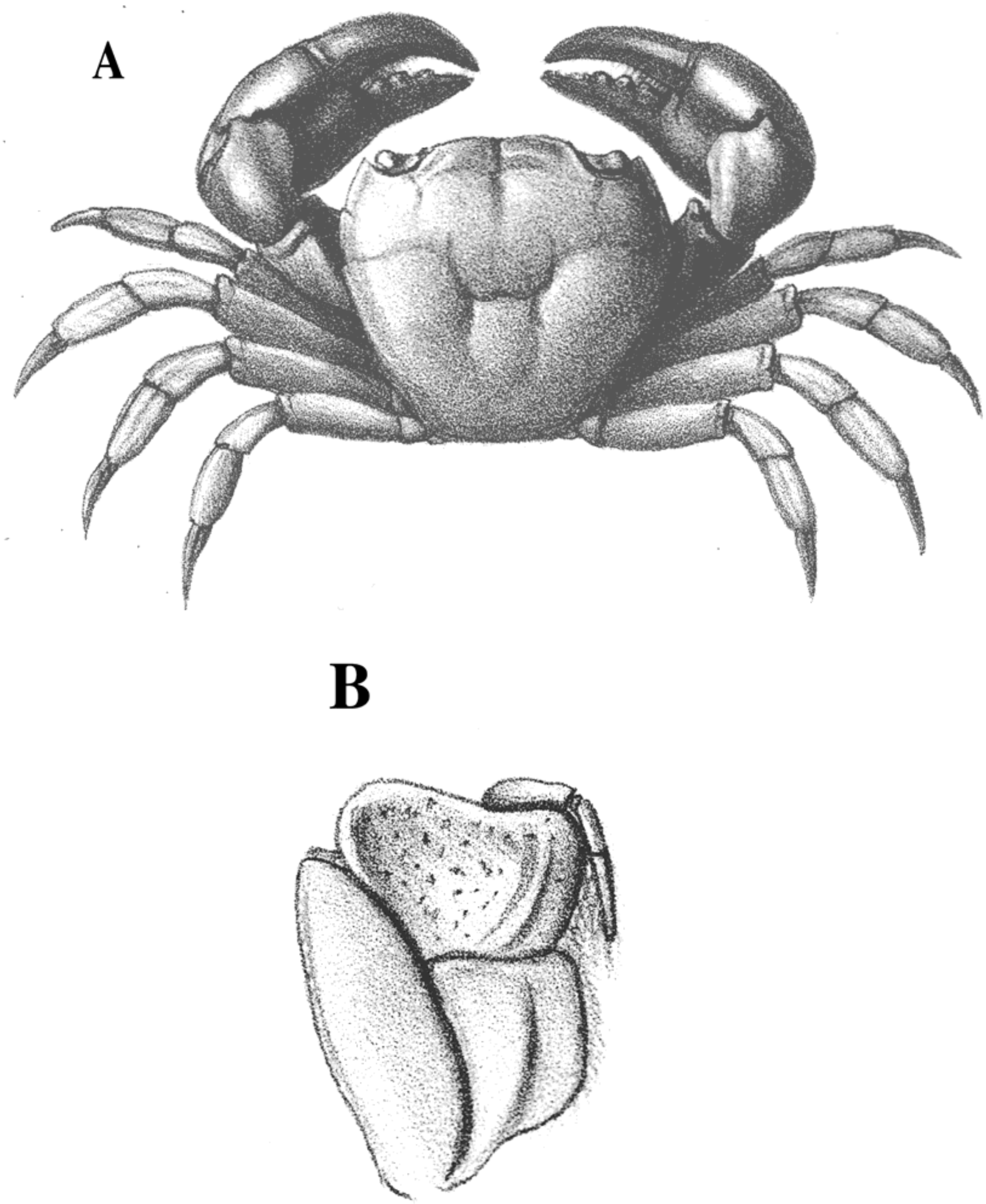



Figure 79. *Gnathograpsus riedelii* A. Milne-Edwards, 1868. A) dorsal view; B) third maxilliped. (After A. Milne-Edwards, 1868).

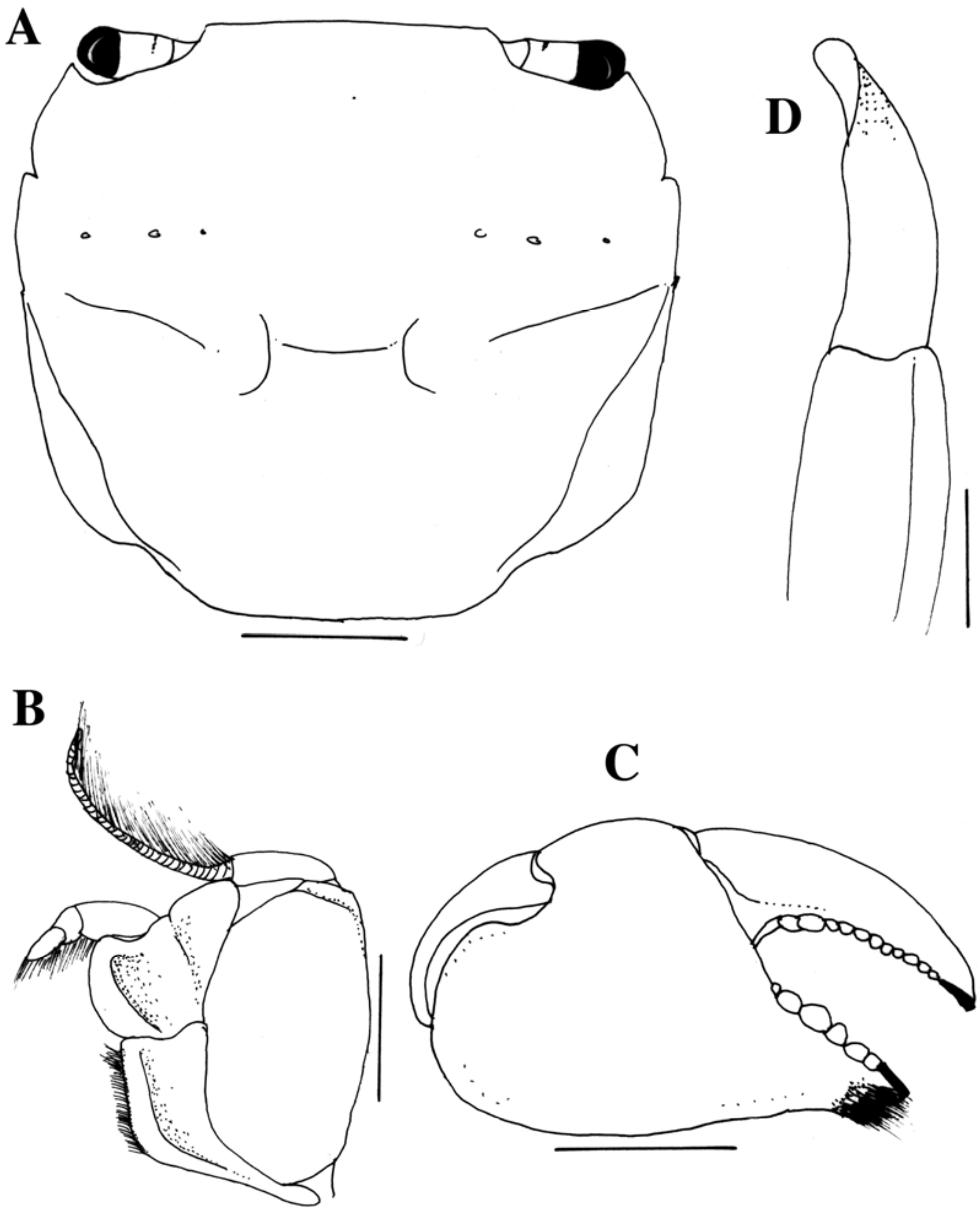



Figure 80. *Gnathograpsus riedelii* A. Milne-Edwards, 1868, male, 13.0mm x 11.8mm) (ZRC-uncatalogued). A) carapace; B) third maxilliped; C) outer view of chela; D) distal end of G1. (Scale=1.0mm).

## *Gnathograpsus setocarpus*, new species

(Figure 81A-C)

*Gnathograpsus riedelii* A. Milne-Edwards, 1868: 182, pl. 27, figs. 1-5 (part) (not *Gnathograpsus riedelii* A. Milne-Edwards, 1868).

**Materials examined.**— **Holotype** – 1 male (34.0mm x 30.0mm) (NMB-622c), Baaguia, Ost (East) Timor, coll. D.A. Buhler, Aug. 1935. – **Paratypes** – 23 males (20.6-33.0mm x 19.2-29.0mm, 7 females (16.8-27.9mm x 15.2-24.4mm) (NMB-622c), Baaguia, Ost (East) Timor, coll. D.A. Buhler, Aug. 1935. – **Others** – 1 male (21.3mm x 18.3mm) (NMB-622a), Fluss bei Buleleng, north Bali, Indonesia, coll. D.E. Stressmann, 1913; 1 male (22.9mm x 19.7mm) (RMNH-2594), Erifeli, Flores, Indonesia, coll. J.G. de Man, & M. Weber; 1 male (18.6mm x 16.8mm), 1 female (16.8mm x 15.3mm) (RMNH-D2077), River Dona by Endeh, Flores, coll. M. Weber; 2 males (14.8-17.4mm x 13.2-15.2mm) (RMNH-D23767), West Flores, coll. J.A.J. Vezhecjen, Apr. 1966; 5 males (17.2-20.0mm x 14.8-17.7mm), 1 female (13.7mm x 11.1mm) (SFM-5287), Solumbara, Flores, coll. Elbert, Sep. 1909; 1 male (23.0mm x 19.6mm), 1 female (21.0mm x18.0mm) (SFM-5255), Taliovcemy, Fambara; 4 males (9.5-24.5mm x 9.0-21.4mm), 1 female (8.4mm x 7.4mm) (ZMA-no cat. number.), river Dona bu Endeh, Flores, coll. Weber, 1888/1889; 4 males (12.0-26.2mm x 11.0-23.4mm), 1 female (20.6mm x 18.1mm), (ZMA-no cat. number), river Ba by Endeh, Flores, no collection date; 4 males (10.3-18.3mm x 9.2-16.3mm), 7 females (6.7-15.4mm x 6.4-13.6mm) (ZMA no cat. number), Indonesia, coll. M. Weber, 1888/1889.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth and flat. Front broad, anterior margin slightly concave medially. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very broad, 2.1 times broader than ischium. Chelipeds large, symmetrical in males, outer-posterior margin of carpus with long soft setae, fingers with a tuft of short setae at the tip of the fixed finger. Ambulatory legs short, flat, margins with rows of very short setae. Telson broadly triangular. G1 slender. Female gonopore with operculum circular in shape.

**Etymology.**— ‘Seto’ is the short form of the Latin ‘Setose”, alluring to the densely setose carpus of the chelipeds. The name is used as a noun in apposition.

**Colour.**— The colour fresh specimens has not been documented, and the colour of all preserved specimens examined is brownish in colour.

**Size.**— The largest male specimen examined is 34.0mm x 30.0mm (holotype), while the largest female specimen examined is 27.9mm x 24.4mm (paratype).

**Habitat.**— The habitat of this species has been recorded, but the author suspects that it is probably found under small rocks and pebbles in the freshwater river beds .

**Remarks.**— This species has always been misidentified as *G. riedelii.* Many of the specimens examined have been mislabeled as *G. riedelii*. This species closely resembles *G. riedelii,* in the external morphology. But closer examination has shown that it can be easily separated from *G. riedelii* by the following features a) the exopod of the third maxilliped is 2.3 times broader than ischium (vs. only 2.0 times in *G. riedelii*), b) the outer distal margin of carpus of chela is fringed is long soft setae (vs. absent in *G. riedelii*), and c) the ambulatory legs are narrower and longer (vs. broader and stouter in *G. riedelii*).

**Distribution.**— Indonesia only.

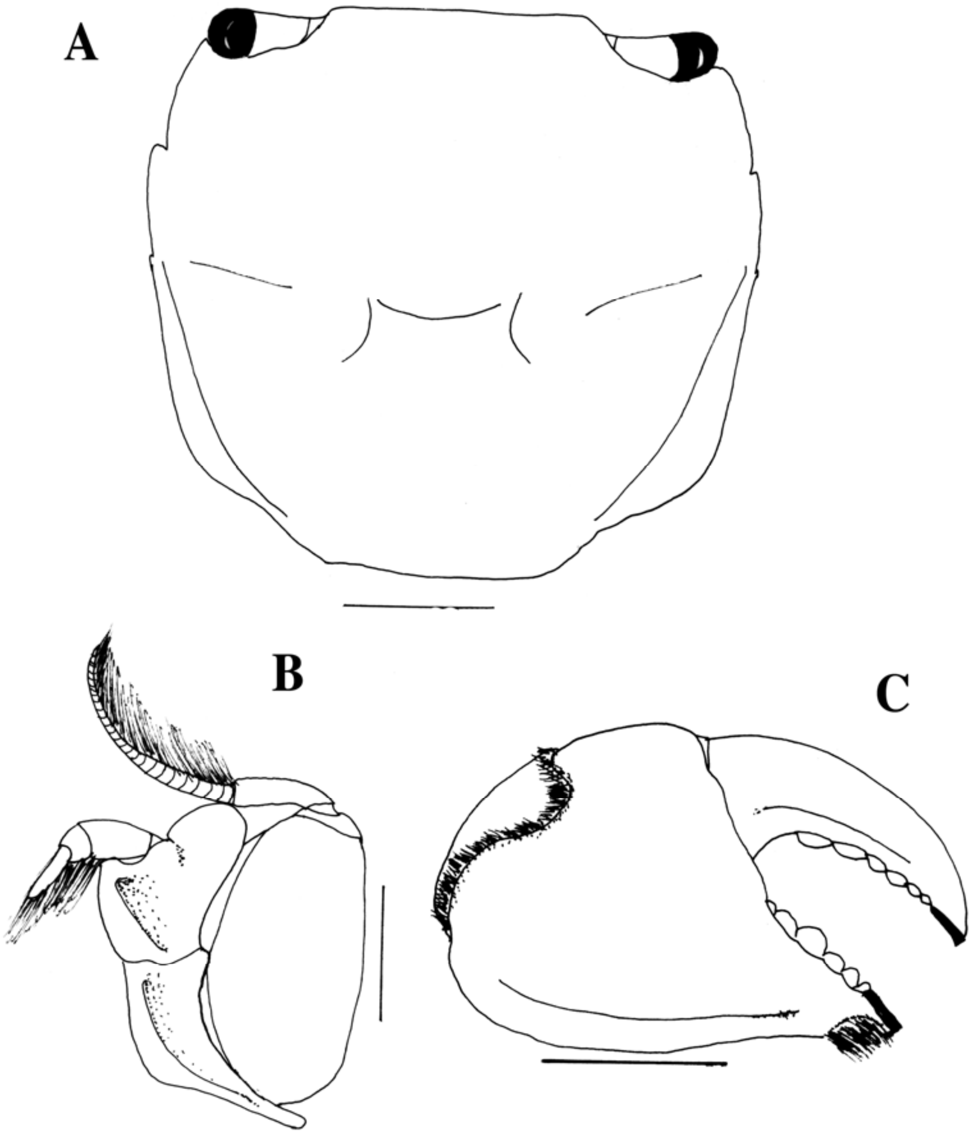



Figure 81. *Gnathograpsus setocarpus* new species, male, holotype, 34.0mm x 30.0mm (NMB-622c) A) carapace; B) third maxilliped; C) outer view of chela. (Scale=1.0mm).

## *Gnathograpsus demani* Roux, 1917

(Figures 82; 83A-E)

*Ptychognathus demani* Roux, 1917: 100.

**Materials examined.**— **Lectotype** – 1 male (17.5mm x 15.9mm) (NMB-673a), Waitjori River, New Guinea, coll. 1916. – **Paralectotype** – 2 males (11.8-25.6mm x 10.7-22.3mm), 3 females (15.3-20.8mm x 13.9-18.3mm) (ZMA-DE-41468), Waitjiri River, New Guniea, leg. New Guinea Expedition, J. Roux, 22 May 1909.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth and flat. Front broad, anterior margin slightly concave medially. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod broad, as broad as ischium. Cheliped large, symmetrical in males, outer outer surface with long, stiff brown setae with some short, soft brown setae at base of fingers. Ambulatory legs slender, flat, margins with stiff brown setae. Telson broadly triangular in shape. G1 slender. Female gonopore with operculum circular in shape.

**Colour.**— The colour fresh specimens has not been documented, and the colour of all the preserved specimens examined is overall brownish in colour, the long, stiff setae are black in colour, while the  long soft setae are brown in colour.

**Size.**— The largest male specimen examined is 25.6mm x 22.3mm (ZMA-DE-41468), while the largest female specimen examined is 20.8mm x 18.3mm (ZMA-DE-41468).

**Habitat.**— There is no documentation on the habitat of this animal, but based on the external morphological features, the species is likely to be found under rocks and pebbles in freshwater streams.

**Remarks.**— This species is very unique. It is very similar to *Pseudograpsus setosus* (Fabricius, 1798) particularly in the form of carapace, and the presence of the long, stiff setae at the base of the fingers. But it is quite different in the following features a) the very broad and convex exopod of the third maxilliped (vs. narrow and slender exopod in *P. setosus*); b) the ischium of third maxilliped is narrow (vs. broad in *P. setosus*); c) the long stiff setae are brown in colour (vs. black in *P. setosus*); d) the presence of soft short setae at the base of the fixed fingers (vs. glabrous in *P. setosus*), and e) the G1 is very long and narrow (vs. broad and stouter in *P. setosus*).

Interestingly, this species has not been reported after its original description.

**Distribution.**— New Guinea only.

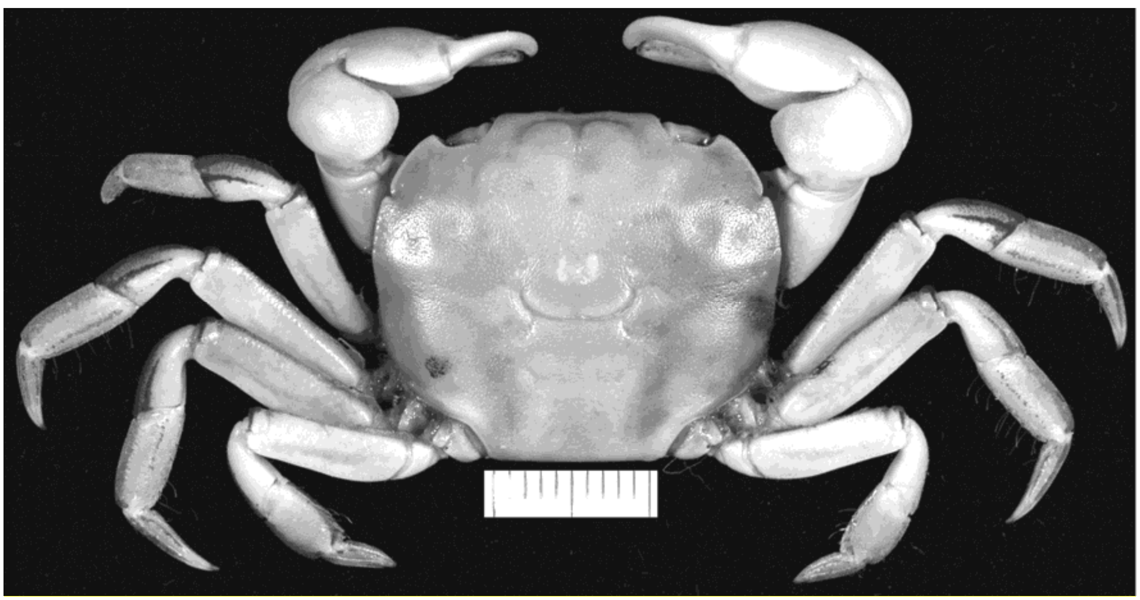


Figure 82. *Gnathograpsus demani* Roux, 1917, male, lectotype, 17.5mm x 15.9mm (NMB-673a). Dorsal view.

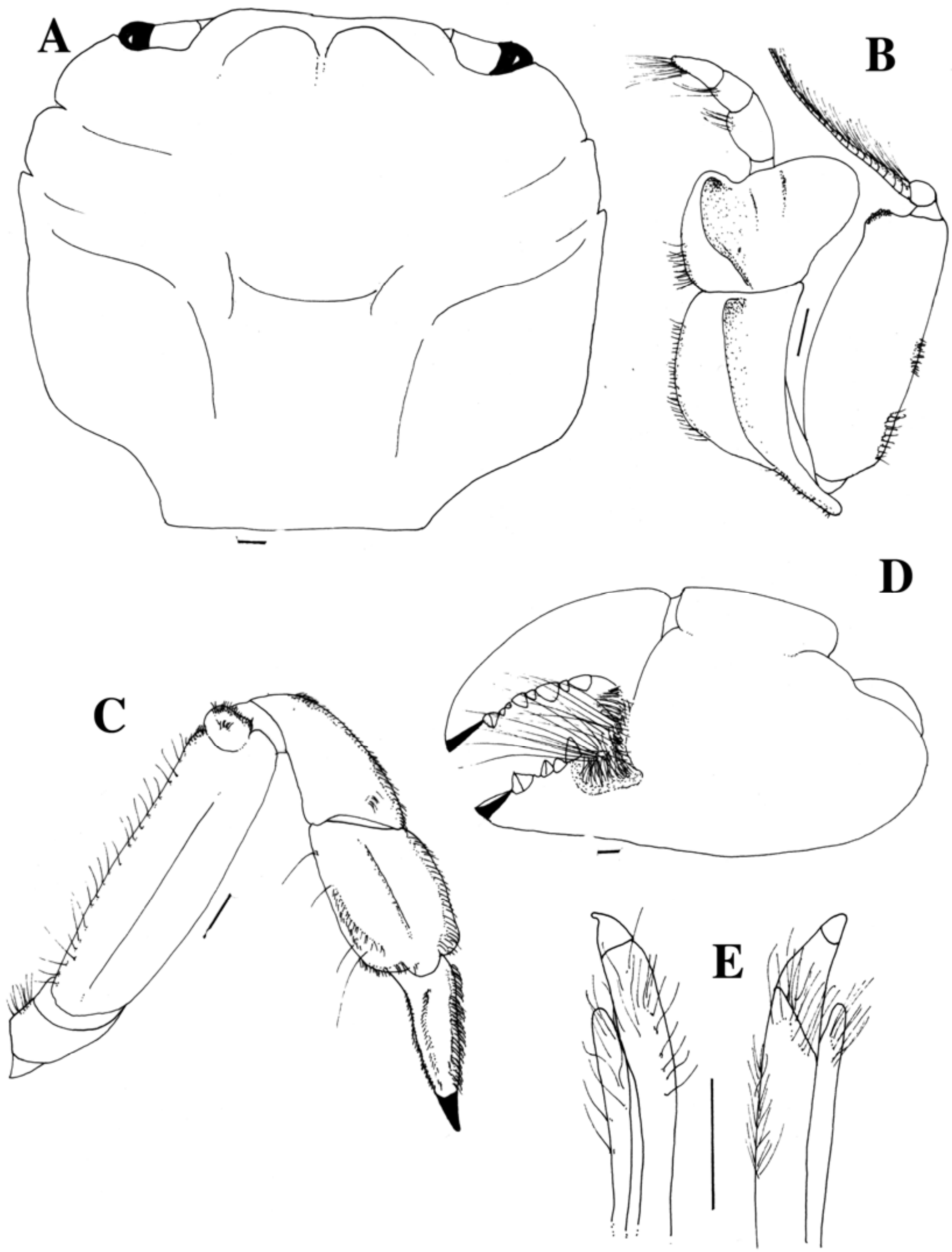



Figure 83. *Gnathograpsus demani* Roux, 1917, male, lectotype, 17.5mm x 15.9mm (NMB-673a). A) carapace; B) third maxilliped; C) last ambulatory leg; D) outer view of chela; E) distal end of G1. (Scale=1.0mm).

## *Gnathograpsus pilosus* (de Man, 1892), new combination

(Figures 84; 85A-D)

*Ptychognathus Riedelii* var. *pilosa* de Man, 1892: 323.

*Ptychognathus pilosus* –Holthuis, 1978: 17; Fransen *et al.*, 1997: 127.

**Materials examined.— Lectotype –** 1 male (16.0mm x 14.1mm) (RMNH-D12595), River by Rea, Flores, Indonesia, coll. M. Weber, 1888. – **Paralectotypes** – 2 males (17.5-18.7mm x 15.2-16.2), 2 females (11.6-12.3mm x 10.6-10.8mm) (NMB-988a), no collection data; (mislabeled as syntype of *P. dentatus*) 8 males (6.7-17.2mm x 6.6-15.2mm) (ZMA-DE-102584), river near Reo, Flores, Indonesia, leg. M. Weber, 1888. – **Others –** 1 male (14.8mm x 13.3mm) (RMNH-1232), river by Rea, Flores, coll. M. Weber, no collection date; 2 males (12.1-15.5mm x 10.5-13.5mm) (ZMA- no cat. number), Station 131, coll. Siboga Expedition, no collection date; 1 male (7.8mm x 5.9mm) (SFM-5252), Bacton, Celebes, leg. Elbert, 1909.

**Diagnosis.—** Carapace subquadrate, distinctly broader than long, dorsal surface smooth. Front broad, anterior margin slightly concave medially. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very broad, 2.2 times broader than ischium. Cheliped large, symmetrical, larger in males, fingers with a tift of setae on outer surface of pollex, manus in addition to a small tuft of short, bristle at the tip of pollex. Ambulatory legs long, flat, anterior margins setose. Telson long. G1 long, slender. Female gonopore small.

**Colour.—** The colour fresh specimens has not been documented, and the colour of all preserved specimens examined (RMNH-D12595) is light brown in colour.

**Size.—** The largest male specimen examined is 16.0mm x 14.1mm (holotype), while the largest female specimen examined is  12.3mm x 10.8mm (paratype).

**Habitat.—** The habitat of this species has not been documented.

**Remarks.**— de Man (1892) had given a comprehensive discussion on *P. riedelii*. In addition, he also provided a short note on what he considered was a new form of *Ptychognathus riedelii*, variety *pilosa*, stating that the juvenile individuals that represent this variety were probably collected at the same time from the same locality as *P. dentatus*. Holthuis (1978) briefly stated that these juveniles belong to de Man's 'subspecies' of *Ptychognathus riedelii*. He did also added that he would referred to this subspecies as *P. pilosa* for easy reference and convenience. These specimens, in addition to small tuft of setae at the tips of the cheliped fingers, also have tufts of setae present on the outer surface of the cheliped, which is distinctly different from *Ptychognathus riedelii*, and hence, I raise this taxa to a full species level.

I examined the type material of *P. pilosus* (RMNH-D-12595) as well as the materials found in Amsterdam labeled as the type materials of *P. dentatus* (ZMA-DE-102584). The two lots of specimens are identical even though they have labels. Both series of specimens have the little tuft of short bristle-like setae at the tip of the pollex, in addition to the tufts on long soft setae on the outer surface of the chela. In addition, the exopods of the third maxillipeds are broad, 2.2 times broader than ischium. Both species have a long telson of the male abdomen, and the anterior margins of the ambulatory legs are all setose. There is a problem with the real identity 'supposed types' of *P. dentatus* in Amsterdam.

The description of *P. dentatus* given by de Man (1892) is totally different from the type specimens (ZMA-DE-102584). In addition to having the broad exopod of the third maxilliped, the other key character is the presence of the thick pelt of soft long setae on the inner surface of the chela (de Man, 1892: 320, p. 3). The label with the specimens is labeled as "river near Reo, Flores, Indonesia, leg. M. Weber, 1888". The type locality of of *P. dentatus* was given as Celebes by de Man (1892: 318). As such, the material labeled as '*P. dentatus* syntypes' in Amsterdam with the catalogue number, ZMA-DE-102584, cannot be the types of *P. dentatus*, but belong to those of *P. pilosus* instead. It is possible that label has been written wrongly or the specimens have been mixed up.

*Gnathograpsus pilosus* is distinct from *P. dentatus* in several ways, viz. a) the exopod of the third maxillipeds is 2.2 times broader than ischium (vs. 2.0 in *P. dentatus*); b) the elongated telson (vs.broad telson in in *P. dentatus*); c) the relatively long and slightly curved fingers (vs. shorter and almost straight fingers in *P. dentatus*); d) presence of setae on the outer surface of pollex and manus (vs. glabrous in *P. dentatus*, even for very young specimens); e) the long ambulatory legs (vs. broad short ambulartory legs in *P. dentatus*); f) the anterior margins of ambulatory legs are covered with long setae (vs. covered with very short bristle-like setae in *P. dentatus*); and g) the G1 is proportionately more slender (vs. broader in *P. dentatus*).

**Distribution.**— Indonesia only.

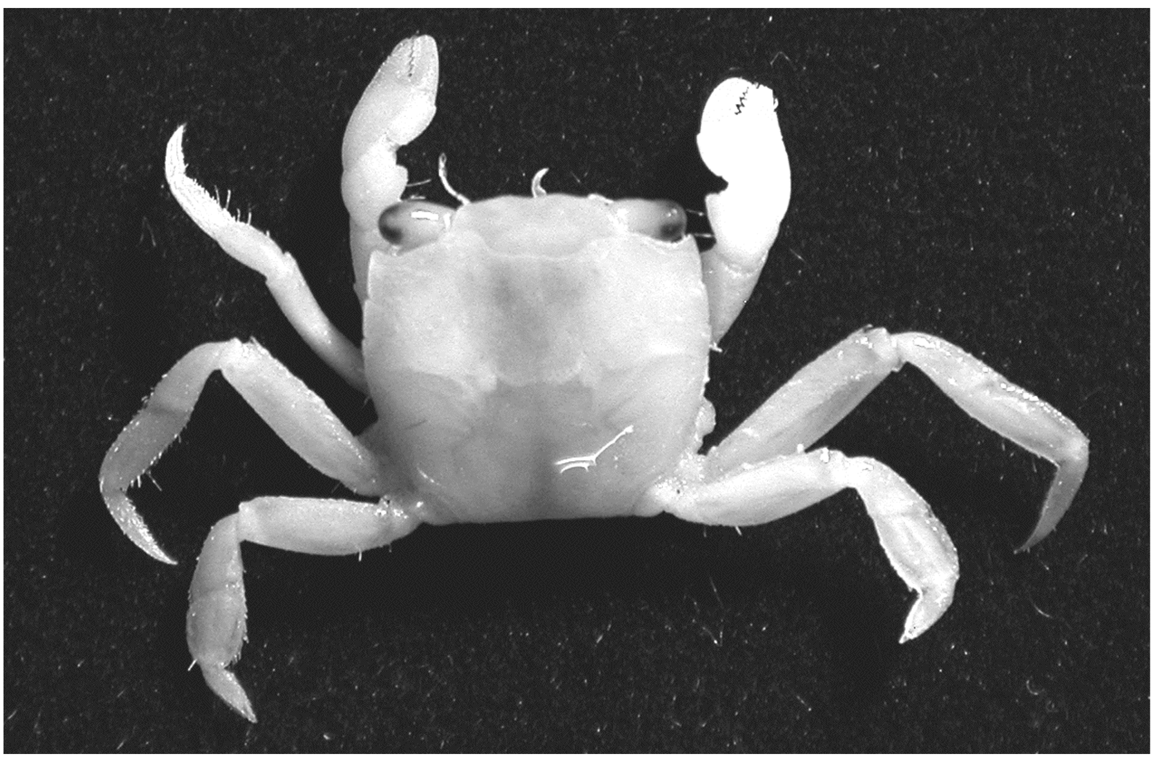


Figure 84. *Gnathograpsus pilosus* de Man, 1892**,** lectotype, 16.0mm x 14.1mm (RMNH-D12595). Dorsal view.

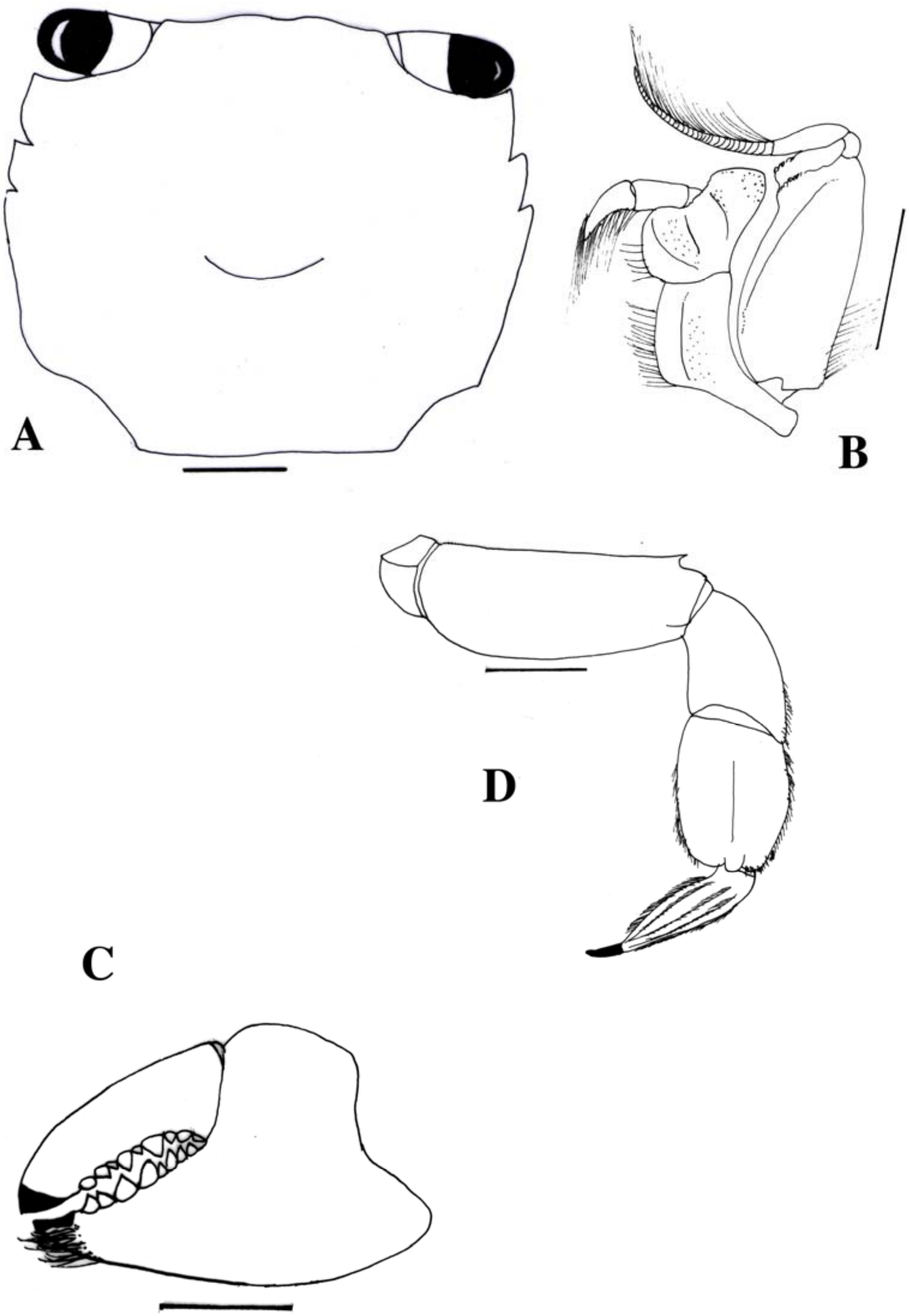



Figure 85. *Gnathograpsus pilosus* de Man, 1892**,** lectotype, 16.0mm x 14.1mm (RMNH-D12595). A) carapace; B) third maxilliped; C) outer view of chela; D) last ambulatory leg. (Scale=1.0mm).

### *Gnathograpsus intermedius* (de Man, 1879), new combination

(Figures 86A-C; 87A-E)

*Ptychognathus intermedius* de Man, 1879: 69; 1892: 322, pl. 19; Ortmann, 1894: 711; Tesch, 1918: 88; Fransen *et al.*, 1997: 127.

**Materials examined.— Lectotype** – 1 male (27.5mm x 23.8mm) (RMNH-197), Molukken (Molluccas), coll. H.L. Mahlot, no collection date. – **Paralectotype** – 1 male (25.6mm x 21.8mm) (RMNH-197), Molukken (Molluccas), coll. H.L. Mahlot, no collection date. – **Others** – **French Polynesia** – 4 males (9.6-11.2mm x 8.6-9.3mm), 1 female (ovigerous) (6.9mm x 6.0mm) (MNHN-no cat. number), Tahiti island, French Polynesia, coll. J. Poupin, Apr. 1995; 6 males (9.2-15.8mm x 8.7-13.8mm) (MNHN), Tahiti island, French Polynesia, coll. J. Poupin, Apr. 1995.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth and flat. Front broad, anterior margin slightly concave medially. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod broad, 1.7 times broader than ischium. Cheliped large, symmetrical in males, outer surface of palm with flat rounded granules, fingers glabrous. Ambulatory legs short, flat, margins densely setose especially at posterior margins of propodus, dactylus; propodus of last ambulatory very broad, almost squarish in shape. Telosn broadly triangular in shape. G1 very long, slender. Female gonopore operculate, circular, small.

**Colour.**— The colour fresh specimens has not been documented, and the colour of all the preserved specimens examined is brownish in colour.

**Size.**— The largest male specimen examined is 27.5mm x 23.8mm (holotype), while the female size unknown as there is no documentation of female specimen.

**Habitat.**— The habitat of this species has not been recorded.

**Remarks.**— The species has been collected from Molluccas, and has never been collected from that locality again thereafter. It has also been found in Tahiti. There is no record of any female specimen.

**Distribution.**— Indonesia (Molluccas) and French Polynesia (Tahiti).

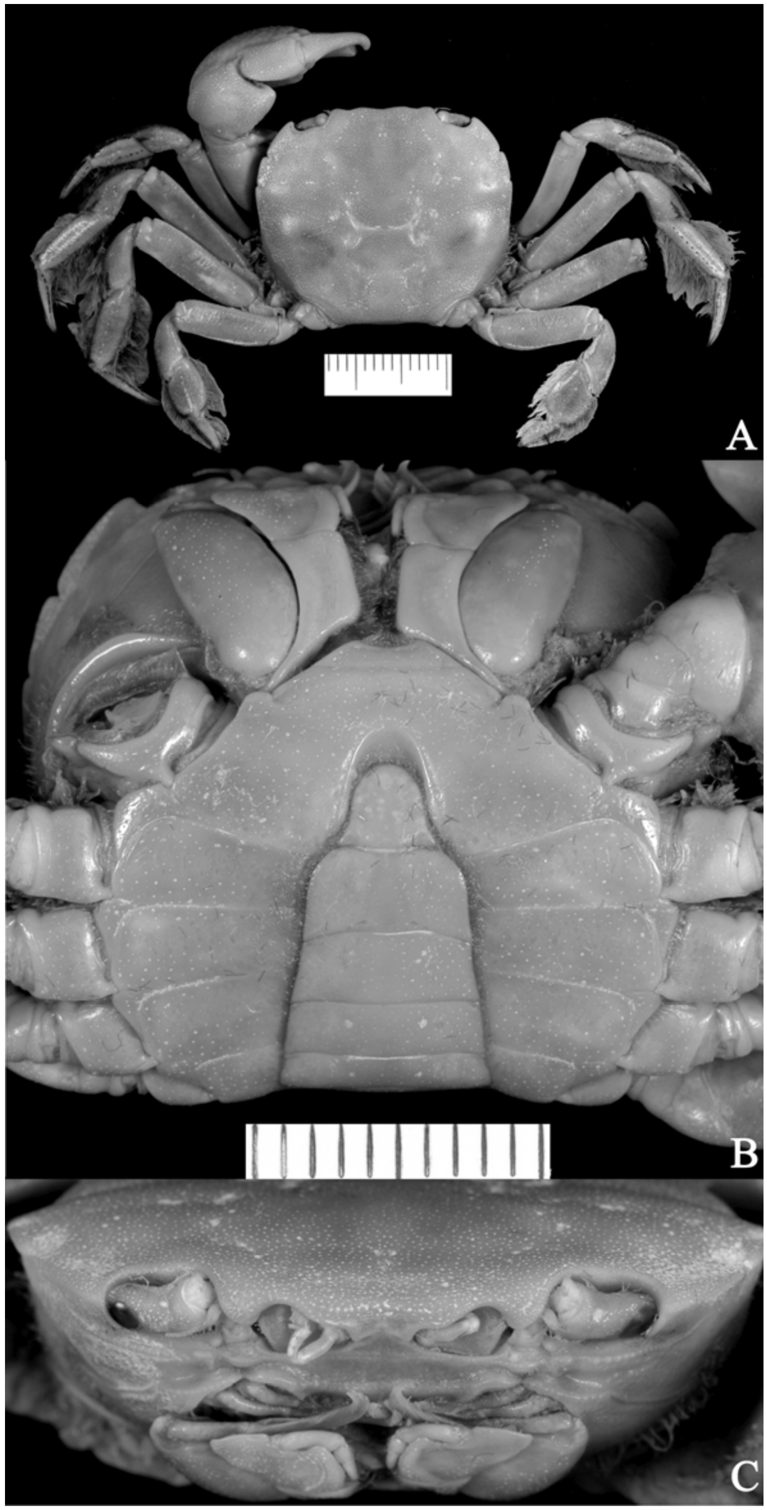



Figure 86. *Gnathograpsus intermedius* de Man, 1879, male, 27.5mm x 23.8mm (RMNH-197). A) dorsal surface; B) ventral surface; C) frontal view.

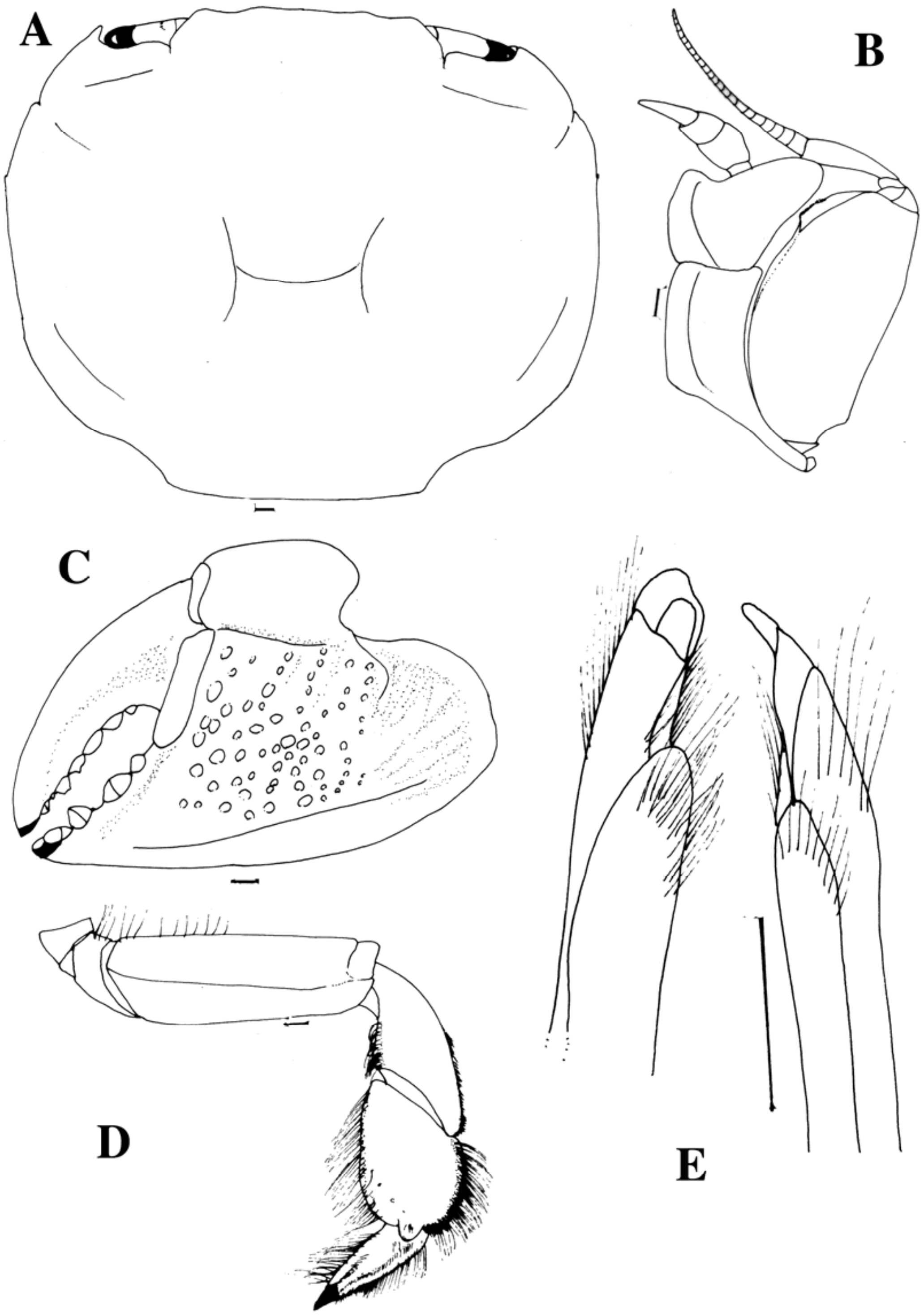



Figure 87. *Gnathograpsus intermedius* de Man, 1879, male, 27.5mm x 23.8mm (RMNH-197). A) carapace; B) third maxilliped; C) outer view of chela; D) last ambulatory leg; E) distal ends of G1. (Scale=1.0mm).

## Genus *Mitragrapsus*, new genus

*Ptychognathus* – de Ma, 1892: 15; de Man, 1887: 719; Ortmann, 1894: 683; de Man, 1895: 90; Alcock, 1900: 402; Stimpson, 1907: 129, pl. 7, fig. 5, 5a; Rathbun, 1914: 69; Tesch, 1918: 85; Finnegan, 1931: 549; Crosnier, 1965: 37; Serène & Moosa, 1971: 7, pl. 3, figs. A, B; Minei, 1972: 49, figs. 1, 2; Crosnier, 1975: 738; Hartnoll, 1975: 305; Nakasone, 1977: 62; Miyake, 1983: 237; Shokita, 1989: table 1, fig. 2; Shokita, 1990: Table 3; Poupin, 1996a: 69, 77, 78; Fransen *et al.*, 1997: 127; Nomoto *et al.*, 1999: 5, pl. 1, fig. 1; Kishino & Wada, 2001: 59; Marumura & Kosaka, 2003: 64; Kishino *et al.*, 2001: 127; Naruse, 2005: 223; Naruse *et al.*, 2005: 69 (All part).

*Varuna* – Rathbun, 1914: 69 (not *Varuna* H. Milne Edwards, 1830).

**Type species.**— *Ptychognathus dentatus* de Man, 1892, by current designation.

**Gender.**— Masculine.

**Diagnosis**.— Carapace subquadrate, distinctly broader than long; dorsal surface glabrous, punctate; regions well defined, flat, epigastric cristae not distinct. Frontal margin produced, straight. Anterolateral margin subcristate with three teeth including orbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly subparallel. Orbits small, eyes completely filling orbit. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum, broader than ischium. Epistome broad, flat, posterior margin entire. Chela with or without setae, fingers usually longer palm. Ambulatory legs with short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular in shape with seven moveable segments (six somites plus telson).

**Etymology.—** In the Vedic hymns, ‘Varuna’ is the Lord of the cosmic rhythm of the celestial spheres, while ‘Mitra’ brings forth the light at dawn, which was covered by ‘Varuna’ (Singh, 1998). ‘Mitra’ is often associated with ‘Varuna’, so that the two are combined as ‘Mitra-Varuna’. ‘Mitra’ is used as a prefix to ‘Grapsus’ alluring to the close affinity of the carapace form to *Varuna*, and its affinity with the grapsoid crab.

**Remarks.**— All the included species in this new genus have a broad and swollen exopod of the third maxilliped and two anterolateral teeth after the orbital tooth. In addition, these species are very closely resemble members of the genus *Varuna* in their external morphology. Due to this great similarity, Rathbun (1914) had in fact transferred them to the genus *Varuna* when she described *V. altimanus* Rathbun, 1914. She justified her action but she had ignored the key character of the exopod of the third maxillipeds. Tesch (1918) subsequently transferred these species back to the genus *Ptychognathus* on basis of their very convex, broad exopod of the third maxilliped.

The genus is distinctly different from *Ptychognathus* sensu stricto in the following characters viz. a) a proportionately broader carapace (vs. narrower carapace in *Ptychognathus*); b) there are three anterolateral teeth including the orbital tooth (vs. only two in *Ptychognathus*); c) the chela is usually long and slender (vs. broader chela in *Ptychognathus*); d) the ambulatory legs are less setose (vs. very setose ambulatory legs in *Ptychognathus*), and e) the ischium of the third maxilliped is narrower (vs. broader in *Ptychognathus*).

As noted, while the new genus is superficially very similar to *Varuna*, it can nevertheless be easily discerned by the following features a) the carapace is slightly broader than long (vs. distinctly broader than long in *Varuna*); b) the anterolateral margin of carapace not vaulted upwards (vs. vaulted upwards in *Varuna*); c) the merus of the third maxilliped foliaceous (vs. non foliaceous merus in *Varuna*); d) the exopod of the third maxilliped very broad and convex (vs. narrow and flat exopod in *Varuna*); d) the ischium of the third maxiliped narrow (vs. broad ischium in *Varuna*), and e) the presence of only one spine on the carpus of the chelae (vs. presence of one strong and small weak spines in *Varuna*).

As defined here, the new genus comprises seven species viz. *M. dentatus* (de Man, 1892) [type species]; *M. spinicarpus* (Ortmann, 1894); *M. onyx* (Alcock, 1900);

*M. polleni* (de Man, 1895)*; M. affinis* (de Man, 1895); *M. altimanus* (Rathbun, 1914) and *M. crassimanus* (Finnegan, 1931).

**Key to species in *Mitragrapsus***

1a. Carapace subquadrate, surface punctate. Chela setose. --------------------------- **2**

1b. Carapace subquadrate, surface glabrous. Chela glabrous. ------------------------ **3**

2a. Chela with setae on the outer surface, near base of pollex. Exopod of third maxilliped 2.3 times broader than ischium. --------------------------------- ***M. onyx***

2b. Chela with setae on inner surface. Exopod of third maxilliped 2.3 times broader than ischium. --------------------------------------------------------------------- ***M. dentatus***

3a. Chela glabrous, with granules on outer and inner surfaces, carpus with a very strong, sharp spine. -------------------------------------------------------------- ***M. spinicarpus***

3b. Chela glabrous, surface smooth, carpus with a weak, blunt spine. ------------ **4**

4a. Chela with weak spine. Exopod of third maxilliped about 1.5 times as broad as ischium. -------------------------------------------------------------------------- **5**

4b. Chela with weak spine. Exopod of third maxilliped about 1.2 times as broad as ischium. ----------------------------------------------------------------------------- **6**

5a. Exopod of third maxilliped 1.5 times as broad as ischium. Ambulatory legs long, slender. ------------------------------------------------------------------- ***M. polleni***

5b. Exopod of third maxilliped 1.6 times as broad as ischium. Ambulatory legs broad, stout. --------------------------------------------------------------- ***M. altimanus***

6a. Expod of third maxilliped 1.2 times as broad as ischium. Ambulatory legs long, slender. ------------------------------------------------------------------ ***M. affinis***

6b. Expod of third maxilliped 1.1 times as broad as ischium. Ambulatory legs broad, stout. --------------------------------------------------------------- ***M. crassimanus***

**_Mitragrapsus dentatus_ (de Man, 1892), new combination**

(Figures 88A-C; 89A-C)

*Ptychognathus dentatus* de Man, 1892: 318, pl. 18, fig. 9; Alcock, 1900: 403; Fransen *et al.*, 1997: 127.

**Materials examined.— Lectotype** – 1 male (34.3mm x 32.5mm), (RMNH-D2593), Lupa Lupa River, Celebes, coll. J.G. de Man, October, 1888, received on 26 Apr. 1930. – **Paralectotypes** – 2 males (31.3-36.4mm x 29.6-34.4mm) (ZMA- no cat. number), River Lupa-Lupa, near Tempe, Celebes, Indonesia, coll. M. Weber, 1888. – **Others** – **Indonesia** –2 males (16.3-24.0mm x 14.5-21.6mm) (ZMA-no cat. number), no collection data; 3 males (16.3-24.0mm x 14.5-21.6mm), 2 females (19.9-21.4mm x 18.0-18.3mm), (ZMA-no cat. number), no collection data. **– New Guinea** – 1 female (ovigerous) (28.9mm x 25.5mm) (NMB-674a), Meranke, New Guinea, don. Museum Amsterdam, ca. 1916; 2 males (35.9-36.8mm x 32.7-33.0mm), 2 females (28.3-35.4mm x 25.8-31.9mm) (ZMA-no cat. number), Meranke, New Guinea, coll. Koch, 1905. – **Philippines** – 1 female (15.1mm x 14.0mm) (USMN-47975), Cattabato, Mindanao, Phililppines, coll. Janyeon, 26 Oct. 1903; 3 males (13.3-29.3mm x 12.6-27.9mm) (USNM-73156), Ilo-Ilo, Panay Island, Philippines, coll. H.C. Hellens, 15 Mar. 1929.

**Diagnosis.**— Carapace subquadrate, distinctly broader than long, dorsal surface smooth, flat. Front produced, broad, anterior margin straight. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very broad, 2.3 times broader than ischium. Cheliped large, symmetrical, larger in males, fingers with setae only on inner surface, a short spine on carpus of cheliped. Ambulatory legs short, flat, margins densely setose. Telson broadly triangular. G1 slender. Female gonopore with rounded operculum.

**Colour.**— The colour of fresh specimens has not been documented, but all the preserved specimens examined are light brown in colour.

**Size.**— This is a large-sized species, the largest male specimen examined is 36.8mm x 34.4mm (ZMA-no cat. number), while the largest female specimens examined is 35.4mm x 31.9mm (ZMA-no cat. number).

**Habitat.**— This species can be found under rock and pebbles by freshwater river mouths or along the river banks (Alcock, 1900).

**Remarks.**— This species strongly resembles *Varuna litterata* and *V. yui* but it can be distinguished from these two species by the following features: a) the anterolateral margin of the carapace is not vaulted upwards (vs. strongly vaulted upwards in *V. litterata* and weakly vaulted in *Varuna yui*); b) the presence of the very broad and swollen exopod of third maxillipeds (vs. narrow and flat exopod of third maxilliped in *V. litterata* and *V. yui*); c) the presence of a very narrow ischium of the third maxilliped (vs. broad and stout ischium in *V. litterata* and *V. yui*); d) the presence of a strong spine on the carpus of the chela (vs. a weaker spine in *V. litterata* and *V. yui*); e) the presence of setae on the inner surface of the chela (vs. glabrous in *V. litterata* and *V. yui*); f) possesson of a very long and slender G1 (vs. broader and stouter G1 in *V. litterata* and *V. yui*), and g) the female gonopore very small (vs. larger female gonopore in *V. litterata* and *V. yui*).

*Mitragrapsus dentatus* is unique in having the tuft of setae on the inner surface of the chela, while in the other species, the tufts of setae are either on the outer surface or both inner and outer surfaces are glabrous. This species is also rare as there are not many specimens in the various museums.

**Distribution.**— India, Indonesia, Philippines, New Guinea.

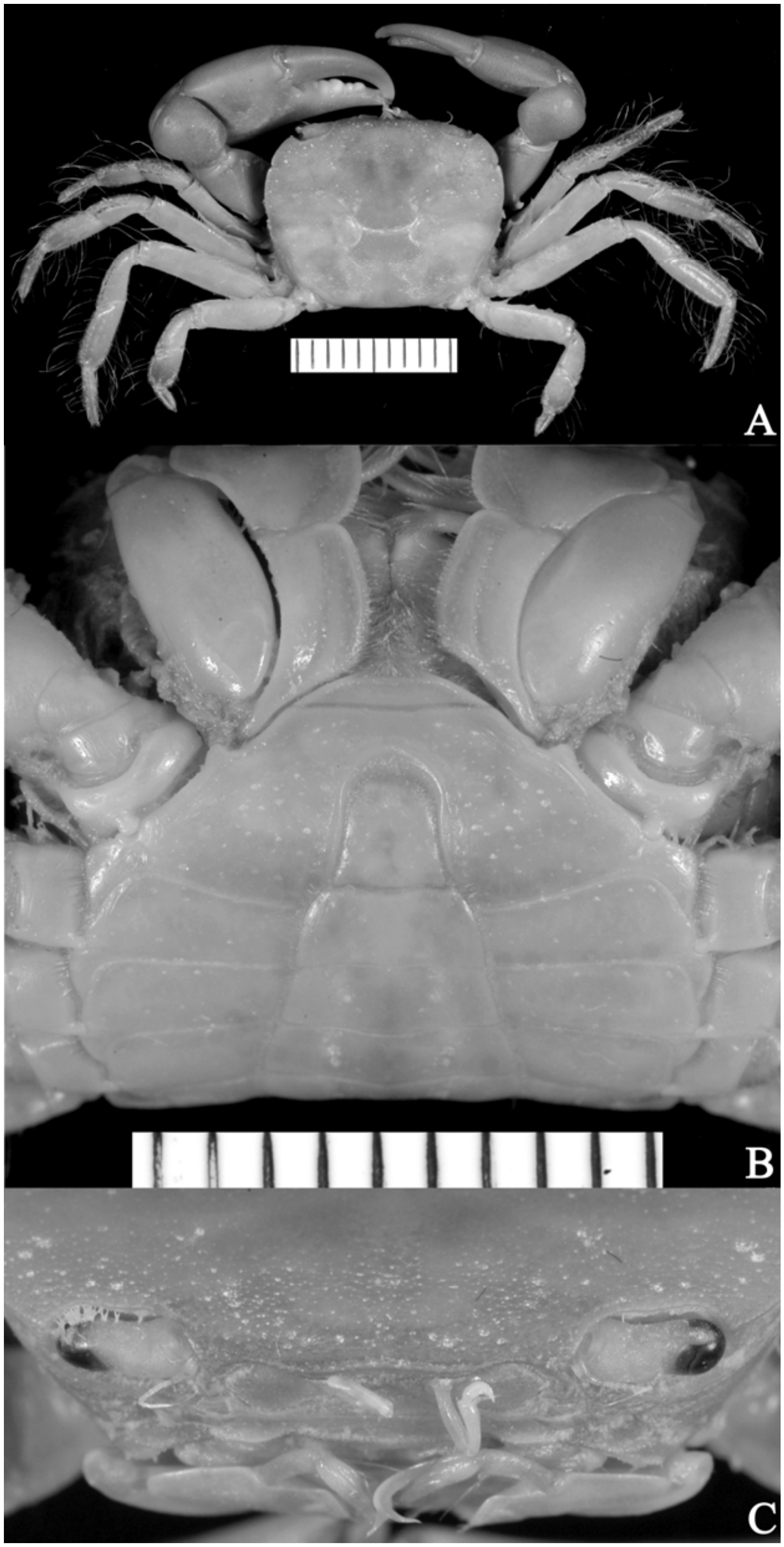



Figure 88. *Mitragrapsus dentatus* de Man, 1892, male, lectotype, 34.3mm x 32.5mm (RMNH-D2593). A) dorsal view; B) ventral view; C) frontal view.

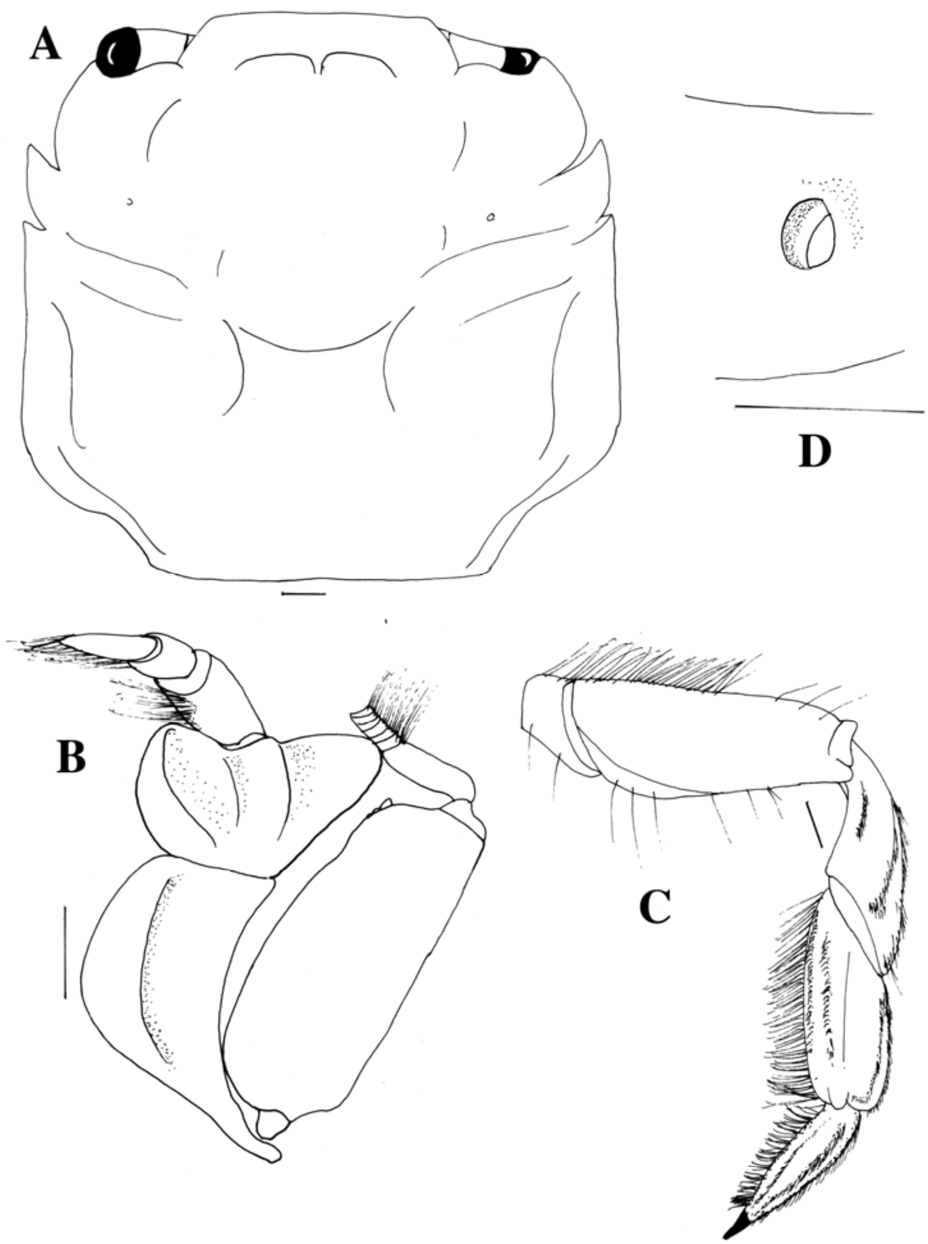



Figure 89. *Mitragrapsus dentatus* de Man, 1892, male, lectotype, 34.3mm x 32.5mm (RMNH-D2593); female, 15.1mm x 14.0mm (USMN-47975). A) carapace; B) third maxilliped; C) last ambulatory leg. (Scale=1.0mm).

### *Mitragrapsus spinicarpus* (Ortmann, 1894), new combination

(Figures 90; 91A-C)

*Ptychognathus spinicarpus* Ortmann, 1894: 711, Pl. 23, fig. 13, 13i; Tesch, 1918: 86.

**Materials examined.**— **Indonesia** – 1 male (25.1mm x 23.3mm) (SFM-5266), Soembara, Bagne, Flores, Sunda Islands group, coll. 1909. – **Philippines** – 11 males (12.0-23.9mm x 10.8-20.8mm), 3 females (14.7-15.9mm x 13.0-15.2mm), (USNM-44659), Nato River, East Coast of Luzon, Philippines, coll. *Albatross*, 18 Jul. 1909; 1 male (6.8mm x 5.9mm), 1 female (9.9mm x 9.4mm) (USNM-44594), Luong River, 3 miles up the river, Luzon River, Philippines, coll. E.A. Mearus, no collection date; 1 female (14.9mm x 14.3mm) (USNM-73754), Siaton River, Negros, Philippines, coll. D. Hart, no collection date. – **Taiwan** – 1 male (6.9mm x 6.3mm) (USNM-57471), Shyojo, Formosa, coll. M. Oshima, Jan. 1923.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth, flat. Front produced, broad, anterior margin straight. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very broad, 1.7 times as broad as ischium. Cheliped very large, carpus with a very strong spine, symmetrical in males, fingers surfaces glabrous. Ambulatory legs short, flat, margins setose.

**Colour.**— The colour of fresh specimens has not been documented, and all the preserved specimens examined are brownish in colour.

**Size.**— The largest male specimen examined is 25.1mm x 23.3mm (SFM-5266), while the largest female specimen examined is 15.9mm x 15.2mm (USNM-44659).

**Habitat.**— It is found under small rocks and pebbles along river banks and river mouths (Tesch, 1918).

**Remarks.**— This species is very similar to *V. litterata* and *V. yui* in overall morphology, but it can be easily discerned from the latter two species by the characters listed above. This species is also characterized by the presence of a very long, strong spine on the carpus of the chela. This spine is very much longer and stronger than any of the species in this genus, and *Varuna*.

I have not been able to locate and examine the type specimen of this species, but the specimens examined so far have fitted the description provided by Ortmann (1894).

This is not a commonly seen species.

**Distribution.**— Indonesia, Philippines, Taiwan.

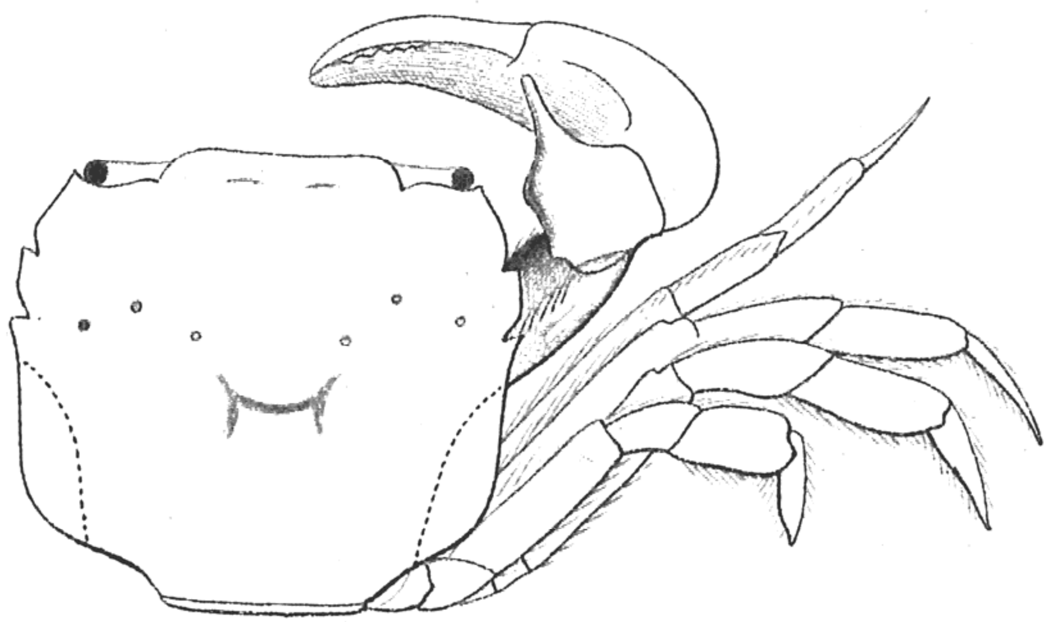


Figure 90. *Mitragrapsus spinicarpus* (Ortmann, 1894). Dorsal view. (After Ortmann, 1894).

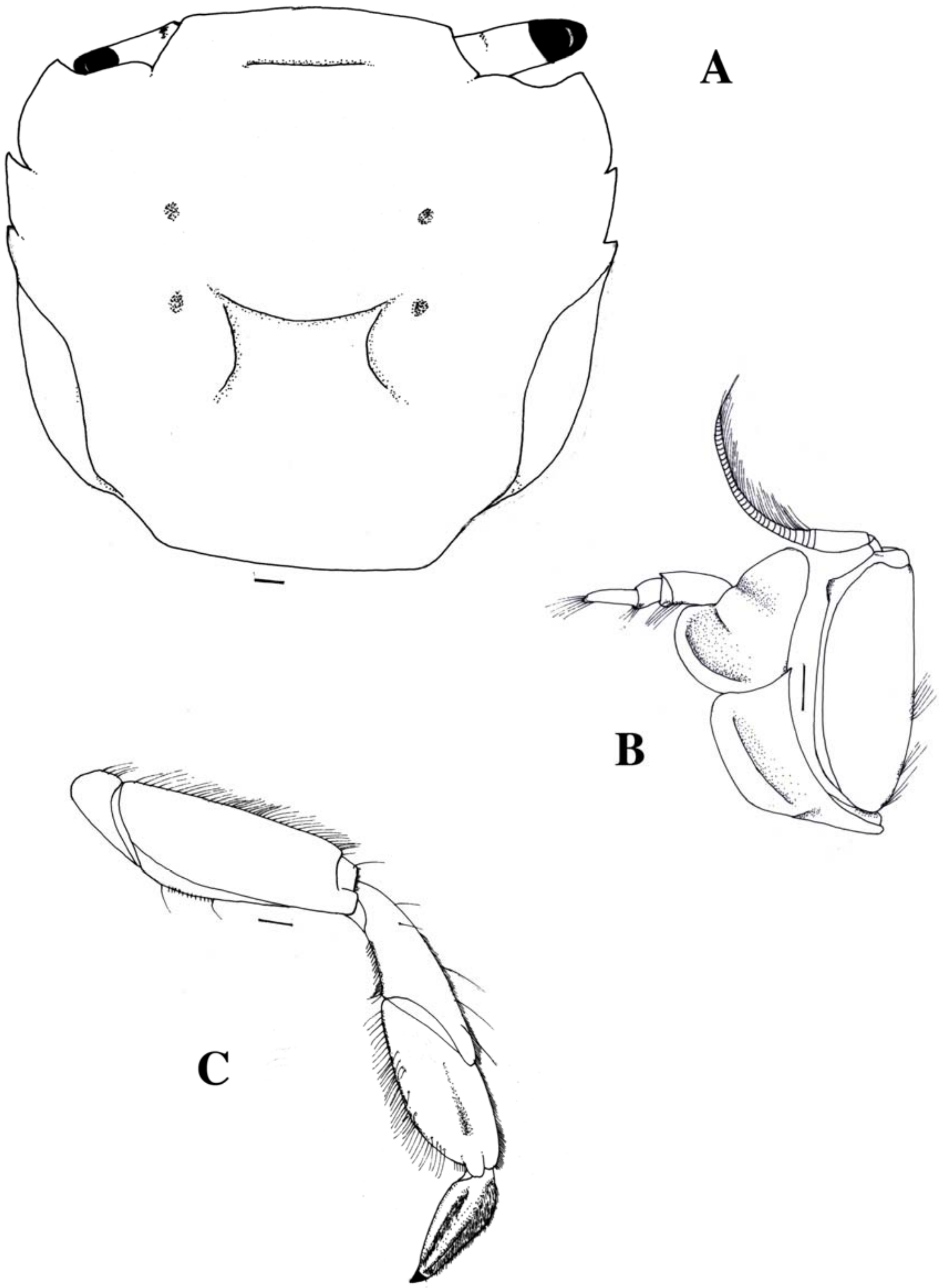



Figure 91. *Mitragrapsus spinicarpus* (Ortmann, 1894), male, 23.9mm x 20.8mm (USNM-44659). A) carapace; B) third maxilliped; C) last ambulatory leg. (Scale=1.0mm).

## *Mitragrapsus altimanus* (Rathbun, 1914), new combination

(Figure 92A-F)

*Varuna altimanus* Rathbun, 1914: 70.

*Ptychognathus altimanus* – Tesch, 1918: 88, pl. 4, fig. 5; Serène & Moosa, 1971: 7, Pl. 3, Figs. A, B; Minei, 1972: 49, figs. 1, 2; Nakasone, 1977: 62; Miyake, 1983: 237; Shokita, 1989: table 1, fig. 2; Shokita, 1990: Table 3; Nomoto *et al.*, 1999: 5, pl. 1, fig. 1; Kishino & Wada, 2001: 59; Marumura & Kosaka, 2003: 64; Kishino *et al.*, 2001: 127; Naruse, 2005: 223; Naruse *et al.*, 2005: 69.

**Materials examined.**— **Holotype** – 1 male (21.3mm x 20.9mm) (USNM-44558), Pt. Jamalo, Luzon, Philippines, coll. 13 Jul. 1908. – **Others** – **Indonesia** – 8 males (11.5-18.3mm x 11.0-17.0mm), 8 females (9.8-19.6mm x 9.4-19.5mm) (USNM-75863), Benkulen, Sumatra, Indonesia, coll. H.C. Kelless, 17 Dec. 1925. – **Philippines** – 2 males (10.7-16.6mm x 10.4-16.1mm) (USNM-44556), Malabang River, Mindanao, Philippines, coll. 21 May 1909; 1 female (14.2mm x 14.0mm) (USNM-44557), shore collection, West coast of Alauild Island, Luzon, Philippines, coll. 19 Nov. 1908, US Bureau of Fisheries, no collection date; 1 male (USNM-44554), on driftwood, coast of Mindanao, no collection date; 1 male (11.4mm x 10.5mm) (USNM-73172), Jaso River, Panay Island, Philippines, coll. H.C.H. Kellerss (Ilo Ilo Expedition), no collection date. – **Taiwan** – 3 males (21.2-24.5mm x 20.6-22.9mm), 1 female (21.8mm x 20.6mm), (NTOU-uncatalogued) Wang-Sha-Xi River, Pingtung County, Taiwan, coll. S.Y. Shy, 5 Aug. 1993; 1 male (21.4mm x 20.6mm), 2 females (18.5-19.2mm x 17.5-18.6mm), (NTOU-uncatalogued), Che-He, southern Taiwan, coll. Apr. 2002.

**Diagnosis.**— Carapace subquadrate, distinctly broader than long, dorsal surface smooth and flat. Front broad, anterior margin slightly concave medially. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very broad, 1.6 times as broad as ischium. Cheliped symmetrical, larger in males, fingers without any seatae on the outer surface. Ambulatory legs short, flat, margins densely setose. Male abdomen triangular in shape with all segments freely moveable (six somites plus telson), distal margin of telson convex in shape. G1 stout, long. Female gonopore with small, rounded operculum.

**Colour.**— The colour of fresh specimens has not been documented, but all the preserved specimens examined are light brown in colour.

**Size.**— This is a relatively large-sized species. The largest male specimen examined is 24.5mm x 22.9mm (NTOU-no cat. number), while the largest female specimen examined is 19.2mm x 18.6mm (NTOU-no cat. number).

**Habitat.**— It can be found along freshwater river banks or under rocks in river mouths (S.Y. Shy, pers. comm.).

**Remarks.**— This species is very similar to *Varuna litterata* and *V. yui* in external morphology but it can be easily distinguished from the two species of *Varuna* by the following characters: a) the presence of a very broad exopod of the third maxilliped (vs. a narrow exopod in *Varuna*); b) the length of the male G1, reaching to sternite 5 (vs. G1 reaching only to sternite 6 in *Varuna*), and c) the width of female abdominal segments (maximum width of the third and fifth abdominal segments). The other distinguishing characters are listed in Table 5 (see below)

Table 5. Key diagnostic characters of *Mitragrapsus altimanus* and *Varuna litterata* (Modified from Naruse *et al.*, 2005).

| Characters | *M. altimanus* | *V. litterata* |
|---|---|---|
| Outer end of granulated ridge of metabranchial region | Separated from the anterolateral tooth by outer length of former anterolateral tooth | Separated from the anterolateral tooth by half length of former tooth |
| Width of exopod of third maxilliped | Wide; larger individuals (especially males) have a wider exopod; width to ischium width 0.6~1.8 in males; 0.68~0.84 in females | Narrow; width to ischium width 0.55~0.8 in males; 0.55~0.71 in females |
| Anterior margin of large male chelipedal merus | Fringed with long setae | Serrated |
| Dorsal margin of large male chela | Proximal part keel-like | Rounded |
| Female sternal knob position | Closer to anterior margin of sternite 5 | Middle of sternite 5 |
| Body size | Smaller in size; male G1 reaches thoracic sternite V in individuals with a CL > 8.3 mm; fifth abdominal segment equal to that of third abdominal segment in an individual with a CL of 13.4 mm | Larger in size; G1 of similar-sized males (CL 7.4~11.8 mm) just reaching thoracic sternite VII or VI; fifth abdominal segment remains narrower than that of third even in individual with a CL of 19.2 mm |

**Distribution.**— Japan (Okinawa), Taiwan, Philippines, Indonesia.

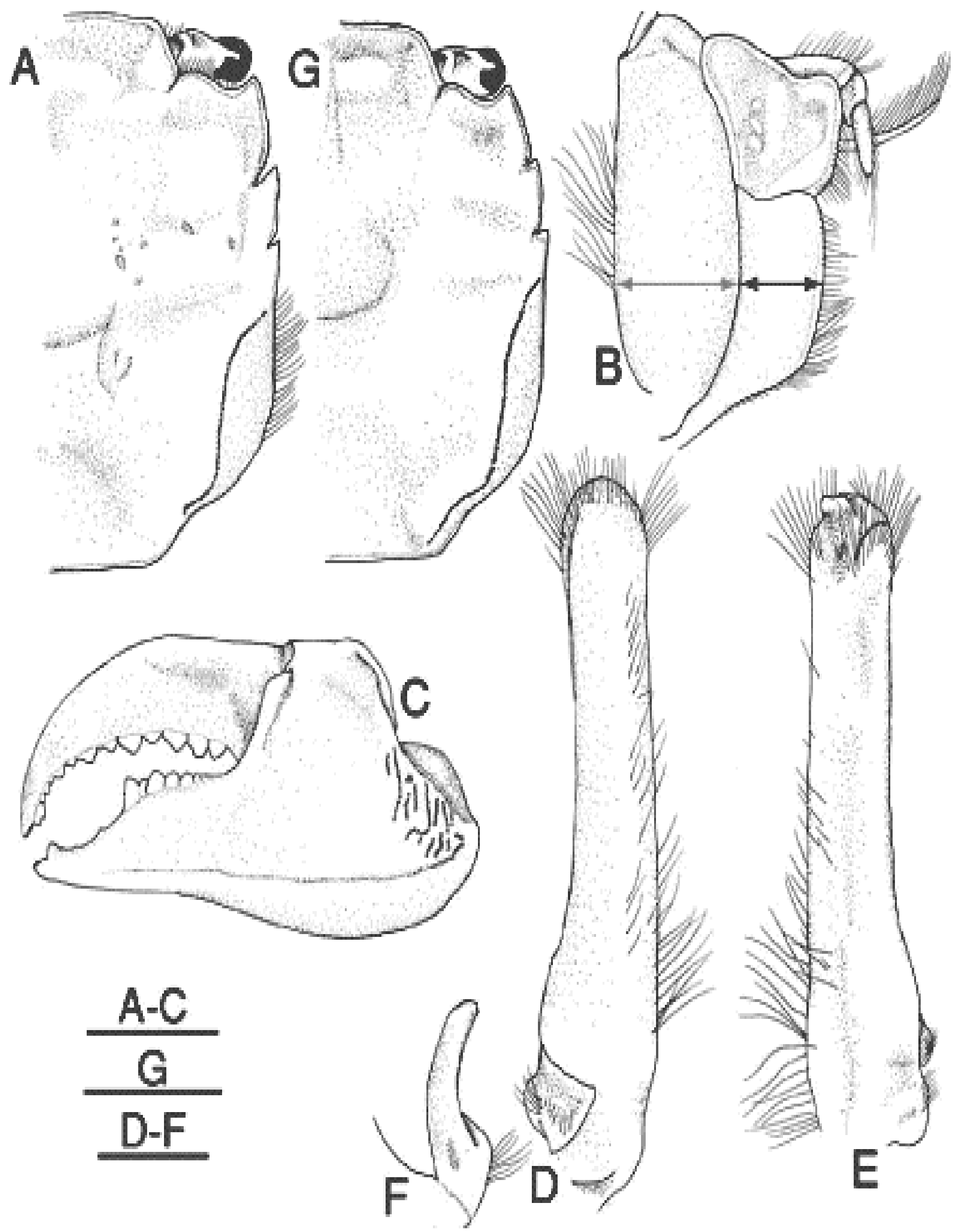



Figure 92. *Mitragrapsus altimanus* Rathbun, 1914, male, holotype, 1.3mm x 20.9mm (USNM-44558). A, B) male carapace; B) third maxilliped; C) outer surface of cheliped; D, E) G1; F) G2. (Scale=1.0mm).

## *Mitragrapsus onyx* (Alcock, 1900), new combination

(Figures 93; 94A-D)

*Ptychognathus onyx* Alcock, 1900: 404; Rathbun, 1914: 70; Tesch, 1918: 86; Hartnoll, 1975: 305.

**Materials examined.**— 3 males (13.7-16.1mm x 12.4-14.4mm) (SFM-5289), Was Kai, Ubernbling des Jurngi, no collection date; 2 females (11.0-15.0mm x 10.0mm-13.8mm) (USNM-44561), Batangas River, Batangas, Luzon, Philippines, coll. 7 Jun. 1908, U.S. Bureau of Fisheries, no collection date; 1 male (30.0mm x 27.9mm) (USNM-44564), Taal Lake, East, Philippines, coll. U.S. Bureau of Fisheries, 26 Dec. 1907; 1 male (20.4mm x 19.3mm) (USNM-no cat. number), Nueua, Vizcaya, coll. Herne, 1931; 1 female (16.9mm x 15.9mm) (USNM-44562), Tilig, Lubang River and beach, Philippines, coll. 14 Jul. 1908; 1 male (6.0mm x 5.2mm), 1 female (5.6mm x 4.7mm), (USNM-44565), Surigao River, East Coast of Mindanao, Philippines, coll. U.S. Bureau of Fisheries, 18 May 1908.

**Diagnosis.**— Carapace subquadrate, broader than long, dorsal surface smooth, flat, regions defined. Front broad, produced, anterior margin slightly concave medially. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, ischium narrow, exopod very broad, 2.3 times broader than ischium. Cheliped symmetrical in males, fingers with a patch of setae on outer surface, at base of pollex, outer surface of merus of chela with distinct strong spine. Ambulatory legs long flat, margins setose. G1 long. Female gonopore small, operculum slightly protruding.

**Colour.**— The colour of fresh specimens has not been documented, and the colour of all preserved specimens examined is brownish in colour (SFM-5289, USNM-44561).

**Size.**— The largest male specimen examined is 30.0mm x 27.9mm (USNM-44564), while the largest female specimen examined is 16.9mm x 15.9mm (USNM-44562).

**Habitat.**— There is no record on the habitat of this species, but the local fishermen have told the author that the bottom of Batangas River in Luzon is covered with small rocks, and pebbles.

**Remarks.**— This species was established on the basis of two young males collected from Tavoy (Alcock, 1900: 404). The description provided by Alcock (1900) is very brief. Alcock stated that this species is closely related to *P. spinicarpus*, *P. polleni* and *P. affinis*, if these species are indeed distinct (Alcock, 1900: 404). It must be noted that the young crabs in this genus are very similar in morphology and not easy to differentiate, which probably led to Alcock's (1900) cynical comment. Nonetheless, he provided some notes on the differences between this species and *P. dentatus*. It is apparent that the key difference is the presence of setae on the outer surface of the cheliped (vs. presence of the setae on the inner surface of the cheliped in *P. dentatus*). There was no report of this species collected from Myanmar or India since Alcock's (1900) report. Hartnoll (1975) reported this species in Tanzania.

Based on Alcock's description, and the examination of the larger size specimens collected from Philippines that are in USNM and SFM, it is clear that *P. onyx* and *P. dentatus* are two distinct species. However, I was unable to examine the type specimens in the Indian Museum, and the identification of the present material of *M. onyx* must be based on Alcock's (1900) descriptions and figures. The specimens from Tanzania reported by Hartnoll (1975) also could not be obtained for examination.

**Distribution.**— Tanzania, India, Philippines.

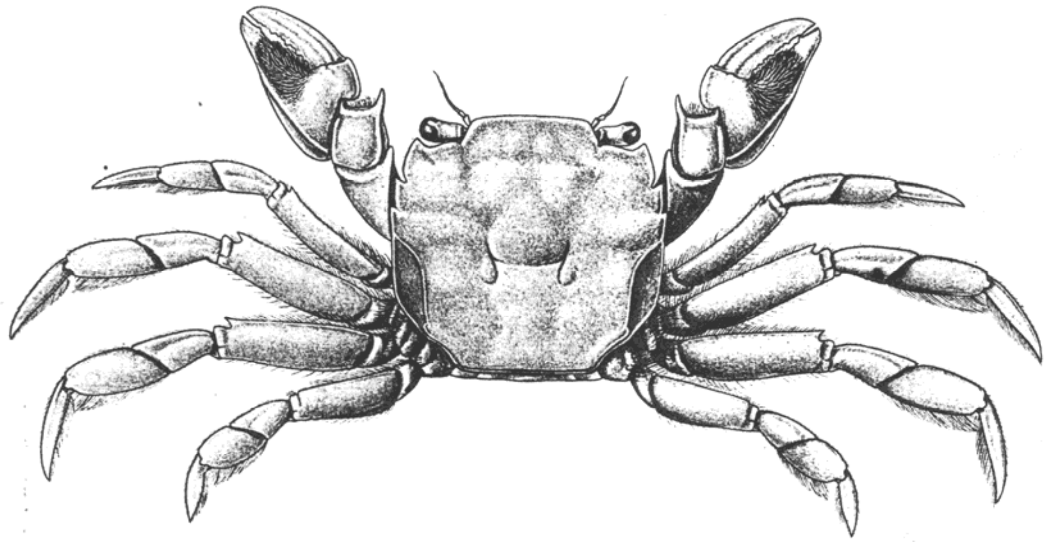


Figure 93. *Mitragrapsus onyx* (Alcock, 1900). Dorsal view. (After Alcock, 1900).

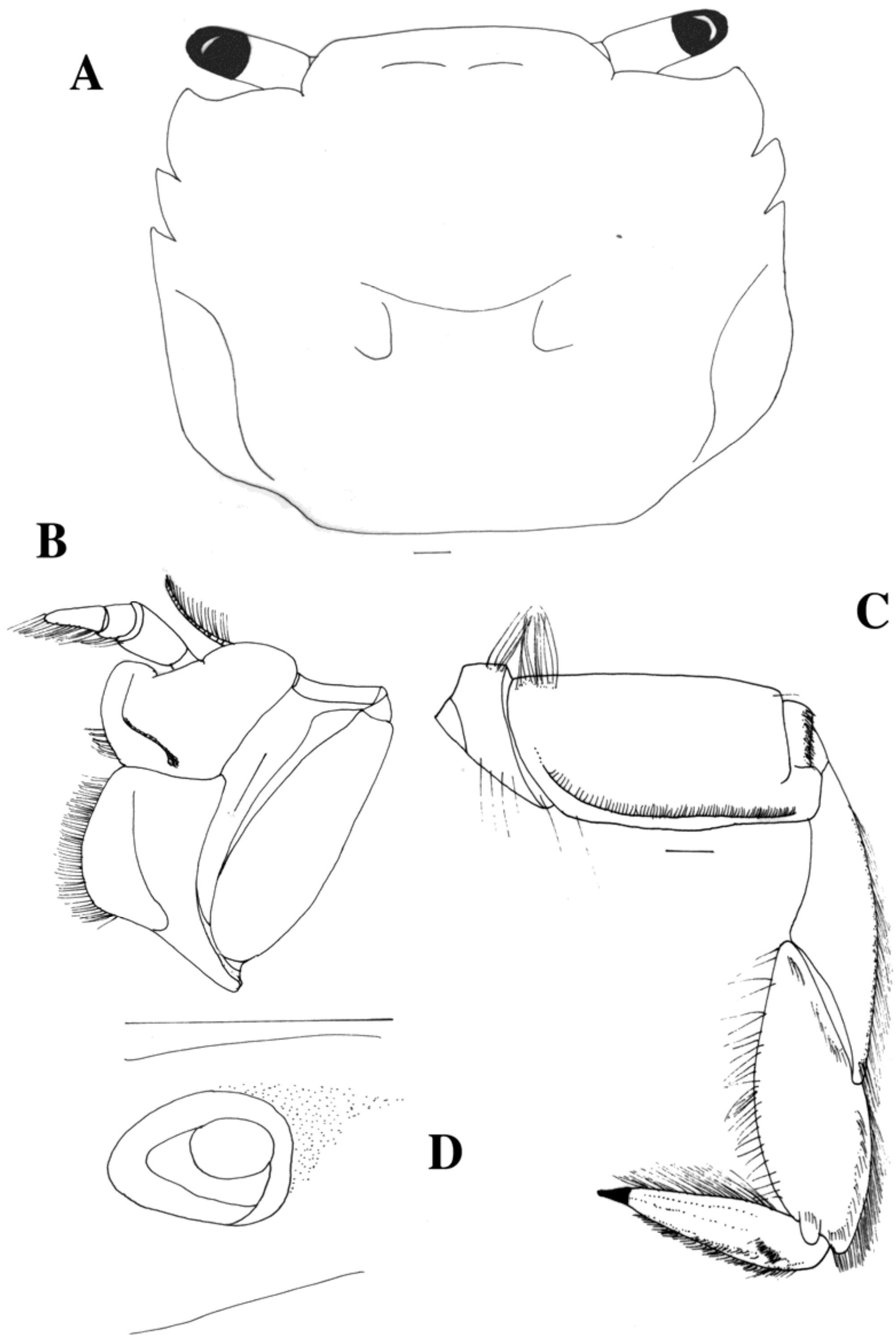



Figure 94. *Mitragrapsus onyx* Alcock, 1900, male, 6.0mm x 5.2mm,;  female, 5.6mm x 4.7mm (USNM-44565)). A) carapace; B) third maxilliped; C) last ambulatory leg; D) female gonopore. (Scale=1mm)

### *Mitragrapsus polleni* (de Man, 1895), new combination

(Figures 95; 96A-E)

*Ptychognathus polleni* de Man, 1895: 94; 1898: pl. 28, fig. 20; Tesch, 1918: 87; Crosnier, 1965: 38; Crosnier, 1975: 735; Fransen *et al.*, 1997: 127.

**Materials examined.— Lectotype** – 1 male (9.7mm x 9.0mm) (RMNH-Colnr-230), Madagascar, coll. Pollen & van Dam, no collection date. – **Others** – 1 male (9.8mm x 9.3mm), (MNHN-B-13225), Madagascar, no collection date.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth, flat. Front produced, broad, anterior margin straight. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod broad, 1.5 times broad as ischium. Cheliped symmetrical in males, fingers glabrous, sparingly granulated. Ambulatory legs short, flat, margins densely setose. Male abdomen triangular in shape with all segments freely moveable (six somites plus telson). G1 short, stout.

**Colour.**— The colour of fresh specimens is not documented, but all the preserved specimens examined are brownish in colour.

**Size.**— The largest male specimen examined is 9.8mm x 89.3mm (MNHN-B-13225), while the largest female size is not known, as only male specimens have been collected so far.

**Habitat.**— It is found under small rocks and pebbles along river banks and river mouths (Crosnier, 1975).

**Remarks.**— This species is found only in Madagascar, there is no other report on this animal from any other locality. So far, only two male specimens have been collected (see Crosnier, 1975).

**Distribution.**— Madagascar only.

Figure 95. *Mitragrapsus polleni* (de Man, 1895), male, lectotype, 9.7mm x 9.0mm (RMNH-Coll Nr-230), Dorsal view.

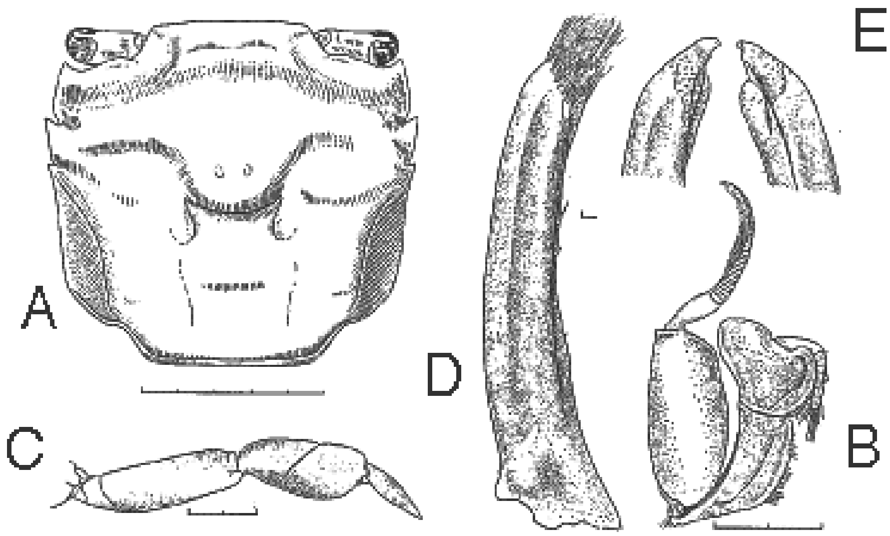



Figure 96. *Mitragrapsus polleni* (de Man, 1895), male, 9.8mm x 9.3mm, (MNHN-B-13225). A) carapace; B) third maxilliped; C) last ambulatory leg; D) G1; E) distal tip of G1. (After Crosnier, 1975).

### *Mitragrapsus affinis* (de Man, 1895), new combination

*Ptychognathus affinis* de Man, 1895: 97, fig. 21; Tesch, 1918: 87.

**Materials examined.**— 1 male (21.1mm x 20.0mm), (ZMA-no cat. number), Kwangdang Bay, Kawa Bay, station 179, Siboga Expedition, coll. & det. Siboga Expedition, 1899; 1 male (10.1mm x 9.8mm), 7 females (5.5-7.7mm x 5.0-7.0mm), 2 juveniles (4.6-4.8mm x 4.0-4.5mm) (ZMA-DE-20143), Kwangdang Bay, Kawa Bay, station 115, Siboga Expedition, coll. & det. Siboga Expedition, 1899.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth, flat. Front produced, broad, anterior margin straight. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very broad, 1.2 times as broad as ischium. Cheliped small, asymmetrical in males, fingers long, surfaces glabrous. Ambulatory legs short, flat, margins setose. Male abdomen triangular in shape with all segments freely moveable (six somites plus telson). G1 stout. Female gonopore with rounded operculum.

**Colour.**— The colour of fresh specimens has not been documented, but all the preserved specimens examined are light brown in colour.

**Size.**— The largest male specimen examined is 21.1mm x 20.0mm (ZMA-no cat. number), while the largest female specimen examined is 7.7mm x 7.0mm (ZMA-DE-20143).

**Habitat.**— There is no documentation of the habitat of this species but the local fishermen told me that the bottom of the bay are covered by pebbles and rocks. The fishermen’s beliefs have been supported by Kilbun (1995).

**Remarks.**— The species have not been recorded since its original description. Attempts to collect this species in Manado and the northern coast of Sulawesi have not been successful.

The type specimen of this species cannot be located in RMNH or ZMA. However, I have examined the specimens collected from the type locality, which have been identified by J.G de Man (ZMA specimens, see above). These specimens are not the types materials as they were collected in 1899, while the species was described in 1895.

**Distribution.**— Indonesia (Kwangdang Bay =Teluk Kuandang, Sulawesi) (Kilbun, 1995).

## *Mitragrapsus crassimanus* (Finnegan, 1931), new combination

*Ptychognathus crassimanus* Finnegan, 1931: 549; Poupin, 1996a: 69, 77, 78.

**Materials examined.**— 1 male (9.8mm x 8.5mm), 1 female (ovigerous) (9.0mm x 8.5mm) river, Ua Pon base Hakabou, no collection date.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth and flat. Front broad, anterior margin slightly concave medially. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very broad, as broader than ischium. Cheliped large, symmetrical in males, fingers glabrous. Ambulatory legs short, flat, margins setose. (Modified from Finnegan, 1931).

**Colour.**— The colour of fresh specimens has not been documented.

**Size.**— The largest male specimen examined is 13.0mm x 11.5mm (Finnegan, 1931), and largest female specimen examined is 9.0mm x 8.5mm (MNHN-no cat. number).

**Habitat.**— The species has been reported to be found under small rocks and pebbles in freshwater streams (Finnegan, 1931).

**Remarks.**— Finnegan (1931) described this species very briefly. She did not provide any figures or photographs. She did, however, comment that the species is closely allied to to *Mitragrapsus polleni*, but gave no other comment. She also listed several differences between *M. crassimanus*, and *N. easteranus*, but she did not describe the form of the third maxillipeds, which is one of the key characters of this genus. Another difference she mentioned was the ‘width of fronto-orbit is much more than seven-eighths that of the carapace’ indicating that the front is very broad, and it should fall into the same genus as *M. polleni* and *M. dentatus.* However, examination of the pair of specimens found in Paris Museum (MNHN-no cat. number) showed that it is more closely allied to the genus *Mitragrapsus*. There are, however, distinctive differences in the forms of the carapace, third maxillipeds and ambulatory legs between *M. crassimanus* and *N. easteranus* as listed by Finnegan (1931) to suggest these are two separate species. There are also differences in the form of the carapace, third maxillipeds and ambulatory legs between *M. crassimanus* and *M. polleni*.

Finnegan (1931) established the species based on one male specimen (13.0mm x 11.5mm) collected from Marquesas Islands. She did not mention if she had a depository for that male specimen. The two specimens I have examined from MNHN are clearly not her type specimen series. I am still trying to locate her type specimen. Interestingly, *M. crassimanus* has not been collected since its original description. In particular, it is not cited by Marquet (1988, 1991, 1993, pers. comm.), who has collected extensively in the Marquesas rivers.

**Distribution.**— French Polynesia (Marquesas Islands) only

## Genus *Neoptychognathus*, new genus

*Ptychognathus* Stimpson, 1858: 104; de Man, 1887: 719; de Man, 1895: 90; Alcock, 1900: 402 (part); Stimpson, 1907: 129, pl. 7, fig. 5, 5a; Rathbun, 1914: 69; Tesch, 1918: 85 (part); Crosnier, 1965: 37

**Type species.**— *Ptychognathus barbatus* A. Milne-Edwards, 1873, by current designation.

**Gender.**— Masculine.

**Diagnosis**.— Carapace quadrangular, broader than long; dorsal surface glabrous, punctate; regions well defined, flat, epigastric cristae not discernible. Frontal margin slightly convex, usually straight. Anterolateral margin subcristate with two teeth including orbital tooth . Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Chela with or without setae, fingers as long as palm. Ambulatory legs with short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular in shape with seven moveable segments (six somites plus telson).

**Etymology.**— 'Neo' is the latin for 'new' is used as a prefix to *Ptychognathus*, indicating that it is a new genus.

**Remarks.**— This new genus is very closely allied to *Ptychognathus* sensu stricto. In addition to the broad exopod of the third maxilliped, all the species in *Neoptychognathus* can be differentiated from *Ptychognathus* sensu stricto by the following features: a) possession of two teeth on the anterolateral margin after the orbital tooth (vs. only one in *Ptychognathus*); b) these species are relatively larger in adult size (vs. smaller in adult size in *Ptychognathus*), and c) the carapace is distinctly broader than long (vs. only slightly broader in *Ptychognathus*).

Preliminary DNA studies done by C. D. Schubart and the current author (unpublished data) have shown that there are distinct differences between *Ptychognathus* sensu stricto, and *Neoptychognathus*, new genus.

*Neoptychognathus*, new genus comprises of six species viz. *N. barbatus* (A. Milne-Edwards, 1873) (type species); *N. pusillus* (Heller, 1865); *N. easteranus* (Rathbun, 1907); *N. johannae* (Rathbun, 1914); *N. guijulugani* (Rathbun, 1914) and *N. capillidigitatus* (Takeda, 1984).

**Key to species in *Neoptychognathus***

1a. Carapace quadrangular; frontal margin straight. ------------------------------- **2**

1b. Carapace quadrangular; frontal margin distinctly sinuous. -------------------- **3**

2a. Anterolateral teeth of carapace sharp. Outer surface of cheliped glabrous. ------------- ---------------------------------------------------------------------- ***N. easternaus***

2b. Anterolateral teeth of carapace blunt. Outer surface of cheliped with tufts of setae on fingers. ------------------------------------------------------------------ ***N. johannae***

3a. Frontal margin of carapace with two lobes at distal ends. --- ***N. guijulugani***

3b. Frontal margin of carapace with no lobes at distal ends. ------------------- **4**

4a. Cheliped with only one tuft of setae on fixed finger. Exopod of third maxilliped 1.4 times broader than ischium. -------------------------------------- ***N. capillidigitus***

4b. Chelipeds with two tufts of setae, one each on movable and fixed fingers. Expod of third maxilliped less than 1.4 times broader than ischium. ------------ **5**

5a. Expod of third maxillipeds 1.2 times broader than ischium. Base of cheliped's fingers with a small palvinus. -------------------------------------------------------- ***N. pusillus***

5b. Exopod of third maxillipeds 1.1 times broader than ischium. Base of cheliped's fingers without pulvinus. --------------------------------------------- ***N. barbatus***

## *Neoptychognathus barbatus* (A. Milne-Edwards, 1873), new combination

(Figure 97A-B)

*Gnathograpsus barbatus* A. Milne-Edwards, 1873: 316, pl. 17: 4.

*Ptychognathus barbatus* – de Man, 1895: 105; Crosnier, 1965: 37; Fransen *et al.*, 1997: 127;

**Materials examined.**— **Lectotype** – 1 male (12.7mm x 9.7mm) (MNHN-10877), New Caledonia, no collection date. – **Paralectotypes** – 2 males (mounted on board) (MNHN-10877), New Caledonia; 1 male (12.3mm x 10.0mm) (RMNH-D192), New Caledonia, no collection date; 1 male (mounted on board) (MNHN-3395), New Caledonia, no collection date; 2 males (mounted on board) (MNHN-3401), New Caledonia, coll. A. Milne-Edwards, 1872; 3 males (9.5-11.9mm x 8.0-9.8mm), 2 females (9.4-9.6mm x 7.8mm) (USNM-20308), New Caledonia, coll. M. Balanca, no collection date. – **Others** – 1 male (8.0mm x 6.7mm), 1 female (7.5mm x 6.1mm) (RMNH-D16691), Point Aux Sabbles, Maritius, coll. C. Michel, 23 Mar. 1960; 2 males (9.3-11.2mm x 7.6-8.9mm), 1 female (10.9mm x 8.7mm) (RMNH-16992), Point Aux Sabbles, South of Port Louis, Maurtius, coll. C. Miche1, 8 Sep. 1960.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth and flat. Front broad, anterior margin slightly concave medially. Anterolateral margin with three teeth including orbital tooth. Regions well defined. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very broad, 1.1 times broader than ischium. Cheliped symmetrical in males, fixed finger with a tuft of long setae at the base of outer surface, absent in female. Ambulatory legs short, flat, slightly setose. Male abdomen triangular in shape with all segments freely moveable (six somites plus telson), telson triangular in shape, distal margin convex. Female gonopore with rounded operculum.

**Colour.**— The colour of fresh specimens has not been documented, the colour of all the preserved specimens examined are light brown in colour.

**Size.**— The largest male specimen examined is 12.7mm x 9.7mm (MNHN-10877), and the largest female specimen examined is 10.9mm x 8.7mm (RMNH-16992).

**Habitat.**— There is no documentation on the habitat of this species.

**Remarks.**— This species is currently reported from New Caledonia only. The very common '*Ptychognathus barbatus*' that is distributed in the Indo-West Pacific and reported on by many authors is actually an undescribed species (see below).

**Distribution.**— New Caledonia only.

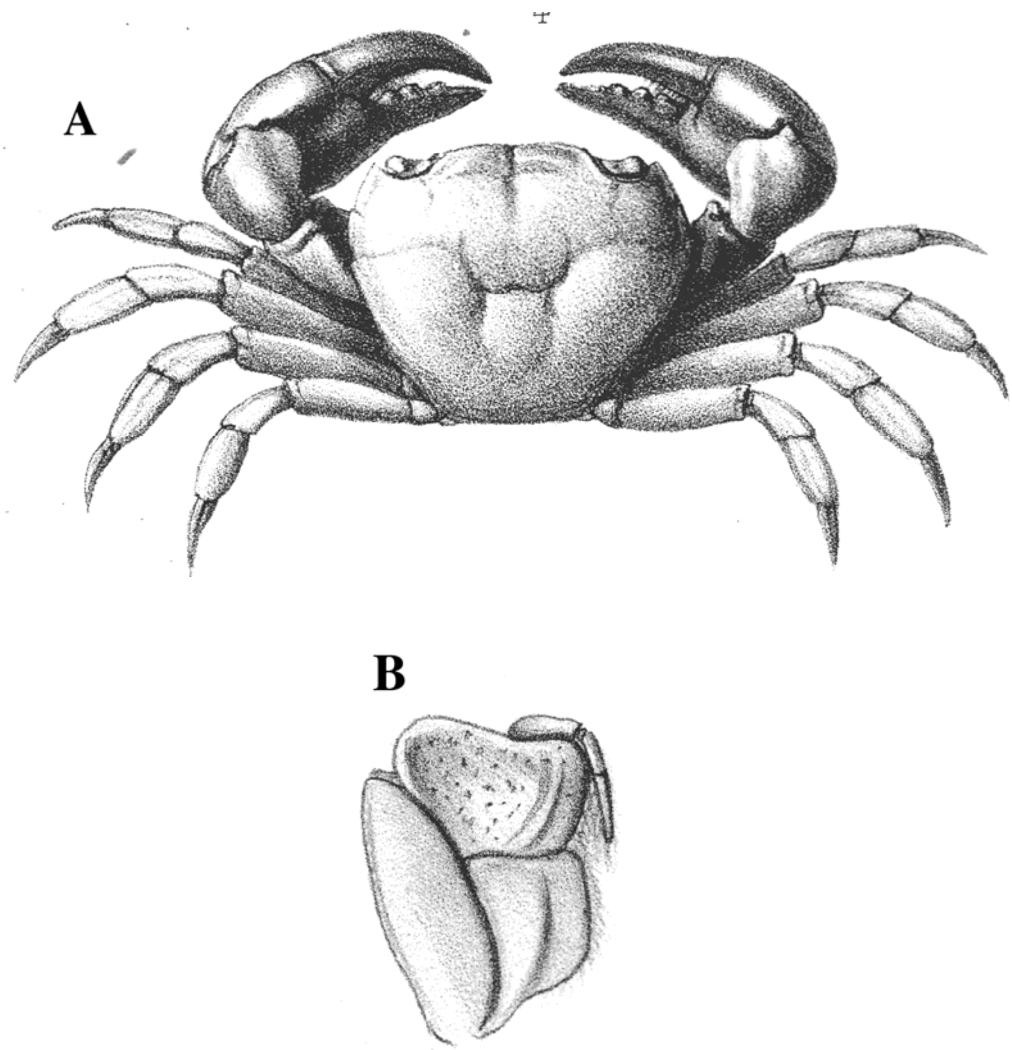



Figure 97. *Neoptychognathus barbatus* (A. Milne-Edwards, 1873). A) dorsal view; B) third maxilliped. (After A. Milne-Edwards, 1873).

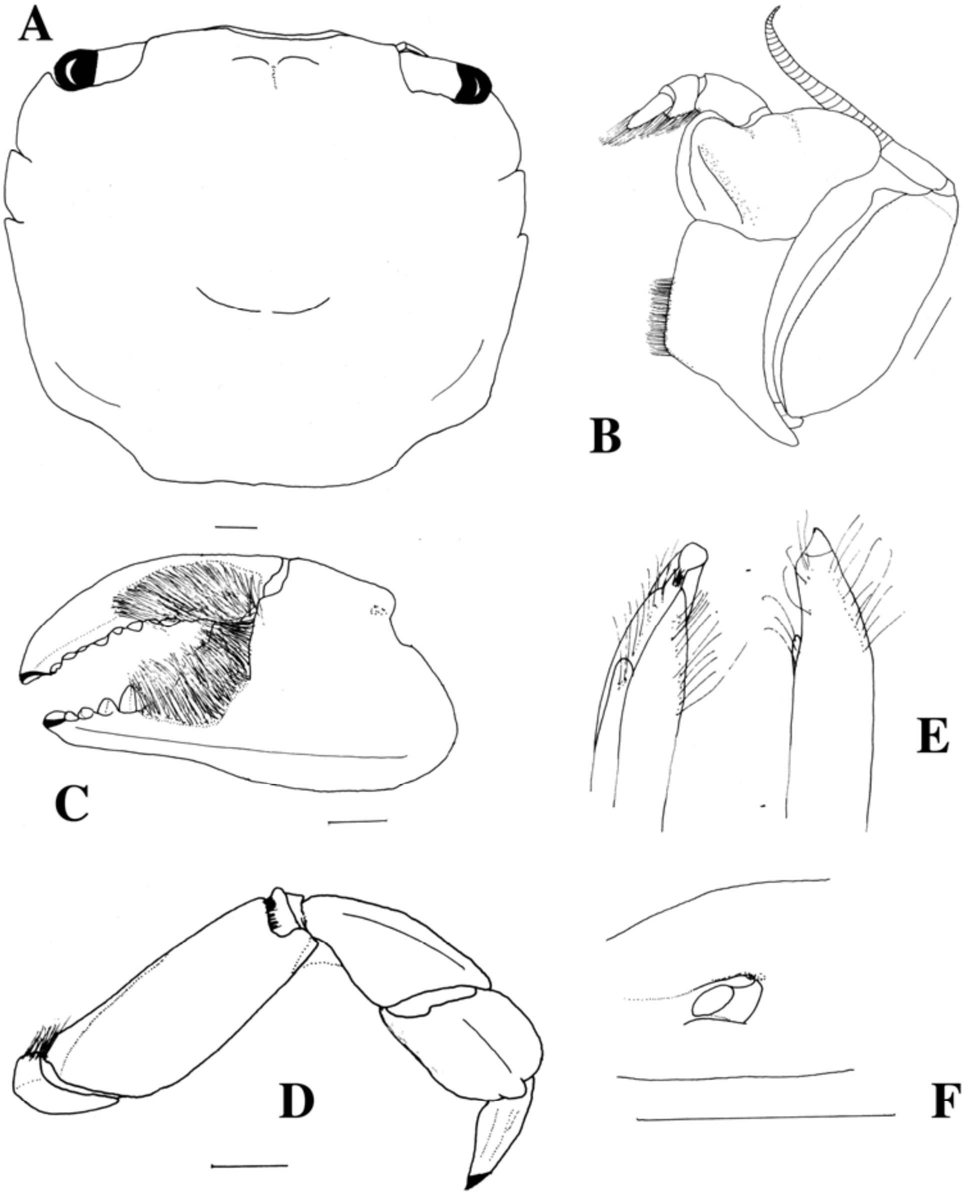



Figure 98. *Neoptychognathus barbatus* (A. Milne-Edwards, 1873), male, 11.9mm x 9.8mm; female, 9.6mm x 7.8mm (USNM-20308). A) carapace; B) third maxilliped; C) outer view of male chela; D) last ambulatory leg; E) distal ends of G1; F) female gonopore. (Scale=1.0mm).

### *Neoptychognathus pusillus* (Heller, 1865), new combination

(Figure 99 A-F)

*Ptychognathus pusillus* Heller, 1865: 60; de Man, 1895: 99, pl. 28, fig. 22; de Man, 1902: 537; Alcock, 1900: 403, 405; Tesch, 1918: 87.

**Materials examined.**— **Australia –** 1 male (22.2mm x 18.3mm) (WAM-uncatalogued), Sale, Christmas Island, coll. H. Yorkston, Jul. 1988; 1 male (11.0mm x 9.9mm), 1 female (WAM-52885), Christmas Island, coll. D. Powell, 10 Nov. 1961; 11 males (6.6-16.5mm x 5.7-13.6mm), 7 females (7.0-11.0mm x 5.7-9.4mm), 1 female (ovigerous) (10.4mm x 9.0mm) (WAM-52785), Dandhoron Bay, Christmas Island, coll. 14-26, Feb. 1978; 1 male (14.8mm x 12.5mm), 1 female (12.3mm x 10.7mm), 1 juvenile (5.5mm x 4.8mm), 2 megalopae (ZRC 1965.7.27.154-155), Dolly Beach, Christmas Island, coll. CAGH, 1939. – **Indonesia** – 6 males (15.6-32.5mm x 12.5-26.8mm), 22 females (15.7-21.4mm x 12.5-18.8mm) (SFM-5357), Celebes, coll. Elbert, 10 Aug. 1909; 1 male (20.9mm x 16.0mm) (SFM–no cat. number), Celebes, coll. Elbert, 1909; 7 males (7.1-10.6mm x 6.2-9.2mm) 2 females (ovigerous) (7.2-9.0mm x 6.0-7.7mm) (NMB-620a), Tirim comalio, Leylou, coll. 1893; 1 female (ovigerous) (8.5mm x 7.4mm) (ZMA-no cat. number), Ambonina, coll. de Man’s collection, no collection date; 1 female (10.3mm x 9.3mm) (ZMA-no cat. number), River by Bambang, Flores, coll. M. Weber, no collection date; 1 male (8.8mm x 7.4mm) (ZMA-no cat. number), river by Pidgot, coll. Siboga expedition, no collection date. – **Sri Lanka** – 1 male (10.9mm x 9.6mm), 1 female (oviergous) (9.2mm x 7.7mm) (NMB-620a), Tuncormapi, Ceylon, coll. GER, 1893.

**Diagnosis.**— Carapace subquadrate, dorsal surface punctate, flat. Front broad, anterior margin concave medially. Anterolateral margin with three teeth including orbital tooth. Regions well defined. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very broad, convex, 1.2 times broader than ischium. Cheliped symmetrical in males, outer surfaces of pollex, manus setose, base of fingers with a small distinct pulvinus. Ambulatory legs short, flat, margins slightly setose. Telson broadly triangular. G1 long. Female gonopore with rounded operculum.

**Colour.**— The colour of fresh specimens has not been documented, all the preserved specimens examined are brownish in colour.

**Size.**— The largest male specimen examined is 32.5mm x 26.8mm (SFM-5357) while the female specimen examined is 21.4mm x 18.8mm (SFM-5357).

**Habitat.**— It is found in freshwater streams (Anonymous, 2002: 69)

**Remarks.**— This species is very closely allied to *N. barbatus* in its morphology. de Man (1902) gave a very detailed of the differences between this species and its relatives, particularly *N. barbatus*. In addition to de Man's list of differences, the most distinct character of this species is the presence of a pulvinus at the base of the fingers (vs. absence of the pulvinus in *N. barbatus*).

This species has not been collected from Indonesia since its original type locality (Celebes). Instead it has been quite abundantly collected from Christmas Island, Australia (G. Marquet, pers. comm.; Anonymous, 2002; 2003/04). One specimen has been collected from Sri Lanka.

The type specimens of this species should be lodged in the Vienna Natural History Museum, I have not been able to borrow the specimen out as it is very fragile. However, I have examined the specimens collected from the type locality which were identified by Heller ((NMB-620a) himself.

**Distribution.**— Australia (Christmas Island), Indonesia (Ambon), Sri Lanka.

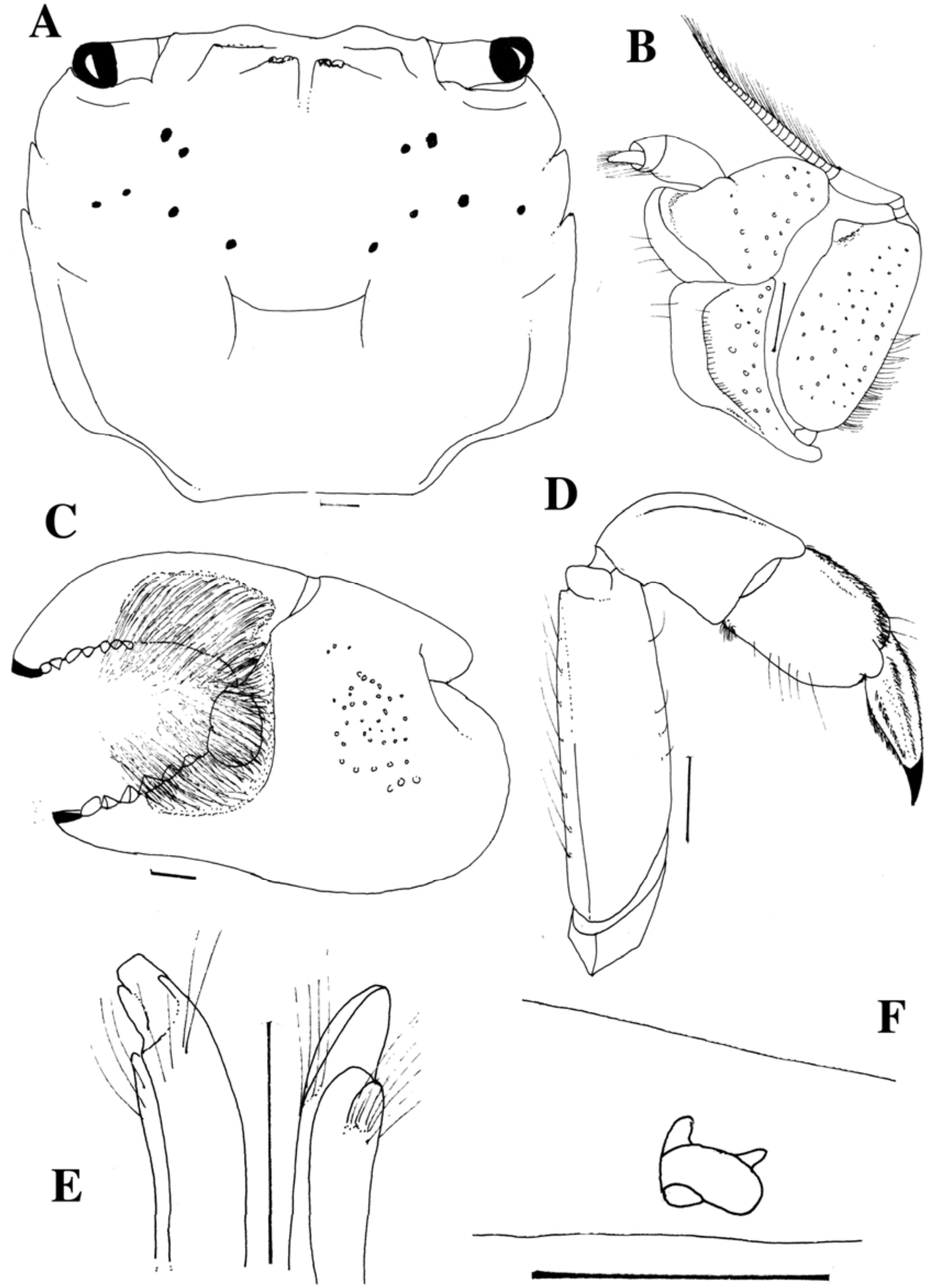



Figure 99. *Neoptychognathus pusillus* Heller, 1865, male, 32.5mm x 12.5-26.8mm; female, 21.4mm x 18.8mm (SFM-5357). A) carapace; B) third maxilliped; C) outer view of male chela; D) last ambulatory leg; E) distal ends of G1; F) female gonopore. (Scale=1.0mm).

## *Neoptychognathus easteranus* (Rathbun, 1907), new combination

(Figure 100A-I)

*Ptychognathus easteranus* Rathbun, 1907: 31, pl. 2, fig. 4, pl. 7. 4, 4a; Tesch, 1918: 86; Garth, 1973: 325; Poupin, 2003: 31.

**Materials examined.— Holotype** – 1 male (12.0mm x 10.8mm) (USNM-32845), shore on Easter Island, coll. 20 Dec. 1904. – **Others** – 5 males (12.5-17.5mm x 10.0-14.5mm), (RMNH-D-37262), Rucutu Fcans, French Polynesia, 22°26'S, 151°20'W, leg. G. Marquet, 1986; 1 male (9.3mm x 7.8mm), 4 females (5.7-16.0mm x 4.8-14.0mm), 1 carapace (10.5mm x 9.1mm), (RMNH-D38389), La Perone Bay, Easter Island, coll. H. Dumont, 29 Aug. 1990; 1 male (16.5mm x 14.3mm), Atuona, Hiva, Oa, French Polynesia, 9°40'S 139°02'W, coll. G. Marquet, 5 Jan. 1987.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth and flat. Front broad, anterior margin slightly concave medially. Regions well defined. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod broad as ischium. Cheliped symmetrical in males, fingers with tufts of setae. Ambulatory legs short, flat, margins slightly setose. Telson narrowly triangular. G1 slender. Female gonopore with rounded operculum.

**Colour.**— The colour of fresh specimens has not been documented, but all the preserved specimens examined are brownish in colour.

**Size.**— The largest male specimen examined is 12.0mm x 10.8mm (USNM-32845), while the largest female specimen examined is 16.0mm x 14.0mm (RMNH-D38389).

**Habitat.**— The species is found in freshwater streams (G. Marguet, pers. comm.)

**Remarks.**— This distribution of this species is rather disjuncted, it is originally reported from Easter Island (Indian Ocean), and later from the French Polynesia. There is no report of this species from any locality between these two places.

There is also very little known about the biology of this animal.

**Distribution.**— Australia (Easter Island), French Polynesia.

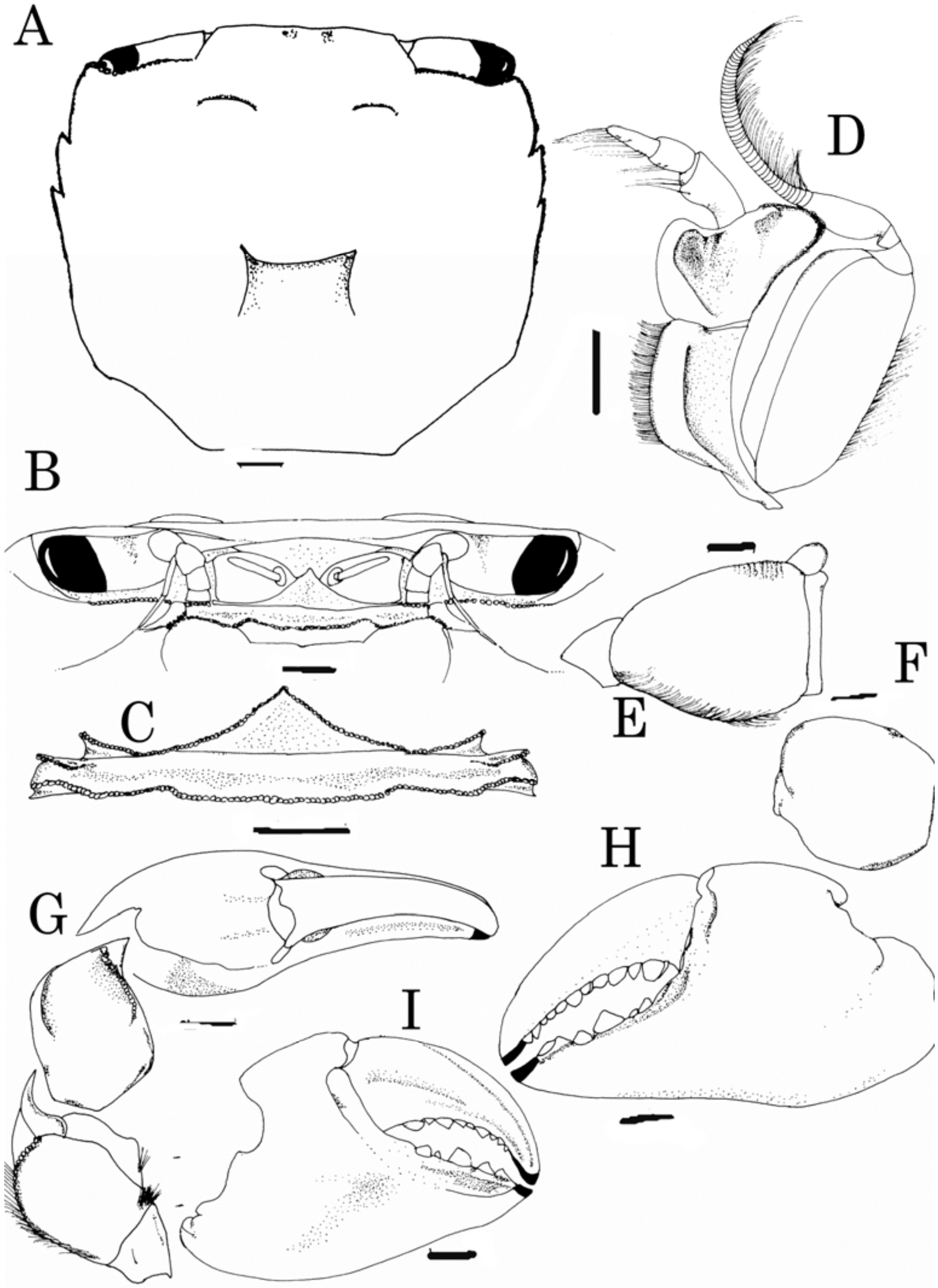



Figure 100. *Neoptychognathus easteranus* Rathbun, 1907, male, holotype, 12.0mm x 10.8mm (USNM-32845). A) carapace; B) frontal veiw; C) endostome; D) third maxilliped; E) merus of chela; F) ischium of chela; G) top view of the chela; H) frontal view of cheliped; I) inner view of cheliped. (Scale=1.0mm).

## *Neoptychognathus johannae* (Rathbun, 1913), new combination

(Figures 101; 102A-C)

*Ptychognathus johannae* Rathbun, 1913: 354, pl. 30; 1918: 88; Tesch, 1918: 88.

**Materials examined.**— **Holotype** – 1 male (18.3mm x 15.9mm) (USNM-22799), Johanna Island, Comoro, West Indian Ocean, from Hildebrunt (Berlin Museum), no collection date.

**Diagnosis.**— Carapace subquadrate, distinctly broader than long, dorsal surface smooth, flat. Front broad, anterior margin slightly concave medially. Regions well defined. Anterolateral margin with three teeth including orbital tooth. Third maxilliped punctate, close with a small gap, merus with antero-external angle broad, exopod very convex, broad, as 1.2 times broader than ischium. Chelae symmetrical, large, cheliped high and broad, long, soft setae on proximal end of fingers. Ambulatory legs short, flat, margins covered with mainly short bristle like setae. Male abdomen broadly triangular in shape with all segments freely moveable (six somites plus telson). G1 short, stout.

**Colour.**— The colour fresh specimens has not been documented, and the colour of the preserved specimens (holotype) examined is brownish in colour.

**Size.**— The largest male specimen examined is 18.3mm x 15.9mm (holotype) while the largest female size is not known, so far, only the holotype has been collected .

**Habitat.**— There is no documentation on the habitat of this species.

**Remarks.**— This species was described based on one male specimen from the Comoros. It has only been reported from the type locality. The female specimen of this species has not been reported. This key character of this species is the form of the third maxillipeds: they are distinctly granulated, especially the exopod. The third maxillipeds of all other congeners are smooth.

**Distribution.**— West Indian Ocean (Comoro Islands).

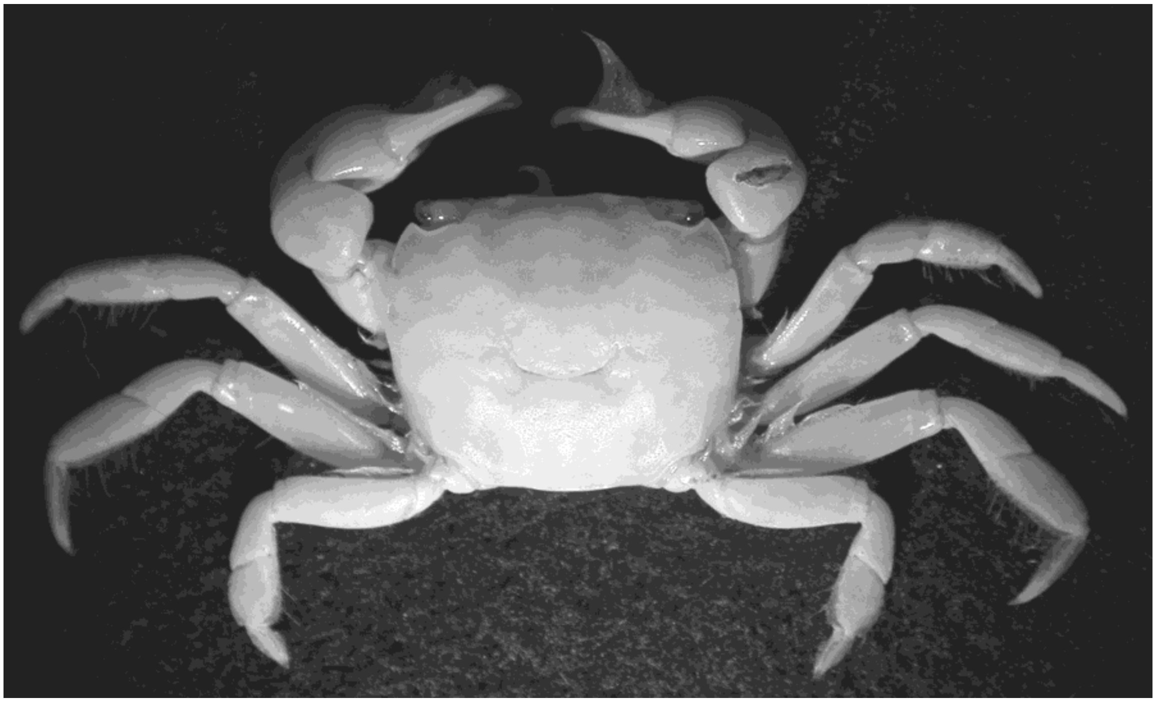


Figure 101. *Ptychognathus johannae* Rathbun, 1913, male, holotype, 18.3mm x 15.9mm (USNM-22799). Dorsal view.

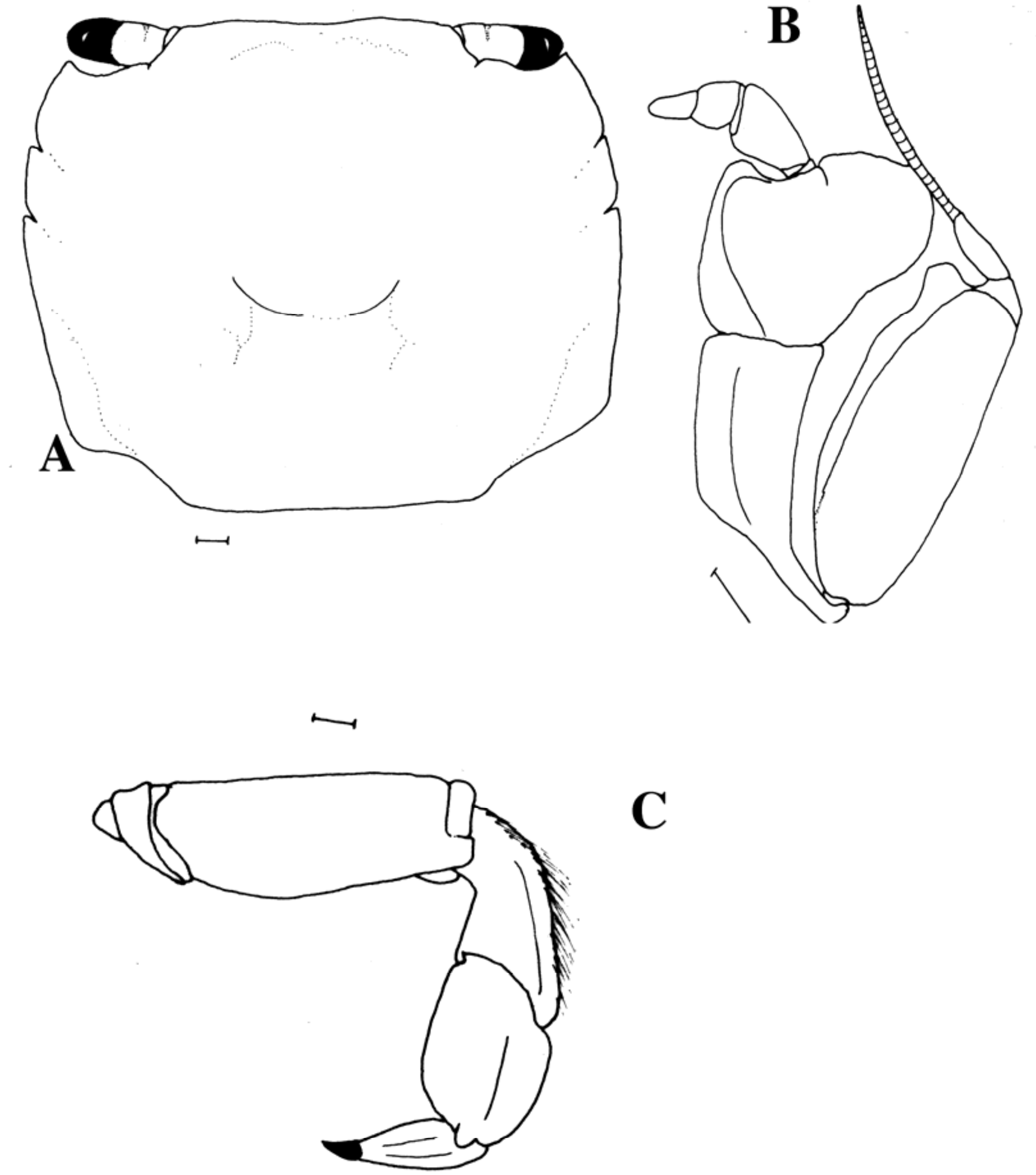



Figure 102. *Ptychognathus johannae* Rathbun, 1913, male, holotype, 18.3mm x 15.9mm (USNM-22799). A) carapace; B) third maxilliped; C) last ambulatory leg. (Scale=1.0mm)

### *Neoptychognathus guijulugani* (Rathbun, 1914), new combination

(Figures 103; 104A-F)

*Ptychognathus guijulugani* Rathbun, 1914: 71; Tesch, 1918: 88.

**Materials examined.**— **Holotype** – 1 male (9.0mm x 7.5mm) (USNM-44668), Guijulugan, Negros, Philippines, coll. 2 Apr. 1908. – **Paratypes** – 1 male (7.2mm x 6.5mm), 1 female (8.2mm x 7.4mm), 1 female (ovigerous) (8.5mm x 7.4mm) (USNM-44668), Guijulugan, Negros, Philippines, coll. 2 Apr. 1908. – **Others – 1 male** (10.8mm x 9.2mm) (ZMA-no cat. number), Station 131, Siboga Expedition, no collection date. – **Marianas** – 18 males (7.7-11.1mm x 6.5-9.4mm), 6 females (4.8-9.0mm x 4.0-7.8mm), 5 juvenile (3.9-4.5mm x 3.2-3.7mm) (USNM-uncatalogued), Rota, Marianas, coll. D.G. Fray, 16 Nov. 1945. – **Philippines** – 4 males (5.1-6.1mm x 4.0-4.7mm), 4 females (ovigerous) (4.5-5.2mm x 3.8-4.3mm) (USNM-44670), Guijuligan, Negros, Philippines, coll. 2 Apr. 1908; – **Taiwan** – 6 males (6.5-10.3mm x 5.9-8.8mm), 2 females (8.6-13.7mm x 7.2-12.0mm), 2 females (ovigerous) (6.7-7.1mm x 6.0-6.2mm), (NMMBA-no cat. number), Laiching Bay, Lanyu Island, coll. H.P. Ho, 19 Apr. 2002.

**Diagnosis.**— Carapace subquadrate, distinctly broader than long, dorsal surface smooth, flat. Front broad, anterior margin slightly concave medially, distal end lobed. Regions well defined. Anterolateral margin with three weak teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very convex, broad, 1.3 times broader than ischium. Chelae symmetrical, large, cheliped high and broad, a square patch of long, soft setae on near distal of palm, continuing to fingers. Ambulatory legs narrow, flat, margins slightly setose. Male abdomen triangular in shape with all segments freely moveable (six somites plus telson). G1 long, stout. Female gonopore with rounded operculum.

**Colour.**— The colour of fresh specimens has not been documented, but the colour of all the preserved specimens examined is brownish in colour.

**Size.**— The largest male specimen examined is 10.3mm x 8.8mm (NMMBA-no cat. number), while the largest female specimen examined is 13.7mm x 12.0mm (NMMBA no cat. number).

**Habitat.**— The species can be found under small rocks and pebbles along river banks and river mouth (H.P. Ho, pers. comm.).

**Remarks.**— This species was reported originally from Philippines, and it has been recently recorded from Taiwan as well. This is a small-sized species, and is very closely allied to *N. barbatus*, but it can be easily distinguished from *N. barbatus* by the following features a) the narrower carapace (vs. broader carapace in *N. barbatus*); b) the frontal margin is sinuous, with a small lobes at the distal end (vs. straight frontal margin and absence of distal lobes), and c) the exopod of the third maxillipeds is 1.3 times broader than ischium (vs. 1.1 times as broad as ischium in *N. barbatus*).

**Distribution.**— Philippines, Taiwan.

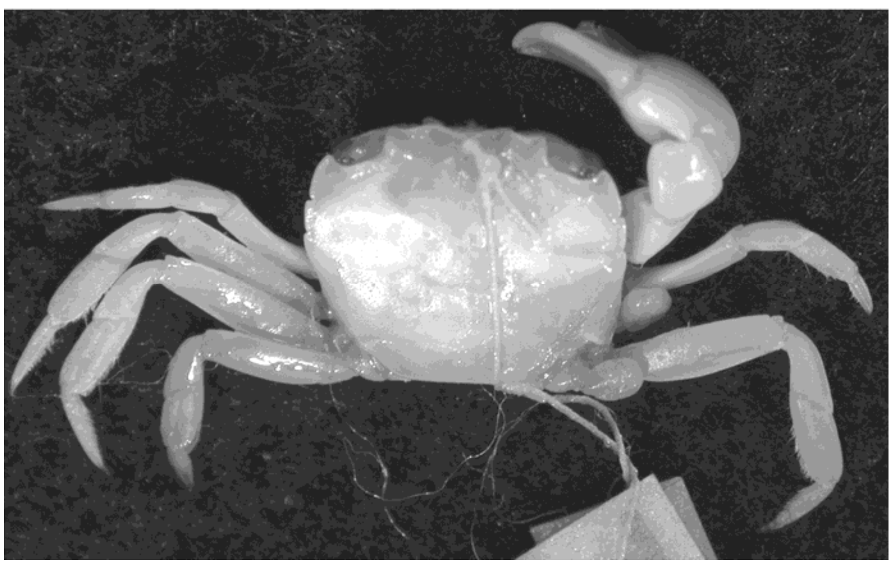


Figure 103. *Neoptychognathus guijulugani* Rathbun, 1914, male, holotype, 9.0mm x 7.5mm (USNM-44668). Dorsal view.

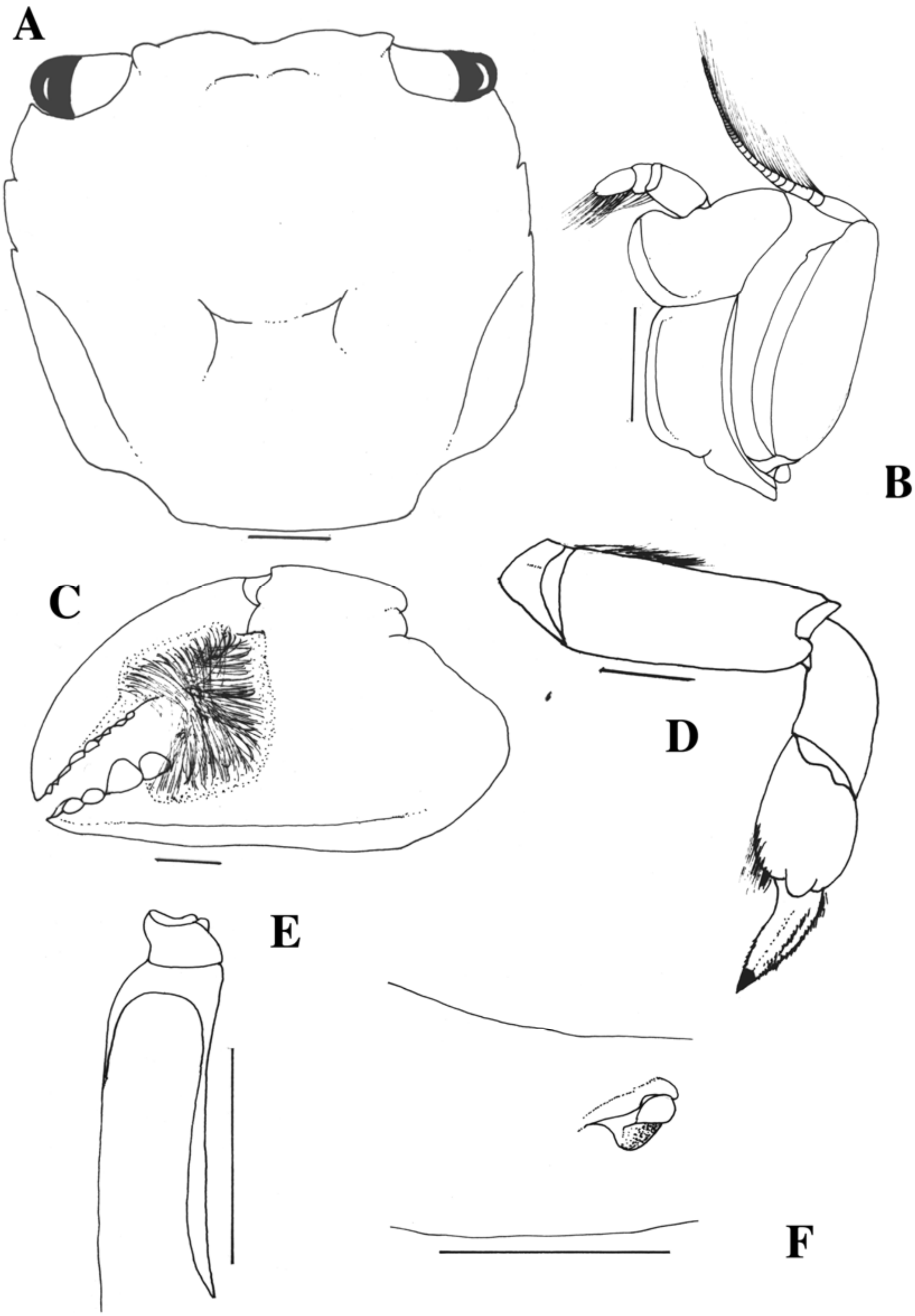



Figure 104. *Neoptychognathus guijulugani* Rathbun, 1914, male, paratype, 7.2mm x 6.5mm; female, paratype, 8.2mm x 7.4mm (USNM-44668). A) carapace; B) third maxilliped; C) outer surface of male cheliped; D) last ambulatory leg; E) distal tip of G1; F) female gonopore. (Scale=1.0mm).

### *Neoptychognathus capillidigitalis* (Takeda, 1984), new combination

(Figure 105A-F)

*Ptychognathus capillidigitalis* Takeda, 1984: 117, figs 1-4; Komai *et al.*,, 2004: 58.

**Materials examined.**— **Holotype** – 1 male (7.9mm x 6.0mm) (NSMT-Cr.-8987), Tonda-Gawa River, Shirahama-Cho, Wakayama, Prefecture, Japan, coll. K. Wada & Y. Fukui, 4 Feb. 1984. – **Others** – 8 females (4.2-7.6mm x 3.4-6.2mm) (RU-no cat. number), Aha River, Okinawa Island, Japan, coll. 7 Aug. 1990; 1 male (7.1mm x 5.4mm) (RU-no cat. number), Takasato River, Kunigami Village, Okinawa Island, Japan, coll. 29 Jul. 1987; 20 males (5.0-7.7mm x 4.0-6.2mm), 7 females (5.2-8.1mm x 4.1-6.6mm), 2 females (ovigerous) (5.5-6.2mm x 4.4-5.2mm) (RU-no cat. number), Aha River, Kunigami Village, Okinawa Island, Japan, 27 Jul. 1987; 11 males (5.6-8.4mm x 4.5-6.7mm), 11 females (6.5-8.9mm x 5.0-7.1mm) (RU-no cat. number), upstream of Kukukana River, Okinawa Island, Japan, coll. Y. Nakasone, 27 Jul. 1987.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth, flat. Front broad, anterior margin slightly concave medially. Regions well defined. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod broad, 1.4 broader than ischium. Cheliped symmetrical in males, fingers setae. Ambulatory legs short, flat, margins setose. Male abdomen broadly triangular in shape with all segments freely moveable (six somites plus telson). G1 long, slender. Female gonopore with rounded operculum.

**Colour.**— The colour fresh specimens has not been documented, and the colour of all the preserved specimens examined is brownish in colour.

**Size.**— The largest male specimen examined is 8.4mm x 6.7mm (RU-no cat. number) while the largest female specimen examined is 8.9mm x 7.1mm (RU-no cat. number).

**Habitat.**— It is found under small rocks and pebbles along river banks and river mouths (Y. Nakasone, pers. comm.).

**Remarks.**— The detailed description and good figures of this species can be found in Takeda (1984). This species has not be been recorded from any locality outside Japan.

**Distribution.**— Japan only.

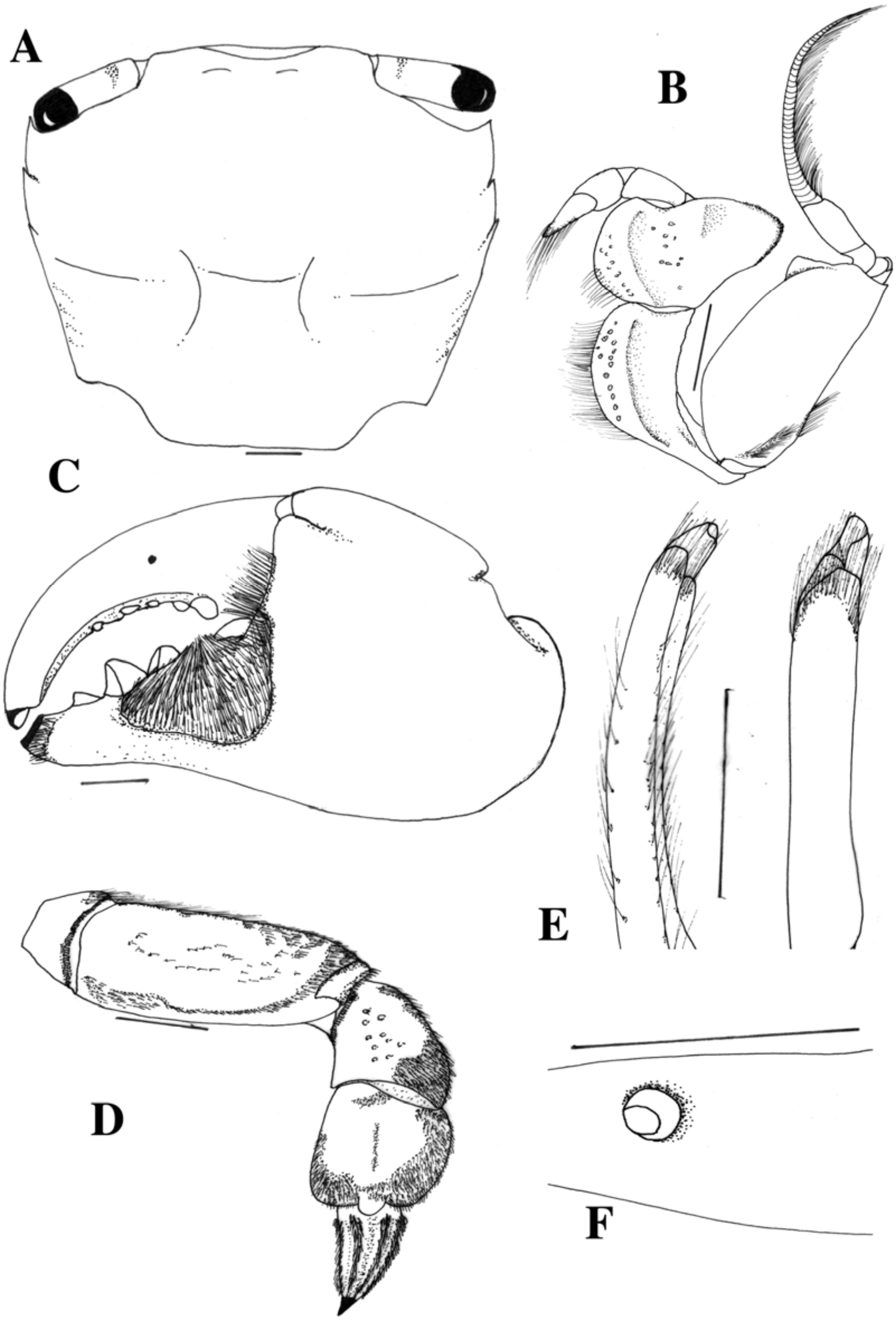



Figure 105. *Neoptychognathus capillidigitalis* Takeda, 1984, male, holotype, 7.9mm x 6.0mm (NSMT-Cr.-8987); female, 7.6mm x 6.2mm, (RU-no cat. number). A) carapace; B) third maxilliped; C) outer surface of male cheliped; D) last ambulatory leg; E) distal tips of G1; F) female gonopore. (Scale=1.0mm).

***Neoptychognathus insolitus* (Osawa & Ng, 2006), new combination**

(Figure 106A-K)

*Ptychognathus* cf. *hachijyoensis* – Kishino, *et al.*, 2001: 16, pl. 1, fig. 5 (not *Ptychognathus hachijyoensis* Sakai, 1955).

*Ptychognathus johannae* – Nakasone & Irei, 2003: 274 (key), fig. 50 (not *Ptychognathus johannae* Rathbun, 1914).

*Ptychognathus insolitus* Osawa & Ng, 2006: 57.

**Materials examined.**— **Holotype** – 1 male (13.9 mm x 9.5 mm) (CMNH-ZC), Nakata, Izena Island, Ryukyu Islands, mouth of a narrow river, interspace of pebbles, coll. M. Osawa, 23 May 2004. – **Paratypes** – 2 males (9.8-9.9mm x 6.9-7.1mm), 2 females (10.5-11.3mm x 7.6-7.8mm), 1 female (ovigerous) (9.7mm x 7.3mm) (CMNH-ZC), Nakata, Izena Island, Ryukyu Islands, mouth of a narrow river, between pebbles, coll. M. Osawa, 23 May 2004.

**Diagnosis.**— Carapace subquadrate, distinctly broader than long, dorsal surface smooth, flat. Front broad, anterior margin slightly concave medially. Regions well defined. Anterolateral margin with three teeth including orbital tooth. Third maxilliped punctate, close with a small gap, merus with antero-external angle broad, exopod very convex, broad, as 1.2 times broader than ischium. Chelae symmetrical, large, cheliped high and broad, long, soft setae on proximal end of fingers. Ambulatory legs short, flat, margins setose. Male abdomen broadly triangular in shape with all segments freely moveable (six somites plus telson). G1 short, stout. Female gonopore operculum oval in shape.

**Colour.**— The colour of fresh specimens is pale yellow or pale brown entirely, setae dark brown. Fingers of cheliped white. All the preserved specimens examined are brownish in colour.

**Size.**— The largest male specimen examined is 13.9mm x 9.5mm (holotype), while the largest female specimen examined is 11.3mm x 7.8mm (paratype).

**Habitat.**— The species is found near the mouth of a narrow river, and hiding among the pebbles in the calm stream. The crab is found together with a species provisionally referred to *Ptychognathus barbatus* (which will be named *Cognatus cavaterminus* in this thesis, see below) (M. Osawa, pers. comm.).

**Remarks.**— Kishino *et al.* (2001) recorded this species (as *P.* cf. *hachijyoensis*) from Amami-oshima Island, and collected from the substrate of sand and pebbles in a freshwater spring at the depth of 0.2 m. Nakasone & Irei (2003: fig. 65, tab. 6) mentioned that their material (as *P. johannae*) collected at a site of the salinity of 30 ‰ in Benoki River of the northern part of Okinawa Island. This probably means that the collection was made near the mouth of river, as the specimens examined from Izena Island.

**Distribution.**— Japan (Okinawa Islands) only.

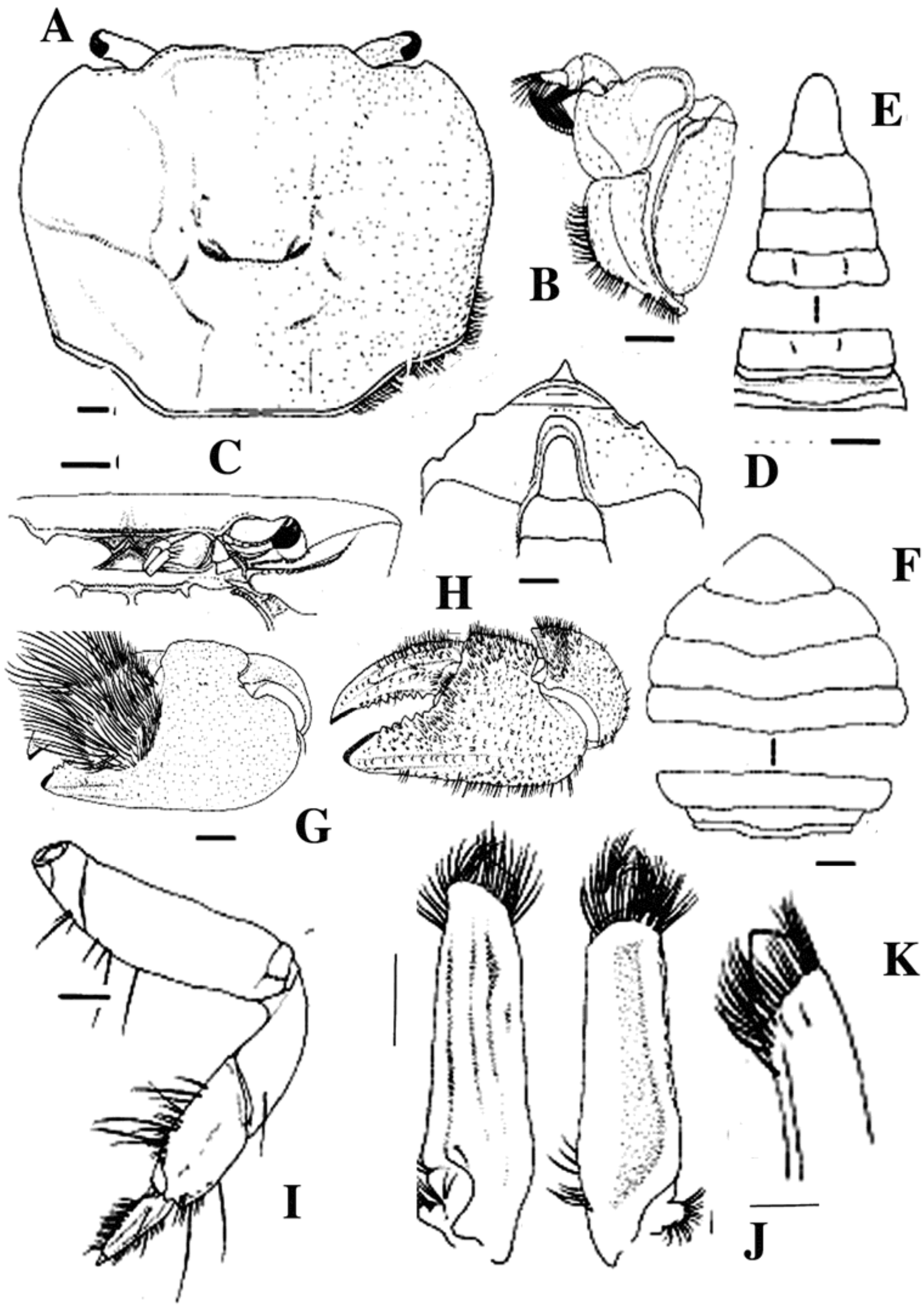



Figure 106. *Neoptychognathus insolitus* Osawa & Ng, 2006, male, holotype, 13.9 mm x 9.5 mm (CMNH-ZC 1960); female, 11.3 mm x 7.8 (CMNH-ZC 1961). A) carapace; B) third maxilliped; C) frontal view; D) sternites 1-4; E) male abdomen; F) female abdomen; G) frontal view of male cheliped; H) frontal view of female cheliped; I) last ambulatory leg; J) two views of G1; K) tip of G1. (Scale=1.0mm).

## Genus *Cognatus*, new genus

*Ptychognathus* – de Man, 1887: 719; de Man, 1895: 90; Alcock, 1900: 402; Tesch, 1918: 85; Sakai, 1939: 647, 658; Crosnier, 1965: 37; Dai *et al*., 1991: 515; Naiyanetr, 1998:102. (not *Ptychognathus* Stimpson, 18858)

**Type species.**— *Cognatus cavaterminus* new species, by current designation (see below).

**Gender.**— Masculine.

**Diagnosis**.— Carapace quadrante, slightly broader than long; dorsal surface glabrous, slightly punctate; regions well defined, flatm epigastric cristae distinct. Frontal margin slightly convex, usually gently bilobed. Anterolateral margin subcristate with three teeth including orbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod broad, with short flagellum. Epistome broad, flat, posterior margin entire, lobulated. Chela swollen, with a tuft of thick setae, fingers as long as palm. Ambulatory legs with short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen narrowly triangular in shape with seven moveable segments (six somites plus telson). Telson with distal margin concave. G1 long, slender. Female gonopore with rounded operculum.

**Etymology.**— "Cognatus' is the Latin for 'affinity'. It is used to indicate its close affinity to it original genus "*Ptychognathus*'. It is used as a noun.

**Remarks.**— *Cognatus* contains a single undescribed species that has always been identified as "*Ptychognathus barbatus*". The new genus possesses the following distinct characters viz. a) the carapace is slightly broader than long (vs. distinctly broader than long in *Ptychognathus*); b) there are three distinct anterolateral teeth (vs. two small teeth in *Ptychognathus*); c) the chela is usually large with setae on the external surface (vs. smaller chelae with/without setae on the external surface in *Ptychognathus*); d) the exopod of the third maxilliped is flat (vs. slightly convex in *Ptychognathus*), and e) the G1 is long (vs. proportionately shorter and stouter G1 in *Ptychognathus*).

The new genus is also different from *Mitragrapsus*, new genus in having a) a very distinct epigastric cristae (vs. indistinct epigastric cristae in *Mitragrapsus*); b) the regions are more well defined (vs. less defined in *Mitragrapsus*), and c) posterior margin of epistome lobulated (vs. almost straight in *Mitragrapsus*).

*Cognatus*, new genus, is also very different from *Neoptychognathus*, new genus, in the following features a) the carapace is more rounded (vs. more quadrate in *Neoptychognathus*); b) the anterolateral teeth are very broad (vs. more acute teeth in *Neoptychognathus*); c) the ambulatory legs are broader and stouter (vs. narrower and more slender in *Neoptychognathus*); d) the telson is very narrowly triangular (vs. more broadly triangular in *Neoptychognathus*), and e) the distal margin of the telson is distinctly concave (vs. distinctly convex in *Neoptychognathus*).

This genus is found mainly in the tropical waters of Indo-West Pacific. There are currently only two species in this genera viz. *C. cavaterminus*, new species (type species), and *C. benokiensis*, new species.

**Key to species in *Cognatus***

1a. Carapace subquadrate. Exopod of third maxilliped as broad as ischium. Merus of last ambulatory legs broad. ---------------------------------------------- ***C. benokiensis***

1b. Carapace subquadrate. Exopod of third maxilliped distinctly broader than ischium. Merus of last ambulatory legs long and narrow. -------------- ***C. cavaterminus***

## *Cognatus cavaterminus*, new species

(Figures 107; 108A-E)

*Ptychognathus barbatus* – Ortmann, 1895: 105; 1902: 515; Alcock, 1900: 406; de Man, 1902: 505; Pesta, 1913: 63; Tesch, 1918: 87; Maki & Tsuchiya, 1923; Horikawa, 1940: 29; Lin, 1949: 28; Dai, Yang, Song & Chen, 1986: 468, fig. 262; Fukui, Wada & Wang, 1989: 229, fig. 14; Dai *et al.*, 1991: 515, fig. 262; Chang & Chen, 1992; Huang, 1994: 596; Jeng, Chan, Fung, Tzeng & Yang, 1996: 100; Wang & Liu, 1996a: 109, figs. 136–137; Wang & Liu, 1996b: 77; Yu, Jeng, Chan, Ho & Shy, 1996: 15; Jeng, Chan, Fung & Tzeng, 1997; Jeng, 1997: 18, 58; Naiyanetr, 1998: 102; Wang & Liu, 1998; Jeng, Shao, Fung, Tzeng & Wu, 1998: 123; Ng, Wang, Ho & Shih, 2001: 46 (not *Ptychognathus barbatus* A. Milne-Edwards, 1873).

**Materials examined.**— **Holotype** – 1 male (13.0mm x 11.7mm) (ZRC-uncatalogued), river mouth, Paya River, Tioman Island, Pahang, Malaysia, coll. Hons. Class 2002, 7-12 Sep. 2002. – **Paratypes** –21 males (6.9-13.0mm x 6.1-11.6mm), 25 females (5.2-10.7mm x 4.1-9.2mm), 2 females (ovigerous) (7.3-8.9mm x 7.0-7.6mm) (ZRC-uncatalogued), river mouth, Paya River, Tioman Island, Pahang, Malaysia, coll. Hons. Class 2002, 7-12 Sep. 2002. – **Others** – **Indonesia** – 1 male (9.1mm x 7.8mm), 1 female (9.2mm x 7.5mm) (RMNH-D1228), Atjeh, Indonesia, coll. Cantstorm Museum, 1896; 1 male (14.6mm x 12.5mm) (RMNH-D193), Banda, Indonesia, coll. 1881; 4 males (5.4-11.3mm x 4.6-10.1mm), 1 female (ovigerous) (8.9mm x 7.9mm) (SFM-7078), Ternate, Indonesia, coll. Kukenthal, no collection date. – **Japan** – 3 males (12.4-14.3mm x 11.0-12.8mm), 3 females (ovigerous) (12.5-13.8mm x 10.8-1.9mm), (NSMT-CR-1001), no locality, coll. M. Takeda, 28 Jul. 1968; 13 males (9.5-14.4mm x 8.0-12.5mm), 3 females (8.9-10.7mm x 8.0-9.3mm), 20 females (ovigerous) (9.0-13.4mm x 7.9-11.4mm) (RU-no cat. number), Benoki River, Okinawa, Island, The Ryukyus, Japan, coll. 28 Jul. 1987. – **Philippines** – 3 males (9.5-11.9mm x 8.0-9.9mm), 4 females (9.8-11.0mm x 8.8-9.2mm) (USNM-46653), Manila, Luzon, Philippines, coll. 1908; 1 male (8.5mm x 7.1mm), 2 females (8.5-8.7mm x 7.0-7.1mm) (USNM-4598), Masin Loc Bay, Tacabales, Philippines, coll. 22 Nov. 1908. – **Somoa** – 17 males (6.2-10.9mm x 5.0-8.8mm), 8 females (6.0-9.5mm x 4.9-7.5mm), 1 female (ovigerous) (10.0mm x 8.4mm) (USNM-44588), Pago Pago, Somoa, coll. Aug. 1902. – **Taiwan** – 3 males (12.1-16.6mm x 10.5-14.1mm) (NTOU-no cat. number), Ho-Mei, Taipei County, coll. Z.H. Pang & J.F. Huang, 1 Dec. 1988; 1 male (15.6mm x 13.4mm) 2 females (12.5-15.2mm x 10.8-13.0mm) (TMCD-no cat. number), Hsin-Kang, Tou-Cheng, I-Lan

County, Taiwan, coll. J.H. Wang, 11 Apr. 1989; 1 male (34.3mm x 30.3mm) (IZAS-no cat. number), Ta-Xi, I-Lan County, Taiwan, coll. M.S. Jeng , 14 Oct. 1995; 3 males (15.5-18.0mm x 13.1-15.0mm) (NTOU-no cat. number), Ao-Ti, Taiwan, coll. 6 Jun. 1971. – **Thailand** – 2 males (14.8-17.0mm x 12.4-14.2mm) (SFM-7123), Phuket, Thailand, coll. 8 Jan. 1972.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth, flat. Front broad, anterior margin slightly concave medially. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, meri with antero-external angle broad, exopod very broad, 1.3 times broader than ischium. Cheliped symmetrical in males, fingers with a tuft of long setae at the base of outer surface, absent in female. Ambulatory legs short, flat, densely setose. Male abdomen triangular in shape with all segments freely moveable (six somites plus telson), telson extremely long, slender, distal margin of telson concave in shape. G1 long, slender. Female gonopore with rounded operculum.

**Etymology.—** 'Cava' and 'terminus' are the Latin words for concave and boundary respectively. The name is used as a noun in apposition, alluring to the concave distal margin of the telson.

**Colour.**— The colour of fresh specimens is dark brown (Wang & Liu, 1996a, 1996b), and all preserved specimens examined are light brown in colour.

**Size.**— This species can grow to quite large in adult size, the largest male specimen examined is 34.3mm x 30.3mm (IZAS-no cat. number), and the largest female specimen examined is 15.2mm x 13.0mm (TMCD-no cat. number).

**Habitat.**— It can be found under pebbles or rocks at river mouths (Wang & Liu, 1996a, 1996b).

**Remarks.**— The new species is commonly found in many parts of the Indo-West Pacific region. It is interesting that this very common species has been ignored for so long. de Man (1895) examined 18 male specimens and 28 female specimens collected from Atjeh (Indonesia) as well as four male and two female specimens from Penang (Malaysia). In his 1985 publication, he gave a brief description of the male abdomen (page 108, para. 4), stating that the abdomen is similar to that of *Ptychognathus riedelii*, but he did not comment on the concave distal end of the telson. I have examined specimens collected from Atjeh (RMNH-D1228), and these specimens too have the concave distal margin in the telson. Sakai (1939) had examined specimens collected from Loo Choo, also gave a good description of the species including the comment that the 'terminal segment of male extremely oblong, and terminally fringed with longish hairs' (Sakai, 1939: 659) but again there was no mention about t the distal margin of the telson. Dai *et al*. (1986: 468) gave a description in Chinese and mentioned the concave distal margin of the telson. They also provided a text-figure of the telson (text-fig. 262, fig. 4). However, they did not provide any further discussion. In Dai *et al.* (1991), they mentioned that '... telson elongately quadrilateral, distal margin haired, concave medially.' (Dai *et al.*, 1986: 516), and provided a good figure on page 515 (Dai *et al.*, 1991: text-fig. 262), showing a telson with concave margins. However, this species continued to be recognised as *Ptychognathus barbatus*.

Extensive examination of the '*Ptychognathus barbatus*' specimens housed in various museums, and freshly collected materials from Malaysia (Tioman), Indonesia (Sulawesi, Sumatra), China (Hainan Island, Guangdong and Fujian Pronvices), Japan (Okinawa), Taiwan and Philippines (Negros, Cebu, Panay, Ilo-Ilo, Leyte, Samar, and Luzon), has shown that the concavity on the telson is a very constant character in all the specimens examined. All of them are distinctly different from the original descriptions and figures of the real *Ptychognathus barbatus* provided by A. Milne-Edwards (1873). There is no doubt that what has been commonly called "*Ptychognathus barbatus*" from many parts of the Indo-West Pacific is actually a separate species, and are here described as new to science.

The new species is certainly superficially similar to *Neoptychognathus barbatus* in the form of the carapace, third maxillipeds and ambulatory legs but it is distinctly different from *N. barbatus* in the following features: a) the carapace shape is more rounded (vs. carapace is more quadrate in *Neoptychognathus*); b) the anterolateral teeth are very broad (vs. more acute teeth in *Neoptychognathus*); c) the exopod of the third maxillipeds is 1.3 times broader than ischium (vs. 1.1 times broader in *Neoptychognathus*); d) the ambulatory legs are broader and stouter (vs. narrower and more slender in *Neoptychognathus*); e) the telson is very narrowly triangular (vs. more broadly triangular in *Neoptychognathus*); f) the distal margin of the telson is distinctly concave (vs. distinctly in *Neoptychognathus*), and g) the G1 is relatively stouter and broader (vs. narrower and more slender G1 in *Neoptychognathus*).

In life, this species is generally more aggressive than its congeners. It is found usually on its own but sometimes with *P. ishii* or even *P. hachijoensis*. When they are kept together in captivity, they tend to fight and loose all their ambulatory legs very easily.

**Distribution.**— Taiwan, China, Japan, Indonesia, Philippines, Malaysia, India (?).

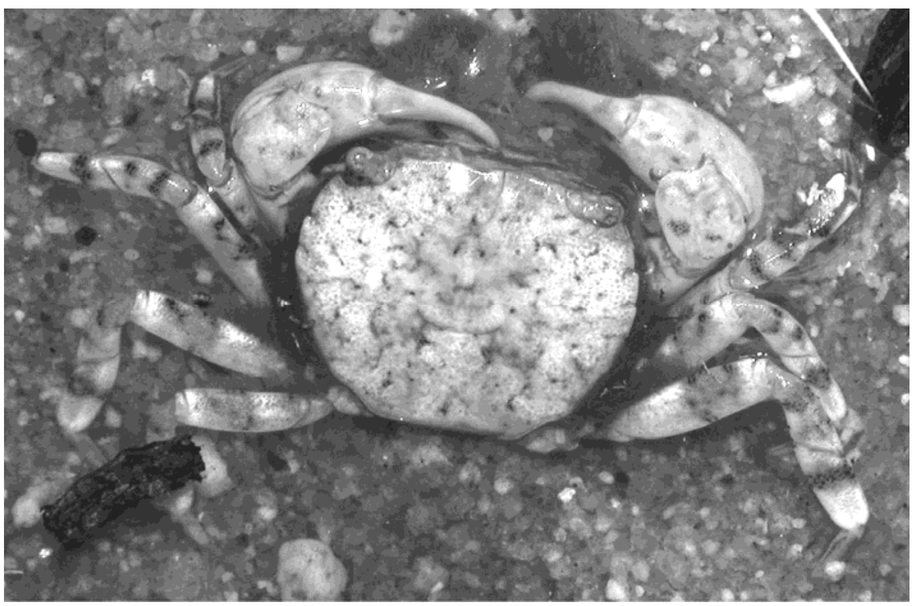


Figure 107. *Cognatus cavaterminus*, new species**,** male, holotype, 13.0mm x 11.7mm (ZRC-uncatalogued). Dorsal view.

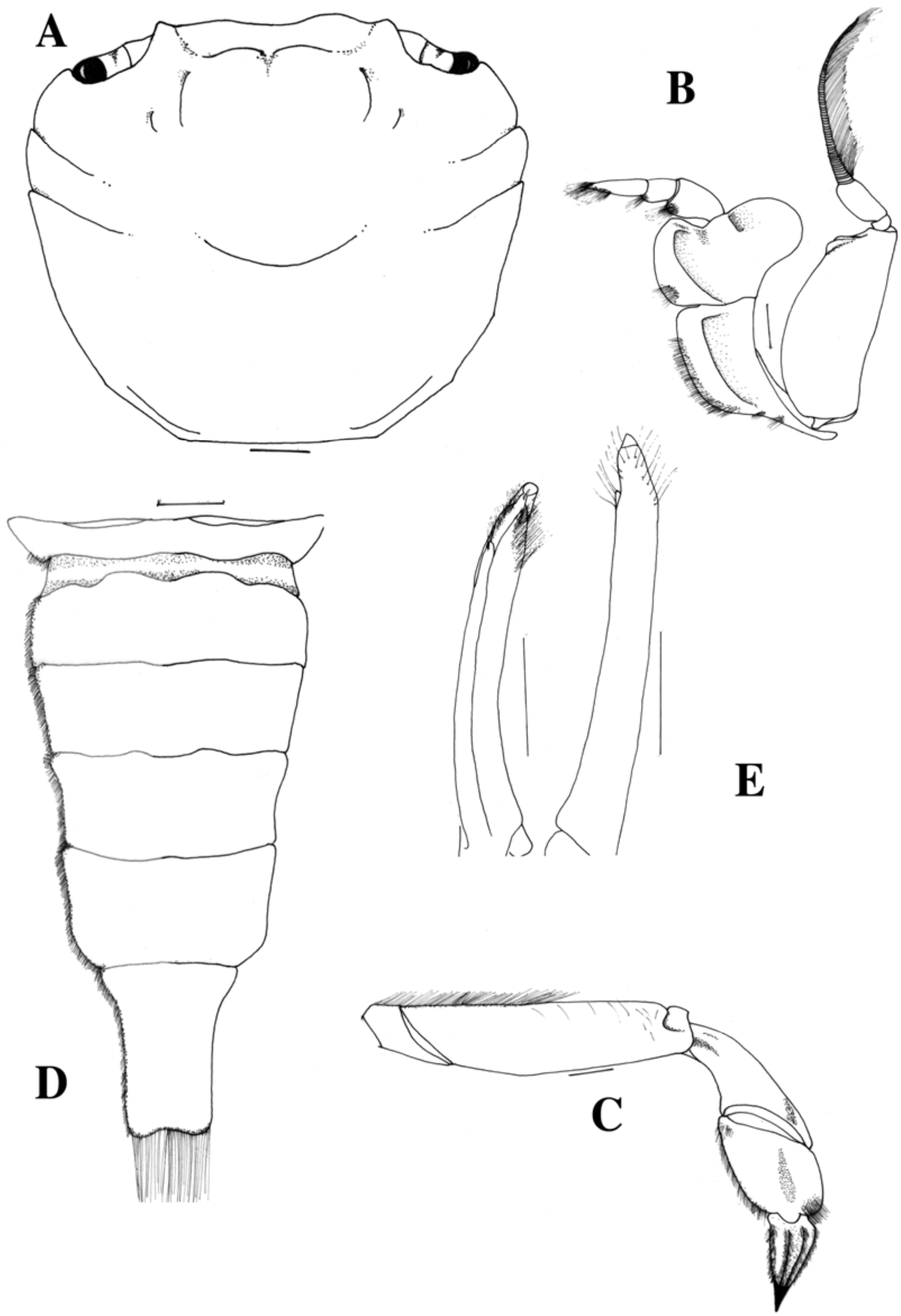



Figure 108. *Cognatus cavaterminus*, new species**,** male, holotype, 13.0mm x 11.7mm (ZRC-uncatalogued). A) carapace; B) third maxilliped; C) last ambulatory leg; D) male abdomen; E) distal tips of G1. (Scale=1.0mm).

## *Cognatus benokiensis*, new species

(Figure 109A-D)

**Materials examined.— Holotype –** male (11.4mm x 10.0mm) (RU-no cat. number), Benoki River, Benoki, Kunigami Village, Okinawa Island, The Ryukyus, Japan, leg. H. Hayashi, 7 Jul. 1990. – **Paratypes –** 27 males (4.5-10.3mm 4.0-9.1mm), Benoki River, Benoki, Kunigami Village, Okinawa Island, The Ryukyus, Japan, leg. H. Hayashi, 7 Jul. 1990.

**Diagnosis.**— Carapace subquadrate, dorsal surface smooth and flat. Front broad, anterior margin slightly concave medially. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod as broad as ischium. Cheliped large, symmetrical in males, fingers setose at proximal ends of pollex and manus. Ambulatory legs short, flat, margins setose. Telson broad, distal margin concave. G1 stout.

**Etymology.—** The species is named after its type locality, Benoki River, Benoki, Kunigami Village, Okinawa Island, Japan.

**Colour.**— The colour fresh specimens has not been documented, and the colour of all preserved specimens examined is brownish in colour.

**Habitat.**— It is found under small rocks and pebbles along river banks, and river mouth (Y. Nakasone, pers. comm.).

**Remarks.**— The new species is similar to *C. cavaterminus*, new species, but can be easily differentiated by the following characters: a) the stouter ischium of the third maxilliped, length to width ratio 2.3 (vs. more slender ischium, length to width ratio 2.5 in *C. cavaterminus*); b) possession of a more slender exopod of the third maxilliped, length to width ratio 3.0 (vs. a stouter exopod, length to width ratio 2.8 in *C. cavaterminus*); c) the exopod of the third maxilliped is as wide as the ischium of the third maxilliped (vs. exopod is broader than the exopod, 1.3 times wider than ischium in

*C. cavaterminus*); d) the stouter merus of the last ambulatory leg, length to width ratio 2.6 (vs. more slender merus, length to width ratio 3.0 in *C. cavaterminus*); e) the stouter propodus of the last ambulatory leg, length to width ratio 1.3 (vs. more slender propodus, length to width ratio 1.7 in *C. cavaterminus*); f) the dactylus of the last ambulatory leg is stouter, the length to width ratio being 2.7 (vs. more slender dactylus, length to width ratio 2.9 in *C. cavaterminus*); and g) a very stout G1, length to width ratio 7.0 (vs. very slender G1, length to width ratio 11.3 in *C. cavaterminus*).

**Distribution.**— Japan (Okinawa) only.

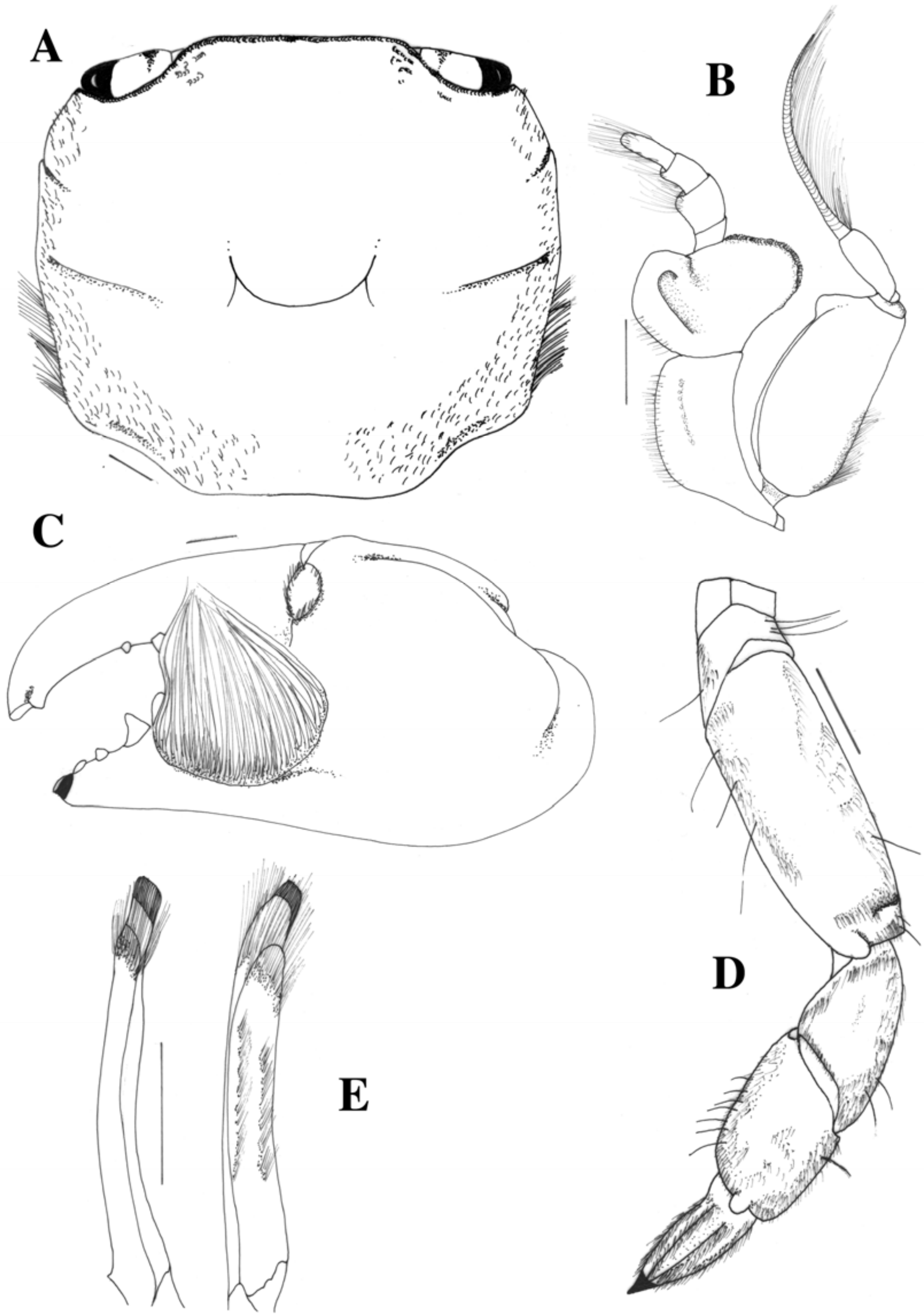



Figure 109. *Cognatus benokiensis*, new species**,** male, holotype, 11.4mm x 10.0mm (RU-no cat. number). A) carapace; B) third maxilliped; C) outer view of male chela; D) last ambulatory leg; D) distal tips of G1. (Scale=1.0mm).

## Genus *Abakos*, new genus

*Ptychognathus* – Sakai, 1939: 647, 658; 1955: 112, 193; 1976: 641 (not *Ptychognathus* Stimpson, 1858).

**Type species.**— *Ptychognathus takahashii* Sakai, 1939, by present designation.

**Gender.**— Masculine.

**Diagnosis**.— Carapace quadrangular, broader than long; dorsal surface glabrous, punctate; regions not well defined, flat. Frontal margin slightly convex, usually straight. Anterolateral margin subcristate with four teeth including a very small orbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly subparallel. Orbits small, eyes completely filling orbit. Third maxilliped short, stout, small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod broad, with short flagellum. Epistome broad, flat, posterior margin entire. Chela with setae, fingers as long as palm. Ambulatory legs with short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular in shape with seven moveable segments (six somites plus telson).

**Etymology.**— 'Abakos' is the Greek word for the numerical 'four', alluring to the presence of four teeth on the anterolateral margin of the carapace. It is used as artificially as a noun.

**Remarks.**— The new genus contains only one species, *P. takahashii*. The new genus is different from *Ptychognathus* by the following features: a) presence of a very small orbital tooth (vs. broad orbital tooth in *Ptychognathus*); b) presence of three anterolateral teeth after the very small orbital tooth (vs. two teeth in *Ptychognathus*); c) front of the carapace is vaulted downwards (vs. front not vaulted in *Ptychognathus*); d) front is distinctly bilobed (vs. front is straight in *Ptychognathus*); e) the very narrow eye stalks (vs. broader eye stalks in *Ptychognathus*), and f) the elongated telson of male abdomen (vs. broad telson in *Ptychognathus*).

### *Abakos takahasii* (Sakai, 1939), new combination

(Figure 110A-E)

*Ptychognathus takahasii* Sakai, 1939: 661; Horikawa, 1940: 29; Lin, 1949: 29; Shih *et al.*, 1991: 142; Ng *et al.*, 2001: 46.

**Materials examined.**— **Holotype** – 1 male (9.1mm x 7.6mm) (KPMNH-6545), Gang-kou, Lanyu, southern Taiwan, coll. S. Takahashi, no date. (Specimen examined by Dr. J. Okuno on behalf of the current author).

**Diagnosis.**— Carapace quadrangular, broader than long; dorsal surface glabrous, punctate; regions not well defined, flat. Frontal margin vaulted dowards, distinctly bilobed. Anterolateral margin subcristate with a very small orbital tooth plus three broader teeth. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly subparallel. Orbits small, eyes completely filling orbit. Third maxilliped short, stout, small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod broad, with short flagellum. Epistome broad, flat, posterior margin entire. Chela with setae, fingers as long as palm. Ambulatory legs with short setae, stout dactyli. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Telson elongated, sixth abdominal segment angular at the distal lateral margins.

**Colour.**— The colour of fresh specimens has not been documented, but the preserved specimen is brown in colour (J. Okuno, pers. comm.).

**Size.**— This is a small-size species, the largest male specimen examined is 9.4mm x 8.0mm (Sakai, 1939), there is no documentation of female specimen.

**Habitat.**— This species has been reported to be found under rocks and pebbles in mudflats in the intertidal region (Sakai, 1939).

**Remarks.**— The type locality of this species is Tanshui, Taiwan, but the species has not been collected in Taiwan since the first collection. I have made several attempts to collect fresh material of this species but none has been successful. The older locals living around Tanshui have told me that there are a lot of changes in the area, and many of the crab species that they used to catch during their childhood have all disappeared.

**Distribution.**— Taiwan only.

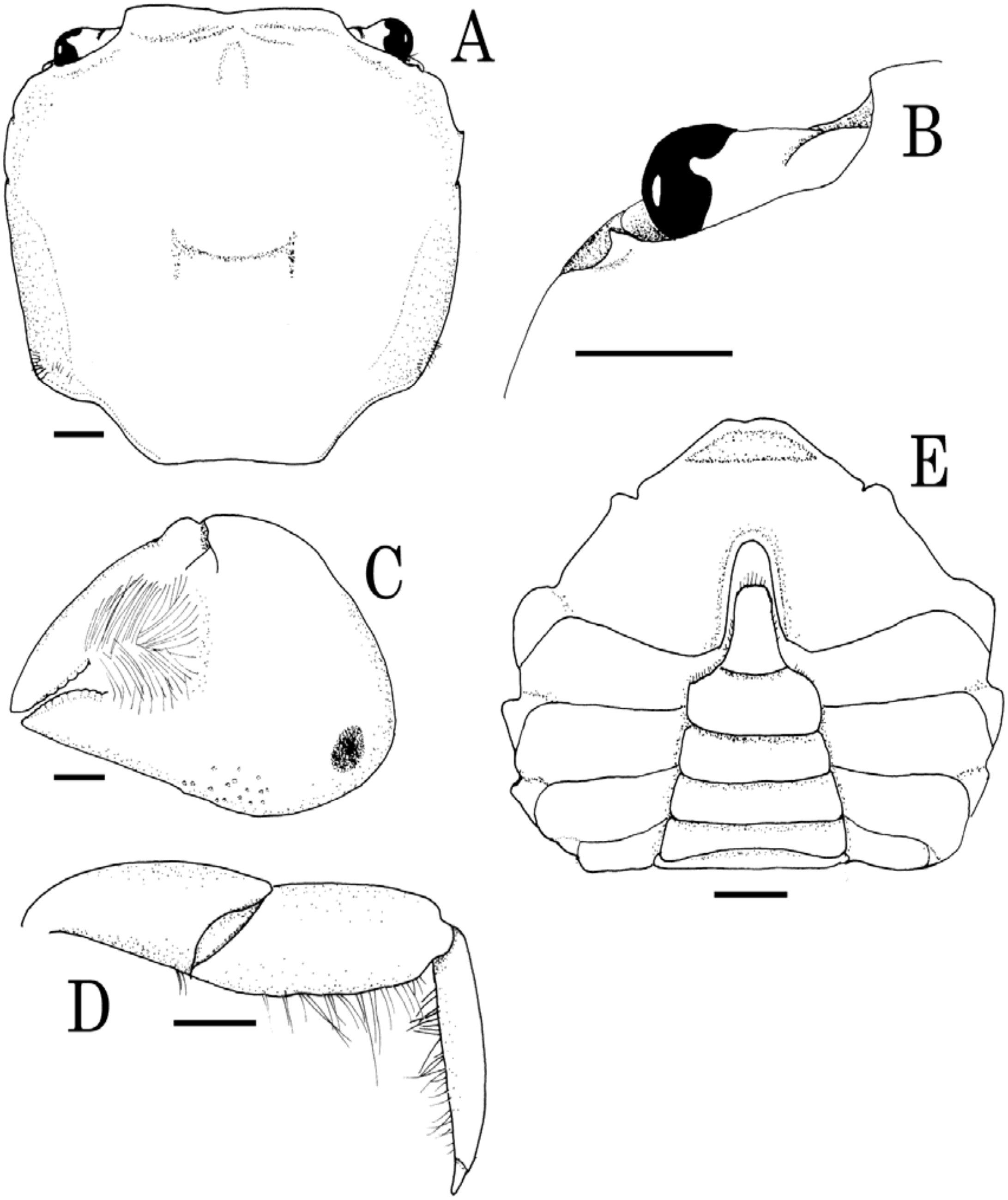



Figure 110. *Abakos takahasii* (Sakai, 1939), male, holotype, 9.1mm x 7.6mm (KPMNH-6545). A) carapace; B) frontal orbit; C) outer surface of cheliped; D) last ambulatory leg; E) sternum with abdomen. (Scale=1.0mm).

## Genus *Pseudogaetice,* new genus

*Gaetice* – Rathbun, 1923: 629 (not *Gaetice* Gistel, 1835).

**Type species.**— *Gaetice americanus* Rathbun, 1923, by monotypy.

**Gender.**— Feminine.

**Diagnosis.**— Carapace quadrangular, broader than long; dorsal surface glabrous, punctate; regions well defined, flat. Frontal margin distinctly bilobed. Anterolateral margin subcristate with three teeth including orbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, distinctly converging. Orbits small, eyes completely filling orbit. Third maxillipeds short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Chelae symmetrical, large in males, rounded, high, outer surface glabrous, inner surface of cheliped with tufts of short stiff setae, fingers slightly shorter than palm. Ambulatory legs glabrous, very broad, stout segments, stout dactyli. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular with all segments freely moveable (six somites plus telson).

**Etymology.**— 'Pseudo' is the latin word for false, it is used a prefix to '*Gaetice*' alluring to the fact that this species has been mistaken as a *Gaetice* species since its establishment.

**Remarks.**— The genus, *Gaetice,* has originally comprised of three species viz. *G. depressus* De Haan, 1933 (type species), *G. ungulatus* Sakai, 1939, and *G. americanus* Rathbun, 1923. The two species, *G. depressus* and *G. ungulatus* are very distinctly different from the *G. americanus* in terms of the external morphology (see below) and feeding habits (see below) that they have been transferred to their own subfamily (see below).

The new genus is very closely allied to the *Gaetice* in the form of the carapace, and ambulatory legs but it is distinctly different from the genus, *Gaetice* in the following features a) the third maxillipeds close with a distinct rhomboidal gap (vs. close without a gap in *Gaetice*); b) the suture line between the merus and ischum of the third maxilliped is straight (vs. oblique suture line in *Gaetice*); c) absence of the long palp on the third maxillipeds (vs. presence of the long palp in *Gaetice*); d) absence of the central medial sulcus which the palp of the third maxillipeds sits on the sternal plastron (vs. presence of the medial sulcus in *Gaetice*); e) the fingers of the chelipeds close with a small gap (vs. the chelipeds of the fingers close with a wide gap in *Gaetice*), f) ambulatory legs are all very broad and stout (vs. long slender legs in *Gaetice*), and g) presence of a tuft of long stiff setae on the inner surface of chelipeds (vs. glabrous in *Gaetice*).

The new genus is more closely allied to *Hemigrapsus* sensu stricto in the form of the third maxillipeds, but it can be easily discerned from the *Hemigrapsus* by the following a) anterolateral teeth are more acute (vs. broader anterolateral teeth in *Hemigrapsus*); b) carapace longer than broad (vs. carapace broader than long in *Hemigrapsus*); c) posterior margin of carapace distinctly converging (vs. subparallel in *Hemigrapsus*); d) the ambulatory legs are all slender and long (vs. broad and stout ambulatory legs in *Hemigrapsus*), and e) male abdomen is narrow (vs. broader male abdomen in *Hemigrapsus*).

There is only one species in this genus, *Psedogaetice americanus* Rathbun, 1923.

### *Pseudogaetice americanus* (Rathbun, 1923), new combination

(Figures 111; 112A-G)

*Gaetice americanus* Rathbun, 1923: 629.

**Materials examined.— Lectotype** – 1 male (15.4mm x 14.2mm) (USNM-17452), San Juns Gonzales, Bay, Gulf of California, coll. Steamer Albatross, 27 Mar. 1889. – **Paralectotypes** – 69 males (6.2-16.8mm x 6.0-15.3mm), 41 females (9.2-12.7mm x 8.5-11.4mm), 27 females (ovigerous) (12.0-12.9mm x 10.7-11.6mm) (USNM-17452), San Juns Gonzales, Bay, Gulf of California, coll. Steamer Albatross, 27 Mar. 1889. – **Others** – 6 male (8.4-14.9mm x 10.0-11.3mm), 1 female (11.3mm x 10.0mm) (USNM-no cat. number), Guaymas son Met, coll. S.A. Glaswell, 15 Jan. 1932; 2 males (8.2-11.7mm x 7.5-10.0mm), 1 female (7.7mm x 7.0mm) (USNM-no cat. number), Puerto San Carlos Sonora, Mexico, coll. E.D.. Richards, 4 Apr. 1940; 5 males (7.6-17.8mm x 5.8-16.0mm), 3 females (10.8-15.3mm x 8.7-13.1mm), 1 female (ovigerous) (10.2mm x 8.7mm) (USNM-no cat. number), San Felipe Bay, California, coll. S.A. Glaswell, 7 Jun. 1933; 5 males (13.6-17.5mm x 12.5-16.7mm), 10 females (ovigerous) (11.6-16.0mm x 10.5-14.6mm) (numerous specimens) (USNM-no cat. number), Pelion Island, Kino Bay, Sonora, Mexico, coll. S.A. Glaswell, 27 Dec. 1931; 2 males (12.4-13.8mm x 11.1-12.4mm), 5 females (ovigerous) (12.8-17.3mm x 11.4-15.3mm) (USNM-68397), Guaymas Bay, Sonora, Mexico, coll. B. J. Yost, 21 Jun. 1923; 1 female (5.3mm x 4.7mm), (USNM-17685), Lower California, no collection date; 1 male (11.5mm x 10.5mm) (USNM-17454), San Bartotone Bay, coll. U.S. Fish Commission, 11 Apr. 1889; 1 male (13.1mm x 11.5mm) (USNM-17453), Puerto Rebugio, Angel Island, coll. U.S. Fish Commission, 29 Nov. 1889; 2 females (ovigerous) (7.2-12.5mm x 6.0-11.0mm) (USNM-31511), shore of Guaymas Bay, Sonora, Mexico, coll. W. Palmer, 20 Feb. 1902; 4 males (13.9-18.4mm x 12.4-16.8mm), 3 females (11.0-13.6mm x 9.2-12.4mm), 14 females (ovigerous) (12.0-18.1mm x 10.6-15.6mm) (numerous specimens) (USNM-no cat. number), coll. S.A. Glaswell, 1931; 10 males (8.7-11.0mm x 7.4-9.4mm), 5 females (7.8-10.3mm x 6.5-9.5mm), 2 females (ovigerous) (8.0-8.2mm x 6.5-6.8mm) (USNM-no cat. number), Peurto Sardo, Sonora, Mexico, coll. S.A. Glaswell, Dec. 1924; 10 males (10.8-15.5mm x 9.9-14.1mm), 2 females (11.6-11.8mm x 10.0mm), 3 females (ovigerous) (11.3-13.4mm x 9.2-11.5mm) (USNM-no cat. number), Puerto San Podro, off San Pedro, Noroso, Gulf of Mexico, Sonora, coll. S.A. Glaswell, 25 Dec. 1931; 6 males (12.7-18.1mm x 11.3-16.3mm), 1 female (ovigerous) (12.5mm x 11.3mm) (USNM-no cat. number), Tiburon Island, east side, coll. S.A. Glaswell, 28 Dec. 1932; 1 female (ovigerous)

(16.7mm x 15.0mm) (USNM-89515), Puerto Penasco, Mexico, coll. Mac'Dinities family, 24 Dec. 1947; 2 males (15.7-17.4mm x 13.6-15.4mm), 1 female (12.6mm x 11.4mm), 1 female (ovigerous) (12.7mm x 11.0mm) (USNM-110649), Tiburon Island, Gulf of California, eastern side, coll. S.A. Glaswell, 28 Dec. 1931; 1 male (7.5mm x 6.4mm), 2 female (8.2-8.4mm x 7.3-7.4mm), 11 females (ovigerous) (7.3-10.1mm x 6.2-8.5mm) (USNM-17293), Guaymas, Mexico, near harbour, coll. P.J. Jouy, 23 Feb. 1891; 10 males (8.6-13.0mm x 6.8-11.4mm), 3 females (7.1-8.3mm x 6.6-7.5mm), 8 females (ovigerous) (7.4-16.7mm x 6.5-14.7mm) (numerous specimens) (USNM-17292), Guaymos, near harbour, Mexico, coll. P.J. Jouy, 23 Feb. 1891; 12 males (7.3-9.9mm x 6.5-8.9mm), 3 females (7.0-7.3mm x 5.8-6.4mm) (numerous specimens) (USNM-no cat. number), Peurto Escondida, coll. S.A. Glaswell, 16 Dec. 1931; 20 males (4.9-14.7mm x 4.0-13.5mm), 9 females (5.2-8.9mm x 4.7-7.5mm), 5 females (ovigerous) (8.3-12.8mm x 7.1-11.7mm) (numerous specimens) (USNM-uncatalogued), Hogolus Bay, B.C., coll. S.A. Glaswell, 4 Jan. 1932; 8 males (12,9-18.3mm x 11.2-16.6mm), 1 female (12.9mm x 11.2mm), 3 females (ovigerous) (11.0-15.5mm x 9.6-12.0mm) (USNM-74526), Punta Penascosa, Sonora, Mexico, coll. H.N. Lowe, Feb. 1934; 8 males (15.9-19.5mm x 14.3-17.3mm) (USNM-no cat. number), Pelican Island, Kino Bay, coll. S.A. Glaswell, 27 Dec. 1931.

**Diagnosis.**— Carapace subquadrate, broadening anteriorly, dorsal surface flat, smooth; frontal margin strongly bilobed. Anterolateral margin with three teeth including orbital tooth. Third maxilliped with merus, ischium squarish in shape. Infraorbital ridge with very few large, round granules. Chelipeds symmetrical, larger in males, high, fingers shorter than palm, fingers close with almost no gape. Ambulatory legs very short, broad. Male abdomen narrowly triangular in shape with all segments freely moveable (six somites plus telson). Telson broad. G1 long, thick, stout. Female gonopore with crescent-shaped operculum.

**Colour.**— The colour of fresh specimens has not been documented, but all the preserved specimens examined are dark cream to brown in colour.

**Size.**— The largest male specimen examined is 19.5mm x 17.3mm (USNM-no cat. number), and the largest female specimen examined is 18.1mm x 15.6mm (USNM-no cat. number).

**Habitat.**— It can be found under small rocks, close to the river mouths (Rathbun, 1923).

**Remarks.—** This species distinctly does not belong to the genus, *Gaetice*, as it lacks the following features that define the genus, *Gaetice* (see above).

**Distribution.**— South America (Mexico) only.

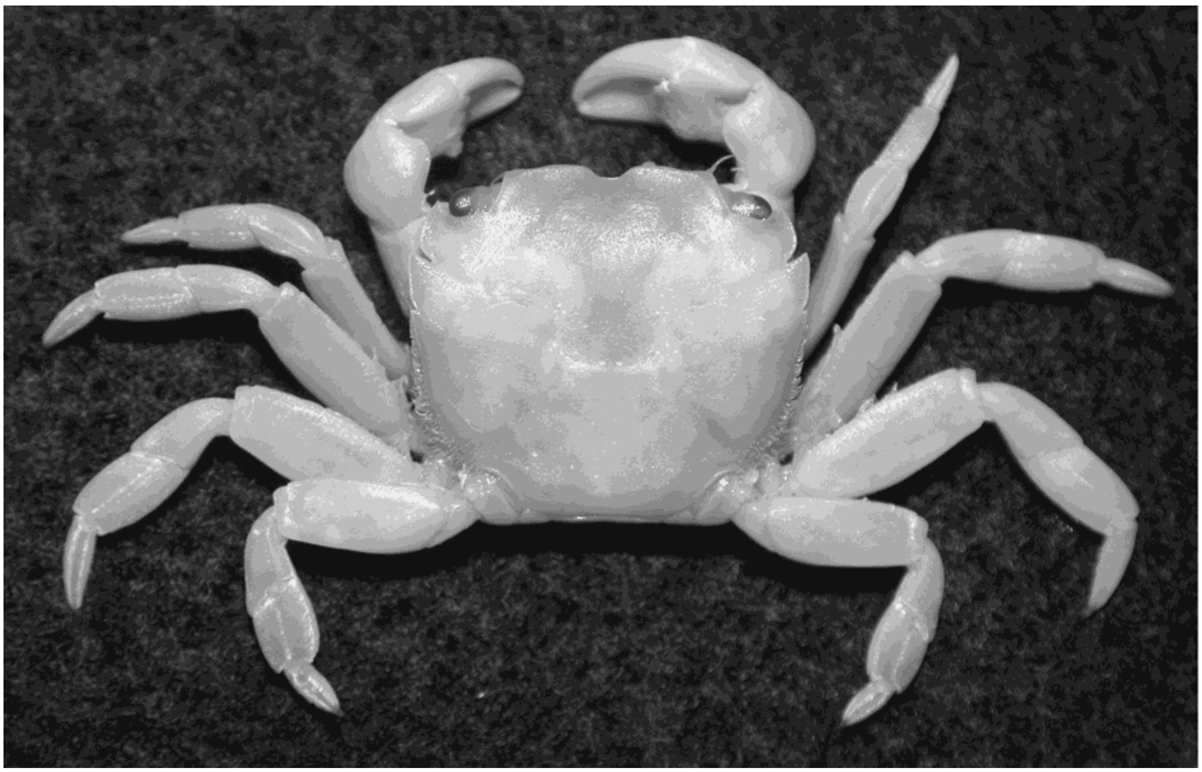


Figure 111. *Pseudogaetice americanus* (Rathbun, 1923), male, lectotype, 15.4mm x 14.2mm (USNM-17452). Dorsal view.

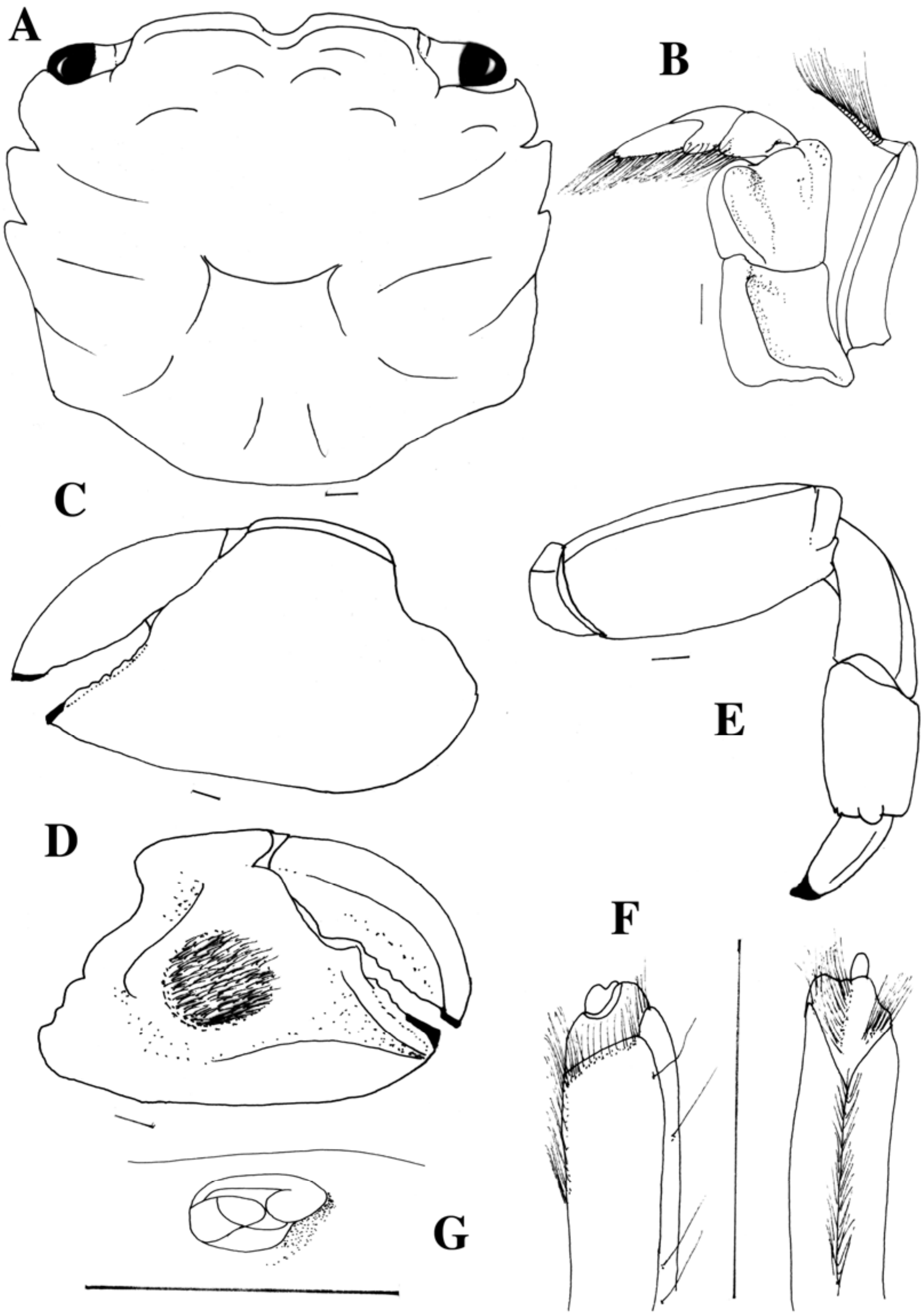



Figure 112. *Pseudogaetice americanus* (Rathbun, 1923), male, 16.8mm x 15.3mm; female 12.7mm x 11.4mm (USNM-17452)A). A) carapace; B) third maxilliped; C) outer view of chela; D) inner view of chela; E) last ambulatory leg; F) distal tips of G1; G) female gonopore. (Scale=1.0mm).

## Genus *Pyxidognathus* A. Milne-Edwards, 1878

*Pyxidognathus* A. Milne-Edwards, 1878: 109; de Man, 1883: 159; 1888: 148, pl. 10, fig. 4-6; Alcock, 1900: 408; 1902: 66, fig.3-3a); Tesch, 1918: 167; Ward, 1941: 15.

*Hypsilograpsus* de Man, 1879: 72.

**Type species.**— *Pyxidognathus granulosus* A. Milne-Edwards, 1878, by monotypy.

**Gender.**— Masculine.

**Diagnosis.**— Carapace subquadrate to rounded, broader than long; dorsal surface punctate; regions well defined, physiognomy very convex. Frontal margin slightly convex, distinctly four-lobe. Anterolateral margin subcristate usually with three teeth including orbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxillipeds short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Inner surface of chela with granulated; outer surface of pollex and manus glabrous; fingers as long as palm. Ambulatory legs with short setae, stout dactyli, posterior margins of all propodi with one large spine plus numerous small spines. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular with all segments freely moveable (six somites plus telson).

**Remarks.**— This genus was established by A. Milne-Edwards (1878) for *P. granulosus* A. Milne-Edwards, 1878. Currently, it comprises of *P. granulosus* A. Milne-Edwards, 1878, P. *subglobsus* Tesch, 1819*, P. deianira* de Man, 1888, and *P. fluviatilis* Alcock, 1900. Ward (1941) has transferred *P. deianira* to its own genus, *Parapyxidognathus* (see above). Serène and Moosa (1971: 9) synonymized *P. subglobsus* under *P. granulosus*. As such there are only two species left in this genus viz. *P. granulosus* and *P. fluviatilis*.

On the other hand, *Pyxidognathus* is very different from *P. fluviatilis* in a) the carapace shape is distinctly broader than long (vs. not distinctly broader than long *P. fluviatilis*); b) the physiognomy of the carapace being very convex (vs. flat in *P. fluviatilis*); c) the anterolateral teeth are broad and blunt (vs. narrow and acute in *P. fluviatilis*), d) the ambulatory legs are broad and stout (vs. long and slender in *P. fluviatilis*); e) presence of a strong spine on the distal end of the posterior margin of the propodi of the ambulatory legs (vs. proximal end in *P. fluviatilis*); f) very long and slender G1 (vs. short and stout G1 *P. fluviatilis*), and g) the female gonopore is very rounded (vs. slightly elliptical in *P. fluviatilis*). All these differences indicate that *P. fluviatilis* does not belong to the genus, *Pyxidognathus*, but it belongs to the genus, *Parapyxidognathus* (see above).

de Man (1879) established *Hypsilograpsus deldeni* for the species, *P. granulosus* independently, probably unaware of A. Milne-Edwards' paper. A few years later, he commented that *Hypsilograpsus* is the same species as *Pyxidognathus* (see de Man, 188l; Tesch, 1918b). I have not examined any *Hypsilograpsus deldeni* specimen, but based on the descriptions provided by de Man (1879, 1883), I believe that *Hypsilograpsus deldeni* is a junior synonym of *P. granulosus*. The genus, *Pyxidognathus* sensu stricto, has been last treated by Tesch (1918b), and Serène and Moosa (1971) in detail. Hence, it will not be treated further here.

## *Pyxidognathus granulosus* A. Milne-Edwards, 1879

(Figure 113A-C)

*Pyxidognathus granulosus* A. Milne-Edwards, 1897: 109; Serène & Moosa, 1971: 9; Holthuis, 1978: 18; Fransen *et al*., 1997: 127.

*Hypsilograpsus deldeni* de Man, 1879: 72.

*Pyxidognathus subglobosus* Tesch, 1918: 170.

**Materials examined.**— ***P. subglobosus*** – **Lectotype** – 1 male (18.5mm x 16.5mm) (ZMA-De-102.513), Nias, west coast of Sumatra, Indonesia, coll. J.P. Kleiwig de Zuraah. – ***P. granulosus* / *Hypsilograpsus deldeni*** – **Holotype —** 1 female (RMNH-1207), near Menado, North Celebes (Sulawesi), coll. 1836, leg. A.J. van Delden. – **Others** –**Indonesia** – 1 female (16.4mm x 14.4mm) (ZMA-no catalogue no.), Reo river, Flores, coll. M. Weber, no collection date.1 female (18.4mm x 16.0mm) (ZMA-no catalogue no.), river by Reo, Flores, coll. Heber, 1889; 1 male (15.8mm x 14.5mm) (NMB-1006a), Bonodokodi river, West Sumba, coll. E. Sutter, 10 Aug. 1949. – **Philippines** – 4 males (12.0-18.0mm x 11.1-16.5mm), 1 female (14.1mm x 12.4mm) (ZRC-uncatalogued), Kawasan Fall, Matutinao, Cebu Island, Philippines, coll. P.K.L. Ng, 30 Jul. 2003; 4 males (14.6-20.8mm x 13.7-17.2mm), 1 female (18.1mm x 16.0mm), 4 females (ovigerous) (13.5-19.6mm x 12.2-17.2mm) (ZRC-uncatalogued), Kawasan Fall, Cebu Island, coll. P.K.L. Ng, 30 Jul. 2003; 2 females (10.7-11.2mm x 9.8-10.2mm) (ZRC-uncatalogued), Inambacan River, Antequerra, Bohol Island, Philippines, coll. P.K.L. Ng, 27 Nov. 2001; 10 males (10.3-19.5mm x 9.6-17.3mm), 4 females (14.9-19.8mm x 13.4-17.2mm) (ZRC-uncatalogued), Ksawasan Fall, Matutinao, Cebu Island, Philippines, coll. H.C. Liu *et al.,* 2-3 Dec. 2001.

**Diagnosis.**— Carapace subquadrate, almost rounded, physiognomy very convex, dorsal surface smooth front broad, anterior margin slightly concave medially, distinctly four-lobed. Anterolateral margin with three teeth including the very small orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very broad. Chelipeds normal, symmetrical in males, large, fingers with without any long setae on outer surface. Ambulatory legs very short, flat, margins sparingly setose, posterior margins of propodi with numerous spines. Male abdomen triangular in shape with all segments freely moveable (six somites plus telson), distal margin of telson convex in shape. G1 stout, short. Female gonopore with rounded operculum.

**Colour.**— The colour of fresh specimens can vary from reddish brown, speckled with bark brown spots, to gray with brown and black spots (unpublished data) The colour of all preserved specimens examined is dark brown, dark grey in colour.

**Size.**— The largest male specimen examined is 20.8mm x 17.2mm (ZRC-uncatalogued), and largest female specimen examined is 19.6mm x 17.2mm (ZRC-uncatalogued).

**Habitat.**— The specimens can be found under rocks and pebbles in freshwater rivers, usually about 50 meters away from the river mouths, where they are subjected to some brackish water influence (unpublished data).

**Remarks.**— The type locality of this species is Ovalau, Fiji Islands. I have not been able to locate the type material of this species in MNHN during my last two visits there (1996 and 1999). However, the specimens of de Man's *Hypsilograpsus deldeni* were collected from near Manado (Celebes), and the holotype of *Hypsilograpsus deldeni* is still extant (see Fransen *et al*., 1997).

This species has been reported from two localities, Philippines and Indonesia. The local fishermen from Philippines (Cebu, Negros) commented that this species used to occur in abundance in the past (ca. 20 years ago) but the population has almost been wiped out in recent years due to coastal development and water pollution. The crabs have the habit of curling up their legs, such that the entire organism becomes round, and you can roll or throw them around like pieces of round rocks, and these crabs usually sustain no injury from such actions. The locals called these crabs 'the stone crabs'. The crab can maintain this 'curled-up' position for as long as an hour! (pers. observ.).

**Distribution.**— Philippines, Indonesia.


Figure 113. *Pyxidognathus granulosus* A. Milne-Edwards, 1868, male, 20.8mm x 17.2 (ZRC-uncatalogued). A) dorsal view; B) ventral view; C) frontal view.

## Genus *Scutumara* Ng & Nakasone, 1993

*Scutumara* Ng & Nakasone, 1993: 1, figs. 1-2; Ng & Komai, 2000: 48.

**Type species.**— *Scutumara enodis* Ng & Nakasone, 1993, by original designation.

**Gender.**— Feminine.

**Diagnosis.**— Carapace elongate, slightly broader than long, surfaces very smooth, glabrous, regions nor defined; epigastric cristae poorly developed or absent; front well produced, anterolateral margin convex, trilobed; posterolateral margins gently concave, distinctly converging. Antennules fold obliquely in large fossae. Posterior margin of epistome with three distinct lateral ridges; endostome with three palatal ridges. Third maxilliped merus broader than long, anterolateral angle strongly produced, auriculiform. Outer surfaces of chela with low but distinct subventral ridge, extending from near proximal edge of palm to just before tip of pollex. Closed fingers with proximal gap. Ambulatory legs glabrous, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular with all segments freely moveable (six somites plus telson).

**Remarks.**— Ng & Nakasone (1993) established *Scutumara*, and transferred two species previously placed in *Pseudograpsus*: *S. laniger* (Tesch, 1918), and *S. miyakei* (Nakamura & Takeda, 1972) to this new genus. Although the type specimen of *S. enodis* was represented only by a sub-adult female, Ng & Nakasone (1993) argued that on the basis of differences on the carapace and ambulatory legs, *S. enodis, S. laniger* and *S. miyakei* are distinct enough to warrant their placement in *Scutumara*. The discovery of the male *S. enodis* provides further evidence to the establishment of *Scutumara* (Ng & Komai, 2000). Ng & Komai (2000) described the male specimen of *Scutumara enodis*, and gave information on the male abdomen and male first pleopod (G1), and provided additional evidence in support of the establishment of the genus.

Based on the studies by Ng & Komai (2000), the genus, *Scutumara* is distinctly different from the genus, *Pseudograpsus* in the following features a) the exopod of the third maxilliped reaches two-thirds the length of the merus (vs. the exopod of the third maxilliped reaches to half the length of the merus in *Pseudograpsus*; b)  all known *Scutumara* species are ivory-cream white colour when alive (vs. all  all known *Pseudograpsus* species are chestnut in colour; c) the lateral margins of the sixth abdominal segment are generally rounded, (vs. the lateral margins are angular at the distal region in *Pseudograpsus*; d) the sixth abdominal segment is narrow, length to width ratio between 3.5 and 5.0 (vs. broad, length to width ratio between 1.5 to 2.0 in *Pseudograpsus*. Noteworthy is that the dentition on the anterolateral margin of the male specimen of *S. enodis* is less prominent than that of the female holotype. I interpret this as intraspecific variation.

There are currently three species in this genus viz. *S. enodis* Ng & Nakasone, 1993; *S. laniger* (Tesch, 1918), and *S. miyakei* (Nakamura & Takeda, 1972).

**Key to species in *Scutumara***

1a. Carapace elongated with gastric and cardiac groves, frontal margin less produced. ------------------------------------------------------------------------------------------ **2**

1b. Carapace elongated without gastric and cardiac groves, frontal margin very much more produced. ---------------------------------------------------------------- ***S. enodis***

2a. Infra-orbital ridge striated. Exopod of third maxilliped very narrow. ------ ***S. laniger***

2b. Infra-orbital ridge slightly striated. Exopod of third maxilliped broader. - ***S. miyakei***

## ***Scutumara enodis* Ng & Nakasone, 1993**

(Figure 114A-J)

*Scutumara enodis* Ng & Nakasone, 1993: 1, figs. 1-2; Ng & Komai, 2000: 48.

**Materials examined.— Holotype** – 1 female (5.8mm x 5.9 mm) (ZRC 1993.1), under littoral coral sand, Kunri-Hama Beach, Sesoko Island, Okinawa, Ryukyus, Japan, coll. P.K.L. Ng & Y. Nakasone, Apr. 1992. – **Others** —1 male (4.9mm x 5.1 mm) (CBM-ZC 3604), beach near Fukido-gawa river-mouth, Ishigaki Island, Yaeyama group, Japan, coll. T. Komai, 24 Mar. 1997.

**Diagnosis.**— Carapace slightly broader than long; dorsal surface smooth, glabrous, without setae; regions not defined. Frontal margin slightly convex, entire. Infraorbital margin not distinctly cristate, slightly raised. Anterolateral margin slightly arcuate, subcristate, with three indistinct teeth including orbital tooth. Orbits small, eyes completely filling orbit. Third maxilliped with foliaceous merus, broader than long; anterolateral angle strongly produced, auriculiform; distal margin distinctly bilobed, outer lobe larger, its base with small median cleft. Ischium longer than broad, sulcus not discernible. Small, distinct rhomboidal gape formed when closed. Chelipeds small, subequal, outer, inner surfaces smooth, glabrous; distinct ventral ridge running from near proximal part of palm to almost tip of pollex, inner surface without setae at base of fingers. Ambulatory legs with second pair longest, smooth, without spines or setae. Male abdomen triangular with all segments freely moveable (six somites plus telson). Lateral margins of thoracic sternites 4-5 finely granulated. G1 relatively slender, weakly curving outwards, terminal lobe elongate, apparently two-articulated, dorsally curved; genital opening lateral to base of terminal lobe.

**Colour.**— The colour fresh specimens is cream white (T. Komai, pers. comm.), all preserved specimens examined are uniformed cream white.

**Size.**— This is a small-sized species, the largest male specimen examined is 4.9mm x 5.1mm (CBM-ZC 3604), and the largest female specimen examined is 5.8mm x 5.9mm (ZRC 1993.1).

**Habitat.**— The specimens are found under littoral coral sand (T. Komai, pers. comm.).

**Remarks.**— *Scutumara enodis* can be easily separated from *S. laniger* and *S. miyakei* by the different structure of the frontal margin, the absence of gastric and cardiac grooves, and absence of setae on the inner surface of the palm (Ng & Nakasone, 1993).

Based on published descriptions and figures of *S. laniger* and *S. miyakei*, *S. enodis* can also be easily separated from the former two species by the following a) the third abdominal segment is narrow, length to width ratio: ca. 4.1 (vs. broader, ca. 3.5 in *S. laniger* and ca. 3.1 in *S. miyakei*); b) the lateral margins of the sixth abdominal segment are weakly rounded (vs. distinctly convex in *S. laniger*, and even more convex in *S. miyake*); c) the sixth abdominal segment is narrower, length to width ratio: ca. 5.0 (vs. broad, ca. 3.5 in *S. laniger*) and ca. 3.8 in *S. miyakei*); d) the length to width ratio of the telson is 1.0, which is similar to *S. laniger* (vs. relatively longer in *S. miyakei*, ca. 1.4); e) the G1 of *S. enodis* is characterised by having an elongated tube, and narrow subterminal lobe (vs. a short distal part and obtuse subterminal lobe in *S. miyakei*, and in having a long beak and small subteminal lobe in *S. laniger*), and f) the G1 is stouter and broader, which is similar to *S. miyakei* (vs. longer and more slender in *S. laniger*).

Specimens of *Scutumara enodis* are small in size, as are the other two known *Scutumara* species. The holotype female (a sub-adult) is only 5.8mm x 5.9mm (Ng & Nakasone, 1993). The smaller adult male specimen, is only 4.9mm x 5.1 mm. Similarly, the holotype of *S. laniger* is only 8.3 mm in carapace length, and that of *S. miyakei* is 3.6 mm.

**Distribution.**— Southern Japan (Okinawa south to Ishigaki Islands, Ryukyus).

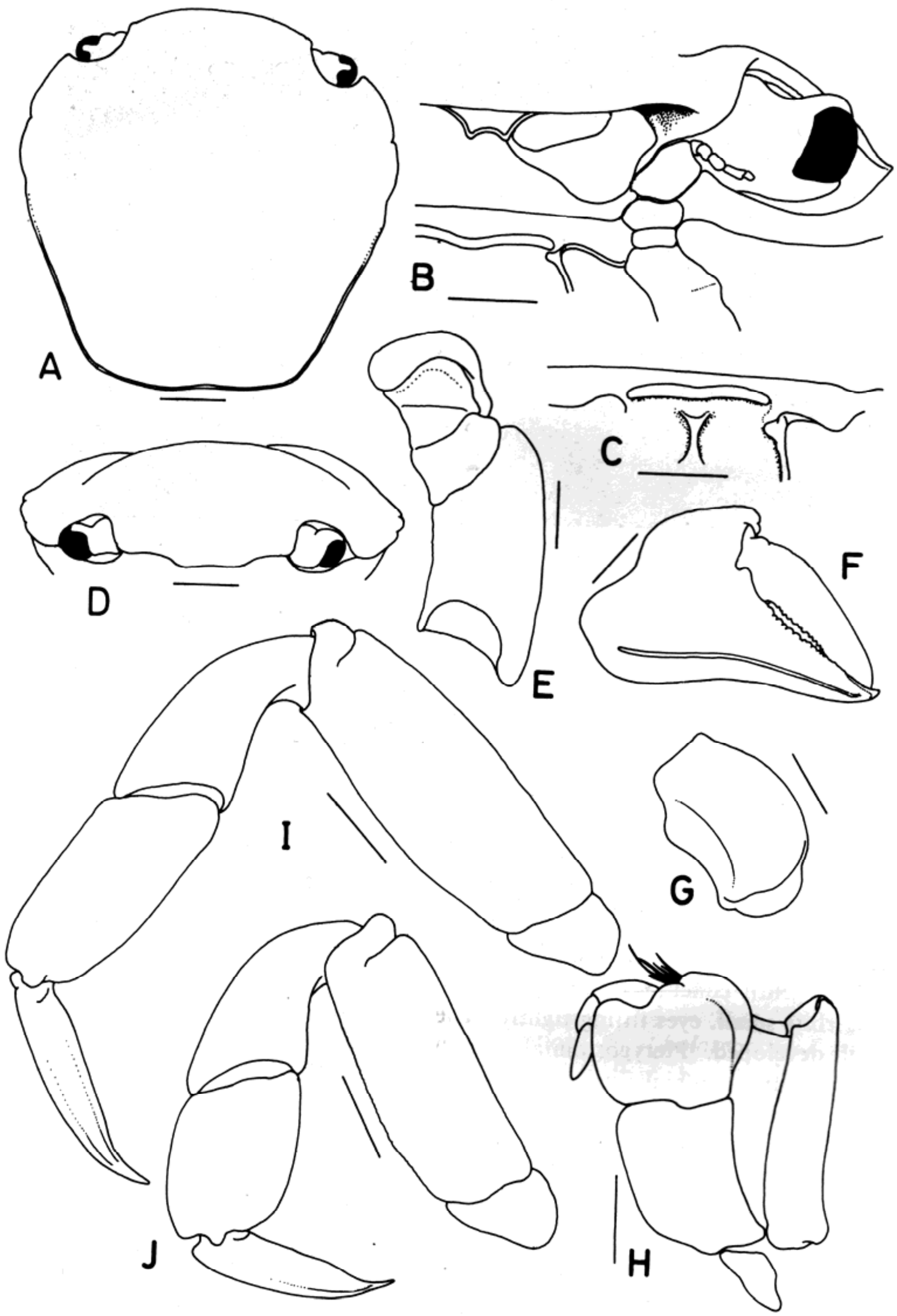



Figure 114. *Scutumara enodis* Ng & Nakasone, 1993, female, holotype, 5.8mm x 5.9 mm (ZRC 1993.1). A) carapace; B) frontal view with epistome; C) epistome; D) frontal view; E) merus of chela; F) outer surface of chela; G) carpus of chela; H) third maxilliped; I) fourth ambulatory leg; J) last ambulatory leg. (Scale=1.0mm).

## *Scutumara laniger* (Tesch, 1918)

(Figure 115A-C)

*Scutumara laniger* (Tesch, 1918) – Ng & Nakasone, 1993: 2; Ng & Komai, 2000: 48.

*Pseudograpsus laniger* Tesch, 1918: 99.

**Materials examined.— Lectotype** – 1 male (8.6mm x 7.9mm) (ZMA-De-102998), Tanah Djampea (sea) station 64, Flores, Indonesia, coll. 4 May 1899. – **Paralectotypes** – 1 female (7.7mm x 7.2mm) (ZMA-De-102999), station 127, Taruna Bay, Great Sangir Island, Indonesia, coll. M. Webber, 20/21 Jul. 1899. – **Others** – 3 males (6.8-7.5mm x 7.0-7.2mm) (USNM-90400), Guam; 2 males (6.8-7.5mm x 6.9-7.7mm) (ZRC 2000.0530), Guam, ex. BPBM, coll. 1925.

**Diagnosis.—** Carapace subquadrate, dorsal surface punctate, flat. Front broad, anterior margin slightly concave medially. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very narrow, narrower than ischium. Chelipeds asymmetrical in males, large, at distal end of fingers with a tuft of short soft setae on inner surface, absent in female. Ambulatory legs short, flat, margins sparsely setose. Male abdomen triangular in shape with all segments freely moveable (six somites plus telson); distal margin of telson convex in shape. G1 short, tip with a small, rounded subterminal lobe.

**Colour.—** The colour of fresh specimens has not been documented, and the colour of all preserved specimens examined is ivory white.

**Size.—** This is a small-sized species, the largest male specimen examined is 8.6mm x 7.9mm (ZMA-De-102998), and the largest female specimen examined is 7.7mm x 7.2mm (ZMA-De-102999).

**Habitat.—** Reportedly to be found under coral pebbles in sandy area along the coast (Tesch, 1918).

**Remarks.**— This is a very rare species.

**Distribution.—** Indonesia, Guam, India.

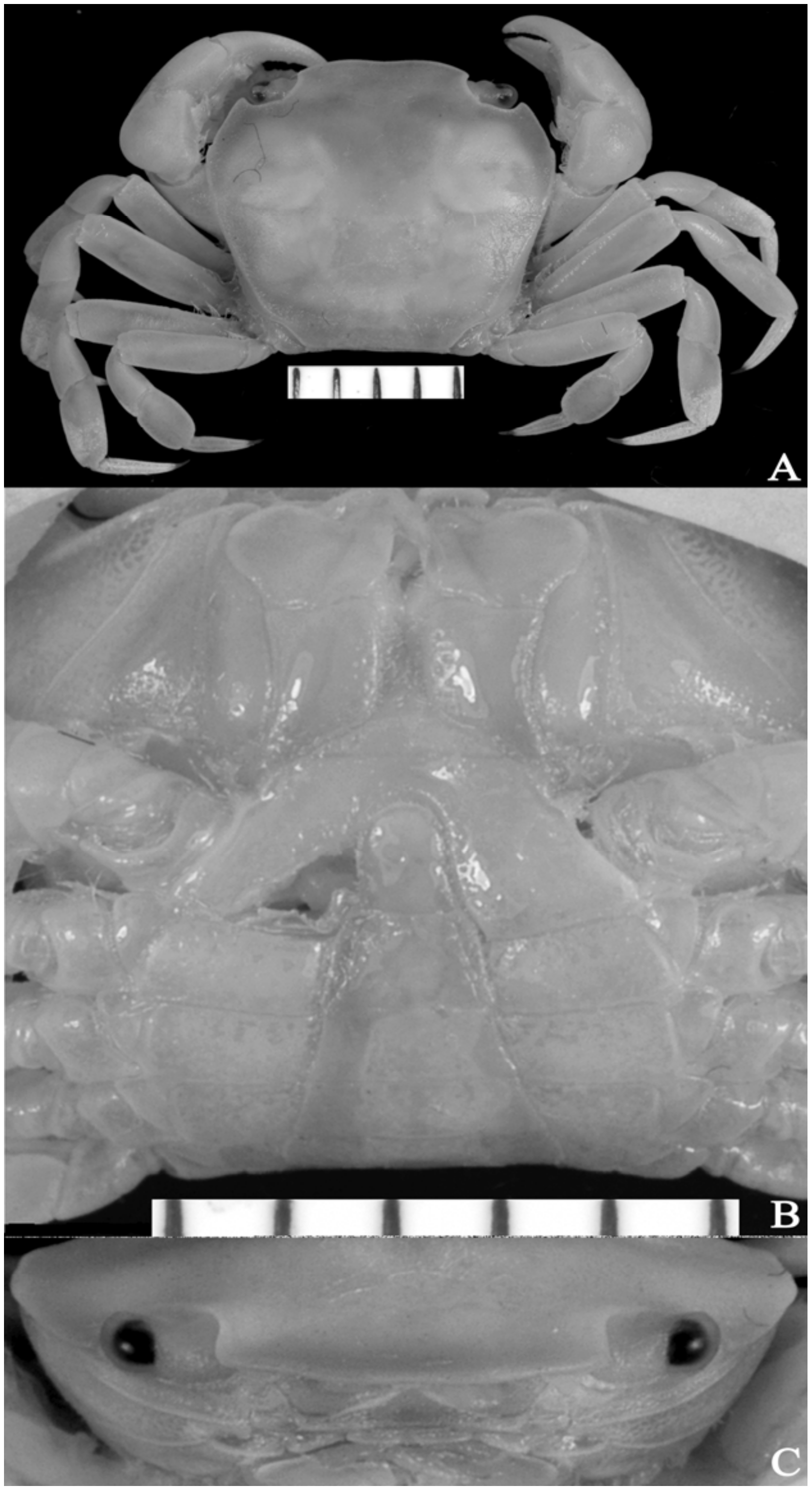



Figure 115. *Scutumara laniger* (Tesch, 1918), male, lectotype, 8.6mm x 7.9mm (ZMA-De-102998). A) dorsal view; B) ventral view; C) frontal view.

## *Scutumara miyakei* (Nakamura & Kurata, 1977)

(Figure 116A-G)

*Scutumara miyakei* – Nakamura & Kurata, 1977: 436.

*Pseudograpsus miyakei* Nakamura & Kurata, 1977: 436.

**Materials examined.— Holotype** – 1 male (3.8mm x 3.6mm) (NSMT-CR-862), Benoa, Bali Island, coll. 24 Aug. 1923.

**Diagnosis.**— Carapace subquadrate, dorsal surface punctate, flat. Front broad, anterior margin slightly concave medially. Anterolateral margin with three teeth including the very small orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very narrow, narrower than ischium. Cheliped symmetrical in males, large, base of fingers with a tuft of short soft setae on outer surface, absent in female. Ambulatory legs short, flat, margins sparsely setose. Male abdomen triangular in shape with all segments freely moveable (six somites plus telson), distal margin of telson convex in shape. G1 short, tip with a small, obtuse subterminal lobe.

**Colour.**— The colour fresh specimens has not been documented but the colour of the only preserved specimen examined is light cream..

**Size.**— This is a small-sized species, the only male specimen examined is 3.8mm x 3.6mm (NSMT-CR-862), the size of female specimen is unknown, as no female specimen has been collected.

**Habitat.**— There is no information on the habitat of this animal.

**Remarks.**— The species was described based on a specimen found in the collections of the National Science Museum in Tokyo, which was collected in 1924. There is no report of any other the specimens after its original report. Bali Island has developed into one of the world's most popular tourist island, and the beaches have been converted into tourist beaches. Attempts to obtain fresh materials from Bali Island and nearby islands have been unfruitful. Hence, there is no certainty if this species could be found on this island.

**Distribution.**— Indonesia (Bali Island) only.

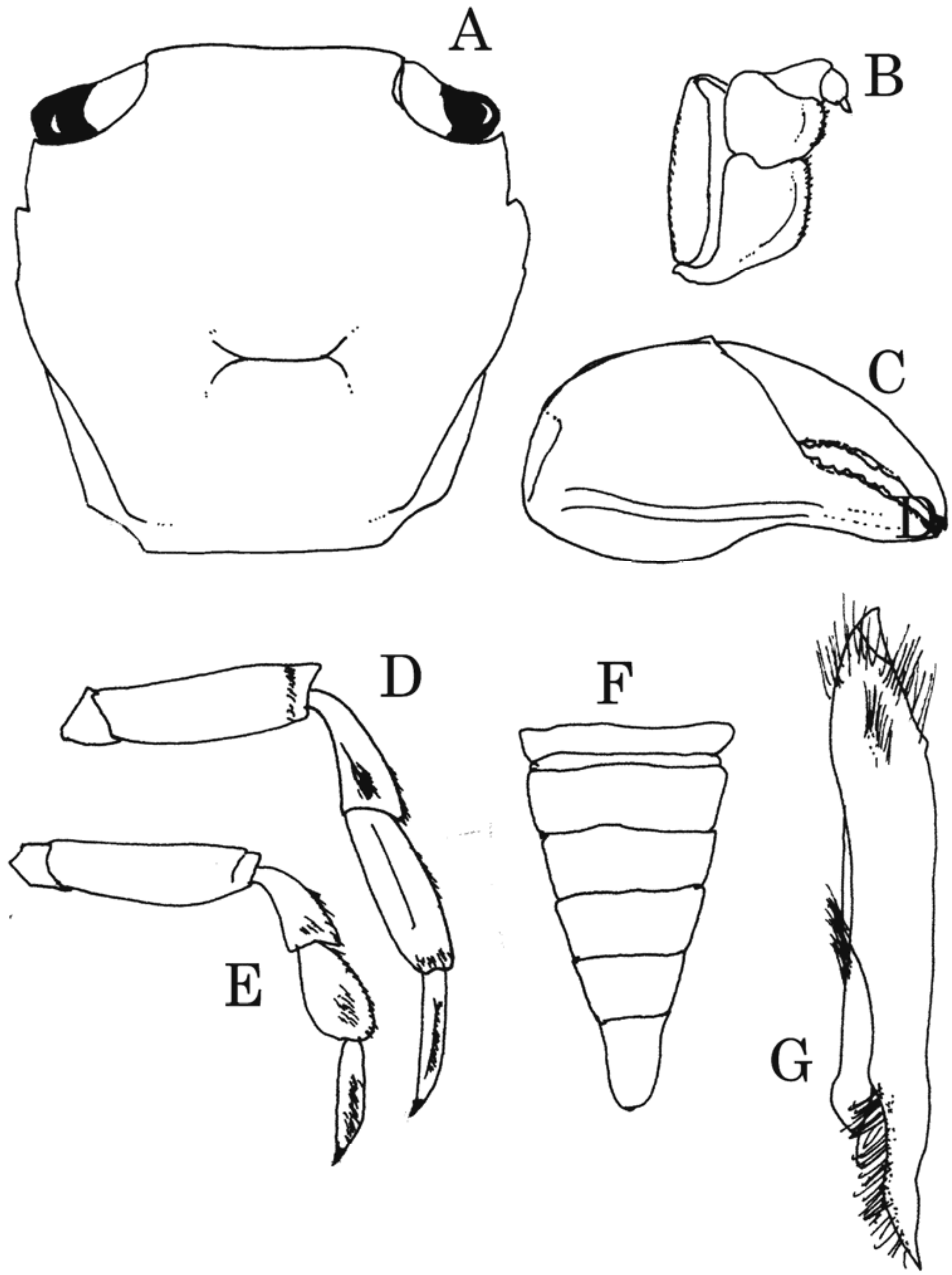



Figure 116. *Scutumara miyakei* (Nakamura & Kurata, 1977), male, holotype, 3.8mm x 3.6mm (NSMT-CR-862). A) carapace; B) third maxilliped; C) outer surface of cheliped; D) fourth ambulatory leg; E) last ambulatory leg; F) G1; H) male abdomen. (Scale=1.0mm).

## Genus *Tetragrapsus* Rathbun, 1918

*Tetragrapsus* Rathbun, 1918: 273; Spivak, 1997: 77; Schubart *et al*. 2000: 179; 2006: 193.

**200**

**Type species.**— *Brachynotus (Heterograpsus) jouyi* Rathbun, 1893, by original designation.

**Gender.**— Masculine.

**Diagnosis.**— Carapace quadrate, broader than long; dorsal surface glabrous, punctate; regions not well defined, slightly convex. Frontal margin curved slightly downwards, straight. Anterolateral margin subcristate with four small teeth including orbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, denticulate, subparallel. Orbits small, incomplete, eyes elongated. Infra-orbital ridge slightly raised, striated. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod narrow with short flagellum. Epistome broad, flat, posterior margin entire. Inner surface of chela with a tuft of soft setae; outer surface of pollex and manus glabrous; fingers shorter than palm. Ambulatory legs with short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen very narrowly triangular with all segments freely moveable (six somites plus telson).

**Remarks.**— This genus is very closely allied to *Hemigrapsus* but it is distinctly different from *Hemigrapsus* by the following characters viz. a) presence of four anterolateral teeth (vs. three teeth on the anterolateral margin in *Hemigrapsus*); b) the ischium of third maxilliped is almost squarish (vs. rectangular in *Hemigrapsus*); c) merus of third ambulatory leg very slender and long (vs. short and broad in *Hemigrapsus*); d) propodus of the third ambulatory legs long and slender (vs. short and broad in *Hemigrapsus*); e) dactylus of third ambulatory legs long and slender (vs. broader and shorter in *Hemigrapsus*), and f) propodus of last ambulatory legs is also very long and slender (vs. broad and short in *Hemigrapsus*).

The genus is also different from *Brachynotus* in the following viz. a) presence of four on the anterolateral margin (vs. presence of 3 teeth in *Brachynotus*); b) the teeth are broad (vs. acute teeth in *Brachynotus*); c) absence of pulvinus on chelipeds (vs. presence of a distinct pulvinus in *Brachynotus*); d) the ambulatory legs are all broader and shorter than those of *Brachynotus*.

This is a monotypic genus.

## *Tetragrapsus jouyi* (Rathbun, 1893)

(Figures 117A-C; 118A-F)

*Tetragrapsus jouyi* – Rathbun, 1918: 273; Spivak, 1997: 77.

*Brachynotus (Heterograpsus) jouyi* Rathbun, 1893: 247.

**Materials examined.— Holotype** – 1 male (12.9mm x 10.2mm) (USNM-17496), Guaymas, Mexico, Gulf of California, coll. P.L. Jouy, 27 Feb. 1891. – **Paratypes** – 4 males (7.5-12.7mm x 5.7-10.5mm), 5 females (5.9-12.8mm x 4.8-10.0mm) (USNM-17496), Guaymas, Mexico, Gulf of California, coll. P.L. Jouy, 27 Feb. 1891. – **Others** – 3 males (8.3-11.3mmm x 6.3-8.8mm), 1 female (7.7mm x 5.8mm), 2 females (ovigerous) (9.4-11.5mm x 8.6-8.8mm) (USNM-no cat. number, labeled as metatypes), Puerto Escondido, British Columbia, coll. S.A, Glaswell, 16 Dec. 1931.1 male (7.0mm x 6.2mm), 2 females (7.8-7.9mm x 6.6-6.9mm) (USNM-99805), Punta Penasco, Sonara, Mexico, coll. E.P. Chance, 13-26 Nov. 1955; 2 males (6.3-8.2mm x 6.4-4.9mm), 1 female (7.5mm x 5.9mm) (USNM-uncatalogued), La Paz, B.C., coll. S.A. Glaswell, 5 Aug. 1932; 2 males(10.3-10.8mm x 7.8-8.0mm), 2 females (ovigerous) (10.4-10.8mm x 8.4-8.5mm) (USNM-no cat. number), Angel de la Garcardia Island, Gulf of California, East central side , near lagoon, coll. S.A. Glaswell, 1 Aug. 1932; 1 male (3.9mm x 3.0mm) (USNM-70887), Juan Inernoulez, Chile, coll. N.L. Schmitt, 8 Dec. 1926.5 males (5.6-11.2mm x 4.1-9.0mm), 3 females (7.9-10.0mm x 5.9-7.9mm), 6 females (ovigerous) (7.7-11.2mm x 5.8-8.9mm) (USNM-110659), Angel de la Guardia Island, Gulf of California, coll. S.A. Glaswell, 1 Aug. 1932.

**Diagnosis.**— Carapace quadrate, broader than long; dorsal surface glabrous, punctate; regions not well defined, slightly convex. Frontal margin curved slightly downwards, straight. Anterolateral margin subcristate with four small teeth including orbital tooth. Posterolateral margin not sharply demarcated from anterolateral margin, denticulate, subparallel. Orbits small, incomplete, eyes elongated. Infra-orbital ridge slightly raised, striated. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae, merus with two slight vertical grooves, ischium broad. Exopod narrow with short flagellum. Epistome broad, flat, posterior margin entire. Inner surface of chela with a tuft of soft setae; outer surface of pollex and manus glabrous; fingers shorter than palm. Ambulatory legs with short setae, stout dactyli.

Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen very narrowly triangular with all segments freely moveable (six somites plus telson). G1 stout, short. Female gonopore with operculum oval in shape.

**Colour.**— The colour of fresh specimens has not been documented, but all the preserved specimens examined are cream to light brown in colour.

**Size.**— The largest male specimen examined is 12.9mm x 10.2mm (holotype), the largest female is 11.5mm x 8.8mm (USNM-no cat. number).

**Habitat.**— This species has been reported to be found under rocks (Rathbun, 1918) on the Gulf side of Mexico.

**Remarks.**— There is very little known about this species except that it is found in the Gulf side of Mexico. There is also very few reports of this species.

**Distribution.**—, Mexico (Guaymas), Chile, Argentina.

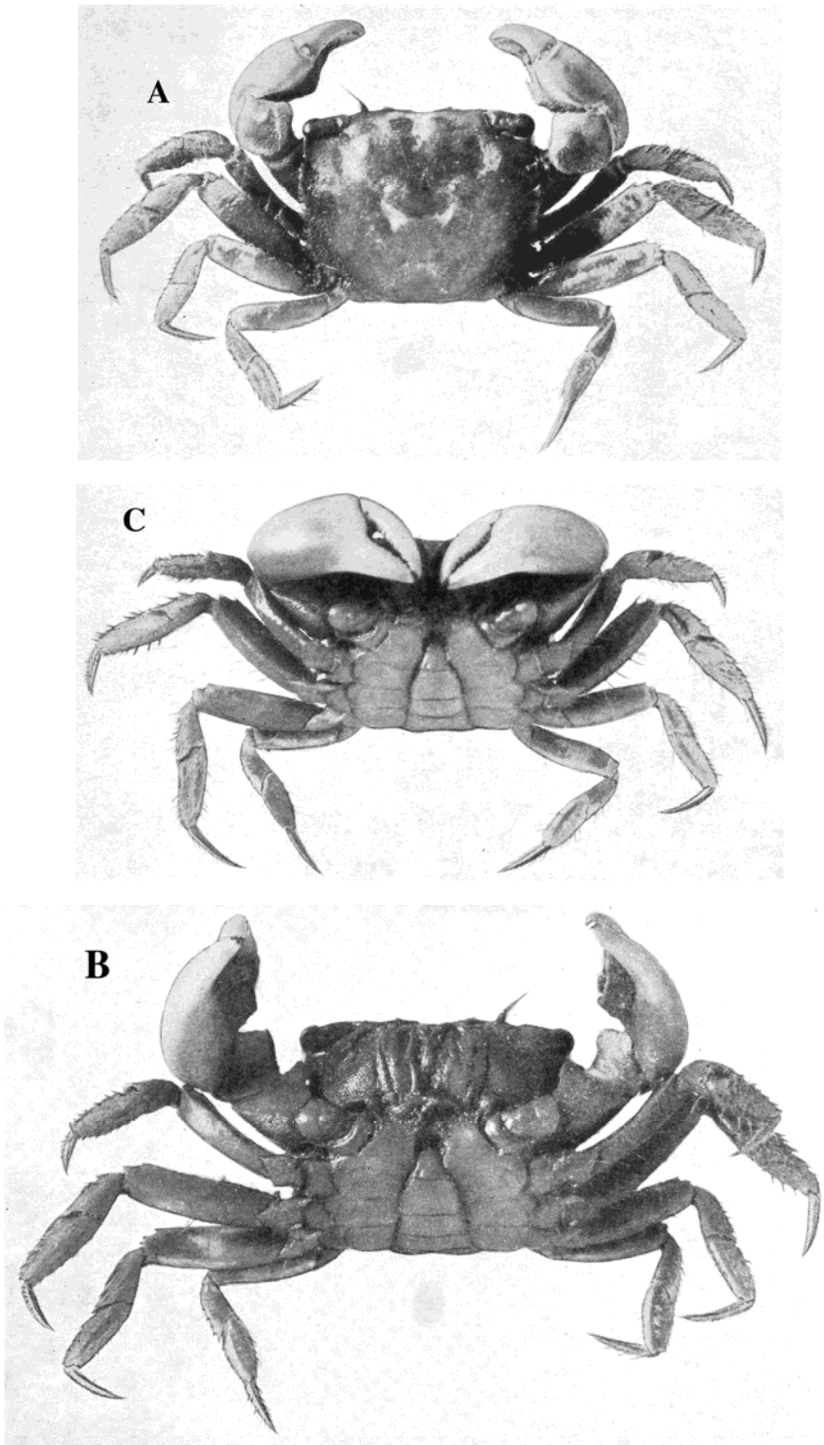



Figure 117. *Tetragrapsus jouyi* Rathbun, 1918. A) dorsal view; B) ventral view; C) ventral view showing inner surface of chela. (After Rathbun, 1918).

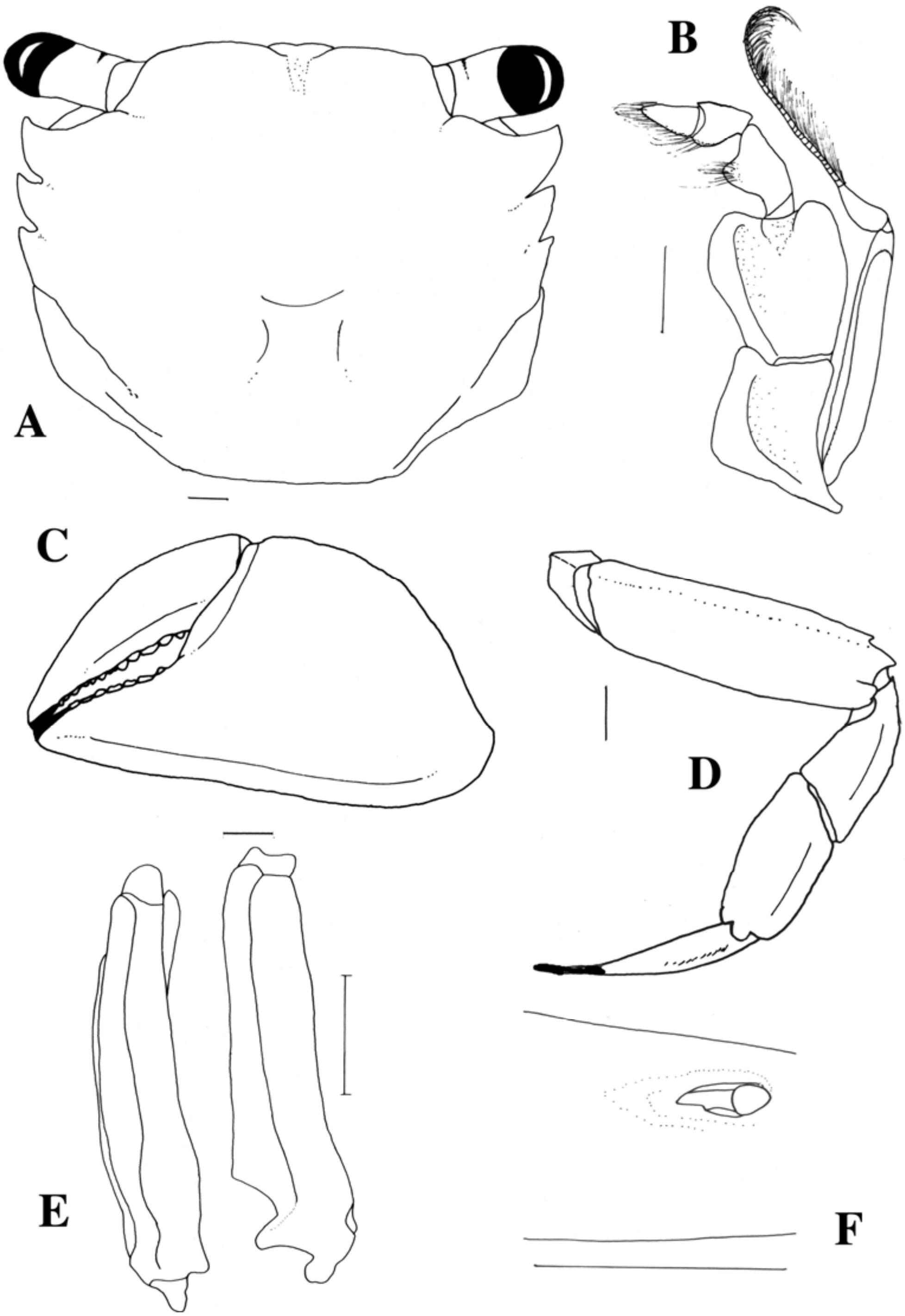



Figure 118. *Tetragrapsus jouyi* Rathbun, 1918, male, paratype, 12.7mm x 10.5mm; female, 12.8mm x 10.0mm (USNM-17496). A) carapace; B) third maxilliped; C) outer view of chela; D) last ambulatory leg; E) distal views of G1; F) female gonopore. (Scale=1.0mm).

## Genus *Utica* White, 1847

*Utica* White, 1847a: 43 (nomon nudum); White, 1847b: 86; White, 1847c: 207; Adams & White, 1849: 53, pl. 13, fig. 6; H. Milne Edwards, 1853: 177, pl. 7, fig. 4; Kingsley, 1880: 206; Ortmann, 1894: 713; de Man, 1895: 113; de Man, 1898: 702, pl. 28, fig. 24; Rathbun, 1910: 308, pl. 2, Figs. 2, 3; Tesch, 1918: 96; Balss, 1934: 234, fig. 12; Estampador, 1937: 539; Minei, 1972: 50, figs. 3-5; Holthuis, 1978: 19; Nagai & Nomura, 1988: 38; Shokita, 1990: 310, Table 3; Kishino & Wada, 2001: 59, fig. 1; Kishino *et al.*, 2001: 127; Shokita *et al.,* 2003: 101; Marumura & Kosaka, 2003: 64; Naruse, Ng, & Hsu.*,* 2005: 211.

*Pseudograpsus* – Schmeltz, 1874: 75 (not *Pseudograpsus* H. Milne Edwards, 1853).

**Type species.**— *Utica gracilipes* White, 1847, by monotypy.

**Gender.**— Feminine.

**Diagnosis.**— Carapace distinctly quadrangular in shape, broader than long; dorsal surface punctate; regions well defined, flat, some regions slightly concave. Frontal margin slightly deflected forward, straight. Anterolateral margin subcristate with three teeth, orbital tooth distinct. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. A distinct wide ‘V’ setose, granulated ridge at gastric region, a distinct horizontal raised setose, granulated ridge across the carapace at branchial region. Orbits small, eyes completely filling orbit. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Inner surface of chela with granules; surfaces of pollex and manus with tufts of long, soft setae; fingers as long as palm. Ambulatory legs long, slender, with short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular with all segments freely moveable (six somites plus telson). G1 long, narrow. Female gonopore with operculum circular in shape.

**Remarks.**— The genus is very easily recognized by the presence of the characteristic wide 'V' ridge on the gastric region and the horizontal setose granulated ridge across the carapace at the branchial region. This genus is primarily found in freshwater, and has the habit of feigning death when they are caught (Adams & White, 1850: 53; pers. observ.).

Currently, there are seven recognized species in this genus viz. *U. gracilipes* White, 1847 (type species); *U. barbimana* A. Milne-Edwards, 1873; *U. glabra*, A. Milne-Edwards, 1873; *U. crassimana* Haswell, 1881; *U. setosipes* Haswell, 1881; *U. nausithoe* de Man, 1898, and *U. borneensis* de Man, 1895. All species from the genus, *Utica* have the distinct flat carapace with the 90°-angled anterolateral teeth, and the wide 'v' ridge on the gastric region, and the raised setose, granulated ridge across the carapace at the branchial region. However, it must be noted that *U. borneensis* lack these four typical characters, and therefore, is transferred to it own genus (see below) in this report.

It must be noted that the genus *Utica* is also rather problematic as many of the types materials of species cannot be located, or are in very bad conditions that made examination of these specimens very challenging.

**Key to species in *Utica***

1a. Carapace distinctly broader than long; surface flat, almost glabrous, characteristic wide ‘V’ ridge and brachial horizontal ridge obvious. ----------- ***U. gracilipe**s*

1b. Carapace broader than long, slightly convex, surface setose, characteristic wide ‘V’ ridge and brachial horizontal ridge not obvious. ---------------------- **2**

2a. Ambulatory legs longer and slender. Chelipeds glabrous. ------------- ***U. glabra***

2b. Ambulatory legs broader. Chelae with setae on chelipeds. -------------------- **3**

3a. Ambulatory legs with surfaces sparingly setose. Cheliped surfaces slightly setose. ----------------------------------------------------------------------------------- ***U. setosipes***

3b. Ambulatory legs with surfaces densely setose. Chelipeds densely setose. --- **4**

4a. Merus of last ambulatory leg long and slender. -------------------------- ***U. crassimana***

4b. Merus of last ambulatory leg broader and shorter. ----------------- ***U. barbimana***

## *Utica gracilipes* Adam & white, 1847

(Figure 119)

*Utica gracilipes* White, 1847a: 43 (nom. nud.); White, 1847b: 86; White, 1847c: 207; Adams & White, 1849: 53, pl. 13, Fig. 6; H. Milne Edwards, 1853: 177, pl. 7, fig. 4; Kingsley, 1880: 206; Ortmann, 1894: 713; Tesch, 1918: 96; Balss, 1934: 234, fig. 12; Estampador, 1937: 539; Minei, 1972: 50, figs. 3-5; Holthuis, 1978: 19; Nagai & Nomura, 1988: 38; Shokita, 1990: 310, Table 3; Kishino & Wada, 2001: 59, Fig. 1; Kishino *et al.* , 2001: 127; Shokita *et al.,* 2003: 101; Marumura & Kosaka, 2003: 64; Naruse, Ng, & Hsu., 2005: 211. (All part)

*Pseudograpsus barbatus* – Schmeltz, 1874: 75 (not *Pseudograpsus barbatus* H. Milne Edwards, 1853).

*Utica nausithoe* de Man, 1895: 113; de Man, 1898: 702, pl. 28, fig. 24; Rathbun, 1910: 308, pl. 2, figs. 2, 3; Tesch, 1918: 96.

**Materials examined.**— **Lectotypes** – 1 female (22.9mm x 21.5mm) (MNHN-B3779), Philippines, don. Mus. Baritonnque. – **Others** – **Indonesia** – 1 female (28.1mm x 26.4mm), (ZRC-uncatalogued), freshwater river by the beach front, Murex Beach Resort, Manado, North Sulawesi, Indonesia, coll. H.H Tan, L.L. Koh & N.K. Ng, 14 Jul. 2003; 1 male (23.2mm x 21.5mm) (NMB-670d), Takoka Beach, West Sumbar, coll. E. Sutter, 31 Aug. 1949; 1 male (24.4mm x 22.3mm) (NMB-670a), Konga River, flores, Gesch. Mus. Amsterdam, 1916; 1 male (24.5mm x 23.5mm), 1 male (18.1mm x 17.5mm) (B-670c), Bondokodi river, West Sumba, coll. E. Sutter, 10 Aug. 1949. **– Philippines** – 1 male (11.4mm x 11.1mm), 1 female (16.1mm x 15.7mm), (ZRC-uncatalogued), Inmabalcan River, Antequerra, Bohol Island, Philippines, coll. P.K.L. Ng & Y. Cai, 16 Dec. 2000; 2 males (9.3-10.5mm x 8.9-10.0mm), 1 female (14.0mm x 13.8mm), (ZRC-uncatalogued), Inmabalcan River, Antequerra, Bohol Island, Philippines, coll. P.K.L. Ng *et al.,* 27 Nov. 2001; 4 males (24.5-28.6mm x 22.4-25.5mm), 2 females (23.3-26.3mm x 22.6-25.8mm) (USNM-44633), Veradero Mountain, Mindanao, Philippines, coll. 23 July 1908. – **Papua New Guinea** – 1 male (25.4mm x 23.9mm) (USNM-190789), Sepik River, Manembeg, Sepik District, Papua New Guinea, South Pacific Ocean, coll. A.W. Herre, 10 May 1929. – **Taiwan** – 1 female (14.0mm x 13.4mm) (USNM-123506), stream in mountains, Shih-Kuang-Chien Village, Chia Tung Hsiang, Pingtung County, coll. 13 Jan. 1961; 1 male (16.0mm x 15.5mm) (NMNS5008-004), Hengchun, Pingtung County, coll. Hsu *et al.*, 28 Jun. 2005.

**Diagnosis.**— Carapace rectangular, slightly broader than long, dorsal surface flat, depressed and punctate. Front broad, anterior margin straight, projected outwards. Anterolateral margin with four teeth including the small orbital tooth. Metabrachial region with a thick, ridge with very short, dense setae. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very broad, broader than ischium, merus and ischium equal in width and length. Cheliped symmetrical in males, large, fingers with a tuft of long setae on outer surface, absent in female. Ambulatory legs short, flat, margins densely setose. Male abdomen triangular in shape with all segments freely moveable (six somites plus telson), distal margin of telson convex in shape.

**Colour.**— The colour of fresh specimens is almost black in colour (pers. observ.), all the preserved specimens examined are dark brown with the black densely setose metabrachial ridge (see above) .

**Size.**— The largest male specimen examined is 28.6mm x 25.5mm (USNM-44633), and the largest female examined is 28.1mm x 26.4mm (ZRC-uncatalogued).

**Habitat.**— They are found in freshwater bodies. Specimens can be collected from still pools along the riverbanks, covered with dead leaves and branches (unpublished data).

**Remarks.**— This species is  not commonly found in the freshwater rivers. The reproductive biology of this species is not known, as there is no report whether this species migrate to the brackish water for spawning.

**Distribution.**— China, Taiwan, Okinawa (Japan), Philippines, and Indonesia.

Figure 119. *Utica gracilipes* White, 1847, female, 28.1mm x 26.4mm (ZRC-uncatalogued). Dorsal view.

## *Utica barbimana* A. Milne-Edwards, 1873

(Figure 120A-B)

*Utica barbimana* A. Milne-Edwards, 1873: 38, pl. 14, fig. 4.

**Materials examined.— Lectotype** – 1 male specimen on a wooden stump (MNHN-3781), New Caledonia, coll. M. Balaosa, no collection date.

**Diagnosis.—** Carapace quadragular, dorsal surface slightly setose, convex. Front broad, anterior margin slightly concave medially. Anterolateral margin with three teeth including very small orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod narrow, narrower than ischium. Cheliped symmetrical in males, large, fingers with a tuft of long setae on outer surface, absent in female. Ambulatory legs short, flat, margins densely setose.

**Colour.—** The colour fresh specimens has not been documented, but the preserved specimen (lectotype) is dark brown in colour.

**Size.—** This is a small-sized species. When I examined the specimen in 1999, I was not able to measure the carapace size, as the specimen was stuck on a wooden stump, which is in turn glued inside a very small box. A. Milne-Edwards had given the size of the specimen as $0^{m}$,01 by $0^{m}$,01 (A. Milne-Edwards, 1873: 297).

**Habitat.—** This species has been reported to be found in freshwater bodies (Milne Edwards, 1873).

**Remarks.—** From the figures provided by A. Milne-Edwards (1873: pl. 14, fig. 4), this species is more closely allied to the new genus, *Pseudoutica* (see below) as it lacks the characteristic 'V' ridge on the gastric region, and lacks the horizontal setose granulated ridge across the carapace at the branchial region. However, the identity of this species is not certain as I was not able to detach the specimen. Alphonse Milne-Edwards described both *Utica barbimana* and *Utica glabra* from the same locality without giving any detailed description of the two species. Examination of the materials in MNHN revealed only one specimen which has been mounted on a wooden stump. The stump has completely covered the ventral region, especially the third maxillipeds. The specimen also has no ambulatory leg or cheliped available for further examination.

Alphonse Milne-Edwards (1873) did not indicate any type material in his publication. He did not indicate on the specimens either, both the available specimens are syntypes. Since the identity of this species is in doubt, in order to stabilize the taxonomy of this species, the collection's curator (D. Guinot) and I (manuscript in preparation) has designated the specimens (MNHN-3871) to be the lectotype. Interestingly, there is no more reports on this species after its description.

**Distribution.**— New Caledonia only.

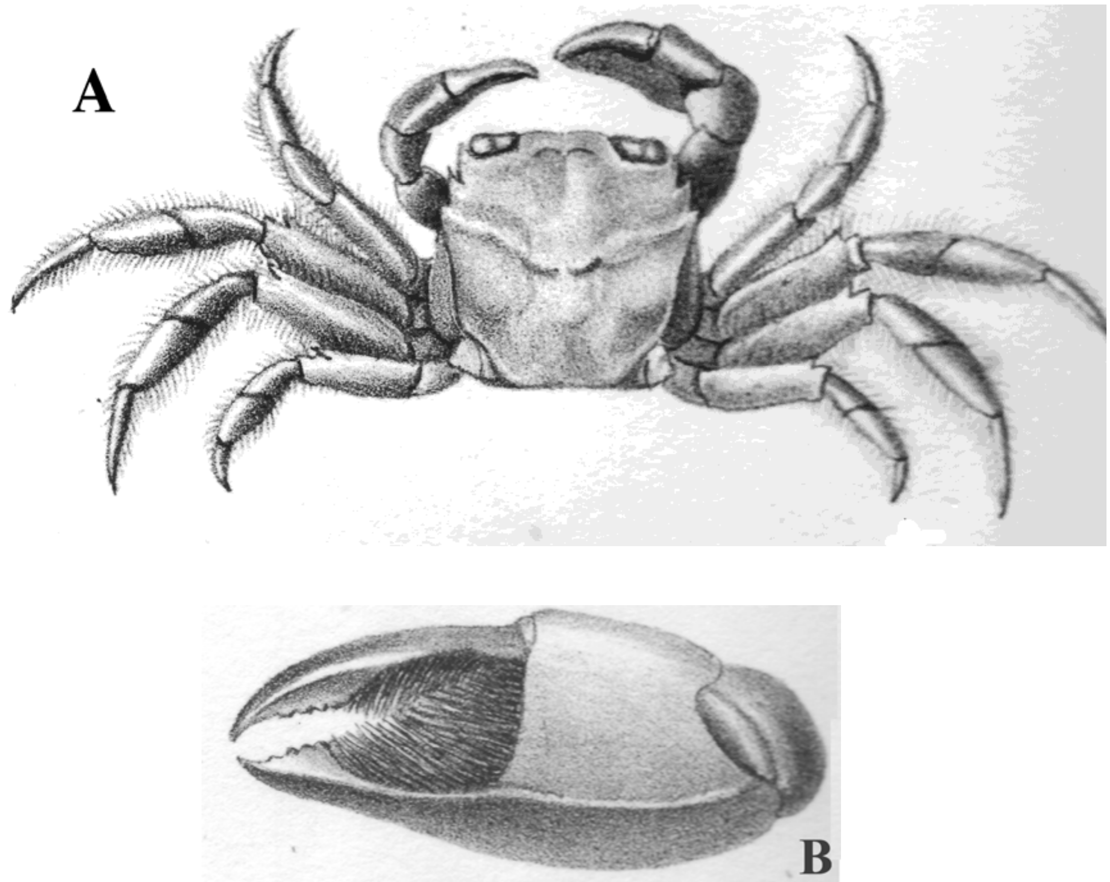



Figure 120. *Utica babimana* A. Milne-Edwards, 1868. A) dorsal view; B) outer surface of cheliped (after A. Milne-Edwards, 1868).

## *Utica glabra* A. Milne-Edwards, 1873

(Figure 121A-B)

*Utica glabra* A. Milne-Edwards, 1873: 296, pl. 14, fig. 3.

**Materials examined.— Lectotype** – 1 dry male specimen (MNHN-3780), Noumea (freshwater), coll. M. Balocsa, no collection date.

**Diagnosis.—** Carapace quadragular, dorsal surface slightly setose, convex. Front broad, anterior margin slightly concave medially. Anterolateral margin with three teeth including very small orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod narrow, narrower than ischium. Chelae symmetrical in males, large, fingers without any setae on cheliped. Ambulatory legs short, flat, margins glabrous.

**Colour.—** The colour of fresh specimen has not been documented, but the preserved dried specimen examined (lectotype) is dark brown in colour.

**Size.—** This is a small-sized species, again, the current author was not able to measure the carapace size, as the specimen was stuck on a wooden stump, which was in turn glued inside a box. A. Milne-Edwards gave the size of the specimen as $0^{m}$,013 x $0^{m}$,013 (A. Milne-Edwards, 1873: 297).

**Habitat.—** The label on the specimen indicated that the specimen was collected from the freshwater area in the type locality (MNHN-3780).

**Remarks.—** The specimen was collected from the type locality of Noumea, and it has not been collected or reported again.

The specimen in MNHN is a dried specimens, mounted inside a small box. The chelipeds and ambulatory legs are very brittle and fragile, a few legs have dropped off, and the legs are not complete. It was also not possible to examine the ventral region of the specimen properly as the specimen was mounted on the ventral surface. Based on the dorsal surface morphology, it is very similar to *Utica borneensis*, with a metabrachial ridge. However, the outer and inner surfaces of the cheliped are distinctly glabrous and smooth. Since, there is only one specimen with only one cheliped available, it is not possible to check if there was any trace of setae on the cheliped, thus, the identity of this species cannot be ascertained without examination of freshly collected materials.

For the time being, I regard this species as a valid good species since it is very distinct as it does not have any setae on the outer and inner surfaces of its chelipeds. Notably, this species has to be revised once fresh materials have been collected from the type locality.

**Distribution.**— New Caledonia only.

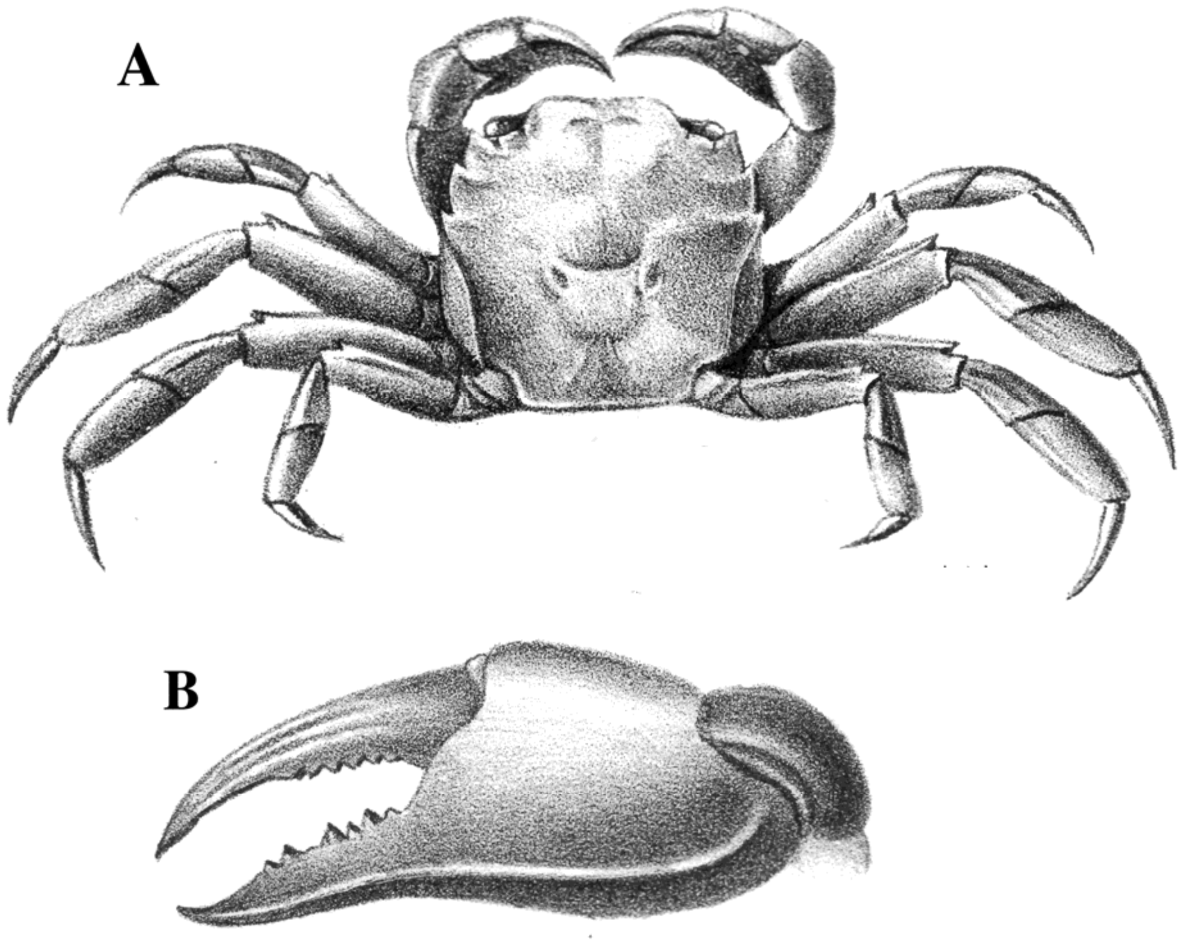



Figure 121. *Utica glabra* A. Milne-Edwards, 1868. A) dorsal view; B) outer surface of cheliped (after A. Milne-Edwards, 1868).

## *Utica crassimana* Haswell, 1881

(Figure 122)

*Utica crassimana* Haswell, 1881: 549; 1882: 102, pl. 2, fig. 3; Davie, 2002: 228.

**Materials examined.**— 1 male (16.2mm x 14.1mm) (QM-W24030), Boggy Creek, Myrtletown, southeast Australia, coll. P. Davie, 2 Jun. 1998. – **Others –** 1 male (15.3mm x 13.5mm), (QM-W8851), Calliope River, Southeast Queensland, coll. 10 Feb. 1977; 1 male (15.4 mm x 13.3mm), (QM-no cat. number), Elimbah Creek, Toorbul, Pumi Cestione passage, South East Queensland, coll. 7 May 1994, P. Davie.

**Diagnosis.**— Carapace subquadrate, upper dorsal surface smooth and flat. Front slightly concave medially. Anterolateral margin slightly vaulted, with four teeth including orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very broad, broader than ischium. Chelipeds symmetrical in males, large, fingers with a tuft of long setae on inner surface, absent in female. Ambulatory legs short, flat, margins densely setose. Male abdomen triangular in shape with all segments freely moveable (six somites plus telson), distal margin of telson convex in shape.

**Colour.**— The colour live specimens is pink with purple marking (Haswell, 1882: 102), but all the preserved specimens examined are uniformly brown in colour.

**Size.**— The largest male specimen examined is 16.2mm x 14.1mm (QM-W24030), the size of largest female is unknown, since only males specimens have been collected.

**Habitat.**— This species can be found in the mangrove, estuarine, low intertidal, mud substrate, shallow subtidal areas (P. Davie, pers. comm.).

**Remarks.**— The specimens examined which are housed in the Queensland Museum are very closely allied to *U. gracilipes* in the overall morphology. According to the descriptions and figures provided by Haswell (1881, 1882), the horizontal raised granulated ridge across the carapace at the branchial region of *U. crassimana* is not obvious. The overall carapace shape of *U. crassimana* is also not as angular as *U. gracilipes*.

The type materials of Haswell are located in the Australian Museums (Griffin & Stanbury, 1970; Ng & Ahyong, 2001), but there is no mention of *Utica* specimens listed in both publications. It is possible that the types specimens of *Utica crassimana* Haswell, 1881 and *Utica setosipes* Haswell, 1881, are lost. Clearly neotypes are needed, and this will be done with my Australian colleague when I reappraised the varunid species in Australia.

**Distribution.**— South East Australia only.

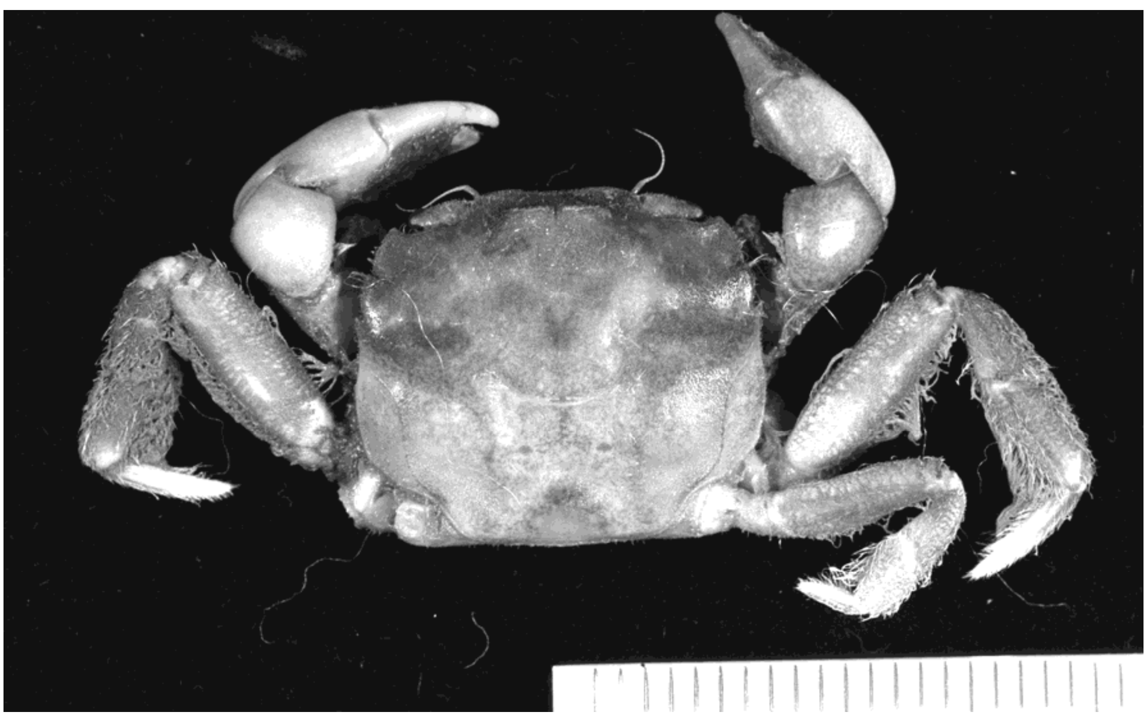


Figure. 122. *Utica crassimana* Haswell, 1881, male, 15.3mm x 13.5mm (QM-W8851). Dorsal view.

## *Utica setosipes* Haswell, 1881

*Utica setosipes* Haswell, 1881: 549; 1882: 101, pl. 2, fig. 2; Davie, 2002: 228.

**Materials examined.**— No material examined.

**Diagnosis.**— Carapace subquadrate, dorsal surface short dense setae. Front not prominent, anterior margin straight. Anterolateral margin with three teeth including very small orbital tooth. Third maxillipeds close with a small gap, merus with antero-external angle broad, exopod very broad, broader than ischium. Cheliped symmetrical in males, large, fingers with a tuft of long setee on outer surface, absent in female. Ambulatory legs short, flat, margins densely setose. Male abdomen unknown. (Modified from Haswell, 1882).

**Colour.**— The colour of fresh specimens is dark brown (Haswell, 1882) but colour of preserved specimens has not been documented.

**Size.**— The largest size of this species is not known, but the only species reported is 12.7mm x 11.1mm (Haswell, 1882: 102).

**Habitat.**— This species has been reported to be found in estuarine, low intertidal, shallow subtidal area (Haswell, 1882).

**Remarks.**— The descriptions (Haswell, 1881; 1882) and figures provided (Haswell, 1882) are very brief and was based on a female specimen. Based on both the descriptions and figure, *Utica setosipes* is closely allied to the only species in the new genus *Pseudoutica* (see below) in the form of the carapace, ambulatory legs and habits. Haswell has also added that the species is closely allied to *U. glabra* but differs from it in having the front being less prominent and more setose ambulatory legs. He further added that this species was found along the shore, while the *Utica* species are fresh water (Haswell, 1882: 102). Since no specimens were examined, it will remain in the genus *Utica* for the time being. This species has only been reported from Queensland, Australia only.

**Distribution.—** North East coast of Australia only

## Genus *Pseudoutica,* new genus

*Utica* White, 1847a: 43 (nomon nudum); White, 1847b: 86; White, 1847c: 207; Adams & White, 1849: 53, pl. 13, fig. 6; H. Milne Edwards, 1853: 177, pl. 7, fig. 4; Kingsley, 1880: 206; Ortmann, 1894: 713; de Man, 1895: 118; Tesch, 1918: 96 (part); Balss, 1934: 234, fig. 12; Estampador, 1937: 539; Minei, 1972: 50, figs. 3-5 (part); Holthuis, 1978: 19; Nagai & Nomura, 1988: 38 (part); Shokita, 1990: 310, Table 3; Kishino & Wada, 2001: 59, Fig. 1; Kishino *et al.*, 2001: 127; Shokita *et al.,* 2003: 101 (part); Marumura & Kosaka, 2003: 64; Naruse, Ng, & Hsu*.,* 2005: 211 (part) (Not *Utica* White, 1847).

**Type species.**— *Utica borneensis* de Man, 1895, by current designation.

**Gender.**— Feminine.

**Diagnosis.**— Carapace quadrangular, broader than long; dorsal surface setose, punctate; regions well defined, convex. Frontal margin slightly convex, straight. Anterolateral margin subcristate with three teeth including orbital tooth,. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Inner surface of chela with granules; outer surface of pollex and manus with tufts of setae manus; fingers as long as palm. Ambulatory legs with short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen triangular in shape with all segments freely moveable (six somites plus telson). G1 stout. Female gonopore with operculum circular in shape.

**Etymology.**— 'Pseudo' is added as a prefix to it original genus, as the species from this genus  has always been mistaken as a *Utica* species.

**Remarks.**— The new genus is very different from *Utica*, it can be easily differentiated from *Utica* by the following characters viz. a) carapace distinctly much long than broad (vs. distinctly broader than long in *Utica*); b) the carapace is convex (vs. flat or even some regions are slightly concave in *Utica*); c) the absence of the raised granulated horizontal ridge across the branchial region of the carapace (vs. presence of such a distinct ridge in *Utica*); d) the frontal region of the carapace is not produced (vs. very produced forward in *Utica*); e) the ischium if the third maxilliped is stouter and shorter (vs. a longer and more slender ischium in *Utica*), and f) it is a very small species when it reaches maturity (vs. large size in *Utica*). The new genus is essentially a brackish water species, found along the coastal region, while *Utica* can be found in freshwater stream at about 100m away from the coast without any tidal influence.

The new genus is very similar to the *Ptychognathus* sensu lato in its size and external morphology, but it is different from the latter by the following characters viz. a) distinctly much broader than long (vs. less broader than long in *Ptychognathus*); b) the ischium of the third maxilliped is very broad and stout (vs. long and slender in *Ptychognathus*); c) the exopod of third maxilliped is narrow (vs. a very broad, convex exopod in *Ptychognathus*), and d) very long and slender ambulatory legs (vs. broad and flat legs in *Ptychognathus*).

The new genus is also different from *Parapyxidognathus* Ward, 1941 in the following features a) carapace punctate (vs. smooth carapace in *Parapyxidognathus*); b) the teeth on the anterolateral margin are less acute (vs. more acute in *Parapyxidognathus*); c) merus of third maxilliped less foliaceous (vs. more foliaceous in *Parapyxidognathus*); d) ischium of third maxilliped is much broader (vs. less broad in *Parapyxidognathus*); e) the exopod of the third maxilliped is narrow (vs. broad in *Parapyxidognathus*); f) the posterior margin of ambulatory legs has no spines (vs. presence of numerous spines in *Parapyxidognathus*); g) the male abdomen is narrowly triangular in shape (vs. broadly triangular in *Parapyxidognathus*).

*Pseudoutica* is definitely different from *Pyxidognathus* by having viz. a) a distinctly quadrangular carapace (vs. subquadrangular carapace in *Pyxidognathus*); b) flat carapace physiognomy (vs. very convex carapace physiognomy in *Pyxidognathus*);

c) the exopod of the third maxilliped is narrow (vs. broad in *Pyxidognathus*); d) the posterior margin of ambulatory legs has no spines (vs. presence of numerous spines in *Pyxidognathus*); e) the male abdomen is narrowly triangular in shape (vs. broadly triangular in *Pyxidognathus*), and f) presence of a tuft of setae on the outer surface of cheliped (vs. absence in *Pyxidognathus*).

This is a monotypic genus.

## *Pseudoutica borneensis* (de Man, 1895), new combination

(Figure 123A-I)

*Utica borneensis* de Man, 1895: 118, pl. 228: 25; Maki & Tsuchiya, 1923: 100; Horikawa, 1940: 30; Lin, 1949: 30, 31; *Dai et al.*, 1986: 470, fig. 264, pl. 66: 3; Dai & Yang, 1991: 516, fig. 264, pl. 66: 3; Huang, 1994: 596; Ng *et al.*, 2001: 46.

**Materials examined.— Indonesia** – 1 male (14.5mm x 12.4mm) (ZRC-uncatalogued), Aple'33, 300m, West Irian, coll. 30 Mar. 2000. 1 male (9.0mm x 8.2mm) (ZRC-uncatalogued), EM272/2, West Irian, coll. R. Hanley, 25 Feb. 1998; 2 males (9.5-12.2mm x 8.1-10.5mm) (ZRC-uncatalogued), Kam 1, 200m, West Irian, coll. 3 Apr. 2000; 1 male (6.3mm x 5.5mm), 1 female (9.0mm x 7.8mm) (ZRC-uncatalogued), Margin area, Land Base Port side, West Irian, coll. 29 Jul. 1999; male (12.7mm x 11.3mm) (ZRC-uncatalogued), S325, 6N, No. 69, West Irian, coll. 20 Mar. 1998; 1 female (12.0mm x 11.4mm) (USNM-75863), Benkulen, Sumatra, Indonesia, coll. H.C. Kelless, 17 Dec. 1925. – **Taiwan** – 2 females (7.6-11.9mm x 6.8-10.1mm) (NMNS-uncatalogued), Wan-Li-Tung, Heng-Chun Ping-Tung County, coll. Z.T. Lee, 7 Nov. 1993; 1 male (11.5mm x 10.7mm) (NMNS-uncatalogued), Qigu, Tainan County, 20 Jan. 1993; 1 male (10.5 x 9.6) (USNM-55404), Tabao Tabao, Formosa, coll. Taihoken Normal School, Aug. 1918.

**Diagnosis.**— Carapace subquadrate, slightly depressed, smooth, with short setae at margins. Metabranchial region with no oblique ridge, densely furnished with short setae. Frontal margin straight, slightly concave medially. Third maxillipeds close with a small gap, merus, ischium quadrate in shape; exopod broad. Chelipeds of male, female stout, densely setose at edge of fingers. Ambulatory legs slender, margins densely setose. G1 long, stout. distal end with a bluntly truncated process. Female gonopore with small operculum, circular in shape.

**Colour.**— The colour of fresh specimens can vary from light brown to dark brown or black (Z.T. Lee, pers. comm.), and the colour of the preserved specimens examined is dark brown.

**Size.**— This is a small-sized species, the largest male specimen examined is 14.5mm x 12.4mm) (ZRC-uncatalogued), and the largest female specimen examined is 11.2mm x 11.4mm) (USNM-75863).

**Habitat.** —It can be found in mangrove or muddy flats at the river mouths (C.H. Wang, pers. comm.).

**Remarks.**— The type materials of this species is supposedly to be in ZMA and/or RMNH but I did not manage to locate the specimen when I was there in the years 1996 and 1999. The type material is also not listed by Fransen *et al.* (1997) for RMNH type materials. So, the materials are probably lost. The type locality of this species is Borneo. I will designate a neotype for this species at a later date when materials from Borneo are available.

This species seems to prefer more saline water as they are usually found in mangroves to muddy flats by the river mouths. This habit also warrants the separation of this species into it own genus as *Utica* species prefer freshwater habitat.

**Distribution.**— Taiwan, Japan, Philippines, Borneo and Singapore

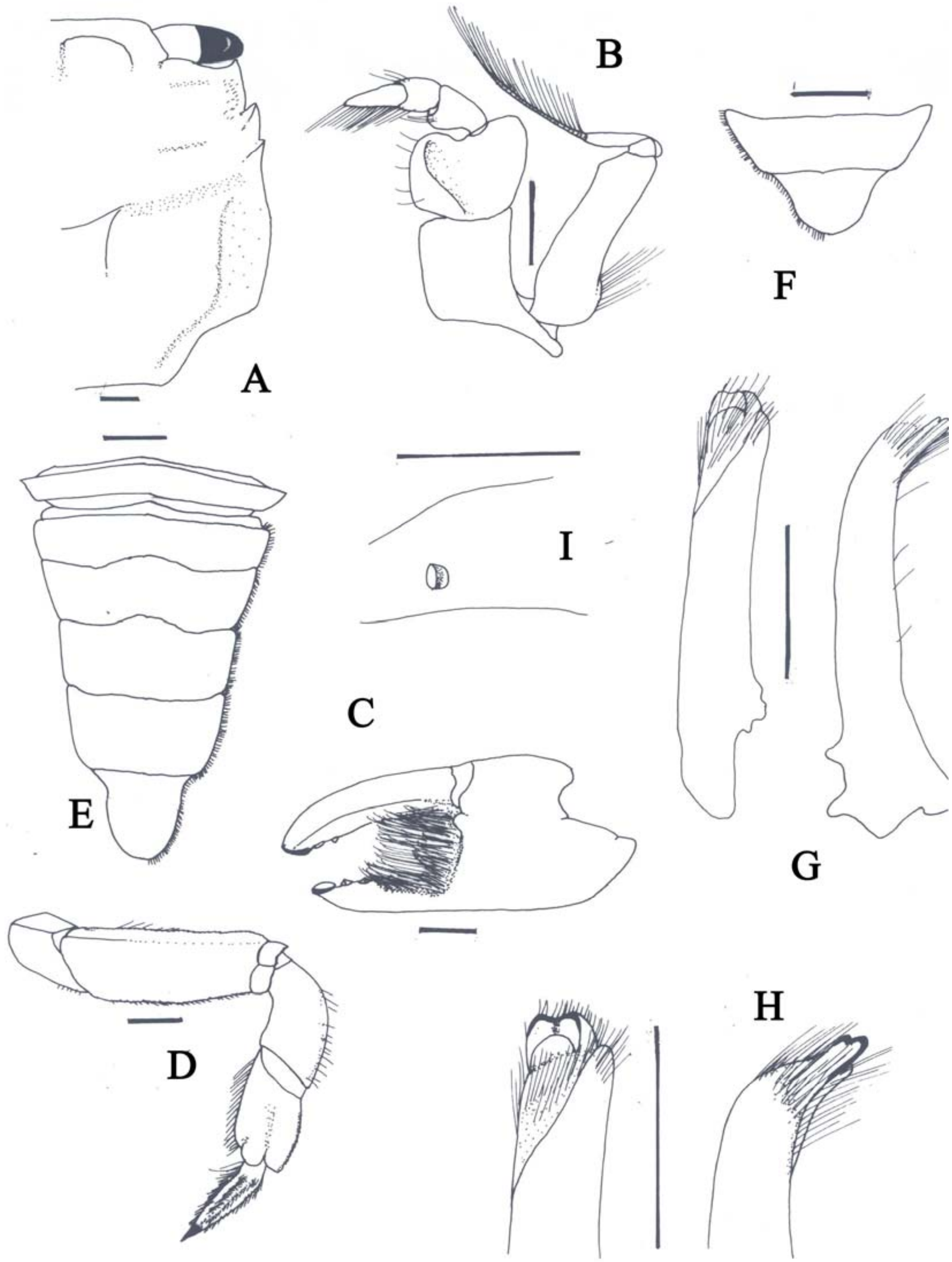



Figure 123. *Utica borneensis* de Man, 1895, male, 14.5mm x 12.4mm, (ZRC-uncatalogued); female, 12.0mm x 11.4mm (USNM-75863). A) carapace; B) third maxilliped; C) outer surface of cheliped; D) last ambulatory leg; E) male abdomen; F) female abdomen; G) G1; H) distal region of G1; I) female gonopore. (Scale=1.0mm).

### Genus *Varuna* H. Milne Edwards, 1830

*Cancer* Fabricius, 1798: 342.

*Trichopus* De Haan, 1835: 32; Dana, 1852: 336, pl. 20, fig.8.

*Varuna* H. Milne Edwards, 1830: 511; Pfiffer, 1889: 30; Alcock, 1900: 401; Stimpson, 1907: 124; Tesch, 1918: 84; Balss, 1922c: 149; Sakai, 1939: 665, pl. 76: 2, pl. 108: 1; Horikawa, 1940: 29; Lin, 1949: 29; Barnard, 1950: 122, fig. 22c, 23f, 24d; Wu *et al.*, 1962: 208; Shen & Dai, 1964: 129; Crosnier, 1965: 34, fig. 40, 41a-b; 46, pl. 6, fig. 1; Wang & Chen, 1981: 156; Dai *et al.*, 1986: 473, fig. 265: 4, pl. 66: 7; Manna, 1988: 754; Fukui *et al.*, 1989: 229; Dai & Yang, 1991: 519, fig. 265: 4, pl. 66: 7; Shih *et al.*, 1991: 142; Huang, 1994: 597; Wang & Liu, 1996a: 110, figs. 138, 139; Wang & Liu, 1996b: 78; Wang & Liu, 1996c: 227; Yu *et al.* , 1996: 15, 67, fig. 79; Ho & Hung, 1997: 85; Jeng, 1997: 18; Jeng, 1998: 83; Jeng *et al.*, 1998: 123; Ng, 1998: 1144; Cai & Ng, 2001: 680; Ng *et al.*, 2001: 46, 53.

**Type species.**— *Cancer litteratus* Fabricius, 1798, subsequent designation by, P.K.L. Ng (1988).

**Gender.**— Masculine.

**Diagnosis.**— Carapace quadrangular, broader than long; dorsal surface glabrous, punctate; region well defined, slightly convex. Frontal margin slightly convex, straight, slightly produced. Anterolateral margin subcristate with three teeth including orbital tooth, Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxillipeds short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire, 3 lobed. Inner surface of chela with granules; outer surface of pollex and manus glabrous; fingers as long as palm. Ambulatory legs with short setae, stout dactyli. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular with all segments freely moveable (six somites plus telson). G1 long, slender. Female gonopore with small, prominent operculum.

**Remarks.**— Currently, the genus *Varuna* comprises of three species viz. *V. litterata* (Fabricius, 1798) (type species), *V. tomentosa* Pfiffer, 1889, and *V. yui* Hwang & Takeda, 1986. *V. tomentosa* has been reported from the East Indian Ocean while the *V. yui* is only reported from the Indo West Pacific, and *V. litterata* is practically found across the tropical belt except Tropical America. This is genus is currently the most wide spread varunid crab around, second to *Eriocheir* De Haan, 1853.

This genus is closely allied to *Mitragrapsus* (see above) as they have the same form of carapace, but *Varuna* can be distinguished from *Mitragrapsus* by the following a) margins of carapace is vaulted (vs. not vaulted in *Mitragrapsus*); b) the anterolateral angle of the merus of the third maxillipeds is not broad and foliaceous (vs. broadened and foliaceous anterolateral angle in *Mitragrapsus*); c) the ischium of the third maxillipeds is broad (vs. narrow in *Mitragrapsus*); d) the exopod of the third maxillipeds is slender and narrow (vs. very broad and convex in *Mitragrapsus*), and e) the cheliped surfaces are glabrous (vs. presence of setae on either outer or inner surface of chelipeds in *Mitragrapsus*).

Hwang & Takeda described *V. yui* based on specimens collected from Taiwan, but *V. yui* has not been accepted by many workers (T.Y. Chan, T. Komai & R.Y. Liu, pers. comm.), stating that the external morphology is no different from those of a young *V. litterata*. Examination of the adult specimens of both species have shown that they are distinctly different in the forms of the carapace, ambulatory legs, and especially the male G1 and female gonopore. Molecular data (on going study with H.T. Shih) has also shown that they are two distinct species (see below).

*V. tomentosa* was established by Pfiffer in 1889 based on specimens collected from Egypt and nearby areas, who stated that it is different from *V. litterata* that it is more densely setose and the legs are less broad. This name has been widely accepted as valid (see Hartnoll, 1975). Examination of the *V. tomentosa* type specimen has shown that it is no different from that of a *V. litterata* (see below). Hence, it is synonymized under *V. litterata* in this report.

*Varuna* is also one of the commercially valuable food crabs in Asia and South East Asia. There is very little known about the biology of this genus except that the females need to go to the deep sea for spawning (S. Shokita, pers. comm.). Gravid females have been found on floatsums or driftwoods (P.K.L. Ng, pers. comm., pers. observ.). The larvae have been known to exhibit swarming behaviour (Ryan & Choy, 1990; M.S. Jeng, pers. comm.).

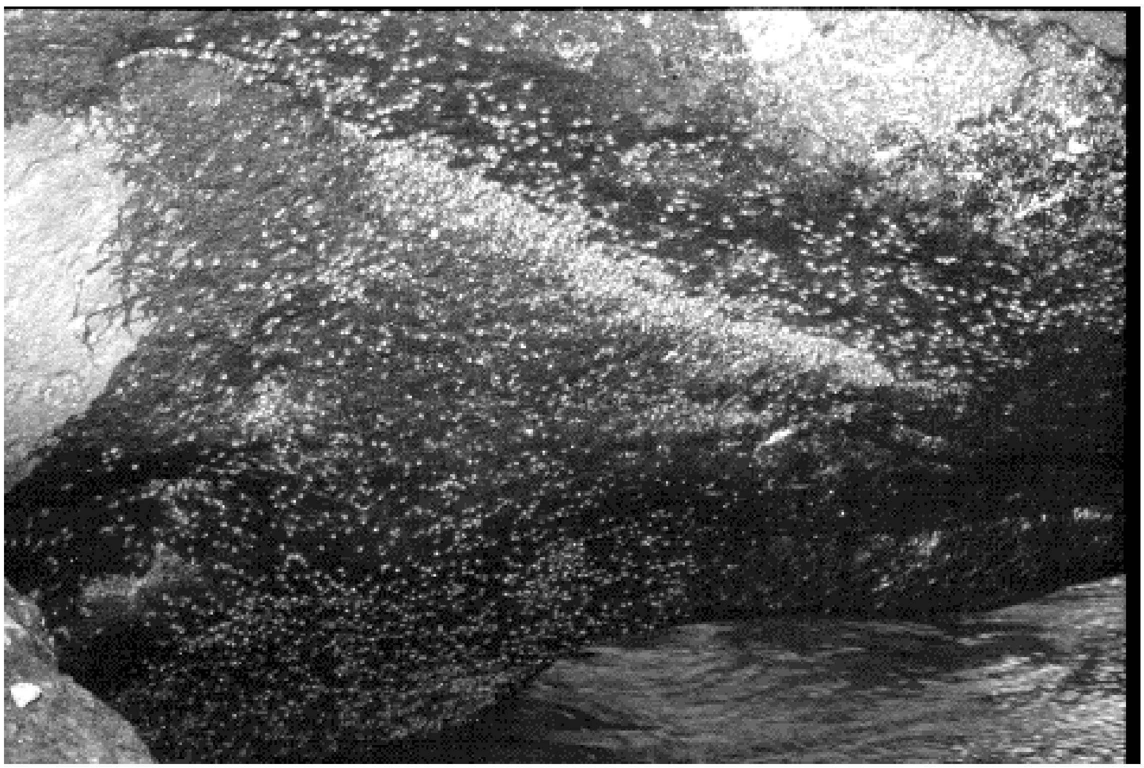


Figure 124. Photograph showing swarming behaviour of *Varuna litterata* megalopae (Courtesy of Dr. H.T. His).

**Key to species in *Varuna***

1a. Carapace with anterolateral margin arched upwards. ------------------------ **2a**

1b. Carapace with anterolateral margin less vaulted. ------------------------------ **2b**

2a. G1 long and stout, length to width ratio 6.9, distal end with a single lobe. Female gonopore with a oval protruding button. ------------------------------ ***V. litterata***

2b. G1 short and stout, length to width ratio 5.5, distal end bi-lobed. Female gonopore has a semi-circular operculum over a small low button. --------------------- ***V. yui***

## *Varuna litterata* (Fabricius, 1798)

(Figure 125)

*Cancer litteratus* Fabricius, 1798: 342.

*Varuna litterata* — H. Milne Edwards, 1830: 511; Alcock, 1900: 401; Stimpson, 1907: 124; Tesch, 1918: 84; Balss, 1922c: 149; Maki & Tsuchiya, 1923: 100; Sakai, 1939: 665, pl. 76: 2, pl. 108: 1; Horikawa, 1940: 29; Lin, 1949: 29; Barnard, 1950: 122, fig. 22c, 23f, 24d; Wu *et al.*, 1962: 208; Shen & Dai, 1964: 129; Crosnier, 1965: 34, fig. 40, 41a-b; 46, pl. 6, fig. 1; Wang & Chen, 1981: 156; Dai *et al.*, 1986: 473, fig. 265: 4, pl. 66: 7; Hwang & Takeda, 1986: 11; Fukui & Manna, 1988: 754; Wada & Wang, 1989: 229; Ryan & Choy, 1990: 237; Dai & Yang, 1991: 519, fig. 265: 4, pl. 66: 7; Shih *et al.*, 1991: 142; Huang, 1994: 597; Wang & Liu, 1996a: 110, figs. 138, 139; Wang & Liu, 1996b: 78; Wang & Liu, 1996c: 227; Yu *et al.*, 1996: 15, 67, fig. 79; Ho & Hung, 1997: 85; Jeng, 1997: 18; Jeng, 1998: 83; Jeng *et al.*, 1998: 123; Naiyanetr,1998: 103; Ng, 1998: 1144; Ng *et al.*, 2001: 46, 53; Keith, Vigneux & Marquet, 2002: 72.

*Trichopus litteratus* De Haan, 1835: 32; Dana, 1852: 336, pl. 20, fig.8.

*Varuna tomemtosa* Pfiffer, 1889: 30.

**Materials examined.—** ***Varuna litterata*** – **Lectotype** – 1 male (34.0mm x 32.3mm) (ZMUC-1201), southeastern India, coll. No collection date. – ***Varuna tomentosa*** – **Lectotype** – 1 male (45.4mm x 42.1mm) (ZIMH). – **Paralectotype** – 1 female (23.9 x 23.5), (ZIMH). – **Others** – 3 males (14.4-20.0mm x 13.8-18.8mm) (USNM-44656), Caluagan River, 3m from rivermouth, near Paluan Bay, Mindoro, coll. 11 Dec. 1908. – **Australia** – 1 male (58.4mm x 51.4mm) (WAM-C24525), Bowes River, north of Geraldton, coll. Jul. 2000; 2 males (56.8-57.0mm x 47.8-50.8mm) (WAM-no cat. number), Gascoyne River, Western Australia, coll. M. Walker, Mar. 1964; 1 male (42.5mm x 37.7mm) (WAM-no cat. number), Gascoyne River, Carnarvon, coll. L. Silvester, Mar. 1974. – **Indian Ocean** – 1 male (38.4mm x 35.0mm) (MNHN-B16790), Indian Ocean; 2 males (27.5-52.5mm x 25.7-46.9mm) (ZRC 1965.8.3.14-15), Christmas Island, Indian Ocean, coll. C.A. G.H., 1940. – **Indonesia** – 1 male (30.0mm x 28.0mm) (USNM- acc no. 122953), Zembeh Strait, Celebes, coll. Heere, 14 Jun. 1929; 4 males (8.2-21.7mm x 8.0-20.3mm), 1 female (27.8mm x 26.1mm) (ZSM, no cat. number), road from Sungei Sengkang, Sungei Bulu Atipesa Ponra, Kecheil Pampanua, Kab. Bone, Sulawesi, Indonesia, coll. M. Kottelat, 10 Jun. 1988; 1 male (38.9mm x 35.6mm) (USNM-23360), Pilo Mobur, Anambas Island, China Sea, coll. M.J. Abbott, 26 Aug. 1899; 17 megalopae, 1 juvenile crab 1, 2 females (12.4-18.5mm x 12.2-17.8mm) (ZRC, no cat. number), lower reaches of south Ifis, Halmahera, coll. D. Robb, Sep. 1994. – **Japan** – 1 male (11.5mm x 11.2mm) (USNM-123431), Gangara Cave, Unago-Go, Tamagusuka Son, Okinawa Island, Japan, coll. D.W. Rhodes, 1 Apr. 1967; 1 male (34.5mm x 32.1mm), 1 female (28.4mm x 27.9mm) (ZRC, no cat. number), Yona River, Kunigami Villager, Okinawa, Japan, coll. 29 Jul. 1987. – **Madascagar** – 12 males (25.6-44.2mm x 24.4-39.0mm), 15 females (26.0-38.8mm x 24.9-33.1mm) (USNM-125809), Nosy Bay, Madascagar, Indian Ocean, coll. W.J. Cross, Aug. 1964; 12 males (25.7-44.2mm x 24.5-39.2mm), 15 females (27.0-32.9mm x 26.0-32.0mm), freshwater, Nossi Be, Madagascar, Indian Ocean, coll. W.J. Gross, Aug. 1964; 1 male (48.3mm x 44.3mm) (MNHN B14023), Dans Casier a langoustes, - 20m, Fort Dauphin, Madagascar, coll. May 1960. **New Guinea** – 1 female (26.8mm x 25.8mm) (USNM, acc no. 122953), Mariemberg, New Guinea, coll. A. Herre, 10 May 1929; 2 males (9.6-16.8mm x 9.2-16.4mm), 2 females (11.0-21.0mm x 9.6-16.4mm) (USNM-59341), Wakijs River, New Guinea, coll. E.A. Briggs, 1925; 2 males (44.5-49.4mm x 39.6-44.3mm), 3 females (29.8-31.6 x 28.6-30.8) (BNHM-1848.31), north coast of New Guinea, coll. HMS 'Challenger', 22 Feb. 1875. – **Palau** – 1 male (35.7mm x 32.8mm) (USNM-172603), reservoir, Arakebesan Island, Palau, Caroline Islands, North Pacific Ocean, 7º21' N, 134º27'E, coll. G. Bright, 5 Jan. 1977; 2 males (11.9-15.2mm x 11.1-14.7mm), 1 female (12.3mm x 11.8mm) (USNM-172605), Ghimal River, Babelthuap Island, Palau, Caroline Islands, 7º23'30"N, 134º32'28"E, coll. G. Bright, 25 Nov. 1976; 1 male (21.4mm x 18.5mm) (USNM-172604), Babelthuap Island, Palau, Caroline Island, 7º22'30"N, 134º32'28"E, coll. G. Bright, 28 Oct. Oct. 1976; 7 juvenile. (3.8-6.4mm x 3.2-6.2mm) (USNM-172602), Negerbekun River, Debris, Babelthuap Island, Palau, Caroline Islands, coll. G. Bright, 1 Jun. 1978. – **Oceania** – 2 males (30.8-43.7mm x 29.2-38.6mm) (USNM-90870), Torokina, Bougainvilla, Solomon Islands, coll. W.L. Necter, 16 Jul. 1944; 1 male (38.7mm x 35.8mm), 1 female (juvenile) (20.1mm x 19.6mm) (MNHN-B-24712), La Foa, New Caledonia, coll. G. Marquet, 6 Sep. 1991. – **Philippines** – 1 male (11.5mm x 10.5mm) (USNM-44652), Taal Lake, East side of Island, Philippines, coll. Dec. 1907; 2 males (8.9-23.3mm x 8.6-21.4mm), 3 females (8.6-29.1mm x 7.3-28.2mm) (USNM-48378), Zamboonga, Mindanao, Philippines, coll. F. Bakar, 27 Feb. 1914; 2 males (25.0-27.3mm x 24.3-25.3mm), 2 females (21.8-26.4mm x 20.9-24.2mm) (USNM-44624), Cabuago River, Catanduanes Islands, Philippine Islands, coll. Albatross Philippines Expeditions, 9 Jun. 1909; 3 males (10.5-40.5mm x 10.0-36.0mm), 5 females (16.0-38.0 x 15.0-35.4) (USNM-73156), Hoilo, Panay Island, Philippines, coll. H.C. Kellers, 15 Mar. 1929; 3 males (11.5-34.0mm x 11.0-30.5mm), 1 female (30.8mm x 29.1mm) (USNM-44666), small stream, Mati, Mindanao, Philippines, coll. 15 May 1908; 2 males (32.8-34.7mm x 30.7-32.3mm) (USNM-44645), 20 feet seine, River at Point Jamelo, Luzon, coll. 13 Jul. 1908; 1 male (30.7mm x 26.3mm), 1 female (15.8mm x 15.5mm) (USNM-169675), stream in Napo Point, near moron, southwest of Subic Bay, Bataan, Luzon, Philippine Islands, coll. M.

McCallough, Mar. 1976; 1 male (8.2mm x 7.7mm), 2 females (11.0-38.8mm x 10.7-37.9mm) (USNM-44641), Batangas River, Batangas, Luzomn, coll. Albatross Philippines Expedition, 27 Jun. 1908; 1 female (23.1mm x 21.2mm) (USNM-44640), Zamboanga, Mindanao, Philippines, coll. 27 May 1908; 1 male (35.2m x 32.7mm), 1 female (35.7mm x 34.3mm) (USNM-44637), Ilo Ilo, Philippines islands, coll. 6 Mar. 1098; 1 female (35.1mm x 32.6mm) (USNM-44644), Tiling, Lubang River and beach, coll. 14 Jul. 1908; 1 female (26.4mm x 25.2mm) (USNM-Balayan Bay, mouth of Santiago River, coll. 10 Feb. 1909; 1 male (54.8mm x 48.0mm) (USNM-44667), Yana River, Legaspsi, coll. Albatross Philippines Expedition, 31 Jun. 1909; 1 male (35.8mm x 33.9mm), 1 female (19.0mm x 18.6mm) (USNM-73208), Jaro River, Panay Island, Philippines, coll. H.C. Kelless, Apr. 1929; 1 female (18.4mm x 17.4mm) (USNM-44665), Dumaca River, Luzon, Philippines, coll. 25 Feb. 1909; 1 male (11.2mm x 10.5mm), 2 females (7.3-9.0mm x 7.0-8.6mm) (USNM-73226), Care, Guimans Island, Philippines, coll. H.C. Kelless, 26 Jun. 1929; 1 female (17.2mm x 16.3mm) (USNM-93755), Siaton, Negros, Philippine Islands, coll. B. V. Hart, no collection date; 1 male (22.8mm x 20.5mm) (USNM-44595), Rio Grande River, Madanao, Philippine Islands, coll. E.A. Mearns, Oct. 1903; 1 male (48.0mm x 42.7mm) (USNM-44649), Varadero Bay, Mindoro, Philippines, coll. 27 Oct. 1909. **– South Africa** – 2 males (52.7-54.6mm x 47.3-49.1mm) (USNM-252321), False Bay, Strand Fontain, South Africa, South Atlantic Ocean, coll. B. Kensley, 25 Mar. 1988. – **Taiwan** – 2 males (32.2-35.3mm x 29.2-30.0mm), 2 females (32.0-33.7mm x 29.6-31.5mm) (USNM-123507), Shih-Keng-Chien village, Ta-Keng Village, Chia-Tung Hsiang, Pingtung hsien, Taiwan, coll. R.E. Kuntz, 17 Apr. 1961; 1 male (35.9mm x 32.5mm), 1 female (27.1mm x 25.5mm) (USNM123512), Shih-Kung-Chien Village, Chia-Tung Hsiang, Pingtung Hsien, Formosa, coll. 13 Jan. 1962; 1 male (37.2mm x 32.1mm), 1 female (32.8mm x 30.5mm) (USNM-123511), Ta-Kung village, Chia-Tung Hsiang, Pingtung Hsien, Formosa, coll. 4 Jan. 1962; 2 males (30.0-35.6mm x 27.3-31.7mm), 2 females (33.8-34.1mm x 31.2-31.3mm) (USNM-123509), Pei-Shih Village, Kaa-Tung Hsiang, Pingtung Hsien, Formosa, coll. 17 Jun. 1961; 1 male (31.3mm x 29.4mm) 1 female (34.8mm x 32.0mm) (USNM-123513), Pei-Shih Village, Kaa-Tung Hsiang, Pingtung Hsien, Formosa, coll. 13 Jun. 1962; 3 males (45.6-50.3mm x 39.8-43.3mm), 2 females (31.5-46.0mm x 29.2-42.2mm) (USNM-123514), I-Lan market, I-Lan Hsien, Formosa, coll. 24 Sep. 1959; 2 males (42.0-43.3mm x 37.2-37.7mm) , 2 females (33.0-37.6mm x 31.4-35.0mm) (USNM-123510), Yueh-Chi Village, Pingtung Hsien, Formosa, coll. 17 Jan. 1961; 1 male (34.4mm x 30.2mm) (USNM-55369), Takao Takao, Formosa, coll. 1918; 2 males (26.0-29.9mm x 24.1-26.2mm), 2 females (21.7-32.2mm x 21.0-30.0mm), Shih-Kung-Chien village, Chia-Tung Hsiang, Pingtung Hsien, Formosa, coll. 13 Jan. 1961; 1 male (16.8mm x 16.5mm) (USNM-93466), Nan-Liao, Hsi-Shi,Ma-Kung District, Taiwan, coll. D.H. Johnson, 27 Apr. 1952; 4 males (43.2-56.8mm x 38.2-49.6mm), 2 females (35.7-36.8mm x 34.6-34.7mm) (ZRC 1998.453), Kang-Kou Si, Taiwan, coll. S.H. Tan, May 1998; 1 male

(51.0mm x 44.6mm) (ZRC-no cat. number), Kang-Kou Xi, Kenting National Park, Pingtung County, Taiwan, coll. P.K.L. Ng, 30 May 1997; 2 males (15.5-39.9mm x 15.1-35.9mm) (ZRC-no cat. number), below Tou-Men Bridge, Hung-Tou Village, Lan-Yu Island, Taiwan, coll. 5 Jun. 1993; 5 males (14.8-26.8mm x 14.4-25.1mm), 4 females (17.5-35.9mm x 16.8-34.0mm) (ZRC-no cat. number), river mouth of Kang-Kou Xi, Kenting National Park, Heng-Chun Peninsula, Pingtung County, Taiwan, coll. S.H. Tan, 19 May 1998; 1 male (31.5mm x 29.4mm) (NTCMST-no cat. number.), Tapei County, Taiwan, coll. 18 May 1991; 2 males (30.4-37.7mm x 28.4-34.2mm) (ZRC-no cat. number), between Nan-Liao Fish Port and Great-White Sand, Green Island, Taitung County, Taiwan, coll. 6 Jun. 1993; 1 1 male (55.0mm x 48.3mm) (ZRC-no cat. number), Ta-Chi Fish Port, Taiwan, coll. P.K.L. Ng, 27 May 1997; 1 male (44.5mm x 40.5mm), 1 female (42.8mm x 40.2mm) (USNM-106148), freshwater stream, coastal plain, I-Lan, I-Lan Hsien, Northeast Taiwan, coll. Oct. 1959; 2 males (32.2-35.3mm x 29.2-30.0mm), 2 females (32.0-33.7mm x 29.6-31.5mm) (USNM-123507), Shih-Keng-Chien village, Ta-Keng Village, Chia-Tung Hsiang, Pingtung hsien, Taiwan, coll. R.E. Kuntz, 17 Apr. 1961; 2 males (30.0-35.6mm x 27.3-31.7mm), 2 females (33.8-34.1mm x 31.2-31.3mm) (USNM-123509), Pei-Shih Village, Kaa-Tung Hsiang, Pingtung Hsien, Formosa, coll. 17 Jun. 1961; 1 male (31.3mm x 29.4mm) 1 female (34.8mm x 32.0mm) (USNM-123513), Pei-Shih Village, Ka-Tung Hsiang, Pingtung Hsien, Formosa, coll. 13 Jun. 1962; 3 males (45.6-50.3mm x 39.8-43.3mm), 2 females (31.5-46.0mm x 29.2-42.2mm) (USNM-123514), I-Lan market, I-Lan Hsien, Formosa, coll. 24 Sep. 1959; 2 males (42.0-43.3mm x 37.2-37.7mm) , 2 females (33.0-37.6mm x 31.4-35.0mm) (USNM-123510), Yueh-Chi Village, Pingtung Hsien, Formosa, coll. 17 Jan. 1961; 1 male (34.4mm x 30.2mm) (USNM-55369), Takao Takao, Formosa, coll. 1918; 2 males (26.0-29.9mm x 24.1-26.2mm), 2 females (21.7-32.2mm x 21.0-30.0mm), Shih-Kung-Chien village, Chia-Tung Hsiang, Pingtung Hsien, Formosa, coll. 13 Jan. 1961; 1 male (35.9mm x 32.5mm), 1 female (27.1mm x 25.5mm) (USNM123512), Shih-Kung-Chien Village, Chia-Tung Hsiang, Pingtung Hsien, Formosa, coll. 13 Jan. 1962; 1 male (37.2mm x 32.1mm), 1 female (32.8mm x 30.5mm) (USNM-123511), Ta-Kung village, Chia-Tung Hsiang, Pingtung Hsien, Formosa, coll. 4 Jan. 1962; 4 males (43.2-56.8mm x 38.2-49.6mm), 2 females (35.7-36.8mm x 34.6-34.7mm) (ZRC 1998.453), Kang-Kou Si, Taiwan, coll. S.H. Tan, May 1998; 1 male (51.0mm x 44.6mm) (ZRC-no cat. number), Kang-Kou Xi, Kenting National Park, Pingtung County, Taiwan, coll. P.K.L. Ng, 30 May 1997; 2 males (15.5-39.9mm x 15.1-35.9mm) (ZRC-no cat. number), below Tou-Men Bridge, Hung-Tou Village, Lan-Yu Island, Taiwan, coll. 5 Jun. 1993; 5 males (14.8-26.8mm x 14.4-25.1mm), 4 females (17.5-35.9mm x 16.8-34.0mm) (ZRC, no cat. number.), river mouth of Kang-Kou Xi, Kenting National Park, Heng-Chun Peninsula, Pingtung County, Taiwan, coll. S.H. Tan, 19 May 1998; 1 male (31.5mm x 29.4mm) (NTCMST-no cat. number), Tapei County, Taiwan, coll. 18 May 1991; 2 males (30.4-37.7mm x 28.4-34.2mm) (ZRC-no cat. number), between Nan-Liao Fish Port and

Great-White Sand, Green Island, Taitung County, Taiwan, coll. 6 Jun. 1993; 1 male (55.0mm x 48.3mm) (ZRC-no cat. number), Ta-Chi Fish Port, Taiwan, coll. P.K.L. Ng, 27 May 1997; 1 male (44.5mm x 40.5mm), 1 female (42.8mm x 40.2mm) (USNM-106148), freshwater stream, coastal plain, I-Lan, I-Lan Hsien, Northeast Taiwan, coll. Oct. 1959; 1 male (16.8mm x 16.5mm) (USNM-93466), Nan-Liao, Hsi-Shi,Ma-Kung District, Taiwan, coll. D.H. Johnson, 27 Apr. 1952.

**Diagnosis.**— Carapace quadrangular. Dorsal surface punctate, regions well defined. Front broad, anterior margin almost straight, slightly produced, sloping downwards. Anterolateral margins arched upwards, with three teeth including orbital tooth. Third maxillipeds closed with a narrow gap. Chelipeds symmetrical, larger in males. Fingers closed without any gap. Ambulatory legs long, slender, merus with a small sub-distal spine on anterior margin, densely setose on anterior, posterior margins, last ambulatory very flattened. G1 long, stout, distal end with a single lobe, length to width ratio 6.9. Female gonopore operculate, with an oval protruding button.

**Colour.**— The colour of fresh specimens can range from light brown to dark brown to almost black (pers. observ.), all the preserved specimens examined are brown in colour.

**Size.**— This species can grow to relatively large size, the largest male specimen examined is 58.4mm x 51.4mm (WAM-C24525), while the largest female specimen examined is 42.8mm x 40.2mm (USNM-106148).

**Habitat.**— Smaller specimens can be found in freshwater streams close to the river mouth (unpublish. data), but large mature specimens can be collected with gill nets or found on floatsum (M.S. Jeng; P.K.L. Ng, pers. comm.)

**Remarks.**— *Varuna litterata* is the most common varunid crab found across the entire Tropics except Tropical America.

Although this species is has a very wide distribution, its biology is not well known. There are only several reports o the swarming behaviour of this species the

(Kemp, 1915; Connell & Robertson, 1986; Mana, 1988; Ryan & Choy, 1990). It is only very recent that the larval development of this species has been studied (Xu, 2003).

*V. litterata* is very closely allied to *V. yui* , but it can be easily distinguished from *V. yui* by the characters listed below (see below *V. yui* ).

Examination of the holotype specimen of *Varuna tomentosa* (ZIMH) has shown that it is a junior synonym of *Varuna litterata*, as there is no morphological difference between *V. tomentosa* and *V. litterata*. The many of the older records of this species require verification, as *V. yui* has not been widely accepted (T.Y Chan, pers. comm.).

**Distribution.—** Indo-west Pacific Oceans (East Africa to Japan).

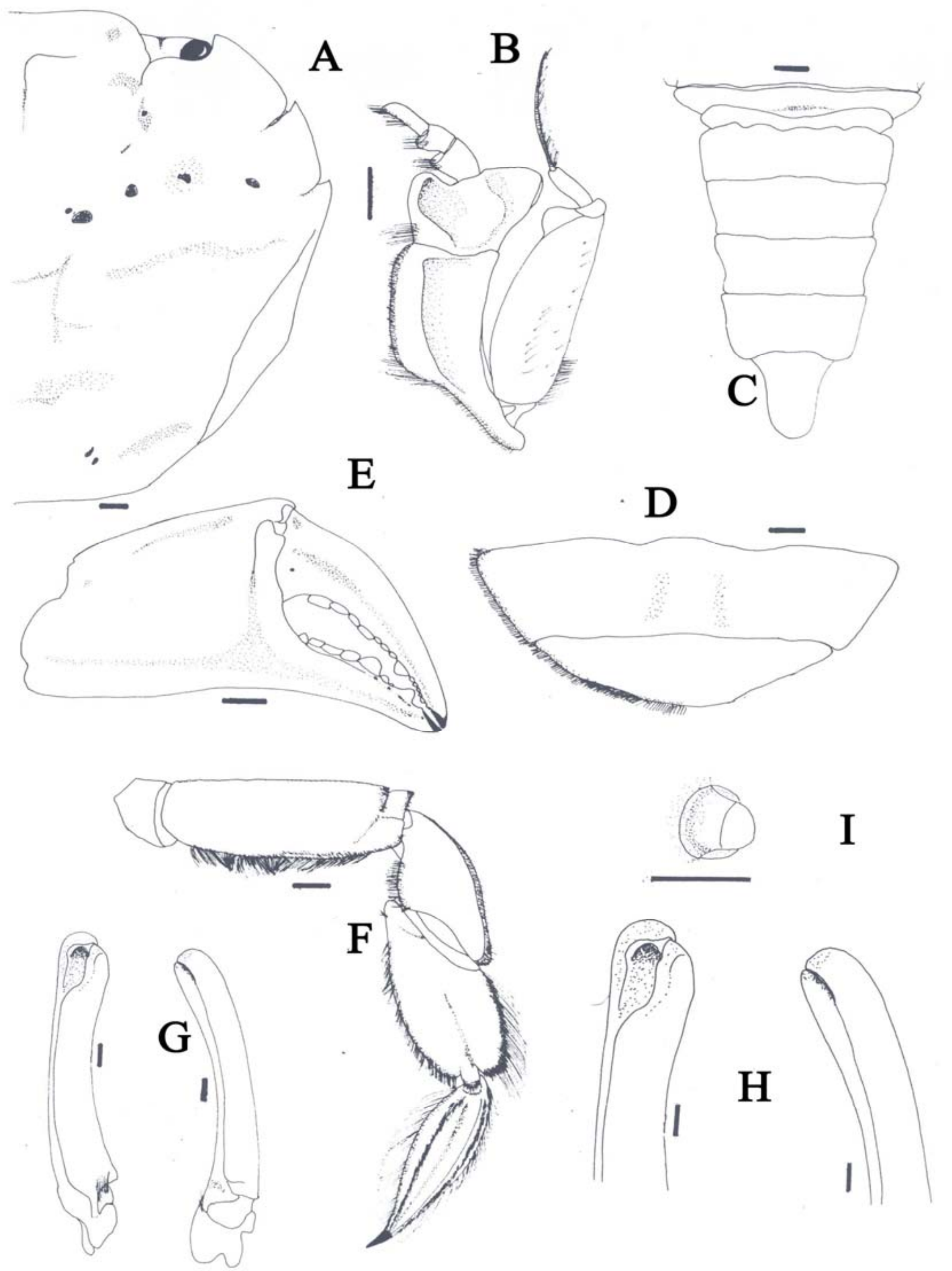



Figure 125. *Varuna litterata* Fabricius, 1798, male, 56.8mm x 49.6mm; female, 36.8mm x 34.7mm (ZRC 1998.453). A) carapace; B) third maxilliped; C) male abdomen; D) female abdomen (part); E) chela; F) last ambulatory leg; G) G1; H) distal end of G1; I) female gonopore. (Scale=1.0mm).

## *Varuna yui* Hwang & Takeda, 1986

(Figure 126A-I)

*Varuna yui* Hwang & Takeda, 1986: 11; Huang, 1994: 597; Jeng *et al.*, 1996: 100; Jeng *et al.*, 1997; Jeng *et al.*, 1998: 123; Ng, 1998: 1144; Ng *et al.*, 2001: 46.

**Materials examined.— Holotype** – 1 male (35.2mm x 32.6mm) (NSMT), Ta-Tung, I-Lan county, Taiwan, coll. J.J. Hwang, 27 Nov. 1983. – **Paratypes** – 1 male (34.3mm x 30.6mm) (NTOU-no cat. number), Ta-Tung, I-Lan county, Taiwan, coll. J.J. Hwang, 27 Nov. 1983; 1 female (31.6mm x 30.4mm), Ta-Tung, I-Lan county, Taiwan, coll. J.J. Hwang, 27 Nov. 1983. – **China** – 4 males (12.2-31.2mm x 11.6-28.9mm), 4 females (15.0-24.8mm x 14.5-22.5mm) (USNM-57022), Amoy China, coll. S.F. Light, no collection date; 3 males (26.8-29.2mm x 25.0-26.8mm), 1 female (32.2 x 31.0) (USNM-44647), Kowloon, China, coll. 22 Aug. 1908; 1 female (30.5mm x 29.0mm) (USNM-59161), Yenting, Che Kiang Province, China, coll. Science Society of China, 1925; 1 male (23.0mm x 21.0mm), 1 female (damaged carapace) (USNM-57021), Foochow, China, coll. S.J. Light, 1922; 1 male (39.8mm x 36.2mm) (USNM-61979), Foochow market, Foochow, China, coll. S.J. Light, no collection date; 1 male (32.1mm x 29.6mm) (USNM-44646), Kowloon Wharf, China, coll. 19 Aug. 1909; 1 male (23.4mm x 22.2mm), 1 female (18.1mm x 17.2mm) (USNM-57794), Amoy, China , coll. S.J. Light, 1923; 1 female (24.9mm x 22.2mm) (USNM-59083), Foochow, Fukien Province, China, coll. R.S. Clarke, Sep-Nov. 1923; 1 male (27.9mm x 26.0mm), 1 female (36.4mm x 35.0mm) (MNHN B16780), Amoy, China, coll. C.F. Wang, Jul. 1925; 2 males (22.5-22.8mm x 21.3-21.8mm), 2 females (9.2-11.4mm x 8.4-10.8mm) (ZRC-uncatalogued), Along road from Changpo to Huiwen Hainan Island, coll. N.K. Ng & Y. Cai, 1 Dec. 1998; 1 male (8.5mm x 8.0mm), 1 female (8.6mm x 8.0) (ZRC-uncatalogued), Yan-Dun village, Hainan Island, coll. N.K. Ng & Y. Cai, 1 Dec. 1998; 12 males (9.0-19.7mm x 8.5-18.4mm), 11 female (9.2-21.3mm x 8.8-20.0mm) (ZRC-uncatalogued), Jimei Beach, Xiamen, Fujian Province, coll. N.K. Ng & Y. Cai, 18 Nov. 1998. – **Hong Kong** – 1 male (25.7mm x 24.7mm), 1 female (ovigerous) (25.6mm x 25.0mm) (ZRC 1997.655), Tai-O, Lantau Island, Hong Kong, coll. D. Dudgeon, no collection date. – **India** – 1 male (30.4mm x 28.0mm) (USNM-19660), Bay of Bengal, Indian Ocean, India (specimen from Kiel Museum); 1 male (31.7mm x 29.2mm), 1 female (ovigerous) (36.7mm x 33.2mm) (USNM19716), Bay of Bengal, from Zoological Museum of Copenhagen, no collection date; 1 male (26.0mm x 24.0mm), 1 female (28.2mm x 25.8mm) (USNM-75431), Canning, India, coll. A.S. Pearse, 4 Jul. 1930. – **Indonesia** – 1 female (ovigerous) (32.7mm x

31.4mm) (USNM-44596), south of Bunke, Java Sea, coll. W.L. Abott, 11 Sep. 1907; 1 female (22.8mm x 17.5mm) (USNM-39183), Atjeh, Sumatra, coll. Captain Storm, no collection date; 1 male (9.8mm x 9.4mm), 3 females (11.3-12.7mm x 10.8-12.2mm) (ZRC-no cat. number), Sungei Umas-Umas, Indonesia, coll. D. Wowor, 29 Sep. 1998; 2 females (11.4-17.9mm x 10.5-16.5mm) (ZRC-no cat. number), found in the stomach of catfish, from Batang Hari River, Indonesia, coll. H.H. Ng, no collection date; 1 female (13.7mm x 13.5mm) (ZSM-no cat. number), road from Sengkang to Palopo, mangrove forest along sungei Bosa at Desa Karanga kechil Belopa, Kab. Luwu, Sulawesi, coll. M. Kottelat, 11 Jun. 1988; 1 male (20.8mm x 19.4mm) (ZSM-no cat. number), road from Sungei Sengkang, Sungei Bulu Atipesa Ponra, Kecheil Pampanua, Kab. Bone, Sulawesi, Indonesia, coll. M. Kottelat, 10 Jun. 1988; 1 male (7.9mm x 6.4mm), 1 female (13.8mm x 12.7mm), Nirwana, Lovina, Bali, Indonesia, coll. M Kotelatt *et al.,* 27 Mar. 1992. – **Japan** – 1 female (15.1mm x 14.7mm) (ZRC-uncatalogued), Tsune Town, Ishigaki Island, Okinawa, no collection date; – **Malaysia** – 1 female (13.0mm x 12.0mm) (ZRC 1996.1727), Sungei Paya, Kampong Paya, Palau Tioman, Pahang, Malaysia, coll. P.K.L. Ng, 25 Jun. 1996; 1 male (9.5mm x 8.9mm) (ZRC 1996.1728), Pool between Sungei Mentawak and Sungei Keliling, Palau Tioman, Pahang,. Malaysia, coll. P.K.L. Ng *et al.,* 27-28 Jun. 1996; 2 males (11.7-19.5mm x 11.3-18.4mm), 4 females (10.3-15.1mm x 10.0-14.4mm) (ZRC 1996.1729), Sungei Keliling, Paulau Tioman, Pahang, Malaysia, coll. P.K.L. Ng *et al.,* 27-28 Jun. 1996; 1 male (24.2mm x 23.0mm), 1 female (12.5mm x 11.3mm) (ZRC 1985.411-412), stream flowing into Jason Bay, near Kuala Sendilii, just above beach, Malaysia, coll. D.S. Johson, 12 Feb. 1962; 3 females (15.6-22.9mm x 15.5-21.9mm) (ZRC 1989.2806-2808), stream behind Idrus Inn, Palau Tioman, Pahang, Malaysia, coll. 1 Jun. 1986; 3 females (16.5-23.8mm x 15.7-22.8mm) (ZRC 1985.1755-1757), in stream near sea, Camp Terendak, Tanjong Bidara, Malacca, Malaysia, coll. P.K.L. Ng, 16 Feb. 1985; 1 female (ovigerous) (33.9mm x 32.4mm) (ZRC 1989.2183), on *Sargassium*, floating, between Palau Tulai and Tekek Bay, Palau Tioman, Pahang, Malaysia, coll. P.K.L. Ng, 26 Jun. 1987; 1 female (8.5mm x 8.2mm) (ZRC 1991.355), ditch at Jason bay, Mawai-Sendilii Road, coll. D.S. Johnson, 18 Jun. 1960; 1 male (7.5mm x 7.0mm), 3 females (7.6-12.7mm x 7.1-12.2mm) (ZRC 1991.357-360), ditch at Jason Bay, Mawai-Sendilii Road, coll. D.S. Johnson, 16 Apr. 1960; 1 male (17.4mm x 16.2mm) (ZRC 1985.413), stream flowing into Jason Bay, near Kuala Sendilii, just above the beach, no collection date; 1 male (5.4mm x 4.9mm), 1 female (7.8mm x 7.6mm), ZRC-no cat. number), Tioman Island, Pahang, Malaysia, coll. Y. Cai, Sep. 1997. – **Philippines** – 1 male (34.5mm x 32.3mm) (USNM-184088), Binoy, Tanan Strait, Negros Island, Philippies, Pacific Ocean, 19º20' N, 123º10'E, coll. fisherman, Apr. 1980; 1 male (17.9m x 16.8mm) (USNM-169675), stream in Napo Point, near moron, southwest of Subic Bay, Bataan, Luzon, Philippine Islands, coll. M. McCallough, Mar. 1976; 1 female (37.2mm x 34.6mm) (USNM-45916), near Malakon, Philippines Islands, coll. Albatross Philippines Expedition, 10 Aug. 1908; 9 males

(8.2-14.2mm x 7.8-13.2mm), 9 females (11.5-24.7mm x 11.1-23.9mm) (USNM-44641), Batangas River, Batangas, Luzon, coll. Albatross Philippines Expedition, 27 Jun. 1908; 4 males (14.5-27.7mm x 13.4-26.8mm), 2 females (18.7-26.6mm x 18.0-24.7mm) (USNM-44624), Cabuago River, Catanduanes Islands, Philippine Islands, coll. Albatross Philippines Expeditions, 9 Jun. 1909; 1 male (37.6mm x 34.9mm), 3 females (16.3-17.9mm x 15.0-17.2mm) (USNM, no cat. number.), Nueua Vizcaya, coll. Herre, 1931; 1 male (37.2m x 34.4mm) (USNM-44650), Philippines islands, don. Chief Bon Rohange, coll. 1907-1909; 3 males (11.4-25.5mm x 10.6-23.6mm), 1 female (23.7mm x 21.9mm) (USNM-44663), small stream south side of Catabato, Mindanao, coll. 20 May 1908; 1 male (28.8mm x 26.2mm), 2 females (28.2-32.2mm x 27.1-30.5mm), 1 female (ovigerous) (31.0mm x 29.1mm) (USNM-44639), below mouth of river, seine, Catabato, Mindanao, Philippines, coll. May 1908; 1 female (ovigerous) (26.1mm x 25.4mm) (USNM-44638), off northern coast of Cebu Island, Philippines, coll. 3 Apr. 1908; 1 male (13.7mm x 12.6mm) (USNM-44664), Reservoir Bacoor, Luzon, Philippines, coll. 17 Jun. 1908; 1 male (7.7mm x 7.2mm) (USNM-44651), Balagas Bay, Philippine Islands, coll. 19 Jan. 1908; 1 male (11.5mm x 10.7mm) (USNM-44653), Batagas market, coll. 6 Jun. 1908; 10 males (31.7-41.8mm x 29.6-36.7mm), 1 female (34.6mm x 32.3mm) (ZRC-no cat. number), ISR Munro Ichthyological Collection, Panay, Philippines, coll. K. Carpenter, Oct. 1995. – **Singapore** – 5 males (27.5-34.9mm x 25.4-32.4mm), 2 females (30.4-31.1mm x 29.1-29.2mm) (ZRC 1996.2042), Seletar, Singapore, coll. S.L. Yang, 24 Sep. 1984; 1 male (29.8 x 27.3) (ZRC 1989.3404), freshwater stream between Ang Mio Kio and Upper Thomson, coll. P.K.L. Ng & H.P Ng, Jun. 1986; 1 female (ovigerous) (32.2mm x 31.0mm) (ZRC 1965.16), Sultan Shoal, Singapore, coll. P.A. Moonteiro, 27 Nov. 1930; 1 male (24.8mm x 23.7mm), 1 female (ovigerous) (28.8mm x 26.1mm), (ZRC 1965.17-18), Sultan Shoal, Singapore, coll. P.A. Monteiro, Nov. 1934; 1 male (37.5mm x 34.4mm) (ZRC 1995.423), canal in Siglap, Singapore, coll. R. Subharaj, 1988; 1 male (27.2mm x 25.4mm), 3 females (24.2-26.4mm x 22.9-24.7mm) (ZRC 1989.3386-3389), Botanic Gardens, Singapore, coll. H.P. Ng & P.K.L. Ng, Apr. 1986; 1 female (25.9mm x 24.1mm) (ZRC 1965.8.3.12), Changi, Singapore, coll. Jun. 1934; 1 male (25.1 x 23.5) (ZRC 1965.8.3.13), Johore Straits, coll. Oct. 1934; 1 female (34.9mm x 33.3mm) (ZRC 1996.2941), Corea House, Singapore, coll. 27 Jul. 1965; 6 juveniles (5.9-8.4mm x 5.9-8.3mm) (ZRC 1965.8.3.19-24), drainage ditches, Pasir Ris, Singapore, coll. Oct. 1937; 1 male (15.9mm x 15.4mm) (ZRC 1985.410), Locality: B61, coll. SRFRS, no collection date; 1 female (32.9mm x 31.2mm) (ZRC 1985.409), locality: B11, coll. SRFRS, no collection date; 3 males (16.2-26.7mm x 15.2-24.6mm), 1 female (ovigerous) (33.5mm x 31.7mm) (ZRC 1985.404-408), station 5, on pieces of wood in a patch of *Sargassium*, coll. SRFRS, 26 Sep. 1955; 1 female (34.2mm x 32.9mm) (ZRC 1992.7925), in brackish water, Sungei Buloh, Singapore, coll. P.K.L. Ng, Jul. 1992; 1 male (32.7mm x 30.2mm), 2 females (25.9-27.1mm x 24.5-25.4mm) (ZRC 1989.3667-3669), on floatsom, Seletar Island, Singapore, coll. P.K.L. Ng, 6 Dec. 1986; 1 male (34.0mm x 31.1mm), 1 female (31.6mm x 30.1mm) (ZRC 1965.8.3.1-2), Singapore Island, coll. 1953;1 male (27.0mm x 25.4mm) (ZRC 1981.8.28.1), Tuas, Singapore, coll. P.K.L. Ng, 14 Apr. 1981; 1 male (47.0mm x 38.9mm) (ZRC 1987.596), Bedok Reservoir, Singapore, coll. C.M. Yang, 16 Jun. 1987; 1 female (9.0mm x 8.6mm) (ZRC 1991.356), 113/4 mile of Jurong Road, Singapore, coll. D.S. Johnson, 18 Mar. 1958; 1 male (17.5mm x 15.9mm), 6 females (9.4-16.3mm x 8.5-15.2mm) (ZRC 1989.2218-2224), under rocks, shallow water, drain to West Coast, Pandan Garden, Singapore, coll. P.K.L. Ng, 1987; 1 male (12.0mm x 11.2mm), 5 females (5.0-14.4mm x 4.5-13.4mm) (ZRC 1989.3390-3395), Penang seashore, Malaysia, don. UMJZ; 1 male (40.7mm x 36.8mm) (ZRC 1965.8.3.3), Siglap, Singapore, coll. M.W.F. Tweedie, Jun. 1934; 1 male (19.7mm x 18.6mm) (ZRC 1965.8.3.4), Siglap, Singapore, coll. M.W.F. Tweedie, Jul. 1934; 1 male (19.4mm x 18.3mm) (ZRC 1965.8.3.5), Siglap, Singapore, coll. M.W.F. Tweedie, Jul. 1934; 1 male (29.5mm x 26.5mm) (ZRC 1965.8.3.6), Siglap, Singapore, coll. M.W.F. Tweedie, May 1935; 1 male (29.5mm x 26.5mm) (ZRC 1965.8.3.7), Siglap, Singapore, coll. M.W.F. Tweedie, May 1935; 1 male (21.1mm x 19.2mm) (ZRC 1965.8.3.8), Siglap, Singapore, coll. M.W.F. Tweedie, May 1935; 1 female (30.4mm x 28.6mm) (ZRC 1965.8.3.9), Siglap, Singapore, coll. M.W.F. Tweedie, Jul. 1934; 1 female (34.2mm x 32.8mm) (ZRC 1965.8.3.4), Siglap, Singapore, coll. M.W.F. Tweedie, no collection date; 1 male (32.8mm x 31.8mm) (ZRC-no cat. number), probably escapee from Siva's tank, most likely from Sungei Buloh, coll. 29 Apr. 1998; 1 male (21.5mm x 19.5mm), 1 female (15.4mm x 14.2mm), (ZRC-no cat. number), Geylang canal, Singapore, coll. Reef Ecology Study Lab, 18 Aug. 1984; 2 males (20.4-21.9mm x 19.1-20.5mm) (ZRC-no cat. number), tide pool in Sungei Buloh, Singapore, coll. Y. Cai, 12 Sep. 1998. – **Taiwan** – 1 male (31.4mm x 28.7mm) (USNM-55370), Hsin-Chuang, Taipei, Formosa, coll. S.H. Lin, Aug. 1919; 1 male (44.4mm x 40.0mm), 1 female (43.0mm x 39.7mm) (USNM-106148), I-Lan, I-Lan County, northeast Taiwan, coll. Oct. 1959; 1 male (23.9mm x 22.5mm) (ZRC-no cat. number), river mouth of Jang-Kou Xi, Heng-Chun Peninsula, Pingtung County, Taiwan, coll. S.H. Tan, 19 May 1998; 1 male (31.7mm x 29.1mm), 1 female (23.5mm x 22.1mm) (NTCMST-no cat. number), Taipei County, Taiwan, coll. 17 Oct. 1990; 1 female (27.4mm x 25.4mm) (USNM-55377), Formosa, coll. Taihoku Normal School, no collection date; 1 male (44.4mm x 40.0mm), 1 female (43.0mm x 39.7mm) (USNM-106148), I-Lan, I-Lan County, northeast Taiwan, coll. Oct. 1959; 1 female (27.4mm x 25.4mm) (USNM-55377), Formosa, coll. Taihoku Normal School, no collection date; 1 male (23.9mm x 22.5mm) (ZRC-no cat. number), river mouth of Jang-Kou Xi, Heng-Chun Peninsula, Pingtung County, Taiwan, coll. S.H. Tan, 19 May 1998; 1 male (31.7mm x 29.1mm), 1 female (23.5mm x 22.1mm) (NTCMST-no cat. number), Taipei County, Taiwan, coll. 17 Oct. 1990. – **Thailand** – 1 female (29.4mm x 27.8mm) (USNM-19660), Nonburi, Thailand, coll. 20 Aug. 1923; 1 male (23.1mm x 21.7mm) (USNM-25218), island west of Siam, coll. W.I. Abbott, no collection date;

2 males (30.2-35.9mm x 28.5-32.5mm), 2 females (29.0-31.9mm x 27.3-29.4mm) (USNM-no cat. number.), Klong Ranode, Siam, no collection date; 1 female (38.9mm x 35.7mm) (USNM-no cat. number), Chao Paya River at Paknam, Thailand, coll. 3 Jun. 1927; 1 female (35.0mm x 33.3mm) (USNM-no cat. number), Paknam, Thailand, no collection date; 2 males (7.6-17.9mm x 7.1-16.5mm), 1 female (9.8mm x 9.2mm) (ZRC-no cat. number), southeast Ban Pliu, Chataburi Province, Thailand, coll. M. Kottelat, 21 Mar. 1980; 1 male (28.3mm x 26.6mm) (CU-no cat. number), information in Thai language; 3 males (27.3-28.3mm x 24.9-26.6mm), 2 females (26.9-32.0mm x 26.0-30.3mm) (CU-no cat. number), Gulf of Thailand, no collection date; 1 male (33.8mm x 30.5mm), 1 female (31.1mm x 29.2mm) (CU-no cat. number), Gulf of Thailand, no other data; 1 male (35.0mm x 32.7mm), 1 female (32.7mm x 31.7mm) (ZRC-uncatalogued), Phuket, Thailand, coll. P.K.L. Ng, 19 Feb. 2001; 1 female (31.3mm x 29.2mm), 1 female (ovigerous) (31.6mm x 29.4mm) (ZRC-uncatalogued), Pichi Port, Phuket, Thailand, coll. N.K. Ng & K.L. Yeo, 17-20 Jan. 2000; 4 males (33.3-35.7mm x 30.8-33.0mm), 1 female (34.1mm x 32.0mm) (CU-no cat. number), Bangkok Market, coll. 3 Aug. 1997; 2 males (20.0-23.8mm x 19.0-22.2mm), 1 female (24.4mm x 23.2mm) (CU-no cat. number), Diem Conp River, Quay Ning Province, Thailand, coll. 23 Mar. 1997. – **Vietnam** – 5 males (34.2-40.2mm x 31.1-36.8mm), 1 female (38.0mm x 36.1mm) (ZRC-no cat. number), Cho Market, Hon, Hanoi, Vietnam, coll. Sep. 1997; 2 males (17.5-21.5mm x 16.6-19.8mm) 6 females (15.4-20.7mm x 14.6-19.6mm), 1 juvenile (4.6mm x 4.4mm) (ZRC-uncatalogued), Tran Chau village, Cat Ba Island, Hai Phong Province, Vietnam, coll. M. Kottelat, 25 Sep. 1998.

**Diagnosis.**— Carapace quadrangular. Dorsal surface punctate, regions well defined. Front broad, anterior margin almost straight, slightly produced and slope downwards. Anterolateral margins less vaulted, with three teeth including orbital tooth. Third maxillipeds closed with a narrow gap. Chelipeds symmetrical, larger in males. Fingers closed without any gap. Ambulatory legs long, slender, merus with a small sub-distal spine on anterior margin, densely setose on anterior, posterior margins. G1 short, stout, length to width ratio 5.5, distal end bi-lobed. Female gonopore with a semi-circular operculum over a small low button.

**Colour.**— The colour of fresh specimen is light or dark brown in colour, with dark brown setae (pers. observ.), all preserved specimens examined are light brown or brown in colour (see above in materials examined).

**Size.**— This species is slightly smaller in adult size when compared to *V. litterata*, largest male is 44.4mm x 40.0mm (USNM-106148), and the largest female specimen examined is 43.0mm x 39.7mm (USNM-106148).

**Habitat.**— This species can be found mainly in freshwater streams, a short distance from the seashore. Gravid females can be found in water with very low salinity (unpublished data).

**Remarks.**— The two species of *Varuna* can be easily discerned by the differences in the form of the carapace, G1 and female gonopore althought many co-workers (T.Y. Chan, pers. comm. etc) do not recognized this as a valid species. The key differences are a) anterolateral margin of the carapace is less vaulted (vs. more vaulted in *V. litterata*); b) the ambulatory meri are more slender (vs. broader in *V. litterata*); c) the propodi of ambulatory legs are more slender (vs.broader in *V. litterata*); d) the male abdomen is more narrowly triangular (vs. more broadly triangular in *V. litterata*); e) the male telson is more narrow (vs. broad in *V. litterata*); f) the tip of G1 is distinctly bilobed to form a V-shape (vs. not distinctly divided in *V. litterata*); g) tip of the G1 is bilobed and split apart forming a 'U' shaped tip (vs. closely packed together in *V. litterata*); h) the female gonopore is circular, with a raised operculum (vs. circular gonopore with a sunken operculum in *V. litterata*).

A recent study on the 16s and COI sequences (an ongoing study with H.T. Shih) has revealed that there are 24 base-pairs differences between *V. litterata* and *V. yui* (unpublished data), confirming that *V. yui* is a good species. The first zoeae of this species has been obtained under relatively lower salinity (≈15ppm) indicating that the larvae prefers shallow waters. It is also interesting to note that swarming behaviour of this species has yet to be reported.

**Distribution.**— Taiwan, Southern China, Vietnam, Indonesia, Philippines, Singapore, West Malaysia, Thailand**.**

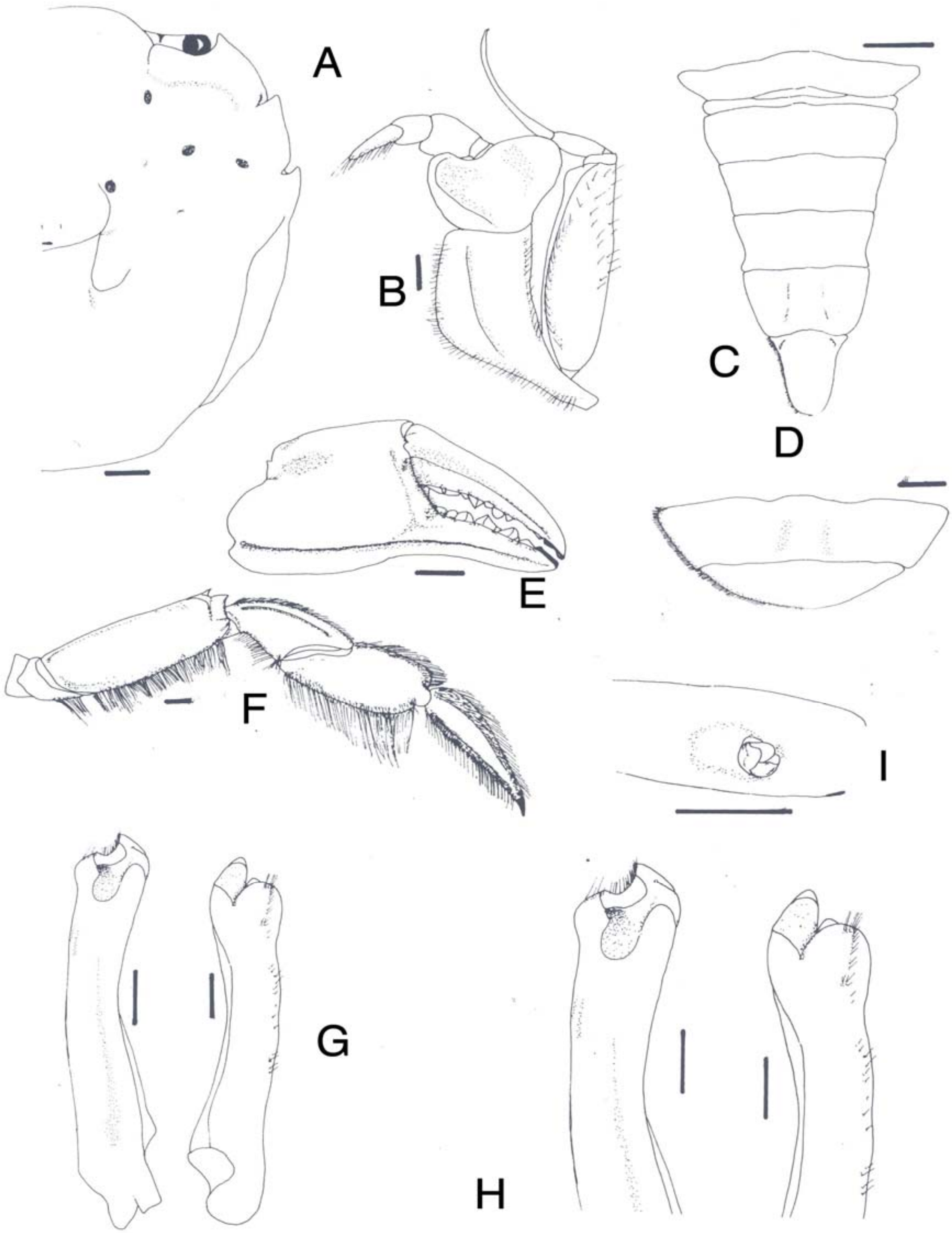



Figure 126. *Varuna yui* Hwang & Takeda, 1986, male, 27.2mm x 25.4mm; female 26.4mm x 24.7mm (ZRC 1989.3386-3389). A) carapace; B) third maxilliped; C) male abdomen; D) female abdomen (part); E) chela; F) last ambulatory leg; G) G1; H) distal end of G1; I) female gonopore. (Scale=1.0mm).

## Subfamily Cyclograpsinae H. Milne Edwards, 1853

Cyclograpsinae H. Milne Edwards, 1853: 191

Cyclograpsacea H. Milne Edwards, 1853: 191.

Helicinae Kossmann, 1877: 57.

**Diagnosis.**— Carapace oval to quadrate or quadrangular, with lateral margins convex to subparallel; regions often discernible; dorsal surface usually glabrous, physiognomy sometimes flat to deeply vaulted; anterolateral margins entire or with one to four epibranchial teeth or notches. Front deflexed; broad, less than half maximum carapace breadth. Orbits open laterally; sub-orbital crest more or less straight, typically long, extending to a short distance across lateral branchial region, typically stridulatory in conjunction with chelipeds; pterygostomial grooves opening into anterolateral corner of buccal cavity; pterygostome, sub-branchial, sub-hepatic regions with or without reticulation of hooked setae; pterygostome with a deep vertical groove placed subparallel to buccal cavity. Third maxilliped with oblique setose crest extending across merus, outer distal corner of ischium; rhomboidal gape when closed; reaching forward to margin of epistome to completely close buccal cavity anteriorly; exopod normal, narrow; flagella of third maxilliped exopods not especially elongated, not noticeably protruding from behind third maxilliped. Endostome smooth, more or less prominent medially.. Chelipeds usually subequal, large in size. Ambulatory legs oval to circular in cross section, typically more or less narrow, not markedly dorso-ventrally flattened; posterodistal margin of meri not armed with spines; propodi, dactyli not armed with strong black bristles. Male abdomen with all segments freely moveable (six somites plus telson). Male gonopore is located some distance from coxa, embedded within thoracic sternite 8. Female gonopore operculate, usually rounded.

**Type Genus.** — *Cyclograpsus* H. Milne Edwards, 1897, by original designation.

**Remarks.**— The Cyclograpsacea H. Milne Edwards, 1853, has always been treated as a junior synonym of Sesarminae Dana, 1852, by most workers in the last century.

When H. Milne Edwards established the ‘famille Catométopes’ in 1837 and the tribe Grapsoïden (see Remarks on family Varunidae), he had included the genera *Sesarma*, *Cyclograpsus* in this tribe. In his genus *Cyclograpsus*, he further subdivided the genus into three different groups based on characters of the anterolateral margin, orbit and third maxillipeds. One group contains *C. punctatus* from the Indian Ocean; *C. audouinii* from New Guinea; and *C. integer* from Brazil. The next group contains *C. quadridentatus* from Australia (=New Holland); *C. sexdentatus* from New Zealand; *C. gaimardii* from Australia (=New Holland); *C. crenulatus* and *C. octodentatus* from King Island (Tasmania, Australia), and the last group, *C. latreillii* from Ile de France.

When Dana (1852: 307) divided the Grapsoidea into five families (see above in Introduction and Remarks for family Varunindae), he noted that the genus *Helice* was ambiguous in its relations with other genera, and both *Metaplax* and *Chasmagnathus* have the ‘oblique piliferous crest’ upon the outer maxilliped which is characteristic of the *Sesarma* group. He further commented that the *Gnathochasmus* of MacLeay (1838) and *Cyclograpsus* of H. Milne Edwards (1833) are identical. A portion of H. Milne Edwards’s ‘Cyclograpsi’ in which have the outer maxilliped has an oblique piliferous crest should belong to the Sesarminae (Dana, 1852: 331), while those without the crest should belong to another group, which he named *Hemigrapsus* Dana, 1852. In his subsequent definition of Sesarminae, Dana (1852) included *Sesarma*, *Sarmatium*, *Cyclograspsus*, *Chasmagnathus* and *Helice* in this subfamily. However, he had grouped *Sesarma* and *Sarmatium* together with the common character of ‘*Articulus maxillipedis externi 3tius apice rotundatus*’; while *Cyclograpsus*, *Chasmagnathus* and *Helice* were put into one group with the common character of ‘*Articulus maxillipedis externi 3tius apice truncatus scepeque excavatus*’. This indicated that Dana (1852) had already recognized two separate groups in his subfamily Sesarminae.

When H. Milne Edwards established Cyclograpsacea in 1853, he used the main characters of the ‘almost oval-shaped carapace, the smooth form of the carapace, as well as the short, stout and almost glabrous ambulatory legs’, and he hand included *Pseudograpsus*, *Heterograpsus* (now *Brachynotus* and *Hemigrapsus*), *Paragrapsus*, *Cyclograpsus*, *Chasmagnathus* and *Platynotus* (now *Gaetice*). In addition to having the same morphological characters, members of all these genera all found along the high tide zones of coastal areas (without freshwater input). It is interesting to note that H. Milne Edwards did not mention the oblique setose crest extending across merus, outer distal corner of ischium of the third maxilliped which is used for channeling water across the pterygostome or the reticulated setose pterygostome.

In his definition of Sesarmacaea, H. Milne Edwards (1853: 181) stated that its members had the "Regions jugales fortment et régulièrement réticulées. Cadre buccal en général échancré aux angles antérieurs, de facon à constituer de chaque côté orifice expirateur spécial. Dactylopodites inermes ou faiblement épineux. Hebdourite souvent enchàssé dans l'hectourite chez la femalle". The main characters he used were the regularly reticulated setae on the pterygostome, and the special form of the mouthparts connecting to breathing apparatus. This would refer to the highly specialized water chanelling groove found only in these crabs. The genera included in his Sesarmacaea were *Sesarma* s. l., *Aratus*, *Holometopus* (now known as *Chiromantes*), *Metasesarma*, *Metagrapsus* (now *Metopograpsus*) and *Helice*. All the genera except *Helice*, share the common character of having this groove, and at the same time, all these genera have very similar habitats, being found in mangroves or mudflats.

With regards to the genus, *Metaplax* H. Milne Edwards, 1852, the original author (H. Milne Edwards, 1852) commented that it was closely related to the *Macrophthalmus* and *Cleistostoma*. It was then placed in the Ocypodoidea but no worker at that time connected it with the Cyclograpsacea or Sesarmacaea.

Although there was no mention of the 'oblique setose piliferous ridge across the external maxilliped', Haswell (1882: 102) placed the genus *Paragrapsus* in the subfamily Sesarminae together with *Cyclograpsus*, *Helice* and *Chasmagnathus*, because *Paragrapsus* has 'orbits and submarginal grooves as in *Cyclograpsus* …. Legs as in *Cyclograpsus*.' He further commented that the genus is scarcely distinct from *Chasmagnathus*' (Haswell, 1882: 104). Examination of this genus by recent workers has confirmed its placement in the Sesarminae (Campbell & Griffin, 1966).

Alcock (1900: 288) divided the family Grapsidae into four distinct subfamilies (1900: 288) viz. Grapsinae, Varuninae, Sesarmine and Plagusiinae. Alcock's subfamily Varuninae is made up of all the H. Milne Edwards' (1853) Varunacea (see above on Remarks for family Varunidae) and part of the H. Milne Edwards' Cyclograpsacea. According to Alcock (1900), the subfamily Sesarminae is made up of Sesarmacea and part Cyclograpsacea, with the following definition: 'Front strongly deflexed: the lower border of the orbit commonly runs downwards towards the angle of the buccal cavern: the external maxilliped leave a wide rhomboidal gap between them, *an oblique hairy crest trasveres them from a point near the antero-external angle of the ischium to a point near the antero-internal angle of the merus*, their palp articulates either at the summit or near the antero-external angle of the merus, and their exognath is slender and either partly or almost entirely concealed. The male abdomen either fills or does not quite fill all the space between the last pair of ambulatory legs. Antennal flagella variable'; with a strong emphasis on the presence or absence of the oblique crest on the maxiilipeds. He included S*esarma, Sarmatium*, *Metasesarma*, *Clistocoeloma* and *Metaplax* in his diagnosis but he did not justify why he had included *Metaplax* (for the first time) in this subfamily.

Interestingly, Kossmann (1877) placed *Cyclograpsus* and *Chasmagnathus* into a new subfamily, Helicinae (1877) on the basis of the morphology of the antennae. Unfortunately, the form of the antennae of the other genera of this subfamily does not support his separation, and his subfamily was never recognized by later workers.

Tesch (1918) argued that the presence of the oblique piliferous ridge across the merus and ischium of the external maxilliped warrants the inclusion of *Metaplax* in the subfamily Sesarminae. He further commented that *Helice* is related to *Metaplax*, as the side walls of the body are vertical and like the pterygostomian regions, ornamented in the usual way of the sesarmine.' (Tesch, 1918). Since Tesch (1918), most workers have considered the subfamily Sesarminae to contain the genera *Sesarma* s. l., *Sarmatium, Aratus, Holometopus* (now known as *Chiromantes*), *Metasesarma, Metagrapsus*, *Cyclograpsus*, *Chasmagnathus, Helice, Metaplax* and *Paragrapsus*. This system has been widely accepted.

Balss (1957) in his study on the systematics of the decapods, agreed with the classification of the Sesarminae proposed by Tesch (1918). However, he noted that in members of the Sesarminae, the male abdomen either filled the sternum completely or nearly so at the fifth ambulatory leg (Balss, 1957), although he did not comment further in detail.

Guinot (1979: 209) stated that ‘Chez d’autres sesarmines comme *Metaplax* H. Milne Edwards (fig. 52J) ou *Cyclograpsus* H. Milne Edwards, don’t l’abdomen est plus étroit à la base et a des bords à peu près rectilignes, la disposition ressemble à celle des varuninae (fig. 52f-h). L’orifice mâle est très éloigné de la coxa, noyé au sein du sternite 8. Une large portion du sternite 8 est exposée: un sillon peut le traverser complètement (*Metaplax crenulatus*, *Cyclograpsus punctatus*, *C. integer*), incomplètement (*Metaplax dentipes*: fig. 52J), ou pas du tout (*Metaplax tredecim*)’. This indicated that both *Metaplax* and *Cyclograpsus* should be transferred to Varuninae. Guinot & Bouchard’s (1998) work on the locking buttons of the sternum of Brachyura also indicated that the Varuninae and Sesarminae at that time are paraphyletic and should be reviewed. Unfortunately, Guinot’s statement was never formalized until Davie (2002) resurrected the subfamily Cyclograpsinae H. Milne Edwards, 1853.

The two most important characters that bind the different species from subfamily Cyclograpsinae to the subfamily Sesarminae are the presence of a reticulated pattern of hooked setae on the pterygostome, subbranchial and subhepatic regions (which is used to re-oxygenate water) (Maitland, 1990; 1992), and the oblique setose crest extending across the merus and outer distal corner of the ischium of the third maxilliped which is used in channeling water flow. According to Davie (2002, 2003), these two characters are highly derived, and while admittedly linked, seem to show the very close relationship between cyclograpsines and the Sesarminae (present Sesarmidae). This suggests that this adaptation has occurred more than once and thus can reasonably be considered as homoplaseious (P. Davie, pers. comm.). However, close morphological comparisons of the detailed structures of these two characters in the cyclograpsines and true sesarmines show that they do differ in some details. Notably, the pattern of the grooves that direct respiratory water to flow across the pterygostome are different, and there is vertical groove running subparallel with the buccal cavity present in cyclograpsines which is absent in sesarmines (sensu stricto).

In addition, genera from the subfamily Cyclograpsinae have a strongly developed, stridulatory sub-orbital crest that is relatively straight. The sub-orbital crest (infra-orbital ridge) which also extends across the lateral branchial region is also very similar to members of the subfamily Varuninae, and this supports an alleged sister-group relationship corroborating the results of Schubart *et al.* (2000), and Kitaura *et al.* (2002). A similar conclusion was reached by Karasawa & Kato (2001) after a phylogenetic analysis of 17 grapsoid genera. The form of the orbital ridge (Crosnier, 1965), the position of the genital opening (Guinot, 1979), and abdominal locking mechanism (Guinot & Bouchard, 1998) of these genera further supported the fact that they should be placed with the Varuninae (present Varunidae) instead of the Sesarminae (present Sesarmidae). These genera have a strongly developed, typically stridulatory, and a sub-orbital crest that is relatively straight.

Recent studies on larval morphology, and 16s mtDNA by Schubart & Cuesta (1998), Schubart *et al.* (2000) and Kitaura *et al.* (2002) have shown that the type genus of the Cyclograpsacea, *Cyclograpsus*, together with *Chasmagnathus*, and *Helice*, have much greater affinities with the Varuninae than Sesarminae. Kitaura *et al.* (2002) examined the 16s mtDNA of four species of *Metaplax*, and found them to be all rooted in the same clade with other cyclograpsine/varunine genera, indicating that they clearly belonged to a different lineage from the Sesarminae, and are clearly different from the ocypodid subfamily Macrophthalminae whose species have similar behaviour and biology to those of *Metaplax*. Similarly, a cladistic study conducted by Sternberg & Cumberlidge (1998) found the Sesarminae to be paraphyletic and that a number of genera like *Chasmagnathus*, *Cyclograpsus*, *Helice*, *Helograpsus*, *Metaplax* and *Paragrapsus* should be reassigned elsewhere within the Grapsoidea. My examination of the specimens from these genera have confirmed that they do not belong to the subfamily Sesarminae, and yet they do not belong to the subfamily Varuninae. They should be transferred to a subfamily of their own but within the Varunidae. Two names are available for the taxa concerned: Cyclograpsacea H. Milne Edwards, 1853, and

Helicinae Kossmann, 1877. Since, H. Milne Edwards' name is the most senior, Davie (2002) recommended the recognition of a resurrected Cyclograpsinae (see below).

In the current report, I recognize the family Varunidae as a full family, and the inclusion of four subfamilies, Varuninae, Cyclograpsinae, Gaeticinae and Thalassograpsinae, the latter two being new. Similarly, the Grapsidae and the Sesarmidae are also recognized as separate families.

With the current definition of Cyclograpsinae, there are now 12 genera in this subfamily. They are *Cyclograpsus* H. Milne Edwards, 1837; *Chasmagnathus* De Haan, 1835; *Austrohelice* Sakai, Türkay & Yang, 2006; *Neohelice* Sakai, Türkay & Yang, 2006; *Parahelice* Sakai, Türkay & Yang, 2006; *Pseudohelice* Sakai, Türkay & Yang, 2006; *Helice* De Haan, 1835; *Helograpsus* Campbell & Griffin, 1966; *Helicana* Sakai & Yatsuzuka, 1980; *Metaplax* H. Milne Edwards, 1852; *Paragrapsus* H. Milne Edwards, 1853, and *Neomeplax* new genus.

**Key to genera in Cyclograpsinae**

1a. Carapace subquadrangular, almost rounded, surface of carapace not clearly defined, anterolateral margin with weak tooth or lobe. ------------------------ ***Cyclograpsus***

1b. Carapace subquadrangular, surface of carapace clearly divided into different regions, anterolateral margin with distinct tooth/teeth. ------------------------------ **2**

2a. Carapace distinctly broader than long, anterolateral margin with two sharp teeth including exorbital tooth. ----------------------------------------------- ***Helograpsus***

2b. Carapace distinctly broader than long, anterolateral margin with three teeth including exorbital tooth. ------------------------------------------------------- **3**

3a. Carapace with frontal margin strongly projecting forward, bilobed. -------------------- ---------------------------------------------------------------------- ***Paragrapsus***

3b. Carapace with frontal margin not projecting forward, weakly bilobed or almost straight. ------------------------------------------------------------------------------- **4**

4a. Overall physiognomy of carapace high. Anterolateral teeth broad, carapace broadest at branchial region. ------------------------------------------------------------------ **5**

4b. Overall physiognomy of carapace low. Anterolateral teeth narrow, carapace broadest at hepatic region. ------------------------------------------------------------- **11**

5a. Merus of third maxilliped nearly half as broad anteriorly as long. ----------------------- --------------------------------------------------------------------- ***Chasmagnathus***

5b. Merus of third maxilliped nearly as broad anteriorly as long. ------------------- **6**

6a. Infra-orbital ridge in male with isomorphic granules or tubercules. -------------- **7**

6b. Infra-orbital ridge in male with heteromorphic granules or tublercules. ---------- **8**

7a. Infra-orbital ridge consist of two rows of granules. -------------------- ***Neohelice***

7b. Infra-orbital ridge consist of a single row of granules. --------- ***Austrahelice***

8a. Lateral part of male infra-orbital ridge with 5 or less large tubercles of different sizes. ------------------------------------------------------------------------------- **9**

8b. Lateral part of male infra-orbital ridge with more than 5 large tubercules of different sizes. -------------------------------------------------------------------------------- **10**

9a. G1 with suture of sperm channel perfectly straight, no torsion distally; horny tip elongate and clearly flattened. ----------------------------------------- ***Pseudohelice***

9b. G1 with or without torsion of the suture of the sperm channel, horny tip not much flattened, rather thick to tubular. ----------------------------------------- ***Parahelice***

10a. Distal part of G1 broad, tip thick, triangular. -------------------------- ***Helice***

10b. Distal part of G1 slender, tip small, poorly developed. ------------- ***Helicana***

11a. Carapace surface distinctly grooved, cheliped very long, slender, ambulatory legs with numerous spines on anterior and posterior margins. -------- ***Neometaplax***

11b. Carapace surface not distinctly grooved, cheliped broad, stout, ambulatory legs without spines on anterior and posterior margins. --------------------- ***Metaplax***

### Genus *Cyclograpsus* H. Milne Edwards 1837

*Cyclograpsus* H. Milne Edwards, 1837: 77; Rathbun, 1918: 325; Tesch, 1819: 125; Bernard, 1950: 131; Crosnier, 1965: 78; Campbell & Griffin, 1966: 127; Griffin, 1968: 235; Kim, 1973: 492; Manning & Holthuis, 1981: 239; Dai *et al.*, 1986: 497; Dai & Yang, 1991: 545. Davie, 2002: 209.

*Gnathochasmus* MacLeay, 1838: 65

**Type species.**— *Cyclograpsus punctatus* H. Milne Edwards, 1837, by monotypy, *Cyclograpsus punctatus* H. Milne Edwards, 1837 (= *Gnathochasmus barbatus* MacLeay, 1838) subsequent designation, see Rathbun, M.J. (1918).

**Gender.**— Masculine.

**Diagnosis.**— Carapace subquadrangular to rounded, broader than long; dorsal surface glabrous, punctate; regions not well defined, convex. Frontal margin slightly convex, almost straight. Anterolateral margin subcristate with two teeth slightly indicated, including external orbital tooth distinct, very broad; second tooth lobiform. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Chelipeds asymmetrical in adults, very large in male, palm swollen, fingers sharp. Ambulatory legs with short setae, stiff setae on dactyli. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular with all segments freely moveable (six somites plus telson).

**Remarks.**— The genus was last revised by Campbell & Griffin (1966), and Griffin (1968), when they synonymized several species; *C. minutus* Jacquinot in Hombron & Jacquinot, 1852 under *C. punctatus* H. Milne Edwards, 1837; *C. whitei* H. Milne

Edwards, 1853, under *C. lavauxi* H. Milne Edwards, 1853; and *C. laevis* Hess, 1865, under *C. audouinii* H. Milne Edwards, 1837. Many unidentified species like *C. tasmanicus* were also treated (Campbell & Griffin, 1966, Griffin, 1968). I concur with the arguments presented by Campbell & Griffin (1966) and Griffin (1968) for these species.

This genus currently comprises of 16 recognized species viz. *Cyclograpsus punctatus* H. Milne Edwards, 1837 (type species); *C. audouinii* H. Milne Edwards, 1837; *C. becarrii* Nobili, 1899; *C. cinereus* Dana, 1852; *C. granulatus* Dana, 1852; *C. escondidensis* Rathbun, 1933; *C. henshawi* Rathbun, 1902; *C. incisus* Shen, 1940 *C. insularum* Campbell & Griffin, 1966; *C. integer* H. Milne Edwards, 1837; *C. intermedius* Ortmann, 1894; *C. granulosus* H. Milne Edwards, 1853; *C. lavauxi* H. Milne Edwards, 1853; *C. longipes* Stimpson, 1858; *C. lucidus* Dai, in Dai & Yang, 1986; and *C. sanctaecrusis* Griffin, 1968.

The genus can be broadly divided into two main groups, one with distinctly quadralateral shaped carapaces viz. *C. intermedius*, *C. henshawi*, *C. audouinii*, *C. incisus*, *C. sanctaecrusis* and *C. escondidensis*, while the rest have a distinctly subquadrangular to rounded carapace. There are, however, not enough morphological characters to divide them into two genera.

The genus is very commonly found in tropical waters.

**Key to species in *Cyclograpsus***

1a. Carapace distinctly quadrangular in shape. --------------------------------------------- **2**

1b. Carapace almost subquadrangular to rounded in shape. ------------------------------- **7**

2a. Carapace with one or two indistinct lobes on the anterolateral margin, including orbital tooth/lobe. ------------------------------------------------------------------------ **3**

2b. Carapace with three indistinct teeth/lobes on anterolateral margin, including orbital tooth/lobe. ----------------------------------------------------------------------------- **4**

3a. Tooth on anterolateral margin sharp. Infra-orbital ridge with a tubercule, and three rounded granules. -------------------------------------------------------- ***C. henshawi***

3b. Tooth on anterolateral margin blunt, more like a lobe. Infra-orbital ridge with three tubercules, and two broad granules. ------------------------------------ ***C. sanctaecrusis***

4a. Anterolateral margin of carapace with three very broad teeth, including orbital tooth. Infra-orbital ridge with 20 isomorphic granules. --------------------- ***C. intermedius***

4b. Anterolateral margin of carapace with three lobes. Infra-orbital ridge with less than 20 isomorphic granules. ----------------------------------------------------------------- **5**

5a. Infra-orbital ridge granulated without setae. ----------------------------------------- **6**

5b. Infra-orbital ridge with setae interspersed among granules. ------ ***C. escondidensis***

6a. Infra-orbital ridge with about 11 isomorphic granules. ----------------- ***C. incidus***

6b. Infra-orbital ridge with 13-21 (mean 17) isomorphic granules. ------ ***C. audouinii***

7a. Anterolateral margin of carapace with only orbital tooth. --------------------------- **8**

7b. Anterolateral margin of carapace with two or more teeth including orbital tooth. ----- ------------------------------------------------------------------------------------------ **13**

8a. Infra-orbital ridge with isomorphic granules. ------------------------------------------- **9**

8b. Infra-orbital ridge with heteromorphic granules. -------------------------------------- **11**

9a. Infra-orbital ridge with two elongated granules only. ------------------ ***C. cinereus***

9b. Infra-orbital ridge with numerous rounded granules. ------------------------------ **10**

10a. Infra-orbital ridge with 12-19 rounded granules. -------------------- ***C. granulosus***

10b. Infra-orbital ridge with more than 20 rounded granules. ------------ ***C. granulatus***

11a. Infra-orbital ridge with 10-17 irregularly-sized rounded granules. ------ ***C. lavauxi***

11b. Infra-orbital ridge with elongated tubercules and rounded granules. ------------- **12**

12a. Infra-orbital ridge with two elongated granules followed by three rounded granules. ----------------------------------------------------------------------------- ***C. lucidus***

12b. Infra-orbital ridge with 15 rounded granules, largest below orbit, decreasing in size towards distal end of pterygostimail region. --------------------------- ***C. insularum***

13a. Carapace with two teeth/lobes including orbital tooth. --------------------------- **14**

13b. Carapace with three teeth including orbital tooth. --------------------------------- **15**

14a. Anterolateral margin with two lobes, infra-orbital ridge with three elongated granules. ---------------------------------------------------------------------- ***C. longipes***

14b. Anterolateral margins with two teeth, infra-orbital ridge with several large rounded granules. --------------------------------------------------------------------------- ***C. beccarii***

15a. Anterolateral margin with three lobes, infra-orbital ridge with three elongated lobes. ------------------------------------------------------------------------------- ***C. integer***

15b. Anterolateral margin with three lobes, infra-orbital ridge with numerous granules. ------------------------------------------------------------------------------------ ***C. punctatus***

## *Cyclograpsus punctatus* H. Milne Edwards, 1837

(Figures 127A-B; 128A-E)

*Cyclograpsus punctatus* H. Milne Edwards, 1837: 78; Smith, 1838: 65, pl. 3; H. Milne Edwards, 1853: 197, pl. 7 fig. 9; Kingsley, 1880: 221; Haswell, 1882: 104; Ortmann, 1894: 729; Stimpson, 1907: 132; Stebbing, 1910: 318; Rathbun, 1911: 590; Tesch, 1918: 126; Campbell & Griffin, 1966: 142; Griffin, 1968: 235; Fransen *et al.*, 1997: 121; Ng & Ahyong, 2001: 94. Guzmán, 2003: 27.

*Gnathochasmus barbatus* MacLeay, 1838: 65, pl. 3.

*Sesarma barbata* Krauss, 1843: 45, pl. 3, fig. 3a-c.

*Cyclograpsus minutus* Jacquinot in Hombron & Jacquinot, 1852: pl. 6; 1853: 75.

*Cyclograpsus punctatus* – Stimpson, 1907: 132; Rathbun, 1918: 328 (not *C. punctatus* H. Milne Edwards, 1837).

**Materials examined.**— No material examined.

**Diagnosis.**— Carapace subquadrangular, almost rounded, broader than long; surface slightly convex, granulated in frontal region; front slightly deflected, anterior margin nearly straight. Anterolateral margin slightly vaulted upwards, with two lobes instead of teeth including orbital lobe, vaulted upwards. Infra-orbital ridge not known. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Chelipeds symmetrical, surfaces smooth, Ambulatory legs flat, stout; meri finely serrated on anterior, posterior margins, propodi, dactyli with short, long setae. (Modified from Rathbun, 1918).

**Colour.**— There is a variety of colours reported for the fresh specimens of this species, they can be purplish brown with black setae (Stimpson, 1858) or greenish-yellow with dark red spots (Krauss, 1843). The colour of preserved specimens has not been documented.

**Size.**— The largest known male specimen reported is 28.5mm x 23.5mm (Rathbun, 1918), the size of largest female specimen reported is 24.5mm carapace width (Campbell & Griffin, 1966).

**Habitat.**— It can be found under rocks and mud holes in brackish water in river mouths (Rathbun, 1918) or in higher tidal areas (Broekhuyen, 1940).

**Remarks.**— *Cyclograpsus punctatus* has been reported to occur from Chile (Garth, 1957) to South Africa (Barnard, 1950), and, Hong Kong (Stimpson, 1907; Rathbun, 1918). Campbell & Griffin (1966) has doubted the presence of this species in Hong Kong, which I agree, that record more likely to be a wrong identification.

This species very closely allied to *C. audouinii* H. Milne Edwards, 1837, which is found in Australia and New Guinea. However, it can be separated from *C. audouinii* by a) a slighty vaulted anterolateral margin of the carapace (vs. non vaulted anterolateral margin in *C. audouinii)*; b) the anterolateral margin of the carapace is distinctly convex (vs. subparallel in *C. audouinii*); c) the propodus of the ambulatory legs are broader and stouter (vs. narrower in *C. audouinii*), and d) the absence of setae at the bases of the ambulatory legs (vs. presence of setae in *C. audouinii*).

*Cyclograpsus punctatus* is primarily found in Africa and Chile. Stimpson (1907) reported the living colour of this species is purplish brown with black punctae, but he did not state the number of specimens he had examined or provide any other descriptions except for the colour and its habitat. The living colour of 'purplish-brown' can refer to *C. integer* H. Milne Edwards, 1837 or *C. intermedius* Ortmann, 1894, which are very common in East Asia.

**Distribution.**— Chile, South Africa.

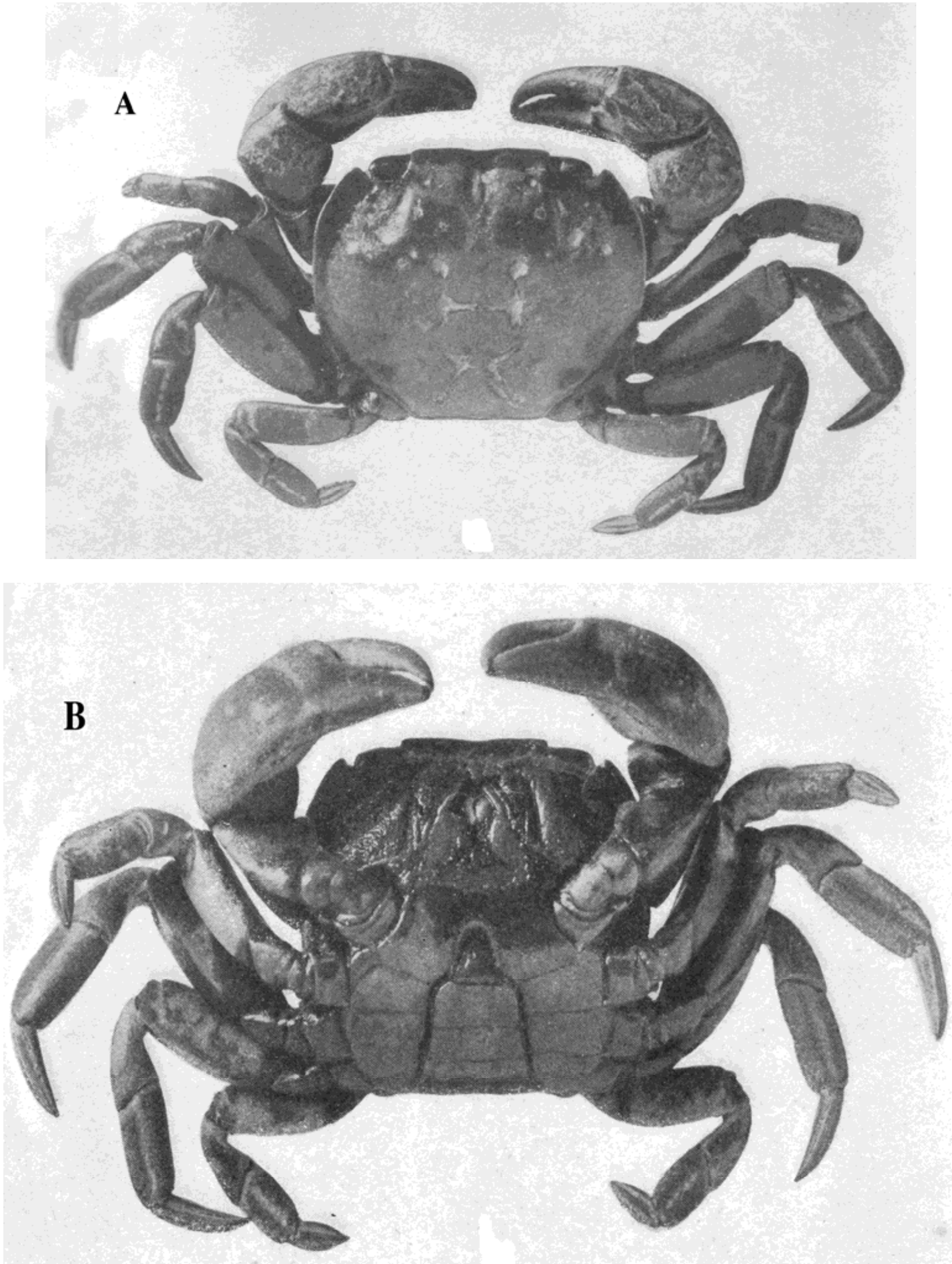



Figure 127. *Cyclograpsus punctatus* H. Milne Edwards, 1837. A) dorsal view; B) ventral view. (After Rathbun, 1918).

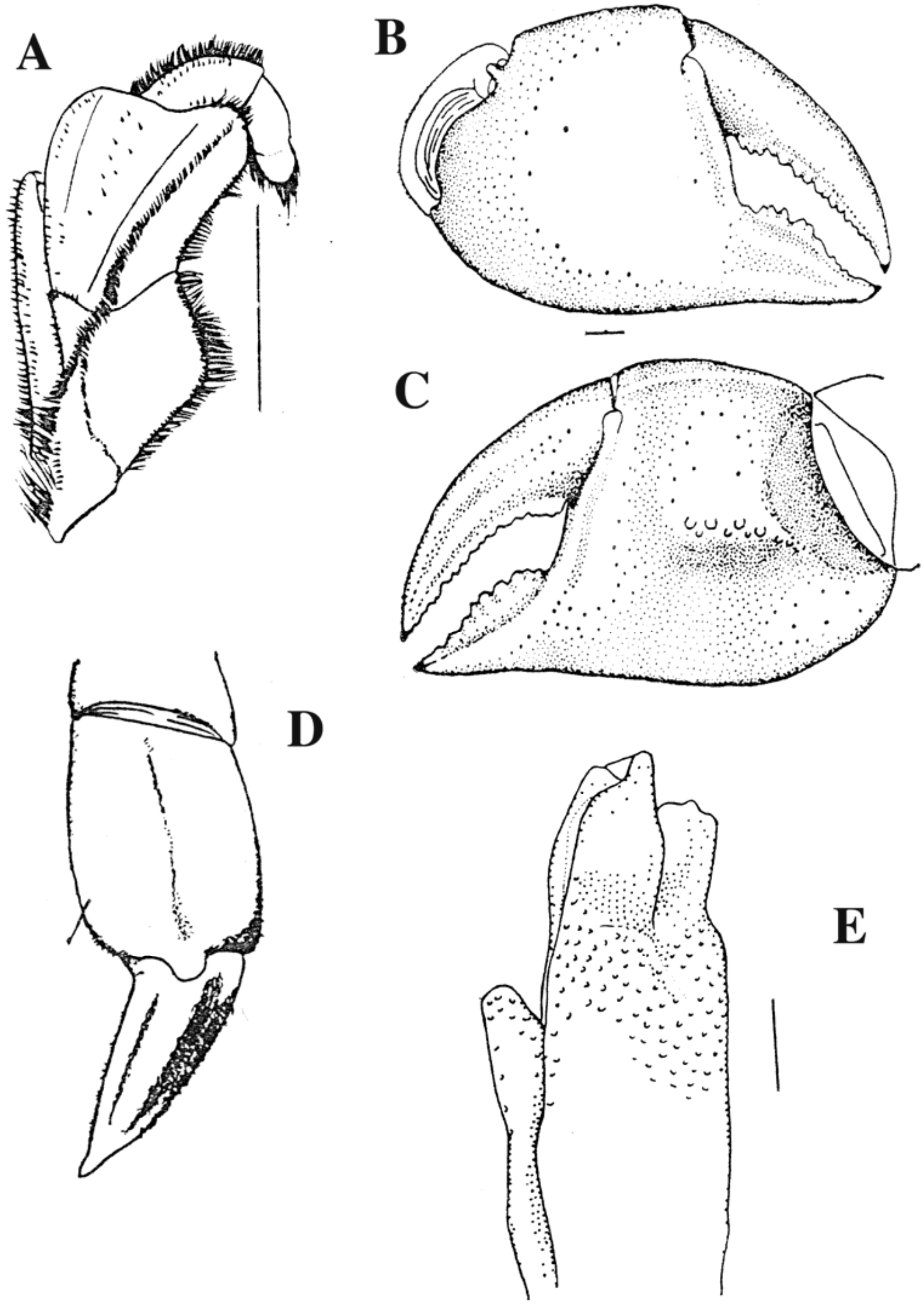



Figure 128. *Cyclograpsus punctatus* H. Milne Edwards, 1837. A) third maxilliped; B) outer view of chela; C) inner view of chela; D) last ambulatory leg; E) tip of G1. (After Campbell & Griffin, 1966).

## *Cyclograpsus audouinii* H. Milne Edwards, 1837

(Figures 129; 130A-E)

*Cyclograpsus Audouini* H. Milne Edwards, 1837: 78; 1853: 197; Stimpson, 1907: 132; Teach, 1918: 126; Hale, 1924: 70; 1927a: 176; 1927b: 312; Montgomery, 1931: 456; Campbell & Griffin, 1966: 150; Jones & Morgan, 1994: 186.

*Cyclograpsus laevis* Hess, 1865: 152; de Man, 1887: 700.

*Cyclograpsus lavauxi* – Haswell, 1882: 103 (not *Cyclograpsus lavauxi* H. Milne Edwards, 1853).

*Cyclograpsus punctatus* – Ortmann, 1894: 729 (not *Cyclograpsus punctatus* H. Milne Edwards, 1837).

*Cyclograpsus punctatus audouini* – Balss, 1935: 142.

**Materials examined.**— 5 males (17.3-31.5mm x 14.6-25.0mm), 2 females (22.5-23.6mm x 17.9-19.4mm), 3 females (ovi.) (17.7-22.6mm x 14.5-19.1mm) (ZRC 1965.7.8.15-25), east coast of Tasmania, coll. W.W.F. Tweedie, 1940.

**Diagnosis.**— Carapace subquadrangular, almost rounded, broader then long; surface slightly convex, granulated in frontal region; front slightly deflected, anterior margin nearly straight. Anterolateral margin with three indistinct lobes instead of teeth including orbital lobe. Infra-orbital ridge with 13-21 (usually 17) granules. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Chelipeds symmetrical, surfaces smooth. Ambulatory legs flat, long; meri finely serrated on anterior, posterior margins, propodi, dactyli with short, long setae.

**Colour.**— The colour of fresh specimens is highly variable, some specimens have mottled patterns of red-brown, purple and yellow (Campbell & Griffin, 1966). Estuarine specimens are mottled with purple, dark-grey or brownish-grey (Jones & Morgan, 1994). The colour of preserved specimens examined is light brown (ZRC 1965.7.8.15-25).

**Size.**— The largest male specimen reported is 40.5mm in carapace width (Campbell & Griffin, 1966), and largest female examined is 23.6mm x 19.4mm (ZRC 1965.7.8.15-25).

**Habitat.**— It can be found intertidally on the rocky shore, among boulders and stones at or above the highest tide limit; extending into shallow waters, associated with seaweeds, logs, rocky platforms, beaches, reefs and estuarine flats (Campbell & Griffin, 1966).

**Remarks.**— This species can be found together with *C. granulosus*. This species is closely allied to *C. granulosus* but it is easily distinguished from *C. granulosus* by a) the presence of three lobes on anterolateral margin (vs. smooth rounded carapace margin without any tooth in *C. granulosus*); b) the carapace is slightly wider than long (vs. very distinctly wider than long in *C. granulosus*); c) the chelae are not very large (vs. huge, massive in *C. granulosus*), and d) the presence of tufts of long setae between the bases of the legs (vs. absence of such setae in *C. granulosus*).

This species has been described and discussed in detail by Campbell & Griffin (1966), and I concur with their conclusion on this species.

**Distribution.**— Australia (Christmas Island, New South Wales, Queensland, South Australia, Victoria, Western Australia, New Guinea.

Figure 129. *Cyclograpsus audouini* H. Milne Edwards, 1837, male, 31.5mm x 25.0mm (ZRC 1965.7.8.15-25). Dorsal view.

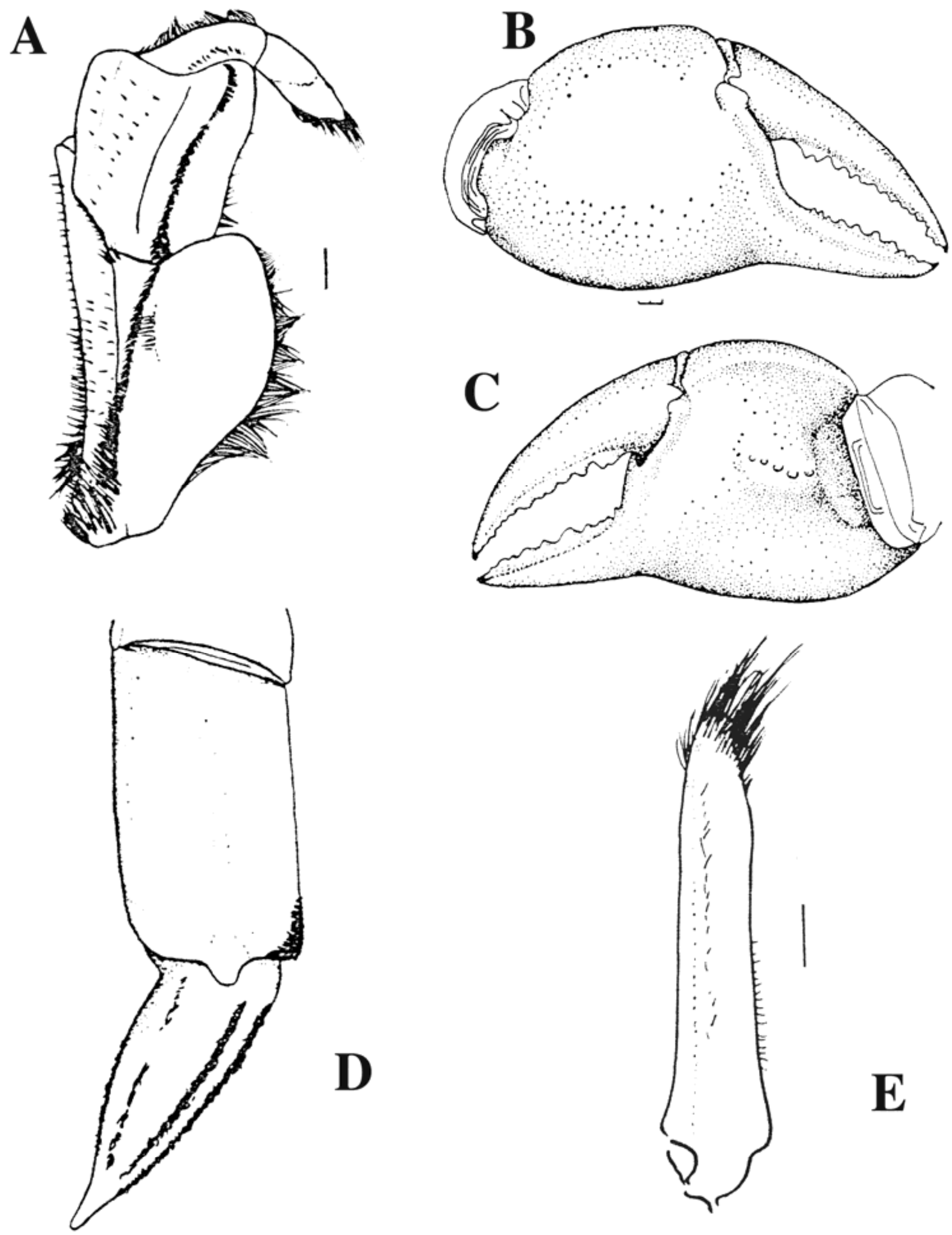



Figure 130. *Cyclograpsus audouini* H. Milne Edwards, 1837. A) third maxilliped; B) outer view of chela; C) inner view of chela; D) last ambulatory leg; E) tip of G1. (After Campbell & Griffin, 1966).

## *Cyclograpsus integer* H. Milne Edwards, 1837

(Figures 131A-B)

*Cyclograpsus integer* H. Milne Edwards, 1837: 79; Rathbun, 1918: 326, pl. 97, figs. 1-2; Balss, 1922: 83; Monod, 1956: 451, figs. 609-610-612; Forest & Guinot, 1961: 160, 162, figs. 175a-c; Crosnier, 1965: 78, figs. 129; Hartnoll, 1965: 114, 115; 137-138; Velez, 1967: 43; Griffin, 1968: 243; Coelho & Ramos, 1972: 202; Fausto-Filho, 1967: 13; 1974: 14; Chace & Hobbs, 1969: 173; Sakai, 1976: 667, pl. 227; Powers, 1977: 132; Manning & Holthuis, 1981: 239; Abele & Kim, 1986: 62, fig. 674b; Dai *et al.*, 1986: 498, text-fig. 281; Fukui *et al.*, 1989: 230; Dai & Yang, 1991: 545; Poupin, 1994: 56; Melo, 1996: 465, 1 fig.; 1998: 31; Castro, 1997: 96; Ng *et al.*, 2001: 44; McLaughlin *et al*, 2005: 60, 119.

*Cyclograpsus occidentalis* A. Milne-Edwards, 1878: 350; A. Milne-Edwards & Bouvier, 1902: 111.

*Cyclograpsus parvulus* de Man 1896: 350; 1898: pl. 32, figs.42a-e; Tesch, 1918: 127.

*Cyclograpsus granulatus* Chen, 1980: 143, pl. IV, fig. 25 (not *Cyclograpsus granulatus* Dana, 1852)

**Materials examined.— China** – 2 males (11.2-13.4mm x 9.1-11.1mm) (QIH-no cat. number), Sanya, Hainan Island, coll. 21 Mar. 1958. – **Taiwan** – 1 male (8.2 x 6.5mm), 1 female (8.2mm x 6.6mm) (TMCD-2546), Xiao-Hsiang-Lan, Fulung, Taipei County, coll. C.H. Wang 20 Apr. 1989; 1 male (9.1mm x 7.4mm) (TMCD-2464), Taishan, Ye-Liu, Taipei County, coll. Y. Fukui, 19 Nov. 1988; 4 males (7.0-9.4mmx 5.4-7.7mm), 2 females (9.6-11.0mm x 7.4-8.7mm) (TMCD-2514), Patouzhi, Keelung, coll. Wang C.H., 12 Apr. 1989; 1 male, 1 female (TMCD-2362), Haban, Xiao Ryukyus, Pingtung County, coll. J.C. Lin, 17 May 1988. 3 males (7.8-10.1mm x 6.1-7.9mm) (NMNS-002253-00084), Houdaizhi, Penghu, coll. P.W. Hseuh, 17 Jul. 1994; 1 male (6.2mm x 5.3mm) (NMMBA-uncataloged) Laiqingwan Bay, Lanyu Island, Taiwan, coll. P.H. Ho, 19 Apr. 2002.

**Diagnosis.**— Carapace subquadrangular, almost rounded, slightly broader then long; surface slightly convex, granulated in frontal region; front slightly deflected, anterior margin nearly straight. Anterolateral margin with three lobes instead of teeth including orbital lobe. Infra-orbital ridge with three elongated tubercules. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Chelipeds symmetrical, surface smooth, Ambulatory legs flat, stout; meri finely serrated on anterior, posterior margins, propodi, dactyli with short, long setae. G1 stout, distal chitinous process truncated. Female gonopore circular in shape with a semicircular operculum.

**Colour.**— The colour of fresh specimens can range from cream to light brown (Melo, 1998), sometimes purplish in colour (H.T. Shih), and all preserved specimens examined are cream to light grey in colour.

**Size.**— The largest male specimen reported is 13.4mm x 11.1mm (QIH specimen), and largest female specimen examined is 11.0mm x 8.7mm (TMCD-2514).

**Habitat.**— It can be found under rocks and shells at the upper intertidal zone (Dai & Yang, 1991; Melo, 1998).

**Remarks.**— This species is problematic. There are several morphological differences between the specimens collected from East Asia and the West Atlantic. Based on descriptions provided by Chace & Hobbs (1966), and Dai & Yang (1991), and in the specimens examined, there seems to be some discrepancies on the morphology. There seems to have two forms, the Asian form and the American form. The Asian form can be distinguished from the American form by the following features a) the anterolateral margin of the Asian form is very convex especially at the anterior half (vs. less convex in the American form); b) the posterolateral margin is distinctly converging (vs. subparallel in the American form); c) the front is produced downwards (vs. not produced downwards in the American form); d) the epigastric cristae are very distinct (vs. indistinct epigastric cristae in the American from); and e) the ambulatory legs are broader and stouter (vs. more slender and narrower legs in the American form). Indications are that we are dealing with two separate species but the lack of material on hand from America makes any decision now premature. There is thus a need to re-examine the *C. integer* specimens from the Eastern and Western Atlantic regions at a later date to ascertain their actual identities. To resolve this problem, the type specimen of *C. integer* has also to be located. Two attempts (1996 and 1999) to locate the specimen in the MNHN have been unsuccessful – it may be lost.

**Distribution.**— Taiwan, China, Polynesian Islands, Indo-West Pacific, Eastern and Western Atlantic.

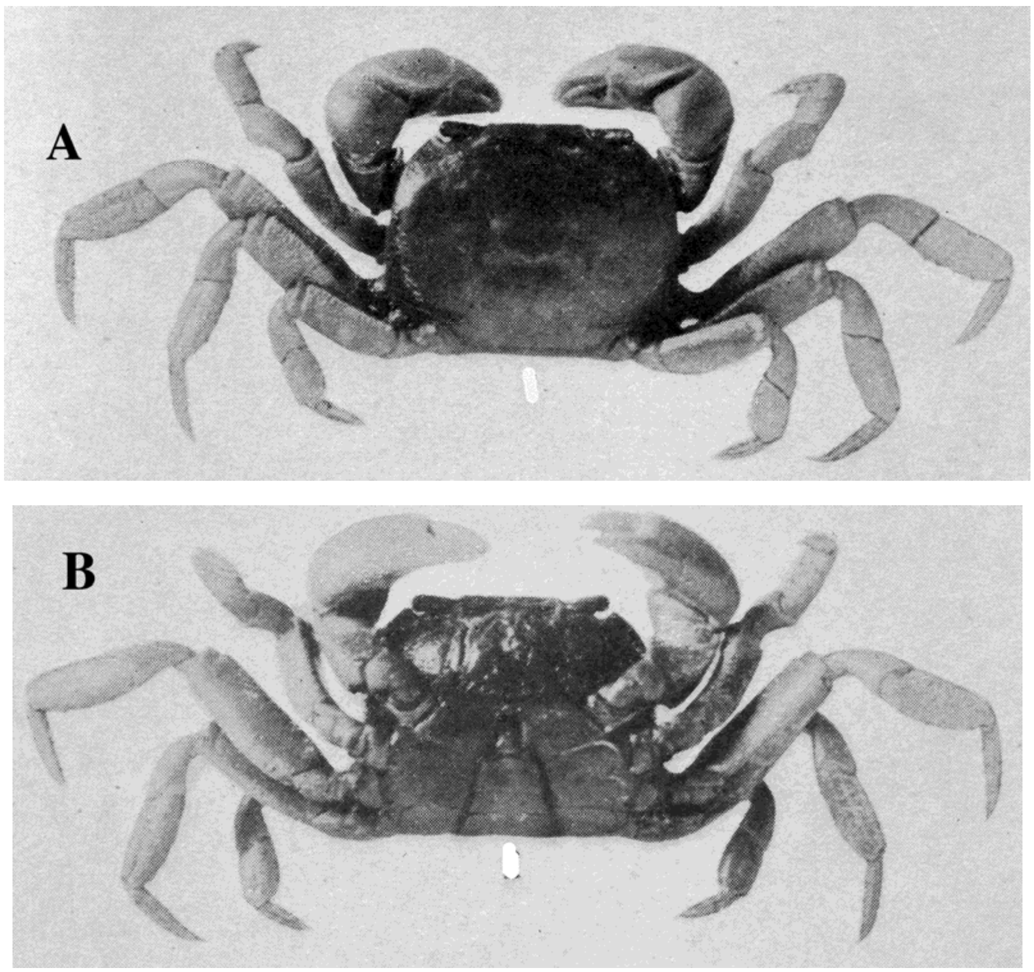



Figure 131. *Cyclograpsus integer* H. Milne Edwards, 1837. A) dorsal view; B) ventral view. (After Rathbun, 1918).

## *Cyclograpsus intermedius* Ortmann, 1894

(Figure 132)

*Cyclograpsus intermedius* Ortmann, 1894: 728; Doflein 1902: 667; Tesch, 1918: 127; Balss, 1922: 21; Sakai, 1934: 324, pl. 17, fig. 1; 1935: 232, pl. 62, fig. 3; 1939: 689, pl. 75, fig. 3; 1965: 200, pl. 94, fig. 4; 1976: 666, pl. 227: 2; Kamita, 1941: 228, text-fig. 125a-b; Campbell & Griffin, 1966: 140; Kim, 1973: 492, text-fig. 220, pl. 46, fig. 171; Dai *et al.*, 1986: 501, fig. 284: 1–2, pl. 71: 1; Dai & Yang, 1991: 549, fig. 284: 1–2, pl. 71: 1; Huang, 1994: 598; Ng *et al.*, 2001: 44.

**Materials examined.**— 1 male (12.5mm x 10.1mm), 2 females (ovigerous) (18.1-21.5mm x 14.5-17.6mm), (TMCD-2557), Hsiao-Hsiang-Lan, Fu Lung, Taipei County, Taiwan, coll. C.H. Wang, 21 Apr. 1989; 1 female (21.7mm x 17.8mm), (TMCD-7478), Patouzih, Keelung, coll. L.H. Sun, 2 Jan. 1989. 1 female (13.0mm x 10.5mm) (TMCD-2565), Badouzhi, Keelung, Taiwan, coll. L.Q. Sun, 7 May 1989.

**Diagnosis.**— Carapace quadrilateral, almost round in shape; surface flat, smooth; front deflected slightly, anterior margin nearly straight. Anterolateral margin with three teeth including orbital lobe. Infra-orbital ridge with 20 granules. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Chelipeds symmetrical, surfaces smooth, Ambulatory legs flat, slender, with distinct rows of very short setae on dactyli. G1 trigonal, distal chitinous process, inner lobe short. Female gonopore operculate, triangular in shape.

**Colour.**— The colour of fresh specimens is light brown in colour (C.H. Wang, pers. com.), and the preserved specimens examined are all cream coloured.

**Size.**— The largest male specimen recorded is 28.0mm x 23.8mm (Dai *et al.* 1986), and largest female examined is 21.5 x 17.6mm (TMCD-2557).

**Remarks.**— Tesch (1918) reported this species from India, but this is primarily an East Asian species. The identity of the specimens found in Indian Ocean will need to be ascertained. I have not been able to locate the type specimen of *C. intermedius*, but, I have been able to examine the specimens from area near the type locality. They fit the descriptions and figures provided by Ortmann (1894).

**Distribution.**— Taiwan, China, Japan, Korea, Indian Ocean.

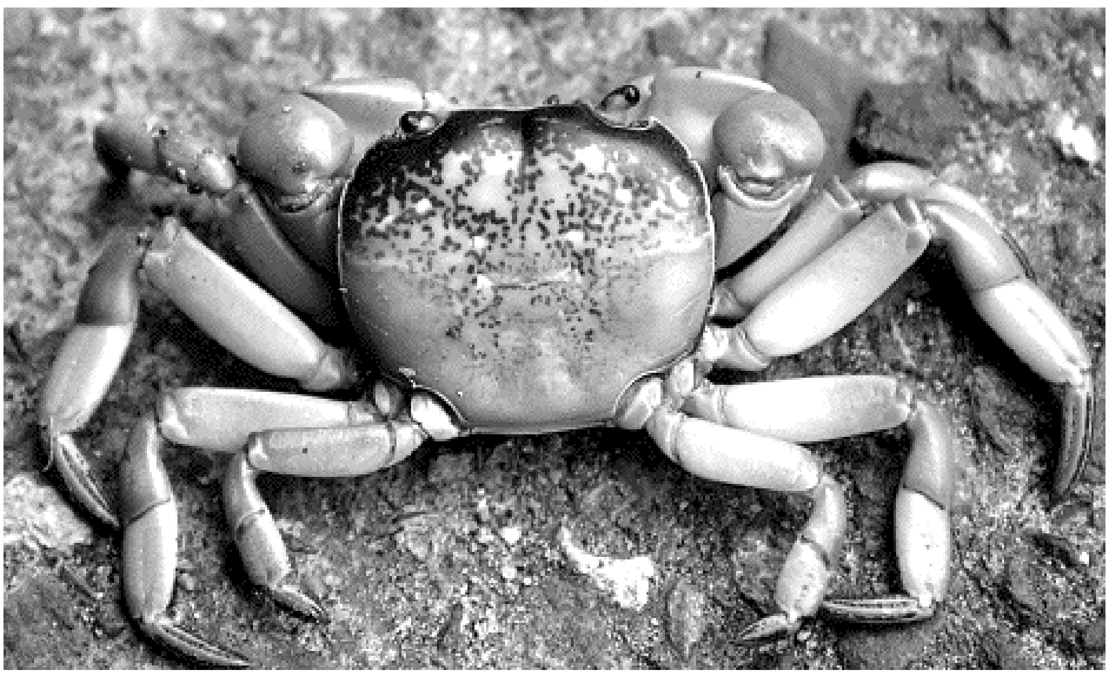


Figure 132. *Cyclograpsus intermedius* Ortmann, 1894. Dorsal view (Courtesy of Dr. H.T. Shih).

### *Cyclograpsus cinereus* Dana, 1852

(Figure 133A-B)

*Cyclograpsus cinereus* Dana, 1852: 251; 1852: 360, pl. 23, fig. 3a; Rathbun, 1918: 327, pl. 98; McLaughlin *et al*, 2005: 59.

**Materials examined.— Paratype** – 1 female (13.8mm x 11.4mm) (USNM-2340), Valparaiso, Aconcagua, Chile, coll. J.D. Dana, .S. Exploring Expedition, no collection date.

**Diagnosis.**— Carapace subquadrangular, almost rounded, slightly broader then long, broadest at hepato-brachial region, surface slightly convex, front slightly deflected, anterior margin nearly straight. Anterolateral margin with only one anterolateral tooth. Infra-orbital ridge with two elongated tubercules. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Chelipeds symmetrical, surfaces smooth, Ambulatory legs flat, stout, glabrous. Male abdomen almost rectangular in shape, telson small. (Modified from Rathbun, 1918).

**Colour.**— The colours of fresh and preserved specimens have not been documented.

**Size.**— The largest male size has not been reported, and the largest female specimen reported is 13.8mm x 11.4mm (Rathbun, 1918).

**Habitat.**— This species has been reported to be found in the intertidal area (Rathbun, 1918).

**Remarks.**— The species seem to favor sandy areas with little rainfall or freshwater (Rathbun, 1918). Although I did not examine any material, the species is easy to recognize, and Rathbun (1918) has provided an excellent figure (Rathbun, 1918: 327, plate 98).

**Distribution.**— Sandwich Island, Hawaii, west coast of Chile (Taltal), Peru, Panama.

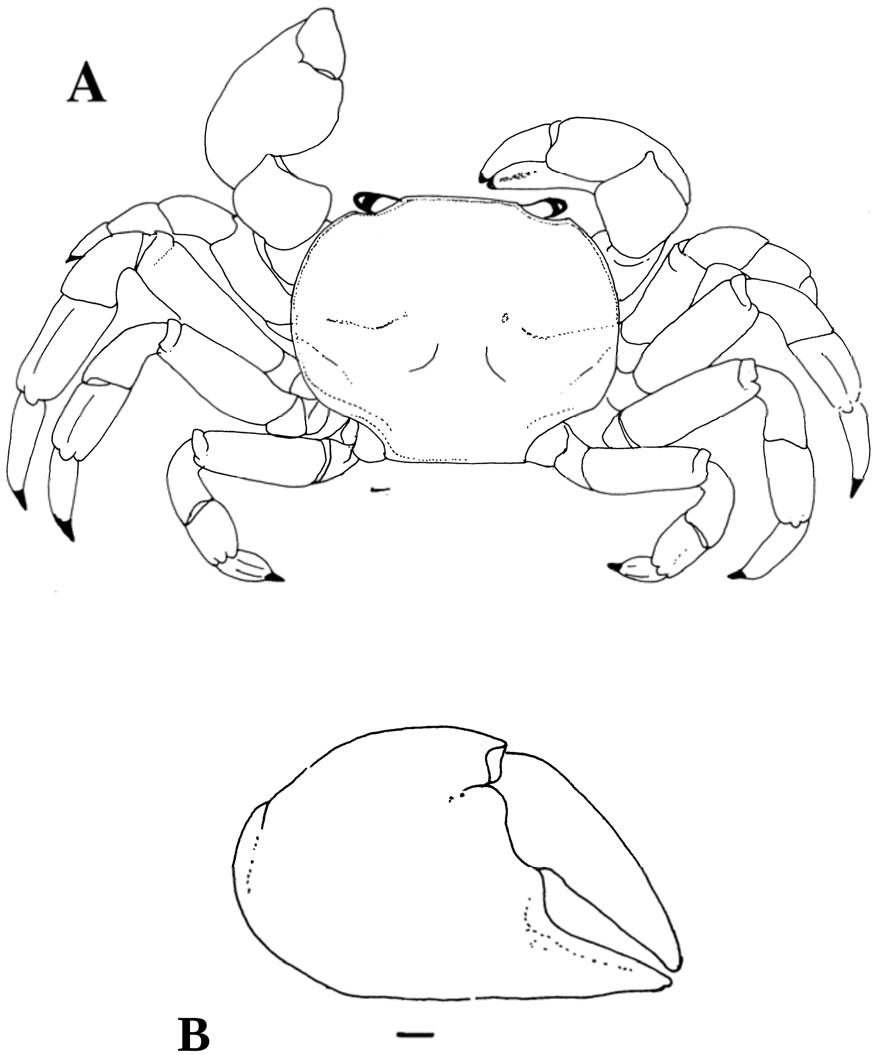



Figure 133. *Cyclograpsus cinereus* Dana, 1852A) dorsal view; B) chela. (After Campbell & Griffin, 1968).

## *Cyclograpsus granulatus* Dana, 1852

*Cyclograpsus granulatus* Dana, 1852: 251; 1852: 361, pl. 23, fig. 4; Rathbun, 1906: 840; McLaughlin *et al*, 2005: 60.

**Materials examined.**— **Neotype** – 1 male (8.3mm x 6.8mm), (ZRC 2000.0523) (ex BPBM-3164), Maui, Hawaii, coll. P. St Sure, 29 Aug. 1928. – **Others** – 3 males (6.9-8.3mm x 5.5-6.8mm) (ZRC 2000.0523) (ex BPBM-3164), Maui, Hawaii, coll. P. St Sure, 29 Aug. 1928; 2 males (7.0-9.8mm x 5.6-8.2mm), 1 female (ovigerous), (7.9mm x 6.4mm) (ZRC-uncatalogued), East Hagataa Bay, Guam, high tide zone, coll. K. & G. Paulay, 2 Feb. 2000.

**Diagnosis.**— Carapace subquadrangular, almost rounded, slightly broader then long, broadest at the hepato-brachial region, surface slightly convex, front slightly deflected, anterior margin nearly straight. Anterolateral margin with one anterolateral tooth. Infra-orbital ridge with more than 20 rounded granules. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Chelipeds symmetrical, surfaces smooth, Ambulatory legs flat, stout, glabrous. Male abdomen almost rectangular with all segments freely moveable (six somites plus telson), telson small.

**Colour.**— The colour of fresh specimens has not been documented, but all preserved specimens examined are dark cream in colour.

**Size.**— The largest male examined is 9.8mm x 8.2mm, and the largest female examined is 7.9mm x 6.4mm (ZRC 2000.0523).

**Habitat.**— It can be found under rocks, in the high tide line (ZRC-uncatalogued).

**Remarks.**— The species has only been found in Hawaii and Guam. There is very little knowledge about the biology of this species. This species is also very small in size, the ovigerous female being only 7.9mm x 6.4mm (ZRC specimens).

I have not been able to locate the type specimen of *C. granulatus* in USNM or elsewhere, and like much of Dana's material, is probably lost. For stability, I select a neotype from Maui, Hawaii (BPBM-3164/ZRC 2000.0523), the type locality.

**Distribution.**— Guam, Hawaii.

## *Cyclograpsus granulosus* H. Milne Edwards, 1853

(Figure 134A-E)

*Cyclograpsus granulosus* H. Milne Edwards, 1853: 197; Haswell, 1882: 104, Guiler, 1952: 40; Campbell & Griffin, 1966: 152.

*Cyclograpsus punctatus* – Haswell, 1882: 104; Guiler, 1952: 40; 1956: 7 (not *Cyclograpsus punctatus* H. Milne Edwards, 1837).

*Cyclograpsus audouinii* – Tweedie, 1942: 18, pl. 18, fig. 4 (not *Cyclograpsus audouinii* H. Milne Edwards, 1837).

**Materials examined.— Lectotype** – 1 female (dry) (22mm x 19mm) (MNHN), Tasmania, coll. M.M Quoy & Gaimard, no collection date. – Others – 2 males (23.7-28.8mm x 20.0-23.55m), 2 females (22.2-22.6mm x 18.4-18.5mm), (QM-W25594), Dunalley, Norfolk Bay, Tasmania, Australia, coll. Y. Fukui, 21 Dec. 2000.

**Diagnosis.—** Carapace subquadrangular, almost rounded, slightly broader then long, broadest at the hepato-brachial region, surface slightly convex, front slightly deflected, anterior margin nearly straight. Anterolateral margin with one anterolateral tooth. Infra-orbital ridge with 12-19 granules (mode 16) in males. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Chelipeds symmetrical, surfaces smooth, Ambulatory legs flat, stout, glabrous. Male abdomen almost rectangular in shape with all segments freely moveable (six somites plus telson), telson small. (Modified from Campbell & Griffin, 1966).

**Colour.—** The colour of fresh specimens has been reported to be deep red to brown, and sometimes purple (Guiler, 1952). The colour of preserved specimens has not been documented.

**Size.—** The largest male specimen reported is 35mm in carapace width, and largest female has a carapace width of 28.5mm (Campbell & Griffin, 1966)

**Habitat.**— It can be found under rocks, in the high tide line, usually near masses of seaweeds (Guiler, 1952; Campbell & Griffin, 1996).

**Remarks.**— This species has always been confused with *C. audouinii* as they are very similar in the form of the carapace but they can be differentiated by the following: a) the widest region of the carapace is nearer to the front (vs. widest region of the carapace near the mid region *in C. audouinii*); b) the frontal margin is four-lobed (vs. bilobed *in C. audouinii*); c) absence of setae at the base of ambulatory legs (vs. presence of setae *in C. audouinii*), and d) the tip of the G1 is straight (vs. curved in *in C. audouinii)*.

**Distribution.**— South Australia.

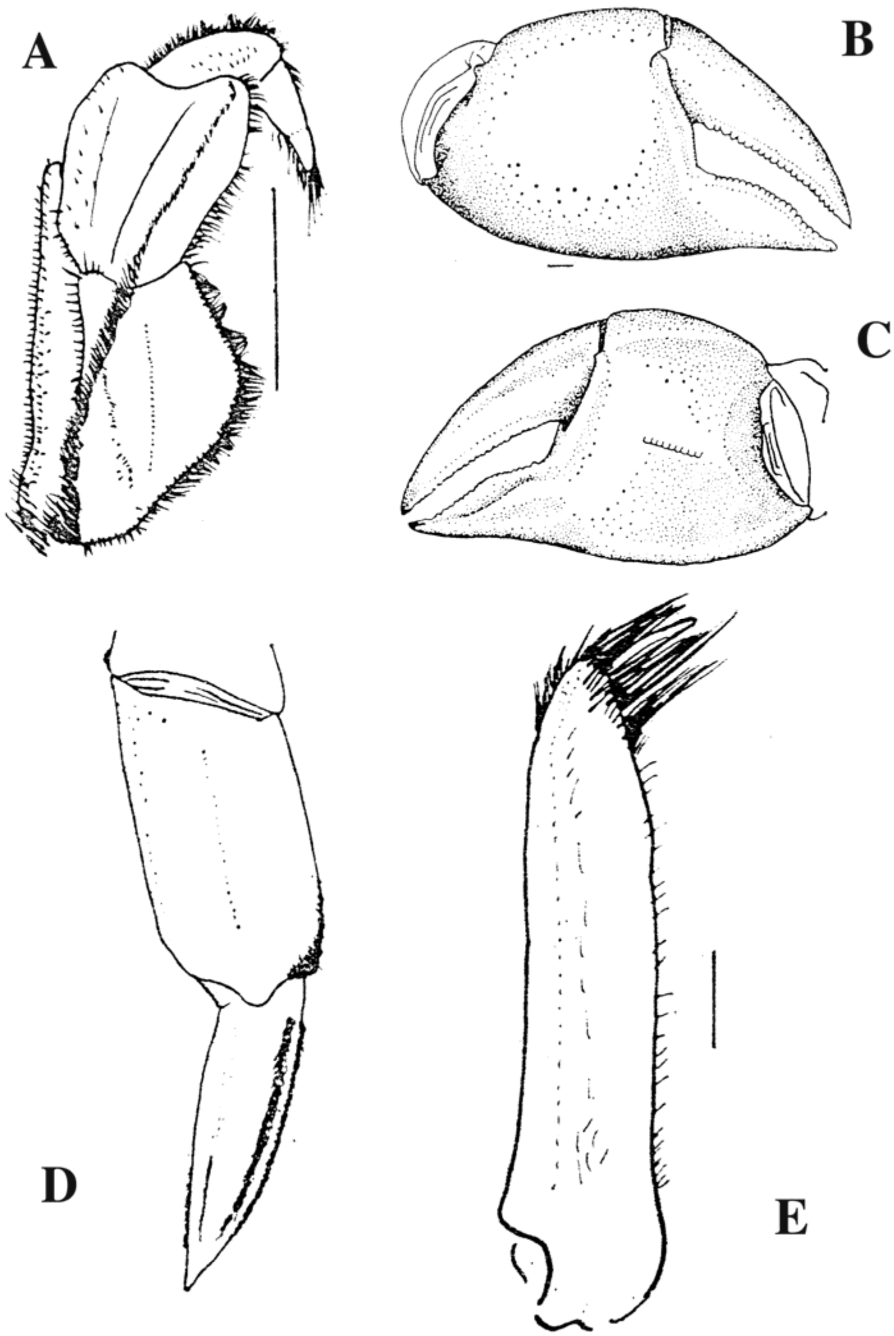



Figure 134. *Cyclograpsus granulosus* H. Milne Edwards, 1853. A) third maxilliped; B) outer view of chela; C) inner view of chela; D) last ambulatory leg; E) tip of G1. (After Campbell & Griffin, 1966).

### *Cyclograpsus longipes* Stimpson, 1858

(Figure 135)

*Cyclograpsus longipes* Stimpson, 1858: 105; Stimpson, 1907: 131; de Man, 1897: 355, pl. 32, figs. 43a-c; Rathbun, 1907: 36; Tesch, 1918: 126; Sakai, 1976: 667, pl. 227, fig. 3; Holthuis, 1953: 32; Forest & Guinot, 1961: 160; Garth, 1973: 325; Báez & Ruiz, 1985: 106; Dai *et al.*, 1986: 501, text-fig. 283; Dai & Yang, 1991: 548, text-fig. 283, pl. 70, fig. 8; Poupin, 2003: 36.

**Materials examined.**— 1 male (9.3 mm x 7.4 mm), 3 females (8.4-9.6 mm x 6.3-7.8 mm) (ZRC 1971.10.30.11-14), Fish market (1137), Indonesia, coll. 18 Feb. 1971.

**Diagnosis.**— Carapace subquadrangular, almost rounded, slightly broader then long; surfacefalt, smooth, granulated, striated in the margins; front slightly deflected, anterior margin nearly straight. Anterolateral margin with two small teeth including orbital teeth. Infra-orbital ridge with three elongated lobes. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Chelipeds symmetrical, surfaces smooth, Ambulatory legs flat, stout; meri finely serrated on anterior, posterior margins, propodi, dactyli with short, long setae. G1 stout, distal chitinous process narrow, long. Female gonopore circular in shape with a semicircular operculum.

**Colour.**— The colour of fresh specimens is cream to light brown (Poupin, 2003), and the colour of preserved specimens examined is cream to light grey (ZRC 1971.10.30.11-14).

**Size.**— The largest male specimen examined is 9.3mm x 7.4mm (ZRC-1971.10.30.11-14), and the size of the largest female specimen examined is 9.6mm x 7.8mm (ZRC-1971.10.30.11-14).

**Habitat.**— It can be found under rocks and shells at the upper intertidal zone (Dai & Yang, 1991).

**Remarks.**— *Cyclograpsus longipes* is not a common species. It is interesting to note that the crab is found mostly in the tropical coastal areas except for the specimens that are found in Bonin Islands of Japan by Sakai (1976: 667).

When Stimpson (1858) described this species, he did not state how many specimens he had examined but he based his description on a male specimen collected from Port Lloyd, Bonin Islands. Since his type specimen are not longer extant (Diess & Manning, 1981; Evans, 1967), I will select a neotype when the Bonin Islands specimens are available.

**Distribution.**— China (Xisha Islands), Japan (Amami Islands, Bonin Islands), Fiji Islands, Tahiti, and Indonesia.

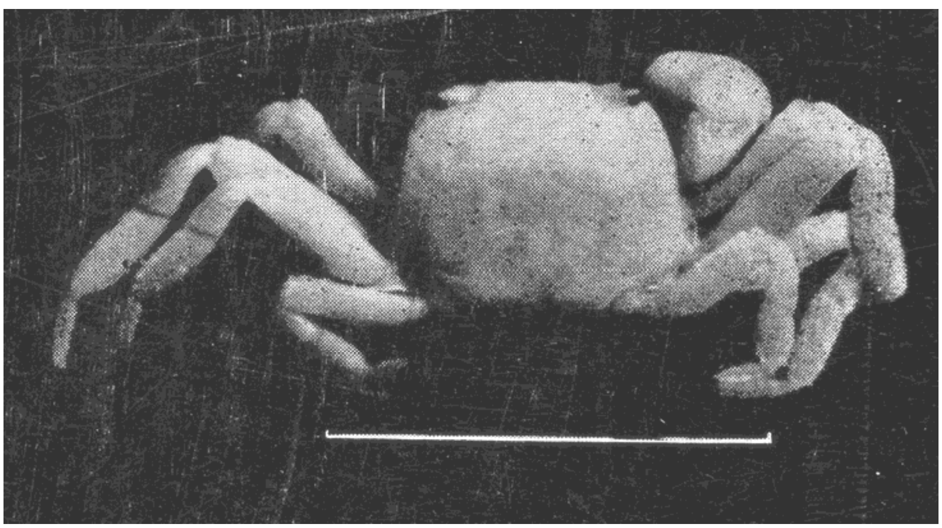


Figure 135. *Cyclograpsus longipes* Stimpson, 1858. Dorsal view. (After Dai & Yang, 1991).

### *Cyclograpsus lavauxi* H. Milne Edwards, 1853

(Figure 136A-B; 137A-E)

*Cyclograpsus lavauxi* H. Milne Edwards, 1853: 197; Miers, 1876: 41; Filhol, 1886: 390; Thomson, 1912: 238; Thomson & Anderton, 1921: 30; Chilton & Bennett, 1929: 770; Richardson, 1949: 29; Trevarthen & Kulka, 1950: 51; Dell, 1963: 50; Bennett, 1964: 84; Campbell & Griffin, 1966: 143; Dell, 1968; Griffin, 1968: 1; Bacon, 1971: 415; Hayward, 1974: 151; Marsden & Fenwick, 1978: 1; Knox & Bolton, 1978: 100; Marsden, 1981: 10; Wear & Fielder, 1985: 1; McLay, 1988: 310.

*Cyclograpsus chavauxi* – Batham, 1956: 447; 1958: 647 (wrong spelling).

*Cyclograpsus Whitei* H. Milne Edwards, 1853: 197; Filhol, 1886: 391.

*Cyclograpsus audoninii* Dana, 1852: 359, pl. 23, fig. 2 (not *Cyclograpsus audoninii* H. Milne Edwards, 1837).

**Materials examined.— Lectotype** (*Cyclograpsus lavauxi* H. Milne Edwards, 1853) **–** 1 male (23.0mm x 21.0mm) (MNHN), New Zealand, collection date.– **Others** – 2 males (10.3-12.3mm x 8.3-10.0mm), 1 female (10.4mm x 8.4mm) (NMNS-uncatalogued), Avon-Heathcote Estuary, mudflat, Christchurch, New Zealand, coll. C. McLay, 5 Jun. 2005; 1 male (12.0mm x 9.9mm) (ZRC-uncatalogued), Kaikoma Penninsular, New Zealand, coll. C. McLay, Aug. 2000. – **Holotype** (*Cyclograpsus whitei* H. Milne Edwards, 1853) – 1 female (27.0mm x 25.0mm) (MNHN), New Zealand, no collection date.

**Diagnosis.**— Carapace subquadrangular, almost rounded, slightly broader then long; surface slightly convex, granulated in frontal region; front slightly deflected, anterior nearly straight. Anterolateral margin smooth with only orbital tooth. Infra-orbital ridge with 10-17 irregularly sized granules. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Chelipeds symmetrical, surface smooth; male chela larger than female. Ambulatory legs flat, stout; meri finely serrated on anterior, posterior margins, propodi, dactyli with short setae or glabrous.

**Colour.**— Fresh specimens are distinctly speckled in dark reddish-brown colour of a varying shade of blue, bluish grey, fawn to yellowish brown. Its underside is pale, chelipeds are white (McLay, 1988). The colour of preserved specimens examined is dark cream in colour.

**Size.**— The largest male specimen reported is 28 mm in carapace width, and the largest female documented is 26 mm in carapace width (McLay, 1988).

**Habitat.**— This species is commonly found on rocky shores, in estuaries and mud flats. Usually hiding at high intertidal levels under boulders (McLay, 1988)

**Remarks.**— *Cyclograpsus lavauxi* is very similar to *C. insularum* but is different in having a) a very wide eye orbit (vs. narrower eye orbit in *C. insularum*), and b) the presence of 10 to 17 strong irregular-sized tubercules on the infra-orbital ridge (vs. 15 tubercules, decreasing in size outwards, in *C. insularum*). This species breeds in September to January (McLay, 1988). They have been observed to grasp stones with its rear legs, presumably to stabilize itself in the presence of wave action. This distribution of this species is very strange. It is found in abundance in New Zealand and Chile. It may well be that the one found in Chile is a different species, but this can only be ascertained when fresh materials from Chile are examined, as there is evidence that speciation has occurred after New Zealand and South America have been separated from the Antarctica (von Ihering, 1891; Veevers *et al*. 1991; Bruce, 2002) (see below in Discussion).

**Distribution.**— New Zealand and Chile (Juan Fernandez).

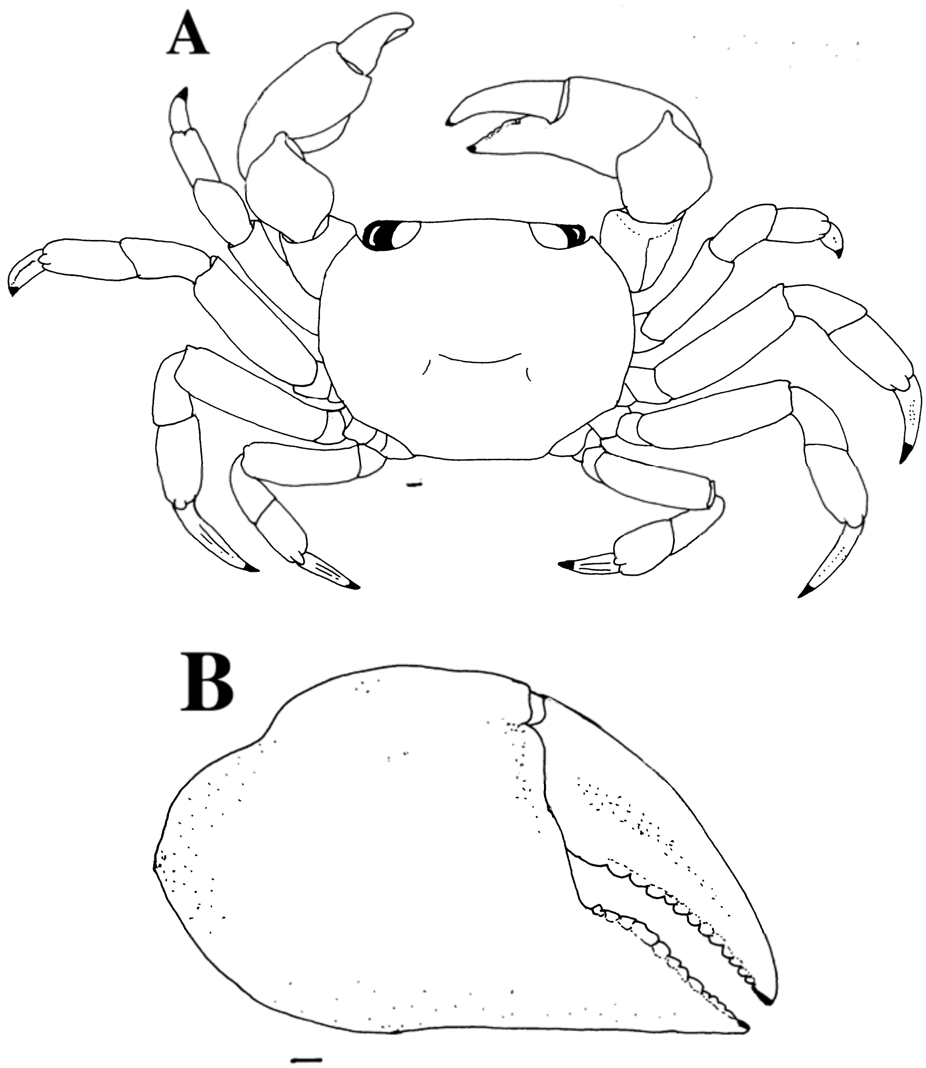



Figure 136. *Cyclograpsus lavauxi* H. Milne Edwards, 1853; A) dorsal view; B) cheliped (after Campbell & Griffin, 1966).

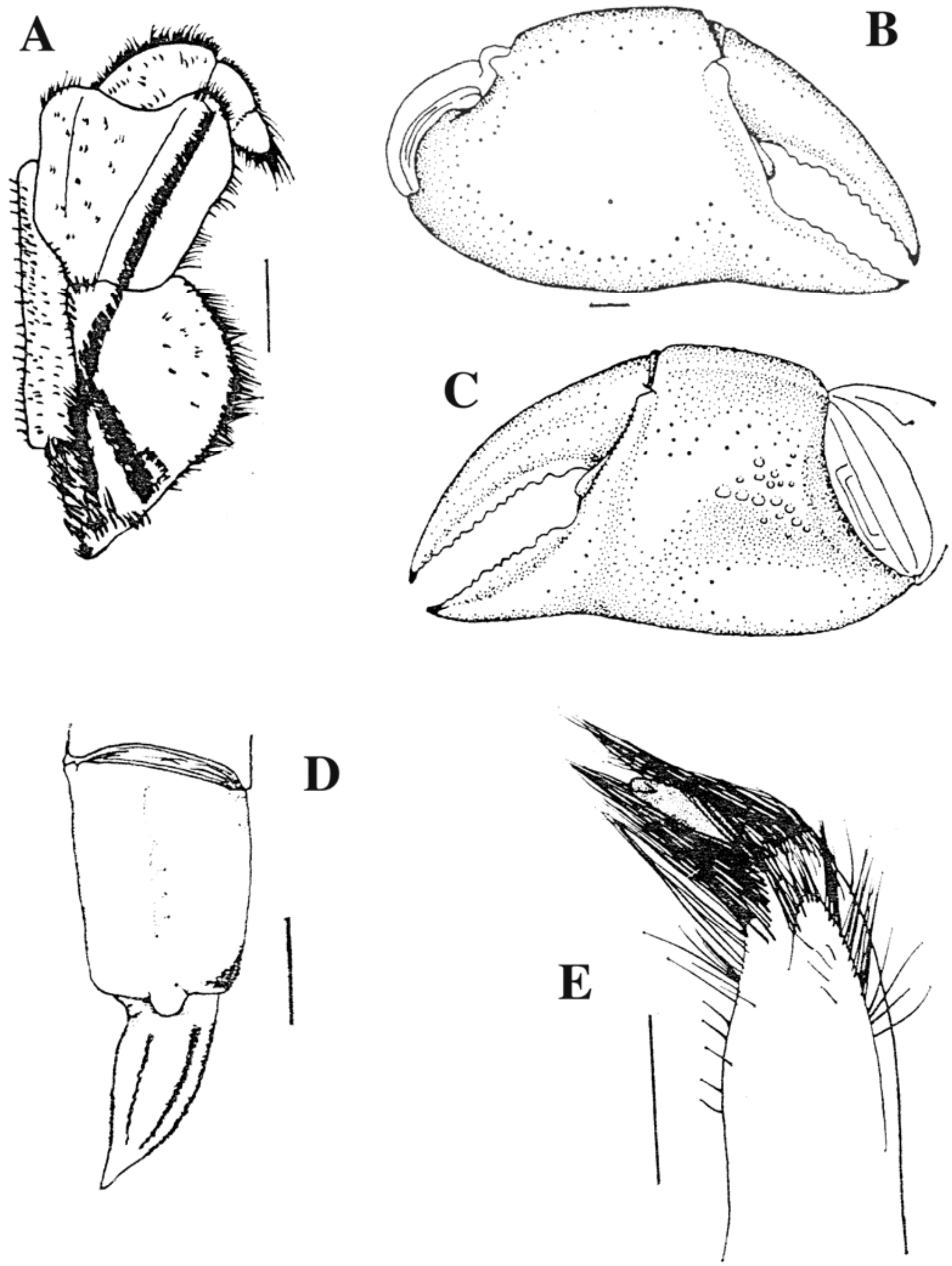



Figure 137. *Cyclograpsus lavauxi* H. Milne Edwards, 1853; A) third maxilliped; B) outer view of cheliped; C) inner view of chela; D) part of last ambulatory leg; E) tip of G1 (after Campbell & Griffin, 1966).

### *Cyclograpsus insularum* Campbell & Griffin, 1966

(Figure 138A-B; 139A-F)

*Cyclograpsus insularum* Campbell & Griffin, 1966: 164; Dell & Marshall, 1967: 1; Dell, 1968: 13; Bacon, 1971: 415; Wear & Fielder, 1985: 80; McLay, 1988: 306.

*Cyclograpsus whitei* Chilton & Bennett, 1929: 769; Dell, 1963: 50; Bennett, 1964: 85 (nomen preoocupum).

**Materials examined.**— No material examined.

**Diagnosis.**— Carapace subquadrangular, almost rounded, slightly broader then long; surface flattened, granulated in frontal region; front not deflected, anterior straight. Anterolateral margin granulated with only orbital tooth. Infra-orbital ridge with about 15 granules, largest beneath eyes. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Chelipeds symmetrical, surfaces smooth; male chela larger than females. Ambulatory legs flat, stout; meri finely serrated on anterior, posterior margins, propodi, dactyli with sparse short setae. (Modified from Campbell & Griffin, 1966; McLay, 1988).

**Colour.**— The colour of fresh specimens is smoothly graded from brown/purple in front, to paler brown towards the back of the carapace (McLay, 1988). The colour of preserved specimens has not been documented.

**Size.**— The largest male specimen reported has a carapace width of 22mm, and largest female a carapace width of 18mm (McLay, 1988).

**Habitat.**— This species can be found on the upper reaches of the intertidal zone, or on exposed shores in the presence of boulders, just lower than high tide level (McLay, 1988).

**Remarks.**— This species can be easily distinguished from *C. lavauxi* by the following characters a) the carapace lacks the distinct white spots found in *C. lavauxi*; b) all the ambulatory legs are broad and short e (vs. slender and narrow in *C. lavauxi*), and c) this is a smaller species compared to *C. lavauxi*, carapace width of mature male is about 22mm (vs. 28mm in *C. lavauxi*) (McLay, 1988). These crabs can be found in relatively high density of over 30/m$^2$, and they breed in winter from June to August, in a very short season of 9 weeks. They produce only one brood (McLay, 1988).

**Distribution.**— New Zealand only.

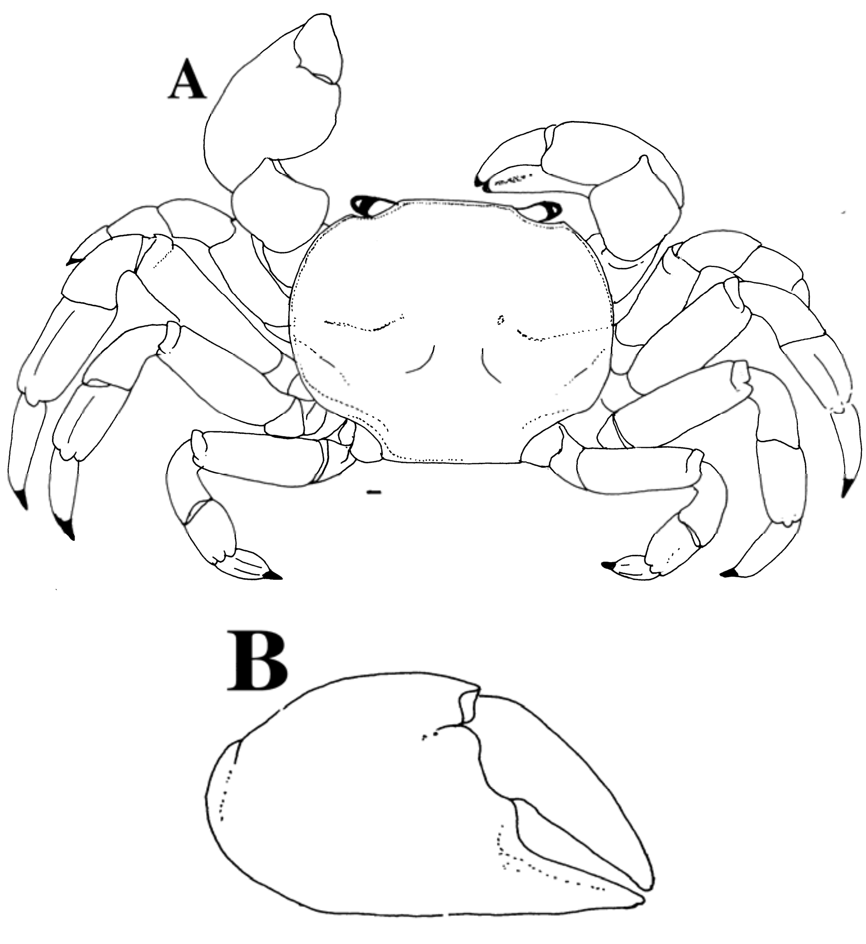



Figure 138. *Cyclograpsus insularum* Campbell & Griffin, 1966. A) dorsal view; B) cheliped (after Campbell & Griffin, 1966).

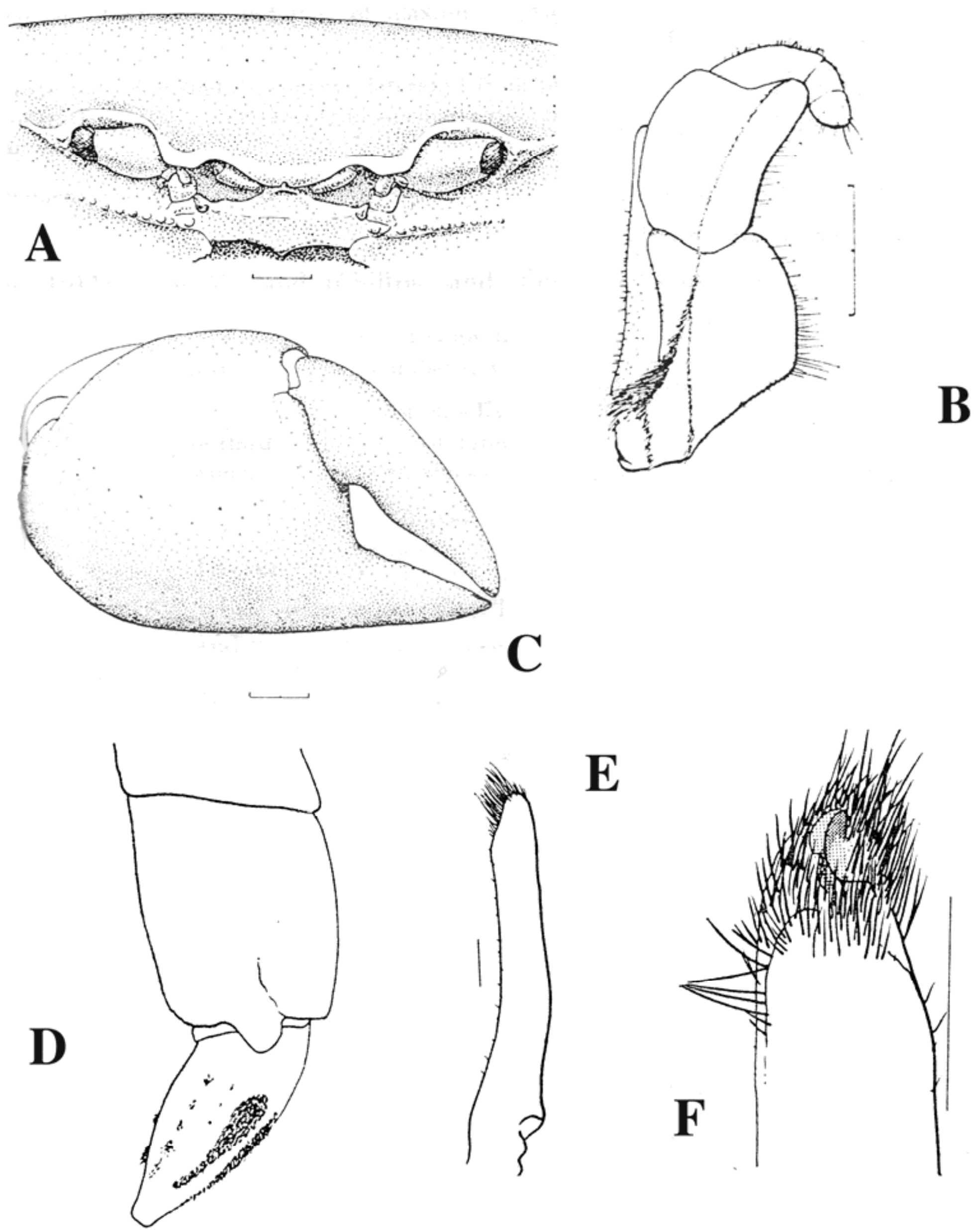



Figure 139. *Cyclograpsus insularum* Campbell & Griffin, 1966. A) frontal view of crab; B) third maxilliped; C) outer view of cheliped; D) inner view of chela; E) part of last ambulatory leg; F) tip of G1 (after Campbell & Griffin, 1966).

***Cyclograpsus henshawi* Rathbun, 1902**

(Figure 140A-C)

*Cyclograpsus henshawi* Rathbun, 1902: 75; Edmondson, 1959: 188; McLaughlin *et al*, 2005: 60

**Materials examined.**— **Holotype** – 1 male (USNM-22857), Hilo Hawaii Island, Hawaii, USA, no collection date. – **Paratype** – 1 female (USNM-22857), Hilo Hawaii Island, Hawaii, USA, no collection date. – **Others** – 2 males (15.9-18.2mm x 13.2-14.7mm), 1 female (12.9mm x10.1mm) (ZRC 2000.0525) (ex BPBM-1598), Kanana Bay, Oahu, Hawaii, coll. C.H. Edmondson, 22 Mar. 1924.

**Diagnosis.**— Carapace subquadrangular, slightly broader then long; surface flattened, smooth, granulated in frontal region; front not deflected, anterior straight. Anterolateral margin granulated with only orbital tooth. Infra-orbital ridge with innermost granule elongated, followed by three granules that are decreasing in size. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Chelipeds asymmetrical, surfaces smooth. Ambulatory legs flat, stout; meri finely serrated on anterior, posterior margins, propodi, dactyli with sparse short setae.

**Colour.**— The colour of both fresh and preserved specimens have not been documented.

**Size.**— The largest male specimens reported is 19.5mm x 16.0mm (Rathbun, 1902), and largest female specimen examined is 12.9mm x 10.1mm (ZRC 2000.0525).

**Habitat.**— It can be found  under rocks at the upper intertidal zone (Rathbun, 1902).

**Remarks.**— This species was reported by Rathbun (1902: 76) to be ‘not rare’ in the Hawaiian islands, and yet there are few specimens available in the museums.

**Distribution.**— Hawaii, Maui, Oahu only.

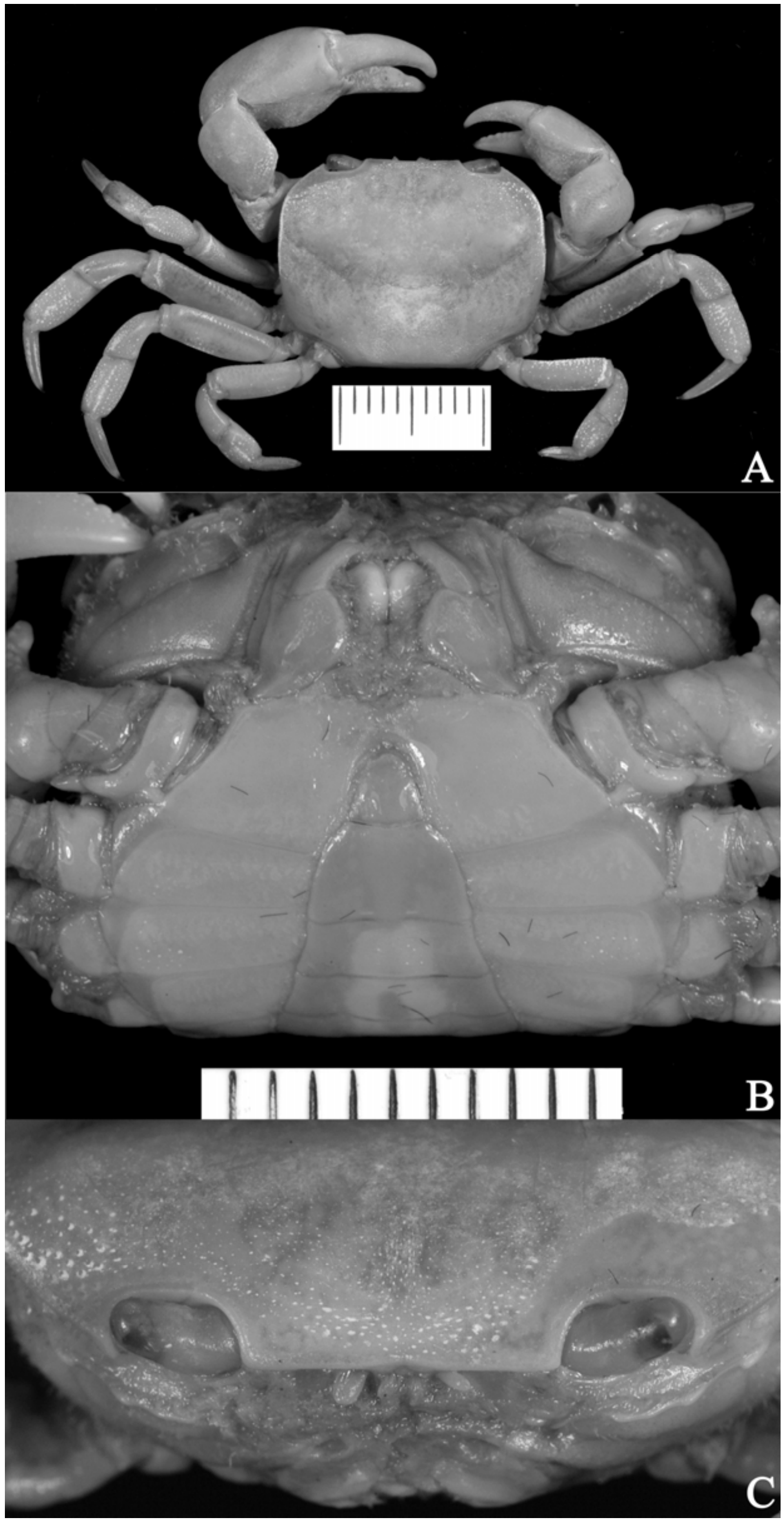



Figure 140. *Cyclograpsus henshawi* Rathbun, 1902 male, 18.2mm x 14.7mm (ZRC 2000.0525). A) dorsal view; B) ventral view; C) frontal view.

### *Cyclograpsus lucidus* Dai, 1986, in Dai, Yang, Song & Chen, 1986

(Figure 141)

*Cyclograpsus lucidus* Dai, 1986: 546, pl.70 (6), text-fig. 282(1); Dai & Yang, 1991: 546, pl. 70, fig. 282.

**Materials examined.—** No material examined.

**Diagnosis.—** Carapace almost rounded, slightly broader then long; surface slightly convex, granulated in frontal region; front slightly deflected, anterior margin nearly straight. Anterolateral margin with only orbital tooth, posterolateral margin slightly diverging. Infra-orbital ridge with five protuberances, innermost two elongated, decrease in size. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Chelipeds asymmetrical, surfaces smooth. Ambulatory legs flat, stout; meri finely serrated on anterior, posterior margins, propodi, dactyli with short setae. G1 stout, distal chitinous process rounded. Female gonopore unknown. (Modified from Dai & Yang, 1991).

**Colour.—** The colour of both fresh and preserved specimen has not been documented.

**Size.—** The largest male specimen is 20.5mm x 16.8mm, and largest female specimen 15.2mm x 13.0mm (Dai *et al.*, 1986).

**Habitat.—** The habitat of this species has not been documented.

**Remarks.—** Dai (1986) described this species based on several specimens collected from the different localities in Hainan Island, southern China. She compared the species with *C. audouinii*, *C. lavauxi*, *C. puntatus* and *C. granulatus*, stating that *C. lucidus* is different from these species only in the form of the G1 but she did not specifically state how different it was.

There was no further report about the species thereafter. Attempts to borrow the specimens from the Institute of Zoology, The Chinese Academy of Sciences, Beijing, has been unsuccessful as the specimens could not be located (first attempt in December 1999, and the second attempt in November in 2005). In November 1998, the author went to the type locality, Sanya, the southern coast of Hainan Island, and Qiongshan in Hainan Island to attempt to collect the species but to no avail. The coastline along the Hainan Island has been very badly degraded, especially Sanya, which is now a very prominent tourist city in China.

**Distribution.**— China (Hainan Island) only.

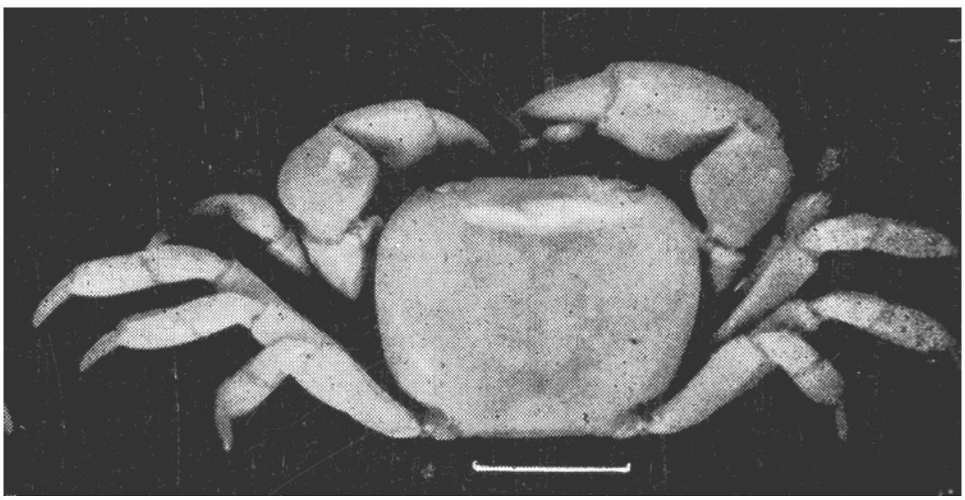


Figure 141. *Cyclograpsus lucidus* Dai, 1986. Dorsal view (After Dai & Yang, 1991).

***Cyclograpsus incidus* Shen, 1940**

(Figure 142)

*Cyclograpsus incidus* Shen, 1940: 259, figs. 10-16; Campbell & Griffin, 1966: 140; Dai *et al.*, 1986: 500: Dai & Yang, 1986: 547.

**Materials examined.**— No material examined.

**Diagnosis.**— Carapace subquadrangular, almost rounded, slightly broader then long; surface flat, smooth, granulated in frontal region; front slightly deflected, anterior margin nearly straight. Anterolateral margin with three weak lobes instead of teeth including orbital lobe. Infra-orbital ridge with 11 granules. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Chelipeds symmetrical, surfaces smooth, Ambulatory legs flat, long; meri finely serrated on anterior, posterior margins, propodi, dactyli with short, long setae. (Modified from Dai & Yang, 1986).

**Colour.**— The colour of both fresh and preserved materials has not been documented.

**Size.**— The largest male specimen reported is 10.0mm x 8.7mm (Dai & Yang, 1986), and no female specimen has been recorded.

**Habitat.**— This species can be found  in shallow waters in the littoral zone (Dai & Yang, 1986).

**Remarks.**— The specimen of this species cannot be located in the Institute of Zoology, The Chinese Academy of Sciences (see above). There is no other report on this species after its original description. I had tried to collect the fresh materials of this species along the coast of Guangdong Province, China, in November 1998 and September

2005, but these trips had been fruitless. There is no mention of female specimens by Dai & Yang (1991).

**Distribution.—** China (Guangdong Province).

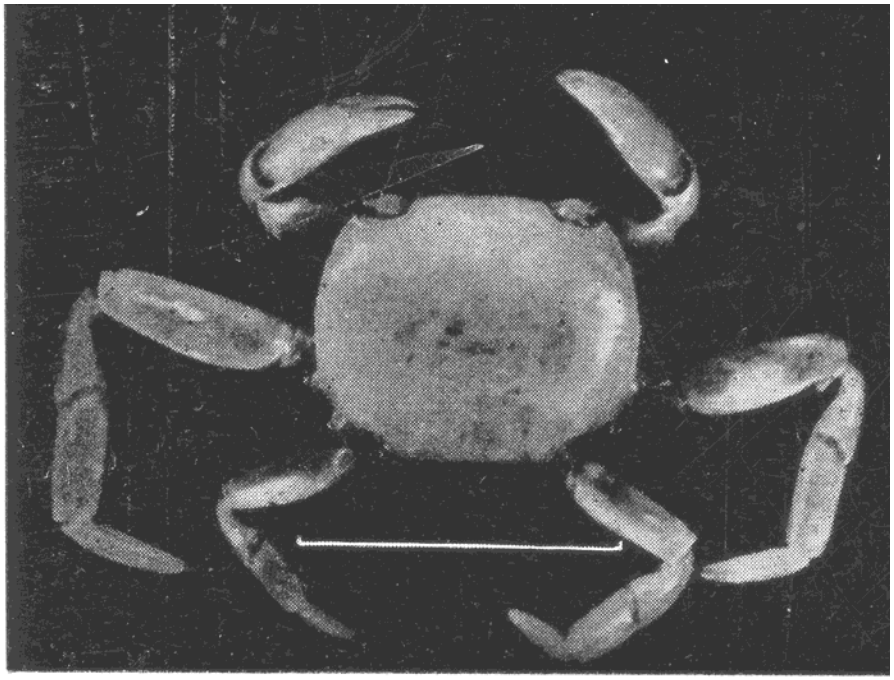


Figure 142. *Cyclograpsus incidus* Shen, 1940. Dorsal view (After Dai & Yang, 1991).

***Cyclograpsus sanctaecrucis* Griffin, 1968**

(Figure 143)

*Cyclograpsus sanctaecrucis* Griffin, 1968: 236, figs. 1, 2a-b, e; 3a-b, 4a-b, g)

*Cyclograpsus minutus* – Ward, 1941: 14 (not *Cyclograpsus minutus* Jacquinot in Hombron & Jacquinot, 1852)

**Materials examined.**— No material examined.

**Diagnosis.**— Carapace subquadrangular, almost rounded, distinctly broader than long; surface slightly convex, granulated in frontal region; front slightly deflected, anterior margin nearly straight. Anterolateral margin with two lobes including orbital lobe. Infra-orbital ridge with three small narrow lobules below orbit, two broader ones at lateral end. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Chelipeds symmetrical, long, surfaces smooth. Ambulatory legs flat, long; meri finely serrated on anterior, posterior margins, propodi, dactyli with short, long setae. (Modified from Griffin, 1968).

**Colour.**— The colour of fresh specimens has not been documented but preserved specimens are cream white and the setae are pale to russet in colour (Griffin, 1968).

**Size.**— The largest male specimen reported is 8.7mm x 7.2mm (Griffin, 1968), and the largest female specimen examined is 7.1mm x 5.8mm.

**Habitat.**— Probably intertidal, there is no other information on this species.

**Remarks.**— Based on the descriptions and diagrams provided by Griffin (1968), this species is very closely allied to *C. integer* in the form of the carapace, but can be differentiated by the following features a) the presence of a notch on the anterolateral margin (vs. absent in *C. integer*); b) the posterolateral margin of the carapace is less strongly divergent (vs. strongly divergent in *C. integer*); c) the male abdomen is broadly triangular in shape (vs. more narrowly triangular in *C. integer*); d) the propodus of the ambulatory legs are more narrow (vs. broad in *C. integer*), and e) the corneous terminal process of the G1 is very short (vs. long in *C. integer*).

*Cyclograpsus sanctaecrucis* is also closely allied to *C. longipes* but can be differentiated from the latter by a) the presence of one notch on the anterolateral margin of the carapace (vs. presence of two notches in *C. longipes*); b) a less divergent posterolateral margin (vs. strongly divergent posteroalteral margin in *C. longipes*), and c) the presence of weakly developed epigastric lobes (vs. absent in *C. longipes*).

This species is, again, not known except for its original report.

**Distribution.**— Santa Cruz, Pacific Ocean only.

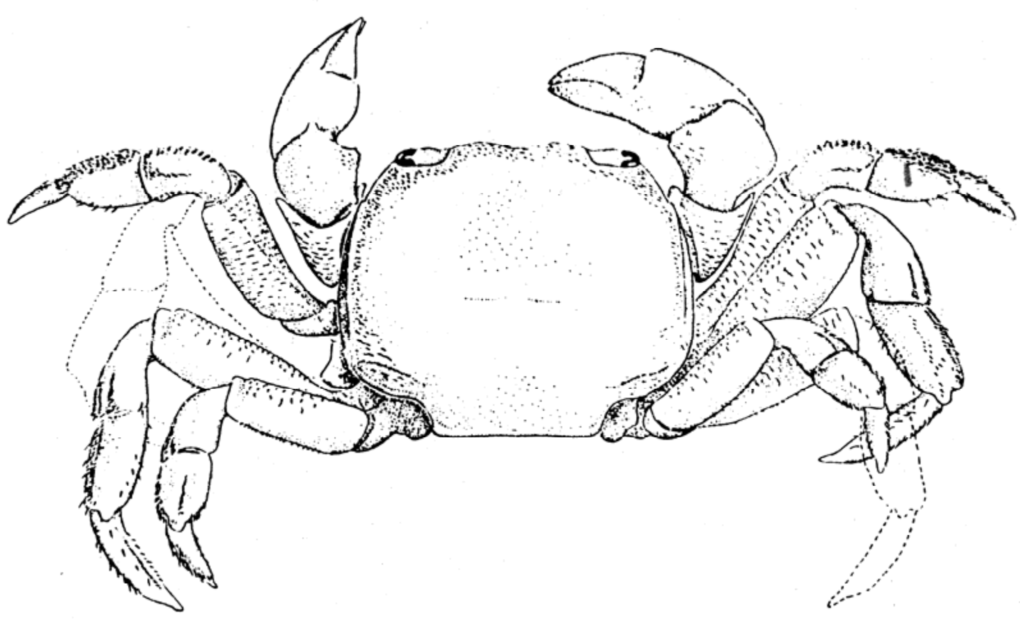


Figure 143. *Cyclograpsus sanctaecrucis* Griffin, 1968. Dorsal view. (After Griffin, 1969).

### ***Cyclograpsus beccarii* Nobili, 1899**

*Cyclograpsus beccarii* Nobili, 1899: 41; Griffin, 1968: 238.

**Materials examined.**— No material examined.

**Diagnosis.**— Carapace subquadrangular, almost rounded, slightly broader then long; surface very convex, granulated in frontal region; front slightly deflected, anterior margin nearly straight. Anterolateral margin with two teeth including orbital teeth, followed by four small notches. Infra-orbital ridge with several large granules. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Chelipeds symmetrical, surfaces smooth. Ambulatory legs flat, long; meri finely serrated on anterior, posterior margins, propodi, dactyli with short, dense setae. (Modified from Griffin, 1968).

**Colour.**— The colour of fresh  and preserved specimens has not been documented,

**Size.**— The sizes of largest male and female specimens have not been documented.

**Habitat.**— The habitat of this species has not been documented.

**Remarks.**— This species has been reported to be closely allied to *C. intermedius* and *C. incisus* in having only two teeth on the anterolateral margins, but it can be easily distinguished from the two species by the presence of four small notches behind the two teeth on the anterolateral margins, and the very convex carapace (see Nobili, 1899). On this basis, Nobili actually suggested this species be transferred to it own genus (Nobili, 1899: 42, Griffin, 1968: 238). Unfortunately, this species has not been reported after its description. The type specimens are located in the Museo Civico di Storia Naturale, Genoa, Italy, but Griffin (1968: 238) reported that it "… cannot be found in the collections of that institution". The identity and validity of this species cannot be ascertained unless the type materials or fresh materials from the type locality are examined. The author had had written to the Museo Civico di Storia Naturale, Genoa, in the years 1999, 2001, and 2005, but she has yet to receive any reply. Attempts to obtain fresh material from West Irian (via R. Rahayu) has been unsuccessful as well. Since there is no material available for examination, I have regarded this taxa as an *incerta sedis*, although I keep it in *Cyclograpsus* for convenience.

**Distribution.**— Dorei (Manokwari) in West Irian (Griffin, 1968).

## *Cyclograpsus escondidensis* Rathbun, in Glassell, 1933

*Cyclograpsus escondidensis* Rathbun, in Glassell, 1933: 336, pl. 23; Griffin, 1968: 241; Brusca, 1980: 56; Boschi, 2000: 76; Enríquez, 2001: 97.

**Materials examined.— Holotype –** 1 male (USNM-67863), collected at high tide under stones, Puerto Escondido, Sonora Gulf of California, Mexico, coll. S.A. Glassell, 17 Dec. 1931. – **Paratypes –** 1 female (USNM-67864), collected at high tide under stones, Puerto Escondido, Sonora Gulf of California, Mexico, coll. S.A. Glassell, 17 Dec. 1931; 1 male, 1 female (USNM-122630), collected at high tide under stones, Baja California, Mexico, coll. S.A. Glassell, 19 Dec. 1931.

**Diagnosis.**— Carapace subquadrangular, almost rounded, slightly broader then long; surface slightly convex, granulated in frontal region; front slightly deflected, anterior margin nearly straight. Anterolateral margin with three lobes instead of teeth including orbital lobe. Infra-orbital ridge with numerous granules interspersed with setae. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Chelipeds symmetrical, inner surface with scattered granules. Ambulatory legs flat, long; meri very flat, broad, finely serrated on anterior, posterior margins, propodi, dactyli with short, long setae.

**Colour.**— The colour of fresh and preserved specimens has not been documented.

**Size.**— The sizes of male and female specimens have not been documented.

**Habitat.**— The habitat of this species has not been documented.

**Remarks.**— This species is very closely allied to *C. integer* and *C. henshawi*, but is distinctive because of the presence of a) a very straight frontal margin; b) the presence of numerous granules interspersed with setae on the male infra-orbital ridge, and c) the presence of very broad meri of the ambulatory legs (Griffin, 1968). This species seems to be relatively uncommon (Griffin, 1968; Brusca, 1980; Boschi, 2000; Enríquez, 2001).

**Distribution.**— Central West America (Puerto Escondido, B.C.S) only (Brusca, 1980; Boschi, 2000; and Enríquez, 2001).

## Genus *Chasmagnathus* De Haan, 1853

*Ocypode* (*Chasmagnathus*) De Haan, 1835: 56; Adams & White, 1849: 52; H. Milne Edwards, 1853: 200; Herklots, 1861: 15.

*Chasmagnathus* – Dana, 1852: 251; Dana, 1852: 364-365; Dana, 1855: 8, pl. 23 figs. 6a-d; Dana, 1880: 222-223; Stimpson, 1858: 105; Miers, 1881: 69; Matsuura, 1894: 56; Ortmann, 1894: 727; Ortmann, 1898: 605; Stimpson, 1907: 133; Terao, 1916: 188; Tesch, 1918: 124; Parisi, 1918: 105; Rathbun, 1918: 329; Urita, 1918: 65; Balss, 1922: 154; Maki & Tsuchiya, 1923: 173, pl. 21 fig. 1; Urita, 1926: 21; Asano, 1933: 556-557, text-fig. 1263; Sakai, 1935: 73; 1936: 232, pl. 64 fig. 1; Kamita, 1936: 320; 1936: 35; Shen, 1940: 74, 94; Sakai, 1939: 690, pl. 77 fig. 1; 1940: 51; Horikawa, 1940: 30; Kamita, 1941a: 88; Kamita, 1941b: 229, text-fig. 127; Kamita, 1941c: 233, 237, 242; Kamita, 1974: 720, 1 text-fig.; Tanaka, 1943: 7; Nakazawa & Sakai, 1947: 652, fig. 1880; 1960: 85, pl. 42, fig. 4; 1965: 205, pl. 98, fig. 4; Tanaka, 1949: 25; Lin, 1949: 30; Sakai, 1950: pl. 3, fig. 2; 1954: 76; Utinomi, 1956: pl. 45, fig. 9; Miyake, 1961: 177; 1962: 131; Kim, 1962: 54, 55; Wu *et al.*, 1962: 203; Shen & Liu, 1963: 142, 144; Park, 1964: 18; Shen & Dai, 1964: 131, 1 fig.; Serène, 1968: 109; Kim, 1970: 23; Coelho & Ramos, 1973: 202; Holcman de Spector, *et al.*, 1973: 217; Kim, 1973: 493, 656, fig. 222, pl 45, fig. 172; Yamaguchi *et al.*, 1976: 41; Sakai, 1976: 668, pl. 228 fig. 1; Kikuchi & Miyake, 1978: 45; Kim & Kim, 1982: 153; Nakasone *et al.*, 1983: 37; Miyake, 1983: 186, pl. 62, fig. 4; Takeda, 1983: 147 (col. fig.), 287; Su & Lue, 1984: 63, 67, fig. 12; Kim & Chang, 1985: 56; Matsuo & Makiya, 1985: 307, 309, 312; Dai *et al.*, 1986: 502, text-fig. 284/3, pl. 71 fig. 2; Clark, 1987: 45; Yamaguchi *et al.*, 1987: 33; Fukui *et al.*, 1989: 230; Yoshimura, 1990: 755, 760, 761; Dai & Yang, 1991: 550, text- fig. 284(3), pl. 71 fig. 2; Yamaguchi & Baba, 1993: 487, fig. 186; Wada, 1995: 410, pl. 116-2; Poupin, 1996: 69; Muraoka, 1998: 54; Islam *et al.*, 2000: 35; Asakura, 2000: 335; Ng *et al.*, 2001: 44; Davie, 2002: 207; Sakai *et al.*, 2006: 8. (part).

**Diagnosis.**— Carapace quadrangular, broader than long, surface convex, well defined, lateral margins convergent. Suborbital ridge in males and females heteromorphic, bearing strong crests in their median region. Merus of third maxilliped nearly half as broad anteriorly as long. Chelipeds equal in males, females; chelae glabrous at base of fingers; short stridulating ridge present at merus in males,females. First to third ambulatory legs with thick velvety setae on carpi, propodi. Third abdominal somite of male projecting laterally. G1 with sperm channel suture totally on ventromesial surface, stem thick and broadened distally, short corneous tip tubular and with a dorsal genital aperture; palp stout, triangular.

**Type species.**— *Chasmagnathus convexus* De Haan, 1835, by monotypy.

**Gender.**— Masculine.

**Remarks.**— Currently, there are four species in this genus viz *Chasmagnathus convexus* de Haan, 1835 (type species); *C. granulatus* Dana, 1852; *C. subquadrata* Dana, 1852, and *C. georgei* Clark, 1987. Sakai *et al.* (2006) recently revised this genus. They have have retained *C. convexus* in *Chasmagnathus*, and transferred *C. granulatus* to an new genus, *Neohelice* Sakai, Türkay & Yang, 2006, and created another genus with two new subgenera viz. *Pseudohelice* (*Parahelice*) Sakai, Türkay & Yang, 2006, for *C. georgei* and *Pseudohelice* (*Pseudohelice*) Sakai, Türkay & Yang, 2006, for *C. subquadrata* respectively. They further added that *Pseudohelice* is the subtropical or tropical counterpart of the temperate *Helice*.

Based on the specimens examined (*C. convexus*, *C. subquadrata*, and *C. granulata*) and the detailed description provided by Clark (1987) for *C. georgei*, the author concurs with Sakai *et al.*'s (2006) splitting up of *Chasmagnathus* into the three genera. I do not agree on the subgenus nomenclature, as there are enough external adult morphological characters to show that they are all separate genera. These morphological characters are robust enough. Preliminary studies on the CO1 and 16s gene carried out by H. T. Shih (in collaboration with the present author), has also supported Sakai *et al.*'s (1986) separation (see text figures 1 and 2 below). This molecular study is not yet published, but follows the protocols established by H.T. Shih for other groups of crabs he has been working on (e.g. see Shih *et al.*, 2004). As Sakai *et al.* (2006) currently define it, *Chasmagnathus* is monotypic, comprising of only *C. convexus* de Haan, 1835.

A comment on the study of Sakai *et al.* (2006) is important here. As the thesis was being written, this important paper has yet to be published, ostensibly in

Senckenbergiana Maritima in Frankfurt, Germany, the institutional organ of the second author, Michael Türkay. The author, and her supervisor, has read several versions of this manuscript, including helping to review the final paper, which was supposed to have been published early 2006. Delays appear to have taken place and indications are that this paper will appear soon. As such, we have used the names proposed by Sakai *et al.* (2006) rather than "new genus 1 or 2" as they complicate the discussion. Before this part of the thesis goes to press, the necessary checks will be made to ensure that no nomen nuda arise. In fact, previous delays and miscommunications with an earlier version of this important paper has resulted in one of the names, *Pseudohelice* being accidentally cited in Guinot & Bouchard (1998: 666), and the name becoming a nomen nudum there.

The genus *Chasmagnathus* sensu lato is relatively common in East Asia, Australia, and South America. Species in this genera like *C. convexus* and *C. granulata* are also very popular experimental animals (de Oliveira, 1940; 1962; Oliveira, 1948; 1950; 1955; 1958; Boschi *et al.*, 1967; Coelho & Ramos, 1973; 2; Holcman *et al.*, 1973; Maldonado *et al.*, 1989; Melo *et al.*, 1989; López *et al.*, 1999; Gimenez & Anger, 2001; Kopin *et al.*, 2001; Rainbow & Black, 2001; Rodríguez *et al.*, 2001; Luquet *et al.*, 2002; Weihrauch1 *et al.*, 2003; Genovese *et al.*, 2004). There are very few reports on the discussion on the taxonomic status on this animal (Stimpson, 1858; Targioni-Tozzetti, 1877; Cuesta *et al.*, 2001).

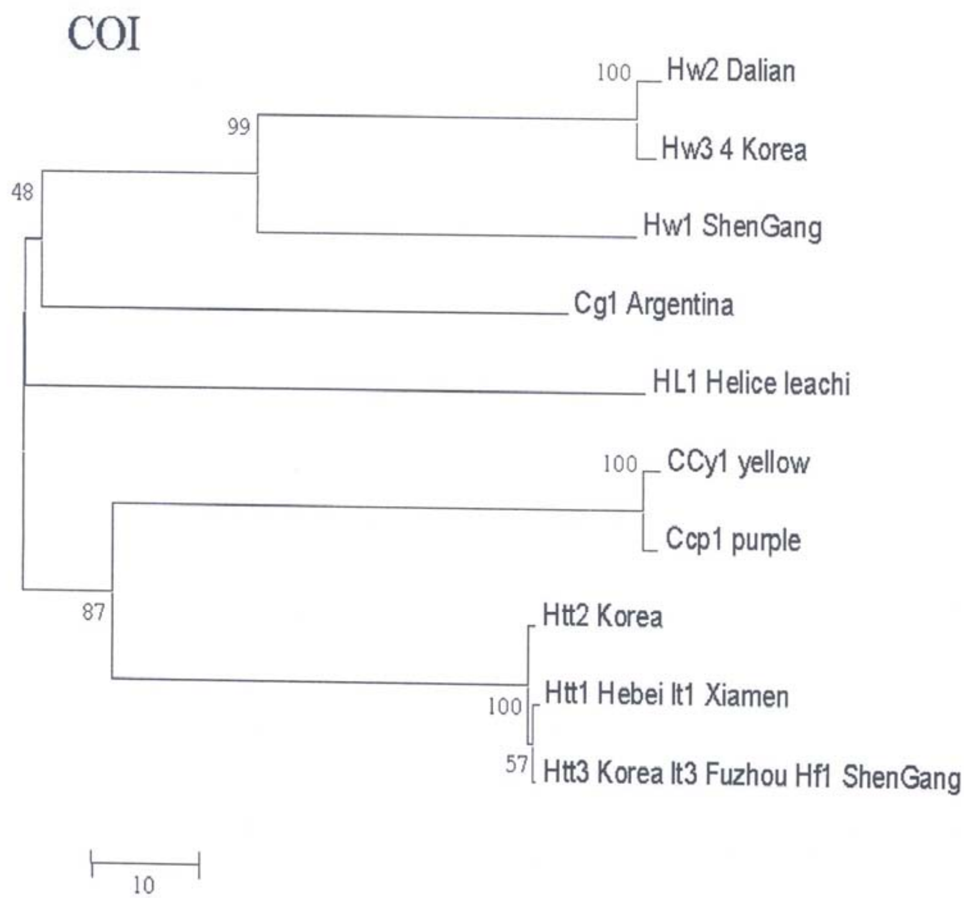



Figure 144. Molecular tree of the CO1 gene showing the differences in *Neohelice granulatus* (Cg), *Chasmagnathus convexus* (Ccp), *Austrohelice crassus* (Hc), *Helicana wuana* (Hw), *Helice formosensis* (Hf), *Helice latimera* (Hlt), *Helice tientiensis* (Htt), *Helice leachi* (HL). (Courtesy of Dr. Shih His-Te).

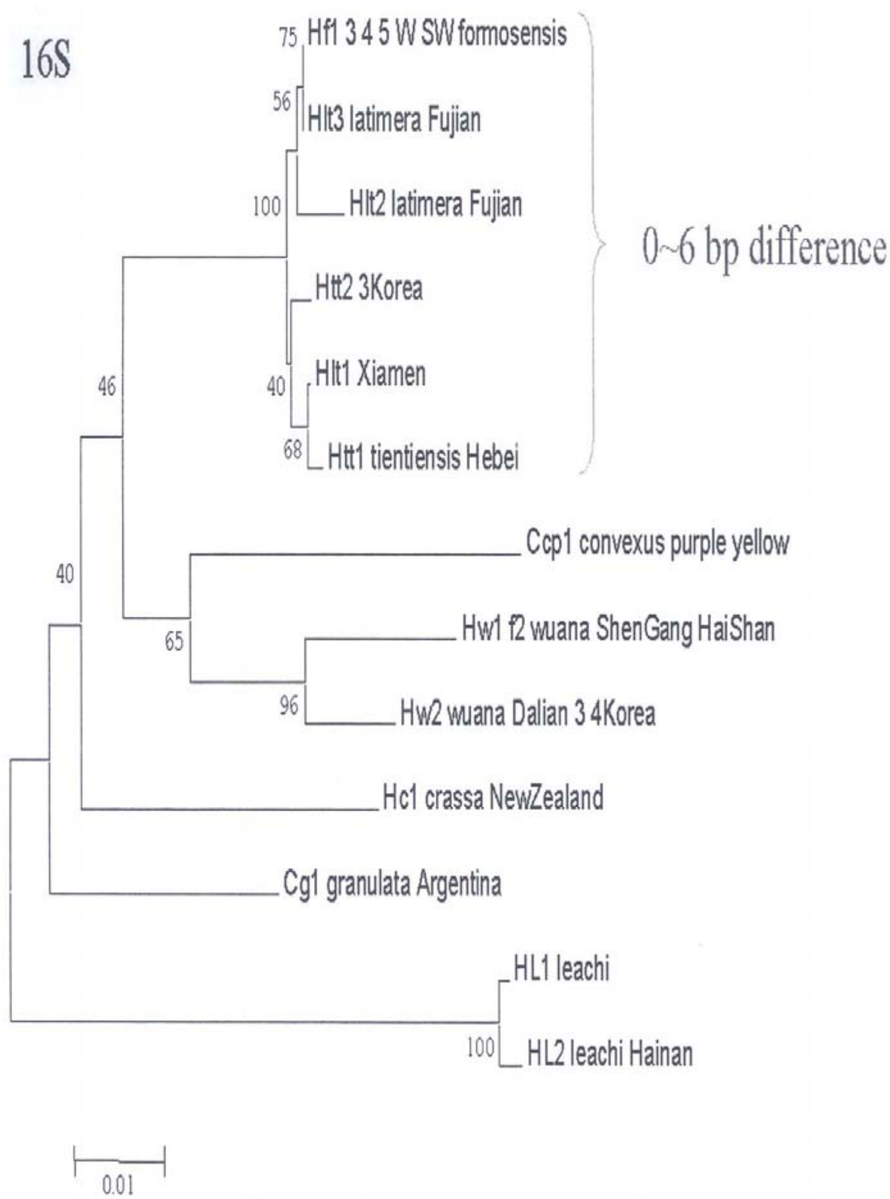



Figure 145. Molecular tree of the 16s gene showing the differences in *Neohelice granulatus* (Cg), *Chasmagnathus convexus* (Ccp), *Austrohelice crassus* (Hc), *Helicana wuana* (Hw), *Helice formosensis* (Hf), *Helice latimera* (Hlt), *Helice tientiensis* (Htt), *Helice leachi* (HL), *Helice crassa* (Hc1). (Courtesy of Dr. Shih His-Te).

## *Chasmagnathus convexus* (De Haan, 1835)

(Figure 146)

*Ocypode* (*Chasmagnathus*) *convexus* De Haan, 1833: pl. 7 fig. 5; 1835: 56-57, pl. C; Adams & White, 1849: 52; H. Milne Edwards, 1853: 200; Herklots, 1861: 15.

*Chasmagnathus convexus* – Stimpson, 1858: 105; Ortmann, 1894: 727; Stimpson, 1907: 133; Terao, 1916: 188; Tesch, 1918: 124; Parisi, 1918: 105; Balss, 1922: 154; Urita, 1926: 21; Asano, 1933: 556-557, text-fig. 1263; Sakai, 1935: 73; 1936: 232, pl. 64 fig. 1; Kamita, 1936: 320; 1936: 35; Shen, 1940: 74, 94; Sakai, 1939: 690, pl. 77 fig. 1; 1940*:* 51; Horikawa, 1940: 30; Kamita, 1941a: 88; 1941b: 229, text-fig. 127; 1941c: 233, 237, 242; 1974: 720, 1 text-fig.; Tanaka, 1943: 7; Nakazawa & Sakai, 1947: 652, fig. 1880; 1960: 85, pl. 42, fig. 4; 1965: 205, pl. 98 fig. 4; Tanaka, 1949: 25; Lin, 1949: 30; Sakai, 1950: pl. 3, fig. 2; 1954: 76; Utinomi, 1956: pl. 45, fig. 9; Miyake, 1961: 177; 1962: 131; Kim, 1962: 54, 55; Wu *et al.*, 1962: 203; Park, 1964: 18; Shen & Dai, 1964: 131, 1 fig.; Serène, 1968: 109; Kim, 1970: 23; Kim, 1973: 493, 656, fig. 222, pl 45, fig. 172; Yamaguchi *et al.*, 1976: 41; Sakai, 1976: 668, pl. 228 fig. 1; Kikuchi & Miyake, 1978: 45; Kim & Kim, 1982: 153; Nakasone *et al.*, 1983: 37; Miyake, 1983: 186, pl. 62, fig. 4; Takeda, 1983: 147 (col. fig.), 287; Kim & Chang, 1985: 56; Matsuo & Makiya, 1985: 307, 309, 312; Dai , *et al.*, 1986: 502, text-fig. 284/3, pl. 71 fig. 2; Yamaguchi *et al.*, 1987: 33; Fukui *et al.*, 1989: 230; Yoshimura, 1990: 755, 760, 761; Dai & Yang, 1991: 550, text-fig. 284(3), pl. 71, fig. 2; Yamaguchi & Baba, 1993: 487, fig. 186; Wada, 1995: 410, pl. 116-2; Fransen *et al.*, 1997: 121; Muraoka, 1998: 54; Islam *et al.*, 2000: 35-43, tables 1-2, text-figs. 1-3; Asakura, 2000: 335; Ng *et al.*, 2001: 44; Sakai *et al.*, 2006: 8.

*Chasmagnathus convex* – Su & Lue, 1984: 63, 67, fig. 12;

*Chasmagnathus convexa* – Matsuura, 1894: 56; Maki & Tsuchiya, 1923: 173, pl. 21 fig. 1.

*Chasmagnathus Convexus* – Urita, 1918: 65.

*Chasmagnathus convexum* – Morton & Morton, 1983: 227, Pl. 19 fig. E.

*Chasmognathus convexus* – Shen & Liu, 1963: 142, 144 (wrong spelling).

*Helice spinicarpa* H. Milne Edwards, 1853: 190; Targioni-Tozzetti, 1877: 161; Tesch, 1918: 119; Serène, 1968: 109.

**Materials examined.**— **Type – Taiwan** – 1 male (29.0mm x 22.0mm) (NTOU-uncatalogued) San-Sin Bridge, Hsinchu County, coll. Huang J.F., 26 Sep. 1987; 1 female

(49.0mm x 37.0mm) (NTOU-uncatalogued), San-Sin Bridge, Hsinchu County, coll. Huang J.F, 29 Mar. 1988. 9 males (13.0-38.2mm x 10.3-29.0mm), 5 females (31.8-37.4mm x 24.2-29.0mm) (NMNS-uncatalogued), Yunliao. Taichung, coll. H.T. Shih, 20 May 2002; 2 females (27.8-31.6mm x 21.5-24.1mm), 1 female (ovigerous) (34.3mm x 25.8mm) (NMNS-001665-0001), Dajiaxi river, south bank, coll. P.W. Hsueh, 9 Dec. 1993. – **Hong Kong** – 1 male (41.0mm x 30.0mm), 1 female (42.4mm x 32.2mm) (ZRC-uncatalogued), Hong Kong (purchased from market), coll. P.K.L. Ng, 28 Feb. 2006.

**Diagnosis.**— Carapace subquadrilateral, almost elliptical in shape; surface convex, punctate, granulated, distinct, wide, medial groove between epigastric regions; frontal margin sinuous. Anterolateral margin vaulted upwards, with four teeth including orbital tooth. Third maxillipeds close with gape, an oblique row of short setae runs diagonally across from inner anterolateral angle of merus, to outer posterolateral angle of ishium. Infra-orbital ridge with three or four large tubercules, a gap, ending with five small tubercules. Cheliped symmetrical in males, surfaces smooth, stridulatory ridge present on merus of chelipeds. Ambulatory legs long, slender, margins of first, second ambulatory legs covered with short setae, interspersed with long setae; meri with a sharp sub-distal spine on anterior margin; third ambulatory legs with carpi setose on dorsal half of anterior surface, propodi on dorsal margin; in fourth ambulatory legs both carpus and propodus setose on respective dorsal margins. G1 with stem stout, broadened distally, short corneous endpiece tubular and with a dorsal genital pore; palp stout and triangular. Female gonopore operculate, protruding.

**Colour.**— The colour of fresh specimens is greyish brown in colour, and the colour of all preserved specimens examined is light brown.

**Size.**— The largest male specimen examined is 41.0mm x 30.0mm (ZRC-uncatalogued), and the largest female is 42.4mm x 32.2mm (ZRC-uncatalogued).

**Habitat.**— It can be found  burrowed in muddy banks by the river mouths (H.T. Shih, pers. comm.).

**Remarks.**— This species has been reported to nocturnal in nature (Sakai *et al.*, 2006: in press). The taxonomy of this species has been treated in detail by Sakai *et al.* (2006), and hence, there is no need to give any further treatment in this report. As mentioned above, the molecular study of this species and its relationships with its previous congeners is currently in progress (in collaboration with H.T. Shih).

*Chasmagnathus* is distinctly different from *Helice* and the other *Chasmagnathus* sensu lato species in its behaviour. The species is very mild and peaceful in nature. It is commonly sold as pets to children in Hong Kong (see above Introduction). *Helice spinicarpa*, described by H. Milne Edwards in 1853, from an unknown locality, is a junior synonym of *C. convexus*. The lectotype of *Helice spinicarpa* (MNHN-B4646S) was examined by Sakai *et al.* (2006), and has been determined to be the present species because of the morphology of the infra-orbital ridge.

**Distribution.**— Taiwan, Hong Kong, China, Japan, Korea.

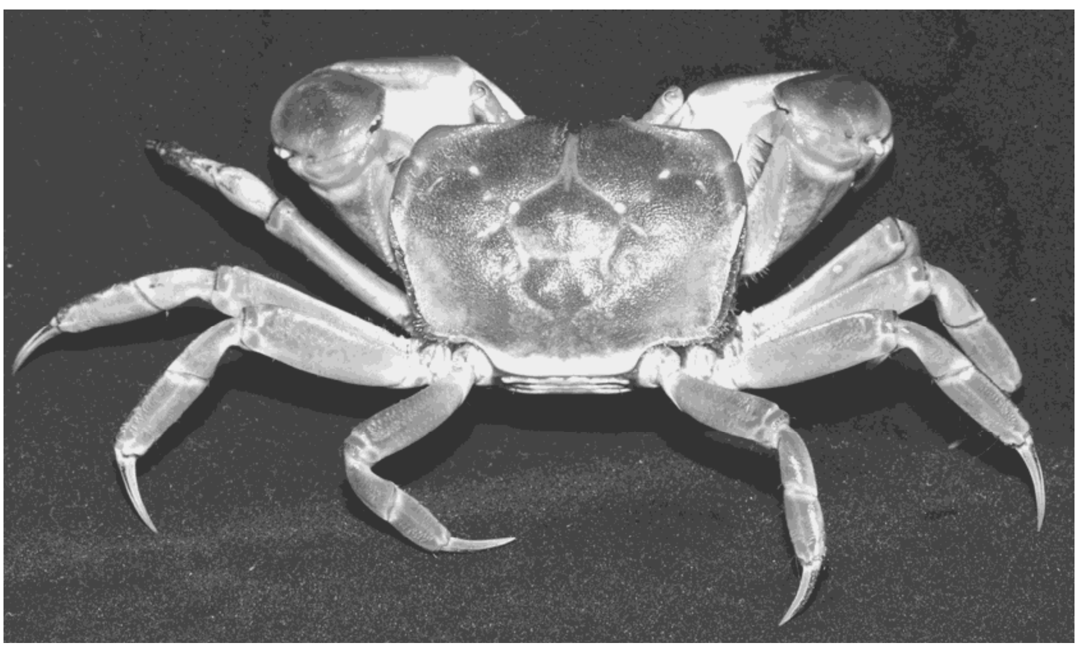


Figure 146. *Chasmagnathus convexus* (De Haan, 1835), 41.0mm x 30.0mm (ZRC-uncatalogued). Dorsal view.

## Genus *Neohelice* Sakai, Türkay & Yang, 2006

*Chasmagnathus* Dana, 1852: 251; Dana, 1852: 364-365; Dana, 1855: 8, pl. 23 figs. 6a-d; Stimpson, 1858: 105; Targioni-Tozzetti, 1877: 161; Dana, 1880: 222-223; Miers, 1881: 69; Hutton, 1882: 264; Ortmann, 1894: 728; Rathbun, 1898: 605; Moreira, 1901: 42, 106; Stimpson, 1907: 133; Parisi, 1918: 105; Rathbun, 1918: 329; Tesch, 1918: 124; Balss, 1922: 154; de Oliveira, 1940: 143; de Oliveira, 1962: 257; Oliveira, 1948: 695, 699; Oliveira, 1950: 371, 389; Oliveira, 1950: 512; Oliveira, 1955: 190, 241; Oliveira, 1958: 52, 57, 58; Boschi, 1964: 62, Boschi, 1966: 453; Boschi *et al.*, 1967: 6, 28; Coelho & Ramos, 1973: 202; Holcman de Spector *et al.*, 1973: 217; Coelho *et al.*, 1979: 236; Melo *et al.*,, 1989: 22, 29; Tavares & Albuquerque, 1989: 104; Maldonado *et al.*, 1989: 1139, text-figs. 1-2; Melo, 1990: 79; Melo, 1996: 464; Melo, 1998: 501; Romano *et al.*, 1990: 113; Boschi *et al.*, 1992: 77; Anger *et al.*, 1994: 446; Poupin, 1996: 69; Ismael *et al.*, 1997: 463, López Greco *et al.*, 1999: 490, text-figs. 1-4; Davie, 2002: 207 (All in part).

*Helice* – H. Milne Edwards, 1853: 190, pl. 7, fig. 6; Heller, 1865: 61; von Martens, 1869: 11-12, pl. 1 figs. 3a-b; Smith, 1869: 37; Targioni-Tozzetti, 1872: 395; 1873: 467: 1877: 60, pl. 10 fig. 3; Targioni-Tozzetti, 1877: 161; Tesch, 1918: 119.

*Neohelice* Sakai, Türkay & Yang, 2006: 61.

**Diagnosis.**— Carapace quadrilateral, broader than long, surface convex, granulated, well defined, lateral margins convergent. Suborbital ridge in males, females with two rows of isomorphic granules. Merus of third maxilliped nearly half as broad anteriorly as long. Chelipeds equal in males and females; chelae glabrous at base of fingers, without meral stridulatory ridge. First three ambulatory legs with carpi and propodi with dense setae dorsally. Third abdominal somite of male not projecting laterally. G1 stout, with suture of sperm channel starting on ventromesial side, displaced to dorsal side distally, palp elongated, triangular in shape.

**Type species.**— *Chasmagnathus granulatus* Dana 1852, original designation by Sakai, Türkay & Yang (2006)

**Gender.**— Masculine.

**Remarks.**— Currently, this is a monotypic genus. Sakai, Türkay & Yang (2006) has given a very detailed description of this genus. They also pointed out that *Neohelice* is probably related to the *Austrohelice* Sakai, Türkay & Yang, 2006. The preliminary study on the 16s RNA (see above, text-figure 2) has also supported their report.

*Neohelice* is distinctly different from *Chasmagnathus* in the following a) the carapace are granulated (vs. smooth in *Chasmagnathus*); b) the presence of two rows of isomorphic granules on the infra-orbital ridge (vs. presence of one row of heteromorphic granules in *Chasmagnathus*), and c) the lack of a stridulatory ridge on the chela (vs. presence of the stridulatory ridge in *Chasmaganthus*).

## *Neohelice granulata* (Dana, 1852), new combination

(Figure 147A-B)

*Chasmagnathus granulatus* Dana, 1852: 251; 1852: 364-365; Dana, 1855: 8, pl. 23 figs. 6a-d; 1880: 222-223; Ortmann, 1894: 728; Rathbun, 1898: 605; Moreira, 1901: 42, 105-106; Rathbun, 1918: 329-330, pl. 100, pl. 159 fig. 9; de Oliveira, 1940: 143; 1962: 257, text-figs. 1-14; Oliveira, 1948: 695, 699; 1950: 371, 389; 1950: 512; 1955: 190; 1955: 241; 1958: 52, 57, 58. Coelho *et al.*, 1979: 236; Melo, Veloso & Oliveira, 1989: 22, 29; Tavares & Albuquerque, 1989: 104; Maldonado *et al.*, 1989: 1139, text-figs. 1-2; Romano *et al.*, 1990: 113, text-figs. 1-3; Boschi *et al.*, 1992: 77, text-fig. 88; Anger *et al.*, 1994: 446, 447, 449, 450, 451, 452, 454, 455, 456, 457, 458, 459, 460, 461, 462, 463; Melo, 1990: 79; 1996: 464, 1 text-fig.; 1998: 501; Ismael *et al.*, 1997: 463, table 1, text-figs. 1-4; López Greco *et al.*, 1999: 490, text-figs. 1-4.

*Helice granulata* – Heller, 1865: 61.; von Martens, 1869: 11-12, pl. 1 figs. 3a-b; Smith, 1869: 37; Targioni-Tozzetti, 1872: 395; 1873: 467: 1877: 60, pl. 10 fig. 3.

*Helice Gaudichaudi* – H. Milne Edwards, 1853: 190, pl. 7, fig. 6;

*Helice gaudichaudi* – Targioni-Tozzetti, 1877: 161; Tesch, 1918: 119; Serène, 1968: 109.

*Chasmognathus granulatus* – Miers, 1881: 69.

*Chasmagnathus granulata* – Boschi, 1964: 62, pls. 3, 17, 20, 22; 1966: 453; Boschi *et al.*, 1967: 6, 28-42, tables 1-3, text-figs. 9-17; Coelho & Ramos, 1973: 202; Holcman de Spector *et al.* , 1973: 217-223, text-figs. 1-5; Boschi, 1979: 140.

*Neohelice granulata* – Sakai *et al.*, 2006: 61, figs 95-96.

**Materials examined.**— **Neotype** – 1 male (USNM-173578), Lagoa Dos Patos, Estuary Rio Grande do Sul Brazil C.E. Bemvenuti, no collection date.– **Others** – 5 males, 5 females, 1 female (ovi) (USNM-173478), Lagoa Dos Patos, Estuary Rio Grande do Sul Brazil C.E. Bemvenuti, no collection date; 1 male (USNM-256491), Lagoa Dos Patos, Estuary Rio Grande, Rio Grande do Sul, Brazil, coll. L. Chaos, 16 Jun. 1980; 9 males (26.7-29.6mm x 22.8-24.6mm), 6 females (24.7-29.6mm x 21.0-26.0mm) (NMNS-uncatalogued), Sam Boromboin, Argentina, coll. R. Ribeiro, 17 Mar. 2001; 1 males (28.0mm x 23.4mm), 1 female (25.8mm x 21.6mm) (ZRC-uncatalogued), Sam Boromboin, Argentina, coll. R. Ribeiro, 17 Mar. 2001.

**Diagnosis.**— Carapace quadrilateral, broader than long; surface convex, sparingly setose, granulated, distinct wide medial groove between epigastric regions; frontal margin sinuous. Anterolateral margin vaulted upwards, with three teeth including orbital tooth. Third maxillipeds close with gap, an oblique row of short setae runs diagonally across from inner anterolateral angle of merus, to outer posterolateral angle of ishium. Infra-orbital ridge consisting of two rows of granules in both sexes; anterior row larger than posterior, consisting of 22-24 isomorphic granules; posterior row bearing 20-28 granules. Cheliped symmetrical in both sexes, surfaces densely granulated, meral stridulatory ridge absent. Ambulatory legs long, slender, only fourth leg covered with dense short setae. G1 stout, subquadrate distally; corneous tip short, broad, with spermatopore opening on dorsal face near to medial sternal groove; palp large, elongated, triangular.

**Colour.**— The colour of fresh specimens has not been documented, and the colour of all the preserved specimens examined is brownish in colour.

**Size.**— The largest male specimen examined is 29.6mm x 24.6mm (NMNS-uncatalogued), and the largest female examined is 29.6mm x 26.0mm (NMNS-uncatalogued).

**Habitat.**— It can be found in sandy mud flats (Sakai, Türkay & Yang, 2006).

**Remarks.**— This is interesting to note that this species is currently found only in South America. This species is a very common experimental animal (see Boschi *et al.,* 1967; Gimenez & Anger, 2001; Rodríguez *et al.*, 2001; Luppi *et al.*, 2002; Luquet *et al.*, 2002; Genovese *et al.*, 2004), but not many workers have commented on its taxonomy.

Since Dana's original type materials could not be found in the USNM, and almost certainly lost; and this species is the type of a recently recognized genus; it is useful to stabilize its taxonomy by selection of a neotype. One such specimen from the type locality is here chosen (USNM-173578).

Sakai *et al.* (2006) has given a very good account of this species and there is no need to elaborate here.

**Distribution.**— Brazil, Uruguay, Argentina.

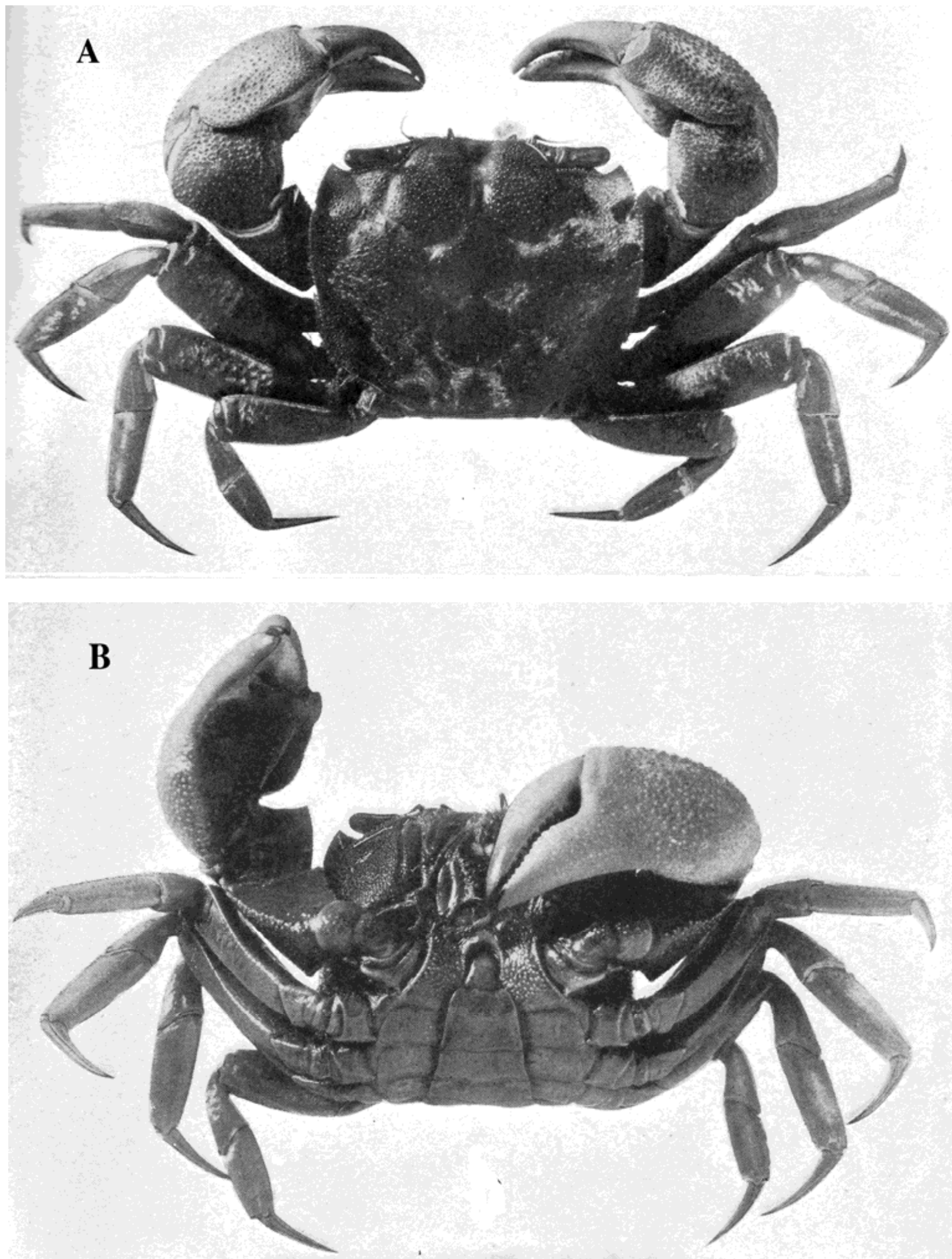



Figure 147. *Neohelice granulatus* (Dana, 1852). Dorsal view; B) ventral view. (After Rathbun, 1918).

## Genus *Parahelice* (Sakai, Türkay & Yang, 2006), new combination

*Chasmagnathus* Dana, 1852: 251; 1852: 364-365; Dana, 1855: 8, pl. 23 figs. 6a-d; 1880: 222-223; Ortmann, 1894: 728; Rathbun, 1898: 605; Moreira, 1901: 42, 105-106; Rathbun, 1918: 329-330, pl. 100, pl. 159 fig. 9; de Oliveira, 1940: 143; 1962: 257-262, text-figs. 1-14; Oliveira, 1948: 695, 699; 1950: 371, 389; 1950: 512; 1955: 190; 1955: 241; 1958: 52, 57, 58; Boschi, 1964: 62, pls. 3, 17, 20, 22; 1966: 453; Boschi, Scelzo & Goldstein, 1967: 6, 28-42, tables 1-3, text-figs. 9-17; Coelho & Ramos, 1973: 202; Holcman de Spector *et al.*, 1973: 217-223, text-figs. 1-5; Coelho *et al.*, 1979: 236; Melo, Veloso & Oliveira, 1989: 22, 29; Clark, 1987: 45; Tavares & Albuquerque, 1989: 104; Maldonado *et al.*, 1989: 1139, text-figs. 1-2; Romano *et al.*, 1990: 113-122, text-figs. 1-3; Boschi *et al.*, 1992: 77, text-fig. 88; Anger *et al.*, 1994: 446, Melo, 1990: 79; 1996: 464, 1 text-fig.; 1998: 501; Ismael *et al.*, 1997: 463, table 1, text-figs. 1-4; López Greco *et al.*, 1999: 490-, text-figs. 1-4; Sakai *et al.*, 2006: 1. (All in part).

*Helice* – H. Milne Edwards, 1853: 190, pl. 7, fig. 6; Heller, 1865: 61; von Martens, 1869: 11-12, pl. 1 figs. 3a-b; Smith, 1869: 37; Targioni-Tozzetti, 1872: 395; 1873: 467: 1877: 60, pl. 10 fig. 3; Miers, 1886: 268, pl. 21 fig. 2; de Man, 1896: 34; 1897: pl. 31 fig. 41; Tesch, 1918: 119; Serène, 1968: 109; Sakai *et al.*, 2006: 1. (All in part).

*Pseudohelice* (*Parahelice*) Sakai *et al.*, 2006: 46.

**Diagnosis.**— Carapace quadrilateral, broader than long, surface convex, granulated, well defined, lateral margins convergent. Suborbital ridge in males, females with two rows of isomorphic granules. Merus of third maxilliped nearly half as broad anteriorly as long. Chelipeds equal in males and females; chelae glabrous at base of fingers, without meral stridulatory ridge. First three ambulatory legs with carpi and propodi with dense setae dorsally.  Third abdominal somite of male not projecting laterally. G1 stout, with suture of sperm channel starting on ventromesial side, displaced to dorsal side distally, palp elongated, triangular in shape.

**Type species.**— *Chasmagnathus pilosa* Sakai, Türkay & Yang, 2006, by original designation.

**Gender.**— Masculine.

**Remarks.**— There are currently five species in this genus viz. *Parahelice pilosa* (Sakai, Türkay & Yang, 2006) (type species); *Parahelice georgei* (Clark, 1987); *Parahelice pilimana* (A. Milne-Edwards, 1873); *Parahelice balssi* (Sakai, Türkay & Yang, 2006); *Parahelice daviei* (Sakai, Türkay & Yang, 2006), and *Parahelice likas*, new species.

Sakai *et al.* (2006) has given a detailed account of the genus and hence, there is no need to treat it further in this report.

**Key to species in *Parahelice***

1a. Chelipeds without a tuft of setae at the base of the fingers. ------------------------ **2**

1b. Chelipeds with a tuft of setae at the base of the fingers. ---------------------------- **3**

2a. Infra-orbital ridge of male with two tubercules, a third elongate striated crest, then a row of irregular protuberances ending in four granules; infra-orbital ridge of female with 16-20 isomorphic rounded granules. ------------------------------------- ***P. pilosa***

2b. Infra-orbital ridge of male with with four tubercles, then an elongate median crest, ending in four interspaced granules; infra-orbital ridge of female with two lateral tubercles, four striated crests, ending in ten simple mesial elongate tubercles. --------- ------------------------------------------------------------------------------- ***P. georgei***

3a. Stridulatory ridge present in merus of chelipeds. -------------------------------------- **4**

3b. Stridulatory ridge absent in merus of chelipeds. ---------------------------------- ***P. likas***

4a. Carpi and propodi of first and second ambulatory legs setose. ---------- ***P. pilimana***

4b. Carpi and propodi of first to third or even fourth ambulatory legs setose. -------- **5**

5a. First to third ambulatory legs setose. Infra-orbital ridge of male with three striated granules. ------------------------------------------------------------------------ ***P. balssi***

5b. First to fourth ambulatory legs setose. Infra-orbital ridge of male with one rounded, then a y-shaped crest, ending in six rounded granules. ------------------------ ***P. daviei***

***Parahelice pilosa*** **(Sakai, Türkay & Yang, 2006), new combination**

(Figure 148)

*Pseudohelice* (*Parahelice*) *pilosa* Sakai, Türkay & Yang, 2006: 51.

**Materials examined.— Holotype** – 1 male (17.6mm x 14.7mm) (USNM 99/798), Philippines, Balayan Bay, coll. 27 Aug. 1927.

**Diagnosis.—** Carapace quadrilateral, slightly broader than long; surface convex, slightly granulated, with a distinct wide, medial groove between epigastric regions,; frontal margin bilobed. Anterolateral margin vaulted upwards, with three teeth including orbital tooth, posterolateral margin setose. Third maxillipeds close with rhomboidal gape. Infra-orbital ridge in male with two lateral separated protuberances, a third elongate striated crest followed by a row of irregularly formed protuberances in its central part, four granules at its mesial end; female infra-orbital ridge consists of a row of 16-20 isomorphic interspaced, rounded tubercles. Cheliped unequal in males, females, surfaces smooth, meral stridulating ridge present in both sexes. Ambulatory legs broad, margins of merus of first to third ambulatoty legs covered with short setae; fourth ambulatory leg without such dense setation. Third male abdomenial segment laterally projecting. G1 broad, stout, distal part with corneous subtubular tip with broad terminal sperm aperature.

**Colour.—** The colour fresh specimens is grey in colour (Sakai *et al.*, 2006), and the colour of preserved specimens has not been documented.

**Size.—** The largest male specimen reported is 15.0mm x 18.5mm (Sakai *et al.*, 2006), and the largest female specimen reported is 18.8mm x 16.5mm (Sakai *et al.*, 2006).

**Habitat.—** It can be found in burrows along mudflats, mangroves (Sakai *et al.*, 2006).

**Remarks.**— This species is closely allied to *P. georgei* (Clark, 1987), but is distinctly different in the following characters: a) the infra-orbital ridge has two lateral separated protuberances, a third elongate striated crest followed by a row of irregularly formed protuberances in its central part, and four granules at its mesial end (vs. four tubercle topped striated crests laterally, an elongate, weakly striated median crest, four interspaced granules in *P. georgei*) and b) the absence of setae on the proximal end of the fingers (vs. presence of setae in *P. georgei*).

**Distribution.**— Philippines, Indonesia

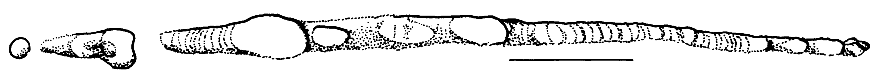


Figure 148. Infra-orbital ridge of *Parahhelice pilosa* Sakai *et al.*, 2006. (After Sakai *et al.*, 2006).

### *Parahelice georgei* (Clark, 1987), new combination

(Figure 149A-B)

*Helice latreilli* – Miers, 1886: 268, pl. 21 fig.2. (part); de Man, 1896: 343; 1897: pl. 31 fig. 41 (non *Cyclograpsus latreilli* H. Milne Edwards, 1837).

*Chasmagnathus georgei* Clark, 1987: 45, text-figs. 1A-B, G & H; 2B & D; pls. 1B, 2B & 3B.

*Pseudohelice* (*Parahelice*) *georgei* – Sakai, Türkay & Yang, 2006: 49.

**Materials examined.**— 1 male (20.5mm x 17.5mm) (RMNH-1985489), intertidal, Rememberance Beach, Bodgaya, Sabah, Borneo, coll. D. George & J. George, 28 Aug. 1980.

**Diagnosis.**— Carapace quadrilateral, slightly broader than long; surface convex, punctate, with a distinct wide, medial groove between epigastric regions,; frontal margin bilobed. Anterolateral margin vaulted upwards, with three teeth including orbital tooth, posterolateral margin setose. Third maxillipeds close with rhomboidal gape. Infra-orbital ridge in male with four tubercle topped striated crests laterally, an elongate, weakly striated median crest, four interspaced granules, in females with weakly heteromorphic consisting of two lateral tubercles, four striated crests, and ten simple mesial elongate tubercles. Cheliped unequal in males, equal in females, surfaces punctate, meral stridulating ridge present in both sexes. Ambulatory legs broad, margins of propodi of first to third ambulatoty legs covered with short setae; fourth ambulatory leg without such dense setation. G1 elongated; distal part tapering, incurved distally, palp triangular; genital pore broadly open towards dorsal face.

**Colour.**— The colour fresh specimens is grey in colour (Clark, 1987) and the colour of preserved specimens has not been documented.

**Size.**— The size of the holotype is 20.5mm x 17.5mm (Clark, 1987). So far, no female specimen has been documented.

**Habitat.**— It can be found  in burrows along grassy banks, or under rocks, and mudflats of mangroves (Clark, 1987)

**Remarks.**— This species has been described in detail by Clark (1987), and it has been further treated by Sakai *et al.* (2006).

**Distribution.**— Sumatra, Borneo, New Guinea, and Fiji.

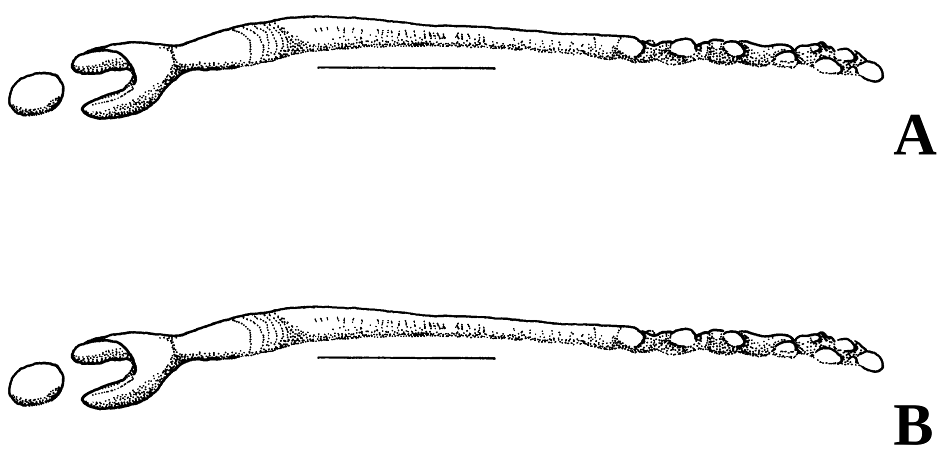



Figure 149. Infra-orbital ridge of *Parahelice georgei* (Clark, 1987). (After Sakai *et al.*, 2006).

## *Parahelice pilimana* (A. Milne-Edwards, 1873), new combination

(Figure 150)

*Helice pilimana* A. Milne-Edwards, 1873: 313, pl. 18 (part), fig. 1a; Serène, 1968: 109.

*Pseudohelice (Parahelice) pilimana S*akai, Türkay & Yang, 2006: 50.

**Materials examined.**— 1 male (26.0mm x 22.3mm), 1 female (23.0mm x 19.8mm) (MNHN-B-10996), New Caledonia, no collection date.

**Diagnosis.**— Carapace quadrilateral, slightly broader than long; surface slightly granular. Anterolateral margin slightly sinuous, with four teeth including orbital tooth. Third maxillipeds close with rhomboidal gape. Infra-orbital ridge in male with two large round tubercles, an elongate, striated crest, and 9-11 rounded tubercles, in females with 22 isomorphic granules. Cheliped unequal in males, females, meral stridulating ridge present in both sexes surfaces smooth, base of fingers with a patch of setae. Ambulatory legs broad, margins of first, second ambulatory legs carpi, propodi setose on dorsal halves of anterior, posterior-surfaces, third, fourth ambulatory legs with carpi, propodi setose only on dorsal margins. Third male abdominal somite produced laterally. G1 slender, curved towards distal end.

**Colour.**— The colour fresh specimens and preserved specimens is unknown.

**Size.**— The largest male specimen reported is 26.0mm x 22.0mm (*S*akai *et al.*, 2006), and the largest female specimen is 23.0mm x 19.8mm (*S*akai *et al.*, 2006).

**Habitat.**— It can be found in mudflats (Sakai *et al.*, 2006).

**Remarks.**— Sakai *et al.* (2006) has given a very detailed account of this species and there is no need to repeat the treatment here.

**Distribution.**— New Caledonia, New Guinea.

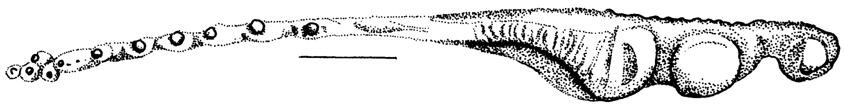


Figure 150. Infra-orbital ridge of *Parahelice pilimana* (A. Milne-Edwards, 1873). (After Sakai *et al.*, 2006).

## *Parahelice balssi* (Sakai, Türkay & Yang, 2006), new combination

(Figure 151)

*Helice leachii* – Emmerson, 1994: 316.

*Pseudohelice* (*Parahelice*) *balssi* Sakai *et al.*, 2006: 46.

**Materials examined.**— 1 male (9.5mm x 8.0mm) (MNHN-B-20894), Madagascar coll. Millot, no collection date.

**Diagnosis.**— Carapace quadrilateral, slightly broader than long; surface punctuated. Anterolateral margin slightly vaulted upwards with three teeth including orbital tooth. Third maxillipeds close with rhomboidal gape. Infra-orbital ridge in male with three striated lateral crests, and a row of 11 mesial granules. Cheliped unequal in males, surfaces smooth, base of fingers with a patch of setae, meral stridulating ridge present. Ambulatory legs broad, margins of carpi, propodi of first to third ambulatoty legs covered with short setae; fourth ambulatory leg setose only on dorsal margin. G1 with stout stem; suture of sperm channel starting on mesio-ventral side and displaced to dorsal side near base of palp.

**Colour.**— The colour fresh specimens and preserved specimens is unknown.

**Size.**— The size of the holotype male is 9.5mm x 8.0mm (Sakai *et al.*, 2006). There is no document of female specimen.

**Habitat.**— There is no habitat data, but the author believes that the species should be found in mudflats.

**Remarks.**— The species was described based on only male specimens.  Sakai *et al.* (2006) has given a detailed account of this species.

**Distribution.**— Madagascar, South Africa.

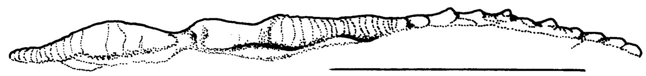


Figure 151. Infra-orbital ridge of *Parahelice balssi* (Sakai, Türkay & Yang, 2006), (After Sakai *et al.*, 2006).

## *Parahelice daviei* (Sakai, Türkay & Yang, 2006), new combination

(Figure 152A-B)

*Pseudohelice* (*Parahelice*) *daviei* Sakai, Türkay & Yang, 2006: 48.

**Materials examined.**— No material examined.

**Diagnosis.**— Carapace quadrilateral, slightly broader than long; surface punctate, Anterolateral margin vaulted upwards, with three teeth including orbital tooth. Third maxillipeds close with rhomboidal gape. Infra-orbital ridge in male with first lateral protuberance a rounded tubercle, second an elongate, laterally Y-shaped crest, and a row of six granules in its mesial part Cheliped unequal in males, equal in females, surfaces smooth, meral stridulating ridge present in both sexes, a conspicuous patch of setae at base of fingers. Ambulatory legs broad, margins of carpi, propodi of first to fourth ambulatoty legs covered with dense setae. Third male abdominal segment laterally projecting. G1 slender, tapering, genital pore opening distally on ventro-mesial face. (Modified from Sakai *et al.*, 2006).

**Colour.**— The colour of fresh specimens and preserved specimens has not been documented.

**Size.**— The largest male specimen reported so far, is 12.7mm x 10.1mm (Sakai *et al.*, 2006). There is no document of female specimen.

**Habitat.**— It can be found  in burrows along mudflats in estuarine area (Sakai *et al.*, 2006).

**Remarks.**— This species was established by Sakai *et al.* (2006) based on two specimens collected from Indonesia. They have also given a full treatment of this species in their report.

**Distribution.**— Indonesia only.

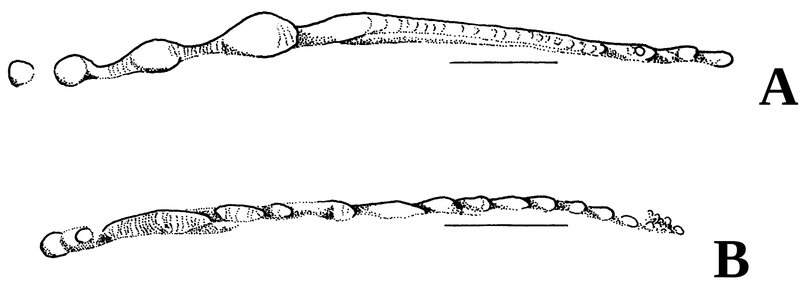


Figure 152. Infra-orbital ridges of *Pseudohelice daviei.* (After Sakai *et al.*, 2006).

***Parahelice likas*, new species**

(Figure 153A-F)

**Materials examined.— Holotype** – 1 male (9.0mm x 7.1mm) (ZRC-uncatalogued), muddy-sandy river bank and among *Avicennia* spp. mangrove area, Kota Kinabalu City Bird Sanctuary, Likas, Sabah, coll. S.N. Leow, 30 Jul. 2004. – **Paratypes –** 1 male (8.0mm x 7.0mm) (BMRI), muddy-sandy river bank and among *Avicennia* spp. mangrove area, Kota Kinabalu City Bird Sanctuary, Likas, Sabah, coll. S.N. Leow, 27 Jul. 2004; 1 male (5.0 x 4.0 mm) (ZRC-uncatalogued), muddy-sandy river bank and among *Avicennia* spp. mangrove area, Kota Kinabalu City Bird Sanctuary, Likas, Sabah, coll. S.N. Leow, 30 Jul. 2004. 1 female (10.0mm x 9.0 mm) (Sabah Museum), muddy-sandy river bank and among *Avicennia* spp. mangrove area, Kota Kinabalu City Bird Sanctuary, Likas, Sabah, coll. S.N. Leow, 13 Aug. 2004.

**Diagnosis.**— Carapace quadrilateral, broader than long, regions well defined, convex, surface punctate. Anterolateral margin with three teeth including orbital tooth. Suborbital ridge in male heteromorphic, consisting of two lateral separated rounded tubercles, followed by an elongate, striated median crest and nine closely placed granules mesially, female with about 12 isomorphic granules. Male chelipeds subequal, lightly punctate externally; meral stridulating ridge absent roughly punctate on fingers, gape between fingers; chela with patch of setae at base of fingers. First to third ambulatory legs with dorsal margins of carpi, propodi setose. Third male abdominal segment laterally projecting. G1, tapering, genital opening on distal ventro-mesial face. Female gonopore operculate, rounded.

**Etymology.**— *Parahelice likas* is named after the type locality Likas. Likas is one of the towns in Sabah, where the Kota Kinabalu City Birds Sanctuary is located.

**Habitat.**— It can be found in mud flats in the mangrove (S.N. Leow, pers. comm.).

**Colour.**— The colour of fresh specimens is light brown, and all preserved specimen examined are brown in colour (holotype and paratypes).

**Remarks.**— The present species is closely allied to *Parahelice pilimana* (A. Milne-Edwards, 1873), in having a conspicuous, well developed patch of setae at the base of the cheliped fingers, and the infra-orbital ridge of males with at least one separated and rounded tubercle laterally. The new species can be discerned from *P. pilimana* by the following features: a) the infra-orbital ridge is with two separated tubercles, the second tubercle larger and nine granules at its mesial end (vs. infra-orbital ridge consists of two large tubercles, followed by elongate and striated crest, and 9-11 rounded tubercles on the meral half in *P. pilimana*) and b) the absence of a stridulatory organ on the merus of the cheliped (vs. presence of stridulatory in *P. pilimana*).

This new species is being described with Miss S. N. Leow.

**Distribution.**— Malaysia (Sabah only).

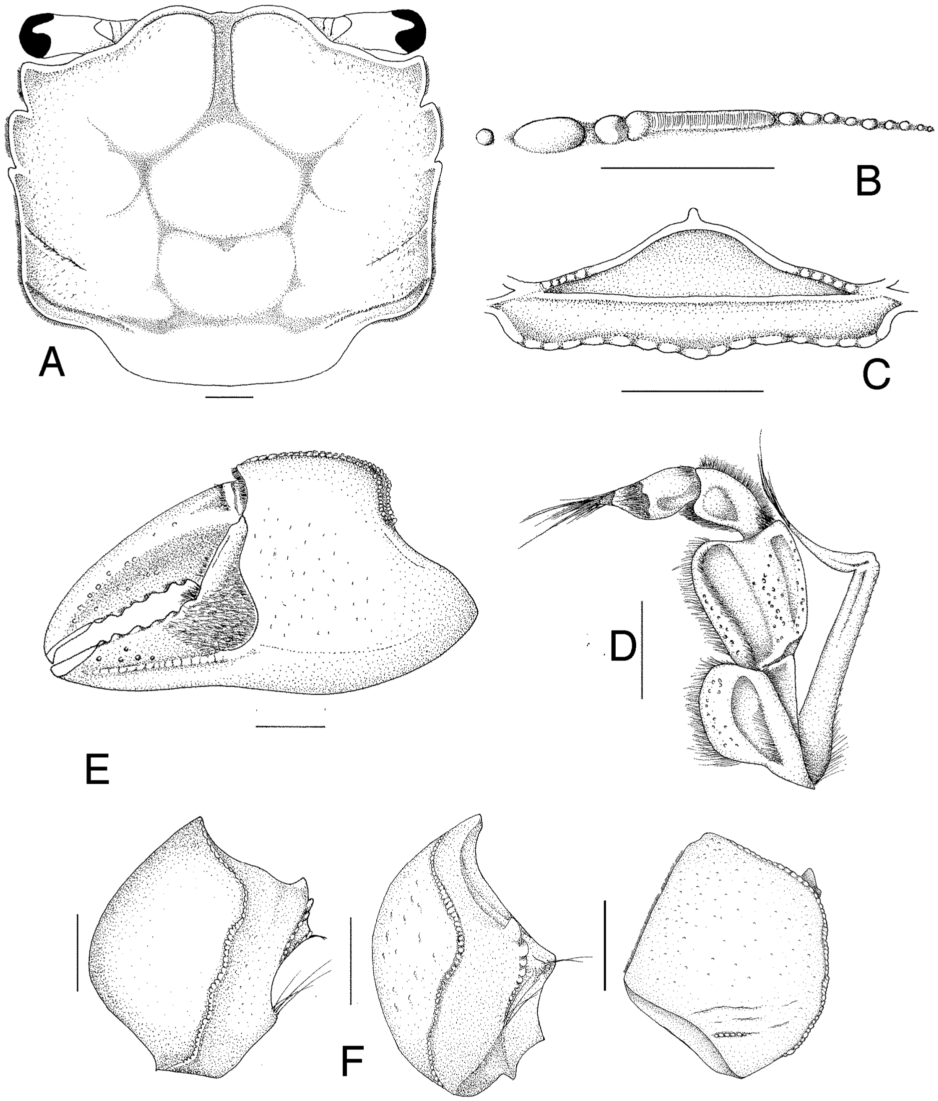



Figure 153. *Parahelice likas*, new species, holotype, 9.0mm x 7.1mm (ZRC-uncatalogued). A) carapace; B) infra-orbital ridge; C) epistome; D) chela; D) third maxilliped; F) different views of the carpus of the chela. (Scale=1.0mm).

## Genus *Pseudohelice* (Sakai, Türkay & Yang, 2006), new combination

*Chasmagnathus* Dana, 1852: 251; 1852: 364-365; Dana, 1855: 8, pl. 23 figs. 6a-d; 1880: 222-223; Ortmann, 1894: 728; Rathbun, 1898: 605; Moreira, 1901: 42, 105-106; Rathbun, 1918: 329-330, pl. 100, pl. 159 fig. 9; de Oliveira, 1940: 143; 1962: 257-262, text-figs. 1-14; Oliveira, 1948: 695, 699; 1950: 371, 389; 1950: 512; 1955: 190; 1955: 241; 1958: 52, 57, 58; Boschi, 1964: 62, pls. 3, 17, 20, 22; 1966: 453; Boschi, Scelzo & Goldstein, 1967: 6, 28, text-figs. 9-17; Coelho & Ramos, 1973: 202; Holcman de Spector *et al.*, 1973: 217, text-figs. 1-5; Coelho *et al.*, 1979: 236; Melo *et al.*, 1989: 22, 29; Tavares & Albuquerque, 1989: 104; Maldonado *et al.*, 1989: 1139, text-figs. 1-2; Romano *et al.*, 1990: 113, text-figs. 1-3; Boschi *et al.*, 1992: 77, text-fig. 88; Anger *et al.*, 1994: 446, 447, 449, 450, 451, 452, 454, 455, 456, 457, 458, 459, 460, 461, 462, 463; Melo, 1990: 79; 1996: 464, 1 text-fig.; 1998: 501; Ismael *et al.*, 1997: 463, text-figs. 1-4; López Greco *et al.*, 1999: 490, text-figs. 1-4; Sakai *et al.*, 2006: 1. (All part)

*Helice* – H. Milne Edwards, 1853: 190, pl. 7, fig. 6; Heller, 1865: 61; von Martens, 1869: 11-12, pl. 1 figs. 3a-b; Smith, 1869: 37; Targioni-Tozzetti, 1872: 395; 1873: 467: 1877: 60, pl. 10 fig. 3; Targioni-Tozzetti, 1877: 161; Tesch, 1918: 119; Serène, 1968: 109. (All part)

*Pseudohelice* Sakai, Türkay & Yang, 1996 – Guinot & Bouchard, 1998: 666 (nomen nudum)

*Pseudohelice* (*Pseudohelice*) – Sakai *et al.*, 2006: 36.

**Diagnosis.**— Carapace quadrilateral, slightly broader than long, broader than long, surface convex, well defined, lateral margins convergent. Suborbital ridge in males heteromorphic, lateral free (non fused) part with at most four or five larger tubercles of different size, some may be higher than fused parts, others smaller, non fused part shorter than fused part; females with heteromorphic or isomorphic granules. Merus of third maxilliped nearly as broad anteriorly as long. Chelipeds subequal or unequal in males and females; chelae glabrous at base of fingers, with meral stridulatory ridge. First three ambulatory legs with carpi, propodi with dense setae dorsally. Third abdominal somite of male projecting laterally.

**Type species.**— *Chasmagnathus subquadrata* Dana 1852, by original designation.

**Gender.**— Masculine.

**Remarks.**— Sakai *et al.* (2006) established two subgenera, *P.* (*Parahelice*) and *P.* (*Pseudohelice*) for *Pseudohelice*. Sakai *et al.* (2006) has given a very consise account for this taxon, and it will not be elaborated further in this report. I feel that there are enough morphological characters to raise it to generic status. The preliminary genetic data (see above) has substantiates my decision.

The generic name *Pseudohelice* Sakai, Türkay & Yang, 1996, was cited by Guinot & Bouchard (1998: 666) in their publication, rendering it a nomen nudum. This name, however, has been validated by their recent publication (see Sakai *et al*., 2006).

**_Pseudohelice subquadrata_ (Dana, 1852), new combination**

(Figure 154A-B)

*Chasmagnathus subquadratus* Dana, 1852: 251; 1852: 363; Dana, 1855: pl. 23, fig. 5; Targioni-Tozzetti, 1877: 161; Hutton, 1882: 264; Ortmann, 1894: 728; Poupin, 1996: 69; Davie, 2002: 207.

*Pseudohelice* (*Pseudohelice*) *subquadrata* – Sakai *et al.*, 2006: 37.

*Helice latreilli* – H. Milne Edwards, 1852: 156; Bouvier, 1915: 306-307; Estampador, 1937: 539; Estampador, 1959: 96; Michel, 1964: 13; Türkay, 1981: 61 (not *Helice latreilli*

*Helice leachii* – Kingsley, 1880: 220; Miers, 1886: 268-269, pl. 21 fig. 2 (part); de Man, 1887: 690; Rathbun, 1907: 36; McNeill, 1920: 109; Sakai, 1939: 696, text-fig. 126; Miyake, 1939: 226; Sakai, 1940: 32; Horikawa, 1940: 30; Lin, 1949: 30; Holthuis, 1958: 51; Crosnier, 1965: 76, fig. 125-128, pl. 5, fig. 2; Kim, 1966: 406-407, text-fig. 7, pl. 3 fig. 3; Campbell & Griffin, 1966: 130; Macnae, 1968: 175, 224, 231; Kim, 1970: 23; Kim, 1973: 502; Hartnoll, 1975: 307; Takeda & Miyake, 1976: 113; Nakasone, 1977: 62; Saenger, 1977: 325; Holthuis, 1977: 175; Vannini & Valmori, 1981: 909; Dai *et al.*, 1986: 505; Hirata *et al.*, 1988: 22; Emmerson, 1994: 316; Yu *et al.*, 1996: 15; Jeng, 1997: 18; Davie, 1998: 47, 1 unnumbered fig.

*Helice leachi* – Ortmann, 1894: 57; Parisi, 1918: 108-110, text-fig. 5, pl. 8 fig. 2; Miyake, 1963: 68; Guinot, 1967: 287; Serène, 1968: 109; Sakai, 1976: 672-673, text-fig. 370, pl. 228 fig. 2; Serène, 1977: 51; Frith, 1977: 6, 8, 13; Kim & Kim, 1982: 153; Baba *et al.*, 1984: 1-10, figs. 1-2; Kikuchi & Miyake, 1978: 45; Kim, 1985: 85; Yamaguchi *et al.*, 1987: 33; Fukui *et al.*, 1989: 230, 234, fig. 21; Shokita, 1990: 313; Wada, 1995: 410, text-fig. 21; Mia & Shokita, 1996: 104; Mia & Shokita, 1997: 70; Shokita *et al.*, 1998: 66, 67; Mia *et al.*, 1999: 31; Mia *et al.*, 1999: 52, 2 text-figs, 5 tables; Islam *et al.*, 2000: 39.

*Helice* (*Helice*) *leachii* – Dai & Yang, 1991: 553, pl. 72 fig. 1, text-fig. 286 (5-6); pl. 72: 1; Dai & Yang, 1991: 553, fig. 286: 5–6, pl. 72: 1; Huang, 1994: 598.

*Pseudohelice leachii* – Guinot & Bouchard, 1998: 666 (nomen nudum).

*Helice Leachii* Hess, 1865: 153; Nauck, 1880: 28-29, figs. 15, 17; Haswell, 1882: 107.

*Helice subquadrata* – Tesch, 1918: 120, pl. 6, fig. 1; Serène, 1968: 109; Ng *et al.*, 2001: 45, fig. 8g.

*Helice tridens* – Borradaile, 1910: 408 (not *Helice tridens* De Haan, 1835).

**Materials examined.**— **Neotype** – 1 male (18.2mm x 16.0) (QM-W2269), Australia, New South Wales, Sydney, Sailors Bay, coll. B. Campbell, no collection date. – **Others** – **China** – 1 male (30.0mm x 24.3mm) (QIH-no cat. number), Yandu, Haikou, Hainan Island, coll. 26 May 1958. – **Taiwan** – 2 males (11.4-12.1mm x 8.9-9.8mm) (TMCD-2429), Chu-Yuen, Tansui, Taipei County, coll. C.H. Wang, 23 Nov. 1988; 2 males (18.0-18.7mm x 16.3-15.5mm), 2 females (12.5-16.4mm x 10.0-14.4mm), (NMMBACDA-652), Dongsha island, Kaohsiung, coll. H.P. Ho, 22 Aug. 2004; 1 female (16.5mm x 13.6mm) (TMCD-2577), Hung-Mao Gang, Hsin Feng, Hsinchu County, coll. C.H. Wang, 4 Aug. 1989.

**Diagnosis.**— Carapace quadrilateral, surface convex, punctate, distinct wide, medial groove between epigastric regions; frontal margin sinuous . Anterolateral margin slightly vaulted upwards, with four teeth including orbital tooth. Third maxillipeds close with gape, an oblique row of short setae runs diagonally across from the inner anterolateral angle of the merus, to the outer posterolateral angle of the ishium. Infra-orbital ridge in males with two to four striated crests in lateral half, four to six low, closely set tubercles, 7-11 more interspaced roundish ones in mesial end; female infra-orbital ridge with 16-20 isomorphic tubercles. Cheliped symmetrical in males, but not in females, surfaces smooth, short meral stridulating ridge present in both sexes. Carpi, propodi of ambulatory legs dorsal margins covered with short setae, interspersed with long setae; merus with a sharp subdistal spine on the anterior margin. G1 corneous endpiece elongate and clearly flattened, with a pointed or truncate tip, separated by a distal V-shaped genital pore opening from its narrow lower endpiece; palp small. Female gonopore operculate, prominent.

**Colour.**— The colour of fresh specimens has not been documented, but preserved specimens examined are brown in colour (see above Material examined).

**Size.**— The largest male specimen examined is (30.0mm x 24.3mm) (QIH specimens), while the largest female specimen examined is 16.5mm x 13.6mm) (TMCD-2577).

**Habitat.**— It can be found on sandy mudflats (Sakai *et al.*, 2006).

**Remarks.**— The distribution of this species is very wide, spreading throughout the Indo West Pacific. From the description provided by Sakai *et al.* (2006), there seems to be a lot of morphological variation in the differenrt specimens collected from different parts of Indo West Pacific. To resolve this problem, a detailed study on the morphometry of the specimens collected from the entire Indo West Pacific has to be carried out. The genetic studies on these specimens can substantiate the morphological data.

Sakai *et al.* (2006) has also taken up the proposals of Ng *et al.* (2001) and Davie (2002) to treat *Helice leachii* as a junior synonym of *Chasmagnathus subquadratus* Dana, 1852. Due to its complex taxonomic past, Sakai *et al.* (2006) selected a neotype for this species.

**Distribution.**— Australia, Taiwan.

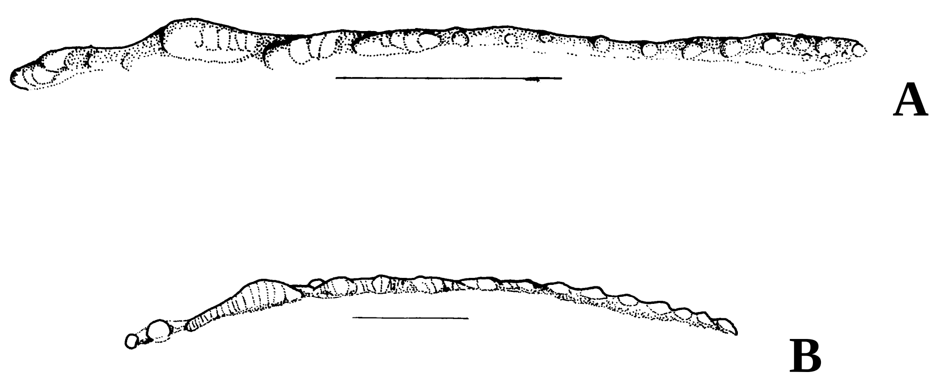



Figure 154. Infra-orbital ridge of *Austrahelice subquadrata* (Dana, 1852). (After Sakai *et al.*, 2006).

## Genus *Helice* De Haan, 1835

*Ocypode* (*Helice*) De Haan, 1835: 28.

*Helice* – Dana, 1852: 252; 1 Dana, 852: 367-368; Dana, 1855: 8, pl. 23 fig. 8; H. Milne Edwards, 1853: 189; Stimpson, 1858: 105; Herklots, 1861: 15; Heller, 1865: 61; Hess, 1865: 153; Miers, 1876: 43, 44; 929: 773; Miers, 1886: 269; Miers, 1879: 38; Kingsley, 1880: 219; Ortmann, 1894: 727; Parisi, 1918: 106; Matsuura, 1894: 56; Doflein 1902: 666; Stimpson, 1907: 133; Terao, 1916: 188; Urita, 1918: 65; 1926: 421; 1928: 21; Tesch, 1918: 117; Balss, 1922: 154; Rathburn, 1931: 90; Shen, 1932: 203; Asano, 1933: 560; Sakai, 1934: 233, 324; Sakai, 1935: 73; Kamita, 1936: 320; Sakai, 1936: 233; Sakai, 1939, 692; Horikawa, 1940: 30; Matsuo, 1940: 5; Shen, 1940: 74, 95; Kamita, 1941a: 89; Kamita, 1941b: 231, text-fig. 128; Kamita, 1941c: 237, 242; Tanaka, 1943: 7; Serène, 1947: 653, fig. 1881; Lin, 1949: 30; Sakai, 1954: 76; Ono, 1959: 146, 147, text-fig. 1; Sakai, 1960: 85, pl. 42, fig. 7; Tanaka, 1960: 121; Guinot-Dumortier, 1961: 83, text-fig. 3; Nakazawa & Miyake, 1961: 177; Kim, 1962: 54; Nakazawa & Miyake, 1962: 131; Tanaka, 1962: 33; Wu *et al.*, 1962: 204; Chang, 1963: 6; Shen & Liu, 1963: 143; Utinomi, 1963: 168; Park, 1964: 18; Shen & Dai, 1964: 131; Sakai, 1965: 204; Kim, 1970: 22; Kim, 1971: 19; Hashiguchi, 1975: 91, 99; Sakai, 1976: 668; Sakai, 1968: 109; Ohshima, 1966: 9; Kim, 1970: 22; Wear, 1970: 5, 23; Kim, 1973: 496, 501, 657, 658; Sakai *et al.*, 1976: 41; Nakasone, 1977: 65: Nye, 1977: 75-89; Kikuchi & Miyake, 1978: 45; Sakai & Yatsuzuka, 1980: 393; 400, figs. 5, 12, 13; Kim & Kim, 1982: 145, 153; Miyake, 1983: 185; Sakai & Nakano, 1983: 89; Tanaka, 1983: 58; Kim, 1985: 85; Kim & Chang, 1985: 56; Matsuo & Makiya, 1985: 307, 309; Dai *et al.*, 1986: 506; Zhou & Sun, 1986: 226; Takeda & Kurihara, 1987: 79-89; Hirata *et al.*, 1988: 22; McLay, 1988: 294; Fukui *et al.*, 1989: 230; Dai & Yang, 1991: 553; Shih *et al.*, 1991: 142; Yamaguchi & Baba, 1993: 488; text-fig. 187A, 187B, pl 13c; Huang, 1994: 598; Sato, 1995: 22; Yoon & Noh, 1995: 330-339; Wada, 1995: 410; Yamanishi & Wada, 1996: 77, 105, 133; Wang & Liu, 1996a: 125; Wang & Liu, 1996b: 100; 227; Ho & Hung, 1997: 105; Omori *et al.*, 1997: 279; Guinot & Bouchard, 1998: 666; Jeng *et al.*, 1998: 66; Mia *et al.*, 1999: 52-61; Takeda *et al.*, 2000: 141; Asakura, 2000: 342; Ng *et al.*, 2001: 44, fig. 8f; Sakai, Türkay & Yang, 2006: 14. (All in part).

**Type species.**— *Ocypode* (*Helice*) *tridens* De Haan, 1835, by monotypy.

**Gender.**— Masculine.

**Diagnosis.**— Carapace rounded, quadrangular, broader than long; dorsal surface setose, punctate; regions not well defined, convex. Frontal margin slightly convex, straight. Anterolateral margin subcristate with four teeth including exorbital tooth, orbital tooth distinct, with a faint notch on posterolateral margins behind third anterolateral tooth. Orbits small, eyes completely filling orbit. Third maxilliped short, stout, merus of third maxilliped nearly as broad anteriorly as long. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Chelipeds equal in both sexes; chelae with or without setae at base of fingers; meral stridulating ridge always conspicuous, well separated from anterior margin in males, more than one-third anterior margin length, in females not conspicuous. First two pairs of ambulatory legs with carpi, propodi with thick short setae, the following two lacking such dense setal tufts. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without medial grooves. Male abdomen broadly triangular with all segments freely moveable (six somites plus telson), third somite of male abdomen protruding laterally.

**Remarks.**— Following Sakai *et al.*'s definition of *Helice*, there are currently only four species in this genus viz. *Helice tridens* De Haan, 1835 (type species), *H. formosensis* Rathbun, 1931; *H. latimera* Parisi, 1918; and *H. tientsinensis* Rathbun, 1931. These four species are all restricted to East Asia. Preliminary studies on the 16s RNA gene of these species supports their new grouping (on-going study).

**Key to species in *Helice***

1a. Infra-orbital ridge of male with isomorphic granules or tubercules on infra-orbital ridge. ------------------------------------------------------------------------------- **2**

1b. Infra-orbital ridge of male with heteromorphic granules or tubercules on infra-orbital ridge. ----------------------------------------------------------------------- **3**

2a. Infra-orbital ridge of male with 33-37 vertically elongated tubercules; female with 26-37 isomorphic granules. --------------------------------------- ***H. tientsinensis***

2b. Infra-orbital ridge of male with 64-67 vertically elongated tubercules; female with 37-55 isomorphic granules. ----------------------------------------------- ***H. latimera***

3a. Infra-orbital ridge of male with 2-8 tublecules; followed by 15-22 rounded granules, female with 24-29 isomorphic granules. ---------------------- ***Helice formosensis***

3b. Infra-orbital ridge of male with 2-3 tublecules; followed by 9-16 rounded granules, female with 15-28 isomorphic granules. ------------------------------ ***Helice tridens***

## *Helice tridens* De Haan, 1835

(Figure 155)

*Ocypode* (*Helice*) *tridens* De Haan, 1835: 57, pl. 11 fig. 2, pl. 15 fig. 6, pl. C.

*Helice tridens* - Milne Edwards, 1853: 189; Stimpson, 1858: 105; Herklots, 1861: 15; Miers, 1879: 38; Kingsley, 1880: 219; Matsuura, 1894: 56; Ortmann, 1894: 727; Koelbel, 1898: 570; Doflein 1902: 666; Stimpson, 1907: 133; Urita, 1918: 65; Tesch, 1918: 119; Balss, 1922: 154 (part); Guinot-Dumortier, 1961: 83, text-fig. 3; Asano, 1933: 560, text-fig. 1273; Sakai, 1954: 76; Guinot-Dumortier, 1961: 83, text-fig. 3; Kim, 1973: 496, 657, fig. 224, pl. 47, fig. 173; Yamaguchi *et al.*,1976: 41; Tanaka, 1983: 58; Miyake, 1983: 185, pl. 62, fig. 1; Takeda, 1983: 147 (col. fig.), 193; Matsuo & Makiya, 1985: 307, 309; Kim & Chang, 1985: 56; Takeda & Kurihara, 1987: 79-89; Yamaguchi *et al.*, 1987: 33, pl. 16 fig. 9; Yamaguchi & Baba, 1993: 488 (part), text-fig. 187A (part) 187B, pl 13c; Sato, 1995: 22; Yamanishi & Wada, 1996: 77, 105, 133; Omori *et al.*, 1997: 279-288, fig. 2A, 3B, 4B, 5B, 7B, 8B, 9B, 10B, 11B, 13; Guinot & Bouchard, 1998: 666; Takeda *et al.*, 2000: 141; Asakura, 2000: 342; Sakai *et al.*, 2006: 23.

*Helice tridens tridens* – Rathbun, 1931: 90, pl. 7; Sakai, 1934: 324: 233, pl. 64 fig. 2; Sakai, 1935: 73; Sakai, 1936: 233, pl. 64 fig. 2; Sakai, 1939 692, text-fig. 121, pl. 77 fig. 2; 1960: 85, pl. 42, fig. 7; 1965: 204; ; Kamita, 1936: 320; Matsuo,1940: 5; Sakai, 1940: 51; Kamita, 1941a: 89; Kamita, 1941b: 231, text-fig. 128; Kamita, 1941c: 237, 242; Tanaka, 1943: 7; Serène, 1947: 653, fig. 1881; Ono, 1959: 146, 147, text-fig. 1;Tanaka, 1960: 121; Nakazawa *et al.*, 1961: 177; Kim, 1962: 54; Nakazawa *et al.*, 1962: 131; Tanaka, 1962: 33; Utinomi, 1963: 168; Park, 1964: 18; Sakai, 1965: 204; Ohshima, 1966: 9; Serène, 1968: 109; Kim, 1970: 22; Kim, 1971: 19; Sakai, 1974: 720; Hashiguchi, 1975: 9; Sakai, 1976: 669; Kim & Kim, 1982: 145, 153; Sakai & Nakano, 1983: 89; Kim, 1985: 85; Yoon & Noh, 1995: 330; Mia *et al.*, 1999: 52.

*Helice (Helice) tridens tridens* – Sakai & Yatsuzuka, 1980: 395; Wada, 1995: 410.

*Helice Latreillii* – Targioni-Tozzetti, 1877: 161.

*Helice latreilli* – Tesch, 1918: 119; Serène, 1968: 109.

*Helis tridens* – Urita, 1928: 21 (wrong spelling).

*Helice ttridens* – Kikuchi & Miyake, 1978: 45 (wrong spelling)

*Gapsus latreillei* H. Milne Edwards, 1837: 80.

**Materials examined.**— **Lectotypes** – 33.0mm x 27.0mm) (RMNH-188), Japan, coll. Ph. F. von Siebold, 1823-1829. – **Paralectotypes** – 3 males (15.6-35.5mm x 18.8-38.3mm), 3 females (20.3-29.2mm x 23.1-32.1mm), Japan, coll 1823-1829, Ph. F. von Siebold. – **Others** – **China** – 1 male (26.3mm x 22.8mm) (QIH-6610), Chengyu Island, coll. R.Y. Liu, 12 Oct. 1952; 1 male (29.3mm x 25.3mm) (QIH-4582), Jinan, Nanbao, Shandong Province, 25 Oct. 1951; 1 male (20.6mm x 17.9mm) (QIH-no cat. number), Tanggu, coll. 8 Oct. 1951; 7 males (9.6-23.9mm x 7.8-20.7mm), 1 female (23.5mm x 18.9mm), 1 female (ovigerous) (14.0mm x 10.1) (QIH-no cat. number), Zhikun, coll. 13 Oct. 1981; 14 males (10.3-23.6mm x 8.2-19.3mm), 1 female (ovigerous) (QIH-06608), Dalian, coll, 29 May 1950. – **Taiwan** – 9 males (13.4-18.8mm x 10.6-15.0mm), 2 females (13.7-14.5mm x 10.6-11.4mm), (NTOU-no cat. number), Fengshan river mouth, Hsinchu County, coll. J.F. Huang, 27 Sep. 1987; 1 female (27.5mm x 21.7mm) (NTOU-no cat. number), Tansui river mouth, Taipei County, coll. J.F. Huang, 1 Apr. 1984; 1 female (26.0mm x 21.4mm) (NTOU-no cat. number), Bu-Dai, Jiayi County, coll. J.F. Huang, 3 Jan. 1988; 2 males (18.4-29.8mm x 15.2-24.0mm) (NTOU-no cat. number), Tansui, Taipei County, coll. J.F. Huang, 15 Nov. 1984; 4 males (15.5-19.0mm x 12.5-17.0mm), 3 females (15.7-18.6mm x 13.3-15.4mm) (NTOU-no cat. number), Tansui river mouth, Taipei County, coll. 3 Mar. 1986; 2 males (18.7-29.5mm x 15.0-24.5mm) (NTOU-no cat. number), Kunshan river, Tainan, coll. J.F. Huang, 30 Jan. 1988; 1 female (26.0mm x 21.4mm) (NTOU-no cat. number), Budai, Jiayi County, coll. J.F. Huang, 3 Jan. 1988.

**Diagnosis.**— Carapace quadrilateral; surface convex, sparingly setose, granulated, distinct wide, medial groove between epigastric regions; frontal margin sinuous . Anterolateral margin vaulted upwards, with four teeth including orbital tooth. Third maxillipeds close with gap, an oblique row of short setae runs diagonally across from inner anterolateral angle of merus, to outer posterolateral angle of ishium. Infra-orbital ridge with of males consisting of row of 9-16 rounded granules including two or three striate mesial ones, females with row of 15-28 isomorphic granules. Cheliped symmetrical in both sexes; surfaces smooth, meral stridulatory ridge present, much reduced or absent in females. Ambulatory legs long, slender, first and second legs covered with dense short setae, interspersed with long setae, following two pairs without such setal areas; merus with a sharp subdistal spine on the anterior margin. G1 with a broadly triangular tip. Female gonopore protruding with operculum, distinct slit present.

**Colour.**— The colour of fresh specimens is not documented, all preserved specimens examined are orange-reddish brown.

**Size.**— The largest male specimen examined is 29.8mm x 24.0mm (NTOU-no cat. number), and the largest female specimen examined is 26.0mm x 21.4mm (NTOU-no cat. number).

**Habitat.**— The species can be found  in sandy mud flats (J.F. Huang, pers. comm.).

**Remarks.** —Sakai *et al.* (2006) examined the two syntypes of *Cyclograpsus latreillii* and found to belong to two different species. They, in conjuction with D. Guinot from the Museum National d'Histoire Naturelle, Paris, designated one of the male specimens of the *Cyclograpsus latreillii* as lectotype of *C. latreillii* (MNHN-B-4647S). With this action, *C. latreillii* becomes a junior subjective synonym of *H. tridens*. The other specimen is apparently a specimen of *C. subquadrata*.

**Distribution.**— Taiwan, Japan (Aomori to Kagoshima), Southern Korea.

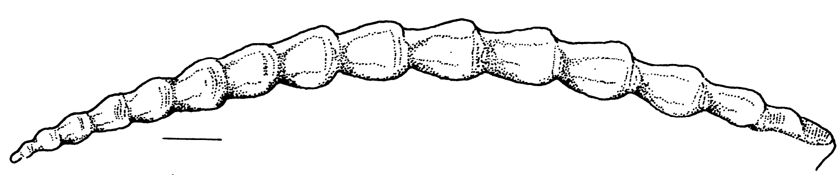


Figure 155. Infra-orbital ridge of *Helice tridens* (After Sakai *et al.*, 2006).

## *Helice formosensis* Rathbun, 1931

(Figure 156)

*Helice formosensis* Rathbun, 1931: 91, pl. 8 fig. 18, pl. 9 fig. 22; Sakai, 1940; 27; Miyake, 1983: 185; Fukui *et al.*, 1989: 230, fig. 22; Shih *et al.*, 1991: 142; Hsueh, 1995: 145; Hsueh, 1996: 35; Wang & Liu, 1996a: 125, figs. 166–169; Wang & Liu, 1996b: 100; Ho & Hung, 1997: 105; Jeng *et al.*, 1998: 66; Wang & Liu, 1998: 100; Ng *et al.*, 2001: 44, fig. 8f; Sakai *et al.*, 2006: 16.

*Helice tridens latimera* – Parisi, 1918: 106 (part), fig. 4b, pl. 8: 3; Sakai, 1939: 693, fig. 122a–b; Horikawa, 1940: 30; Lin, 1949: 30; Wu *et al.*, 1962: 204; Sakai, 1976: 669, text-fig. 366 c; Nakasone, 1977: 65 (not *Helice* (*tridens*) *latimera* Parisi, 1918)

*Helice tridens tridens* – Rathbun, 1931: 90 (part), pl. 7: 6, pl. 8: 16, pl. 9: 21; Lin, 1949: 30; Wu *et al.*, 1962: 204; Chang, 1963: 6 (not *Ocypode* (*Helice*) *tridens* De Haan 1835).

*Helice tridens* – Stimpson, 1858: 105 (part; 1907: 133 (part); Terao, 1916: 188; Hirata *et al.*, 1988: 22, 1 fig.

*Helice (Helice) formosensis* – Sakai & Yatsuzuka, 1980: 400, figs. 5, 12, 13; Huang, 1994: 598; Dai *et al.*, 1986: 506, Dai & Yang, 1991: 553.

*Helice (Helice) latimera* – Wang & Liu, 1996c: 227 (not *Helice* (*Helice) latimera* Parisi, 1918).

*Helice tridens sheni* – Shen & Dai, 1964: 132, 1 fig.

*Helice tridens formosensis* – Serène, 1968: 109.

*Helice latimera* – Dai *et al.*, 1986: 506-507, text-figs. 287/1-2, pl. 72 fig. 2 (not *Helice* (*Helice) latimera* Parisi, 1918).

**Materials examined.**— **Holotype** – 1 male (USNM-55371), Giran, Taitung, Taiwan, coll. Aug. 1918. – **Others** – **Taiwan** – 3 males (17.5-27.3mm x 14.0-23.2mm), 4 females (16.9-24.1 x 13.5-18.6mm), (NMNS-uncatalogued), Yanliao, Taichung, coll. H.T. Shih, 20 May 2002; 1 males (16.0mm x 13.6mm), 1 female (14.9mm x 12.6mm), 2 females (ovigerous) (20.8-21.5mm x 17.7-17.8mm), (NMNS-uncatalogued), Tzaiwei, Tansui, coll. H.T. Shih, 18 Jun. 1996; 2 females (26.2-31.0mm x 21.3-24.9mm), (NTOU-uncatalogued), Hsiangshan, coll. M.S. Hung, May 1998; 2 males (21.5-25.7mm x 19.7-21.3mm), 1 female (29.2mm x 22.6mm) (NMNS-004657-00024), Shenggang fish port, coll. H.T. Shih, 1 Oct. 2004; 1 male (16.6mm x 14.0mm) (NMNS-uncatalogued), Dajiaxi river, coll. S.M. Chao, 14 Oct. 1998; 4 males (11.4-17.7mm x

8.8-13.9mm), 5 females (14.3-28.2mm x 11.6-22.6mm) (NMNS-001470-00003), Dajiaxi rivermouth, coll. Z.D. Lee, 12 Oct. 1993.

**Diagnosis.**— Carapace quadrilateral, slightly broader than long; surface convex, granulated, with a distinct wide, medial groove between epigastric regions; frontal margin bilobed. Anterolateral margin vaulted upwards, with four teeth including orbital tooth. Third maxillipeds close with rhomboidal gape. Infra-orbital ridge of males with row of 15-22 rounded granules including 2-8 striated mesial ones, females with row of 24-29 isomorphic granules. Cheliped symmetrical in males, surfaces smooth, meral stridulating reige present in males, reduced or absent in females. First to second ambulatory legs broad, margins of propodus covered with short setae; third, fourth ambulatory legs without such dense setation. G1 stout, slightly bent dorsally inwards, tip suddenly narrowed at about half its length. Female gonopore with protruding but small operculum.

**Colour.**— The colour fresh specimens is greyish brown, and the colour of all preserved specimens examined is brown.

**Size.**— The largest male specimen examined is 27.3mm x 23.2mm (NMNS-uncatalogued), while the largest female examined is 31.0mm x 24.9mm (NTOU-uncatalogued).

**Habitat.**— It can be found in burrows along grassy banks, or under rocks, and mudflats of mangroves (H.T. Shih, pers. comm.).

**Remarks.**— *Helice formosensis* can be easily separated from *H. tridens* by the morphology of its infra-orbital crest, the setation on the ambulatory legs, and by the structure of the male first pleopod. However, Sakai *et al.* (2006) reported that adult specimens showed some characters in common with *H. formosensis* from localities within the range of typical *H. tridens.* The examination of a series of smaller specimens from these areas have showed that there is some tendency for characters to overlap. Preliminary results on the 16s rRNA has also indicated that the *Helice* species are still very closely affliated with each other. The possible solution to resolve this doubt is to do an extensive, detailed morphormetic study of the four species, and its population structure and dynamics.

The species has been first described from Taiwan, and believed to be restricted to Taiwan.

**Distribution.**— Taiwan only.

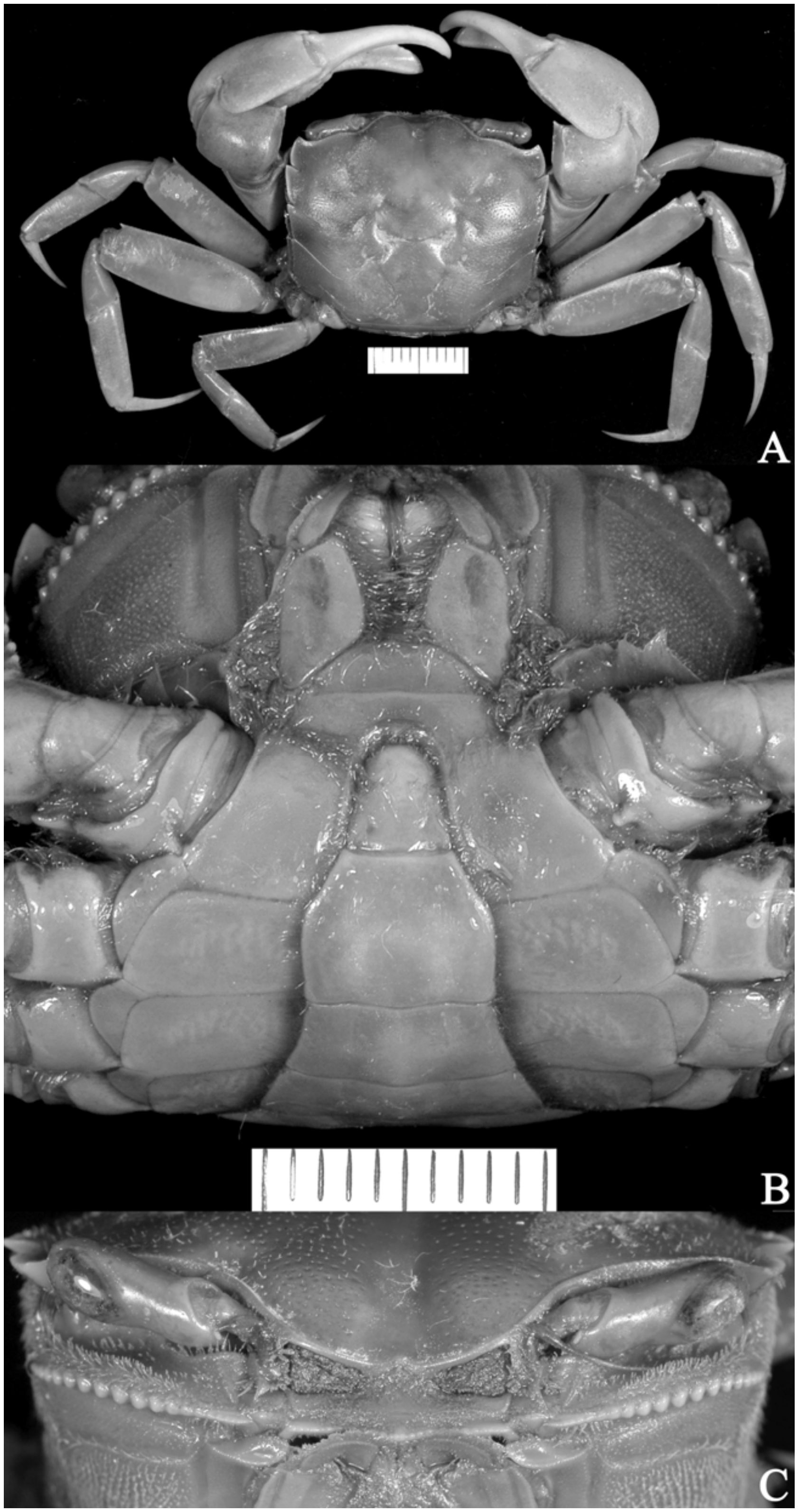



Figure 156. *Helice formosensis* Rathbun, 1931, male, 27.3mm x 23.2mm (NMNS). A) dorsal view; B) ventral view; C) frontal view.

### ***Helice latimera* Parisi, 1918**

(Figure 157)

*Helice latimera* Parisi, 1918: 106 (part), text figs, 4a, 4c-d, pl. 8 fig. 3.

*Helice tridens latimera* – Sakai, 1976: 669; Serène, 1968: 109.

*Helice* (*Helice*) *latimera* – Sakai & Yatsuzuka, 1980: 403; Dai & Yang, 1991: 552, pl. 71 fig. 6, text-figs. 286 (3-4).

*Helice latimera* – Sakai *et al.*, 2006: 20.
*Helice formosensis* – Miyake, 1983: 185.

*Helice tridens pingi* Rathbun, 1931: 91, pl. 8, fig. 15, pl. 9 figs. 23-24; Shen, 1940: 95; Serène, 1965: 109; Sakai, 1976: 672.

*Helice* (*Helice*) *latimera* – Sakai & Yatsuzuka, 1980: 403, text-figs 6, 14-15.

*Helice tridens* – Morton & Morton, 1983: 227, 228, text-fig. 11.11/7 (not *Ocypode* (*Helice*) *tridens* De Haan 1835).

*Helice pingi* – Dai *et al.*, 1986: 505, text-figs. 286/3-4, pl. 71 fig. 6.

**Materials examined.**— **Neotype** – 1 male (33.2mm x 26.0mm)  4 males (31.6-33.2mm x 24.9-26.0mm), 3 females (28.8-33.9mm x 22.0-27.7mm) (ASIZ-no cat. number), Yandu, Haikou, Hainan Island, coll. 3 Nov. 1959.  **China** – 1 male (24.4mm x 19.8mm), 1 female (23.5mm x 18.3mm) (ASIZ-C2463), Wenzhou, Zhejinag Province, coll. 2 Jul. 1962; 1 male (29.5mm x 24.3mm), 2 females (12.8-9.4mm x 28.6-23.0mm) (ASIZ-no cat. number), Amoy coll. 11 Nov. 1959; 1 males (29.2mm x 24.4mm) (ASIZ-C02429), Nanpukou, Haikou, Haina Island, coll. 21 Feb. 1958; 1 males (26.1mm x 20.8mm), 2 females (28.0-29.4mm x 21.8-23.9mm) (ASIZ-no cat. number), Haikou, Hainan Island, coll. 26 May 1958; 2 males (27.0-30.3mm x 22.6-24.3mm) (ASIZ-no cat. number), no other data; 2 males (28.9-31.0mm x 20.0-20.8mm), 1 female (31.4mm x 25.3mm) (ASIZ-no cat. number), Xiamen, Fujian Province, coll. 11 Aug. 1928; 2 males (28.9-31.0mm x 22.9-25.9mm) (ASIZ-C2432), Xingmeng, Hainan Island, coll. 1 Jun. 1956; 1 female (26.3mm x 21.0mm) (ASIZ-no cat. number), Haikou, Hainan Island, coll. 11 May 1959; 1 males (31.0mm x 25.6mm) (ASIZ-C2428), Xiongshan, Beigang, Hainan Island, coll. 12 Jan. 1960; 1 males (22.0mm x 17.8mm) (ASIZ-no cat number), don. Swire Marine Laboratory, no collection date; 6 males (21.1-30.1mm x 27.3-24.6mm) (QIH-no cat. number), Yandu, coll. 11 Jun. 1960; 1 male (34.2mm x 28.8mm), 1 female (29.4mm x 23.5mm) (QIH-no cat. number), Haikou, Hainan Island, coll. 11 Jun. 1958. – **Taiwan** – 5 males

(13.0-23.0mm x 10.0-20.0mm), 2 females (23.0mm x 19.0mm), (NTOU-no cat. number), San-Shin Bridge, Hsinchu County, coll. 26 Sep. 1987; 1 male (30.0mm x 24.0mm), (NTOU-no cat. number), Ilan river, coll. J.F. Huang, 4 Sep. 1987; 1 male (31.3mm x 26.3mm) (NTOU-uncatalogued), Tansui rivermouth, Taipei County, coll. J.F. Huang, 21 Mar. 1992; 1 male (26.4mm x 23.0mm), 1 female (30.8mm x 25.4mm), (NMNS-uncatalogued), Jinmen, coll. L.R. Tung, 8 May 1989; 1 male (25.6mm x 21.4mm), 1 female (17.5mm x 14.9mm) (NMNS-uncatalogued), Jinmen, coll. L.R. Tung, 23 May 1988.

**Diagnosis.**— Carapace quadrilateral; surface convex, sparingly setose, granulated, distinct wide, medial groove between epigastric regions; frontal margin sinuous . Anterolateral margin slightly vaulted upwards, with four teeth including orbital tooth. Third maxillipeds close with gap, an oblique row of short setae runs diagonally across from inner anterolateral angle of merus, to outer posterolateral angle of the ishium. Infra-orbital ridge with regularly tapering from center towards both ends, made of row of 64-67 vertically expanded and striated ridges, females with row of 37-55 isomorphic granules. Cheliped symmetrical in males, surfaces smooth, meral stridulatory ridge present in male, smaller in female. Ambulatory legs long, slender, first pair densely setose; dorsal margin of second carpus covered with dense short setae, interspersed with long setae; merus of all ambulatory legs with a sharp subdistal spine on the anterior margin. Last two ambulatory legs without conspicuous setae. G1 with a triangular tip; terminal endpiece with a narrow genital pore distally. Female gonopore with protruding operculum, slit semi-oval in shape.

**Colour.**— The colour fresh specimens has not been documented, all preserved specimens examined are range-reddish brown in colour.

**Size.**— The largest male specimen examined is 31.3mm x 26.3mm (NTOU-no cat. number), while the largest female specimen examined is 33.9mm x 27.7mm (ASIZ-no cat. number).

**Habitat.**— It can be found in sandy mud flats along the coast or river banks (J.F. Huang, pers. comm.).

**Remarks.**— This species has been usually confused with *H. formosensis* but it can be easily discerned by a) the form of the infra-orbital ridge that has 64-67 vertically expanded striated tubercules (vs. 15-22 rounded granules followed by 2-8 striated tubercules in *H. formosensis*), and b) the G1 is slender (vs. broader G1 in *H. formosensis*). Sakai *et al.* (2006) has treated this species in their report and there is no need to do so again here.

**Distribution.**— Taiwan, China (Southern Zhejiang Province to Hainan Province), Vietnam.

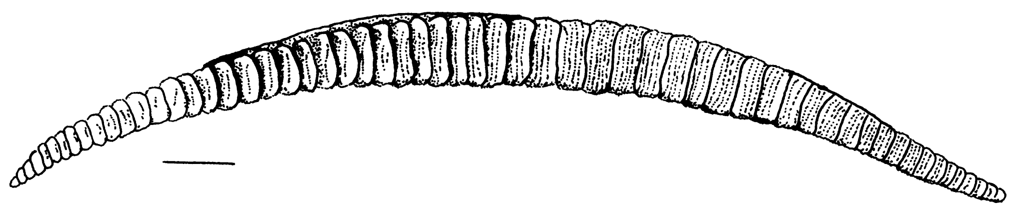


Figure 157. Infra-orbital ridge of *Helice latimera* (After Sakai *et al.*, 2006).

### *Helice tientsinensis* Rathbun, 1931

(Figure 158)

*Helice tridens* – Urita, 1926: 421.

*Helice tridens tientsinensis* Rathbun, 1931: 92, pl. 7 fig. 9, pl. 8 fig. 19, pl. 9 figs. 27-28; Shen, 1932: 210, text-fig. 130-131, pl. 8 fig. 5-6; Kamita, 1936: 3-4, text-figs. 3-4; 1941a: 89; 1941b: 238, text-fig. 131; 1941c: 235, 242; Sakai, 1939: 696, 732, text-fig.125; Matsuo, 1940: 5; Shen, 1940: 74, 95; Kim, 1962: 54; Shen & Liu, 1963: 143; Shen & Dai, 1964: 131; Park, 1964: 18; Serène, 1968: 109; Kim, 1970: 22; 1973: 501, 658, fig. 227, pl. 48, fig. 176; Sakai, 1976: 671, text-fig. 369; Sakai & Yatsuzuka, 1980: 398, text-figs 4, 10-11; Kim & Kim, 1982: 145, 153; Zhou & Sun, 1986: 226.

*Helice* (*Helice*) *tientsinensis* – Dai & Yang, 1991: 551, pl. 71 fig. 4, text-fig. 285 (3-4).

*Helice tientsinensis* – Dai *et al.*, 1986: 504, text-figs. 285/3-4, pl. 71 fig. 4; Sakai *et al.*, 2006: 21.

**Materials examined.**— **Holotype** – 1 male (USNM-25431), Tianjin, Hebei Province, China, coll. M.L. Robb, May 1901. – **Paratypes** – 3 males, 4 females (USNM-25431), Tianjin, Hebei Province, China, coll. M.L. Robb, May 1901. – **Others** – **China** – 4 males (20.6-27.8mm x 17.0-23.4mm), 2 females (22.8-26.6mm x 18.3-21.3mm) (QIH-no cat. number), Yangkou market, Shandong Province, coll. R.Y. Liu, 24 Jul. 1953; 11 males (24.0-28.1mm x 20.1-23.9mm), 2 females (23.3-24.9mm x 18.4-20.5mm) (QIH-no cat. number), Changkou, Qingdao; 2 males (25.3-28.3mm x 20.8-25.1mm) (QIH-0622), Daicheng, Fishery, Shandong Province, coll. 30 Jul. 1951; 3 males (22.7-31.1mm x 17.7-27.0mm), 1 female (ovigerous) (22.0mm x 17.7mm) (QIH-no cat. number), Zhuang River, coll. X. Cheng, 19, May 1950; 3 males (20.8-27.4mm x 17.0-23.2mm), 2 females (17.1-22.9mm x 13.7-22.2mm), 2 females (ovigerous) (23.8-26.4mm x 19.2-20.8mm) (QIH-06622), Beidaihe River, coll. 1 May 1950; 1 male (28.6mm x 23.2mm) (QIH-no cat. number), Lidao, Jing Jiao Port, coll. 2 May 1951; 1 male (20.3mm x 16.5mm), 1 female (15.9mm x 13.2mm) (QIH-no cat. number), Changkou, coll. 18 Oct. 1958; 1 male (0.4mm x 16.5mm), 2 females (10.0-16.4mm x 7.7-12.7mm) (QIH-no cat. number), Changkou, coll. 18 Oct. 1958; 4 males (27.5-33.2mm x 22.8-26.9mm) (QIH-no cat. number), Wannainjiao, Tanggu, coll. 31 May 1951; 2 males (24.0-25.2mm x 20.6-21.3mm) (QIH-06615), Changkou, Qingdao, coll. 7 May 1951; 3 males (25.8-28.8mm x 21.3-24.3mm), 2 females (27.5-28.1mm x 22.5-22.8mm), (QIH-06863), Yanzhao, Nuyukou, coll. 15 Sep. 1958; 1 male (26.1mm x 22.2mm), 1 female (24.3mm x 17.4mm) (ASIZ-02409), Dupujiang, Shandong, coll. 3 May 1956. – **Taiwan** – 3 males (15.6-24.9mm x 11.7-20.0mm), 2 males (23.3-25.7mm x 19.1-20.8mm) (NMNS-uncatalogued), Jinmen, coll. H.T. Shih, 13 Apr. 2000.

**Diagnosis.**— Carapace quadrilateral; surface convex, sparingly setose, granulated, distinct wide, medial groove between epigastric regions; frontal margin sinuous . Anterolateral margin vaulted upwards, with four teeth including orbital tooth. Third maxillipeds close with gap. Infra-orbital ridge consisting of row of 33-37 heteromorphic protuberances in males of which middle ones clearly higher than others, 10-15 mesial granules quite small, lateral ones similarly small and confluent with one another; male infra-orbital crest thus appears strongly constricted on both sides of its center; infra-orbital ridge of females with 26-37 isomorphic tubercles. Chelipeds symmetrical in males, females, surfaces smooth, stridulatory ridge present on the merus of chelipeds. First ambulatory leg with propodus and carpus provided with thick setae on anterior faces; second ambulatory leg with setal tufts on anterior face of carpus, and on dorsal half of anterior face of propodus; last two ambulatory legs without conspicuous setation. G1 with broad tip; corneous endpiece distally with small genital pore. Operculum clearly protruding, with oval slit on mesial side.

**Colour.**— The colour fresh specimens has not been documented, all preserved specimens examined are orange-reddish brown in colour.

**Size.**— The largest male specimen examined is 33.2mm x 22.8-26.9mm (QIH-no cat. number), and the largest female specimen is 28.1mm x 22.8mm (QIH-06863).

**Habitat.**— It can be found in sandy mud flats (Dai & Yang, 1991).

**Remarks.** — This species is very easy to recognise as the infra-orbital ridges are very distinct in both male and female specimens (see figure below).

This species is found mainly along the coast China. The Taiwanese specimens were found on Jinmen Island, situated along the Straits of Taiwan.

**Distribution.**— China (Liaoning Province to Fujian Province), Korea (southern coast).

Figure 158. Infra-orbital ridge of *Helice tientsinensis*. (After Sakai *et al.*, 2006).

## Genus *Austrohelice* Sakai, Türkay & Yang, 2006

*Helice* Dana, 1852: 252; 1852: 367-368; H. Milne Edwards, 1853: 190; Dana, 1855: 8, pl. 23 fig. 8; Hess, 1865: 153; Heller, 1865: 61; Miers, 1876: 43-44; Targioni-Tozzetti, 1877: 161; Kingsley, 1880: 220; Hutton, 1882: 264; Filhol, 1886: 391; Miers, 1886: 269; Thomson & Anderton, 1921: 101; Oliver, 1923: 541-544; Chilton & Bennett, 1929: 772; Richardson, 1949: 34, fig.13; Beer, 1959: 197-203, text-fig. 1A, C; Wood, 1963: 9, 14; Dell, 1963: 55, text-fig.; Bennett, 1964: 83, text-fig. 140; Campbell & Griffin, 1966: 129; Dell, 1968: 26; Dell, 1968: 232, 233, 237; Serène, 1968: 109; Cameron, 1970: 439, 440; Wear, 1970: 5, 23, figs. 50-58; Bedford, 1972: 113; Miller & Batt, 1973: 99, fig. 125; Hayward, 1974: 160; Jones, 1976: 580, 586, fig. 1; Carpenter, 1976: 15, 16, text-fig. 2; Cox, 1976: 155-156; Nye, 1977: 75-89; Knox *et al.*, 1977: 27; Bolton & Knox, 1977: 7; Knox & Fenwick, 1978: 5; Knox *et al.*, 1978: 44; Fenwick, 1978: 208; Latham, 1978: 355; Fielder & Jones, 1978: 42-43, text figs. 1-2; Jones, 1980: 433-443, tables 1-6, text-figs. 1-3; Shumway & Jones, 1981: 551-553; Jones, 1981: 271-282; Johnson *et al.*, 1981: 245; Jones & Simons, 1982: 49; Hawkins & Jones, 1982: 103; Hawkins *et al.*, 1982: 341; Knox, 1983: 27: 7; & Simons, 1983: 656; Williams *et al.*, 1985: 269; Palmer & Williams, 1986: 270; McLay, 1988: 294, text-fig. 64; Dowse & Palmer, 1992: 106, 108, 115; Guinot & Bouchard, 1998: 666; Morrisey, 1999: 231, tables 1-4, text-figs. 1-6. (All part).

*Austrohelice* Sakai, Türkay & Yang, 2006: 53.

**Type species**.— *Helice crassa* Dana, 1852, designation by Sakai, *et al.*, 2006.

**Gender.**— Feminine.

**Diagnosis.—** Carapace subquadrangular, physiognomy very high, faint notch on posterolateral margins behind third anterolateral tooth. Infraorbital ridge heteromorphic in males, isomorphic in females. Merus of third maxilliped nearly as broad anteriorly as long. Chelipeds equal in both sexes, chelae without a patch of setae at base of fingers; meral stridulating ridge absent, well separated from anterior margin in males, absent in females. First two pairs of ambulatory legs with thick soft setae on carpi, propodi, fourth pair glabrous. G1 with suture of sperm channel beginning on ventromesial surface, displaced distally to dorsal side. Female gonopore with rounded, protruding operculum. (Modified from Sakai *et al*., 2006).

**Remarks**.— There is only one species included in this genus viz. *A. crassa* (Dana, 1852).

This genus is very similar to *Neohelice* Sakai, Türkay & Yang, 2006, in lacking a stridulatory ridge on the merus but, it can be easily discerned by the following features: a) the presence of only one row of granules on the infra-orbital ridge (vs. presence of two rows of granules in *Neohelice*); b) the margins of first two pairs ambulatory legs are setose (vs. only fourth ambulatory legs setose in *Neohelice*), and c) the ambulatory legs are broad and stout (vs. long and slender in *Neohelice*).

## *Austrohelice crassa* (Dana, 1852), new combination

(Figure 159)

*Helice crassa* Dana, 1852: 252; 1852: 367; H. Milne Edwards, 1853: 190; Dana, 1855: 8, pl. 23 fig. 8; Hess, 1865: 153; Heller, 1865: 61; Miers, 1876: 43; Targioni-Tozzetti, 1877: 161; Kingsley, 1880: 220; Filhol, 1886: 391; Miers, 1886: 269; Thomson & Anderton, 1921: 101; Oliver, 1923: 541; Chilton & Bennett, 1929: 772; Richardson, 1949: 34, fig.13; Beer, 1959: 197, text-fig. 1A, C; Wood, 1963: 9, 14; Dell, 1963: 55; Bennett, 1964: 83, text-fig. 140; Campbell & Griffin, 1966: 129; Dell, 1968: 26; Dell, 1968: 232, 233, 237; Serène, 1968: 109; Cameron, 1970: 439, 440; Wear, 1970: 5, 23-25, figs. 50-58; Bedford, 1972: 113; Miller & Batt, 1973: 99, fig. 125; Hayward, 1974: 160; Jones, 1976: 580, 586, fig. 1; Carpenter, 1976: 15, 16, text-fig. 2; Cox, 1976: 155; Nye, 1977: 75; Knox *et al.*, 1977: 27; Bolton & Knox, 1977: 7; Knox & Fenwick, 1978: 5; Knox *et al.*, 1978: 44; Fenwick, 1978: 208; Latham, 1978: 355; Fielder & Jones, 1978: 42, text figs. 1-2; Jones, 1980: 433, tables 1-6, text-figs. 1-3; Shumway & Jones, 1981: 551; Jones, 1981: 271; Johnson *et al.*, 1981: 245; Jones & Simons, 1982: 49; Hawkins & Jones, 1982: 103; Hawkins *et al.*, 1982: 341; Knox, 1983: 27: 7; & Simons, 1983: 656; Williams *et al.*, 1985: 269; Palmer & Williams, 1986: 270; McLay, 1988: 294, text-fig. 64; Dowse & Palmer, 1992: 106, 108, 115; Guinot & Bouchard, 1998: 666; Morrisey, 1999: 231, tables 1-4, text-figs. 1-6. (All in part).

*Chasmagnathus subquadratus* – Thomson, 1913: 238 (not *Chasmagnathus subquadratus* Dana, 1852).

*Helice lucasi* H. Milne Edwards, 1853: 190; Miers, 1876: 44; Hutton, 1882: 264; Filhol, 1886: 391-393; Chilton & Bennett, 1929: 773; Serène, 1968: 109. (not *Helice lucasii* H. Milne Edwards, 1853).

*Austrohelice crassus* – Sakai, Türkay & Yang, 2006: 54.

**Materials examined.**— 5 males (9.2-16.9mm x 7.2-13.1mm) (NMNS-uncatalogued), Avon-Heathcote Estuary, mudflat, Christchurch, New Zealand, coll. C. McLay, 5 Jun. 2005.

**Diagnosis.**— Carapace quadrilateral, slightly broader than long; surface convex, granulated, with a distinct wide, medial groove between epigastric regions; frontal margin bilobed. Anterolateral margin vaulted upwards, with three teeth including orbital tooth. Third maxillipeds close with rhomboidal gape. Infra-orbital ridge consisting of isomorphic granules, 21-30 in males, 25-34 in females. Chelipeds symmetrical in both sexes, surfaces smooth, without any setae, meral stridulating ridge absent. Ambulatory legs broad, margins of propodi from first, second legs covered with short setae; following two ambulatory legs with propodi and carpi bearing only sparse setal tufts on their respective anterodorsal margin. G1 stout, incurved and rounded distally, tip suddenly narrowed at about half its length. Female gonopore operculate, protruded, broadly triangular.

**Colour.**— The colour of fresh specimens is grey, olive green in colour (C. McLay, pers. comm.), and the colour of the preserved specimens examined is brown in colour (NMNS-uncatalogued).

**Size.**— The largest male specimen reported is 21.7mm in carapace width, and the largest female size reported is 20.9mm in carapace width (McLay, 1988).

**Habitat.**— It can be found in burrows on mudflats (McLay, 1988).

**Remarks.**— Based on the description given by H. Milne Edwards (1853) of *Helice lucasii*, it seems to be the junior synomym of this species. This has been confirmed by Sakai *et al.* (2006).

This species has been reported to climb trees to about a meter in height to feed on the thin film of mud left behind on the branches and leaves immediately after the high tide has receeded (Cox, 1977). This is the only species in the Varunidae that has been reported to exhibit such kind of behaviour. The biology of this speices has been studied in detail (see McLay, 1988; Morrisey, 1999).

**Distribution.**— New Zealand only.

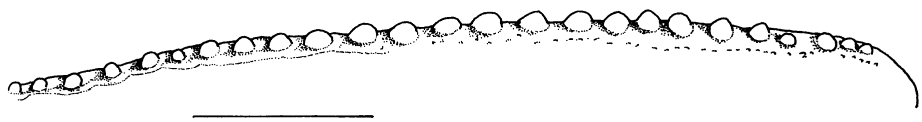


Figure 159. Infra-orbital ridge of *Austrohelice crassa* (After Sakai *et al.*, 2006).

## *Helicana* Sakai & Yatsuzuka, 1980

*Helice* (*Helicana*) Sakai & Yatsuzuka, 1980: 404.

*Helicana* – Sakai *et al.*, 2006: 26.

**Type species**.— *Helice tridens wuana* Rathbun, 1931, by original designation.

**Gender.**— Feminine.

**Diagnosis.—** Carapace subquadrangular, physiognomy very high, faint notch on posterolateral margins behind third anterolateral tooth. Infra-orbital ridge heteromorphic in males, isomorphic in females. Merus of third maxilliped nearly as broad anteriorly as long. Chelipeds equal in both sexes, chelae without a patch of setae at base of fingers; meral stridulating ridge present, well separated from anterior margin in males, absent in females. First three pairs of ambulatory legs with thick soft setae on carpi, propodi, fourth pair glabrous. G1 usually slim, tubular, bent distally, tip with corneous endpiece hardly discernible, genital pore subterminal, facing ventral side; palp small. Female gonopore with rounded, protruding operculum.

**Remarks**.— akai & Yatsuzuka described *Helicana* as a subgenus of *Helice* (1980: 404). It has been raised to a full genus due to the differences in the endophragmal system, together with the basic differences in the form of the first male pleopod, female gonopore form, and setae being resent on the ambulatory legs (see Sakai *et al.*, 2006). Sakai *et al.* (2006) have stressed that the identification of females in this genus is difficult, and it is only possible with the morphology of the female reproductive duct.

A recent study by Irawan *et al.* (1993) found that the genetic difference between *Helice tridens* and *H. japonica* is greater than expected. In fact, the difference is greater than the different species in the different genus. Thus, Irawan *et al.* (1993) treated them as two taxa in separate subgenera but within *Helice*. The differences between *Helice tridens* and *H. japonica* are even greater than the difference between *Helice tridens* and

*Chiromanthes dehanni*. These results further indicated that the Sesarminae might be polyphyletic within the *Helice* and *Chasmagnathus* genera, forming a separate lineage from the "*Sesarma*" line, as represented by *Chiromantes*. Their results supported Sakai & Yatsuzuka's (1980) recognition of *Helicana*. However, a valid comparison at the genetic level of the different species within the *Helice, Helicana* and *Chasmagnathus* with *Chiromantes* has to be carried out. This study is currently in progress (on going collaboration with H. T. Shih). Preliminary molecular data on the 16s and CO1 concurs with Sakai *et al.*'s (2006) report.

There are currently only three species found in this genus viz. *Helicana wuana* (Rathbun, 1931), *H. japonica* (Sakai & Yatsuzuka, 1980), and *H. doerjesi* Sakai, Türkay & Yang, 2006.

**Key to species in *Helicana***

1a. Infra-orbital ridge of male with 13 or more granules. -------------------------------- **2**

1b. Infra-orbital ridge of male with 10-12 granules. ------------------------ ***H. japonica***

2a. Propodus of ambulatory legs with a subdistal spine. ------------------- ***H. wuana***

2b. Propodus of ambulatory legs without subdistal spine. ------------------ ***H. doerjesi***

## *Helicana japonica* Sakai & Yatsuzuka, 1980

(Figure 160)

*Helice tridens wuana* – Sakai, 1939: 695 (part); Sakai, 1940: 51 (part); Kamita, 1941a: 89; Kamita, 1941b: 236, text-fig. 130; Kamita, 1941c: 233, 242; Tanaka, 1943: 7; Ono, 1959: 146, 147, text-fg. 1: Miyake, 1961: 24; Miyake *et al.*, 1962: 131; Tanaka, 1962: 33; Kim, 1970: 22; Baba & Moriyama, 1972: 49, 10 text-figs 5; Kim, 1973: 499, 658, fig. 225, pl. 48, fig. 175; Sakai, 1976: 671, text-fig. 368; Nakasone, 1977: 62, 65, 67.

*Helice tridens sheni* Sakai, 1939: 695 (part); Sakai, 1976: 671, fig. 368.

*Helice* (*Helicana*) *japonica* Sakai & Yatsuzuka, 1980: 408; Wada, 1995: 411.

*Helice japonica* – Miyake, 1983: 185, pl. 62, fig. 3; Tanaka, 1983: 58; Sakai & Nakano, 1983: 89; Takeda, 1983: 147 (col. fig.), 292; Yamaguchi *et al.*, 1987: 34, pl. 17 fig. 1; Irawan *et al.*, 1993: 101, figs. 1-2; Irawan & Kijima, 1994: 39; Yamanishi & Wada, 1996: 77, 105; Omori *et al.*, 1997: 279, text-figs. 2B, 3A, 4A, 5A, 7A, 8A, 9A, 10A, 11A, 12; Takeda *et al.*, 2000: 141.

*Helicana japonica* –Takeda *et al.*, 2000: 141; Sakai *et al.*, 2006: 32.

*Helice wuana* – Yamaguchi *et al.*, 1976: 41; Takeda, 1976: 158; Sato, 1995: 22 (not *Helice wuana* (Rathbun, 1931))

*Helice tridens sheni* – Matsuo, 1940: 5; Kikuchi & Miyake, 1978: 45 (not *Helice tridens sheni* Sakai, 1939)

**Materials examined.**— **Paratype** – 1 female (USNM-171513), Hakata Bay, Kyushu Island, Fukuoka, Japan, coll. K. Sakai, Apr. 1978. – **Others** – **China** – 1 male (17.6mm x 14.0mm), (ASIZ-no cat. number), Yantai, coll. Nov. 1932; 1 female (11.3mm x 8.0mm) (ASIZ-uncatalogued), Shenjiamen, Zhejiang Province, coll. 1974. – **Taiwan** – 1 female (11.0mm x 7.8mm) (NTOU-no cat. number), coll. J.F. Huang, no collection date; 1 female (14.4mm x 10.3mm), (NTOU-no cat. number), Wuchao, Taichung County, coll. J.F. Huang, 24 Apr. 1988.

**Diagnosis.**— Carapace quadrilateral; surface convex, sparingly setose, granulated, distinct wide, medial groove between epigastric regions; frontal margin sinuous . Anterolateral margin vaulted slightly upwards, with four teeth including orbital tooth, posterolateral margin divergent posteriorly. Third maxillipeds close with gap, an oblique row of short setae runs diagonally across from inner anterolateral angle of merus, to outer posterolateral angle of ishium. Infra-orbital ridge with 10-12 rounded tubercules, and usually one or two, vertically striated, tubercle-sized protuberances; in females infra-orbital ridge of 12-14 isomorphic granules. Chelipeds symmetrical in males, surfaces smooth, meral stridulatory ridge present. Ambulatory legs long, slender, first, second ambulatory legs covered with dense short setae, interspersed with long setae; merus with a sharp subdistal spine on the anterior margin; third ambulatory leg with pelt on anterior and dorsal halves of posterior surfaces of carpus and propodus; last ambulatory leg with carpus and propodus naked. G1 slender, stem incurved distally; palp obtuse, short and fused with stem along its whole length. Female gonopore operculate, sunken below sternal surface, narrow.

**Colour.**— The colour fresh specimens has not been documented, all the preserved specimens examined are brown in colour.

**Size.**— The largest male examined is 17.6mm x 14.0mm (ASIZ-no cat.number), but the largest female specimen examined is 11.3mm x 8.0mm (ASIZ-no cat. number).

**Habitat.**— It can be found in muddy, blackish sediment in the intertidal zone (Dai & Yang, 1991)

**Remarks.**— *Helicana japonica* can be easily discerned from its congeners by the following features a) the presence of only 10-12 granules present on the infra-orbital ridge of male (vs. presence of 15-17 granules in *H. wuana* and *H. doerjesi*); b) the presence of 12-14 isomorphic granules on the infra-orbital ridge of female (vs. 19-21 in *H. wuana* and 12-13 in *H. doerjesi*); c) the finger tip of chela being denticulate (vs. tips sharp in *H. wuana* and tips truncate and spoon-shaped in *H. doerjesi*); d) the carpus and propodus of the first and second pair of ambulatory legs have thick setae on anterior and dorsal half of posterior surfaces (vs. sparingly setose on carpus and propodus of third ambulatory leg in *H. wuana*, and very thickly setose in *H. doerjesi*), and e) the distal end of G1 is slender (vs. long and slender in *H. wuana*, and short and stout in *H. doerjesi*) (see Sakai *et al.*, 2006).

I had only managed to examine the paratype of this speices is the USNM.

**Distribution.**— Japan, Taiwan, China (Shangdong Province), South Korea

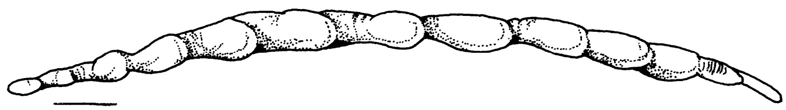


Figure 160. Infra-orbital ridge of *Helicana japonica* (After Sakai *et al.*, 2006).

## *Helicana wuana* (Rathbun, 1931)

(Figure 161)

*Helice tridens wuana* Rathbun, 1931: 92, pl. 7 fig. 8, pl. 8 fig. 17, pl. 9 figs. 25-26; Shen, 1932: 208, text-figs. 128-129; Kamita, 1936: 6, fig. 5, 7; Horikawa, 1940: 30; Shen, 1940: 74, 94. (part); Sakai, 1940: 51. (part); Kim, 1962: 54; Serène, 1968: 109; Kim, 1970: 22; Kim & Kim, 1982: 145, 153; Kim, 1985: 85. Lin, 1949: 30; Wu *et al.*, 1962: 205.

*Helice tridens wuana* – Kamita, 1936: 6, fig. 6 (not *Helice tridens wuana* Rathbun, 1931)

*Helice tridens sheni* Sakai, 1939: 694, fig. 123; Sakai, 1940: 51; Kamita, 1941a: 88; 941b: 234, text-fig. 129; 1941c: 235, 242; Kim, 1962: 54; Shen & Liu, 1963: 143; Serène, 1968: 109; Kim, 1970: 22; Kim, 1973: 498, 657, fig. 225, pl. 47, fig. 174; Sakai, 1976: 670, text-fig. 367; Kim & Kim, 1982: 145, 153; Lee & Koh, 1994: 83-85, 87, text-fig. 4-1, 4-2, 4-3, 4-4, 4-5.

*Helice wuana* – Sakai, 1940; Fan, 1976: 398; Dai *et al.*, 1986: 505. (part); Fukui *et al.*, 1989: 230, fig. 23; Shih *et al.*, 1991: 142; Wang & Liu, 1996a: 127, fig. 170; Wang & Liu, 1996b: 102; Hsueh, 1996: 97; Ho & Hung, 1997: 107; Jeng *et al.*, 1998: 67; Lin, 1998: 89; Wang & Liu, 1998: 87.

*Helice (Helice) tridens sheni* – Sakai & Yatsuzuka, 1980: 398.

*Helice tridens tridens* – Shen, 1932: 203, text-figs. 126-127, pl. 8 figs 1-2. [non *Ocypode* (*Helice*) *tridens* De Haan, 1835.]; Baba & Moriyama, 1972: 49-55, text-figs. 6-10, 16-20, 26-30, 36, 50-54, 60-64, 75, 87-96.

*Helice (Helicana) wuana* — Sakai & Yatsuzuka, 1980: 405, figs. 7, 16, 18; Dai *et al.*, 1986: 505, fig. 285: 1–2, pl. 71: 3; Dai & Yang, 1991: 554, fig. 285: 1–2, pl. 71: 3; Huang, 1994: 598; Wang & Liu, 1996c: 227.

*Helice sheni* – Dai *et al.*, 1986: 503, text-figs. 285/1-2, pl. 71 fig. 3.

*Helice tridens* – Irawan *et al.*, 1993: 101-110, figs. 1-2.

*Helice tridens tridene* – Zhou & Sun, 1986: 226 (wrong spelling).

*Helice tridens* var. – Sakai, 1931: 130 (incomplete name).

*Helice* sp.— Ng *et al.*, 2001: 45, 53, fig. 8h.

*Helicana wuana* – Sakai *et al.*, 2006: 34.

**Materials examined.**— **Holotype** – 1 male (USNM-61874), Wenzhou, Zhejiang Province, China, coll. H.W. Wu, no collection date. – **Paratypes** – 1 male, 1 female (USNM-61874), Wenzhou, Zhejiang Province, China, coll. H.W. Wu, no collection date. – **Others** – **China** – 3 females (12.4-18.5mm x 9.5-14.5mm) (QIH-no cat. number), Qikou, coll. 22 Jul. 1951. – **Taiwan** – 3 males (16.0-23.8mm x 12.9-19.5mm), 2 females (13.7-16.3mm x 10.6-12.8mm) (NMNS-uncatalogued), Korea, leg. H.T. Shih, no collection date; 2 males (17.0-18.0mm x 14.0-15.3mm), 7 Jun. (2.5-7.5mm x 1.2-6.0mm) (NMNS-004657-00107), Wuzaiwei, coll. H.T. Shih & H.T. Lung, 3 May 2003; 1 male (24.4mm x 19.7mm) 1 female (ovigerous) (15.3mm x 12.3mm), (TMCD-no cat. numbern), Sheng Gang, Zhanghua County, coll. J.C. Lin, 15 Dec. 1990; 1 female (20.7mm x 15.7mm), (TMCD-no cat. number), De-Zhi-Kou river, Ilan County, coll. 20 Mar. 1991; 3 males (15.6-21.9mm x 12.7-18.4mm), (TMCD-no cat. number), Sheng Gang, Zhanghua County, coll. C.H. Wang, no collection date; 1 female (13.8mm x 10.7mm) (TMCD-2641), Baoli rivermouth, Checheng, Pingtung County, coll. C.H. Wang, 15 Feb. 1990; 1 male (10.5mm x 8.0mm) (TMCD-2588), Shenggang, coll. 30 Aug. 1988; 6 males (7.4-14.4mm x 5.8-11.2mm), 4 females (12.6-14.5mm x 9.8-11.0mm) (ZRC-uncatalogued), Tanchienxi, rivermouth, Hshinchu, coll. N.K Ng & J. Lai, 29 Nov. 2003.

**Diagnosis.**— Carapace quadrilateral; surface convex, sparingly setose, granulated, distinct wide, medial groove between epigastric regions; frontal margin sinuous . Anterolateral margin vaulted upwards, with four teeth including orbital tooth. Infra-orbital ridge of males with 13-15 granules and a confluent striated crest about 0.4 times infra-orbital ridge length, female infra-orbital ridge with 21-22 granules, which innermost 10-11 are more closely set together. Chelipeds asymmetrical in males, surfaces smooth, stridulatory ridge present on the merus of chelipeds; fingers largely gaping; female chelipeds equal. Ambulatory long, slender, carpi, propodi of first, second legs with dorsal margin covered with dense short setae, interspersed with long setae; merus with a sharp subdistal spine on anterior margin; third ambulatory leg with carpus, propodus setose on dorsal parts of anterior surfaces; fourth ambulatory leg without setae. G1 slender, stem incurved distally; suture of sperm channel beginning on dorsal side. Female gonopore operculate, broadly oval, sunken below surface of sternum.

**Colour.**— The colour of fresh specimens has not been documented, but all the preserved specimens examined are orange-reddish brown in colour.

**Size.**— The largest male specimen examined is 24.4 x 19.7mm (TMCD-no cat. number), while the largest female specimen examined is 21.9mm x 18.4mm (TMCD-no cat. number).

**Habitat.**— It can be found in sandy mud flats (H.T. Shih, pers. comm.).

**Remarks.**— The species can be easily recognized by the morphology of the male infra-orbital ridge, with 13-15 free granules, and the female ridge is also heteromorphic and bearing 20 or 21 protuberances. This species has been discussed in detail by Sakai & Yatsuzuka (1980) and Sakai *et al.* (2006). Hence, there is no need to treat it again here.

**Distribution.**— China (central to northern coast), Korea, Taiwan.

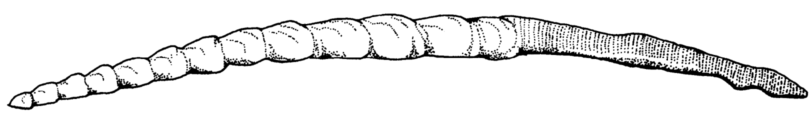


Figure 161. Infra-orbital ridge of *Helicana wuana*.(After Sakai *et al.*, 2006).

## *Helicana doerjesi* Sakai, Türkay & Yang, 2006

(Figure 162)

*Helice tridens wuana* – Sakai, 1939: 695,732 (part); 1940: 51. (part); Shen, 1940: 74, 94. (part); Lin, 1949: 30; Wu *et al.*, 1962: 205.

*Helice tridens sheni* – Lin, 1949: 30; Sakai, 1976: 670 (part).

*Helice wuana* – Dörjes, 1978: 121; Dai & Song, 1986: 60; Dai *et al.*, 1991: 505 (part). text-figs. 285/3-4, pl. 71 fig. 4; Fukui *et al.*, 1989: 230, 234, text-fig. 23 (not *Helice tridens wuana* Rathbun 1931).

*Helice (Helicana) wuana* – Sakai & Yatsuzuka, 1980: 405 (part).

*Helice (Helicana) japonica* – Dai & Yang, 1991: 555, text-fig. 286 (1-2) (part).

*Helicana doerjesi* Sakai, Türkay & Yang, 2006: 29.

**Materials examined.**— **Paratypes** – 1 female (IZAS-uncatalogued), Putuo, Zhoushan, Zhejiang Province, China, coll. Jul. 1955; 1 male (BNHM-84159), Dinghai, Zhoushan, Zhejiang Province, China, coll. 4. Nov. 1983. – **Others** – 5 males (13.0-23.9mm x 10.0-19.8mm), 2 females (22.4-23.0mm x 18.0-19.0mm) (NTOU-no cat. number), Sanshen bridge, Hsinchu, coll. J.F. Huang, 26 Sep. 1987; 1 male (18.2mm x 15.4mm) (NTOU-no cat. number), Taiwan, coll. H.P. Ho, no collection date; 1 male (24.0mm x 20.8mm) (NTOU-no cat. number), Taiwan, coll. H.P. Ho, no collection date; 1 male (16.7mm x 13.0mm) (TMCD-2829), Zhuyuan, Taipei County, coll. J.H. Wang, no collection date; 1 male (22.4mm x 18.0mm) (TMCD-2261), Tamsui, Taipei County, coll. J.H. Wang, 7 Jun. 1987; 1 female (20.7mm x 15.6mm) (TMCD-2704), Dezhikou river, I-Lan County, coll. 20 Mar. 1990; 1 male (24.4mm x 19.7mm), 1 female (ovigerous) (15.3mm x 12.3mm) (TMCD-2695), Sheng Gang, Zhanghua County, coll. J.C. Lin, 15 Dec. 1990.

**Diagnosis.**— Carapace quadrilateral; surface convex, punctate, distinct wide, medial groove between epigastric regions; frontal margin sinuous. Anterolateral margin vaulted slightly upwards, with four teeth including orbital tooth, posterolateral margin divergent posteriorly. Third maxillipeds close with gap. Infra-orbital ridge with 14-15 rounded tubercules, plus a striated ridge which is 0.22 times the infra-orbital length; in females, infra-orbital ridge of about 10 isomorphic granules. Chelipeds asymmetrical in males, surfaces smooth, meral stridulatory ridge present. Ambulatory legs long, slender, first two pairs of ambulatory legs covered with dense short setae, interspersed with long setae; merus with no subdistal spine on anterior margin; third ambulatory leg with pelt on anterior, dorsal halves of posterior surfaces of carpi, propodi; last ambulatory leg with carpus, propodus naked. G1 elongate, terminal part of stem strongly curved towards dorsal side, female gonopore operculate, sunken below sternal surface, narrow.

**Colour.**— The colour fresh specimens has not been documented, all preserved specimens examined are orange-reddish brown in colour.

**Size.**— The largest male examined is 24.4mm x 19.7mm (TMCD-2695), and the largest female specimen examined is 20.7mm x 15.6mm (TMCD-2704).

**Habitat.**— It can be found  in muddy, blackish sediment in the intertidal zone (J.H. Wang, pers. comm.).

**Remarks.**— The present species is very closely allied to *H. wuana* in adult morphology, but it can be easily discerned in the following features: a) the carapace is narrower (vs. broader carapace in *H. wuana*); b) the anterolateral margin is convergent anteriorly (vs. subparallel margin in *H. wuana*); c) the fingers of chelipeds have sharp tips (vs. fingers of chelipeds spoon-shaped in *H. wuana*), and d) the meri of the ambulatory legs are without a subdistal spine (vs. distinct subdistal spine in *H. wuana*).

I had only managed to examine the parartype, as the holotype is in SFM.

**Distribution.**— Taiwan, China (Zhejiang Province to Guangxi Province).

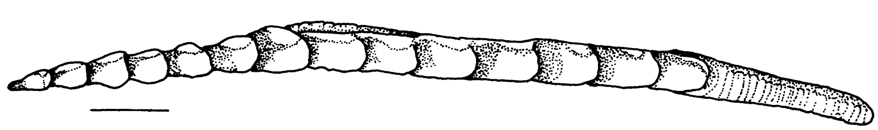


Figure 162. Infra-orbital ridge of *Helicana doerjesi* (After Sakai *et al.*, 2006).

## Genus *Helograpsus* Campbell & Griffin, 1966

*Helograpsus* Campbell & Griffin, 1966: 134; Anonymous, 1984: 118**;** Bennett, 1987: 231; Davey, 1988: 55; Jones & Morgan 1994: 187; Davie *et al.*, 1998: 48; Davie, 2002: 207.

*Helice* – Hale, 1927: 177, fig. 177; Tweedie, 1942: 19, fig. 5 (not *Helice* De Haan, 1835).

*Chasmagnathus* – Haswell, 1882: 550, fig. 2, pl. 33; Whitelegge, 1889: 229 (not *Chasmagnathus* De Haan, 1835).

**Type species.—** *Chasmagnathus haswellianus* Whitelegge, 1889, by original designation.

**Gender.**— Masculine.

**Diagnosis.** — Carapace quadrangular, broader than long; dorsal surface smooth; regions not well defined. Frontal margin slightly deflexed, straight. Anterolateral margin vaulted, subcristate with two teeth including external orbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxillipeds short, stout. Small, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Chela asymmetrical, inner surface of chela with granules; outer surface of pollex and manus with tufts of long, stiff setae, a patch of short stiff setae near posterior margin of manus; fingers as long as palm. Ambulatory legs with short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular with all segments freely moveable (six somites plus telson).

**Remarks.**— The genus was established by Campbell & Griffin (1966) for one species, *Chasmagnathus haswellianus* Whitelegge, 1889. This species only occurs in Australia.

Based on the descriptions provided by Campbell and Griffin (1966), the genus is closely allied to *Cyclograpsus* and *Paragrapsus* in the form of the orbit of the eye, the frontal margin of the carapace and epistome. However, this genus is different from *Paragrapsus* as the carapace physiognomy of *Helograpsus* is far more inflated (vs. less inflated in *Paragrapsus*). This genus is also different from *Cyclograpsus* as the lateral margins of the carapace in *Helograpsus* is much more vaulted (vs. less so in *Cyclograpsus*).

This is a monotypic genus.

This species can be found in abundance in certain parts of Australia. It would be worthwhile to study this genus in detail, as this species has been reported to create different types of very complicated burrowing systems on different substrates (Katrak & Dittmann, 2006), and it has reported that the construction of the tunnels for mosquito control has apparently affected the population of this taxa (Breitfuss *et al.*, 2004; Webb & Russell, 2005).

## *Helograpsus haswellianus* (Whitelegge, 1889)

(Figure 163A-F)

*Chasmagnathus convexus* – Haswell, 1882: 550, fig. 2, pl. 33 (not *Chasmagnathus convexus* De Haan, 1835)

*Chasmagnathus haswellianus* – Whitelegge, 1889: 229.

*Helograpsus haswellianus* – Campbell & Griffin, 1966: 135; Anonynous, 1984: 118**;** Bennett, 1987: 231; Davey, 1988: 55; Jones & Morgan 1994: 187; Davie *et al.*, 1998: 48; Davie, 2002: 207.

*Helice haswellianus* – Hale, 1927: 177, fig. 177; Tweedie, 1942: 19, fig. 5.

**Materials examined.**— 1 male (21.0mm x 17.0mm), 1 female (16.1mm x 12.6mm) (ZRC 1995.951), Jackson's Creek, South East Queensland, Australia, coll. Campbell et al., 12 Oct. 1972; 6 males (11.8-17.0mm x 8.9-13.6mm), 1 female (14.4mm x 11.6mm), 2 females (ovigerous) (13.0-13.4mm x 9.9-10.5mm) (ZRC 1965.7.26.213-221), south coast of Tasmania, Australia, coll. Mupt, 1940-1941; 5 males (8.8-12.3mm x 7.1-10.3mm), 1 female (14.8mm x 12.2mm) (QM-W23982), Dunwich, North Strahbroke Island, south east Queensland, Australia, coll. P. Davie *et al.*, 18-19 Aug 1997.

**Diagnosis.**— Carapace subrectangular, distinctly broader than long, surface convex, punctate, granulated; frontal margin sinuous. Anterolateral margin vaulted longidutinally, with two lobes including orbital lobe. Third maxillipeds close with gap. Infra-orbital ridge with 9-17 rounded granules in male. Chelipeds asymmetrical in males. Ambulatory legs long, slender; merus with a sharp subdistal spine on anterior margin, one or more sharp spines on posterior margins of merus. G1 long, slender. Female gonopore unknown. (Modified from Campbell & Griffin, 1966).

**Colour.**— The colour of fresh specimens is reddish brown (Davie *et al.*, 1998), and the colour of preserved materials has not been documented.

**Size.**— The largest male specimen reported has a carapace width of 25mm, and the largest female documented is 18mm in fcarapace width (Campbell & Griffin, 1966).

**Habitat.**— This species is found on the intertidal zone with sandy muddy substrate (Davie *et al.*, 1998)

**Remarks.**— This species is endemic to eastern and southern Australia, and is found in abundance. There is not much publication on the biology of this animal except the larval development (Fielder & Greenwood, 1985), and its burrow morphology (Breitfuss *et al.,* 2004; Webb & Russell, 2005).

**Distribution.**— Australian (New South Wales, Queensland, South Australia, Tasmania, Victoria).

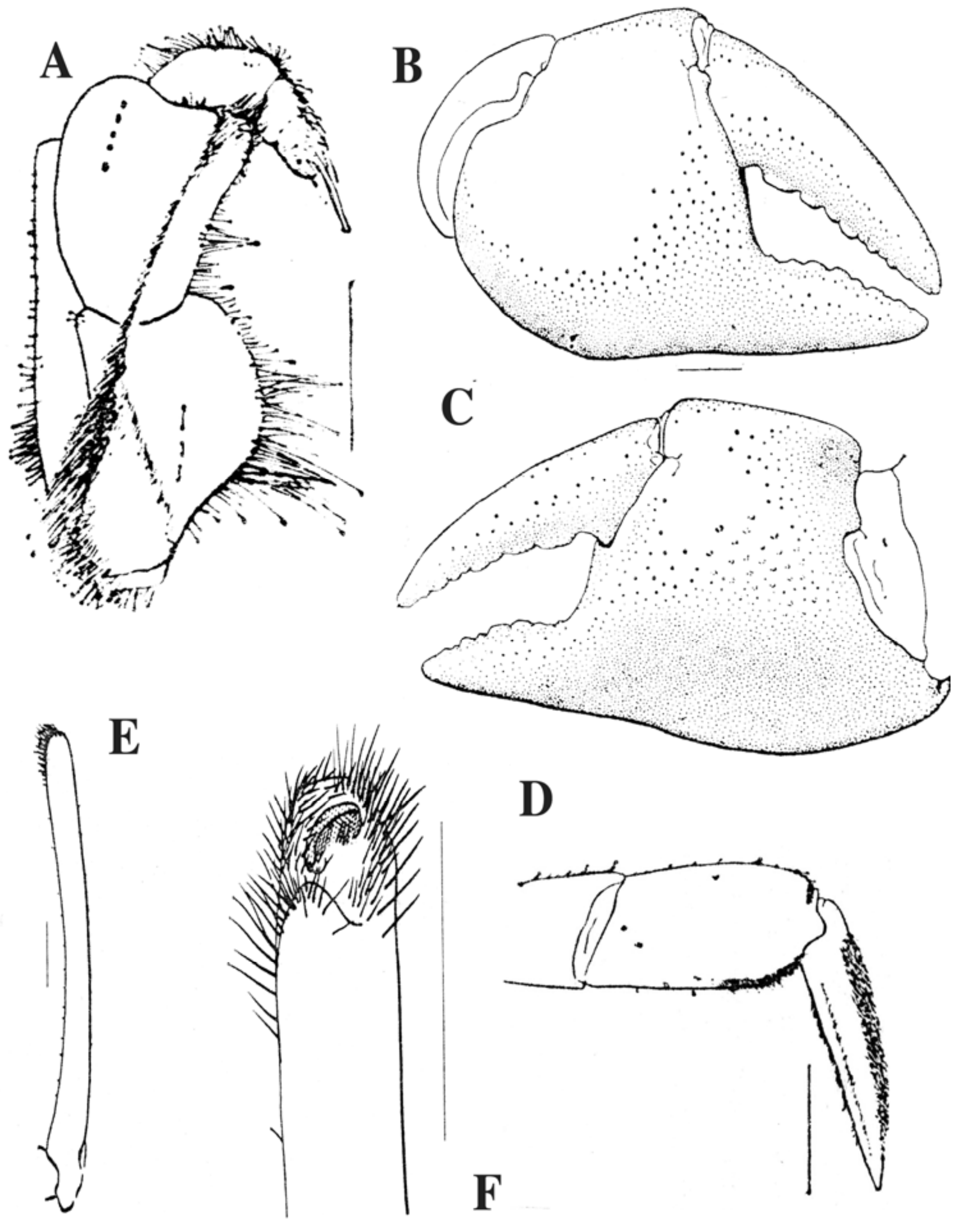



Figure 163. *Helograpsus haswellianus* (Whitelegge, 1889). A) third maxiliiped; B) outer view of chela; C) inner view of chela; D) last ambulatory leg; E) G1; F) distal end of G1. (After Campbell & Griffin, 1966).

## Genus *Metaplax* H. Milne Edwards, 1852

*Metaplax* H. Milne Edwards, 1852: 161; de Man, 1887: 153; Alcock, 1900: 430; Tesch, 1918: 115; Balss, 1922: 153; Sakai, 1939a: 548, 688; Sakai, 1939b: 648, 698; Sakai, 1976: 673; Dai *et al.*, 1986: 507; Dai & Yang, 1991: 555; Davie & Nguyen, 2003: 379.

*Rhaconotus* Gerstaeker, 1856: 142; Kingsley, 1880: 213.

**Type species.**— *Metaplax distincta* H. Milne Edwards, 1852, designation by Davie & Nguyen (2003).

**Gender.**— Feminine.

**Diagnosis.**— Carapace quadrangular, broader than long; dorsal surface setose, punctate; regions well defined, slightly convex. Frontal margin, narrow, slightly convex, straight. Anterolateral margin subcristate with four teeth including orbital tooth. Posterolateral margins not sharply demarcated from anterolateral marginn, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit Infraorbital ridge with heteromorphic or isomorphic granules. Third maxilliped short, stout. Large, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Inner surface of chela with granules; a patch of short stiff setae near posterior margin of manus; fingers as long as palm. Ambulatory legs with short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen broadly triangular with all segments freely moveable (six somites plus telson).

**Remarks.**— Currently, the genus *Metaplax* H. Milne Edwards, 1852, contains 11 species viz. *M. distincta* H. Milne Edwards, 1852 (type species), *Metaplax crenulata* (Gerstaecker, 1856), *M. dentipes* (Heller, 1865), *M. elegans* de Man, 1888 (= *M. crassipes* de Man, 1892), *M. indica* H. Milne Edwards, 1852, *M. intermedia* de Man, 1888, *M. longipes* Stimpson, 1858, *M. occidentalis* Pretzmann, 1971 (originally described as a subspecies of *M. indica* but here raised to species rank here, see later), *M.*

*sheni* Gordon, 1931, *M. takahashii* Sakai, 1939, and *M. tredecim* Tweedie, 1950. *M. crenulatus* (Gerstaecker, 1856) has been transaferred to its own genus (see later).

The genus *Metaplax* can be broadly divided into two main groups by the number of granules or tubercules found on the infra-orbital ridge viz. a) one group with species with more than 25 granules or tubercules like *M. elegans*, *E. intermedius*, *M. distincta*, and *M. dentipes*, and b) the other group containing the rest of the species that have less than 25 tubercules on the infra-orbital ridge. There are, however, not enough other morphological characters to divide them into two separate genera. The taxonomy of this genus will be re-appraized as the identity of many species within the genus is uncertain. For example, there is great confusion over the identity of *M. longipes* and *M. takahashii* (see Davie & Nguyen, 2003). *M. elegans* specimens collected from different parts of China, and Taiwan and Singapore seems to have different forms of carapaces, third maxillipeds, endostomes, and ambulatory legs. These differences are probably not intra-specific differences (see below).

Gerstaecker (1856) estesblished the genus *Rhaconotus* for the species, *Rhaconotus crenulatus*. However, the genus name is already occupied by *Rhaconotus* Ruthe, 1854, a wasp from the family Braconidae, Order Hymenoptera. In any case, since de Man (1888) later synonymised *Rhaconotus* with *Metaplax* (see below), and almost every worker has accepted this, there has not been no need to replace Gerstaecker's (1856) name. However, it must be noted that *Metaplax crenulata* is distinctly different from the other *Metaplax* sensu stricto, and it will be transferred to a new genus in this report (see below).

Although *Metaplax* is a very common genus in mudflats, and seems to be a very common prey for birds and other organisms, there is very little known about the biology of its constituent species. The presence of the stridulatory ridge on the infra-orbital ridge indicates that these organisms could have made use of sound for communication, and the presence of the strong chelipeds, perhaps, also has the same function as the large chelipeds in male *Uca*. Pretzmann (1971) reported the courtship behaviour of *Metaplax occidentalis*, which showed that the male crabs actually wave the long and stout chelipeds, but unlike the *Uca*, both chelipeds are used.

**Key to species in *Metaplax***

1a. Carapace rectangular. Infra-orbital ridge with more than 25 granules. ------- **2**

1b. Carapace rectangular. Infra-orbital ridge with less than 25 granules. --------- **5**

2a. Infra-orbital ridge with isomorphic granules. ----------------------------------- **3**

2b. Infra-orbital ridge with heteromorphic granules. -------------------------------- **4**

3a. Infra-orbital ridge with 40-50 granules in males. Palm of cheliped as long as broad. - **--------------------------------------------------------------------------- *M. intermedius***

3b. Infra-orbital ridge with 50-60 granules in males. Palm of cheliped long than broad. - **------------------------------------------------------------------------- *M. elegans***

4a. Infra-orbital ridge of male with 20-25 granules, eight to ten granules below orbit. --- **---------------------------------------------------------------------- *M. distincta***

4b. Infra-orbital ridge of male with 25-30 granules, six granules below orbit. ------------- **------------------------------------------------------------------------ *M. dentipes***

5a. Carapace with three distinct teeth on anterolateral margin including orbital tooth. --- **-------------------------------------------------------------------------------- *M. tredecium***

5b. Carapace with four or more teeth on anterolateral margin including orbital tooth. ---- **---------------------------------------------------------------------------------------------- 6**

6a. Carapace with five distinct teeth on anterolateral margin including orbital tooth. -- **7**

6b. Carapace with four distinct teeth on anterolateral margin including orbital tooth. -- **9**

7a. Carapace with length to width ratio of 1.5, infra-orbital ridge with 10 or more granules. ------------------------------------------------------------------------------ **8**

7b. Carapace with length to width ratio of 1.4, infra-orbital ridge with 8 elongated granules, length to width ratio of propodus of leg 4 is 3.0. -------------- ***M. takahashii***

8a. Infra-orbital ridge with seven large, three small granules. Length to width ratio of propodus of leg 4 is 4.6. ------------------------------------------------------- ***M. neosheni***

8b. Infra-orbital ridge with 15-19 granules. Length to width ratio of propodus of leg 4 is 4.2. ---------------------------------------------------------------------------------- ***M. sheni***

9a. Carapace with length to width ratio of 1.3, infra-orbital ridge with 15-18 granules. Length to width ratio of P4 is 3.5. -------------------------------------- ***M. gocongensis***

9b. Carapace with length to width ratio of 1.4, infra-orbital ridge with less than 15 granules. Length to width ratio of P4 is about 4.0. ------------------------------------- **10**

10a. Infra-orbital ridge with four to five elongated granules below orbit. Ambulatory legs and chelipeds broad, stout. ------------------------------------------------------------ **11**

10b. Infra-orbital ridge with seven rounded granules below orbit. Ambulatory legs and chelipeds very long, slender. ---------------------------------------------------- ***M. longipes***

11a. Infra-orbit ridge with four or five elongated granules, followed by two large and three small granules. ------------------------------------------------------- ***M. indica***

11b. Infra-orbit ridge with five elongated granules, followed by five large, two oval and three small granules. ------------------------------------------ ***M. occidentalis***

## *Metaplax distincta* H. Milne Edwards, 1852

(Figure 164A-C)

*Metaplax distinctus* H. Milne Edwards, 1852: 162, pl. 4, fig. f; Stimpson, 1858: 97; 1907: 100; Nobili, 1903: 23; Naiyanetr, 1998: 98.

*Metaplax distincta* – de Man, 1888: 158, pl. 10, fig. 7-9; Henderson, 1893: 391; Alcock, 1900: 432; Tesch, 1918: 117; Krishnan & Kannupandi, 1989: 633.

**Materials examined.**— 1 male (15.5mm x 11.0mm) (ZRC 2001.2330), Kampuan mangrove, Ranong, Thailand, coll. P. Clark, 18 Nov. 2001.

**Diagnosis.**— Carapace rectangular, surface slightly convex, punctate, granulated; frontal margin sinuous. Anterolateral margin with four teeth including orbital tooth. Third maxillipeds close with gap. Infra-orbital ridge with 25-30 small lobulated granules in male, first 8-10 under orbit, the rest decreasing in size. Cheliped symmetrical in males, stridulatory ridge present on merus of chelipeds. Ambulatory legs long, slender, merus with a sharp subdistal spine on anterior margin, one or more sharp spines on posterior margins of merus. G1 long, slender.

**Colour.**— The colour of fresh specimens is reddish brown (T. Kannupandi & S. Ravichandran, pers. comm.) but preserved specimens are brown in colour (ZRC 2001.2330).

**Size.**— The largest male specimen examined is can grow up to 16.9mm x 11.5mm (H. Milne Edwards, 1852: 162), and size of largest female is only about 15mm by 10mm (T. Krishnan, T. Kannupandi & S. Ravichandran, pers. comm.).

**Habitat.**— It can be found on the intertidal zone with sandy muddy substrate (P. Clark & S. Ravichandran, pers. comm.).

**Remarks.**— Henri Milne Edwards described *M. distincta* and *M. indica* based on specimens collected from India. Since he had only provided figures for *M. distincta*, Davie & Nguyen (2003) selected *M. distincta* as the type species for the genus. Unfortunately, both the type specimens of both *M. distincta* and *M. indica* could not be located when the present author went to the MNHN to check type specimens in the years 1996 and 1999. They are believed to be lost (see also Davie & Nguyen, 2003).

*Metaplax distincta* has been reported to be a very common species found in the mangroves of the tropical India (Krishnan & Kannupandi, 1989; S.A. Fernando & O. Fernando, pers. comm.), but during her field trip to Tamil Nadu in Year 2001, the author failed to collect any specimen. It appers that the species has become rather uncommon in the last two decades, probably due to mangrove destruction (S.A. Fernado & T. Kannupandi, pers. comm.). Krishnan & Kannupandi published the larval development of *M. distincta* in 1989, unfortunately, they did not keep the female specimen or any other specimens after their studies so their identification cannot be verified (T. Kannupandi, pers. comm.).

**Distribution.**— India (Bombay), Thailand.

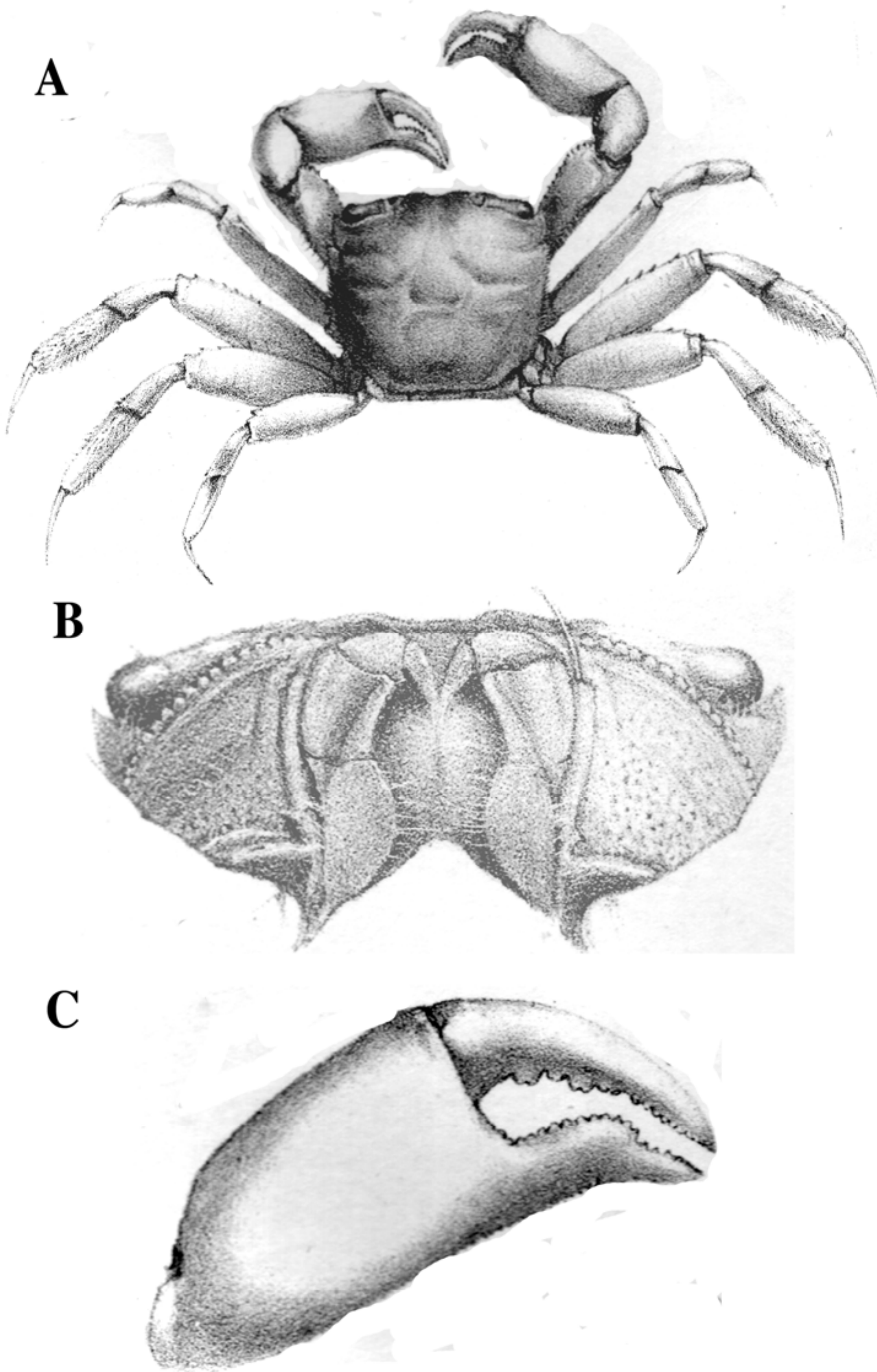



Figure 164. *Metaplax distinctus* H. Milne Edwards, 1852. A) dorsal view; B) frontal view; C) outer view of chela. (After de Man, 1888).

## *Metaplax elegans* de Man, 1888

(Figures 165; 166A-C)

*Metaplax elegans* de Man, 1888: 164, pl. 11: 4–6; Fukui *et al.*, 1989: 230, fig. 25; Shih *et al.*, 1991: 142; Kuo, 1995: 64; Wang & Liu, 1996a: 128, figs. 170–172; Wang & Liu, 1996b: 103; Fransen *et al.*, 1997: 124; Ho & Hung, 1997: 108; Jeng *et al.*, 1998: 68; Naiyanetr, 1998: 98; Wang & Liu, 1998: 103; Ng & Sivasothi, 1999: 73; Ng *et al.*, 2001: 45; Sastrangara *et al.*, 2003: 1.

**Materials examined.**— **Holotype** – 1 male (RMNH-D-13), Burma, Anadman Sea, Mergui Archipelago, coll. 25 Nov. 1881 – 13 Apr. 1882, J. Anderson. – **Others** – **China** – 1 male (8.3mm x 5.6mm) (QIH-no cat. number), Guanghai, Guangdong Province, coll. 29 Mar. 1958; 1 male (14.0mm x 8.6mm) (QIH-no cat. number), Beigang, Hainan Island, coll. 12 Jan. 1960; 1 male (9.0mm x 6.2mm), Xiamen, Fujian Province, coll. 7 Jun. 1958; 1 male (11.8mm x 8.0mm) (QIH-no cat. number), no data, coll. 7 Jun. 1958; 1 male (13.7mm x 9.2mm) (QIH-no cat. number), Xiongshan, Hainan Island, coll. 7 Jun. 1958. – **Taiwan** – 2 males (11.0-11.3mm x 7.2-7.4mm), 2 females (11.6-11.7mm x 7.7-7.8mm) (TMCD-uncatalogued), Bei-Men, Tainan County, coll. C.H. Wang, 9 Nov. 1988; 5 males (7.4-12.5mm x 4.8-9.9mm), 3 females (7.2-12.8mm x 5.0-6.5mm) (NMNS-uncatalogued), Fu-Long river mouth, coll. 15 Nov. 1993; 2 males (12.0-14.5mm x 7.7-9.5mm) (NTOU-uncatalogued), coll. M.S. Hung, 21 Aug. 1998; 6 males (8.7-15.4mm x 7.9-10.1mm), 4 females (11.0-20.0mm x 7.5-18.4mm) (NMNS-001491-00053), Bazhang river, coll. J.D. Lee, 21 Oct. Oct. 1993; 5 males (7.4-12.9mm x 12.5-17.9mm), 3 females (7.2-12.8mm x 5.0-8.5mm) (NMNS-uncatalogued), Houlong rivermouth, coll. 15 Nov. 1993. – **Singapore** – 1 male (14.1mm x 9.5mm), 1 female (ovigerous) (9.3mm x 6.5mm) (ZRC-uncatalogued), Kranji Beach, coll. May 1996; 1 female (ovigerous) (6.9mm x 4.3mm) (ZRC 1993.411), Sungei Buloh, coll. 15 Aug. 1992. – **Thailand** – 4 males (7.4-10.4mm x 5.1-6.8mm) (ZRC 1993.212.217), Phuket Island, Thailand, coll. S. Harminto, Jun. 1987.

**Diagnosis.**— Carapace rectangular, broader than long, surface convex, punctate, granulated; frontal margin sinuous . Anterolateral margin four teeth including orbital tooth. Third maxillipeds close with gap. Infra-orbital ridge with 50-60 small, rounded granules in males, 35-40 in females. Chelipeds symmetrical in males, stridulatory ridge present on merus of chelipeds. Ambulatory legs short, broad; merus with a sharp subdistal spine on anterior margin, one or more sharp spines on posterior margins of merus. G1 long, slender; female gonopore operculate, circular in shape.

**Colour.**— The colour of the fresh specimens are bright reddish brown in colour (Wang & Liu, 1998), and all preserved specimens are brown in colour.

**Size.**— The largest male specimen examined is 14.5mm x 9.5mm (NTOU-uncatalogued), and the largest female specimen examined is 20.0mm x 18.4mm (NMNS-001491-00053).

**Habitat.**— It can be found  in mud burrows in mangroves river mouths (Wang & Liu, 1996a; 1996b; 1998).

**Remarks.**— This species is easily spotted in its natural habitat due to its distinctive purplish coloration (Wang & Liu, 1996a; 1996b, 1998). The species has not been well studied even though it is one of the most common crabs that can be found in mangrove mudflats in the Tropics.

*M. elegans* is different from the most of the other *Metaplax* species in the form of the infra-orbital ridge. Most of the the species have very few, large granules, which are usually rounded in shape or elongated in shape on the infra-orbital ridge; but *M. elegans* has about 50 to 60 small, isomorphic, rounded granules on the ridge. This sole difference does not warrant the separation of *M. elegans* into its own genus, as the overall morphology still fits the broader definition of *Metaplax*.

*Metaplax elegans* has been collected Taiwan, southern Mainland China (Guangxi Province, Zhejiang Province, and Fujian Province) and Singapore, and the various populations differ slightly in the forms of the third maxilliped, endostome, ambulatory legs and G1s. These characters are, however, not strong enough to separate each morphotype into their own new species. It is very probable that *M. elegans* is a species-group complex and will need more thorough study. However, more material still needs to be collected to ascertain if the differences observed are discrete or part of a cline.

**Distribution.**— Taiwan, Mergui, China, Sarawak, Singapore, Thailand.

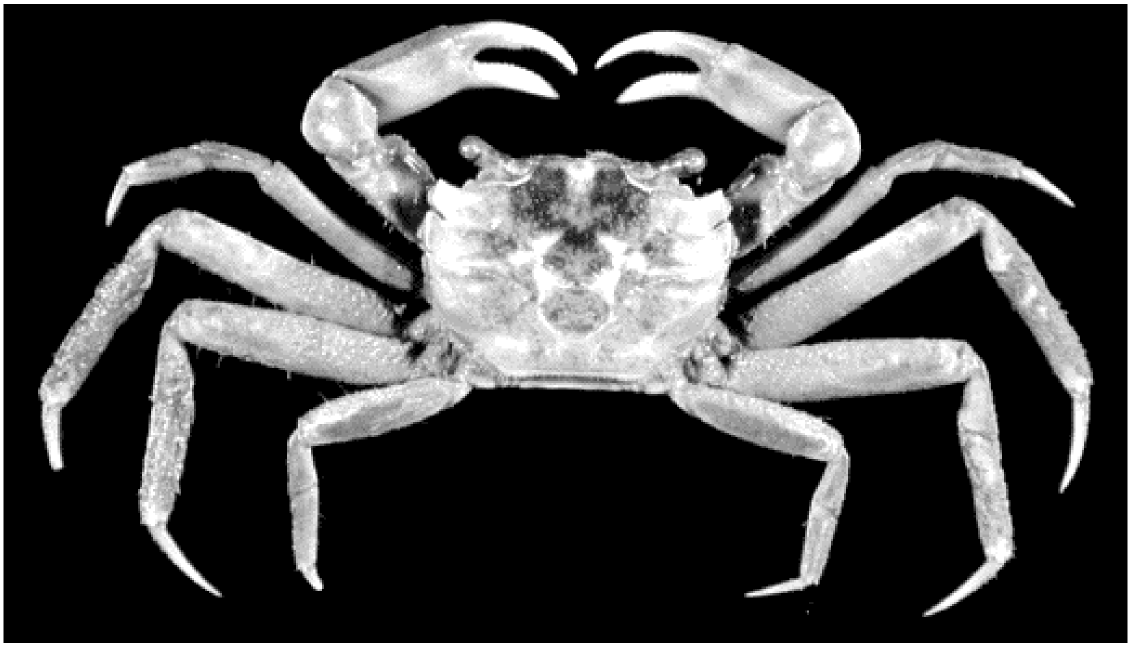


Figure 165. *Metaplax elegans* de Man, 1888, male, 14.1mm x 9.5mm (ZRC-uncatalogued). Dorsal view.

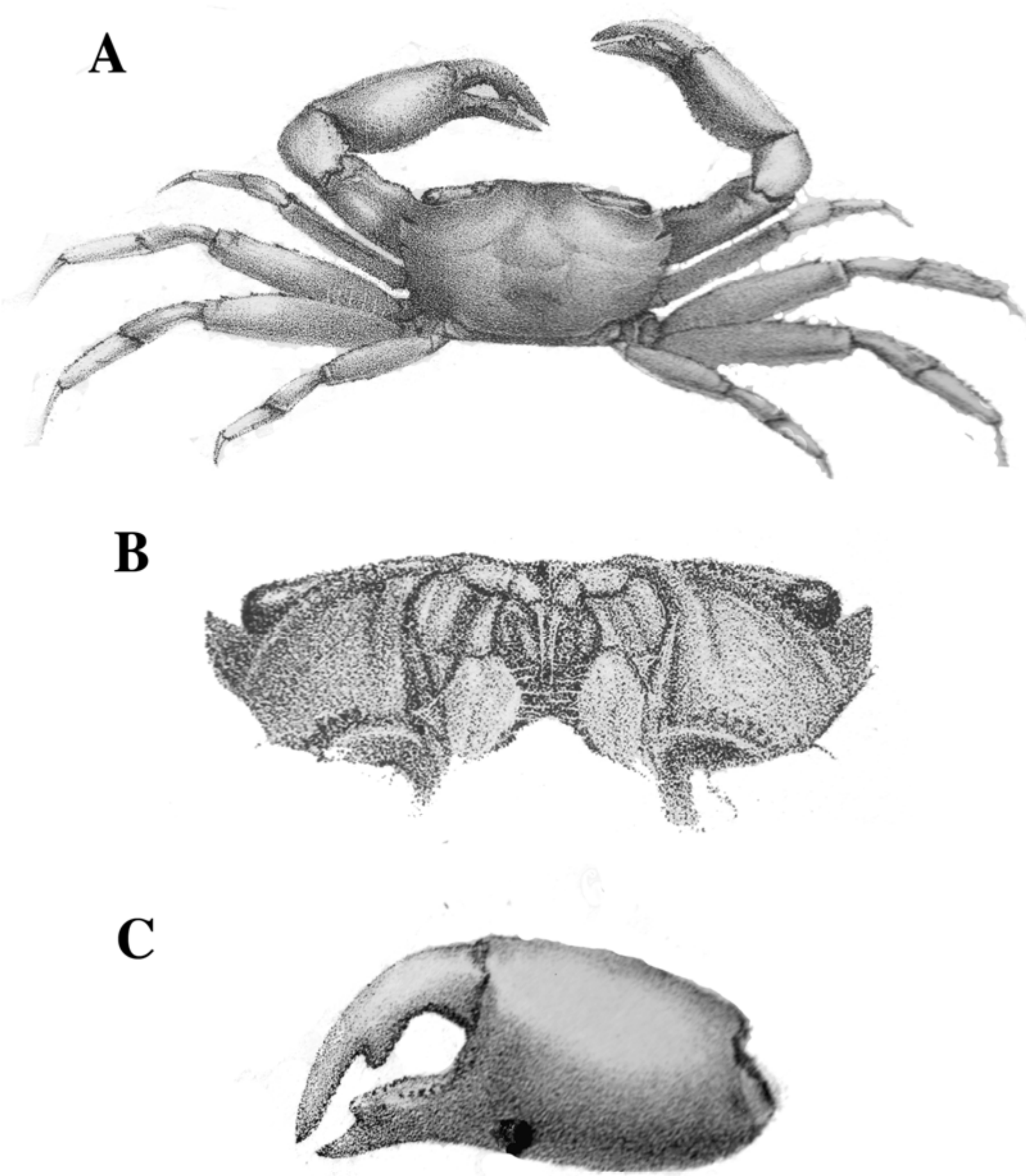



Figure 166. *Metaplax elegans* de Man, 1888. A) dorsal view; B) frontal view; C) outer view of chela. (After de Man, 1888).

### *Metaplax longipes* Stimpson, 1858

(Figure 167)

*Metaplax longipes* Stimpson, 1858: 97; Koelbel, 1898: 569; Stimpson, 1907: 99; Tesch, 1918: 116; 1940a: 236; 1940b: 95; Lee, 2001: 115; Wang & Liu, 1996c: 227; Naiyanetr, 1998: 98; Ng *et al.*, 2001: 53; Davie & Nguyen, 2003: 384.

**Materials examined.**— **Neotype** – 1 male (18.7mm x 13.9mm) (QIH-no cat. number), Nandukou, Haikou, Hainan Island, coll. 21 May 1958. – **Others** – **China** – 9 males (12.5-22.4mm x 8.8-15.6mm), 1 female (15.5mm x 11.3mm), 5 females (ovigerous) (14.0-19.1mm x 10.6-13.3mm) (BNHM-C-02369), Shenxingmen, Zhoushan, Zhejiang Province, coll. 1934; 6 males (7.9-16.0mm x 6.1-11.1mm), 1 female (11.0mm x 7.0mm), 3 females (ovigerous) (11.0-12.1mm x 7.7-8.5mm) (BNHM-no cat. number), Xiamen, no other data; 8 males (11.0-21.6mm x 8.3-15.3mm), 5 females (6.2-14.3mm x 4.3-10.2mm) (QIH-no cat. number), Fangcheng, Guangxi Province, coll. 6 Jun. 1980; 1 female (19.5mm x 14.7mm) (QIH-no cat. number), Nandukou, Haikou, Hainan Island, coll. 21 May 1958; – **Taiwan** – 2 males (16.5-18.5mm x 13.5-15.5mm) (NMNS-uncatalogued), Taduxi river, Taichung County, coll. 28 Oct. 1993; 4 males (16.2-21.9mm x 13.2-19.0mm), 4 females (18.4-22.3mm x 14.3-17.5mm) (NMNS-uncatalogued), Houlongxi river mouth, coll. 7-8 Dec. 1992.

**Diagnosis.**— Carapace rectangular, surface convex, punctate, granulated; frontal margin sinuous . Anterolateral margin with four teeth including orbital tooth. Third maxillipeds close with gap. Infra-orbital ridge with seven rounded granules in males. Chelipeds symmetrical in males, stridulatory ridge present on merus of chelipeds. Ambulatory legs long, slender; merus with a sharp subdistal spine on anterior margin, one or more sharp spines on posterior margins of merus. G1 long, slender.

**Colour.**— The fresh specimens are brown in colour (H.C. Liu, pers. comm.), and all preserved specimens examined are dark cream in colour.

**Size.**— The largest male specimen examined is 22.4mm x 115.6mm (BNHM-C-02369), and the largest female examined is 22.3mm x 17.5mm (NMNS-uncatalogued).

**Habitat.**— It can be found on the intertidal zone with sandy muddy substrate (H.C. Liu, pers. comm.; Wang & Liu, 1996c; Davie & Nguyen, 2003).

**Remarks.**— *Metaplax longipes* Stimpson, 1858, is one of the most problematic species in this genus. Many workers believed *M. longipes* to be senior synonym of *M. takahashii* Sakai, 1939 (T.Y. Chan, pers. comm.; Davie & Nguyen, 2003) but *M. longipes* is distinctly different from *M. takahashii* in the form of the carapace, infra-orbital ridge and ambulatory legs (see below).

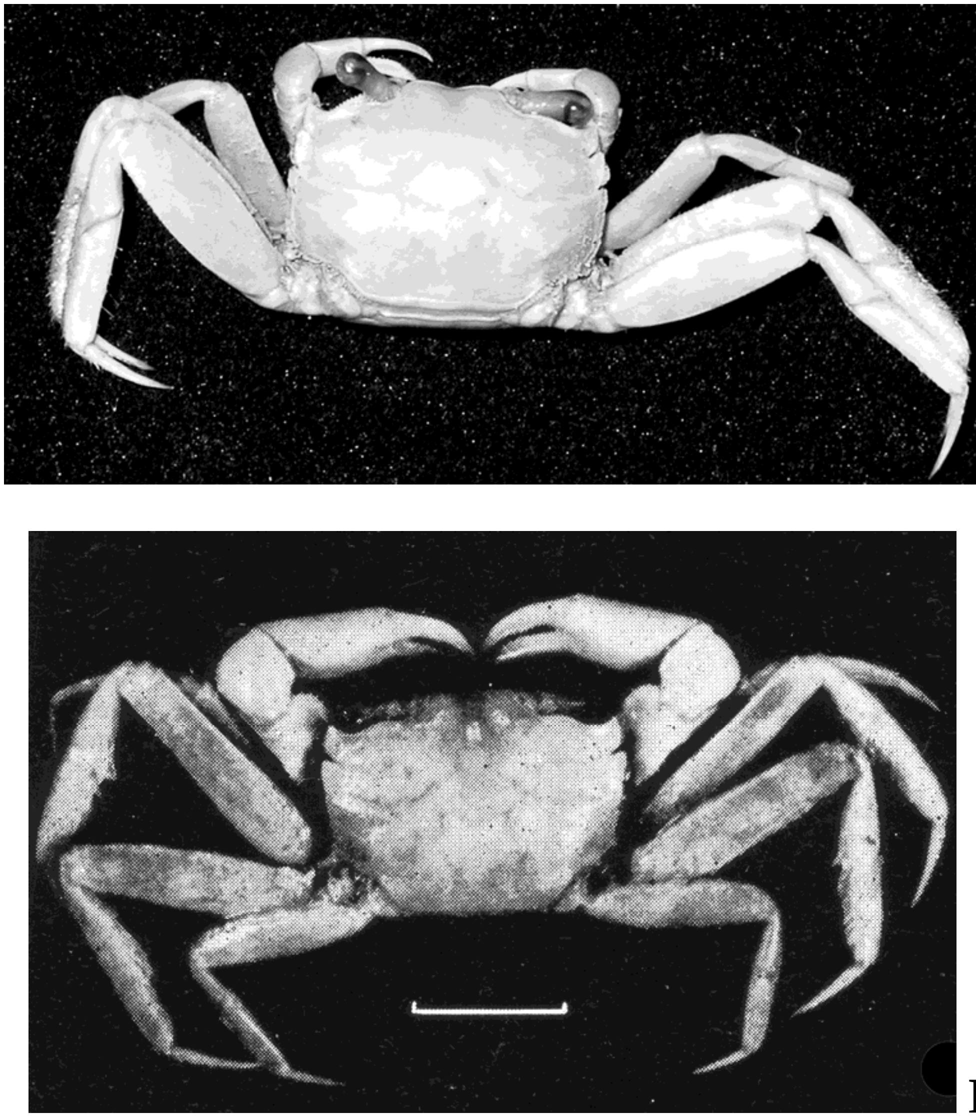
Stimpson (1858) first described *M. longipes* based on one male specimen collected from Hong Kong port. Later, in his English description of *M. longipes* (Stimpson, 1907: 98), he clearly stated that the "Infra-orbital margin seven-lobed, lobes rounded, smooth, glossy, decreasing in size outwardly, the innermost lobe being the largest and most projecting, somewhat curving downward."

Subsequently, four male specimens were recorded from Tai Po, Hong Kong by Shen (1940a: 236). Another four males from Fujian and Zhejiang Provinces were also reported by Shen (1940b: 95) but he did not provide any description of the specimens he obtained from Hong Kong, Fujina or Zhejiang provinces, China. He also did not state hoe he had determined the identities of those specimens. Shen & Dai (1964) further noted that *M. longipes* had nine or ten lobes on the infraorbital ridge, slightly more than the seven originally recorded by Stimpson (1858, 1907). Dai & Yang (1991) had also recorded what they thought to be *M. longipes* from Guangdong, Fujian, and Zhejiang Provinces, China, but their key character for this species is the presence of 11-15 tubercles on the infraorbital crest of males. Strangely, however, they have two separate figures of the infraorbital ridge, one with seven lobes, and the other with nine. Davie & Nguyen (2003) interpreted 'the shorter ridge with fewer lobules is the "typical" form for *M. longipes* since it fits Stimpson's description better than the other with numerous lobules' (see Davie & Nguyen, 2003). Lee (2001:115) also recorded *M. longipes* from the small Taiwanese controlled islands of Kinmen, and along the coast of mainland China but not from the main island of Taiwan.

The description given by Stimpson (1858) for *M. longipes* also seems to fit the description of *M. takshashii*, especially for the infra-orbital crest except that Sakai's description of *M. takahashii* supposedly has five teeth on the anterolateral margin as compared to the four teeth in *M. longipes*. However, the last tooth can be very indistinct, and may have been overlooked by Stimpson and fellow workers. Sakai (1939) also did not mention or compare with Stimpson's species in his report. Davie (1992) has recorded *M. takahashii* from Hong Kong but also did not check the identity of *M. longipes*.

The type specimen of Stimpson is no longer extant (Diess & Manning, 1981; Evans, 1967), and the identity of this species is doubt. In order to stabilize the taxonomy of this species, a neotype, preferably from the type locality, Hong Kong, should be selected. Two of the four male specimens reported by Shen (1940a) which he had collected from Hong Kong, were supposedly housed in Institute of Zoology, The Chinese Academy of Sciences (ASIZ), Beijing (S.L. Yang, pers. comm.). One of the male specimens could be selected as a neotype for *M. longipes* if these specimens are found. The curator of Crustacea in the Insitute of Zoology, The Chinese Academy of Sciences, found a bottle containing a piece of paper labeled 'Maipo', with two male specimens (one has been crushed, while the other is very soft, and folded) and a female specimen. The infra-orbital ridge of the male specimens has seven granules below the orbit (see insert photograph A). As there were no other label in that bottle, and the curator has no other information to offer, it is not possible to ascertain if the specimens in the bottle were those collected by Shen (1940a). Due to the dubious nature of this material, I prefer that the name of this problematic species be fixed on the basis of a fresh specimen on hand, which keeps the name for a species best understood as defined by Stimpson and Shen. To this effect, we select a neotype from Hainan Island, which is near Hong Kong (see materials examined).

**Distribution.**— Taiwan, Hong Kong, China.



A

B

Figure 167. *Metaplax longipes* Stimpson, 1858, (A) male, neotype, 18.7mm x 13.9mm (QIH). Dorsal view; B) dorsal view. (After Dai & Yang, 1991).

## ***Metaplax takahashii* Sakai, 1939**

(Figure 168)

*Metaplax takahashii* Sakai, 1939: 698, fig. 127a–c; Sakai, 1976: 673, fig. 371a–c; Dai *et al.*, 1986: 508, fig. 288: 3–4, pl. 72: 4; Dai & Yang, 1991: 556, fig. 288: 3–4, pl. 72: 4; Ng *et al.*, 2001: 46.

*Metaplax takahasii* – Horikawa, 1940: 30; Lin, 1949: 31; Fukui *et al.*, 1989: 230, fig. 24; Shih *et al.*, 1991: 142 (wrong spelling).

**Materials examined.— Holotype** – 1 male (14.4mm x 10.5mm) (KPMNH-107076), Tansui, Taiwan, coll. 1933. – **Others** – **China** – 1 male (15.8mm x 11.6mm) (QIH-no cat. number), Shuidong market, Guangdong Province, coll. 24 Dec. 1954; 1 male (8.4mm x 6.6mm) (QIH-no cat. number), coll. 5 Jul. 1958; 1 male (20.9mm x 15.1mm) (QIH-no cat. number), Dachi district, Leqing, coll. X.T. Ma, 7 Jun. 1953; 1 female (6.9mm x 5.3mm) (QIH-no cat. number), Haikou, Hainan Island, coll. 26 May 1958; 2 females (6.2-7.0mm x 4.9-5.3mm) (BHNM-C2366), Guanghai, Guangdong Province, Jul. 1957; 1 male (7.2mm x 5.3mm) (BNHM-no cat. number), Fuguichi, Fijian Province, coll. 31 Mar. 1974; 3 males (8.5-11.5mm x 7.0-8.7mm), 3 females (7.3-12.9mm x 5.0-9.4mm) (BNHM-no cat. number), Guanghai, Guangdong Province, coll. 26 Mar. 1956. – **Taiwan** – 1 male (16.0mm x 11.0mm) (NTOU-no cat. number), Tam-Shui River, Taipei County, coll. J.F. Huang, 25 Mar. 1984; 1 male (14..0mm x 10.0mm) (NTOU-no cat. number), Tam-Shui River, Taipei County, coll. J.F.Hunag, 18 Oct. 1987; 1 female (13.0mm x 9.0mm) (NTOU-no cat. number), Tai-Xi, Yunlin County, coll. J.F. Huang, 25 Mar. 1984; 3 males (8.6-14.7mm x 6.0-12.1mm), 1 female (17.8mm x 14.0mm) (TMCD-uncatalogued), Houlong river mouth, coll. 15 Nov. 1992; 1 male (17.7mm x 12.8mm) (TMCD-2654), Guandu, Taipei County, coll. C.H. Wang, 18 May 1990.

**Diagnosis.—** Carapace rectangular, surface convex, punctate, granulated; frontal margin sinuous. Anterolateral margin with four teeth including orbital tooth. Third maxillipeds close with gap. Infra-orbital ridge with eight tubercules (six elongated and two smaller) tubercles in male, 15-20 small granules in females. Cheliped symmetrical in males, stridulatory ridge present on merus of chelipeds. Ambulatory legs short, broad; meri with a sharp subdistal spine on the anterior margin, one or more sharp spines on posterior margins of merus.

**Colour.**— The fresh specimens are grey in colour with brown spots (J.-F. Huang, pers. comm.), and all preserved specimens examined are brown in colour.

**Size.**— The largest male examined examined is 20.9mm x 15.1mm (QIH-no cat. number), and the largest female specimen examined is 17.8mm x 14.9mm (TMCD specimens).

**Habitat.**— It can be found  in mud flats, mangroves (J.F. Huang, pers. comm.).

**Remarks.**— This species is believed to be the junior symnoym of *M. longipes* by many workers (see above), but *M. takahashii* is distinctly different from *M. longipes* in the following a) the carapace is broader, with length to width ratio 1.4 (vs. narrower carapace, length to width ratio 1.1 in *M. longipes*);  b) the infra-orbital ridge with eight elongated tubercules (vs. seven rounded granules in *M. longipes*); c) the ambulatory legs are broad and stout (vs. very much longer and more slender in *M. longipes*).

**Distribution.**— Taiwan, Hong Kong (see Dai *et al.*, 1986), China, Japan.

Figure 168. *Metaplax takahashii* Sakai, 1939. Dorsal view. (After Dai & Yang, 1991).

## *Metaplax sheni* Gordon, 1931

(Figure 169)

*Metaplax sheni* Gordon, 1931: 533, figs. 31-32; Tweedie, 1936: 69; Shen & Dai, 1964, 133; Dai *et al.*, 1986: 509; Dai & Yang, 1991: 558.

**Materials examined.— Holotype** – 1 male (13.2mm x 8.6mm) (BNHM), Amoy, no collection date. – **Paratype** – 1 male (12.8mm x 8.5mm) (BNHM), Amoy, no collection date. – **Others – China –** 4 males (17.0-23.8mm x 12.5-17.3mm) (QIH-no cat. number), Xiamen fish market, Fijian Province, coll. H.L. Chen, 13 Jun. 1975; 2 males (4.5-4.8mm x 3.2-3.6mm) (QIH-no cat. number), Zuopu, coll. 26 Jul. 1976; 1 male (6.9mm x 4.4mm) (QIH-no cat. number), Sanya, Hainan Island, coll. 25 May 1958; 1 male (8.3mm x 5.5mm) (QIH-no cat. number), Yandu, Haikou, Hainan Island, coll. 26 May 1958; 3 males (10.5-13.6mm), 2 females (7.3-10.6mm x 5.0-5.8mm) (ASIZ-uncatalogued), Beigang, Xiongshan, Hainan Island, coll. 24 May 1958; 7 males (9.0-11.0mm x 6.0-7.4mm) (ASIZ-uncatalogued), Longmen, Guangdong Province, coll. 4 Apr. 1981; 1 male (9.2mm x 6.0mm), 1 female (6.6mm x 4.2mm) (ASIZ-uncatalogued), Pingyan, Xingfuyang, Fujian Province, coll. 20 Nov. 1984; 1 male (13.7mm x 8.9mm) (ASIZ-uncatalogued), Xiamen, coll. 21 Jul. 1931; 1 male (9.4mm x 6.3mm) (ASIZ-uncatalogued), Hangxi, Fenghua, Zhejiang Province, coll. 18 Jun. 1976; 8 males (7.4-12.0mm x 5.3-8.0mm), 4 females (7.5-10.0mm x 5.0-6.2mm), 1 female (ovigerous) (8.2mm x 6.3mm) (ASIZ-C-2347), Shatian, Hepu, Guangxi Provincve, coll. 3 Jun. 1980; 3 males (8.8-13.8mm x 6.2-8.9mm), 1 female (ovigerous) (10.2mm x 7.0mm) (ASIZ-uncatalogued), Qingjing, Zhejiang Province, coll. 20 Sep. 1970. – **Indonesia** – 4 males (7.4-8.3mm x 5.2-5.5mm), 2 females (8.5-8.7mm x 6.0-6.1mm), 3 females (ovigerous) (7.4-8.4mm x 5.3-6.0mm) (ZRC 1964.81257-65), Tanjong Balai, Karimun, Kalimantan, Indonesia, coll. M.W.F. Tweedie, 1950.

**Diagnosis.—** Carapace rectangular, surface convex, punctate, granulated; frontal margin sinuous. Anterolateral margin with four teeth including orbital tooth. Third maxillipeds close with gap. Infra-orbital ridge with 15-20 tubercules in male, innermost five elongated. Cheliped symmetrical in males, stridulatory ridge present on merus of chelipeds. Ambulatory legs long, slender; merus with a sharp subdistal spine on anterior margin, one or more sharp spines on posterior margins of merus. G1 long, slender, distal process vent ventrally outwards.

**Colour.**— The fresh specimens are brown in colour (H.L. Chen, pers. comm.), and all the preserved specimens examined are usually dark cream in colour.

**Size.**— The largest male examined is 23.8mm x 17.3mm (QIH specimens), and the largest female examined is 10.2mm x 7.0mm (ASIZ-uncatalogued specimens).

**Habitat.**— It can be found on the intertidal zone with sandy muddy substrate (Dai & Yang, 1991)

**Remarks.**— This species has been reported only from China but there are numerous specimens collected and reported by Tweedie (see Tweedie, 1950) from Karimun (Kalimantan, Indonesia).

**Distribution.**— China (Fujian, Zhejiang, Guangxi, and Guangdong Provinces), Indonesia (Karimun).

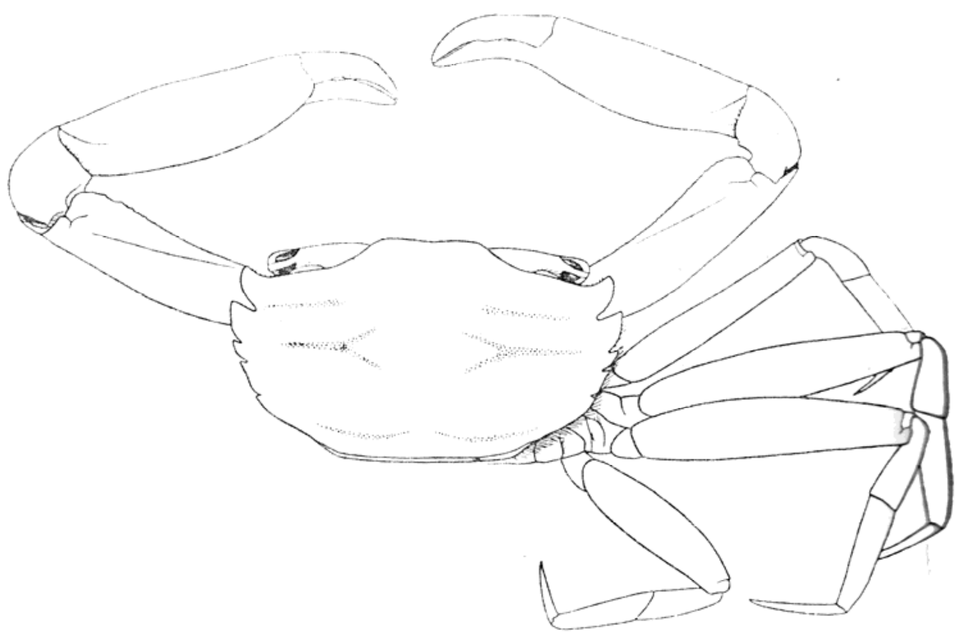


Figure 169. *Metaplax sheni* Gordon, 1931. (After Gordon, 1931)

### *Metaplax dentipes* (Heller, 1865)

(Figure 170)

*Helice dentipes* Heller, 1865: 62.

*Metaplax dentipes* – de Man, 1865: 162; Alcock, 1900: 433; de Man, 1908: 219; Rathbun, 1910: 329; Tesch, 1918: 117; Naiyanetr, 1998: 98; Davie & Nguyen, 2003: 379.

**Materials examined.**— 3 males (20.9-21.6mm x 11.1-16.3mm), 2 females (14.7-18.8mm x 10.9-14.2mm) (ZRC 2000.1636), Song Khram, Samut, Thailand, coll. SYC, 1994.

**Diagnosis.**— Carapace rectangular, surface convex, punctate, granulated; frontal margin sinuous. Anterolateral margin with four teeth including orbital tooth. Third maxillipeds close with gap. Infra-orbital ridge with 25-30 granules in male, of which 6 are just below the orbit. Cheliped symmetrical in males, stridulatory ridge present on merus of chelipeds. Ambulatory legs long, slender; merus with a sharp subdistal spine on anterior margin, one or more sharp spines on posterior margins of merus. G1 long, slender.

**Colour.**— The colour of fresh specimens has not been documented, but all preserved specimens examined are brown in colour (ZRC 2000.1636).

**Size.**— The largest male specimen examined is 21.6mm x 16.3mm, and the largest female examined is 18.8mm x 14.2mm (ZRC 2000.1636).

**Habitat.**— This species is found on the intertidal zone with sandy muddy substrate (Tesch, 1918).

**Remarks.**— The species was originally described by Heller (1865) in the genus *Helice* based on a young female specimen. The description provided by Heller is short. This species falls into the same category as *M. distincta* where there are 25 to 30 granules on the infra-orbital ridge, but this species is distinctly different from *M. distincta* the presence of 6 granules below the orbit on the infra-orbital ridge (vs. 8-10 below the orbita on the infra-orbital ridge in *M. distincta*). *M. dentipes* is similar to *M. intermedius* by the presence of one or more sharp spines on the posterior margin of the merus of the ambulatory legs but the infra-orbital ridge has only 25-30 granules (vs. about 40 granules in *M. intermediu*s). De Man (1888) provided a detailed description of the adult, and transferred the taxon to *Metaplax*.

The descriptions provided by Heller (1865) is clear enough fot me to distinguish *M. dentipes* and its congeners.

**Distribution.**— Mergui, Sri Lanka, India, Thailand.

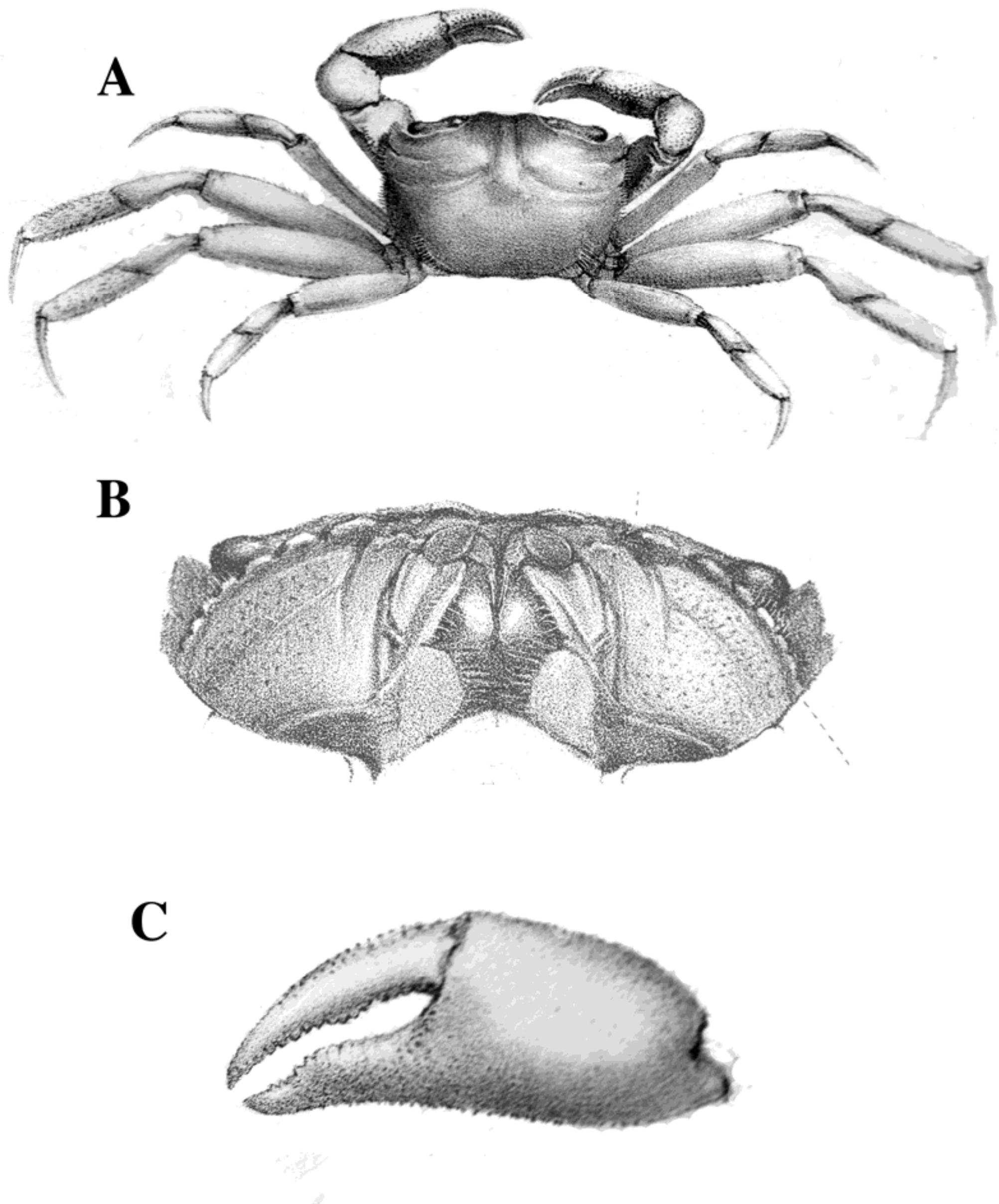



Figure 170. *Metaplax dentipes* (Heller, 1865). A) dorsal view; B) frontal view; C) outer view of chela. (After de Man, 1888).

## *Metaplax gocongensis* Davie & Nguyen, 2003

(Figure 171A-D)

*Metaplax gocongensis* Davie & Nguyen, 2003: 397.

**Materials examined.— Holotype** – 1 male (29.0mm x 20.6 mm) (QMW-26683), My Loi Commune, Vai co River, ca. 40 km south of Ho Chi Minh City, Go Cong Province, Vietnam, 106°39'E, 10°28'N, in dike wall of tiger prawn pond near river bank, coll. V.X. Nguyen, 28 Jul. 2002. – **Paratypes** – 2 males (29.1 x 20.7, 18.9 x 14.2 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, 106°42'E 10°17'N, coll. Nguyen, 2 Feb. 2002. – **Others** – 1 male (26.1mm x 19.4mm), 1 female (22.9mm x 19.4mm) (ZRC 1969.10.1.2-3), Cantho, Vientam, coll. T.L. Nguyen, Aug. 1969.

**Diagnosis.**— Carapace subquadrangular, almost rounded, slightly broader then long; surface slightly convex, granulated in frontal region; front slightly deflected, anterior margin nearly straight. Anterolateral margin with four teeth including orbital teeth. Infra-orbital ridge of male with one elongated tubercle, followed by numerous granules decreasing in size. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Cheliped symmetrical, surfaces smooth, palm of cheliped very high. Ambulatory legs flat, stout, merus finely serrated on anterior, posterior margins, propodus, dactylus with short, long setae. G1 stout, distal chitinous process truncated. Female gonopore circular in shape with a semicircular operculum.

**Colour.**— The colour of fresh specimens is greyish brown (Davie & Nguyen, 2003), and all the preserved specimens examined are all brown in colour (ZRC 1969.10.1.2-3).

**Size.**— The largest male specimen reported is 29.0mm x 20.6mm (Davie & Nguyen, 2003), and largest female specimen examined is 22.3mm x 16.4mm (ZRC 1969.10.1.2-3).

**Habitat.**— This species can be found in the intertidal silty mud zone along the river banks or ricefields subjected to tidal influence where salinity ranges from 0-15p.p.t. (Davie & Nguyen, 2003). It has been reported that this is a gregarious species (Davie & Nguyen, 2003).

**Remarks.**— Davie & Nguyen (2003) described the this species based on numerous specimens collected from Go Cong, Vietnam. This species has its closest allies amongst the *Metaplax* species with less than 20 lobules/tubercles on the male infraorbital crest, i.e. *M. indica* H. Milne Edwards, 1852, *M. longipes* Stimpson, 1858, *M. occidentalis* Pretzmann, 1971, *M. sheni* Gordon, 1931, *M. takahashii* Sakai, 1939, and *M. tredecim* Tweedie, 1950, but *M. gocongensis* differs from all of these by the presence of prominent black, slender, fixed spines on the outer surface of the merus of the chelipeds.

Davie & Nguyen (2003) stressed that *M. gocongensis,* is closely allied to *M. tredecim* Tweedie, 1950, in having the same numbers (12-14) lobules or tubercles on the infra-orbital ridge but in *M. tredecim,* these lobules decrease in size and length more-or-less progressively from the inner orbit outwards, and there is not an obviously much larger and longer inner lobe. *Metaplax tredecim* also has only two lateral teeth behind the external orbital angle (versus three), and the meri of the ambulatory legs are more slender (merus of P4 ca. 4.3 times longer than wide versus 3.5).

*Metaplax gocongensis* is also very similar to *Metaplax sheni* Gordon, 1931, in having the innermost lobule of the infraorbital ridge by far the largest, but in *M. sheni*, it is not as long and pronounced as that of *M. gocongensis*. Davie & Nguyen (2003) stated that *M. sheni* is a small species, apparently less than about 15 mm in carapace width (Gordon, 1930, 1931; Tweedie, 1936). *Metaplx gocongensis* is also different from *M. sheni* in having broader and stouter chelipeds and ambulatory legs.

**Distribution.**— Southern Vietnam only.

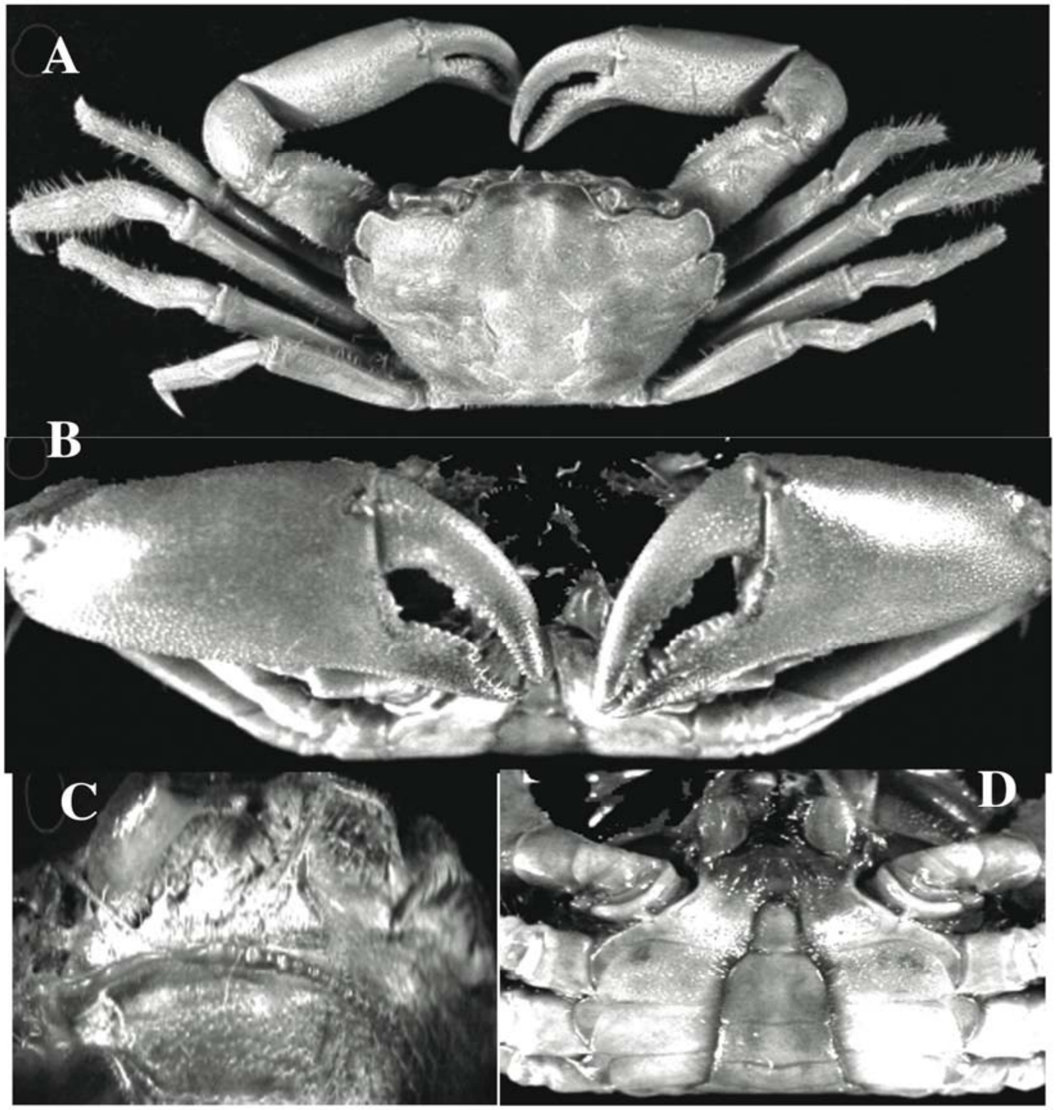



Figure 171. *Metaplax gocongensis* Davie & Nguyen, 2003, male, holotype 29.0mm x 20.6mm (QMW26683). A) dorsal view; B) cheliped; C) infra-orbital ridge; D) ventral view. (from Davie & Nguyen, 2003).

**_Metaplax intermedius_ de Man, 1888**

(Figure 172A-C)

*Metaplax intermedius* de Man, 1888: 166, pl. 11; Alcock, 1900: 435; Tesch, 1918: 117.

**Materials examined.**— No material examined.

**Diagnosis.**— Carapace rectangular, surface convex, punctate, granulated; frontal margin sinuous . Anterolateral margin with four teeth including orbital tooth. Third maxillipeds close with gap. Infra-orbital ridge with 40-50 rounded granules in male, with first 5 below orbit elongated. Cheliped symmetrical in males, stridulatory ridge present on merus of chelipeds. Ambulatory legs long, slender; merus with a sharp subdistal spine on anterior margin, one or more sharp spines on posterior margins of merus. (Modified from de Man, 1888; Alcock, 1900).

**Colour.**— Both live and preserved colour unknown.

**Size.**— Unknown.

**Habitat.**— Unknown, but probably in muddy intertidal zone (Tesch, 1918)

**Remarks.**— This species is very similar to *M. elegans* but the infra-orbital ridge has far fewer granules, about 40 (vs. 50-60 granules in *M. elegans*), and . The type material is probably in Zöologisch Museum Amsterdam (ZMA) but the author could not locate the specimens during her trip to the ZMA in 1999.

**Distribution.**— Mergui Archipelago.

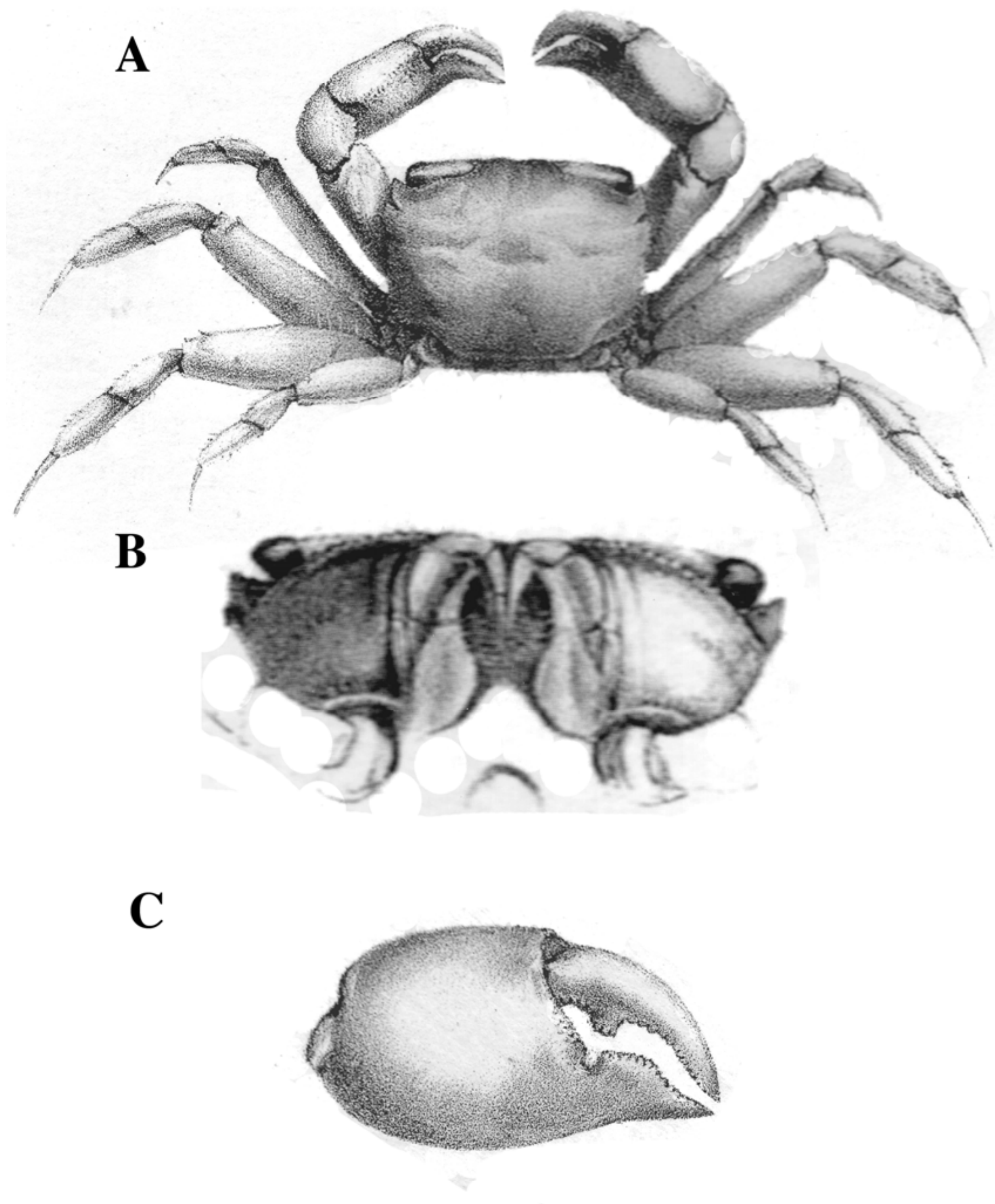



Figure 172. *Metaplax intermedius* de Man, 1888. A) dorsal view; B) frontal view; C) outer view of chela. (After de Man, 1888).

## *Metaplax tredecim* Tweedie, 1950

(Figure 173A-B; 174)

*Metaplax tredecim* Tweedie, 1950: 354, fig. 6; Choy & Booth, 1994: 273.

**Materials examined.**— **Paratypes** – 8 males (9.7-15.7mm x 7.6-11.8mm), 2 females (11.6-15.0mm x 9.2-11.5mm), 3 females (ovigerous) (13.8-15.8mm x 10.2-11.8mm) (ZRC 1964.7.14.4-18), Labuan, North Borneo, coll. G. Nunong, Aug. 1950. – **China** – 1 female (ovigerous) (10.6mm x 7.5mm) (QIH-no cat. number), Zhejiang Province, coll. 1974; 1 male (9.5mm x 7.0mm) (QIH-no cat. number), Sanya, Hainan Island, coll. 18 Mar. 1958; 2 males (11.8-17.0mm x 9.0-12.1mm), 2 females (7.6-13.7mm x 5.2-10.4mm), Beigang, Hainan Island, coll. 12 Jan. 1960; 2 males (10.0-14.7mm x 7.0-11.0mm) (QIH-no cat. number), Sanya, Hainan Island, coll. 23 Nov. 1959; 1 male (24.2mm x 17.2mm) (QIH-no cat. number), Fenghua, Zhejiang Province, coll. 6 Oct. 1976. – **Brunei** – 3 males (14.1-21.3mm x 10.8-16.0mm), 1 female (15.3mm x 11.5mm), 1 female (ovigerous) (13.0mm x 9.0mm) (ZRC-uncatalogued), Tutong, Brunei, coll. 16 Sep. 1990.

**Diagnosis.**— Carapace rectangular, surface convex, punctate, granulated; frontal margin sinuous. Anterolateral margin with three teeth including orbital tooth. Third maxillipeds close with gap. Infra-orbital ridge with 12-14 rounded granules in male, with the leargest on the innermost and decreasing in size; female with about 20 small isomorphic granules. Cheliped symmetrical in males, stridulatory ridge present on merus of chelipeds. Ambulatory legs long, slender; merus with a sharp subdistal spine on anterior margin, one or more sharp spines on posterior margins of merus. G1 long, slender.

**Colour.**— The colour of fresh specimen is not known but all the preserved examined are brown in colour.

**Size.**— The largest male specimen examined is 24.2mm x 17.2mm (QIH specimens), and the largest female examined is 15.3mm x 11.5mm (ZRC specimens).

**Habitat.**— The speciesh can be found  on the intertidal zone with sandy muddy substrate (Tweedie, 1950).

**Remarks.**— This species is very commonly found in the mangroves or mudflats in sub-tropical and tropical regions.

**Distribution.**— Southeast China, and South East Asia.

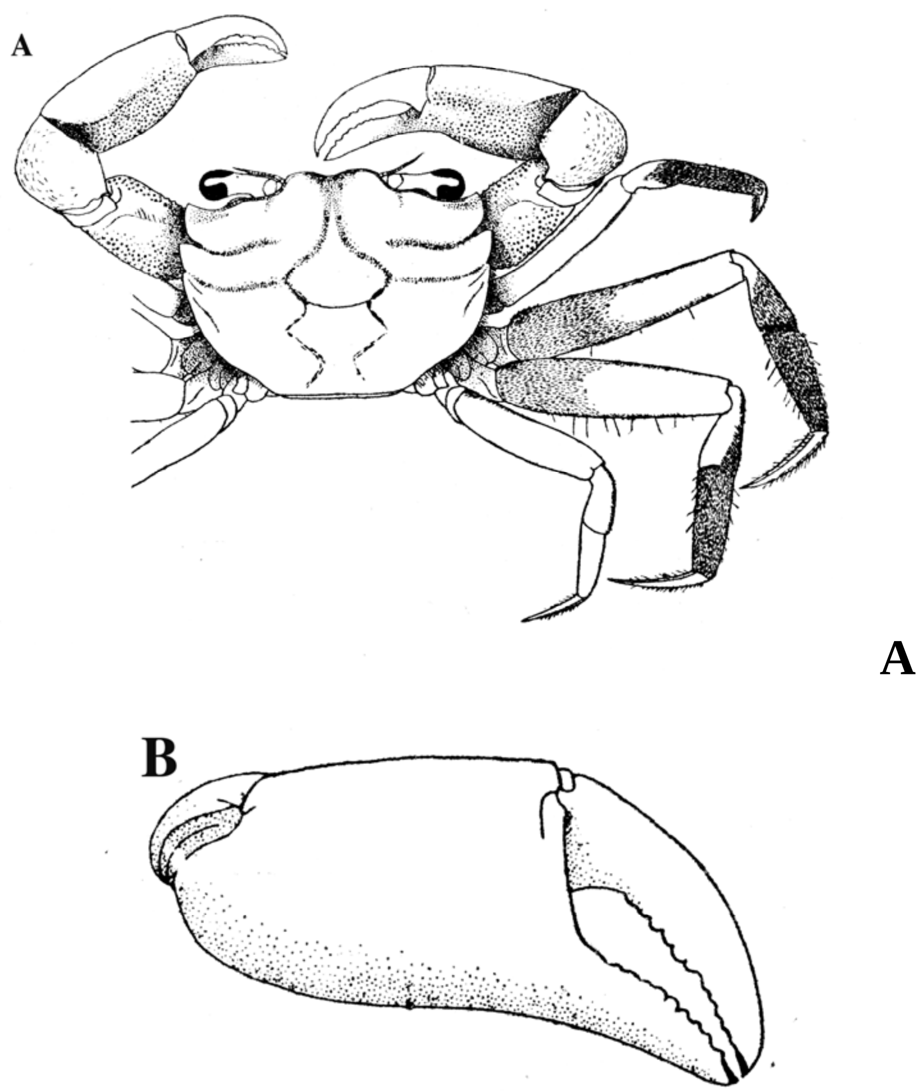



Figure 173. *Metaplax tredecim* Tweedie, 1950. A) dorsal view; B) outer surface of cheliped. (After Tweedie, 1950).

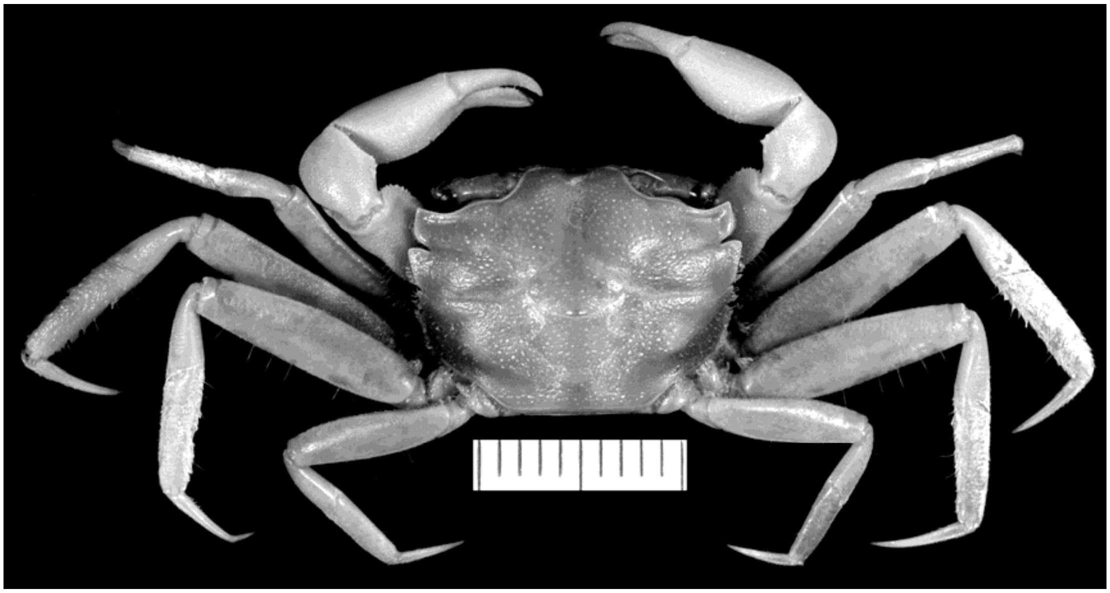


Figure 174. *Metaplax tredecim* Tweedie, 1950, 15.7mm x 11.8mm (ZRC 1964.7.14.4-18). Dorsal view.

### ***Metaplax occidentalis* Pretzmann, 1971**

*Metaplax occidentalis* Pretzmann, 1971: 478; Davie & Nguyen, 2003: 383.

**Materials examined.**— No material examined.

**Diagnosis.**— Carapace rectangular, surface convex, punctate, granulated; frontal margin sinuous . Anterolateral margin with four teeth including orbital tooth. Third maxillipeds close with gap. Infra-orbital ridge with five small granules, followerd by two elongated granules and ending with three granules decreasing in size in male. Cheliped symmetrical in males, stridulatory ridge present on merus of chelipeds, finger long, recurved. Ambulatory legs long, slender; merus with a sharp subdistal spine on anterior margin, one or more sharp spines on posterior margins of merus. G1 long, slender. (Modified from Pretzmann, 1971).

**Colour.**— The colours of fresh and preserved specimens have not been documented.

**Size.**— The sizes of male and female specimens have not been documented.

**Habitat.**— This species can be found on sandy beaches (Pretzmann, 1971).

**Remarks.**— *Metaplax occidentalis* Pretzmann, 1971, was originally described as a subspecies of *M. indica* H. Milne Edwards, 1852. Pretzmann (1971) stated that it differs from *Metaplax indica* by the following characters: a) the infra-orbital border beginning with five small granules, followed by five more granules that become larger and more tubercular; followed by two oval, vesicular structures, and ending with three small closely-packed teeth, b) the fingers of the chela are somewhat longer, and more strongly bent downwards, c) the carapace lateral margins have a large exorbital tooth, followed by a second tooth of similar size, and a third tooth in the form of an indistinct projection, d) carpus of cheliped bearing distinct, inwardly placed spine, and e) the G1 does not have a forwardly directed apical spine. Based on these differences, Davie & Nguyen (2003) regarded it as a full species.

Pretzmann (1971) did not mention about the specimen deposit and a check with Berlin Museum and Senckenberg Natural History Museum, Frankfurt am Main, Germany about the wherebouts of the type specimens have been fruitless. I am now waiting for the curator from Vienna Museum to send me the type specimens.

**Distribution.**— Iran (Bandarabass), Persian Gulf only (Pretzman, 1971).

## *Metaplax neosheni,* new species

**Materials examined.— Holotype** – 1 male (13.3mm x 8.6mm) (QIH-no cat. number), Station 1, Beigang, Xiongshan, Hainan Island, coll. 7 Jun. 1958. – **Paratypes** – 3 males (9.4-12.3mm x 6.5-7.5mm), 2 females (7.8-9.9mm x 5.2-6.7mm) (QIH-no cat. number), Station 1, Beigang, Xiongshan, Hainan Island, coll. 7 Jun. 1958.

**Diagnosis.**— Carapace rectangular, surface convex, punctate, granulated; frontal margin sinuous . Anterolateral margin with four teeth including orbital tooth. Third maxillipeds close with gap. Infra-orbital ridge of male with seven large granules below the orbit, followed by two to three round granules decreaing in size. Cheliped symmetrical in males, stridulatory ridge present on merus of chelipeds, palm very much longer than fingers. Ambulatory legs long, slender; merus with a sharp subdistal spine on anterior margin, one or more sharp spines on posterior margins of merus. G1 stout. Female gonopore with small operculum.

**Etymology**.— 'Neo' is the Latin for the word 'new' and it is used with 'sheni' to indicate its close alliance with *M. sheni*.

**Colour.**— The colour of fresh specimens is unknown but all the preserved specimens examined are brown in colour.

**Size.**— The largest male specimen examined is 13.3mm x 8.6mm (holotype), and the largest female specimen examined is 9.9mm x 6.7mm (paratype).

**Habitat.**— It can be found on the intertidal zone with sandy muddy substrates.

**Remarks.**— This species is very closely allied to *M. sheni*, but it can be discerned from the latter species by a) the form of the male infra-orbital ridge which has seven large and three small granules in *M. neosheni* (vs. 15-19 isomorphic granules in *M. sheni*); b) the third maxilliped is very narrow in M. *neosheni* (vs. very broad in *M. sheni*), and c) the relatively very long and slender ambulatory legs (vs. broader and stouter in *M. sheni*).

This species is very similar to *M. longipes* and *M. takahashii* (based on the description provided by Sakai, 1939) of in the form of the infra-orbital ridge, but it can be separated from the latter two by the forms of the presence of very long and slender dactylus for all its ambulatory legs (vs. presence of broader and shorter dactylus in *M. longipes* and *M. takahashii*).

**Distribution.**— China.

## Genus *Neometaplax*, new genus

*Metaplax* H. Milne Edwards, 1852: 161; de Man, 1886: 256 (not *Metaplax* H. Milne Edwards, 1852).

*Rhaconotus* Gerstaeker, 1856: 142; Kingsley, 1880: 213.

**Type species.—** *Rhaconotus crenulatus* Gerstaecker, 1856, by present dersignation.

**Gender.—** Masculine.

**Diagnosis.** — Carapace quadrangular, distinctly broader than long; dorsal surface setose, punctate; regions well defined by deep grooves, flat. Frontal margin slightly convex. Anterolateral margin cristate with five teeth including orbital tootht, last tooth small. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped short, narrow. Large, distinct rhomboidal gape when closed, palp short, with short setae. Exopod with short flagellum. Epistome broad, flat, posterior margin lobulated. Cheliped very long, slender. Inner surface of chela with granules; palm distinctly longer than fingers. Ambulatory legs long, slender, anterior and posterior margins of legs all covered with numerous spines. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Thoracic sternites 1-3 sunken medially. Male abdomen narrowly triangular with all segments freely moveable (six somites plus telson).

**Etymology.**— 'Neo' is new in Latin, and it is used as a noun, as a prefix with the original generic name, '*Metaplax*', indicating the close affiliations with the existing genus, *Metaplax.*

**Remarks.**— Gerstaecker (1856) established the genus *Rhaconotus* based on the specimens collected from an unknown location, and named the species, *Rhaconotus crenulatus*. However, the genus name is preoccupied by *Rhaconotus* Ruthe, 1854, used for a group of parasitic wasps from family Braconidae. De Man (1888) synonymised *Rhaconotus crenulatus* under the genus *Metaplax*, based on the form of the carapace, third maxilliped, and chelipeds. This has been accepted by most workers, and therefore, there has not been a need to find a replacement name for *Rhaconotus* Gerstaecker, 1856. However, the present study shows that *M. crenulatus* is distinctly different from *Metaplax* sensu stricto. These differences warrant the separation of this species into its own genus. It would be ideal to use the original generic name, *Rhaconotus*, but since it is pre-occupied, a new genus *Neometaplax*, gen. nov is established for this taxa.

*Neometaplax* is very similar to *Metaplax*, in that both genera share the same habitats, and have similar form of oblique grooves on the third maxillipeds. The new genus differs from *Metaplax* in the following features: a) the presence of a medial cristae from the frontal margin to the gastric region of the carapace (vs. absent in *Metaplax*); b) the presence of small spines along the anterolateral margins in addition to the anterolateral teeth (vs. either glabrous or presence of beads or in *Metaplax*); c) the presence of numerous strong spines on the anterior and posterior margins of chelipeds (vs. absence of such spines in *Metaplax*); d) the presence of numerous (usually seven or more) strong spines on the anterior and posterior margins of all the ambulatory legs except the dactylus (vs. presence of few (usually five or less) small spines only on the anterior margins of the propodus of the ambulatory legs in *Metaplax*); e) the posterior margin of the epistome possessing five lobes (vs. three lobes in *Metaplax*); f) the sixth abdominal segment is distinctly rectangular (vs. trapezoidal in *Metaplax*); and g) the presence of a vertical medial groove on the sternal segments 5-8 (vs. only on sternites 6-8 in *Metaplax*).

The new genus is also very similar to the genus, *Euchirograpsus* H. Milne Edwards, 1853 in size, and form, especially in the presence of strong and broad spines on the dorsal and ventral margins of the ambulatory legs, but it is different from *Euchirograpsus* in the following features: a) the carapace is distinctly broader than long (vs, not as distinctly in *Euchirograpsus*); b) the surface of the carapace is sparingly covered with soft setae or granules and deep grooves demarcating the different regions (vs. carapace is covered with short stiff setae, without deep groove in *Euchirograpsus*); c) the anterolateral teeth are very strong and salient (vs. anterolateral teeth not as strong and salient in *Euchirograpsus*); d) the frontal margin is not clefted or there is no trace of any cleft to receive the antennae (vs. the forntal margin has some trace of a cleft); e) the orbit has a ‘U’ shaped sulcus at the lateral end (vs. orbit almost closed except for a slit at the lateral end in *Euchirograpsus*); f) there are no ridges across the segments of the ambulatory legs (vs. presence of ridges in *Euchirograpsus*); g) the telson has seven free segments (vs. segments 3-6 fused in *Euchirograpsus*), and the G1 is long and slender, and lack a twist at midway (vs. short and flat G1, with a midway twist in *Euchirograpsus*).

There is only one species in this new genus i.e. *N. crenulatus* (Gerstaecker, 1856). Its biology is quite different from *Metaplax* as well. Specimens of *N. crenulatus* are not easy to catch. These crabs are found in the softest region of the mudflats, where the mud is so‘gluey’ or in ‘semi-liquid state’, making it impossible for their predators to walk or run after these crabs. These crabs have been spotted in the daytime during the low tide to foraging for food on the surface of these mudflats. On the other hand, all *Metaplax* species prefers more ‘solid’ mudflat where the substrate is made up of sand and mud. Another interesting observation is that *N. crenulatus* tends to wander very far away from their burrows. Unlike *Metaplax* species, *N. crenulatus* does not burrow when they are startled or frightened, they run (P.K.L. Ng, pers. comm.)!

### *Neometaplax crenulata* (Gerstaecker, 1856), new combination

(Figure 175)

*Rhaconotus crenulata* Gerstaecker, 1856: 142.

*Metaplax crenulata* – de Man, 1888: 156; 1889: 439; Alcock, 1900: 435; Tesch, 1918: 116; Naiyanetr, 1998: 98; Davie & Nguyen, 2003: 380.

**Materials examined.**— **Singapore** – 2 males (33.8-44.0mm x 26.4-32.6mm), 1 female (ovi ) (22.6mm x 18.2mm) (ZRC 1997.696), Tanjong Kling mudflat, Singapore, coll. I. Polunin, 12 Jul. 1965; 2 females (31.8-32.6mm x 25.0-25.7mm) (ZRC 1989.2081-2082), Mandai mangrove, Singapore, coll. D. H. Murphy, 1985. – **Thailand** – 1 female (22.3mm x 15.8mm), 2 juveniles (3.9-4.6mm x 3.10-3.4mm) (ZRC 1998.1205), Ao Nam Bo mangrove, Phuket, coll. P.K.L Ng, Dec. 1998.

**Diagnosis.**— Carapace subquadrangular, distinctly broader then long; surface flat, with deep grooves demarcating the different regions, granulated, setose in frontal region; front slightly deflected, anterior margin nearly straight. Anterolateral margin with three teeth including orbital tooth. Infra-orbital ridge raised with 25 small granules. Third maxillipeds close with rhomboidal gape, merus with broad longitudinal groove medially. Cheliped symmetrical, surfaces smooth, very long, slender. Ambulatory legs flat, long, glabrous but anterior and posterior margins of all legs covered with small spines. G1 stout, distal chitinous process truncated. Female gonopore operculate, circular, small.

**Colour.**— The colour of fresh specimens is brown (D.H. Murphy, pers. comm.), all preserved specimens examined are also brown in colour (ZRC 1997.969).

**Size.**— The largest male specimens examined is 44.0mm x 32.6mm (ZRC 1997.696), and largest female specimen examined is 32.6mm x 25.0mm (ZRC 1998.1205).

**Habitat.**— It can be found  in mud holes in mudflats, especially on very soft mud (P.K.L. Ng, pers. comm.).

**Remarks.**— This species is difficult to collect as  its preferred habitat is the softest mud in the mangroves. The characters listed for the generic and species definition for this taxa is also very consistant in the juvenile stage.

The type materials are probably in Berlin Museum, I am waiting for Dr. Oliver Coleman’s reply about the loan.

**Distribution.**— Mergui, Thailand, Malaysia, and Singapore.

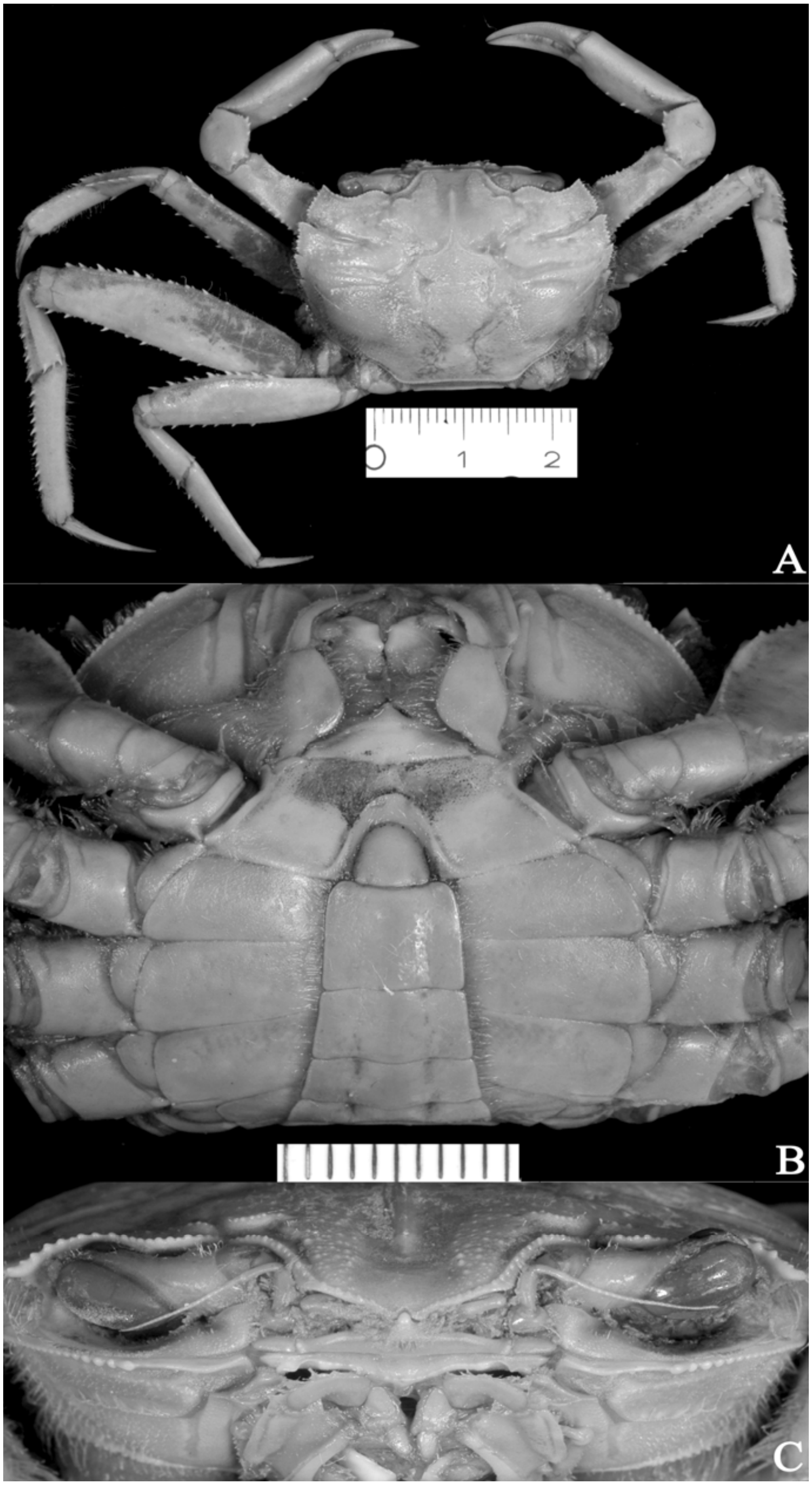



Figure 175. *Neometaplax crenulatus* (Gerstaecker, 1856), male, 44.0mm x 32.6mm (ZRC 1997.696). A) dorsal view; B) ventral view; C) frontal view.

## Genus *Paragrapsus* H. Milne Edwards, 1853

*Paragrapsus* H. Milne Edwards, 1853: 195; Tesch, 1918: 125; Campbell & Griffin, 1966: 159; Davie *et al.*, 1998: 48; Davie 2002: 207.

**Type species.**— *Cyclograpsus quadridentatus* H. Milne Edwards, 1837, subsequent designation by Tesch (1918).

**Gender.**— Masculine.

**Diagnosis.**— Carapace subquadrangular, broader then long; surface slightly convex, granulated in frontal region; front slightly deflected, anterior margin nearly straight, regions not well defined. Anterolateral margin with two or three teeth including orbital tooth. Third maxillipeds close with rhomboidal gape, merus with broad longitudinal groove medially. Cheliped asymmetrical in both sexes, surfaces smooth, smaller in females. Ambulatory legs flat, stout, merus finely serrated on anterior, posterior margins, propodus, glabrous.

**Remarks.-** This genus is found only in Eastern part of Australia. The genus was last revised by Campbell & Griffin (1966).

It is interesting to note that crabs from this genus are very similar to members of *Hemigrapsus* sensu lato. The genus is distinctly different from *Hemigrapsus* in having the water chanelling groove, the oblique crested setose ridge on the third maxillipeds and the absence of setae on the chelipeds and ambulatory legs.

**Key to species in *Paragrapsus***

1a. Carapace distinctly broader than long. Anterolateral margin with two teeth including orbital tooth. **------------------------------------------------------- *P. quadridentatus***

1b. Carapace distinctly broader than long. Anterolateral margin with three teeth including orbital tooth. **--------------------------------------------------------------- 2**

2a. First ambulatory leg with carpus, propodus and dactylus setose. Ridge absent on suture between sternites 1 and 2. **-------------------------------------------------- *P. laevis***

2b. First ambulatory leg with propodus and dactylus setose. A distinct granulated ridge present on suture between sternites 1 and 2. **-------------------------------- *P. gaimardii***

## *Paragrapsus quadridentatus* (H. Milne Edwards, 1837)

(Figures 176; 177A-F)

*Cyclograpsus quadridentatus* H. Milne Edwards, 1837: 79; Hess, 1865: 152.

*Paragrapsus quadridentatus* – Haswell, 1882: 105, pl. 3, fig. 1.; de Man, 1889: 441; Tesch, 1918: 125; Tweedie, 1942: 21, fig. 7; Campbell & Griffin, 1966: 160, text-fig. 9, 10, pl. 12, fig. 1.

*Chasmagnathus quadridentatus* – Ortmann, 1894: 728.

**Materials examined.**— 8 males (16.0-33.0mm x 13.9-26.6mm), 3 females (19.3-22.8mm x 16.6-19.3mm) (ZRC 1965.7.271.172-182), south coast of Tasmania, coll. Mupt, 1940-1941.

**Diagnosis.**— Carapace subquadrangular, slightly broader than long; surface slightly convex, granulated, front slightly deflected, anterior margin nearly straight. Anterolateral margin with two teeth including orbital tooth. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Infra-orbital ridge with about 25 low granules. Cheliped asymmetrical, bigger in males, surfaces smooth, Ambulatory legs flat, stout, merus finely serrated on anterior. Male abdomen broadly triangular. G1 and female gonopore unknown. (Modified from Campbell & Griffin, 1966).

**Colour.**— The colour of fresh specimen has been reported to be greenish grey or pale brown in colour (Campbell & Griffin, 1966), and the colour of preserved specimens has not been documented.

**Size.**— The largest sizes of male and female specimens have not been documented.

**Habitat.**— This species can be found in the intertidal, rocky shore, sand beaches, usually under stones on sand or shingle beaches, or rocky coasts, at lower mid-intertidal level, and appears to prefer exposed to semi-exposed coastal areas (Campbell & Griffin, 1966).

**Remarks.**— The species has been revised by Campbell & Griffin (1966). It is a very common shore crab found in the coastal area. It is endemic to Australia.

**Distribution.**— Australia **(**Tasmania, Victoria).

Figure 176. *Paragrapsus quadridentatus* H. Milne Edwards, 1837 (source: www.museum.vic.gov.au/crust/mov1660t.html).

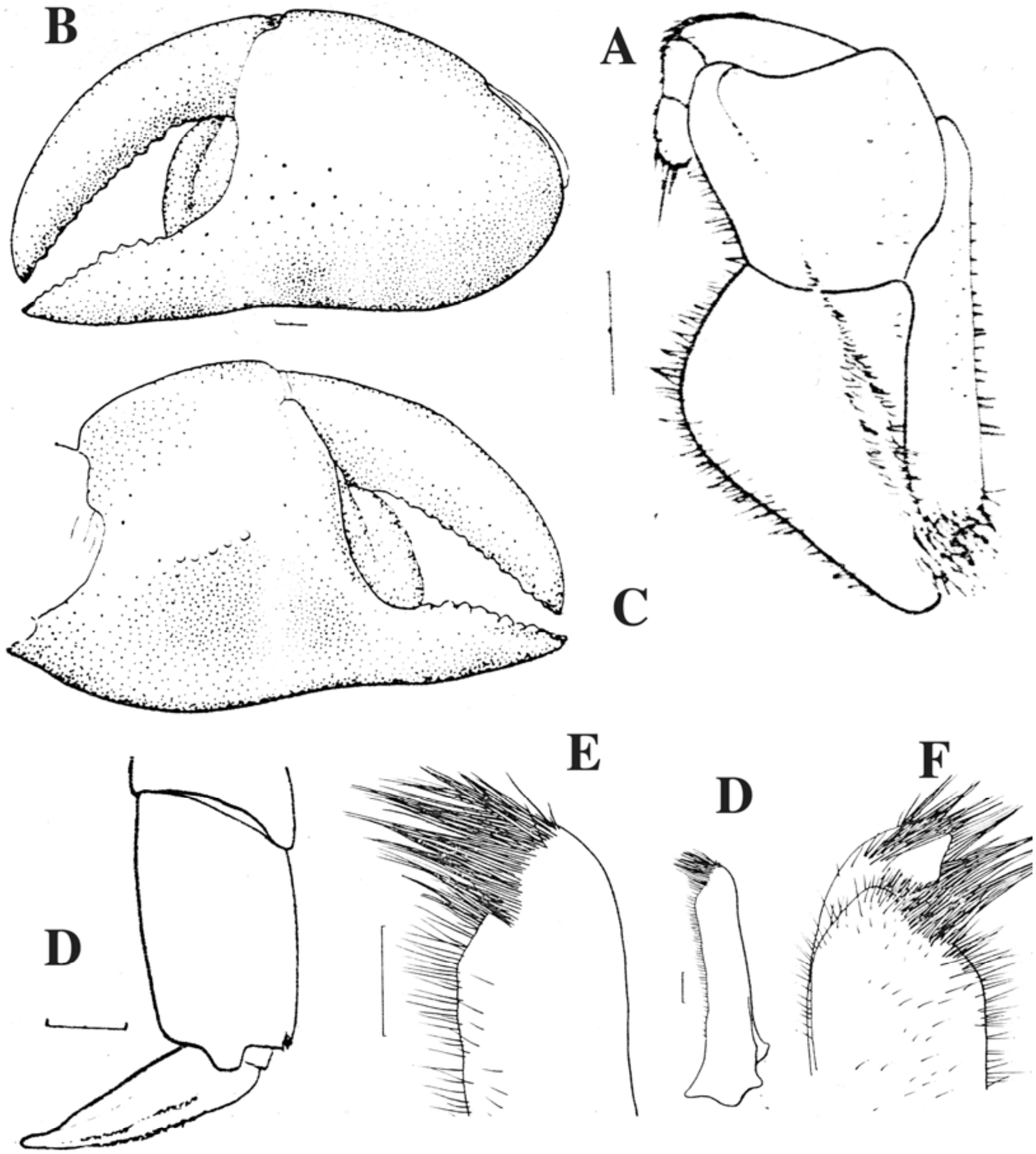



Figure 177. *Paragrapsus quadridentatus* H. Milne Edwards, 1837. A) third maxilliped; B) outer view of chela; C) ineer view of chela; D) part of last ambulatory leg; D) G1; E, F) distal tips of G1. (After Campbell & Griffin, 1966).

### *Paragrapsus gaimardii* (H. Milne Edwards, 1837)

(Figures 178)

*Cyclograpsus gaimardii* H. Milne Edwards, 1837: 79.

*Paragrapsus gaimardii* -H. Milne Edwards, 1853: 196; Haswell, 1882b: 105, pl. 2, fig. 4; Hale, 1927a: 77-80; Tweedie, 1942: 210; Campbell & Griffin, 1966: 164.

*Helice gainardii*– Tesch, 1918: 119.

**Materials examined.**— 1 female (26.4mm x 2.5mm) (QM-W5170), Germatine creek, coll. Campbell *et al*., 20 Sep 1972; 5 males (21.0-39.8mm x 18.9-37.4mm), 3 females (21.6-29.0mm x 19.2-26.2mm), (ZRC 1965.7.271.164-171), south coast of Tasmania, Australia, coll. Mupt, 1940-1941.

**Diagnosis.**— Carapace subquadrangular, almost rounded, slightly broader than long; surface slightly convex, granulated in frontal region; front slightly deflected, anterior margin distinctly bilobed. Infra-orbital ridge with 25 rounded granules. Anterolateral margin with three teeth including orbital tooth, third tooth more like a lobe. Cheliped asymmetrical, surfaces smooth, large in males. Ambulatory legs flat, stout, merus finely serrated on anterior, margins glabrous. (Modified from Campbell & Griffin, 1966).

**Colour.**— The colour of fresh specimens is specimens are yellow brown with dark red spots, chelipeds are orange in colour (Campbell & Griffin,1996), and colour of preserved specimens has not been documented.

**Size.**— The largest male specimen reported is 41mm in carapace width (Campbell & Griffin, 1966), and the size of  female specimen is unknown.

**Habitat.**— It can be found  under stones or in burrows, on sheltered sandy or slightly muddy shores, and on shingly or pebbly beaches, in the shallow subtidal or intertidal areas.

**Remarks.**— The species has been revised by Campbell & Griffin (1966). It has been reported to be a very common shore crab (Campbell & Griffin, 1966) but attempts by the author to make collections in Dampier (Western Australia)and Moreton Bay (Queenland) on towe separate occasions have been futile.

**Distribution.**— Australia (South Australia, Tasmania, Victoria).

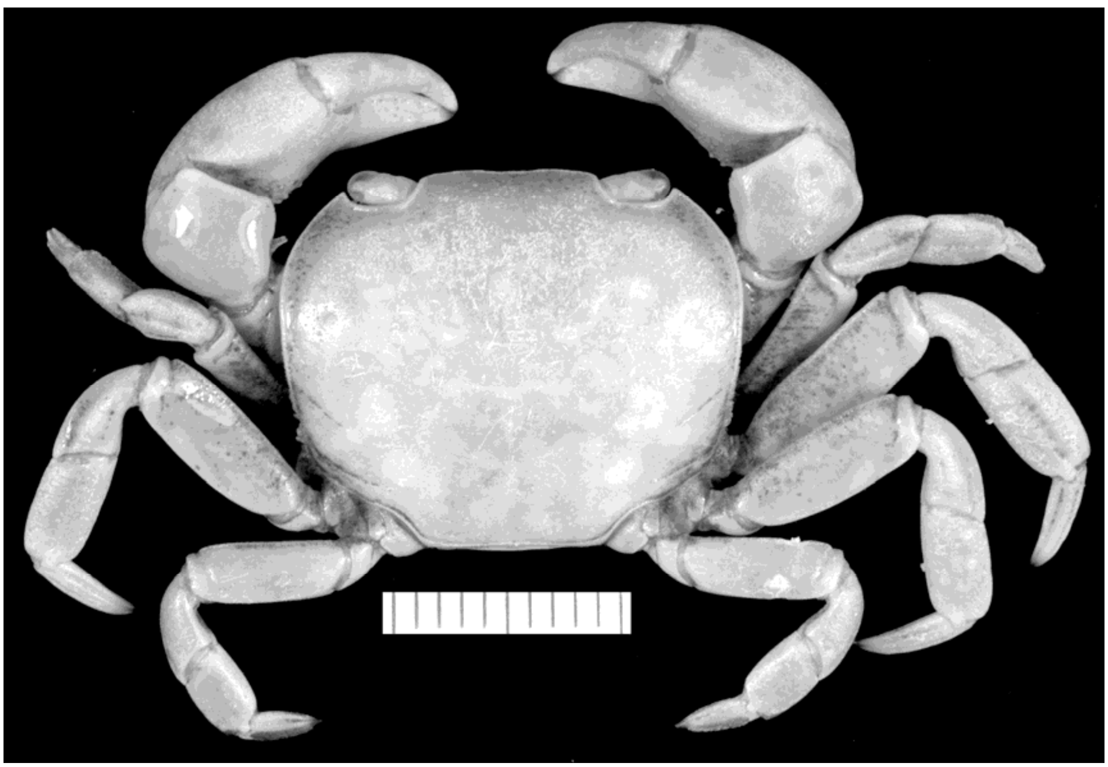


Figure 178. *Paragrapsus gaimardii* (H. Milne Edwards, 1837), male, 29.0mm x 26.2mm (ZRC 1965.7.271.164-171). Dorsal view.

### ***Paragrapsus laevis*** **(Dana, 1852)**

(Figures 179A-C; 180A-F)

*Chasmagnathus laevis* Dana: 1852: 1852: 365, pl. 23,fig. 7; Kingsley, 1880: 222; Haswell, 1882: 106; Miers, 1884: 246; Ortmann, 1894: 728; Fulton & Grant, 1906: 19.

*Paragrapsus laevis* – Heller, 1865: 55; Tesch, 1918: 125; Campbell & Griffin, 1966: 162, text-fig. 8; pl. 12, fig. 2; Davie *et al.*, 1998: 48; Davie 2002: 207.

*Paragrapsus verreauxi* H. Milne Edwards, 1853: 195; Haswell, 1882: 105

**Materials examined.**— 2 males (31.0-34.7mm x 26.0-29.4mm), 1 female (20.7mm x 17.7mm), 1 female (ovigerous) (22.0mm x 18.3mm) (ZRC 1965.7.27.161-163), Sailor's Bay, Syndey, New South Wales, Australia, coll. M.W.F. Tweedie, 1941.

**Diagnosis.**— Carapace quadrangular, slightly broader than long; surface convex, granulated, punctate; front slightly deflected, anterior margin four lobes Anterolateral margin with 3 teeth including orbital tooth, rest of margin beaded. Third maxillipeds close with rhomboidal gape, merus with a broad longitudinal groove medially. Infra-orbital ridge with about 25 large distinct tubercules. Cheliped symmetrical, surfaces smooth. Larger in males. Ambulatory legs flat, stout; First leg setose, other legs glabrous. Male abdomen broadly triangular. G1 narrow, slender. Female gonopore operculate, small.

**Colour.**— The colour of fresh specimens is specimens with numerous red spots (Campbell & Griffin, 1966). The colour of preserved specimens is dark cream to light brown (ZRC 1965.7.27.161-163).

**Size.**— The largest male specimen examined is 34.7mm x 29.4mm, and largest female specimen is 22.0mm x 18.3mm (ZRC 1965.7.27.161-163).

**Habitat.**— It can be found  under stones or in burrows, not penetrating far along estuaries (Campbell & Griffin, 1966).

**Remarks.**— The species has been revised by Campbell & Griffin (1966). It is a very common shore crab.

This is an interesting species. The carapace and male abdomen of this species looks very much like those of *Hemigrapsus* species, but the third maxillipeds of this species have the 'oblique setose piliferous ridge across the external maxilliped' which is typically found in Cyclograpsinae. Hence, this species does not belong to the genus *Hemigrapsus*. have the forms of the mouthparts are typical of *Cyclograpsus* s. l..

It would be interesting to compare the larval development and the DNA data between *Hemigrapsus* sensu stricto and this species, to see how closely related is this taxon to the *Hemigrapsus* sensu stricto.

**Distribution.**— Australia (New South Wales, Queensland, Tasmania, Victoria, Tasmania) only.

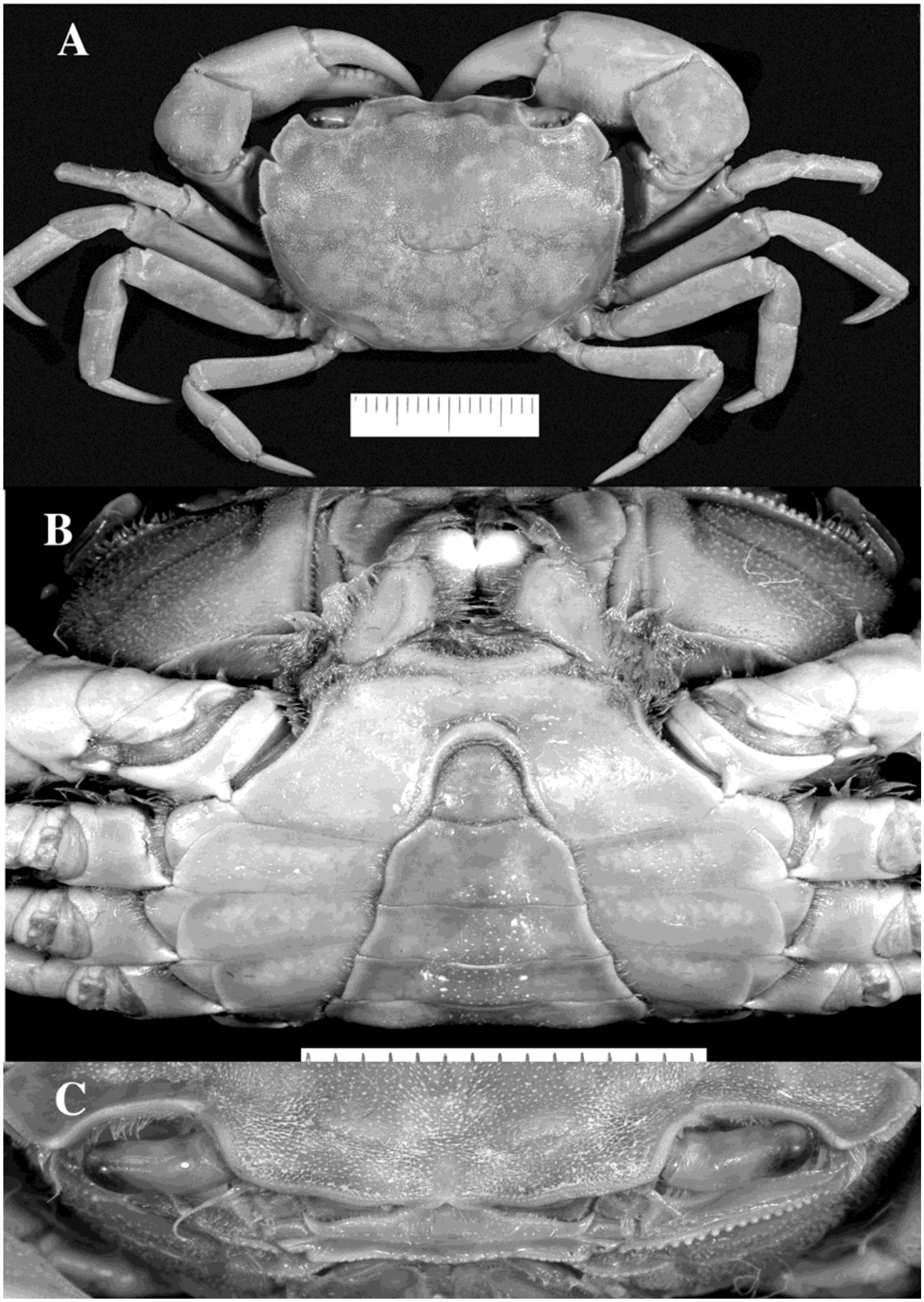



Figure 179. *Paragrapsus laevis* (Dana, 1852), male, 34.7mm x 29.4mm (ZRC 1965.7.27.161-163). A) dorsal view; B) vental view; C) frontal view.

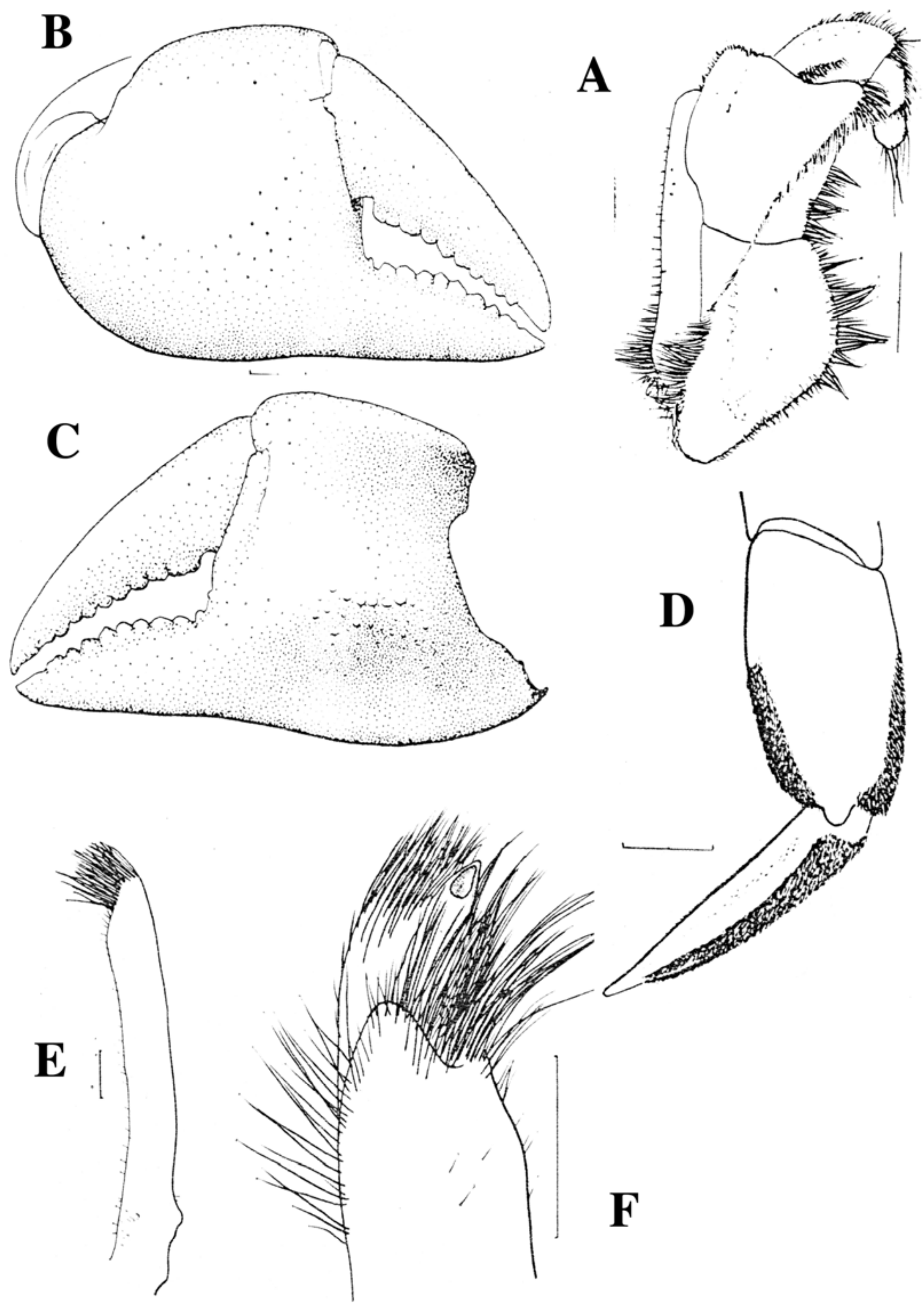



Figure 180. *Paragrapsus laevis* (Dana, 1852). A) third maxilliped; B) outer view of chela; D) inner view of chela; D) part of last ambulatory leg; E) G1; F) distal end of G1. (After Campbell & Griffin, 1966).

### Subfamily Gaeticinae, new subfamily

Varuninae H. Milne Edwards, 1853: 191 (part).

**Diagnosis.**— Carapace subquadrate to elliptical in shape, broader than long, lateral margins usually convex to subparallel; regions discernible, dorsal surface usually glabrous, smooth, physiognomy usually flat; anterolateral margins entire or with one or two or three epibranchial teeth or notches. Front not deflexed; broad, less than half maximum carapace breadth. Orbits open laterally; sub-orbital crest more or less straight, typically long, extending to a short distance across lateral branchial region, stridulatory in conjunction with chelipeds; pterygostomial grooves not opening into anterolateral corner of buccal cavity; pterygostome, sub-branchial, sub-hepatic regions without any reticulation of hooked setae; pterygostome without a deep vertical groove placed subparallel to buccal cavity. Third maxilliped without oblique setose crest extending across merus, outer distal corner of ischium; elongated narrow gape when closed; reaching forward to margin of epistome to completely close buccal cavity anteriorly; exopod normal, narrow; flagella of maxilliped exopods especially elongated, noticeably protruding from behind third maxilliped; palp of exopod markedly elongated, armed with very long brush of setae that reaches almost to abdomen when folded. Endostome smooth, more or less medially prominent. Plastron of sternum with more or less deep longitudinal sulcus anterior to abdomen, into which setal brush of the third maxilliped is folded for protection. Chelipeds usually symmetrical, large in size. Ambulatory legs laterally flattened, oval in cross section, typically more or less narrow, not markedly dorso-ventrally flattened; posterodistal margin of meri not armed with spines; propodi, dactyli not armed with strong black bristles. Abdomen usually with all segments freely moveable (six somites plus telson). Male gonopore is located very far away from coxa, embedded within sternite 8. Female gonopore operculate, usually rounded.

**Type Genus.**— *Gaetice* Gistel, 1835 (replacement name for *Grapsus* (*Platynotus*) De Haan, 1833.

**Gender.**— Masculine.

**Remarks.**— Members of the new subfamily Gaeticinae can be easily recognized, and separated from all other subfamlies by the following suite of characters viz. a) the orbit is open laterally; b) the sub-orbital crest is present, straight, variable in length and stridulatory in function; c) the pterygostomial grooves do not open into the anterolateral corner of the buccal cavity; d) the third maxilliped is without an oblique setose crest extending across the merus and outer distal corner of the ischium; e) the third maxilliped leaves a narrow gape when closed; f) the distal part of the third maxilliped reaches as far as the posterior margin of the epistome, completely closing the buccal cavity; g) the palp of the third maxilliped is markedly elongated and the tip is armed with a very long brush of setae that reaches almost to the abdomen when folded (used for suspension feeding); h) the sternal plastron has a deep longitudinal sulcus anterior to abdomen, into which setal brush of the third maxilliped is folded when not in use; i) the third maxilliped may have a strongly inwardly oblique ishio-meral articulation (*Gaetice*) or normal horizontal articulation (*Setostoma*); j) the exopod of the third maxilliped is normal (*Setostoma*) or slightly enlarged (*Gaetice*); k) the endostome is smooth, more or less medially prominent, and l) the male abdomen has segments 3–6 fused although the suture lines are still evident. Other key characters are also listed in Table 6.

There are currently two genera in this subfamily viz. *Gaetice* Gistel, 1853 consisting of *G. depressus* (De Haan, 1833), and *G. ungulatus* Sakai, 1939, and *Setostoma* which is a new genus established for *Acmeopleura balssi* Shen, 1932, *A. toriumii* Takeda, 1971, and *A. depressa* Sakai, 1965 (see below).

The subfamily Gaeticinae is the only subfamily that exhibits the suspension feeding behaviour. Suspension feeding amongst the Brachyura has been previously reported only in *Gaetice depressus* by Depledge (1989). Suspension feeding is very commonly observed in porcellanid crabs (Robinson & Tully, 2000; Valdovia & Stotz, 2006). Harminto & Ng (1991) have noted that the camptandriid crab, *Baruna* is a also a suspension feeder but in a different way from gaeticinid crabs.

*Setostoma* and *Gaetice* species appear to be quite different from each other in carapace morphology, and the likelihood of a close relationship seems difficult to accept initially. Nevertheless the two genera share three important apomorphies: 1) the palp of the third maxilliped carries long setae clearly used for suspension feeding; 2) the anterior segments of the sternum have a longitudinal sulcus, into which the maxillipedal setae rest; and 3) the male abdomen has segments 3–6 fused and immoveable event hough the suture loines are still evident. This set of characters is unique among the grapsoid crabs, and it seems to point strongly to a monophyletic lineage.

There is strong evidence that all the *Setostoma* species live as commensals in the burrows of thalassinidean shrimps or other burrowing invertebrates such as large polychaetes or perhaps echiuroids. Davie (1989) and Sakai (2000) have reported the probable association of *D. toriumii* with the large mud-shrimp *Upogebia major* and *Upogebia yokoyai*, and this has been confirmed by recent work by Itani (2001, 2003, 2004). Sakai (1976) reported *D. balssi* as "found associated with annelids". Itani *et al.* (2002, 2004) has found *D. depressa* in the burrows of thalassinideans.

Given that *Setostoma* species are commensals with other animals in burrows, this would place significant constraints on their morphology, leading to the loss of anterolateral teeth, small, slender, unarmed legs, and a smooth, glabrous rounded carapace. Thus, a commensal versus a free-living habit helps explain the substantial differences between *Gaetice* and *Setostoma* species.

**Key to genera in Gaeticinae**

1a. Carapace distinctly rounded, dorsal surface punctate,convex. --------- ***Setostoma***

1b. Carpace distinctly quadrangular, dorsal surface glabrous, flat. --------------- ***Gaetice***

## Genus *Setostoma*, new genus

*Acmaeoplerua* – Stimpson, 1858: 106; 1907: 130; Kim, 1973: 461, 463 (part, not *Acmeopleura* 1858).

**Type species.**— *Acmeopleura balssi* Shen, 1932, by present designation.

**Diagnosis.**— Carapace rounded, eliptical, broader than long; dorsal surface glabrous, regions not well defined, very convex. Frontal margin slightly convex, bilobed. Anterolateral margin subcristate without teeth, external orbital tooth distinct, acute. Posterolateral margins not sharply demarcated from anterolateral margin distinctly converging. Orbits small, eyes completely filling orbit, Third maxilliped short, broad. Small, distinct rhomboidal gape when closed, palp slender, long, with long setae. Exopod with short flagellum. Epistome broad, flat, posterior margin entire. Inner, outer surface of chela setose; outer surface of pollex and manus with tufts of long, stiff setae; fingers shorter than palm. Ambulatory legs slightly setose, long dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates with distinct medial grooves. Male abdomen narrowly triangular, segments 3-6 fused but sutures still visible.

**Etymology.**— From the Greek, *sestron*, meaning sieve, and *stoma* for mouth. It is used as a noun.

**Gender.**— Neuter.

**Remarks.**— *Setostoma* is here restricted to three species viz. *A. balssi* Shen, 1932, *A. depressa* Sakai, 1965, and *A. toriumii* Takeda, 1971. All three species are associated with upogebiids and callianassids (Itani, 2004). The two ‘real’ *Acmeopleura* species are free living and they have been retained in the subfamily Varuninae (see above).

*Setostoma*, new genus, is distinctly different from *Acmeopleura* in the the following key characters a) its carapace almost elliptical (vs. subquadrangular in *Acmeopleura*), b) the inner surface of the chela setose (vs. inner surface granulated in *Acmeopleura*); c) the anterior sternal plates has a distinct medial sulcus (vs. absent of medial sulcus in *Acmeopleura*); and d) the male abdomen has segments 3-6 fused (vs. seven free segments in *Acmeopleura*). The other differences are list in Table 5 (see below).

*Setostoma* is also distinctly different from *Gaetice* the following features a) the carapace is almost elliptical in shape (vs. quadrangular in shape in *Gaetice*); b) the anterolateral margin is entire (vs. with three teeth in *Gaetice*); c) the third maxillipeds are short and broad (vs. long and slender in *Gaetice*); and d) the suture between merus and ischium of third maxillipeds is horizontal (vs. diagonal in *Gaetice*). The other differences between *Setostoma* and *Gaetice* are fully documented in the Table 5 below.

Although the habits of this genus have been studied in details by Itani and co-workers (2002, 2005) in recent years, the reproductive biology of these taxa are still not known. It will be interesting to see how they reproduce as they are living in association with upogebiids and callianassids in the burrow. Questions like how does the female leave the burrow to spawn or how do the juveniles seek a suitable host, or is the larval development abbreviated etc. all need to be investigated.

Table 6. Table showing the key characters between the three genera *Acmaeopleura* (subfamily Varuninae), *Setostoma* and *Gaetice* from subfamily Gaeticinae.

| **Characters** | ***Acmaeopleura*** | ***Setostoma*** | ***Gaetice*** |
|---|---|---|---|
| **Carapace shape** | Subquadrangular | Elliptical | Quadrangular |
| **•Anterolateral teeth** | No obvious tooth | No tooth | Three teeth |
| **•Carapace surface** | Setose | Glabrous | Punctate |
| **Third maxilliped** | Short, stout | Short, stout | Long, slender |
| **•Suture between merus, ishchium of third maxillipeds** | Horizontal | Horizontal | Diagonal |
| **•Palp of third maxiliped** | Short palp with short setae | Short palp with long setae | Long palp with very long setae |
| **Chelipeds** | Short, stout | Narrow, slender | Short, stout |
| **•Cheliped fingers** | Distinctly longer than palm, long with numerous teeth | Distinctly shorter than palm, very short with teeth | Longer than palm, long with very few teeth |
| **•Inner surface of cheliped** | Large granules present | Covered with short setae | Small granules present |
| **Last ambulatory legs** | Short, stout, densely setose | Long, slender, slightly setose | Short, stout, slightly setose |
| **•Dactylus of last leg** | Short, stout | Long, slender | Long, slender |
| **Abdomen (male)** | Broadly triangular, seven free segments | Triangular, segments 3-6 fused | Narrowly triangular segments 3-6 fused |
| **Male telson** | Subrectangular | Subtriangular | Triangular |
| **Female telson** | Broadly triangular | Quadrangular | Broadly triangular |
| **Sternum - anterior sternal plates** | No medial sulcus | With broad medial sulcus | Deep, narrow, medial sulcus |

| | | | |
|---|---|---|---|
| **Habitat** | Found under stones with grasses | Found with thalassinidean shrimp | Found under stones on sandy or rocky shores |

**Key to species in *Setostoma***

1a. Carapace rounded; front produced. Ambulatory legs broad, short. ------ ***S. depressa***

1b. Carapace rounded; front produced. Ambulatory legs long, slender. --------- **2**

2a. Ambulatory very long, slender. Male abdomen narrowly triangular. ------ ***S. balssi***

2b. Ambulatory long, slender. Male abdomen broadly triangular. ------------ ***S. toriumii***

## *Setostoma balssi* (Shen, 1932), new combination

(Figure 181)

*Acmaeopleura balssi* Shen, 1932: 155, text-figs. 98-101, pl. 6, fig. 1-2; Shen & Dai, 1964: 125; Crosnier, 1965: 44, figs. 60-62; Sakai, 1965: 197, text-fig. 26b; Sakai, 1976: 643, pl. 220, fig. 1; Kim, 1973: 463, text-fig. 200, pl. 92, fig. 153; Dai *et al.*, 1986: 472, text-fig. 265, pl. 66, fig. 5; Dai & Yang, 1991: 518, text-fig. 265, fig. 2-3, pl. 66, fig. 5; Ghani & Tirmizi, 1991: 93; Itani, 2002: 129: Itani *et al.*, 2002: 43; Itani, 2004: 33; Itani *et al.*, 2005: 1.

**Materials examined.**— **Neotype** – 1 male (IZAS) (cracked carapace), Yantai, Shangdong Province, China, coll. 1 Feb. 1948. – **Others** – 1 male (3.7mm x 3.0mm) (MNHN-MPB-18854), Madagascar, coll. 11 Jul. 1967; 1 male (13.2mm x 9.6mm), 1 female (10.3mm x 8.0mm) (NSMT-Cr-11327), Sagami Bay, Japan, coll. H. Ikeda, no collection date; 1 female (6.1mm x 4.5mm) (SFM spec, dry), Marayama, Japan, coll. 18 Dec. 1952, no collection date; 1 specimen (SFM spec, dry), Hiroshima, Japan, collected with *Upogebia*, coll. 1958; 1 male, 1 female in pieces (SFM specs, dry), Hiroshima, Japan, collected in the *Upogebia* tunnels, coll. 17 Oct. 1958; 1 male (stuck to bottle) (SFM-no cat. number, dry), Japan, coll. 1 Aug. 1932; 1 male (16.9mm x 13.4mm) (SFM, ex T. Sakai collection), Fushiki, Toyama, Japan, no collection date; 1 dried specimen stuck to bottle (SFM, ex T. Sakai collection), Hiroshima, found in *Upogebia* tunnel, coll. 1958.

**Diagnosis.**— Carapace almost subcircular, dorsal surface convex, punctate, regions not defined. Anterolateral margins with only orbital tooth. Third maxilliped very broad; ischium, merus broad, an elongated narrow gape when closed, plap with very long bristle extending beyond first sternal segment, exopod very narrow. Cheliped symmetrical, large, glabrous, finger shorter than palm. Ambulatory legs long, slender, sparingly setose. Male abdomen narrowly triangular in shape, telson broadly triangular. G1 long, slender. Female gonopore operculate, circular in shape.

**Colour.**— The colour of fresh specimens is unknown but all preserved specimens examined are cream to light brown in colour (see above under Materials examined).

**Size.** — The largest male specimen examined is 16.9mm x 13.4mm (SFM, ex T. Sakai collection), and largest female examined is 10.3mm x 8.0mm (NSMT-Cr-11327).

**Habitat.**— It can be found in tunnels with upogebiids and callianassids, under rocks or muddy vegetation, along the banks of rivers (Itani 2000, Itani *et al.*, 2002).

**Remarks.**— This species is very rare, and not easily collected, and it has been reported to be found in burrows of annelids, echiurans, and upogebiids (Sakai, 1976; Ghani & Tirmizi, 1991; Itani *et al.*, 2004).

The type specimen of *S. balssi* (Shen, 1932) is believed to be lost. Several checks with the Institute of Zoology, The Chinese Academy of Sciences, Beijing (G.X. Chen, pers. comm.); Beijing Natural History Museum (S.L. Yang, pers. comm.); Institute of Oceanography, The Chinese Academy of Sciences, Qingdao (R.Y. Liu, H.L. Chen, pers. comm.), and the British Museum of Natural History (P.F. Clark, pers. comm.) could not track down the location of the specimen. The type locality of this species is Shangdong Province in northeastern China. Several attempts to collect fresh specimens for a neotype from the coastal region of China (Fujian and Guangdong Provinces in 1998, Tianjin and Qingdao in 2000, Guangdong Province in 2005, Fijian Province in 2005, Tianjin and Qingdao in 2005) have been unsuccessful. As such, the male specimen with a cracked carapace from Yantai (IZAS) will be selected as the neotype from Yantai (IZAS) is here selected as the neotype to stabilize the taxonomy of the species.

This species can be found from East Asia to Madagascar (Crosnier, 1965).

**Distribution.**— Taiwan, China, Japan, Pakistan, Madagascar.

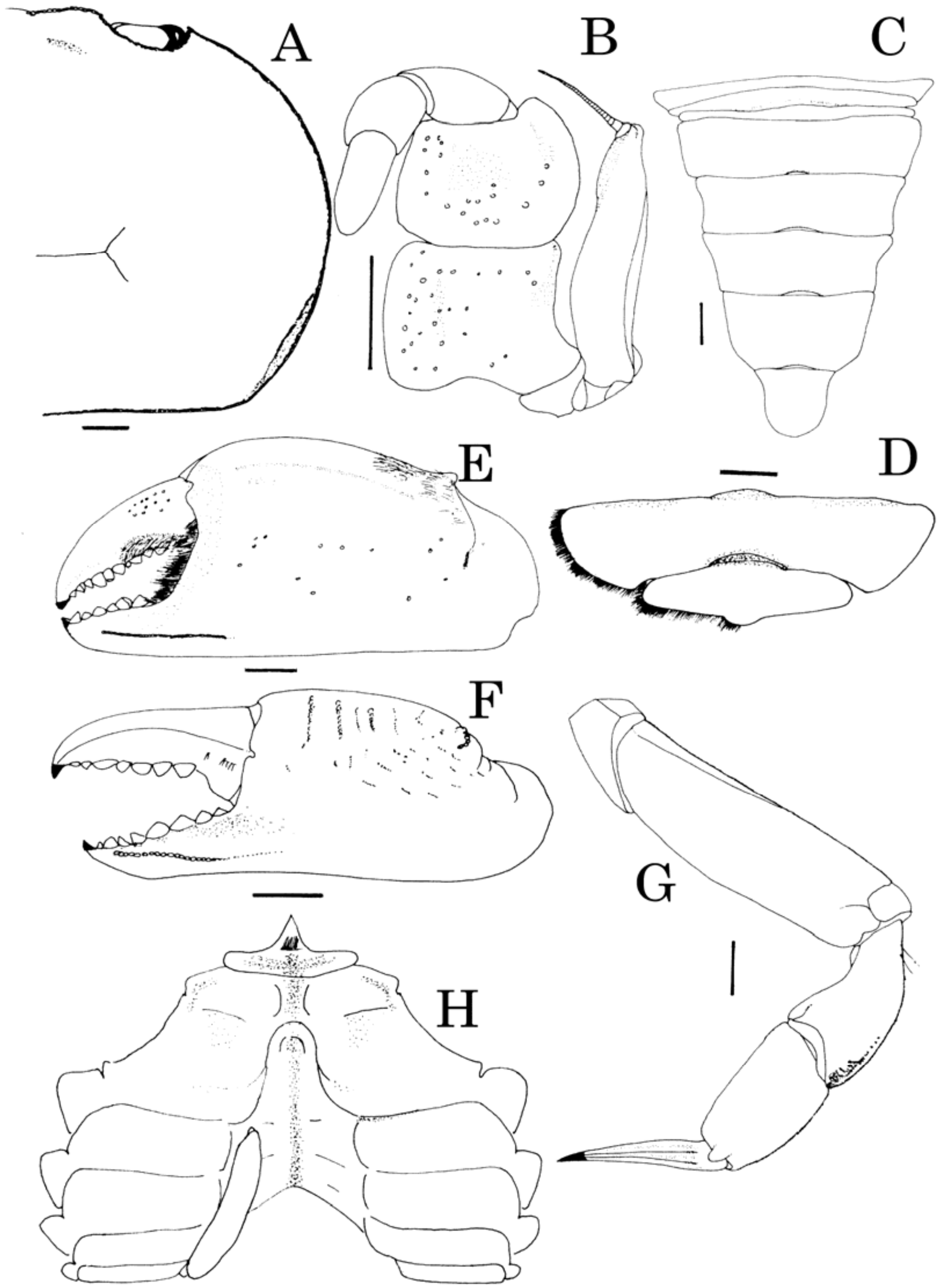



Figure 115. *Setostoma balssi* (Shen, 1932), male, 13.2mm x 9.6mm; female, 10.3mm x 8.0mm (NSMT-Cr-11327). A) carapace; B) third maxilliped; C) male abdomen; D) female abdomen (part); E) male chela; F) female chela; G) last ambulatory leg; H) male sternum. (Scale=1.0mm)

### *Setostoma depressa* (Sakai, 1965), new combination

*Acmaeopleura balssi* – Sakai, 1939: 663, text-fig. 116.

*Acmaeopleura depressa* Sakai, 1965: 191, pl. 91, fig. 4, text-fig. 26a; 1976: 643, text-fig. 352; Itani, 2004: 33; Itani *et al.*, 2005: 1.

**Materials examined.— Holotype** – 1 female (5.5mm x 4.5mm) (SFM-24720, ex T. Sakai collection), Japan, leg. K. Sakai, no collection date.

**Diagnosis.**— Carapace almost subcircular, dorsal surface convex, punctate, regions not defined. Anterolateral margins with only orbital tooth. Third maxilliped very broad; ischium, merus broad, exopod very narrow. Cheliped large, with a tift of long soft setae on outer surface of immovable finger. Ambulatory legs short, slender, covered with short setae. G1 long, slender, length to width ratio 8.2, almost straight, distal end slightly bilobed. Female gonopore operculate, circular in shape.

**Colour.**— The colour of fresh specimens has not been documented, the only preserved specimen examined (holotype) is cream in colour.

**Size.**— The largest male size is has not been recorded, but the largest female is 5.5mm x 4.5mm (holotype).

**Habitat.**— They were probably dug out from under rocks or muddy vegetation, along the banks of the river, associated with upogebiids and callianassids (Itani, 2004; Itani *et al.*, 2004).

**Remarks.**— This species is symbiotic with upogebiids and callianassids (Itani, 2004; Itani *et al*., 2004). No drawings was done as the holotype was a dried specimen.

**Distribution.**— Japan only.

### *Setostoma toriumi* (Takeda, 1971), new combination

(Figure 182A-H)

*Acmaeopleura toriumi* Takeda, 1971: 13; Itani *et al.*, 2002: 43; Itani, 2004: 33; Itani *et al.*, 2005: 1; Karasawa & Tanaka, 2005: 95; Anker *et al.*, 2005: 179.

**Materials examined.**— **Holotype** – 1 male (4.5mm x 4.0mm), (NSMT-Cr-971), shore of Onagawa Bay, Japan, coll. M. Toriumi, 10 Jul. 1972. – **Others** – 2 males (5.6-5.9mm x 4.7-4.9mm), 1 female (ovigerous) (5.6mm x 4.7mm) (QM-no cat. number), Yamaguchi Bay, Seto Inland Sea, Yamagichi Prefecture, Japan, coll. G. Itani, 7 May 1997.

**Diagnosis.**— Carapace almost subcircular, dorsal surface convex, punctate, regions not defined. Anterolateral margins with only orbital tooth. Third maxilliped very broad; ischium, merus broad, exopod very narrow. Cheliped large, with a tuft of soft setae at base of immovable finger. Ambulatory legs short, slender, covered with short setae. Male abdomen broadly triangular. Telson broad. G1 long, slender. Female gonopore operculate, circular in shape.

**Colour.**— The colour of fresh specimens has not been documented but all preserved specimens examined are cream to light brown in colour.

**Size.** — The largest male specimen examined is 5.9mm x 4.9mm (QM-no cat. number), and the largest female examined is 5.6mm x 4.7mm (QM-no cat. number).

**Habitat.**— It can be found associated with echiurans, upogebiids and callianassids along the banks of the river (Davie, 1992; Itani, 2002, 2004).

**Remarks.**— The species is reportd to be the co-habitant of burrows of echiurans, upogebiids, and callianassids (Davie, 1992; Itani, 2002, 2004).

**Distribution.**— Japan only.

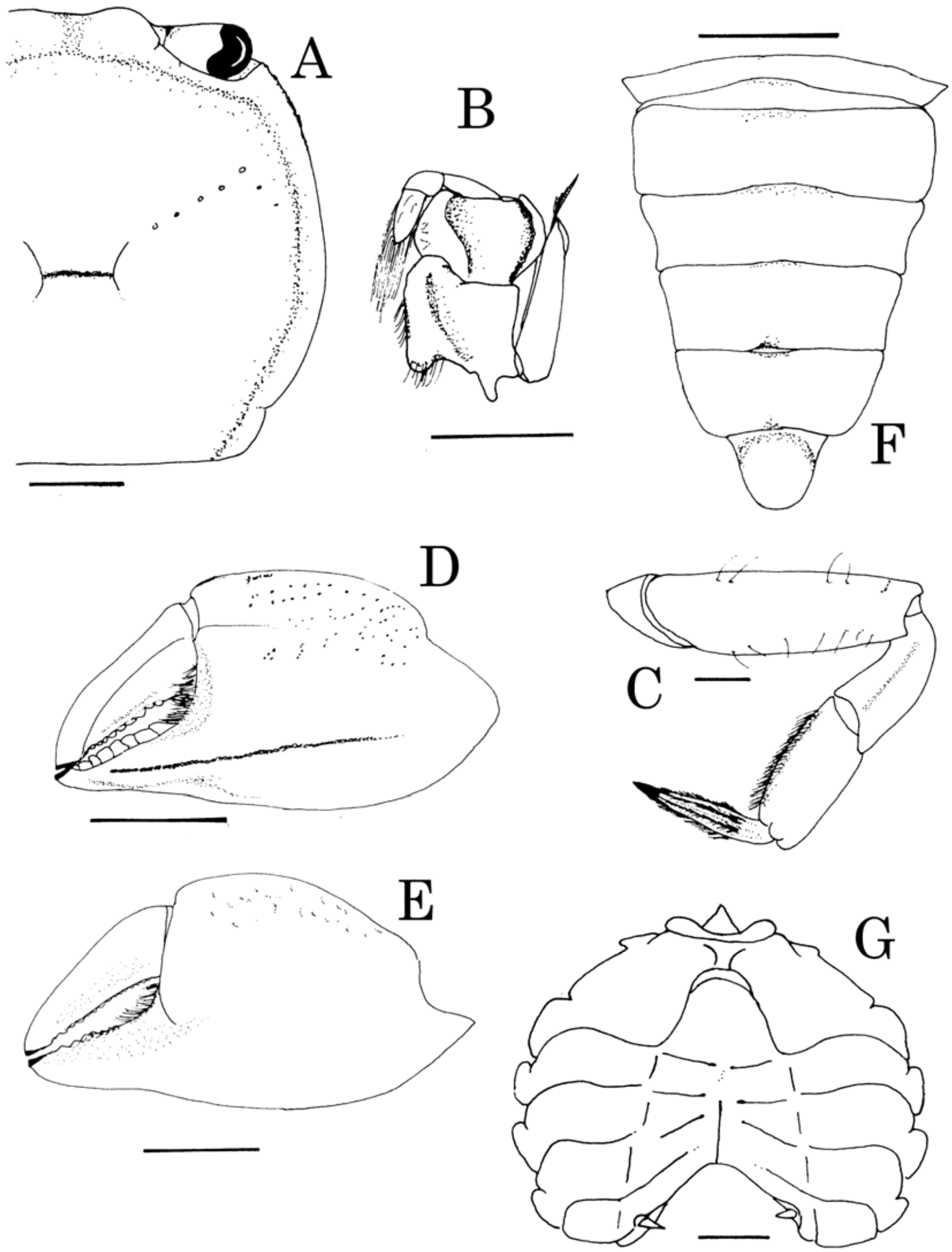



Figure 182. *Setostoma toriumii* (Takeda, 191971), male, 5.9mm x 4.9mm; female, 5.6mm x 4.7mm (QM-no cat. number). A) carapace; B) third maxilliped; C) male abdomen; D) female abdomen (part); E) male chela; F) female chela; G) last ambulatory leg; H) male sternum. (Scale=1.0mm).

## Genus *Gaetice* Gistel, 1835

*Grapsus (Platygrapsus)* De Haan, 1833: 63.

*Gaetice* Gistel, 1835: 10; Tesch, 1918: 84; Sakai, 1939: 677, pl. 47: 3; 1976: 652; Horikawa, 1940: 29; Lin, 1949: 29; Kim, 1973: 744; Miyake, 1983: 176; Dai *et al.*, 1986: 482; Fukui *et al.*, 1989: 229; Dai & Yang, 1991: 528; Shih *et al.*, 1991: 142; Huang, 1994: 597; Wang & Liu, 1996a: 113, figs. 144, 145; Wang & Liu, 1996b: 86; Jeng *et al.*, 1998: 59; Ng *et al.*, 2001: 44.

*Platynotus* De Haan, 1853: 34.

*Platygrapsus* Stimpson, 1858: 107; 1907: 128.

**Type species.**— *Grapsus (Platygrapsus) depressus* De Haan, 1853, by monotypy.

**Gender**.— Feminine.

**Diagnosis.**— Carapace quadrangular, broader than long; dorsal surface glabrous punctate; regions well defined, flat Frontal margin convex, bilobed. Anterolateral margin subcristate with three teeth including orbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, concave at branchial region, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped with an oblique suture between merus, ischium. Medial sulcus on anterior sternal plates narrow. Infraorbital ridge with numerous small, round granules. Small, distinct elongated gape when closed, palp with a brush of long setae. Epistome broad, flat, posterior margin entire. Chela large, sometimes asymmetrical, surfaces glabrous, fingers as long as palm. Ambulatory legs with short setae, stout dactylus. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates with distinct medial grooves for the setal brush to sit in. Male abdomen narrowly triangular with all segments freely moveable (six somites plus telson).

**Remarks.**— The genus *Gaetice* used to comprise three species viz. *G. depressus* De Haan, 1833, *G. ungulatus* Sakai, 1939 and *G. americanus* Rathbun, 1923. However, *G.*

*americanus* is distinctly different from its two genera and it has been removed to it new genus, *Pseudogaetice* (see above), and remains in the subfamily Varuninae. As such, there are only two species in *Gaetice* as defined here

**Key to species in *Gaetice***

1a. Carapace subquadrate; frontal margin strongly lobed. ------------------------ **2a**

1b. Carapace subquadrate; frontal margin weakly lobed. --------------------------- **2b**

2a. Infraorbital ridge with numerous small, round granules. Propodus of last ambulatory leg short, broad. --------------------------------------------------------- ***G. depressus***

2b. Infraorbital ridge with few large, round granules. Propodus of last ambulatory leg longer, more slender. ----------------------------------------------------- ***G. ungulatus***

## *Gaetice depressus* (De Haan, 1833)

(Figures 183; 184A-I)

*Grapsus* (*Platynotus*) *depressus* De Haan, 1833: 63, pl. 8, fig. 2.

*Platygrapsus convexiusculus* Stimpsom, 1858: 104; 1907: 128, pl. 17, fig. 3.

*Gatice depressus*— Jeng *et al.*, 1994: 98; Yu *et al.*, 1996: 15; Jeng *et al.*, 1996: 100; Jeng, 1997: 18; Jeng *et al.*, 1998: 123 (wrong spelling).

*Gaetice depressus* — Blass, 1922: 50; Maki & Tsuchiya, 1923: 100; Urita, 1926: 25; Gordon, 1931: 528; Shen, 1932: 180, text-fig. 114-116, pl. 7, fig. 4; Sakai, 1934: 323; 1935: 230, pl. 61, fig. 3; 1939: 677, pl. 47: 3; Sato, 1936c: 1951; 1936d: 137; Horikawa, 1940: 29; Kamita 1941: 209, text-fig. 116; Lin, 1949: 29; Kim, 1973: 477, text-fig. 211, pl. 43, fig. 162; Miyake, 1983: 176; Dai *et al.*, 1986: 482, fig. 270: 3–4, pl. 68: 1; Fukui *et al.*, 1989: 229; Dai & Yang, 1991: 528, fig. 270: 3–4, pl. 68: 1; Shih *et al.*, 1991: 142; Yamaguchi & Baba, 1993: 470, fig. 179; Huang, 1994: 597; Hsueh, 1996: 35; Wang & Liu, 1996a: 113, figs. 144, 145; Wang & Liu, 1996b: 86; Jeng *et al.*, 1997: 100; Jeng *et al.*, 1998: 59; Ng *et al.*, 2001: 44.

**Materials examined.**— **Lectotype** – 1 male (25.6mm x 21.3mm) (RNHM-1226), Japan, coll. P.F. von Siebold, 1823-1829 (det by Yamaguchi & Baba, 1993). – **Paralectotype** – 1 female (12.1mm x 10.0mm) (RNHM-1227), Japan, coll. P.F. von Siebold, 1823-1829; 4 specimens mounted on board (RNHM-D-42279, dry), Japan, coll. P.F. von Siebold, 1823-1829. – **Others** – **China** – 11 males (8.9-20.9mm x 7.2-17.8mm), 9 females (10.0-17.0mm x 8.0-15.2mm), 3 females (ovigerous) (12.3-12.8mm x 10.0-10.3mm) (MNHN-B-12089), Amoy, China, coll. C.F. Wang, Jul. 1925; 1 male (11.3mm x 9.9mm), 6 females (8.9-13.3mm x 7.0-10.9mm) (MNHN-B-12091), Tonkin, coll. 1897; 11 specimens mounted on board (RNHM-D-45218, dry), Amoy, China, coll. 1859-1862, leg. G. Schlead; 8 males (16.2-24.3mm x 15.7-20.4mm), 8 females (11.4-20.5mm x 9.6-17.3mm) (SFM-22115), Shilaroren, Qingdao, Shangdong Province, China, coll. M. Tuerkay, 16 Apr. 1992; 1 male (22.2 x 18.5mm) 1 female (11.5 x 10.0mm) (USNM64952), Amoy China, coll. C.J. Shen, Nov. 1928; 4 males (10.5-17.0 x 9.1-14.5mm) 8 females (9.0-15.5 x 7.8-13.0mm) (ZRC-uncatalogued), Seashore along road from Changpo to Huiren, Hainan Island, China, coll. N.K. Ng & Y. Cai, 1 Dec. 1998; 10 males (14.5-21.3 x 12.3-17.5mm) 2 females (13.3-16.6 x 11.7-13.8mm) (ZRC-uncatgalogued), Bainu Beach, Nan'ao Island, Guangdong Province, China, coll. N.K. Ng & Y. Cai, 13 Nov. 1998; 4 males (10.5-17.8mm x 9.1-15.2mm), 4 females (9.6-15.2mm x 8.2-13.0mm), 4 females (ovigerous) (9.0-

14.7mm x 7.8-12.0mm), (ZRC-uncatalogued/nnk0053), Seashore along from Changpo to Huiwen, Hainan Island, Guangdong Province, China, coll. Y. Cai & N.K. Ng, 1 Dec. 1998; 10 males (14.5-21.3mm x 12.3-17.5mm), 2 females (13.3-16.0mm x 11.7-13.3mm) (ZRC-uncatalogued), Bainu Beach, Nan'ao Island, Guangdong Province, China, coll. Y. Cai & N.K. Ng, 13 Nov. 1998; 7 males (6.2-16.6mm x 5.5-14.2mm), 6 females (9.6-16.8mm x 8.1-13.0mm), (ZRC- uncatalogued/nnk0062), Feng'er Beach, Nan'ao Island, Guangdong Province, China, coll. Y. Cai & N.K. Ng, 14 Nov. 1998. – **Hong Kong** – 1 males (12.1-22.5mm x 10.0-18.8mm), 3 females (12.3-15.3mm x 10.3-12.8mm), (ZRC 1998.1023), inner Tolo Habour, Wu Kwai Sha, New Territories, Hong Kong, coll. P.K.L. Ng & S.Y. Lee, 6 Jun. 1996; 10 males (1.4-21.9mm x 10.3-18.3mm), 4 females (10.5-17.2mm x 8.8-14.1mm), 1 female (ovigerous) (14.5mm x 11.9mm), (SFM-12042), Hong Kong, coll. Galathea Expedition, leg. Behn, no collection date; 1 male (12.0mm x 10.7mm) (MNHN-B-9133), Hong Kong. – **Japan** – 2 specimens mounted on board, cracked carapace, (MNHN-10911), Japan, no collection date; 3 specimens mounted on board, (MNHN-10808), exchanged from Leiden Museum, Japan, no collection date; 2 specimens mounted on small board, (MNHN-3622), Japan, no collection date; 2 specimens mounted on board (MNHN-3620), Japan, coll. 1865; 1 specimen mounted on board, carapace damaged, (MNHN-3619), exchanged from Leiden Museum, Japan, no collection date; 10 males (6.8-17.3mm x 6.0-14.9mm), 6 females (9.3-11.7mm x 8.5-9.8mm), 3 females (ovigerous) (10.1-17.7mm x 8.6-14.5mm), (MNHN-B-12090), Tokyo area, Japan, coll. Harmand, 1906. 1 male (17.0mm x 14.2mm) (QM-uncatalogued), Sakada, Shirahama, Wakayama Prefecture, Japan, coll. Y. Fukui, 6 Aug. 1996; 8 specimens mounted on board (RNHM-D-45217, dry), no collection data; 1 mounted specimen found among other species (RHNM-D-45219), Japan, coll. leg. P.F. von Siebold, 1823-1824; 9 males (13.5-22.2mm x 11.8-19.2mm), 1 female (20.0mm x 17.8mm), 5 females (ovigerous) (13.6-21.4mm x 12.0-17.5mm) (RNHM-D-1225), Amoy, China, coll. G. Schlegel, no collection date; 2 males (10.3-20.0mm x 8.9-17.2mm), 3 females (10.0-15.8mm x 9.3-12.3mm) (RMNH-D-12461), Shirahama, Wakayama Prefecture, Japan, coll. S. M. Shino, 7 Aug. 1958; 1 male (21.2mm x 17.9mm), 1 female (ovigerous) (16.0mm x 13.3mm) (RMNHM-D-25135), Sagami Bay, Kanagawa Prefecture, coll. H. Suzuki, 10 Sep. 1968; 1 female (9.4mm x 8.2mm) (RNHM-D-25136), Ariake Bay, northwest of Simabara, Kyukyus, Japan, coll. T. Sakai & L.B. Holthuis, 8 Sep. 1968; 13 males (17.9-24.7mm x 15.4-21.2mm), 1 female (20.6mm x 16.8mm), 1 female (ovigerous) (16.2mm x 13.3mm), (RHNM-D-41894), Matsushima, Amakusa, Kyushu, Japan, coll. T. Yamguchi, 4 Sep. 1985; 3 males (12.7-15.2mm x 11.1-12.8mm) (RU-uncatalogued), rivermouth of Okukubi River, Okinawa Island, Ryukyus, Japan, coll. 27 Jun. 1987; 1 male (12.6mm x 10.8mm) (RU-uncatalogued), Mizura River, Iriomote Island, Ryukyus, Japan, coll. 2 Oct. 1987; 3 males (10.0-14.4mm x 8.5-12.4mm), 2 females (11.4-13.2mm x 9.3-11.3mm) (RU-uncatalogued), Okinawa, Japan, coll. 5 Aug. 1984; 1 male (7.6mm x 6.2mm), 3 females (7.1-8.4mm x 6.0-6.8mm), (RU-uncatalogued), Okinawa, Japan; 1 male (30.4mm x 27.0mm) (SFM-7655), Sagami Bay, Japan, leg. T. Sakai; 4 males (6.0-15.2mm x 4.8-12.9mm), 1 female (13.5mm x 11.2mm), (SFM-7685), Ishigaki Island, Okinawa, Japan, leg. T. Sakai; 2 males (22.3-25.4mm x 18.2-20.9mm), 3 females (15.9-19.3mm x 13.0-15.6mm) (SFM-no cat. number), Minamizu, Japan, leg. T. Watanabe, no collection date; 8 males (7.0-14.4mm x 6.1-12.2mm), 4 females (7.0-11.2mm x 5.9-9.4mm) (SFM-22487), Okinawa, Japan, coll. Aug. 1983, leg. R. Hiza; 1 male (16.7mm x 14.4mm) (SFM-no cat. number), Ohsima, Amami, Japan, coll. 31 Mar. 1968; 41 males (6.6-15.1mm x 6.4-13.2mm), 8 females (8.4-14.5mm x 7.1-12.4mm), (SFM-no cat. number), Okinawa, Japan, leg. T. Sakai, no collection date; 1 male (16.0mm x 13.5mm) (USNM-60247), Hokkaido Imperial University, Wakayma Prefecture, Honshu, Japan, coll. M. Sasaki, 1925; 2 males (24.0-31.2 x 21.0-26.0mm) (USNM-54500), Hokkaido, Japan, coll. M. Sasaki, Jul. 1916; 2 males (16.6-20.5mm x 13.8-17.1mm) (USNM-18834), Ohosima, Yokata Coast, Japan, coll. Sakamoto, no collection date; 2 males (16.7-24.0 x 14.0-20.4mm) 1 female (20.1mm x 16.6mm) (USNM-62867), Misaki, Japan, coll. A.S. Pearse 7 Aug. 1929; 2 males (12.0-15.3mm x 10.0-12.8mm), 1 female (13.0mm x 11.8mm), (ZMA-de-240140), Tokyo, Japan, coll. Harmond, 1906**. – Korea** – 5 males (11.0-27.3mm x 9.5-22.6mm), 1 female (ovigerous) (20.mm x 16.9mm), (ZRC-uncatalogued/nnk0186), rocky tidal pools, Seong San Beach, Cheju Island, South Korea, coll. N.K. Ng & J.C.Y. Lai, 28 Aug. 2002. – **Taiwan** – 3 males (15.4-19.6mm x 12.3-16.0mm), 1 female (16.6mm x 14.0mm) (ASIZ-71687), He-Mei, Taiwan, coll. M.S. Jeng, 4 Nov. 1997; 1 female (16.2mm x 14.4mm) (TMCD/CHCD-no cat. number), no data, coll. H.C. Liu, no collection date; 3 males (16.7-20.4mm x 13.7-17.4mm), (TMCD/CHCD -no cat. number), Ao-Di, Taiwan, coll. H.C. Liu, 6 Jun. 1971; 4 males (18.3-21.2mm x 16.0-18.0mm) (TMCD/CHCD -no cat. number), no other data, coll. H.C. Liu, no collection date; 2 females (ovigerous) (11.9-12.7mm x 9.4-10.5mm) (TMCD/CHCD -no cat. number), Xiang-Shan, Hsin-Chu, Taiwan, coll. H.C. Liu, 25 Apr. 1992; 3 males (16.7-20.4 x 13.7-17.4) (NTOU-no cat. number), Ao-Di, I-Lan County, Taiwan, coll. 6 Jun. 1971; 1 male (18.2mm x 15.5mm), 1 female (14.4mm x 11.4mm) (NTOU-no cat. number), Ao-Di, I-Lan County, Taiwan, coll. 6 Jun. 1982; 1 male (18.3mm x 15.3mm), 1 female (13.6mm x 1.0mm) (NTOU-no cat. number), no data; 1 male (11.2mm x 9.2mm) (NTOU-no cat. number), small drains near Lun-Ta Harbour, Kao-Hsiung, coll. J.F. Huang, 3 Apr. 1988; 3 males (16.7-20.4mm x 13.7-17.4mm) (NTOU-no cat. number), Ao-Di, I-Lan County, Taiwan, coll. 6 Jun. 1971; 1 male (18.2mm x 15.5mm), 1 female (14.4mm x 11.4mm) (NTOU-no cat. number), Ao-Di, I-Lan County, Taiwan, coll. 6 Jun. 1982; 21 males (7.3-17.2mm x 6.2-14.5mm), 10 females (7.5-13.5mm x 6.0-11.5mm), (NTOU-no cat. number), Peng-Hu islands, coll. 11 Oct. 1984; 1 male (12.0mm x 10.6mm) (NTOU-no cat. number), Tan-Hai, Taipei County, coll. 21 Nov. 1985; 1 male (11.0mm x 9.5mm) (NTOU-no cat. number), Kao-Hsiung, coll. 3 Apr. 1988; 6 males (15.5-18.7mm x 14.3-15.0mm), 3 females (12.3-16.7mm x 10.7-13.8mm) (NTOU-no cat. number), He-Mei, Taipei County, Taiwan, coll. Z.L. Pang &

R.F. Huang, no collection date; 9 males (10.2-19.3mm x 8.5-16.3mm), 2 females (8.9-9.5mm x 7.5-8.0mm), (NTOU-no cat. number), Peng-Hu Islands, Taiwan, coll. 11 Oct. 1984; 1 male (18.0mm x 15.7mm), 1 female (14.0mm x 11.5mm) (NTOU-no cat. number), Ao-Di, Taiwan, coll. 6 Jun. 1982; 2 males (17.1-19.3mm x 14.0-15.5mm), 1 female (10.4mm x 8.8mm) (TMCD-2128), Sha-Gang, Peng-Hu Islands, Taiwan, coll. C.H. Wang, 28 Jan. 1986; 20 males (15.7-24.4mm x 13.7-21.0mm) (TMCD-2335), Jin-Cheng, Jin-Men Islands, Taiwan, coll. L.R. Dong, 29 Jan. 1988; 1 male (10.5mm x 8.9mm), 1 female (10.7mm x 9.4mm) (TMCD-3275), Cheng-Gong Town, Taipei County, Taiwan, no collection date; 1 female (14.1mm x 11.8mm) (TMCD-2681), Bi-Nan Village, Taipei County, coll. C.H. Wang, 24 Oct. 1990; 1 male (18.4mm x 15.4mm), 1 female (16.5mm x 14.0mm) (TMCD-2199), Fu-Lung, He-Mei, Taipei County, coll. C.H. Wang, 18 Jun. 1986; 4 males (11.3-16.8mm x 9.3-14.6mm), 1 female (11.0mm x 9.2mm) (TMCD-2436), Ba-Li-Hai Beach, Taipei County, Taiwan, coll. C.H. Wang, 4 Nov. 1988; 9 males (8.2-25.6mm x 6.9-20.5mm), 3 females (7.9-21.0mm x 6.7-16.8mm) (TMCD-2415), Te-Mao Village, Taipei County, coll. C.H. Wang, 1 Nov. 1988; 2 males (18.0-24.3mm x 14.9-19.7mm), 1 female (17.8mm x 14.4mm) (TMCD-2515), Ba-Dou-Zhi, Keelung, Taiwan, coll. C.H. Wang, 12 Apr. 1989; 3 males, 1 female (TMCD-2461), Keelung, Taiwan, no collection date; 2 males, 1 female (TMCD-2128), Sa-Gang, Peng-Hu Islands, Taiwan, coll. 28 Jan. 1986; 1 male, 1 female (TMCD-2199), Fu-Lung, Taipei County, coll. 19 Jun. 1986; 1 female (17.0mm x 13.6mm) (TMCD-2233), Shi-Men Village; Taipei County, Taiwan, coll. X.X. Wu, 2 Feb. 1987; 29 males, 37 females (TMCD-2338), Yang-Shan, Jin-Men Island, coll. L.R. Dong, 30 Jan. 1988; 6 males (9.6-19.3mm x 8.3-16.5mm), 1 female (12.1mm x 9.8mm), (USMN-220516), Tan-Sui beach, northeastern Taiwan, coll. 15 Aug. 1956; 1 male (23.8mm x 19.8mm) (USNM 55392), Formosa, coll. Taihoku Normal School, no collection date.

**Diagnosis.**— Carapace subquadrate, broadening anteriorly, dorsal surface flat, smooth; frontal margin strongly lobed. Anterolateral margin with three teeth including orbital tooth. Third maxilliped with an oblique suture between merus, ischium. Medial sulcus on anterior sternal plates narrow. Infraorbital ridge with numerous small, round granules. Chelipeds symmetrical, occasionally unequal, larger in male, fingers close with a large gap, usually with one or two large teeth near base of movable finger. Propodus of last ambulatory legs short, broad.

**Colour.**— The colour fresh specimen can range from light cream colour to dark brown, with dark brown and/or black spots (unpublished data). All preserved specimens examined are dark cream to brown in colour.

**Size.**— This is small-size species, the largest male specimen examined is 25.6mm x 21.3mm (lectotype), and the largest female specimen examined is 20.1 x 16.6mm (USNM-62867).

**Habitat.**— It can be found  under small rocks, on coral sand substrate close to the river mouth, they can be found stack on top of each other in huge numbers (unpublished data).

**Remarks.**— The colour of this species is highly variable, it can range form cream colour to black, with spots or blotches or with all sorts of patterns (see above).

This species can be can easily distinguished from *G. ungulatus* by the following features a) the lateral lobes of the frontal margin are very distinct (vs. not distinct in *G. ungulatus*); b) the infra-orbital ridge has numerous small isomorphic granules, usually more than 12 granules (vs. few large isomorphic granules, usually less than eight in *G. ungulatus*); c) the anterolateral angle of the merus of the third maxillipeds is very convex (vs. less convex in *G. ungulatus*); f) the propodus of the last ambulatory leg is broad and short (vs. long and narrow in *G. ungulatus*); g) the sixth abdominal segment is broad and stout (vs. long and narrow in *G. ungulatus*), and h) the male telson is broadly triangular (vs. more elongated in *G. ungulatus*).

**Distribution.**— Taiwan, China, Japan, Hong Kong, and Korea.

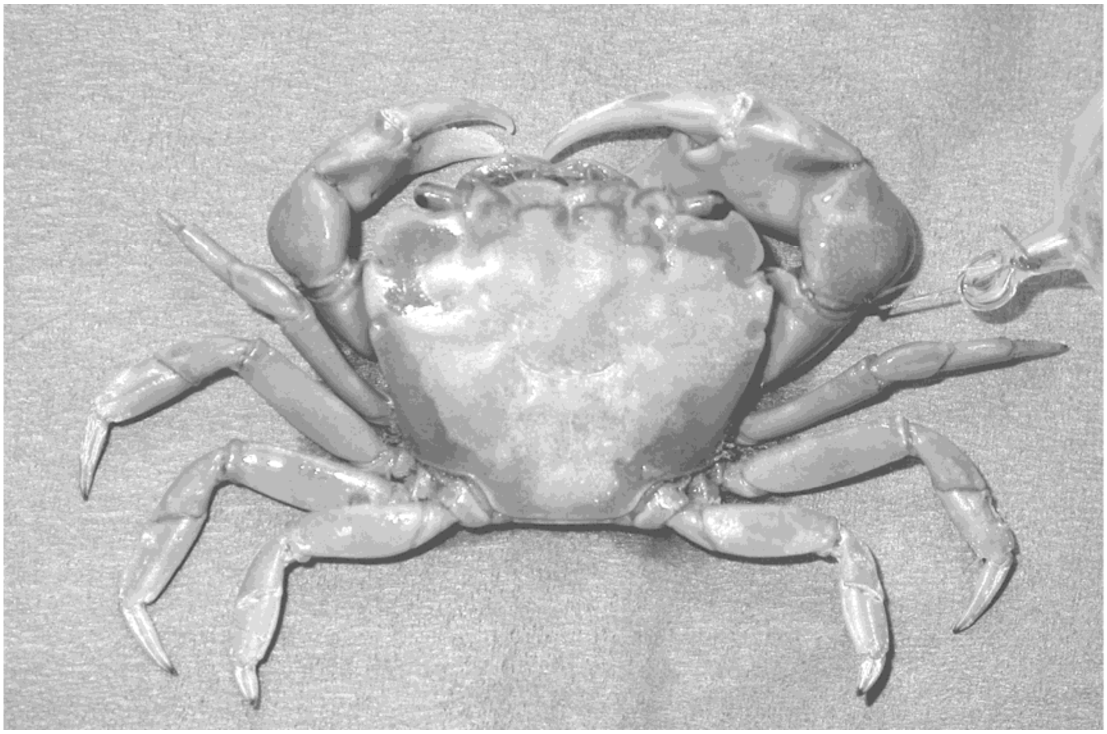


Figure 183. *Gaetice depressus* (De Haan, 1833) male, lectotype, 25.6mm x 21.3mm (RNHM-1226). Dorsal view.

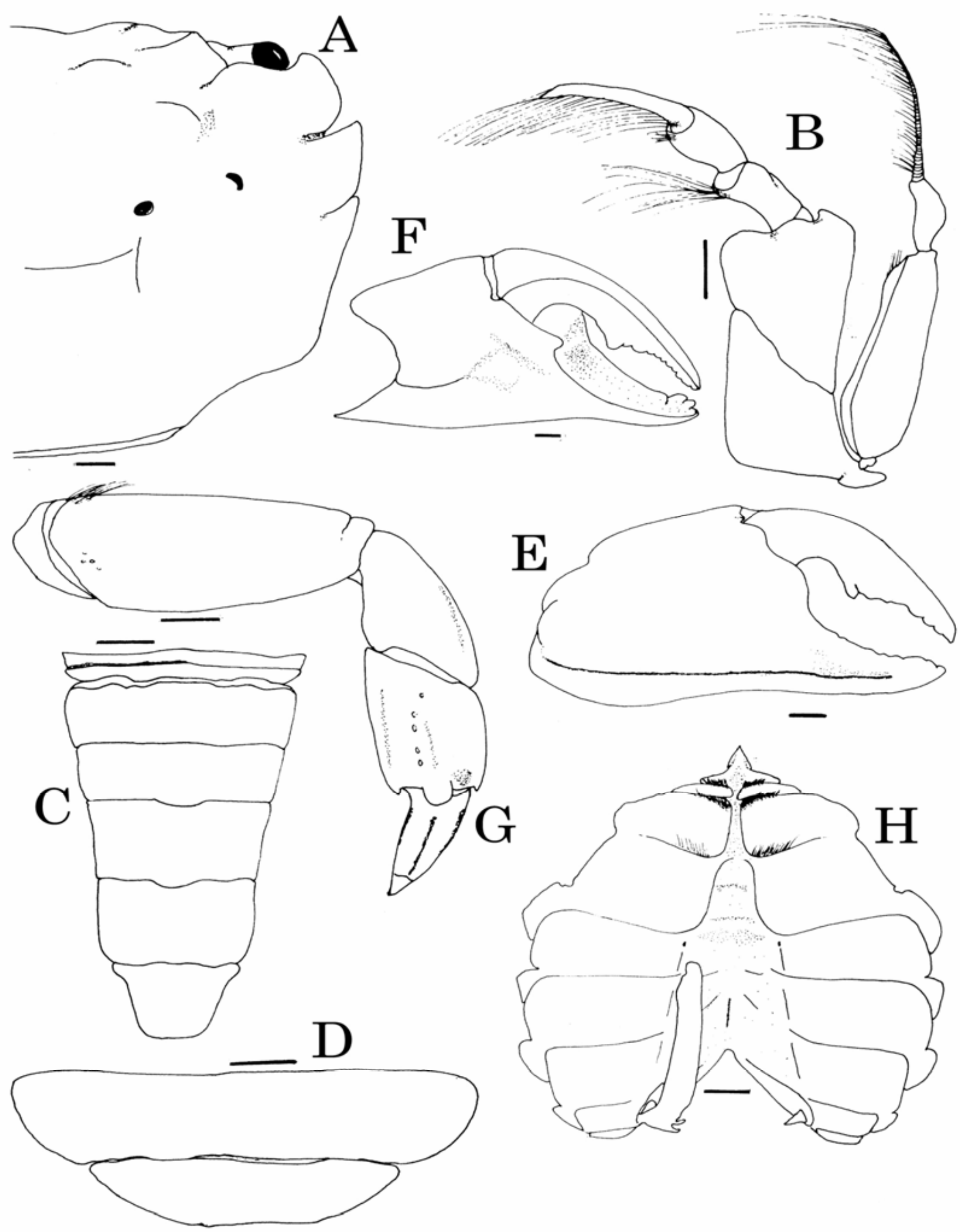



Figure 184. *Gaetice depressus* (de Haan, 1833), male, 18.3mm x 15.3mm; female, 13.6mm x 1.0mm (NTOU-no cat. number). A) carapace; B) third maxilliped; C) male abdomen; D) female abdomen (part); E) outer surface of chela; F) inner surface of chela; G) last ambulatory leg; H) male sternum. (Scale=1.0mm).

## *Gaetice ungulatus* Sakai, 1939

*Gaetice ungulatus* – Sakai, 1939: 678, fig. 120a-e; Sakai, 1976: 653, text-fig. 358a-c.

**Materials examined.**— **Neotype** – 1 male (10.4mm x 8.4mm) (RU-uncatalogued), Minatogawa, Okinawa, coll. 25 Aug. 1972. – **Others** – **China** – 26 males (10.5-23.8mm x 8.0-19.4mm), 3 females (11.1-16.4mm x 9.8-13.8mm), 7 females (ovigerous) (13.0-17.5mm x 11.9-14.9mm) (ASIZ-C00203), Jiaopo, Guangdong Province, coll. 27 Jun. 1957; 45 males (6.0-20.0mm x 5.5-17.0mm), 12 females (6.0-18.1mm x 4.9-14.9mm), 3 females (ovigerous) (11.1-16.4mm x 9.8-13.8mm) (ASIZ-C02541), Haimen, Guangdong Province, coll. 10 Aug. 1957; 7 males (13.1-19.8mm x 110-16.7mm), 7 females (12.2-17.3mm x 9.8-14.8mm), 5 females (ovigerous) (9.0-17.8mm x 7.8-15.0mm) (ASIZ-C02567), Puqian, Hainan Island, coll. 17 May 1957; 24 males (12.4-24.0mm x 10.7-20.1mm), 2 females (12.5-20.3mm x 10.8-16.2mm), 8 females (ovigerous) (9.0-19.0mm x 7.7-16.0mm), (ASIZ-C-00198), Puqian, Hainan Island, coll. 17 May 1957; 5 males (9.2-13.4mm x 8.0-12.3mm), 2 females (16.1-17.5mm x 13.0-15.2mm), 5 females (ovigerous) (8.0-11.8mm x 6.9-9.8mm) (ASIZ-C00206), Beihai, Guangxi Province, coll. 19 Apr. 1956; 2 males (18.2-20.6mm x 14.6-17.2mm) (QIH-no cat. number), Gulangyu, Fujian Province, coll. no date; 1 male (16.8mm x 4.7mm) (QIH-no cat. number), Qingzhou, Longmen, coll. 12 May 1950; 2 males (8.4-12.3mm x 7.5-10.6mm) (QIH-no cat. number), Dicun, Guangzhou, Guangdong Province, 10 May 1963; 11 males (7.9-10.1mm x 7.0-10.1mm), 3 females (8.4-10.5mm x 7.0-9.0mm) (ZRC-uncatalogued/nnk0194), seashore outside Institute of Oceanology, Qingdao, Shandong Province, P.R. China, coll. P.K.L. Ng & H.L. Chen, 22 Aug. 2002. – **Hong Kong** – 7 males (7.8-15.6mm x 8.0-12.3mm), 2 females (8.5-12.7mm x 7.2-10.5mm) (ASIZ-C00216), Hong Kong; 1 male (9.3mm x 8.5mm) (MNHN-B-9139), Hong Kong; 1 male (14.9mm x 13.1mm) (USNM-19979), Hong Kong (from Stockholm Museum); 1 male (14.0mm x 12.0mm) (USNM-19674), Hong Kong (from Kiel Museum). – **Japan** – 2 males (6.7-7.0mm x 5.7-5.8mm) (RU-uncatalogued), Aha River, Okinawa River, Ryukyus, Japan, coll. 27 July 1987; 5 males (10.7-15.3mm x 9.7-13.1mm), 1 female (10.0mm x 9.3mm), 3 females (ovigerous) (10.8-12.6mm x 9.2-10.mm) (QM-no cat. number), Uchinoura, Tanabe, Wakayama Prefecture, Japan, coll. Y. Fukui, 7 Aug. 1996; 1 male (9.5mm x 8.0mm) (RU-uncatalogued), no location or data; 4 males (10.7-15.3 x 9.7-13.1mm) (QM-no cat. number), Uchinoura, Tanabe, Wakayama Prefecture, Japan, coll. Y. Fukui, 7 Aug. 1996; 1 juvenile specimen (RU-uncatalogued), Yawadi, Japan, coll. 4 May 1985; 1 female (18.7mm x 14.9mm) (USNM-48350), Beach at Kagoshima, Japan (under stones), coll. T. Urita. – **Taiwan** – 1 male (16.9mm x

14.1mm), (NTOU-no cat. number), Tong-Lei, Coll. 17 Aug. 2000; 1 male (16.6mm x 14.2mm) (NMNS-no cat. number), Ma-Gang Fish port, coll. 11 Aug. 1995.

**Diagnosis.**— Carapace subquadrate, broadening anteriorly, dorsal surface flat, smooth; frontal margin weakly lobed. Anterolateral margin with three teeth including orbital tooth. Third maxilliped with an oblique suture between merus, ischium. Medial sulcus on anterior sternal plates broad. Infraorbital ridge with very few large, round granules. Chelipeds symmetrical, occasionally unequal, larger in male, fingers close with a large gap, usually with one or two large teeth near base of movable finger. Propodus of last ambulatory legs long, narrow.

**Colour.**— Similar to its congeners, there is great variability in the coloration of this species. The colour of the fresh specimens can range from light cream colour to dark brown, with dark brown and/or black spots (Y. Nakasone, pers. comm.), and all preserved specimens examined are dark cream to brown in colour (see above Materials examined).

**Size.**— This species is small in size, largest male specimen examined is 24.0mm x 20.1mm (ASIZ-C-00198), and the largest female specimen examined is 20.3mm x 16.2mm (ASIZ-C-00198).

**Habitat.**— It can be found  under small rocks, on coral sand substrate close to the river mouth, they can be found stack on top of each other in huge numbers (pers. observ., Y. Nakasone, pers. comm.).

**Remarks.**— This species can be easily separated from *Gaetice depressus* by the following features a) the oblique groove by the lateral ends of the carapace's frontal margin of the carapace is very distinct (vs. indistinct in *G. depressus)*; b) the presence of about eight or less granules on the infra-orbital ridge (vs. presence of more than 12 small rounded granules on the infra-orbital ridge in *G. depressus*); c) the anterolateral angle of the merus of the third maxilliped is very convex (vs. less convex in *G. depressus*); c) the propodus of the last ambulatory leg is narrower and more slender (vs. broader and stouter in *G. depressus*); d) the sixth abdominal somite is broad (vs. more narrow in *G. depressus*), and e) the telson is broadly triangular in shape (vs. narrowly triangular in shape in *G. depressus*).

This species is not commonly found. The type materials of this species is not in Kanagawa Prefecture Natural History Museum or National Science Museum, Tokyo or Research Institute and Natural History Museum, Senkenberg. So, it is likely that the species is lost. As such, I have designated a male, 10.4mm x 8.4mm, (RU-uncatalogued), collected from Minatogawa, Okinawa as the neotype for this species.

**Distribution.**— Taiwan, China, Hong Kong, and southern Japan.

### Subfamily Thalassograpsinae, new subfamily

**Diagnosis.**— Carapace quadrate with lateral margins subparallel; regions often discernible; dorsal surface glabrous, physiognomy flat; anterolateral margins with three teeth including orbital angle. Front deflexed; broad, less than half maximum carapace breadth, four-lobed. Orbits open laterally; sub-orbital crest more or less straight, typically long, extending to a short distance across lateral branchial region; pterygostomial grooves opening into anterolateral corner of buccal cavity; pterygostome, pterygostome non setose, with no vertical groove subparallel to buccal cavity. Third maxilliped with merus squarish in shape, ischium broad, with a faint longitudinal sulcus, leaving almost no gap when closed; not reaching forward to margin of epistome to completely close buccal cavity anteriorly; exopod narrow; flagella of maxilliped exopods not especially elongated, not noticeably protruding from behind third maxilliped. Endostome granulated, medially prominent very narrow. Chelipeds usually subequal, large in size. Ambulatory legs flat, dorso-ventrally flattened; margin of meri not armed with spines; propodi, dactyli not armed with strong black bristles. Telson broadly triangular in shape. Male gonopore is located very far away from coxa, embedded within sternite 8. Female gonopore usually with oval operculum.

**Type Genus.**— *Thalassograpsus* Tweedie, 1950, by present designation.

**Gender.**— Masculine.

**Remarks.**— The Thalassograpsinae can be differentiated from the other subfamilies within the family Varunindae by the following suite of characters viz. a) the orbit is open laterally, similar but not as wide as those in Varuninae, Cyclograpinae and Gaeticinae; b) it has no pterygostomial grooves (vs. presence of a shallow groove in Cyclograpsinae); c) the third maxilliped has no oblique setose crest extending across the merus and the outer distal corner of the ischium (vs. presence of a simple crest in Cyclgrapsinae); d) the third maxilliped has no gape when closed (vs. presence of a gap in Varuninae, Cyclograpsinae and Gaeticinae); e) the anterolateral margin of the third maxilliped merus is not convex, unlike other varunines, f) the sulcus is almost not visible on the merus and ischium of the third maxilliped (vs. distinctly visible in the other subfamilies); g) the posterior margin of the epistome ends in two elongated lobes (not seen in other subfamilies as small protusions); h) the fingers of of the chelipeds are very short with numerous small teeth (other subfamilies have typical longer fingers and fewer, larger teeth); i) the sternal plastron is without a medial groove, not even a slight indentation (vs. deep furrow in Gaeticinae and no furrow in Varuninae); j) thoracic sternites 3-4 are flat and broad (vs. slightly convex in the other subfamilies); k) the anterolateral margin of the sternal plastron is straight and horizontal (all other families and subfamilies are slopping downwards, and with lobes); l) the suture of thoracic sternite 3/4 is not visible (vs. slightly visible in all the others subfamilies); and m)the proportionately wider medial groove in thoracic sternites 7 and 8 (other subfamilies with narrower medial groove in sternite 8). The differences are also listed in Table 7 (see below).

There is only one genus in this subfamily.

## Genus *Thalassograpsus* Tweedie, 1950

*Brachynotus* Hilgendorf 1892: 38 (part).

*Thalassograpsus* Tweedie, 1950: 133; Sakai, 1976: 652; Dai *et al*., 1986: 481; Dai & Yang, 1991: 527.

**Type species.**— *Brachynotus harpax* Hilgendorf, 1892, by monotypy.

**Gender.**— Masculine.

**Diagnosis.**— Carapace quadrangular, broader than long; dorsal surface glabrous, punctate; regions well defined. Frontal margin with four lobes. Anterolateral margin subcristate with three teeth including orbital tooth. Posterolateral margins not sharply demarcated from anterolateral margin, distinctly converging. Orbits small, eyes completely filling orbit. Third maxilliped short, stout. Small, or almost no gape when closed, palp short, with short setae. Exopod narrow with short flagellum. Epistome narrow flat, posterior margin entire, with elongated lobes at the end. Inner surface of chela with granules; outer surface of pollex and manus glabrous. Ambulatory legs flat, short, sparingly setose; posterior margin of merus end in a sharp spine, stout dactylus, with a few chitinous spines. Lateral margins of thoracic sternites 4-5 finely granulated; anterior sternal plates without any medial grooves. Male abdomen narrowly triangular with all segments freely moveable (six somites plus telson), telson broadly triangular. G1 long, slender. Female gonopore with operculum oval in shape.

**Remarks.**— *Thalassograpsus* was established by Tweedie (1950) for *Brachynotus harpax* Hilgendorf, 1892, on the basis of the following features: a) the frontal margin and supra-orbital margin do not form a continuous margin (vs. continuous in *Utica* and other varunine taxa); b) the third maxilliped meet completely in the middle line leaving no gap between them (vs. a distinct rhomboidal gap in other varunine taxon); c) there is no raised line on the branchial region cutting off a posterolateral facet (vs. present in *Brachynotus* and other varunine taxon) (see Tweedie, 1950). In addition to the three characters listed by Tweedie (1950), *Thalassograpsus* is also different from *Brachynotus* in the following: a) the anterolateral teeth are relatively broader (vs. more acute and sharp in *Brachynotus*); b) the the chelipeds do not have a pulvinus at the base of the fingers (vs. presence of a distinct pulvinus in *Brachynotus*); c) the merus of the third maxilliped is squarish in shape (vs. foliate in shape in *Brachynotus*); d) the longitudinal sulcus on the merus and ischium of the third maxilliped is very faint and almost invisible. (vs. distinct in *Brachynotus*); e) there is a distinct, sharp subdistal spine on the anterior margin of the last ambulatory legs (vs. absence of such spine on *Brachynotus*), and f) the dactylus of the last ambulatory legs has a few small chitinous spines (vs. absence in *Brachynotus*).

### *Thalassograpsus harpax* (Hilgendorf, 1892)

(Figure 185A-I)

*Brachynotus harpax* Hilgendorf, 1892: 38; Sakai, 1939: 675, figs. 119a–c; Horikawa, 1940: 29; Lin, 1949: 29.

*Thalassograpsus harpax* – Harntoll, 1975: 305; Sakai, 1976: 652, pl. 223: 1; Vannini & Valmori, 1981: 57; Dai *et al.*, 1986: 481, fig. 271: 1–4, pl. 67: 8; Dai & Yang, 1991: 527, fig. 271: 1–4, pl. 67: 8; Ng *et al.*, 2001: 46.

**Materials examined.**— **Lectotype** – 1 male (11.0mm x 9.7mm) (ZMB-8472), Fundorf, Aden, leg Hildebrandt. – **Paralectotypes** – 3 males (8.0-10.0mm x 8.8-9.0mm), 3 females (ovigerous) (7.8-10.3mm x 6.7-9.0mm), (ZMB – 8472), Fundorf, Aden, leg Hildebrandt; 11 males (6.8-12.0mm x 5.9-10.3mm), 4 females (6.1-10.8mm x 5.7-9.1mm), (MNHN-MPB-12534), Aden, coll. 1904 (written as types of Hilgendorf. – **Others** – **Japan** – 1 female (8.2mm x 7.3mm), 1 female (ovigerous) (6.7mm x 6.2mm) (RU-uncatalogued), Japan; 1 male (8.7mm x 7.4mm) (RU-uncatalogued), Japan, coll. 28 May 1984; 1 male (10.9mm x 9.3mm) (RU-uncatalogued, coll. 28 Jul. 1985. – **Philippines** – 1 male (6.0mm x 5.3mm) (MNCR-uncatalogued, spec No. 531), University of Philippines collection; 5 males (4.7-10.7mm x 3.0-9.5mm), 1 female (8.8mm x 7.5mm), 1 female (ovigerous) (9.0mm x 8.0mm) (NMNS-uncatalogued), Cumming Island, Philippines, coll. H.T. Shih, 30 Aug. 2003. – **Taiwan** – 1 male (8.9mm x 7.6mm), (NMNS-uncatalogued), Chi-Han, coll. 15 May 1994. – **Red Sea** – 2 females (ovigerous) (MNHN-MPB-12531), Perim D'Jousseamusre, coll. 1897; 1 male (11.3mm x 9.8mm) (MNHN-MPB-12532), Red Sea area, coll. 1897; 1 male (7.6mm x 6.6mm), 1 female (6.1mm x 5.4mm) (MNHN-MPB-12535), Red Sea area, coll. 1897; 1 male (9.4mm x 8.1mm) (MNHN-MPB-12537), Red Sea area, coll. 1897;1 male (6.9mm x 6.0mm), 3 females (ovigerous) (6.4-7.3mm x 5.5-6.0mm) (MNHN-MPB-12536), Ues Musch Mission, coll. 1933; 5 males (7.8-10.1mm x 6.6-9.0mm), 2 females (6.0-8.1mm x 4.6-7.5mm), 3 females (ovigerous) (6.6-7.8mm x 5.8-6.8mm) (MNHN-MPB-12533), Djibouti Adem Soback. D'Jousseaumre, coll. 1897; 1 female (7.2mm x 6.0mm) (SFM-17272), Bjibouli, Djibouti, Stadlogebrel, plage de Triton, eulitoral, leg. F. Allspach, 18 Mar. 1987.

**Diagnosis.**— Carapace subquadrate, with dorsal surface flat, front broad, anterior border concave medially, divided into four lobes. Dorsal orbital margin with a suture. Ventral orbital margins with three long ridges. Third maxillipeds close with almost no gap, merus squarish, ischium broad, exopod narrow. Chelipeds stout, with numerous small teeth on cutting edge of fingers. Ambulatory legs flat, broad, sparsely setose; merus with sub-distal spine, dactylus with few stiff setae. Male abdomen narrowly triangular in shape with all segments freely moveable (six somites plus telson). G1 long, slender, slightly arched. Female gonopore operculate, small, oval in shape.

**Colour.**— The colour of fresh specimens is cream colour to light brown (H.T. Shih, pers. comm.), and all preserved specimens examined are light brown in colour.

**Size.**— The species is relatively small in size, largest male specimen examined is only 11.3mm x 9.8mm (MNHN-MPB-12532), and largest female specimen examined is 9.0mm x 8.0mm (NMNS-uncatalogued).

**Habitat.**— It can be found under coral stones or rocks, or pebbles in sheltered rocky shores (H.T. Shih, pers. comm.).

**Remarks.**— This species is relatively uncommon despite the fact that it has a very wide distribution. The biology of this species is also unknown.

**Distribution.**— Taiwan, China, Japan, Samoa Island, Indonesia, Singapore, Australia, and Red Sea.

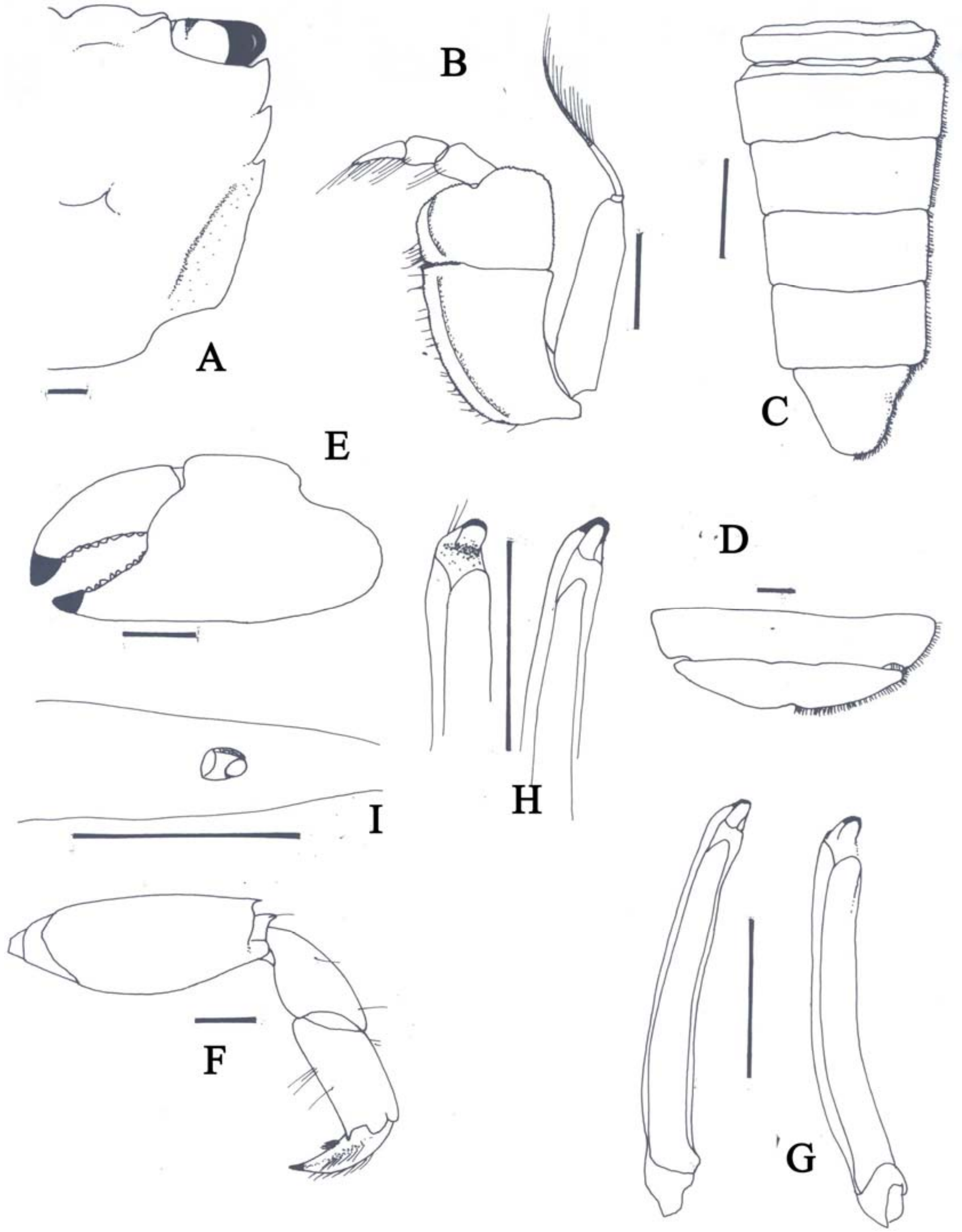



Figure 117. *Thalassograpsus harpax* (Hilgendorf, 1882); male, 10.0mm x 9.0mm; female, 10.3mm x 9.0mm (ZMB – 8472). A) carapace; B) third maxilliped; C) male abdomen; D) female abdomen (part); E) chela; F) last ambulatory leg; G) G1; H) distal end of G1; I) female gonopore. (Scale=1.0mm).

## Family XENOGRAPSIDAE, new family

**Type genus.**— *Xenograpsus* Takeda & Kurata, 1977, by monotypy.

**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 articleimmobile, 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 fingers 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 with a tuft of short setae. Male abdomen with all segments freely moveable (six somites plus telson). Male gonopore narrowly separated from the coxa of fifth ambulatory legs by an elongation of episternite 7 meeting thoracic sternite 8.

**Remarks.**— Takeda & Kurata (1977) described an unusual new genus and new species, *Xenograpsus novaeinsularis*, from Nishino-shima island in the Ogasawara Islands, Japan, from an area with steep cliffs and violent waves; shortly after the island was first formed in 1973 (Kido & Koike, 1975; Nakamura & Koike, 1975; Takeda & Kurata, 1977). They referred it to the subfamily Varuninae (present Varunidae). Sixteen years later, this species was reported from Akuseki-jima Island, Tokara Islands, south of Kyushu, as well as from Kita-Iwo-jima Island, Iwo Islands, to the south of the Ogasawara Islands (Takeda *et al.,* 1993). It was subsequently reported from the sediment of Esmeralda Bank, an active submarine volcano in the Mariana Arc (Türkay & Sakai, 1995). In 2000, a second species, *X. testudinatus*, was described from Taiwan (Ng *et al.*, 2000).

The genus *Xenograpsus* Takeda & Kurata (1977) is a peculiar genus of grapsoid crab which has been found thus far only around shallow-water sulphur-rich hydrothermal vents. Three species are currently known, viz., *X. novaeinsularis* Takeda & Kurata, 1977 (type species) from Japan, and the Marianas Arc; *X. testudinatus* Ng, Huang & Ho, 2000, from the Taiwan Arc, and *X. ngatama* McLay, 2006.

Takeda & Kurata (1977) had referred the genus to the subfamily Varuninae (family Grapsidae), commenting that it had a ridge running parallel to the infra-orbital border, the third maxilliped were quite broad and entirely covered 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 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 the chelipeds are related to those of Macrophthalminae of the Ocypodidae (Takeda & Kurata, 1977). In the discussion of *X. novaeinsularis*, they even compared the species to *Camptandrium japonicum* (Sakai, 1934) (family Camptandriidae) (Takeda & Kurata, 1977: 105). Clearly, Takeda & Kurata (1977) recognized that the placement of *Xenograpsus* is more complicated than just placing it in the subfamily Varuninae.

Takeda & Kurata (1977) recognized that the placement of *Xenograpsus* in the subfamily Varuninae was problematic, but nevertheless, decided to retain 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 there is a deep split between *Xenograpsus* and other grapsoid families that requires separate family recognition. The full suite of characters from adults, larvae and DNA is presented below.

## MORPHOLOGICAL EVIDENCE

**Male gonopore position** (Figure 186A-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 radiation of grapsoid crabs into the intertidal, terrestrial and freshwater habitats (Glaessner, 1957; Guinot, 1998). 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. 186A). This condition is almost identical for the Sesarmidae (Fig. 186B) and the Plagusiidae (Fig. 186C).

In this respect, the Grapsidae represent the most plesiomorphic condition with the gonopore/penis in free contact with the coxa of P5 (Fig. 186D). 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. 186E). 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. 186F), but failed to recognise how phlogenetically 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. 186G). 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. 186H). 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 currently also being reviewed.

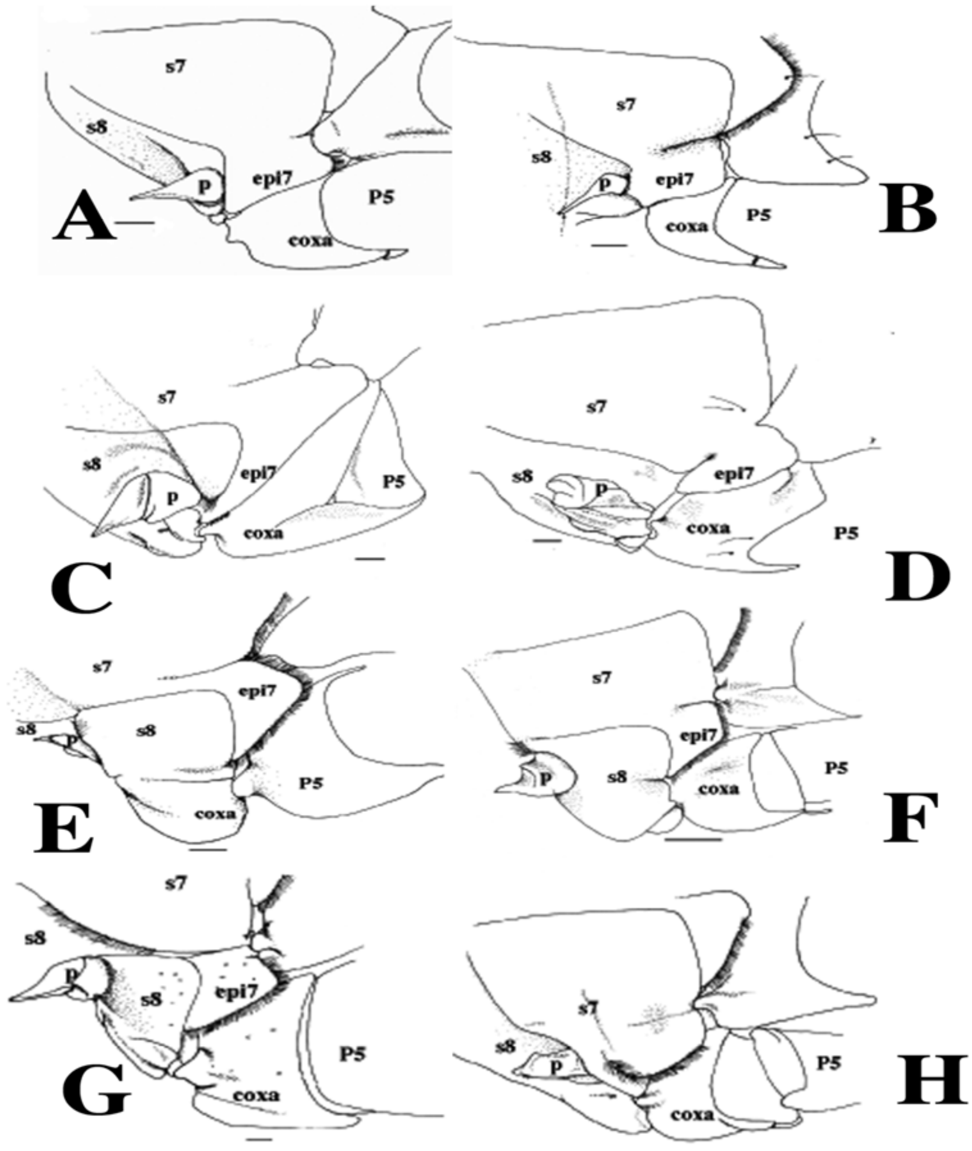



Figure 186. Different gonopore position of different families. A) *Xenograpsus testudinatus* Ng, Huang & Ho, 2000 (new family), male (19.8mm x 18.0 mm) (TMCD-uncatalogued); B) *Sesarma reticulatum* Say, 1817 (Sesarmindae), male (25.4mm x 21.3mm) (ZRC.1970.8.4.6); C) *Plagusia squamosa* (Herbst, 1790) (Plagusidae), male (41.7mm x 49.6mm) (SAM-A-39677); D) *Grapsus tenuicrustatus* Herbst, 1783 (Grapsidae), male (54.7mm x 52.1mm) (ZRC.2000.0574); E) *Varuna litterata* (Fabricius, 1798) (Varunidae), male (55.0mm x 48.3mm) (ZRC-uncatalogued); F) *Cyclograpsus henshawi* Rathbun, 1902 (Varunidae), male (18.2mm x 14.7mm) (ZRC.2000.0525); G) *Platychirograpsus spectabilis* de Man, 1896 (Glyptograpsidae) male (43.7mm x 36.6mm (RMNH-D25479), and H) *Gecarcinus weileri* Sendler, 1912 (Gercarcinidae), male (59.4mm x 46.4mm) (ZMK).

**Orbital structure** (Figures. 187A-G)

*Xenograpsus* is unusual in having an almost complete orbit in the form of a deep sunken cavity (Fig. 187A), a condition very different from all other grapsoids. The lower margin of the exorbital tooth of *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 suborbital margin that is the homologue of that in the Grapsidae (for example) 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. 187B) and Plagusiidae (Fig. 187C), the orbit 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. 187D), 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. 187E, 187F) and Glyptograpsidae (Fig. 187G), 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. 187H), but none approach the condition in Xenograpsidae.

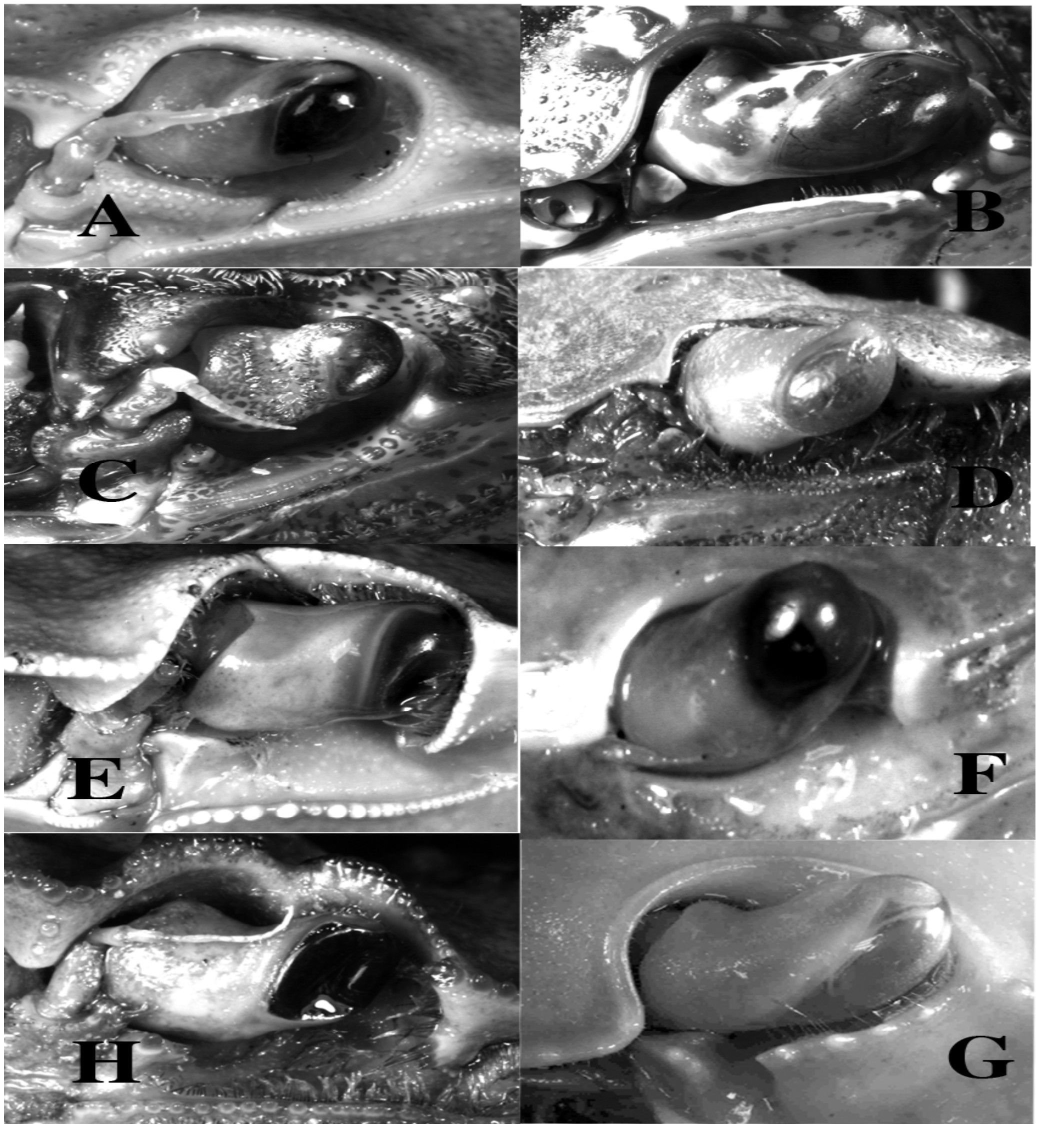



Figure 187. Different forms of eye orbits of different families. A) *Xenograpsus testudinatus* Ng, Huang & Ho, 2000 (new family), male (19.8mm x 18.0 mm) (TMCD-uncatalogued); B) *Grapsus tenuicrustatus* Herbst, 1783 (Grapsidae), male (54.7mm x 52.1mm) (ZRC.2000.0574); C) *Plagusia squamosa* (Herbst, 1790) (Plagusidae), male (41.7mm x 49.6mm) (SAM-A-39677); D) *Sesarma reticulatum* Say, 1817 (Sesarmindae), male (25.4mm x 21.3mm) (ZRC.1970.8.4.6); E) *Varuna litterata* (Fabricius, 1798) (Varunidae), male (55.0mm x 48.3mm) (ZRC-uncatalogued); F) *Cyclograpsus henshawi* Rathbun, 1902 (Varunidae), male (18.2mm x 14.7mm) (ZRC.2000.0525); G) *Platychirograpsus spectabilis* de Man, 1896 (Glyptograpsidae), male (43.7mm x 36.6mm (RMNH-D25479); H), and H) *Gecarcinus weileri* Sendler, 1912 (Gercarcinidae), male (59.4mm x 46.4mm) (ZMK).

**Interantennular Septum** (Figure 188A-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. 188A), and in this respect, it resembles all other higher taxa (Figs. 188B) except the Grapsidae (Fig. 188B) and Sesarmidae (Fig. 188C). These latter two families have a broad anteriorly convex septum, meeting but not obviously inserted into the frontal margin.

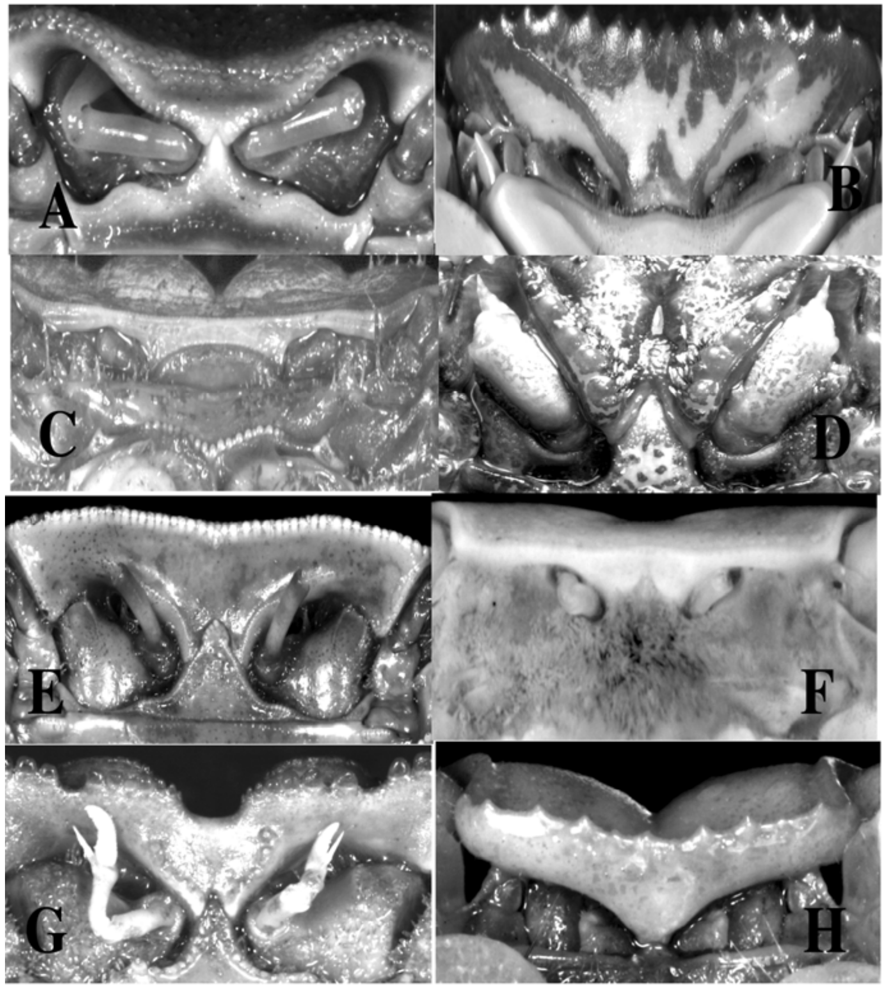



Figure 188. Different Interantennular septum of different families. A) *Xenograpsus testudinatus* Ng, Huang & Ho, 2000 (new family), male (19.8mm x 18.0 mm) (TMCD-uncatalogued); B) *Grapsus tenuicrustatus* Herbst, 1783 (Grapsidae), male (54.7mm x 52.1mm) (ZRC.2000.0574); C) *Sesarma reticulatum* Say, 1817 (Sesarmindae), male (25.4mm x 21.3mm) (ZRC.1970.8.4.6); D) *Plagusia squamosa* (Herbst, 1790) (Plagusidae), male (41.7mm x 49.6mm) (SAM-A-39677); D) E) *Varuna litterata* (Fabricius, 1798) (Varunidae), male (55.0mm x 48.3mm) (ZRC-uncatalogued); F) *Cyclograpsus henshawi* Rathbun, 1902 (Varunidae), male (18.2mm x 14.7mm) (ZRC.2000.0525); G) *Platychirograpsus spectabilis* de Man, 1896 (Glyptograpsidae), male (43.7mm x 36.6mm (RMNH-D25479, and H) *Gecarcinus weileri* Sendler, 1912 (Gercarcinidae), male (59.4mm x 46.4mm) (ZMK).

## 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** (Figure 189A-H)

The broad flat subrectangular third maxillipeds of *Xenograpsus*, with their inner margins meeting and not leaving a rhomboidal gap (Fig. 190A) (versus a broad gap in all other families), also appears to be unique amongst the Grapsoidea (Figs 190B-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. 190H), 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.

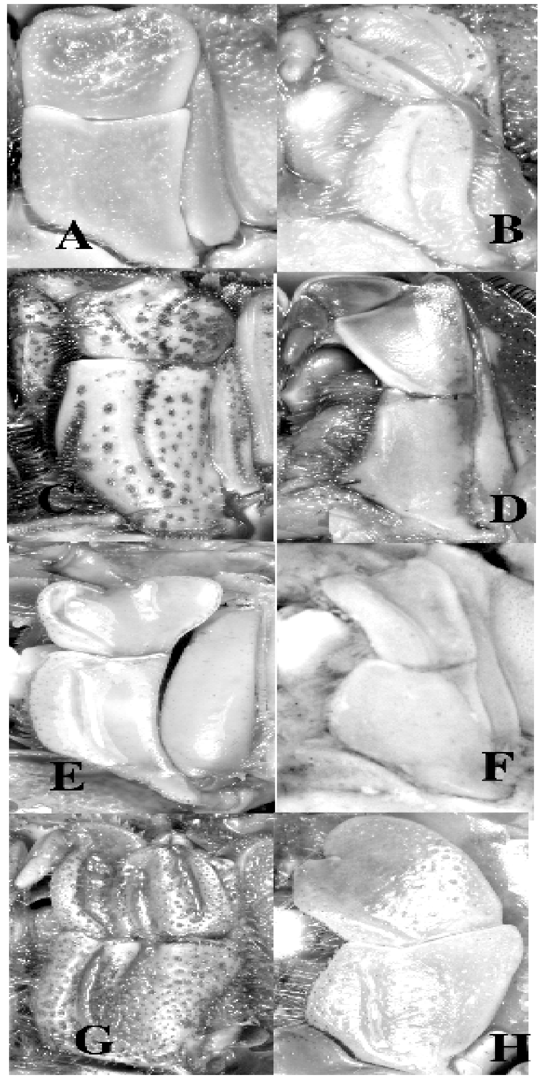


Figure 189. Different forms of third maxillipeds of different families. A) *Xenograpsus testudinatus* Ng, Huang & Ho, 2000 (new family), male (19.8mm x 18.0 mm) (TMCD-uncatalogued); B) *Sesarma reticulatum* Say, 1817 (Sesarmindae), male (25.4mm x 21.3mm) (ZRC.1970.8.4.6); C) *Plagusia squamosa* (Herbst, 1790) (Plagusidae), male (41.7mm x 49.6mm) (SAM-A-39677); D) *Grapsus tenuicrustatus* Herbst, 1783 (Grapsidae), male (54.7mm x 52.1mm) (ZRC.2000.0574); E) *Varuna litterata* (Fabricius, 1798) (Varunidae), male (55.0mm x 48.3mm) (ZRC-uncatalogued); F) *Cyclograpsus henshawi* Rathbun, 1902 (Varunidae), male (18.2mm x 14.7mm) (ZRC.2000.0525); G) *Platychirograpsus spectabilis* de Man, 1896 (Glyptograpsidae), male (43.7mm x 36.6mm (RMNH-D25479), and H) *Gecarcinus weileri* Sendler, 1912 (Gercarcinidae), male (59.4mm x 46.4mm) (ZMK).

## LARVAL EVIDENCE

Jeng *et al*. (2004a) described the first stage zoea and megalopa of *X. testudinatus*, and compared them with other known varunid larval characters (*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) (see Cuesta *et al.*, 2001). In addition, the larval characters of *Eriocheir hepuensis* (Ng *et al.*, 1998) and *Johngarthia planatus* (Cuesta *et al.*, 2007) are also compared with *X. testudinatus*. The results are summarized in Tables 8-11.

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 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 from any 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. a) the absence of an antennal exopod, and a setal formula for the maxillular endopod (see Jeng *et al.*, 2004a). Other shared characters include a) the basal endite armature of the maxillule; b) the formula of the endopod setation; c) the setal formula on the basis of the first maxilliped, and d) 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. There are nevertheless some major differences between the two genera including the differences in spinulation of the antennal protopod (see Jeng *et al.*, 2004a).

Table 7. List of adult morphological characters distinguishing the six families Xenograpsidae, Varunidae, Grapsidae, Plagusiidae, Glyptograpsidae, Sesarmidae and Gercarcinidae.

| Characters | Family | | | | | | |
|---|---|---|---|---|---|---|---|
| | **Xenograpsidae** | **Varunidae** | **Grapsidae** | **Plagusiidae** | **Glytograpsidae** | **Sesarmidae** | **Gercarcinidae** |
| **Eye Orbit** | Totally closed | Open laterally (wide) | Open laterally (small) | closed | Open laterally (small slit) | Open laterally (small) | Both closed and open |
| **Frontal cleft to receive antennules** | No | No | No | Yes | No | No | No |
| **Basal segment of antenna** | Immobile | Mobile | Immobile | Immobile | Mobile | Immobile | Immobile |
| **Suborbital crest form** | Small granules | Small granules | Small granules | Straight | Small granules | Small granules | Straight |
| **Pterygostomial region - reticulated setae** | Totally absent | Absent | Sparingly present | Sparingly present | Almost absent | Present | Present, very thick or absent |
| **Third Maxilliped – gape** | No gape/very narrow gape | Narrow rhomboidal gape | Normal rhomboidal gape | Wide gape | Narrow gape | Wide rhomboidal gape | Wide gape |
| **Third maxilliped - no of suclcus on merus** | One but very faint | One | One | One but faint | Three | One | One |
| **Third maxilliped - no of suclcus on ischium** | One but very faint | One | One | One | Two | One | One |
| **Third maxilliped -** | Absent | Absent | Absent | Absent | Absent | Present | Absent |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **oblique setose crest** | | | | | | | |
| **Third maxilliped - reaching epistome** | Yes | No | No | No | No | Yes | No |
| **Third maxilliped - closing entire cavity** | Yes | No | No | No | No | Yes | No |
| **Third maxilliped - palp** | Normal length | Normal length | Normal length | Normal length | Normal length | Normal length | Variously vestigial or normal length |
| **Third maxilliped - length of plap when folded** | Not reaching abdomen when folded | Reaching abdomen when folded | Not reaching abdomen when folded | Not reaching abdomen when folded | Not reaching abdomen when folded | Not reaching abdomen when folded | Not reaching abdomen when folded |
| **Articulation of third maxilliped** | Horizontal | Nearly vertical | Horizontal | Horizontal | Horizontal | Horizontal | Horizontal |
| **Sternite 3/4 with depressed sulcus** | Yes | No | Yes | No | Yes | No | Yes |
| **Sternite 3/4 suture** | Not visible | Visible | Visible | Visible | Visible | Visible | Not visible |
| **Medial groove reaching anterior margin of Sternite 3** | Yes | No | No | No | No | No | Yes |
| **Abdomen – segments** | 7 free segments | 7 free segments | 7 free segments | 3-5/3-6 fused | 3-5 fused | 7 free segments | 7 free segments |
| **Position of male gonopore** | Gonopore narrowly separated from coxa of P5 by an | Gonopore embedded in sternite 8, no | Gonopore on sternite 8, meeting coxa of | Gonopore by edge of sternite 7 and separated from the | Gonopore separated from coxa of P5, embedded in sternite | Gonopore separated from coxa of P5, by | Gonopore narrowly separated from |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | elongation of episternite 7 meeting sternite 8 | contact with coxa of P5 or sternite 7 | P5 and episternite 7 | coxa of P5, by a small extension of episternite 7 | 8, beside sternite 7 | episternite 7, edge of sternite 8 | coxa of P5 by distal edge of sternite 8 |
| **Presence of mobile setae on dactylus of ambulatory legs** | No | No | Yes | No | No | No | Yes |
| **Presence of spines on ambulatory dactylus** | Small minute spines | No | No | Fixed chitinous spines | Fixed chitinous spines | No | Strong fixed chitinous spines |
| **Form of G1** | Slender, short | Long, slender | Short, slender | Slender with a twist | Broad, flat | Long and slender | Long slender |
| **Ambulatory legs - longest** | Second pair | Second pair | Third pair | Second pair | Third pair | Third pair | Second pair |

Table 8. A comparison between the first stage zoeae of *Brachynotus sexdentatus* described by Cuesta *et al.* 2001a, b, *Eriocheir hepuensis* by Ng *et al.*, 1998, *Johngarthia planatus* by Cuesta *et al.*, 2007, and *Xenograpsus testudinatus* from Jeng *et al.*, 2004a.

| **Zoea 1 characters** | *Brachynotus sexdentatus* (after Cuesta *et al.*, 2001a, b) | *Eriocheir hepuensis* (after Ng *et al.*, 1998) | *Johngarthia planatus* by (after Cuesta *et al.*, 2007) | *Xenograpsus testudinatus* (after Jeng *et al.*, 2004a) |
|---|---|---|---|---|
| **Carapace - lateral spines** | present | present | present | absent |
| **Antenna - exopod** | present with two 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 9. A comparison between the first stage zoeas of *Gecarcinus lateralis* (Gecarcinidae) by Willems 1982; *Johngarthia planatus* (Gecarcinidae) by Cuesta et al., 2007; *Glytograpsus impressus* (Glytograpsidae) by Cuesta & Schubart, 1997; *Grapsus adscensionis* (Grapsidae) by Cuesta et al., 1999; *Plagusia depressa* (Plagusiidae) by Wilson & Gore, 1980; *Sesarma aequatoriale* (Sesarmidae) by Cuesta et al., 1998; *Brachynotus sexdentatus* (Varunidae) by Cuesta et al., 2001a, b; *Eriocheir hepuensis* by Ng et al, 1998, and *Xenograpsus testudinatus* from Jeng et al., 2004a.

| **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 subterminal + 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<br>2,2,3,3 | 10<br>2,2,3,3 | 8<br>2,2,2,2 | 8<br>2,2,2,2 | 8<br>2,2,2,2 | 10<br>2,2,3,3 | 10<br>2,2,3,3 | 10<br>2,2,3,3 | 10<br>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 10. A comparison between the zoeal characters of the Varunidae as suggested by Cuesta *et al*. 2001a, b and those of *Xenograpsus testudinatus* described by Jeng *et al.*, 2004a.

| *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 |

Table 11. A comparison between the more pronounced megalopa characters of *Brachynotus sexdentatus* described by Cuesta *et al.* 2001a, b, *Eriocheir hepuensis* by Ng *et al.*, 1998, *Johngarthia planatus* by Cuesta *et al*, 2007, and *Xenograpsus testudinatus* described by Jeng *et al.*, 2004a.

| *Megalopal characters* | *Brachynotus sexdentatus* by Cuesta *et al.*, 2001a, b | *Eriocheir hepuensis* by Ng *et al.*, 1998 | *Johngarthia planatus* by Cuesta *et al.*, 2007 | *Xenograpsus testudinatus* by 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 (3 8 subterminal & 2 terminal) | | 1,4 (2 subterminal & 2 terminal) setae |
| **Maxillule - exopod setation** | 1 seta | 2 setae | | 2 setae |
| **Maxilla - coxal endite setation** | 15+5 | 14,9 | | *ca*. 22+9 |

| | | | |
|---|---|---|---|
| **Maxilla - basial endite setation** | 11+16 | 11,14 | 8+12 |
| **Maxilla - endopod setation** | 0 | 0+(4or 5) | 1 basal + 2 marginal |
| **Maxilla - exopod (scaphognathite) margin setation** | 46 | 80-90 | *ca*. 64 |
| **Maxilla - exopod (scaphognathite) lateral setation** | 5 | 5 | 3 |
| **First maxilliped - epipod setation** | 7 | 12 | 14 |
| **First maxilliped - coxal endite setation** | 17 | 17 | 12 |
| **First maxilliped - basial endite setation** | 17 | 23 | 12 |
| **First maxilliped - endopod setation** | 2 subterminal, 2 terminal | 4 terminal | 2 subterminal |
| **Second maxilliped - endopod setation** | 0,2,1,8,11 | 1,0,1,5,10 | 0,0,2,6,10 |
| **Third maxillipeds- epipod** | 13 long setae | 13 long setae | 32 long setae |

## DNA EVIDENCE

The trees in figures 190-192. 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, 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 evidently too early to put much confidence in the topology of this section of the tree.

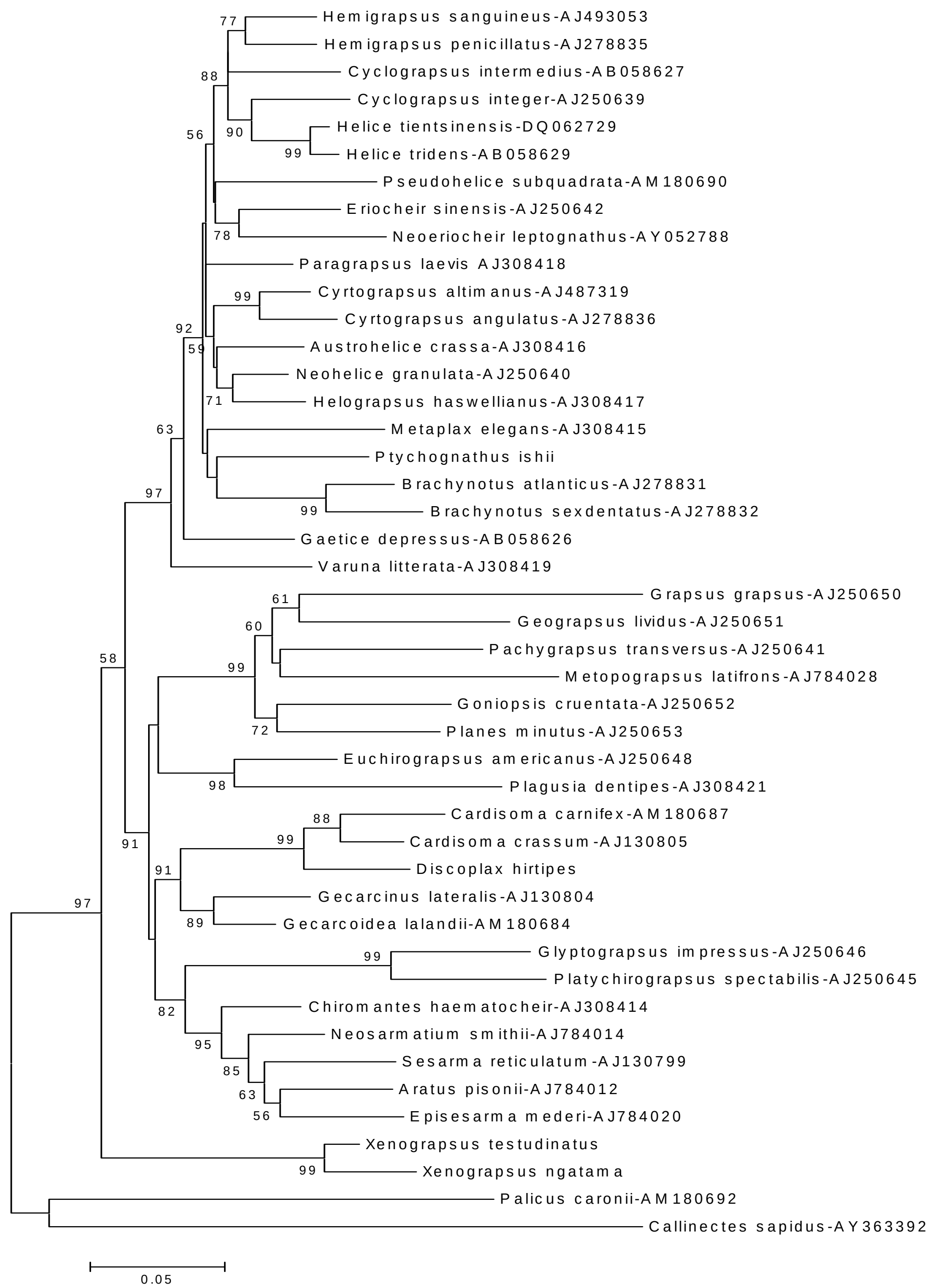



Figure 190. Phylogenetic consensus tree of 45 brachyuran crabs constructed with the neighbor joining method. Tamura-Nei distances with a gamma correction of 0.5. Confidence values according to an Interior-Branch Test with 2000 replicates. *Callinectes sapidus* and *Palicus caronii* were included as outgroups. Only confidence values higher than 50% are shown.

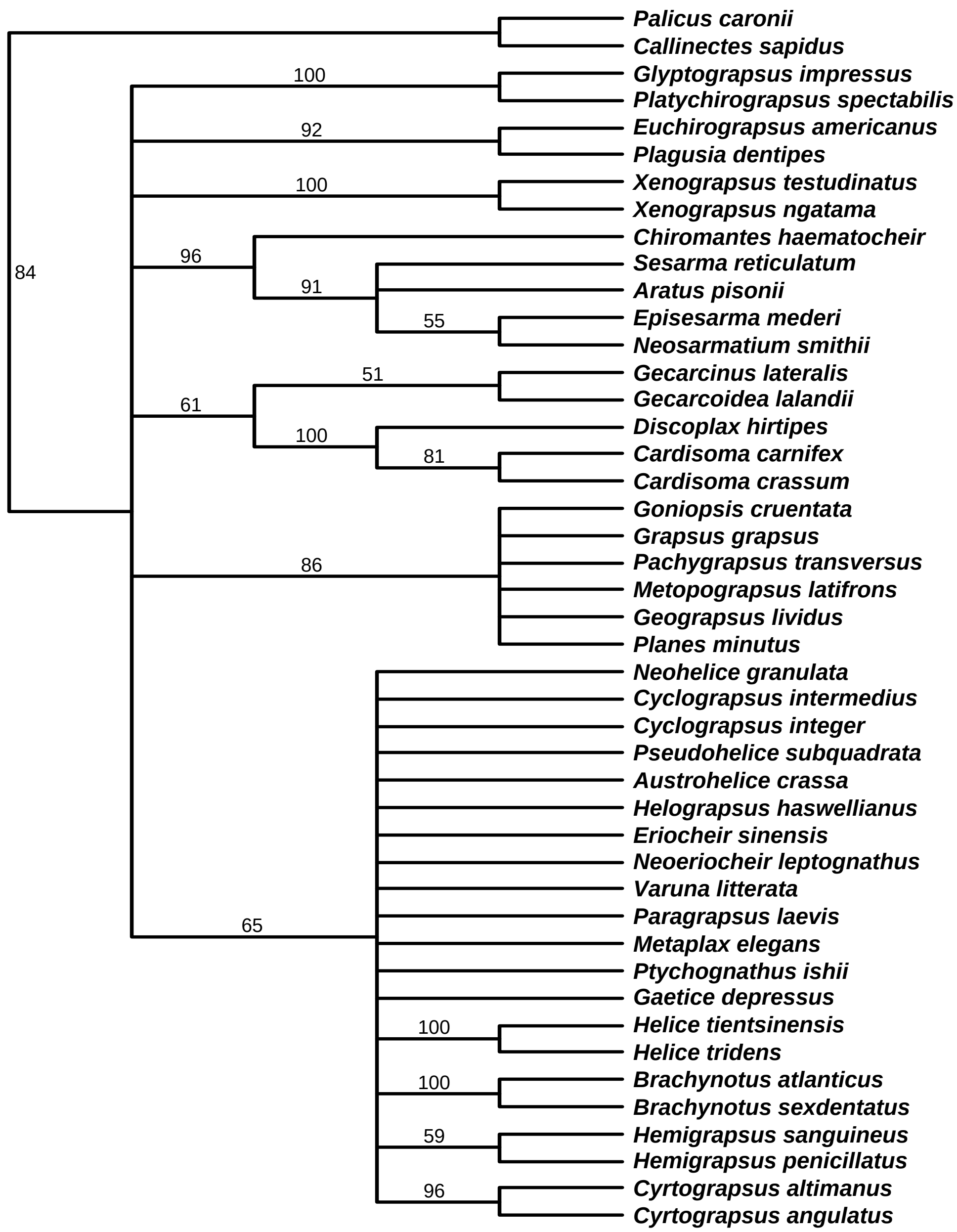



Figure 191. Phylogenetic consensus tree of 45 brachyuran crabs constructed with the maximum parsimony method resulting in one shortest tree of the length 1989 (CI=0.33, RI=0.36). Tranversions were weighed three times transitions. Confidence values after running 2000 bootstrap pseudoreplicates. *Callinectes sapidus* and *Palicus caronii* were defined as outgroups. Only confidence values higher than 50% are shown.

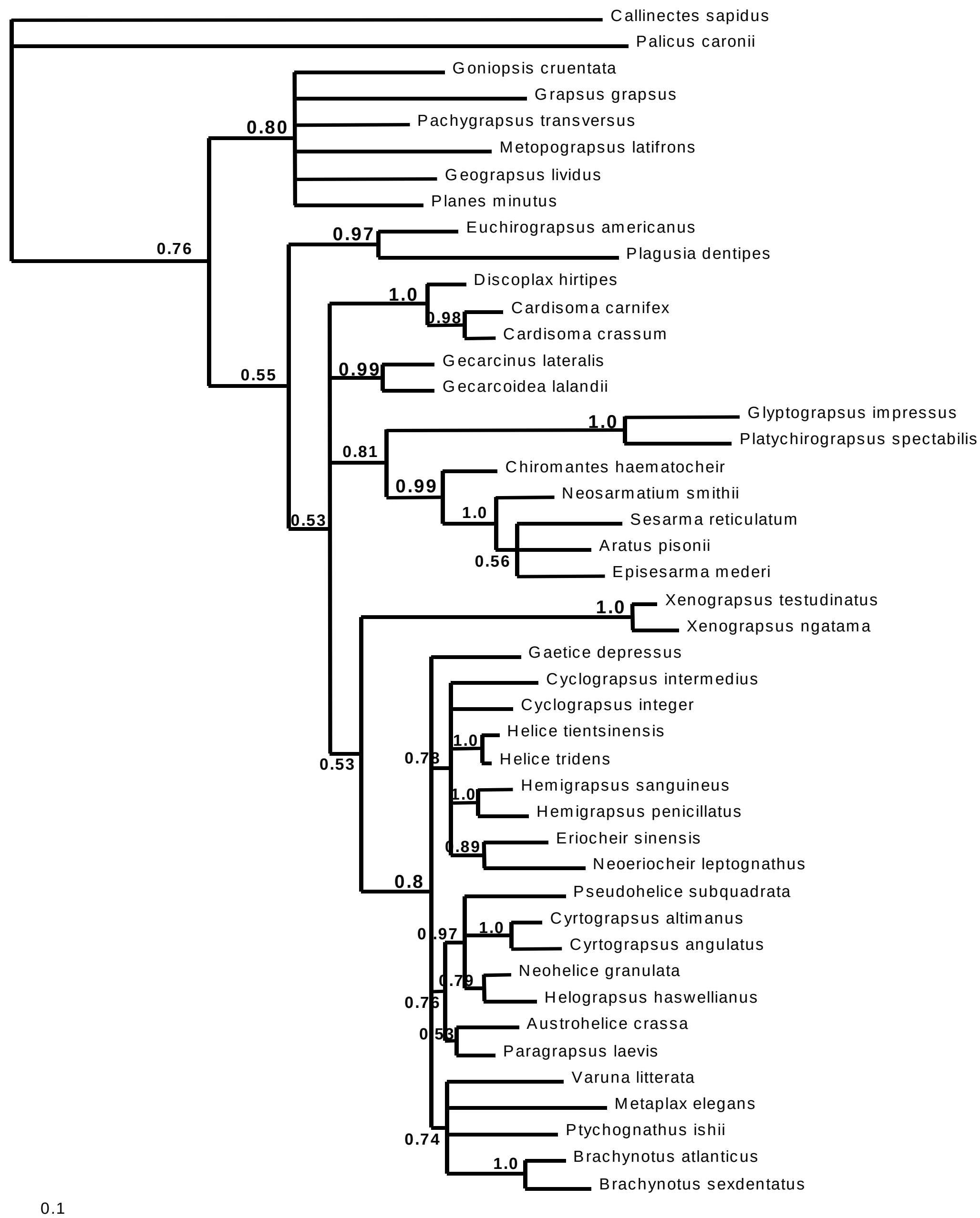



Figure 192. Phylogenetic consensus tree of 45 brachyuran crabs constructed with Bayesian inference based on the General time reversible model (GTR+I+G) as calculated with MODELTEST. Confidence values reflect posterior probabilities after running 4 chains for 2 million generations, excluding 20 thousand as burnin. *Callinectes sapidus* was defined as outgroup. Only confidence values higher than 0.5 are shown in the tree.

**DISCUSSION**

The overall evidence (adult morphology, larval features and DNA datasets) strongly supports the recognition of a separate family for the genus *Xenograpsus*. The adult features (Table 7), larval characters (Tables 8-11) and the molecular evidence (Figures 190-192) all corroborate, and leave little doubt that *Xenograpsus* represents a separate lineage, i.e. as a distinct new family, the Xenograpsidae.

With the recognition of the new family, the Grapsoidea now contains seven families: Grapsidae, Sesarmidae, Varunidae, Plagusiidae, Gecarcinidae, Glyptograpsidae and Xenograpsidae.

In addition, to the characters listed by Takeda & Kurata (1977), the following suite of characters also shows *Xenograpsus* to be significantly different from genera of other subfamilies in the Varunidae viz.

a) the infra-orbital crest with small granules, extending slightly beyond the orbits, and with no stridulatory function (vs. infra-orbital crests with a stridulatory function as in the subfamily Cyclograpsinae);

b) the third maxilliped lacks an oblique setose crest extending across the merus and outer distal corner of ischium (vs. oblique setose crest present in the family Sesarmidae and subfamily Cyclograpisnae, it must be noted that structure and form of the oblique setose crest in the Cyclograpsinae differs from that in the Sesarmidae (see above remarks on the subfamily Cyclograpsinae);

c) the infra-orbital and ptyergostomial grooves are present in the genus *Xenograpsus* but not as developed as those grooves found in the other subfamilies especially in the Cyclograpsinae. c) the palp of the third maxilliped is normal, with a long brush of setae not reaching the sternum when folded (vs. reaching beyond the sternum in subfamily Gaeticinae);

d) the thoracic sternal plastron is narrow with afairly depressed sulcus, the sternite 3/4 being narrow, the suture is not visible, and a medial groove which almost reaches the anterior margin of sternite 3 (vs. medial groove reaching anterior margin of the fourth sternite in other subfamilies);

e) the penis size is relatively much smaller (vs. much larger in all the other families); and

f) the base of the male abdomen is proportionately broader (vs. narrower in other families). The differences are also listed in Table 7 (see below).

### Genus *Xenograpsus* Takeda & Kurata, 1977

*Xenograpsus* Takeda & Kurata, 1977: 100; 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; McLay, 2007: in press.

**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 maybe present, oblique granulate crista absent on carapace above base of fifth ambulatory leg; cervical groove prominent. 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 calcifled, relatively short, stout. Female gonopore operculate, rounded in shape.

**Remarks.—** Currently, there are only three species found in this genus, viz. *X. novaeinsularis* Takeda & Kurata, 1977, from Japan; *X. testudinatus* Ng, Huang & Ho, 2000, from Taiwan; and a species off New Zealand, *X. ngatama* McLay, 2007. The latter is also the first record of the genus in the southern hemisphere. The specimens were from somewhat deeper waters but apparently still associated with vents (C. McLay, pers. comm.). Both *X. novaeinsularis* from Ogasawara islands and Mariana arc (Türkay & Sakai, 1995) and *Xenograpsus ngatama* from New Zealand (C. McLay, pers. comm.) are associated with black smokers, while *X. testudinatus* is associated with yellow smokers (Jeng *et al.*, 2004b).

**Key to species of *Xenograpsus***

1a. Carapace with one distinct protogastric tubercle. --------------------------- **2**

1b Carapace with many distinct protogastric tubercles. ----------- ***X. ngatama***

2a. Carapace with anterolateral tooth present, oblique granulated crista absent on carapace above base of fifth ambulatory legs. ------ ***X. novaeinsularis***

2b Carapace without anterolateral tooth, oblique granulated crista present on carapace above base of fifth ambulatory legs. -------------------- ***X. testudinatus***

### *Xenograpsus novaeinsularis* Takeda & Kurata, 1977

(Figure 193)

*Xenograpsus novaeinsularis* Takeda & Kurata, 1977: 100; Takeda *et al.*, 1993: 59; Türkay & Sakai, 1995: 25; Ng *et al.*, 2000: 46; Ng *et al.*, 2001: 191; Schubart *et al.*, 2002: 42; Jeng *et al.*, 2004: 969.

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

**Diagnosis.**— Carapace anterolateral margin without epibranchial tubercle; epigastric cristae prominent, one protogastric tubercule present; dorsal surface of the even, distinctly convex; oblique granulate crista absent on carapace above base of fifth ambulatory legs; cervical groove prominent. Margin of third maxilliped merus weakly convex. Cheliped merus short with length to width ratio 1.8. Tips of fingers spoon-shaped with a tuft of short setae. Ambulatory legs with lateral margins of meri subparallel; propodi relatively short, stout, with length to width ratio 1.5; dactylus stout, length to width ratio 2.3. Male telson broadly rounded distally. Male G1 strongly calcified, relatively short, stout, with length to width ratio 5.4.

**Colour.—** The colour of fresh specimens is reddish to greyish-brown in colour overall (Takeda & Kurata, 1977), and all preserved specimens examined are lighter in shade.

**Size.**— The largest male specimen examined is specimens so far is 20.4mm x 19.0mm (NSMT-Cr.6570), and the largest female so far is 10.0mm x 9.0mm (SFM-22945).

**Habitat.**— The crabs can be found hiding in the crevices of sulphur chimneys close to hydrothermal vents, or found on volcanic islands, sometimes in the tides pools on the shore (Takeda & Kurata, 1977).

**Remarks.**— Takeda & Kurata (1977) described *Xenograpsus novaeinsularis* from Nishino-shima island in the Ogasawara Islands, from an area with steep cliffs and violent waves; shortly after the island was first formed in 1973 (Kido & Koike, 1975; Nakamura & Koike, 1975; Takeda & Kurata, 1977). This species 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 subtile differences in the form of the carapace, and ratio of the chelipeds and ambulatory legs. The 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 further supports the fact they have very limited dispersal from their home ranges. The presence of a third species from New Zealand (see below) strongly indicates that the crabs are separated by the natural barrier of the open ocean. The specimens from the Mariana Arc should be re-examined in detail, and fresh materials collected for DNA study, as there is a possiblility that the *X. testudinatus* collected from Mariana Arc may be a cryptic new species, as it has been shown by numerous species found in hydrothermal environments (see Tunnicliffe & Fowler, 1996; McArthur & Tunnicliffe, 1998, van Dover, 2000, see below) I also have an ongoing project with Dr. C.D. Schubart to compare the DNA sequences of the three species currently available. However, the author is still trying to obtain fresh specimens of *X. novaeinsularis* from the Mariana Arc and Ogasawara Islands. Previous material has all been preserved in formalin.

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

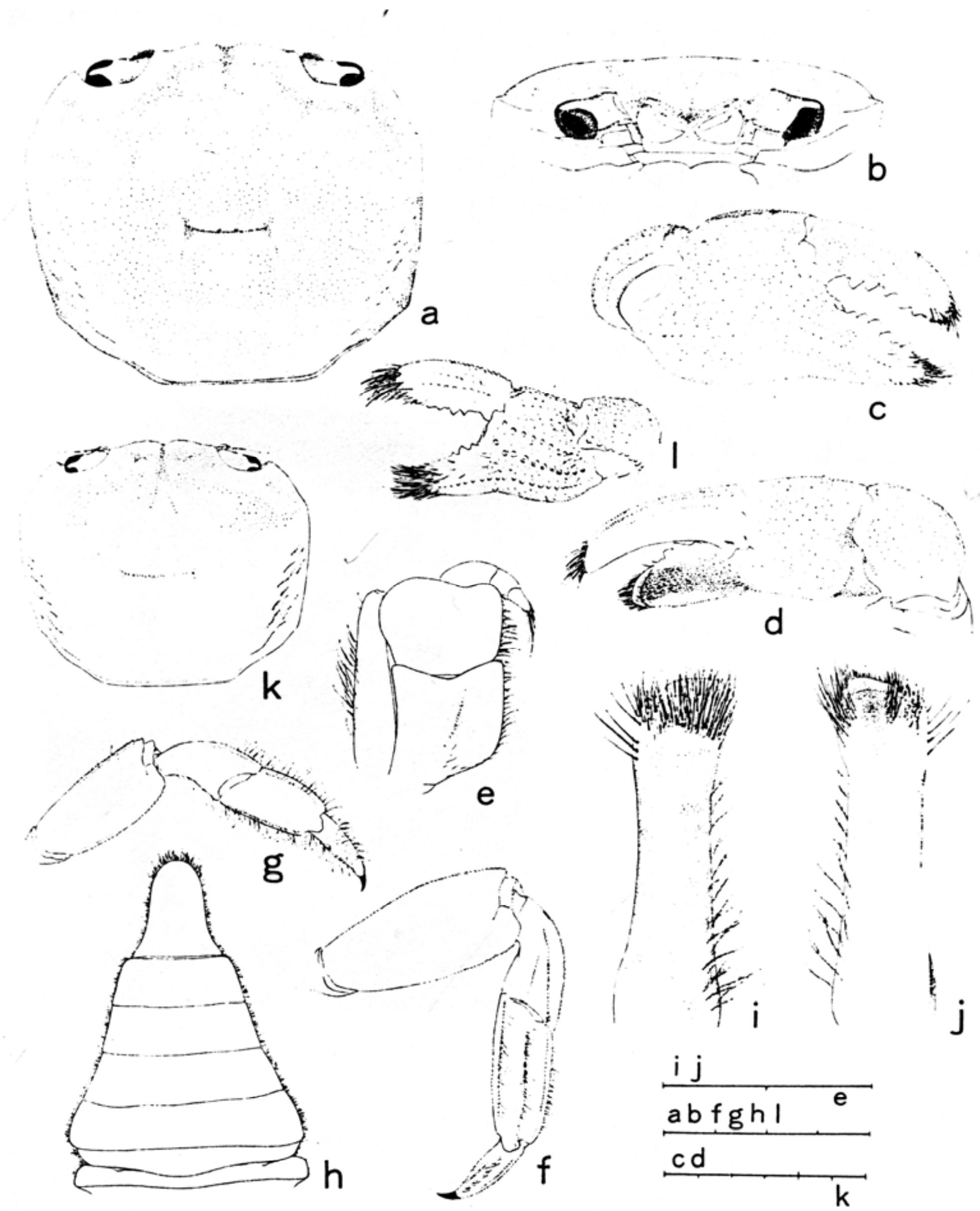



Figure 193. *Xenograpsus novaeinsularis* Takeda & Kurata, 1977.(From Takeda & Kurata, 1977).

## *Xenograpsus testudinatus* Ng, Huang & Ho, 2000

(Figures 194A-C; 195A-J)

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

**Materials examined.— Holotype** – 1 male (19.8mm x 18.0 mm) (TMCD-uncatalogued), Geng-Xin Fish Port, Pei-Kuan, 15m depth in rocky reef, I-Lan County, Taiwan, coll. P.H. Ho, 3 Oct. 1991. – **Paratypes** – 1 male (21.7mm x 20.1 mm) (TMCD-uncatalogued), Geng-Xin Fish Port, Pei-Kuan, 15m depth in rocky reef, I-Lan County, Taiwan, coll. P.H. Ho, 3 Oct. 1991; 1 male (15.8mm x 14.4 mm) (NTOU-uncatalogued), Geng-Xin Fish Port, Pei-Kuan, 15m depth in rocky reef, I-Lan County, Taiwan, coll. P.H. Ho, 3 Oct. 1991; 1 male (17.4 x 16.1 mm) (USNM-uncatalogued), Geng-Xin Fish Port, Pei-Kuan, 15m depth in rocky reef, I-Lan County, Taiwan, coll. P.H. Ho, 3 Oct. 1991; 3 males, 4 females (ZRC-uncatalogued), Kuei-Shan (= Turtle Mountain) Island, I-Lan County, Taiwan; 5 males, 7 females (ASIZ72116-2), 16m depth, near thermal vent, coll. 18 Apr. 1999.

**Diagnosis.**— Carapace anterolateral margin with epibranchial tubercle; epigastric cristae prominent; dorsal surface of the even, distinctly convex. Margin of third maxilliped merus weakly convex. Cheliped merus short with length to width ratio 1.8. Tips of fingers spoon-shaped with a tuft of short setae. Ambulatory legs with lateral margins of meri subparallel; propodi relatively short, stout, with length to width ratio 1.5; dactylus stout, length to width ratio 2.3. Male telson broadly rounded distally. Male G1 strongly calcifled, relatively short, stout, with length to width ratio 5.4.

**Colour.—** The colour of fresh specimens is reddish to greyish-brown in colour overall (Ng *et al.*, 2000). All preserved specimens examined are lighter in colour shade.

**Size.**— The largest male specimen examined is 21.7 x 20.1mm (paratype), the largest female reported is 21.6mm x 20.2mm (Ng *et al.*, 2000) .

**Habitat.**— It can be found hiding in the crevices of sulphur chimneys close to hydrothermal vents (Jeng *et al*., 2004a).

**Remarks.**— This species was described from the vents of Kueishan Island in northeastern Taiwan, and was separated from the allied *X. novaeinsularis* by the following characters: a) the absence of an epibranchial tubercle or tooth on the anterolateral margin of the carapace (vs. presence of a distinct epibranchial tooth in *X. novaeinsularis*); b) the epigastric cristae are relatively more prominent (vs. not prominent in *X. novaeinsularis*); c) the dorsal surface of carapace is relatively more convex (vs. less convex in *X. novaeinsularis*); d) the margin of the merus of the third maxilliped is weakly convex (vs. strongly convex in *X. novaeinsularis*); e) the merus of the cheliped is short, with the length to width ratio 1.8 (vs. relatively longer merus with a length to width ratio of 2.2 in *X. novaeinsularis*); f) the relatively shorter and stouter ambulatory propodus, with length to width ratio of 1.5 (vs. length to width ratio 2.4 in *X. novaeinsularis*); g) the shorter and stouter ambulatory dactylus, with a length to width ratio of 2.3 (vs. length to width ratio 3.8 in *X. novaeinsularis*); h) the lateral margins of the ambulatory meri are subparallel (vs. more convex in *X. novaeinsularis*); i) the distal margin of male telson being broadly rounded (vs. narrowly rounded in *X. novaeinsularis*); k) the G1 is proportionately shorter and stouter with a length to width ratio of 5.4, and more strongly calcified (vs. relatively longer and more slender G1, with the length to width ratio 6.0, and only weakly calcified in *X. novaeinsularis*); and l) the female gonopore is slightly raised (vs. sunkened in *X. novaeinsularis*) (see Ng *et al.*, 2000).

*Xenograpsus testudinatus* also appears to be a generally larger species than *X. novaeinsularis*, with most of the specimens examined measuring more than 18mm in carapace width. In contrast, most of the specimens of *X. novaeinsularis* examined by Ng *et al*. (2000), and reported thus far are relatively small (cf. Takeda & Kurata, 1977; Takeda *et al*., 1993; Türkay & Sakai, 1995). The largest specimens of *X. novaeinsularis* from Ogasawara, which measures 20.4mm in carapace width (NSMT-Cr.6570), compares well with the type series of *X. testudinatus*, allowing good comparisons to be made (see above). Examination of the good series of specimens of *X. novaeinsularis* on hand shows that larger specimens tend to have a more convex carapace dorsal surface, prominent epigastric cristae, more acute epibranchial teeth, third maxilliped which do not completely cover the buccal cavity, a male telson which does not completely cover the medial grooves of the third and fourth thoracic sternites, and ambulatory legs that are less setose to glabrous. However, none of these age- or size-related infra-specific variations, however, are substantial enough to account for the differences between *X. novaeinsularis* and *X. testudinatus* (see above).

**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 to feed on the zooplankton kill (or marine snow) resulting from the toxic plumes discharged by the vents. Such feeding behaviour was the first ever reported for any hydrothermal vent species (Jeng *et al.*, 2004a, b; see Appendix II). *Xenograpsus testudinatus* seems to be the only brachyuran crab present in this environment (Jeng *et al*., 2004 a, b). The biology this species is still under study (J.F. Huang & J.S. Hwang, pers. comm.).

**Distribution.**— Taiwan.

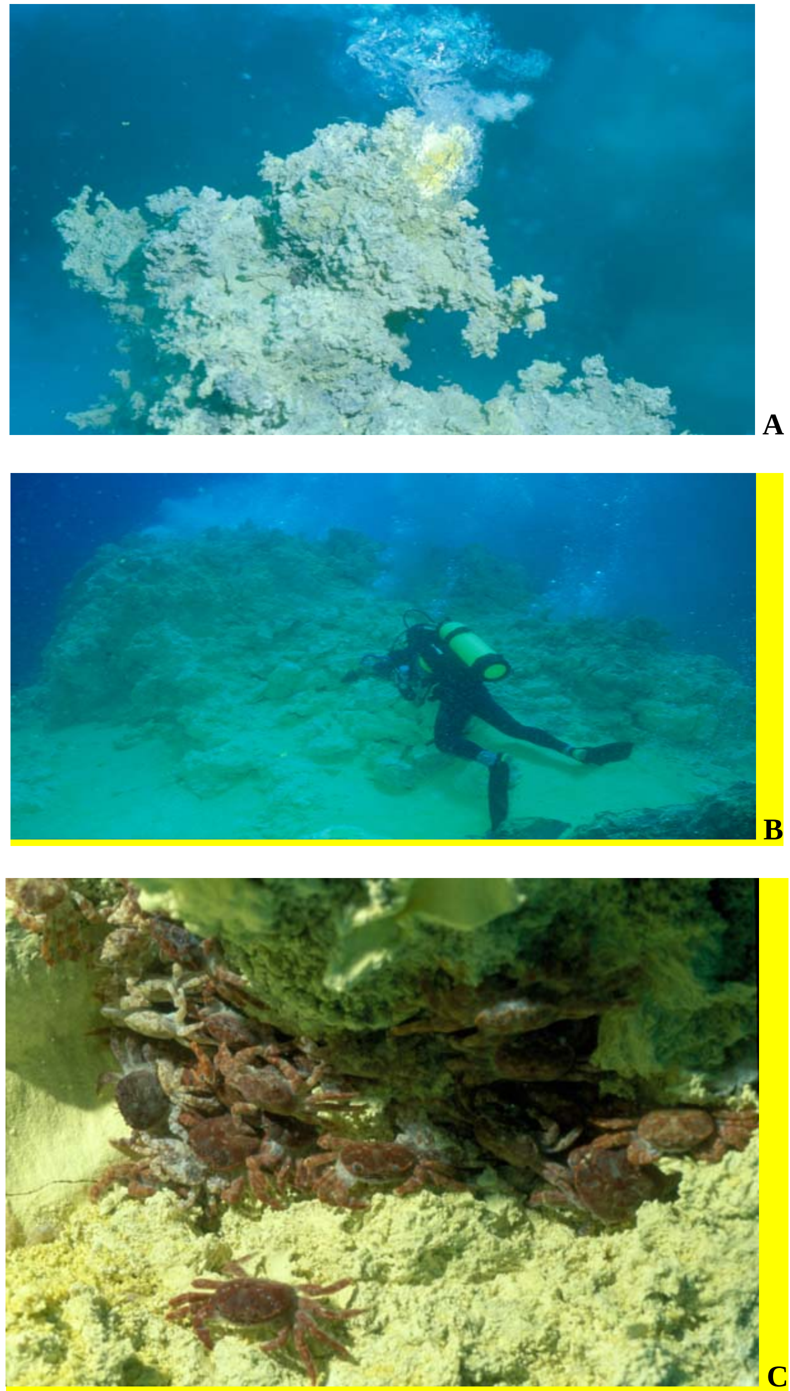



Figure 194. A, B) Yellow smoker around Kueishan Island; C) Cluster of *X. testudinatus* crabs in one of the crevices.

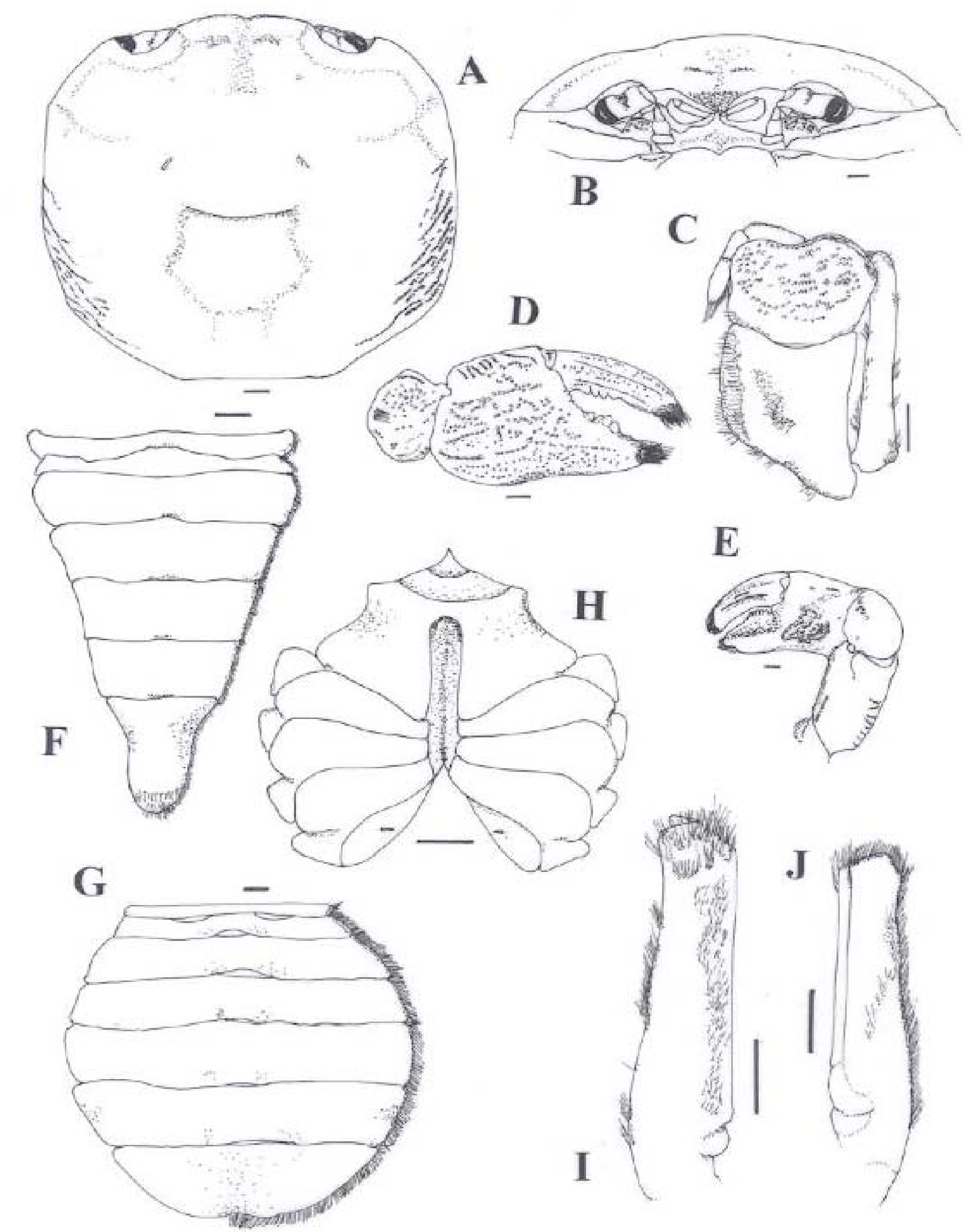



Figure 195. *Xenograpsus testudinatus*, male, holotype, 19.8mm x 18.0 mm, (TMCD). A) carapace; b) frontal view; c) third maxillipeds; d) right cheliped; e) inner view of chela; f) male abdomen; g) female abdomen; h) male sternum; i-j) different views male G1. (Scale=1.0mm).

## *Xenograpsus ngatama* McLay, 2007

(Figure 196)

*Xenograpsus ngatama* McLay, 2007: 1.

**Material examined.**— **Holotype** – 1 male (27.1mm x 25.8 mm) (NIWA), collected at NZOI stn. Z10782, during a *Tangaroa* cruise from 35º44.22 -44.04'S, 178º29.72 – 29.63'E, at a depth of 270 – 239 m, coll. 21 May 2001. – **Paratype** – 1 male (17.3mm x 15.7mm) (ZRC-uncatalogued), Brothers Seamount, near Kemadec Island, New Zealand, coll. C.M McLay, 2005.

**Diagnosis.**— Carapace anterolateral margin with epibranchial tubercle; epigastric cristae present but tubercles not arranged in cristae with many large tubercules; dorsal surface even, distinctly convex; three broad anterolateral teeth present, including the first orbital tooth; blique granulate crista present on carapace above base of fifth ambylatory leg cervical groove prominent. Margin of third maxilliped merus weakly convex. Cheliped merus short with length to width ratio 1.7. Tips of fingers spoon-shaped with a tuft of short setae. Ambulatory legs with lateral margins of meri subparallel; propodi relatively short, stout, with length to width ratio 1.5; dactylus stout, length to width ratio 2.3. Male telson broadly rounded distally. Male G1 strongly calcifled, relatively short, almost straight, with length to width ratio 5.3.

**Colour.**— The colour of fresh specimens is cream to reddish brown in colour (C. McLay, pers. comm.), and the colour of all preserved specimens examined is brown in colour.

**Size.**— The largest male specimen examined is 17.3mm x 15.7mm (NIWA-uncatalogued), and the largest female is not known as so far no female have been collected (C. McLay, pers. comm.).

**Remarks.**— The new species from New Zealand was just recently described by McLay (2006). The three species can be easily separated from each other by the form of the carapace and other morphological features (Mclay, 2007). In addition to the morphological differences, preliminary studies on 560 base-pairs of 16s rRNA of this species, has shown that this species clusters with *X. testudinatus*. There are still a number of differences in the sequence (ongoing study with C. D Schubart), that warrant its status as a new species.

**Distribution.**— New Zealand only.

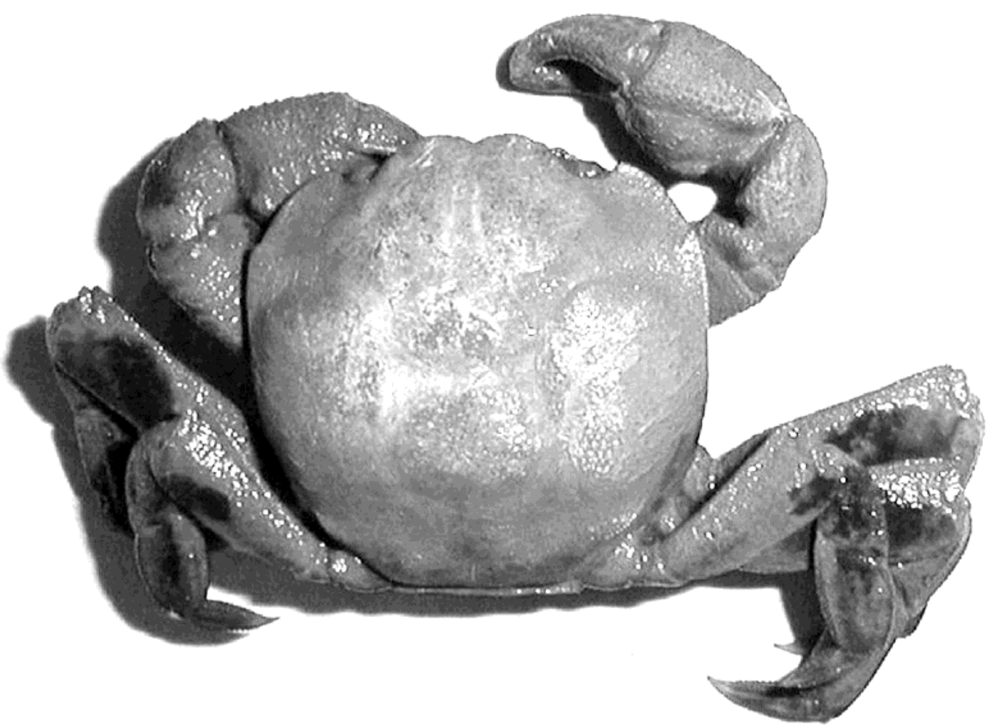


Figure 196. *Xenograpsus ngatama* McLay, 2007, from New Zealand, male, holotype, 17.3mm x 15.7mm (ZRC-no cat. number). Dorsal view.

**COMARATIVE MATERIALS**

The following is a list of comparative material that were used for adult morphology comparisons to elucidate the family status of the Xenograpsidae.:

**Family Grapsidae MacLeay, 1838:**

*Geograpsus crinipes* (Dana, 1852): 1 male (55.8mm x 45.9mm) (ZRC 2001.0727), Pago Bay, Guam, coll. P.K.L. Ng, 28 Jul. 2001.

*Planes cyaneus* Dana, 1852: 1 male (14.9mm x 14.5mm), 1 female (ovigerous) (9.8mm x 9.7mm) (ZRC 2000.0453), Heeia, Hawaii, coll. D. Takada, 23 Jan. 1999.

*Metopograpus oceanicus* Jacquinot, 1852: 1 male (24.0mm x 19.5mm), 2 females (ovigerous) (28.8-29.6mm x 24.6-24.4mm) (ZRC), Changi, Singapore, coll. Tweedie, Jun. 1934.

*Pachygrapsus fakaravensis* (Rathbun, 1907): 2 males (18.7-19.0mm x 17.3-17.6mm), 1 female (ovigerous) (18.3mm x 16.7mm) (ZRC 2000.0406), Kewalo, on seawall, Ala Moana, Waikiki, Oahu, Hawaii, coll. S.H Tan & P.K.L. Ng, 22 Jan. 2000.

**Family Glytograpsidae Schubart, Cuesta & Felder, 2002:**

*Glyptograpsus impressus* Smith, 1870: 1 male (7.8mm x 6.0mm) (USMN-168826), Panama, no collection date; 1 male (9.1mm x 7.3mm) (USNM-uncatalogued), no other data; 2 male (15.4-17.8mm x 13.6-15.4mm), 1 female (13.8mm x 11.5mm) (RMNH-D9745), El Salvador, coll. M. Boeseman, 27 Feb. 1953; 1 male (11.6mm x 10.0mm), 1 female (20.1mm x 16.8mm) (RMNH-D9746), Rio Conchalio, El Salvador, coll. M. Boeseman, 21 Mar. 1953.

*Platychirograpsus spectabilis* de Man, 1896: 3 males (36.2-43.7mm x 29.5-36.6mm) (RMNH-D25479), Veracruz, Mexico, coll. E.A. Charex, 20 Sep.1965; 1 male (45.1mm x 38.5mm) (SFM-7498), Veracruz, Mexico, leg. Burmeister, 7 Nov. 1973.

**Family Sesarmidae Dana, 1852:**

*Sesarma reticulata* Say, 1817: 1 male (25.4mm x 21.3mm) (ZRC 1970.8.4.6), Atlantic coast of North America, det. R. Serène, 10 Jul. 1970.

*Chiromantes haematocheir* (de Haan, 1833): 1 male (41.0mm x 34.0mm) (NHM-1880), Chufoo, Shangtung, China, coll. S. Hindle, no collection date.

*Bresedium brevipes* (de Man, 1889): 1 male (21.9mm x 19.9mm) (QMW-8810), Daintree river, North Queensland, Australia, coll. B. Campbell, 3 Dec. 1975.

*Aratus pisoni* H. Milne Edwards, 1837: 1 male (18.9mm x 18.8mm) (NHM-1923.8.14.50-64), Marajo Island, Amazon, Brazil, no collection date.

*Episesarma singaporense* (Tweedie, 1936): 1 male (19.1mm x 16.5mm), 1 female (15.1mm x 12.0mm) (ZRC 1999.0565), Chonburi Province, Thailand, coll. P.K.L. Ng, 29 Sep.1998.

*Neosarmatium smithi* H. Milne Edwards, 1853: 1 male (36.6mm x 35.8mm) (ZRC 1971.7.29.2), Singapore, Johore Straits, coll. C.L. Soh, 18 Jul. 1971.

**Family Plagusiidae Dana, 1852:**

*Plagusia speciosa* Dana, 1852 (additional to Ng *et al.*, 2001): 1 male (34.4mm x 32.2 mm), 1 female (ovigerous) (22.6mm x 20.9mm) (ZRC 2000.2234), Chuanfanshi, Hengchun, Pingtung County, Taiwan, coll. H.C. Liu, 16 Oct. 1997; 3 males (14.6-25.3mm x 13.2-23.3mm) (TMCD-CHCD), Jiupeng, Pingtung County, Taiwan, coll. H.C. Liu, 23 Mar. 1997; 2 males (23.3-26.3mm x 21.2-23.6 mm), 1 female (20.7mm x

18.4mm), 1 female (ovigerous) (25.5mm x 23.0 mm) (TMCD-CHCD-1764), no other data; 1 male (30.8mm x 27.8 mm) (TMCD-CHCD-1779), Fengchuisha, Hengchun, Pingtung County, Taiwan, coll. H.C. Liu, 11 Aug. 1997; 1 male (36.0mm x 32.6mm), 1 female (ovigerous) (36.6mm x 32.8mm) (TMCD-CHCD-1765), Jialuoshui, Hengchun, Pingtung County, Taiwan, coll. H.C. Liu, 12 Aug. 1997; 1 male (29.9mm x 27.8mm) (TMCD-CHCD-1799), Hengchun, Pingtung County, Taiwan, coll. H.C. Liu, 17 Nov. 1997; 1 male (31.8mm x 29mm) (TMCD-CHCD), Chuanfenshi, Hengchun, Pingtung County, Taiwan, coll. H.C. Liu, 11 Dec. 1997; 12 males (20.6-38.0mm x 18.7-34.4mm), 12 females (11 ovi) (23.2-35.2mm x 20.7-31.1mm) (TMCD-CHCD), Lutao, Taitung County, Taiwan, coll. H.C. Liu, 10-12 Sep. 1999; 1 male (31.0mm x 29.5mm) (TMCD-CHCD), Shitiping, Hualian County, Taiwan, coll. H.C. Liu & C.H. Wang, 7 May. 2000.

*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; 2 females (ZRC 1965.7.27.121-122), Cocos-Keeling Islands, coll. C. A. Gibbson-Hill, 1941; 1 male, 1 female (ZRC 1999.1413), night market in Keelung, Taiwan, coll. N.K. Ng & Y. Cai, 27 Nov. 1997; 1 female (TMCD-uncatalogued), Hengchun, Taiwan, coll. H.C. Liu, no collection date.

*Plagusia squamosa* (Herbst, 1790): 1 male (41.7mm x 49.6mm) (SAM-A-39677), Isipingo Natal, coll. ULT Ecological Survey, 12 Jul. 1935; 2 males, 1 females (ovigerous) (ZRC 1999.0988), night market in Keelung, Taiwan, coll. N.K. Ng & Y. Cai, 27 Nov. 1997; 1 female (TMCD-uncatalogued); Chuanfanshi, Hengchun, Taiwan, coll. H.C. Liu, 30 Jun 1999; 1 female (TMCD-uncatalogued), Hengchun, Taiwan, coll. H.C. Liu, 28 Jul. 1999; 1 male (41.0mm x 38.4mm) (ZRC-uncatalogued), Pritidian Point, Guam, coll. G. Paulay, 19 Jan. 1997.

*Percnon affinis* Nobili, 1907: 2 males (28.8-37.3mm x 30.4-41.1mm), 1 female (40.4mm x 41.6mm), Kenting National Park, Taiwan, coll. 7 Apr. 2004.

*Miersiograpsus kingsleyi* (Miers, 1885): 4 males (6.5-12.1mm x 6.2-11.3mm), 2 females (ovigerous) (8.1-8.1mm x 7.8-8.2mm) (SFM-13555), station 48, coll. 1 Aug.

1984; 1 male (broken carapace), 1 female (6.0mm x6.0mm) (SFM-8339), coll. 1898-1899.

*Echirograpsus madagascarensis* Türkay, 1978: 1 male (9.4mm x 9.4mm), 1 female (10.0mm x 9.7mm) (SFM-7794), Madagascar, coll. A. Crosnier, 3 Mar. 1973;

*Euchirograpsus americanus* H. Milne Edwards, 1880 : 1 male (13.4mm x 12.7mm), 1 female (ovigerous) (16.4mm x 15.3mm) (SFM-no cat. number), Florida, USA, leg. W.L. Schmitt, 4 Aug. 1931; 1 female (ovigerous) (13.5mm x 13.9mm) (USNM-155628), Bahama Island, Straits of Florida, USA, coll. 29 Mar. 1975; 1 male (11.5mm x 11.2mm), 1 female (ovigerous) (9.6mm x 9.4mm) (USNM-232638), off south Carolina, USA, coll. 9 Mar. 1981; 1 male (8.7mm x 8.1mm), 1 female (6.3mm x 5.8mm) (USNM-202806), off north Carolina, 99m depth, coll. 14 May. 1981; 1 female (10.0mm x 6.4mm) (USNM-276579), off Florida, Gulf of Mexico, coll. 10 Dec. 1983; 1 female (18mm x 12.4mm) (USNM-276578), off Florida, Gulf of Mexico, coll.10 Dec. 1983.

*Euchirograpsus liguricus* H. Milne Edwards, 1853: 1 female (23.5mm x 20.8mm) (SFM), Morokkan, kurste, station 9c-82a, coll. Meteor Expedition, 18-19 Jun 1967; 7 males (8.8-20.4mm x 7.9-17.8mm), 4 females (8.3-10.9mm x 7.4-9.2mm) (SFM), Marokkan, station 8-13a, 120-180 depth, coll. Meteor Expedition, 23 Jan. 1967.

*Euchirograpsus timorensis* Türkay, 1975: 1 male (18.1mm x 17.1mm), 3 females (12.8-23.5mm x 12.7-22.5mm) (USNM-308983), New Caledonia, coll. 18 Oct. 1992; 2 males (15.4-17.2mm x 15.0-16.7mm), 3 females (18.8-23.3mm x 18.5-22.2mm) (USNM-308984), New Caledonia, coll. 29 Jan. 1993.

*Euchirograpsus turekayii* Crosnier, 2001: 2 males (34.1-37.8mm x 33.2-367mm), (ZRC-uncatalogued), Balicasaq Island, off Panglao Island, Bohol, Phlilppines, coll. P.K.L. Ng, 25-30 Jul. 2003.

**Family Gecarcinidae MacLeay, 1838:**

*Epigrapsus notatus* (Heller, 1865): 1 male (33.8mm x 28.8mm) (ZRC-uncatalogued), Siang-Chiao-Wan, Heng-Chun Peninsula, Pingtung County, Taiwan, coll. H.C. Liu, 19 Jan. 1998.

*Gercarcinus weileri* Sendler, 1912: 2 males (52.7-59.4mm x 41.6-46.4mm), (ZMK-no cat. number), Sao Thome, West Africa, coll. Galathea Expedition, no collection date.

*Cardisoma crassus* Smith 1870: 2 males (37.0-39.9mm x 29.4-33.25mm) (ZMK-no cat. number), El Salvador, Triunfo, coll. 20-21 Feb. 1953.

*Discoplax hirtipes* (Dana, 1852): 1 male (69.1mm x 53.5mm) (ZRC 2004.0462),Hinagdanan Cave, Panglao Island, Bohol, The Visayas, Philippines, coll. P.K.L. Ng, 3 Mar. 2004.

## PHYLOGENETIC ANALYSIS

### Introduction

In the last few years, there have been numerous reports on the phylogeny of the Grapsoidea (see Sternberg & Cumberlidge, 2000; Kitaura *et al*, 2001; Schubart *et al*., 2000a; 2000b; 2002, 2006; Cuesta & Schubart, 1997 etc.). Most of the phylogenetic studies, so far, have been based on molecular data (Kitaura *et al*, 2001; Schubart *et al*., 2000a; 2000b; 2002, 2006), and/or larval data (Cuesta & Schubart, 1998; 1999; Cuesta *et al*., 2000; Schubart *et al*., 2001). There is only one paper that has dealt with adult morphology, larval morphology and the molecular data sets (Schubart *et al*, 2002). So far, there are only two reports that have dealt with adult morphology including fossil evidence (Sternberg & Cumberlidge, 2000; Karasawa & Kato, 2001).

The recent publication of the phylogeny of Grapsoidea by Schubart *et al*. (2000a, 2002; 2006) has elevated the subfamilies Vauninae, Sesarminae, Plagusinae to family level, and it has been widely accepted (Martin & Davies, 2001, Schubart *et al*., 2002; 2006). The use of larval characters has also more or less supported the new classification system (Cuesta, 1997; 2000; 2001; Jeng *et al*., 2004). There is no proper detailed study on the adult morphology of this group of crabs, and there are doubts if the molecular and larval classification would agree with the adult classification system. As such, the aim of the cladistic analysis is to use adult morphology a) to elucidate the relationships between the six previously recognized grapsoid families; b) to show if the Varunidae is monophyletic; c) to show that the Cyclograpsinae is a subfamily of the Varunidae and not Sesarmidae; and d) to determine the phylogenetic position of the Xenograpsidae.

## MATERIALS AND METHODS

A data matrix comprising of 48 species, 47 genera (2 species of *Xenograpsus*) and 113 characters (Appendix 1) was edited with MacClade Release Version 4.05 for OS X (Maddison & Maddison, 2002). The ingroup consists of 46 species from the different genera (listed in Appendix 2). The two outgroup species are *Holotheres halingi* from the family Pinnotheridae, and *Expixanthus frontalis* from the family Eriphiidae. The ingroup species were selected to represent a broad diversity of external adult morphologies. The outgroup species were selected based on their hypothesized relationships to the ingroup. Both the ingroups and outgroups are found roughly in the same distribution range as well as habitat. The phylogeny presented is rooted with the two outgroups.

To search for the most parsimonious phylogenetic tree, the morphological data were analyzed using the heuristic search option in the PAUP* version 4.0b10 for Macintosh, with 100 random addition replicates via stepwise addition and TBR branch swapping (Swofford *et al.*, 1996; Swofford, 2000; 2002). PAUP was used to calculate tree length (TL), Consistency Index (CI), Retention Index (RI), rescaled Consistency Index (RC), and the strict consensus of the most parsimonious tree.

Clade stability was assessed by using Bootstrap analysis (Felsenstein, 1985a; 1985b), and Jackknife analysis (Ferris *et al*., 1996). TNT Version 1 (Goloboff, 1993a; 1993b; 1993-97; 1999) was used to perform 100 replicates of the Bootstrap analyses, in addition to the strict consensus of the most parsimonious tree. Synapomorphies and characters optimizations were obtained using the character tree trace option in MacClade Release Version 4.05 for OS X (Maddison & Maddison, 2002). All characters analyzed were unordered and unweighted.

Appendix 1. Data matrix for the analysis of 46 ingroups and two outgroups, <-> indicates unknown data.

| **Species\Characters** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Xenograpsus testudinatus* | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Xenograpsus novaeinsularis* | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Grapsus albolineatus* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Metopograpsus oceanicus* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Planes cyaneus* | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Pachygrapsus fakavaraensis* | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Varuna litterata* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ptychognathus ishii* | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Hemigrapsus penicillatus* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Eriocheir sinensis* | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 |
| *Platyeriocheir formosa* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Neoeriocheir leptognathus* | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Scutumara enodis* | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Pseudograpsus setosus* | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Orcovita saltatrix* | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Pyxidognathus granulosus* | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Noarograpsus lobulatus* | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Austrograpsus spinosus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Cyrtograpsus angulatus* | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 4 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Gnathograpsus riedelii* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Parapyxidognathus deianira* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Quadragrapsus albus* | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Utica gracilipes* | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Mitragrapsus dentatus* | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Pseudoutica borneensis* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Brachynotus lucasii* | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Cyclograpsus audouinii* | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Chasmagnathus convexus* | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Helice formosensis* | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Metaplax elegans* | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Paragrapsus laevis* | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Gaetice depressus* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Setostoma balssi* | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 |
| *Thalassograpsus harpax* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Gercarcinus weileri* | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Epigrapsus notatus* | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Discoplax hirtipes* | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Platychirograpsus typicus* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 4 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| *Glyptograpsus impressus* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 4 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| *Plagusia squamosa* | 1 | 0 | 2 | 0 | 2 | 0 | 1 | 1 | 2 | 0 | 0 | 3 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Percnon affine* | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 3 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Euchirograpsus tuerkayi* | 1 | 2 | 2 | 0 | 2 | 0 | 1 | 0 | 2 | 0 | 0 | 3 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Sesarma reticulata* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Episesarma singaporense* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Aratus pisoni* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Neosarmatium smithi* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Holotheres halingi* | 2 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 |
| *Epixanthus frontalis* | 3 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |

| Species\Characters | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Xenograpsus testudinatus* | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Xenograpsus novaeinsularis* | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Grapsus albolineatus* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 |
| *Metopograpsus oceanicus* | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 |
| *Planes cyaneus* | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 |
| *Pachygrapsus fakavaraensis* | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 |
| *Varuna litterata* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Ptychognathus ishii* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Hemigrapsus penicillatus* | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Eriocheir sinensis* | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Platyeriocheir formosa* | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Neoeriocheir leptognathus* | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Scutumara enodis* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Pseudograpsus setosus* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Orcovita saltatrix* | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Pyxidognathus granulosus* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Noarograpsus lobulatus* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Austrograpsus spinosus* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Cyrtograpsus angulatus* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Gnathograpsus riedelii* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Parapyxidognathus deianira* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Quadragrapsus albus* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Utica gracilipes* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Mitragrapsus dentatus* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Pseudoutica borneensis* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Brachynotus lucasii* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Cyclograpsus audouinii* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Chasmagnathus convexus* | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Helice formosensis* | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Metaplax elegans* | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Paragrapsus laevis* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Gaetice depressus* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Setostoma balssi* | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Thalassograpsus harpax* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Gercarcinus weileri* | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Epigrapsus notatus* | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Discoplax hirtipes* | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Platychirograpsus typicus* | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Glyptograpsus impressus* | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Plagusia squamosa* | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| *Percnon affine* | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| *Euchirograpsus tuerkayi* | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| *Sesarma reticulata* | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| *Episesarma singaporense* | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| *Aratus pisoni* | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| *Neosarmatium smithi* | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| *Holotheres halingi* | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 |
| *Epixanthus frontalis* | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 |

| Species\Characters | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Xenograpsus testudinatus* | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Xenograpsus novaeinsularis* | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Grapsus albolineatus* | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Metopograpsus oceanicus* | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Planes cyaneus* | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Pachygrapsus fakavaraensis* | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Varuna litterata* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Ptychognathus ishii* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 |
| *Hemigrapsus penicillatus* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Eriocheir sinensis* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Platyeriocheir formosa* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Neoeriocheir leptognathus* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Scutumara enodis* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | - | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Pseudograpsus setosus* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Orcovita saltatrix* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 |
| *Pyxidognathus granulosus* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Noarograpsus lobulatus* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Austrograpsus spinosus* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Cyrtograpsus angulatus* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Gnathograpsus riedelii* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 |
| *Parapyxidognathus deianira* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Quadragrapsus albus* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Utica gracilipes* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Mitragrapsus dentatus* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | - | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 |
| *Pseudoutica borneensis* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 |
| *Brachynotus lucasii* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Cyclograpsus audouinii* | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| *Chasmagnathus convexus* | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| *Helice formosensis* | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| *Metaplax elegans* | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| *Paragrapsus laevis* | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| *Gaetice depressus* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Setostoma balssi* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Thalassograpsus harpax* | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| *Gercarcinus weileri* | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 2 |
| *Epigrapsus notatus* | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 2 |

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Discoplax hirtipes* | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 2 |
| *Platychirograpsus typicus* | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | - | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 2 |
| *Glyptograpsus impressus* | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | - | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 2 |
| *Plagusia squamosa* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | - | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Percnon affine* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | - | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Euchirograpsus tuerkayi* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | - | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Sesarma reticulata* | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 0 |
| *Episesarma singaporense* | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 0 |
| *Aratus pisoni* | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 0 |
| *Neosarmatium smithi* | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 0 |
| *Holotheres halingi* | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Epixanthus frontalis* | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 |

| Species\Characters | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Xenograpsus testudinatus* | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *Xenograpsus novaeinsularis* | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *Grapsus albolineatus* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| *Metopograpsus oceanicus* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| *Planes cyaneus* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| *Pachygrapsus fakavaraensis* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| *Varuna litterata* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Ptychognathus ishii* | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Hemigrapsus penicillatus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Eriocheir sinensis* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Platyeriocheir formosa* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Neoeriocheir leptognathus* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Scutumara enodis* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Pseudograpsus setosus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Orcovita saltatrix* | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Pyxidognathus granulosus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Noarograpsus lobulatus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Austrograpsus spinosus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Cyrtograpsus angulatus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Gnathograpsus riedelii* | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Parapyxidognathus deianira* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Quadragrapsus albus* | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Utica gracilipes* | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Mitragrapsus dentatus* | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Pseudoutica borneensis* | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Brachynotus lucasii* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Cyclograpsus audouinii* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 |
| *Chasmagnathus convexus* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 |
| *Helice formosensis* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 |
| *Metaplax elegans* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 |
| *Paragrapsus laevis* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 |
| *Gaetice depressus* | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 |
| *Setostoma balssi* | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 |
| *Thalassograpsus harpax* | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 |
| *Gercarcinus weileri* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *Epigrapsus notatus* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Discoplax hirtipes* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *Platychirograpsus typicus* | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Glyptograpsus impressus* | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Plagusia squamosa* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 |
| *Percnon affine* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 |
| *Euchirograpsus tuerkayi* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 |
| *Sesarma reticulata* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Episesarma singaporense* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Aratus pisoni* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Neosarmatium smithi* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Holotheres halingi* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 |
| *Epixanthus frontalis* | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |

| Species\Characters | 81 | 82 | 83 | 85 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Xenograpsus testudinatus* | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Xenograpsus novaeinsularis* | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Grapsus albolineatus* | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 |
| *Metopograpsus oceanicus* | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 |
| *Planes cyaneus* | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 |
| *Pachygrapsus fakavaraensis* | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 |
| *Varuna litterata* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Ptychognathus ishii* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Hemigrapsus penicillatus* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Eriocheir sinensis* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 |
| *Platyeriocheir formosa* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 |
| *Neoeriocheir leptognathus* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 |
| *Scutumara enodis* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Pseudograpsus setosus* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Orcovita saltatrix* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Pyxidognathus granulosus* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Noarograpsus lobulatus* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 |
| *Austrograpsus spinosus* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 |
| *Cyrtograpsus angulatus* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Gnathograpsus riedelii* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Parapyxidognathus deianira* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Quadragrapsus albus* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Utica gracilipes* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Mitragrapsus dentatus* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Pseudoutica borneensis* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Brachynotus lucasii* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Cyclograpsus audouinii* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Chasmagnathus convexus* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Helice formosensis* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Metaplax elegans* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Paragrapsus laevis* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Gaetice depressus* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Setostoma balssi* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Thalassograpsus harpax* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Gercarcinus weileri* | 0 | 1 | 0 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Epigrapsus notatus* | 0 | 1 | 0 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Discoplax hirtipes* | 0 | 1 | 0 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Platychirograpsus typicus* | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *Glyptograpsus impressus* | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| *Plagusia squamosa* | 1 | 1 | 2 | 1 | 0 | 2 | 0 | 2 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| *Percnon affine* | 1 | 1 | 2 | 1 | 0 | 2 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| *Euchirograpuis tuerkayi* | 1 | 1 | 2 | 1 | 0 | 2 | 0 | 2 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| *Sesarma reticulata* | 0 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Episesarma singaporense* | 0 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Aratus pisoni* | 0 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Neosarmatium smithi* | 0 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Holotheres halingi* | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Epixanthus frontalis* | 0 | 1 | 1 | 1 | 1 | 4 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 0 |

| **Species\Characters** | **101** | **102** | **103** | **104** | **105** | **106** | **107** | **108** | **109** | **110** | **111** | **112** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Xenograpsus testudinatus* | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 |
| *Xenograpsus novaeinsularis* | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 |
| *Grapsus albolineatus* | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Metopograpsus oceanicus* | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Planes cyaneus* | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Pachygrapsus fakavaraensis* | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Varuna litterata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Ptychognathus ishii* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hemigrapsus penicillatus* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Eriocheir sinensis* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Platyeriocheir formosa* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Neoeriocheir leptognathus* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Scutumara enodis* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Pseudograpsus setosus* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Orcovita saltatrix* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Pyxidognathus granulosus* | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 |
| *Noarograpsus lobulatus* | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Austrograpsus spinosus* | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *Cyrtograpsus angulatus* | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| *Gnathograpsus riedelii* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Parapyxidognathus deianira* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Quadragrapsus albus* | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Utica gracilipes* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Mitragrapsus dentatus* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Pseudoutica borneensis* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Brachynotus lucasii* | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Cyclograpsus audouinii* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 |
| *Chasmagnathus convexus* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Helice formosensis* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 |
| *Metaplax elegans* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Paragrapsus laevis* | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 2 |
| *Gaetice depressus* | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 1 |
| *Setostoma balssi* | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| *Thalassograpsus harpax* | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 |
| *Gercarcinus weileri* | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 2 |
| *Epigrapsus notatus* | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Discoplax hirtipes* | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 2 |
| *Platychirograpsus typicus* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *Glyptograpsus impressus* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *Plagusia squamosa* | 1 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 2 |
| *Percnon affine* | 1 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 2 |
| *Euchirograpsus tuerkayi* | 1 | 1 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 2 |
| *Sesarma reticulata* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Episesarma singaporense* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 |
| *Aratus pisoni* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Neosarmatium* smithi | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Holotheres halingi* | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| *Epixanthus frontalis* | 1 | 1 | 1 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 2 |

The species list is provided below:

| No | Species | Specimens |
|---|---|---|
| 1. | *Xenograpsus testudinatus* | Material examined in Taxonomy |
| 2. | *Xenograpsus novaeinsularis* | Material examined in Taxonomy |
| 3. | *Grapsus albolineatus* | Material examined in Taxonomy |
| 4. | *Metopograpsus oceanicus* | Material examined in Taxonomy |
| 5. | *Planes cyaneus* | Material examined in Taxonomy |
| 6. | *Pachygrapsus fakavarensis* | Material examined in Taxonomy |
| 7. | *Varuna litterata* | Material examined in Taxonomy |
| 8. | *Ptychognathus ishii* | Material examined in Taxonomy |
| 9. | *Hemigrapsus penicillatus* | Material examined in Taxonomy |
| 10. | *Eriocheir sinensis* | Material examined in Taxonomy |
| 11. | *Platyeriocheir formosa* | Material examined in Taxonomy |
| 12. | *Neoeriocheir leptognathus* | Material examined in Taxonomy |
| 13. | *Scutumara enodis* | Material examined in Taxonomy |
| 14. | *Pseudograpsus setosus* | Material examined in Taxonomy |
| 15. | *Orcovita saltatrix* | Material examined in Taxonomy |
| 16. | *Pyxidognathus granulosus* | Material examined in Taxonomy |
| 17. | *Noarograpsus lobulatus* | Material examined in Taxonomy |
| 18. | *Austrograpsus spinosus* | Material examined in Taxonomy |
| 19. | *Cyrtograpsus angulatus* | Material examined in Taxonomy |
| 20. | *Gnathograpsus riedelii* | Material examined in Taxonomy |
| 21. | *Parapyxidognathus deianira* | Material examined in Taxonomy |
| 22. | *Quadragrapsus albus* | Material examined in Taxonomy |
| 23. | *Utica gracilipes* | Material examined in Taxonomy |
| 24. | *Mitraptycho dentatus* | Material examined in Taxonomy |
| 25. | *Pseudoutica borneensis* | Material examined in Taxonomy |
| 26. | *Brachynotus lucasii* | Material examined in Taxonomy |
| 27. | *Cyclograpsus audouinii* | Material examined in Taxonomy |
| 28. | *Chasmagnathus convexus* | Material examined in Taxonomy |
| 29. | *Helice formosensis* | Material examined in Taxonomy |
| 30. | *Metaplax elegans* | Material examined in Taxonomy |
| 31. | *Paragrapsus laevis* | Material examined in Taxonomy |

| | | |
|---|---|---|
| 32. | *Gaetice depressus* | Material examined in Taxonomy |
| 33. | *Setostoma balssi* | Material examined in Taxonomy |
| 34. | *Thalassograpsus harpax* | Material examined in Taxonomy |
| 35. | *Gercarcinus weileri* | Material examined in Taxonomy |
| 36. | *Epigrapsus notatus* | Material examined in Taxonomy |
| 37. | *Discoplax hirtipes* | Material examined in Taxonomy |
| 38. | *Platychirograpsus typicus* | Material examined in Taxonomy |
| 39. | *Glyptograpsus impressus* | Material examined in Taxonomy |
| 40. | *Plagusia squamosa* | Material examined in Taxonomy |
| 41. | *Percnon affine* | Material examined in Taxonomy |
| 42. | *Euchirograpsus tuerkayi* | Material examined in Taxonomy |
| 43. | *Sesarma reticulata* | Material examined in Taxonomy |
| 44. | *Episesarma singaporense* | Material examined in Taxonomy |
| 45. | *Aratus pisonii* | Material examined in Taxonomy |
| 46. | *Neosarmatium smithi* | Material examined in Taxonomy |
| 47. | *Holotheres halingi* (Outgroup) | 1 male (6.7mm x 6.5mm), 1 female (9.6mm x 9.4mm) (ZRC 1999.1234), Solomon Island, Halingi, from sea cucumber, coll. 1999. |
| 48. | *Epixanthus frontalis* (Outgroup) | 3 males (16.2-22.8mm x 10.3-14.7mm) (ZRC-uncatalogued), Dumpo Beach, East Sarmar, Philippines, coll. N.K. Ng & Z. Jaafar, 10 July 2002. |

**Characters**

The characters used in this analysis are described below. '-' indicates unknown data. The state assignments do not reflect a priori polarization of the characters.

a) Carapace (figures of the carapace): The carapace shapes of the specimens examined are either quadrate (like the *Varuna*, *Helice*) or subquadrate (*Pyxidognathus*) or almost rounded (as in *Setostoma*). The carapace are usually broader than long (0) or it can be as broad as long or square in shape (1), or longer than broad (2) as in *Scutumara.* The widest region of the carapace (or Maximum carapace width) is usually at the middle of carapace (0), but it can be very near the front of carapace (1) as in *Metopograpsus* or *Gercarcinus* or near posterior region of carapace (2) *Plagusia* or *Austrograpsus*. The physiognomy of the carapace can either be flat (0) in most of the species examined or convex (1) as in *Eriocheir*, *Pseudograpsus* and *Pyxidognathus*. The carapace surface is usually smooth (0) or punctated (1) or granulated (2). The epi-gastric cristae are usually present (0), but in some genera, it can be absent (1). The gastric regions can be clearly defined (0) or not defined. Likewise for the branchial regions of the carapace, it can be defined (1), or not defined (0) by the presence (1) or absence (0) of the branchial ridges. The lateral margins of the carapace can be subparallel (0) or distinctly convergent (1) or distinctly divergent (2) towards the posterior margin. The anterolateral margin, excluding first orbital tooth, can be either entire (1) without any teeth (0) or dentate or lobulate (0) with different numbers of teeth tooth like one tooth (1); two teeth (2); three teeth (3); four or more teeth (4). The posterolateral margin can be almost straight (0) or convex (1).

The front of carapace is usually very narrow with the width ratio of 0.5 times as broad as carapace or less (0) or in some of the genera it can be greater than 0.5 times as broad as carapace (1). The front can be produced forward (1) or not produced forward (0), and in some genera, it is deflexed downwards (1), but in some genera it is not deflected downwards (0. The front can be entire (or not cleft to receive antennae) (0) or clefted to receive antennae (1). The frontal margin can be entire (0) without lobes or teeth (2) or lobulated (1) or the lobes are very acute and sharp like teeth (1). The frontal teeth which are present just next to the orbital margin of the carapace can be absent (0) or present (1).

b) Eyes and Orbit (figures of the orbits): The eye orbits in *Varuna*, *Eriocheir*, *Ptychognathus* and most of the varunid crabs are opened with a wide gap (0) at the end. In the sesarmid and grapsid crabs, the orbit is opened with a very narrow gap (1), and in *Xenograpsus*, there is no gap (2). The first orbital angle in the varunid crabs do not form protective cap (0) but it does form a protective cup (1) in *Xenograpsus*. The orbital width can be narrow (0) or broad (1). The length of the eye stalk can be short (0) or long (1) while the width of the eye stalk can be broad (0) or slender (1). The cornea pigment – (0) not reduced; (1) reduced, constricted.

The antennules are not visible dorsally (0) in most genera but in *Plagusia* it can be seen dorsally (1). The basal antennular segment is normally not swollen (0) but in some genera, it can be swollen (1).

The basal article of antenna is mobile (0) in the varunid crabs but usually it is immobile (1) in other families. The antennal flagellum is normally short, it stays within orbit (0); but it can be very long, extend beyond orbit (1), and in some genera, it is vestigial or reduced (2).

The suborbital crest is usually entire (0) but in some genera, it can be granulate (1). The crest can be flat (0) or raised (1). It may be non-stridulatory (0) or stridulatory (1) with the merus of the chelipeds.

The infra orbital ridge in most of the grapsoid crabs closes the orbit to form a sulcus (0), but it may not close orbit (1) in some genera. In the infra-orbital ridge usually is not displaced ventrally to from suborbital crest (0) but in some genera, it may be displaced ventrally to form suborbital crest (1). In the varunid crabs, lower orbital angle is confluent with ex-orbital angle leaving a notch (0), while in *Xenograpsus*, it is not confluent with ex-orbital angle leaving a notch (1). The lower orbital margin does not displaced to form suborbital ridge (0) but in varunid crabs, it is displaced to form suborbital crest (1). In some genera, the suborbital crest may be absent or indistinct (0), while it can be very distinct (1). The lower orbital border can be weak (0) or strong (1). In most genera, the lower orbital margin forms a ‘V-shaped’ notch (0); while the varunid crabs form do not (1), instead the varunid crabs form a ‘U-shaped’ sulcus (0) but the other subfamilies do not form U-shaped sulcus (1). In the *Xenograpsus*, the lower orbital margin continues with outer orbital angle and close orbit laterally (0) but in varunid crabs, the lower orbital margin does not continue with outer orbital angle (1).

Inner orbital tooth is usually present (0), but it can be reduced or absent (1 in the varunid and glyptograpsid crabs (1), and distinctly broadened in *Xenograpsus* (2).
45. The inner orbital tooth forms a broad lobe and excludes antennular flagellum from orbit (0) or it does not form a broad lobe (1).

c) Pterygostomial region: At the pterygostomial region, the groove parallel to buccal cavity can be absent (0) or present (1). In addition, there can be an oblique groove opening to the pterygostomian region present (1), in some genera it is absent (0); The proximal surface of the pterygostomian region may have setae present (1) or absent (0), so the pterygostomial region can be glabrous (0) like in *Xenograpsus*, or sparingly setose (1) as in *Varuna*, or moderately setose (2) as in *Sesarma* or very densely setose (3) as in *Gercarcinus*.

The setal form can be simple setae (0) or reticulated (1) as in the *Sesarma*. The distal lateral surface of pterygostomian region can is usually flat (0), in some genera, it can be swollen (1), and in some genera it can be concave (2). This surface can be glabrous (0) or setose (1).

d) Third maxillipeds: The third maxilliped can articulate at the sternite either horizontally (0) or vertically (1). When the third maxillipeds close it can either close completely with no gap (0), sometimes, it can leave a small rhomboidal gap (1) or a large rhomboidal gap (2). The third maxillipeds can also close entire cavity (0), it may not close up the entire cavity (1), reaching to the epistome (0) in some genera do not reach the epistome (1).

The meri of the third maxillipeds can be quadrate (broader than long) (0) or very broad (1) or less broad (longer than broad) (2). The width of the meri can be broader than long (0) or longer than broad (1). The anterolateral margin of the meri is usually not foliate (0), but in *Ptychognathus*, *Gnathograpsus* etc., it can very foliate (1). The inner margin of the merus also has posterior concavity (0) in most of the genera, but in some genera, this concavity is absent (1). The overall width of the meri can broader than ischium (0) or narrower than ischium (1). In the genera *Sesarma*, *Episesarma*, there is an obilque setose crest on merus, in *Varuna* and *Grapsus*, such crest is absent (0). In addition, there is an oblique narrow canal distally parallel to oblique crest (1), this canal can be absent (0). The number of suclus present on merus can range from absent /indistinct (0) to one (1) or three (2).

The palp of the third maxillipeds articulate at the anterior margin of merus (0), and in some genera, the articulation occurs at the anteromesial angle of merus(1). The length of the palp normally reaches mid-length of third maxillipeds (0), but sometimes, it can be very long, reaching beyond mid-length of third maxillipeds (1), and occassionaly, it can be very short, not even reaching mid-length of third maxillipeds (2).The setal length of the plap when folded normally do not reach the sternal plastron (0), in some cases, it just reaches the sternal plastron (1), but in *Gaetice*, and *Setostoma*, it reaches beyond sternal plastron (2).

The ischium of the third maxillipeds is usually rectangular in shape (0), and in some genera, it can be almost squarish in shape (1). The number of suclus present on ischium can range from absent / indistinct (0) to one (1) or two (2).

The exopod in most genera is more slender than ischium (0), but in the Ptychognathus, Orvcovita, the exopod is distinctly broader than ischium (1). The exopod can also be flat (0) or convex (1), with its surface punctate (0) or smooth (1).

e) Epistome (figures of the epistomes): The margin of the epistome can be entire (0), no lobulation at the lateral end; (1) lobulated at the lateral ends. These lobes can be small (0) or elongated lobes at the distal ends (1). The margin may also be protruding outwards (0) or not protruding outwards (1) with granules (0) or tubercles (1). The overall epistome height can be high (0) or low (1).

f) Sternum (figures of the sternum): The sternite 3/4 is either narrow (0) or broad (1); with suclus present on sternite 3/4 that can be depressed (0), and in some genera, not depressed (1). The suture line of sternite 3/4 can be visible (0) or not visible (1). The longitudinal medial groove may (1) or may not reach sternite 3 (1). The pleurobranch is absent on sternite 6 (0), but in *Glyptograpsus*, it is present (1). The lateral margin of sternite 3/4 can be concave (0) or flat (1) or convex (2). When the crab is viewed from the posterior end, the sternite 8 is visible (0) or not visible (1). Likewise, when the crab is viewed from the ventral end, sternite 8 can be visible (0) or not visible (1).

There are several forms with regards to the position of male gonopore. The gonopore can be embedded inside sternite 8, no contact with sternite 7 or coxa of periopod 5 (0); or the gonopore is located between sternite 8, sternite 7 and coxa of periopod 5 (1); or gonopore is located between sternite 8 and sternite 7 but there is no contact with coxa of periopod 5 (2); gonopore is located between sternite 8 and coxa of periopod 5 but no contact with sternite 7 (3), and gonopore is located at coxa of pereiopod 5 (4).

g) G1 (first male gonopod): The G1 of these animals can be broad (0) or narrow (1); straight (0) or sinuous (1). The overall length can normally reach sternite 5 (0), it can be very long, reaching to sternite 4 (1), or it can be very short, reaching only to sternite 6. 90. In some cases, there is a twist at the middle of G1 (0) while most G1 do not have a twist (1).

h) Male abdomen: The male abdomen is usually broadly triangular (0), but sometimes, it can be narrowly triangular (1), with its lateral margins sub-parallel (0) or distinctly divergent towards segment one (1). There are usually 7 free segments (including telson) (0), but in some genera, segments 3-5 may be fused (1) or segments 3-6 are fused (2). The widest segment is usually segment three (0) or segment one (1).

The shape of telson can be broadly triangular (0) or narrowly triangular (1). The locking mechanism may be present (0) or absent (1)**.**

i) Ambulatory legs: The longest pair of the ambulatory legs is usually the second pair (0); but sometimes, it can be the third pair (1) or even the first pair (2). The legs can be densely setose (0) or sparsely setose (1) or glabrous (2). The propodi of ambulatory legs 2-5 is usually dorsa-ventrally flattened (0); but sometimes, it can be cylindrical (1) in cross section. The meri of ambulatory legs 2-5 can be smooth, without priddles cross the lateral surfaces (0), but in some genera, lateral faces can be filled with priddles (1). The meri of periopods 2-4 are usually broad (0), but sometimes, they can be narrow (1). Similarly for the propodi of periopods 2-4, they can be broad (0) or narrow (1). The merus of the last ambulatory leg is usually broad (broad), but sometimes narrow (1).

Similarly for propodus of the last ambulatory leg, it can be broad (0) or narrow (1). The length of the dactylus of the last ambulatory legs can be quite significant, it can be longer than propodus (0) or as long as propodus (1) or shorter than propodus (2).

The dactlyi of all the ambulatory legs can be dorso-ventrally flattened (0) or cylindrical (1) in shape. There are mobile setae present (1) on dactylus or absent (0). In some genera, acute tubercles can be present (1) or absent (0) on the dactyli.

j) Chelipeds: The pectinated crests on the dorsal region of the chelipeds are very distinct in the family Sesarmidae, but not as obvious in other species. The stridulatory ridge on the merus is very distinctly seen in the *Episesarma singaporense*.

k) Size: The adult size of the animals ranges from small (in *Scutumara, Ptychognathus* etc. in which the gravid female is less than 20mm in carapace length) to medium (most of the species examined fall into this category, in which the carapace length of the gravid female is between 21mm to 40mm) to large (like *Varuna*, *Eriocheir*, species from the family Gercarcinidae, in which the carapace length of the gravid female is greater than 41mm).

## List of characters and states

### Carapace

01. Carapace shape – (0) quadrate (1) sub-quadrate; (2) almost rounded; (3) trapezoid.
02. Carapace ratio – (0) broader than long; (1) as broad as long; (2) longer than broad.
03. Maximum carapace width – (0) middle of carapace; (1) front of carapace; (2) near posterior of carapace.
04. Carapace physiognomy – (0) flat; (1) convex.

05. Carapace surface – punctate; (0) smooth; (1) punctuated; (2) granulated.

06. Carapace gastric regions – (0) defined; (1) not defined.

07. Carapace branchial regions – (0) not defined; (1) defined.

08. Carapace - branchial ridges – (0) absent; (1) present.

09. Carapace - lateral margins – (0) subparallel; (1) convergent; (2) divergent.

10. Carapace front to carapace width ratio – (0) 0.5 times as broad as carapace or less; (1) greater than 0.5 times.

11. Carapace anterolateral margin (exclude first orbital tooth) – (0) dentate or lobulated; (1) entire.

12. Carapace anterolateral margin number of teeth (exclude first orbital tooth) – (0) no tooth; (1) 1 tooth; (2) 2 teeth; (3) 3 teeth; (4) 4 or more.

13. Carapace – posterolateral margin – (0) almost straight; (1) convex.

14. Front produced forward – (0) not produced forward; (1) produced forward.

15. Front deflexed downwards – (0) not deflected downwards; (1) deflexed downwards.

16. Front cleft – (0) not cleft to receive antennae; (1) cleft to receive antennae.

17. Front entire or lobulated - (0) entire; (1) lobulated.

18. Front lobule type – (0) lobes; (1) sharp lobes (like teeth); (2) no lobe.

19. Frontal teeth – (0) absent; (1) present.

20. Epi-gastric cristae; (0) present; (1) absent.

**Eyes and Orbit Region**

21. Eye Orbit – (0) closed; (1) open.

22. Eye Orbit – (0) open with a wide gap; (1) open with a very narrow gap; (2) no gap

23. Orbit form – (0) first orbital angle not forming protective cap; (1) first orbital angle form a protective cup.

24. Orbital width – (0) narrow; (1) broad.

25. Eye stalk – length – (0) short; (1) long.

26. Eyes stalk – width – (0) broad; (1) slender.

27. Eyes - cornea pigment – (0) not reduced; (1) reduced, constricted.

28. Antennules not visible dorsally – (0) not visible dorsally; (1) visible dorsally.

29. Basal article of antenna – (0) mobile; (1) immobile.

30. Antennal flagellum – (0) short (within orbit); (1) long (extend beyond orbit); (2) vestigial (reduced).

31. Basal antennular segment – (0) not swollen; (1) swollen.

32. Suborbital crest form – (0) entire; (1) granulate.

33. Sub-orbital crest – (0) flat; (1) raised.

34. Sub-orbital crest – function – (0) non stridulatory; (1) stridulatory.

35. Infra orbital ridge – (0) closing orbit to form a sulcus; (1) not closing orbit.

36. Infra-orbital ridge – (0) not displaced ventrally to from suborbital crest; (1) displaced ventrally to form suborbital crest.

37. Lower orbital angle – (0) confluent with ex-orbital angle leaving a notch; (1) not confluent with ex-orbital angle leaving a notch.

38. Lower orbital margin – (0) not displaced to form suborbital ridge; (1) displaced to form suborbital crest.

39. Lower orbital margin – (0) absent; (1) present.

40. Lower orbital border – (0) weak; (1) strong.

41. Lower orbital margin – v-shaped notch – (0) form a V-shaped notch; (1) do not form a V-shaped notch.

42. Lower orbital margin – u-shaped sulcus – (0) form U-shaped sulcus; (1) do not form U-shaped sulcus.

43. Lower orbital margin – (0) continue with outer orbital angle and close orbit laterally; (1) do not continue with outer orbital angle.

44. Inner orbital tooth – (0) present; (1) reduced or absent; (2) broadened.

45. Inner orbital tooth – (0) form a broad lobe and exclude antennular flagellum from orbit; (1) do not form a broad lobe.

**Pterygostomian region**

46. Pterygostomian groove parallel to buccal cavity – (0) absent; (1) present.

47. Pterygostomian region – oblique groove opening to pterygostomian region – (0) absent; (1) present.

48. Pterygostomian region – setae on proximal surface – (0) absent; (1) present.

49. Pterygostomian region – setae – (0) glabrous; (1) sparingly setose; (2) setose; (3) very densely setose.

50. Pterygostomian setae type – (0) simple setae; (1) reticulated setae.

51. Pterygostomian distal lateral surface – (0) flat; (1) swollen; (2) concave.

52. Pterygostomian setae on distal posterior region – (0) glabrous; (1) setose.

**Third maxillipeds**

53. Third maxillipeds – articulation at sternite – (0) horizontal; (1) vertical.
54. Gap of third maxillipeds when closed – (0) no gap; (1) small rhomboidal gap; (2) large rhomboidal gap.
55. Third maxillipeds – closing entire cavity – (0) closing entire cavity; (1) not closing entire cavity.
56. Third maxllipeds – reaching epistome – (0) reaching epistome; (1) not reaching epistome.
57. Third maxillipeds – number of sulci on merus – (0) 0; (1) 1; (2) 3.
58. Third maxillipeds – obilque setose crest on merus – (0) absent; (1) present.
59. Third maxillipeds – oblique narrow canal distally parallel to oblique crest – (0) absent; (1) present.
60. Third maxillipeds – merus size – (0) quadrate (broader than long); (1) very broad; (2) less broad (longer than broad).
61. Third maxillipeds – length of palp – (0) normal length (reaching mid-length of third maxillipeds); (1) very long (reaching beyond mid-length of third maxillipeds); (2) very short (not reaching mid-length of third maxillipeds).
62. Third maxillipeds – anterolatermal margin – (0) not foliate; (1) foliate.
63. Third maxillipeds – merus width – (0) broader than long; (1) longer than broad.
64. Third maxillipeds - merus - inner margin - posterior concavity – (0) concavity present; (1) concavity absent.
65. Third maxillipeds – merus broader than ischium – (0) merus broader than ischium; (1) merus narrower than ischium.
66. Third maxillipeds – ischium – (0) rectangular in shape; (1) almost squarish in shape.
67. Third maxillipeds – number of sulci on ischium – (0) 0; (1) 1; (2) 2.
68. Third maxillipeds – length of setae of plap when folded – (0) not reaching sternal plastron; (1) reaching sternal plastron; (2) reaching beyond sternal plastron.
69. Third maxillipeds – articulation of palp – (0) anterior margin of merus; (1) anteromesial angle of merus.
70. Third maxillipeds – exopod shape – (0) more slender than ischium; (1) broader than ischium.
71. Third maxillipeds – exopod shape – (0) flat; (1) convex.
72. Third maxillipeds – expod surface – (0) punctate; (1) smooth.

**Epitsome**

73. Epistome margin – (0) entire, no lobulation at the lateral end; (1) lobulated at the lateral ends.

74. Epistome margin lobulation – (0) small lobes; (1) elongated lobes at the distal ends.

75. Epistome margin protrusion – (0) protruding outwards; (1) not protruding outwards.

76. Epistome margin – types of granules – (0) granules; (1) tubercles.

78. Epistome height – (0) high; (1) low.

**Sternum**

79. Sternite 3/4 – sulcus – (0) with depressed sulcus; (1) without depressed sulcus.

80. Sternite - suture of sternite 3/4 – (0) visible; (1) not visible.

81. Sternite – (0) medial groove not reaching sternite 3; (1) medial groove reaching sternite 3.

82. Male sternum- sternite 3/4 – (0) narrow; (1) broad.

83. Pleurobranch on sternite 6 – (0) absent; (1) present.

84. Sternum – lateral margin of sternites3/4 – (0) concave; (1) flat; (2) convex.

85. Sternite 8 – (0) Sternite 8 visible from posterior view; (1) Sternite 8 not visible from posterior view.

86. Sternite 8 – (0) Sternite 8 visible from ventral view; (1) Sternite 8 visible from ventral view.

87. Position of male gonopore – (0) gonopore embedded inside sternite 8, no contact with sternite 7 or P5's coxa; (1) gonopore between sternite 8 and sternite 7 and P5's coxa; (2) gonopore between sternite 8 and sternite 7, no contact with coxa P5; (3) gonopore between sternite 8 and coxa of P5, no contact with sternite 7; (4) gonopore at coxa of P5.

**G1**

88. Form of G1 – width – (0) broad; (1) narrow.

89. Form of G1 – overall length – (0) reaching to sternite 5 (normal); (1) reaching to sternite 4 (long); (2) reaching only to sternite 6 (short).

90. Form of G1 – straight or sinuous – (0) straight; (1) sinuous.

91. Form of G1 – twist – (0) middle of G1 without a twist; (1) middle of G1 with a twist.

**Male Abdomen**

92. Male abdomen – fused segments – (0) 7 free segments; (1) 3-5 fused; (2) 3-6 fused.

93. Male abdomen – widest segment – (0) segment 3; (1) segment 1.

94. Male abdomen – overall shape – (0) broadly triangular; (1) narrowly triangular.

95. Male abdomen – lateral margins – (0) sub-parallel; (1) divergent towards segment 1.

96. Male abdomen – shape of telson – (0) broadly triangular; (1) narrowly triangular.

97. Male abdomen – locking mechanism – (0) present; (1) absent.

**Ambulatory legs**

98. Ambulatory legs – longest legs – (0) second pair; (1) third pair; (2) first pair.

99. Ambulatory legs – merus with priddles - (0) without priddles; (1) with priddles.

100. Ambulatory legs – merus of 2-4 – (0) broad; (1) narrow.

101. Ambulatory legs – propodus of 2-4 – (0) broad; (1) narrow.

102. Ambulatory legs – last merus – (0) broad; (1) narrow.

103. Ambulatory legs – last propodus – (0) broad; (1) narrow.

104. Ambulatory legs – last dactylus – (0) longer than propodus; (1) as long as propodus; (2) shorter than propodus.

105. Ambulatory legs – mobile setae on dactylus – (0) absent; (1) present.

106. Ambulatory legs – acute tubercles on dactylus – (0) absent; (1) present.

107. Ambulatory legs – dactylus 2-5 – (0) dorso-ventrally flattened; (1) cylindrical

108. Ambulatory legs – overall setation – (0) densely setose; (1) sparsely setose; (2) glabrous

109. Ambulatory legs – 2-5 propodus - cross section – (0) dorsa-ventrally flattened; (1) cylindrical.

**Chelipeds**

110. Chelipeds – pectinated crest on dorsal region of fixed finger – (0) absent; (1) present.

111. Chela – stridulatory ridge on merus – (0) absent; (1) present.

112. Cheliped fingers – (0) finger longer than palm; (1) finger shorter than palm.

**Size**

113. Adult size – (0) small; (1) medium; (2) large.

## DISSCUSSION

The cladistic analysis carried out on the morphological characters of 48 species from 47 genera by PAUP* version 4.0b10 for Macintosh, has generated 26 trees with 403 steps (RI = 0.685, CI=0.304). The strict consensus of the 8 trees with bootstrap support and jackknife proportions over 50% is provided below.

The analysis clearly shown that the Varunidae is monophyletic, and that *Xenograpsus* should be removed to its own family. The strict consensus tree below clearly showed six distinct clades viz. the Xenograpsidae clade, the Grapsidae clade, the Varunidae clade, the Glyptograpsidae clade, the Sesarmidae clade, the Gercarcinidae clade, and the Plagusiidae clade. These six clades correspond to the six families that this study duly recognizes.

It is interesting to note that *Xenograpsus novaeinsularis* and *X. testudinatus* are always grouped together as one clade, and is always very far from the Varunidae. In fact, the *Xenograpsus* clade comes out as a basal clade to all the other five families, regardless of the type of cladistic analyses that were carried out. This clearly warrants the separation of *Xenograpsus* from Varunidae into its own family. The larval evidence (Jeng *et al*., 2004) and molecular analysis (in collaboration with C.D. Schubart) of the genus *Xenograpsus* also supports this action. The Xenograpsidae come out as basal as one of the outgroup, *Epixanthus frontalis* (Eriphiidae) suggesting that it could be the ancestral taxon to the Grapsoidea (see later).

The Plagusiidae and Gercarcinidae came out as two separate clades at the same level but at different nonde or poin. The Gercarcinidae has long been treated at the superfamily level. However, Schubart *et al*. (2000a, 2002, 2006) has placed it at the same level as the Varunidae and Sesarmidae. As for the Plagusiidae, the family is distinct on its own, although it must be noted that the genus *Percnon* needs to be re-evaluated. The Grapsidae (*Grapsus albolineatus*, *Metopograpsus oceanicus*, *Planes cyaneus* and *Pachygrapsus fakavaraensis*) come out together as one clade, but *Pachygrapsus fakavarensis* is separated from the other three taxa, but is still in the same clade.

Fraaije (2003) estimated that the Grapsidae sensu lato first appeared in the Late Eocene (40 Ma), while the Varunidae first came about in the Middle Miocene (about 12 Ma). However, the Gercarcinidae and Sesarmidae arose only in recent times (< 12 Ma, Late Miocene). The 'Grapsidae' that Fraaije (2003) referred to could have been Grapsidae sensu lato, before the recent revision, which was used to include the currently accepted Plagusiidae and Grapsidae. This would have supported the result of the cladistic tree of having Plagusiidae coming out as one of the basal groups. The Gercarcinidae has been postulated to only appear about the same time as the Sesarmidae (see Fraaije, 2003), which is much later then the Varunidae. However, based on the present cladistic trees, the Gercarcinidae is more basal than both the Varunidae and Sesarmidae. This suggests that the Gercarinidae appeared much earlier than the Varunidae, and probably at about the same time as the Xenograpsidae and the Plagusiidae. The present cladogram contradicts Fraaije's (2003) results. One possible explanation is the characters chosen for the cladistic analysis on the evolution of the Gercarcinidae are not robust enough.

The Sesarmidae and the Grapsidae came out at the same level but different node, as basal clades with respect to the Glyptograpsidae and Varunidae. The Glyptograpsidae came out basal with respect to Varunidae. It is the common belief that the Sesarmidae came about when the sea level has dropped low enough for the mangrove formation (69-23 Ma) (Ellison *et al*., 1999; Hogarth, 1999).

In the TNT bootstrap tree, *Glyptograpsus* and *Platychirograpsus* came out as one single clade, at the same node as Varunidae. The current author feels that it is more appropriate that *Glyptograpsus* and *Platychirograpsus* be treated as one of the subfamily under the family Varuninidae rather than family level since the external morphology of the animal is very close to the varunid crabs, particularly the poisition of the male gonopore and form of the eye orbit..

The 28 species within the Varunidae come out together as a single clade, next to the Sesarmidae. The resolution within the Varunidae clade is not perfect, as only 28 genera out of 41 genera have been used for the cladistic analysis. However, the Cyclograpsinae and Gaeticinae come out as separate clades within the Varunidae clade but the Thalassograpsinae comes out with Gaeticinae. The different genera of the Varuninae are scattered within the Varunidae clade.

The Cyclograpsinae (*Metaplax elegans*, *Helice formosensis*, *Chasmagnathus convexus*, *Cyclograpsus audounii* and *Paragrapsus laevis*) come out as a distinct clade within the Varunidae clade, supporting the resurrection of Cyclograpsinae by Davie (2002) and Davie & Nguyen (2002). Within the Cyclograpsinae, *Paragrapsus* and *Cyclograpsus* come out as a single clade, while *Metaplax, Helice* and *Chasmagnathus* come out as a separate clade. It is interesting to note that *Helice* and *Chasmagnathus* come out as two separate clades, supporting Sakai & Türkay's recent revision (2006) that *Helice* and *Chasmagnathus* are two separate genera, and not a genus-complex. The genus *Metaplax* come out with *Helice* and *Chasmagnathus*. It is worth looking into the distribution patterns of some of the genera in this subfamily. The genus *Paragrapsus* is found mainly in the cooler region in Australia, while *Cyclograpsus* is very widely distributed in the topical area. This is similar for *Metaplax*, *Helice* and *Chasmagnathus*. Both *Helice* and *Chasmagnathus* are very commonly found in the temperate zone, the two genera appear to prefer cooler waters. The southernmost locality of the genus is at the southern region of Hainan Island, China, in the northern hemisphere. In the southern hemisphere, *Helice* is found in New Zealand. *Metaplax* are found mainly in the tropics and the subtropics, with a few species found as north as Shangdong Province in China. The overall morphology of both *Helice* and *Metaplax* are very similar (see section on Cyclograpsinae), and both genera are found living in mudflats. It is possible that both *Helice* and *Metaplax* have split to occupy similar niches but in different climatic conditions. The possible cause of isolation could be the changes along the path of the Kuroshio Current (H.T. Shih, pers. comm.).

The Gaeticinae, comprising of *Setostoma* and *Gaetice* came out as a clade together with Thalassograpsinae. The feeding biology of *Setostoma* and *Gaetice* is unique as they are the only two genera in the Varunidae that filter-feed (see earlier section on Gaeticinae). The feeding biology of *Thalassograpsus* is unknown, and the adult morphology of *Thalassograpsus* is distinctly different from *Gaetice* and *Setostoma* (see section on Thalassograpsinae).

It is interesting to note that the external morphology of *Austrograpsus spinosus* and *Cyrtograpsus angulatus* are very similar, particularly in the form of the carapace with its fourth anterolateral tooth broadest and most distinct. The distribution of the two genera is in Australia and Patagonia respectively, both genera come out as separate clades in all the cladograms. The species, *Hemigrapsus sexdentatus* has similar distribution as well (see Taxonomy above). Von Ihering (1891) hypothesized that New Zealand, eastern Australia and India form one continent in the early Mesozoic times, and during the Lower Cretaceous period, this land mass was extended to New Guinea and Chile, with most of South America all submerged. In the Upper Cretaceous period, New Zealand became separated, and the South Pacific continent divided between Samoa and Society Islands. The eastern region was elevated, the central portion sank, and became what is known as Chile, La Plata and Patagonia. Veevers *et al*. (1991) reported that Australia and New Zealand separated about 80 Ma, while Australia and South America remained more or less connected by Antarctica until about 38 Ma. Bruce's (2002) study on the Mesozoic geology of the Puerto Ingeniero Ibanez Region, 46 degrees South Chilean Patagonia, has additional supporting evidence on the vicariance events suggested by Veevers *et al.*, 1991. The recent molecular data (Waters & Burridge, 1999; Waters *et al.*, 2000) on the 16s haplotypes of the very common freshwater fish, *Galaxias macilatus*, has suggested that there is a phylogentetic separation up to 36 Ma which is consistent with the vicariance model proposed by von Ihering (1891), Bruce (2002) and Veevers *et al*. (1991).

The poor resolution of the other genera within the Varunidae clade has indicated that perhaps the external morphological characters used here are inadequate in revealing the relationships of these genera. The very diverse forms in the morphology of the adults have greatly reduced the numbers of shared characters they have,hence, making it difficult to score the characters properly for cladistic analysis. Molecular analysis on the 16s rRNA, and 12S rRNA, has not been very helpful either (see Schubart *et al*., 2000, 2002, 2006). Larval characters have been used so far to elucidate the phylogeny of the varunid crabs (see Cuesta, 1998, Cuesta *et al*., 2000, 2001 etc.) but larvae are often not easy to obtain, as most of the varunid crabs are seasonal in their breeding, and much of the larval hatching occurs in the deeper waters. It is very likely that internal morphological characters like gastric mills will have to be used for further analysis.

The molecular analysis of the brachyuran crabs currently, has only centered around a few genes: mitochrondrial genes like 16s rRNA and 12S rRNA (see Kitaura, 2002, Schubart, 1999), CO1 genes and tRNA-gene re-arrangements (see Kitaura, 2002), 18S rRNA and 28S rRNA genes (see Giribet *et al*., 2005). These sequences or loci do not clearly reflect the genetics of the entire organism. The sequences, if they could illustrate the differences between the taxon, could be used as additional characters on the overall analysis. The study of morphology allows the study of the organism coded by many different genes, if these genes are correlated, the overall expression will be seen on the entire organism. This is definitely more useful than looking at one or two or nine genes.

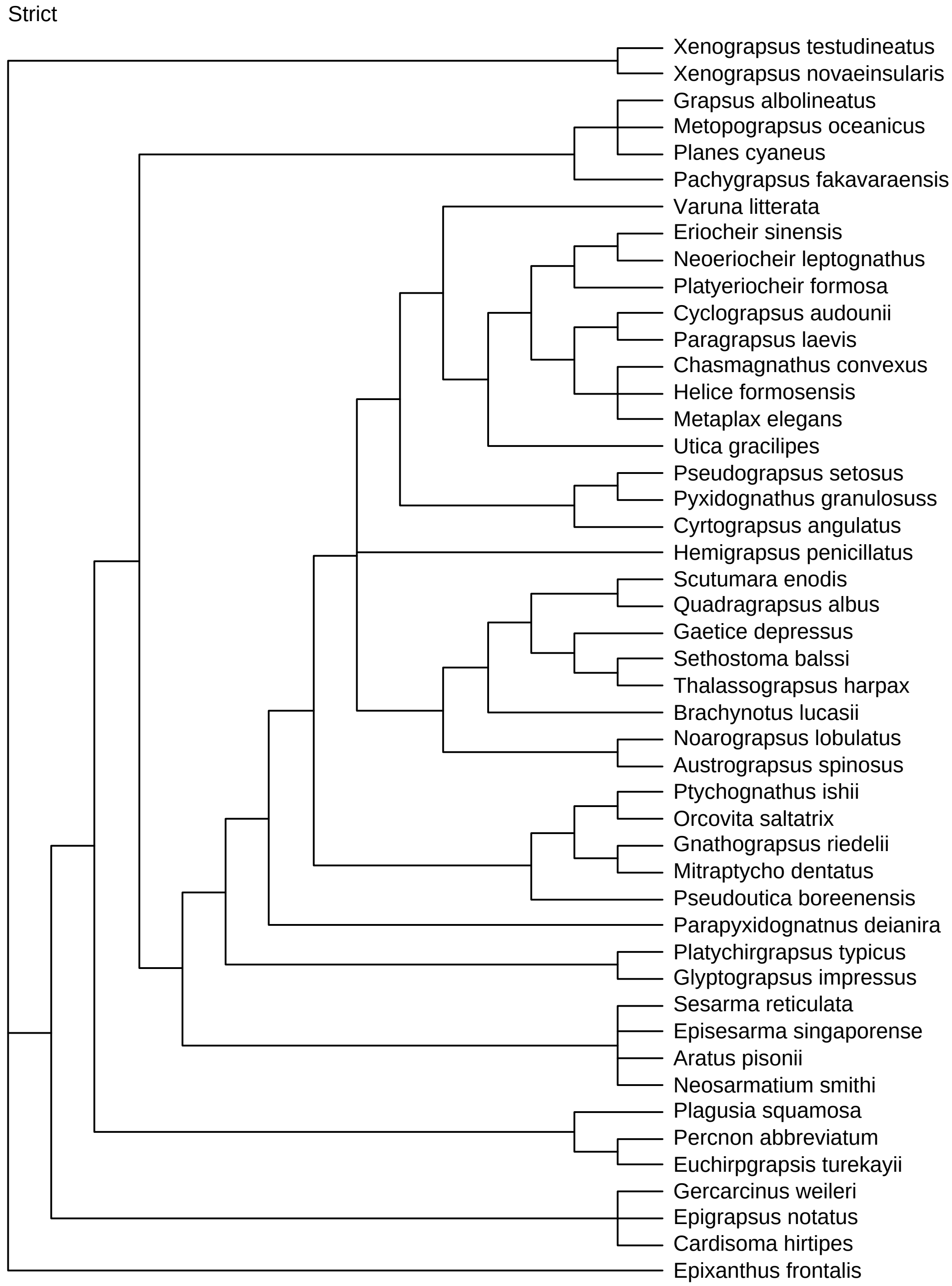



Figure 197. The strict consensus tree of 8 trees at 403 steps for the parsimony analysis of the morphological data of Appendix 1 (PAUP).

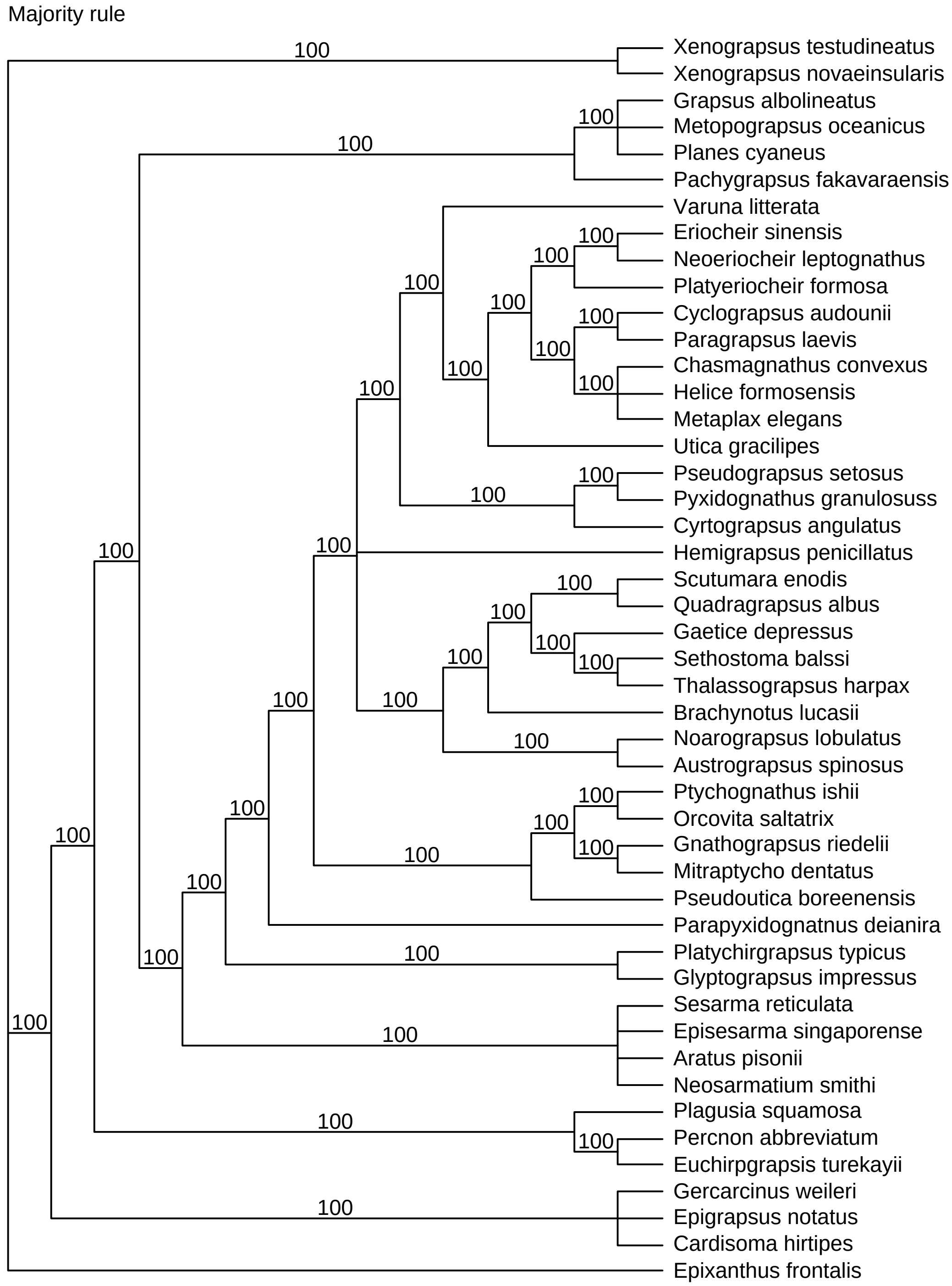



Figure 198. The Majority-rule tree, derived from PAUP on 112 characters and 46 genera.

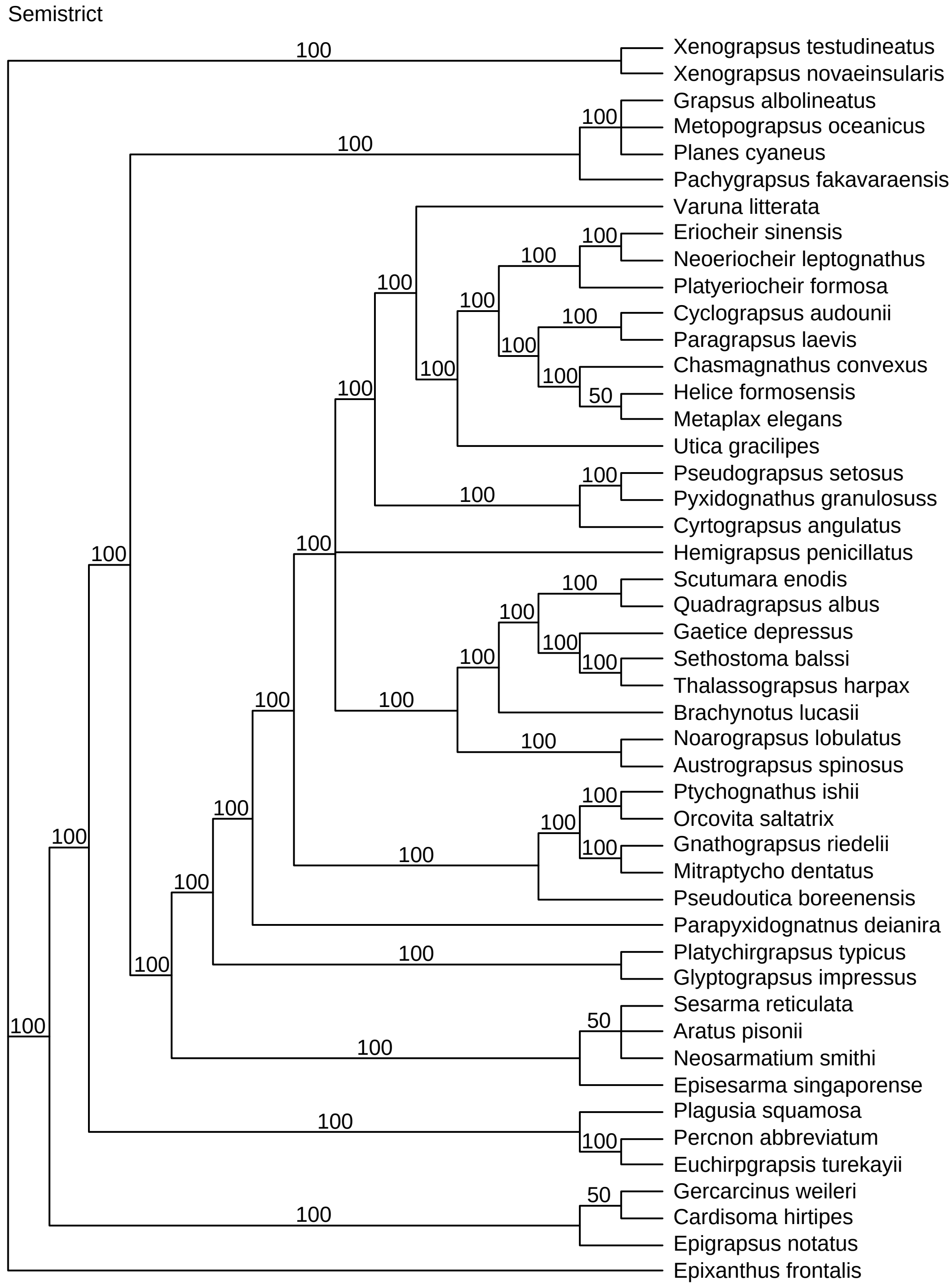



Figure 199. The Semi-strict consensus tree from PAUP on 112 characters and 46 genera.

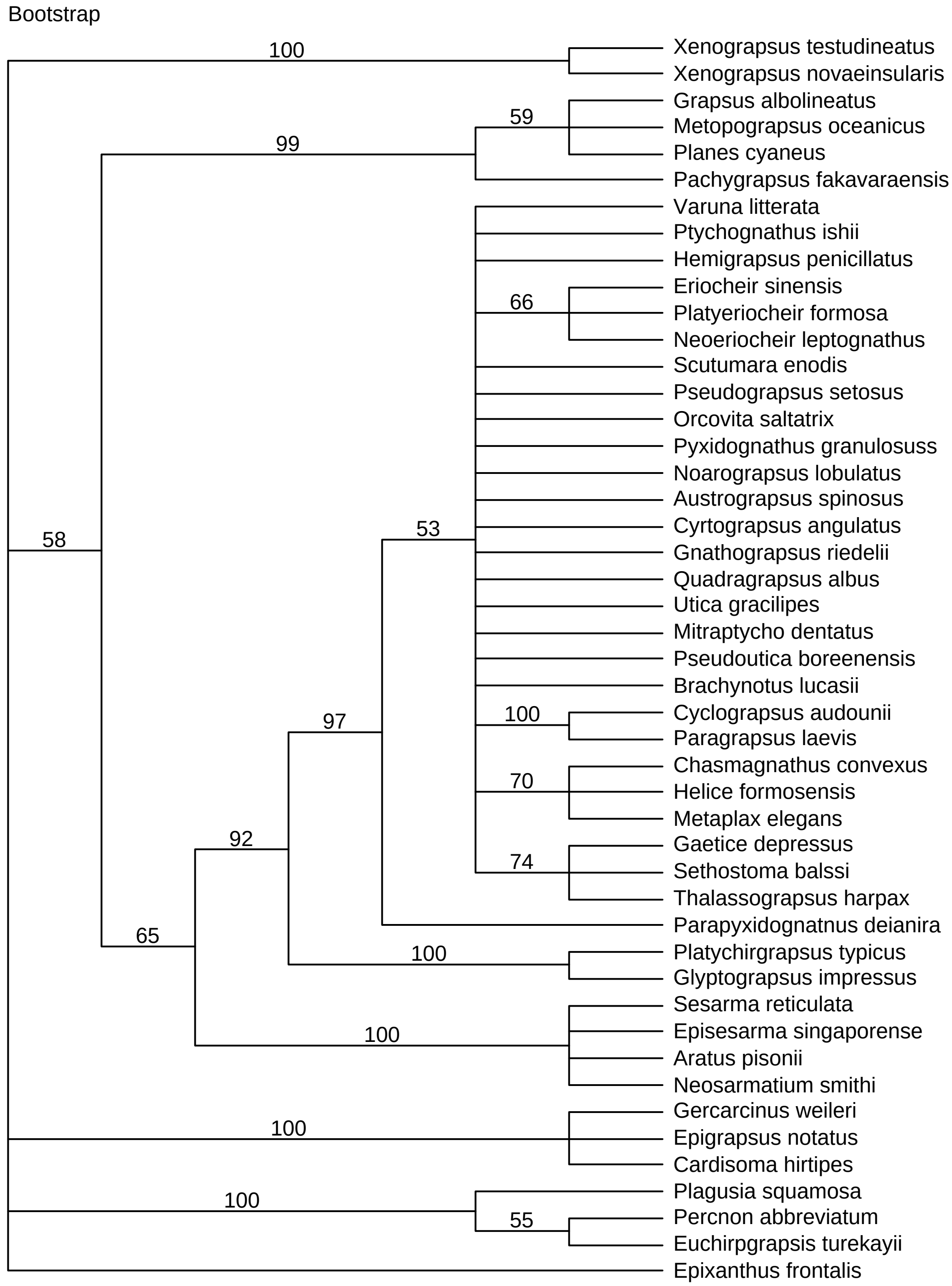



Figure 200. The bootstrap tree from PAUP on 112 characters and 46 genera.

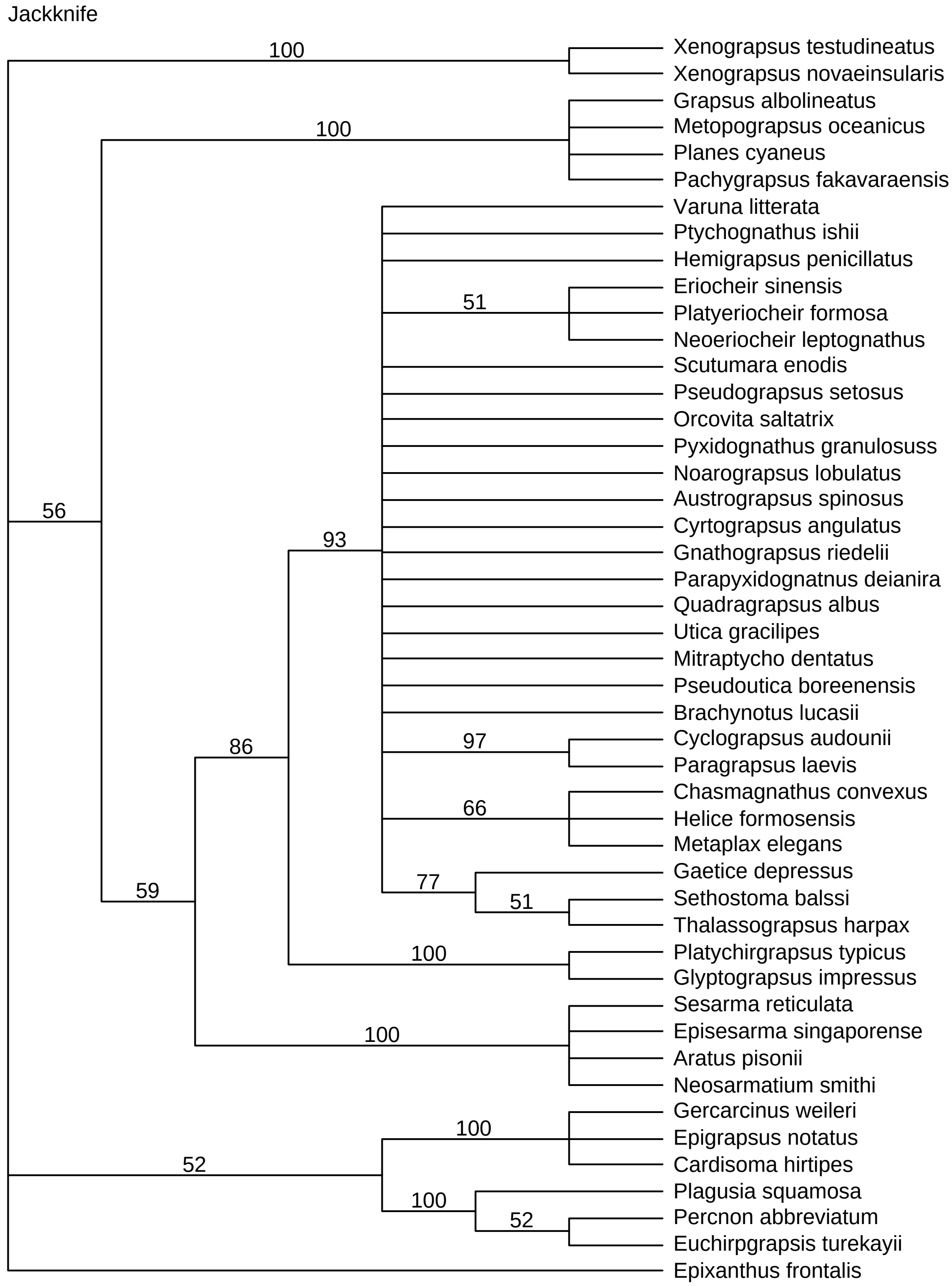



Figure 201. The jackknife tree from PAUP on 112 characters and 46 genera.

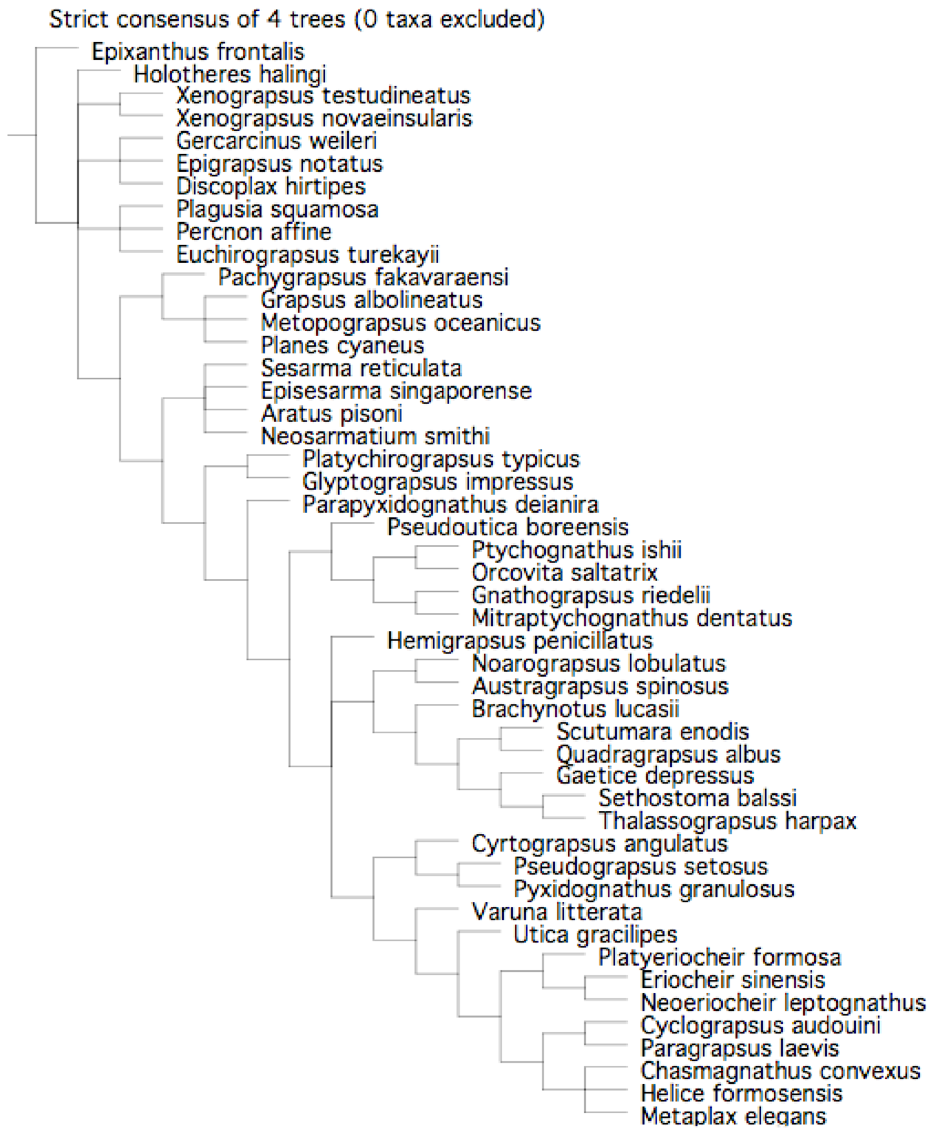



Figure 202. The Strict Consensus Tree of four most parsimonious trees based on 112 characters, derived from TNT, with a Driven Search at an Initial Level at 50, and a minimum of three hits. There are 403 steps.

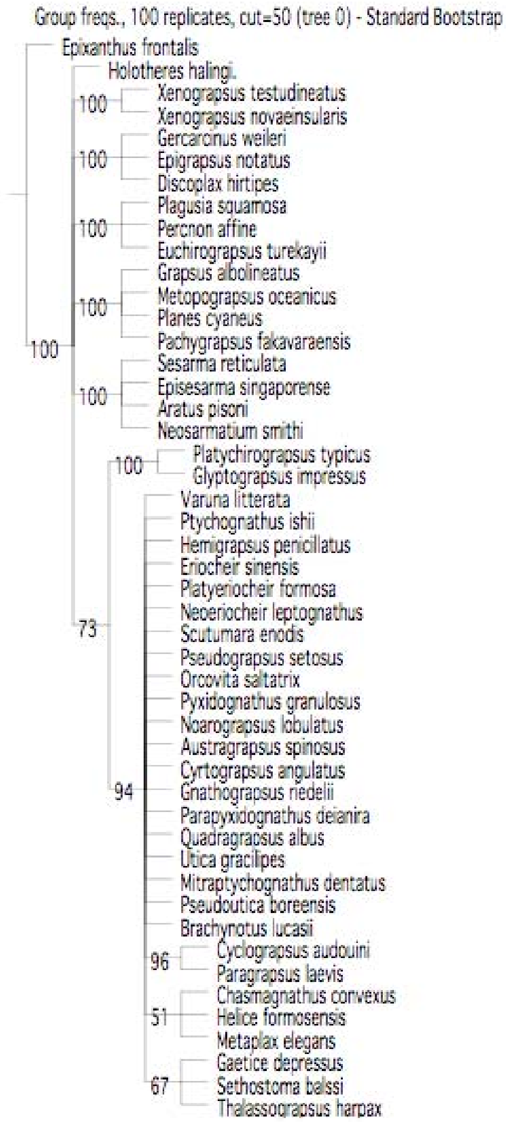



Figure 203. The Bootstrap tree derived from TNT, with a Driven Search at an Initial Level at 50, and a minimum of three hits. There are 403 steps. The numbers at the branches indicate bootstrap support values above 50%.

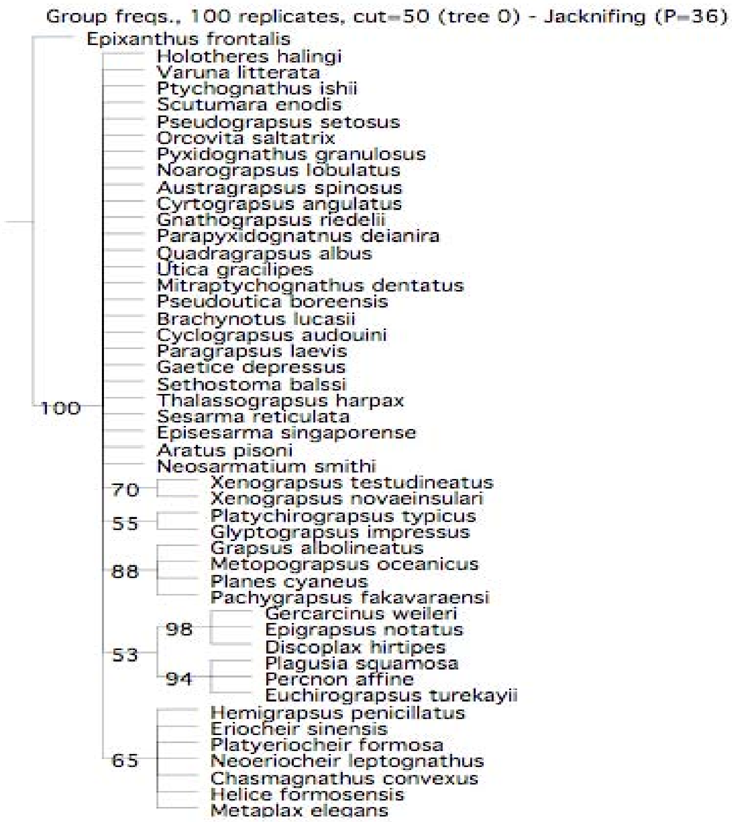



Figure 204. The Jackknife tree derived from TNT, with a Driven Search at an Initial Level at 50, and a minimum of three hits. There are 403 steps. The numbers at the branches indicate bootstrap support values above 50%.

## CONCLUSION

The discovery of hydrothermal vents communities in 1977 by J.B. Corliss and J.M. Edmond, has provided a lot of surprises and information about life in the deep sea and in extreme environments. The discovery of hydrothermal vent organisms also has prompted extensive research on extreme environments, and the possible origin of life on earth (Corliss *et al*., 1979; Corliss *et al*., 1981; Edmond *et al*., 1982; Sleep, 1986; Nisbet, 1987; Maher & Stevenson, 1988; Corliss, 1990; Knoll, 2003).

The hydrothermal vents communities are characterized by their dependence on geochemical energy sources (mainly $H_2S$). The most abundant are the Archaea and the bacteria that are able to withstand the high temperatures. They assimilate the resources at the vents directly by oxidizing the available chemicals found in the environment (van Dover, 2000). Other invertebrates like the polychaete worms, gastropods, vestimentiferan tube worms, vent clams, vent mussels, copepods crustaceans, bresiliid shrimps, vent crabs etc. that dominate the vents exploit these reduced compound indirectly by grazing and/or filtering these free-living chemoautotrophs (Little & Vrijrnhoek, 2003). A recent paper by Jeng *et al*. (2004), reported that one species of hydrothermal crabs, *Xenograpsus testudinatus* described from shallow water sulphur-rich hydrothermal vents in Taiwan, swarm out of their crevices during slack tide to feed on the zooplankton kill ('marine snow') which has resulted from the toxic plumes discharged by the vents. However, the feeding habit of its sister species, *X. novaeinsularis* is not known.

Currently, there are more than 500 new species, and more than a dozen new families being described from these vents since their discovery. More than 90% of vent species appear to be endemic (Tunnicliffe & Fowler, 1996; McArthur & Tunnicliffe, 1998). Many of the new species discovered from the hydrothermal vents have no close relative outside the chemosynthetic environment, and must be placed in its own genera or even family. Some examples are the bresiliid shrimps, *Rimicaris exoculata* (see Bruce, 2005); vent crabs, *Bythograea thermydron*, (see Guinot & Segonzac, 1997); squat lobster, *Munidopsis subquamosa* (see Ahyong & Poore, 2004); galatheid crab, *Shinkaia crosnieri* (see Chan *et al*., 2000), the callianassid shrimp, *Paraglypturus calderus* (see Türkay & Sakai, 1995); hydrothermal limpets and vent barnacles. Such high level of taxonomic endemism indicates either a long evolutionary history or high rate of evolution (Cohen & Haedrich, 1983; van Dover, 2000). Newman (1985) addressed the issue, noting that some of the taxa found in the vents are immigrants which belongs to the wide-ranging deep-sea genera (probably Mid to Late Cenozoic in age), and he put forth the idea that the vents have provided a refuge or shelter for these taxa during the major extinction events that have eliminated the shallow water relatives. This idea was later expanded by Tunnicliffe (1992) stating that the food web in the hydrothermal system is indirectly dependent of the sun, and thus, such system would be immune from the prolong periods of blocked sunlight of the major meteor impact in the late Cretaceous that is thought to wipe out the dinosaurs and other organisms.

Many of the hydrothermal taxon has been shown to be 'ancient' or 'relic'. Archaea which is most abundant in the hydrothermal vents, have been shown to be more ancient than bacteria (Makarova & Koonin, 2003). Newman (1985) hypothesized that the 'average generic age' for the stalked scalpellid barnacle, *Neolepas zevinae* the sessile Verrucocorpha, *Neoverruca*, and the sessile Balanomorpha, *Eochionoelasmus* to at 28 million years, 81 million years and 153 millions years respectively. Based on the form of the 8-plated capitulum, Newman (1979) recognized *Neolepas zevinae* as a Mesozoic relic. The asymmetric barnacle, *Neoverruca brachylepadoformis*, which is very common in the Mariana Arc, has been reported to be to be the missing link between two barnacle orders (Brachylepadomorpha and Verrucomorpha), and as a living fossil with close affinities to the extinct Brachylepadomorphs from the Jurassic-Miocene (Newman & Hessler, 1989) based on its juvenile development. Based on shell morphology, Yamaguchi and Newman (1990) described the primitive Balanomorph, *Eochionoelasmus ohtai*, from a vent in the North Fiji Basin. In addition to cirripeds, the vents have also yielded several relic mollusc species like the limpet, *Neomphalus fretterae*, which has been placed in its own superfamily Neomphalacea, and family Neomphalidae (McLean, 1981). McLean (1981) suggested that *Neomphalus* must represent one outcome of a basic gastropod theme previously undescribed, and the family have risen between the Late Paleozoic and Late Mesozoic (70-250 million years ago). When a more primitive neomphalid gastropod, *Symmetromphalus*, from Mariana vents was described (McLean, 1990), and the coiled members of the Neomphalacea from the East Pacific Rise vents, were described by Warén & Bouchet (1989), McLean

(1990) places the two genera into a new family, Cyathermiidae within the Neomphalidae, indicating the radiation potential of this group.

Little & Vrijenhoek (2003) questioned the validity of this 'relic theory'. They argued, using mytilid bivalves, bresiliid shrimps, vesicomyids and a few other vents organism as case studies, that fossil vents contain both fossil and modern taxon, and there are also discrepancies between evolutionary ages inferred from molecular divergences versus fossil evidence for several taxon. They further showed that taxonomic composition of the vent communities changed considerably through time, indicating that deep-sea chemosynthetic environments might not be immune from global extinction events that affect diversity in the photic zone. Shank *et al*. (1999) also reported that molecular evidence indicated that vent and the seep-endemic bresiliid shrimp only diversified very recently, probably less than 20 Ma. Little & Vrijenhoek (2003) concluded that many of these vent animals are not living fossils but re-invasions of the habitat after anoxic/dysoxic events in the ocean during the Cenomanian-Turonian boundary or at the end Palaeocene (Jacobs *et al*., 1998). It must be noted that the study carried out by Little & Vrijenhoek (2003) was carried out on a very small group of animals, and there are still a lot of discrepancy involving fossiliferous vents sites, and there is a need to re-assess the 'relic theory'.

The cladistic analysis has clearly shown that Xenograpsidae is probably not a grapsoid crab, although it may be one of the 'relic' or ancestral taxon to the modern grapsoids. The different species of Xenograpsidae could have taken refuge in the hydrothermal vents during the global extinction events (see above), especially in the deeper vents in the the Izu-Bonin-Mariana Arc. There could have been re-colonization at the shallow water vents after these catastrophic events are over.

The variety of vent animals have shown that the ability to live at the vents has evolved many times (van Dover, 2000). The selective advantage for the adaptation to vent conditions – a virtually unlimited food supply is strong (van Dover, 2000). Hessler & Lonsdale (1991) hypothesized that if convergent adaptation to vent conditions is such a ready possibility, then vent fauna totally isolated from the others might yield a completely different, separately evolved set of species filling the same niches.

The history of Izu-Bonin-Mariana since subduction began about 43 Ma (Robert *et al*., 2006). The fore-arc, Izu-Bonin arc has been estimated to be to be about 35 Ma, the Kyushu-Palau plate was > 40 Ma (Cosa *et al*., 1998), while the Opening of the Okinawa Trough commenced during the middle Miocene (~10–6 Ma) (Sibuet *et al*., 1995; Miki, 1995), but it became inactive after the arc-continent collision of Taiwan and the Philippine. Ujiié (1994) believed that the Southern Okinawa Trough and Ryukyu arc, Kueishan Island is currently situated, was formed only 1.7 and 0.5 Ma. Based on Fraaije's (2003) estimate, *Xenograpsus* could have been present in the Izu-Bonin-Mariana Arc a few millions years after it was formed, and perhaps it was widely distribution along the arc and the fault lines. Sibuet *et al*. (1998) suggested that the block faulting along the central axis of the Okinawa Trough took place at about 2 Ma and the uplift of the Ryukyu arc during the Pleistocene between 1.7 and 0.5 Ma (Ujiié, 1994), had probably separated the Okinawa arc from the Izu-Bonin arc. Ujiié *et al*. (1991) and Ujiié and Ujiié (1999) further suggested that there was a bridge connecting the central–southern part of the Ryukyu arc with Taiwan, preventing inflow of the Kuroshio Current to the Okinawa Trough during the last glacial stage. All these factors could have contributed to the isolation of the *Xenograpsus testudinatus* in Keuishan Island.

Along the Bonin-Mariana arc, *Xenograpsus novaeinsularis* is found in the Ogasawara Islands and edges of the Mariana Trench. However, based on the observed abbreviated larval development of the *Xenograpsus testudinatus* (see Jeng *et al*., 2004), it is very likely that the distribution of *Xenograpsus* is localized. The current author believes that there is a need to reappraise the *Xenograpsus novaeinsularis* found in the Mariana Trench, as it could be a possibly be a new species at the Mariana Trench. Initial examination of the *Xenograpsus novaeinsularis* specimen from the Mariana Trench indicated that there are subtle differences morphological differences between the specimen from Ogasawara Islands and the Mariana Trench (see Ng *et al*., 2000). These differences are not significant enough to divide them into two distinct species but they could be genetically distinct. Unfortuntaley, all the material we have had been preserved in formalin and cannot be used for any DNA work. There are numerous examples of cryptic species found in vent communities (van Dover, 2000).

The other possible refuge from global extinction events are underwater and/or underground caves, particularly anchialine caves that have been isolated for millions of years. Iliffe (1987; 1992; 2004) reported more than 250 new species of marine animals, mainly crustaceans, living in the caves on islands in the Atlantic, Caribbean and Indo-Pacific. Many of these animals are exceptionally primitive ‘living’ fossils, others are related to the deep sea forms. *Orcovita* Ng & Tomascik, 1994, is one such group of animals that is known only from anchialine caves. This genus could be one of the possible ‘relic’ taxon of the Varunidae but in our analysis, it did not come out as a basal group. The morphological characters used for the analysis are perhaps not robust enough, but it is also possible the evolution of the anchialine habit is a recent event. The other anchialine species is *Hemigrapsus estellinensis*, or commonly known as the obligate cave crab in USA, is found in Estelline Salt Springs, which is a group of brine springs less than a mile east of Estelline at the Childress county line in east central Hall County (at 34°33' N, 100°25' W). The springs are located on the floodplain of the Prairie Dog Town Fork of the Red River, Texas. The current status of this crab is unclear, it is believed to be extinct after the United States Corps of Engineers built a dike around the springs to stop the flow and prevent the salt from entering the river in 1964.

Brachyuran crab diversity has been shown to increase in time, implying a strong evolutionary radiation from the Late Jurassic onwards, for example, the appearance of Dynomenidae during the Late Jurassic. After a rapid evolution during the Late Cretaceous and they declined from the Eocene onwards (Fraaije, 2003). The first grapsid crab was estimated to have appeared during the late Eocene (40 Ma), and the first varunid crab appeared by the middle Miocene (12 Ma). It is in recent times that the Gercacinidae and Sesarmidae appeared and evolved rapidly. Beside the other paleoecological factors and possible destruction after death, the early crabs are all relatively very small in size, which probably explained their scarcity in paleontological collections (Fraaiji, 2003). The average size of anomurans and brachyurans crabs which remains in the Masstrichtian type area are all less than 10mm in size. The periods of increase in crab size and diversity of crabs have been linked with global sea level high stands (Haq *et al*., 1987). Haq *et al*. (1987) stated that the major explosive adaptive radiations among crabs occurred during the Late Jurassic, the Albian-Cenomanian, the Campanian-Maastrichtian, and during many shallow, more or less isolated seas. During these periods, the high stand is characterized by the presence of many shallow and isolated areas, with more eco-space and new niches for the crabs to invade (Yacobucci, 1996). And when the sea level fell, the newly evolved crab populations were forced to retreat to the sea. The mixing has probably led to stronger competitions which probably led to extinction and faunal turnovers (Fraaye, 1996b). This was followed by a period of stasis, during which a slower and stabilized evolutionary pattern dominated. After each period, more and more ecological niches were successfully filled, leading to the recent diversity in the crab size, morphology and feeding strategy (Fraaije, 2003).

The invasion of brachyuran crabs into the terrestrial environment has perhaps aided the increase in crab size. For example, among the six families, the adults of the Gercarcinidae are the largest in size. For the gercarcinid crabs, there is basically no competition for food resource, and ecological niches. The largest crabs are found in the Plagusiidae, Varunidae and Sesarmidae are also more or less terrestrial. For example, *Plagusia squamosa*, *Grapsus albolineatus*, *Varuna litterata*, *Eriocheir sinensis*, *Helice*, *Episesarma singaporense* are all relatively large-size animals in adulthood. The increase in size also corresponded to the increase in the thickness of the carapace, especially the branchial regions, which could have aided in respiration by increasing the amount of water retained in the gill chamber when the crabs move on land. This is very clearly seen in all the Gercarcinidae. In the genera *Plagusia* and *Grapsus*, which inhabit cliffs and rocky shores, have their branchial regions inflated. *Helice, Eriocheir* and *Episesarma* have very high carapace physiognomies, indicating that the carapace has, very likely, increased in its capacity to store or trap moisture inside the branchial region, which enable the animal to make use the trapped moisture for respiration.

The cyclograpsine crabs have never been reported to venture into the freshwater region even thought they are be found in river mouths or mangroves where there are aquifers or freshwater inputs. This indicates that these animals are adapted to or still require a higher salinity for their physiology. A simple experiment involving *Chasmaganthus convexus* and *Metaplax elegans* has shown that these animals survive better in water with higher salinity (pers. observ.). Unlike the cyclograpsine crabs, almost all the varunine crabs are able live in freshwater, except the anachialine genus, *Orcovita*, and a few other genera like *Hemigrapsus*, *Asiagrapsus* and *Quadragrapsus.*

Genera like *Varuna*, *Ptychognathus*, *Gnathograpsus*, *Pyxidognathus*, *Utica* and *Pseudograpsus* can be found in areas that have little or no seawater influence.

Although the adults need to go back to the brackish water for spawning, observation on the larval development of several species of varunine crabs have shown that the eggs and larvae of some species are able to hatch and survive well in low salinity water, or even fresh water! Experiments with the spawning and larval development of *Gnathograpsus palipes* and *Pyxidognathus granulsus* have shown that the two different species have their own preference for salinity, and they can even control the spawning if the water salinity becomes too high or too low respectively (pers. observ.). It is interesting to note that some genera of sesarmid crabs like *Geosesarma* need not go back to marine water for spawning. The larvae have abbreviated development, and hatched as juvenile crabs (Yeo & Ng, 1999; Ng & Tan, 1995).

The development of the stridulatory organ on the infra-orbital ridge and the mersial organ on the chelipeds has further indicated that it is an adaptation for the cyclograpsine crab to live in mudflat habitats. This is particularly obvious in genera like *Helice* and *Metaplax*. These crabs inhabit mud flats which probably make ‘seeing’ each other difficult. The stridulatory organ would probably enable the crabs to communicate each other effectively, particularly in searching for its mate or defending its territory. It is interesting to note that the stridulatory organ is very well developed in males, it is presumed that the sound is produced by the males to attract the females, very much like the waving of the *Uca* species. Other genera like *Cyclograpsus*, *Paragrapsus* that do not live in the mudflat habitats, but amongst rock and pebbles at the upper tidal zone do not posses such well-developed stridulatory organs. In *Metaplax elegans*, crabs have been observed to ‘rub’ either one of their chelae against the infra-orbital ridge region when they are standing by the entrance of their burrows when there is still a thin film of water left on the mudflat (pers. observ.). So far, there has bee no report of any social behavior from this taxon of crab except for *Metaplax occidentalis* (see Pretzmann, 1981).

It is worthwhile to note that the development of the oblique piliferous or setose crest on the third maxillipeds and the parallel groove along the buccal cavity as well as the development of the reticulated setae on pterygstomial region have revealed that these animals are somewhat adapted to terrestrial life. The type of oblique piliferous crest between the cyclograpsine crabs and the sesarmid crabs are very different. The oblique setose crest is found on the sesarmid crabs are very thick and the grove is very deep, while the crest found in the cyclograpsine crabs are simple, and the groove not as deep. The reticulated setae found on the pterygostomial region of the sesarmid crabs are neatly arranged in an orderly manner, while the setae in cyclograpsine crabs are not neatly arranged or in any orderly manner. Despite the differences in forms, both serve the same function in channeling water movement across the pterygostomial region and buccal cavity for respiration.

Maitland (1990, 1992) reported that in the *Heloecius cordiformis* (Heloeciinae, Ocypodidae), the branchial chambers are modified for both air breathing and water circulation. Water is held within the branchial chambers, is used for feeding and, to a certain extent, respiration. The branchial water is continuously pumped out by the scaphognathites over specialized setae-bearing regions of the carapace, and back through the branchial chambers over the gills. Water falling ventrally is collected by the abdomino-sternal cavity (formed between the abdomen and sternum) from where it returns to the branchial chambers via branchio-sternal canals. The crabs also exhibited several water retaining or water acquiring behaviour like a) ‘water shoogling’ where branchial water is drawn out between the ambulatory legs where it is worked by scissor-like up and down movements of the legs; b) abdomen flap where the branchial water volume is adjusted by the extension and flexion of the abdomen against the cephalothorax; c) ‘water dumping’ behaviour by tilting forwards and kissing the substrate, branchial water is voided to allow an entirely fresh load to be taken up; d) ‘statuesque posing’ in which the crabs remain erect and motionless for long period of time. During the statuesque posing, there is no branchial water and external body surfaces dry out. Posing behaviour may function in thermoregulation, osmoregulation or as an anti-fouling mechanism against settling organisms. Similar behaviour has alos been reported for the sesarmid crabs (Foskett, 1977; Felgenhauer & Abele, 1983). The cyclograpsine crabs exhibit similar behaviour (pers. observ.) but the current author cannot confirm the actual mechanism of water transport.

The varunid crabs that do not have the 'oblique crest' across the merus of the third maxillipeds. They also lack the reticulated setae on the pterygostomial region. The varunine crabs are able to live under terrestrial condition for hours. This can be easily seen during the transport of live *Eriocheir* from China to Singapore, and many of the varunine crabs were also caught during the low tide when they were hiding under rocks and pebbles (pers. observ.). The varunine crabs have developed this unique system of water transport across the pterygostome and buccal cavity by the evolution of the basal segment of the antenna from a fixed, immobile segment to mobile segment. The mobility of the segment probably helps to channel water movement from the end of the orbit where the wide 'U-shape' sulcus is, across the eye, into the pterygostomial groove that open into the buccal cavity.

Crab size has thought to be related to predation pressure, and was probably controlled by the predation pressure of the simultaneously evolving teleost fishes. In order to avoid predation, the crabs have probably devised strategies like a) hiding and living in crevices, b) camouflage their carapace, c) burrow into loose sediments, and d) swim in the open waters (Vermeji, 1978).

Varunid crabs have developed the strategies of hiding and living in crevices further by associating itself with another organism. This is observed in the genus *Setostoma*, from the subfamily Gaeticinae, which is found living as commensals in the burrows of thalassinidean shrimps or other burrowing invertebrates such as large polychaetes or perhaps echiuroids. Davie (1989) and Sakai (2000) have reported the probable association of *S. toriumii* with the large mud-shrimps *Upogebia major* and *U. yokoyai*, respectively. This has been confirmed by recent work by Itani (2001, 2003, 2004). Sakai (1976) reported *S. balssi* as "found associated with annelids". Itani *et al.* (2002, 2004) has found *S. depressa* in the burrows of thalassinideans (see section on Gaeticinae). It is, however, not known if these crabs are also ecto-parasite to its associates. The gaeticine crabs are essentially filter feeders (see section on Gaeticinae), but only *Gaetice* is free living (Delgpage, 1989).

Camouflage has been exploited extensively in the Varunidae. For example, the carapace of *Hirtograpsus i*s covered with thick, dense, short setae while the carapace of *Noarograpsus* is covered with granules. Both genera are found living in the mudflat environment. The presence of granules and setae has helped in camouflaging their carapace as they burrow into sediments. The colour variation of the carapace in the genus *Gaetice* and *Scutumara* are so variable that it is almost impossible to distinguish the animals from the sand particles if they stay motionless.

It has been shown that the antennae and antennule play an important role in the feeding process in varunid crabs. Tay (1998) has shown that in *Eriocheir sinensis*, the removal of antennae has seriously affected the feeding of the animal. The feeding efficiency has decreased three folds, but it did not totally hinder the feeding behaviour of *Eriocheir sinensis*. This is very likely because the crab is able to detect food or other chemical stimulant by means of other chemsosensory setae fund on other parts of the body such as the chela, third maxillipeds and ambulatory legs. The threshold for food detection in *Eriocheir* has been shown to be very low, and it could probably one of the adaptations that varunid crabs has adopted for living on land. The low threshold had probably enable the crab is able to detect food sources more readily than other organisms.

The presence of setae of on the third maxillieds, chelipeds and ambulatory legs in varunid crabs have been shown to be of sensory function. A study on the types of setae found in the *Eriocheir* by Tai (1997) has shown that the *Eriocheir* has five different types of setae present on the third maxillipeds namely simple, pappose, serrulate, plumodenticulate and triserrulate. The threshold of chemical and mechanoreception have been studied (Perarson *et al.*, 1979; Rebach *et al.*, 1990, Tai, 1997), and the threshold for food detection can be as low as $10^{-16}$ g/l (Pearson & Olla, 1977)! The pappose and plumodenticulate setae are mechanorecepters, while the simple, serrulate and triserrulate setae are both chemical and mechanoreceptors. The threshold for detection for the various types of setae has been  these various The pappose setae are also found on the tuft of setae on the chelipeds and the ambulatory legs (pers. observ.) of *Eriocheir* and *Ptychognathus*. The pappose setae and serrulate setae are also found on the ambulatory legs of *Varuna*, *Pseudograpsus* and *Utica* (unpublished data). The sensory setae enable the crab to detect changes in the environment, detect food, and hence, aided in the crab’s adapttabilies.

The process of carcinization (Borradaile, 1916; Stevcic, 1971; McLaughlin & Rafael, 1997; Guinot & Bouchard, 1998; McLaughlin *et al.*, 2004) which leads to the formation of crab-like forms has many derived conditions like the broadening of the carapace, front, buccal cavity, sternal plates and abdomen. The intercalation of a wide sternal plate, between the bases of the legs produces a greater distance between the coxa of P5 and the gonopods, with the resulting effect of having the coxal sexual male opening, and the penis further separated from the formamina at the bases of the gonopods (Guinot & Bouchard, 1998). The migration of the gonopores to the sternal position is a derived condition, which entailed the re-organization of the thorax, especially the muscle attachments and the exoskeleton, improving the mechanism of locomotion, particularly for walking and running. This process leads to the strong adaptative radiation and dispersal to the terrestrial and freshwater habitats (Glaessner, 1957, Guinot & Bouchard, 1998). The position of the gonopore, therefore, also shows the ancestry, and the possible phylogenetic lineages between the different taxon. In the Eriphiid crab (*Epixanthus frontalis*) the male gonopore opening is in the coax of the fifth ambulatory leg. In the *Xenograpsus*, the gonopore opening is only narrowly separated from the coxa of P5 by an elongation of episternite 7. This is very similar to the grapsid, sesarmid and plagusid crabs, but different from the varunid and glyptograpsid crabs. In the varunid and glyptograpsid crabs, the gonopore opening is embedded deep inside sternite 8, and with no contact with coxa of P5 or thoracic sternite 7.

The numerous new genera described here is testament to how poorly the family is known. Many of these new genera were established to accommodate those species that are different from their sister species in the original genus i.e. there are enough characters to split them, but they still have very close affinities to their original genera, in terms of their biology, habits and even some of the morphological characters. Recent molecular clocking in the genus *Varuna* (with H.T. Shih, in prep.) has shown that the genus is still very young, perhaps only about four million years old.

Recent publications by Martin & Davies (2001) and Schubart *et al*., (2006) have recognized five families in the Grapsoidea. The current study has added one additional family, Xenograpsidae in the Grapsoidea The true lineage of Xenograpsidae has to be determined as well to illustrate the phylogeny of the Grapsoidea. Kitaura *et al*. (2002)

and Schubart *et al* (2006), in their molecular phylogenetic studies of the grapsoid and ocypodoid crabs have strongly indicated that there is a possibility that Macrophthalminae is a sister taxon of Varunidae; with the Ocypodinae and Dortillinae not closely related. The latter they argue may also be separate lineage or family. The true lineage of the grapsoid and ocypodoid crabs has yet to be understood. Currently, only preliminary molecular evidences have been generated to initiate the in-depth study of these two major taxa, and molecular evidence, at it stands now, is not enough to give further details about the phylogeny of these coastal organisms. As such, there is an urgent need to re-appraise the Grapsoidea using adult and larval morphology. The morphological evidences (based on external adult characters, internal adult characters like the gastric mills, and larval characters), in conjunction with the molecular evidences should be able to bequeath us a better understanding of the evolution of these brachyuran crabs.

## Appendix I. Cladistics Analysis for the genus *Eriocheir*.

| **Species / Characters** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Eriocheir sinensis* | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 |
| *Eriocheir japonica* | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ericoheir hepuensis* | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Eriocheir ogasawaraensis* | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Neoeriocheir leptoganthus* | 0 | 0 | 0 | 3 | 0 | 3 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 |
| *Platyeriocheir formo* | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Gecarcinus weileri* | 2 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Epixanthus frontalis* | 1 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |

| **Species / Characters** | **16** | **17** | **18** | **19** | **20** | **21** | **22** | **23** | **24** | **25** | **26** | **27** | **28** | **29** | **30** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Eriocheir sinensis* | 0 | 2 | 2 | 0 | 0 | 0 | 2 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Eriocheir japonica* | 1 | 0 | 0 | 2 | 2 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Ericoheir hepuensis* | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Eriocheir ogasawaraensis* | 2 | 0 | 0 | 2 | 2 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Neoeriocheir leptoganthus* | 2 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Platyeriocheir formo* | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 2 |
| *Gecarcinus weileri* | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 1 |
| *Epixanthus frontalis* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |

| Species / Characters | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Eriocheir sinensis* | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 1 |
| *Eriocheir japonica* | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 1 |
| *Ericoheir hepuensis* | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 1 |
| *Eriocheir ogasawaraensis* | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 1 |
| *Neoeriocheir leptoganthus* | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Platyeriocheir formo* | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 1 |
| *Gecarcinus weileri* | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 |
| *Epixanthus frontalis* | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |

**Characters and character states:**

1. Carapace physiognomy
    - 0: flat
    - 1: slightly convex
    - 2: very convex

2. Frontal margin
    - 0: straight
    - 1: lobed

3. Frontal margin - teeth
    - 0: absent
    - 1: present

4. Frontal margin - medial teeth
    - 0: acutely triangular
    - 1: slightly triangular
    - 2: very broadly triangular
    - 3: absent

5. Frontal margin - medial cleft
    - 0: absent
    - 1: present

6. Frontal margin - type of medial cleft
    - 0: V-shaped
    - 1: U-shaped
    - 2: broad U-shaped

3: absent

7. Epi & protogastric cristae
   0: absent
   1: present

8. Epi & protogastric cristae
   0: low
   1: high

9. Epi & protogastric cristae
   0: weak
   1: strong

10. Epi & protogastric cristae
   0: blunt
   1: granular
   2: sharp

11. Chela - merus
   0: short
   1: long

12. Chela - merus
   0: broad
   1: slim

13. Cheliped - distal tooth
   0: weak
   1: strong

14. Cheliped - distal tooth
   0: blunt
   1: sharp

15. Fourth ambulatory leg
   0: short
   1: long

16. Fourth ambulatory leg
   0: slender
   1: broad

17. Male 6th abdomen somite - latero-distal margin
   0: roundish
   1: slightly arched
   2: arched

18. Female 6th abdomen somite
   0: roundish

1: slightly arched
2: arched

19. Male telson - distal end
    0: narrow
    1: broader
    2: very broad

20. G1 - gonopore position
    0: close to distal end
    1: half way from distal end
    2: 1/3 way from distal end

21. Female gonopore
    0: semicircular
    1: triangular
    2: bluntly triangular

22. Female gonopore
    0: not concave
    1: concave
    2: very concave

23. Carapace anterolateral margin - teeth
    0: 0 teeth
    1: 3 teeth
    2: 4 teeth

24. Eye stalks
    0: narrow
    1: broad

25. Epistome
    0: no lobes
    1: 3 lobes

26. Third maxillipeds
    0: long
    1: short

27. Third maxillipeds
    0: narrow
    1: broad

28. Thoracic sternites - suture 2-3
    0: straight
    1: convex

29. Thoracic sternites - lateral margins of sternites 3-4
    0: entire

1: slightly sinuous
2: strongly sinuous

30. Thoracic sternites - 5-6 - medial groove
    0: narrow
    1: broad
    2: very broad

31. Thoracic sternites - space on sternite 8
    0: narrow throughout length
    1: narrow proximally, broad distally

32. Cheliped - setae
    0: inner surface only
    1: outer surface only
    2: both inner and outer surface
    3: no setae

33. Cheliped merus - distal tooth
    0: absent
    1: present

34. Tips of cheliped dactyli
    0: sharp
    1: blunt

35. Tips of cheliped dactyli
    0: corneous
    1: spoon-shaped

36. Fourth ambulatory leg - setae
    0: absent
    1: present

37. Fourth ambualtory leg - propodi
    0: short
    1: long
    2: very long

38. Fourth ambulatory leg - propodi
    0: broad
    1: slender

39. Fourth ambulatory leg - dactylus
    0: slightly dorso-ventrally compressed
    1: rounded with angular margins
    2: dorso-ventrally compressed

40. G1
    0: short

1: long

41. G1
0: stout
1: narrow

42. Female gogopore operculum
0: crenulated
1: triangular
2: reactangular

43. Female gonopore
0: flat
1: concave

44. Spawning season
0: All year round
1: May to June (Summer)
2: October to January (Autum to Winter)

45. Spawning behavior - adult migration
0: no
1: yes

46. Spawning behaviour - larvae migration
0: no
1: yes

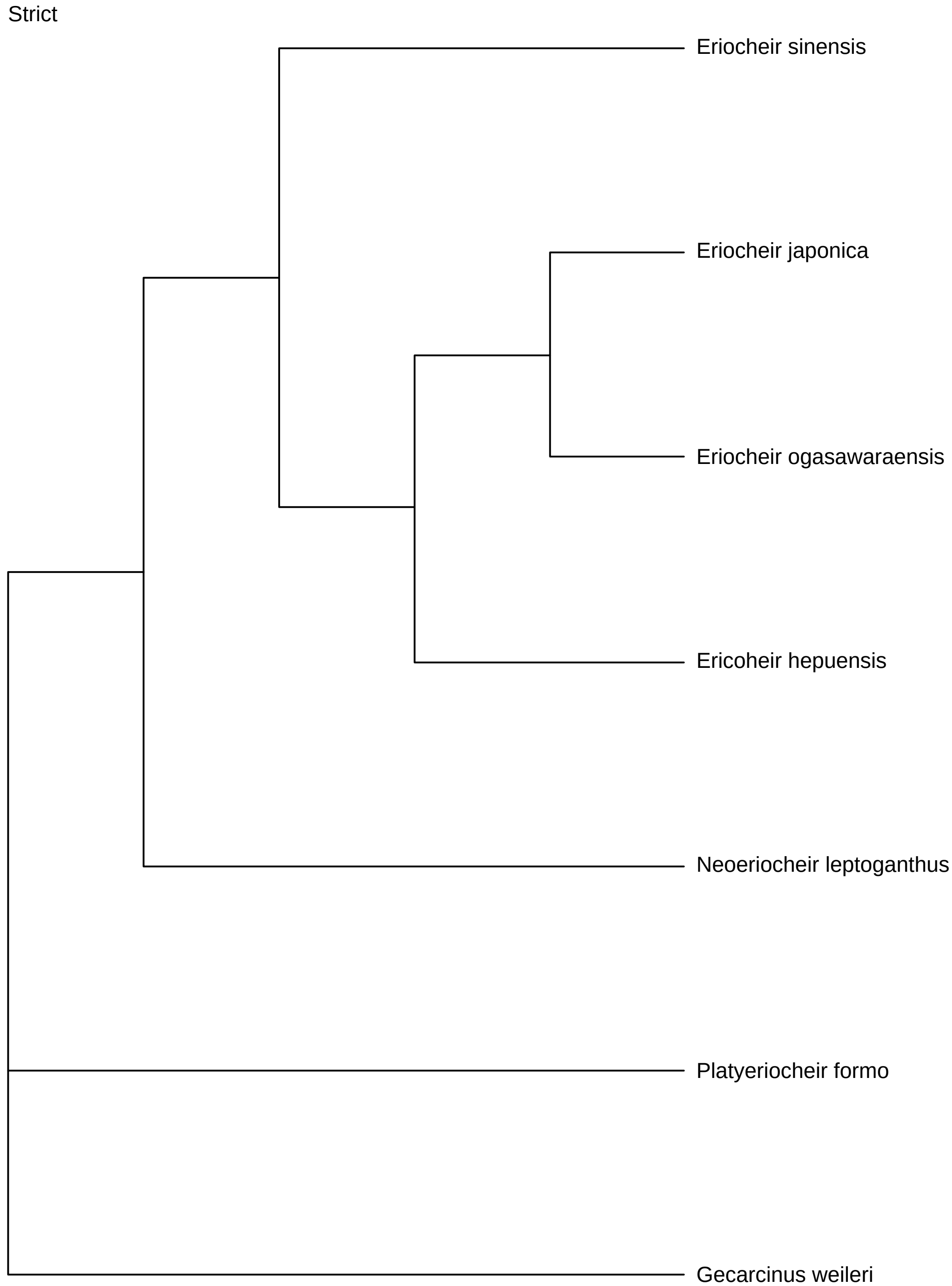



Figure 205. The strict consensus tree of 31 trees at 98 steps for the parsimony analysis of the morphological data of Appendix II (PAUP).

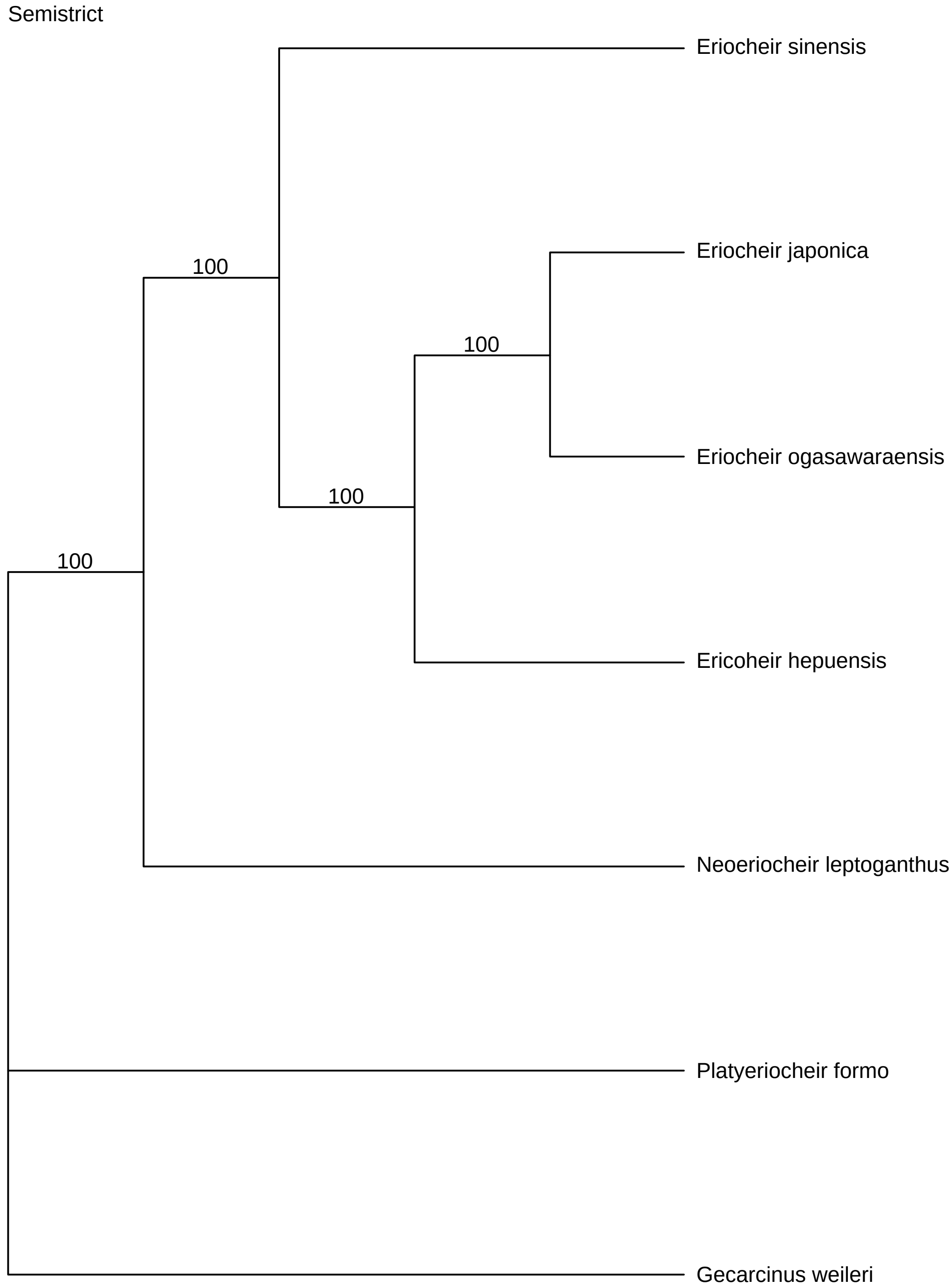



Figure 206. The semi-strict consensus tree of 31 trees at 98 steps for the parsimony analysis of the morphological data of Appendix II (PAUP).

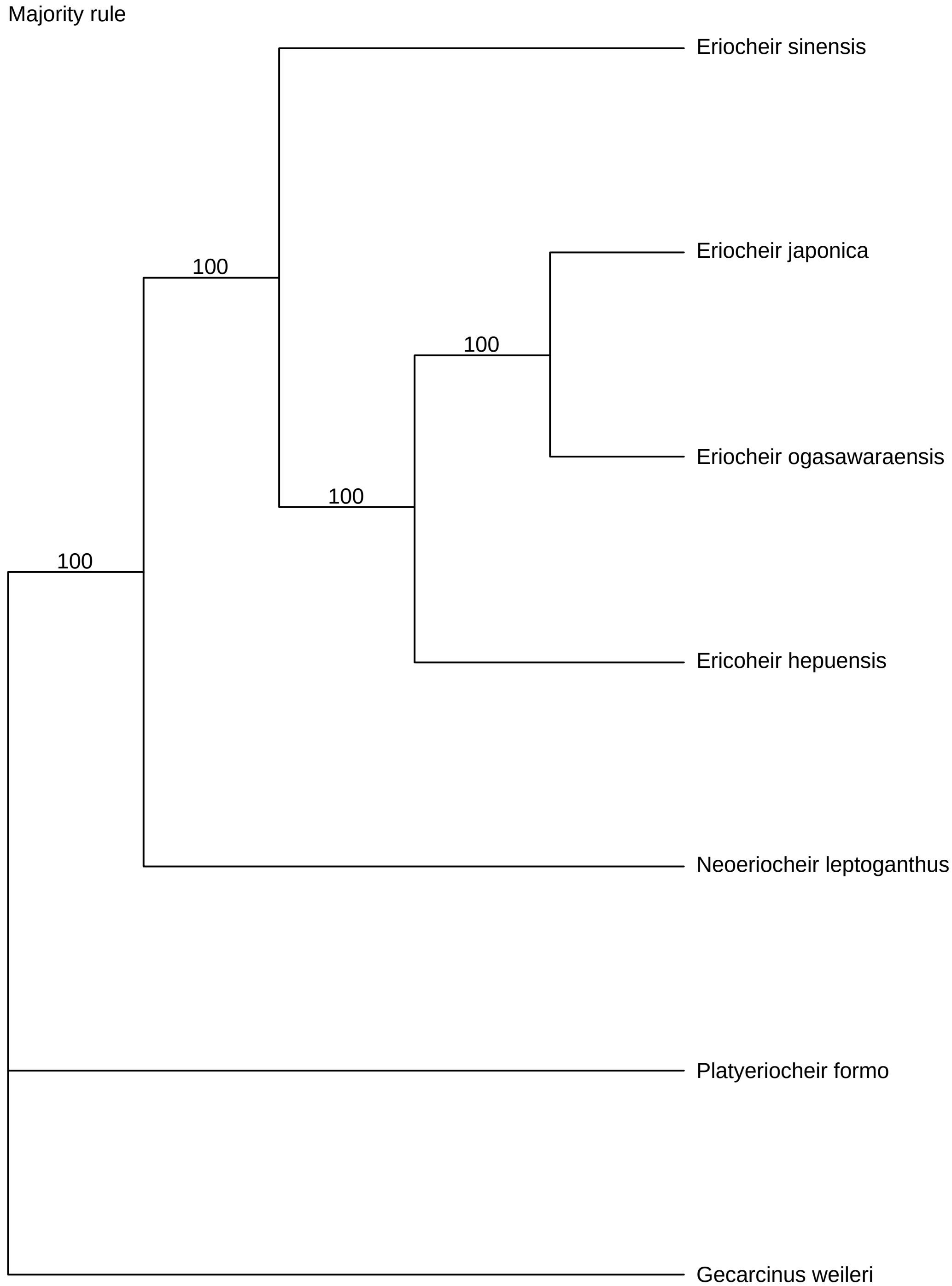



Figure 207. The majority tree of 31 trees at 98 steps for the parsimony analysis of the morphological data of Appendix 1I (PAUP).

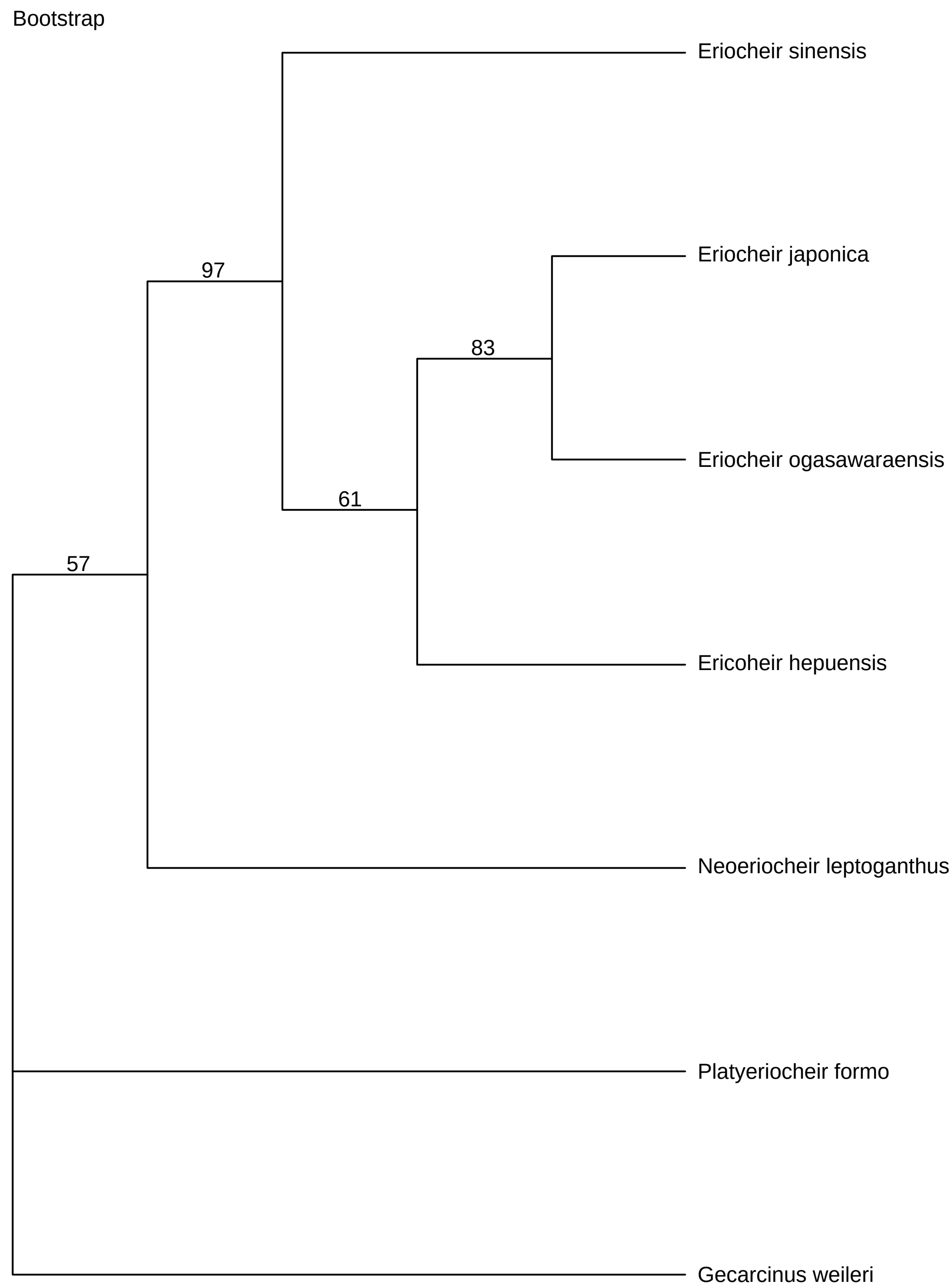



Figure 208. The bootstrap tree with bootstrap vales of 31 trees at 98 steps for the parsimony analysis of the morphological data of Appendix II (PAUP).

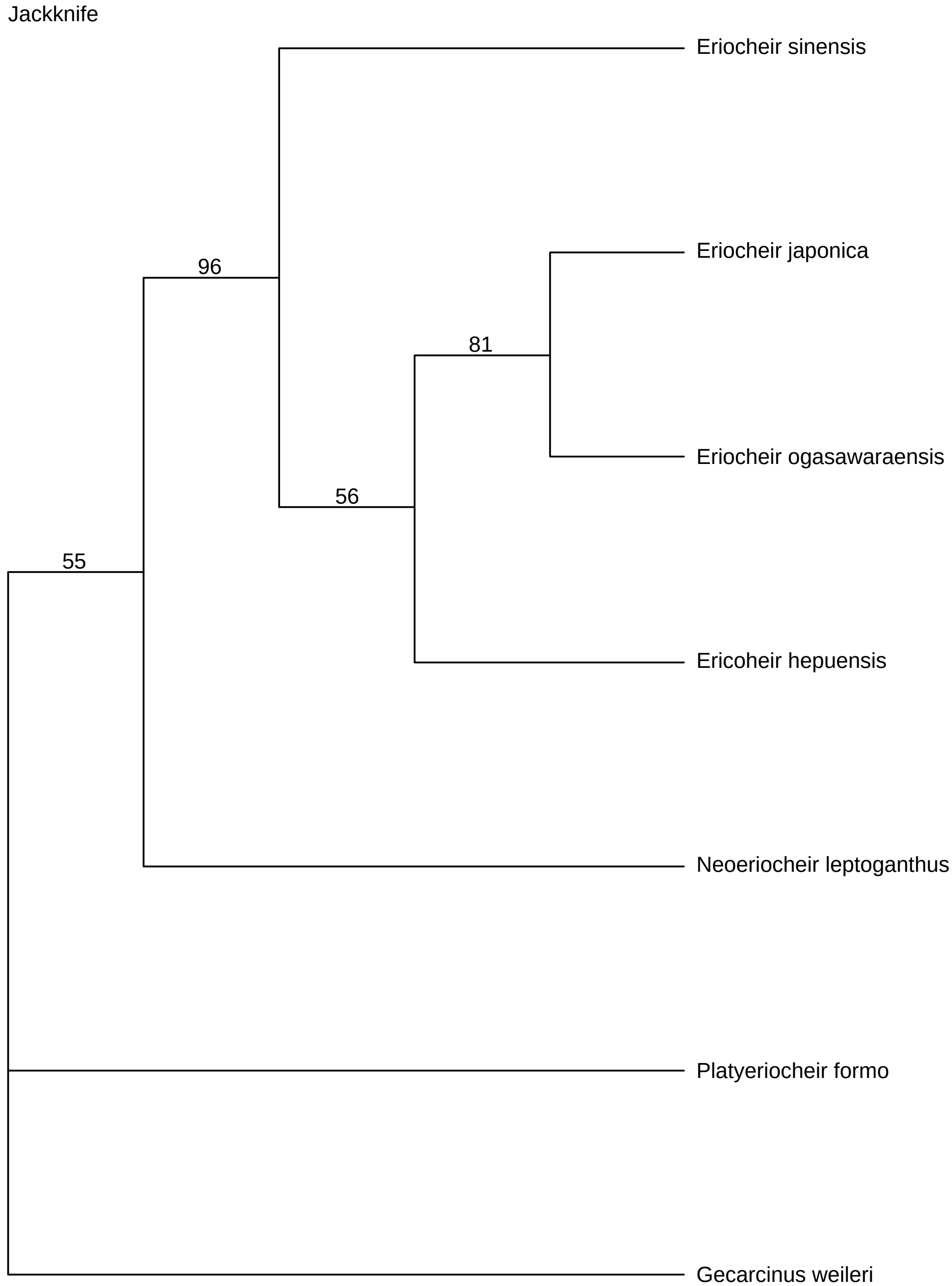



Figure 209. The jackknife tree with jackknife vlaue of 31 trees at 98 steps for the parsimony analysis of the morphological data of Appendix II (PAUP).

**<u>APPENDIX III. Ecology of the crab species, *Xenograpsus testudinatus* (adapted from Jeng *et al.*, 2004b)</u>**

The hydrothermal crab *Xenograpsus testudinatus* was found to occur in very high densities (over 300 crabs/m$^{2)}$ in nutrient-poor shallow-water Sulphur-rich hydrothermal vents (8-20 m depth) in northern Taiwan. My co-authors and I (2004b) has shown that the crabs swarm out of their hiding places during slack tides to feed on the plankton kill resulting from the toxic Sulphur plumes discharged by the vents that rains down during this period ("marine snow").

While there has been substantial work on the ecology of deepwater hydrothermal vent animals (Grassle, 1986; Tunicliff, 1991; van Dover, 2000), the same cannot be said of shallow-water vent systems (less than 200 m depth). In fact, there is a dearth of data on shallow-water hydrothermal vents, with published information only from California Stein, 1984), Iceland (Fricke *et al.*, 1989), Aegean Sea (Dando *et al.*, 1995), Azores and Kuriles (Tarasov *et al.*, 1986), Marianas (Barone *et al.*, 1992; Stüben *et al.*, 1992; Sakai & Türekay, 1995), Brothers Mount in New Zealand (McLay, 2007). The animal diversity in such vent systems is poor compared to deep-water systems (Fricke *et al.*, 1989; van Dover, 2000) and no complex communities have been reported as yet. The recently discovered shallow water vents at Kueishan Island (121°57'E 24°50'N) in I-lan County, northeastern Taiwan, is one such system and is considered to be part of the Okinawa Arc and associated geological area (Fig. 210) (Lee *et al.*, 1980; Chen, 1980; Liu, 1995)

Until 1997, Kueishan Island was under strict military control, the area outside it being used as a live-firing area, and there was no civilian access. Although the local fishermen have long reported there was volcanic activity in the area and the smell of Sulphur was often strong, no scientific explorations were possible. While many earlier studies have discussed the geological origin of the island and associated areas (Lee *et al.*, 1980; Chen, 1980; Liu, 1995), they were not aware of the presence of hydrothermal vents there. In 1997, the island was degazetted as a live-firing zone, and scientists started to enter the area to examine the island's biodiversity. Only in 1999 was the island freely accessible by scientists. Coincidentally, the discovery of the first specimens of *X. testudinatus* was from the shores of I-Lan, near Kueishan in fishing nets in 1991 (Ng *et al.*, 2000), without any indication of their hydrothermal affinities. Only subsequent enquires established its natural habitat (Ng *et al.*, 2000; Ng *et al.*, 2001).

The Kueishan vents were discovered only in 1997, and the geology and ecology of these shallow-water vents are now just being studied (Jeng, 1980; Song & Yang, 1980; Kuo, 2001; Jeng *et al.*, 2004b). Vents are present only on the eastern edge of the island (Fig. 2), with most of them (ca. 80%), including all the large ones, at 8-20m depths (shallowest 5m, deepest known, 26m). At any one time, there can be up to nine large smokers between 2-6m high (Fig. 211), with numerous small vents at other depths, all spewing Sulphur rich plumes with emergent temperatures of up to 65-112°C and a low pH of 1.9-4.6 (present data) although a temperature of 116°C and pH of 1.75 has been reported (Kuo, 2001). The extensive bubbling is the result of gas discharges consisting mainly of $CO_2$, $N_2$, $O_2$ and $H_2S$ (Kuo, 2001). The narrow 200m wide island-shelf drops off abruptly to 50m (Fig. 2). One of the unusual features of the Kueishan system is that the vent discharges are highly acidic and Sulphur rich (Gamo et al., 1997; Kuo, 2001). The only macro-invertebrate associated with these Sulphur rich vents is *Xenograpsus testudinatus* (Fig. 212), a crab discovered from the area only in 2000 (Lee *et al.*, 1980; Chen, 1980; Liu, 1995). This is in sharp contrast to active deep-water vents which have a diverse community of worms, clams, crustaceans etc. (Grassle, 1986; Tunicliffe, 1991; van Dover, 2000). The genus *Xenograpsus* comprises two other species from volcanic islands in the Mariana Arc (*X. novaeinsularis*) (Takade & Kurata, 1977, Takeda *et al.*, 1993; Türekay & Sakai, 1995), and Brothers Mount in New Zealand (*X. ngamata*) (McLay, 2007). *Xenograpsus* is unusual in that it is the only shallow-water obligate hydrothermal brachyuran genus known and the only crab that lives in such an extreme environment.

While *Xenograpsus* crabs are known to be associated with Sulphur rich systems, almost nothing is known about their ecology and adaptations. *Xenograpsus novaeinsularis* is known to be closely associated with shallow-water vents and has been observed to feed on the nearby ocean floor with its setae-tipped pincers (Takeda &

Kurata, 1977, Takeda *et al.*, 1993) and has been speculated to be tolerant of the high temperatures adjacent to the vents (Türkay & Sakai, 1995). No mention was made as to what they are feeding on. As *X. testudinatus* aggregates in large numbers (average density of 364 crabs/$m^2$) at the Kueishan vents (Ng *et al.*, 2000; Jeng *et al.*, 2004b), the perplexing question is how this nutrient-poor ecosystem can support such a substantial crab population. What are the crabs feeding on?

To ascertain the crab population, sampling was conducted of the area adjacent to the vents. This was done by wrapping a 0.25$m^2$ area of surface and subsurface rubble with a net and bringing it onshore. The rubble was broken up and the crabs were counted (megalopae excluded). The data suggests that the entire vent area (ca. 200 x 500m) has a population of some 3.6 million crabs, a remarkably high density. Even then, this is likely to be an underestimate as this was based on the collectable rubble only, with the larger masses harboring visibly higher densities. In such areas, the crabs are highly concentrated, completely filling up all available crevices. Interestingly, *X. testudinatus* is a placid species and will not fight even when crowded in the aquaria and is non-aggressive even when manhandled.

*In-situ* observations using SCUBA are complicated by the toxic Sulphur-rich environment and severe acoustic disturbance caused by the intense bubbling seriously reducing the available working time underwater (Fig. 211). In addition, the area is subjected to strong and unpredictable currents with the vent discharges often making the waters too murky in which to work. There is also active seismic activity, with tremors and frequent undersea landslides. As the vents are near shore, landslides from the adjacent cliffs pose a constant danger. Observations by SCUBA can thus only be conducted under optimal conditions between April and September, and during the hour-long slack water period during the day. Even then, this is highly dependent on daily seismic activity and water turbidity.

Jeng *et al*. (2004b) studies over the last four years have shown that *X. testudinatus* dwells in the rubble interspaces at the base of the vents. The rubble there is Sulphur rich and other studies have shown the crab to be highly tolerant of Sulphur in its gut and body tissues (unpublished data). The suggestion that the crabs have a high-thermal tolerance (Türekay & Sakai, 1995) is not borne out in our study as the waters inhabited by the crabs has temperatures of 16-25°C, the high temperatures of the plumes dissipating rapidly in the surrounding cold water. In the laboratory, they die rapidly in temperatures approaching 35-40°C and do best in aquaria with waters ranging between 20-24°C. Aquarium populations have been continuously maintained for over four years under such conditions, with some individuals already four years old, and others spawning annually with the larvae metamorphosing into juveniles (Jeng *et al.*, 2004a).

Observations of the crab aggregations at the Kueishan shallow-water vents over the last four years as well as studies in the laboratory and aquaria, show that *X. testudinatus* is feeding on the plankton kill (sometimes called “marine snow”) resulting from the toxic plumes and gases generated by the vents in the relatively still water column during slack tide. The vent discharges at Kueishan have a high concentration of Sulphur, $H_2S$ and $CO_2$ and will kill any small organism directly exposed to it (Kido, 1975, Stüben *et al.*, 1992).

During slack water, *Xenograpsus* crabs swarm out of the hiding places by the thousands (Fig. 212, video clip) and begin frantically feeding on the sea floor with their pincers. This swarming behaviour has only been observed during slack water and has never been reported before. Dissections of numerous *Xenograpsus* specimens collected between 2000 and 2003 revealed that their guts were consistently full of zooplankton (mainly copepods) and not planktons as plants materials are not affected by Sulphur. Studies of the mouthparts, mandibles and gastric mill of *Xenograpsus* confirm that it is not a filter-feeder, the structures being consistent with what is seen in typical bottom scavengers and/or detrital feeders (Schaefer, 1970; Caine, 1975; Felgenhauer & Abele, 1989; Ng *et al*., in prep.). Interestingly, my co-authors and I have observed that freshly caught and even four-year old aquarium specimens will only feed on minced animal matter and not when it is intact. Since there is no large fish or other large organism around the vents because Sulphur is toxic to these animals. There is no known predator of *Xenograpsus*!

On all occasions when slack water conditions were optimal for observation, my co-authors and I have witnessed a gradual precipitation of fine particulate matter, sometimes including small dead fish, around the vents. Analysis of water samples collected at this time revealed a high concentration of fine Sulphur and other inorganic particles and zooplankton of various types. During slack water when the currents are weak or absent, the vent plumes are directed vertically and the plankton as well as small animals in the water column killed by the toxic plumes descend straight down. The crabs time their foraging to coincide with this "marine snow" to maximize their feeding efficiency. As soon as the currents increase and the plume veers after slack water, the crabs immediately return to their rubble cover (Fig. 212). As tides in Taiwan are semidiurnal, my co-authors and I believe this feeding run takes place twice daily although night dives have been ruled out for the moment due to safety restrictions.

*Xenograpsus* crabs have only been collected from volcanically active Sulphur rich vents with substantial bubbling thus far. *Xenograpsus novaeinsularis* from a depth of 120m, while *X. testudinatus* has been collected in deeper waters immediately off Kueishan Island at depths of between 100-200m (T.Y. Chan, pers. comm.). The deeper waters, however, are still well within the mesopelagic zone and while plankton loads at these, provide sufficient food for the crabs. While no equivalent population study has been conducted at these depths, our available data suggests they are scarcer than in the shallower waters, suggesting plankton availability may be a limiting factor.

It has been demonstrated that vent discharges with high sulphide levels are integral to the establishment of a chemolithotrophic food web (van Dover, 2000) and/or growth of Sulphur-bacteria mats (Childress & Fisher, 1992). As the vent discharges in Kueishan have a high concentration of almost pure elemental Sulphur (99.5% purity) (Kuo, 2001) (and the area is covered with Sulphur deposits) which inhibits microbial growth, it is not surprising that the habitat is nutrient-deficient and species-poor. The consistently high density of *X. testudinatus* in the vent area of Kueishan, however, can only be explained if there is a constant food source. This, my coauthors and I believe, is the twice daily rain of plankton carcasses during slack water resulting from Sulphur plumes generated by the vents. My co-authors and I believe the crabs' reliance on this food source is novel, and the feeding behaviour observed is a remarkable adaptation to maximizing their ability to harvest the plankton kill. This form of feeding behaviour is hitherto unknown for any hydrothermal organism.

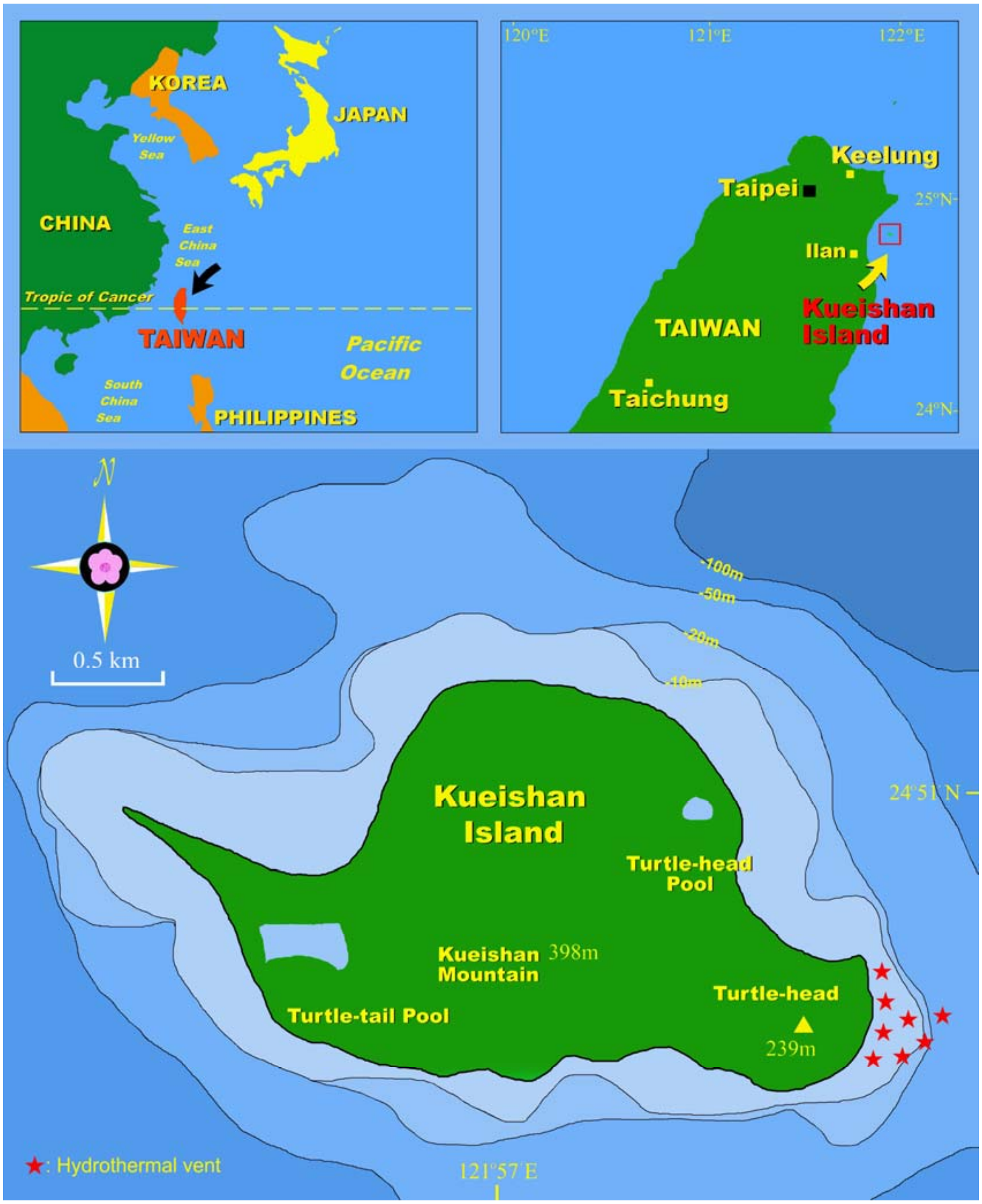



Figure 210. Map of Taiwan and Kueshan Island. (Top left) Map showing the Okinawa Arc and associated geological area. (Top right) Position of Kueishan Island with respective to Taiwan. (Bottom) Map of Kueishan Island.

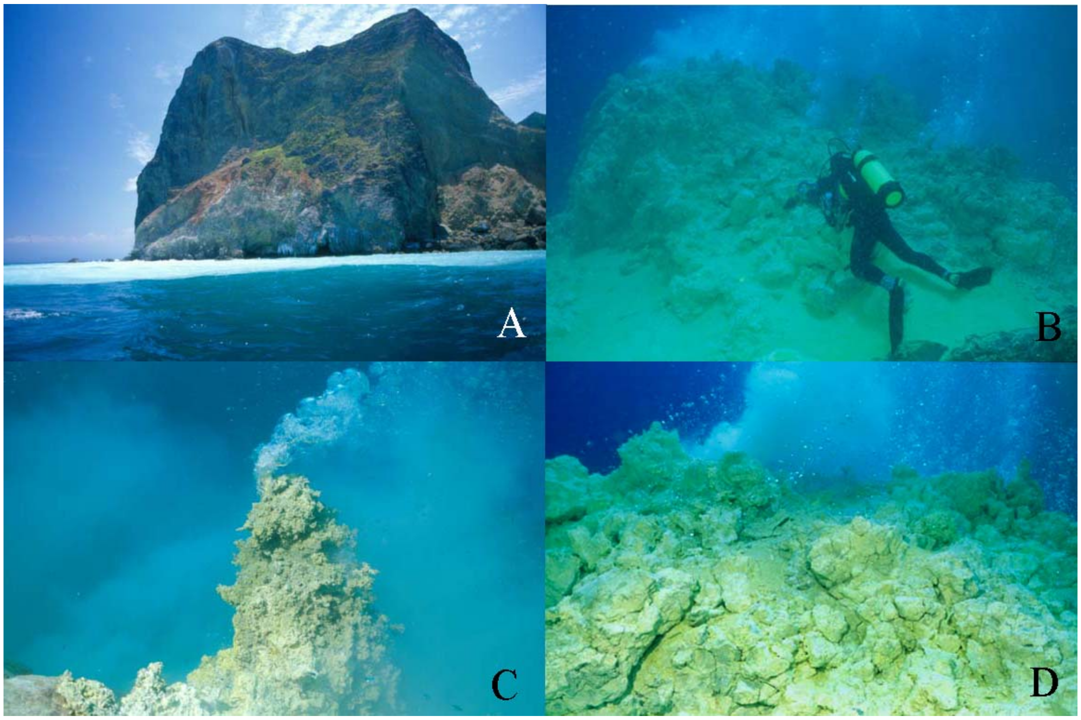



Figure 211. Shallow-water hydrothermal vents. A) northern end of Kueishan Island, with strong bubbling and Sulphur particles (white area); B) SCUBA diver working in bubbling zone; C) one of the 'yellow' chimneys spewing out gases and Sulphur particles; D) close-up of active vent area.

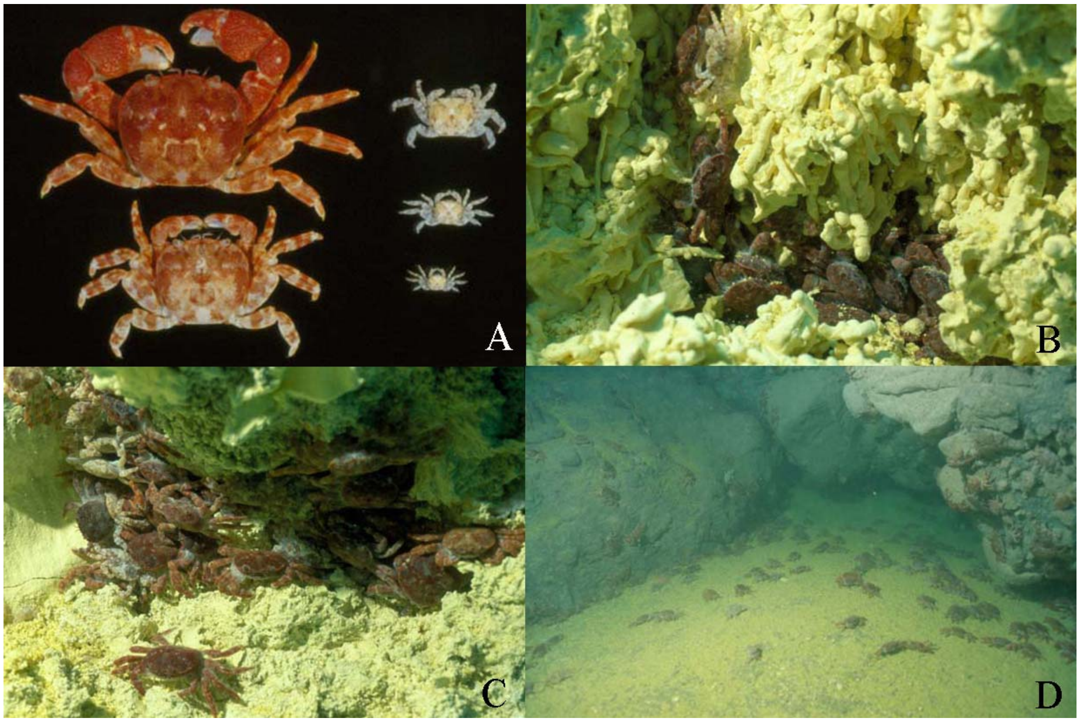


Figure 212. Shallow-water hydrothermal vent crabs. A) Various sizes of the hydrothermal crab, *Xenograpsus testudineatus*; B) crab aggregates in the interspaces of the Sulphur deposits; C) as currents slow, crabs begin to move out; D) during slack tide, the crabs swarm over the landscape feeding on the marine snow.

**<u>Appendix IV. Video clips showing the swarming behaviour and feeding behaviour of the hydrothermal vents crab species, *Xenograpsus testudinatus* (adapted from Jeng *et al.*, 2004b).</u>**

Commentary to the short video

| Time Start | Time End | Remarks |
|---|---|---|
| 0:00:00 | 0:00:15 | Title of the video. View of Kueishan Island from the north, as seen from the public ferry. Kueishan Island is also called the 'Turtle Hill' Island because the island is shaped like a turtle from lateral view. |
| 0:00:15 | 0:00:18 | The hydrothermal vents are found in the eastern part of the island. This clip shows the first author standing at the eastern edge of Kueishan island. The floating sulphur particles from the vents can be seen drifting eastwards towards the Pacific Ocean. |
| 0:00:18 | 0:00:20 | The floating sulphur particles, as seen from the boat. The air is filled with a strong and very pungent smell of sulphur. |
| 0:00:20 | 0:00:25 | The waves around the eastern part of the island are choppy, and it is not easy to find a suitable point to anchor the boat. Here, the first author's boat is attempting an approach from the north. |
| 0:00:25 | 0:00:29 | Close up of the floating sulphur particles. The density of the particles tends to vary with the number of chimneys below the sea and the wave and current conditions on the day. |
| 0:00:29 | 0:00:33 | The boat eventually had to approach from another side. The timing for when the divers descend into the sea is important and they try to stay in the water as short as possible. The acidic water, strong sulphur concentrations, sonic disturbance from the intense bubbling etc. make diving extremely unpleasant and uncomfortable. Most divers are only able to stay underwater for about half an hour at most. |
| 0:00:33 | 0:00:39 | The boat is slowly travelling in the direction of the current flow (as indicated by the sulphur particles), looking for the suitable site for the divers to go down. It is important that they do not dive directly above the vents. |
| 0:00:39 | 0:00:42 | The first author is preparing here to descend with his assistant, and equipment. Specific safety instructions are also given to the assistant still on board the boat to look out for bubbles, turn of the tides and any other incidents which may endanger the divers below. |
| 0:00:42 | 0:00:47 | The prominent sulphur plumes, as observed during the dive descent. The mixture of sulphur particles and gases is clearly evident |
| 0:00:47 | 0:00:52 | One of the yellow chimneys spewing out a high concentration of sulphur particles and hot gases that comprise mainly of $CO_2$, |

| | | |
|---|---|---|
| | | $N_2$, $O_2$ and $H_2S$. |
| 0:00:52 | 0:00:56 | Close up view of a yellow chimney. The temperature of the water is 112$^oC$ at the chimney mouth but is cooled rapidly by the surrounding seawater. Just a few metres from the plume, the water is only about 16-25$^oC$. |
| 0:00:56 | 0:01:04 | A view of another, larger yellow chimney. |
| 0:01:04 | 0:01:11 | The first author and his assistant examining a particularly large chimney. The chimneys are fragile and unstable, with a tendency to crumble when handled. |
| 0:01:11 | 0:01:20 | The first author digging out *Xenograpsus testudinatus* from the crevices near the base of the chimney. This is the only genus of brachyuran crab known to be associated with shallow-water sulphur-rich hydrothermal vents. |
| 0:01:20 | 0:01:35 | A close up on the first author's attempt to get the crabs. Crabs removed from the rubble scramble back into the crevices immediately on release. Nothing is known about the ecology and adaptations of these peculiar crabs. |
| 0:01:35 | 0:01:38 | Crabs of various sexes and sizes hiding in the crevices. They are known to aggregate in huge numbers (average 364 crabs/$m^2$). |
| 0:01:38 | 0:01:40 | Close up of the crabs hiding in the crevices. These crabs are relatively mild-tempered and can be kept in aquaria 'peacefully' even in large numbers. |
| 0:01:40 | 0:01:54 | The first author and his assistant waiting by one of the chimney, waiting for slack water. The spewing of the chimneys is continuous, producing a consistent pulsating noise. This noise causes great discomfort to divers. As such, the divers can stay underwater for only a very short time. This makes the *in-situ* study of the crabs very difficult and time consuming. |
| 0:01:54 | 0:02:09 | Once slack water occurs, all the particles in the plume will start to fall down vertically, making the entire water column very hazy and cloudy. At this point, the crabs swarm out of their crevices onto the sea-floor in huge numbers; and start frantically foraging for food. They feed rapidly on the freshly killed plankton ("marine snow") lying on the sea-floor even as more plankton continues descending down the water column. The plankton is killed almost instantly by the toxic plumes discharged by the vents and in the absence of currents, drifts downwards. |
| 0:02:09 | 0:02:27 | The swarming of the crabs … The forage only a short distance from their crevices, usually within a few metres radius. As the slack water period is very short, the crabs have to feed rapidly. Once the tide turns, the marine snow is carried away and dispersed by the strong currents. |

| | | |
|---|---|---|
| 0:02:27 | 0:02:41 | Close up of the feeding behaviour. The crabs are generally not very selective in their food. They will consume any food particles that are small enough to go through their mouths. |
| 0:02:41 | 0:02:55 | At tide turns, the currents push the sulphur particles away and the water column starts to clear. This is when the crabs start moving back into their crevices. |
| 0:02:55 | 0:03:01 | The end of the video showing the first author gradually swimming away. |

There is no commentary for the long video.

## LITERATURE CITED


Abele, L.G., 1975. The identity of *Sesarma hanseni* Rathbun, 1897, a supprosedly west Indian species, with *S. dehaani* H. Milne Edwards, 1853, from the West Pacific (Decapoda, Grapsidae). *Crustaceana*, 28(1): 48-52.

Abele, L.G., 1976. Comparative species composition and relative abundance of decapod crustaceans in marine habitats of Panama. *Marine Biology*, 38: 263-278.

Abele, L.G., 1982. Biogeography. In: D.E. Bliss (ed.). *The biology of Crustacea*. Vol. 1: Systematics, the fossil record, and biogeography. Pp. 242-304. Academic Press, New York, United States of America.

Abele, L.G., 1987. Book review: Schram, Frederick R. 1986. Crustacea. Oxford University Press, New York. Pp. I-xiv, 1-606. *Journal of Crustacean Biology*, 7(1): 200-201.

Abele, L.G. 1991. Comparison of morphological and molecular phylogeny of the Decapoda. *Memoirs of the Queensland Museum 31:*101-108.

Abele, L.G., 1992. A review of the grapsid crab genus *Sesarma* (Crustacea: Decapoda: Grapsidae) in America, with the description of a new genus. *Smithsonian Contribution in Zoology*, 527: 1-60. Abele, L.G. & B.E. Felgenhauer, 1986. Phylogenetic and phenetic relationships among the lower Decapoda. *Journal of Crustacean Biology*, 6: 385-400.

Abele, L.G. & D.B. Means, 1977. *Sesarma jarvisi* and *Sesarma cookei*: Montane, terrestrial grapsid crabs in Jamaica (Decapoda). *Crustaceana* 32(1): 91-93.

Abele, L.G. & W. Kim, 1986. *An illustrated guide to the marine Decapod crustaceans of Florida*. Technical Series 8(1), part 2, 760 pp. Florida Department of Environmental Regulation, United States of America.

Abele, L.G. & W. Kim, 1989. The decapod crustaceans of the Panama Canal. *Smithsonian Contribution in Zoology*, 482: 1-50.

Abele, L.G., P.J. Campanella & M. Salmon, 1986. Natural history and social organization of the semiterrestrial grapsid crab *Pachygrapsus transversus*. *Cahiers de Biologie Marine*, 38: 291-299.

Adams, A. & A. White, 1849. Crustacea. In: Arthur Adams (ed.), T*he Zoology of the Voyage of H.M.S. Samarang: under the command of Captain Sir Edward Belcher, during the year 1843-1846 by John Edward Gray, John Richardson, Arthur Adams, Lovell Reeve, and Adam White*, pp. i-viii, 1-66, Pls. 1-13.

Adams, A. & A.White, 1848-1849. Crustacea. In: A. Adams (ed.), *The zoology of the voyage of H. M. S. Samarang under the command of Captain Sir Edward Belcher, C. B., F. R. A. S., F. G. S. during the years 1843-1846*, 4, VIII, pp. 1-32, pls.1-6 (1848); pp. 33-67, pl. 7-13 (1849). Reeve, Benham, and Reeve, London, United Kingdom.

Adema, J.P.H.M. 1991. *De krabben van Nederland en België (Crustacea, Decapoda, Brachyura)*. 244 pp. Nationaal Natuurhistorisch Museum, Leiden, The Netherlands.

Ahyong, S.T., & G.C.B. Poore, 2004. Deep-water Galatheidae (Crustacea: Decapoda: Anomura) from soutrhern and eastern Australia. *Zootaxa*, 472: 1-76.

Aikawa, H., 1929. On larval forms of some Brachyura. *Records of Oceanographic Works in Japan*, 2(1): 17-55, pls. 1–5, tabs. 1–6.

Akiwa, R., 2003. Distribution of two morphotypes of *Hemigrapsus penicillatus* within Tokyo Bay, Japan. Department of Aquatic Biosciences. Bachelor of Science thesis, Tokyo University of Fisheries, Tokyo, Japan. [Unpublished].

Albert, F., 1883. *Ueber das Kaugerüst der Makruren. Inaugural-Disseration zur Erlangung der philosophischen Doctorwürde an der Georg-August-Universität zu Göttingen*. Pp. 80, text-fig. 1; Göttingen, Dieterich'sche Universiti Buchdruckerei, Germany.

Alcock, A., 1895. Materials for a carcinological fauna of India. No. 1. The Brachyura Oxyrhyncha. *Journal of the Asiatic Society of Bengal*, 64(2): 157-291.

Alcock, A., 1896. Materials for a carcinological fauna of India. No. 2. The Brachyura Oxystoma. *Journal of the Asiatic Society of Bengal*, 65(2): 133-296.

Alcock, A., 1899. Natural History Notes from the Royal Indian Marine Survey Ship 'Investigator', Commander T. H. Heming, R. N., commanding. Series III. No. 3. On some notable new and rare species of Crustacea. *Journal of the Asiatic Society of Bengal*, 68(2): 111-119.

Alcock, A., 1900. Materials for a carcinological fauna of India. No. 6. The Brachyura Catometopa or Grapsoidea. *Journal of the Asiatic Society of Bengal*, 67: 279-486.

Alcock, A., 1901. *A Descriptive Catalogue of the Indian Deep-Sea Crustacea Decapoda Macrura and Anomula, in the Indian Museum*.. Pp. 1-286, pls. I-III. Indian Museum, Calcutta, India.

Alcock, A., 1902. *A Naturalist in Indian Seas*. Pp. 328. John Murray, London. United Kingdom.

Amestoy, F., 1985. Biología reproductora de *Cyrtograpsus angulatus* (Dana, 1851) (Decapoda, Brachyura). *Actas de las Jornadas de Zoologia del Uruguay (Montevideo)*, 1985 : 51.

André, M., 1947. L'envahissement du reseau hydrographique francais par le Crabe chinois (*Eriocheir sinensis* H. M. Edw.). *Revue Scientific, Revue Rose*, 3264: 33–38.

Anger, K., E. Spivak, C. Bas, D. Ismael, & T. Luppi, 1994. Hatching rhythms and dispersion of decapod crustacean larvae in a brackish coastal lagoon in Argentina. *Helgoländer Meeresunteruchungen*, 48(4): 445-466, table 1, text-figs. 1-8.

Anker, A., M. Galena-Vantsetti, C. Lira, J.A.V. Caripe, A.R. Palmer & M.S. Jeng, 2005. Macrofauna associated with Echiuran Burrows: A review with new onservations of the the innkeeper worm, *Ochetostoma erythrogrammon* Leuckart and Rüppel, in Venezuela. *Zoological Studies*, 44(2): 157-190.

Anonymous, 1984. *Coastal Invertebrates of Victoria*, 117 pp. Marine Research Group of Victoria, The Museum of Victoria, Victoria, Australia.

Anonymous, 2001. Washington Sea Grant Program. February 2001. "Non-indigenous species facts: Chinese Mitten Crab." Available: http://nsgl.gso.uri.edu. (accessed on 26 September 2006)

Anonymous, 2002. *Christmas Island National Park Management Plan.* Part 1. A description of Christmas Island and the National Park. Christmas Island National Park Management Plan. Parks Australia. Australia.

Asakura, A., 2000. Decapod Crustacea. In: Natural Conservation for Wild Life (ed). *Red Data Book for Wild Life in Chiba Prefecture*. 438 p. Chiba Prefectual Goverment, Japan.

Asakura, A., 2006. The story behind the discovery of *Hemigrapsus takanoi* Asakura & Watanabe, 2005, a cryptic species of crab, previously thought to be the common Japanese intertidal crab, *H. penicillatus* (Decapoda: Brachyura: Grapsoidea). *TAXA, Proceedings of the Japanese Society of Systematic Zoology*, 21: 33-39.

Asakura, A. & S. Watanabe, 2005. *Hemigrapsus takanoi*, new species, a sibling species of the common Japanese intertidal crab *H. penicillatus* (Decapoda: Brachyura: Grapsoidea). *Journal of Crustacean Biology*, 25(2): 279-292.

Asano, H., 1933. *Illustrated Fauna of Fisheries*. P. 924 + 49 + 39 pp., 2144 text-figs., Seikokan, Tokyo, Japan.

Ates, A.S., 1999. *Liocarcinus depurator* (Linneaus, 1758) and *Brachynotus sexdentatus* (Risso, 1827) (Deapopda, Bracyhura), two new records for the Turkish Black Sea Fauna. *Turkish Journal of Zoology*, 23: 116-118.

Ates, A.S., T. Katagan, A. Kocatas, & F. Erkan Yurdabak, 2005. Decapod (Crustacea) Fauna of Saros Bay (Northeastern Aegean Sea). *Turkish Journal of Zoology*, 29: 119-124.

Baba, K. & Y. Fukuda, 1972. Larval development of *Chasmagnathus convexus* de Haan (Crustacea, Brachyura) reared under laboratory conditions. *Memoirs of the Faculty of Education, Kumamoto University*, 21(1): 90-96, text-figs. 1-2.

Baba, K. & M. Moriyama, 1972. Larval development of *Helice tridens wuana* Rathbun and *H. tridens tridens* de Haan (Crustacea, Brachyura) reared in the laboratory. *Memoirs of the Faculty of Education, Kumamoto University*, 20: 49-68.

Baba, K., Y. Fukuda & Y. Nakasone, 1984. Zoeal morphology of the sesarmine crab, *Helice leachi* (Hess) (Crustacea: Decapoda: Brachyura). *Memoirs of the Faculty of Education, Kumamoto University, Natural Sciences*, 33: 5-10.

Bacescu, M.C., 1967. *Crustacea. Decapoda*. Fauna of the *Republica Socialista România*. Vol. 4 fasc. 9. Pp. 1-351, 141 figs., 2 pls.

Bacon, M.R., 1971. Distribution and ecology of the crabs *Cyclograpsus lavauxi* and *C. insularum* in Northern New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 5: 415-426.

Báez, P & R. Ruiz, 1985. Crustáceos de la isles oceánicas de Chile depositados en el Museo Nacional de Historia Natural de Santiago. In: P. Arana (ed.), *Investigaciones Marinas en el archipiélagp de Juan Fernández*. Pp. 93-108. Escuelade Ciencias de Mar, Universidad Católica de Valparaiso. Chile.

Baker, A.N., 1971. Food and feeding of kahawai (Teleostei: Arripodidae). *New Zealand Journal of Marine and Freshwater Research*, 5: 415-426.

Baker, M. C., 1973. Stochastic properties of the foraging behavior of six species of migratory shorebirds. *Behaviour* 45: 242-270.

Balss, H., 1922. Diagnosen neuer japanischer Decapoden. *Zoologischer Anzeiger*, 54(1/2): 1-7.

Balss, H., 1922. Ostasiatische Decapoden. IV. Die Brachyrhynchen. *Archiv Naturgesche* (A), 88(11): 94-166, pls. 1-2.

Balss, H., 1925. Macrura der Deutschen Tiefsee-Expedition. 1. Natantia, Teil A. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898-1899* 20: 221-315.

Balss, H., 1930. Zoologische Ergebuisse der Reisen von Dr. L. Kohl-Lassen nach den Subantarktischen Inseln bei Neuseeland und nach Sudiorgien. Die Dekapoden (Crustaceen). *Senkenbergiana*, 12: 195-210, 6 figs.

Balss, H., 1934. Die Krabben der Reise J. W. Harms' nach der Christmas-Insel und dem Malaiischen Archipel. *Zoologischer Anzeiger*, 106(10): 225-237.

Balss, H., 1935. On three South Indian crabs (Decapoda, Brachyura) of the Madras Museum. *Records of Indian Museum*, 37: 45-48.

Balss, H., 1938. Die Dekapoda Brachyura von Dr. Sixten Bocks Pazifik-Expedition 1917-1918. *Göteborgs Kungl. Vetenskaps och Vitterhets Samhälles, Series B*, 5(7): 1-85 figs 1-18 pls 1-2.

Balss, H., 1940-1944. Morphologischer Teil. In: Dr. H. G. Bronns (ed.) *Klassen und Ordnungen des Tierreichs*, 5(1, 7): 22-667, text-figs. 7-740; Leipzig (Akademische Verlagsgesellschaft Geest & Portig K.-G.) [Lief. 1: pp. 1-160, 1940; Lief. 2: pp. 161-320, 1941; Lief. 3: 321-862, 1944.]

Balss, H., 1957. VIII. Systematik. Decapoda. Klassenund Ordnungendes Tierreichs. In H. G. Bronns, Klassenund Ordnungendes Tierreichs. Bd5, IAbt., 7. Buch, 12 Lief: pp. 1505–1672, abb. 1131–1199. Leipzig, Akademische Verlagsgesellschaft, Germany.

Barnard, K. H., 1950. Descriptive catalogue of South African decapod Crustacea. *Annals of South African Museum,* 38: 1-837.

Barnard, K.H., 1955. Additions to fauna list of South African Crustacea and Pycnogonida. *Annals of the South African Museum*, 43: 1-107, Figs. 1-53.

Barnes, D.J., B.E. Chalker & K.W. Kinsey, 1986. Reef metabolism. *Oceanus* 29(2): 20-26.

Barone, A., A. Lange, S. Wu, C. Li & D. Zhang, 1992. First results of study of sulphur rich hydrothermal activity from an island-arc environment: Esmeralda Bank in the Mariana Arc. *Marine Geol*ogy, 103, 521-528.

Baross, J.A. & S.E. Hoffman, 1985. Submarine hydrothermal vents and associated gradient environments as sites for the origin and evolution of life. *Origins of Life and Evolution of Biospheres* (Formerly Origins of Life and Evolution of the Biosphere), 15 (4): 327-345.

Bas, C.C. & E.D. Spivak, 2000. Effect of salinity on embryos of two southwestern Atlantic Esturine grapsid crab species cultured in vitro. *Journal of Crustacean Biology*, 20(4): 647-656.

Batham, E.J., 1956. Ecology of a southern New Zealand sheltered rocky shore. *Transactions of the Royal Society of New Zealand*, 84(2): 447-465.

Batham, E.J., 1958. Ecology of a southern New Zealand exposed rocky shore at Little Papanui, Otago Peninsular. *Transactions of the Royal Society of New Zealand*, 85(4): 647-658.

Batham, E.J., 1965. Rocky shore ecology of a southern New Zealand fiord. *Transactions of the Royal Society of New Zealand*, 6(21): 215-227.

Bedford, J.J., & J.P. Leader, 1977. The composition of the haemolymph and muscle tissue of the shore crab, *Hemigrapsus edwardsii*, exposed to different salinities. *Comparative Biochemistry and Physiology,* 57A: 341-345.

Bedford, J.J., 1972. The composition of the blood of the grapsid crab, *Helice crassa* Dana. *Journal of Experimental Marine Biology and Ecology,* 8: 113-119.

Beer, C.G., 1959. Notes on the behaviour of two estuarine crab species. *Transactions Royal Society of New Zealand*, 86(3/4): 197-203.

Bennett, E.W., 1930. Notes on New Zealand Brachyura and related crustacean. *Records of Cantebury Museum*, 3(4): 255-261.

Bennett, E.W., 1964. The Marine Fauna of New Zealand: Crustacea Brachyura. *New Zealand Department of Science and Industry Research Bulletin*, No. 53. New Zealand Oceanography Institute Memoir 22. 120 pp, 141 figures.

Bennett, I., 1987. *Australian Seashores: W.J. Dakin's classic study*. Pp. 255, Angus & Robertson. Australia.

Bolton, L.A. & G.A. Knox, 1977. The ecology of selected sites near Mapua, Waimea Inlet. *Estuary Research Unit Reports, Depsrtment of Zoology, Universitgy of Canterbury*, 10: 1-30.

Boone, L., 1934. Scientific results of the World Cruise of the Yacth Alva, 1931, William K. Vanderberbilt, commanding. Crustacea: Stomatopoda and Brachyura. *Bulletin of the Vanderberbilt Marine Museum, Huttington, L. I. New York, USA*, 5: 1-210, pls. 1-109.

Borradaile, L.A., 1898. On some Crustaceans from the South Pacific-Part I: Stomatopoda. *Proceedings of the Zoological Society of London*, 1898: 32-38, pls 5-6.

Borradaile, L.A., 1907. On the classification of the Decapod Crustaceans. *The Annals and Magazine of Natural History*, 114:32-62.

Borradaile, L.A., 1910. On the land and amphibious Decapoda of Aldabra. *Transactions of the Linnean Society of London*, 13(2): 405-409.

Borradaile, L.A., 1916. Crustacea. Part II. *Porcellanopagurus*; an instance of carcinixation. In: British Antarctic (‘Terra Nova’) Exploration 1910. *Natural History Report Zoology*, 3(3): 111-126.

Boschi, E.E., 1964. Los crustáceos decápodos Brachyura del litoral Bonaerense (R. Argentina). *Bollotin of Institute of Marine Biology*, *Mar del Plata*, 6: 1-96.

Boschi, E.E., 1966. Preliminary note on the geographic distribution of the decapod crustaceans of the marine waters of Argentina (South-west Atlantic Ocean).

*Proceedings of the Symposium of Crustacea, Ernakulam*, 1: 449-456, tables 1-2, 1 map.

Boschi, E.E., 1976. Nuevos aportes al conocimiento de la distribucion geografica de los crustáceos Decápodos del Mar Argentino. *Physis, (A)*, 35(90): 59-68, table 1, text-figs. 1-3.

Boschi, E.E., 1979. Geographic distribution of Argentinian marine decapod crustaceans. *Bulletin of the Biological Society of Washington*, 3: 134-143, text-fig. 1, table 1.

Boschi, E.E., 1979. Los crustáceos decápodos en las comunidades bentonicas del mar epicontinental argentino. In: *Ecologia bentónica y sedimentación de la plataforma continental del Atlántico sur*. Memorias del Seminario organizado por Unesco con el auspicio del Gobierno del Uruguay (Montevideo, 9-12 de mayo de 1978): 279-290, text-figs. 1-3. UNESCO: Oficina regional de ciencia y tecnologia para América Latina y el Caribe. Montevideo, Uruguay.

Boschi, E.E., 1981. Larvas de Crustacea Decapoda. Pp. 699-758, figs. 234-241. In: D. Boltovsky (ed.). *Atlas del Zooplancton del Atla´ntico Sudoccidentaly Metodos de Trabajocon Zooplancton Marino*. Pp. xxix, 936. NIDEP, Publicación especial, República Argentina.

Boschi, E.E., 2000. *Species of decapod crustaceans and their distribution int he American marine zoogeographic provinces*. Revista de Investigación y Desarrollo Pesquero. No. 13. Mar del Plata, República Argentina.

Boschi, E.E., M.A. Scelzo & B. Goldstein, 1967. Desarrollo larval de dos especies de Crustáceos Decápodos en el laboratorio. *Pachycheles haigae* Rodrigues da Costa (Porcellanidae) y *Chasmagnathus granulata* Dana (Grapsidae). *Boletim do Instituto del Biologica marina Mar del Plata*, 12: 1-46.

Boschi, E.E., C.E. Fischbach & M.I. Iorio, 1992. Catálogo ilustrado de los crustáceos estomatópodos y decápodos marinos de Argentina. *Frente maritimo*, 10(A): 7-94, text-figs. 1-98.

Bourdillon-Casanova, L., 1960. Leme´roplancton du Golfede Marseille: les larves de Crustace´s Decapodes. *Recueildes Travaux de la Station Marined' Endoume Marseille*, 30: 1–286, figs. 1–78, tabs. 1–27.

Bouvier, E.L., 1915. Décapodes marcheurs (Reptantia) et Stomatopodes recueillis à l'île Maurice par M. Paul Carié. *Bulletin of Science, France and Belgium* (7) 48(3): 178-318, text-figs. 1-42, pls. 4-7.

Bouvier, E.L., 1940. Décapodes marcheurs. *Faune de France*, 37: 1-404.

Bowdich, E.T. (1825). *Excursions in Madeira and Porto Santo During the autumn of 1823, while on his Third Voyage to Africa.*: [s.n.] pp. i-xii, 1-278, 12 pls. London, United Kingdom.

Brandis, D., V. Storch, & M. Türkay, 1999. Morphology and function of the copulatory system in freshwater crabs of the genus *Potamon*. *Journal of Morphology,* 239(2): 157-166.

Brashnikov, V., 1907. Beitrage zur fauna der russischen ostlichen Meere, gesammelt von dem Schoner Storosh i. d. 1899-1902. In: *St. Peterburg Memoires Ac. Sc. series 8,* 20, part 6, 2 Taf., 1 Karteu 26 Abb. i. T. Russia.

Breitfuss, M.J., R.M. Connolly & P.E.R. Dale, 2004. Densities and aperture sizes of burrows constructed by *Helograpsus haswellianus* (Decapoda: Varunindae) in saltmarshes with and without mosquito-control runnels. *Wetlands*, 24(1): 14-22.

Breton G., M. Faasse, N. Pierre, & T. Vincent, 2002. A new alien crab in Europe: *Hemigrapsus sanguineus* (Decapoda: Brachyura: Grapsidae). *Journal of Crustacean Biology*, 22(1): 184-189.

Broekhuysen, G.J., 1941. The life history of *Cyclograpsus punctatus*, M. Edw.: breeding and growth. *Transactions of the Royal Society of South Africa,* 28(4): 331-366.

Bruce, A.J., 2005. Note on a new species of *Bresilia* (Crustacea: Decapoda: Bresiliidae) from Zanzibar. *Memoirs of the Queensland Museum,* 51(2): 385-390.

Bruce, Z.R., 2002. Mesozoic Geology of the Puerto Ingeniero Ibanez Region, 46 degrees South Chilean Patagonia. Ph.D. thesis submitted to University of Canterbury, New Zealand. [Unpublished].

Brune, G., 1981. *Springs of Texas*, Vol. 1. Fort Worth: Branch-Smith, United States of America.

Brusca, R.C., 1980. *Common Intertidal Invertebrates of the Gulf of California.* 2nd

Edition. 513 pp., figs. 1.1-27.36. The University of Arizona Press, United States of America.

Buden, D.W., 2001. Decapod Crustaceans of the Headwater Streams of Pohnpei, Eastern Caroline Islands, Federated States of Micronesia. *Pacific Science*, 55(3): 257-265.

Buhk, F., 1938. Zu Fortpflanzungs biologieder Wollhand-krabbe. *Wochenschrift für Aquariemund Terrarienkunde*, 35: 776–780.

Cabral, H.N. & M.J. Costa, 1999. On the Occurrence of the Chinese Mitten Crab, *Eriocheir sinensis*, in Portugal (Decapoda, Brachyura). *Crustaceana*, 72(1): 55-58.

Cai, Y. & P.K.L. Ng, 2001. The freshwater decapod crustaceans of Halmahera, Indonesia. *Journal of Crustacean Biology*, 21: 665–695.

Caine, E.A., 1975. Feeding and masticatory structures of selected Anomura: (Crustacea). *Journal of Experimental Marine Biology and Ecology*, 18: 277-301.

Cameron, J., 1970. Biological aspects of pollution in the Heathcote River, Christchurch, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 4(4): 431-444.

Campbell, B.M. & D.J.G. Griffin, 1966. The Australian Sesarminae (Crustacea: Brachyura): genera *Helice*, *Helograpsus* nov., *Cyclograpsus*, and *Paragrapsus*. *Memoirs of the Queensland Museum*, 14: 127-174, text-figs 1–10,pls. 20-23.

Campbell, J.A., 1967. *Rhythmic spontaneous activity in an intertidal crab, Cyclograpsus lavauxi*. Bachelor of Science (Honours) thesis submitted to Department of Zoology, Univerisity of Canterbury. 28 pp. [Unpublished].

Cano, G., 1889. Crostacei brachiuri ed anomuri raccolti nel viaggo della "Veltor Pisani" intorno al globo. *Bollutin de la Societie National Napoli, Series 1*, 3: 79-105, 169-268, pl. 7.

Carlton, J.T., 1985. Transoceanic and interoceanic dispersal of coastal marine organisms:the biology of ballast water. *Oceanography and Marine Biology: An Annual Review*, 23: 313-371.

Carlton, J.T., 1987. Patterns of transoceanic marine biological invasions in the Pacific Ocean. *Bulletin of Marine Science*, 41: 452-465.

Carlton, J.T., 1992. Blue immigrants: the marine biology of maritime history. The Log. *Mystic Seaport Museum, Mystic, CT*, 44: 31-36.

Carpenter, A., 1976. A guide to the crabs (Crustacea: Decapoda) of the Avon-Heathcote estuary, Canterbury. *Mauri Ora*, 4: 15-18.

Castro, C.B., 1997. *Desenvolimento de um Plano de Ação para Conserção dos Recursos Marinhos do Complexode Abrolhos. Projecto Abrolhos*. 104 pp. Conservation International Brazil & IBAMA, Brazil.

Chace Jr., F.A. & Hobbs Jr., H.H. 1969. The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica. Bredin-Archbold-Smithsonian Biological Survey of Dominica. *Bulletin of the United States National Museum,* 292: 1-258.

Chakraborty, A., S.K. Otta, B. Joseph, S. Kumar, Md. S. Hossain, I. Karunasagar, M.N. Venugopal & I. Karunasagar, 2002. Prevalence of white spot syndrome virus in wild crustaceans along the coast of India. *Current Science,* 82(11): 1392-1397.

Chan, T.Y., D.A. Lee & C.S. Lee, 2000. The first deep-sea hydrothermal animal reported from Taiwan: *Shinkaia crosnieri* Baba and Williams, 1998 (Crustacea: Decapoda: Galatheidae), *Bulletin of Marine Sciences,* 67(2): 799-804.

Chan, T.Y., M.S. Hung & H.P. Yu, 1995. Identity of *Eriocheir recta* (Stimpson, 1858) (Decapoda: Brachyura), with description of a new crab from Taiwan. *Journal of Crustacean Biology*, 15(2): 301-308.

Chan, T.Y., P.K.L. Ng & N.K. Ng, 2005. The nomenclature and taxonomy of *Eriocheir formosa* Chan, Hung and Yu, 1995 (Brachyura, Varunidae) from Taiwan: A rebuttal of Tang *et al*. (2003, 204). *Crustaceanea*, 78(4): 457-464.

Chang, C.M., 1963. A check-list of Taiwan crabs with descriptions of 19 new records. *Biological Bulletin of the Tunghai University*, 14: 1-23.

Chang, C.M., 1965. *Edible Crustacea of Taiwan.* Pp 60. Chinese-America Joint Commission on Rural Reconstruction, Taipei, Taiwan.

Chang, K.H., & Y.S. Chen, 1992. *Seashore life of Northeast Taiwan.* Pp. 240. Northeastern Coast National Scenic Area Adminstration, Taipei.

Chapman, HF, P.E. Dale, B.H. Kay, 1998. A method for assessing the effects of runneling on salt marsh grapsid crab populations. *Journal of American Mosquito Control Association*, 14 (1): 61-68.

Chen, C.H., 1980. *Taiwan's volcanic rocks*. Ministry of Economics Central Geological Survey Special Issue. Ministry of Economics, Taipei, Taiwan, Taiwan. [In Chinese].

Chen, J.F., 1998. Biology of the mitten crab *Eriocheir formosa* (Crustacea: Decapod) in the Shakatang stream of the Taroko National Park. M.Sc. thesis submitted to National. Taiwan Ocean University, Keelung. 55pp. [Unpublished].

Chen, W.J., 1995. Studies on the taxonomy of the crab megalopae collected from Tungkang coast. MS. Thesis submitted to National Sun Yat-Sen University, Kaoshiung, Taiwan. 137pp. [Unpublished].

Chen, W.J., J.H. Cheng, & J.Y. Shy, 2005. On two new species of freshwater crabs (Crustacea: Decapoda: Brachyura: Potamidae) from southern Taiwan. *Raffles Bulletin of Zoology*, 53(1): 103-110.

Chhapgar, B.F., 1957. On the marine crabs (Decapoda: Brachyura) of Bombay State. Part I. *Journal of the Bombay Natural History Society*, 54: 399-439.

Childress, J.J. & C.R. Fisher. 1992. The biology of hydrothermal vent animals: physiology, biochemistry, and autotrophic symbioses. *Oceanography and Marine Biology: Annual Review,* 30: 337-441.

Chilton, C. & E.W. Bennett, 1929. Contributions for a revision of the Crustacea Brachyura of New Zealand. *Transactions of Proceedings of New Zealand Institute*, 59(4): 731-778.

Chiu, J.K., 1964. Prevalence of *Paragonimus* infection in crab hosts in Taiwan. *Bulletin of the Institute of Zoology, Academia Sinica*, 3: 63-73.

Choy, S.C. & W.E. Booth, 1994. Prolonged inundation and ecological changes in an *Avicennia* mangrove: implications for conservation and management. *Hydrobiologia*, 285(1-3): 237-247.

Christiansen, M.E., 1969. Crustacca Decapoda Brachyura. *Marine Invertebrates of Scandinavia, Oslo*, 2:1-143.

Chu, K.H., H.Y. Ho, C.P. Li & T.Y. Chan, 2003. Molecular phylogenetics of the mitten crab species in *Eriocheir*, sensu lato (Brachyura: Grapsidae). *Journal of Crustacean Biology*, 23(3): 738-746.

Chui A., C. Chang & Z. Feng, 2001. Advance in taxonomic researches on *Paragonimus* sp. *Chinese Journal of Parasitology and Parasitic Diseases*, 19(5): 312-315.

Clark, P.F., 1984. Recent records of alien crabs in Britain. *Naturalist*, 109: 111-112.

Clark, P.F., 1987. A new species of *Chasmagnathus* (Crustacea: Brachyura: Grapsidae) from the Bodgaya Island Group (Semporna), Sabah, Borneo. *Malayan Nature Journal*, 41: 45-53.

Clark, P.F., 2006. *Eriocheir sinensis*: H. Milne Edwards 1853 or 1854? *Aquatic Invasions*, 1: 17-27.

Clark, P.F. & B.S. Galil, 1998. Redescription of *Tetralia cavimana* Heller, 1861 and *Trapezia cymodoce* (Herbst, 1799) 1ststage zoeas with implications for classification within the superfamiliy Xanthoidea (Crustacea, Brachyura). *Proceedings of the Biological Society of Washington*, 101: 853-860.

Clark, P.F. & W.R. Webber, 1991. A redescription of *Macrocheira kaempferi* (Temminck, 1836) zoeas witha discussion of the classification of the Majoidea Samouelle, 1819 (Crustacea: Brachyura). *Journal of Natural History*, 25: 1259-1279.

Clark, P.F., D.K. Calazans & G.W. Pohle, 1998 Accuracy and standardisation of brachyuran larval descriptions. *Invertebrate Reproduction and Development*, 33: 127-144.

Coelho, P.A. & M.A. Ramos, 1972. A constituição e a distribuição da fauna de decápodos do litoral leste da América do Sul, entre as latitudes de 5° e 39°. *Trabalhos Oceanográficos da Universidade Federal de Pernambuco, Recife*, 13: 133-236.

Coelho, P.A., M. Ramos-Porto & M.L. Koening, 1979. Crustáceos marinhos do Brasil, do Uruguai e da Argentina (ao norte de Mar del Plata). *Consideraçoes* *biogeográficas*. *Anais da Universidade Federal Rural de Pernambuco, Recife,* 2/3: 227-256.

Cohen, A.N. & J. T. Carlton, 1997. Transoceanic transport mechanisms: the introduction of the Chinese mitten crab *Eriocheir sinensis* to California. *Pacific Science*, 51(1): 1-11.

Cohen, D.M. & R.L. Haedrich, 1983. The fish fauna of the Galapagos thermal vent region. *Deep-Sea Research*, 30: 371-379.

Colbert, E.H., 1974. *Lystrosaurus* from Antarctica. *American Museum Novitates*, No. 2535: 1-44.

Connell, A.D., & W. Robertson, 1986. Recent records of megalopae of the crab *Varuna litterata* (Fabr.) entering Natal estuaries. *South African Journal of Zoology*, 21: 184-185.

Cope, E.D., 1870. The Lystrosaurusfrontosus. *Proceedings of the American Philosophy Society*, 11: 419.

Corliss, J.B., 1990. Hot springs and the origin of life. *Nature,* 347: 624.

Corliss, J.B., J. Daymond, L.I. Gordon, J.M. Edmond, R.P. von Herzen, R.D. Ballard, K. Green, D. Williams, A. Bainbridge, K. Crane & T.H. van Andel, 1979. *Submarine thermal springs on the Galapagos Rift. Science*, 203: 1073-1083.

Corliss, J.B., J.A. Baross, & S.E. Hoffman, 1981. A hypothesis concerning the relationship between submarine hot springs and the origin of life on earth. *Oceanological Acta, supplement*, 4: 59-69.

Cosa, M.A., R.J. Arculus, J. A. Pearce & J.G. Mitchell, 1998. $^{40}$Ar/$^{39}$Arand K-Ar geochronological age constraints for the inception and early evolution of the Izu—Boinin-Mariana arc system. *The Island Arc*, 7: 579-596.

Costlow, J.D., Jr., & E. Fagetti, 1967. The larval development of the crab *Cyclograpsus cinereus* Dana, under laboratory conditions. *Pacific Science,* 21: 166–177.

Cox, G.J., 1976. A note on tree climbing by the crab *Helice crassa* in mangrove swamps. *Tane,* 22: 155-156.

Crane, J., 1975. *Fiddler crabs of the world. Ocypodidae: Genus Uca*. XXIII + 736 p., 101 text-figs., 21 maps, 50 pls., 24 tabs; Princeton University Press, Princeton, New Jersey, United States of America.

Creel, G.C. 1964. *Hemigrapsus estellinensis*: A new grapsooid crab from North Texas. *Southwestern Naturalist*, 8(4): 236-241.

Cronin, T.W. & R.B. Forward, Jr., 1982. Tidally timed behavior: Effects on larval distributions in estuaries. 505-520 pp. In: V.S. Kennedy (ed.). *Estuaries Comparisions*. Academic Press, New York, United States of America.

Cronin, T.W. & R.B. Forward, Jr., 1986. Vertical migration cycles of crab larvae and their role in larval dispersal. *Bulletin of Marine Science*, 39(2): 192-201.

Crosnier, A., 1965. *Crustacés decapodés, Grapsidae et Ocypodidae*. *Faune de Madagascar.* Publiée sous les auspices du Gouvernement de la République Malgache. XVIII. O.R.S.T.O.M.. 143 pp, 11 pls. France.

Crosnier, A., 1975. Sur quelques Portunidae, Grapsidae et Ocypodidae (Crustacea Decapoda Brachyura) de Madagascar ou des Iles avoisinantes, noveuax, rares ou non encore signales. *Bulletin du Muséum National d'Hitoire Naturelle, Paris*, 304: 711-741.

Crosnier, A., 2001. Grapsidae (Crustacea, Decapoda, Brachyura) d'eau profonde du Pacifique sud-ouest. *Zoosystema*, 23(4): 783-796.

Cuesta, J.A., 1999. Morfología larval de la familia Grapsidae (Crustacea, Decapoda, Brachyura). Ph.D. Thesis submitted to Universidad de Sevilla, Spain. Pp. 291. [Unpublished].

Cuesta J.A., R. Diesel, & C.D. Schubart, 2001. Re-examination of the zoeal morphology of *Chasmagnathus granulatus*, *Cyclograpsus lavauxi*, *Hemigrapsus sexdentatus,* and *H. crenulatus* confirmed consistent chaetotaxy in the Varunidae (Decapoda, Brachyura). *Crustaceana*, 74(9): 895-912.

Cuesta, J.A. & C.D. Schubart, 1997. The first zoeal stage of *Glyptograpsus impressus*, with comments on the subfamilial arrangement of Grapsidae (Crustacea: Brachyura). *Cahiers de Biologie Marine*, 38: 291–299.

Cuesta, J.A. & C.D. Schubart, 1999. First zoeal stages of *Geograpsus lividus* and *Goniopsis pulchra* from Panama confirm consistent larval characters for the subfamily Grapsinae (Crustacea: Brachyura: Grapsidae). *Ophelia*, 51: 163-176.

Cuesta, J.A., C.D. Schubart & A. Rodriguez, 2001a. Larval development of *Brachynotus sexdentatus* (Risso, 1827) (Decapoda, Brachyura) reared under laboratory conditions, with notes on the larval characters of the Varunidae. *Invertebrate Reproduction and Development*, 38(3): 207–223, figs 1–12, tabs 1–4.

Cuesta, J.A., J.I. González-Gordillo & A. Rodríguez, 1997. First zoeal stages of *Grapsus adscensionis* (Osbeck) and *Planes minutus* (Linnaeus) (Brachyura: Grapsidae) described from laboratory hatched material, with notes on larval characters of the Grapsinae. *Journal of Natural History*, 31: 887-900.

Cuesta, J.A., M.U. García-Guerrero & M.E. Hendrickx, 2007. The complete larvaal development of *Johngarthia planatus* (Brachyura: Grapsiodea: Gercarcinidae) described from laboratory reared material with notes on the affinity of *Gecarcinus* and *Johngarthia*. *Journal of Crustacean Biology*, 27(2): 263-277.

Cuesta, J.A., R. Diesel & C.D. Schubart, 2001b. Re-examination of the zoeal morphology of *Chasmagnathus granulatus, Cyclograpus lavauxi, Hemigrapsus crenulatus,* and *H. sexdentatus* confirms consistent chaetotaxy in the Varunidae (Decapoda, Brachyura). *Crustaceana*, 74(9): 895-912.

Cuesta, J.A. & A. Rodríguez, 2000. Zoeal stages of the intertidal crab *Pachygrapsus marmoratus* (Fabricius, 1787) (Brachyura, Grapsidae) reared in the laboratory. *Hydrobiologia*, 436: 119-130.

Cuesta, J.A. & C.D. Schubart, 1997. The zoeal stage of *Glyptograpsus impressus*, with comments on the subfamilial arrangement of Grapsidae (Crustacea: Brachyura). *Cahiers de Biologie Marine*, 38: 291-299.

Cuesta, J.A. & C.D. Schubart, 1998. Morphological and molecular differentiation between three allopatric populations of the littoral crab, *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura: Grapsidae). *Journal of Natural History*, 32: 1499-1508.

Cuesta, J.A., C.D. Schubart & A. Rodríguez, 2000. Larval development of *Brachynotus sexdentatus* (Risso, 1827) (Decapoda, Brachyura) reared under laboratory conditions, with notes on larval characters of the Varunidae. *Invertebrate Reproduction and Development*, 38: 207-223.

Cuesta, J.A., H.C. Liu & C.D. Schubart, 2002. First zoeal stages of *Epigrapsus politus* Heller, *E. notatus* Heller, and *Gecarcoidea lalandii* H. Milne Edwards, with remarks on zoeal morpholgy of the Gecarcinidae Macleay (Crustacea: Brachyura). *Journal of Natural History,* 36(14): 1671-1685.

Cuesta, J.A., J.I. González-Gordillo & A. Rodríguez, 1997. First zoeal stages of *Grapsus adscensionis* (Osbeck) and *Planes minutus* (Linnaeus) (Brachyura: Grapsidae) described from laboratory hatched material with notes on larval characters of the Grapsinae. *Journal of Natural History*, 31: 887-900.

Cuesta, J.A., R. Diesel & C.D. Schubart, 2001. Re-examination of zoeal morphology of *Chasmagnathus granulata, Cyclograpus lavauxi, Hemigrapsus crenulatus, a*nd *H. sexdentatus* confirms consistent chaetotaxy in Varunidae (Decapoda: Brachyura). *Crustaceana*, 74(9): 895-912.

Cuesta, J.A., M. Schuh, R. Diesel & C.D. Schubart, 1999. Abbreviated larval development of *Armases miersii* (Grapsidae: Sesarminae), a crab that breeds in supralittoral rock pools. *Journal of Crustacean Biology*, 19: 26-41.

Cui, Z., J. Xiang,  L. Song & L. Zhou, 2000. Genetic differentiation within Eriocheir sinensis (Milne Edwards) revealed by allozyme and RAPD. *Chinese Journal of Oceanology and Limnology*, 18(1): 234-240.

Dahdouh-Guebas, F., 1994. Kenyan Mangrove Crabs: Feeding ecology and behavioural ecology of some selected species. Thesis submitted to the Free University of Brussels, Belgium. 150 pp. [Unpublished].

Dai, A, S.Yang, Y. Song & G. Chen, 1986. *Crabs of the China Seas*.. Pp. 1-642. China Ocean Press, Beijing, People's Republic of China. [In Chinese].

Dai, A. Y. & S.L. Yang, 1991. *Crabs of the China Seas*. 2nd ed. 682 pp., 74 pls. China Ocean Press, Beijing, People's Republic of China.

Dai, A., 1991. Studies on the subspecies differentiation of the genus *Eriocheir* (Decapoda: Brachyura). S*cientific Treatise Systematics, Evolutionary Zoology,* Beijing, 1: 61-71. [In Chinese and with English abstract].

Dai, A., 1993. Systematic and biological studies on *Eriocheir japonica hepuensis* Dai, 1991, International Senckenberg Symposium Crustacea Decapoda.  Frankfurt. 18-22, October, 1993.

Dai, A.Y. & Y.Z. Song, 1977. On Grapsidae (Crustacea: Brachyura) of China. *Acta Zoologica Sinica*, 23(4): 360-376, 1 pl., 8 text-figs.

Dai, A.Y. & Y.Z. Song, 1986. Intertidal crabs from Beibu Gulf of Guangxi. *Transaction of Chinese Crustacean Society*, 1: 54-62, pl. 1.

Dana, J.D. 1851. Conspectus Crustaceorum quæ in Orbis Terrarum circumnavigatione, Carolo Wilkes e Classe Reipublicæ Fæderatæ Duce, Lexit et descripsit J.D. Dana. Pars VIII. Proceedings of the Academy of Natural Sciences of Philadelphia 5(10): 247–254. [Reprint: Conspectus Crustaceorum quæ in Orbis Terrarum circumnavigatione, Carolo Wilkese Classe Reipublicæ Fæderatæ Duce, Lexit et descripsit J.D. Dana. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 5: 1-8 (247–254).]

Dana, J.D., 1851. On the classification of the Crustacea Grapsoidea. *American Journal of Sciences and Arts*, 12: 283-290.

Dana, J.D., 1852. Conspectus Crustaceorum, &c. Conspectus of the Crustacea of the Exploring Expedition under Capt. Wilkes, U.S.N. I. CRUSTACEA CANCROIDEA. Proceedings of the Academy of Natural Sciences of Philadelphia, VI (no. III), 73–86. [meeting of May 1852]. [REPRINT: Crustacea Cancroidea & Corystoidea. Conspectus Crustaceorum, &c. Conspectus of the Crustacea of the Exploring Expedition under Capt. Wilkes, U.S.N. including the Crustacea Cancroidea & Corystoidea. *Proceedings of the Academy of Natural Sciences of Philiadelphia*, VI: 73–86.

Dana, J.D., 1855. Crustacea, part 1. In: United *States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N.*, Altas. 13: 1-27, pls. 1-96. United States of America.

Dando, P.R., J.A. Hughes & F. Thiermann, 1995. Preliminary observations on biological communities at shallow hydrothermal vents in the Aegean Sea. 303–317 pp. In: Parson, L.M., D.R. Walker & C.L. Dixon (eds). *Hydrothermal vents and processes*. Geological Society Special Publication No. 87. United Kingdom.

Davey, K., 1998. *A Photographic Guide to Seashore Life of Australia.* Pp.53, New Holland Press, Sydney. Australia.

Davie, P.J.F., 1992. A new species and new records of intertidal crabs (Crustacea: Brachyura) from Hong Kong. 345-359 pp. In: B. Morton (ed.). *Proceedings of the Fourth International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 11-29 April 1989.Vol*. Hong Kong University Press, Hong Kong.

Davie, P.J.F., 1994. Variations in diversity of mangrove crabs in tropical Australia. *Memoir of Queensland Museum.* 36(1): 55-58.

Davie, P.J.F., 1998. Crustaceans. In: P.J.F. Davie (ed.), *Wild Guide to Moreton Bay*: 18-19, 41-49, 95-101, 144-152, 209-220, 250-253, [whole volume xxiv + 408 pp., many unnumbered colour pictures]. Queensland Museum, Brisbane, Australia.

Davie, P.J.F., 2002. Crustacea: Malacostraca: Eucarida (Part 2): Decapoda - Anomura, Brachyura. In: Wells, A., & W.W.K. Houston (eds.). *Zoological Catalogue of Australia.* Volume 19.3B. xiv, 641pp.CSIRO Publishing, Melbourne, Australia.

Davie, P.J.F. & N.K. Ng, 2001. A review of *Acmaeopleura* Stimpson (Crustacea: Brachyura: Grapsidae) with description of a new species. Fifth International Crustacean Congress, 9-13 July 2001, Melbourne, Australia.

Davie P.J.F. & N.V. Xuan, 2003. A new species of *Metaplax* (Crustacea: Brachyura: Varunidae: Cyclograpsinae) from Vietnam. *The Raffles Bulletin of Zoology*, 51(2): 379-386

Davis, G.M., C.E. Chen, Z.B. Kang, & Y.Y. Liu, 1994. Snail hosts of *Paragonimus* in Asia and the Americas. *Biomedical Environmental Science*, 7: 369-82.

Dawson, E.W., 1987. A key to the world species of *Plagusia* (Crustacea: Brachyura), with a new record of *P. depressa tuberculata* Lamarck from New Zealand. *National Museum of New Zealand Records*, 3(4): 37-45.

Dei-Cas, E., Z. Copes, F. Mañe-Garzón & B. Holcman-Spector, 1975. Estudio sobre la biologia del cangrejo de estuario *Chasmagnathus granulata* Dana, 1851. III. Proteinograma electroforetico de *Chasmagnathus granulata* Dana, 1851. *Revista de Biologia del Uruguay*, 3(1): 43-51.

Deiss, W.A. & R.B. Manning, 1981. The fate of the Invertebrate Collections of the North Pacific Exploring Expedition, 1853-1856. In: (A. Wheeler & J.H. Price (eds.). *History in the Service of Systematics*. Papers from the Conference to

Celebrate the Centenary of the British Museum (Natural History), 13-16 April, 1981. Pp. 79-85. British Museum of Natrual History, London, United Kingdom.

Delesalle, B., 1985. Mativa atoll. Tuamotu archipelago. In: B. Delesalle, R. Galzin & B. Salvat (eds.). *Proceedings of the Fifth International Coral Reef Congress, Tahiti, 27 May - 1 June 1985*, 1: 269-307, figs. 1-44.

Dell, K.R., & B.A. Marshall, 1967. The rediscovery of the crab *Cyclograpsus insularum* Campbell & Griffin in New Zealand. *Records of Dom. Museum*, 6(1): 1-3.

Dell, R.K., 1963. *Nature in New Zealand. Native Crabs*. 64 pp., 43 unnumbered figs. A. H. & A. W. Reed, Wellington and Auckland, New Zealand.

Dell, R.K., 1968. Composition and distribution of the New Zealand brachyuran fauna. *Tranactions of the Royal Society of New Zealand* (Zoology), 10(25): 225-240, 2 figs., table 1.

Dell, R.K., 1968. Notes on New Zealand crabs. *Records of Dominion Museum*, 6(3): 13-28, pls. 1-3.

Denny, C.M. & D.R. Schiel, 2001. Feeding ecology of the banded wrasse *Notolabrus fucicola* (Labridae) in southern New Zealand: prey items, seasonal differences and ontogenetic variation. *New Zealand Journal of Marine and Freshwater Research*, 35: 925–933.

Denti, A., B. Dimant & H. Maldonado, 1988. Passive avoidance learning in the crab *Chasmagnathus granulatus*. *Physiology & Behaviour*, 43: 317-320.

Depledge, M.H., 1989. Observations on the feeding behaviour of *Gaetice depressus* (Grapsidae: Varuninae) with special reference to suspension feeding. *Marine Biology*, 100(2): 253-259.

Desmarest, A.G., 1825. *Considérations générales sur la classe des Crustacés et description des espéces de ces animaux, qui vivent dans la mer, sur les côtes, ou dans les eaux douces de la France.*: p. XIX+446 pp., 56 pls.

Diesel, R. & C.D. Schubart, 2000. Die außergewöhnliche Evolutionsgeschichte jamaikanischer Felsenkrabben. *Biologie in unserer Zeit*, 30(3): 136-147.

Diesel, R., C.D. Schubart & M. Schuh, 2000. A reconstruction of the invasion of land by Jamaican crabs. *Journal of Zoology, London*, 250(2): 141-160.

Diess, W.A. & R.B. Manning, 1981. The fate of the invertebrate collections of the North Pacific Exploring Expedition, 1853-1856. *In*: History in the Service of Systematics. London: Society for the Bibliography of Natural History.

Dineen, J.F., P.F. Clark, A.H. Hines, S.A. Reed & H.P. Walton, 2001. Life history, larval description and natural history of *Charybdis hellerii* (A. Milne Edwards, 1867) (Crustacea, Decapoda, Brachyura, Portunidae), an invasive crab in the western Atlantic. *Journal of Crustacean Biology*, 21: 774-805, figs. 1-24.

Do, V.N., & N.K. Hoang, 2004. Some results of research on Grapsidae in mangrove forest of Giao Thuy District, Nam Dinh Province. *Scientific Journal of Hanoi University of Education*, 4: 106-114.

Doflein, F., 1902. Ostasiatische Dekapoden. *Abhandlungen der. Bayerischen Akademie der Wissenschaften, München*, (2)21(3): 613-670, figs 1-4, pls 1-6.

Dörjes, J., 1978. Sedimentologische und faunistische Untersuchungen an Watten in Taiwan. II. Faunistische und aktuopaläontologische Studien. *Senckenbergiana maritima*, 10: 117-138, pls. 1-3.

Dowse, H.B. & J.D. Palmer, 1992. Comparative studies of tidal rhythms XI. Ultradian and circalunidian rhythmicity in four species of semiterrestrial intertidal crabs. *Marine Behavor and Physiology*, 21: 105-119.

d'Udekem d'Acoz, C. & M. Faasse, 2002. De huidige status van *Hemigrapsus sanguineus* (de Haan, 1835) en *H. penicillatus* (de Haan, 1835) in de noordelijke Atlantische Oceaan, in het bijzonder in Nederland, met opmerkingen over hun biologie (Crustacea, Decapoda, Brachyura). *Het Zeepaard*, 62(4): 101-115.

Dumoulin, E., 2004. Snelle areaaluitbreiding van het peneelkrabbetje *Hemigrapsus penicillatus* (de Haan, 1835) langs de kusten van de Zuidelijke Bocht van de Noordzee, status van haar opmars in de Westerschelde en beschouwingen over de ecologie en het gedrag van de sort. *De Strandvlo*, 24: 5-35.

Edgar, G. J., 1989. *Australian Marine Life: the plants and animals of temperate waters*, pp. 213, Reed, Australia.

Edgecombe, G.D. (editor), 1998. Arthropod fossils and phylogeny. Columbia University Press. New York, United States of America.

Edmond, J.M., K.L. von Damm, R.E. McDuff, & C.I. Measures, 1982. Chemistry of hot springs on the East Pacific Rise and their effluent dispersal. *Nature*, 297: 187-191.

Edmondson, C.H., 1959. Hawaiian Grapsidae. *Occassional Papers of Bernice P. Bishop Museum*, 22(10): 153-202.

Edmondson, C.H., 1962. Xanthidae of Hawaii. *Occassional Papers of Bernice P. Bishop Museum*, 22(13): 215-309 figs 1-34

Ellison, A.M., E.J. Farnsworth & R.E. Merkt, 1999. Origins of mangrove ecosystems and the mangrove biodiversity anomaly. *Global Ecology and Biogeography*, 8: 95-115.

Elton, C.S., 2000. *The Ecology of Invasions by Animals and Plants*. Pp 27-28. University of Chicago Press. Chicago, Illinois, United States of America.

Emmerson, W.D., 1994. A note on three uncommon African grapsids, *Helice leachii* Hess, 1865, *Sesarma* (*Sesarma*) *longipes* Krauss, 1843 and *Sesarma* (*Sesarma*) *smithi* H. Milne Edwards, 1853. *Crustaceana*, 67(3): 316-323.

Emparanza, E.J.M., G.L. Guzmán & P.K.L. Ng, 2007. A redescription of *Acanthonyx petiverii* H. Milne Edwards, 1834, and designation of a neotype for *Acanthonyx simplex* Dana, 1852 (Brachyura, Majidae). Crustaceana: In press.

Enríquez, R.E., E. y G.D Velard, G. de la Selva, & S.A. Lorax Consultores, 2001. *Estudio Justificativo Para El Decreto Del Parque Nacional "Archipélago De San Lorenzo, B.C." Presentado al Fondo Mundial para la Naturaleza*. World Wildlife Fund, Switzerland.

Estampador, E.P. 1937. A checklist of Philippine crustacean decapods. *Philippines Journal of Zoology*, 62(4): 465-560.

Estampador, E.P., 1959. Revised checklist of Philippine crustacean decapods. *National Applied Science Bulletin*, 17(1): 1-127.

Evans, A.C., 1967. Syntypes of Decapoda described by William Stimpson and James Dana in the collections of the British Museum (Natural History). *Journal of Natural History*, 1: 399-411.

Faasse, M.A., R. Nijland, C. d'Udekem d'Acoz, & J.M. Duivenvoorde, 2002. Opmars van de penseelkrab *Hemigrapsis penicillatus* De Haan, 1935 in Nederland. *Het Zeepaard*, 62(2): 41-44.

Fabricius, J.C., 1798. *Supplementum Entomologiae systematicae*. 573 pps. Proft et Storch, Hafniae, Copenhagen, Denmark.

Fagetti, E. & I. Campodonico, 1971. The larval development of the crab *Cyclograpsus punctatus* H. Milne Edwards, under laboratory conditions (Decapoda, Brachyura, Grapsidae, Sesarminae). *Crustaceana*, 21: 183-195.

Fan, Z.G., 1976. Ecology and burrow observations on crabs of the infauna of the intertidal zone, Qingdao. *Studies in Marine Sciences*, 11: 397-403, pls. 1-2 [In Chinese].

Farris, J.S., V.A. Albert, M. Källersjö, D. Lipscomb & A.G. Kluge, 1996. Parsimony jackknifing outperforms neighbour-joining. *Cladistics*, 12: 99-124.

Fausto-Filho, J., 1967. Segunda contribuição ao inventário dos crustáceos decápodos marinhos do Nordeste brasileiro. *Arquivos da Estação de Biologia Marinha da Universidade Federal do Ceará 7*(1): 11-14.

Fausto-Filho, J., 1974. Stomatopod and decapod crustaceans of the Archipelago of Fernando de Noronha, Northeast Brazil. *Arquivos de Ciências do Mar*, 14(1): 1-35.

Felderman, R.M. & C.L. McLay, 1993. Geological history of brachyuran decapods from New Zealand. *Journal of Crustacean Biology*, 13: 443–455.

Felgenhauer, B.E. & L.G. Abele, 1983. Branchial water movement in the grapsid crab *Sesarma reticulatum* Say. *Journal of Crustacean Biology*, 3(2): 187-195.

Felgenhauer, B.E. & L.G. Abele, 1989. Evolution of the foregut in the lower Decapoda. In: B.E. Felgenhauer, L. Watling & A.B. Thistle (eds.). Functional Morphology of Feeding and Grooming in Crustacea. In: F.R. Schram (general ed.). *Crustacean Issues*, 6: 205-219.

Felsenstein, J., 1985a. Phylogenies and the comparative method. *The American Naturalist*, 125(1): 1-15.

Felsenstein, J., 1985b. Confidence limits on Phylogenies: an approach using the bootstrap. *Evolution*, 39(4): 783-791.

Fenwick, G.D., 1978. Decapoda of the Snares Islands, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 12(2): 205-209.

Ferraris, J.D. & S.R. Palumbi (eds.), 1996. *Molecular Zoology*. Wiley-Liss, New York, New York.

Fielder, D.R. & J.G. Greenwood, 1983. The zoeal stages and megalopa of *Bresedium brevipes* (De Man, 1899) (Crustacea: Decapoda: Grapsidae), reared in the laboratory. *Journal of Plankton Research*, 5: 585-598.

Fielder, D.R. & J.G. Greenwood, 1984. The complete larval development of *Helograpsus haswellianus* (Whitelegge) (Decapoda, Grapsidae), reared in the laboratory. *Proceedings of the Royal Society of Queensland*, 95: 11-22.

Fielder, D.R. & J.G. Greenwood, 1985. The complete larval development of the sand bubbler crab, *Scopimera inflata* H. Milne Edwards, 1837 (Decapoda, Ocypodidae), reared in the laboratory. *Crustaceana*, 48: 133-146.

Fielder, D.R. & M.B. Jones, 1978. Observations on the feeding behaviour in two New Zealand mud crabs. *Mauri Ora*, 6: 41-46.

Fihol, H., 1885. 1. Zoologie. 3. *Crustace´s, in Recherches zoologiques, botaniques et ge´ologiques faites a` l'ile Campbell et en Nouvelle-Ze´lande*. Recueil de Me´moires, Rapports et Documents relatifs a` l'Observation du Passage de Ve´nus sur le Soleil du 9 De´cembre 1874, Mission de Ile Campbell, Institut de France, Acade´mie des Sciences, Paris, Zoologie, 3 (2) 1 (text): 349–510.

Filhol, H., 1886. Catalogue des Crustacés de la Nouvelle-Zélande, des îles Auckland et Campbell. In: *Recueil de Mémoires, Rapports et Documents relatifs à l'observation du passage de Venus sur le Soleil*. Mission de l'Ile Campbell. *Records Vénus Zoology*, 3(2): 349-510; 3(4), Atlas, pls 38-55.

Finnegan, S., 1931. Report on the brachyura collected in Central America, the Gorgona and Galapagos islands, by Dr. Crossland on the St George Expedition to the Pacific, 1924-25. *Linnean Society Journal, Zoology*, 37(255): 607-673, fig. 1-6.

Fishelson, L., 1971. Ecology and distribution of the benthic fauna in the shallow waters of the Red Sea, *Marine Biology*, 10(2): 113-133.

Flores, A.A.V., J. Paula & T. Dray, 2003. First zoeal stages of grapsoid crabs (Crustacea: Brachyura) from the East African coast. *Zoological Journal of the Linnean Society*, 137 (3): 355-383.

Fontoura, N.F., G. Bond & M. Achaval, 1987. Sistema arterial e veias branquicardíacas de *Chasmagnathus granulata* Dana, 1851 (Crustacea, Decapoda, Grapsidae). *Review of Brasilian Biology*, 47(3): 283-288.

Forest, J., 1957. Mise au point sur les *Brachynotus* de Me´diterrane´e et d'Afrique occidentale: *Brachynotus sexdentatus* Risso et *Brachynotus atlanticus* nov. sp., *Bulletin de l'Institut Franc¸ais d'Afrique Noire, ser. A*, 19, 501–510, figures 1–14.

Forest, J. & H. Gantés, 1960. *Sur une collection de Crustacés Décapodes Marcheurs du Maroco. Bulletin of Museum nationale Histoire naturelle*, Paris, 32(2): 346-358, 3 figs.

Forest, J. & D. Guinot, 1961. Crustacés Décapodes Brachyoures de Tahiti et des Tuamotu. *Expedition française sur les recifs coralliens de la Nouvelle-Calédonie*. Volume préliminaire. Pp. ix-xi, 1-195, 178 text-figs, 18 pls., Paris, Frnace.

Forest, J. & D. Guinot, 1962. Remark biogeographiques sur las crabes des archipels de la Society et des Tuamontu. *Cahiers du Pacifique*, 4: 41-75, fig. 1, tabs. 1-2.

Forskål, P., 1775. Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quæ in itinere orientali observavit Petrus Forskål. Post mortem auctoris edidit Carsten Niebuhr. Adjuncta est materia medica Kahirina atque tabula maris rubri geographica. 20, XXXIV, 164 p., 1 map. Hauniæ. (Möller).

Forward, R.B., Jr., 1987. Larval release rhythms of decapod crustaceans: An overview. *Bulletin of Marine Science*, 41(2): 165-176.

Forward, R.B., Jr., 1989. Depth regulation of larval marine decapod crustaceans: test of an hypothesis. *Marine Biology*, 102: 195-201.

Foskett, J.K., 1977. Osmoregulation in the larvae and adults of the grapsid crab *Sesarma reticulatum* Say. *Biological Bulletin*, 153: 505-526.

Fraaije, R.H.B., 2003. Evolution of reef-associated decapod crustaceans through time, with particular reference to the Maastrichtian type area. *Contribution to Zoology*, 72 (2/3). Article 10.

Fraaye, R.H.B., 1996. *Graptocarcinus maastrichtensis* and *Caloxanthus kuypersi* from the type Maastrichtian. *Journal of Paleontology,* 70: 463-465.

Fransen, C.H.J.M., L.B. Holthuis & J.P.H.M. Adema, 1997. Type-catalogue of the Decapod Crustacea in the collections of the Nationaal Natuurhistorisch Museum, with appendices of pre-1900 collectors and material. *Zoologische Verhandelingen*, 311: 1-344.

Fransozo, A., J.A. Cuesta & M.L. Negeiros-Fransozo, 1998. The first zoeal stage of two species of Grapsidae (Decapoda, Brachyura) anda key to such larvae from the Brazilian coast. *Crustaceana*, 71: 331-343.

Fricke, H., O. Giere, K. Stetter, G. Alfredsson, J. Kristjansson, P. Stoffers, J. Svavarsson, 1989. Hydrothermal vent communities at the shallow subpolar Mid-Atlantic Ridge. *Marine Biology*, 102: 125-129.

Frith, D.W., 1977. A preliminary list of Macrofauna from a mangrove forest and adjacent biotopes at Surin Island, western peninsular Thailand. *Research Bulletin of the Phuket Marine Biological Center*, 17: 1-14

Froglia C., & R.B. Manning, 1978. *Brachynotus gemmellari* (Rizza, 1839), the third Mediterranean species of the genus (Crustacea, Decapoda, Brachyura). *Proceedings of the Biological Society of Washington*, 91(3): 691-705.

Fukui, Y., 1993. Timing of copulation in the molting and reproductive cycles in a grapsid crab, *Gaetice depressus* (Crustacea: Brachyura). *Marine Biology*, 117(2): 221-226.

Fukui, Y., K. Wada & C.H. Wang, 1989. Ocypodidae, Mictyridae and Grapsidae (Crustacea: Brachyura) from some coasts of Taiwan. *Journal of Taiwan Museum*, 42(1): 225-23.

Fulton, S.W. & F.E. Grant, 1906. Some little known Victorian decapod Crustacea, with descriptions of new species. No. III. *Proceedings of the Royal Society of Victoria,* 19(1): 5-15, pls. 3-5.

Galil, B., C. Froglia & P. Noël, 2002. Crustaceans: decapods and stomatopods. In: F. Briand (ed.), *CIESM Atlas of Exotic Species in the Mediterranean*. Vol. 2. Pp. 192. CIESM Publishers, Monaco.

Gamô, S. 1958. On the post-larval stage of two species of crabs of the subfamily

Varuninae, Grapsidae, brachyuran Crustacea. *Zoological Magazine*, 67: 373–379, figs.1–4, tab.1.

Gamô, S., 1960. On the post-larval stage of the shore crab, *Acmaeopleura parvula* Stimpson, of the sub-family Varuninae, Grapsidae, Brachyura Crustacea. *Zoological Magazine*, 67: 373-379.

Gamô, T., K. Okamura, J.L. Charlou, T. Urabe, J.M. Auzende, J. Ishibashi, K. Shitashima & H. Chiba, 1997. Acidic and sulfate-rich hydrothermal fluids from the Manus back-arc basin, Papua New Guinea. *Geology*, 25: 139-142.

Gao, T., 2000. Study on mitochondrial DNA sequences of Japanese mitten crab, *Eriocheir japonica*: 1. 12S rRNA. *Journal of Ocean University, Qingdao*, 30(1): 106, 43-47.

Garrill, A. & P. Kirk, 2000. Mycoloical Research News. *Mycological Research*, 104: 516-517.

Garth, J.S., 1957a. Reports of the Lund University Chile Expedition 1948-49. 29. The Crustacea Decapoda Brachyura of Chile. *Acta Universitatis Lundensis, Series 2*, 53(7): 1-127, pls. I-IV.

Garth, J.S., 1957b. The Crustacea Decapoda Brachyura of Chile. *Lunds Universitets Arsskrift, N.F.* (2), 53(7): 1-130, 11 figs., 4 pls.

Garth, J.S., J. Haig, & J.C. Yaldwyn, 1967. The decapod Crustacea of the Royal Society Expedition to southern Chile, 1958-59. *Transactions of the Royal Society of New Zealand*, 8(16): 169-186.

Geldiay, R. & A. Kocatas, 1968b. Two species of crabs new for Turkey: *Brachynotus sexdentatus* Risso vs *Brachynotus* sp. *Scientific Report of Faculty of Science, Ege University*, 51: 1-13.

Geldiay, R. & A. Kocatas, 1972. A preliminary study on the benthos in Zmir Bay. *Scientific Report of Faculty of Science, Ege University*, 12: 1-34.

Genovese, G., C.G. Luchetti, & C.M. Luquet, 2004. Na+/K+, ATPase activity and gill ultrastructure in the hyper-hypo-regulating crab *Chasmagnathus granulatus* acclimated to dilute, normal, and concentrated seawater. *Marine Biology*, 144(1): 111-118.

Georgiadis, C. & G. Georgiadis, 1974. Zur Kenntnis des Crustacea Decapoda des Golfes von thessaloniki. *Crustaceana*, 26(3): 239-248.

Gerstaecker, A., 1856. Carcinologishes Beitrage. *Archiv für Naturgeschichte, Berlin,* 22(1): 101-162, pls. 4–6.

Ghani, N. & N.M. Tirmizi, 1991. *Acmaeopleura balssi* Shen, 1932: a grapsid genus and species hitherto unknown from the northern Arabian Sea (Decapoda, Brachyura). *Crustaceana*, 61, 93-95.

Gill B.J., 1998. *Powell's Native Animals of New Zealand*. 94 pp. David Bateman, Auckland, New Zealand.

Gilles, B.R., 1996. Toxicity and Accumulation of Mercury in Three Species of Crabs with Different Osmoregulatory Capacities, *Bulletin of Environmental Contamination and Toxicology*, 57(1): 91-98.

Gimenez, L. & K. Anger, 2001. Relationships among salinity, egg-size, embryonic development and larval biomass in esturine crab, *Chasmagnathus granulata* Dana, 1851. *Journal of Experimental Marine Biology and Ecology*, 260(2): 241-257.

Giribet, G. & C. Ribera, 2000. A review of arthropod phylogeny: new data based on ribosomal DNA sequences and direct character optimization. *Cladistics*, 16: 204-231.

Giribet, G., G.D. Edgecombe, & W.C. Wheeler, 2001. Arthropod phylogeny based on eight molecular loci and morphology. *Nature*, 413: 157-161.

Giribet, G., G.D. Edgecombe, W.C. Wheeler, & C. Babbitt, 2002. Phylogeny and systematic position of Opiliones: a combined analysis of chelicerate relationships using morphological and molecular data. *Cladistics*, 18: 5-70.

Giribet, G., S. Richter, G.G. Edecombe & W.C. Wheeler, 2005. The position of crustaceans within Arthopoda – Evidence from nine molecular loci and morphology. *Crustacean Issues*, 16: 307-352.

Gistel, J.N.F.X., 1848. *Naturgeschichtedes Tierreichsfu ¨rho¨ here Schulen*. i–xvi. 216 pp., Pls. 1–32. Stuttgart, Germany.

Glaessner, M.F., 1933. New Tertiary crabs in the collection of the British Museum.

*Annuals Magazine in Natural History*, 10/12: 1–28.

Glaessner, M.F., 1957. Evolutionary trends in Crustacea (Malacostraca). *Evolution*, 11: 178-184.

Glassell, S.A., 1933. Descriptions of five new species of Brachyura collected on the west coast of Mexico. *Transactions of the San Diego Society of Natural History*, 7(28): 331-343.

Gnazzo, G., F. Mañe-Garzon & J. Leymonié, 1978. Estudios sobre la biologia del cangrejo de estuarion *Chasmagnathus granulata* Dana, 1851, IV. *Ionograma normal en poblaciones de diferente salinidad. Revista de Biología del Uruguay*, 6(1): 5-17.

Gollasch, S., 1999. The Asian decapod *Hemigrapsus penicillatus* (de Haan, 1835) (Grapsidae, Decapoda) introduced in European waters: status quo and future perspective. *Helgolander Meersuntersuhungen,* 52: 359-366.

Goloboff, P.A., 1993-97. PEE-WEE. Parsimony and Implied Weights, Version 2.8. Program and documentation, distributed by the author, New York, United States of America.

Goloboff, P.A., 1993a. NONA, Version 1.8. Program and documentation. New York, United States of America.

Goloboff, P.A., 1993b. Estimating character weights during tree search. *Cladistics*, 9, 83-91.

Goloboff, P.A., 1999. Analyzing large data sets in reasonable times: solutions for composite optima. *Cladistics*, 15: 415-428.

González-Gordillo, J.I., S. Tsuchida & C.D. Schubart, 2000. Redescription of the megalopa of *Plagusia dentipes* (Brachyura: Plagusiidae) from Japan. *Crustacean Research*, 29: 143-151.

Gordon, I., 1930. Seven new species of Brachyura from the coasts of China. *Annals and Magazine of Natural History Series*, 10, 6: 519-525.

Gordon, I., 1931. Brachyura from the Coasts of China. *Journal of the Linnean Society of London*, 37: 525-558, figs 1-36.

Gordon, I., 1947. The mitten crab - a Chinese immigrant to Europe. In: *Illustrated London News*, 1947, 4 October: 384.

Gore, R.H. & L. Scotto, 1982. *Cyclograpsus integer* H. Milne Edwards, 1837 (Brachyura, Grapsidae): the complete larval development in the laboratory, with notes on larvae of the genus *Cyclograpsus*. *Fisheries Bulletin, United States*, 80: 501–521.

Gorny, M., 1999. On the biogeography and ecology of the southern ocean decapod fauna. *Scientia Marina*, 63(1): 367-382.

Graham, D.H., 1939, Food of the fishes of Otago Harbour and adjacent sea. *Transactions and Proceedings of the Royal Society of New Zealand*, 68, 421–436.

Grassle, J.F., 1986. The ecology of deep-sea hydrothermal vent communities. *Advances in Marine Biology*, 23, 301-362.

Grecoa, L.S.L. & E.M. Rodríguez. 2003. Reproductive Performance in *Cyrtograpsus angulatus* and *Cyrtograpsus altimanus* (Brachyura, Varunidae) from Jabalí Island, Argentina. *Journal of Crustacean Biology*, 24(1): 213–216.

Green, J., 1961. A Biology of Crustacea. Quadrangle Books, Inc. Chicago, Illinois, United States of America.

Green, P.A. & D.T. Anderson, 1973. The first zoea larvae of the estuarine crabs *Sesarma erythrodactyla* Hess, *Helograpsus haswellianus* (Whitelegge) and *Chasmagnathus laevis* Dana (Brachyura, Grapsidae, Sesarminae). *Proceedings of the Linnaean Society of New South Wales*, 98: 13-28.

Griffin, G.J.G., 1968. A new species of *Cyclograpsus* (Decapoda, Grapsidae) and notes on five others from the Pacific Ocean. *Crustaceana*, 15: 235-248.

Griffin, D.J.G., 1969a. Breeding and moulting cycles of two Tasmanian Grapsid crabs (Decapoda, Brachyura). *Crustaceana*, 16(2): 88-94.

Griffin, D.J.G., 1969b. Notes on the taxonomy and zoogeography of the Tasmanian Grapsid and Ocypodid crabs (Crustacea, Brachyura). *Records of Australian Museum*, 27: 323-347.

Griffin, D.J.G., 1971. The ecological distribution of grapsid and ocypodid shore crabs (Crustacea, Brachyura) in Tasmania. *Journal of Animal Ecololgy*, 40: 597-621, 5 figs.

Griffin, D.J.G., 1972. Brachyura colleted by Danish expeditions in southeastern Australia (Crustacea, Decapoda). *Steenstrupia, Copenhagen,* 2: 49-90, 3 figs.

Griffin, D.J.G., 1973. A revision of the southern temperate shore crabs *Leptograpsus variegatus* (Fabricius) and *Plagusia chabrus* (Linnaeus) (Crustacea, Decapoda, Grapsidae). *Journal of the Royal Society of New Zealand*, 3: 415-440, 15 figs.

Griffin, D.J.G. & J.C. Yaldwyn, 1971. Port Phillip Survey 1957-1963, 2. Brachyura (Crustacea, Decapoda). *Memoir of National Museum, Victoria*, 32: 43-64, 4 figs.

Gu, J., 1986. An ecological survey of *Eriocheir sinensis*. *Transactions of the Chinese Crustacean Society,* 1: 268-269.

Guerao, G., C.D. Schubart & J.A. Cuesta, 2001. The first zoeal stage of *Grapsus grapsus* Linnaeus and *Geograpsus lividus* (H. Milne Edwards) (Decapoda, Brachyura, Grapsidae) from the western Atlantic. *Nauplius,* 9(2): 111-121. (Published in 2003)

Guerao, G., J.A. Cuesta, P.A Belló & J.I. González-Gordillo, 1995. Larval development of *Brachynotus gemmellari* (Rizza, 1839) (Brachyura, Grapsidae) reared under laboratory conditions. *Journal of Plankton Research*, 17: 1143–1161, figs.1–11, tabs.1–3.

Guiler, E.R., 1952. A list of the Crustacea of Tasmania. *Records of Queen Victoria Museum,* 3: 15-44.

Guinot, D., 1966. *Les crabes comestibles de l'Indo-Pacifique*. Deuxieme volume preliminaire: 1-145, pls. 1-10. Editions de la Foundation Singer-Polingnac, Paris, France.

Guinot, D., 1967. La faune carcinologique (Crustacea, Brachyura) de l'Océan Indien occidental et de la Mer Rouge. Catalogue, remarques biogeographiques et bibliographie. *Mémoir du L'Institut Français [now Fondamentale] d'Afrique Noire*, 77: 235-352.

Guinot, D., 1977. Données nouvelles sur la morphologie, la phylogene` se et la taxonomiedes Crustacés Décapodes Brachyoures, a `l' Université Pierre-et-Marie-Curie: 2 vols., infolio, pp. I–XV, 1–486, XVI–XXIV; feuilles n. n. 56, fig.78, pls. 31, figs. n. n. 2, tabs.14 (Ronéotypé).

Guinot, D., 1978. Principes d'une classification évolutive des Crustacé Décapodes Bracyuoures. *Bulletin Biologique de la France et de la Belique n.s.*, 112(3): 211-292, fig. 1-3, Tab. 1.

Guinot, D., 1979. Données nouvelles sur la morphologie, la phylogenese et la taxonomie des Crustacés Décapodes Brachyoures. *Mémoires du Museum National d'histoire Naturelle (A),* 112: 1-354, pls. 1-27.

Guinot, D., 1985. Crustacea. In: G. Richard (ed.). *French Polynesia coral reefs, fauna and flora. A first compendium of French Polynesian sea-dwellers.* Proceedings of the Fifth International Coral Reef Congress, Tahiti 27 May - 1 June 1985, 1: 446-455.

Guinot, D. & J.M. Bouchard, 1998. Evolution of the abdominal holding systems of brachyuran crabs (Crustacea, Decapoda, Brachyura). *Zoosystema*, 20(4): 613-694.

Guinot, D., & M. Segonzac, 1997. Description dun crabe hydrothermal nouveau du genre *Bythograea* (Crustacea Decapoda Brachyura) et remarques sur les Bythograeidae de la dorsale du Pacifique oriental. *Zoosystema,* 19(1): 121-149.

Guinot-Dumortier, D., 1961. Crabes, crevettes et langoustes ne sont pas toujours silencieux. *La Nature*, 89: 82-89.

Guinot-Dumortier, D. & B. Dumortier, 1960. La stridulation chez les crabes. *Crustaceana*, 1(2): 117-155.

Guo, J.Y., N.K. Ng, A.Y. Dai & P.K.L. Ng, 1997. The taxonomy of three commercially important species of mitten crabs of the genus *Eriocheir* de Haan, 1835 (Crustacea: Decapoda: Braehyura: Grapsidae). *The Raffles Bulletin of Zoology,* 45 (2): 445-476.

Gurney, R., 1924. Report on the British Antarctic "Terra Nova" Expedition, 1910. *Zoology*, 8 (2): 37-202.

Gurney, R., 1942. *Larvae of Decapod Crustacea.* Royal Society of London. 306 pp. London, United Kingdom.

Guzmán, G., 2003. *Crustáceos Chilenos: Orden Decapoda*. Guías de Identificación y Biodiversidad Fauna Chilena. Apuntes de Zoología, Universidad Arturo Prat, Iquique, Chile. 28 pp.

Haahtela, I., 1963. Pohjois-selkämeri ja perämeri littyneet kiinan villasaksiravun (*Eriocheir sinensis*) löytöalueeseen. *Eripainos (Suomen Kalastuslehti)*, 6: 1-3, 4 figs.

Haahtela, I., 1963. Some new observations and remarks on the occurrence of the mitten crab, *Eriocheir sinensis* Milne-Edwards (Crustacea, Decapoda), in Finland. *Aquilo, Zoology*, 1: 9-16, 4 figs.

Haan, W. d. 1833. Crustacea.In: Siebold, P.F.De. *Fauna Japonica, sive Descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batava imperium tenent, suscepto, annis* 1823-1830 *collegit, notis, observationibus et adumbrationibus illustravit* P.F. de Siebold. *Conjunctis studiis* C.J. Temminck *et* H. Schlegel *pro Vertebratis atque* W. de *Haan pro Invertebratis elaborata Regis aupicus edita*. in P. F. von Siebold. Leiden, Lugduni-Batavorum. Decas I: pp. ix-xvi, 1–24, pls 1–8, A, B, circ. 2. (For dates see Sherborn & Jentink, 1895; Holthuis, 1953 and Holthuis & T. Sakai, 1970).

Hale, H.M., 1876. T*he Crustaceans of South Australia*. Pts. I & II. 177pp. South Australia Government Press, Australia.

Hale, H.M., 1924. Notes on Australian Crustacea. No. III. *Transactions and Proceedings of the Royal Society of South Australia*, 48: 209-225.

Hale, H.M., 1927a. The crustaceans of south Australia, part 1. In: *Handbook of the Flora and Fauna of South Australia*. 201pp. 202 text-figs. Government Printer. Adelaide.

Hale, H.M., 1927b. The fauna of Kangaroo Island, south Australia, No. 1. The Crustaces. *Transactions of the Royal Society of South Australia*, 51: 307-325.

Hale, H.M., 1927-29. *The Crustaceans of South Australia. Part I and II.*: 380 pp, 364 figs. Government Printer, Adelaide, South Australia.

Haq, B.U., J. Hardenbol, & P.R. Vail, 1987. Chonology of fluctuating sea-levels since the Triassic. *Science*, 235: 1156-1167.

Harminto, S. & P.K.L. Ng, 1991. A revision of the camptandriine genus *Baruna* Stebbing, 1904 (Crustacea: Brachyura: Decapoda: Ocypodidae), with descriptions of two new species from the Indo-West Pacific. *The Raffles Bulletin of Zoology*, 39(1): 187-20.

Hart, J.F.L., 1935. The larval development of British Columbia Brachyura. Xanthidae, Pinnotheridae (inpart) and Grapsidea. *Canadian Journal of Research*, 12: 411-432, figs. 1-7.

Hartnoll, R., 1965. Notes on the marine grapsid crabs of Jamaica. *Proceedings of the Linnean Society of London,* 176 (2): 113-147.

Hartnoll, R., 1968. Morphology of the genital ducts in female crabs. *Journal of the Linnean Society, London*, 176: 113-147.

Hartnoll, R.G., 1975. The Grapsidae and Ocypodidae (Decapoda: Brachyura) of Tanzania. *Journal of Zoology, London*, 177: 305-328.

Hashiguchi, Y., 1975. *Biotope of Decapod Crustacea in Urado Bay, Kochi-city, Japan*. Report on an Environmental Assessment for the construction of Tanezaki Habour in relation of Decapod Crustacea, Kochi Prefectural Goverment: 82-100. [In Japanese].

Hashmi, S.S., 1964. Some addition to the checklist of crabs of Karachi and notes on habit and habitat of *Psedophthalmus vigil* (Fabricius) and *Macrophthalmus* species. *Agriculture, Pakistan,* 15: 451-454.

Hassain, S.M., 2006. *Brief report on the Biodiveristy in the coastal areas of Pakistan*. Prepared for Regional Technical Assistance (RETA) of ADB in collaboration with IUCN. Pakistan.

Hassler R.R. & P.F. Lonsdale, 1991. Biogrography of of Mariana Trough hydrothermal vent communities. *Deep Sea Research*, 38: 185-199.

Haswell, W.A., 1881. On some new Australian Brachyura. *Proceedings of the Linnean Society of New South Wales,* 6(3): 540-551 [549].

Haswell, W.A., 1882. *Catalogue of the Australian Stalk- and Sessile-eyed Crustacea*. 326 pps., 4 pls. Australian Museum, Sydney, Austalia.

Hawkins, A.J.S. & M.B. Jones, 1982. Gill area and ventilation in two mud crabs, *Helice crassa* Dana (Grapsidae) and *Macrophthalmus hirtipes* (Jacquinot) (Ocypodidae), in relation to habitat. *Journal of Experimental Marine Biology and Ecology*, 60: 103-118.

Hawkins, A.J.S., M.B. Jones & I.D. Marsden, 1982. Aerial and aquatic respiration in two mud crabs, *Helice crassa* Dana (Grapsidae) amd *Macrophthalmus hirtipes* (Jacquinot) (Ocypodidae), in relation to habitat. *Comparative Biochemistry and Physiology*, 73A(3): 341-347.

Hayasaka, S., 1988. Geology of Tane-ga-shima. *Modern Geology*, 12: 169–183.

Hayward, B.W., 1974. Kewerau crabs. *Tane*, 20: 159-161.

Heller, C., 1862. Nenue Crustaceen, gesammelt während der Weltumseglung der k. k. Fregatte Novara. Zweiter vorläufiger Bericht. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, 12: 519–528.

Heller, C., 1865. *Crustaceen*. In: Reise der österreichischen Fregatte *NOVARA* um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorf-Urbair. *Zoologischer Theil*, 2(3): 1-280, pls. 1-25; Wien (Kaiserliche-Königliche Hof- und Staatsdruckerei). Vienna.

Henderson, J.R., 1893. A contribution to Indian Carcinology. *Transanction of the Linnean Society of London*, 5(2): 325-458, pls. 36-40.

Herborg L.M., S.P Rushton, A.S. Clare, & M.G. Bentley, 2005. The invasion of the Chinese mitten crab (*Eriocheir sinensis*) in the United Kingdom and its comparison to continental Europe. *Biological Invasions*, 7(6): 959-968.

Herbst, J.F.W., 1782-1804. *Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten.* 1-3. Pp. 62. Germany.

Herklots, J.A., 1861. *Symbolae Carcinologicae.* Etudes sur la classe des Crustacés. 43 pp. E.J. Brill, Leiden, The Netherlands.

Hess, W., 1865. Beiträge zur Kenntniss der Decapoden-Krebse Ost-Australiens. *Archiv für Naturgeschichte,* 31: 127-173, pls., 6-7.

Hessler, R.R. & P.F. Lonsdale, 1991. Biogeography of Mariana Trough hydrothermal vent communities. *Deep-Sea Research,* 38: 185-199.

Hicks, G.R.F., 1973, Combined effects of temperature and salinity on *Hemigrapsus edwardsi* (Hilgendorf) and *H. crenulatus* (Milne Edwards) from Wellington

Harbour, New Zealand. *Journal of Experimental Marine Biology and Ecology*, 13, 1–14.

Hieb, K.M. & T. Veldhuizen, 1998. “Mitten crabs on the move.” IEP Newsletter. Vol. 11 (2) Spring 1997.

Hilgendorf, F., 1882. *Identität der Crustaceen-Gattungen Brachynotus und Heterograpsus. Berlin Sitzungsberichte de Gesellschaft Naturforschender Freunde zu Berlin*, 1882: 68-70.

Hilgendorf, F., 1892. Eine neue *Brachynotus* Art aus Aden. *Berlin Sitzungsberichte de Gesellschaft Naturforschender Freunde zu Berlin*, 4: 37-40.

Hills, D. M. & C. Moritz, 1990. Molecular systematics. In: D.M. Hills, C. Moritz & B.K. Mable (eds). *Molecular Systematics*. Pp. 45-126. Sinauer Associates Inc., Sunderland, Massachustetts, United States of America.

Hill, D.M., C. Moritz & B.K. Mable, 1996. *Molecular Systematics*. Second Edition. 655pp. Sinauer Associates Inc., Sunderland, Massachustetts, United States of America.

Hillis, D.H., B.K. Mable & C. Moritz, 1996. Applications of molecular systematics: the state of the field and a look to the future. In: D. H. Hillis, C. Moritz & B. K. Mable (eds.). *Molecular Systematics*. Pp. 515-543. Sinauer, Sunderland, United States of America.

Hinrichs, K. & K.G. Grell. 1937. Entwicklungsstadien von *Eriocheir sinensis*, H. Milne Edwards, im helgolander plankton. *Zoologischer Anzeiger*, 119: 217-221.

Hirata, Y., Y. Nakasone & S. Shokita, 1988. *Okinawa Decapods and Shells in Color*. 144 pp., unnumbered colour figs. Fudokisha Publishing, Naha, Japanese. [In Japanese].

Hiriart, J.L.V., J.C.N. Rodriguez, A.C. D.Barriga, M.D.V. Martinez, P.F. Hernandez, E.L. Fernandezi & P. Schmidtsdorf, 1989. *Listados faunisticos de Mexico. I. Crustaceos estomatopodoes y Decapodos intermareales de Las Islas del Golfo de California, Mexico.* Universidad Nacional Autonoma de Mexico, Mexico.

Ho, P.H. & M.S. Hung. 1997. *Seashore crabs of Hsin-Chu City*. 122 pp. Hsinchu City Government, Hsinchu, Taiwan.

Ho, P.H., 1996. Crabs. In: K. C. Shao (ed.). *Common Seafood of Taiwan*. Part 1. Pp. 71-90, Taiwan Fisheries Department, Taipei, Taiwan.

Ho, P.H., P.K.L. Ng, T.Y. Chan, & D.A. Lee. 2004. New records of 31 species of brachyuran crabs from the joint Taiwan-France expeditions, "Taiwan 2000" and "Taiwan 2001", off deep waters in Taiwan. *Crustaceana* 77: 641-668.

Hoestlandt, H., 1948. Recherches sur la Biologie de L'*Eriocheir sinensis* en France (Crustace Brachyoure). In: E.T.C. Masson (ed.). *Annales de L'Institut Oceanographique*. Paris, France.

Hogarth, P.J., 1999. *The biology of mangroves*. 228 pp, 9 figs. Oxford University Press, Oxford, United Kingdom.

Holcman de Spector, B., E. V. Dei-Cas, J. Leymonié & F. Mañe-Garzón, 1971. Biologia del cangrejo de estuario *Chasmagnathus granulata* Dana 1851. (II) Variaciones del peso corporal en relacion con la salinidad en *Chasmagnathus granulata* Dana 1851. *Trab. V Congr. Latinamer. Zoologia (Montevideo)*, 1: 217-223, text-figs. 1-5.

Holcman-Spector, B., F. Mañe-Garzón & E. Dei-Cas, 1977. Una larva *Cystacantha* (Acanthocephala) de la cavidad general de *Chasmagnathus granulata* Dana 1851. *Revista de Biología del Uruguay (Montevideo)*, 5(2): 67-76.

Holmes, S.J., 1900. Synopsis of stalk eyed Crustacea. *Occasional Papers of the California Academy of Sciences*, 7: 1-262, pls. 1-5.

Holthuis, L.B., 1953a. Enumeration of the Decapod and Stomatopod Crustacea from Pacific coral islands. *Atoll Research Bulletin,* 24: 1-66.

Holthuis, L. B., 1953b. On the dates of publication of W. De Haan's volume on the Crustacea of P.F. Von Siebold's "Fauna Japonica". *The Journal of the Society for the Bibliography of Natural History*, 3(1): 36-47, 1 pl.

Holthuis, L.B., 1958. Crustacea Decapoda from the northern Red Sea (Gulf of Aqaba and Sinai Peninsula). II. Hippidea and Brachyura (Dromiacea, Oxystomata, and Grapsoidea). Contribution to the knowledge of the Red Sea. *Bulletin of Sea Fisheries Research Station, Israel*, 17(9): 41-54.

Holthuis, L.B., 1959. The Crustacea Decapoda of Suriname (Dutch Guiana). *Zoologische Verhandelingen,* 44: 1-296, 68 figs., 16 pls.

Holthuis, L.B., 1961. Report on a collection of Crustacea Decapoda and Stomatopoda from Turkey and the Balkans. *Zoologische Verhandelingen,* 47: 1-67, 15 figs., 2 pls.

Holthuis, L. B., 1973. Caridean shrimps found in land-locked saltywater pools at four Indo-West Pacific localities (Sinai Peninsula, Funafuti Atoll, Maui and Hawaii Islands), with the descriptions of one new genus and four new species. *Zoologische Verhandelingen*, 128: 1-48, pls. 1-7.

Holthuis, L.B. 1977. The Grapsidae, Gecarcinidae and Palicidae (Crustacea: Decapoda: Brachyura) of the Red Sea. *Israel Journal of Zoology*, 26: 141-192.

Holthuis, L.B. 1978. A collection of decapod Crustacea from Sumba, Lesser Sunda Islands, Indonesia. *Zoologische Verhandelingen*, 162: 1-55.

Holthuis, L.B., 1987. *Vrais Crabes*. Fiches FAO d' identification des especes pour les besoins de la peche. Mediterranee et Mer Noire. Zone de peche 37. Vegetaux et invertebres, 1. Pp. 321-367.

Holthuis, L.B. & E. Gottlieb, 1958. An annotated list of the Decapod Crustacea of the mediterranean coast of Israel, with an appendix listing the Decapoda of the eastern Mediterranean. *Bulletin of the Research Council of Israel*, 7B: 1-126, 15 figs.

Holthuis, L.B. & T. Sakai, 1970. *Ph.F. Von Siebold and Fauna Japonica. A history of early Japanese Zoology*. i-xviii + part I, 1-132, (in English) + part II, 207-323, (in Japanese) + plates I-XXXII. Academic Press of Japan, Tokyo, Japan.

Hombron, J.B. & H. Jacqinot, 1842–1845. Crustace´s. *Atlas d'Histoire Naturelle Zoologie*. Voyage au Poˆ le Sud et dans l'Oceanie sur les corvettes l'Astrolabe et la Ze´le´e pendant les anne´es 1837–1838–1839–1840, pls 1–9.

Hombron, J.B. & H. Jacquinot, 1843. Atlas d'Histoire Naturelle Zoologie par MM. Hombron et Jacquinot, chirurgiens de l'expédition. In: *Voyage au pôle sud et dans l'Océanie sur les Corvettes l'*Astrolabe *et la* Zélée; exécuté par ordre du roi pendant les années 1837-1838-18391840 sous les commandement de M. Dumont d'Urville capitaine de vaisseau publié sous les auspices du département de la marine et sous la direction superieure de M. Jacquinot, capitaine de Vaisseau, commandant de La Zelee. Livraison 16. Mammifères pl. 2; Poissons pl. 2; Oiseaux pls 2, 3; Crustacés pl. 1. Gide, Paris, France.

Horikawa, Y., 1940. A list of Formosan crabs. *Scientific Taiwan,* 8: 21-31.

Hsueh, P.W., 1995. Notes on the biology of a poorly known grapsid crab *Clistocoeloma sinense* Shen, 1933 (Decapoda, Brachyura) from Taiwan. *Bulletin of the National Museum of Natural Science,* 5: 143-146.

Hsueh, P.W., 1996. Brachyuran composition and its associated microhabitats at the Kaomei coastal wetland, west-central Taiwan. *Bulletin of the National Museum of Natural Science*, 8: 35-42.

Huang, Z.G., 1994. Brachyura. In: *Marine species and their distributions in China's Seas.* Pp. 576-600. Department of Ocean Management and Monitoring State Oceanic Administration. China Ocean Press, Beijing, People's Republic of China.

Huelsenbeck, J.P. & F. Ronquist, 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics*, 17: 754-755.

Hung, M.S., 1993. Population dynamics and biology of the mitten crab *Eriocheir rectus* in Nanao stream. Masters of Science thesis submitted to National Taiwan Ocean University, Keelung, Taiwan. Pp.1-67. [Unpublished].

Hung, M.S. & H.P. Yu, 1996. A new mitten crab from Taiwanese eastern part - the Taiwan mitten crab. *Nature Conservation Quarterly, Taiwan Endemic Species Research Institute*, 13: 42-46.

Hung, M.S., H.P. Ho & H.P. Yu, 1993. Freshwater mitten crab of Taiwan. *China Fisheries Monthly, China Fisheries Association, Taipei*, 479: 9-20

Hutton, F.W., 1882. The stalk-eyed Crustacea of New Zealand. *New Zealand Journal of Science*, 1(6): 263-264.

Hutton, F.W., 1904. I*ndex Faunae Novae Zealandiae*. 372 pp. Philosophical Institute of Canterbury, Dulau and Co., London, Ynited Kingdom.

Hwang, J.J. & K. Mizue, 1985. Freshwater crabs of Taiwan. *Bulletin of the Faculty of Fishery*. *Nagasaki University, Japan,* 57: 1-22, pls. 1-2.

Hwang, J.J. & M. Takeda, 1986. A new freshwater crab of the family Grapsidae from Taiwan. *Proceedings of the Japanese Society of Systematic Zoology*, 33: 11-18.

Hwang, S.G. & C.H. Kim, 1995. Zoeal stages and megalopa of *Hemigrapsus penicillatus* (De Haan, 1835) (Decapoda, Brachyura, Grapsidae) reared in the laboratory. *Korean Journal of Systematic Zoolog*y, 11: 389-409, figs. 1-7, tabs. 1-5.

Hwang, S.G., C.K. Lee & C.H. Kim, 1993. Complete larval development of *Hemigrapsus sanguineus* (Decapoda, Brachyura, Grapsidae) reared in the laboratory. *Korean Journal of Systematic Zoology,* 9: 69-86, figs. 1-7, tabs. 1-4.

Hymanson, Z., J. Wang & T. Sasaki, 1999. "Lessons from the Home Of the *Eriocheir sinensis*." Department of Fish and Game.  Sacramento, California. Available: http://www.iep.water.ca.gov/report/newsletter/1999summer/ (accessed on 26 September 2006).

Icely, J.D. & J.A. Nott, 1992. Digestion and absorption: Digestive System and associated organs. In: F.W. Harrison & A.G. Humes (eds.). *Microscopic anatomy of invertebrates, Volume 9. Decapod Crustacea.* pp. 147-201, tabs. 1-7, figs. 1-42. A John Wiley & Sons Inc. New York, Unites States of America.

Iliffe, T.M., 1987. Observations on the biology and geology of anchialine caves. In: H.A. Curran (ed.). *Proceedings of the Third Symposium on the Geology of the Bahamas*. Pp. 73-80.CCFL Bahamian Field Station. Bahamas.

Iliffe, T.M., 1992. Anchialine Cave Biology. In: A.I. Camacho (ed.). *The Natural History of Biospeleology*. Pp. 613-636. Museo Nacional de Ciencias Naturales, Madrid, Spain.

Iliffe, T.M., 2004. Anchialine caves, biodiversity. In: D.C. Culver & W.B. White (eds.). *Encyclopedia of Caves*. Pp. 24-30, Elsevier, Burlington, MA, United States of America.

Im, J.G., K.H. Chang & M.M. Reeder, 1997. Current diagnostic imaging of pulmonary and cerebral paragonimiasis, with pathological correlation. *Seminars in Roentgenolog,* 32: 301-324.

Ingle, R. W., 1980. *British Crabs*. 222 pp. Oxford University Press, New York, United States of America.

Ingle, R.W. & M.J. Andrews, 1976. Chinese crab reappears in Britain. *Nature London,* 263: 638.

Ingle, R.W., 1986. The Chinese mitten crab *Eriocheir sinensis* H. Milne Edwards - a contentious immigrant. *The London Naturalist*, 65: 101–105, fig.1.

Ingle, R.W., 1991. *Larval Stages of Northeastern Atlantic crabs. An Illustrated Key*. 363 pp, figs. 1-2, 7 pls. Natural History Museum Publications and Chapman and Hall. London.

International Code of Zoological Nomenclature, 1999. 4th edition. Pp. 1-126. The International Trust for Zoological Nomenclature, London, United Kingdom.

Irawan, B. & A. Kijima, 1994a. Difference of salinity requirements among the three estuarine crab species, *Chiromanthes dehaani, Helice tridens* and *H. japonica* (Brachyura: Grapsidae). *Tohoku Journal of Agriculteral Research*, 44(1-4): 39-47.

Irawan, B. & A. Kijima, A., 1994b. Degree of genetic differentiation among different river populations in two estuarine crabs, *Helice tridens*, and *Chiromanthes dehaani*. *Tohoku Journal of Agriculture Research*, 44(1-4): 49-57.

Irawan, B., A. Kijima & Y. Fujio, 1993. Genetic divergence among the three species of estuarine crab, *Helice tridens*, *H. japonica* and *Chiromanthes dehaani* (Sesarminae, Grapsidae; Decapoda). *Tohoku Journal of Agriculteral Research*, 43(3-4): 101-110.

Ishikawa, M. & K. Yatsuzuka, 1948. On the artificial rearing of larvae of Japanese wood hand-crab (*Eriocheir japonicus* De Haan). *Suisan Gakkai Shi*, 10: 35–39.

Ishikawa, M., 1976. Ecology and Aquaculture of *Eriocheir japonicus*. In Reports of the Research carried out in 1974, *Buzen Fisheries Experimental Station, Fukuoka*: 1–40, figs.1–5, tabs.1–10. [In Japanese].

Islam, S., S. Shokita & H. Kawaguchi, 2000. Effects of Salinity on the larval development of a sesarmid crab, *Chasmagnathus convexus* (De Haan). *Bulletin of the Faculty of Science, University of Ryukyus*, 69: 35-43.

Ismael, D., K. Anger & G.S. Moreira, 1997. Influence of temperature on larval survival, development, and respiration in *Chasmagnathus granulata*. (Crustacea, Decapoda) *Helgoländer Meeresunters*, 51(4): 463-475.

Ismid, M., H. Suzuki & T. Saisho, 1994. Occurance of Brachyuran larvae in the surf zone of Fukiage Beach, Kagoshima Prefecture, Japan. I. Families Grapsidae and Ocypodidae. *Benthos Research*, 16: 11-24, figs. 1-12.

Itani, G., 2000. Distribution of *Acmaeopleura parvula* (Brachyura, Grapsidae) in Izu-Ogasawara Archipelago. *Nankiseibutu*, 42: 69-71. [In Japanese with English abstract].

Itani, G., 2002. Two types of symbioses between grapsid crabs and a host thalassinidean shrimp. *Publications of the Seto Marine Biological Laboratoy*, 39: 129-137.

Itani, G., 2003. Symbiotic relationships in shrimp burrows. In: Asakura, A. (ed). *Biology of crustaceans - recent topics.* Pp. 233-253. Tokai University Press, [In Japanese].

Itani, G., 2004. Host specialization in symbiotic animals associated with thalassinidean shrimps in Japan. In: Tamaki, A. (ed). *Proceedings of the symposium on "Ecology of large bioturbators in tidal flats and shallow sublittoral sediments -from individual behavior to their role as ecosystem engineers.* Pp. 33-43, Nagasaki University. [In Japanese].

Itani, G., M. Izichi, & H. Ueda, 2005. Crab species collected from the burrows of *Urechis unicinctus* in Hiuchi-nada, the central Seto Inland Sea, Japan. *Cancer*, 14, 1-4. [In Japanese with English Abstract].

Itani, G., P.J.F. Davie, & M. Takeda, 2002. Taxonomic notes of *Acmaeopluera balssi* Shen, 1932 and *A. toriumii* Takeda, 1974 (Crustacea, Brachyura, Grapsidae). *Bulletin of the National. Science Museum, Series A*, 28: 43-50.

Ives, J.E., 1891. Echinoderms and Arthropods from Japan. *Proceedings of the Academy of Natural Sciiences, Philadephia*, 1891(2): 210-223, pls 7-12.

Jacobs, D.K. & D.R. Lindberg, 1998. Oxygen and evolutionary patterns in the sea: onshore/offshore trends and recent recruitment of deep sea faunas. *Proceedings of the National Academy of Science, USA*, 95: 9396-9401.

Jacquinot, H., 1852. Crustacés. In: H. Jacquinot, & H. Lucas, *Voyage au Pôle Sud et dans l'Océanie sur les Corvettes l'Astrolabe et la Zélée; executé par ordre du roi pendant les années 1837-1838-1839-1840 sous le commandement de M.J. Dumont d'Urville*. Atlas, (1852), 9 pl. (by H. Jaquinot); Zool., 3(3) (1853) pp. 1-107 (by H. Lucas). Gide & Baudry, Paris, France.

Jang, I.K. & C.H. Kim, 1989. Complete larval development of a sand bubbler crab, *Scopimera longidactyla* (Brachyura, Ocypodidae), reared in the laboratory.

*Korean Journal of Systematic Zoology*, 5(2): 121-137, figs.17, tabs.1-3.

Jeng, M.-S. 1997. *Studies on the land and aquatic decapod crustacean fauna of the Kenting National Park (II)*. Communities of decapod crustaceans around the sea. ii+66 pp. Ministry of the Interior, Taipei, Tawian. [In Chinese].

Jeng, M.-S. 1998. *The Prawns and Crabs of Kenting National Park*. 133 pp. Kenting National Park Hand Guides No. 14. [In Chinese].

Jeng, M.-S., 2000. Volcanic crabs. *Nature World*, 68: 38-45. [In Chinese].

Jeng, M.-S., K.T. Shao, H.R. Fung, C.S. Tzeng, & S.H. Wu. 1998. *Northeast Coast Area. Investigations into ecological resources and monitoring (IV)*. 182 pp. Ministry of Transport and Tourism, Taipei, Taiwan. [In Chinese].

Jeng, M.-S., P.F. Clark & P.K.L. Ng, 2004a. The first zoea, megalopa, and first crab stage of the hydrothermal vent crab, *Xenograpsus testudinatus* (Decapoda: Brachyura: Grapsoidea) and systematic implications for the Varunidae. *Journal of Crustacean Biology*, 24(1): 188-212.

Jeng, M.-S., N.K. Ng & P.K.L. Ng. 2004b. Hydrothermal vent crabs feeds on marine snow. *Nature*, 432: 969.

Jeng, M.-S., R.G. Chan, H.R. Fung, & C.S. Tzeng. 1997. *Northeast Coast Scenic Area. Investigations into ecological resources and monitoring (III)*. 194 pp. Ministry of Transport and Tourism. Taipei, Taiwan. [In Chinese].

Jeng, M.-S., R.G. Chan, H.R. Fung, C.S. Tzeng, & C.T. Yang. 1994. *Northeast Coast Area. Investigations into ecological resources and monitoring (I)*. 205 pp. Ministry of Transport and Tourism, Taipei, Taiwan. [In Chinese].

Jeng, M.-S., R.G. Chan, H.R. Fung, C.S. Tzeng, & C.T. Yang. 1996. *Northeast Coast Area. Investigations into ecological resources and monitoring (II)*. 184 pp. Ministry of Transport and Tourism, Taipei, Taiwan. [In Chinese].

Johnson R.J. & J.R. Johnson, 1983. Paragonimiasis in Indochinese refugees: roentgenographic findings with clinical correlations. *American Review of Respiratory Diseses*, 128: 534-538.

Johnson, I., N. Flower & M.W. Loutit, 1981. Contribution of periphytic bacteria to the concentration of chromium in the crab *Helice crassa*. *Microbial Ecology*, 7: 245-252.

Jones, D.S. & G.J. Morgan, 1994. *A field guide to Crustaceans of Australian Waters*. 216 pp. Reed, Chatswood, New South Wales, Australia.

Jones, D.S., 1993. A new *Neolepas* (Cirripedia: Thoracica: Scalpellidae) from an abyssal hydrothermal vent, Southwest Pacific. *Bulletin of Marine Sciences*, 52: 937-948.

Jones, M.B., 1976. Limiting factors in the distribution of intertidal crabs (Crustacea: Decapoda) in the Avon-Heathcote estuary, Christchurch. *New Zealand Journal of Marine and Freshwater Research*, 10(4): 577-587.

Jones, M.B., 1980. Reproductive ecology of the estuarine burrowing mud crab, *Helice crassa* (Grapsidae). *Estuarine and Coastal Marine Sciences*, 11: 433-443.

Jones, M.B., 1981. Effect of temperature, season, and stage of life cycle on salinity tolerance of the estuarine crab *Helice crassa* Dana (Grapsidae). *Journal of Experimental Marine Biology and Ecology*, 52: 271-282.

Jones, M.B. & M.J. Simons, 1982. Habitat preferences of two estuarine burrowing crabs *Helice crassa* Dana (Grapsidae) and *Macrophthalmus hirtipes* (Jacquinot) (Ocypodidae). *Journal of Experimental Marine Biology and Ecology*, 56: 49-62.

Jones, M.B. & M.J. Simons, 1983. Latitudinal variation in reproductive characteristics of a mud crab, *Helice crassa* (Grapsidae). *Bulletin of Marine Science*, 33(3): 656-670.

Jones, M.B.J., 1983. *Animals of the Estuary Shore: Illustrated Guide and Ecology*. University of Canterbury Publication No. 32. 162 pp. University of Canterbury, Canterbury, Newe Zealand.

Jones, M.L., 1981. *Riftia pachyptilia* Jones: Observation on the vestimentiferan worm from the Galapagos Rift. *Science*, 213: 333-336.

Kamita, T., 1936a. Crab fauna of Cheju-Do Island. *Zoological Magazine, Tokyo*, 48(6): 314-321. [In Japanese].

Kamita, T., 1936b. Crabs from the coast of Korea Strait. *Journal of the Chosen Natural History Society*, 21: 30-35, pl. 1. [In Japanese].

Kamita, T., 1936c. Identity and distribution of Korean Ashiharagani (= *Helice*) crabs. *Fisheries of Korea*, 133: 1-6. [In Japanese].

Kamita, T., 1941a. Catalogue of Crabs in Korea. *Chosen*, 309: 61-90. [In Japanese].

Kamita, T., 1941b. On the distribution of brachyuran Crustaceans in Korea. *Zoological Magazine, Tokyo*: 53(5): 232-244. [In Japanese].

Kamita, T., 1941c. *Studies of the Decapod Crustaceans of Chosen. 1. Crabs.* The Fisheries Society of Chosen, Keijo. 289 pp. 147, 2 pls., 1 map.

Karasawa, H. & K. Inoue, 1992. Decapod crustaceans from the Miocene Kukinaga Group, Tanegashima Island, Kyushu, Japan. *Tertiary Research*, 14, 73–96.

Karasawa, H. & H. Kato, 2001. 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). *Paleontological Research*, 5: 259–275.

Karasawa, H. & T. Tanaka, 2005. A first notice of *Acmaeopleura* Stimpson (Crustacea: Decapoda: Brachyura) from the Miocene of Japan. *Bulletin of the Mizunami Fossil Museum*, 32: 95-96, 1 fig.

Kato, N., 1974. On an andromous phenomenon of megalopae of a grapsoid crab, *Varuna litterata* (Fabricius). *Researches on Crustacea*, 6: 25–29, figs.1, 2.

Katrak, G. & S. Dittmann, 2006. Variation in burrow morphology of the grapsid crab, *Helograpsus haswellianus*, between saltmarsh sites in South Australia. International Society of Wetland Scientist - 27th Annual Conference. Cairns, 9-14 July 2006.

Keenan, C.P., P.J.F. Davie & D.L. Mann, 1998. A revision of the genus *Scylla* de Haan, 1833 (Crustacea: Decapoda: Brachyura: Portunidae). *The Raffles Bulletin of Zoology*, 46(1): 217-245.

Keith, P., E. Vigneux & G. Marquet, 2002. Atlas des poissons et des crustacés d'eau douce de Polynésie française. *Patrimoines naturels*, 55: 1-175, illustré. French Polynesia.

Kemp, S., 1918. Zoological results of a tour in the Far East. Crustacea Decapoda and Stomatopoda. *Memoirs of the Asiatic Society of Bengal*, 6: 217-297, figs. 1-12.

Kemp, S.W., 1915. Fauna of the Chilka Lake. Crustacea Decapoda. *Indian Museum*, 5: 199-325).

Khan, S.A., S.M. Raffi, & P.S. Lyla, 2005. Brachyuran crab diversity in natural (Pitchavaram) and artificially developed mangroves (Vellar Estuary). *Current Science*, 88(8): 1316-1324.

Kido, T., 1975. On the living environment for fish in the coastal waters surrounding the new and old volcanic island, "Nisi-No-Sima". *Journal of Tokyo University, Fish*eries, 61: 59-63.

Kido, T. & Y. Koike, 1975. On the survey in the inlet of "Nisinosima-Sin To". *Journal of Tokyo University, Fisheries*, 61(1-2): 41-47. [In Japanese with English abstract].

Kikuchi, T. & S. Miyake, 1978. *Fauna and Flora of the Sea around the Amakusa Marine Biological Laboratory, 2, Decapod Crustacea* (Revised edition), 52 pp. Amakusa Marine Biological Laboratory, Kyushu University, Amakusa, Japan.

Kilburn, R.N., 1995. Turridae (Mollusca: Gastropoda) of southern Africa and Mozambique, Part 8, Conidae subfamily Mangeliinae, sect. 3. *Annals of the Natal Museum*, 36: 261-269.

Kim, C.H., 1979. Complete larval development of *Hemigrapsus penicillatus* (De Haan) reared in the laboratory and its taxonomic significance. *Journal of Science (Pusan National University, Korea)*, 18: 43–54.

Kim, C.H. & D.Y. Moon, 1987. Complete larval development of *Hemigrapsus sinensis* Rathbun (Brachyura, Grapsidae) reared in the laboratory. *Korean Journal of Zoology*, 30: 277-291, figs.1-7, tab.1.

Kim, C.H. & H.J. Lee. 1983. Zoeal development of *Gaetice depressus* (De Haan) (Decapoda, Garpsidae) reared in the laboratory. *Journal of Science (Pusan National University, Korea)*, 35: 195-200.

Kim, C.H. & I.K. Jang, 1986. The complete larval development of *Cyclograpsus intermedius* Ortmann reared in the laboratory (Decapoda: Brachyura: Grapsidae). *Journal of Science (Pusan National University, Korea)*: 42: 143-158.

Kim, C.H. & I.K. Jang, 1987. The complete larval development of *Acmaepleura parvula* Stimpson (Brachyura, Grapsidae) reared in the laboratory. *Bulletin of the Korean Fishery Society*, 20: 543-560.

Kim, C.H. & S.G. Hwang, 1990.The complete larval development of the mitten crab *Eriocheir sinensis* H. Milne Edwards, 1853 (Decapoda, Brachyura, Grapsidae) reared in the laboratory and a key to the known zoeae of the Varuninae. *Crustaceana*, 68: 793-812, figs. 1-7, tabs.1-7.

Kim, C.H. & S.G. Hwang, 1995. The complete larval development of *Eriocheir japonica* De Haan (Crustacea, Brachyura, Grapsidae) reared in the laboratory. *Korean Journal of Zoology*, 33: 411-427, figs. 1-7, tabs. 1–4.

Kim, H.S., 1962. Fauna of the crabs on the coasts of the western islands of Korea. *Korean Journal of Zoology*, 5(2): 51-54.

Kim, H.S., 1966. Unrecorded species of brachyuran decapods from Korea. *Sung Kyun Kwan University Journal*, 11: 399-412, pls. 1-3.

Kim, H.S., 1970. A checklist of the Anomura and Brachyura (Crustacea, Decapoda) of Korea. *Seoul National University Journal (B)*, 21: 1-34, pls. 1-5.

Kim, H.S., 1973. Anomura & Brachyura. In: *Illustrated encyclopedia of fauna and flora of Korea*, 14: 694 p., 112 pls., Samwha Publishing Co., Seoul, Korea.

Kim, H.S., 1985. Systematic studies on crustaceans of Korea. 1. Decapods. *Proceedings of the College of Natural Sciences, Seoul National University*, 10(1): 63-94.

Kim, H.S. & B.J. Rho, 1971. On the distribution of the benthic animals of Korean coastal seas. 1. Jeju Island Region. The Report for IBP no. 5. Pp 7-21. Korea.

Kim, H.S. & C.Y. Chang, 1985. The brachyuran crabs of Cheju Island, Korea (Crustacea: Decapoda). *Korean Journal of Systematic Zoology*, 1(1-2): 41-60.

Kim, W. & H.S. Kim, 1982. Classification and geographical distribution of Korean crabs (Crustacea, Decapoda, Brachyura). *Proceedings of the College of Natural Sciences, Seoul National University*, 7(1): 133-159.

Kinahan, J.R., 1856. Remarks on the habits and distribution of marine crustacea on the eastern shores of Port Philip, Victoria, Australia, with descriptions of undescribed species and genera. *Journal of the Royal Dublin Society*, 1: 111-134, pls. 3-4.

Kingsley, J.S., 1880. Carcinological notes. IV. Synopsis of the Grapsidae. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 32: 187-224.

Kishino, T. & K. Wada. 2001. Record of *Utica gracilipes* (Crustacea: Brachyura: Grapsidae) from Yakushima-Island, Kagoshima Prefecture, Japan. *Nankiseibutsu*, 43: 59-60. [In Japanese].

Kishino, T., A. Nomoto, S. Kimura, T. Yonezawa & K. Wada. 2001. Brachyuran crab species recorded in the brackish waters of Amami-Oshima Island, Kagoshima Prefecture, Japan. *Nankiseibutsu*, 43: 125-131.

Kishino, T., T. Yonezawa, A. Nomoto, S. Kimura & K. Wada. 2001. Twelve rare species of brachyuran crabs recorded in the brackish waters of Amami-Oshima Island, Kagoshima Prefecture, Japan. *Nankiseibutsu*, 43: 15–22.

Kitaura, J., K. Wada & M. Nishida, 1998. Molecular phylogeny and evolution of unique mud-using territorial behaviour in ocypodid crabs (Crustacea: Brachyura: Ocypodidae). *Molecular Biology and Evolution*, 15(6): 626-637.

Kitaura, J., K. Wada & M. Nishida, 2002. Molecular phylogeny of grapsoid and ocypodoid crabs with special reference to the genera *Metaplax* and *Macrophthalmus*. *Journal of Crustacean Biology*, 22(3): 682-693.

Kitching, J.A. & J. Lockwood, 1974. Observations on shell form and its ecological significance in thaisid gastropods of the genus *Lepsiella* in New Zealand. *Marine Biology*, 28, 131–144.

Knoll, A.H., 2003. *Life on a Young Planet: the First Three Billion Years of Evolution on Earth*. Princeton University Press, Princeton, New Jersey, United States of America.

Knowlton, N., 1986. Cryptic and sibling species among the decapod Crustacea. *Journal of Crustacean Biology*, 6: 356-363.

Knowlton, N., 1993. Sibling species in the sea. *Annual Review of Ecology and Systematics*, 24: 189-216.

Knox, G.A., 1969. The plants and animals of the rocky shores. In: G.A. Knox (ed.). The Natural History of Canterbury. Pp. 536–552. A. H. Reed and A.W. Reed, Wellington, New Zealand.

Knox, G.A., 1975. The marine benthic ecology and biogeography. In: G. Kuschel (ed.). *Biogeography and Ecology in New Zealand* (The Hague: Junk). Pp. 353–403.

Knox, G.A., 1983. *An ecological survey of the Wairau River Estuary*. Estuary Research Unit Report. No. 27. 141 pp. Department of Zoology, University of Canterbury, New Zealand.

Knox, G.A. & A.R. Kilner, 1973. *The Ecology of the Avon-Heathcote Estuary*. Estuarine Research Unit Report, Department of Zoology, University of Canterbury, unnumbered volume, 358 pp.New Zealand.

Knox, G.A. & L.A. Bolton, 1978. *An ecological survey of Shakespeare Bay, Queen Charlotte Sound*. Estuarine Research Unit Report, Department of Zoology, University of Canterbury, 18, 143 pp, New Zealand.

Knox, G.A. & G.D. Fenwick, 1978a. *The ecology of the Riwaka-Tapu Bay intertidal sand beaches*. Estuary Research Unit Report. No. 13. 32 pp. Department of Zoology, University of Canterbury, New Zealand.

Knox, G.A., & L.A. Bolton, 1978b. *An ecological survey of Shakespeare Bay, Queen Charlote Sound*. Estuary Research Unit Report. No. 18. 143 pp. Department of Zoology, University of Canterbury, New Zealand.

Knox, G.A., L.A. Bolton & K. Hackwell, 1977. *Report on the ecology of Parapara Inlet, Golden Bay*. Estuary Research Unit Report. No. 11. 66 pp. Department of Zoology, University of Canterbury, New Zealand.

Knox, G.A., L.A. Bolton & K. Hackwell, 1978. *Report on the ecology of benthic macroflora and fauna of Brookland lagoons, Waimakiri Estuary*. Estuary Research Unit Report. No. 16. 125pp. Department of Zoology, University of Canterbury, New Zealand.

Kobayashi, S. & S. Matsuura, 1991. Longitudinal distribution of the Japanese mitten crab in the Kaminokawa River, Kagoshima. *Nippon Suisan Gakkaishi*, 57: 1029-1034.

Kobayashi, S., M. Kagehira, T. Yoneji & S. Matsuura, 1997. Questionnaire research on the ecology and fishery of the Japanese mitten crab *Eriocheir japonica* (De Haan). *Scientific Bulletin of Faculty of Agriculture, Kyushu University*, 52: 89-104.

Kobjakova, Z.I., 1966. Order Decapoda. In: (E.N. Pavlovskii). Atlas of the invertebrates of the far eastern seas of the USSR. Jerusalem, Israel Program for Scientific Translations, IPST. Cat.No.1672. [Translated from the original 1955 Russian edition].

Kobjakova, Z.I., 1976. Animals and plants of Peter the Great Bay, Sea of Japan. Nauka, Leningrad, Russia. [In Russian].

Kocatas, A., 1971. Izmir Körfezi ve Civarı Yengeçlerinin “Brachyura” Taksonomi ve Ekolojisi Üzerine Arastırmalar [Investigations on the taxonomy and ecology of crabs ‘Brachyura’ from Izmir Bay and its adjacent areas. *E. Ü. Fen Fak. Ilmi Raporlar Serisi (Scientific Reports of the Faculty of Science, Ege University) 76: 1–77 (in Turkish)*. 76, 1-77.

Kocatas, A., 1981. Liste préliminare et repartition des Crustaces Décapodes de eaux Turques. *Rapp. Comm. Int. Mer Medit.*, 27(2): 161-162.

Koelbel, K., 1898. Beschreibung der Krebse. *Wiss. Ergebn. der Reise des Grafen Bela Sczechenyi in Ostasien*, 2: 565-579, 1 pl.

Komai, T., I. Yamasaki, S. Kobayashi, T. Yamamoto & S. Watanbe, 2006. *Eriocheir ogasawaraensis*, a new species of mitten crab (Crustacea: Decapoda: Brachyura: Varunidae) from Ogasawara Islands, Japan, with notes on the systematics of *Eriocheir* De Haan, 1835. *Zootaxa*, 1168: 1-20.

Komai, T., T. Nagai, A. Yogi, T. Naruse, Y. Fujita & S. Shokita. 2004. New records of four grapsoid crabs (Crustacea: Decapoda: Brachyura) from Japan, with notes on four rare species. *Natural History Research*, 8: 33–63.

Kopin, C.Y., C.E. Epifanio, S. Nelson, & M. Stratton, 2001. Effects of chemicals cues on metamorphosis of the Asian shore crab *Hemigrapsus sanguineus*, an invasive species on the Atlantic Coast of North America. *Journal of Experimental Marine Biology and Ecology*, 265(2): 141-151.

Kossmann, R., 1877. Malacostraca (1. Theil: Brachyura). Chapter Erste Halfte, III. In: R. Kossmann, (ed.), *Zoologische Ergebnisse einer im Auftrage der Königlichen Academie der Wissenschaften zu Berlin ausgeführten Reise in die Küstengebiete des Rothen Meeres*. Pp. 1-66, pls. 1-3. W. Engelmann, Leipzig, Germany.

Koukouras, A., 1992. Decapod crustacean fauna of the Aegean Sea: New information, checklist, affinities. *Senckenbergiana Maritima*, 22: 217-244, 2 figs., 4 tabs.

Krauss, F., 1843. *Die südafrikanischen Crustaceen. Eine Zusammenstllung aller bekannten Malacostraca, Bemerkungen über deren Lebensweise und georgraphische Verbreitung, nebst Beschreibung und Abildung mehrer neuen Arten.* Pp. 1-68, 4 pls. Stuttgart, Germany.

Krishnan, T. & T. Kannupandi, 1989. Laboratory cultured zoeae and megalopa of the mangrove crab *Metaplax distincta* H. Milne Edwards. *Journal of Plankton Research*, 11: 633-648.

Kumar, S., K. Tamura & M. Nei, 2004. MEGA3: Integrated software for Molecular Evolutionary Genetics Analysis and sequence alignment. *Briefings in Bioinformatics*, 5: 150-163**.**

Kuo, F.W., 2001. *Preliminary investigations of the hydrothermal activities off Kueishan Island.* M.Sc. thesis submitted to Institue of Marine Geology and Chemistry, National Sun Yat Sen University, Taiwan. [Iin Chinese with English abstract][Unpublished].

Kurata, H., 1968a. Larvae of Decapoda Brachyura of Arasaki, Sagami Bay I, *Acmaeopleura parvula* Stimpson (Grapsidae). *Bulletin of the Tokai Regional Fisheries Research Laboratory*, 56: 259–263, fig.1, tabs.1-2.

Kurata, H., 1968b. Larvae of Decapoda Brachyura of Arasaki, Sagami Bay II, *Hemigrapsus sanguineus* (DeHaan) (Grapsidae). *Bulletin of the Tokai Regional Fisheries Research Laboratory,* 56: 161-165, fig. 1.

Lai, H., J. Shy & H. Yu, 1986. Morphological observation on the development of larval *Eriocheir japonica* De Haan (Crustacea, Decapoda, Grapsidae) reared in the laboratory. *Journal of the Fisheries Society of Taiwan*, 13(2): 12-21, figs. 1-9, tabs. 1-3.

Lai, H.T., J.Y. Shy & H.P. Yu. 1986. Morphological observation on the development of the larval *Eriocheir japonica* de Haan, 1835 (Crustacea, Decapoda, Grapsidae) reared in the laboratory. *Journal of Fisheries Society*, 13: 12-21. [In Chinese].

Lai, W. & J. Lu, 1992. Study on the decapod crustacean community in Chiangjiang River estuary. *Transactions of the Chinese Crustacean Society*, 3: 23-29. [In Chinese].

Lamarck, J.B., 1801. Crustacés. In: J.B. Lamarck (ed.). *Système des animaux sans vertèbres*. Pp. 1-432. Maillard, Paris, France.

Lamarck, J.B.P.A., 1818. *Histoire Naturelle des Animaux sans vertèbres*, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une Introduction offrant la Détermination des caractères essentiels de l'Animal, sa distinction du végétal et des autres corps naturelles, enfin, l'Exposition des Principes fondamentaux de la Zoologie. Vol. 5. 612 pp. France.

Latham, K., 1978. Asiatic whimbrel catching crabs. *Notornis*, 25: 355.

Latreille, P.A., 1803. *Histoire naturelle, générale et particulière, des Crustacés et des Insectes.* Vol. 6. Pp. 1-391, 44 pls. F. Dufart, Paris, France.

Latreille, P.A., 1804. Tableau méthodique des Crustcés. In: *Nouveau dictionnaire d'historie naturelle appliqu aux Arts, principalement à l'agriculture et à l' économie rurale et demostique: par une Société de naturalistes et d'Agriculteurs: avec des figures tirées des trois règnes de la nature*, 24: 125-127.

Latreille, P.A., 1817a. Glasime, *Gelasimus* (Buffon). In: *Nouveau dictionnaire d'histoire naturelle, applique aux arts, l'agriculture, l'economie rurale et domestique, la medicine, etc*. Second edition, 12: 517-520.

Latreille, P.A., 1817b. Les crustacés, les arachnides et les insectes. *In*, Cuvier, G. (ed.) *Le règne animal distribué d'après son organization, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée.* Paris : [s.n.] Vol. 3 First edition. xxix + 653 pp.

Latreille, P.A., 1817c. *Nouveau dictionnaire d'histoire naturelle*, appliquée aux arts, à l'agriculture, à l'economie rurale et domestique, à la médecine, etc. Vol. 10, 404 pp.

Latreille, P.A., 1819. *Nouveau dictionnaire d'histoire naturelle*, appliquée aux arts, à l'agriculture, à l'economie rurale et domestique, à la médecine, etc. Second edition. Vol. 30. Pp. 71-72

Latreille, P.A., 1825. *Familles naturelles du règne animal*, exposées succinctement et dans un ordre analytique, avec l'indication de leurs genres. Second Edition. 570

pp. Baillère , Paris, France.

Latreille, P.A., 1828. Encyclopédie Méthodique. Histoire Naturelle. Entomologie, ou Histoire naturelle des Crustacés, des Arachnides et des Insectes. *Serville et Guérin : Le Peletier de St-Fargeau*, 10(2): 345-852.

Lebour, M.V., 1934. The life history of *Dromia vulgaris*. *Proceedings of the Zoological Society of London*, 1934: 241-249.

Lee, C.S., G.G. Shor, L.D. Bibee, Jr., R.S. Lu & Y.W.C. Hilde, 1980. Okinawa Trough: Origin of a back-arc basin. *Marine Geology,* 35:219-241.

Lee, J.H., 2001. *Crabs of Taiwan*: *Revelations*. 176 p. Big Tree Culture Enterprise Co., Taipei, Taiwan.

Lee, Y.H. & C.H. Koh, 1994. Biogenic sedimentary structures on a Korean muf flat: Spring-neap variations. *Netherland Journal Sea Research,* 32(1): 81-90.

Lenz, H., 1901, Crustaceen. Ergebnisse einer Reise nach und dem Pazifik (Schauinsland 1896–1897). *Zoologische Jahrbucher, Abtheilung fur Systematik, Geographie und Biologie der Thiere*, 14, 429–482.

Lenz, H., 1902. Die Crustaceen der Sammlung Plate. (Decapoda und Stomatopoda). *Zoologsiche Jahrbucher, Systematics, Suppl.* 5: 731-772, pl. 23.

Leslie, M.A., 1968, Animals of the Rocky Shore of New Zealand. 128 pp. A.H. Reed & A.W. Reed, Wellington, New Zealand.

Levin, H., 1999. *Ancient invertebrates and their living relatives*. First Edition. Prentice-Hall, New Jersey, United States of America.

Lewinsohn, C. & L.B. Holthuis, 1964. New records of Decapod Crustacea from the Mediterranean coast of Israel and the eastern Mediterranean. *Zoologische Mededelingen, Leiden,* 40: 45-63, 5 figs.

Li, G., Q. Shen & Z. Xu, 1993. Morphomentric and biochemical genetic variation of the mitten crab, *Eriocheir,* in southern China. *Aquaculture,* 111: 103-115.

Li, M., Z. Kuang, H. Zhen & M. Wang, 1992. The morphological development of the larvae of the *E. hepuensis*. *Guangxi Fisheries Technology,* 3: 1-12, figs. 1-4.

Liang, X.Q., S.L. Yan, D.C. Zheng & D.D. Guo, 1974. Larval development of *Eriocheir sinensis* H. Milne-Edwards. *Acta Zoologica Sinica*, 20: 61-66, pls. 1-6.

Lin, C.C., 1949. A catalogue of brachyourous Crustacea of Taiwan. *Quartary Journal of Taiwan Museum*, 2(1): 10-33.

Linnaeus, C., 1756. *Systema Naturae*. Ninth edition. Theodor Haak, Leiden (Lugdunum Batavorum). Thje Netherlands.

Linnaeus, C., 1758. Cancer. pp. 625-634 *In:* (10th edn), *Systema naturae per Regna Tria Naturae*, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. 824 pp. L. Salvius, Holmiae.

Little, C.T.S. & R.C. Vrijenhoek, 2003. Are hydrothermal vent animals living fossils? *Trends in Ecology and Evolution*, 18 (11): 582-588.

Liu, C.C., 1995. The Ilan plain and the southwestward extending Okinawa trough. *Journal of the Geological Society, China*, 38(3), 229-242.

Liu, H.C., 1998. *Biological Resources of Kaomei Wetland*. 150 pp. Taichung County Government, Taichung, Taiwan.

Lopez de Levy, M., 1989. Estudio histologico del ovario de *Chasmagnatus granulata* Dana 1851. (Decapoda, Grapsidae). *Bolatim Societe Zoologia del Uruguay Segunda Epoca*, 5: 46-47.

Lopez-Greco, L.S., G.C. Lopez, & E.M. Rodriguez, 1999. Morphology of spermathecae in the estuarine crab *Chasmagnathus granulata* Dana 1851. (Grapsidae, Sesarminae). *Journal of Zoology*, 249(4): 490-493.

Lowe, S., M. Browne, S. Boudjelass & M. De Poorter, 2004. *100 of the World's Worst Invasive Species Database*. Published by The Invasive Species Specialist Group (ISSG), a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), 12 pp.

Lucas, H., 1846. *Crustacés, Arachnides, Myriopodes et Hexapodes: Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842*. Sciences physiques, Zoologie I. Histoire Naturelle des Animaux Articulés. 403 pp., 8 pls. France.

Lucas, M., 1840. *Histoire naturelle des Crustaces, des Arachnides et des Myriapodes*. Pp. 240-243. Dumenil, Paris, France.

Luppi, T.A., E.D. Spivak, & K. Anger, 2002. Postsettlement growth of two estuarine crab species, *Chasmagnathus granulata* and *Cyrtograpsus angulatus* (Crustacea, Decapoda, Grapsidae): laboratory and field observations. *Helgoland Marine Research*, 55: 293-305.

Luquet, C., G. Genovese, G. Rosa & G. Pellerano, 2002. Ultrastructural changes in the gill epithelium of the crab *Chasmagnathus granulatus* (Decapoda: Grapsidae) in diluted and concentrated seawater. *Marine Biology*, 141(4): 753-760.

MacLeay, W.S., 1838. Illustrations of the Annulosa of South Africa; being a portion of the objects of natural history chiefly collected during an expedition into the interior of South Africa, under the direction of Dr. Andrew Smith, in the years 1834, 1835 and 1836; fitted out by " The Cape of Good Hope association for exploring Central Africa". *In*: A. Smith, *Illustrations of the Zoology of South Africa; consisting chiefly of figures and descriptions of the objects of natural history chiefly collected during an expedition into the interior of South Africa, under the direction of Dr. Andrew Smith, in the years 1834, 1835 and 1836*; fitted out by " The Cape of Good Hope association for exploring Central Africa," (Invertebrates). Pp. 1-75 + pls. 1-4. Sith Elder and Co., London, United Kingsom.

Macleod, G., C. McKeown, A.J. Hall & M.J. Russell, 1994. Hydrothermal origin and oceanic pH conditions of the relevance to the origin of life. *Origin of Life Evolution and Biosphere*, 24: 19-41.

Macnae, W., 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-Pacific region. *Advances in Marine Biology*, 6: 74-270.

Magalhães, C. & M. Türkay, 1996. Taxonomy of the neotropical freshwater crab family Trichodactylidae. I. The generic system with description of some new genera (Crustacea: Decapoda: Brachyura). *Senckenbergiana Biologia*, 75(1/2): 63-95.

Maher, K.A. & D.J. Stevenson, 1988. Impact frustrations of the origin of life. *Nature*, 331: 612-614.

Maitland, D.P., 1990. Carapace and branchial water circulation, and water-related behaviours in the semaphore crab, *Heloecius cordiformis* (Decapoda: Brachyura: Ocypodidae). *Marine Biology*, 105(2): 275–286.

Maitland, D.P., 1992. Carapace movements aid air breathing in the semaphore crab, *Heloecius cordiformis* (Decapoda: Brachyura: Ocypodidae). *Journal of Comparative Physiology B: Biochemical, Systemic and Environmental Physiology*, 162 (4): 375–382.

Makarova, K.S. & E.V. Koonin, 2003. Comparative genomics of archaea: how much have we learned in six years, and what's next? *Genome Biology*, 4(8): 115.

Maki, M. & K. Tsuchiya, 1923. *A monograph of the Decapoda Crustacea of Formosa*. pp. xi, 215, 4. Report of the Department of Agriculture, Government of Research Institute of Taihoku, 3: 1-215, 24 pls.

Maldonado, H., A. Romano & M. Lozada, 1989. Opioid action on response level to danger stimulus in the crab (*Chasmagnathus granulatus*). *Behavioral Neurosciences*, 103(5): 1139-1143.

Man, J.G. de, 1879. On some new or imperfectly known Podophthalmous Crustacea of the Leyden Museum. *Notes Leyden Museum*, 1: 53-73.

Man, J.G. de, 1887. Übersicht der indo-pacifischen Arten der Gattung *Sesarma* Say nebst einer Kritik der von W. Hess und Nauck in den Jahren 1865 und 1880 beschriebenen Decapoden. *Zoologische Jahrbucher Abteilung fur Systematik*, 2: 639-722, pl. 17.

Man, J.G. de, 1888. Report on the Podophthalmous Crustacea of the Mergui Archipelago, collected for the Trustees of the Indian Museum, Calcutta, by Dr John Anderson, F.R.S., Superintendent of the Museum. Parts I–V. *Journal of the Linnean Society*, 22(136–140): 1–312, pls 1–19.

Man, J.G. de, 1890. Carcinological studies in the Leyden Museum, No. 4. *Notes from Leyden Museums*, 12 (13): 49-126, pls. 3-6.

Man, J.G. de, 1891. Carcinological studies in the Leyden Museum. No 5. *Notes Leyden Museum,* 13: 1-61, pls. 1-4.

Man, J.G. de, 1892. Decapoden des Indischen Archipels. pp. 265-527 pls 15-29. In: Weber, M. (ed.). *Zoologische Ergebnisse einer Reise nach Niederländisch Ost-Indien.* Vol. 2. E.J. Brill, Leiden.

Man, J.G. de, 1895a. Bericht uber die von Herrn Sciffscaptan Storm zur Atejeh, an den westlichen Kuchen von Malakka, Borneo und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden. *Zoologsiche Jahrbucher, Systematics*, 8: 485-609, pls. 12-14.

Man, J.G. de, 1895b. Bericht über die von herrn Schiffscapitän Storm zu Atjeh, an den westlichen Küsten von Malakka, Borneo und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden (Part 2). *Zoologsiche Jahrbucher, Systematics*, 9: 75-218, figs 16-39.

Man, J.G. de, 1896a. Ueber neue und wenig bekannte Brachyuren des Hamburger und Pariser Museums. *Mittheilungen aus dem Naturhistorischen Museum zu Hamburg*, 13: 75-118, Pls-3.

Man, J.G. de, 1896b. Bericht über die von herrn Schiffscapitän Storm zu Atjeh, an den westlichen Küsten von Malakka, Borneo und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden (Part 3). *Zoologsiche Jahrbucher, Systematics*, 9: 339-386, figs. 40-49.

Man, J.G. de, 1896c. *Platychirograpsus spectabilis*, nov. gen. n. sp., eine neue Form der Grapsidae vom Gabun, Westküste von Africa. *Zoologischer Anzeiger*, 19: 292-294, 1 fig.

Man, J.G. de, 1897. Bericht über die von herrn Schiffscapitän Storm zu Atjeh, an den westlichen Küsten von Malakka, Bornio und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden (Part 5). *Zoologsiche Jahrbucher, Systematics*, 9: 725-788 figs 60-73.

Man, J.G. de, 1898. Bericht über die von Herrn Schiffscapitän Storm zu Atjeh, an den westlichen Küsten von Malakka, Borneo und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden. Sechster Theil. *Zoologische Jahrbucher Abteilung fur Systematiks*, 10: 677-708, pls. 28-38.

Man, J.G. de, 1902. Die von Herrn Professor Kükenthal im Indischen Archipel gesammelten Dekapoden und Stomatopoden. In: Kükenthal, W. Ergebnisse einer Zoologischen Forschungsreise in den Molukken und Borneo. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 25: 467-929, pls 19-27.

Man, J.G. de, 1908. The fauna of brackish ponds at Port Canning, Lower Bengal. Part. X: Decapod Crustacea, with an account of a small collection from brackish water near Calcutta and in the Dacca district, eastern Bengal. *Records of Indian*

*Museum*, 2: 211-231, pls. 18-19.

Man, J.G. de, 1889. Über einige neue oder seltene indopacifische Brachyuren. *Zoologsiche Jahrbucher, Systematics*, 4: 409-552 pls 9-10.

Man, J.G. de, 1895a. Bericht über die von Herrn Schiffscaptän Storm zu Atjeh, an den westlichen Küsten von Malakka, Borneo und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden. Zweiter Theil. *Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere*, 9: 75–218.

Man, J.G. de, 1895b. Bericht uber die von Herrn Sciffscaptan Storm zur Atejeh, an den westlichen Kuchen von Malakka, Borneo und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden. *Zoologsiche Jahrbucher, Systematics*, 8: 485-609, pls. 12-14.

Man, J.G., de, 1914. Note sur quelques Crustacès Brachyures terrestres et d'eaux douce apparteenant au Musee Civique de Gene. *Annals de Museum Storia naturalis Genova*, 46: 122-138.

Mana, A.K., 1988. Behavioural study of a small edible crab *Varuna litterata* in the coastal water of Bay of Bengal. *Environemnt and Ecology*, 6(3): 754-755.

Mañe-Garzón, F. & R. Montero, 1973. Una nueva especie de Rotifera Bdelloidea, *Anomopus chasmagnathii* n. sp, de la cavidad branquial del cangrejo de estuario *Chasmagnathus granulata* Dana, 1851 (Decapoda, Brachiura). *Revisão na Biologia, Uruguay,* 1(2): 139-144.

Mañe-Garzón, F., E. Dei-Cas, B. Holcman-Spector & J. Leymonié, 1974. Estudios sobre la biologia del cangrejo de estuario *Chasmagnathus granulata* Dana, 1851. I. Osmorregulacion frente a cambios de salinidad. Physis. *Seccion A: Los Oceanos y sus Organismos*, 33(86): 163-171.

Manning, R.B., & L.B. Holthuis, 1981. West African brachyuran crabs (Crustacea: Decapoda). *Smithsonian Contributions to Zoology*, 306:1-379.

Manuel, M.R., P.C. Gonzales & L. Basmayor, 1991. The crustacean fauna of Natunawan Cove in Tabaco, Albay (Crustacea: Brchyura: Macrura and Stomapoda). *National Museum Papers, Manila*, 2(1): 59-102.

Margulis, L. & K.V. Schwartz, 2000. *Five Kingdoms: An Illustrated Guide To the*

*Phyla of Life on Earth*. Third Edition. W.H. Freeman and Company, New York, United States of America.

Marques, F. & G. Pohle, 1995. Phylogenetic analysis of the Pinnotheridae (Crustacea, Brachyura) based on larval morphology, with emphasis on the *Dissodactylus* species complex. *Zoologica Scripta*, 24: 347-364.

Marquet, G., 1988. Les eaux intérieures de la Polynésie française. Principales caractéristiques physiques, chimiques et biologiques. Thèse de Doctorat de l'université Paris VI, spécialité Sciences de la Vie (Océanologie Biologique). Pp. 233, 64 figs.

Marquet, G., 1991. Freshwater crustaceans of French Polynesia: taxonomy, distribution and biomass (Decapoda). *Crustaceana*, 61: 125-140.

Marquet, G., 1993. Etude biogéographique de la faune d'eau douce de Polynésie française. *Biogeographica,* 69 (4): 157-170, fig. 1-3.

Marsden, I.D., 1981. Marine. *Biology of the Kaikoura Peninsula, quantitative intertidal survey*. Estuary Research Unit Report. No. 25. 93 pp. Department of Zoology, University of Canterbury, New Zealand.

Marsden I.D. & G.D. Fenwick, 1978. *Preliminary survey of intertidal areas from Cape Campbell to Haumuri Bluffs.* Estuary Research Unit Report. No. 18. 41 pp. Department of Zoology, University of Canterbury, New Zealand.

Martens, E. von, 1869. Südbrasilische Süß- und Brackwasser-Crustaceen nach den Sammlungen von Dr. Reinh. Hensel. *Archiv fur Naturgeschies*, 35(1): 1-37, pls. 1-2.

Martin, Joel W. & G.E. Davis. 2001. *An Updated Classification of the Recent Crustacea.* Natural History Museum of Los Angeles, Science Series 39. Pp. i-vii, 1-124.. Natural History Museum of Los Angeles County. United States of America.

Marumura, M. & A. Kosaka. 2003. *Catalogue of the Brachyuran and Anomuran crabs donated by the late Mr. Seiji Nagai to the Wakayama Prefectural Museum of Natural History*. Wakayama Prefectural Museum of Natural History, Wakayama, Japan.

Mathews, L.M., C.D. Schubart, J.E. Neigel & D.L. Felder, 2002. Genetic, ecological, and behavioural divergence between two sibling snapping shrimp species (Crustacea: Decapoda). *Molecular Ecology*, 11: 1427-1437.

Matsuo, K. & K. Makiya, 1985. Ecological studies on the lung fluke, *Paragonimus ohirai* Miyazaki, 1939. 1. Infection rate with *P. ohirai* metacercariae of brackish water crabs collected from six rivers in the Tokai district, central Japan. *Japanese Journal of Tropical Medical Hygiene*, 13(4): 307-313.

Matsuo, M., 1940. Crabs and their distribution in the ajacent sea of Manchu (= N. China). *Journal of Manchourian Biological Society*, 3(1): 1-7.

Matsuura, K. 1894. Brachyura of Japan. *Zoological Magazine*, 6(23): 51-57.

McArthur, A.G. & V. Tunnicliffe, 1998. Relics and antiquity revisited in the modern vent fauna. In: R. Mills & K. Harrison  Modern (eds.). *Ocean Floor Processes and the Geological Record*. Pp. 271–291, Special Publication of the Geological Society of London, United Kingdom.

McDermott, J.J., 1998. The western Pacific brachyuran *Hemigrapsus sanguineus* (Grapsidae) in its new habitat along the Atlantic coast of the United States: geographic distribution and ecology. *ICES Journal of Marine Science*, 55(2): 289-298.

McLaughlin, P.A. & R. Lemaître, 1997. Carcinization in the Anomura - fact or fiction. 1. Evidence from adult morphology. *Contributions to Zoology*, 67(2): 79-123

McLaughlin, P.A., 1980. *Comparative morphology of recent crustacea*. 170pp. W.H. Freeman, San Francisco, United States of America.

McLaughlin, P.A., D.K. Camp, M.V. Angel, E.L. Bousfield, P. Brunei, R.C. Brusca, D.Cadien, A.C. Cohen, K. Conlan, L.G. Eldredge, D.L. Felder, J.W. Goy, T. Haney, B. Hann, R.W. Heard, E.A. Hendrycks, H.H. Hobbs, III, J.R. Holsinger, B. Kensley, D.R. Laubitz, S.E. LeCroy, R. Lemaitre, R.F. Maddocks, J.W. Martin. P. Mikkelsen, E. Nelson, W.A. Newman, R.M. Overstreet, W.J. Poly, W.W. Price, J.W. Reid, A. Robertson, D.C. Rogers, A. Ross, M. Schotte, F.R. Schram, C.-T. Shih, L. Watling, G.D.F. Wilson & D.D. Turgeon, 2005. *Common and scientific names of aquatic invertebrates from the United States and Canada:*

*crustaceans*. American Fisheries Society, Special Publication, 31. Bethesda, Maryland, United States of America.

McLaughlin, P.A., R. Lemaître & C.C. Tudge, 2004. Carcinization in the Anomura - fact or fiction. 2. Evidence from larval, megalopal and early juvenile morphology. *Contributions to Zoology*, 73(3): http://dpc.uba.uva.nl/ctz/vol73/nr03/art01 (accessed 23 September 2006).

McLay, C.L., 2007. New crabs from hydrothermal vents of the Kermadec Ridge submarine volcanoes, New Zealand: *Gandalfus gen. nov.* (Bythograeidae) and *Xenograpsus* (Varunidae) (Decapoda: Brachyura). *Zootaxa*, 1524: 1-22.

McLay, C.L. & C.D. Schubart, 2004. On the correct name for *Hemigrapsus edwardsii* (Hilgendorf, 1882) (Brachyura: Varunidae) from New Zealand. *Journal of Natural History*, 38(20): 695-704.

McLay, C.L. & D.J. McQueen, 1995. Intertidal zonation of *Cyclograpsus lavauxi* H. Milne Edwards, 1853 (Brachyura: Grapsidae) along the coast of the South Island of New Zealand. *Crustacean Research*, 24, 49–64.

McLay, C.L., 1988. Brachyura and crab-like Anomura of New Zealand. *Leigh Laboratory Bulletin*, 22: I-IV, 1-463, text-figs. 1-85.

McLean, J.H., 1981. The Galapagos Rift limpet Neomphalus: Relevance to understanding the evolution of a major Paleozoic-Mesozoic radiation. *Malacology*, 21: 291-336.

McLean, J.H., 1985. Preliminary report on the limpets at hydrothermal vents. *Biological Society of Washington Bulletin*, 6: 159-166.

McLean, J.H., 1990. A new genus and species of neomphalid limpet limpet from the Mariana vents with a review of Neomphalacea and Peltospiracea. *Nautilus*, 104: 77-86.

McNeill, F.A., 1920. Studies in Australian Carcinology. No. 1. *Records of the Australian Museum*, 13(3): 105-109, pl. 19.

Melo, G.A.S., 1990. A presença, no litoral sudeste brasiliero, de espécies de Brachyura (Crustacea: Decapoda) originárias das regiões biogeográficas Magelânica e Argentina de Atlântico Sul. *Atlântica*, 12(2): 71-83.

Melo, G.A.S., 1996. *Manual de identificação dos Brachyura (Caranguejos e Siris) do litoral brasiliero*, 604 pp., numerous unnumbered text-figs. Plêiade/FAPESP, São Paulo. Brazil.

Melo, G.A.S., 1998. Malacostraca, Eucarida. Brachyura. Oxyrhyncha and Brachyrhyncha. In: P.S. Young (ed.). *Catalogue of Crustacea of Brazil*. Série Livros n. 6. Pp. 455-515. Museu Nacional, Rio de Janeiro, Brazil.

Melo, G.A.S., V.G. Veloso, & M.C. Oliveira, 1989. A fauna de Brachyura (Crustacea: Decapoda) do litoral do Estado de Paraná. Lista preliminar. *Neritica*, 4(1/2): 1-31.

Merques, F. & G. Pohle, 1995. Phylogenetic analysis of the Pinnotheridae (Crustacea, Brachyura) based on larval morphology, with emphasis on the *Dissodactylus* species complex. *Zoological Science*, 24: 347-364.

Mia, M., Y.R. Fuseya, & S. Watanabe, 1999. Genetic variation among the three species of grapsid crabs, *Helice tridens latimera*, *H. tridens tridens* and *H. leachi*. *Crustacean Research*, 28: 52-61, 2 text-figs, 5 tables.

Mia, M.Y. & S. Shokita, 1996. Description of larval and juvenile stages of the grapsid crab *Helice leachi* Hess (Brachyura: Grapsidae) reared under laboratory conditions. *Crustacean Research*, 25: 104-120.

Mia, M.Y. & S. Shokita, 1997a. Larval development of grapsid crab *Helice formosensis* Rathbun (Crustacea: Brachyura) reared in thelaboratory. *Species Diversity*, 2: 7-23.

Mia, M.Y. & S. Shokita, 1997b. Optimal salinity required for the larval development of two grapsid crabs, *Helice leachi* Hess and *H. formosensis* Rathbun. *Crustacean Research*, 26: 70-74.

Mia, M.Y., S. Shokita, S. Shinzato & M. Kinjo, 1999. Feeding habits of the grapsid crab, *Helice leachii* Hess, under laboratory conditions. *Bulletin of the Faculty of Sciences, University of Ryukyus*, 68: 31-44.

Michel, C., 1964. Check List of the Crustacea Brachyura (Crabs) recorded from Mauritius. *Bulletin of Mauritius Institute*, 6(1): 1-48.

Miers, E.J., 1876. *Catalogue of the Stalk- and Sessile-eyed Crustacea of New Zealand*. pp. xii+1–136, 3 pls . Colonial Museum and Geological Survey Department, London, United Kingdom.

Miers, E.J., 1878. Revision of the Plagusiinae. *Annual Magazine of Natural History*, (5)1: 147-154.

Miers, E.J., 1879. On a collection of Crustacea made by Capt. M. C. St. John, R.N., in the Korean and Japanese Seas. *Proceedings of the Zoological Society of London*, 1879: 18–61, pls I–III.

Miers, E.J., 1881. Crustacea. In: A. Günther (ed.). *Account on the zoological collections made during the survey of H. M. S. 'ALERT' in the Straits of Magellan and on the coast of Patagonia*. Proceedings of the Zoological Society of London, 1881: 61-79, pl. 7.

Miers, E.J. 1884. Crustacea. Report on the Zoological Collections in the Indo-Pacific Ocean during the voyage of H.M.S. "Alert" 1881-1882. London. Pp. 178-322, 513-575, pls. 18-34.

Miers, E. J., 1885. The Brachyura. pp. 585-592 pls 196-198. In: C.W. Thomson, C. Wyville & J. Murray (eds). *Report on the Scientific Results of the Voyage of the H.M.S.* Challenger *During the Years 1873-1876.* London : H.M.S.O. Vol. 1(2).

Miers, E.J., 1885. The Brachyura. pp. 585-592 pls 196-198 *in* Thomson, C.W., Wyville C. & Murray, J. (eds). *Report on the Scientific Results of the Voyage of the H.M.S.* Challenger *During the Years 1873-1876.* London : H.M.S.O. Vol. 1(2).

Miers, E.J., 1886. The voyage of H.M.S. Challenger. Zoology. In: Report on the Brachyura collected by H.M.S. Challenger during the years 1873–76, Report on the Scientific Results of the Voyage of H.M.S. Challenger During the Years 1873–76, 17, i–xvi,1–362, pls. 1-29.

Miki, M., 1995. Two-phase opening model for the Okinawa Trough inferred from paleomagnetic study of the Ryukyu arc. *Journal of Geophysics Research*, 100 (B5): 8169–8184.

Miller, M. & G. Batt, 1973. Reef and Beach Life of New Zealand. 141 pp. Collins, Auckland and London.

Milne Edwards, A., 1867. Descriptions de quelques espèces nouvelles de Crustacés Brachyures. *Annales de la Société entomologique de France, series 4,* 7: 263-288.

Milne Edwards, A., 1868a. Description de quelques Crustacés nouveaux provenant des voyages de M. Alfred Grandidier à Zanzibar et à Madagascar. *Nouelle Archive*

*Museum Histoire Nationale, Paris* 4: 69-92 pls. 19-21.

Milne Edwards, A., 1868b. Observations sur la faune carcinologique des îles du Cap. *Nouvelles Archives du Muséum d'Histoire naturelle (Paris),* 4: 49-68.

Milne-Edwards, A., 1869. Description de quelques espèces nouvelles de Crustacèes provenant du voyage de M. A. Bouvier ant Iles du Cap Vert. *Revue et Magasin de Zoologie,* 21: 350-355, 375-378, 409-412.

Milne Edwards, A., 1873. Recherches sur la faune carcinologique de la Nouvelle-Calédonie, Deuxième Partie. *Nouvelles Archives du Muséum d'Histoire naturelle (Paris),* 9: 155-332, pls. 4-18.

Milne Edwards, A., 1873–1881. Études sur les Xiphosures et les Crustacés de la region Mexicaine. In *Mission scientific au Mexique et dans l'Amérique centrale, Recherches Zoologiques pour servir à l'histoire de la faune del'Amérique centrale et du Mexique*, 5: 1-368, plates 1-61.

Milne Edwards, A., 1874. Recherches sur la faune carcinologique de la Nouvelle-Calédonie. Pt. 3. Groupe des Oxystomes. *Nouvelles Archives du Muséum d'Histoire naturelle (Paris),* 10: 39-58 pls 2, 3.

Milne Edwards, A., 1878. Etudes sur les Xiphosures et les Crustacés de la région Mexicaine. I: *Mission scientifique au Mexique et dans l'Amérique centrale, Recherches Zoologiques pour servir à l'histoire de la faune de l'Amérique centrale et du Mexique*. Part 5. Pp. 121-184; pls. 21-27, 29, 30.

Milne Edwards, A., 1879. Description de quelques Crustacés nouveaux. *Bulletin de la Société Philomathique de Paris, Series 7,* 3: 103-110, pls.1-2.

Milne Edwards, A., 1879. Etudes sur les Xiphosures et les Crustacés Podophthalmiens, pts v & vi. pp. 185-224 pls xxxi-xxxix, pp. 225-264 pls xv. a, xxviii, xl-xliii & xlv-xlviii . *In, Mission scientifique au Mexique et dans l'Amérique centrale*, Recherches Zoologiques pour servir à l'histoire de la faune de l'Amérique centrale et du Mexique. Pt 3.

Milne Edwards, A., 1880. Etudes sur les Xiphosures et les Crustacés de la région Mexicaine. *Mission scientifique au Mexique et dans l'Amérique centrale*, pp. 1-368, 61Recherches Zoologiques pour servir à l'histoire de la faune de l'Amérique centrale et du Mexique. Pt. 5.

Milne Edwards, A., 1880. No. 1. Reports on the results of dredging under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, '78, '79, by the U.S. Coast Survey Steamer "Blake". Lieut.-Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., Commanding. VIII. Etudes préliminaires sur les Crustacés. *Bulletin of Museum of Comparative Zoology*, 8(1): 1-68 pls 1-2.

Milne Edwards, A.,1880. Etudes sur les Xiphosures et les Crustacés podophthalmaires. pp. 265-372 pls xlix-lxi *In, Mission scientifique au Mexique et dans l'Amérique centrale*, Recherches Zoologiques pour servir à l'histoire de la faune de l'Amérique centrale et du Mexique. Pt. 5.

Milne-Edwards, A. & E.L. Bouvier, 1900. *Crustacés Décapodes I. Brachyures et Anomoures*. Exp. Sci. Travailleur et Talisman (1880-1883). Volume 6. Pp. 1-396, pls. 1-32.

Milne Edwards, H., 1830. Varune. [*Varuna*]. In: Audouin, Isid. Bourdon, Ad. Brongniart, Cambassèdes, De Candolle, G. Delafosse, Deshayes, E. Deslonchamps, Drapiez, Dumas, Edwards, H.-M. Edwards, A. Fée, Geoffroy Saint-Hilaire, Isid. Geoffroy Saint-Hilaire, Guérin, Guillemin, A. De Jussieu, Kunth, Latreille, Lesson, C. Prévost, A. Richard, et Bory de Saint-Vincent. p. 511, *Dictionnaire classique d'Histoire naturelle*, Vol. 16 (T-Z) J. Tastu, Paris. 748. [in 17 volumes published between 1822 and 1831 (16 vols text, 1 vol. Atlas).

Milne Edwards, H., 1833. Note sur un nouveau genre de Crustacés de l'ordre des Stomapodes. *Annals du Societie Entomologie, France*, 1: 336-340 pl. 12.

Milne Edwards, H., 1834. *Histoire naturelle des Crustacés*, comprenant l'anatomie, la physiologie et la classification de ces Animaux. Vol. 1, xxxv + 468 pp. Librairie encyclopédique de Roret, Paris, France.

Milne Edwards, H., 1837. *Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux*. Vol. 2, 532 pp., Atlas 32 pp., 42 pls. Librairie de Roret, Paris, France.

Milne Edwards, H., 1837. Les Crustacés. In G. Cuvier (ed.) *Le Règne Animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux, et d'introduction à l'anatomie comparée*. 278 pp., Atlas, pls 1–80. Déterville, Paris, France.

Milne Edwards, H., 1852. De la famille des ocypodides (Ocypodidae). Second Mémoire. In Observations sur les affinités zoologiques et la classification naturelle des Crustacés. *Annales des Sciences Naturelles, Series 3 (Zoology)*, 18: 128-166, pls. 3, 4. [Reprinted with separate pagination in undated Mélanges Carcinologique s pp. 73-128].

Milne Edwards, H., 1853. De la famille des ocypodides (Ocypodidae), suite. *Annales des Sciences Naturelles series 3 (Zoology),* 20: 163–228, pls. 6-11. [A continuation of H. Milne Edwards, 1852, and reprinted in undated Mélanges Carcinologiques pp. 129-196.].

Milne Edwards, H., 1854. Notes sur quelques Crustaces nouveaux on peu connus conserves dans la collection du Museum d'Historic Naturelle. *Archives du Museum d historie Naturelle* (Paris), 7:145-192.

Milne Edwards, H. & H. Lucas, 1841. Description des Crustacés nouveau ou peu connus conservés dans la collection du Museum d'Histoire Naturelle. *Archiv du Museum d'Histoire Naturelle, Paris,* 2: 461-473.

Minei, H., 1972. Distribution and ecological notes of two Japanese grapsids (Decapoda, Crustacea). *Scientific Bulletin of Faculty of Agriculture, Kyushu University,* 27: 49-53.

Mingkid, W.M., S. Akiwa, & S. Watanabe, 2006. Morphological characters, pigmentation, and distribution of the sibling penicillate crabs, *Hemigrapsus penicillatus* (De Haan, 1835) and *H. takanoi* Asakura & Watanabe, 2005 (Decapoda, Brachyura, Grapsidae) in Tokyo Bay. *Crustaceana*, 79(9): 1107-1121.

Miyake, S., 1939. Notes on Crustacea Brachyura collected by Professor Teiso Esaki's Micronesia Expeditions 1937-1938 together with a checklist of Micronesian Brachyura. *Records of Oceanographic Works of Japan*, 10(2): 168-247, pls 12-17.

Miyake, S., 1961a. A list of the decapod Crustacea of the Sea of Ariaké, Kyushu. *Records of oceanography Workshops, Japan, Special number,* 5: 165-178.

Miyake, S., 1961b. *Fauna and Flora of the Sea around the Amakusa Marine Biological Laboratory,* 2. *Decapod Crustacea*. 30 pp, 1 text-fig. Amakusa Marine Biological Laboratory, Kyushu University, Amakusa, Japan.

Miyake, S., 1963. On decapod crustaceans from the Yaéyama Group, Ryukyu Islands. *Reports on Commission of Foreign Scientific Research, Kyushu University*, 1: 61-73, pl. 1.

Miyake, S., 1983. *Japanese Crustacean Decapods and Stomatopods in color. Vol. II. Brachyura (Crabs)*. VIII, 277 p., 64 pls. Hoikusha, Osaka., Japan.

Miyake, S., K. Sakai & S. Nishikawa, 1962. A fauna-list of the decapod Crustacea washed by the Tsushima warm current. *Records of Oceanographic Works of Japan, Special Nnumber*, 6: 121-131.

Mo, J.L., B.P. Devos & G. Trausch, 2003. Asprption of Cl- and Na+ in posterior gills of the Chinese crab, *Eriocheir sinensis*: Modulation by Dopamine and cAMP. *Journal of Crustacean Biology*, 23(3): 505–512.

Mocquard, M.F., 1883. L'estomac des Crustacés podophthalmaires. *Annales des Sciences Naturelles*, 16(1): 1-313, pls. 1-11.

Ferraris, J.D. & S.R. Palumbi, 1996. Molecular Zoology: Advances, Strategies and Protocols. 580 pp. 10 maps. Wiley-Liss, New York, United States of America.

Monod, Th., 1930. Über einige Indo-pazifische Decaopden de meeresfauna Syriens, *Zoologischer Anzeiger*, 92: 135-141, 8 text figs., 1 map.

Monod, Th., 1933. Brachyura Maroccana. 1. Pinnotheridae, avec description d'*Asthenognsthus atlanticus* nov. sp. II. Dromiidae, Oxystomata, Oxyrhyncha, Brachyrhyncha (excl. Pinnotheridae). *Bulletin of the Society of National Sciences, Morocco*, 12: 142-155, 9 figs., 199-220, 7 figs.

Monod, Th., 1956. Hippidea et Brachyura ouest-africains. *Mémior Institute du France Afrika Noire*, 45: 1-674, 884 figs.

Monteforte, M., 1984. *Contibution à la connaissance de la faune carcinologique de French Polynésia. Inventaire faunistique, répartition bionomique et données quantitatives sur les Crustacés Décapodes Reptantia (Brachuyra, Bonomura, Macrura) et les Crustacés Stomatopodes habitant les complexes récifo-lagonaires de quelque îles hautes et atolls*. Thèse de l'Ecole Pratique des Hautes Etudes, 3ème section: 1-196, figs. 1-33, ta. a-s, photographies.

Montgomery, S.K., 1931. Report on the Crustacea Brachyura of the Percy Sladen Trust Expedition to the Abrolhos Islands under the leadership of Professor W.J. Dakin, in 1913; along with other crabs from Western Australia. *Journal of the Linneanus Society*. 37: 405-465 1 text-fig. Pls. 24-30.

Montú, M., K. Anger & C. de Bakker, 1996. Larval development of the Chinese mitten crab *Eriocheir sinensis* H. Milne Edwards (Decapoda: Grapsidae) reared in the laboratory. *Helgoländer Meeresunteruchungen*, 50: 223-252, figs.1-16, tab. 1.

Moreira, C., 1901. Contribuções para o conhecimento da fauna Brazileira. Crustaceos do Brazil. *Archive of Museum, Rio de Janeiro*, 11: I-IV, 1-152, pls 1-5.

Morita, T., 1974. Morphological observation on the development of larva of *Eriocheir japonica* De Haan. *Zoological Magazine*, 83: 24-81.

Morrisey, D.J., T.H. de Witt, D.S. Roper & R.B. Williamson, 1999. Variation in the depth and morphology of burrows of the mud crab *Helice crassa* among different types of intertidal sediment in New Zealand. *Marine Ecology Progress Series*, 182: 231-242, tables 1-4, text-figs. 1-6.

Morrison, J.P., 1954. Animal Ecology of the Raroia atoll, Tuamotu. Part 1. Ecological notes on the mollusks and other animals of Raroia. *Atoll Research Bulletin*, 34: 1-18.

Morton, B. & J. Morton, 1983. *The sea shore ecology of Hong Kong*. XIV, 350 p., 28 pls. Hong Kong University Press, Hong Kong.

Morton, J.E. & M. Miller, 1968. *New Zealand Seashore*. 638 pp. Collins, London, United Kingdom.

Morton, J.E., 1973. The seashore. In: G.R. Williams (ed.). *The Natural History of New Zealand: An Ecological Survey*. Pp. 93–130. A.H. & A.W. Reed, Wellington, New Zealand.

Motoh, H., 1999. *Edible shrimps and crabs from the Sea of Japan*. 98 pp. with colour plates., Ashigara Printing Co. Ltd., Minami-Ashigara City, Japan.

Mukae, H., H. Taniguchi & N. Matsumoto, 2001. Clinicoradiologic features of pleuropulmonary *Paragonimus westermani* on Kyusyu Island, Japan. *Chest*, 120: 514-520.

Murano, M., 1975. Phytoplankton in the waters surrounding a new active volcanic island, Nisinosima-sin-To. *Journal of Tokyo University, Fisheries*, 61(1-2): 93-

107.

Muraoka, K., 1971. On the post-larval characters of the two species of shore crabs. *Researches on Crustacea,* 4/5: 225-234, figs.1-4.

Muraoka, K., 1974. On the megalopa of *Hemigrapsus penicillatus* (De Haan), Brachyuran crab. *Researches on Crustacea*, 6: 52-57, figs. 1-2, tab.1.

Muraoka, K., 1998. Catalogue of the Brachyuran and Anomuran Crabs donated by Prof. Dr. Tune Sakai to the Kanagawa Prefectural Museum. *Catalogue of the Collection in the Kanagawa Prefectural Museum of Natural History*, 11: 5-67, pls 1-16.

Muraoka, K. & S. Satoh, 1977. On the post-larval stage of *Ptychognathus barbatus* (A. Milne Edwards) (Crustacea, Brachyura, Grapsidae). *Bulletin of the Kanagawa Prefecture Museum,* 10: 15-21, figs. 1-3, tab. 1.

Nagai, S. & K. Nomura, 1988. *Okinawan Marine Organisms.* No. 7, Crab. Shinsei Tosho, Okinawa, Japan. [In Japanese].

Naiyanetr, P., 1998. Checklist of Cruatacean fauna in Thailand (Decapoda and Stomatopoda). 161 pp. Office of Enviromental Policy and Planning, Thailand.

Nakamura, I. & M. Takeda, 1972. A new species of the Grapsidae (Crustacea, Brachyura) from Bali Island in the collection of the National Science Museum, Tokyo. *Bulletin of the National Science Museum*, *Zoology*, Tokyo, 15(3): 435-439.

Nakamura, Y. & Y. Koike, 1975. On the change of the bottom topography in the surrounding area of the island Nisino-sima. *Journal of Tokyo University, Fisheries*, 61(1-2): 37-40. [In Japanese with English abstract].

Nakamura-Uchiyama, F, H. Mukae, & Y. Nawa, 2002. Paragonimiasis: a Japanese perspective. *Clinical Chest Medicine*, 23: 409-420.

Nakasone, Y., 1977. Crab zonation in the Yuhi River, Okinawa Island. *Japanese Journal of Ecology*, 27(1): 61-70.

Nakasone, Y. & M. Irei. 2003. Grapsidae. Pp. 272–282. In: Nishida, M, N. Shikatani, & S. Shokita (eds.). *The flora and fauna inland waters in the Ryukyu Islands*. 572 p. Tokai University Press, Tokyo, Japan.

Nakasone, Y., Y. Ono & S. Goshima, 1983. Daily activity and food consumption of the sesarmid crab *Chasmagnathus convexus* (Decapoda, Brachyura). *Bulletin of the College of Education, University of Ryukyus*, 26(2): 37-53.

Nakazawa, K. & T. Sakai, 1947. Decapoda, Brachyura. In: S. Uchida *et al.* (eds.). *Encyclopaedia Zoologica*. Pp. 649-730, figs. 1875-2114. Hokuryukan, Tokyo, Japan.

Naruse, T. & H. Tamura, 2006. A first record of anchialine crab of the genus *Orcovita* Ng & Tomascik, 1994 (Decapoda: Brachyura: Varunidae) from Japan, with descriptopn of the species. *Limnology,* 7(3): 147-151.

Naruse, T. 2005. *Ptychognathus altimanus*. In: Nature Conservation Division (Department of Cultural and Environmental Affairs, Okinawa Prefectural Government) (ed.). *Threatened wildlife in Okinawa.* Second edition (Animals) - Red Data Okinawa, p. 223. Nature Conservation Division, Department of Cultural and Environmental Affairs, Okinawa Prefectural Government, Okinawa, Japan.

Naruse, T., H.T. Shih, N.K. Ng, & H.L. Hsu, 2005. On two new records of varunid crabs (Crustacea: Brachyura: Varunidae) from Southern Taiwan. *Collections and Research Taiwan*, 18: 69-79.

Nauck, E., 1880. Das Kaugerüst der Brachyuren [mit Beshreibung neuer Gattungen und Arten, z. T. von C. Semper]. *Zeitschrift Fur Wissenschaftliche Zoologie*, 34(1): 1-69, pl. 1.

Naylor, E., 1957. *Brachynotus sexdentatus* (Risso), a grapsoid crab new to Britain. *Annual Magazine of Natural History*, 10(12): 521-523, 1 fig.

Naylor, E. & B.G. Williams, 1984. Phase-responsiveness of the circatidal locomotor activity rhythm of *Hemigrapsus edwardsi* (Hilgendorf) to simulated high tide. *Journal of the Marine Biological Association, United Kingdom*, 64: 81-90.

Nepszy, S.J. & J.H. Leach, 1973. First records of the Chinese mitten crab, *Eriocheir sinensis* (Crustacca: Brachyura) from North America. J*ournal of the Fisheries Research Board of Canada*, 30: 1909-1010.

Newman, W.A., 1979. A new scalpellid (Cirripedia); A Mesozoic relic living near an abyssal hydrothermal spring. *Transactions of the San Diego Society of Natural History*, 19: 153-167.

Newman, W.A., 1985a. Preliminary report on the limpets at hydrothermal vents. *Bulletin of the Biological Society of Washington*, 6: 159-166.

Newman, W.A., 1985b. The abyssal hydrothermal vents invertebrate fauna. A glimpse of antiquity? *Bulletin of the Biological Society of Washington*, 6: 231-242.

Newman, W.A. & R.R. Hessler, 1989. A new abyssal hydrothermal verrucomorphan (Cirripedia; Sessilia): The most primitive living sessile barnacle. *Transactions of the San Diego Society of Natural History*, 21: 259-273.

Ng, N.K. & T. Komai. 2000. Notes on the male of *Scutumara enodis* Ng & Nakasone, 1993 (Crustacea: Decapoda: Brachyura: Grapsidae). *Proceedings of the Biological Society of Washington* (USA), 113 (1): 48-53.

Ng, N.K. & P.K.L. Ng. 2002. *Orcovita mcneiceae*, a new species of anchialine crab (Brachyura, Grapsidae, Varuninae) from the Loyalty Islands. *Crustaceana*, 75: 663–670.

Ng, N.K. & P.K.L. Ng, 2007. *Cancer setosus* Fabricius, 1798: (currently *Pseudograpsus setosus*; Crustacea, Decapoda): Proposed replacement of syntypes by a neotype. *Bulletin of Zoological Nomenclature* (United Kingdom). [In press].

Ng, N.K. & M. Segonzac, 2006. Arthropoda, Crustacea, Decapoda, Brachyura, Grapsidae. *Denisia* 18: 474.

Ng, N.K., J. Guo & P.K.L. Ng, 1999. On the generic affinities of *Eriocheir leptognathus* Rathbun, 1913, and *Eriocheir formosa* Chan, Hung and Yu, 1995, with description of a new genus (Crustacea: Grapsidae: Varuninae). *Journal of Crustacean Biology*, 19: 154-170.

Ng, N.K., J.-F.Huang & P.-H. Ho. 2000. Description of a new species of hydrothermal crab, *Xenograpsus testudinatus* (Crustacea: Decapoda: Brachyura: Grapsidae). In: Hwang, J.-S., Wang, C.-H., Chan, T.-Y. (Eds). *Proceedings of the International Symposium on Marine Biology in Taiwan – Crustacean and Plankton Taxonomy, Ecology and Living Resources.* 26-27 May, 1998, Taiwan. National Taiwan Museum Special Series, No. 10, March 2000: 191–199, figs 1–3.

Ng, N.K., M.S. Jeng & P.K.L. Ng, 2002. On the taxonomy of *Pseudograpsus setosus* (Fabricius, 1778) (Decapoda, Brachyura, Grapsidae). *Crustaceana*, 75(6): 759-776.

Ng, N.K., H.C. Liu & P.H. Ho, 2001. *Plagusia speciosa* Dana, 1851, a new record for Taiwan (Crustacea: Decapoda: Brachyura: Plagusiinae) with a key to the genus for Taiwan. *National Taiwan Museum Special Publication* (Taiwan), 53(2): 13-22.

Ng, N.K., M.R. Manuel & P.K.L. Ng. 2006. A new genus of varunid crabs from the Philippines (Crustacea: Decapoda: Grapsidae). *Proceedings of the Biological Society of Washington*, 119(1): 49-57.

Ng, N.K., S. Yang & A. Dai. Notes on the Varunine crabs of China. *Fauna Sinica*. Beijing Ocean Press, People's Republic of China. [In press].

Ng, N.K., S. Yang & P.K.L. Ng. Comparative studies on the gastric mills of *Eriocheir* De Haan, 1835, *Neoeriocheir* Sakai, 1983, and *Platyeriocheir* Ng, Guo and Ng, 1999 (Crustacea: Decpapoda: Grapsidae). *Crustaceana.* (Submitted)

Ng, N.K., A.Y. Dai, J. Guo & P.K.L. Ng, 1998. The complete larval development of the southern Chinese mitten crab, *Eriocheir hepuensis* Dai, 1991 (Decapoda, Brachyura, Grapsidae) reared under laboratory conditions. *Crustaceana*, 71: 493-517.

Ng, P.K.L., 1988. *The Freshwater Crabs of Peninsular Malaysia and Singapore.* Pp 1-152, i-viii. Department of Zoology, National University of Singapore & Shinglee Publishers Pte. Ltd,. Singapore.

Ng, P.K.L., 1998. Crabs. In: K. E. Carpenter & V. H. Niem (eds.). *FAO Species identification guide for fishery purposes. The living marine resources of the Western Central Pacific.* Volume 2. Cephalopods, crustaceans, holothurians and sharks. Pp. 1045-1155. Food and Agriculture Organisation, Rome.

Ng, P.K.L. & D. Dudgeon, 1992. The Potamidae and Parathelphusidae (Crustacea: Decapoda: Brachyura) of Hong Kong. *Invertebrate Taxonomy*, 6: 741-768.

Ng, P.K.L. & Y. Nakasone, 1993. *Scutumara enodis*, a new genus and species of grapsid crab (Decapoda: Brachyura) from Okinawa, Ryukyus, Japan. *Crustacean Research, Tokyo, Japan*, 22: 1-6.

Ng, P.K.L. & T. Tomascik. 1994. *Orcovita saltatrix*, a new genus and species of anchialine varunine crab (Crustacea: Decapoda: Brachyura: Grapsidae) from Kakaban Island, Indonesia. *Raffles Bulletin of Zoology,* 42(4): 937-948.

Ng, P.K.L. & C.G.S. Tan, 1995. *Geosesarma notophorum* sp. nov. (Decapoda, Brachyura, Grapsidae, Sesarminae), a terestrail crab from Sumatra, with novel brooding behaviour. *Crustaceana*, 68(3): 390-395.

Ng, P.K.L. & N. Sivasothi (eds). 1999. A Guide to Mangroves of Singapore", Volume 2: Animal Diversity. Pp. 168. BP Guide to Nature Series published by the Singapore Science Centre, sponsored by British Petroleum, Singapore.

Ng, P.K.L. & P.F. Clark, 2000. The eumedonid file: a case study of systematic compatibility using larval and adult characters (Crustacea: Decapoda: Brachyura). *Invertebrate Reproduction and Development*, 38 (3): 225-252.

Ng, P.K.L. & P.F. Clark, 2000. The Indo-Pacific Pilumnidae XII. On the familial placement of *Chlorodiella bidentata* (Nobili, 1901) and *Tanaocheles stenochilus* Kropp, 1984 using adult and larval characters with the establishment of a new subfamily, Tanaochelinae (Crustacea: Decapoda: Brachyura). *Journal of Natural History*, 34: 207-245.

Ng, P.K.L., & S.T. Ahyong, 2001. The brachyuran crab types in the MacLeay Collection. *Raffles Bulletin of Zoology*, 49(1): 83–100

Ng, P.K.L. & C.D. Schubart, 2002. *Haberma nanum*, a new genus and new species of mangrove crab (Crustacea: Decapoda: Brachyura: Sesarmidae) from Singapore. *Raffles Bulletin of Zoology*, 50(2): 437-442.

Ng, P.K.L. & H.C. Liu. 2003. On a new species of tree-climbing crab of the genus *Labuanium* (Crustacea: Decapoda: Brachyura: Sesarmidae) from Taiwan. *Proceedings of Biological Society of Washington*, 116: 601-616.

Ng, P.K.L., H.C. Liu, & C.D. Schubart. 2004. *Geosesarma hendon*, a new species of terrestrial crab (Crustacea: Decapoda: Brachyura: Sesarmidae) from Taiwan and the Philippines. *Raffles Bulletin of Zoology*, 52: 239-249.

Ng, P.K.L., D. Guinot & T.M. Iliffe, 1996. Revision of the anchialine varunine crabs of the genus *Orcovita* Ng & Tomascik, 1994 (Crustacea: Decapoda: Brachyura: Grapsidae), with descriptions of four new species. *The Raffles Bulletin of Zoology*, 44(1): 109-134.

Ng, P.K.L., C.H. Wang, P.H. Ho & H.T. Shih, 2001. An annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). *National Taiwan Museum*

*Special Publication Series,* Taipei, Taiwan, 11: 1-86, 8 colour pls.

Nicolet, H., 1849. *Crustaceos*. In: C. Gay (ed.). *Historia fisica y politica de Chile*. Pp. 115-318. Paris, Frnace.

Nijland, R., 2000. Huidige verspreiding penseelkrab (*Hemigrapsus penicillatus*) in Nederland. *Het Zeepaard,* 60(6): 316-318.

Nijland, R., 2003. *Hemigrapsus penicillatus*: een niewe krab in Nederland. *Natura*, 100: 72-74.

Nijland, R. & J. Beekman, 2000. *Hemigrapsus penicillatus* De Haan 1835 waargenomen in Nederland. *Het Zeepaard*, 60(3): 169-171.

Nisbet, E.G., 1987. *The Young Earth*. Allen & Unwin, Winchester, Massachusett, United States of America.

Nisbet, E.G., & N.H. Sleep, 2001. The habitat and nature of early life. *Nature*, 409:1083-1091.

Nixon, K.C., 1999. The Parsimony Ratchet, a new method for rapid parsimony analysis. *Cladistics*, 15: 407-414.

Nixon, K.C. & J.M. Carpenter, 2000. On the other ‘phylogenetic systematics’. *Cladistics*, 16: 298-318.

Nobili, G., 1899. Contribuzioni alla conoscenza della fauna carcinologica della Papuasia, delle Molucche e dell' Australia. *Annuals Museum Civic Stor. Nat. 'Giacomo Doria'*, 20: 230-282, 358, 473-523

Nobili, G., 1903. Crostacei di Singapore. *Bolletin Museum of Zoologi Comp., Torino,* 18(455): 1-39, 1 pl.

Nobili, G., 1907. Ricerche sui Crostacei della Polinesia. Decapodi. Stomatopodi, Anisopodi e Isopodi. *Memori della Reale Accademia delle Scienze di Torino, ser. 2*, 57: 351-430, pls. 1-3.

Noël, P.Y., E. Tardy & C.d. d'Acoz, 1997. Will the crab *Hemigrapsus penicillatus* invade the coasts of Europe? *Comptes Rendus de l'Academie des Sciences Series III Sciences de la Vie,* 320(9): 741-745.

Nomoto, A., S. Yodo, S. Kimura, T. Kishino, M. Sakano & K. Wada. 1999. Six rare brachyuran species of the family Grapsidae, recorded from the Kinokawa River Estuary, Wakayama Prefecture. *Nankiseibutsu*, 41(1): 5–9.

Normant, M., A. Wiszniewska, & A. Szanlaska, 2000. The Chinese mitten crab *Eriocheir sinensis* (Decapoda: Grapsidae) from Polish Waters. *Oceanologia*, 42(3): 375-383.

Nye, P.A., 1977. Reproduction, growth and distribution of the grapsid crab *Helice crassa* (Dana, 1851) in the southern part of New Zealand. *Crustaceana*, 33(1): 75-89, pl. 1.

Ogura, M. & Y. Kishi, 1985. Reproductive period and occupation of empty beverage cans by males of the crabs, *Hemigrapsus penecillatus* (De Haan). *Japanese Journal of Ecology*, 35: 377-385.

Okamoto, K. & Y. Kurihara, 1987a. Seasonal variation of population structure of *Hemigrapsus penicillatus* (De Haan) (Crustacea: Brachyura). *Japanese Journal of Ecology*, 37: 81-89.

Okamoto, K. & Y. Kurihara, 1987b. Cannibalism in a grapsid crab, *Hemigrapsus penicillatus* (De Haan) (Crustacea: Brachyura). *Marine Ecology Progress Series*, 41: 123-127.

Okamoto, K. & Y. Kurihara, 1989. Feeding habit and food selection of the grapsid crab *Hemigrapsus penicillatus* (De Haan) (Crustacea: Brachyura). *Japanese Journal of Ecology*, 39: 195-202.

Oliveira, L. de, 1948. Estudo hidrobiológico das lagôas de Piratininga e Itaipú. *Memórias do Instituto Oswaldo Cruz*, 46(4): 673-718, maps 1-4.

Oliveira, L. de, 1950. Levantamento biogeográfico de Baía de Guanabara. *Memórias do Instituto Oswaldo Cruz*, 48: 365-391.

Oliveira, L. de, 1958. Poluição das áquas marítimas. *Memórias do Instituto Oswaldo Cruz*, 56(1): 39-78, pls 1-9.

Oliveira, L. de & L. Krau, 1953. Levantamento biogeográfico de Baía de Guanabara. II Crescimento do manguezal na Ilha do Pinheiro. *Memórias do Instituto Oswaldo Cruz*, 51: 503-544.

Oliveira, L. de, R. Nascimento, L. Krau & A. Miranda, 1955. Biogegraphic and hydrobiologic observartions on the Lake of Maricá. *Memórias do Instituto Oswaldo Cruz,* 53(2-4): 228-262, tables 1-12, text-figs. 1-18.

Oliveira, L.P.H., de, 1940. Contribuição ao conhecimento dos crustaceos do Rio de Janeiro. *Memórias do Instituto Oswaldo Cruz,* 35(1): 137-151.

Oliveira, L.P.H., de, 1962. Estádios larvários do caranguejo "catanhen" *Chasmagnathus granulata* Dana, 1851 (Crustacea, Grapsidae). *Memórias do Instituto Oswaldo Cruz,* 60(2): 257-262.

Oliver, W.R.B., 1923. Marine littoral plant and animal communities in New Zealand. *Proceedings of the New Zealand Institute,* 54: 496-545, pls. 42-50.

Omori, K., K. Shiraishi & M. Hara, 1997. Life histories of sympatric mud-flat crabs, *Helice japonica* and *H. tridens* (Decapoda: Grapsidae) in a Japanese estuary. *Journal of Crustacean Biology*, 17(2): 279-288.

Ono, Y., 1959. The ecological studies on Brachyura in the estuary. *Bulletin of the Marine Biological Station, Asamushi, Tohoku University*, 9(4): 145-148.

Ortmann, A., 1894. Die Decapoden-Krebse des Strassbuger Museum. VIII, Catametopa. *Zoologischen Jahrbuchern, Abtheilung fur Systematik, Jena*, 8: 683-772, pl. 23.

Ortmann, A., 1894a. Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berückishtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen. VIII Theil. Abtheilung: Brachyura (Brachyura genuina Boas), III. Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 2. Gruppe: Catametopa. *Zooloische Jahrbücher Abteilung Systematic Geograph Biologische Tiere,* 7: 683-772, Pl. 23.

Ortmann, A., 1894b. Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen. *Zoologischen Jahrbuchern, Abtheilung fur Systematik*, Jena, 8: 683-772, pl. 23.

Ortmann, A.E. 1898. Gliederfüssler: Arthropoda. In: *Dr. H. G. Bronn's Klassen und Ordnungen des Tierreichs*. Vol. 5(2), Crustacea, Malacostraca, (47-52) [Systematik] pp. 1057-1168.

Ortmann, A.E., 1894c. Crustaceen. In: R. Semon, (ed.). *Zoologische Forschungsreisen in Australien und dem Malayischen Archipel ausgeführt in den Jahren 1891-93.* V. Denkschr. mediz.-naturwiss. Ges. Jena, 8: 1-80, pls 1-13.

Ortmann, A.E., 1902. The geographical distribution of freshwater Decapoda and its bearing upon ancient geography. *Proceedings of the American Philosophical Society*, 41: 267-400, 8 figs.

Osawa, M. & N.K. Ng, 2006. A new species of *Ptychognathus* Stimpson, 1858 (Crustacea: Decapoda: Brachyura: Varunidae) from the Ryukyu Islands, southwestern Japan. *Zootaxa*, 1260: 57-66.

Oshima, M., 1921a. Supplement to the species list of the crabs and shrimps from Formosa. *Zoological Magazine*, 33: 122-124.

Oshima, M., 1921b. Supplement to the species list of the decapod crustaceans from Formosa. *Zoological Magazine*, 33: 226-227.

Oshima, K., 1966. Burrows of intertidal crabs I. Marsh crab *Helice tridens tridens* de Haan. *Chikyu Kagaku* (= Earth Science), 87: 9-12, pls. 1-2.

Owen, R., 1860. On the Order of Fossil and Recent Reptilia, and their Distribution in Time. *Report of the British Association for the Advancement of Science*, 1859:153-166.

Ozaki, K., 1956. Crabs at Minabe, Wakayama Pref., Japan. *Nanki Kyodo-gakkai* (=Provincial Society of South Wakayama), 40: 1-12. [In Japanese].

Palmer, J.D. & B.G. Williams, 1986. Comparative studies of tidal rhythms. II. The dual clock control of the locomotor rhythms of two decapod crustaceans. *Marine behavior and Physiology*, 12: 269-278.

Palumbi, S., A. Martin, S. Romano, W.O. McMillan, L. Stice, & G. Grabowski, 1991. The simple fools guide to PCR, Version 2.0. University of Hawaii, United States of America.

Panning, A. & N. Peters, 1933. Die chinesische Wollhandkrabbe (*Eriocheir sinensis* H. Milne-Edwards) in Deutschland. *Zoologischer Anzeiger*, 101: 265-271, 6 figs.

Panning, A., 1933. In: N. Peters, A. Panning & Schnakenbeck (ed.) *Die chinesische Wollhandkrabbe in Duetschland*. *Zoologischer Anzeiger*. Erg.-Bd. zu Bd. 104.

Panning, A., 1938. Systematisches uber *Eriocheir sinensis* H. Milne-Edwards. In: *Reports of the Hamburg Zoological Museum and Institute*. Vol. 47.

Panning, A., 1939. *The Chinese mitten Crab*. Annual Report, Smithsonian Institution, 1938: 361-375.

Panning, A., 1939. Die larven von *Eriocheir sinensis* H. M-Edw. *Zoologischer Anzeiger*, 125: 273-283.

Panning, A., 1952. *Die chinesische Wollhandkrabbe.* Neue Brehmbüch. 70: 1-45, 11 figs., 2 maps.

Parisi, B., 1916. I Decapodi Giapponesi del Museuo di MI-Lano. IV. Cyclometopa. *Atti della Societa Italiana di Scienze Naturali*, 55: 153-190.

Parisi, B., 1918. I Decapodi giapponesi del Museo di Milano. VI. Catometopa e Paguridea. *Atti de la Societa Italiana di Scienze Naturali (Milano)*, 57: 90-115, pl. 8.

Park, T.K., 1964. On the crabs in the eastern sea of Korea. *Korean Journal of Zoology*, 7(1): 15-19.

Park, Y.S. & H.S. Ko, 2002. Complete larval development of *Hemigrapsus longitarsis* (Miers, 1879) (Crustacea, Decapoda, Grapsidae), with a key to the known grapsid zoeas of Korea. *Korean Journal of Biological Sciences*, 6: 107-123, figs. 1-12, tab. 1.

Pastore, M., 1976. Decapoda Crustacea in the Gulf of Taranto and the Gulf of Catania with a discussion of a new species of Dromiidae (Decapoda: Brachyura) in the Mediterranean Sea. *Thalassia Jugoslavica*, 8(1): 105-117.

Pasupathi, K. & T. Kannupandi, 1988. The zoeae, megalopa and the first crab of the mangrove crab *Metaplax elegans* de Man, cultured in the laboratory. *Mahasagar*, 21: 145-160.

Paunovic, M., P. Cakic, A. Hegedis, J. Kolarevic, & M. Lenhardt, 2004. A report of *Eriocheir sinensis* (H. Milne Edwards, 1854) (Crustacea: Brachyura: Grapsidae) from the Serbian part of the Danube River. *Hydrobiologia*, 529(1-3): 275-277.

Pearson, W.H. & B.L. Olla, 1977. Chemoreception in the blue crabs, *Callinectes sapidus*. *The Biological Bulletin*, 153: 346-354.

Pearson, W.H., P.C. Sugarman & D.L. Woodruff, 1979. Thresholds for detection and feeding behaviour in the Dungeness crab, *Cancer magister* (Dana). *Journal of Experimental Marine Biology and Ecology*, 39: 65-78.

Pellegrino, C.R., 1984. The role of desiccation pressures and surface/volume relationships in seasonal zonation and size distribution of four intertidal decapod crustaceans from New Zealand: implications for adaptations to land. *Crustaceana*, 47: 251–268.

Peng, W., 1986. Preliminary study on the problem of variation of *Eriocheir sinensis* in Zhujiang river valley. *Information of Fisheries Science and Technology*, 2: 19-22.

Péqueux, A. & R. Gilles, 1981. $Na^+$-fluxes across isolated perfused gills of the Chinese crab *Eriocheir sinensis*. *Journal of Experimantal Biology*, 92: 173-186.

Péqueux, A, A. Bianchini & R. Gilles, 1996. Mercury and Osmoregulation in the euryhaline crab, *Eriocheir sinensis*. *Comparative Biochemistry and Physiology, Part C: Pharmacology, Toxicology and Endocrinology*, 113(2): 149-155.

Péqueux, A., A. Marchal, S. Wanson, & R. Gilles, 1984. Kinetic characteristics and specific activity of (Na++K+)-ATPase in the euryhaline crab *Eriocheir sinensis* during acclimation. *Marine Biological Letters*, 5: 35-45.

Péqueux, A., P. Le Bras, C. Cann-Moisan, J. Caroff & P. Síbert, 2002. Polyamines, indolamines, and catecholamines in gills and haemolymph of the euryhaline crab, *Eriocheir sinensis.* Effects of high pressure and salinity. *Crustaceana*, 75(3-4): 567-578.

Pereyra Lago, R., 1993a. Larval development of *Sesarma guttatum* A. Milne Edwards (Decapoda, Brachyura, Grapsidae) reared in the laboratory with comments on larval generic and familial characters. *Journal of Crustacean Biology*, 13: 745-762.

Pereyra Lago, R., 1993b. Zoeal developmentof *Sesarma eulimene* De Man (Decapoda, Brachyura, Grapsidae), and identification of larvae of the genus *Sesarma* in South African waters. *South African Journal of Zoology*, 28: 173-181.

Pesta, O., 1913. Zur Kenntnis einiger Tiefsee-Decapoden der Adria. *Zoologischer Anzeiger*. 42: 60-72, 14 figs.

Pestana, D. & A. Ostrensky, 1995. Occurrence of an alternative pathway in the larval development of the crab, *Chasmagnathus granulata* Dana, 1851 under laboratory conditions. *Hydrobiologia,* 306: 33-40.

Peters, N. & A. Panning, 1933. Die Chinesische Wolhandkrabbe (*Eriocheir sinensis* H. Milne Edwards) in Deutsch-land. *Zoologischer Anzeiger*, 104: 1-180.

Petriella A.M. & E.M. Boschi, 1997. Crecimiento en crustáceos decápodos: resultados de investigaciones realizadas en Argentina. *Investigaciones Marias Valparaíso*, 25: 135-157.

Pfiffer, G., 1889. Crustacea. Übersicht der von Herrn Dr. Franz Stuhlmann in Ägypten, auf Sanibar und dem gegenüberliegenden Festlande gesammelten Reptilien, amphibien, Fische, Mollusken und Krebse. *Jahresbericht. Hamburg Wissenschaften Anstalt,* 6: 28-36.

Poinar, G.O. & A. Brocherhoff, 2001. *Nectonema zealandica* n. sp. (Nematomorpha: Nectonematoidea) parasitising the purple rock crab *Hemigrapsus edwardsi* (Brachyura: Decapoda) in New Zealand, with notes on the prevalence of infection and host defence reactions. *Systematic Parasitology*, 50: 149–157.

Porter, C.E., 1936a. Carcinologia Chilena. Enumeracion metodica de los Crustaceos podoftalmos de la Bahia de Talcahuano. *Communcio Museum concepcion*, 1: 150-154.

Porter, C.E., 1936b. Carcinologia Chilena XXVII. Enumeracion metodica de los Crustaceos podoftalmos de la Bahia de Talcahuano. *Review of the Chilena History Nature*, 40: 336-339.

Porter, C.E., 1937. Carcinologia Chilena XXVIII. Introduccion al estudio de los Grapsidos. *Review of the Chilena History Nature,* 41: 20-24, pl. 4, fig 1.

Posada, D., & K. A. Crandall, 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics*, 14: 817-818.

Poupin, J., 1994. *Quelques crustacés décapodes communs de Polynésie française*. Rapport Scientifique du Service Mixte de Surveillance Radiologique et Biologique: 1-86, fig. 1-68, pls. 1-8.

Poupin, J., 1996. Crustaca decapoda of French Polynesia (Astacidea, Palinuridea, Anomura, Brachyura). *Atoll Research Bulletin*, 442: 1-114, figs. I-IV, 1 map.

Poupin, J., 2003. Crustacea Decapoda and Stomatopoda of Easter Island and surrounding areas. A documented checklist with historical overiew and biogeographic comments. *Atoll Research Bulletin*, 500: 1-56.

Powell, A.W.B., 1937. Animal communities of the sea bottom in Auckland and Manukau Harbours. *Transactions of the Royal Society of New Zealand*, 66: 354-401.

Powell, A.W.B., 1947. *Native Animals of New Zealand*. First edition. 96 pp. Unity Press, Auckland, New Zealand.

Powell, A.W.B., 1987. Native Animals of New Zealand. Third edition. 88 pp. Auckland Institute and Museum, Auckland, New Zealand.

Powers, L.W. 1977. A catalogue and bibliography to the crabs (Brachyura) of the Gulf of Mexico. *Contributions in Marine Sciences*, 20: 1-190.

Pretzmann, G., 1971. Ergebnisse einiger Sammelreisen nach Vorderasien. 2. Teil: Marine Brachyura. *Annalen des Naturhistorischen Museums, Wien,* 75: 477-487.

Pretzmann, G., 1981. *Gefährdete Arten decapoder Krebse in der Steiermark.* Rote Listen gefährdeter Tiere der Steiermark. 135-136, 1 fig.

Pretzmann, G., 1984. Results of the Austrian-Indian Hydrobiological Mission 1976 to the Andaman-Islands: Part III: Brachyura from the Andaman Islands. *Annals of Naturhistoire Museum, Wien,* 86B: 141-144, 3 pls.

Rainbow, P.S. & W.H. Black, 2001. Effects changes of salinity on the apparent water permeability of three crab species: *Carcinus maenas, Eriocheir sinensis* and *Necora puber*. *Journal of Experimental Marine Biology and Ecology*, 2604(1): 1-13.

Ramadan, S.E. & N.M. Dowidar, 1976. Brachyura (Decapoda Crustacea) from the Mediterranean waters of Egypt. *Thalassia jugoslavica*, 8(1): 127-139.

Randall, J.W., 1839 (1840). Catalogue of the crustacea brought by Thomas Nuttall and J.K. Townsend, from the West Coast of North America and the Sandwich islands, with description of such species as are apparently new, among which are included several species of different locaiities, previously existing in the collection of the Academy. *Journal of the Academy of natural Science of Philadelphia* 8 (1): 106-147, pl. 3-7.

Rathbun, M.J., 1893. Descriptions of new genera and species of crabs from the west coast of North America and the Sandwich Islands. In: Scientific Results of Exploration by the U.S. Fish Commission "Albatross". No XXIX. *Proceedings of the United States National Museum*, 16(933): 223–260.

Rathbun, M.J., 1898. The Brachyura collected by the U.S. Fish Commission Steamer "Albatross", on the voyage from Norfolk, Virginia, to San Francisco, California, 1887-1888. *Proceedings of the United States National Museum*, 21(1162): 567-616, pls 41-44.

Rathbun, M.J., 1900. Synopses of North-American invertebrates. XI. The catometopous or grapsoid crabs of North America. *American Naturalist*, 34: 583–529.

Rathbun, M.J., 1900. The Decapod Crustaceans of West Africa. *Proceedings of the United States National Museum*, 22: 271-316, 2 figs.

Rathbun, M.J., 1902. Japanese stalk-eyed Crustaceans. *Proceedings of the United States National Museum*, 26: 23-55, 24 figs.

Rathbun, M.J., 1906. The Brachyura and Macrura of the Hawaiian Islands. *Bulletin of United States Fishery Commission*, 23(3): 827-930, text-figs 1-79 pls 1-24

Rathbun, M.J., 1907. Reports on the scientific results of the expedition to the Tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission steamer Albatross, from August 1899, to March 1900, Commander Jefferson F. Morser, U.S.N., commanding - IX. ibidem. from October 1904, to Match 1905, lieut.-commander L. M. Garrett, U. S. N., commanding - X. The brachyura. *Memoirs of the Museum of Comparative Zoology at Harvard College*, 35(2): 23-74, pls. 1-9.

Rathbun, M.J., 1909. New crabs from the Gulf of Siam. *Proceedings of the Biological Society of Washington*, 22, 107–114.

Rathbun, M.J., 1910a. Decapod Crustaceans collected in Dutch East India and elsewhere by Mr. Thomas Barbour in 1906-1907. *Bulletin of Museum of Comparative Zoology*, 52(16): 305-317, Pls. 1-6.

Rathbun, M.J., 1910b. The Danish Expedition to Siam 1899-1900. V. Brachyura. *Kongelige Danske Videnskabernes. Selskabs. Skrifter. Kjobenhavn*, 7(4): 303-368, pls. 1-2.

Rathbun, M.J., 1910c. The stalk-eyed Crustacea of Peru and the adjacent coast.

*Proceedings of the United States National Museum*, 38: 531-620, pls. 36-56.

Rathbun, M.J., 1913. Descriptions of new species of crabs of the families Grapsidae and Ocypodidae. *Proceedings of U.S. National Museum*, 46: 353-358, pls. 30-33. [The date of publication of this volume was stated as December 1913, not 1914 as indicated by the reprint.]

Rathbun, M.J., 1914a. New genera and species of American Brachyrhynchous Crabs. *Proceedings of the United States National Museum*, 47: 117-129, 5 figs., pls. 1-10.

Rathbun, M.J., 1914b. New species of crabs of the families Grapsidae and Ocypodidae. Scientific results of the Philippine cruise of the fisheries steamer "Albatross." 1907–1910. No. 31. *Proceedings of U. S. National Museum*, 47: 69-85.

Rathbun, M.J., 1918, The grapsoid crabs of America. *United States National Museum Bulletin*, 97: 1-461, figs. 1-172, pls. 1-161.

Rathbun, M.J., 1921. New species of crabs from Formosa. *Proceedings of the Biological Society of Washington*, 34: 155-156.

Rathbun, M.J., 1926. Brachyuran crabs from Australia and New Guinea. *Records of Australian Museum,* 15(2): 177-182, pls. 14-16.

Rathbun, M.J., 1931. New and Rare Chinese Crabs. *Lingnan Science Journal*, 8: 75-125. (Date on paper printed as 1929 but note on back of original reprint indicates the paper was only released in 1931).

Rathbun, M.J., 1932. Preliminary descriptions of new species of Japanese crabs. *Proceedinsg of the Biological Society of Washington,* 45: 29-38.

Rebach, S., D.P. French, F.C., von Staden, M.B. Wilber & V.E. Barrd, 1990. Antenunular sensitivity of the rock crab, Cancer irroratus to food substances. *Journal of Crustacean Biology*, 10(2): 213-217.

Reimer, J., C.D. Schubart & R. Diesel, 1998. Description of a new freshwater crab of the genus, *Sesarma* Say, 1817 (Brachyura: Grapsidae: Sesarminae) from western Jamaica. *Crustaceana*, 71(2): 185-196.

Rice, A.L., 1976. The first zoeal stage of *Scopimera crabricauda* Alcock (Crustacea, Brachyura, Ocypodidae). *Bulletin of the British Museum* (Natural History)

(Zoology series), 30(6): 243-246, fig.1.

Rice A.L., 1979. A plea for improved standards in descriptions of crab zoeae. *Crustaceana*, 37: 214-218.

Rice, A.L., 1980. Crab zoeal morphologyand its bearing on the classication of the Brachyura. *Transaction of the Zoological Society of London*, 35: 271-424.

Richardson, L.R., 1949a. A guide to the Brachyrhynchous crabs. *Tuatara*, 2(1): 29-36.

Richardson, L.R., 1949b. Corrections and additions for the guides to the Brachyura, *Tuatara*, 2: 130.

Rieger, P.J. & R.R.R. Vieira, 1997. De senvolvimento larvalde *Cyrtograpsus angulatus* Dana (Crustacea, Decapoda, Grapsidae) em laboratorio. *Revista Brasileira Zoologia*, 14: 601-623, figs. 1-15, tabs. 1-8.

Risso, A., 1826. *Histoire naturelle des principales productions de l'Europe Méridionale. Decapoden.* Vol. 5. Pp. 2-81, pls 1-4. Strassbourg & Paris, Paris.

Risso, A., 1827. *Histoire naturelle des principales productions de l'Europe Méridionale et particulièrement de celles des environs de Nice et les Alpes Maritimes*. Volme 5, vii + 403 pages, 62 figures, 10 unnumbered pages, Strassburg.

Rizza, A., 1839. Descrizione di alcuni crostacei nuovi del Golfo di Catania. *Atti Accademia Gioenia Scienze naturali in Catania*, 15, 367–390.

Robert H.R., 1982. Evolution within the Crustacea. In: D.E. Bliss (ed.). *The Biology of Crustacea*. Pp 149-185. Academic Press, New York, United States of America.

Robinson, M. & O. Tully, 2000. Dynamics of a subtidal population of the porcellanid crab, *Pisidia longicornis* (Decapoda: Crustacea). *Journal of Amrine Biological Assoaciation of the United Kingdom*, 80: 75-83.

Rodríguez, A., J.I. González-Gordillo & J.A. Cuesta, 1992. Larval stages of *Brachynotus atlanticus* Forest, 1957 (Crustacea, Decapoda, Grapsidae) reared under laboratory conditions. *Journal of Plankton Research*, 14: 867-883, figs. 1-12, tabs. 1-3.

Rodríguez, E.M., R. Bigi1, D.A. Medesani, V.S. Stella, L.S.L. Greco, P.A.R. Moreno, J.M. Monserrat, G.N. Pellerano & M. Ansaldo, 2001. Acute and chronic effects of cadmium on blood homeostasis of an estuarine crab, *Chasmagnathus granulata*, and the modifying effect of salinity. *Brazilian Journal of Medical and Biological Research*, 34(4): 509-518.

Romano, A, M. Lozada & H. Maldonado, 1990. Effect of naloxone pretreatment on habituation in the crab *Chasmagnathus granulatus*. *Behavioral Neurobiology and Biology*, 53: 113-122.

Roper, D.S., M.J. Simons & M.B.J. Jones, 1983. Distribution of zooplankton in the Avon-Heathcote Estuary, Christchurch. *New Zealand Journal of Marine and Freshwater Research*, 17: 267–278.

Rosecchi, E., P.Y. Noël & A.J. Crivelli, 1998. Fresh and brackish water decapod crustacea of the Camargue (Rhône delta, France). *Crustaceana*, 71: 280-298.

Roux, J., 1917. Crustacés. *Resultats de l'expedition scientifique neerlandaise a la Nouvelle Guinea. Nova Guinea.* No 5: 589-621 pls. 27, 28.

Rudnick, D.H., K.M. Halat & V.H. Resh, 2000. *Distribution, ecology, and potential impacts of the Chinese mitten crab (Eriocheir sinensis) in San Francisco Bay.* University of California Water Resources Center. Riverside, California, United States of America.

Rumphius, G.E., 1705. *D'Amboinsche Rariteitkamer*, behelzende eene beschryvinge van allerhande zoo weeke als harde schaalvisschen, te weeten raare Krabben, Kreeften, en diergelyke Zeedieren, als mede allerhande Hoorntjes en Schulpen, die men in d'Amboinsche Zee vindt : daar beneven zommige Mineraalen, Gesteenten, en soorten van Aarde, die in d'Amboinsche, en zommige omleggende Eilanden gevonden worden: Verdeelt in drie bocken, & Rumpf, Georg Eberhard, 1627-1702. Amsterdam Vol. 1. 340 pp. 60 pls.

Ryan, P.A. & S.C. Choy, 1990. Observation of mass upstream migration of *Varuna litterata* (Fabricius) megalopae (Decapoda, Brachyura, Grapsidae) in Fiji. *Crustaceana*, 58: 237-249.

Saba, M., 1974. On the larval development of *Chasmagnathus convexus* De Haan (Grapsinae). *Researches on Crustacea*, 6: 71–85.

Sakai, K. & K. Yatsuzuka, 1980. Notes on some Japanese and Chinese *Helice* with *Helice* (*Helicana*) n. subgen., including *Helice* (*Helicana*) *japonica* n. sp.. *Senckenbergiana Biologica*, 60: 393–411.

Sakai, K., 2007. Comments on an invalid nominal species, *Hemigrapsus takanoi* Asakura & Watanabe, 2005, a synonym of *Hemigrapsus penicillatus* (De Haan, 1835) (Decapoda, Brachyura, Grapsidae). *Crustaceana*, 80(4): 503-508.

Sakai, K. & T. Nakano, 1983. List of decapod Crustacea in laboratory of Crustacea, Shikoku Woemen's University, Tokushima. I. *Bulletin of Shikoku Women's University*, 3(1): 73-94, 1 map.

Sakai, K., Türkay, M. & S.L. Yang, 2006. Revision of the *Helice/Chasmagnathus* complex (Crustacea: Decapoda: Brachyura). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaf*, 565: 1-77, 98 figs, 3 tab.

Sakai, T., 1934. Brachyura from the coast of Kyushu, Japan. *Scientific Report of Tokyo Bunrika Daigaku (B)*, 1(25): 281-330, text-figs 1-26, pls 17-18.

Sakai, T., 1935a. *Crabs of Japan*. 239 p., figs 1-122, 27 pages of bibliography & index, frontispiece (in color), pls 1-66 (color). Sanseido, Tokyo, Japan.

Sakai, T., 1935b. Crustacea of Japan. (Brachyura) (Order Decapoda). *Report of First Scientific Expedition to Manchoukuo*, section V, division 1, part II, article 7: 1-16.

Sakai, T., 1935.c List of Marine Animals around Shimoda. *Reports of the Shimoda Marine Biological Station*, 1: 23-85.

Sakai, T. 1936a. *Studies on the crabs of Japan, I. Dromiacea.* Science Reports of the Tokyo Section B, Volume 3, Supplement No. 1: 1–66, fig. 1–13, pls. 1–9. Bunrika Daigaku, Japan.

Sakai, T., 1936b. [no title]. *Zoological Magazine of Japan,* 48(4): 233

Sakai, T., 1936c. Crabs of Japan: 66 plates in life colours with descriptions. , [1935]: 1-239, figs 1-122, 27 pages of bibliography & index, frontispiece (in color), pls 1-66 (color). [1935]: 1-239, figs 1-122, 27 pages of bibliography & index, frontispiece (in color), pls 1-66 (color). Sanseido, Tokyo, Japan [In Japanese].

Sakai, T., 1937. Studies on some Japanese crabs [Nihonsan-kanirui no kennkyu-shiryou]. *Hakubutsugaku zasshi* [Mus. Sci.], 35(60): 127-130, pl. 3.

Sakai, T. 1939. *Studies on the crabs of Japan. IV. Brachygnatha, Brachyrhyncha*. 365–741 p., 42–111 pls. Yokendo, Tokyo, Japan.

Sakai, T. 1940. Biogeographic review on the distribution of crabs in Japanese waters. *Records of Oceanographic Works of Japan*, 11: 27-63.

Sakai, T., 1954. Preliminary report on the brachyuran Crustacea of Hachijo Island. *Records of Oceanographic Works in Japan*, (*New Series*), 1(2): 73-77.

Sakai, T., 1955. Further notes on the brachyuran Crustacea of the Hachijo Island. *Records of Oceanographic Works in Japan*, 2: 193–202.

Sakai, T., 1960s. Crabs. In: K. Nagata & T. Nishimura (eds.). *The crabs of Akita*. 11 pls., no pagination; Funakawa Fisheries Association, Japan.

Sakai, T., 1960b. Decapoda, Brachyura. In: K. Okada, & T. Uchida (eds.). *Encyclopaedia zoologica Illustrated in Colours*, 4: 28-87, pls 14-43. Hokuryukan, Tokyo, Japan.

Sakai, T., 1965a. *The Crabs of Sagami Bay collected by His Majesty the Emperor of Japan.* p. I-XVI, 1-206, 1-92, 1-32, 100 pls. Tokyo, Japan.

Sakai, T., 1965b. *The Crabs of Sagami Bay*. XVI, 206, 92, 32 p., 100 pls., 1 map. Maruzen Co., Ltd., Tokyo, Japan.

Sakai, T., 1974. Brachyura. In: New illustrated encyclopedia of the fauna of Japan, New print of second revised edition:  653-721. Hokuryukan. Tokyo, Japan.

Sakai, T., 1976. *Crabs of Japan and the Adjacent Seas.* 3 vols: xxix 773 pp. [English vol.]; 1-16, 251 pls [Plates vol.]; 461 pp. [Japanese vol.]. Kodansha, Tokyo, Japan.

Sakai, T., 1983. Description of new genera and species of Japanese crabs, together with systematically and biogeographically interesting species (I). *Researches on Crustacea*, 12: 1–23, 1 frontpiece, 8 pls.

Sakai, Toshimaru, 1950. *Crabs in Hata District, S.W. Kochi Prefecture*. 34 pp, 20 pls. Hata Mille High School, Japan.

Salvat, B. & G. Richard, 1985. Takapoto Atoll, Tuamotu archipelago. In: B. Delesalle, R. Galzin & B. Salvat (eds.). *Proceedings of the Fifth international Coral Reef Congress, Tahiti, 27 May - 1 June 1985*, 1: 323-362, figs. 1-34.

Sastrangara, M.H., H. Fermon, & M. Muånhlenberg, 2003. Diversity and Abundance of Intertidal Crabs at the East Swamp-Managed Areas in Segara-Anakan Cilacap, Central Java, Indonesia. Technological and Institutional Innovations for Sustainable Rural Development. Pp. 1-8. Deutscher Tropentag, October 8-10, 2003, Göttingen. Germany.

Sato, H., 1936a. On the littoral fauna of Formosa. *Scientific Taiwan*, 4: 137-144.

Sato, H. 1936b. The collections of the littoral animals of Formosa (1). *Botany and Zoology*, 4: 1435-1442.

Sato, H. 1936c. The collections of the littoral animals of Formosa (2). *Botany and Zoology*, 4: 1619-1624.

Sato, H. 1936d. The collections of the littoral animals of Formosa (4). *Botany and Zoology*, 4: 1951-1957.

Sato, M., 1995. *Ecosystem on Shigetomi Beach, Aira-cho, Kagoshima Prefecture*. Pp. 1-24. Laboratory of Eco-Biology, Science Department, Kagoshima University, Japan.

Satoshi, K, K. Masaaki, Y. Takashi, & S. Matsuura, 1997. Questionnaire research on the ecology and fishery of the Japanese mitten crab *Eriocheir japonica* (De Haan). *Scientific Bulletin of Faculty of Agriculture, Kyushu University*, 52: 89-104.

Say, T., 1817-1818. An account of the Crustacea of the United States. *Journal of the Academy of Natural Sciences of Philadephia*, 1(1-2): 57-63, 65-80 (plate 4), 97-100, 155-160, 161-169 [all 1817], 235-253, 313-319, 374-380, 381-401, 423-441 [all 1818]. [See Holthuis, 1969: vi, vii for dates of publication.]

Scelzo, M.A. & E.E. Boschi, 1973. Aportes al conocimiento de la distribución geográfica de los crustáceos decápodos anomura del Atlántico sudoccidental, frente a las costas Argentinas. *Trabajos del V Congreso Latinoamericano de Zoología*, 1: 204-216.

Scelzo, M.A. & V. Lichtschein de Bastida, 1979. Des arrollo larvaly metamorfosis del cangrejo *Cyrtograpsus altimanus* Rathbun, 1914 (Brachyura, Grapsidae) en laboratorio, con observacion essobrele ecología della especie. *Physis. Seccion A: Los Oceanos y sus Organismos*, 38(94): 103–126, pls. 1-7.

Schaefer, N., 1970. The functional morphology of the foregut of three species of decapod crustacea: *Cyclograpus punctatus* Milne Edwards, *Diogenes brevirostris* Stimpson, and *Upogebia africana* (Ortmann). *Zoologica Africana*, 5, 309-326.

Schellenberg, A., 1928. Decapoda. In: *Die Tierwelt Deutschlands*. Jena (Fisher) Teil, 10: 1-146, 110 figs.

Schmeltz, J.D.E., 1874. *Museum Godeffroy Catalog V. Nebst einer Beilage enthaltend topographische und zoologische Notizen*. L. Friedrichsen & Co., Hamburg, Germany.

Schmitt, W.L., 1931. Shelled invertebrates of the past and present: Crustaceans. *Smithsonian Science Series*, 10(2): 87-247, pls. 32-71.

Schmitt, W.L., 1965. *Crustaceans*. 204 p. The University of Michigan Press, Ann Arbor, MI, Unites States of America.

Schnakenbeck, W., 1933. Larven underste Boden formen. In: N. Peters & A. Panning, (eds.). Die Chinesische Wollhankrabbe (*Eriocheir sinensis* H. Milne Edwards) in Deutschland. *Zoologischer Anzeiger*, 104: 157–170.

Schram, F.R. & C.H.J. Hoff, 1998. Fossils and the Interrelationship of Major Crustacean Groups. In: G.D. Edgecombe (ed.). *Arthropod fossils and phylogeny*. Pp. 233-302. Columbia University Press. New York, United States of America.

Schram, F.R. (Editor), 1983. *Crustacean Issues 1: Crustacean Phylogeny*. A.A. Balkema. Rotterdam, Netherlands.

Schram, F.R., 1982. The Fossil Record and Evolution of Crustacea. In: D.E. Bliss (ed.). *The Biology of Crustacea*. Pp. 93-147. Academic Press New York, United States of America.

Schram, F.R., 1986. *Crustacea*. Oxford University Press. New York, United States of America.

Schubart, C.D., 2002. Book review: An updated classification of the recent Crustacea Crustacea by J.W. Martin and G.E. Davis (2001). *The Raffles Bulletin of Zoology*, 50(1): 279-280.

Schubart, C.D., 2003. The East Asian shore crab *Hemigrapsus sanguineus* (Brachyura: Varunidae) in the Mediterranean Sea, an independent introduction. *Scientia Marina*, 67(2): 195-200.

Schubart, C.D. & J.A. Cuesta, 1998. The first zoeal stages of four *Sesarma* species from Panama, with identification keys and remarks on the American Sesarminae

(Crustacea: Brachyura: Grapsidae). *Journal of Plankton Research*, 20: 61-84.

Schubart, C.D. & R. Diesel, 1998. Osmoregulatory capacities and penetration into terrestrial habitats: a comparative study of Jamaican crabs of the genus *Armases* Abele, 1992 (Brachyura: Grapsidae: Sesarminae). *Bulletin of Marine Science* 63(2): 743-752.

Schubart, C.D. & R. Diesel, 1999. Osmoregulation and the evolution from marine to freshwater and terrestrial life: a comparative study of Jamaican crabs of the genus *Sesarma*. *Archiv für Hydrobiologie*, 145(3): 331-347.

Schubart, C.D. & P.K.L. Ng, 2000. On the identities of the rafting crabs, *Cancer depressus* Fabricius, 1775, *Cancer squamosus* Herbst, 1790, *Plagusia immaculata* Lammarck, 1818 and *Plagusia tuberculata* Lammarck, 1818 (Crustacea: Decapoda: Brachyura: Plagusiidae). *The Raffles Bulletin of Zoology*, 48(2): 327-336.

Schubart, C.D. & P.K.L. Ng, 2002. The sesarmid genus *Neosarmatium* (Decapoda: Brachyura): new distributionary records and a new species from Sulawesi. *Crustacean Research*, 31: 28-38.

Schubart, C.D., J.A. Cuesta & A. Rodríguez, 2001. Molecular phylogeny of the crab genus *Brachynotus* (Brachyura: Varunidae) based on the 16S rRNA gene. *Hydrobiologia*, 449: 41–46.

Schubart, C.D., J.A. Cuesta & R. Diesel, 2002. Glyptograpsidae, a new brachyuran family from Central America: larval and adult morphology, and a molecular phylogeny of the Grapsoidea. *Journal of Crustacean Biology*, 22: 28-44, figs 1–8, tabs 1–2.

Schubart, C.D., R. Diesel & S.B. Hedges, 1998. Rapid evolution to terrestrial life in Jamaican crabs. *Nature*, 393: 363-365.

Schubart, C.D., D. Horst & R. Diesel, 1999. First record of *Sesarma rectum* Randall (Brachyura: Grapsidae: Sesarminae) from the Lesser Antilles. *Crustaceana*, 72(5): 537-538.

Schubart, C.D., H.C. Liu, & J.A. Cuesta, 2003. *Scandarma lintou*, a new genus and new species of tree-climbing crab (Crustacea: Brachyura: Sesarmidae) from Taiwan with notes on its ecology, larval morphology and phylogeny. *The Raffles Bulletin of Zoology*, 51(1): 49-63.

Schubart, C.D., J.E. Neigel & D.L. Felder, 2000b. The use of the mitochondrial 16S rRNA gene for phylogenetic and biogeographic studies of Crustacea. *Crustacean Issues*, 12: 817-830.

Schubart, C.D., J. Reimer & R. Diesel, 1998. Morphological and molecular evidence for a new endemic freshwater crab, *Sesarma ayatum* sp. n., (Grapsidae, Sesarminae) from eastern Jamaica. *Zoologica Scripta*, 27(4): 373-380.

Schubart, C.D., J. Reimer & R. Diesel, 1999. Gonopod morphology and 16S mtDNA sequence alignment of the freshwater crabs S*esarma bidentatum* and *S. ayatum* (Grapsidae: Sesarminae) from Jamaica. *Zoologica Scripta*, 28(3-4): 367-369.

Schubart, C.D., J.A. Cuesta, R. Diesel & D.L. Felder, 2000a. Molecular phylogeny, taxonomy, and evolution of nonmarine lineages within the American grapsoid crabs (Crustacea: Brachyura). *Molecular Phylogentics and Evolution*, 15(2): 179-190.

Schubart, C.D., J.I. González-Gordillo, N. Reyns, H.C. Liu, & J.A. Cuesta, 2001. Are Atlantic and Indo-Pacific populations of the rafting crab, *Plagusia depressa*, distinct? New evidence from larval morphology and mtDNA. *The Raffles Bulletin of Zoology*, 49(2): 301-310.

Schubart, C.D., S. Cannicci, M. Vannini & S. Fratini, 2006. Molecular phylogeny of grapsoid crabs and allies based on two mitochondrial genes and a proposal for refraining from current superfamily classification. *Journal of Zoological Systemtcis and Evolution Research*, 44(3): 193–199.

Schweitzer, C.E., K.J. Lacovara, J.B. Smith, M.C. Lamanna, M.A. Lyon & Y. Attia, 2003. Mangrove-dwelling crabs (Decapoda: Brachyura: Necrocarcinidae) associated with Dinosaurs from the Upper Cretaceous (Cenomanian) of Egypt. *Journal of Paleontology*, 77(5): 888-894.

Sendler, A., 1912. Zehnfusskrebse aus dem Wiesbadener Naturhistorischen Museum. *Jahrbücher des Nassauischen Vereins für Naturkunde*, 65: 189-207. (Wiesbaden [191, Abb. 4-5]).

Sendler, A., 1923. Die Decapoden und Stomatopoden der Hanseatischen Südsee-Expedition. *Abhandlungen Herausgegeben von der Senkenbergischen Naturforschenden Gesellschaft*, 38: 21-47, figs. 1-3, pls. 5-6.

Serène, R., 1968. The Brachyura of the Indo-West Pacific region. In: Prodromus for a check list of the non-planctonic marine fauna of South East Asia. *Singapore National Academy of Sciences, Special publication,* 1 (Fauna IIIC3): 33-112.

Serène, R., 1974. Note on the genera and species of the Camptandriinae Stimpson, 1858 (Decapoda, Brachyura, Ocypodidae). *Treubia* 38(3): 59-68.

Seréne, R., 1977. Crustacés hippidés et brachyoures des îles Séchelles (1 ère partie). *Review of Zoologie Africa* (Tervuren), 91(1): 45-68.

Serène, R. & C.L. Soh, 1970. New Indo-Pacific genera allied to *Sesarma* Say, 1817 (Brachyura, Decapoda, Crustacea). *Treubia,* 27(4): 387-416, pls 1-8.

Serène, R., & M.K. Moosa. 1971. New and few known species of brachyura from Ambon. *Marine Research of Indonesia*, 11: 1-18, Pls. 1-6.

Sethuramlingam, S., 1983. Studies on Brachyuran crabs from Veller estuary - Kille Backwaters complex of Portonovo coast. Ph.D Thesis submitted to  Centre for Advanced Study in Marine Biology, Annamalai University, Tamil Nadu, India. [Unpublished].

Shank, T.M., M.B. Black, K. Halanych, R.A. Lutz, & R.C. Vrijenhoek 1999. Miocene radiation of deep-sea hydrothermal vent shrimp (Caridea: Breesillidae): evidence from mitochondrial cyctochrome oxidase subunit I. *Molecular Phylogenetics and Evolution*, 13(2): 244-254.

Shen, C.J., 1932a. The brachyuran Crustacea of North China. *Zoologica Sinica*, *Series A*, 9: 1–321, 171 text-figs., 10 pls., 1 map.

Shen, C.J., 1932b. The crabs of Hong Kong, Part III. *Hong Kong Naturist*, 3(1): 32-45, pls. 6-9, 10 text-figs.

Shen, C.J., 1937. On some account of the crabs of North China. *Bulletin of the Fan Memmorial Institute of Biology (Zoology),* 7: 167-185.

Shen, C.J., 1940a. On the collections of crabs of South China. *Bulletin of the Fan Memorial Institute of Biology. Peiping*, 10: 69-104.

Shen, C.J., 1940b. The Brachyuran Fauna of Hong Kong. *Journal of the Hong Kong Fisheries Research Station*, 1: 211-242.

Shen, C.J. & A.Y. Dai, 1964. *Illustration of animals in China, Crustacea 2*. 172 pp., 277 figs. Beijing, People's Repulblic of China.

Shen, C.J. & J.Y. Liu, 1963. Preliminary studies on the characteristics of the crab fauna of China seas. *Oceanology Limnology Sinica*, 5(1): 139-153.

Shen, C.R., 1931a. The crabs of Hong Kong. Part I. *Hong Kong Naturalist*, 3(1): 92-110, pls. 4-10.

Shen, C.R., 1931b. The crabs of Hong Kong. Part II. *Hong Kong Naturalist*, 2(3): 185-197, pls. 12-14, 1-13 text-figs.

Shen, C.R., 1935. On some new and rare crabs of the families Pinnotheridae, Grapsidae and Ocypodidae. *Chinese Journal of Zoology*, 1: 19-40, 15 text-figs.

Shen, C.R., 1940. On the collections of crabs of South China. *Bulletin of the Fan Memorial Institute of Biology (Zoology)*, 7(5): 167-185.

Shen, C.R., 1940. The brachyuran fauna of Hong Kong. *Journal of Hong Kong Fisheries Research Station*, 1(2): 211-242.

Sherborne, C.D., 1922. Part 1. Introduction, Bibliography and Index A-Aff, in: Index Animalium sive nominum quae ab A. D. MDCCLVIII generibus et speciebus animalium imposita sunt. Societabus eruditorum adiuvantibus, cxxxix + 128pp. British Museum, London, United Kingdom.

Sherborn, C.D. & J.A. Jentink, 1895. On the dates of the Parts of Siebold's 'Fauna Japonica' and Giebel's 'Allgemeine Zoologie' (first edition). *Proceedings of the Zoological Society of London*, 1895: 149-150.

Shih, H.T., K.Y. Lue, & C.H. Wang. 1991. Crab fauna and the activities of ten crab species in Tanshui mangrove swamp of Taiwan. *Annuals of Taiwan Museum*, 34: 121-140. (in Chinese)

Shih, H.T., P.K.L. Ng & H.W. Chang, 2004. The systematics of the genus *Geothelphusa* (Crustacea, Decapoda, Brachyura, Potamidae) from southern Taiwan: a molecular appraisal. *Zoological Studies*, 43(3): 561-570.

Shin, D.D. & C.Y. Joo, 1990. Prevalence of *Parogonimus westermani* in some Ulchin school children. *Acta Pediatrics of Japan*, 2: 269-274.

Shokita, S., 1989. Longitudinal distribution and abundance of inlandwater and its adjacent crustaceans in Okinawa Island, the Ryukyus. In: Nature Conservation Bureau (Environment Agency) (ed.). *Study of essential factors for preservation of wildlife in Nansei Islands*.. Pp. 483–499. Nature Conservation Bureau (Environment Agency), Tokyo, Japan.

Shokita, S., 1990. Inland-water decapods and their distribution in Iriomotejima Island of the Ryukyu Islands. In: Nature Conservation Bureau (Environment Agency) (ed.). *Study of essential factors for preservation of wildlife in Nansei Islands*. Pp. 305–317. Nature Conservation Bureau (Environment Agency), Tokyo, Japan.

Shokita, S. & S. Nishijima, 1976. Faunal list of inland water Malacostraca of Amami Group, the Ryukyu Islands. *Ecological Studies on Natural Consservation of Ryukyu Island*, 2: 31-38.

Shokita, S., M. Iriondo, A. Kawakami & V. Havanot, 1998. Distribution and abundance of Crustaceans in the mangrove swamp of the Okukubi River, Okinawa Island. Annual *Report on interdisciplinary Research, Institute of Environmental Sciences*, 17: 61-71.

Shokita, S., Y. Fujita, T. Nagai, A. Ito, T. Kawahara & H. Noho, 2003. Distribution and abundance of crustaceans in the mangrove swamp and upper reaches of the Nagura River, Ishigaki Island, Japan. In: Research Institute for Subtropical Regions (ed.). *Reports on the researches for mangrove forests and swamps, Okinawa.* Pp. 97-111. [In Japanese].

Shumway, S.E. & M.B. Jones, 1981. Influence of salinity on the respiration of an estuarine mud crab, *Helice crassa* (Grapsidae). *Comparative Biochemistry and Physiology*, 70A: 551-553.

Shy, J.Y., 2005. A new species of freshwater crab of the genus *Geothelphusa* Stimpson, 1858 (Crustacea, Decapoda, Brachyura, Potamidae) from Taiwan. *The Raffles Bulletin Zoology*, 53: 99-102.

Shy, J.Y. & H.P. Yu, 1992. Complete larval development of the mitten crab *Eriocheir rectus* Stimpson, 1858 (Decapoda, Brachyura, Grapsidae) reared in the laboratory.

*Crustaceana*, 63: 277–290.

Shy, J.Y., & H.P. Yu. 1999. *The Freshwater Crabs of Taiwan*. 116 pp. National Museum of Marine Biology and Aquarium, Kaohsiung, Taiwan. [In Chinese].

Sibuet, J.C., S.K.Hsu, C.T. Shyu, & C.S. Liu, 1995. Structural and kinematic evolution of the Okinawa Trough backarc basin. In: Taylor, B. (Ed.). *Backarc Basins: Tectonics and Magmatism*. Pp. 343–378. Plenum Press, New York, United States of America.

Sibuet, J.C., B. Deffontaines, S.K. Hsu, N. Thareau, J.P. Formal, C.S. Liu & the ACT party, 1998. Okinawa Trough backarc basin: early tectonic and magmatic evolution. *Journal of the Geophysical Research*, 103: 30245–30267.

Silfverberg, C., 1999. A provisional list of Finnish Crustacea. *Memoranda of the Society of Fauna and Flora Fennica*, 75: 15-37

Singh, S., 1998. Sindhu and Sarasvati in the Reg Veda and their Archaeological implications Puratattva. *Bulletin of the Indian Archeaological Society*, 28: 26-38.

Sleep, N.H., 1986. Physical conditions on early earth: Implications for the origin of life. *Origins of Life and Evolution of Biospheres* (Formerly *Origins of Life and Evolution of the Biosphere*), 16: 179-180.

Smith, S.I., 1869. Notice of the Crustacea collected by Prof. C.F. Hartt on the coast of Brazil in 1867. *Transactions of the Connecticut Academy of Arts and Sciences*, 2: 1-42, 1 pl.

Smith, S.I., 1870. Notes on American Crustacea. No. 1. Ocypodoidea. *Transactions of the Connecticut Academy of Arts and Science*, 2: 113–176.

Song, S.R. & C.Y. Yang, 2000. Crabs from strange environment. *Nature World*, 68: 14-19. [In Chinese].

Sourie, R., 1954. Contribution à l'étude écologique des côtes rocheuses du Sénégal. *Memoires de I'Institut Francais d'Afrique Noire*. No. 38, Pp. 1-232, 33 pls.

Southward, A.J., E.C. Southward, P.R. Dando, J.A. Hughes, M.C. Cunnicutt II, J. Alcala-Herrera & Y. Leahy, 1997. Behaviour and feeding of the nassariid gastropod *Cyclope neritea*, abundant at hydrothermal brine seeps off Milos

(Aegean Sea). J*ournal of the Marine Biological Association of the United Kingdom,* 77: 753-771.

Spears, T. & L.G. Abele, 1997. Crustacean phylogeny inferred from 18S rDNA. In: R.A.Fortey & R.H. Thomas (eds.). *Arthropod Relationships*. Systematics Association Special Volume Series 55. Pp. 169-187. Chapman & Hall, London, United Kingdom.

Spivak, E.D., 1997. Los crustáceos decápodos del Atlántico Sudoccidental (25º-55ºS): Distribución y ciclos de vida. *Investigaciones Marinas*, 25: 69-91.

Spivak, E.D., 1999. Effects of reduced salinity on juvenile growth of two co-occurring congeneric grapsid crabs. *Marine Biology,* 134: 249-257.

Spivak, E.D. & J.A. Cuesta, 2000. Larval development of *Cyrtograpsus affinis* (Dana) (Decapoda, Brachyura, Varunidae) from Rio de la Plata estuary, reared in the laboratory. *Scientia Mariana,* 64: 29-47.

Spivak, E.D. & C.D. Schubart, 2003. Species status in question: a morphometric and molecular comparison of *Cyrtograpsus affinis* (Dana) and *C. altimanus* Rathbun (Decapoda, Brachyura, Varunidae). *Journal of Crustacean Biology,* 23(1): 212-222.

Stebbing, T.R.R., 1910. General Catalogue of South African Crustacea (Part V of S. A. Crustacea, for the Marine Investigations in South Africa). *Annuals of South African Museum,* 6: 281-593, pls. 15-22.

Stein, J. L., 1984. Subtidal gastropods consume sulfur-oxidizing bacteria: evidence from coastal hydrothermal vents. *Science,* 223: 696-698.

Stern, R., P. Fryer, S. Klemperer, T. Plank, N. Takahashi, D. Wiens & A. Shaw. *Perspectives on the Adnean Arc from the Izu-Bonin-Mariana Arc system in the Western Pacific*. Backbone of the Americas - Patagonia to Alaska, The Geological Society of America., Mendoza, Argentina, 3-7 April 2006.

Sternberg, R. von & N. Cumberlidge, 2000. Taxic relationships within the Grapsidae MacLeay, 1838 (Crustacea: Decapoda: Eubrachyura). *Journal of Comparative Biology*, 3(2): 115–136.

Sternberg, R. von, N. Cumberlidge & G. Rodriguez, 1999. On the marine sister groups of the freshwater crabs (Crustacea: Decapoda: Brachyura). *Journal of Zoological*

*Systematics & Evolutionary Research*, 37(1): 19-38.

Stevcic, Z., 1998. Evolutionary arrangement of the brachyuran families together with a checklist. Period. *Biology,* 100: 101-104.

Stevcic, Z., 1969: Systematic position of the family Tymolidae. *Arhiv Bioloskih Nauka,* 21: 71-81.

Stevcic, Z., 1971. The main features of Brachyurans Evolution. *Systematic Zoology*, 20(3): 331-340.

Stevcic, Z., 1971. The pathways of brachyuran evolution. In: Zbornik referata sa I simpozijuma biosistematirara Jugoslavije. Proceedings of the First Symposium of the Biosystematists of Yugoslavia). Sarajevo. Pp. 187-193. Yugoslavia.

Stevcic, Z., 1973. The systematic position of the family Raninidae. *Systematic Zoology* 22:625-632

Stevcic, Z., 2000: Adaptive radiation of the brachyuran crabs. Period. biol. 102, 149-155.

Stevcic, Z., 2001: Decapoda: Brachyura. In: J.W. Martin & G.E. Davis. An updated classification of the recent Crustacea. Science Series 39. Pp. 112. Natural History Museum of Los Angeles County, United States of America.

Stevcic, Z., 2005. The reclassification of Brachyuran Crabs (Crustacea: Decapoda: Brachyura). *Fauna Croatica*, 14(1): 1-159.

Stimpson, W., 1853. Synopsis of the marine Invertebrata of Grand Manan: or the region about the mouth of the Bay of Fundy, New Brunswick. *Smithsonian Contribution to Knowledge,* 4: 43-44 (nur Tanais).

Stimpson, W. 1858. Crustacea Ocypodoidea: Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, *observavit et descripsit W. Stimpson*. Pars V. *Proceedings of the Academy of Natural Science of Philadelphia,* 10: 93-110 [page numbers 39-56 on separate reprint].

Stimpson, W. 1858. Prodromus descriptionis animalium evertebratorum, quae in expeditione ad oceanum pacificum septentrionalem, a republica federata missa, Cadwaladaro Ringgold et Johanne Rodgers ducibus, observavit et descripsit. Pars VII. Crustacea Anomura. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 10: 225–252.

Stimpson, W., 1859. Notes on North American Crustacea. No. 1. *Proceedings of the Lyceum of Natural History in the City of New York*, 7: 49-93, pl. 1.

Stimpson, W., 1860a. Notes on North American Crustacea, in the Museum of the Smithsonian Institution. No. II. *Proceedings of the Lyceum of Natural History in the City of New York,* 7: 176-246, pls. 25.

Stimpson, W., 1860b. Prodromus descriptionis animalium evertebratorum, Pars VIII. Crustacea Macrura. *Proceedings of the Academy of National Sciences, Philadephia*. 1860: 22-47.

Stimpson, W., 1870. Preliminary report on the Crustacea dredged in the Gulf Stream in the Straits of Florida, by L. F. de Pourtales. Part. I. *Brachyura. Bulletion of Museum of Comparative Zoology, Harvard*, 2: 109-160.

Stimpson, W., 1907. Report on the Crustacea (Brachyura and Anomura) collected by the North Pacific Exploring Expedition 1853-1856. *Smithsonian Miscellaneous Collection*, 49(1717): 1-240, pls. 1-26.

Stuart, I.G. & M. Mallen-Cooper, 1999. An assessment of the effectiveness of a vertical-slot fishway for non-salmonid fish at a tidal barrier on a large tropical/subtropical river. *Regulated Rivers: Research & Management*, 15(6): 575-590.

Stüben, D., S. H. Bloomer, N. E. Taïbi, T. H. Neumann, V.Bendel, U. Püschel, A. Barone, A. Lange, S. Wu, C. Li & D. Zhang, 1992. First results of study of sulphur rich hydrothermal activity from an island-arc environment: Esmeralda Bank in the Mariana Arc. *Marine Geology*, 103: 521-528.

Su, H.J. & K.Y. Lue, 1984. The crab fauna of Tan-shui mangrove swamp. *Biological Bulletin of National Taiwan Normal Universit*y, 19: 61-70.

Sullivan, J.K., 1977. Effects of salinty and temperature on the acute toxicity of cadmium to the estuarine crab *Paragrapsus gaimardii* (Milne Edwards). *Australian Journal of Marine and Freshwater Research*, 28(6) 739 – 743.

Sun, B.L., G.J. Liu, G.Q. Zhang, & W.M. Liu, 1997. Primary study on the crab (*Helice tridens tientsinensis* Rathbun) being infected with baculovius diseases of shrimp and prevention and treatment for explosive epidemic shrimp disease. *Fisheries Sciences*, (Liaoning), 16(2): 3-6.

Sun, H., K. Zhou & X. Yang, 2003. Phylogenetic relationships of the mitten crabs inferred from mitochondrial 16S rDNA partial sequences (Crustacean, Decapoda). *Acta Zoollogica Sinica*, 49(5): 592-599.

Suzuki, H., 1985. A list of the macro-crustaceans collected from Formosa. *Report on the Ocean Environment of the southern Ryukyu Islands*, 2: 49-59.

Swofford, D.L., 2000. *Phylogenetic Analysis Using Parsimony (and Other Methods).* PAUP 4.0b4. Sinauer Associates, Sunderland, Massachusetts, United States of America.

Swofford, D.L. 2002. PAUP*. *Phylogenetic Analysis Using Parsimony* (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts, United States of America.

Swofford, D.L., G.J. Olsen, P.J. Waddell & D.M. Hillis, 1996. Phylogenetic inference. In: D.M. Hillis, C. Moritz & B.K. Mable (eds.). *Molecular Systematics*. Pp. 407-514. Second edition. Sinauer, Sunderland, Massachusetts, United States of America.

Tai, S. 1997. The bioessays of the food stimulants of the juvenile Chinese hairy crab, *Eriocheir sinensis*. Bachelor of Science (Honours) thesis submitted to National University of Singapore, in partial fulfillment for the degree of the Bachelor of Science with Honours in Zoology for the Academic Year 1997/1998.

Takano, M., M. Ikeda & A. Kijima, 1997. Biochemical and morphological evidence of two sympatric forms, interpreted as sibling species, in the estuarine grapsid crab *Hemigrapsus penicillatus* (De Haan). *Benthos Research*, 52: 111-117.

Takeda, M. 1984. A new species of the family Grapsidae from Japan. *Bulletin of the National Science Museum, Tokyo, Series A, Zoology*, 10: 117–120.

Takeda, M., 1971. New and rare crabs from the Palau Islands. *Micronesica*, 7: 185-213, text-figs. 1-4, pls. 1-7.

Takeda, M., 1974. Accounts of some crabs from Mutsu Bay, with description of a new grapsid from Onagawa Bay. *Bulletin of Marine Biological Station of Asamushi, Tôhoku Uni*versity, 15, 13–21.

Takeda, M., 1976. Littoral and inshore decapod crustaceans of Tanega-Shima Island, Southwest Japan. *Memior of National Science Museum, Tokyo*, 9: 151-161.

Takeda, M., 1982. *Keys to the Japanese and foreign Crustaceans, fully illustrated in colours*. 284 p. Hokuryukan, Tokyo, Japan.

Takeda, M., 1983. Brachyura. In: H. Utinomi (ed.). *The Aquatic Lower Animals of Japan*. 340 pp. Gakken, Tokyo, Japan.

Takeda, M & K. Iwasaki, 1983. Remarkable crabs from the Ryukyus Islands (I). *Bulletin of the Biogeographical Society of Japan*, 38(9): 87-91.

Takeda, M. & Y. Kurata, 1977. Crabs of the Ogasawara  Islands. IV. A collection made at the new volcanic island, Nishino-shima-shinto, in 1975. *Bulletin of National Science Museum (A), Zoology*, 3(2): 91-111, figs. 1-9.

Takeda, M. & S. Miyake, 1976. Crabs of Ogasawara Islands. I. List of known species. *Reseraches on Crustacea*, 7: 101-115.

Takeda, M., H. Takeuchi & H. Suganuma, 1993. Occurrence of *Xenograpsus novaeinsularis* Takeda & Kurata (Crustacea: Decapoda: Brachyura) in the Tokara and Iwo Islands. *Nature and Environmental Science Research*, 6: 59-64.

Takeda, M., K. Sakai, S. Shinomiya & H. Suga, 2000. Crabs from the Steto Inland-Sea, Japan. *Memior of National Science Museum*, Tokyo, 33: 135-144.

Takeda, S. & Y. Kurihara, 1987. The effects of burrowing of *Helice tridens* (De Haan) on the soil of a salt marsh habitat. *Journal of Experimental Marine Biology and Ecology*, 113: 79-89.

Tan, C.G.S. & P.K.L. Ng, 1994. An annotated checklist of mangrove brachyuran crabs in Malaysia and Singapore. *Hydrobiologia*, 285: 75-84.

Tan, L.W H & P.K.L. Ng, 1988. *A Guide to Seashore Life*. 160 pp. Published by the Singapore Science Centre and sponsored by BP, Raffles Museum of Biodiversity Research and Singapore Science Centre, Singapore.

Tanaka, G.I., 1949. Crabs in the Bay of Osaka, Japan. *Osaka Hakubutsu-Gakkai (Osaka Natural History Society)*, 9: 22-25.

Tanaka, S.I., 1943. Crabs in South Ise, Mie prefecture, Japan (=Minami Ise no Kani), *Mie Seibutsu* (=Biology), 3-4: 1-7.

Tanaka, S.I., 1960. Crabs in Kumano, Mie Prefecture, Japan (=Kumano-ji no Kani). Survey for the expanding plan of Coastal National Park at Kumano-nada. *Report on Coastal National Park of Kumano-nada*, 11: 113-121, 1 pl. [In Japanese].

Tanaka, S.I., 1962. A Checklist of Crabs in Mie Prefecture, Japan. *Mie Seibutsu* (=Biology), 12: 1-35.

Tanaka, S.I., 1983. Research group on Brachyura. Brachyuran Fauna of Ise Bay, and the Northern and the Middle parts of Kumano-nada. *Bulletin of the Mie Prefecture Museum, (Natural Sciences)*, 5: 1-67, 11 pls.

Tang, B., K. Zhou & D. Song, 2004. A neotype of *Eriocheir recta* (Crustacea, Decapoda). *Acta Zootaxa Sinica*, 29(2): 255-259. [In Chinese with English abstract].

Tang, B., K. Zhou, S. Song, S. Yang & A. Dai. 2003. Molecular systematics of the Asian mitten crabs, genus *Eriocheir* (Crustacea: Brachyura). *Molecular and Phylogenetics Evolution*, 29: 309-316.

Tarasov, V.G., M.V. Propp, L.N. Propp, S.V. Blinov & G. Kamenev, 1986. Shallow hydrothermal vents of Kraternaya Caldera and the ecosystem of Kurile Islands. *Biologiya Morya*, 2: 72-74.

Targioni-Tozzetti, A. 1873. Catalogo di Crostacei Podottalmi Brachiuri e Anomuri raccolti nel viaggio di circumnavigazione della fregata Italiana *MAGENTA* riportati dal Prof. Enrico Giglioli. *Atti de la Societa Italiana di Scienze Naturali (Milano)*, 15: 460-471.

Targioni-Tozzetti, A., 1872. Catalogo di Crostacei Podottalmi Brachiuri e Anomuri raccolti nel viaggio di circumnavigazione della fregata Italiana *MAGENTA* riportati dal Prof. *Enrico Giglioli. Bollettino della Societa Entomologica Italiana*, 4: 389-399.

Targioni-Tozzetti, A., 1877. Zoologia del viaggio intorno al globo della R. pirocorvetta *MAGENTA* durante gli anni 1865-68. Crostacei brachiuri e anomouri. *R. Istituto di Studi Superiori, Practici e di Perfezionamento in Firenze*, 1: I-XXIX, 1-257, pls. 1-13.

Tavares, M.S. & E.F. Albuquerque, 1989. Levantamento taxonômico preliminar dos Brachyura (Crustacea: Decapoda) de Lagoa de Itaipu, Rio de Janeiro, Brasil. *Atlântica*, 11(1): 101-108.

Terada, M., 1976a. Comparison of the larval developments of nine crabs belonging to the subfamily Sesarminae. *Researches on Crustacea,* 7: 138-169.

Terada, M., 1976b. Comprison of the larval development of *Scopimera globosa* De Haan and *Ilyoplax pusillus* (De Haan). *Zoological Magazine*, 85: 17–27.

Terada, M., 1981. Zoea larvae of five crabs in the subfamily Varuninae. *Researches on Crustacea*, 11: 66–76.

Terada, M., 1982. The zoeal development of *Nanosesarma gordoni* (Shen) (Brachyura, Sesarminae) in the laboratory. *Proceedings of the Japanese Society of Systematic Zoology*, 22: 3345.

Terao, A., 1915a. The second intermediate host of Lung Distoma. Part 2. *Zoological Magazine*, 27: 502-503.

Terao, A., 1915b. The second intermediate host of Lung Distoma. Part 3. *Zoological Magazine*, 27: 555.

Terao, A. 1915c. The second intermediate host of Lung Distoma. Part 4. *Zoological Magazine*, 27: 642.

Terao, A., 1916. Crabs wrong to Paddy fields. *Zoological Magazine*, 28(331): 188-189.

Tesch, J.J., 1918. The Decapoda Brachyura of the Siboga-Expedition. I. Hymenosomidae, Retroplumidae, Ocypodidae, Grapsidae, and Gecarcinidae. *Siboga-Expedition Decapoda Monograph*s, 39(c): 1-148, 6 pls.

Thomson, G.M., 1905. The Portobello Marine Fish-Hatchery and Biological Station. *Transactions and Proceedings of the New Zealand Institute,* 38: 529-558.

Thomson, G.M., 1913. The natural history of Otago Harbour and the adjacent sea, together with a record of the researches carried on at the Portobello marine fish-hatchery. *Transactions of the Proceedings of New Zealand Institute*, 45: 225-251, pl. 10.

Thomson, G.M. & T. Anderton, 1912. *History of the Portlbello Marine Fish-Hatchery and Biological Station.* Dom. New Zealand, Board of Science and Arts Bulletin, 2. 131pp.

Thomson, G.M. & T. Anderton, 1921. History of the Portobello Marine Fish-Hatchery and Biological Station. IX. The Crustacea of Otago Harbour and neighbouring seas. *New Zealand Bulletin of the Board of Sciences and Arts*, 2: 97-119, 16 figs.

Tirmizi, N.M. & N. Ghani, 1996. *Marine Fauna of Pakistan: 5: Crustacea: Brachyura, Brachyrhyncha, Part 1: Xanthidae, Goneplacidae, Pinnotheridae, Ocypodidae, Grapsidae.* Pp. 1-188. Center of Excellence, University of Karachi, Karachi. Pakistan.

Tirmizi, N.M. & Q.B. Kazami, 1983. Carcinological studies in Pakistan, with remarks on species of the Red Sea and the Mediterranean. *Bulletin of the Institute of Oceanography and Fisheries*, 9: 347-380.

Tomita, Y. & S.I. Tanaka, 1968. *Crabs around Kii-Nagashima, Mie Prefecture, Japan*. 1-69 pp., 11 pls. In: Marine Biology around Kii-Nagashima, Mie Prefecture. 3. Reports of Biological Survey at the coast of Kumano-Nada, Mie Prefectural Museum & Toba Aquarium, Japan.

Tran, T.K.D., 1997. *The circulated regions of Parqagonimiasis.* Tap Chi Y Hoc, Ho Chi Minh, No, Series 1: 26-30.

Trevarthen, C. & D. Kulka, 1950. A study of the life of a pebble beach – Coromandel Peninsula. *Tane*, 6: 51-56.

Tsalolikhin, S.J., 1995. *Key to Freshwater Invertebrates of Russia and adjacent lands*. St. Petersburg. Russia.

Tunnicliffe, V., 1991. Hydrothermal vent biology: ecology and evolution. *Oceanography and Marine Biology Annual Review*, 29: 319-407.

Tunnicliffe, V., 1992. Hydrothermal vent communities of the deep sea. *American Scientist*, 80: 336-349.

Tunnicliffe, V. & C.M.R. Fowler, 1996. Influence of sea-floor spreading on the global hydrothermal vent fauna. *Nature*, 379: 531-533.

Türkay, M., 1970. Die Gecarcinidae Amerikas. Mit einem Anhang über *Ucides* Rathbun. (Crustacea: Decapoda). *Senckenbergiana Biologica,* 51(5/6): 333-354, 1 pl.

Türkay, M., 1973. Die Gecarcinidae Afrikas (Crustacea: Decapoda). *Senckenbergiana Biologica,* 54(1/3): 81-103, pls. 1-2.

Türkay, M., 1974. Die Gecarcinidae Asiens und Ozeaniens (Crustacea: Decapoda). *Senckenbergia Biologica*, 55(4/6): 223-259 figs 1-19.

Türkay, M., 1975. Zur Kenntnis der Gattung *Euchirograpsus* mit Bemerkungen zu *Brachygrapsus* and *Litocheira* (Crustacea: Decapoda). *Senckenbergiana Biologica,* 56(1): 103-132.

Türkay, M., 1976. Decapodensammlungen in der Bundesrepublik Deutschland, Nr. 1: Die Crustacea Decapoda des Wiesbadener Museums. *Jahrbücher des Nassauischen Vereins für Naturkunde,* 103: 69-72; Wiesbaden.

Türkay, M., 1978. Zwei neue Grapsiden-Arten aus dem Indopazifik (*Echirograpsus madagascariensis* n. sp. und *Miersiograpsus australiensis* n. sp.) mit Einführung von *Miersiograpsus* n. gen. (Crustacea: Decapoda: Grapsidae). *Senckenbergiana Biologia*, 59: 133-141, 6 figs.

Türkay, M., 1981. Die Expedition von Karl Möbius nach Mauritius und den Seychellen (1874-75) und die dort gesammelten Crustacea Decapoda Reptantia. I. Brachyura excl. Dromiacea, mit Beschreibung von *Menaethiops moebii*. *Mitteilungen aus dem Zoologischen Museum, University of Kiel,* 1(7): 35-64, Abb.1-28.

Türkay, M., 1983. Morphologisch-taxonomische Monographie der Gecarcinidae. Ein Beitrag zur vergleichenden Morphologie der Brachyura (Crustacea: Decapoda). Doctoral Diss. Univ. Frankfurt a. M. (short version), 111 pp., 106 figs.; Frankfurt a. M., Germany.

Türkay, M., 1987. Das vorkommen der Chinesischen wollhandkrabbe (*Eriocheir sinensis*) in Suedhessen und angrenzenden Gebieten (Crustacea: Decapoda: Grapsidae). In: *Hessishe Faunistische Briefe, Institut fur Naturschutz Darmstadt*. Jahrgang 7. Heft 3. Seiten 37-54. Darmstadt, Germany.

Türkay, M., 1988. Göttinger Crustaceensammlung als Dauerleihgabe bei Senckenberg. *Natur und Museum*, 118(8): 253-254.

Türkay, M., 1992. Dr. Jürgen Dörjes, 1936-1991. *Senckenbergiana Maritima*, 22(1/2): 1-9, 1 portrait.

Türkay, M. & K. Sakai, 1976. Die Gecarcinidae von Japan (Crustacea, Decapoda). *Researches on Crustacea, Tokyo*, 7: 11-22, 9 figs., 2 pls.

Türkay, M. & K. Sakai, 1995. Decapod crustaceans from a volcanic hot spring in the Marianas. *Senckenbergiana Maritima*, 26(1/2): 25–35.

Tweedie, M.W.F., 1936. On the crabs of the family Grapsidae in the collection of the Raffles Museum. *The Bulletin of the Raffles Museum*, 12: 44-70, pls. 14, 15.

Tweedie, M.W.F., 1942. The grapsid and ocypodid crabs of Tasmania. *Papers of the Royal Society of Tasmania*, 1941: 13-25.

Tweedie, M.W.F., 1950a. Grapsoid crabs from Labuan and Sarawak. *Sarawak Museum Journal*, 5(2): 338–369.

Tweedie, M.W.F., 1950b. The fauna of Cocos-Keeling Islands, Brachyura and Stomatopoda. *The Bulletin of Raffles Museum, Singapore*, 22: 105-148, text-figs 1-4 pls 16, 17.

Tzeng, C.S. & Y.S. Chen, 1992. *Guide to the seashore life in the East Coast, National Scenic Area of Taiwan*. 221 pp. East Coast National Scenic Area Administration. Taiwan.

Udekem d'acoz, C. d', 1998. kolonisatic van de Europees-Atlantische kusten door de borstelkrab *Hemigrapsus penicillatus* (de Haan, 1835). *De Strandvlo*, 18: 45-48.

Udekem d'Acoz, C. d', 1999. Inventaire et distribution des crustace´s de´capodes l'Atlantique nord-oriental, de la Me´diterrane´e et des eaux continentales adjacents au nord de 25°N. *Patrimoines Naturels* (*Museum National d'Histoire Naturelle, Service du Pattrimoine Naturel, Paris*). No. 40. 383pp.

Udekem d'Acoz, C. d', & M. Frasse, 2002. De huidige status van *Hemigrapsus sanguineus* (de Haan, 1835) en *H. penicillatus* (de Haan, 1835) in de noordelijke Atlantische Oceaan, in het bijzonder in Nederland, met opmerkingen over hun biologie (Crustcea: Decapoda, Brachyura). *Het Zeepaard*, 62: 101-115.

Ujiié, H., 1994. Early Pleistocene birth of the Okinawa Trough and Ryukyu Island arc at the northwestern margin of the Pacific: evidence from late Cenozoic planktonic foraminiferal zonation. *Palaeogeography, Palaeoclimatololgy and Palaeoecology,* 108: 457–474.

Ujiié, H. & Y. Ujiié, 1999. Late Quaternary course changes of the Kuroshio Current in the Ryukyu arc region, northwestern Pacific Ocean. *Marine Micropaleontology*, 37: 23–40.

Ujiié, H., Y. Tanaka, & T. Ono, 1991. Late Quaternary paleoceanographic record from the middle Ryukyu Trench slope, northwest Pacific. *Marine Micropaleontology*, 18: 115–128.

Ujiié, Y., H. Ujjié, A. Taira, Nakamura, T. & K. Oguri, 2003. Spatial and temporal variability of surface water in the Kuroshio source region, Pacific Ocean, over the past 21,000 years: evidence from planktonic foraminifera. *Marine Micropaleontology*, 49: 335–364.

Umemoto, M. & H. Karasawa, 1998. Decapod crustaceans from the Holocene Nanyo Formation of Aichi Prefecture, Japan. *Kaseki no tomo*, 45: 1–19.

Urita, T., 1918. Crabs around Kagoshima-city, Japan, 2. *Rigaku-Kai* (=Sciences), 15(1): 67-72.

Urita, T., 1926a. *A check list of Brachyura found in Kagoshima Prefecture*. III, 41 p. The Tsingtao Times, Qingdao. People's Republic of China.

Urita, T., 1926b. Crabs and Shrimps around Tsingtao, China. *Zoological Magazine* (=Doubutugaku Zasshi), 38(458): 421-438. [In Japanese].

Utinomi, H., 1956. *Coloured Illustrations of Seashore Animals of Japan*. 168 p., 64 pls, I-VII, Hoikusha, Osaka, Japan.

Utinomi, H., 1963. Invertebrata. In: A. Inaba (ed). F*auna and Flora of the Inland Sea of Seto*. 336 p., 6 pls. Mukaishima Marine Biological Station, Hiroshima, Japan.

Valdovia, N & W. Stotz, 2006. Feeding behaviour of the porcellanid crab *Allopetrolisthes spinifrons*, symbiont of the sea anemone *Phymactis papillosa*. *Journal of Crustacean Biology*, 26(3): 302-315.

Van Dover, C. L., 2000. *The ecology of deep-sea hydrothermal vents*. Princeton University Press, New Jersey, United States of America.

Van Dover, C.L., C.R. German, K.G. Speer, L.M. Parson & R.C. Vrijenhoek, 2002. Evolution and Biogeography of deep sea vent and seep invertebrates. *Science*, 29: 11253-1257.

Vannini, M. & P. Valmori. 1981. Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 30. Grapsidae (Decapoda, Brachyura). *Monitore Zoologico Italiano*, (N.S.), suppl. 14: 57-101.

Veevers, J.J., 1991. Phanerzoic Australia in the changing configuration of Proto-Pangea through Gondwanaland and Pangea to the present dispersed continents. *Australian systematic Botany*, 4: 1-11.

Veldhuizen, T. 1997. The first annual IEP monitoring survey of the Chinese Mitten crab in the Delta and Suisun Marsh. IEP Newsletter Vol. 10 (4). Autumn 1997.

Veldhuizen, T. & K. Hieb, 1998. *What difference can one crab species make? The ongoing tale of the Chinese Mitten crab and the San Francisco Estuary*. Outdoor California. May-June 1998. Pp 19-21.

Vélez, I.D., J.E. Ortega, & L.E. Velasquez, 2002. Paragonimiasis: a view from Colombia. *Clinical Chest Medicine*, 23: 421-431.

Vélez, M.J., Jr., 1967. Checklist of the terrestrial and freshwater decapoda of Puerto Rico. *Caribbean Journal of Science*, 7(1-2): 41-44.

Verany, G.B., 1846. *Catalogo degli animali invertebrati marini del Golfo di Genova e Nizza*. Genova, 30 pp., 4 unnumbered pls. Genova, Italy.

Vermeij, G.J., 1978. *Biogeography and adaptation – Pattersn of marine life*. Cambridge: Havard Univeristy Press, United States of America.

Vigneux, K.P.E. & G. Marquet, 2002. Atlas des poissons et des crustacés d'eau douce de Polynésie française. *Patrimoines naturels*, 55: 1-175, illustré.

Vijayakumar, G. & T. Kannupandi, 1986. Zoeae and megalopa of the mangrove crab *Sesarma andersoni* De Man reared in the laboratory. *Mahasagar*, 19: 245-255.

Vijayakumar, G. & T. Kannupandi, 1987. Laboratory reared zoeae and megalopa of the mangrove crab *Sesarma brockii* De Man. *Indian Journal of Fisheries*, 34: 133--144.

Vincent, Th. & G. Brenton, 1999. Présence du crabe *Hemigrapsus penicillatus* (de

Haan, 1835) dans les bassins du port du Havre (Normandie, France). *Bulletin Trimestriel de la Société Géologiquede Normandie et des Amis du Muséum du Havre*, 86: 19-23.

Vincent, Th. & P.Y. Noél, 2002. Les mysidacés et décapoda capturés, collectés et observés entre 1978 et 2000 dans le port du Havre (Seine-Martime, France). *Bulletin Trimestriel de la Société Géologiquede Normandie et des Amis du Muséum du Havre*, 87: 71-91.

Vine, P., 1986. *Red Sea Invertebrates.* 224 pp. Immel Publishing, London, United Kingdom.

Vinuesa, J.H., 1977. Aportes al conocimiento de los crustáceos decápodos de Tierra del Fuego, con algunas observaciones zoogeográficas. *Physis, sección A*, 36(92): 9-19.

Vinuesa, J.H., 2005. Distribution of decapod and stomatopod crustaceans from San Jorge Gulf, Argentina. *Revista de Biología Marina y Oceanografía*, 40(1): 7-21.

Vinuesa, J.H., G.A. Lovrich & F. Tapella, 1999. New localities for Crustacea Decapoda in the Magellan Region, Southern South America. *Scientia Marina*, 63(1): 321-323.

Viola, H. J. & C. Margolis, 1985. *Magnificent Voyagers. The U. S. Exploring Expedition, 1838-1842.* 303 p., numerous unnumbered figs., Smithsonian Institution Press, Washington, D. C., United States of America.

Von Ihering, H., 1891. On the Ancient Relations between New Zealand and South America. Transactions and Proceedings of the New Zealand Insitute, 24(1891): 431-445. *In*: C.H. Smith (ed.): Early Classics in Biogeography, Distribution, and Diversity Studies: to 1950. (http://www.wku.edu/~smithch/biogeog/IHER1891.htm) (accessed on 15 April 2006)

Wada, K., 1995. Brachyura. Pp. 379-418, 101-118 pls, 21, 297-21 figs. In: S. Nishimura (ed.). *Guide to Seashore Animals of Japan with Color Pictures and Keys, 2*. xii, 1-663 p., 144 pls. Hoikusha, Osaka, Japan.

Walossek, D. & K.J. Muller, 1998. Early Arthropod Phylogeny in Light of the Cambrian "Orsten" Findings. In: G.D. Edgecombe (ed.). *Arthropod fossils and* *phylogeny*. Pp. 185-231. Columbia University Press. New York, United States of America.

Wang, C.H. & C.W. Chen, 1981. The list of brachyurous collections at Taiwan Museum (I). *Annual of Taiwan Museum*, 24: 149-156.

Wang, C.H. & H.C. Liu, 1996a. *Common Seashore Crabs of Taiwan*. (First edition). 136 pp. Taiwan Museum, Taipei, Taiwan.

Wang, C.H. & H.C. Liu, 1996b. *Estuarine Crabs of Taiwan*. 113 pp. Wild Bird Society of Kaohsiung, Kaohsiung, Taiwan.

Wang, C.H. & H.C. Liu, 1996c. Preliminary investigations of the crab diversity of Wu-Jiang estuary mangrove area in Kinmen. Pp. 223-229. In: Proceedings of a conference on mangrove ecology, Taiwan Endemic Species Institute. Taiwan.

Wang, C.H. & H.C. Liu, 1998. *Common Seashore Crabs of Taiwan*. (Second edition) 136 pp. Taiwan Museum, Taipei, Taiwan.

Ward, M., 1941. New Brachyura from the Gulf of Davao, Mindanao, Philippine Islands. *American Museum Novitates*, 1104: 1–17, figs.1–30.

Warén, A., & P. Bouchet, 1989. New gastropods from East Pacific Rise hydrothermal vents. *Zoological Scripta*, 18: 67-102.

Warner, G.F., 1977. *The biology of crabs*. xv, 202 p., Elek Science, London, United Kingdom.

Waters, J.M. & C.P. Burridge, 1999. Extreme intraspecific mitochrondrial DNA divergence in *Galaxias maculatus* (Osteichthyes: Galaxiidae), one of the worls's most widespread freshwater fish. *Molecular Phylogenetics and Evolution*, 11: 1-12.

Waters, J.M., L.H. Dijkstra & G.P. Walls, 2000a. Biogeography of a southern hemisphere freshwater fish: how important is marine fishes? *Molecular Ecology*, 9: 1815-1821.

Wear, A., 1843. List of the annulose animals hitherto recorded as found in New Zealand, with descriptions of some new species. In: *E. Dieffenbach Travels in New Zealand; with Contributions to the Geography, Geology, Botany and Natural History of that Country*. Vol. 2, 396 pp.

Wear, R.G., 1965. *Zooplankton of Wellington Harbour, New Zealand.* Zoological Publication of Victoria, University of Wellington. No. 38: p. 1-31, 9 figs.

Wear, R.G., 1970. Life History studies on New Zealand Brachyura. 4. Zoea larvae hatched from the family Grapsidae. *New Zealand Journal of Marine and Freshwater Research*, 4(1): 3-35.

Wear, R.G. & D.R. Fielder, 1985. The marine fauna of New Zealand: larvae of the Brachyura (Crustacea, Decapoda). *New Zealand Oceanographic Institute Memoirs*, 92: 1–90.

Webb, C.E. & R.C. Russell, 2005. *Living With Mosquitoes in the Lower Hunter and Mid-North coast region of NSW*. 84 pp. Department of Medical Entomology, Institute of Clinical Pathology & Medical Research, Westmead Hospital. Australia.

Weihrauch1, D., Morris, S., & D.W. Towle, 2003. Ammonia excretion in aquatic and terrestrial crabs. J*ournal of Experimental Biology*, 207: 4491-4504

Westerkov, K. & K. Probert, 1981. The Seas Around New Zealand. 181 pp. A.H. Reed & A.W. Reed, Wellington. New Zealand.

White, A. 1847a. List of the specimens of Crustacea in the collection of the British Museum. British Museum, London, United Kingdom.

White, A., 1847b. Short descriptions of some new species of Crustacea in the collection of the British Museum. *Annual Magazine of Natural History*, (1) 20: 205-207.

White, A., 1847c. No. VIII. Descriptions of a new genus and five new species of Crustacea. Appendix. In: J. Beete Jukes, *Narrative of the surveying voyage of H.M.S. Fly, commanded by Captain F.P. Blackwood, R.N. in Torres Strait, New Guinea, and other Islands of the Eastern Archipelago, during the years 1842-1846: together with an excursion into the interior of the eastern part of Java*. Vol. II: 335-338, Figs 1–3. London: T. & W. Boone, New Bond Street. [British Library copy date stamped 47.7.28.25]

White, A., 1847d. Short descriptions of some new species of Crustacea in the collection of the British Museum. *Proceedings of Zoological Society of London*, 15: 84-86.

Whitelegge, T., 1901. Scientific results of the Trawling Expedition of H. M. C. S. "Thetis", off the coast of New South Wales, in February and March, 1898.

Crustacea. *Memoir of Australian Museum*, 4: 201-246.

Whitelegge, T., 1902. Scientific results of the Trawling Expedition of H. M. C. S. "Thetis", off the coast of New South Wales, in February and March, 1898. Crustacea. *Memoir of Australian Museum*, 4: 247-283.

Whitelegge, T., 1904. Scientific results of the Trawling Expedition of H. M. C. S. "Thetis", off the coast of New South Wales, in February and March, 1898. Crustacea. *Memoir of Australian Museum*, 4: 403-416.

Willems, K.A. 1982. Larval development of the land crab *Gecarcinus lateralis lateralis* (Fréminville, 1835) (Brachyura: Gecarcinidae) reared in the laboratory. *Journal of Crustacean Biology*, 2: 180–121, figs 1-10, tabs 1-3.

Williams, B.G., 1969. The rhythmic activity of *Hemigrapsus edwardsi* (Hilgendorf), *Journal of Experimental Marine Biology and Ecology*, 3, 215–223.

Williams, B.G., E. Naylor & T.D. Chatterton, 1985. The activity patterns of New Zealand mud crabs under field and laboratory conditions. *Journal of Experimental Marine Biology and Ecology,* 89: 269-282.

Williamson, D.I., 1965. Some larval stages of three Australian crabs belonging to the families Homolidae and Raninidae, and observations on the affinities of these families (Crustacea: Decapoda). *Australian Journal of Marine and Freshwater Research*, 16(3): 369-398.

Wills, M.A., D. Briggs, R. Fortey, M. Wilkinson & P. Sneath, 1998. An Arthropod Phylogeny Based on Fossils and Recent Taxa. In: G.D. Edgecombe (ed.). *Arthropod fossils and phylogeny*. Pp. 33-105. Columbia University Press. New York, United States of America.

Wills, M.A., 1998. A phylogeny of recent and fossil Crustacea derived from morphological characters. In: R.A.Fortey & R.H. Thomas (eds.). *Arthropod Relationships*. Pp. 189-209. Chapman & Hall, London, United Kingdom.

Wilson, K.A., 1980. Studies on decapod Crustacea from the Indian River region of Florida. XV. The larval development under laboratory conditions of *Euchirograpsus americanus* A. Milne Edwards, 1880 (Crustacea: Decapoda: Grapsidae) with notes on grapsid subfamilial larval characters. *Bulletin of Marine Sciences,* 30: 756-775.

Wilson, K.A. & R.H. Gore, 1980. Studies on the decapod Crustacea from the Indian River region of Florida. XVII. Larval stages of *Plagusia depressa* (Fabricius, 1775) cultured under laboratory conditions (Brachyura: Grapsidae). *Bulletin of Marine Sciences*, 30: 776-789, figs 1–6.

Wood, D.H., 1963. A study of the macrofauna of an exposed ‘iron sand’ beach and nearby estuary. *Tane*, 9: 1-15.

Wood, D.H., 1968. An ecological study of a sandy beach near Auckland, New Zealand. *Transactions of the Royal Society of New Zealand (Zoology)*, 10(11): 89-115.

World Health Organization, 1995. *Control of foodborn trematode infection*. Report of a WHO study group. WHO technical report Series: 849.

Wu, J.S., 1992. Biological study of mangrove swamp in Shin-Chu, Taiwan. *Biological Bulletin of National Taiwan Normal University*, 27: 97-111. [In Chinese].

Wu, Y.C., C.M. Ling, J. Shieh & Y.H.M. Wang, 1962. Preliminary studies on the crabs found in the Tansui and the Keelung Rivers and the adjacent area. *Quartery Journal of Taiwan Museum*, 15(3/4): 193-210.

Xie, G., 1996. Studies on the relationship of three kinds of mitten crabs using RAPD Technique. Master of Science thesis submitted to Peking University, Bejing, People’s Republic of China. 47 pp. [Unpublished].

Xu, Z.B., 1991. Studies on clinical manifestations, diagnosis and control of paragonimiasis in China. *Southeast Asian Journal of Tropical Medicine, Public Health*, 22: 345-8.

Xu, C.H., 2002. Studies on the larval culture of *Varuna litterata*. Masters of Science thesis submitted to National Zhongshan University, Taiwan. 80 pp. [Unpublished].

Yacobucci, M,M., 1996. Plasticity of developmental timing as the underlying cause of high speciation rates in ammonoids: an example from the Cenomanian Western Interior Seaway of North America. Pp. 166-167. *Fourth International Symposium on Cephalopods – Present and Past*. Granada, Spain.

Yamaguchi, T. & K. Baba, 1993. Crustacean specimens collected in Japan by Ph. F. Von Siebold and H. Bürger and held by the Nationaal Natuurhistorisch Museum in Leiden and other Museums. In: T. Yamaguchi (ed.). *Ph.F. von Siebold and*

*Natural History of Japan Crustacea.* Pp. 145-570, text-figs. 200 + I-III. Leiden, The Netherlands.

Yamaguchi, T. & L.B. Holthuis, 1993. Kurimoto suiken and bis Kai-ka Rui Siya-sin. In: T. Yamaguchi (ed.). *Von Siebold and Natural History of Japan, Crustacea*. Pp. 647-668. Carcinological Society of Japan, Tokyo, Tokyo, Japan.

Yamaguchi, T. & W.A. Newman, 1990. A new and primitive barnacle (Cirripedia: Balanomorpha) from the North Fiji Basin abyssal hydrothermal field, and its evolutionary implications. *Pacific Science*, 44: 135-155.

Yamaguchi, T. (editor), 1993. *Ph. F. von Siebold and the Natural History of Japan. Crustacea.* 731 pp. The Carcinological Society of Japan, Tokyo, Tokyo, Japan.

Yamaguchi, T., 1994. Barnacles as living fossils from deep-sea hydrothermal vents. *Fossils and Paleontological Society, Japan,* 56: 37-41.

Yamaguchi, T., M. Takeda, & K. Tokudome, 1976. A list of crabs collected in the vicinity of the Aitsu Marine Biological Station and a preliminary report on cheliped asymetry of the crabs. *Calanus, Bulletin of the Aitsu Marine Station, Kumamoto University*, 5: 31-46.

Yamaguchi, T., K. Harada, M. Takeda & T. Kikuchi, 1987. Crab Fauna of the Amakusa Islands, *Calanus, Bulletin of the Aitsu Marine Station, Kumamoto University*, 10: 1-71, pls. 1-19.

Yamanishi, R. & K. Wada, 1996. Benthos in Japan. *WWF Japan Science Report*, 3: 1-183, 10 pls, 58 text-figs, 10 tables.

Yamazi, I., & M. Wakamiya, 1975. Zooplankton in the waters surroundings a new active volcanic islands, Nisinosima-Sin-To. *Journal of Tokyo University Fisheries*, 61(1-2): 71-92.

Yang, C.M., 1979. *A List of Brachyura in the Zoological Reference Collection of the Department of Zoology*. 60 pp. (mimeographed). Department of Zoology, University of Singapore, Singapore.

Yang, H.C., & P.J. Chang, 1996. *The fishes of Quemoy (Kinmen) (part IV)*. 59 pp. Quemoy (Kinmen) Fisheries Research Institute, Quemoy. Taiwan.

Yang, S.L., 1986. The diagnostic value of gastric mills construction as taxonomic character on the classification of crabs. *Acta Zootaxonomica Sinica*, 11(2): 151-159.

Yeo, D.C.J., & P.K.L. Ng, 1999. A new species of *Geosesarma* (Crustacea: Decapoda: Brachyura: Grapsidae) from Paulau Tioman, Peninsular Malaysia. *Raffles Bulletin of Zoology, Supplement No. 6*: 189-196.

Yokoya, Y. 1928. Report of the Biological Survey of Matsu Bay, 10. Brachyura and crab-shaped Anomura. *Science Reports of the Tohuku Imperial Univeristy, Series 4, Biology Sendai, Japan*, 3(4): 757-784, text-figs. 1-8.

Yoon, S.S. & Y.T. Noh, 1995. Morphological studies on hemocytes of the common shore crab, *Helice tridens tridens* (Decapoda, Crustacea). *Korean Journal of Zoology*, 38(3): 330-339, text-figs. 1-13.

Yoshimura, K., 1990. Two new species of the genus *Monhystrium* Cobb, 1920 (Monhysteridae: Nematoda) from terrestrial crabs of subfamily Sesarminae (Brachyura) in Japan. *Zoological Science*, 7: 755-761.

Yu, H.P. & P.H. Ho, 1986. Notes on the freshwater crabs of the genus *Eriocheir* (Crustacea, Decapoda, Grapsidae) from Taiwan. *Annuals of Taiwan Museum*, 29: 111-116.

Yu, H.P., M.S. Jeng, T.Y. Chan, P.H. Ho & J.Y. Shy, 1996. *Studies on the land and aquatic decapod crustacean fauna of the Kenting National Park*. ii+79 pp. Ministry of the Interior, Taipei, Taiwan.

Yu, S., 1996. Control of parasitic diseases in China, current status and prospects. *Chinese Medical Journal*, 109: 259-65.

Yu, S., L. Xu, Z. Jiang, S. Xu, J. Han & Y. Zhu, 1994. Report on the first nationwide survey of the distribution of human parasites in China. 1. Regional distribution of parasite species. *Chinese Journal of Parasitology and Parasitic Diseases*, 12: 241-247.

Zariquiey Alvarez, A.R., 1968. Crustàceos Decápodos Ibéricos. *Investigación Pesquera (Barcelona)*, 32: 1-510.

Zeng, H. & J. Yu, 2002. *Culture chronology of river crabs*.. 364 pp, 59 tabs., 64 pls. Jindun Publishing Company, Beijing, People’s Republic of China.

Zhao J., T.J. Lam & J.Y. Guo, 1997. A cute toxicity of ammonia to the early stage-larvae and juveniles of *Eriocheir sinensis* H. Milne-Edwards, 1853 (Decapoda: Grapsidae) reared in the laboratory. *Aquaculture Research*, 28(7): 517-529.

Zhao, N., N. Du, X. Bao & L. Zhang, 1988. *Artificial Breeding, Propagation and Culture of Chinese Mitten Crab*. Pp. 134-136. Anhui Science and Technology Press, Hefei, People's Republic of China. [In Chinese].

Zhong, H., L. He, Z. Xu, & W. Cao, 1981. Recent progress in studies of *Paragonimus* and paragonimiasis control in China. *Chinese Medical Journal*, 94: 483.

Zhou, N. & L. Sun, 1986. Preliminary report on a survey of brachyuran crustacea from the coast of Liaoning Province, China. *Transactions of the Chinese Crustacean Society*, 1: 223-226.

Zimsen, E., 1964. The type material of I. C. Fabricius. 656 pp. Munksgaard, Copenhagen, Denmark.