

TWO NEW SUBFAMILIES OF VARUNIDAE (CRUSTACEA: BRACHYURA), WITH DESCRIPTION OF TWO NEW GENERA

Peter J. F. Davie

Queensland Museum, PO Box 3300, South Brisbane, Queensland, Australia

Email: Peter.Davie@qm.qld.gov.au

N. K. Ng

Department of Biological Sciences, National University of Singapore, Kent Ridge,

Singapore 119260, Republic of Singapore

Email: ngankee@nus.edu.sg

ABSTRACT. – A number of genera traditionally placed in the Varunidae or Varuninae have been reappraised and found to represent two new subfamilies. The Thalassograpsinae, for *Thalassograpsus harpax* Hilgendorf, 1892, has a number of unique apomorphies including the form of the frontal margin, maxillipeds, endostome, thoracic sternites, and the male abdomen with segments 5 and 6 functionally fused. The Gaeticinae is remarkable for having mouthparts and sternum highly modified for suspension feeding, and having male abdominal segments 3–6 fused. The subfamily includes the type genus *Gaetice* Gistel, 1848, and a new genus *Sestrostoma* split from the Varuninae genus *Acmaeopleura* Stimpson, 1858. *Gaetice americanus* Rathbun, 1923, does not belong to *Gaetice* as here redefined and is transferred to a new genus in the Varuninae.

KEY WORDS. – Taxonomy, Varunidae, *Thalassograpsus*, *Gaetice*, new subfamily, new genera, suspension feeding, commensalism.

INTRODUCTION

The higher phylogenetic relationships within the Grapsoidea have been the subject of much interest during recent years. A new family from the Americas, Glyptograpsidae, affiliated with the Varunidae, was recognised by Schubart et al. (2002). Davie (2002) removed the Plagusiinae to a separate family, the Plagusiidae, but he otherwise took the conservative approach of treating the Grapsinae, Sesarminae, Cyclograpsinae and Varuninae as subfamilies of the Grapsidae. It has nevertheless become increasingly clear over the intervening years, that the Grapsidae, Sesarminae and Varunidae must be recognised as families, with the Cyclograpsinae included as a subfamily of the Varunidae. This seems well supported on the basis of adult and larval morphology, and 16S mtDNA (see Schubart & Cuesta, 1998; Sternberg & Cumberlidge, 1998; Schubart et al., 2000, 2002, 2006; Karasawa & Kato, 2001; Kitaura et al., 2002; and Davie, 2002). Another significant change is the establishment of the Xenograpsidae N. K. Ng, Davie, Schubart & P. K. L. Ng, 2007, for the aberrant *Xenograpsus* that inhabits hydrothermal-vents. Schubart et al. (2006) have more recently suggested that the superfamily groupings Grapsoidea and Ocypodoidea are not monophyletic in their current composition. We consider this still an open question as their

trees may not be sufficiently resolved at higher taxonomic levels, and our own morphological work, aimed at understanding the phylogenetic relationships of the Grapsoidea, still supports its traditional superfamilial structure.

We examined all genera in the Varuninae and found that some genera showed significant patterns of divergence that cannot be accommodated within this subfamily. Two new subfamilies are thus established for these genera.

Specimens examined are deposited in the: Institute of Zoology, Academia Sinica, Taipei (IZAS); Muséum national d'Histoire Naturelle, Paris (MNHN); Museum Zoologicum Bogoriense, Bogor (MZB); Zoologisk Museum, Natural History, Basel (NMB); National Museum, Crustacean Collection, Manila (NMCR); National Museum of Natural History, Taichung (NMNS); National Science Museum, Tokyo (NSMT); National Taiwan Ocean University, Institute of Marine Biology, Keelung (NTOU); Queensland Museum, Brisbane (QM); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); Senckenberg Museum, Frankfurt (SMF); Taiwan Museum, Taipei (TMCD); Zoological Museum of Amsterdam, (ZMA); Zoological Museum, Berlin (ZMB); Zoological Reference Collection, Raffles Museum of

Biodiversity Research, National University of Singapore, Singapore (ZRC).

All measurements provided are of the carapace widths and lengths respectively. The abbreviations G1 and G2 are used for the male first and second gonopods respectively; cw = carapace width.

TAXONOMY

VARUNIDAE Alcock, 1900

Thalassograpsinae, new subfamily

Type genus. – *Thalassograpsus* Tweedie, 1950, by present designation.

Diagnosis. – Carapace glabrous, flat, regions moderately defined; anterolateral margins with 3 teeth including exorbital angle; posterior margin convex; no raised line on the branchial region defining posterolateral facet. Front deflexed; broad, less than half maximum carapace breadth; broadly bilobed, but with short distinct lateral sulcus adjacent to inner orbital edge, such that the frontal and supra-orbital margins are not continuous. Orbits open laterally; sub-orbital crest relatively straight, extending short distance across lateral branchial region, stridulatory against inner edge of cheliped merus; pterygostomial grooves opening into anterolateral corner of buccal cavity; pterygostome non-setose, lacking vertical groove subparallel to buccal cavity. Third maxillipeds with subtriangular ischium, with a faint longitudinal sulcus; merus subquadrate without convex lateral margins; almost no gape when closed; exopod narrow. Epistome granular, medially prominent, very narrow. Chelipeds subequal, large in size. Ambulatory legs dorso-ventrally flattened; posterodistal border of propodus of walking legs with subapical spine. Thoracic sternites 3 and 4 flat, broad; sternite 3 lateral margins relatively straight; the suture of thoracic sternite 3/4 not visible (vs. slightly visible in all other subfamilies); and medial groove in thoracic sternites 7, 8 proportionately wide. Male gonopores fully sternal. Abdomen with segments 5, 6 functionally fused, although suture still present.

Remarks. – The *Thalassograpsinae* can be differentiated from the other subfamilies within the family Varunidae by the following unique suite of apomorphies:

- 1) Frontal margin of carapace with short distinct lateral sulcus just posterior to lateral frontal margin, and separated from inner orbital margin (frontal margin continuous with orbital margin in other Varunidae).
- 2) Epistome has a prominent, outwardly projecting, elongated, transverse lobe laterally.
- 3) Third maxillipeds leave no gape when closed (more or less gaping in Varuninae, Cyclograpsinae and Gaeticinae).
- 4) Merus and ischium of the third maxillipeds lack a visible longitudinal sulcus (distinctly visible in the other Varunidae subfamilies).

- 5) Ischium of third maxillipeds subtriangular (vs. subquadrate in other varunines);
- 6) Male abdomen with segments 5 and 6 fused and immovable, but with suture line still visible.
- 7) Posterodistal border of propodus of walking legs with a subapical spine.
- 8) Thoracic sternites 3, 4 are flat and broad (slightly convex and narrower in the other subfamilies);
- 9) Anterolateral margin of the sternal plastron is straight and horizontal (lobular and sloping downwards in all other grapsoid families and subfamilies);
- 10) Suture of thoracic sternite 3/4 is not visible (moderately visible in all other subfamilies);
- 11) Medial groove in thoracic sternites 7 and 8 are proportionately wider (with narrower medial groove in sternite 8 of other subfamilies).

Thalassograpsus Tweedie, 1950

Brachynotus Hilgendorf, 1892: 38 (part).

Thalassograpsus Tweedie, 1950: 133; Sakai, 1976: 652; Dai et al., 1986: 481; Dai & Yang, 1991: 527; Davie, 2002: 229.

Type species. – *Brachynotus harpax* Hilgendorf, 1892, by monotypy; gender masculine.

Diagnosis. – Genus monotypic; characters are the same as for the new subfamily, *Thalassograpsinae*.

Remarks. – *Thalassograpsus* was established by Tweedie (1950) for *Brachynotus harpax* Hilgendorf, 1892, because it was clear that it differed from typical *Brachynotus* in many features: 1) the frontal and supra-orbital margins are not continuous (continuous in other varunine taxa); 2) the third maxillipeds meet completely in the middle line leaving no gape between them (a distinct rhomboidal gape in other varunine taxa); 3) there is no raised line on the branchial region defining a posterolateral facet (present in *Brachynotus* and other varunine taxa). In fact, there are many other significant character differences between these genera, and the resemblance to the typical varunine *Brachynotus* is at best, superficial.

Thalassograpsus harpax (Hilgendorf, 1892) (Figs. 1, 2, 3)

Brachynotus harpax Hilgendorf, 1892: 38; Sakai, 1939: 675, Figs. 119a–c; Horikawa, 1940: 29; Lin, 1949: 29.

Thalassograpsus harpax – Harntoll, 1975: 305; Holthuis, 1977: 169; 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; Davie, 2002: 229.

Material examined. – Types: Lectotype – 1 male (11.0 × 9.7 mm) (ZMB 8472), Fundorf, Aden, coll. Hildebrandt. Paralectotypes – 3 males (8.0–10.0 × 8.8–9.0 mm), 3 females (ovig.) (7.8–10.3 × 6.7–9.0 mm) (ZMB 8472), Fundorf, Aden, coll. Hildebrandt; 11 males (6.8–12.0 × 5.9–10.3 mm), 4 females (6.1–10.8 × 5.7–9.1 mm)

(MNHN-B12534), Aden, coll. 1904 (written as types of Hilgendorf). Other material: **Red Sea** – 2 females (ovig.) (MNHN-B12531), Perim D’Jousseume, coll. 1897; 1 male (11.3 × 9.8 mm) (MNHN-B12532), Red Sea, coll. 1897; 1 male (7.6 × 6.6 mm), 1 female (6.1 × 5.4 mm) (MNHN-B12535), Red Sea, coll. 1897; 1 male (9.4 × 8.1 mm) (MNHN-B12537), Red Sea, coll. 1897; 5 males (7.8–10.1 × 6.6–9.0 mm), 2 females (6.0–8.1 × 4.6–7.5 mm), 3 females (ovig.) (6.6–7.8 × 5.8–6.8 mm) (MNHN-B12533), Djibouti, D’Jousseume, coll. 1897; 1 female (7.2 × 6.0 mm) (SMG-17272), Bjbouli, Djibouti, Stadlogebel, Triton beach, eulitoral, coll. F. Allspach, 18 Mar.1987. **Japan** – female (8.2 × 7.3 mm), ovig. female (6.7 × 6.2 mm) (RU), Japan; 1 male (8.7 × 7.4 mm) (RU), Japan, coll. 28 May 1984; 1 male (10.9 × 9.3 mm) (RU), coll. 28 Jul.1985. **Taiwan** – male (8.9 × 7.6 mm) (NMNS), Chi-Han, coll. 15 May 1994. **Philippines** – 1 male (6.0 × 5.3 mm) (NMCR No. 531), University of Philippines collection; 5 males (4.7–10.7 × 3.0–9.5 mm), 1 female (8.8 × 7.5 mm), 1 female (ovig.) (9.0 × 8.0 mm) (NMNS), Cumming Island, Philippines, coll. H.T. Shih, 30 Aug.2003. **Singapore** – male, 12.3 mm cw (ZRC 19657922), Singapore, coll. R. Serène.

Diagnosis. – Carapace subquadrate, with dorsal surface flat, front broad, anterior border concave medially, divided into four lobes. Dorsal orbital margin with suture. Ventral orbital margins with 3 long ridges. Third maxillipeds with merus quadrate, ischium broad, exopod narrow. Chelipeds stout, with numerous small teeth on cutting edge of fingers. Ambulatory legs flat, broad, sparsely setose; merus with subdistal spine, dactylus with few stiff setae. Male abdomen narrowly triangular. G1 long, slender, slightly arched. Female gonopore small, oval in shape.

Colour. – Fresh specimens cream to light brown (H. T. Shih, pers. comm.). Preserved specimens are light brown.

Size. – A relatively small species. Largest male specimen examined 11.3 × 9.8 mm (MNHN-B12532), largest female 9.0 × 8.0 mm (NMNS).

Habitat. – Reported from under corals and stones, or among pebbles on sheltered rocky shores.

Distribution. – Indo-West Pacific (China, Japan, Taiwan, Singapore, Indonesia, Samoa, Cocos (Keeling) Islands and Red Sea).



Fig. 1. *Thalassograpsus harpax* (Hilgendorf, 1882). Male, 12.3 mm cw, Singapore, coll. R. Serène, ZRC 1965.7922. Dorsal view.

Remarks. – Relatively uncommon despite its wide distribution. Nothing is known of its biology.

GAETICINAE, new subfamily

Type genus. – *Gaetice* Gistel, 1848 [replacement name for *Grapsus* (*Platynotus*) De Haan, 1833]; gender masculine.

Included genera. – *Gaetice* Gistel, 1848, and *Sestrostoma*, new genus.

Diagnosis. – Varunidae with orbit open laterally; sub-orbital crest straight, variable in length; stridulatory pterygostomial grooves not opening into anterolateral corner of buccal cavity. Third maxillipeds leaving narrow gape when closed; without oblique setose crest on merus, ischium; reaching as far as epistome, completely closing buccal cavity anteriorly; ischiomeral articulation strongly, inwardly oblique (*Gaetice*) or normal (horizontal); exopod normal, not swollen or unusually enlarged; palp markedly elongated, armed with very long brush of setae used for suspension feeding reaching almost to abdomen when folded. Sternal plastron with relatively deep longitudinal sulcus anterior to abdomen, into which setal brush of third maxillipeds is folded for protection. Epistome smooth, relatively prominent medially. Male abdomen with segments 3–6 functionally fused although suture lines still evident.

Remarks. – The most striking apomorphy of the new subfamily Gaeticinae is the modified third maxillipeds having elongated palps each bearing a long setal brush that lies, at rest, in a corresponding longitudinal, anterior sternal sulcus. These mouthparts are used for suspension feeding. Suspension feeding amongst the Brachyura has been previously reported for *Gaetice depressus* by Depledge (1989), but the phylogenetic significance of this has not been previously emphasised. The only other reference to a crab using suspension feeding that we are aware of is Harminto & Ng (1991), who noted such behaviour in a camptandriid crab (*Baruna*), but in a different way from gaeticine crabs. Suspension feeding is common in porcellanid crabs (Robinson & Tully, 2000; Valdovia & Stotz, 2006).

The other important character of the Gaeticinae is the effective fusion of the male abdominal segments 3–6, even though the suture lines are still evident.

In reviewing the varunine genus *Acmaeopleura* Stimpson, 1858 (considered to consist of five species viz. *A. parvula* Stimpson, 1858; *A. rotunda* Rathbun, 1909; *A. balssi* Shen, 1932; *A. depressa* Sakai, 1965, and *A. toriumii* Takeda, 1971), we realised that *A. balssi*, *A. depressa* and *A. toriumii* have third maxillipeds strongly modified for suspension feeding, as well as a medial sulcus on the anterior sternal plates. A new genus was needed to accommodate these two species, here named *Sestrostoma*. On this basis, the affinities of *Sestrostoma* thus appeared to be with *Gaetice* in the Gaeticinae. *Sestrostoma* and *Gaetice* species are dramatically 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 maxillipeds carries long setae clearly used for suspension feeding; 2) the anterior segments of the sternum have a longitudinal sulcus, into which the maxilliped setae extend; 3) the male abdomen has segments 3–6 fused and immovable. This set of characters is unique among grapsoid crabs, and strongly points to a monophyletic lineage.

There is strong evidence that all the *Sestrostoma* species live as symbionts in the burrows of thalassinidean shrimps or other burrowing invertebrates such as large polychaetes and perhaps echiuroids. Davie (1992) and Sakai (2000) have reported the probable association of *S. toriumii* with the large mud-shrimps *Upogebia major* and *U. yokoyai*, which has been confirmed by recent work by Itani (2002, 2004). Sakai (1976) reported *S. balssi* as “found associated with annelids”. Itani (pers. com.) has found *S. depressum* in the burrows of thalassinideans. Given that *Sestrostoma* species live in burrows of invertebrates, this would result in several morphological adaptations such as the loss of anterolateral teeth, the presence of small, slender and unarmed legs, and a smooth, glabrous rounded carapace. Thus a symbiotic in contrast to a free-living habit can help explain the dramatic differences in carapace morphology between *Gaetice* and *Sestrostoma* species.

Key to genera of Gaeticinae

1. Carapace distinctly quadrangular; dorsal surface glabrous, flat.
Third maxilliped suture line between merus and ischium oblique
..... ***Gaetice* Gistel, 1848**
- Carapace distinctly rounded; dorsal surface punctate, convex.
Third maxilliped suture line between merus and ischium straight
..... ***Sestrostoma*, new genus**

Gaetice Gistel, 1848

Grapsus (*Platynotus*) De Haan, 1833: 63 (type species *Grapsus* (*Platynotus*) *depressus* De Haan, 1835, by monotypy; gender masculine; preoccupied name).

Gaetice Gistel, 1848: 10 (replacement name for *Grapsus* (*Platynotus*) De Haan, 1833; gender masculine); 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.

Platygrapsus Stimpson, 1858: 107; 1907: 128.

Type species. – *Grapsus* (*Platynotus*) *depressus* De Haan, 1833.

Diagnosis. – Carapace quadrangular, broader than long; dorsal surface glabrous, punctate; regions well defined, flat.

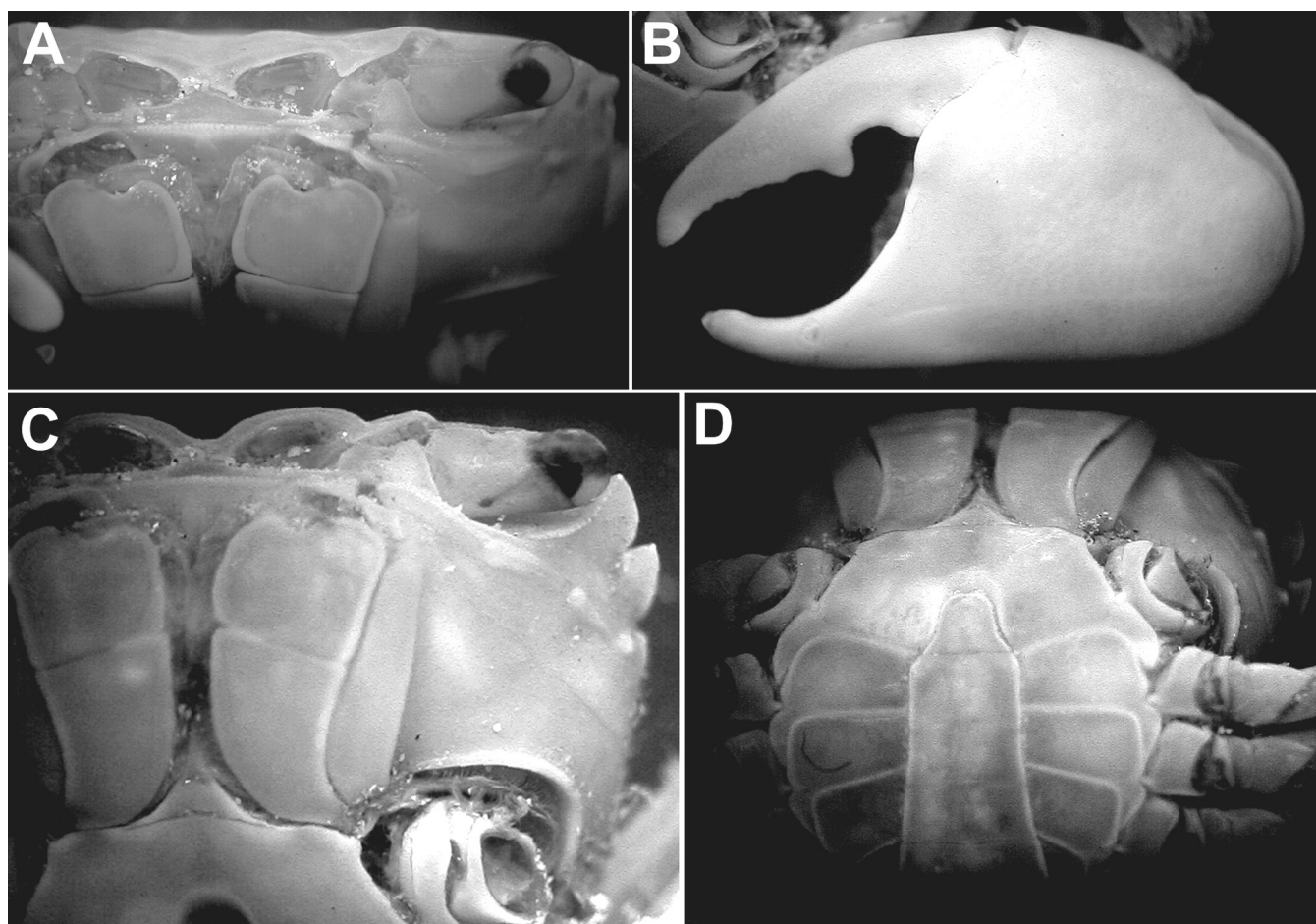


Fig. 2. *Thalassograpsus harpax* (Hilgendorf, 1882). Male, 12.3 mm cw, Singapore, coll. R. Serène, ZRC 1965.7922: A, Frontal view; B, large male chela; C, third maxillipeds and pterygostome; D, male abdomen and sternum.

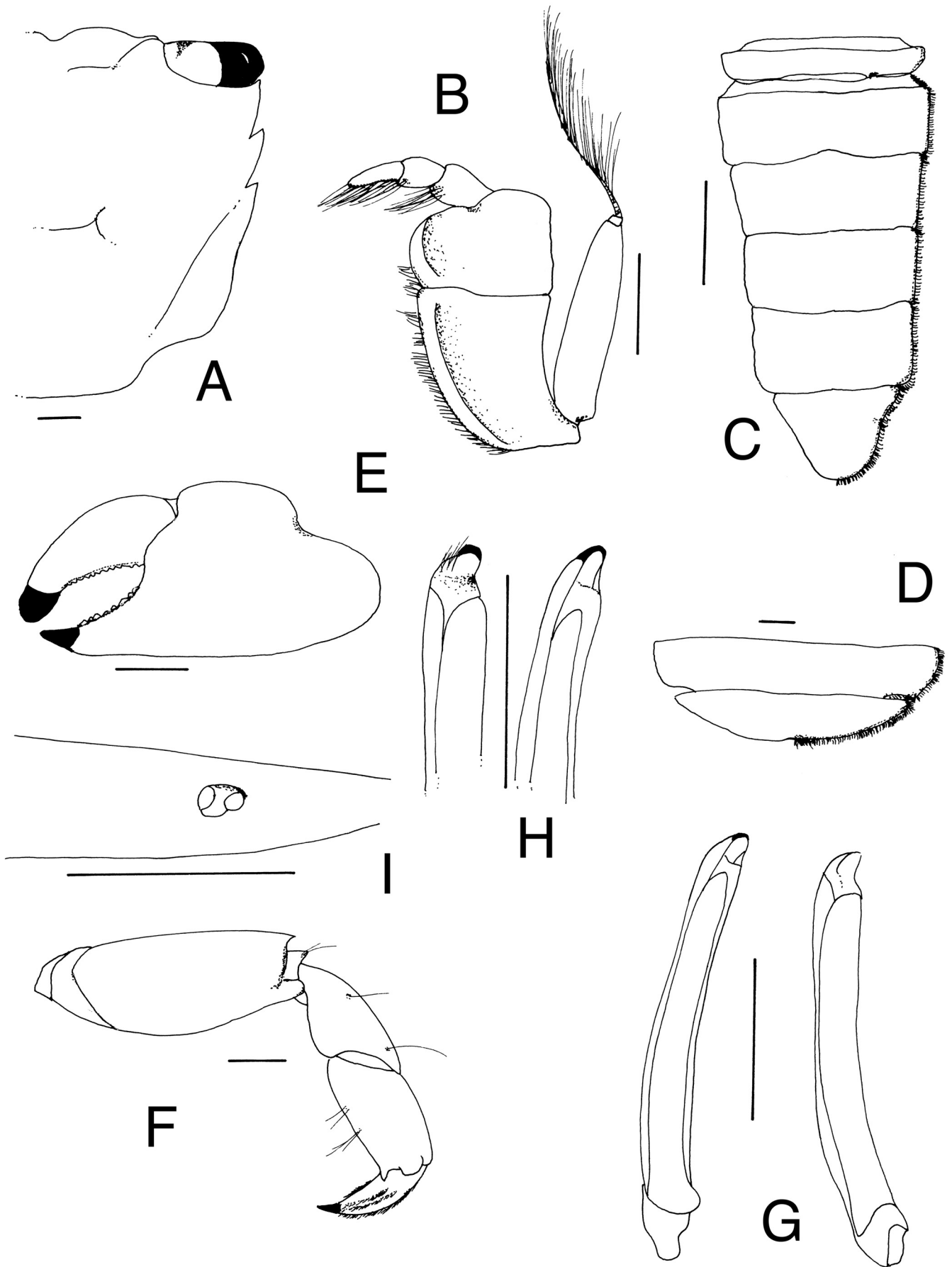


Fig. 3. *Thalassograpsus harpax* (Hilgendorf, 1882). Male, 10.0 × 9.0 mm; female, 10.3 × 9.0 mm (ZMB 8472): A, carapace; B, third maxilliped; C, male abdomen; D, female abdomen (part); E, chela; F, last ambulatory leg; G, G1; H, distal end of G1; I, female gonopore. Scale bars = 1.0 mm.

Frontal margin convex, bilobed. Anterolateral margin subcristate with 3 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 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 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 groove to receive the third maxilliped setal brush. Male abdomen narrowly triangular, with segments 3–6 functionally fused.

Remarks. – *Gaetice americanus* Rathbun, 1923, clearly does not belong to *Gaetice* because it does not have the mouthpart and sternal modifications for suspension feeding that are characteristic of true *Gaetice* species. It is here transferred to a new genus in the Varuninae (see below). *Gaetice* thus includes only two known species, *G. depressus* De Haan, 1833, and *G. unguatus* Sakai, 1939.

Key to species of *Gaetice*

1. Carapace subquadrate; frontal margin strongly lobed; infraorbital ridge with numerous small, round granules. Propodus of last ambulatory leg short, broad *G. depressus*
- Carapace subquadrate; frontal margin weakly lobed; infraorbital ridge with few large, round granules. Propodus of last ambulatory leg longer, more slender *G. unguatus*

Gaetice depressus (De Haan, 1833) (Figs. 4–6)

Grapsus (*Platynotus*) *depressus* De Haan, 1833: 63, Pl. 8 Fig. 2. *Platygrapsus convexusculus* Stimpson, 1858: 104; 1907: 128, Pl. 17 Fig. 3.

Gaetice 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 – Balss, 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, 1936a: 1951; 1936b: 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.

Material examined. – Types: Lectotype – male (25.6 × 21.3 mm) (RMNH-1226), Japan, coll. P. F. von Siebold, 1823–1829 (det. Yamaguchi & Baba, 1993). Paralectotype – 1 female (12.1 × 10.0 mm) (RMNH-1227), Japan, coll. P. F. von Siebold, 1823–1829; 4 specimens mounted on board (RMNH-D-42279, dry), Japan, coll. P. F. von Siebold, 1823–1829.

Other material. **Japan** – 10 males (6.8–17.3 × 6.0–14.9 mm), 6 females (9.3–11.7 × 8.5–9.8 mm), 3 ovig. females (10.1–17.7 × 8.6–14.5 mm) (MNHN-B-12090), Tokyo area, Japan, coll. Harmand, 1906. 1 male (17.0 × 14.2 mm) (QM), Sakada, Shirahama, Wakayama Prefecture, Japan, coll. Y. Fukui, 6 Aug. 1996; 9 males (13.5–22.2 × 11.8–19.2 mm), 1 female (20.0 × 17.8 mm), 5 ovig. females (13.6–21.4 × 12.0–17.5 mm) (RMNH-D-1225), Amoy, coll. G. Schlegel, no collection date; 2 males (10.3–20.0 × 8.9–17.2 mm), 3 females (10.0–15.8 × 9.3–12.3 mm) (RMNH-D-12461), Shirahama, Wakayama Prefecture, Japan, coll. S. M. Shino, 7 Aug. 1958; 1 male (21.2 × 17.9 mm), 1 ovig. female (16.0 × 13.3 mm) (RMNH-D-25135), Sagami Bay, Kanagawa Prefecture, coll. H. Suzuki, 10 Sep. 1968; 13 males (17.9–24.7 × 15.4–21.2 mm), 1 female (20.6 × 16.8 mm), 1 ovig. female (16.2 × 13.3 mm) (RMNH-D-41894), Matsushima, Amakusa, Kyushu, Japan, coll. T. Yamaguchi, 4 Sep. 1985; 3 males (12.7–15.2 × 11.1–12.8 mm) (RU-uncatalogued), river mouth of Okukubi River, Okinawa Island, Ryukyus, Japan, 27 Jun. 1987; 1 male (30.4 × 27.0 mm) (SMF-7655), Sagami Bay, Japan, coll. T. Sakai; 4 males (6.0–15.2 × 4.8–12.9 mm), 1 female (13.5 × 11.2 mm) (SMF-7685), Ishigaki Island, Okinawa, Japan, coll. T. Sakai; 1 male (16.0 × 13.5 mm) (USNM 60247), Hokkaido Imperial University, Wakayama Prefecture, Honshu, Japan, coll. M. Sasaki, 1925; 2 males (12.0–15.3 × 10.0–12.8 mm), 1 female (13.0 × 11.8 mm) (ZMA-de-240140), Tokyo, Japan, coll. Harmond, 1906. **South Korea** – 5 males (11.0–27.3 × 9.5–22.6 mm), 1 ovig. female (20. × 16.9 mm) (ZRC), rocky tidal pools, Seong San Beach, Cheju Island, South Korea, coll. N. K. Ng & J. C. Y. Lai, 28 Aug. 2002. **China** – 11 males (8.9–20.9 × 7.2–17.8 mm), 9 females (10.0–17.0 × 8.0–15.2 mm), 3 ovig. females (12.3–12.8 × 10.0–10.3 mm) (MNHN-B-12089), Amoy, coll. C. F. Wang, Jul. 1925; 1 male (11.3 × 9.9 mm), 6 females (8.9–13.3 × 7.0–10.9 mm) (MNHN-B-12091), Tonkin, coll. 1897; 11 specimens mounted on board (RMNH-D-45218, dry), Amoy, coll. 1859–1862, coll. G. Schlegel; 8 males (16.2–24.3 × 15.7–20.4 mm), 8 females

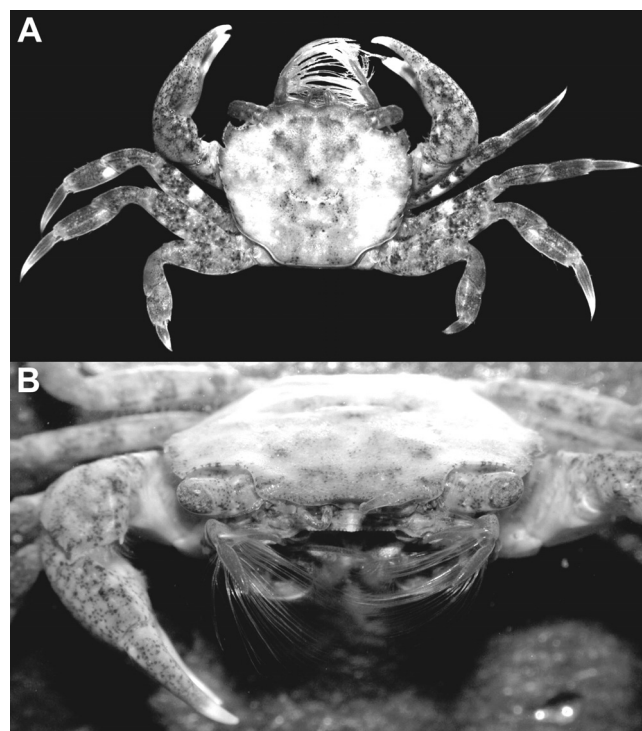


Fig. 4. *Gaetice depressus* (de Haan, 1833), male (ZRC 2005.0095), Qindao, beach adjacent Institute of Oceanology, coll. P.K.L. Ng & H.L. Chen, 22 Aug. 2002. Pictures taken in life, showing setation and movement of third maxillipeds: A, dorsal view; B, anterior frontal view. Photos by P. K. L. Ng.

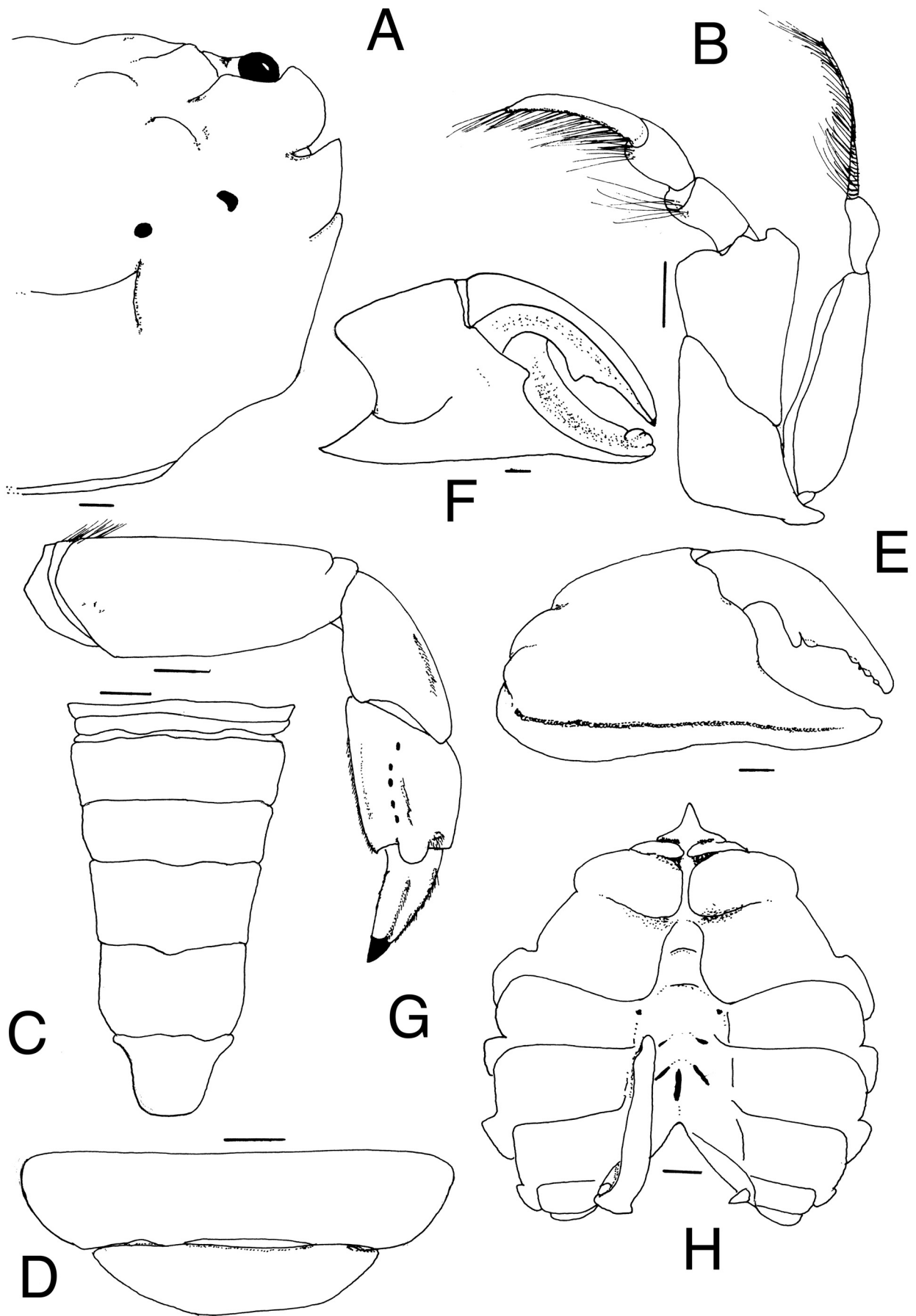


Fig. 5. *Gaetice depressus* (de Haan, 1833), male, 18.3 × 15.3 mm; female, 13.6 × 10.0 mm (NTOU): A, carapace; B, third maxilliped; C, male abdomen; D, female abdomen (part); E, outer surface of chela; F, inner surface of chela; G, last ambulatory leg; H, male sternum. Scale bars =1.0 mm.

(11.4–20.5 × 9.6–17.3 mm) (SMF-22115), Shilaroren, Qingdao, Shangdong Province, coll. M. Türkay, 16 Apr.1992; 1 male (22.2 × 18.5 mm) 1 female (11.5 × 10.0 mm) (USNM 64952), Amoy, coll. C. J. Shen, Nov.1928; 4 males (10.5–17.0 × 9.1–14.5 mm) 8 females (9.0–15.5 × 7.8–13.0 mm) (ZRC), seashore along road from Changpo to Huiren, Hainan Island, coll. N. K. Ng & Y. Cai, 1 Dec.1998; 10 males (14.5–21.3 × 12.3–17.5 mm), 2 females (13.3–16.0 × 11.7–13.3 mm) (ZRC), Bainu Beach, Nan'ao Island, Guangdong Province, coll. Y. Cai & N. K. Ng, 13 Nov.1998. **Hong Kong** – 1 males (12.1–22.5 × 10.0–18.8 mm), 3 females (12.3–15.3 × 10.3–12.8 mm) (ZRC 1998.1023), inner Tolo Harbour, Wu Kwai Sha, New Territories, Hong Kong, coll. P. K. L. Ng & S. Y. Lee, 6 Jun.1996; 10 males (1.4–21.9 × 10.3–18.3 mm), 4 females (10.5–17.2 × 8.8–14.1 mm), 1 ovig. female (14.5 × 11.9 mm) (SMF-12042), Hong Kong, coll. Galathea Expedition, no collection date; 1 male (12.0 × 10.7 mm) (MNHN-B-9133), Hong Kong. **Taiwan** – 3 males (15.4–19.6 × 12.3–16.0 mm), 1 female (16.6 × 14.0 mm) (ASIZ-71687), He-Mei, Taiwan, coll. M. S. Jeng, 4 Nov.1997; 3 males (16.7–20.4 × 13.7–17.4 mm) (TMCD), Ao-Di, Taiwan, coll. H. C. Liu, 6 Jun.1971; 21 males (7.3–17.2 × 6.2–14.5 mm), 10 females (7.5–13.5 × 6.0–11.5 mm) (NTOU), Peng-Hu islands, coll. 11 Oct.1984; 20 males (15.7–24.4 × 13.7–21.0 mm) (TMCD-2335), Jin-Cheng, Jin-Men Islands, Taiwan, coll. L. R. Dong, 29 Jan.1988.

Diagnosis. – Carapace subquadrate, broadening anteriorly, dorsal surface flat, smooth; frontal margin strongly lobed. Anterolateral margin with 3 teeth including orbital tooth. Third maxilliped with 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, large gape between fingers of adult males, usually with one or two large teeth near base of moveable finger. Propodus of last ambulatory legs short, broad.

Colour. – Highly variable, ranging from light cream to dark brown, with dark brown and/or black spots (unpublished data).

Size. – Largest male specimen examined 25.6 × 21.3 mm (lectotype), largest female 20.1 × 16.6 mm (USNM 62867).

Habitat. – Found under small rocks, on coral-sand substrate close to the river mouth. They sometimes stack on top of each other in large numbers. Actively suspension feed while covered by high tide.

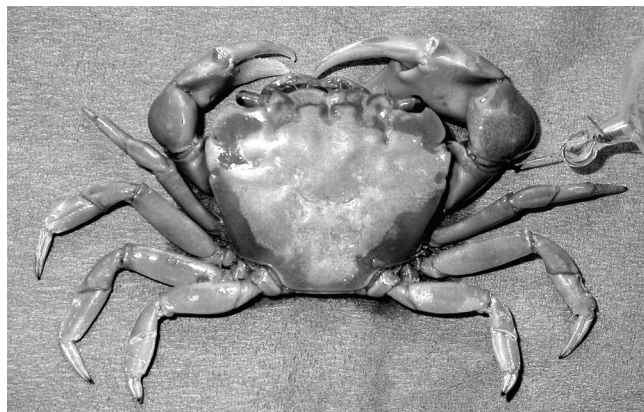


Fig. 6. *Gaetice depressus* (De Haan, 1833), male, lectotype, 25.6 × 21.3 mm (RMNH 1226). Dorsal view.

Distribution. – Japan, Korea, China and Taiwan.

Remarks. – This species can be easily distinguished from *G. unguulatus* by the following: 1) the lateral lobes of the frontal margin are very distinct (not distinct in *G. unguulatus*); 2) the infraorbital ridge has numerous (usually more than 12) small, isomorphic granules (usually less than 8 larger granules in *G. unguulatus*); 3) the anterolateral angle of the merus of the third maxillipeds is very convex (less convex in *G. unguulatus*); 4) the propodus of the last ambulatory leg is broad and short (long and narrow in *G. unguulatus*); 5) the sixth abdominal segment is broad and stout (long and narrow in *G. unguulatus*), 6) the male telson is broadly triangular (more elongated in *G. unguulatus*).

Gaetice unguulatus Sakai, 1939

Gaetice unguulatus Sakai, 1939: 678, Fig. 120a–c; Sakai, 1976: 653, text-fig. 358a–c.

Material examined. – **Japan** – 5 males (10.7–15.3 × 9.7–13.1 mm), 1 female (10.0 × 9.3 mm), 3 ovig. females (10.8–12.6 × 9.2–10. mm) (QM), Uchinoura, Tanabe, Wakayama Prefecture, Japan, coll. Y. Fukui, 7 Aug.1996; 4 males (10.7–15.3 × 9.7–13.1 mm) (QM), Uchinoura, Tanabe, Wakayama Prefecture, Japan, coll. Y. Fukui, 7 Aug.1996; 1 juvenile specimen (RU), Yawadi, Japan, coll. 4 May 1985; 1 female (18.7 × 14.9 mm) (USNM 48350), Beach at Kagoshima, Japan (under stones), coll. T. Urita. **China** – 26 males (10.5–23.8 × 8.0–19.4 mm), 3 females (11.1–16.4 × 9.8–13.8 mm), 7 ovig. females (13.0–17.5 × 11.9–14.9 mm) (ASIZ-C00203), Jiaopo, Guangdong Province, coll. 27 Jun.1957; 45 males (6.0–20.0 × 5.5–17.0 mm), 12 females (6.0–18.1 × 4.9–14.9 mm), 3 ovig. females (11.1–16.4 × 9.8–13.8 mm) (ASIZ-C02541), Haimen, Guangdong Province, coll. 10 Aug.1957; 24 males (12.4–24.0 × 10.7–20.1 mm), 2 females (12.5–20.3 × 10.8–16.2 mm), 8 ovig. females (9.0–19.0 × 7.7–16.0 mm), (ASIZ-C-00198), Puqian, Hainan Island, coll. 17 May 1957; 5 males (9.2–13.4 × 8.0–12.3 mm), 2 females (16.1–17.5 × 13.0–15.2 mm), 5 ovig. females (8.0–11.8 × 6.9–9.8 mm) (ASIZ-C00206), Beihai, Guangxi Province, coll. 19 Apr.1956; 11 males (7.9–10.1 × 7.0–10.1 mm), 3 females (8.4–10.5 × 7.0–9.0 mm) (ZRC-uncatalogued/nnk0194), seashore outside Institute of Oceanology, Qingdao, Shandong Province, coll. P. K. L. Ng & H. L. Chen, 22 Aug.2002. **Hong Kong** – 7 males (7.8–15.6 × 8.0–12.3 mm), 2 females (8.5–12.7 × 7.2–10.5 mm) (ASIZ-C00216), Hong Kong; 1 male (9.3 × 8.5 mm) (MNHN-B-9139), Hong Kong; 1 male (14.0 × 12.0 mm) (USNM 19674), Hong Kong. **Taiwan** – 1 male (16.9 × 14.1 mm), (NTOU), Tong-Lei, Coll. 17 Aug.2000; 1 male (16.6 × 14.2 mm) (NMNS), Ma-Gang Fish port, coll. 11 Aug.1995.

Diagnosis. – Carapace subquadrate, broadening anteriorly, dorsal surface flat, smooth; frontal margin weakly lobed. Anterolateral margin with 3 teeth, including orbital tooth. Third maxilliped with 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 wide gape, usually with one or two large teeth near base of moveable finger. Propodus of last ambulatory legs long, narrow.

Colour. – Similar to *G. depressa*, ranging from light cream to dark brown, with dark brown and/or black spots (Y. Nakasone, pers. comm.).

Size. – Largest male examined 24.0 × 20.1 mm (ASIZ-C-00198), largest female 20.3 × 16.2 mm (ASIZ-C-00198).

Habitat. – Found under small rocks, on coral-sand substrate close to river mouths. They can stack on top of each other in large numbers (pers. observ.; Y. Nakasone, pers. comm.).

Distribution. – China, Taiwan and southern Japan.

Remarks. – Differences with *Gaetice depressus* are discussed under that species. This species is less common. The type material is not in Kanagawa Prefecture Natural History Museum, National Science Museum, Tokyo, or Research Institute and Natural History Museum, Senkenberg, so it can probably be assumed to be lost though this is not certain. As *G. depressus* is currently easily recognised from the description, no neotype designation is required (see Article 75.1 of the International Code of Zoological Nomenclature (1999) which states that a neotype is not to be erected unless "... an author considers that a name-bearing type is necessary to define the nominal taxon objectively."). If in the future a new species is discovered that can be potentially confused with *G. depressus*, it will then be necessary to erect a neotype.

Sestrostoma new genus

Type species. – *Acmaeopleura balssi* Shen, 1932, by present designation.

Diagnosis. – Carapace rounded, elliptical, longer than broad; dorsal surface glabrous, regions not well defined, convex or depressed. Frontal margin slightly convex, bilobed. Anterolateral margin subcristate without teeth. Posterolateral margins not clearly demarcated from anterolateral margin. Orbits small, eyes completely filling orbit, Third maxilliped short, broad; either no gape, or narrow rhomboidal gape when closed; palp slender, long, with long setae. Exopod with short flagellum. Epistome broad, flat, posterior margin relatively medially pointed. Chelae robust, fingers shorter than palm; males, at least, with a relatively well developed tuft of setae at base of gape. Anterior sternal plates with distinct medial groove. Male abdomen narrowly triangular; segments 3–6 functionally fused.

Etymology. – From the Greek *sestron* for "sieve" and *stoma* for "mouth." Gender is neuter.

Remarks. – The reasons for splitting *Sestrostoma* from *Acmaeopleura*, and its placement alongside *Gaetice* in the newly created Gaeticinae, is discussed under the **Remarks** for Gaeticinae.

Acmaeopleura balssi of Ghani & Tirmizi, (1991) was misidentified but we defer giving it a new name until the type can be examined. Similarly, *Acmaeopleura* cf. *balssi* of

Crosnier (1965: 44, Figs. 60–62, Pl. 6 Fig. 3) does not belong to the true *A. balssi* but we defer its description until we have properly examined available material.

Sestrostoma thus includes *S. balssi* (Shen, 1932), *S. depressum* (Sakai, 1965), and *S. toriumii* (Takeda, 1971).

Key to species of *Sestrostoma*

1. Ambulatory legs long, slender; posterolateral epimera visible in dorsal view; carapace with dorsal surface depressed, obviously punctate and minutely granular; margin strongly emarginated; anterior margin of meri of walking legs cristate *S. depressum*
- Ambulatory legs broad, short; posterolateral epimera not visible in dorsal view; carapace more or less convex; anterior margin of meri of walking legs not cristate **2**
2. Male suborbital crest consisting of two elongate crests and one tubercle; third maxillipeds do not close the buccal cavity completely; tips of cheliped fingers obviously cross apically; larger species (to ca. 17 mm cw) *S. balssi*
- Male suborbital crest consisting of nine tubercles; third maxillipeds completely close the buccal cavity; tips of cheliped fingers typically meet, or cross only slightly; smaller species (to ca. 7 mm cw) *S. toriumii*

Sestrostoma balssi (Shen, 1932), new combination (Figs. 7, 8)

Acmaeopleura balssi Shen, 1932: 155, text-figs. 98–101, Pl. 6, Fig. 1–2; 1948: 114, text-fig. 5; Shen & Dai, 1964: 125; 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, Figs. 2–3, Pl. 66 Fig. 5; Takeda & Miyauchi, 1992: 149; Itani, 2002: 129; Itani et al., 2002: 43; Itani, 2004: 33; Itani et al., 2005: 1.

Acmaeopleura toriumii – Komai, Maruyama & Konishi 1992: 202. [Not] *Acmaeopleura balssi* – Sakai 1939: 663, text-fig. 116 [= *A. depressa* Sakai, 1965].

Material examined. – **Japan** – 1 male (13.2 × 9.6 mm), 1 female (10.3 × 8.0 mm) (NSMT-Cr-11327), Sagami Bay, Japan, coll. H. Ikeda, no collection date; 1 female (6.1 × 4.5 mm) (SMF spec., dry), Marayama, Japan, coll. 18 Dec. 1952, no collection date; 1 specimen (SMF spec., dry), Hiroshima, Japan, collected with *Upogebia*, coll. 1958; 1 male, 1 female in pieces (SMF; dried), Hiroshima, Japan, collected in *Upogebia* tunnels, coll. 17 Oct. 1958; 1 male stuck to bottle (SMF; dried), Japan, coll. 1 Aug. 1932; 1 male (16.9 × 13.4 mm) (SMF ex T. Sakai collection), Fushiki, Toyama, Japan, no collection date; 1 dried specimen stuck to bottle (SMF, ex T. Sakai collection), Hiroshima, in *Upogebia* tunnel, coll. 1958. **China** – 1 male (IZAS) (cracked carapace), Yantai, Shangdong Province, China, coll. 1 Feb. 1948.

Diagnosis. – Carapace transversely ovate, approx. 1.1–1.3 times wider than long, dorsal surface convex, punctate, regions not defined. Frontal margin with moderate medial concavity. Lateral margins slightly emarginate, unarmed. Male suborbital crest consisting of 2 elongated crests and one tubercle. Epimera visible posterolaterally in dorsal view. Third maxilliped broad, leaving a narrow gape when closed;

setae of palp very long, extending beyond first sternal segment. Cheliped symmetrical, large, glabrous, finger shorter than palm; tips of cheliped fingers obviously cross apically. Ambulatory legs long, slender, sparingly setose. G1 long, slender, chitinous process at apex. Female gonopore operculate, circular in shape. Large species reaching approximately 17 mm cw.

Colour. – Colour in life typically light buff; specimens from Sone-higata tidal flat in Japan, with red or brown spots (Itani et al., 2002).

Size. – The largest male specimen examined was 16.9 × 13.4 mm (SMF, ex T. Sakai collection), largest female 10.3 × 8.0 mm (NSMT-Cr-11327).

Habitat. – This species is not easily collected. While it has been reported to be found in burrows of annelids, echinurans and possibly thalassinideans, none of these associations have been definitely confirmed (Sakai, 1976; Itani et al., 2002).

Distribution. – Japan, China and Taiwan.

Remarks. – The type specimen of *S. balssi* (Shen, 1932) is believed to be lost. The following institutions were contacted, but none could find a type: The Institute of Zoology, The Chinese Academy of Sciences, Beijing (G. Chen, pers. comm.); Beijing Natural History Museum (S. Yang, pers. comm.); Institute of Oceanography, The Chinese Academy of Sciences, Qingdao (R. Liu, H. Chen, pers. comm.) and the Museum of Natural History, London (P. F. Clark, pers. comm.). The type locality is Shangdong Province in northeastern China. Several attempts to collect a fresh specimen from China with the intention of erecting a neotype were unsuccessful. With the redescription of Itani et al. (2002), the identity of the species seems clear for the moment, and a neotype is thus probably not necessary. If future collections were to cast doubt on the Japanese and Chinese specimens being conspecific then a neotype should be established.

Itani et al. (2002) commented that “Japanese specimens are readily assigned to *Acmaeopleura balssi* by the form of the male sub-orbital crest. The only notable difference from Chinese specimens, as described by Shen (1932, 1948) and Dai & Yang (1981), is in the presence of dense setae in the gape of the cheliped.” Shen (1932, 1948) did not mention the presence or absence of setae, but the figure in Shen (1932) shows that there are short sparse setae in the gape. Otherwise, the exact conformity of the Japanese specimens with those from China in the shape of the carapace, male suborbital crest, third maxilliped, and ambulatory legs, suggests that the presence of setae in the chela gape may be simply due to infraspecific geographic variation.

Itani et al. (2002) listed numerous major characters by which *S. balssi* can be separated from its closest relative, *S. toriumii*. *Sestrostoma balssi* has a narrower fronto-orbital width than *S. toriumii*; the male suborbital crest has two elongated crests and one tubercle in *S. balssi*, while there are nine tubercles in *S. toriumii*; the tip of the cheliped dactylus more curved inwardly in *S. balssi* so that the cheliped fingers clearly cross apically, whereas the tips of the fingers typically meet or cross only slightly at the very tip in *S. toriumii*; the chitinous cusps at the tips of the cheliped fingers are smaller in *S. balssi*. The third maxillipeds do not completely close the buccal cavity in *S. balssi* whereas they do in *S. toriumii*. In *S. balssi* the dactylus of the third maxilliped is longer, the inner-distal projection of the merus less conspicuous, and the inner-proximal projection of ischium also less conspicuous than in *S. toriumii*. *Sestrostoma balssi* has a larger chitinous process at the tip of the male first gonopod, and the setae on the outer margin are denser than in *S. toriumii*.

Adult size differs greatly between the two species, with *S. balssi* reaching as large as 17 mm carapace width, while *S. toriumii* is a smaller species with the largest specimens attaining a maximum carapace width of about 8 mm. *Sestrostoma depressum* is similarly, a small-sized species, reaching to about 7 and 6 mm in maximum carapace width.

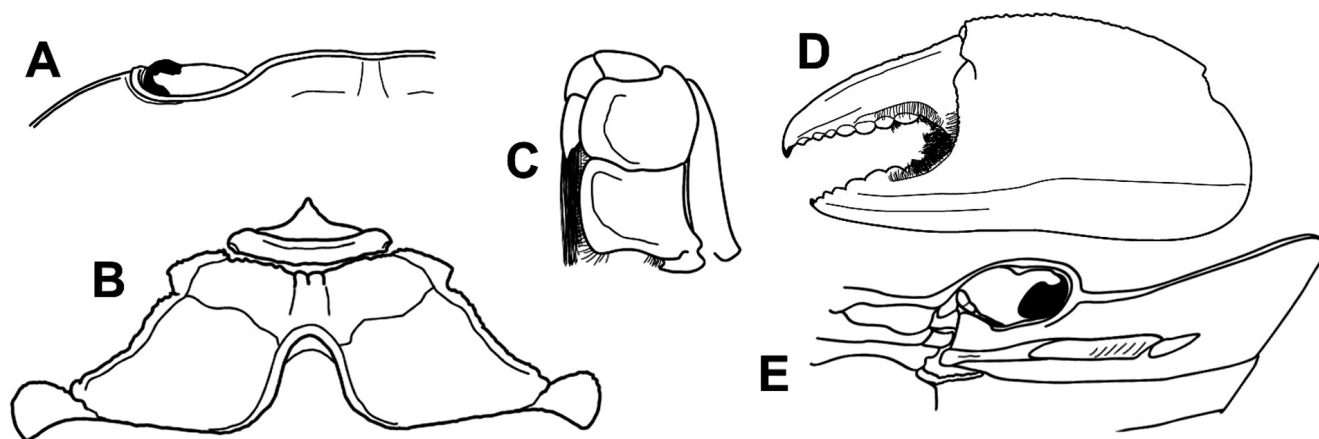


Fig. 7. *Sestrostoma balssi* (Shen, 1932), male (16.2 mm cw), NSMT-Cr 11261: A, frontal region in dorsal view; B, frontal view showing orbit and pterygostome; C, left third maxilliped, showing elongated palp with very long setae; D, anterior sternum showing anterior medial sulcus; E, frontal view of orbit and pterygostome. (After Itani et al., 2002).

Sestrostoma depressum (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. – Syntype, 1 female (5.5 × 4.5 mm) (SMF 24720, ex T. Sakai collection), Japan, coll. K. Sakai, no collection date.

Diagnosis. – Carapace ovate, approx. 1.3 times wider than long; dorsal surface depressed, clearly evenly punctate, microscopically granulated; regions not defined. Frontal margin finely granular; almost straight, not medially emarginated; breadth much less than one-third of carapace. Lateral margins unarmed but markedly emarginate; epimera not visible posterolaterally in dorsal view. Ambulatory legs short, relatively robust; meri cristate along anterior border.

Colour. – This species has been illustrated in colour by Sakai (1965: Pl. 91 Fig. 4), being apparently a relatively uniform pale brown to buff; the dry female examined was cream.

Size. – The largest specimen recorded is a female syntype (7.2 × 6.0 mm) (see Sakai 1965: 196).

Habitat. – Originally recorded from “among pebbles in upper tidal zone, and littoral zone of rocky beach” (Sakai, 1965). It is believed to be associated with upogebiids and callianassids (Itani, 2004; Itani *et al.*, 2004).

Remarks. – This species was originally described from four females from Arasaki, Tenjinjima and Manazura, Japan, without a holotype being designated. Therefore all must be considered syntypes. The only syntype we have examined is in SMF. It is unfortunately dry, and the information on its exact locality in Japan is no longer preserved with the specimen so we refrain from designating this specimen as the lectotype. Apparently no specimen of this species was donated to the Kanagawa Prefectural Museum of Natural History by Tune Sakai (see Muraoka, 1998). This species is still poorly known. The male has not been described.

Distribution. – Japan.

Sestrostoma toriumii (Takeda, 1974), new combination

Acmaeopleura toriumii Takeda 1974: 17–20, Figs. 2, 3; Marumura, 1994: 65, Fig. 2; Davie, 1992: 351; Sakai, 2000: 1158, Fig. 1i–j; Takeda *et al.*, 2000: 138, 141; Itani *et al.*, 2002: 43; Itani, 2004: 33; Itani *et al.*, 2005: 1; Karasawa & Tanaka, 2005: 95; Anker *et al.*, 2005: 179.

[Not] *Acmaeopleura toriumii* - Komai, Maruyama & Konishi 1992: 202 [= *Acmaeopleura balssi* Shen, 1932]

Materials examined. – Types: Holotype – 1 male (4.5 × 4.0 mm) (NSMT-Cr-971), shore of Onagawa Bay, Japan, coll. M. Toriumi, 10 Jul. 1972.

Other material: 2 males (5.6–5.9 × 4.7–4.9 mm), 1 ovig. female (5.6 × 4.7 mm) (QM-W25610), Yamaguchi Bay, Seto Inland Sea, Yamaguchi Prefecture, Japan, coll. G. Itani, 7 May 1997; 4 males, 3 females (QM-W16485), Starfish Bay, Wu Kwai Sha, mud and coarse sand, associated with burrows of *Upogebia major* and the echinurid *Ochetostoma erythrogrammon*, coll. P. Davie, 15 Apr. 1989.

Diagnosis. – Carapace transversely ovate, approx. 1.2–1.5 times wider than long, dorsal surface convex, punctate, regions not defined. Frontal margin with slight medial concavity. Lateral margins smooth, slightly emarginate, without teeth; epimera visible posterolaterally in dorsal view. Male suborbital crest consisting of 9 tubercles. Third maxillipeds broad, completely closing buccal cavity when closed. Chelae large, with tuft of setae on outer face at base of fingers; tips of fingers meet, or cross only slightly. Ambulatory legs relatively long, slender. G1 long, slender, with corneous process apically. Female gonopore operculate, circular in shape. Small species (to ca. 7 mm cw).

Colour. – Not documented for fresh specimens; preserved specimens cream to light brown.

Size. – Largest male 8.4 mm cw; largest female 6.2 mm (see Itani *et al.*, 2002).

Habitat. – Seems primarily associated with a thalassinidean shrimp, *Upogebia major*, although other burrow hosts such as callianassids and echinurans have been reported (Davie, 1992; Sakai, 2000; Itani, 2002, 2004).

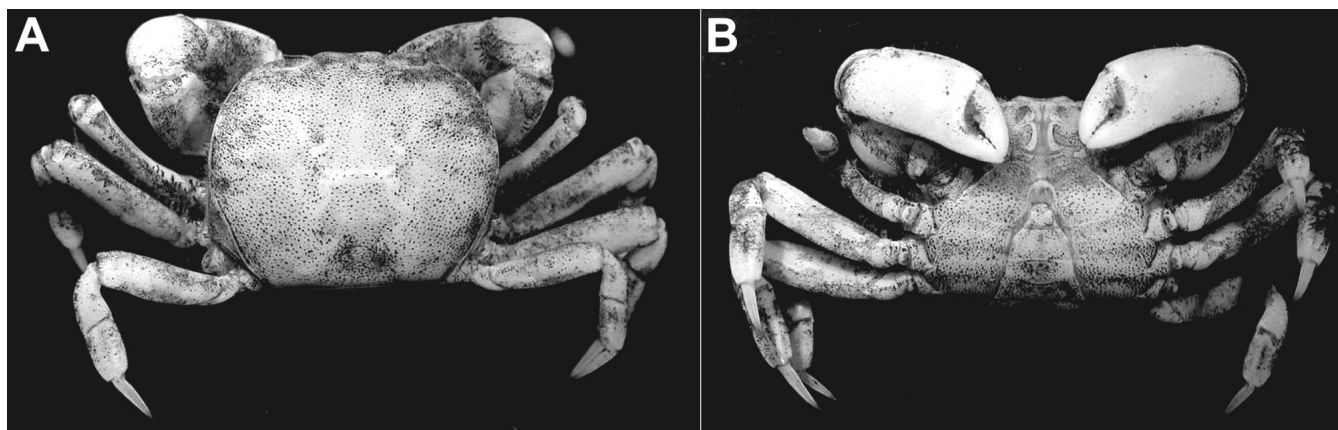


Fig. 8. *Sestrostoma balssi* (Shen, 1932), male (cw = 9.8 mm), collected at Sone-higata tidal flat: A, dorsal view; B, ventral view. (After Itani *et al.*, 2002).

Distribution. – Only known from Japan.

Remarks. – Differences with its closest relative, *S. balssi* are discussed under the **Remarks** for that species.

VARUNINAE Alcock, 1900

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, flat to deeply vaulted or very convex; anterolateral margins entire, or with 1, 2 or 4 epibranchial teeth or notches. Front deflexed; broad, less than half maximum carapace breadth. Orbits open laterally; sub-orbital crest relatively straight, typically long, extending some distance across lateral branchial region, not stridulatory; pterygostomial grooves opening into anterolateral corner of buccal cavity; pterygostome, sub-branchial, sub-hepatic regions may be setose but without regular reticulation of hooked setae; pterygostome without vertical groove placed subparallel to buccal cavity. Third maxillipeds without oblique setose crest extending across merus and outer distal corner of ischium; merus normal or markedly produced; with small rhomboidal gape when closed; reaching forward to margin of epistome to completely close buccal cavity anteriorly; exopod narrow to broad, inflated; flagella not especially elongated, not noticeably protruding from behind third maxilliped. Endostome smooth, more or less medially prominent. Chelipeds usually symmetrical, large in adults. Ambulatory legs moderately flattened, oval in cross section, relatively narrow; posterodistal margin of meri not armed with spines. Male abdomen with all segments freely moveable. Male gonopore sternal, embedded within sternite 8. Female gonopore usually rounded.

Remarks. – The Varuninae is being revised by N. K. Ng and therefore the relationships of its many genera will not be further discussed at this time. We here create a new genus for *Gaetice americanus* Rathbun, 1923, which we have removed from *Gaetice* as part of its revised concept.

Pseudogaetice, new genus

Gaetice – Rathbun, 1923: 629 (not *Gaetice* Gistel, 1848).

Type species. – *Gaetice americanus* Rathbun, 1923, here designated; gender feminine.

Diagnosis. – Carapace subrectangular, broader than long, dorsal surface flat, smooth; frontal margin bilobed. Anterolateral margins short, not strongly convex. Third

maxilliped with merus/ischium subrectangular; merus longer than ischium; palp strongly developed, reaching distal end of ischium when folded; exopod narrow, flagellum short. Infraorbital ridge granular. Chelipeds symmetrical, larger in males, fingers shorter than palm, with marked gape developing in males. Ambulatory legs of moderate length; meri convex anteriorly; dactyli short, broad. Male abdomen narrowly triangular in shape with all segments freely moveable. G1 thick, stout; corneous projection apically.

Etymology. – *Pseudo*, Greek for “false” in combination with *Gaetice* alluding to the confusion of the new species with species of *Gaetice*. Gender masculine.

Remarks. – *Gaetice* Gistel, 1848, has been considered to include three species: *G. depressus* De Haan, 1933 (type species), *G. unguilatus* Sakai, 1939, and *G. americanus* Rathbun, 1923. The first two species, both from the north-west Pacific, are distinctly different from *G. americanus* (from the Pacific coast of Mexico) in morphology and feeding habits, and are here transferred to the new subfamily Gaeticinae. “*Gaetice*” *americanus* must therefore be reallocated, and is here transferred to a new genus, *Pseudogaetice*.

Although *Pseudogaetice americanus* superficially resembles species of *Gaetice* sensu lato in the form of the carapace and ambulatory legs, it is otherwise morphologically similar to typical Varuninae genera. The differences with the Gaeticinae have been discussed above.

Pseudogaetice is most closely related to *Hemigrapsus* Dana, 1851 (a revision of *Hemigrapsus* is in preparation by the second author) and *Tetragnathus* (*T. jouyi* Rathbun, 1918). It differs from these two genera as follows: A) the merus of the third maxilliped is noticeably longer than the ischium, and both segments are subrectangular in *Pseudogaetice*; while in *Tetragnathus* the merus is subequal in length to the ischium and the margins are rounded and strongly diverging distally. In *Hemigrapsus* the merus is typical of most varunines, being shorter than the ischium and with the lateral margins obviously convex and narrowing proximally; B) the palp of the third maxilliped is strongly developed in *Pseudogaetice*, reaching the distal end of the ischium when folded; in the other two genera the palp is much shorter; C) the anterolateral margins in *Pseudogaetice* are relatively shorter, first anterolateral tooth not as broad, margins subparallel, and not markedly narrower than the second anterolateral tooth; this condition is similar to *Tetragnathus*, but unlike *Hemigrapsus*, which typically has broader, more convex anterolateral teeth; D) the frontal lobes are separated by a much stronger medial concavity in *Pseudogaetice* than in the other two genera; E) the chela of *Pseudogaetice* can develop a very broad gape between the fingers of adult males, something not shown by either of the two other genera; F) the moveable finger of the chela has a large, broad tooth in the proximal half, that is absent from both *Hemigrapsus* and *Tetragnathus*; G) the dactyli of the walking legs of *Tetragnathus* are very long, narrow, and relatively strongly curved; whereas those of *Pseudogaetice* and *Hemigrapsus* are broad and not markedly curved.

Pseudogaetice americanus (Rathbun, 1923),
new combination
(Fig. 9)

Gaetice americanus Rathbun, 1923: 629.

Material examined. – Types: Holotype – 1 male (15.4 × 14.2 mm) (USNM 17452), Mexico, San Luis Gonzales Bay, Gulf of California, coll. U.S. Fish Commission Steamer ALBATROSS, 27 Mar.1889. Paratypes, 69 males (6.2–16.8 × 6.0–15.3 mm), 41 females (9.2–12.7 × 8.5–11.4 mm), 27 ovig. females (12.0–12.9 × 10.7–11.6 mm) (USNM 17452), San Luis Gonzales Bay, Gulf of California, coll. U.S. Fish Commission Steamer ALBATROSS, 27 Mar.1889.

Other material: 2 males (12.4–13.8 × 11.1–12.4 mm), 5 ovig. females (12.8–17.3 × 11.4–15.3 mm) (USNM 68397), Guaymas Bay, Sonora, Mexico, coll. B. J. Yost, 21 Jun.1923; 1 female (5.3 × 4.7 mm) (USNM 17685), Baja California, no collection date; 1 male (11.5 × 10.5 mm) (USNM 17454), San Bartolomé Bay, coll. U.S. Fish Commission, 11 Apr.1889; 1 male (13.1 × 11.5 mm) (USNM

17453), Puerto Refugio, Angel Island, coll. U.S. Fish Commission, 29 Nov.1889; 2 ovig. females (7.2–12.5 × 6.0–11.0 mm) (USNM 31511), shore of Guaymas Bay, Sonora, Mexico, coll. W. Palmer, 20 Feb.1902; 1 ovig. female (16.7 × 15.0 mm) (USNM 89515), Puerto Peñasco, Mexico, coll. Mac'Dinities family, 24 Dec.1947; 2 males (15.7–17.4 × 13.6–15.4 mm), 1 female (12.6 × 11.4 mm), 1 ovig. female (12.7 × 11.0 mm) (USNM 110649), Tiburón Island, Gulf of California, eastern side, coll. S. A. Glaswell, 28 Dec.1931; 1 male (7.5 × 6.4 mm), 2 female (8.2–8.4 × 7.3–7.4 mm), 11 ovig. females (7.3–10.1 × 6.2–8.5 mm) (USNM 17293), Guaymas, Mexico, near harbour, coll. P. J. Jouy, 23 Feb.1891; 10 males (8.6–13.0 × 6.8–11.4 mm), 3 females (7.1–8.3 × 6.6–7.5 mm), 8 ovig. females (7.4–16.7 × 6.5–14.7 mm) (numerous specimens) (USNM 17292), Guaymas, near harbour, Mexico, coll. P. J. Jouy, 23 Feb.1891; 8 males (12.9–18.3 × 11.2–16.6 mm), 1 female (12.9 × 11.2 mm), 3 ovig. females (11.0–15.5 × 9.6–12.0 mm) (USNM 74526), Punta Peñascosa, Sonora, Mexico, coll. H. N. Lowe, Feb.1934; 5 males (7.5–6.6 × 9.9–8.8 mm) (QM-W25613), Camp Archelon, Bahía de Los Angeles, Baja California, coll. E. & A.R. Campus, 28 Jul.1996.

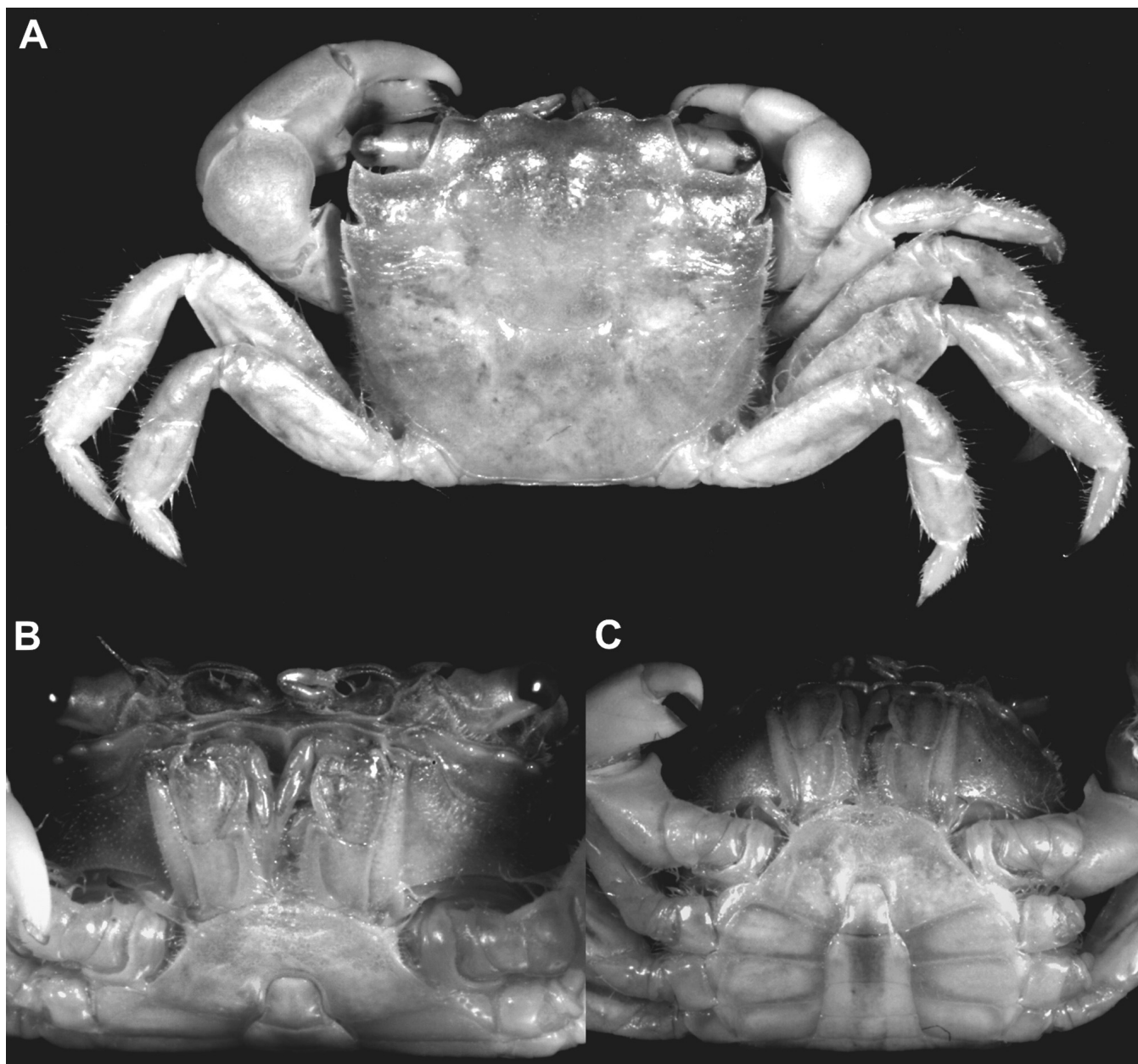


Fig. 9. *Pseudogaetice americanus* (Rathbun, 1923), male (9.9 × 8.8 mm), QM-W25613, Camp Archelon Bahía de Los Angeles, Baja California: A, dorsal view; B, frontal view; C, sternum and abdomen.

Diagnosis. – Carapace subrectangular, broader than long, dorsal surface flat, smooth; frontal margin strongly bilobed. Anterolateral margins relatively short, first anterolateral tooth not particularly broad, margins subparallel, not markedly narrower than the second anterolateral tooth. Third maxilliped with merus, ischium subrectangular; merus longer than ischium; palp very strongly developed, reaching distal end of ischium when folded; exopod narrow, flagellum short. Infraorbital ridge with very few large, round granules. Chelipeds symmetrical, larger, high, fingers shorter than palm in males; fingers close with almost no gape in females, young males, but can develop wide gape in males; dactylus often with large broad tooth on proximal half of cutting margin. Ambulatory legs of moderate length; meri convex anteriorly; dactyli short, broad. Male abdomen narrowly triangular, with all segments freely moveable; telson broad. G1 thick, stout; short corneous projection apically. Female gonopore with crescent-shaped operculum.

Colour. – Not documented to our knowledge. All preserved specimens are dark cream to brown.

Size. – The largest male specimen examined is 19.5 × 17.3 mm (USNM), largest female 18.1 × 15.6 mm (USNM).

Habitat. – Found under small rocks, close to river mouths (Rathbun, 1923).

Distribution. – Only recorded from the west coast of Baja California and the Gulf of California, Mexico.

Remarks. – The affinities of this species with species of *Gaetice*, *Hemigrapsus* and *Tetragrapsus* are discussed under Remarks for the genus *Pseudogaetice*.

ACKNOWLEDGEMENTS

The first author is grateful to the Raffles Museum of Biodiversity Research, National University of Singapore, for travel funds that allowed this research to be completed. We are both very grateful to Peter K. L. Ng (Raffles Museum of Biodiversity Research) for valuable discussions, encouragement and comments on the manuscript. The first author is also grateful to Ernesto Campos and Christoph Schubart for sending him specimens of *Gaetice americanus*, and for early discussions on the status of the American *Gaetice*.

LITERATURE CITED

- 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.
- 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 observations of the innkeeper worm, *Ochetostoma erythrogrammon* Leuckart and Rüppel, in Venezuela. *Zoological Studies*, **44**(2): 157–190.
- Balss, H., 1922. Ostasiatische Decapoden. IV. Die Brachyrrhynchen (Cancridea). *Archiv für Naturgeschichte*, **88A**(11): 94–166, text-Figs. 1–2, Pls. 1–2.
- Crosnier, A., 1965. Crustacés décapodés, Grapsidae et Ocypodidae. *Faune de Madagascar*, **18**: 1–143, 11 pls.
- Dai, A. & S. Yang, 1991. *Crabs of the China Seas*. Second edition. China Ocean Press, Beijing. 682 pp., 74 pls.
- Dai, A. S. Yang, Y. Song & G. Chen, 1986. *Crabs of the China Seas*. China Ocean Press, Beijing China. 642 pp. [in Chinese.]
- Dana, J. D., 1851. On the classification of the Crustacea Grapsoidea. *American Journal of Sciences and Arts*, **12**: 283–290.
- Davie, P. J. F., 1992. A new species and new records of intertidal crabs (Crustacea: Brachyura) from Hong Kong. In: Morton, B. (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. Pp. 345–359.
- 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*, Vol. 19.3B. CSIRO Publishing, Melbourne. xiv, 641 pp.
- 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.
- Edmondson, C. H., 1959. Hawaiian Grapsidae. *Occasional Papers of Bernice P. Bishop Museum*, **22**(10): 153–202.
- 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.
- 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.
- 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.
- Gistel, H., 1848. *Naturgeschichte de Thierreiches. Für höhere Schulen bearbeitet*, Stuttgart. xvi, 1–220 pp., 132 pls.
- Gordon, I., 1931. Brachyura from the Coasts of China. *Journal of the Linnean Society of London*, **37**: 525–558, Figs. 1–36.
- Haan, H. M. De, 1833–1849. Crustacea. In: P. F. von Siebold, *Fauna Japonica, sive Descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batavia imperium tenent, suscepto, annis 1823–1830 collegit, notis, observationibus a adumbrationibus illustravit. Lugduni Batavorum*, fasc. 1–8: i–xxi + vii–xvii + ix–xvi + 1–243, Pls. 1–55, A–Q, circ., Pl. 2.
- 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. *Raffles Bulletin of Zoology*, **39**(1): 187–207.
- Hartnoll, R. G., 1975. The Grapsidae and Ocypodidae (Decapoda: Brachyura) of Tanzania. *Journal of Zoology*, London, **177**: 305–328.
- Hilgendorf, F., 1892. Eine neue *Brachynotus* Art aus Aden. *Sitzungsberichte Gesellschaft Naturforschenden Freunde, Berlin*, **4**: 37–40.

- Holthuis, L. B., 1977. The Grapsidae, Gecarcinidae and Palicidae (Crustacea: Decapoda: Brachyura) of the Red Sea. *Israel Journal of Zoology*, **26**: 141–192.
- Horikawa, Y. 1940. A list of Formosan crabs. *Scientific Taiwan*, **8**: 21–31.
- 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*. Department of Ocean Management and Monitoring State Oceanic Administration. China Ocean Press, Beijing. Pp. 576–600.
- Itani, G., 2002. Two types of symbioses between grapsid crabs and a host thalassinidean shrimp. *Publications of the Seto Marine Biological Laboratory*, **39**: 129–137.
- 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"*, November 1–2, 2003, Nagasaki University, Nagasaki, Japan: 33–43.
- Itani, G., P. J. F. Davie & M. Takeda, 2002. Taxonomic notes on *Acmaeopleura balsii* Shen, 1932 and *A. toriumii* Takeda, 1974 (Crustacea, Brachyura, Grapsidae) from Japanese waters. *Bulletin of the National Science Museum, Series A (Zoology)* **28**(1): 43–50.
- Itani, G., M. Izuchi & H. Ueda, 2005. Crab species collected from the burrows of *Urechis unicinctus* in Hiuchi-nada, the central Seto Inland Sea. *Cancer*, **14**: 1–4. (in Japanese with English abstract)
- 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. Ministry of the Interior, Taipei. II, 66 pp. (In Chinese)
- Jeng, M.-S., R.-G. Chan, H.-R. Fung, & C.-S. Tzeng. 1997. *Northeast Coast Scenic Area. Investigations into ecological resources and monitoring (III)*. Ministry of Transport and Tourism, Taipei. 194 pp. (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)*. Ministry of Transport and Tourism, Taipei. 205 pp. (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)*. Ministry of Transport and Tourism, Taipei. 184 pp. (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)*. Ministry of Transport and Tourism, Taipei. 182 pp. (In Chinese)
- Kamita, T., 1941. *Studies of the Decapod Crustaceans of Chosen. I. Crabs*. The Fisheries Society of Chosen, Keijo. 289 pp., 2 pls.
- 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.
- 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., 1973. Anomura & Brachyura. In: *Illustrated encyclopedia of fauna and flora of Korea*, **14**: 1–694, Pls. 1–112.
- 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.
- Kitaura, J., K. Wada & M. Nishida, 2002. Molecular phylogeny of grapsoid and ocypodoid crabs with special reference to the genera *Metaplex* and *Macrophthalmus*. *Journal of Crustacean Biology*, **22**(3): 682–693.
- Lin, C. C., 1949. A catalogue of brachyurous Crustacea of Taiwan. *Quarterly Journal of Taiwan Museum*, **2**(1): 10–33.
- Maki, M., & K. Tsuchiya, 1923. *A monograph of the Decapoda Crustacea of Formosa*. Report of the Department of Agriculture, Government of Research Institute of Taihoku, **3**: i–xi, 1–215, Pls. 1–24.
- Marumura, M., 1994. New localities of two rare crabs of the family Grapsidae. *Nanki Seibutu* **36**: (1): 65–66.
- Miyake, S., 1983. *Japanese Crustacean Decapods and Stomatopods in color. Vol. II. Brachyura (Crabs)*. Hoikusha, Osaka. VIII, 277 pp., 64 pls.
- 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., 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., P. J. F. Davie, C. D. Schubart & P. K. L. Ng, 2007. Xenograpsidae, a new family of grapsoid crabs (Crustacea: Brachyura) associated with shallow water hydrothermal vents. *Raffles Bulletin of Zoology*, Supplement **16**: 233–256.
- 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.
- Rathbun, M. J., 1909. New crabs from the Gulf of Siam. *Proceedings of the Biological Society of Washington*, **22**: 107–114.
- Rathbun, M. J., 1918. The grapsoid crabs of America. *United States National Museum Bulletin*, **97**: i–xxii, 1–461, Figs. 1–172, Pls. 1–161.
- Rathbun, M. J., 1923. The Brachyuran crabs collected by the U.S. Fisheries steamer 'Albatross' in 1911, chiefly on the west coast of Mexico. *Bulletin of the American Museum of Natural History*, **48**(8): 619–637.
- Robinson, M & O. Tully, 2000. Dynamics of a subtidal population of the porcellanid crab, *Pisidia longicornis* (Decapoda: Crustacea). *Journal of Marine Biological Association of the United Kingdom*, **80**: 75–83.
- Sakai, K. 2000. On the occurrence of three species of crabs on Shikoku Island, Japan, and a new species, *Pinnotheres taichungae* nov. spec., from Taiwan (Decapoda, Brachyura). *Crustaceana*, **73**: 1152–1162.

- Sakai, T., 1934. Brachyura from the coast of Kyushu, Japan. *Scientific Report of Tokyo Bunrika Daigaku (B)*, **1**(25): 281–330, Pls. 17–18.
- Sakai, T., 1935. *Crabs of Japan*. Sanseido, Tokyo. 239 pp., Figs. 1–122, 27 pages of bibliography & index, frontispiece (in colour), Pls. 1–66 (colour).
- Sakai, T. 1939. *Studies on the crabs of Japan*. IV. Brachygnatha, Brachyrhyncha. Yokendo, Tokyo. Pp. 365–741, text-figs. 1–129, Pls. 42–111, 6 tables.
- Sakai, T. 1965. *The crabs of Sagami Bay, collected by His Majesty the Emperor of Japan*. Edited by the Biological Laboratory, Imperial Household, Tokyo. 206 pp., text-figs. 1–27, Pls. 1–100.
- Sakai, T. 1976. Crabs of Japan and the adjacent seas. Kodansha, Tokyo. 3 vols. i-xxix + 1–773, text-figs. 1–379, maps 1–3 [in English]; 1–16, Pls. 1–251, 1–461, text-figs. 1, 2 [in Japanese].
- Sato, H. 1936a. The collections of the littoral animals of Formosa (4). *Botany and Zoology*, **4**: 1951–1957.
- Sato, H. 1936b. On the littoral fauna of Formosa. *Scientific Taiwan*, **4**: 137–144.
- 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., J. A. Cuesta & D. L. Felder, 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.
- Schubart, C. D., J. A. Cuesta, R. Diesel & D. L. Felder, 2000. Molecular phylogeny, taxonomy, and evolution of nonmarine lineages within the American grapsoid crabs (Crustacea: Brachyura). *Molecular Phylogenetics and Evolution*, **15**(2): 179–190.
- 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 Systematics and Evolution Research*, **44**(3): 193–199.
- Shen, C. J. 1932. The brachyuran Crustacea of North China. *Zoologia Sinica*, series A, **9**: 1–321.
- Shen, C. J. 1948. On a collection of crabs from the Shantung Peninsula, with notes on some new and rare species. *Contributions from the Institute of Zoology, National Academy of Peiping*, **4**: 105–117.
- Shen, J. R. & A. Dai, 1964. *Illustrations of Animals in China (Crustacea Part II)*. Peking. 142 pp., 277 figs.
- Shih, J.-T., K.-Y. Lue, & C.-H. Wang. 1991. Crab fauna and the activities of ten crab species in Tanshui mangrove swamp of Taiwan. *Annals of Taiwan Museum*, **34**: 121–140. [in Chinese]
- Sternberg, R. von, & N. Cumberlidge, 1998. Taxonomic relationships within the Grapsidae MacLeay, 1838 (Crustacea: Decapoda: Eubrachyura). *Journal of Comparative Biology*, **3**(2): 115–136.
- Stimpson, W., 1858. Prodromus descriptionis animalium evertibratorum, quae in expeditione and Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit, Pars VII. Crustacea Anomoura. *Proceedings of the Academy of Natural Science of Philadelphia*, **10**(4): 225–252.
- 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.
- 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 rare crabs from Mutsu Bay, with some description of a new grapsid from Onagawa Bay. *Bulletin of the Marine Biological Station of Asamushi, Tohoku University*, **15**: 13–21.
- Takeda, M. & T. Miyauchi, 1992. Anomuran and brachyuran crustaceans from the Soya Strait, northern Hokkaido. *Memoirs of the National Science Museum (Tokyo)*, **25**: 143–153. [In Japanese with English abstract]
- Takeda, M., K. Sakai, S. Shinomiya & H. Suga, 2000. Crabs from the Seto Inland Sea, Southern Japan. *Memoirs of the National Science Museum (Tokyo)*, **33**: 135–144. [In Japanese with English abstract]
- Terada, M., 1981. Zoea larvae of five crabs in the subfamily Varuninae. *Researches on Crustacea*, **11**: 66–76.
- Tesch, J. J., 1918. The Decapoda Brachyura of the Siboga-Expedition. I. Hymenosomatidae, Retroplumidae, Ocypodidae, Grapsidae, and Gecarcinidae. *Siboga-Expedition Decapoda Monographs*, **39**(c): 1–148, 6 pls.
- Tweedie, M. W. F., 1950. Grapsoid crabs from Labuan and Sarawak. *Sarawak Museum Journal*, **5**(2): 338–369.
- Urita, T., 1926. A checklist of Brachyura found in Kagoshima Prefecture, Japan. *Tsingtao Times, Tsingtao*, **1–3**: 1–41.
- 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.
- 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, Nuova Serie, Supplemento* **14**(6): 57–101.
- Wang, C.-H., & H.-C. Liu, 1996a. *Common Seashore Crabs of Taiwan*. (First edition). Taiwan Museum, Taipei. 136 pp.
- Wang, C.-H., & H.-C. Liu, 1996b. *Estuarine Crabs of Taiwan*. Wild Bird Society of Kaohsiung, Kaohsiung. 113 pp.
- 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.
- 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*. Ministry of the Interior, Taipei. ii, 79 pp.