



Taxonomy of the sand bubbler crabs *Scopimera globosa* De Haan, 1835, and *S. tuberculata* Stimpson, 1858 (Crustacea: Decapoda: Dotillidae) in East Asia, with description of a new species from the Ryukyus, Japan

KINGSLEY J. H. WONG^{1,2}, BENNY K. K. CHAN^{1,2} & HSI-TE SHIH^{3,4}

¹Institute of Ecology and Evolutionary Science, National Taiwan University, Taipei 106, Taiwan

²Biodiversity Research Center, Academia Sinica, Taipei 115, Taiwan

³Department of Life Science, National Chung Hsing University, Taichung 402, Taiwan.

⁴Corresponding author. E-mail: htshih@dragon.nchu.edu.tw

Abstract

Sand bubbler crabs of the genus *Scopimera* are common on sandy shores in East Asia yet the taxonomy of the species remains unclear. *Scopimera globosa* De Haan, 1835, the type species, was described from Japanese specimens and also occurs in Korea and China. *Scopimera tuberculata* Stimpson, 1858, described from Japan, has been regarded a junior synonym of *S. globosa*, but the types had long been lost. Some workers have considered the two taxa distinct and *S. tuberculata* has been recorded from South China. In the present study, we confirm using male gonopod morphology and molecular analysis, that the early records of *S. tuberculata* from Hong Kong and *S. globosa* from Taiwan are in fact *S. intermedia* Balss, 1934. The present study regards *S. tuberculata* as a subjective junior synonym to *S. globosa*. A new species, *Scopimera ryukyuensis* **sp. nov.** from the Ryukyus, is identified and described herein. The new species is close to *S. globosa* but can be separated by carapace characters. The mitochondrial cytochrome oxidase I (COI) gene revealed basepair (bp) difference between the new species and other *Scopimera* spp. to be at the interspecific level, at least 28 bp (4.3%).

Key words: *Scopimera ryukyuensis*, Dotillidae, cytochrome oxidase I, taxonomy, Ryukyus, Japan

Introduction

Sand bubble crabs of the genus *Scopimera* De Haan, 1835, are common on Indo-West Pacific tropical and subtropical sandy shores (Yamaguchi & Tanaka 1974; Koga 1995). Taxonomic studies of *Scopimera* in the region, especially in East Asia, have not yet been received extensive attention, resulting in confusions of some morphologically similar species. De Haan (1835) identified the type species of *Scopimera*, *S. globosa* (as *Ocypode (Scopimera) globosa*) from Japan, without stating a precise locality (see also De Haan's re-examined material by Yamaguchi & Baba 1993). Miyake (1983) reported *S. globosa* as being distributed in Korea, North China, mainland Japan, the Ryukyus and Taiwan, implying a wide distribution in the region. Stimpson (1858) identified *S. tuberculata* from Simoda (= Shimoda), Japan, during his North Pacific Exploration Expedition and argued that *S. tuberculata* was different from *S. globosa* by having a rough, tubercle-covered carapace surface (Stimpson 1858, 1907). Stimpson's description of the new species was, however, too brief and uninformative, fitting more than one species of the genus and making realistic comparisons with other species difficult. In addition, the type specimen of *S. tuberculata* was almost certainly destroyed in the Great Chicago Fire of 1871 (Stimpson 1907; Evans 1967; Vasile *et al.* 2005; Manning & Reed 2006). Subsequently, *S. tuberculata* has been considered a junior synonym of *S. globosa* since Koelbel (1897) (see Tesch 1918; Kemp 1919; Sakai 1939, 1976; Tweedie 1950; Ng *et al.* 2001, 2008).

Shen (1935) reported on the specimens of *Scopimera* from South China (including Hong Kong). He reported that *S. tuberculata* was present and suggested that both *S. globosa* and *S. tuberculata* should be treated as distinct species. This recommendation was supported by several workers (e.g., Tweedie 1937; Dai

& Yang 1991; Huang 1994). The distinctive male first gonopod (G1) of “*S. tuberculata*” from South China was first illustrated by Dai & Yang (1991), who recorded its distribution as “Guangdong” only. On the other hand, Tweedie (1950), who received Chinese specimens of *S. tuberculata* collected by Shen, which agreed with Shen (1935) of the species identification (see Tweedie 1937), referred them to *Scopimera intermedia* Balss, 1934 instead. This species was described from Johore in Malay Peninsula. Tweedie (1950) made this decision on the advice of H. Balss who also examined Shen’s material. This was further discussed in Serène & Moosa (1981) who figured G1 of *S. intermedia*. The overall relationship between these three nominal species remained unclear: are *S. globosa* and *S. tuberculata* different species, is the Chinese species *S. tuberculata* or *S. intermedia*, and how many valid species there really are?

Using both morphological and molecular approaches, we examined the taxonomic status of the three species. *Scopimera globosa* and *S. tuberculata* are here shown to be synonyms; while *S. intermedia* is determined to be a good species. A new species of *Scopimera* from the Ryukyus is also identified and described.

Materials and methods

Collection sites. *Scopimera* specimens were collected from the sandy shores in the Wakayama and Chiba, Honshu, and Sedake and Awase, Okinawa in Japan; Cigu, Tainan and Penghu in Taiwan; Tai Po, Starfish Bay and Bui O in Hong Kong; and Lim Chu Kang in Singapore. All specimens were preserved in 75–95% ethanol. Comparative and reference specimens included the collections in Research Museum, Biodiversity Research Center, Academia Sinica, Taipei, Taiwan (ASIZCR); Natural History Museum and Institute, Chiba, Japan (CBM); Coastal Ecology Laboratory of Academia Sinica, Taipei, Taiwan (CEL); the Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOO); the National Museum of Natural Science, Taichung, Taiwan (NMNS); the National Museum of Nature and Science, Tokyo, Japan (NSMT); National Taiwan Museum, Taipei, Taiwan (NTM); The Naturalis, Leiden, Netherlands (RMNH); Ryukyu University Museum, Fujukan, Okinawa, Japan (RUMF); and the Zoological Reference Collection of the Raffles Museum, Singapore (ZRC).

Morphological analysis. The external morphology was examined under stereomicroscopes. Detailed studies on the morphology of the male first gonopod (G1) were conducted under compound light microscopes and scanning electron microscopes (SEM). G1s photographed were air dried, gold coated prior to SEM studies (see Chan *et al.* 2007a, b). The abbreviations cw and cl stand for carapace width and carapace length, respectively.

Molecular analysis. Total genomic DNA was extracted from soft tissue of specimens, using the commercial QIAamp Tissue Kit (QIAGEN, Hilden, Germany). For amplifying mitochondrial COI sequences with a polymerase chain reaction (PCR), the universal primers LCO1490 and HCO2198 (Folmer *et al.* 1994) was used: 5'-GGTCAACAAATCATAAAGATATTGG-3' and 5'-TAAACTTCAGGGTGACCAAAAATCA-3'. The PCR conditions for COI were as follows: 2 min. at 95°C for initial denaturing, then 35 cycles of 1 min. at 95°C, 1 min. at 50°C, 1 min. at 72°C with a final extension for 5 min. at 72°C. Sequences were generated using the same sets of primers and determined on an Applied Biosystems (ABI) 3100 automated sequencer using the ABI Big-dye Ready-Reaction mix kit, following the standard cycle sequencing protocol and were aligned with the aid of CLUSTAL W (vers. 1.4, Thompson *et al.* 1994) and Bioedit (vers. 5.09, Hall 2001), after verification with the complementary strand. Sequences of the different haplotypes were deposited in the DNA Data Bank of Japan (DDBJ) database (accession nos. given in Table 1).

Sequence analysis. The best-fitting model for sequence evolution of the COI dataset was determined by MrModeltest (vers. 2.2, Nylander 2005), selected by the AIC (Akaike information criterion), and was subsequently applied to the minimum evolution (ME), maximum likelihood (ML), and Bayesian inference (BI) analyses. The ME tree was constructed with the PAUP* program (vers. 4.0b10, Swofford 2003) with 2000 bootstrap reiterations. A maximum parsimony (MP) tree was constructed using the PAUP* with 2000 bootstrap reiterations of a simple heuristic search, TBR (tree bisection-reconnection) branch-swapping, and 100 randomly added sequence replications. All characters were equally weighted. The ML analysis was also

calculated by PAUP* with 2000 bootstrap replications with the same parameters as in the MP analysis. The BI analysis was performed with MrBayes (vers. 3.1.1, Ronquist & Huelsenbeck 2003) with 4 independent runs. The search was run with 4 chains for 10⁷ generations, with trees being sampled every 1000 generations (the first 5000 trees were later discarded as the burn-in). Basepair (bp) difference and pairwise estimates of Kimura 2-parameter distance (Kimura 1980) for inter- and intraspecific genetic diversities were also calculated by PAUP*.

Results

Systematic account

Superfamily Ocypodoidea Rafinesque, 1815

Family Dotillidae Stimpson, 1858

Genus *Scopimera* De Haan, 1833

Scopimera globosa De Haan, 1835

(Figs. 1a, b, 2a, b, 3a–c, 4a, b, 6)

Ocypode (Scopimera) globosa De Haan 1835: 53, pl. 11 (3, 3a, 3b), pl. C.

Scopimera globosa — H. Milne Edwards 1852: 153. — Ortmann 1894: 747. — Koebel 1897: 713. — Parisi 1918: 97, fig. 2. — Tesch 1918: 46, pl. 3(3). — Kemp 1919: 312, pl. 12(2). — Yokoya 1928: 779. — Shen 1932: 253, pl. 10(5), text-figs. 155, 157. — Sakai 1934: 320; 1935: 214, pl. 59(4); 1939: 636, pl. 72(4); 1965: 191, pl. 91(1); 1976: 621, pl. 212(2); 1982: 714 (in part). — Kamita 1941: 175, text-fig. 96. — Nishimura & Suzuki 1971: 121, pl. 44(9). — Kim 1973: 641. — Takeda 1975: 144, 243 (in part); 1982: 212; 1994: 260. — Miyake 1983: 168 (in part). — Dai & Yang 1991: 496, fig. 253(2), pl. 63(5) (in part). — Yamaguchi & Baba 1993: 506, fig. 195. — Minemizu 2000: 309. — Ng *et al.* 2008: 235 (in part).

Scopimera tuberculata Stimpson 1858: 98; 1907: 102.

Material examined. Lectotype and paratype: 2 males (RMNH 282), Japan, 1823–1829, coll. Ph. F. von Siebold.

Additional material. Japan: 7 females (NSMT-Cr-3729), Usu Bay, Hokkaido, 27 Jul. 1934, coll. M. Iwasa; 2 males, 2 females (NSMT-Cr-3739), Funabashi, Chiba, 17 Apr. 1957; 3 males (NSMT-Cr-3741), Moiwa, Sopporo; 1 male (NSMT-Cr-6504), Tokyo Bay, 7 Mar. 1977, coll. M. Suzuki; 2 males, 2 females (NSMT-Cr-6797), Ena Bay, Kanagawa, 15 Jun. 1980, coll. M. Takeda; 5 females (CBM-ZC-7979), Usu Bay, Hokkaido, 18 Aug. 2004, coll. T. Komai; 10 males, 2 females (CEL-CRU-2008-02), Wakayama, 7 Aug. 2008, coll. B. K. K. Chan.

Diagnosis. External maxillipeds merus slightly shorter than or subequal to ischium; external orbital angle blunt, crests behind external orbital angles diverging posteriorly (Figs. 1a, 6); cheliped length more than twice of carapace length in mature males, carpus elongated; tooth on inner margin of movable finger triangular (Fig. 2a); male sixth abdominal somite approximately as broad as long (Fig. 2b); G1 slender, tip rounded, with inward radiating setae of similar length (Fig. 3a, b, c).

Description. Carapace inflated, slightly broader than long, regions indistinct, surface covered by rounded tubercles, being densest on branchial regions, smooth on cardiac and intestinal regions; posterior margin longer than width between both external orbital angles (Figs. 1a, 6); suborbital ridge lined with at least 20 equal-sized small rounded granules (Fig. 1b); external orbital angle obtuse, directing slightly anterior, leaving single notch along lateral border, followed by longitudinal crest extending two-thirds of carapace length (Figs. 1a, 6). Pterygostomian regions covered with rounded granules (Fig. 1b). External maxillipeds convex, outer surface covered with rounded tubercles, merus slightly smaller than ischium, suture between them oblique, dactylus of palp just reaching suture. Ventral surface devoid of setae except short dense tufts of light-colored soft setae between bases of first and second ambulatory legs.

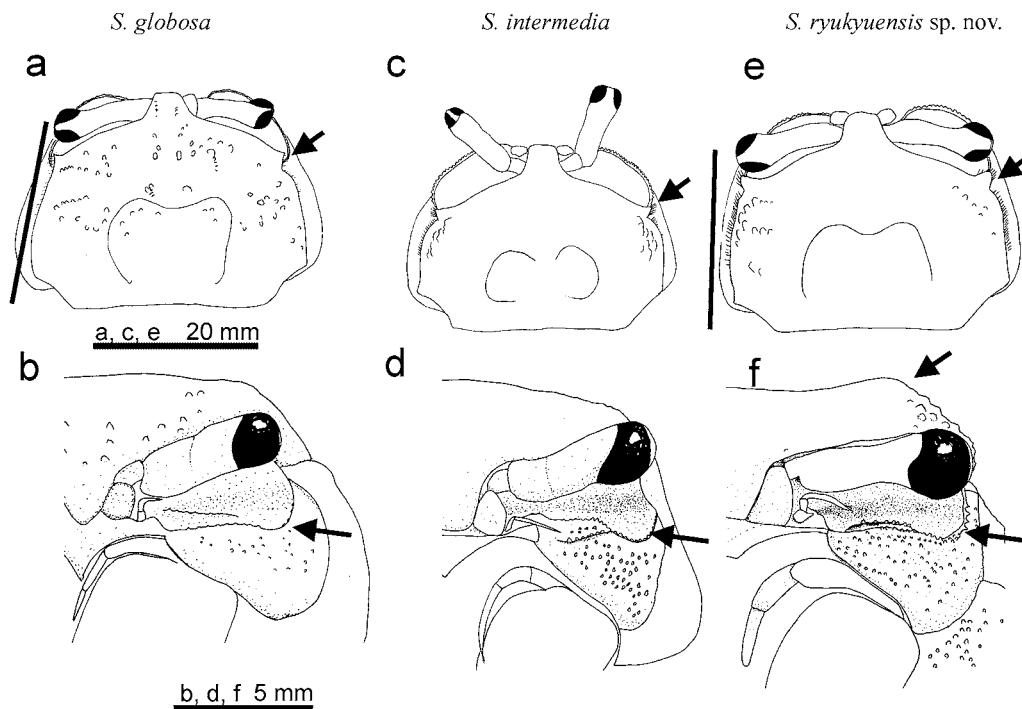


FIGURE 1. *Scopimera globosa* De Haan, 1835: dorsal view of carapace (a) and suborbital ridge and pterygostomian region (b); *S. intermedia* Balss, 1934: dorsal view of carapace (c) and suborbital ridge and pterygostomian region (d); *S. ryukyuensis* **sp. nov.**: dorsal view of carapace (e) and suborbital ridge and pterygostomian region (f). a, c, e: note arrow highlighting relative size of extra-orbital angle and solid line indicating direction of ridge behind the extra-orbital angle (which is diagnostic between *S. ryukyuensis* **sp. nov.** and *S. globosa*). b, d, f: arrow noting raised branchial region viewed from front in *S. ryukyuensis* **sp. nov.** (e) and relative conspicuousness of sub-orbital ridge: that of *S. ryukyuensis* **sp. nov.** being most pronounced.

Entire cheliped covered with fine granules, total length about twice of carapace length in adult males, merus with single longitudinal ovate tympana on inner surface; carpus longitudinally ovate, slightly shorter than merus in adult males; palm as long as merus and fingers; tips of both fingers tapered to sharp points, inner margins of both weakly serrated, movable finger with faint triangular tooth on inner margin (Fig. 2a). Ambulatory legs relatively elongated, slender, first and second legs longest, subequal to each other; fourth leg shortest; merus laterally compressed, tympana entire, occupying most of segment; dactylus tapered to sharp tip, slightly longer than propodus; fourth dactylus curved slightly upwards. Posterior border of merus, carpus, propodus of ambulatory legs lined sparsely with long stiff dark-colored setae.

Male abdomen elongated, telson distally rounded, sixth somite as long as broad, lateral borders of fifth conspicuously concave on proximal half, proximal margin much narrower; fourth somite broad, distal margin very convex (Fig. 2b). G1 slender, curved dorsally, distal end rounded with inward-dorsal radiating brush of longer setae of approximately same length, and a row of short setae around the opening on the inner surface (Fig. 3a–c).

Coloration. Grayish carapace, merus of external maxillipeds dark or with random blotches, chelipeds gray with pale palm and fingers, ambulatory legs banded dark and light gray (Fig. 4a, b) (also see Miyake 1983: Pl. 56(8); Minemizu 2000: 309).

Distribution. Japan (type locality), Korea (Kamita 1941; Kim 1973) and North China (Shen 1932).

Remarks. *Scopimera globosa* is a common species on muddy and sandy shores in Honshu, Japan (Sakai 1939, 1976). Sketch of G1 of *S. globosa* De Haan, 1835 lectotype matches the present material collected from Honshu, Japan. However, of the over 300 *Scopimera* specimens collected and observed from more than four localities from Hong Kong (in South China) and more than six localities from Taiwan, no *S. globosa* was found. Shen (1940) reported *S. globosa* from Tsuen Wan, Wong Chuk Hang, and Tai Po in Hong Kong, but the first two sites are today already heavily urbanized and almost devoid of any natural coasts. Morton & Morton

(1983: 185) stated “*Scopimera globosa* is as common at Tai Tam as *S. intermedia* is at Shiu Hau...”. The second author visited both Tai Po and Tai Tam, and specimens from Tai Po are *S. intermedia* while no *Scopimera* sp. was found in Tai Tam, where a reservoir has been constructed. It is thus unclear whether *S. globosa* really exists in Hong Kong. As for Taiwanese records of *S. globosa*, the first was reported from Danshuei (= Tamsui), Taipei County, by Takahasi (1934) and have been recorded on numerous localities on the main island and Penghu. In a review of ocy podoid crabs, however, a typical *S. intermedia* G1 was illustrated under the name *S. globosa* (see Huang *et al.* 1992: fig. 16). Checking available specimens in National Taiwan Museum and National Museum of Natural Science which has been collected and named as *S. globosa* between 1980s and today, we could find no specimens referable to *S. globosa*. All this material has proven to be *S. intermedia* instead. Thus the presence of *S. globosa* in Taiwan and Hong Kong is not verified in this study and its southern limit along the Chinese coast remains unclear. However, our extensive collections in Taiwan and Hong Kong fail to yield any *S. globosa*, suggesting this species is probably absent in these two regions. There was one record of “*S. globosa*” from Singapore (Tan & Ng 1994) which may be misidentified with *S. intermedia* or other unrecorded species.

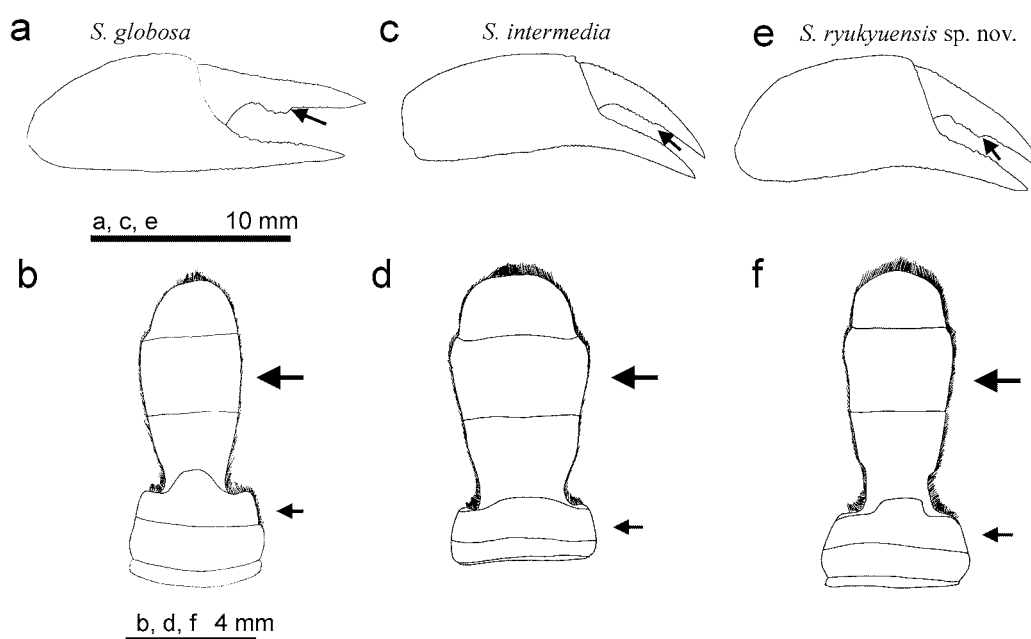


FIGURE 2. *Scopimera globosa* De Haan, 1835: chela (a) and male abdomen (b); *S. intermedia* Balss, 1934: chela (c) and male abdomen (d); *S. ryukyuensis* sp. nov.: chela (e) and male abdomen (f). a, c, e: arrow pointing tooth at inner margin of movable finger: that of *S. intermedia* Balss, 1934, being most rudimentary. b, d, f: large arrows showing dimensions of the sixth abdominal somite and small arrow indicating the convexity of distal border of the fourth somite.

Scopimera tuberculata Stimpson, 1858

(Fig. 6)

Scopimera tuberculata Stimpson 1858: 98; 1907: 102.

Material examined.- Neotype for *Scopimera tuberculata*: male (cw 9.9 mm; cl 7.6 mm) with label “NEOTYPE” of CBM- ZC 4195, *Scopimera globosa*, 2 males, Hashikui Beach, Kushimoto, Kii Peninsula, Japan, 8 Aug. 1976, coll. S. Yamaguchi.

Remarks. The description of *Scopimera tuberculata* in Stimpson (1858) was too brief and it does not provide diagnostic character to differentiate *S. tuberculata* from most of other known species of *Scopimera*. Stimpson (1907) later commented that *Scopimera tuberculata* “differs from De Haan’s *S. globosa* in the character of the upper surface of the carapax and in the obliquity of the meros-joint in the outer maxillipeds”.

Koelbel (1897), using specimens from Hong Kong, suggested *S. tuberculata* was a junior synonym as *S. globosa*. Tesch (1918) examined De Haan's type in Leiden Museum and added to the description of *S. globosa*, agreeing with Koelbel (1897) that Stimpson's descriptions on *S. tuberculata* fell well within the intra-specific variation of *S. globosa*. This view has been supported by a number of authors (e.g., Parisi 1918; Kemp 1919; Sakai 1939, 1965, 1976; Ng *et al.* 2001, 2008). Sakai (1939) further stated that *S. globosa* were found in numerous locations of Japan and the variation observed only involved one species. On the contrary, unlike his previous report (Shen 1932), Shen (1935) argued for the presence of *S. tuberculata* along the Chinese coasts, and Dai & Yang (1991) illustrated the G1 of the species. In the present study, we show that the old records of *S. tuberculata* from South China and Taiwan should be referred to *S. intermedia* instead. Our morphological and molecular analyses support the original identification by Tweedie (1950). Interesting enough specimens of "*S. tuberculata*" in Shen (1935) also included material from North China (nine males from Bohai Bay (= Peichihli Bay), also see Shen 1937a, b). However, without further discussion, Dai & Yang (1991) excluded the North China record, restricting the distribution of the species to only Guangdong in South China. The presence of "*S. tuberculata*" in North China, as well as the northern distributional limit of the species remains unclear. The record of "*S. tuberculata*" from Pam River, Vietnam, by Kosuge *et al.* (1997), are likely to be *S. intermedia* as well on the basis of the geographical distribution. The type specimen of *S. tuberculata* was lost in the great Great Chicago Fire in 1871 (Stimpson 1907; Evans 1967; Vasile *et al.* 2005; Manning & Reed 2006) thus no direct comparison can be made possible. A visit to the type locality of *S. tuberculata*, "Simoda", by the second author in 2007 failed to collect any specimens of *Scopimera*. The entire area around Port Shimoda has been urbanized and the natural beaches and sand flats have long been developed and lost. To eliminate further taxonomic confusion, we now designate a male specimen of *Scopimera globosa* collected from nearby Kii Peninsula in Japan (CSM-ZC 4195), deposited in Chiba Museum, as the neotype of *Scopimera tuberculata* Stimpson, 1858 (Fig. 6). This will settle the taxonomic confusion of related species found in the associated region once and for all and contribute to stability. Through this action, *Scopimera tuberculata* Stimpson, 1858 becomes a subjective junior synonym of *Scopimera globosa* De Haan, 1835.

***Scopimera intermedia* Balss, 1934**

(Figs. 1c, d, 2c, d, 3d–f, 4c, d)

Scopimera intermedia Balss 1934: 233. – Tweedie 1950: 360. – Serène & Moosa 1981: 4, fig. 1. – Morton & Morton 1983: 153, figs. 9.4(4, 5). – Ng *et al.* 2008: 235.

Scopimera globosa — Huang *et al.* 1992: 153, fig. 16, pl. 2D. – Fukui *et al.* 1989: 227. – Shih *et al.* 1991: 126. – Lee 2001: 98. – Ng *et al.* 2001: 39. – Shao *et al.* 2008: 642.

Scopimera tuberculata — Shen 1935: 36, fig. 15; 1940: 233. – Tweedie 1937: 146. – Dai & Yang 1991: 497, fig. 254, pl. 63(7). – Wang & Liu 1996: 225. – Kosuge *et al.* 1997: 182. – Wang 2003: 104. (not *Scopimera tuberculata* Stimpson, 1858 s. str.)

Material examined.- Taiwan: 3 males, 1 female (CEL), Siangshan, Hsinchu, 14 Nov. 2008, coll. P.-C. Tsai *et al.*; 7 males (CEL), Cigu, Tainan, 12 Jul. 2007, coll. B. K. K. Chan; 1 male, 1 female (NMNS 003566-00029), Wujiang estuary, Kinmen, 21 Feb. 2001, coll. K.-S. Lee *et al.*; 1 male (NMNS 001667-00001), Tiesian, Magong, Penghu, 2 Sep. 1990, coll. J.-F. Huang; 9 males, 1 female (CEL), Cingluo, Penghu, 17 Oct. 2008, coll. H.-T. Shih. **Hong Kong:** 27 males (CEL), Starfish Bay, Sep. 2008, coll. K. J. H. Wong; 4 males, 1 female (CEL), Bui O, Sep. 2008, coll. K. J. H. Wong; 3 males, 4 females (CEL), Yuen Chau Tsai, Tai Po, 26 Oct. 2008, coll. B. K. K. Chan. **Singapore:** 1 male, 3 females (ZRC 1969.12.20.1-10), Johore Strait, 19 Feb. 1969, coll. R. Serène; 1 male, 2 females (ZRC 2008.0728), Lim Chu Kang, 24 Nov. 2006, coll. K. L. Yeo.

Diagnosis. External maxillipeds merus slightly shorter than ischium; external orbital angle blunt, crest behind which diverge posteriorly (Fig. 1c); cheliped length more than twice of carapace length, carpus very elongated; tooth on inner margin of movable finger inconspicuous or absent (Fig. 2c); sixth somite of male abdomen broader than long (Fig. 2d); G1 slender, tip tapering, with typical kink and long setae extended from distal end (Fig. 3d, e, f).

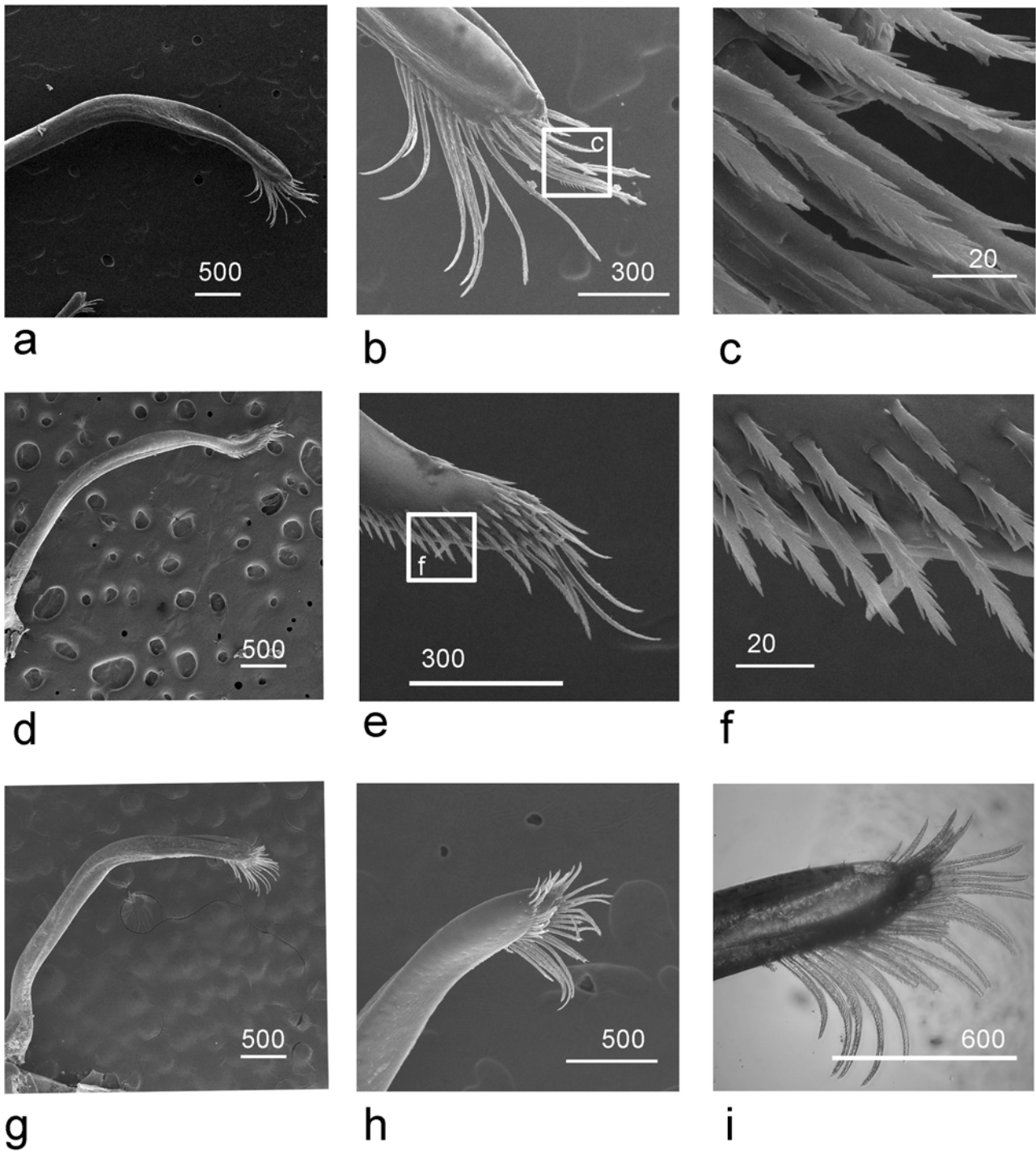


FIGURE 3. *Scopimera globosa* De Haan, 1835: G1 entire view (a), tip (b) and magnification of setae (c); *S. intermedia* Balss, 1934: G1 entire view (d), tip (e) and magnification of setae (f); *S. ryukyuensis* **sp. nov.**: G1 entire view (g), tip (h) and tip observed under light microscope (i). Scale bars in μm .

Description. Carapace convex, globular, slightly broader than long, covered by tubercles, densest around branchial regions and along lateral margins, nearly smooth on cardiac and intestine regions; posterior margin slightly longer than width between both external orbital angles (Fig. 1c); suborbital ridge granulated, composed of at least 25 coarsely bead-like granules, most larger than granules randomly distributed on pterygostomian regions (Fig. 1d); external orbital angle obtuse, leaving single notch along lateral border, followed by longitudinal crest extending most of carapace length (Fig. 1c). External maxillipeds convex, merus slightly smaller than ischium, suture between them oblique, dactylus palp not reaching suture between

merus and ischium. Ventral surface glabrous, smooth, except short dense tufts of light-colored soft setae between bases of first and second ambulatory legs.

Entire cheliped covered by fine granules, total length more than twice of carapace length in adult males; merus with single longitudinal ovate tympana on inner surface, carpus ovate, elongated, as long as merus and longer than palm in adult males, palm longer than fingers, fingers tapered to sharp tips, inner margins of both weakly serrated, tooth on inner margin of movable finger very faint if present (Fig. 2c). Ambulatory legs relatively elongated, slender, third leg longest, first and second legs subequal, fourth leg shortest; merus laterally compressed, tympana entire, occupying most of segment, dactylus tapered to a sharp tip, subequal in length with propodus; anterior border of merus, carpus, both borders of propodus lined sparsely with long stiff dark-colored setae.

Male abdomen elongated, telson broader than long, distal end rounded; sixth somite rectangular, broader than long, distal margin slightly broader; lateral margins of fifth somite conspicuously concave on proximal half, proximal margin narrower; fourth somite broad, distal margin less as convex (Fig. 2d). G1 slender, curved dorsally, tapered to a fine tip with distinctive ventral-outward kink near distal end; several long stiff setae extended from very tip (Fig. 3d–f).

Distribution. From Malay Peninsula (type locality: Johore), Singapore, Borneo, Indonesia (Tweedie 1950), Vietnam (Kosuge *et al.* 1997), to Hong Kong, South China (Shen 1935, 1940; present study) and the southern and western coast of Taiwan, including Penghu (present study). May be present in North China but the northern limit remains unclear (see “Remarks” under *S. tuberculata* above).

Remarks. *Scopimera intermedia* has been recorded under *S. tuberculata* (*sensu* Shen 1935, 1940) from Vietnam (Kosuge *et al.* 1997; see “Remarks” under *Scopimera tuberculata*), Hong Kong, South China (Shen 1935, 1940; Dai & Yang 1991), and Kinmen (Wang & Liu 1996; Ng *et al.* 2001), and *S. globosa* from Taiwan (e.g. Huang *et al.* 1992, see “Remarks” under *S. globosa*). *Scopimera intermedia* is therefore a new record for Taiwan, China, and Vietnam.

Scopimera ryukyuensis sp. nov.

(Figs. 1e, f, 2e, f, 3g–i, 4e, f, 5a–f)

Scopimera globosa — Takeda 1975: 144, 243 (in part, Okinawa, the Ryukyus). – Sakai 1982: 714 (in part, the Ryukyus).
– Miyake 1983: 168, pl. 56(8) (in part, Ishigaki, the Ryukyus). – Nagai & Nomura 1988: 56. – Ng *et al.* 2008: 235 (in part).

Material examined. Holotype: 1 male (RUMF-ZC-00865), Awase, Okinawa, Ryukyus, Japan, 11 April 2008, coll. H.-T. Shih, T. Naruse & N.-H. Jang-Liaw. **Paratypes:** 1 male (RUMF-ZC-00866), data same as for holotype; 2 males (NSMT-Cr 18234, 18235), data same as for holotype; 1 female (NSMT-Cr 18236), Sedake, Okinawa, Ryukyus, Japan, Jun. 2007, coll. B. K. K. Chan; 1 male (NMNS-5687-001), data same as for holotype; 1 male (ASIZCR000199), data same as for holotype; 2 females (ASIZCR000200, 000201), Sedake, Okinawa, Ryukyus, Japan, Jun. 2007, coll. B. K. K. Chan; 1 male (NCHUZOOL 13230), data same as for holotype; 1 male (ZRC 2008.0024), data same as for holotype.

Additional material: 2 males, 10 females (CEL-SG-OK062007), Sedake, Okinawa, Ryukyus, Japan, Jun. 2006, coll. B. K. K. Chan; 14 males, 13 females (inc. 1 ovig.) (NCHUZOOL 13224), data same as for holotype; 4 males (CEL), south of Naha, Okinawa, Ryukyus, Japan, Nov. 2008, coll. B. K. K. Chan.

Diagnosis. External maxillipeds merus shorter than or subequal to ischium; branchial regions raised (Fig. 1f), external orbital angle prominent, crest behind which subparallel (Fig. 1e); cheliped length less than twice of carapace length for mature males, rectangular tooth on inner margin of movable finger (Fig. 2e); male sixth abdominal somite as broad as long, posterior margin shorter (Fig. 2f); G1 similar to *S. globosa*, tip rounded, with inward radiating setae of similar length (Fig. 3g–i).

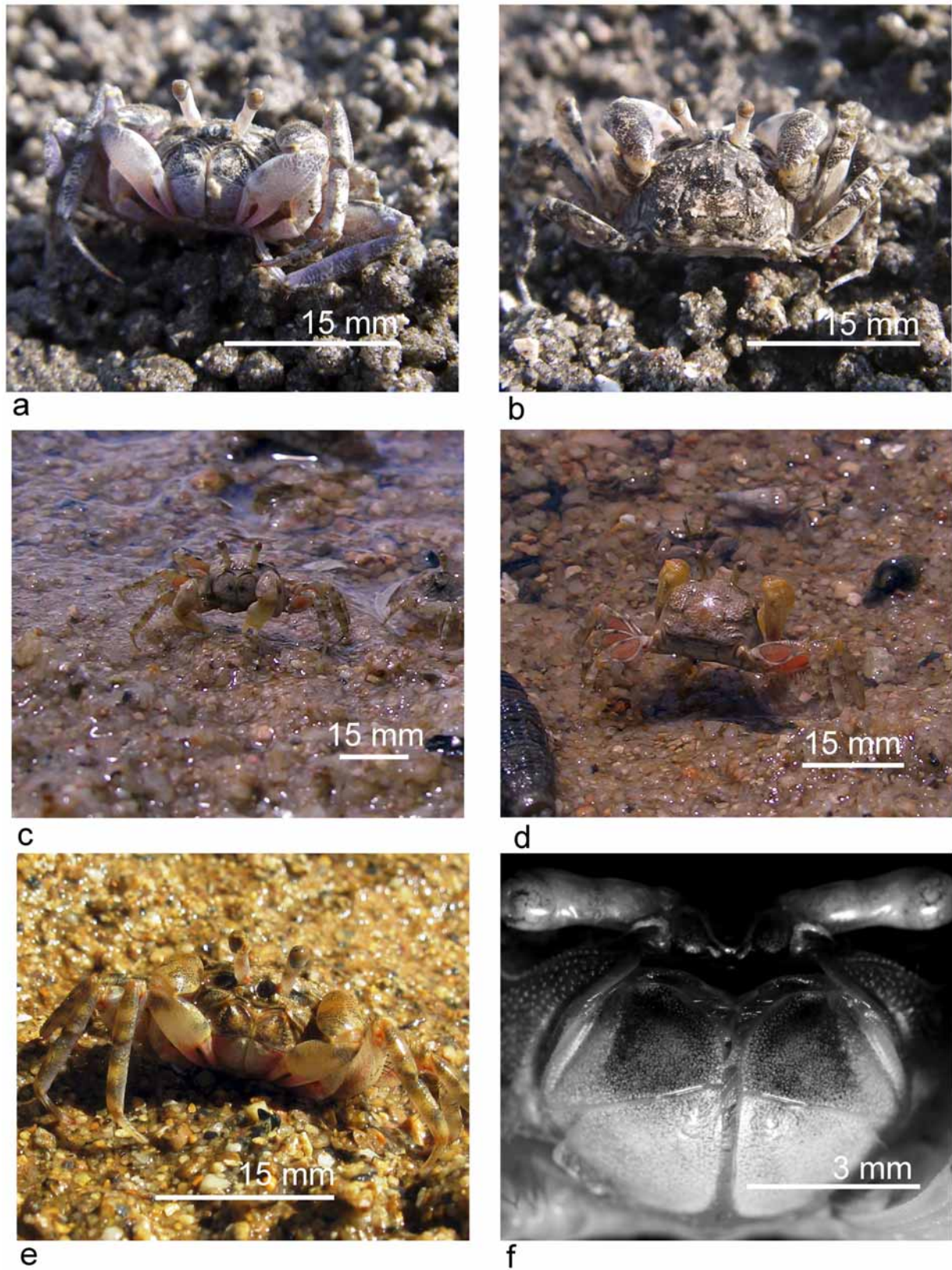


FIGURE 4. Photographs in life (a–e). *Scopimera globosa* De Haan, 1835: male frontal view (a) and dorsal view (b); *S. intermedia* Balss, 1934: male frontal view (c) and dorsal view (d); and *S. ryukyuensis* **sp. nov.**: male frontal view (e) and close-up of external maxillipeds from preserved specimens, showing ring-like marking on merus (f).



a



b



c



d



e



f

FIGURE 5. Photographs in life *Scopimera ryukyuensis* **sp. nov.** (a–e): dorsal view (a), frontal view (b) and ventral view (c) of male and dorsal view (d) and frontal view (e) of female. External architecture of burrow at Sedake, Okinawa, the Ryukyus (f).

Description. Carapace inflated, slightly broader than long, regions indistinct, surface covered by rounded tubercles, more prominent on branchial region, nearly smooth on cardiac and intestinal regions (Fig. 1e); branchial regions extremely raised (Fig. 1f), length of posterior margin subequal to distance between both

external orbital angles. Suborbital ridge composed of at least 20 equal-sized rounded granules (Fig. 1f); external orbital angle triangular, notch behind which prominent, followed by roughly parallel longitudinal crest extending most of carapace length (Fig. 1e). Pterygostomian regions covered with rounded granules (Fig. 1f). External maxillipeds convex, outer surface covered with rounded tubercles, merus slightly smaller than ischium, suture between them slightly oblique, dactylus of palp approximately reaching suture between merus and ischium. Ventral surface glabrous, smooth, except for short dense tufts of light-colored soft setae between bases of first and second ambulatory legs.

Entire cheliped covered with fine granules, total length less than twice of carapace length on adult male; single longitudinal ovate tympana on outer surface of merus; carpus ovate, shorter than merus; palm as long as merus and fingers; tips of fingers tapered to sharp tips, inner margins weakly serrated, inner margin of movable finger with small rectangular tooth (Fig. 2e). Ambulatory legs relatively elongated, slender; first and second legs longest, subequal in length, fourth leg shortest; merus laterally compressed, tympana entire, occupying most of segment; dactylus tapered to sharp tip, length subequal to respective propodus, fourth dactylus curved slightly upwards. Anterior border of merus, carpus and both margins of propodus, dactylus lined sparsely with long stiff dark-colored setae.

Male abdomen elongated, telson distally rounded, sixth somite as long as broad, lateral margins converging slightly posteriorly; fifth elongated, slightly narrower than the anterior segment; fourth somite broad, distal margin very convex (Fig. 2f). G1 largely resembling that of *S. globosa*, slender, curved dorsally, distal end rounded with brush of longer inward-dorsal radiating setae of roughly same length, and a row of short setae around opening on the inner surface (Fig. 3g–i).

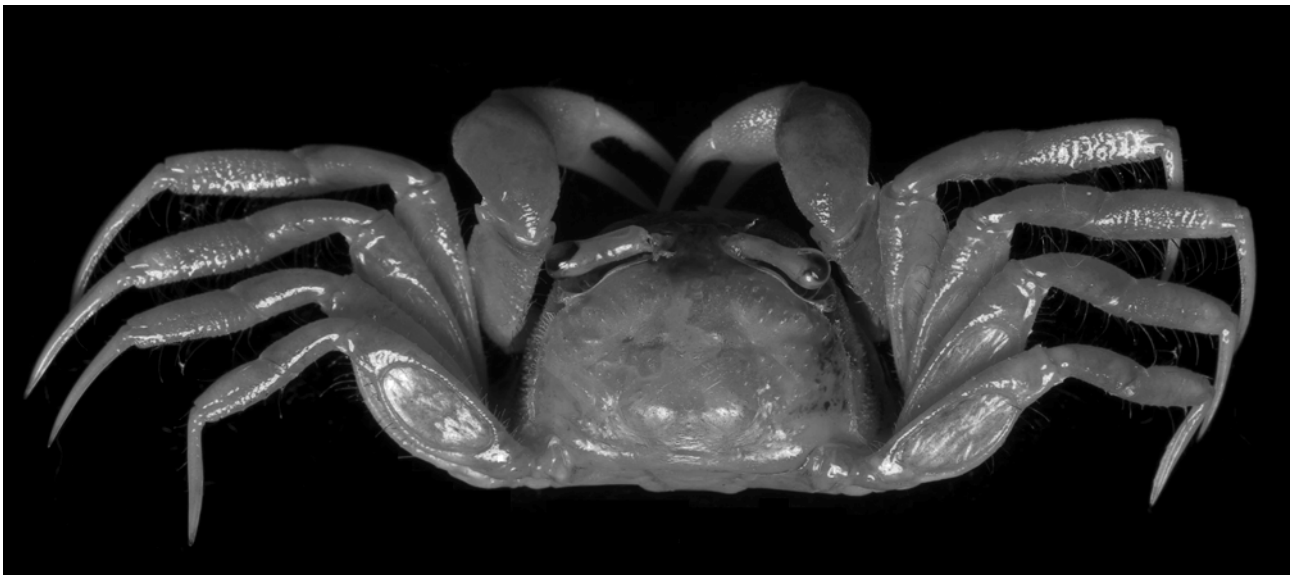


FIGURE 6. Dorsal view of the neotype of *Scopimera tuberculata* Stimpson, 1858. A male (cw 9.9 mm, cl 7.6 mm) (CBM-ZC 4195) deposited in Natural History Museum and Institute, Chiba, Japan.

Size. cw 7.4 mm, cl 6.5 mm for the holotype.

Coloration. Dorsal carapace appears brownish gray, appendages yellow with brownish bands except palm and fingers of chelipeds (Figs. 4e, 5a–e). A brownish circular pattern on merus of external maxillipeds (Fig. 4f) (not observed in any *S. globosa* individual).

Etymology. The name denotes the Ryukyu Archipelago, where the new species was discovered.

Habitat and ecology. On mid-low shores of open, exposed sandy shores. Burrow opening with small radiating sand balls (Fig. 5f) (also see Nagai & Nomura 1988: 56). Smallest female collected that was ovigerous had a carapace width of 5 mm.

Distribution. The present localities are recorded from Okinawa (present study) and Ishigaki (Miyake 1983) in the Ryukyus. This species is probably endemic to the Ryukyu Archipelago.

Remarks. *Scopimera ryukyuensis* **sp. nov.** morphologically resembles *S. globosa* but there are several diagnostic features. Although both species share a similar G1 morphology, *S. ryukyuensis* has a more prominent or pointed triangular external orbital tooth and notch behind, and a subparallel ridge which follows along the lateral margin.

Genetic divergence

For the COI gene from 30 specimens of the genus *Scopimera*, a 658-bp segment was compared, resulting in 11 different haplotypes (Table 1). The studied segment of the COI sequences was AT rich (62.9%) (35.5% T, 27.4% A, 17.9% G, 19.3% C). In this gene fragment, 179 positions were variable and 162 were parsimoniously informative. The best model selected by MrModeltest for COI was the GTR+I model (Pinvar = 0.6662). Both the ME and MP trees are shown (Fig. 7), with the respective confidence values from the ME, MP, BI and ML analyses. For the MP analysis, a single tree was recovered with a tree length of 317 steps, a consistency index of 0.82 and a retention index of 0.88.

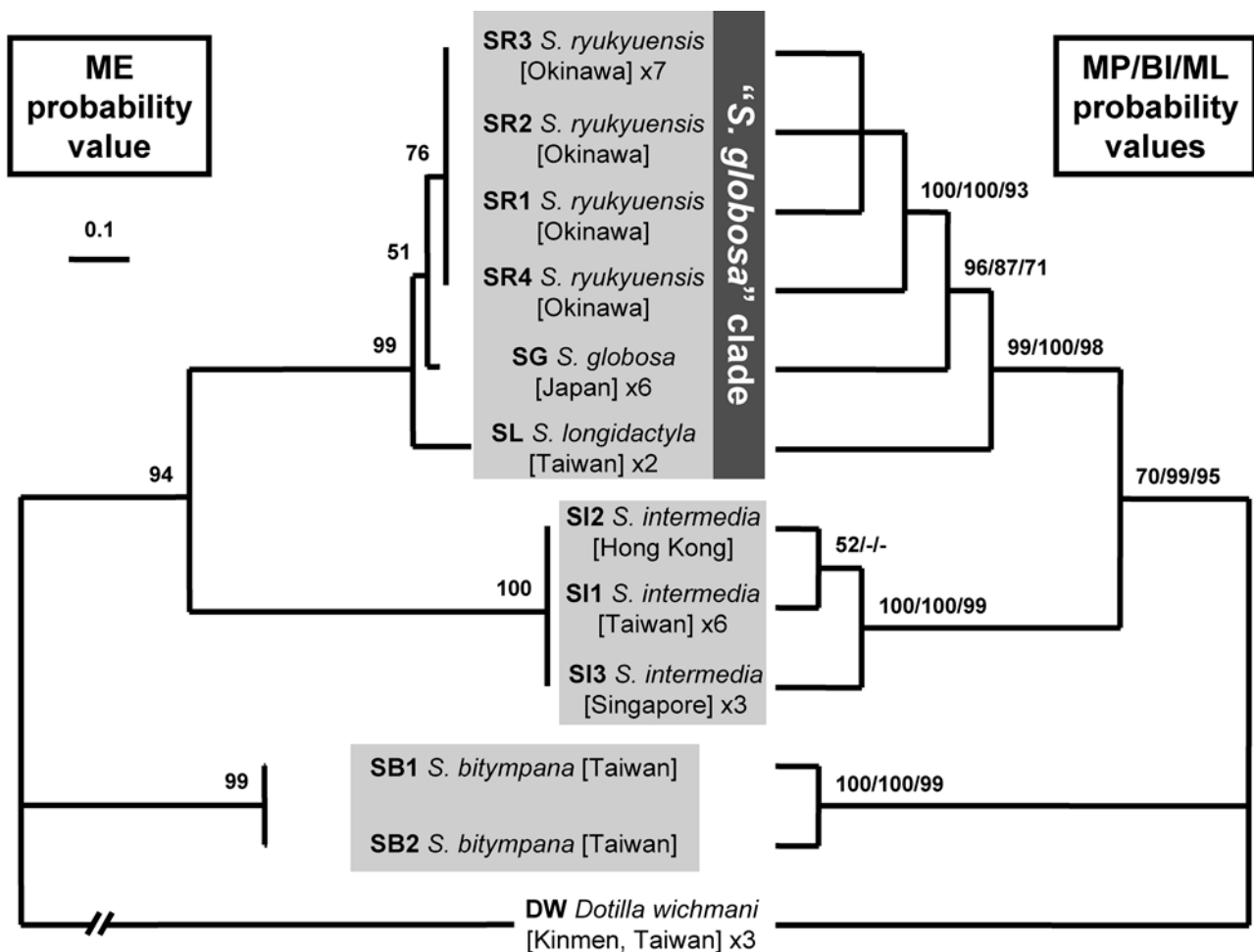


FIGURE 7. A minimum evolution (ME) tree (left) and maximum parsimony (MP) tree (right) of the *Scopimera* species from East Asia and *Dotilla*, based on 658 basepairs of the cytochrome oxidase I genes. Probability values at the nodes represent confidence values for ME (left), MP, Bayesian inference (BI) and maximum likelihood (ML) (right). For haplotype names see Table 1. Species name and locality are behind each haplotype name.

In Figure 7, the *Scopimera* spp. from East Asia could be divided into three main clades, viz. “*S. globosa*” clade (including *S. globosa*, *S. longidactyla*, *S. ryukyuensis* **sp. nov.**), *S. intermedia* and *S. bitympana*. In the “*S. globosa*” clade, although the branch length of the three species are short in ME tree, they can be separated

with high confidence values of ME, MP, BI and ML analyses. The three species differ in the number of bp differences with 28–55 bp, and the pairwise nucleotide percentage divergence among them are from 4.43% to 9.04% (Table 2).

TABLE 1. Specimens and localities used for molecular study. There are 12 haplotypes of cytochrome oxidase I genes of *Scopimera* and the outgroup *Dotilla wichmani*.

Species	Localities	Catalog no.	Sample size	Haplotypes of COI	DDBJ access. no.
<i>S. ryukyuensis</i> sp. nov.	Awase, Okinawa, the Ryukyus	CEL-SG-OA1	1	SR1	AB515318
	Awase, Okinawa, the Ryukyus	CEL-SG-OA2	1	SR2	AB515319
	Awase, Okinawa, the Ryukyus	CEL-SG-OA3,4	2	SR3	AB515317
	Sedake, Okinawa, the Ryukyus	CEL-SG-OK1-5	5	SR3	AB515317
	Sedake, Okinawa, the Ryukyus	CEL-SG-OK6	1	SR4	AB515316
<i>S. globosa</i> (De Haan, 1835)	Wakayama, Japan	CEL-SG-J1-6	6	SG	AB515320
“ <i>S. tuberculata</i> ” Stimpson, 1858 (= <i>S. intermedia</i> Balss, 1934)	Cigu, Tainan, Taiwan	CEL-ST-CQ1-2	2	SI1	AB515326
	Cingluo, Penghu, Taiwan	NCHUZOOOL 13225, 13226, 13227, 13228	4	SI1	AB515326
	Starfish Bay, Hong Kong	CEL-ST-HK1	1	SI2	AB515324
<i>S. intermedia</i> Balss, 1934	Lim Chu Kang mangroves, Singapore	ZRC 2008.0728	3	SI3	AB515325
<i>S. longidactyla</i> Shen, 1932	Danshuei, Taipei, Taiwan	CEL-SL-A1-2	2	SL	AB515323
<i>S. bitympana</i> Shen, 1930	Danshuei, Taipei, Taiwan	CEL-SB-A1	1	SB1	AB515321
	Danshuei, Taipei, Taiwan	CEL-SB-A2	1	SB2	AB515322
<i>Dotilla wichmani</i> De Man, 1892	Kinmen, Taiwan	CEL-D-K1-3	3	DW	AB515327

CEL: Collections in the Coastal Ecology Laboratory of Academia Sinica, Taipei, Taiwan; NCHUZOOOL: Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan; ZRC: Zoological Reference Collection, Raffles Museum, National University of Singapore, Singapore.

TABLE 2. Pairwise nucleotide percentage divergence matrix (lower-left) and the base-pair (bp) differences (upper right) based on 658 bp of the cytochrome oxidase subunit I (COI) gene between haplotypes of *Scopimera* and *Dotilla* (Table 1). For abbreviations of haplotypes see Table 1.

	<i>Scopimera ryukyuensis</i>				<i>Scopimera globosa</i>	<i>Scopimera longidactyla</i>	<i>Scopimera intermedia</i>			<i>Scopimera bitympana</i>		<i>Dotilla wichmani</i>
	SR1	SR2	SR3	SR4	SG	SL	SI1	SI2	SI3	SB1	SB2	DW
SR1	—	2	1	2	29	55	111	112	113	108	108	119
SR2	0.30	—	1	2	29	55	113	114	115	106	106	119
SR3	0.15	0.15	—	1	28	54	112	113	114	107	107	118
SR4	0.30	0.30	0.15	—	29	53	112	113	114	106	106	117
SG	4.59	4.59	4.43	4.59	—	49	113	114	115	109	107	124
SL	9.04	9.04	8.86	8.68	8.00	—	112	113	112	111	111	114
SI1	19.34	19.76	19.55	19.55	19.78	19.59	—	1	2	119	119	125
SI2	19.55	19.97	19.76	19.76	19.99	19.80	0.15	—	3	120	120	126
SI3	19.76	20.18	19.97	19.97	20.20	19.59	0.30	0.46	—	118	118	124
SB1	18.66	18.25	18.45	18.25	18.87	19.27	20.93	21.14	20.72	—	3	115
SB2	18.66	18.25	18.45	18.25	18.47	19.27	20.93	21.14	20.72	0.46	—	115
DW	20.78	20.78	20.58	20.37	21.82	19.73	22.03	22.24	21.82	20.05	20.05	—

Discussion

Without settling the taxonomic identity of *Scopimera globosa* and *S. tuberculata*, the taxonomy of congeners in the West Pacific is difficult. In the present study, we showed the previous records of *S. tuberculata* in South China (Hong Kong) are incorrect and should be referred to *S. intermedia* instead. The taxonomy of these East Asian *Scopimera* species is now stabilized in making *S. tuberculata* as a subjective junior synonym of *S. globosa* through the judicious selection of a neotype for the former species.

In the present study, *Scopimera ryukyuensis* **sp. nov.** is identified from Okinawa in the Ryukyus, and it has diagnostic morphological features and is also genetically distinct compared to other East Asian *Scopimera* species. Based on the studies of other decapods, the bp difference of the mitochondrial COI can be used as an indicator of species boundary (e.g., in freshwater crabs of the genera *Geothelphusa*: Shih *et al.* 2007b, 2008; *Somanniathelphusa*: Shih *et al.* 2007a; and *Johora*: Yeo *et al.* 2007; intertidal crabs like *Helice*, *Chasmagnathus* and allies: Shih & Suzuki 2008; *Uca*: Shih *et al.* 2009; *Mictyris*: Davie *et al.* in press). In our study, the genetic difference of COI of *Scopimera* is at least 28 bp (4.3%), which is slightly more than the suggested criterion of freshwater crabs (Shih *et al.* 2007b: 3.7%) but close to coastal crabs (Shih & Suzuki 2008: 4.6%; Davie *et al.* in press: 4.4%). This provides genetic evidence to support the recognition of this new species. The close relationship among *S. globosa*, *S. longidactyla* and *S. ryukyuensis* **sp. nov.** is shown by the highly-supported monophyletic clade (Fig. 7).

The geographical distribution of *Scopimera* in West Pacific is distinct, with *S. globosa* (see discussion in Sakai 1939, 1976) in mainland Japan, North China, and Korea; and *S. intermedia* on both shores of the Taiwan Strait (including western Taiwan, Penghu, and Kinmen), Hong Kong (present study), and Malaysia (including Singapore and Sarawak) (Balss 1934; Tweedie 1950). Geographical distribution of *S. ryukyuensis* **sp. nov.** is at present only recorded in Okinawa and has not been observed in Taiwan and South China (personal observation), suggesting this species could have narrow geographical distribution within the Ryukyus. There are several intertidal or catadromous crabs which appear to have endemic populations in the Ryukyus, including *Mictyris* (Davie *et al.* in press) and *Eriocheir* (Xu *et al.* 2009). Further studies should define the geographical distribution of this new species in the East Asian region.

Acknowledgments

This study was supported by a grant from the National Science Council (NSC) of Taiwan (NSC96-2621-B-001-007-MY3) and an internal research fund from the Academia Sinica to BKKC and an NSC grants (NSC96-2621-B-005-005-MY3; 98-2621-B-005-001-MY3) to HTS. We wish to thank P. K. L. Ng and S. H. Tan (National Singapore University) for sending relevant literature and specimens from Singapore; C. H. J. M. Fransen (RMNH) for checking the type specimens of *S. globosa* and sketching the G1; H. Komatsu (NSMT), T. Komai (CBM), and K.-S. Lee (NMNS) for allowing study of museum collections and provision of working space; T. Naruse (University of the Ryukyus) and N.-H. Jang-Liaw (NMNS) for helping the collection in the field; S.-L. Yang (Beijing Natural History Museum) for discussion and communications with KJHW; T. Koga (Wakayama University) and K. Wada (Nara Women's University) for their discussions during the TCS Summer Meeting 2009; Yi-Chun Fan, Hsin-Ying Lee and Fu-lung Shih (Academia Sinica, Taiwan) for assistance in the laboratory analysis of morphology and molecular materials; and T.-L. Lin (Academia Sinica, Taiwan) for the assistance in the SEM preparations. We acknowledge P. K. L. Ng and P. Castro for greatly helped o improve this manuscript.

References

- Balss, H. (1934) Die Krabben der Reise J.W. Harms' nach der Christmas-Insel und dem Malaiischen Archipel. *Zoologischer Anzeiger*, 106(10), 225–237.
- Chan, B.K.K., Tsang, L.M. & Chu, K.H. (2007a) Morphological and genetic differentiation of *Tetraclita squamosa* (Crustacea: Cirripedia) in East Asia and description of a new species of *Tetraclita*. *Zoological Scripta*, 36, 79–91.

- Chan, B.K.K., Tsang, L.M. & Chu, K.H. (2007b) Cryptic diversity of *Tetraclita squamosa* complex (Crustacea, Cirripedia) in Asia: description of a new species from Singapore. *Zoological Studies*, 46, 46–56.
- Dai, A.-Y. & Yang, S.-L. (1991) *Crabs of the China Seas*. China Ocean Press, Beijing, 682 pp.
- Davie, P.J.F., Shih, H.-T. & Chan, B.K.K. A new species of *Mictyris* (Decapoda, Brachyura, Mictyridae) from the Ryukyu Islands, Japan. *Crustaceana Monographs* (in press).
- 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.
- Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vriegenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.
- Fukui, Y., Wada, K. & Wang, C.-H. (1989) Ocypodidae, Mictyridae and Grapsidae (Crustacea: Brachyura) from some coasts of Taiwan. *Journal of Taiwan Museum*, 42, 225–238.
- Haan, H.M. de. (1833–1849) Crustacea. In: von Siebold, P.F. (Ed.), *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, Noitis, Observationibus et Adumbrationibus Illustravit*. Lugduni-Batavorum, Leiden, i–xvii, i–xxxii, ix–xvi, pp. 1–243.
- Hall, T.A. (2001) *Bioedit: A User-Friendly Biological Sequence Alignment Editor and Analysis, version 5.09*. Department of Microbiology, North Carolina State University, North Carolina.
- Huang, J.-F., Yu, H.-P. & Takeda, M. (1992) A review of the ocypodid and mictyrid crabs (Crustacea: Decapoda: Brachyura) in Taiwan. *Bulletin of the Institute of Zoology, Academia Sinica*, 31, 141–161.
- Huang, Z.-G. (1994) *Marine Species and Their Distribution in China's Seas*. China Ocean Press, Beijing, 764+134 pp. (in Chinese)
- Kamita, T. (1941) *Studies of the Decapod Crustaceans of Chosen. Pt. 1. Crabs*. The Fisheries Society of Chosen, Keijo, Korea, 289 pp. (in Japanese)
- Kemp, S. (1919) Notes on Crustacea Decapoda in the Indian Museum. XII. Scopimerinae. *Records of the Indian Museum*, 16, 305–348.
- Kim, H.S. (1973) Anomura-Brachyura. In: *Illustrated Encyclopedia of Fauna & Flora of Korea. Vol.14*. Samhwa, Seoul, pp. 589–682. (in Korean)
- Kimura, M. (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, 16, 111–120.
- Koelbel, K. (1897) Beschreibung der Krebse. Wissenschaftliche Ergebnisse der Reise des Grafen Béla Széchenyi in Ostasien, 2, 709–718.
- Koga, T. (1995) Movements between microhabitats depending on reproduction and life history in the sand-bubbler crab *Scopimera globosa*. *Marine Ecology Progress Series*, 117, 65–74.
- Kosuge, T., Wada, K. & Trong, P.D. (1997) Crab distribution in the Cam River estuary, Haiphong, northern Vietnam. In: Anh, P.N., Brands, J.T. & Hong, P.N. (Eds.), *National Workshop on the Relationship Between Mangrove Rehabilitation and Coastal Aquaculture in Vietnam*. Cres & Actmang, Hanoi, pp. 178–184.
- Lee, J.-H. (2001) *A Field Guide to Crabs in Taiwan*. Bigtrees Co., Taipei, 174 pp. (in Chinese)
- Manning, R.B. & Reed, K.J. (2006) Decapod crustaceans deposited in the Zoological Museum of Copenhagen by William Stimpson in 1859. *The Raffles Bulletin of Zoology* 54, 283–293.
- Milne Edwards, H. (1852) Observations sur les affinités zoologiques et la classification naturelle des Crustacés. *Annales des Sciences naturelles*, (3)18, 109–166.
- Minemizu, R. (2000) *Marine Decapod and Stomatopod Crustaceans Mainly from Japan*. Bunnichi-Sogo Shuppan, Tokyo, 344 pp. (in Japanese)
- Miyake, S. (1983) *Japanese Crustacean Decapods and Stomatopods in Color. II Brachyura (Crabs)*. Hoikusha, Osaka, 277 pp. (in Japanese)
- Morton, B. & Morton, J. (1983) *The Sea Shore Ecology of Hong Kong*. Hong Kong University Press, Hong Kong, 350 pp.
- Nagai, S. & Nomura, K. (1988) *Marine Animals of Okinawa, No. 7 (Crustacea)*. Shinsei Tosho Publication, Okinawa, Japan, 250 pp. (in Japanese)
- Ng, P.K.L., Wang, C.-H., Ho, P.-H. & Shih, H.-T. (2001) An annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). *National Taiwan Museum Special Publication Series*, 11, 1–86.
- Ng, P.K.L., Guinot, D. & Davie, P.J.F. (2008) Systema Brachyurorum: Part I. An annotated checklist of the extant brachyuran crabs of the world. *The Raffles Bulletin of Zoology Supplement*, 17, 1–286.
- Nishimura, S. & Suzuki, K. (1971) *Common Seashore Animals of Japan in Color (Kaigan Dobutsu)*. Hoikusha, Osaka, 196 pp. (in Japanese)
- Nylander, J.A.A. (2005) *MrModeltest version 2.2*. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.
- Ortmann, A. (1894) Die Decapoden – Krebse des Strassburger Museums, mit besonderer Berücksichtigung der van

- 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 genuine Boas) III. Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 2. Gruppe: Catametopa. *Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere*, 7, 683–772, pl. 23.
- Parisi, B. (1918) I Decapodi giapponesi del Museo di Milano. VI. Catometopa e Paguridea. *Atti della Societa Italiana de Scienze Naturali*, 57, 5–42.
- Rafinesque, C.S. (1815) *Analyse de la Nature, ou Tableau de l'Univers et des Corps Organisés*. L'Imprimerie de Jean Barravecchia, Palermo. 224 pp. (not seen)
- Ronquist, F. & Huelsenbeck, J.P. (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
- Sakai, T. (1934) Brachyura from the coast of Kyushu, Japan. *Science Reports of the Tokyo Bunrika Daigaku, Section B*, 1(25), 281–330.
- Sakai, T. (1935) *Crabs of Japan*. Sansendo, Tokyo, 239 pp.+66 pls. (in Japanese)
- Sakai, T. (1939) *Studies on the Crabs of Japan. IV. Brachygnatha, Brachyrhyncha*. Yokendo, Tokyo, pp. 365–741+pls. 42–111.
- Sakai, T. (1965) *The Crabs of Sagami Bay*. Maruzen, Tokyo, 206 pp.+100 pls..
- Sakai, T. (1976) *Crabs of Japan and the Adjacent Seas*. Kodansha, Tokyo, 773 pp+251 pls.
- Sakai, T. (1982) Brachyura. In: Uchida, T. (Ed.), *New Illustrated Encyclopedia of the Fauna of Japan (Shin Nihon Doubutsu Zukan)*. Hokuryukan, Tokyo, pp. 653–721. (in Japanese)
- Serène, R. & Moosa, M.K. (1981) Description de *Scopimera gordonae* sp. nov. (Crustacea, Decapoda, Brachyura), une espèce des eaux orientales d'Indonesie. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, 53, 1–9.
- Shao, K.-T., Peng, C.-I. & Wu, W.-J. (2008) 2008 Taiwan Species Diversity II. *Species Checklist*. Biodiversity Research Center, Academic Sinica, Taipei, 796 pp.
- Shen, C.-J. (1932) The brachyuran Crustacea of North China. *Zoologia Sinica, Series A*, 9, 1–300.
- Shen, C.-J. (1935) On some new and rare crabs of the families Pinnotheridae, Grapsidae and Ocypodidae from China. *The Chinese Journal of Zoology*, 1, 19–40.
- Shen, C.-J. (1937a) Second addition to the fauna of brachyuran Crustacea of North China, with a check list of the species recorded in this particular region. *Contributions from the Institute of Zoology, National Academy of Peiping*, 3(6), 277–314.
- Shen, C.-J. (1937b) On some account of the crabs of North China. *Bulletin of the Fan Memorial Institute of Biology (Zoology)*, 7(5), 167–185.
- Shen, C.-J. (1940) The brachyuran fauna of Hong Kong. *Hong Kong Fisheries Research Station Journal*, 1, 211–242.
- Shih, H.-T. & Suzuki, H. (2008) Taxonomy, phylogeny and biogeography of the endemic mudflat crab *Helice/Chasmagnathus* complex (Crustacea: Brachyura: Varunidae) from East Asia. *Zoological Studies*, 47, 114–125.
- Shih, H.-T., Fang, S.-H. & Ng, P.K.L. (2007a) Phylogeny of the freshwater crabs genus *Somaniathelphusa* Bott (Decapoda: Parathelphusidae) from Taiwan and the coastal regions of China, with notes on their biogeography. *Invertebrate Systematics*, 21, 29–37.
- Shih, H.-T., Kamrani, E., Davie, P.J.F. & Liu, M.-Y. (2009) Genetic evidence for the recognition of two fiddler crabs, *Uca iranica* and *U. albimana* (Crustacea: Brachyura: Ocypodidae), from the northwestern Indian Ocean, with notes on the *U. lactea* species-complex. *Hydrobiologia*, 635, 373–382.
- Shih, H.-T., Naruse, T. & Yeo, D.C.J. (2008) A new species of *Geothelphusa* Stimpson, 1857, from Taiwan (Crustacea: Brachyura: Potamidae) based on morphological and molecular evidence, with notes on species from western Taiwan. *Zootaxa*, 1877, 37–48.
- Shih, H.-T., Ng, P.K.L., Schubart, C.D. & Chang, H.-W. (2007b) Phylogeny and phylogeography of the genus *Geothelphusa* (Crustacea: Decapoda, Brachyura, Potamidae) in southwestern Taiwan based on two mitochondrial genes. *Zoological Science*, 24, 57–66.
- Shih, J.-T., Lue, K.-Y. & Wang, C.-H. (1991) Crab fauna and the activities of ten crab species in Tanshui mangrove swamp of Taiwan. *Annual of Taiwan Museum*, 34, 121–140. (in Chinese)
- Stimpson, W. (1858) Crustacea Ocypodoidea. Prodromus descriptionis animalium evertibratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers ducibus, observavit et descripsit, Pars 5. *Proceedings of the Academia of Natural Science, Philadelphia*, 10, 93–110.
- Stimpson, W. (1907) Report on the Crustacea (Brachyura and Anomura) collected by the North Pacific Exploring Expedition, 1853–1856. *Smithsonian Miscellaneous Collections*, 49(1717), 1–240.
- Swofford, D.L. (2003) *PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods)*, version 4. Sinauer, Sunderland, Massachusetts.
- Takahasi, S. (1934) An ecological study of the littoral animals near the mouth of the Tamsui. *Transactions of the Natural History Society of Formosa*, 24, 1–14. (in Japanese)
- Takeda, M. (1975) Brachyura. In: Utinomi, H. (Ed.), *The Aquatic Lower Animals of Japan*. Gakken, Tokyo, pp. 188–331. (in Japanese)

- Takeda, M. (1982) *Keys to the Japanese and Foreign Crustaceans Fully Illustrated in Colors*. Hokuryukan, Tokyo, 58+284 pp. (in Japanese)
- Takeda, M. (1994) Anomura and Brachyura. In: Okutani, T. (Ed.), *Living Things of Seashores*. Yama-Kei Publisher, Tokyo, pp. 221–264. (in Japanese)
- Tan, C.G.S. & Ng, P.K.L. (1994) An annotated checklist of mangrove brachyuran crabs from Malaysia and Singapore. *Hydrobiologia*, 285, 75–84.
- Tesch, J.J. (1918) The Brachyura of the Sigoba Expedition. Hymenosomidae, Ocypodidae, Grapsidae and Gecarcinidae. *Sigoba Expeditie Monographie*, 39c, 1–148.
- Thompson, J.D., Higgins, D.G. & Gibson, T.J. (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, 22, 4673–4680.
- Tweedie, M.W.F. (1937) On the crabs of the family Ocypodidae in the collection of the Raffles Museum. *Bulletin of Raffles Museum, Singapore*, 13, 104–170.
- Tweedie, M.W.F. (1950) Grapsoid crabs from Labuan and Sarawak. *Sarawak Museum Journal*, 5, 328–369.
- Vasile, R.S., Manning, R.B. & Lemaitre, R. (2005) William Stimpson's journal from the North Pacific Exploration Expedition, 1853–1856. *Crustacean Research Special Number*, 5, i–v, 1–220.
- Wang, C.-H. (2003) Crabs. In: Chen, C.-P. & J.-Y. Wu (Eds.), *Kinmen Coastal Creatures Guide*. Kinmen County Government, Kinmen, Taiwan, pp. 86–111. (in Chinese)
- Wang, C.-H. & Liu, H.-C. (1996) Preliminary investigations of the crab diversity of Wujiang estuary mangrove area in Kinmen. In: *Proceedings of a Conference on Mangrove Ecology*. Taiwan Endemic Species Research Institute, Nantou, Taiwan, pp. 223–229. (in Chinese)
- Xu, J.-W., Chan, T.-Y., Tsang, L.M. & Chu, K.H. (2009) Phylogeography of the mitten crab *Eriocheir sensu stricto* in East Asia: Pleistocene isolation, population expansion and secondary contact. *Molecular Evolution and Phylogenetics*, 52, 45–56.
- Yamaguchi, T. & Baba, K. (1993) Crustacean specimens collected in Japan by Ph. F. von Siebold and H. Burger and held by the Nationaal Natuurhistorisch Museum in Leiden and other museums. In: Yamaguchi, T. (Ed.), *Ph. F. von Siebold and Natural History of Japan: Crustacea*, The Carcinological Society of Japan, Tokyo, pp. 145–570.
- Yamaguchi, T. & Tanaka, M. (1974) Studies on the ecology of a sand bubble crab, *Scopimera globosa* De Haan (Decapoda: Ocypodidae). I. Seasonal variation of population structure. *Japanese Journal of Ecology*, 24, 165–174.
- Yeo, D.C.J., Shih, H.-T., Meier, R. & Ng, P.K.L. (2007) Phylogeny and biogeography of the freshwater crab genus *Johora* (Crustacea: Brachyura: Potamidae) from the Malay Peninsula, and the origins of its insular fauna. *Zoologica Scripta*, 36, 255–269.
- Yokoya, Y. (1928) Report of the biological survey of Mutsu Bay. 10. Brachyura and crab-shaped Anomura. *Science Reports of the Tohoku Imperial University, 4th Series (Biology)*, 3, 757–784.