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A review of the *Chaenostoma boscii* species-complex (Decapoda: Brachyura: Macrophthalmidae) from the Indo-West Pacific

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Abstract.— The sentinel crabs, *Chaenostoma orientale* Stimpson, 1858, and *C. crassimanus* Stimpson, 1858, were both described from the Ryukyu Islands, Japan, and have both been long considered junior synonyms of *C. boscii* (Audouin, 1826). After examining specimens of the *C. boscii* species-complex from East Africa, the Malay Peninsula, Indonesia, New Caledonia, Papua New Guinea, the Philippines, Taiwan, and the Ryukyus, we now consider both *C. crassimanus* and *C. orientale* to be valid species, and *C. lisae* (Poupin & Bouchard, 2010) is found to be a synonym of *C. crassimanus*, based on the morphology of the carapace, male cheliped and male first gonopod, supported by molecular evidence from mitochondrial cytochrome oxidase subunit I (COI) sequences. Both *C. orientale* and *C. crassimanus* are found sympatrically in Taiwan (including Penghu), and possibly in the Ryukyus and New Caledonia. While *C. boscii* is endemic to the Red Sea, the distribution of *C. sinuspersici* is limited to the western Indian Ocean (East Africa and the Persian Gulf).

Key words: Chaenostoma orientale, C. crassimanus, C. lisae, C. boscii, C. sinuspersici, *morphology, taxonomy, cytochrome oxidase subunit I*

■ Introduction

Chaenostoma Stimpson, 1858, is a genus of small-sized (carapace width below 15 mm) macrophthalmid crabs that inhabit tropical and subtropical rocky shores (Litulo, 2005; Davie, 2012). This genus for many years was considered to include only two species, *C. boscii* (Audouin, 1826) and *C. punctulatus* (Miers, 1884), but in recent years three new species have been added, viz., *C. lisae* (Poupin & Bouchard, 2010), *C. sinuspersici* (Naderloo & Türkay, 2011), and *C. java* Naderloo, 2013. Most recently, Shih *et al*. (2015), using morphological characters, reinstated two species previously considered junior synonyms of *C. boscii*, *C. orientale* Stimpson, 1858 and *C. crassimanus* Stimpson, 1858, and further suggested that *C. lisae* may be a synonym of *C. crassimanus*. As a result, the *Chaenostoma boscii* species-complex, used by Ng *et al.* (2008) and Naderloo & Türkay (2011) for the taxonomic complexity of this group previously identified as *C. boscii*, includes *C. boscii*, *C. crassimanus*, *C. java*, *C. lisae*, *C. orientale* and *C. sinuspersici*.

Chaenostoma was originally established for *C. orientale* Stimpson, 1858, and *C. crassimanus* Stimpson, 1858, both from "Loo Choo" (= Ryukyu Islands or the Ryukyus) (Stimpson, 1858, 1907). Stimpson (1907) also considered Dana's (1852) record of "*Cleistostoma boscii*" from Fiji as *C. orientale*, while *Macrophthalmus boscii* Audouin, 1826 was treated within another genus *Euplax* H. Milne Edwards, 1852. Several authors (Milne-Edwards, 1873; Ortmann, 1894; Stebbing, 1910; Tesch, 1918) suggested that any morphological differences between *C. orientale*, *C. crassimanus* and *Euplax boscii* could simply be attributed to intraspecif-

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ic variation, and thus that all three species were synonymous. Thus, it followed that Stimpson's *Chaenostoma* had to be treated as a synonym of *Euplax*. Kemp (1919) stated he could find no clear difference between *Euplax* and *Macrophthalmus* sensu lato, and assigned *E. boscii* into *Macrophthalmus*, and this was followed by later authors until recently. Barnes (1967), as a part of his broader review studies of the genus, erected a subgenus *Macrophthalmus* (*Mopsocarcinus*) to include *C. boscii* and *C. punctulatus*. Later *Chaenostoma* was reinstated to replace *Mopsocarcinus*, because the latter is considered as a subjective junior synonym (Ng *et al*., 2001, 2008; Mendoza & Ng, 2007; Barnes, 2010). Recently, Davie (2012) revised the Australian macrophthalmids and treated *Chaenostoma* as a full genus. *Euplax* was later synonymized under *Macrophthalmus* (*Venitus*) Barnes, 1967, by Barnes (1977), but is also now regarded as a good subgenus by Mendoza & Ng (2007), or indeed possibly a good genus (see Kitaura *et al*., 2010; McLay *et al*., 2010). Nevertheless, its type species *Euplax leptophthalmus* H. Milne Edwards, 1852, is clearly generically unrelated to the species of *Chaenostoma* treated here.

Chaenostoma boscii has long been considered to be widely distributed in the Indo-West Pacific (see Ng *et al*., 2008), however a recent study has shown that *C. boscii* is limited to its type locality, the Red Sea (Naderloo & Türkay, 2011). Naderloo & Türkay (2011) initially considered their new species *C. sinuspersici* (type locality: the Persian Gulf) to be widespread throughout the Indo-West Pacific, but Rahayu & Nugroho (2012) suggested the specimens from the West Pacific needed to be re-examined and their status reassessed. Two additional species within this complex have now been described, viz. *C. lisae* (type locality: Mayotte), and *C. java* (type locality: Java).

Recently, the authors examined a series of specimens of this species-complex from numerous localities across the Indo-West Pacific, including the Red Sea, East Africa, the Malay Peninsula, Indonesia, New Caledonia, Papua New Guinea, the Philippines, Taiwan, and the Ryukyus. Among them, two species agreed with the description of *C. orientale* and *C. crassimanus*, and therefore these species are here again recognized as distinct species (Stimpson, 1858, 1907; Shih *et al*., 2015). In addition, specimens of *C. boscii*, *C. sinuspersici* and *C. lisae* were also examined and this has enabled us for the first time to compare the morphology of all these nominal species, and to consider further molecular evidence from mitochondrial cytochrome oxidase subunit I (COI) sequences.

Materials and Methods

Specimens examined were from the Red Sea (Egypt and Saudi Arabia), East Africa (Madagascar, Mayotte, Kenya and Djibouti), Malay Peninsula (Tioman), Indonesia (Bali), New Caledonia, Papua New Guinea, the Philippines (Bohol), Taiwan (including Penghu), and the Ryukyus. These specimens are deposited in the following institutions: Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL); Institute of Zoology, Academia Sinica, Taipei, Taiwan (ASIZ); Coastal Ecology laboratory, Biodiversity Research Center, Academia Sinica, Taipei, Taiwan (CEL); Museum National d'Histoire Naturelle, Paris, France (MNHN); National Museum of Marine Biology and Aquarium (NMMB); Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University, Keelung, Taiwan (NTOU); Senckenberg Museum, Frankfurt am Main, Germany (SMF), and Lee Kong Chian Natural History Museum (formerly Raffles Museum of Biodiversity Research), National University of Singapore, Singapore (ZRC) (Table 1; Appendix 1). Specimens were illustrated with the help of a drawing tube attached to a stereomicroscope. G1 is an abbreviation for the male first gono-

Table 1. The haplotypes of COI gene of the *Chaenostoma boscii* species-complex from the Indo-West Pacific, and the outgroups, used in this study. Abbreviations of museums or universities see Materials and Methods.

Species	Locality	Catalogue no.	Haplotype of COI	Access. no. of COI
C. crassimanus	Ryukyus, Japan: Okinawa	CEL-Oki-124	Cc1	LC155114
	Taiwan: Siaoliuciou, Pingtung	NCHUZOOL 13958	Cc1	LC155114
	Taiwan: Houwan, Pingtung	NCHUZOOL 13959	Cc4	LC155115
	Taiwan: Yingueibi, Pingtung	NCHUZOOL 13960	Cc1	LC155114
	Taiwan: Daguang, Pingtung	NCHUZOOL 13965	Cc2	LC155116
	Taiwan: Daguang, Pingtung	NCHUZOOL 13966	Cc1	LC155114
	Taiwan: Mudan, Pingtung	NCHUZOOL 13967	Cc1	LC155114
	Taiwan: Mudan, Pingtung	NCHUZOOL 13968	Cc3	LC155117
	Taiwan: Lyudao, Taitung	NTOU 20100528b	Cc1	LC155114
	Taiwan: Fengguei, Penghu	NCHUZOOL 13972	Cc1	LC155114
	Taiwan: Fengguei, Penghu	NCHUZOOL 13972	Cc5	LC155118
	Taiwan: Wang-an, Penghu	NTOU 19900903	Cc6	LC155119
	New Caledonia: Noumea	MNHN-IU-2013-9292	Cc1	LC155114
	New Caledonia	MNHN-IU-2009-2591	Cc5	LC155118
	Mayotte (id. as *C. lisae*)	MNHN-IU-2009-993	Cc7	LC155120
	Mayotte (id. as *C. lisae*)	MNHN-IU-2009-993	Cc8	LC155121
C. orientale	Taiwan: Mao-ao, New Taipei City	NTOU 20070208	Co1	LC155122
	Taiwan: Hemei, New Taipei City	NTOU 20070421	Co2	LC155123
	Taiwan: Daguan, Pingtung	NCHUZOOL 13973	Co3	LC155124
	Taiwan: Fengguei, Penghu	NCHUZOOL 13975	Co4	LC155125
	Taiwan: Siyu, Penghu	NCHUZOOL 13982	Co5	LC097137
	Taiwan: Siyu, Penghu	NCHUZOOL 13980	Co6	LC155126
	Malaysia: Para Beach, Tioman	NCHUZOOL 13986	Co2	LC155123
	Indonesia: Nusa Dua, Bali	NCHUZOOL 13987	Co3	LC155124
	New Caledonia: Noumea	MNHN-IU-2013-9291	Co7	LC155127
C. sinuspersici	Iran: Gulf of Oman	NCHUZOOL 13988	Cs1	LC155128
	Mayotte	MNHN-IU-2009-992	Cs2	LC155129
C. boscii	Saudi Arabia: Farasan Islands	NCHUZOOL 13989	Cb1	LC155130
outgroups				
Macrophthalmus banzai	Taiwan: Fangyuan, Changhua	NCHUZOOL 14807		LC155131
Macrophthalmus purpureocheir	Taiwan: Kenting, Pingtung	NMMB CDA890		LC097132

pod. Measurements, in millimeters (mm), are of the carapace width (CW).

Except *Chaenostoma java*, specimens of other species of the *C. boscii* species-complex were used in molecular study (Table 1). Genomic DNA was isolated from the muscle tissue of legs by using the GeneMark tissue and cell genomic DNA purification kit (Taichung, Taiwan). A portion of the COI gene was amplified with PCR using the primers LCO1490 (5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′), HCO2198 (5′-TAAACTTCAGGGTGACCAAAAAATCA-3′) (Folmer *et al*., 1994), and COH6 (5′-TAD ACT TCD GGR TGD CCA AAR AAY CA-3′) (Schubart & Huber, 2006). The PCR conditions for the above primers were denaturation for 50 s at 94°C, annealing for 70 s at 45–47°C, and extension for 60 s at 72°C (40 cycles), followed by extension for 10 min at 72°C. Sequences were obtained by automated sequencing (Applied Biosystems 3730) and were aligned manually, after verification with the complementary strand. *Macrophthalmus banzai* Wada & Sakai, 1989 and *M. purpureocheir* Teng & Shih, 2015 were used as outgroups. Sequences of the different haplotypes were deposited in the DNA Data Bank of Japan (DDBJ), and the accession numbers are given in Table 1. Maximum likelihood (ML) analysis was conducted in RAxML (v. 7.2.6, Stamatakis, 2006), with the model GTR + G (*i.e.* GTRGAMMA) and 100 runs, and found the best ML tree by comparing the likelihood scores. The robustness of the ML tree was evaluated by 1000 bootstrap pseudoreplicates under the model GTRGAMMA. The Kimura (1980) 2-parameter distance (K2P distance) between haplotypes was calculated by the software MEGA 5 (Tamura *et al*., 2011).

Results

Morphological comparison

The five species of the *Chaenostoma boscii* species-complex can be distinguished by a suite of morphological characters (Table 2; Fig. 1). The most reliable features include the direction of the first anterolateral tooth (= external orbital tooth), the depth and shape of the incision between the anterolateral teeth, the shape of the dactylar tooth of the cheliped and presence and extent of a setal patch in the cheliped gape, and the shape of the G1 (Table 2).

The specimens from Mayotte and Madagascar deposited in MNHN and identified as *C. lisae* (Table 1; Appendix 1) were also compared, but no significant morphological difference could be found to separate *C. lisae* from *C. crassimanus* (Table 2; Fig. 1). The morphology of *C. crassimanus* is very different from other members of the species-complex, especially by the shape of the chelipeds, and the position and shape of large tooth on the dactylus of the male cheliped (see Table 2; Fig. 1).

Chaenostoma orientale, *C. boscii* and *C. sinuspersici* are similar in their slender chela morphology (palm length to fixed finger ratio of 1.5–2.0), but can be distinguished by the position and shape of the first and second anterolateral teeth, and their G1 morphology (Table 2; Fig. 1).

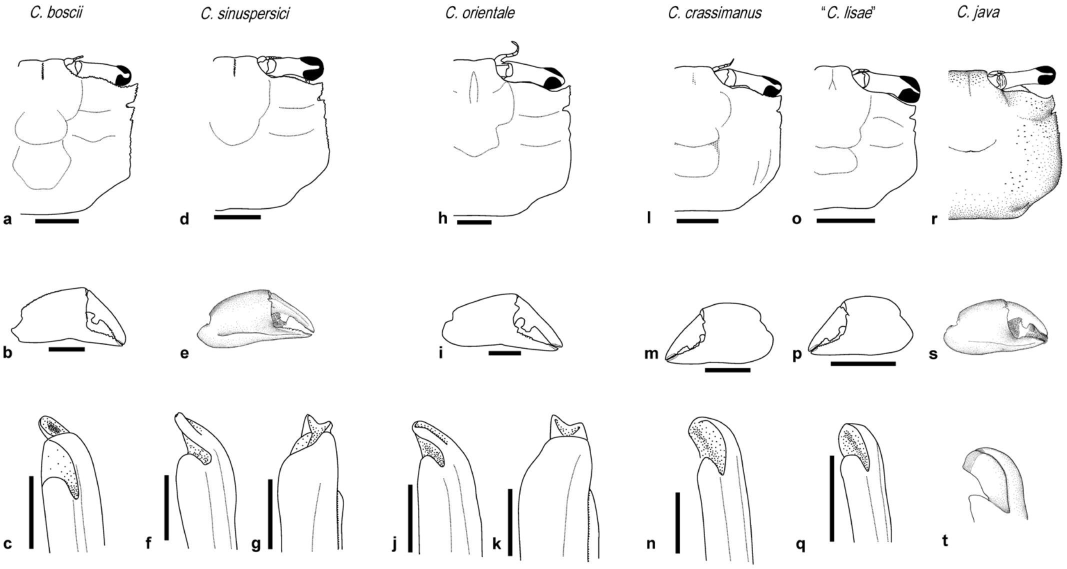

Fig. 1. a–c: *Chaenostoma boscii* (Audouin, 1826), ♂ (NCHUZOOL 13989), CW 8.8 mm. d–g: *C. sinuspersici* (Naderloo & Türkay, 2011), d, f, g: ♂ (NCHUZOOL 13988), CW 7.5 mm; e: after Naderloo & Türkay (2011). h–k: *C. orientale* Stimpson, 1858, ♂ (NCHUZOOL 13981), 12.3 mm. l–n: *C. crassimanus* Stimpson, 1858, ♂ (NCHUZOOL 13968), CW 8.0 mm. o–q: "*C. lisae*" (= *C. crassimanus*), ♂ (MNHN-IU-2009-2591), CW 6.1 mm. r–t: *C. java* Naderloo, 2013, after Naderloo (2013). a, d, h, l, o, r: carapace; b, e, i, s: right cheliped; m, p: left cheliped; c, f, j, n, q, t: ventral view of G1; g, k: mesial view of G1. Scale bars = 2 mm (a, b, d, h, i, l, m, o, p) and 0.5 mm (c, f, g, j, k, n, q).

Table 2. Morphological comparison among five species of the *Chaenostoma boscii* species-complex.

		C. boscii	*C. sinuspersici*	*C. orientale*	*C. crassimanus*	*C. java*
carapace	1st anterolateral tooth	protruding anteriorly	protruding anteriorly	protruding anteriorly	protruding laterally	protruding anteriorly
	incision between 1st and 2nd teeth	deep	deep	deep	shallow	shallow
	extent of lateral protrusion of anterolateral teeth	1st tooth extending far beyond 2nd tooth	tips of both teeth having same extent	1st tooth extending slightly beyond 2nd tooth	tips of both teeth having same extent	2nd tooth extending slightly beyond 1st tooth
	posterolateral margin	slightly converging posteriorly	straight, with the same position of margins of anterolateral teeth	straight, less than the margins of anterolateral teeth	straight, with the same position of margins of anterolateral teeth	diverging posteriorly
	frontal margin	concave	concave	concave	convex	concave
third maxilliped	length ratio of ischium: merus	1.5	1.3	1.4–1.5	1.2–1.3	2.0
cheliped	large tooth on cutting margin of dactylus	subquadrate, proximal	subquadrate, proximal	subquadrate, proximal	low wide rectangular, middle	subquadrate, middle
	shape of palm	slender	slender	slender	globular	globular
	extent of setal patch on inner face of palm	both palm and fingers	both palm and fingers	both palm and fingers	only palm	both palm and fingers
	stridulating ridge on inner merus	absent	present	present	absent	absent
G1	apical part	plate-shaped, quadrate	mesial surface of apical part deeply depressed, from the top of apical part to chitinous process	mesial surface of apical part deeply depressed, only on chitinous process	apical chitinous process short, with distal margin slightly rounded	lateral surface of apical process distinctly depressed, concave on apical surface

DNA analyses

A 658-bp segment of COI from 17 specimens of *C. crassimanus* (including specimens identified as "*C. lisae*"), 11 specimens of *C. orientale*, 2 specimens of *C. sinuspersici* and 1 specimen of *C. boscii* was amplified, resulting in 8, 7, 2 and 1 different haplotypes, respectively (Table 1). According to the phylogenetic tree constructed by COI (Fig. 2), the haplotypes of *C. orientale*, *C. sinuspersici* and *C. boscii* form a clade, and the haplotypes of *C. crassimanus* form another clade, but the support value for the relationship between the two clades is weak (66%). The nucleotide divergences with the K2P distance within and between species are shown in Table 3. With regard to *C. crassimanus*, although the intraspecific nucleotide divergence is relatively large (≤0.92%), there are no natural subgroupings (Fig. 2) that might suggest more than one species, and otherwise,

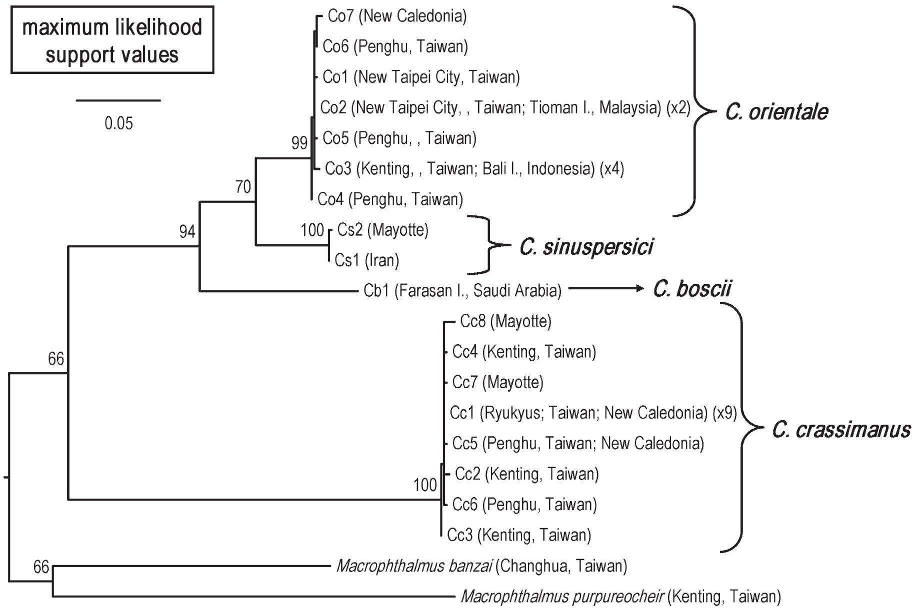

Fig. 2. A maximum likelihood tree of four species of the *Chaenostoma boscii* species-complex, based on the cytochrome oxidase subunit I (COI) gene. See Table 1 for details of the specimens. Probability values at the nodes represent support values for maximum likelihood.

Table 3. Matrix of percentage pairwise nucleotide divergences with K2P distance (lower left) and mean number of differences (upper right) based on 658 bp of COI within and between species of the *Chaenostoma boscii* species-complex. Values of range are shown in parentheses.

	Intraspecific		Interspecific			
	Nucleotide divergence	Mean nucleotide difference	*C. crassimanus*	*C. orientale*	*C. sinuspersici*	*C. boscii*
C. crassimanus	0.21	1.4	—	108.65	111.97	109.07
(incl. "*C. lisae*")	(0–0.92)	(0–6)		(104–112)	(110–116)	(108–110)
C. orientale	0.34	2.25	18.85	—	41.05	71.64
	(0–0.76)	(0–5)	(17.91–19.54)		(38–43)	(70–73)
C. sinuspersici	0.15	1	19.52	6.58	—	75.5
			(19.12–20.38)	(6.06–6.91)		(75–76)
C. boscii	—	—	18.93	12.07	12.79	—
			(18.71–19.12)	(11.76–12.31)	(12.7–12.89)	

the smallest interspecific divergence values within this species-complex are at least 6.06% (Table 3). The largest interspecific divergences occur between *C. crassimanus* and either *C. orientale* or *C. sinuspersici* (≥17.91% and ≥19.12% respectively) (Table 3), but while *C. crassimanus* forms a separate monotypic clade (reflected in morphology: Table 2; Fig. 1), the genetic support value between the two clades is weak (Fig. 2).

Discussion

The synonymy of *C. lisae* under *C. crassimanus* was suggested in Shih *et al*. (2015), and this study supports that action (Table 2; Fig. 1). Although most of the East African specimens tend to be smaller, the largest female reported has a CW of 9.1 mm (Poupin & Bouchard, 2010: 62), which is similar in size to the largest specimens of *C. crassimanus* that we examined from the West Pacific (see Appendix 1). Molecular evidence (Table 3; Fig. 2) also supports *C. lisae* as a junior synonym of *C. crassimanus* (see below).

The smallest interspecific COI divergence value between species in this complex (≥6.06%) (Table 3), is larger than that between other closely related intertidal crab species, *e.g.* 2.49% between *Uca splendida* (Stimpson, 1858) and *U. crassipes* (White, 1847) (Shih *et al.*, 2012); 3.62% between *Mictyris guinotae* Davie, Shih & Chan, 2010 and *M. brevidactylus* Stimpson, 1858 (Davie *et al.*, 2010); 4.1% for the *Sesarma reticulatum* (Say, 1817) group (Schubart *et al.*, 1998); 4.43% between *Scopimera ryukyuensis* Wong, Chan & Shih, 2010 and *S. globosa* De Haan, 1835 (Wong *et al.*, 2010); 4.74% between *Helice tridens* (De Haan, 1835) and the *H. latimera* Parisi, 1918 clade (Shih & Suzuki, 2008); and 4.77% between *Uca jocelynae* Shih, Naruse & Ng, 2010 and *U. neocultrimana* (Bott, 1973) (Shih *et al.*, 2010). Thus the degree of COI divergence convincingly supports the recognition of *C. crassimanus*, *C. orientale*, *C. sinuspersici* and *C. boscii* as different species, but does not support *C. lisae* as separate from *C. crassimanus*.

Chaenostoma crassimanus and *C. orientale* are sympatric in some areas (see below), and similar in coloration (Shih *et al.*, 2015), but can be easily separated using the morphological characters listed in Table 2 and Fig. 1. As previously mentioned, there is a deep phylogenetic split from the other species in the complex (Table 3; Fig. 2).

Chaenostoma java is close to *C. boscii*, *C. orientale*, and *C. sinuspersici* in the subquadrate and protruding tooth on the cutting edge of movable finger of male cheliped, and in the form of the first anterolateral tooth, but the male chela of *C. java* is not as slender as that of the above species (Table 2; Fig. 1r–t; Naderloo, 2013: fig. 1).

Stimpson (1907) considered Dana's specimen from Fiji to be *C. orientale*, based on the morphology of its third maxillipeds. The chela and carapace shown in Dana's (1852) figures (pl. 19(3)) also suggest the Fijian specimen is close to *C. orientale*, however the margins of the sixth somite of the male abdomen of our specimens of *C. orientale* are more swollen centrally compared to Dana's specimen which appears to have straight lateral margins. The identity of Fijian specimens therefore still needs to be fully confirmed.

Barnes (1967) identified specimens from Australia (Queensland), New Caledonia, New Guinea and Solomon Islands (Santa Cruz Islands) as "*M. boscii*". The slender chelipeds of his samples would suggest they may be *C. orientale*, but the figures of the G1 and the male abdomen (Barnes, 1967: fig. 9) appear to differ from that species. Unfortunately, Barnes (1967) did not indicate the provenance of the specimen that he figured (Queensland is presumed but not certain), or for that matter, in what museum most of the specimens he examined are housed. It is possible that several species within the *C. boscii* species-complex (as presently conceived) were represented in the samples he examined. Davie (2012) similarly recorded *C. boscii* from numerous Queensland localities, apparently overlooking the review paper by Naderloo & Türkay (2011) which described *C. sinuspersici* as the widespread species that occurred in Australia. Davie (2012) did not describe his specimens in detail, and did not figure the G1, so it is difficult to be sure of the identity of the Queensland species. The shape of the carapace margins and anterolateral teeth (Davie, 2012: fig. 38a, b) appear most similar to *C. orientale*, however the broad quadrangular palm of the male chela, and the shape of the basal tooth of the dactylus (Davie, 2012: fig. 38c; P. J. F. Davie, personal communication) are more like *C. sinuspersici*. The specimens examined by both Barnes (1967) and Davie

(2012), particularly those from Australia, will need to be re-examined before their identity can be confirmed.

Two records of "*Macrophthalmus boscii*" from Japan were most likely based on misidentifications. Miyake (1983: 168) identified a female specimen form Ishigaki, the Ryukyus, as *Macrophthalmus boscii*, but based on the photograph (Miyake, 1983: pl. 56 (5)), it appears to have long eyestalks, a narrow front, and a clear second anterolateral tooth, and so is most probably a juvenile *M. convexus*. Takeda (1982) also recorded *Macrophthalmus boscii* from Japan, but the short eyestalks, the wide front, the shape of carapace, and the presence of only one anterolateral tooth (as shown by his unnumbered photograph on page 211) suggests it is more likely a varunid (either in *Thalassograpsus* or *Baruna*).

With regard to the distribution of the *C. boscii* species-complex group, *C. boscii* s. str. is limited to the Red Sea (Naderloo & Türkay, 2011); *C. sinuspersici* ranges from the Persian Gulf to East Africa (Naderloo & Türkay, 2011; this study); *C. crassimanus* is the most widely-distributed species, from East Africa to New Caledonia (Stimpson, 1858, 1907; Sakai, 1939; Chen, 1980; Poupin & Bouchard, 2010; Poupin *et al.*, 2012; Bouchard *et al.*, 2013; Shih *et al.*, 2015; this study); *C. orientale* also has wide distribution, between Phuket (Thailand) and Fiji, including Southeast Asia and East Asia (Stimpson, 1858, 1907; Dai *et al.*, 1986; Dai & Yang, 1991; Huang, 1992; Komai *et al.*, 1995; Juncker & Poupin, 2009; Rahayu & Nugroho, 2012; Shih *et al.*, 2015; this study); and *C. java* is so far only recorded from Java, Indonesia (Naderloo, 2013). There is still no study on the larval development of this group, however, the wide distribution of *C. crassimanus* is probably caused by longer larval development periods, as suggested for *Cyclograpsus integer* H. Milne Edwards, 1837 (Gore & Scotto, 1982).

Some species in the *C. boscii* species-complex occur sympatrically, *e.g.*, *C. orientale* and *C. crassimanus* in southern Taiwan and Penghu, as well as possibly in the Ryukyus and New Caledonia; and *C. sinuspersici* and *C. crassimanus* in Mayotte and Madagascar (this study; Stimpson, 1858, 1907; Naderloo & Türkay, 2011; Naderloo, 2013). However, it seems that *C. orientale* and *C. crassimanus* prefer different microhabitats. In Taiwan *C. orientale* prefers to hide under large stones with sandy sediment, while *C. crassimanus* likes to form burrows under reef rock into coarse sandy sediments in seagrass areas (SJT, personal observation). In southern Taiwan, *C. orientale* and *C. crassimanus* are also sympatric with *Macrophthalmus purpureocheir* (Shih *et al.*, 2015; Teng & Shih, 2015).

Although previous studies have suggested that *C. sinuspersici* is widely distributed in the Indo-West Pacific, our study shows that *C. sinuspersici* is limited to East Africa and the Persian Gulf. In contrast, both *C. orientale* and *C. crassimanus* are reinstated as distinct species on the strength of morphological and molecular evidence, with *C. lisae* being treated as a synonym of *C. crassimanus*. While *C. crassimanus* is widely distributed in Indo-West Pacific (reflected in the larger intraspecific COI variation), *C. orientale* is limited to the eastern Indian Ocean and the West Pacific.

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Literature Cited

Barnes, R. S. K., 1967. The Macrophthalminae of Australasia; with a review of the evolution and morphological diversity of the type genus *Macrophthalmus* (Crustacea: Brachyura). Transactions of the Zoological Society of London, 31: 195–161.

Barnes, R. S. K., 1977. Concluding contribution towards a revision, and a key to, the genus *Macrophthalmus* (Crustacea: Brachyura). Journal of Zoology, London, 182: 267–280.

Barnes, R. S. K., 2010. A review of the sentinel and allied crabs (Crustacea: Brachyura: Macrophthalmidae), with particular reference to the genus *Macrophthalmus*. Raffles Bulletin of Zoology, 58: 31–49.

Bouchard, J. M., Poupin, J., Cleva, R., Dumas, J., & Dinhut, V., 2013. Land, mangrove and freshwater decapod crustaceans of Mayotte region (Crustacea Decapoda). Atoll Research Bulletin, 592: 1–60.

Chen, H.-L., 1980. Studies on the crabs of the Xisha Islands, Guangdong Province, China. II. Studia Marina Sinica, 17: 117–147, pls. I–IV. (In Chinese)

Dai, A.-Y., & Yang, S.-L., 1991. Crabs of the China Seas. 21 + 608 pp., 74 pls. China Ocean Press, Beijing and Springer-Verlag, Berlin.

Dai, A.-Y., Yang, S.-L., Song, Y.-Z., & Chen, G.-X., 1986. Crabs of the China Seas. 17 + 568 pp., 74 pls. China Ocean Press, Beijing. (In Chinese)

Dana J. D., 1852. Crustacea. In: United States Exploring Expedition during the Years 1838, 1839, 1840, 1841, 1842. Under the Command of Charles Wilkes, U.S.N., 13(2): i–viii, 1–685.

Davie, P. J. F., 2012. A review of *Macrophthalmus* sensu lato (Crustacea: Decapoda: Macrophthalmidae) from Australia, including two new species and new records. Memoirs of the Queensland Museum, 56: 149–219.

Davie, P. J. F., Shih, H.-T., & Chan, B. K. K., 2010. A new species of *Mictyris* (Decapoda, Brachyura, Mictyridae) from the Ryukyu Islands, Japan. Crustaceana Monographs, 11: 83–105.

Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek, 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.

Gore, R. H., & Scotto, L. E., 1982. *Cyclograpsus integer* H. Milne Edwards, 1837 (Brachyura, Grapsidae): the complete larval development in the laboratory, with notes on larvae of the genus *Cyclograpsus*. Fishery Bulletin, 80: 501–521.

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.

Juncker, M., & Poupin, J., 2009. Crustacés de Nouvelle-Calédonie. Illustration des espèces communes et liste documentée des espèces terrestres et des récifs. 77 pp., 33 pls. Rapport Scientifique du CRISP, Nouméa Cedex, Nouvelle-Calédonie.

Kemp, S., 1919. Notes on Crustacea Decapoda in the Indian Museum. xiii. The Indian species of *Macrophthalmus*. Records of the Indian Museum, 16: 383–394.

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.

Kitaura, J., Wada, K., Fukui, Y. & McLay, C. L., 2010. Molecular phylogenetic position of the New Zealand sentinel crab, *Macrophthalmus* (*Hemiplax*) *hirtipes* (Jacquinot, in

Hombron & Jacquinot, 1846) (Decapoda, Brachyura, Macrophthalmidae). Crustaceana, 83: 1315–1326.

Komai, T., Goshima, S., & Murai, M., 1995. Crabs of the genus *Macrophthalmus* of Phuket, Thailand (Crustacea: Decapoda: Ocypodidae). Bulletin of Marine Science, 56: 103–149.

Litulo, C., 2005. Life history of the crab, *Macrophthalmus boscii* (Audouin, 1826) (Decapoda, Brachyura, Ocypodidae). Crustaceana, 78: 665–676.

McLay, C. L., Kitaura, J., & Wada, K., 2010. Behavioural and molecular evidence for the systematic position of *Macrophthalmus* (*Hemiplax*) *hirtipes* Hombron & Jacquinot, 1846, with comments on macrophthalmine subgenera (Decapoda, Brachyura, Macrophthalmidae). Studies on Malacostraca: Lipke Bijdeley Holthuis Memorial Volume. In: Fransen, C. H. J. M., De Grave, S. & Ng, P. K. L., (eds.). Crustaceana Monographs, 14: 483–503.

Mendoza, J. C. E., & Ng, P. K. L., 2007. *Macrophthalmus* (*Euplax*) H. Milne Edwards, 1852, a valid subgenus of ocypodoid crab (Decapoda: Brachyura: Macrophthalmidae), with description of a new species from the Philippines. Journal of Crustacean Biology, 27: 670–680.

Milne-Edwards, A., 1873. Recherches sur la faune carcinologique de la Nouvelle-Calédonie, II. Nouvelles Archives du Muséum d'Histoire Naturelle, 9: 155–332.

Miyake, S., 1983. Japanese Crustacean Decapods and Stomatopods in Color. vol. II: Brachyura (Crabs). 8 + 277 pp., 64 pls. Hoikusha Publishing Co., LTD., Osaka, Japan. (In Japanese)

Naderloo, R., 2013. The sentinel crabs of the genus *Chaenostoma* (Stimpson, 1858) (Crustacea: Brachyura: Macrophthalmidae), with description of a new species and new records. Journal of Natural History, 47: 2835–2848.

Naderloo, R., & Türkay, M., 2011. A new species of the *Macrophthalmus boscii*-group (Decapoda: Brachyura: Macrophthalmidae) from the Persian Gulf with designation of a neotype for *M. boscii* Audouin (1826). Marine Biodiversity, 41: 503–515.

Ng, P. K. L., Guinot, D., & Davie, P. J. F., 2008. Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. Raffles Bulletin of Zoology, Supplement, 17: 1–296.

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.

Ortmann, A. E., 1894. Crustaceen. In: Semon, R. (ed.), Zoologische Forschungsreisen in Australien und dem malayischen Archipel. Denkschriften der Medicinisch-Naturwissenschaftlichen Geselschaft zu Jena, Verlag von Gusta Fischer, Jena, Germany, 8: 3–80.

Poupin, J., & Bouchard, J. M., 2010. A new dwarf sentinel crab from Mayotte Island, western Indian Ocean (Decapoda: Brachyura: Macrophthalmidae). Zootaxa, 2501: 61–67.

Poupin, J., Zubia, M., Gravier-Bonnet, N., Chabanet, P., & Malay, M., 2012. Illustrated checklist of the Decapoda at Europa Island. Western Indian Ocean Journal of Marine Science, 11: 1–25.

Rahayu, D. L., & Nugroho, D. A., 2012. The Indonesian species of *Macrophthalmus* Desmarest, 1823, with the description of a new species (Crustacea: Decapoda: Brachyura: Macrophthalmidae). Zootaxa, 3158: 20–36.

Sakai, T., 1939. Studies on the Crabs of Japan. IV. Brachygnatha, Brachyrhyncha. vol. 3: 365–741.

Schubart, C. D., Diesel, R., & Hedges, S. B., 1998. Rapid evolution to terrestrial life in Jamaican crabs. Nature, 393: 363–365.

Schubart, C. D., & Huber, M. G. J., 2006. Genetic comparisons of German populations of the stone crayfish, *Austropotamobius torrentium* (Crustacea: Astacidae). Bulletin Français de la Pêche et de la Pisciculture, 380–381: 1019–1028.

Shih, H.-T., Chan, B. K. K., Teng, S.-J., & Wong, K. J. H., 2015. Crustacean Fauna of Taiwan: Brachyuran Crabs, Vol II—Ocypodoidea. 320 pp. National Chung Hsing University, Taichung, Taiwan.

Shih, H.-T., Naruse, T., & Ng, P. K. L., 2010. *Uca jocelynae* sp. nov., a new species of fiddler crab (Crustacea: Brachyura: Ocypodidae) from the western Pacific. Zootaxa, 2337: 47–62.

Shih, H.-T., Ng, P. K. L., Wong, K. J. H., & Chan, B. K. K., 2012. *Gelasimus splendidus* Stimpson, 1858 (Crustacea: Brachyura: Ocypodidae), a valid species of fiddler crab from the northern South China Sea and Taiwan Strait. Zootaxa, 3490: 30–47.

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.

Stamatakis, A., 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics, 22: 2688–2690.

Stebbing, R. T. R. R., 1910. General catalogue of South African Crustacea. (Part V of S. A. Crustacea, for the marine investigations in South Africa). Annals of the South African Museum, 6: 281–593.

Stimpson, W., 1858. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars V. Crustacea Ocypodoidea. Proceedings of the Academy of Natural Sciences of 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.

Takeda, M., 1982. Keys to the Japanese and Foreign Crustaceans Fully Illustrated in Colors. 58 + 284 pp. Hokuryukan Ltd., Tokyo. (In Japanese)

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., & Kumar, S., 2011. MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Molecular Biology and Evolution, 28: 2731–2739.

Teng, S.-J., & Shih, H.-T., 2015. A new species of *Macrophthalmus* Desmarest, 1823 (Crustacea: Decapoda: Brachyura: Macrophthalmidae) from Taiwan, with notes on four new records. Zootaxa, 4058: 451–470.

Tesch, J. J., 1918. The Decapoda Brachyura of the Siboga Expedition. I. Hymenosomidae, Retroplumidae, Ocypodidae, Grapsidae and Gecarcinidae. Siboga-Expeditie, 39(c): 1–148, pls. 1–6.

Wong, K. J., Chan, B. K. K., & Shih, H.-T. 2010. 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. Zootaxa, 2345: 43–59.

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Appendix 1. Specimens of the genus *Chaenostoma* examined.

Chaenostoma boscii. **Saudi Arabia**: 1 ♂ (8.8 mm), 1 ♀ (7.0 mm) (NCHUZOOL 13989), Farasan Islands. **Egypt**: 1 ♂ (not measured) (SMF 26292), Manteqad al-Bahr al Ahmar, coll. C. Rhode and N. Dressler, 6 Sep. 1994.

Chaenostoma sinuspersici. **Iran**: holotype ♂ (9.1 mm) (SMF 36904), Hormozgan, coll. R. Naderloo, 12 July 2006; 1 ♀ (not measured) (SMF 38349), Qeshm I., coll. R. Naderloo, 11 May 2008; 1 ♂ (7.5 mm), 1 ♀ (8.3 mm) (NCHUZOOL 13988), Gulf of Oman, Iran, coll. S. Ebrahimneged, 21 Jan. 2015. **Mayotte**: 1 ♀ (9.8 mm) (MNHN-IU-2009-992), coll. J. Dumas *et al.*, 1 Nov. 2009. **Djibouti**: 2 ♂♂, 2 ♀♀ (not measured) (SMF 24496), Ras Siyyan, coll. U. Zajonz and F. Krupp, 24 June 1996.

Chaenostoma crassimanus. **Ryukyus, Japan**: 1 ♂ (6.2 mm), CEL-Oki-124, Okinawa Island, 6 July 2009. **Taiwan**: 12 ♂♂ (2.3–5.6 mm), 10 ♀♀ (2.6–5.2 mm, incl. 6 ovig.), NCHUZOOL 13969, Wushihbi, Taitung, coll. S.-J. Teng *et al.*, 29 July 2014; 1 ♂ (3.7 mm), NCHUZOOL 13970, Chenggong, Taitung, coll. S.-J. Teng *et al.*, 28 June 2014; 9 ♂♂ (4.1–6.1 mm), 5 ♀♀ (4.2–5.7 mm), NCHUZOOL 13971, Shanyuan, Taitung, coll. S.-J. Teng *et al.*, 27 July 2014; 6 ♂♂ (3.9–7.1 mm), 8 ♀♀ (4.6–7.1 mm), NCHUZOOL 13967, Mudan, Pingtung, S.-J. Teng *et al.*, 25 June 2014; 1 ♂ (8.0 mm), 1 ♀ (7.3 mm), NCHUZOOL 13968, Mudan, Pingtung, S.-J. Teng *et al.*, 25 June 2014; 1 ♂ (3.4 mm), NTOU 19920110, Jioupeng, Pingtung, coll. J.-F. Huang, 10 June 1992; 1 ♀ (6.0 mm), ASIZ 70772, Jioupeng, Pingtung, coll. M.-S. Jeng, 10 Dec. 1996; 1 ♂ (3.0 mm), 1 ♀ (3.2 mm), NCHUZOOL 13962, Houwan, Pingtung, coll. S.-J. Teng *et al.*, 22 June 2014; 34 ♂♂ (3.2–5.6 mm), 24 ♀♀ (3.5–5.5 mm), NCHUZOOL 13959, Houwan, Pingtung, coll. S.-J. Teng *et al.*, 26 June 2014; 3 ♂♂, NCHUZOOL 13961, Houwan, Pingtung, coll. L.-G. Tseng, 9 Mar. 2014; 5 ♂♂ (3.5–4.9 mm), 3 ♀♀ (4.2–4.7 mm, incl. 1 ovig.), NCHUZOOL 13963, Wanlitong, Pingtung, coll. L.-G. Tseng, 29 Apr. 2014; 3 ♀♀ (5.1–5.5 mm, incl. 2 ovig.), NCHUZOOL 13964, Wanlitong, Pingtung, coll. L.-G. Tseng *et al.*, 16 May 2014; 1 ♂ (4.0 mm), 1 ♀ (4.8 mm), ASIZ 710017, Nanwan, Pingtung, coll. M.-S. Jeng, 5 Mar. 1997; 1 ♂ (5.8 mm), NCHUZOOL 13965, Daguang Pingtung; 29 ♂♂ (3.2–5.5 mm), 42 ♀♀ (3.1–6.5 mm), NCHUZOOL 13966, Daguang, Pingtung, coll. S.-J. Teng *et al.*, 24 June 2014; 22 ♂♂ (3.7–5.8 mm), 20 ♀♀ (4.4–6.7 mm, incl. 6 ovig.), NCHUZOOL 13960, Yingueibi, Pingtung, coll. Y.-H. Wang *et al.*, 24 June 2014; 4 ♂♂ (1.5–3.1 mm), NCHUZOOL 13958, Siaoliuciou, Pingtung, coll. J.-H. Lee *et al.*, 11 Nov. 2013; 1 ♂ (6.1 mm), NTOU 20100527, Lyudao, coll. C.-H. Yang, 27 May 2010; 10 ♀♀ (4.3–6.7 mm, incl. 2 ovig.), NTOU 20100528b, Lyudao, coll. H.-Y. Kuo, 28 May 2010; 4 ♂♂ (3.7–4.7 mm), 3 ♀♀ (3.6–6.1 mm), NTOU, Lyudao, coll. C.-H. Yang, 28 May 2010; 2 ♂♂ (5.0, 5.3 mm), 1 ♀ (5.7 mm), NCHUZOOL 13972, Fengguei, Penghu, coll. S.-J. Teng *et al.*, 1 Sep. 2014; 1 ♂ (4.6 mm), 3 ♀♀ (3.8–4.7 mm), NTOU 19900903, Wang-an, Penghu, coll. J.-F. Huang, 3 Sep. 1990. **Philippines**: 1 ♂ (5.3 mm), 1 ♀ (5.5 mm), ZRC M51, Panglao 2004 Expedition, Panglao, Bohol, Philippines, coll. T. Naruse, 2004. **New Caledonia**: 1 ♂ (4.9 mm), MNHN-IU-2013-9292, Noumea, coll. J. Poupin and M. Juncker, 5 Mar. 2009; 1 ♂ (6.1 mm), 1 ♀ (7.2 mm), MNHN-IU-2009-2591 (=MNHN B32603), coll. J. Poupin, 2009. **Mayotte**: 2 ♂♂ (3.8, 4.9 mm), MNHN-IU-2009-993, Bandrele, coll. J. Poupin and R. Cleva, 19 Nov. 2009. **Madagascar**: 2 ♂♂ (5.4, 5.7 mm), 2 ♀

♀ (3.8, 6.6 mm), MNHN-IU-2009-2590 (=MNHN B10717), coll. S. Crosnier, Feb. 1962.

***Chaenostoma orientale*.** **Taiwan**: 1 ♂ (7.1 mm), NTOU 19891019, Danhai, New Taipei City, coll. J.-F. Huang, 19 Oct. 1989; 1 ♂ (9.2 mm), NTOU 20070421, Hemei, New Taipei City, coll. I.-J. Chen *et al*., 21 Apr. 2007; 1 ♂ (9.8 mm), NTOU 20070801a, Hemei, New Taipei City, coll. J.-M. Chen, 1 Aug. 2007; 2 ♂♂ (5.6, 6.2 mm), NTOU 20070801b, Hemei, New Taipei City, coll. J.-M. Chen, 1 Aug. 2007; 1 ♂ (7.7 mm), NTOU 20070208, Mao-ao, New Taipei City, coll. C.-H. Yang, 8 Feb. 2007; 1 ♂ (6.8 mm), NCHUZOOL, Shanyuan, Taitung, coll. S.-J. Teng *et al*., 27 July 2014; 1 ♂ (4.6 mm), ASIZ 710017, Nanwan, Pingtung, coll. M.-S. Jeng, 5 Mar. 1997; 3 ♂♂ (4.8–6.8 mm), 4 ♀♀ (6.8–9.2 mm), NTOU 19900905, Jibei, Penghu, coll. J.-F. Huang, 5 Sep. 1990; 10 ♂♂ (4.5–6.9 mm), 3 ♀♀ (5.1–7.6 mm, incl. 2 ovig.), NCHUZOOL 13976, Citou, Penghu, coll. S.-J. Teng *et al*., 2 Sep. 2014; 1 ♂ (4.1 mm), 6 ♀♀ (4.0–7.3 mm), NCHUZOOL 13977, Watong, Penghu, coll. S.-J. Teng *et al*., 2 Sep. 2014; 13 ♂♂ (4.6–10.3 mm), 10 ♀♀ (3.9–11.0 mm, incl. 6 ovig.), NCHUZOOL 13979, Chihsi, Siyu, Penghu, coll. S.-J. Teng *et al*., 3 Sep. 2014; 1 ♂ (9.7 mm), NCHUZOOL 13980, Chihsi, Siyu, Penghu, coll. S.-J. Teng *et al*., 3 Sep. 2014; 2 ♂♂ (10.7, 12.3 mm), 1 ♀ (12.5 mm), NCHUZOOL 13981, Chihsi, Siyu, Penghu, coll. S.-J. Teng *et al*., 3 Sep. 2014; 1 ♀ (4.5 mm, juv.), NCHUZOOL 13978, Chihsi, Siyu, Penghu, coll. S.-J. Teng *et al*., 31 Aug. 2014; 8 ♂♂ (5.7–7.2 mm), 3 ♀♀ (5.9–6.8 mm, incl. 1 ovig.), NCHUZOOL 13983, Chihdong, Siyu, Penghu, coll. S.-J. Teng *et al*., 31 Aug. 2014; 1 ♀ (7.7 mm, ovig.), NCHUZOOL 13982, Chihdong, Siyu, Penghu, coll. H.-T. Shih, 18 Oct. 2008; 3 juv. ♂♂, NCHUZOOL 13984, Nei-an, Penghu, coll. S.-J. Teng *et al*., 3 Sep. 2014; 10 ♂♂ (3.7–5.2 mm), 4 ♀♀ (4.4–6.9 mm, incl. 1 ovig. 3 juv.), NCHUZOOL 13975, Fengguei, Penghu, coll. S.-J. Teng *et al*., 1 Sep. 2014; 2 ♂♂ (6.3, 8.7 mm), 2 ♀♀ (6.6, 10.4 mm), NTOU 19900902, Fengguei, Penghu, coll. J.-F. Huang, 2 Sep. 1990; 4 ♂♂ (6.1–7.5 mm), 3 ♀♀ (6.1–10.9 mm, incl. 2 ovig.), NCHUZOOL 13985, Magong, Penghu, coll. Y.-H. Wang *et al*., 30 Aug. 2014. **Indonesia**: 19 ♂♂ (2.5–10.5 mm), 12 ♀♀ (4.9–11.3 mm), NCHUZOOL 13987, Bali, coll. H.-T. Shih, 16 July 2014; 2 ♂♂ (not measured) (SMF 5439), Moluccas, Aru Islands, coll. H. Merton, 20 Feb. 1908. **Papua New Guinea**: 1 ♂, 1 ♀ (not measured) (SMF 38539), New Ireland, Ulul Plantation, coll. M. Türkay, 19 July 1998. **New Caledonia**: 1 ♂ (9.1 mm), MNHN-IU-2013-9291, Noumea, coll. J. Poupin and M. Juncker, 5 Mar. 2009. **Malaysia**: 9 ♂♂ (5.7–9.0 mm), 18 ♀♀ (5.1–10.4 mm), NCHUZOOL 13986, Tioman, coll. H.-T. Shih, 20 Aug. 2003.