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Resurrection of *Gelasimus variegatus* Heller, 1862, A Fiddler Crab Closely Related to *Austruca bengali* (Crane, 1975) and *A. triangularis* (A. Milne-Edwards, 1873) (Decapoda, Brachyura, Ocypodidae), from the Bay of Bengal, Indian Ocean

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The identity of the fiddler crab, *Gelasimus variegatus* Heller, 1862 (type locality: Madras, India), has long been uncertain. Examination of specimens from the Bay of Bengal shows that it is a valid species belonging to the genus *Austruca* Bott, 1973. *Austruca variegata* (Heller, 1862) can be separated from the closely related *A. bengali* (Crane, 1975) and *A. triangularis* (A. Milne-Edwards, 1873) by characters of the carapace, orbital floor, major and minor chelae, male first gonopod, vulva (female gonopore), gastric mill, and coloration in life. The three species are also supported by genetic data (nuclear 28S rDNA, mitochondrial 16S rDNA and cytochrome oxidase subunit I (*COI*)). Biogeographically, *A. variegata* is distributed in the Bay of Bengal and reaches to the Laccadive Sea; *A. bengali* is present in the Andaman Sea; and *A. triangularis* is widely distributed in the West Pacific.

Key words: Fiddler crab, *Austruca variegata*, *A. bengali*, *A. triangularis*, Morphology, Cytochrome oxidase subunit I, 16S rDNA, 28S rDNA.

BACKGROUND

The most recent revision of the systematics of the family Ocypodidae recognized a total of 11 genera and 105 species of fiddler crabs in two subfamilies (Shih et al. 2016 2018). With regard to *Austruca* Bott, 1973, 11 Indo-West Pacific species are now recognised, composed of three main clades: the *A. lactea*, *A. triangularis* and *A. sindensis* groups (Shih et al. 2016). In Crane's (1975) system, *Gelasimus triangularis* (A. Milne-Edwards, 1873) contains two subspecies that have since been treated as two species, *Austruca triangularis* (A. Milne-Edwards, 1873) and *A. bengali* (Crane, 1975), which also have genetic support (see Shih et al. 2016). Biogeographically, *A. triangularis* is widely distributed in the West Pacific while *A. bengali* occurs in the eastern Indian Ocean (Bay of Bengal and Andaman Sea) (Crane 1975). However, the distribution of *A. bengali* seems to be disjunct, with a westermost population isolated in the southeastern Indian subcontinent (Crane 1975:

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611, fig. 7), and populations apparently having a wider distribution in eastern and northeastern India, as well as Bangladesh (see Bairagi 1995; Rath and Dev Roy 2011; Hossain 2015; Akash and Chowdhury 2017).

One broad-fronted species, *Gelasimus variegatus* Heller, 1862, with the type locality of Madras (= Chennai, Tamil Nadu, southeastern India), has long been treated as a species with "systematic uncertainties" (Crane 1975: 326). Crane (1975: 326) suspected *G. variegatus* was the same as *Cranuca inversa* (Hoffmann, 1874) because Heller (1862: 521) described the species with a denticulate crest on the merus of major cheliped (see below). As a result, Ng et al. (2008: 240) listed *G. variegatus* as a doubtful synonym of *Uca inversa*. However, *C. inversa* occurs in eastern Africa and is not known to extend to eastern India, and as such, Crane (1975: 326) considered the possibility that Heller's label and locality data may be erroneous. *Gelasimus variegatus* was not included or even mentioned in the later publication of Heller (1865), probably because by then, he had decided it was synonymous with *Gelasimus perplexus* H. Milne Edwards, 1852. Heller (1865: 38) recorded "*Gelasimus perplexus* H. Milne Edwards, 1852" (Fig. 1a, b) and included Madras and Ceylon in the distribution. Based on the figure of the major chela of "*G. perplexus*" (cf. Fig. 1C; Heller 1865: pl. 5(4)) (not *Gelasimus perplexus* H. Milne Edwards, 1852 s. str.), Crane (1975: 291) identified it as *A. bengali* instead. In the short type diagnosis, however, Heller (1862) described *Gelasimus variegatus* as "*G. annularis* affinis, sed brachium chelipedum ad marginem superiorem carinatum et dentatum, index dactylo paulo brevior, acuminatus" [close to *G. annulipes*, merus of cheliped with higher carinate and dentate margin; dactylus of cheliped a little shorter, pointed], which agrees well with the structure of *Austruca bengali* or *A. triangularis* (cf. Huang et al. 1989: pl. 1A–D; Toyota and Seki 2014: 227; Shih et al. 2015: fig. 157), but apparently differ from the dorsal margin of major cheliped merus of *Cranuca inversa*, which has a crest without serration or only minutely serrate (Fig. 1d; cf. Crane 1975: pl. 16A; Bouchard et al. 2013: fig. 36B; Shih et al. 2016: fig. 9A). In addition, the description and figure of "*G. perplexus*" in Heller (1865: 38-39, pl. 5(4); Fig. 1C) also agree with the characters of major cheliped of *G. variegatus*, which support the idea that both are conspecific. It would appear that Heller (1862) had originally believed his material was a new species but decided in later work that it was just a synonym of *G. perplexus* H. Milne Edwards, 1852. We believe, however, that *Gelasimus variegatus* Heller, 1862, is a valid species in *Austruca*, with a similar morphology to *A. triangularis* and *A. bengali*.

On the basis of a series of specimens recently examined from West Bengal and Tamil Nadu, we found a species that agrees very well with the original description of *G. variegatus* by Heller (1862: 3), notably in the morphology of the merus and dactylus of the major cheliped. In addition, their morphology also agrees well with the description and figure of "*Gelasimus perplexus*" from Madras and Ceylon in Heller (1865: 38–39, fig. 5(4); Fig. 1C). The molecular evidence from the nuclear 28S rDNA and mitochondrial 16S rDNA and cytochrome oxidase subunit I (*COI*) supports the hypothesis that this species is in fact distinct but closely related to *A. triangularis* and *A. bengali*. We herein formally recognize *Gelasimus variegatus* Heller, 1862, as a valid species of *Austruca* Bott, 1973.

MATERIALS AND METHODS

Specimens of the *Austruca triangularis* complex obtained from various sources in the Bay of Bengal, Andaman Sea and West Pacific and deposited in the Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL); the Naturhistorisches Museum, Wien, Austria (NHMW); the Queensland Museum, Brisbane, Australia (QM); and the Zoological Reference Collection of the Lee Kong Chian Natural History Museum (formerly Raffles Museum of Biodiversity Research), National University of Singapore, Singapore (ZRC), were examined and illustrated with the help of a drawing tube attached to a stereomicroscope. Multiple photographic images of some structures were stacked using Helicon Focus 5.0. The abbreviation G1 is used for male first gonopod. Measurements, in millimeters (mm), are of the maximum carapace width (CW), carapace length (CL) and pollex length (PL). The terminology used essentially follows Crane (1975) and Davie et al. (2015).

The gastric mill of the stomach from the three species was studied following the methods and terminology in Shih (2015). Multiple photographic images of the mill under the stereo-microscope were stacked using Helicon Focus and the scanning electron microscopy (SEM), mainly following Shih et al. (1999).

Sequences of the nuclear 28S rDNA and the mitochondrial 16S rDNA and cytochrome oxidase subunit I (*COI*) were obtained following the method described by Shih et al. (2016), after verification with the complimentary strand. Sequences of the different haplotypes have been deposited in the DNA Data Bank of Japan (DDBJ) (accession numbers in Table 1). The sequences of other related species of the *A. triangularis* complex (see Shih et al. 2016), viz. *A. albimana* (Kossmann, 1877), *A. annulipes* (H. Milne Edwards,

1837), *A. iranica* (Pretzmann, 1971), *A. lactea* (De Haan, 1835), *A. occidentalis* (Naderloo, Schubart & Shih, 2016), *A. mjoebergi* (Rathbun, 1924), *A. perplexa* (H. Milne Edwards, 1852), and *A. sindensis* (Alcock, 1900), were used as outgroups in this paper.

For the combined 28S, 16S and *COI* dataset, the best-fitting models for sequence evolution of individual datasets were determined by jModelTest (vers. 2.1.4, Guindon and Gascuel 2003; Darriba et al. 2012), selected by the Bayesian information criterion (BIC). The best models obtained were HKY + I, HKY + I + G and TIM3 + I, and were subsequently applied to the partitioned Bayesian inference (BI) analysis. The BI analysis was performed with MrBayes (vers. 3.2.6, Ronquist et al. 2012). The search was run with 4 chains for 10 million generations and 4 independent runs, with trees sampled every 1000 generations. The convergence of chains was determined by the average standard deviation of split frequency values below the recommended 0.01 (Ronquist et al. 2005) and the first 100 trees were discarded as burnin. The relationships of the *COI* haplotypes among *A. variegata*, *A. bengali* and *A. triangularis* were examined using the program PopART (vers. 1.7, Leigh and Bryant 2015). Basepair (bp) differences and the pairwise estimates of Kimura 2-parameter (K2P) distance (Kimura 1980) for genetic diversities between haplotypes were also calculated by MEGA (vers. 10.0.5, Kumar et al. 2018).

RESULTS

TAXONOMY

Family Ocypodidae Rafinesque, 1815
Subfamily Gelasiminae Miers, 1886 (*sensu* Shih et al. 2016)
Genus *Austruca* Bott, 1973

Table 1. The haplotypes of 28S rRNA, 16S rRNA and *COI* genes of specimens of *Austruca* species used in this study. *: species of the *A. variegata* complex, with additional *COI* haplotypes used in table 3 and figure 13

Species	Locality	Catalogue no.	DDBJ Access. no. of 28S	DDBJ Access. no. of 16S	DDBJ Access. no. *COI*	haplotype of *COI*
A. albimana	Egypt: Nabq, Sinai	NCHUZOOL 13242	AB813689	AB471893	AB471906	
A. annulipes	Thailand: Phuket	NCHUZOOL 13258	AB813686	AB471894	AB491161	
*A. bengali**	Malaysia: Selangor	NCHUZOOL 13575	AB813695	AB813651	AB813672	Ab2
	Thailand: Phuket	QM W27320	-	-	LC465132	Ab1
	Thailand: Ranong	NCHUZOOL 13646	-	-	LC015064	Ab3
A. iranica	Iran: Gavbandi	NCHUZOOL 13245	AB813688	AB471896	AB471908	
A. lactea	Hong Kong	NCHUZOOL 13250	AB813693	AB471898	AB471912	
A. mjoebergi	Australia: Bedford I., West Australia	QM-W20253	AB813690	AB471900	AB471914	
A. occidentalis	southern Madagascar	ZRC THH04-30	AB813687	AB813648	AB813669	
A. perplexa	Taiwan: Dulanwan, Taitung	NTOU	AB813691	AB471901	AB471915	
	New Caledonia: Ouano Bay	NCHUZOOL 13573	AB813692	AB813649	AB813670	
	Wallis and Futuna:Pointe Utu	NCHUZOOL 14912	LC150460	LC150339	LC150400	
A. sindensis	Iran: Qeshm	NCHUZOOL 13576	AB813696	AB813652	AB813673	
*A. triangularis**	Taiwan: Baoli R. estuary	NCHUZOOL 13254	-	-	AB471916	At1
	Philippines: Cebu	NCHUZOOL 13574	AB813694	AB813650	AB813671	At2
	Philippines: Cebu	NCHUZOOL 13574	-	-	LC465133	At3
	Philippines: Mindanao	NCHUZOOL 14354	-	-	LC465134	At4
	Indonesia: Bali	NCHUZOOL 14347	-	-	LC465135	At5
	Australia: Queenslands	QM W19251	-	-	LC465136, LC465137	At6, At7
	New Caledonia: Pam	QM W29056	-	-	LC465138	At8
	New Caledonia: Dumbea Point	QM W29057	-	-	LC465139	At9
*A. variegata**	India: Tamil Nadu	ZRC 2001.0853	LC465129	LC465130	LC465131	Av5
	India: Tamil Nadu	ZRC 2001.0853	-	-	LC465140, LC465141, LC465142	Av8, Av1, Av3
	India: Tamil Nadu	NCHUZOOL 14366, 14364, ZRC 2018.1375 (neotype)	-	-	LC465143, LC465144, LC465145	Av6, Av7, Av9
	India: West Bengal	ZRC 2017.0917	-	-	LC465146, LC465146	Av2, Av4

Austruca variegata **(Heller, 1862)**

(Figs. 1a–c, 2, 3a–b, 4a–d, 5a–d, 6a–c, f, 7a, b, e, 8a–d, 9)

urn:lsid:zoobank.org:act:3E16AD8E-C907-4E0A-B14C-3026181664DC

Gelasimus variegatus Heller, 1862: 521 (type locality: Madras, India); Crane 1975: 326.

Gelasimus perplexus – Heller 1865: 38, pl. 5(4) (Madras, India; Ceylon); A. Milne-Edwards 1873: 274 (India). (not *Gelasimus perplexa* H. Milne Edwards, 1837)

Gelasimus triangularis – Henderson 1893: 388 (Madras and Ennore, India); Alcock 1900: 356 (Bay of Bengal). (not *Gelasimus triangularis* A. Milne-Edwards, 1873)

Uca triangularis – Nobili 1903: 20 (Pondicherry, India); Altevogt 1957: 3, 5, figs. 11, 23, 27 (southeastern India); Feest 1969: 159, figs. 6, 7, 9, 11, 13, 14, 16, 18, 19, 20, 22, 24, 26, 28, 29 (Pondicherry, India); Dev Roy and Bhadra 2005: 509, pl. 3(8) (Andhra Pradesh, India); Dev Roy and Nandi 2007: 181, 188 (Tamil Nadu, India); Dev Roy and Bhadra 2008: 155 (list); Rath and Dev Roy 2008: 77, pl. 5(5) (Krishna, India); Dev Roy and Bhadra 2011: 207 (Tamil Nadu, India); Rath and Dev Roy 2011: 60, pl. 4(2) (Orissa, India); Kappalli et al. 2012: 967 (Muzhapilangad estuary, North Kerala, India); Satheeshkumar 2012: 315 (Pondicherry, India); Fredrick and Ravichandran 2013: 442 (Tamil Nadu, India); Hossain 2015: 202 (part; 1 unnumbered fig. = *Metaplax* sp.) (Bangladesh); Sen and Homechaudhuri 2015: 82 (Sundarban, India); Supriya et al. 2017: 647 (Muzhapilangad estuary, North Kerala, India). (not *Gelasimus triangularis* A. Milne-Edwards, 1873)

Uca (*Celuca*) *triangularis bengali* Crane 1975: 286, figs. 24I, J, 32N, O, 59A, 68C, 101 (part); Krishnan 1992: 471, pl. 1; Bairagi 1995: 274 (West Bengal, India). (not *Uca* (*Celuca*) *triangularis bengali* Crane 1975)

Uca bengali – Rosenberg 2001: 860, 866 (part). (not *Uca* (*Celuca*) *triangularis bengali* Crane 1975)

Uca (*Paraleptuca*) *bengali* – Beinlich and von Hagen 2006: 26 (list), fig. 5i (part); Ng et al., 2008: 241 (list, part). (not *Uca* (*Celuca*) *triangularis bengali* Crane 1975)

Uca triangularius bengali [sic] – Ravichandran and Kannupandi 2007: 334 (Pichavaram, India). (not *Uca* (*Celuca*) *triangularis bengali* Crane 1975)

Uca triangularis bengali – Soundarapandian et al. 2008: 115 (Pichavaram, India); Chatterjee and Das 2014: 113, fig. 5 (West Bengal, India). (not *Uca* (*Celuca*) *triangularis bengali* Crane 1975)

Uca inversa – Satheeshkumar and Khan 2011: 315; Satheeshkumar 2012: 315 (Pondicherry, India). (not *Gelasimus inversa* Hoffmann, 1874)

?*Uca inversa* – Dev Roy and Nandi 2012: 218 (list) (Andaman and Nicobar, India).

Uca lactea – Talapatra et al. 2014: 908, fig. 4 (Odhissa, India). (not *Ocypode* (*Gelasimus*) *lactea* De Haan, 1835)

Austruca bengali – Shih et al. 2016: 153 (list, part); Trivedi et al. 2018: 54. (not *Uca* (*Celuca*) *triangularis bengali* Crane 1975)

?*Uca* (*Austruca*) *bengali* – Akash and Chowdhury 2017: 201, fig. 2 (?) (Bangladesh).

Austruca triangularis – Trivedi et al. 2018: 54 (part). (not *Gelasimus triangularis* A. Milne-Edwards, 1873)

Cranuca inversa – Trivedi et al. 2018: 54. (not *Gelasimus inversa* Hoffmann, 1874)

Material examined: Lectotype, ♂ (CW 16.7 mm, PL 24.7 mm) (NHMW 25656; original Novara label, #74 = AN. 1866.II.74.; labelled as "*Gelasimus perplexus* M. Edw."), Madras, India, coll. Johann Zelebor.

Others: 1 ♂ (17.2 mm) (NHMW 12974; no original label), Madras, India, coll. J. Zelebor. 5 ♂♂ (11.6–16.6 mm) (ZRC 2001.0853), Vellar River estuary, Parangipettai (= Porto Novo), Tamil Nadu, India, coll. N. N. Ng, 23 Mar. 2001; 1 ♂ (18.6 mm) (ZRC 2018.1375), 9 ♂♂ (9.8–17.3 mm) (NCHUZOOL 14362), 12 ♂♂ (8.8–17.8 mm) (NCHUZOOL 14363), Vellar River estuary, Parangipettai (= Porto Novo), Tamil Nadu, India, coll. M. Prema and S. Ravichandran, 6 Aug. 2017; 5 ♂♂ (12.0–17.1 mm), 1 ♀ (13.7 mm) (NCHUZOOL 14366), 1 ♀ (16.6 mm) (NCHUZOOL 14365), 6 ♂♂ (10.2–16.9 mm), 7 ♀♀ (9.7–15.4 mm) (NCHUZOOL 14367), Vellar River estuary, Parangipettai (= Porto Novo), Tamil Nadu, India, coll. M. Prema and S. Ravichandran, July–Aug. 2017; 2 ♂♂ (16.1–17.2 mm), 1 ♀ (14.5 mm) (ZRC 2003.0463), mangroves, Pitchavaram, Tamil Nodu, India, coll. N. Sivasothi and Chongsing, 12 Mar. 2000; 10 ♂♂ (14.5–18.4 mm) (ZRC 2017.0917), Danthadhpatrobar, Cantai, Midnapure, West Bengal, India, coll. Z. Jaafar, 25 Nov. 2004; 2 ♂♂ (18.5–18.9 mm) (ZRC 2017.0915), Kolkata aquarium trade, Mar. 2010.

Comparative material: *Austruca bengali*: Thailand: 1 ♂ (9.7 mm) (NCHUZOOL 13646), 1 ♀ (9.9 mm), 5 juv. (NCHUZOOL 14359), Bang Rin mangroves, Ranong, coll. H.-T. Shih, 27 May 2012; 2 ♂♂ (9.1–10.1 mm), 7 juv. (NCHUZOOL 14360), 3 ♂♂ (10.4–11.4 mm), 3 juv. (NCHUZOOL 14361), Tha Thiap Ruea Bang Rong, Phuket, coll. H.-T. Shih, 30 May 2012. Malaysia: 1 ♂ (8.0 mm) (NCHUZOOL 13575), 18 ♂♂ (10.4–14.5 mm), 8 ♀♀ (9.8–12.0 mm), 12 juv. (NCHUZOOL 14345), estuary of Sungai Sementa Besar, Kampung Perepat Kapar, Selangor, coll. H.-T. Shih, 10 Feb. 2009. *Austruca triangularis*: New Caledonia: 1 ♂ (10.4 mm), 2 ♀♀ (8.2–8.6 mm) (QM W29057), Dumbea Point, coll. P. Davie, 8 Feb. 1992; 2 ♂♂ (9.0–11.4 mm) (QM W29056), 1 ♀ (12.4 mm) (QM W29058), Pam, New Caledonia, coll. P. Davie, 10 Oct. 1992. Australia: 3 ♂♂ (9.8–12.1 mm), 1 ♀ (10.2 mm) (QM W19251), Thomatis Creek, Queensland, coll. P. Davie et al., 30 Oct. 1993. Indonesia: 2 ♂♂ (13.1–15.3 mm) (NCHUZOOL 14347), Badung, Kuta, Bali, coll. H.-T. Shih, 16 July 2014; 2 ♂♂ (11.3–11.4 mm) (QM W24251), Pantuan, Kalimantan, coll. E. Dutrieux, unknown date. Malaysia: 1 ♀ (8.3 mm) (NCHUZOOL 14346), Labuan, coll. H.-T. Shih, 24 July 2010. Philippines: 1 ♂ (10.6 mm) (NCHUZOOL 14354), 4 ♂♂ (10.9–12.5 mm), 1 ♀ (12.2 mm) (NCHUZOOL 14355), Zamboanga, Mindanao, coll. C. K. R. Ong, 10 June 2006; 6 ♂♂ (12.4–17.1 mm) (NCHUZOOL 14357), Pago R., Mindanao, coll. H.-C. Liu, 13

July 2007; 5 ♂♂ (12.4–14.2 mm), 1 ♀ (11.9 mm) (NCHUZOOL 13574), 1 ♂ (14.8 mm) (NCHUZOOL 14358), Cebu, coll. L. Liao, 2 Sep. 2003; 1 ♂ (11.5 mm), 2 ♀♀ (10.3–10.4 mm) (NCHUZOOL 14349), 1 ♀ (14.6 mm) (NCHUZOOL 14350), 1 ♂ (11.2 mm) (NCHUZOOL 14351), 1 ♂ (10.6 mm), 2 ♀♀ (10.4–12.4 mm) (NCHUZOOL 14352), Matutinao R. Badian, Cebu, coll. H.-T. Shih, 6 Sep. 2003; 3 ♂♂ (8.1–10.1 mm), 2 juv. (NCHUZOOL 14356), Puerto Galera, coll. P.-C. Tsai and K. Wong,

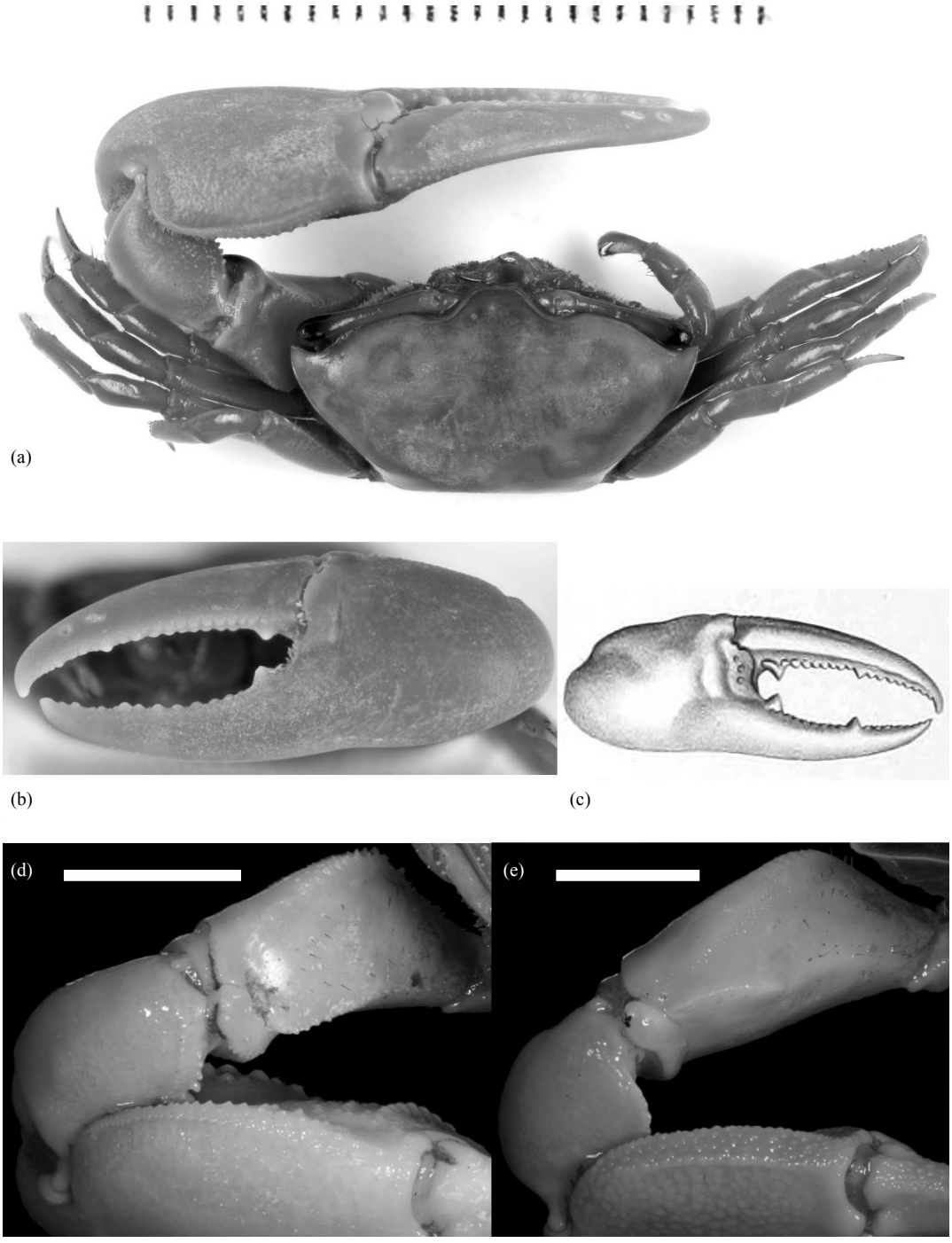

Fig. 1. Male *Austruca variegata* (Heller, 1862) (a–d) and *Cranuca inversa* (Hoffmann, 1874) (e). (a) habitus; (b, c) major cheliped; (d, e) merus of right major cheliped. (a, b) lectotype, CW 17.2 mm (PL 24.7 mm, NHMW 25656; Madras, India), originally identified as *A. perplexa*. (c) "*Gelasimus perplexus*" in Heller (1865: pl. 5(4)). (d) male (CW 18.6 mm, ZRC 2018.1375; Tamil Nadu, India). (e) CW 19.9 mm (NCHUZOOL 14904; Al Darb, Arabia). Scale bars = 5.0 mm.

5 June 2009. Taiwan: 2 ♂♂ (9.1–12.5 mm), 2 ♀♀ (8.8–12.3 mm) (NCHUZOOL 14710), Baoli River estuary, Pingtung, coll. H.-T. Shih, 14 Sep. 1997; 1 ♂ (13.2 mm), 1 ♀ (5.2 mm) (NCHUZOOL 14712), Baoli River estuary, Pingtung, 20 July 2011; 3 ♂♂ (11.4–13.0 mm) (NCHUZOOL 14745), Yanshuei River estuary, Tainan, coll. students, 4 Aug. 2009; 1 ♀ (8.7 mm) (NCHUZOOL 14711), Yanshuei River estuary, Tainan, coll. students, 18 Oct. 2011; 2 ♂♂ (10.2–11.5 mm), 1 ♀ (11.9 mm) (NCHUZOOL 14709), Lanyang River estuary, Yilan, 25 July 2004. *Cranuca inversa*: 1 ♂ (19.9 mm) (NCHUZOOL 14904), Al Darb, Red Sea, Arabia, coll. Anand. Jeya Kumar, 25 Apr. 2017.

Diagnosis: Male. Front moderately broad. Carapace (Figs. 1a, 2a, 3a, b) with orbits slightly oblique; anterolateral angles (= external orbital angles) broadly triangular, directed anteriorly; anterolateral margins short; dorsolateral margin long, definite, converging. Floor of orbits with some weak tubercles medially (Fig. 4a–d). Major cheliped (Fig. 1a–c, with posterodorsal margin of merus with a single row of

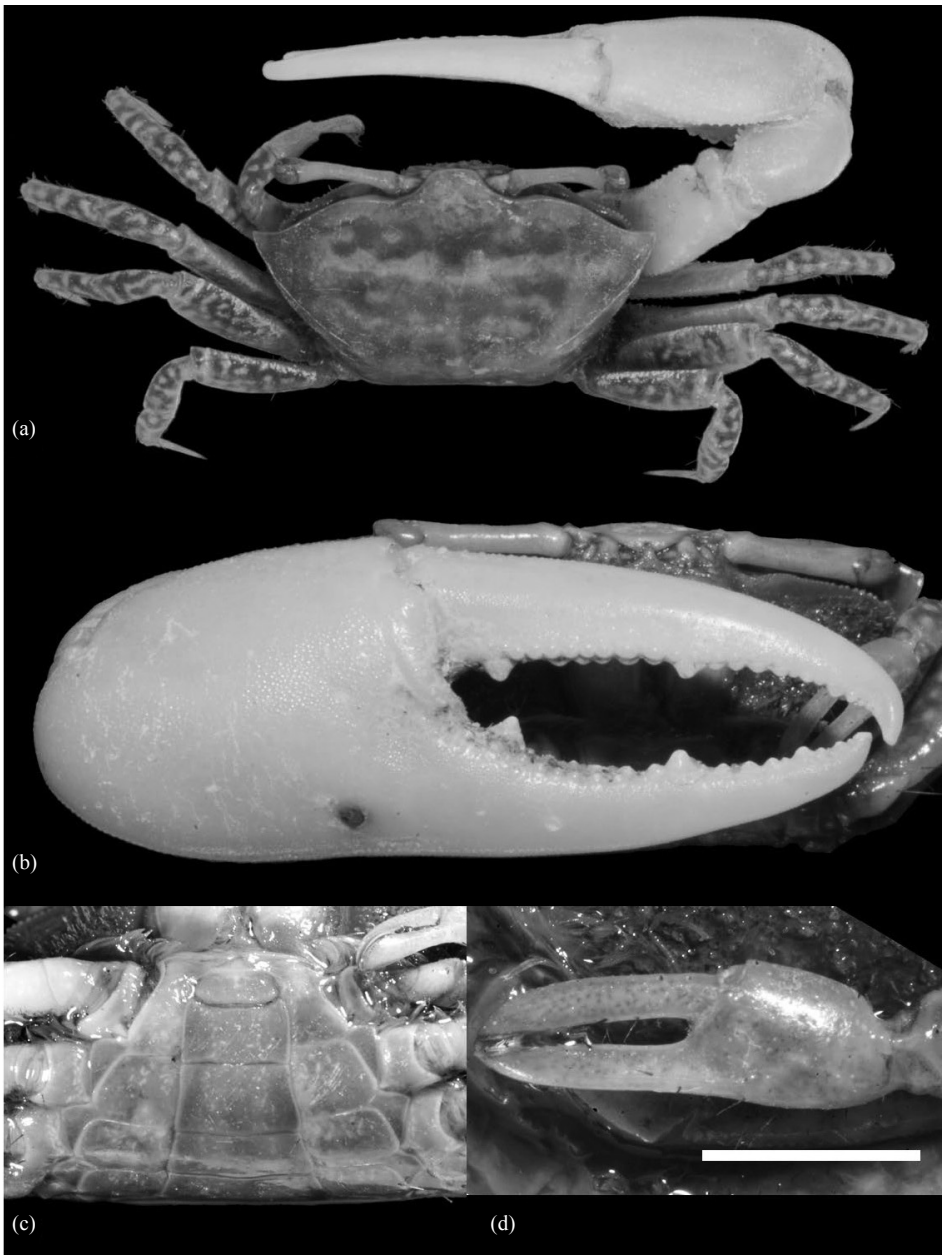

Fig. 2. *Austruca variegata* (Heller, 1862). a–d, male (CW 18.6 mm, CL 10.7 mm, PL 26.6 mm, ZRC 2018.1375). (a) habitus; (b) major cheliped; (c) pleon; (d) minor cheliped. Scale bar = 5.0 mm.

small, sharp tubercles or serrations at convex crest, anterodorsal margin not arched, with serrated row (Fig. 1c); palm broad, with minute tubercles on outer surface, inner surface with proximal predactylar ridge strong and oblique row of granules proximoventrally; dactylus broad, with 1 short shallow groove proximal and subdorsally; pollex broad. Merus of minor cheliped with weak longitudinal row of tubercles above posteroventral margin, curves abruptly upward at distal end, short distance before end of segment. Gape of minor cheliped with serrations on distal part. Meri of second, third ambulatory legs moderately wide, dorsal margin of first, fourth meri almost straight. G1 with flange short, slightly curved, distal edge slightly expanded, almost truncate; thumb tumid, broad as adjacent shaft, extending well beyond flange base (Fig. 6a–c, f). Urocardiac ossicles of gastric mill moderately complex, with 4 or 5 pairs of transverse ridges of median tooth, separated by gaps reached deeply near central ridge, on posterior tooth plate; 4 pairs of cusps on stem region (Fig. 7a, b, e).

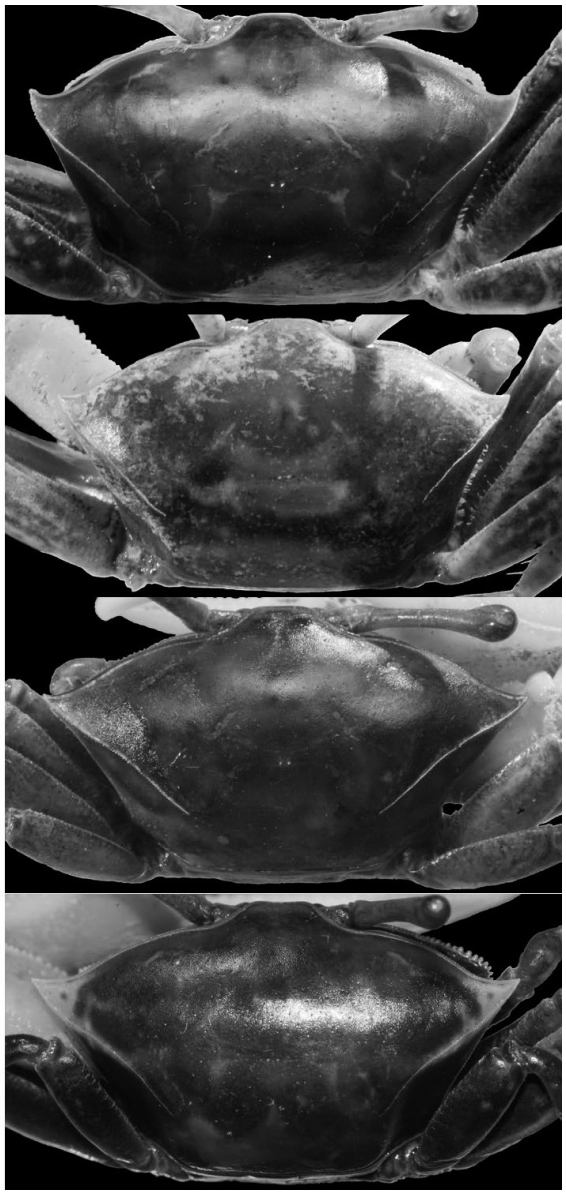

Fig. 3. Carapaces of male *Austruca variegata* (Heller, 1862) (a, b), *A. bengali* (Crane, 1975) (c) and *A. triangularis* (A. Milne-Edwards, 1873) (d). (a) CW 16.6 mm (ZRC 2001.0853; left-handed; Tamil Nadu, India); (b) CW 14.5 mm (ZRC 2017.0917; left-handed; West Bengal, India); (c) CW 14.5 mm (NCHUZOOL 14345; right-handed; Selangor, Malaysia); (d) CW 14.8 mm (NCHUZOOL 13574; left-handed; Cebu, Philippines).

Female. Anterolateral (Fig. 8a) margins long, almost straight, turning at angle into dorsolateral margins. Meri of ambulatory legs moderately wide (Fig. 8a). Vulva (female gonopore) (Fig. 8d) in shallow sternal depression, but not tuberculate.

Coloration in life (Fig. 9): Carapace interlaced with black and pale blue (or yellowish white) transverse bands, some individuals with wider black bands on posterior portion. Eyestalks and major cheliped yellow. Legs pale blue (or yellowish white) with black speckles.

Ecological notes: According to Krishnan (1992), this species in Madras "exhibits a patchy distribution, restricted to the high saline areas where the substratum is clay-mud". *Austruca annulipes* (H. Milne Edwards, 1837) is the only sympatric species in southeastern India (Altevogt 1957; Feest 1969; Krishnan 1992; Dev Roy and Bhadra 2005; Fredrick and Ravichandran 2013). In the northern Bay of Bengal, it was reported to be sympatric with *Austruca annulipes*, *Tubuca rosea* (Tweedie, 1937), *T. paradussumieri* (Bott, 1973), *Gelasimus hesperiae* (Crane, 1975) (see Talapatra et al. 2014; Sen and Homechaudhuri 2015).

Distribution: From the Bay of Bengal (including Sri Lanka) to the Laccadive Sea (see the synonym list). According to Krishnan (1992), the distribution may be extended to the whole eastern side of the Indian subcontinent (from Ganges Delta to Karaikal). Kappalli et al. (2012) and Supriya et al. (2017) studied the population (as *Uca triangularis*) from southwestern India in the Laccadive Sea.

Remarks: As discussed earlier, Heller (1862: 521) briefly diagnosed *Gelasimus variegatus* from Madras (present day Chennai) in India but did not indicate how many specimens he had. Later, even after he synonymized it with "*Gelasimus perplexus*" (not *Gelasimus perplexa* H. Milne Edwards, 1837, s. str.), he did not indicate how many specimens he had from Madras. Crane (1975: 326) searched for the types in vain, commenting that "I have been unable to locate any material referred to this species. In particular the type-specimen was not found in the museum in

Vienna when I asked for it in 1963. According to the short type description in Latin, this species is close to *annulipes* but includes a denticulate crest on the major merus. Almost certainly *variegatus* and *inversa* are synonymous. However, *inversa* has not been recorded from eastern India, while *variegatus* was described from Madras. The specimens were collected on the round-the-world expedition of the "Novara". According to oral reports, mistakes on the labels have been encountered in other material resulting from that trip, and it is not unlikely that the type-material of *variegatus* was collected farther west." A fresh search for "*Gelasimus variegatus*" in the Naturhistorisches Museum Wien failed to find specimens under this name, but there

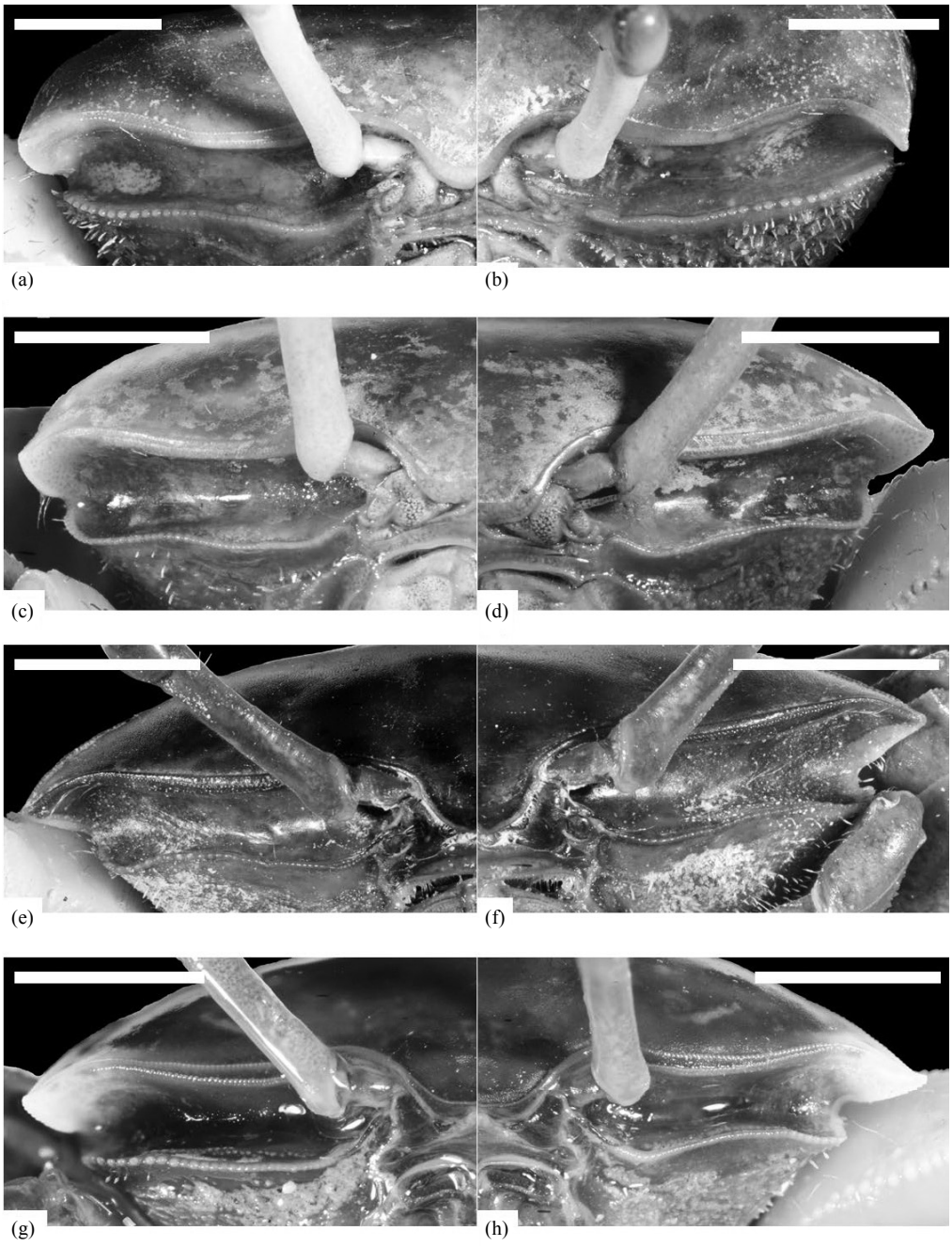

Fig. 4. Floors of orbit of male *Austruca variegata* (Heller, 1862) (a–d), *A. bengali* (Crane, 1975) (e, f) and *A. triangularis* (A. Milne-Edwards, 1873) (g, h). (a, b) CW 18.6 mm (ZRC 2018.1375; right-handed; Tamil Nadu, India); (c, d) CW 14.5 mm (ZRC 2017.0917; left-handed; West Bengal, India); (e, f) CW 14.5 mm (NCHUZOOL 14345; right-handed; Selangor, Malaysia); (g, h) CW 14.8 mm (NCHUZOOL 13574; left-handed; Cebu, Philippines). Scale bars = 5.0 mm.

are two extant lots labelled as "*Gelasimus perplexus*" among Heller's material from Madras (P. C. Dworschak, personal communication). They were all collected by Johann Zelebor who was a staff member during the Novara Expedition. One of these lots (NHMW 25656 and 12980) still carries the original Novara label which states "#74 = AN. 1866.II.74" and contains 100 males and 2 females. The other lot (NHMW 12974), with seven males, does not have the original label but is also part of the expedition material. Although these specimens do not carry the name "*Gelasimus variegatus*", it is quite clear that they are part of the type

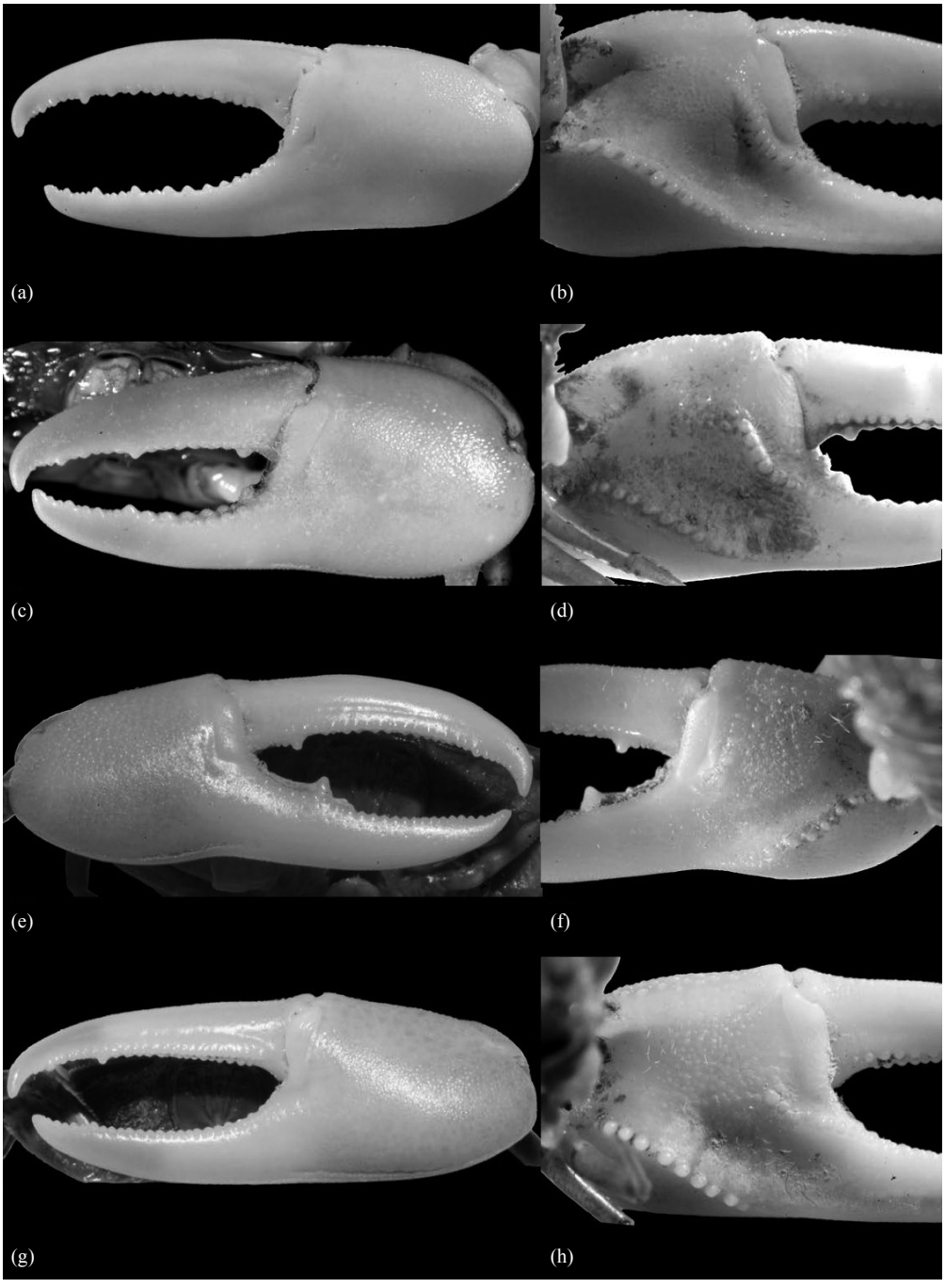

Fig. 5. Outer and inner sides of major palm of *Austruca variegata* (Heller, 1862) (a–d), *A. bengali* (Crane, 1975) (e, f) and *A. triangularis* (A. Milne-Edwards, 1873) (g, h). (a, b) CW 16.6 mm (ZRC 2001.0853; left-handed; Tamil Nadu, India); (c, d) CW 14.5 mm (ZRC 2017.0917; left-handed; West Bengal, India); (e, f) CW 14.5 mm (NCHUZOOL 14345; right-handed; Selangor, Malaysia); (g, h) CW 14.8 mm (NCHUZOOL 13574; left-handed; Cebu, Philippines).

series and are thus syntypes. It would appear that Heller (1865) decided that his "*Gelasimus variegatus* Heller, 1862" was the same as "*Gelasimus perplexus*" and removed all the labels with the former name in the lots, retaining only the accepted name at that time. That was why Crane (1975) failed to find the type specimens of *Gelasimus variegatus*. Based on the labels in these two lots, the specimens were actually examined by the late Hui-Lian Chen as well as Diana Jones who identified them as "*Uca triangularis* (H. Milne Edwards, 1852)" and "*Uca bengali* Crane, 1975", respectively, although none of this information has been published to our knowledge. While we have not managed to examine all the specimens in both lots, Peter Dworschak was kind

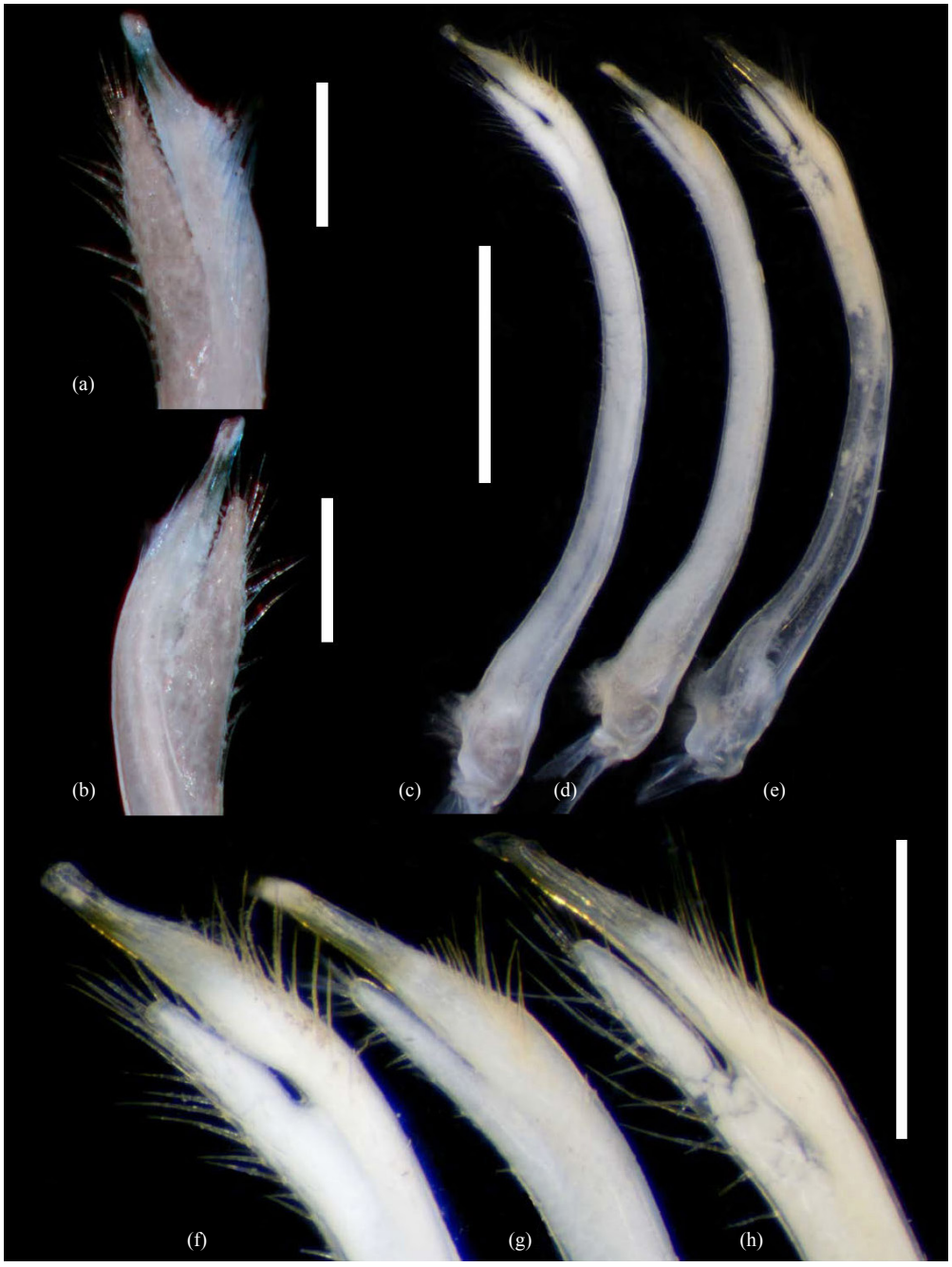

Fig. 6. Right G1s of *Austruca variegata* (Heller, 1862) (a, b, c, f), *A. bengali* (Crane, 1975) (d, g) and *A. triangularis* (A. Milne-Edwards, 1873) (e, h). (a, f–h) lateral view of distal part; (b) mesial view of distal part; (c–e) lateral view. (a, b) CW 16.6 mm (ZRC 2001.0853; Tamil Nadu, India); (c, f) CW CW 14.5 mm (ZRC 2017.0917; West Bengal, India); (d, g) 14.5 mm (NCHUZOOL 14345; Selangor, Malaysia); (e, h) 14.8 mm (NCHUZOOL 13574; Cebu, Philippines). Scale bars: a, b, f–h = 0.5 mm, c–e = 1.0 mm.

enough to photograph for us the best specimens in these lots and allow us to acertain their identities. To stabilize the taxonomy of the species and to leave no doubt about its identity, we here select a male specimen with CW 16.7 mm (NHMW 25656) as the lectotype of *Gelasimus variegatus* Heller, 1862 (Fig. 1a, b).

Austruca variegata closely resembles *A. bengali* and *A. triangularis*, but can be distinguished easily by the morphology of carapace, major and minor chelipeds, G1, gastric mill structure and coloration (see Table 2 for details). In *A. variegata*, the orbit is only slightly oblique in position (Fig. 3a, b) (distinctly oblique in other species; Fig. 3c, d); the anterolateral angles are broadly triangular and directed anteriorly (Fig. 3a, b) (acute and directed laterally in other species, but that on *A. bengali* is very acute; Fig. 3c, d); the anterolateral margins is short (Fig. 3a, b) (absent in *A. bengali* and very short in *A. triangularis*; Fig. 3c, d); the dorsolateral margin is converging (Fig. 3a, b) (strongly converging in other species; Fig. 3c, d); the tubercles on the orbital floor are weak and only present medially (Fig. 4a–d) (none in *A. bengali* (Fig. 4e–f); with strong tubercles in females and males (at least on minor side) in *A. triangularis* (Fig. 4g–h)); the chelae of major cheliped is broad (Fig. 5a, c) (slender in other species; Fig. 5e, g); the groove on major dactylus is one short shallow groove proximally and subdorsally (Fig. 5a, c) (one shallow groove proximally and subdorsally and another long shallow groove just above gape in other species; Fig. 5e, g); the proximal predactylar ridge is long and very strong (Fig. 5b, d) (long and strong in *A. bengali* (Fig. 5f); short and the tubercles fewer or, rarely, absent in *A. triangularis* (Fig. 5h)); the longitudinal row of tubercles above the posteroventral margin on the minor merus is weak (strong in other species; see Crane 1975: fig. 51A); the G1 flange is short and the thumb is stout

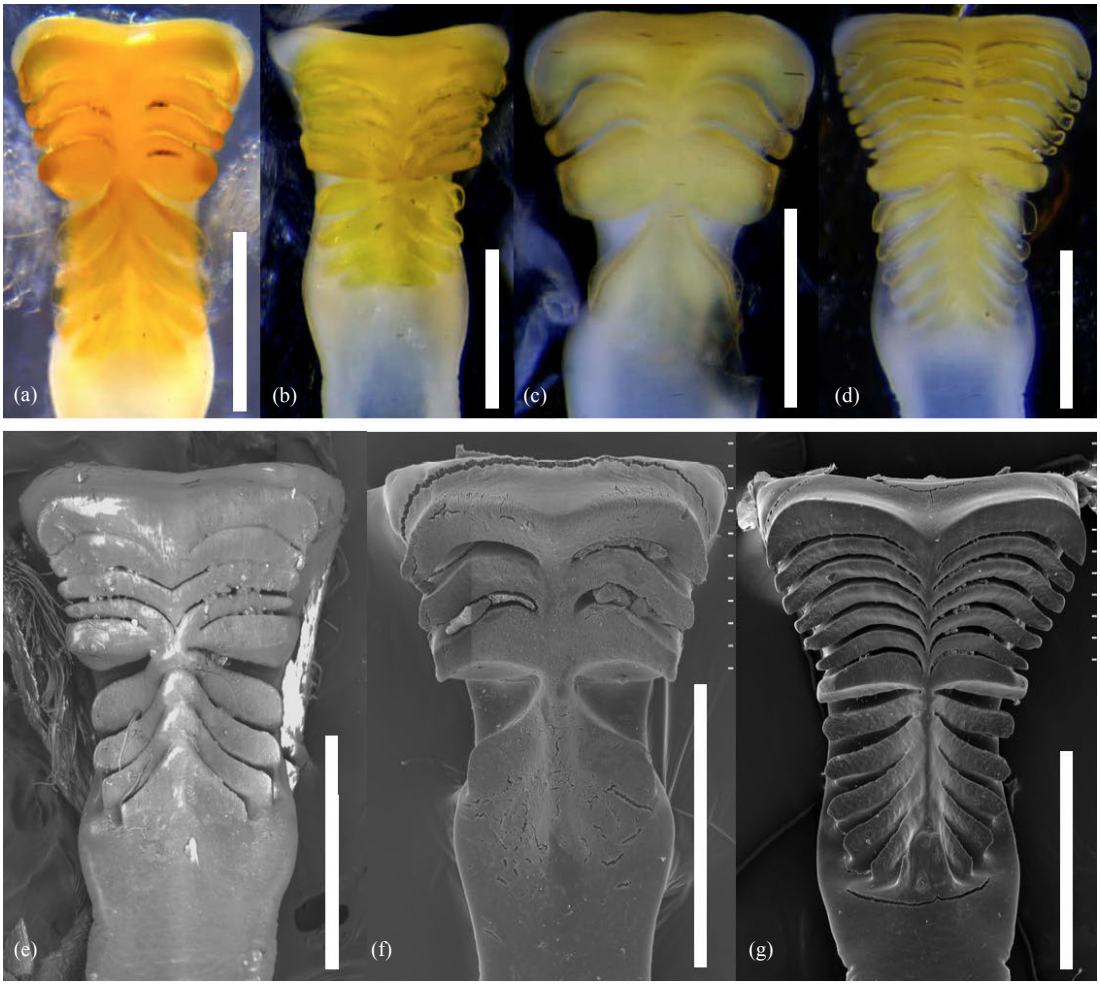

Fig. 7. Urocardiac ossicles of *Austruca variegata* (Heller, 1862) (a, b, e), *A. bengali* (Crane, 1975) (c, f) and *A. triangularis* (A. Milne-Edwards, 1873) (d, g). (a) male (CW 16.1 mm, ZRC 2003.0463; Tamil Nadu, India); (b, e) female (CW 14.5 mm, ZRC 2003.0463; Tamil Nadu, India); (c) male (CW 13.1 mm, QM W27320; Phuket, Thailand); (d) male (CW 14.8 mm, NCHUZOOL 13574; Cebu, Philippines); (f) male (CW 12.5 mm, QM W27320; Phuket, Thailand); (g) female (CW 14.6 mm, NCHUZOOL 14350; Cebu, Philippines). Scale bars = 0.5 mm.

and broad as the adjacent shaft (Fig. 6a–c, f) (flange short and thumb slender in *A. bengali* (Fig. 6d, g); flange long and the thumb is less stout but also broad as adjacent shaft in *A. triangularis* (Fig. 6e, h)); the female vulva is a shallow depression and not tuberculate (Fig. 8d) (with a blunt tubercle in *A. bengali* (Fig. 8e); with a definite apex directed internally in *A. triangularis* (Fig. 8f)); and the gastric mill is moderately complex with 4 or 5 pairs of ridges of median tooth and 4 pairs of cusps on stem region (Fig. 7a, b, e) (simple, 3 pairs and 1 pairs in *A. bengali* (Fig. 7c, f); complex, 7 or 8 pairs and 5 or 6 pairs in *A. triangularis* (Fig. 7d, g)).

The color and patterns of the three species (Figs. 9–11) are different enough to distinguish them in the

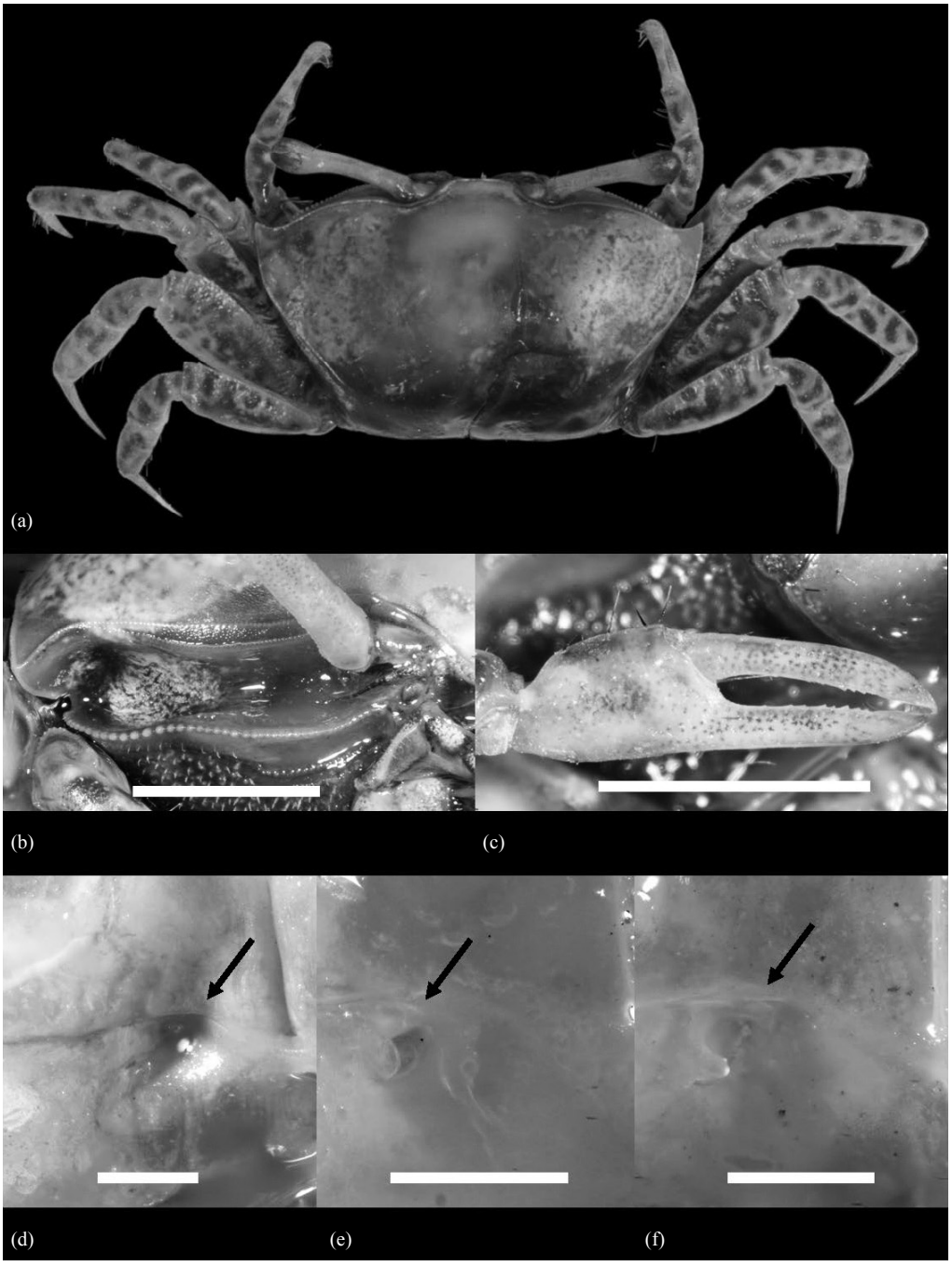

Fig. 8. Female *Austruca variegata* (Heller, 1862) (a–d), *A. bengali* (Crane, 1975) (e) and *A. triangularis* (A. Milne-Edwards, 1873) (f). (a) habitus; (b) floor of right orbit; (c) right minor cheliped; (d–f) right vulva (gonopore). (a–d) CW 16.6 mm (NCHUZOOL 14365; Tamil Nadu, India); (e) CW 12.4 mm (QM W27320; Phuket, Thailand); (f) CW 14.6 mm (NCHUZOOL 14350; Cebu, Philippines). Scale bars: b, c = 5.0 mm, d–f = 0.5 mm

Fig. 9. The live coloration of *Austruca variegata* (Heller, 1862) (a–h). (a, b) dorsal view of male; (c, d) frontal view of male; (e) dorsal view of female; (f) two males fighting; (g) two males moving to low intertidal zone for feeding; (h) a male *A. variegata* (left) and a male *A. annulipes* (H. Milne Edwards, 1837) (right) sympatric in one locality. Specimens not captured. Photos taken from Vellar River estuary, Porto Novo, Tamil Nadu, India.

field. The color of major cheliped is yellow with no speckles in *A. variegata*; yellowish orange with no speckles in *A. bengali*; but it is pale brown, covered with brown speckles in *A. triangularis*. The color of ambulatory legs is also diagnostic, being mottled (pale background with black speckles) in *A. variegata*, neither mottled nor banded in *A. bengali* and dark brown with paler bands in *A. triangularis*.

Among the three species of this complex, *Austruca variegata* was published in 1862, and predates *Austruca triangularis* (A. Milne-Edwards, 1873) and *A. bengali* (Crane, 1975); so it is perhaps better to name this the "*Austruca variegata* complex".

It is pertinent to note that in discussing *Gelasimus tetragonon* (Herbst, 1790), H. Milne Edwards (1837: 52, footnote) listed the name "*Gelasima variegata*, Latr. Coll. du Mus. (fem.)" under its synonymy. This name is clearly a nomen nudum, and on the basis of the synonymy, not the same taxon as what is here regarded as *Austruca variegata* (Heller, 1862).

Key to the species of the *Austruca variegata* complex

1. Carapace with orbit not oblique; anterolateral angles broadly triangular and directed anteriorly; anterolateral margins short. Major chela broad; proximal predactylar ridge long and very strong. Major cheliped yellow, no speckles; ambulatory legs mottled (pale ground with black speckles) ..... *A. variegata*
– Carapace with orbit very oblique; anterolateral angles acute and directed laterally; anterolateral margins absent or very short.

Table 2. Morphological comparison among *Austruca variegata* (Heller, 1862), *A. bengali* (Crane, 1975) and *A. triangularis* (A. Milne-Edwards, 1873)

	A. variegata	*A. bengali*	*A. triangularis*
Carapace:			
orbits	slightly oblique (Figs. 1a, 2a, 3a, b, 8a)	distinctly oblique (Fig. 3c)	distinctly oblique (Fig. 3d)
anterolateral angles	broadly triangular and directed anteriorly (Figs. 1a, 2a, 3a, b, 8a)	very acute and directed laterally (Fig. 3c)	acute and directed laterally (Fig. 3d)
anterolateral margins	short (Figs. 1a, 2a, 3a, b, 8a)	absent (Fig. 3c)	very short (Fig. 3d)
dorsolateral margin	converging (Figs. 2a, 3a, b, 8a)	strongly converging (Fig. 3c)	strongly converging (Fig. 3d)
Orbital floor:			
tubercles on orbital floor	some weak tubercles medially (Fig. 4a–d)	none (Fig. 4e–f)	strong tubercles in females and males (at least on minor side) (Fig. 4g–h)
Major cheliped:	broad (Figs. 1b, 2b, 5a, c)	slender (Fig. 5e)	slender (Fig. 5g)
major chela			
grooves on major dactylus	one short shallow groove proximal and subdorsally (Fig. 2b, 5a, c)	one shallow groove proximal and subdorsally; another long shallow groove just above gape (Fig. 5e)	one shallow groove proximal and subdorsally; another long shallow groove just above gape (Fig. 5g)
proximal predactylar ridge	long and very strong (Fig. 5b, d)	long and strong (Fig. 5f)	short and the tubercles fewer or, rarely, absent (Fig. 5f)
Minor cheliped:			
longitudinal row of tubercles above posteroventral margin on minor merus	weak	strong	strong (Crane 1975: fig. 51A)
G1	flange short; thumb stout and broad as adjacent shaft (Fig. 6a, b, c, f)	flange short; thumb slender (Fig. 6d, g)	flange long; thumb less stout but broad as adjacent shaft (Fig. 6e, h)
Female vulva (gonopore)	in shallow sternal depression and not tuberculate (Fig. 8d)	with a blunt tubercle on later side (Fig. 8e)	with a definite apex on lateral side, directed internally (Fig. 8f)
Gastric mill:			
complexity (pairs of ridges of median tooth; pairs of cusps on stem region)	moderately complex form (4 or 5; 4) (Fig. 7a, b, e)	simple form (3; 1) (Fig. 7c, f)	complex form (7 or 8; 5 or 6) (Fig. 7d, g)
Coloration:			
major cheliped	Yellow with no speckles (Fig. 9)	Yellowish orange with no speckles (Fig. 10)	Pale brown, covered with brown speckles (Fig. 11)
ambulatory legs	mottled (pale ground with black speckles) (Fig. 9)	homogenous (neither mottles or banded) (Fig. 10)	with banding (dark brown with paler bands) (Fig. 11)

Fig. 10. The live coloration of *Austruca bengali* (Crane, 1975) (a–g). (a, b) dorsal view of adult male; (c, d) dorsal view of juvenile male; (e) frontal view of adult male; (f) frontal view of juvenile female; (g) a female in the field (not captured; Phuket, Thailand); (h) habitat in Phuket, Thailand. (a) male (not captured; Selangor, Malaysia); (b) male (not captured; Phuket, Thailand); (c, d) male (CW 7.3, 7.8 mm, NCHUZOOL 14361; Phuket, Thailand); (e) male (CW 14.5 mm, NCHUZOOL 14345; Selangor, Malaysia); (f) female (CW 8.1 cm, NCHUZOOL 14361; Phuket, Thailand).

Major chela slender 2
2. Anterolateral margins absent. Orbital floor without tubercles. Major cheliped with proximal predactylar ridge long and strong. Major cheliped yellowish orange, no speckles; ambulatory legs without mottles or banding ..... *A. bengali*
– Anterolateral margins very short. Orbital floor with tubercles in females and males (at least on minor side). Major cheliped with proximal predactylar ridge short and the tubercles fewer or, rarely, absent. Major cheliped pale brown, covered with brown speckles; ambulatory legs with banding (dark ground with paler bands) ..... *A. triangularis*

Fig. 11. The live coloration of *Austruca triangularis* (A. Milne-Edwards, 1873). (a–d) dorsal view of adult male; (e, f) dorsal view of juvenile male; (g, h) frontal view of adult male. (a, g) NCHUZOOL 14347 (140716, Bali, Indonesia); (b, h) male (CW 11.5 mm, NCHUZOOL 14349; Cebu, Philippines); (c, d) specimens lost (Baoli River estuary, Pingtung, Taiwan); (f) NCHUZOOL 14346 (Labuan, Malaysia).

Molecular analyses

A 624 bp segment of the 28S, 571 bp segment of 16S, and 658 bp segment of *COI* from 11 species of the genus *Austruca* were amplified and aligned (Table 1). The bp differences and nucleotide divergences with the K2P distance of haplotypes, based on 616 bp of *COI*, of the three species of the *A. variegata* complex is shown in table 3. With regard to *A. variegata*, the bp difference and nucleotide divergence within species are ≤ 5 (0.81%) and ≤ 0.82%, respectively; and are ≥ 76 (12.34%) and ≥ 13.7%, respectively, between species (Table 3). Thus, the interspecific divergence is at least 15 times more than intraspecific values, supporting *A. variegata* as a distinct species.

A phylogenetic tree of the combined markers was reconstructed using BI analysis (Fig. 12), with *A. variegata* as sister to *A. triangularis* + *A. bengali*. The haplotype network based on the *COI* haplotypes (Fig. 13) shows that the three species were separated by 34–42 steps, which is consistent with the large genetic distances among them.

DISCUSSION

In this study, we formally recognize *Gelasimus variegatus* Heller, 1862, as a valid species, belonging to the genus *Austruca* Bott, 1973. This species can be separated from the closely related *A. bengali* (Crane, 1975) and *A. triangularis* (A. Milne-Edwards, 1873) by characters of the carapace, orbital floor, major and minor chelae, male first gonopod, vulva (female gonopore), gastric mill, and coloration in life, as well as the genetic data of nuclear 28S rDNA, mitochondrial 16S rDNA and *COI*.

With regard to the molecular evidence, the phylogenetic tree of the three combined markers (Fig. 12) supports *A. variegata*, *A. triangularis* and *A. bengali* as three closely related species. In addition, the interspecific distances of *COI* among the three species are high (Table 3), which are consistent with most studies of other fiddler crab species from the Indo-West Pacific (Chu et al. 2015; Shih et al. 2018).

In southeastern India, *A. variegata* and *A. annulipes* are always sympatric (Fig. 9g), but their distributional ranges are different. While *A. annulipes* is widely distributed from the eastern Indian Ocean to the South China Sea (Shih et al. 2009; Naderloo et al. 2016), *A. variegata* appears to be limited in the Bay of Bengal. Their different ranges are believed to be related to several factors, including the ocean currents, pelagic larval duration, larval behavior etc. (Young 1995; Levin 2006; López-Duarte et al. 2011; Anger et al. 2015; Chai et al. 2017). Apparently, the two sympatric species are exposed to the same ocean currents in the

Table 3. Matrix of percentage pairwise nucleotide divergences with K2P distance (lower-left) and number of bp differences (upper-right) based on 616 bp of *COI* among specimens (see Table 1) of *Austruca variegata*, *A. bengali* and *A. triangularis*

		A. variegata									*A. bengali*			*A. triangularis*								
		Av1	Av2	Av3	Av4	Av5	Av6	Av7	Av8	Av9	Ab1	Ab2	Ab3	At1	At2	At3	At4	At5	At6	At7	At8	At9
A. variegata	Av1	-	0	1	2	1	2	1	3	1	80	79	78	82	84	84	86	85	84	85	85	84
	Av2	0.00	-	1	2	1	2	1	3	1	80	79	78	82	84	84	86	85	84	85	85	84
	Av3	0.16	0.16	-	3	2	3	2	4	2	81	80	79	83	85	85	87	86	85	86	86	85
	Av4	0.33	0.33	0.49	-	3	4	3	5	3	82	81	80	83	85	85	87	86	85	86	86	85
	Av5	0.16	0.16	0.33	0.49	-	3	2	4	2	81	80	79	83	85	85	87	86	85	86	86	85
	Av6	0.33	0.33	0.49	0.65	0.49	-	1	5	3	78	77	76	80	82	82	84	83	82	83	83	82
	Av7	0.16	0.16	0.33	0.49	0.33	0.16	-	4	2	79	78	77	81	83	83	85	84	83	84	84	83
	Av8	0.49	0.49	0.65	0.82	0.65	0.82	0.65	-	4	79	78	77	80	82	82	84	83	82	83	83	82
	Av9	0.16	0.16	0.33	0.49	0.33	0.49	0.33	0.65	-	81	80	79	81	85	83	85	84	83	84	84	83
A. bengali	Ab1	14.53	14.53	14.74	14.95	14.74	14.12	14.33	14.33	14.74	-	2	6	83	82	83	85	84	85	84	83	83
	Ab2	14.33	14.33	14.53	14.74	14.53	13.91	14.12	14.12	14.53	0.33	-	4	81	80	81	83	82	83	82	82	81
	Ab3	14.12	14.12	14.33	14.53	14.33	13.70	13.91	13.91	14.33	0.98	0.65	-	80	79	80	82	81	82	81	81	80
A. triangularis	At1	14.94	14.94	15.15	15.15	15.15	14.52	14.73	14.52	14.73	14.99	14.58	14.38	-	6	4	4	3	6	5	9	4
	At2	15.36	15.36	15.57	15.57	15.57	14.94	15.15	14.94	15.57	14.79	14.38	14.17	0.98	-	4	4	3	6	5	9	4
	At3	15.36	15.36	15.57	15.57	15.57	14.94	15.15	14.94	15.15	14.99	14.58	14.38	0.65	0.65	-	2	1	4	3	7	2
	At4	15.79	15.79	16.00	16.00	16.00	15.36	15.57	15.36	15.57	15.41	14.99	14.79	0.65	0.65	0.33	-	1	4	3	7	2
	At5	15.57	15.57	15.79	15.79	15.79	15.15	15.36	15.15	15.36	15.20	14.79	14.58	0.49	0.49	0.16	0.16	-	3	2	6	1
	At6	15.36	15.36	15.57	15.57	15.57	14.94	15.15	14.94	15.15	15.41	14.99	14.79	0.98	0.98	0.65	0.65	0.49	-	5	9	4
	At7	15.57	15.57	15.79	15.79	15.79	15.15	15.36	15.15	15.36	15.20	14.79	14.58	0.82	0.82	0.49	0.49	0.33	0.82	-	8	1
	At8	15.55	15.55	15.77	15.77	15.77	15.13	15.34	15.13	15.34	14.98	14.78	14.57	1.48	1.48	1.15	1.15	0.98	1.48	1.31	-	7
	At9	15.36	15.36	15.57	15.57	15.57	14.94	15.15	14.94	15.15	14.99	14.58	14.38	0.65	0.65	0.33	0.33	0.16	0.65	0.16	1.15	-

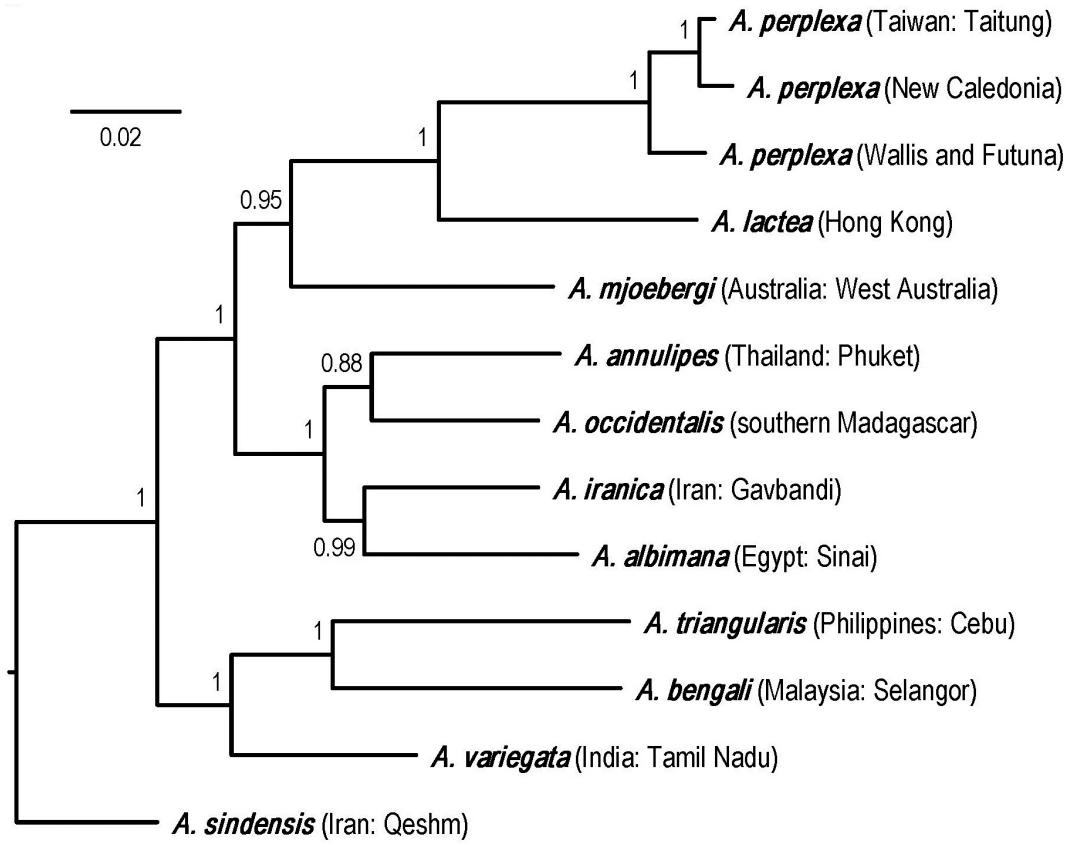

Fig. 12. A Bayesian inference tree of the *Austruca variegata* complex, with the outgroups of other congeneric species, based on the combined 28S, 16S and *COI* markers. Values at the nodes are Bayesian posterior probabilities.

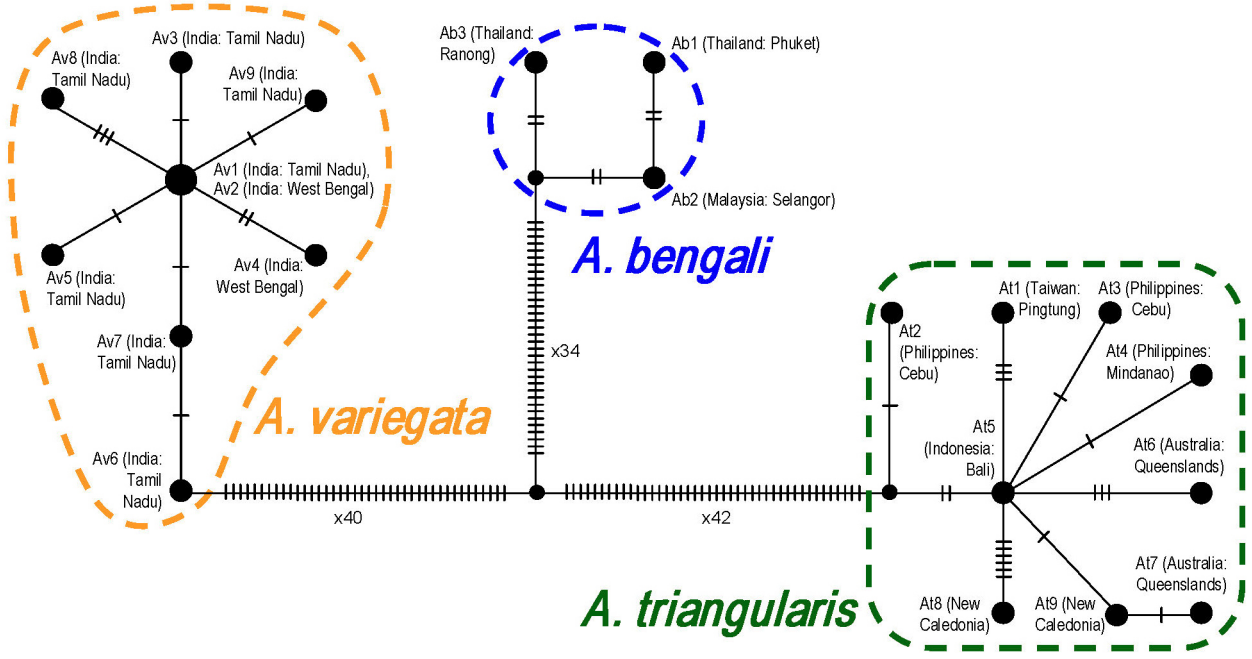

Fig. 13. Genealogical network for the *COI* haplotypes observed within the clades of *Austruca variegata* (Heller, 1862), *A. bengali* (Crane, 1975) and *A. triangularis* (A. Milne-Edwards, 1873). Unlabelled hatches indicate inferred haplotypes not found in the sampled population. For haplotype names, see table 1.

Bay of Bengal, and their total larval duration (from zoea I to megalopa) is similar (42–43 days; Feest 1969). According to López-Duarte et al. (2011), the estuarine species of fiddler crabs express a stronger circatidal rhythm in vertical swimming by larvae than that of the coastal species, which may explain the different distributional ranges between the coastal *A. annulipes* and the estuarine *A. variegata*. More studies on the larval behaviors of the two species will clarify the possible mechanisms of distribution.

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Authors' contributions: HTS conceived this study, performed the morphological description and the molecular analysis, and drafted the manuscript. PKLN performed the discussion and drafted the manuscript. SR and MP collected and processed the samples, performed the ecological observation, and drafted the manuscript. All authors read and approved the final manuscript.

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