

A New Fiddler Crab of *Austruca* Bott, 1973, Closely Related to *A. perplexa* (H. Milne Edwards, 1852) (Crustacea: Brachyura: Ocypodidae), from the South Pacific Islands

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A new species of fiddler crab, *Austruca citrus* n. sp. from Fiji, Wallis & Futuna, and Samoa, in the South Pacific is described based on morphological and molecular evidence. This species is closely related to *Austruca perplexa* (H. Milne Edwards, 1852), but can be distinguished by a suite of characters, including adult size, carapace morphology, shape and coloration of the major chela, the ratio of major pollex length as a function of carapace width, and male first gonopod form. The molecular evidence of the mitochondrial 16S rDNA and cytochrome oxidase subunit I (COI) supports these morphological differences.

Key words: Fiddler crabs, *Austruca perplexa*, *A. citrus*, New species, 16S rDNA, Cytochrome oxidase subunit I.

BACKGROUND

Fiddler crabs of the genus *Austruca* Bott, 1973 are small crabs with a wide front, inhabiting the sandy or muddy sand sediments in the upper intertidal zones of the Indo-West Pacific (Bott 1973; Crane 1975; Shih et al. 2016b). There are three groups in this genus: *A. lactea* complex (8 spp.), *A. variegata* (= *A. triangularis*) complex (3 spp.) and *A. sindensis* (Shih et al. 2016b 2019). Crane (1975) considered the *A. lactea* complex to be a single species, *Uca lactea*, with four subspecies, which were raised to the specific level in Ng et al. (2008a): *A. annulipes* (H. Milne Edwards, 1837), *A. lactea* (De Haan, 1835), *A. mjoebergi* (Rathbun, 1924) and *A. perplexa* (H. Milne Edwards, 1852). Four species were added, viz. *A. albimana* (Kossmann, 1877), *A. cryptica* (Naderloo, Türkay & Chen, 2010), *A. iranica* (Pretzmann, 1971) and *A. occidentalis* (Naderloo, Schubart & Shih, 2016) (Shih et al. 2009 2016b;

Naderloo et al. 2010 2016). According to the phylogeny of Shih et al. (2016b), these species can be divided into three subgroups: (1) *A. albimana*, *A. annulipes*, *A. cryptica*, *A. iranica*, *A. occidentalis*; (2) *A. lactea*, *A. perplexa*; and (3) *A. mjoebergi*.

Of these species, *Austruca perplexa* is widely distributed in the West Pacific and the East Indian oceans (Crane 1975; Shih et al. 2009 2016b; Naderloo et al. 2010). The taxonomy of *A. perplexa*, however, needs to be discussed here as it is closely related to the new species recognized here. *Gelasimus perplexus* H. Milne Edwards, 1852 was described based on an unspecified number of specimens (H. Milne Edwards 1852: 150, pl. 4(18); Fig. 2A) with the following brief description: “Espèce très voisine du *G. annulipes*, mais ayant le pouce de la grande pince beaucoup plus élevé et plus comprimé. - Java” [A species very similar with *G. annulipes* but having the dactylus of the major chela much higher and more compressed. Java]. This agrees

with his figure of the major chela (H. Milne Edwards 1852: pl. 4(18a)). Henri Milne Edwards (1852) also included his earlier record of “*Gelasimus marionis*” (see H. Milne Edwards 1837: 53) under the synonymy of his new species *G. perplexus*, redefining *Gelasimus marionis* Desmarest, 1823 s. str. as a separate taxon (H. Milne Edwards 1852: 145). Henri Milne Edwards’ (1837: 53) record of “*Gelasimus marionis*” was not accompanied by locality information or number of specimens. *Gelasimus marionis* s. str. is now a junior synonym of *Gelasimus vocans* (Linnaeus, 1758) (see Holthuis 1959: 115; Crane 1975: 89).

Alphonse Milne-Edwards (1873: 274), using specimens from New Caledonia, noted that *G. perplexus*, in addition to the high and more compressed major dactylus on the cheliped, also had a diagnostic strong predistal tooth on the pollex. Hilgendorf (1879: 806), however, believed that *G. perplexus* was identical to *G. annulipes* (cf. Fig. 2B), although he had received New Caledonian specimen(s) from A. Milne-Edwards (ZMB Crust. 4300, the Museum für Naturkunde, Berlin). Hilgendorf’s treatment was followed by De Man (1888: 118). *Gelasimus perplexus* was also treated as the “western form” of *G. annulipes* by Nobili (1906a: 312; Red Sea) (= *Austruca albimana* (Kossmann, 1877)) and Nobili (1906b: 151; Persian Gulf) (= *Austruca iranica* (Pretzmann, 1971)). Serène (1973a: 138–139) suggested that the specimen examined by H. Milne Edwards (1852) was only a young male of *G. annulipes*, noting that it had a much smaller predistal pollex tooth, and that the high major dactylus of *G. perplexus* mentioned by H. Milne Edwards (1852) is a character also present in *G. annulipes* (cf. Serène 1973a: fig. 12).

Crane (1975: 295, 300–301) redefined *Uca perplexa* (as *Uca lactea perplexa*), separating it from *Uca annulipes* s. str. (as *Uca lactea annulipes*) by male chela characters (notably by the relatively wider proximal half of the dactylus and the larger predistal pollex tooth). This is the concept of *Uca perplexa* that is now followed by most workers (see the synonymy of *U. perplexa* later). Crane (1975: 298) examined two male syntype specimens in the MNHN: “2 males in same box with the label ‘*Gelasimus perplexus* M. Besukuj Javae.’ They are listed as ‘types non spécifiés.’ Condition very poor, the specimens having been dried, wired, and somewhat crushed. It seems undesirable to designate a lectotype or neotype at present. The larger specimen, about 9 mm long with the propodus 27 mm, was relaxed; the gonopod is clearly of the form referred in the present study to the subspecies, *U. lactea perplexa*; the claws are also of characteristic shape. (!)”

There are indeed two supposed syntypes of *G. perplexus* in the MNHN collection, one rehydrated male (broken, carapace width (CW) 15–16 mm,

propodus length (PL) 28.2 mm) and one dry male (CW 13.8 mm, PL 25.7 mm) (MNHN-IU-2008-10646 = MNHN-B.12005) (Fig. 3), both labelled as from M. Besukiil, Java, Indonesia. The way the labels are written suggest “Besukiil” is a person but it should be a location. “Besukiil” is just an alternate spelling name for “Besuki”, a province in East Java (PKL Ng, personal communication). This location “Prov. Besukil” is also in the website for vascular plants in the MNHN (https://science.mnhn.fr/institution/mnhn/collection/p/item/list?lang=en_US&full_text=Heteropogon+contortus), for specimens collected there in 1845. Danièle Guinot in 1972 had examined the two specimens and her unpublished notes (placed with the specimens) note some problems. Their chelae do not match the drawing in H. Milne Edwards (1852: pl. 4(18)) (Fig. 2A) and while the chela in his plate 4(18) is right-handed, both supposed syntypes are left-handed (Fig. 3). The chela of the two supposed syntypes differ from H. Milne Edwards’ figure in having the dactylus and pollex both more elongate (vs. relatively shorter), the distal part of the dactylus is less prominently tapering (vs. sharply tapering to a slender structure), the pollex is not tapering gradually to the tip, being more or less of the same width along most of its length (vs. pollex gradually tapering proximally to distally), and the predistal tooth on the pollex is large and high (vs. small and low). Nevertheless, these were the specimens Crane (1975) used to define what she called *Uca perplexa* and these characters continue to be used today.

Although Crane (1975) regarded both specimens as types during her study in the MNHN, aided by Jacques Forest and Danièle Guinot, the differences between their chelae and what H. Milne Edwards (1852) originally figured cast doubt. The specimen on which the figure was based cannot be found and is almost certainly lost. Are the two extant specimens in the MNHN, both with the same catalogue number (MNHN B 12005) actually part of the original type series? One specimen is rehydrated and in very poor condition, with only parts of the carapace still present, and there is a question mark next to the type status. The labels associated with it are not the original. The major chela and gonopods, however, are still present (Figs. 3A–B, 6E–F). The second more intact specimen (Fig. 3D–E) has the original labels, one that says “*Gelasimus marionis*”, the other “*Gelasimus perplexus*”. The chelae of both specimens are almost identical (Fig. 3A, B, E).

Looking at the original descriptions and figures in H. Milne Edwards (1837 1852) for *Gelasimus perplexus* and all the available evidence still extant, we are of the opinion that the more intact dried specimen (MNHN-B.12005) is almost certainly one of the syntypes. We are less certain about the type status of

the other specimen as it has less associated information. As discussed above, the specimens H. Milne Edwards (1837: 53) had identified as “*Gelasimus marionis*” from an unspecified location were later referred to as the new species *G. perplexus*. Since H. Milne Edwards (1852) did not select a holotype for *Gelasimus perplexus*, all the material of “*Gelasimus marionis*” reported by H. Milne Edwards (1837) as well as any specimens he may have had with him (none were indicated at that time) in 1852 must be regarded as syntypes. The fact that the more intact MNHN specimen still had the original label identifying it as “*Gelasimus marionis*” and has a second label with the name “*Gelasimus perplexus*” is very indicative. It is important to note here that H. Milne Edwards (1852: 150) distinguished *G. perplexus* from *G. annulipes* by just one character – whether the dactylus of the cheliped is higher and more compressed. He never mentioned the other features of the fingers or the size of the predistal tooth on the pollex, not using them as characters. The two MNHN specimens possess this character: the proximal part of the dactylus is distinctly higher and slightly more compressed compared to typical specimens of *G. annulipes*. That H. Milne Edwards’ (1852: pl. 4(18)) figure of the chela shows shorter and more tapering fingers with a small predistal pollex tooth is actually of secondary importance. Henri Milne Edwards (1852) thus almost certainly identified all his Javanese specimens with a higher dactylus to *G. perplexus* on this basis. It was A. Milne Edwards (1873: 274) who used the proportionately larger predistal pollex tooth as a character and identified New Caledonian specimens as *G. perplexus*, and he would very likely have also examined H. Milne Edwards’ (1852) specimens as well, including the two present MNHN specimens (although he made no mention of them).

We therefore here select the more intact male (CW 13.8 mm, PL 25.7 mm) (MNHN-B.12005) from Besukil, Java as the lectotype of *Gelasimus perplexus* H. Milne Edwards, 1852. This selection will ensure stability as it will preserve how the name is widely used in the future. The other presumptive syntype is here recognized as the paralectotype for the time being. The morphology of the lectotype of *Gelasimus perplexus* as defined here agrees with that of *Uca annulipes* var. *orientalis* Nobili, 1901 (p. 13, fig. A; type locality Buntal, Kuching, Sarawak, Malaysia) (Fig. 2C), especially in the large predistal pollex tooth and the high major dactylus from the base to the position of the adjacent predistal pollex tooth. The two taxa are thus clearly subjective synonyms. Serène (1973a: 138) considered *A. perplexa* (as *Uca annulipes* var. *orientalis*) to be an “intermediate form” of *A. annulipes* for specimens from Phuket, Singapore and Sulawesi, although he identified material from New

Caledonia as “*Uca (Minuca) lactea*”, probably because the specimens were small (max. CW 16.8 mm).

The shape of the major dactylus and the large predistal pollex tooth of the two specimens (Fig. 3A, B, E) are also typical of the large specimens examined (e.g., Fig. 8B, CW 14.9 mm; Crane 1975: fig. 18D–F), except in the case of regenerated major chelae (e.g., Fig. 8A, CW 17.3 mm; Fig. 8D, CW 12.0 mm) and the major chelae of young crabs (e.g., Fig. 8C, CW 12.5 mm; Fig. 8D). The G1 of the rehydrated (Fig. 6E, F) is within the range of variation of specimens from different regions (Crane 1975: fig. 19C–H).

As discussed before, *G. perplexus* H. Milne Edwards, 1852 has been identified as *G. annulipes* H. Milne Edwards, 1837 (Hilgendorf 1879; De Man 1888; Nobili 1906a b; Serène 1973a), if only based on the drawing of the major chela (H. Milne Edwards 1852: pl. 4(18)). As a result, the East African *Austruca occidentalis* (Naderloo, Schubart & Shih, 2016), a species very similar with *A. annulipes*, with only minor difference in minor chela and G1 (Naderloo et al. 2016), cannot be *G. perplexus* H. Milne Edwards, 1852 as well.

The synonymization of *Gelasimus perplexus* H. Milne Edwards, 1852 under *G. chlorophthalmus* H. Milne Edwards, 1837 by Kingsley (1880: 151–152) is not correct, because the morphology of the oblique ridge on inner palm between them is different (much higher with tubercles largest on highest point of the *Austruca lactea* complex (H. Milne Edwards 1852: pl. 4(15b, 16); Forest and Guinot 1961: fig. 151) vs. lower with few tubercles restricted on the lower apex of *Paraleptuca* (H. Milne Edwards 1852: pl. 4 (17a, 19, 20a); Forest and Guinot 1961: figs. 140–142, 146) (cf. Crane 1975: 98, 293).

Due to their similar morphology and coloration, the three common West Pacific species, *A. annulipes*, *A. lactea* and *A. perplexa*, are easily confused and the taxa may have been misidentified in various reports (see Crane 1975: 301–303). For example, after *A. perplexa* (as different names, see synonymy in *A. perplexa*) was confirmed to be distributed in Taiwan (Fukui et al. 1989), several old records of *A. lactea* were revised as *A. perplexa*, including in the offshore islands of Penghu and Dongsha (see Shih et al. 2015a: 190). In addition, *A. perplexa* was always identified as *A. annulipes* in many Singaporean booklets (Ng and Sivasothi 1999: 76; Ng et al. 2007: 75–76; Ng et al. 2008b: 102). Similarly, several old records of “*A. annulipes*” and “*A. lactea*” in Micronesia (Sakai 1936 1976; Miyake 1938 1939, 1940a b) should be referred to as *Paraleptuca crassipes* (White, 1847) and *A. perplexa*, respectively. This is based on the distribution and collecting records for the *A. lactea* complex (Crane 1975: 611–612, map 21; Takeda and Ueshima 2006).

Within the distribution of *A. perplexa*, Crane (1975: 295, figs. 19B, 20A–C, 41B) emphasized that the easternmost population (*i.e.*, from Samoa and Fiji) possesses several different characters, including the coloration of the major cheliped, relative width of the major dactylus, presence of a predistal triangular tooth on the major pollex, possession of tuberculate ridge on the major pollex, and the structures of the distal parts of both posterior and anterior flanges on the male first gonopod. Accordingly, we examined specimens from the easternmost populations and other populations, as well as the supposed syntypes of *A. perplexa* (MNHN-IU-2008-10646).

The fresh series of specimens now also show that the material from Fiji, Wallis & Futuna, and Samoa, while superficially similar to *A. perplexa* as defined here, are nevertheless sufficiently different morphologically to be recognized as a separate taxon. This distinction is supported by molecular evidence from the mitochondrial 16S rDNA and cytochrome oxidase subunit I (*COI*). We therefore propose that a new species be recognized from Fiji and the eastward islands, described herein as *Austruca citrus* n. sp.

MATERIALS AND METHODS

The systematics of the family Ocypodidae (including the fiddler crabs) revised by morphology as well as mitochondrial and nuclear markers (Shih et al. 2016b) is followed in this study (also see Sasaki 2019). Another system proposed recently (Rosenberg 2019) of splitting the subfamily Ocypodinae into Ocypodinae and Uciniae is not followed because the subfamily Uciniae he recognized was wholly based on an assumption that it may be monophyletic in the future. This is not supported by current available genetic data (Shih et al.

2016b). The subgeneric and tribal system proposed by Rosenberg (2019) is also not adopted here because we are not convinced that the groupings are justified based on the current knowledge. Some of the Rosenberg's groupings were based on the clades in Shih et al. (2016b) and others are probably paraphyletic (see Shih et al. 2016b).

Specimens of *Austruca perplexa* *sensu lato* were collected from localities in East Asia, Southeast Asia, and Oceania (Table 1; Fig. 1) and preserved in 70–95% ethanol. Specimens deposited in museums or institutes were also examined: Australian Museum, Sydney, Australia (AM); Biodiversity Research Museum, Academia Sinica, Taiwan (ASIZ); Museum National d'Histoire Naturelle, Paris, France (MNHN); Museum Zoologicum Bogoriense, West Java, Indonesia (MZB); Museo Zoologico dell'Università di Firenze, Italy (MZUF); Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL); Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University, Keelung, Taiwan (NTOU); Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands (RMNH); Senckenberg Museum, Frankfurt am Main, Germany (SMF); Queensland Museum, Brisbane, Australia (QM); Florida Museum of Natural History, University of Florida, Florida, USA (UF); and Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore (ZRC).

Morphological characters were illustrated with the aid of a drawing tube attached to a stereomicroscope. The abbreviation G1 is used for the male first gonopod. Measurements, in millimeters (mm), are of the carapace width (CW), carapace length (CL) and propodus length (= pollex length + manus length; PL) of the

Table 1. The haplotypes of *COI* and 16S rRNA genes of *Austruca citrus* n. sp. and *A. perplexa* (H. Milne Edwards, 1852), as well as the outgroups, from the Indo-West Pacific region. See MATERIALS AND METHODS for abbreviations of museums and universities

Species	Localities [site no.]	Catalogue no. of museum	Sample size	Haplotype of <i>COI</i>	DDBJ Access. no.	Sample size	Haplotype of 16S	DDBJ Access. no.
<i>A. citrus</i> n. sp.	Fiji: Viti Levu [1]	UF 1488; NCHUZOOL 15037	5	Ac-C1	LC508734	5	Ac1	LC508752
	Wallis & Futuna [2]	MNHN IU-2017-9122, IU-2017-9123; NCHUZOOL 14912, 15035	5	Ac-C2	LC150400	5	Ac2	LC150339
	Wallis & Futuna [2]	MNHN IU-2017-9122	1	Ac-C3	LC508735	1	Ac3	LC508753
	Wallis & Futuna [2]	MNHN IU-2017-9123	1	Ac-C4	LC508736	1	Ac4	LC508754
	Samoa [3]	SMF 5675				1	Ac2	LC150339
	Samoa [3]	SMF 5675				1	Ac5, 6	LC508755, LC508756

Table 1. (Continued)

major cheliped. The morphological terminology used essentially follows that of Crane (1975) and Davie et al. (2015). The gastric mill of the stomach was studied following the methods and terminology in Shih (2015). The scanning electron microscopy (SEM) mainly followed Shih et al. (1999).

Genomic DNA was isolated from the muscle tissue of legs using the GeneMark tissue and cell genomic DNA purification kit (Taichung, Taiwan). A region of approximately 510–550 base pairs (bp) of the 5'-end of the 16S rRNA gene was selected for amplification with a polymerase chain reaction (PCR) using the primers 1471 and 1472 (Crandall and Fitzpatrick 1996). A portion of the *COI* gene was amplified with PCR using the primers LCO1490, COL14, HCO2198 and COH6 (Folmer et al. 1994; Roman and Palumbi 2004; Schubart and 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 another extension for 10 min at 72°C. Sequences were obtained by automated sequencing (Applied Biosystems 3730) and aligned with the aid of the MUSCLE function of MEGA (vers.

10.0.5, Kumar et al. 2018), after verification with the complementary strand. Sequences of different haplotypes have been deposited in the DNA Data Bank of Japan (DDBJ), with other sequences published in earlier papers of HTS (Table 1).

The best-fitting model for the *COI* dataset was obtained from jModelTest (vers. 0.1.1, Posada 2008) selected by the Bayesian information criterion (BIC) and was subsequently applied for the Bayesian inference (BI) analysis. BI was performed with MrBayes (vers. 3.1.2, Ronquist et al. 2012), and the search was run with four chains for 10 million generations, with trees sampled every 1000 generations. The chains were deemed to have converged when the average standard deviation of split frequency values fell below the recommended 0.01 (Ronquist et al. 2019), with the first 5000 trees accordingly discarded as burnin. The maximum likelihood (ML) analysis was calculated by MEGA, with the model GTR+I+G and 2000 bootstrap replications (heuristic method = nearest-neighbor-interchange (NNI), initial tree = default-NJ/BioN, branch swap filter = Moderate). A maximum parsimony (MP) consensus tree was also constructed using MEGA, with 2000 bootstrap

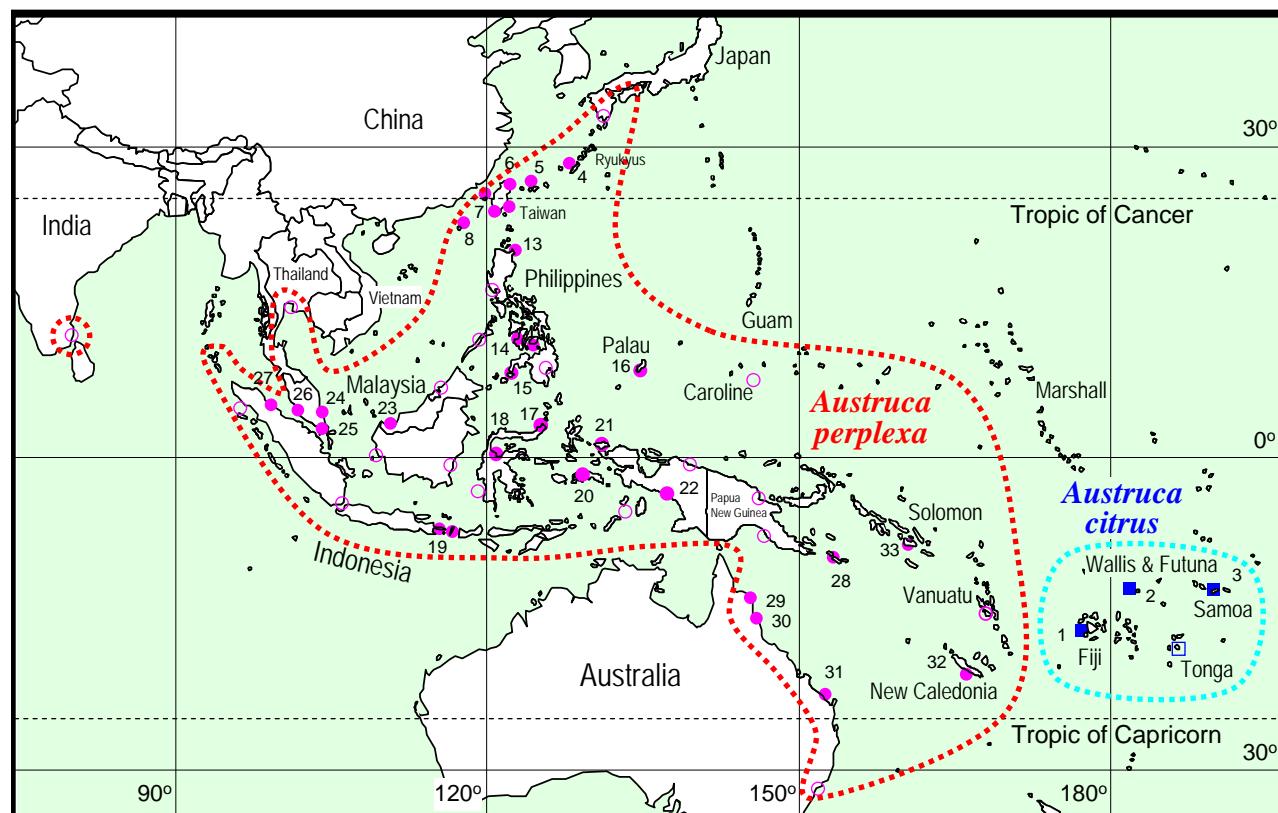


Fig. 1. Collection sites for specimens of *Austruca citrus* n. sp. and *A. perplexa* (H. Milne Edwards, 1852) used in this study: blue solid squares (nos. 1–3) for *A. citrus* and pink solid circles (nos. 4–33) for *A. perplexa* (see Table 1). Blue empty square and pink empty circles indicate additional records of the two species from other references (see synonymy under *A. perplexa*). Different lines indicate the updated ranges of the two species.

reiterations of a simple heuristic search, TBR branch-swapping (tree bisection-reconnection) (100 random-addition sequence replications; max no. of trees to retain = 10000). Other analyses of 16S rDNA and *COI*, the nucleotide composition, variable and parsimony informative positions were calculated using MEGA; and the pairwise estimates of Kimura's (1980) 2-parameter (K2P) distance for inter- and intraspecific genetic diversities were calculated using the PAUP program (vers. 4.0b10, Swofford 2003).

For morphometric analyses, the following measurements of males (except the specimens with apparent regenerated short cheliped) were used: CW and PL. Because the CWs of male specimens from the Fiji-Samoa region ranged from 8.3 to 14.6 mm, the measurements of specimens with CW between 8.3–14.6 mm from other areas were analyzed separately. Three groups of specimens were used in the analyses: 38 males (CW 8.3–14.6 mm) of *A. citrus*, 175 males (CW 6.7–17.5 mm) of all *A. perplexa* and 135 males of *A. perplexa* with CW between 8.3–14.6 mm. The regression lines of PL on CW were calculated for the three groups and their slopes and intercepts were compared by one-way ANCOVA (analysis of covariance) using the software PAST (vers. 3.2.3, Hammer et al. 2001).

RESULTS

TAXONOMY

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

***Austruca perplexa* (H. Milne Edwards, 1852)**
(Figs. 2A, C, D, 3, 5A, C, 6E–I, 7A–C, F, G, 8A–D, 9A–C, 10)

Gelasimus perplexus H. Milne Edwards, 1852: 150, pl. 4(18) [type locality: Java]; A. Milne-Edwards 1873: 274 [New Caledonia]; Hilgendorf 1879: 806.
Gelasimus annulipes – Kingsley 1880: 148 [part; Australia]. (not *Gelasimus annulipes* H. Milne Edwards, 1837).
Uca annulipes var. *orientalis* Nobili, 1901: 13, fig. A [type locality: Buntal, Kuching, Sarawak, Malaysia]; Nobili 1903: 21 [Indonesia: Samarinda, Kalimanda Timur]; MacCagno 1928: 36, fig. 21 [Malaysia: Buntal, Kuching, Sarawak]; Nobili 1906b: 151 [Malay Archipelago]; Oliveira 1939: 131 [list; Borneo].
Uca perplexa – Rathbun 1910: 306, pl. 1(1–2) [Indonesia: Maluku; Sulawesi]; Rathbun 1924: 10; Barnwell 1980: 957 [central Philippines; Indonesia: Jakarta]; Davie 1982: 205 [Australia]; George and Jones 1982: 83, figs. 6, 7b, 54a–f, 58e [Australia]; Takeda 1982: 209 [Japan: Ryukyus]; Ho et al. 1993: 20 [Taiwan: Taitung]; Yamaguchi and Baba 1993: 506 [Japan: Okinawa];

Jones and Morgan 1994: 199, 1 unnumbered fig. [eastern Australia]; Okutani 1994: 214, fig. 1 [Japan: Ryukyus]; Tan and Ng 1994: 83 [Singapore; Malay Peninsula]; Yamaguchi 1994: 165 [Malaya; Indonesia; Thailand]; Wang and Liu 1996: 61, 2 unnumbered figs. [Taiwan]; Hung 2000: 140–1, figs. 438–439 [Penghu, Taiwan]; Lee 2001: 103, 3 unnumbered figs. [Taiwan]; Ng et al. 2001: 37 [list; Taiwan]; Rosenberg 2001: 860 [Philippines: Batangas Bay, Luzon]; Yoshigou 2001: 4, fig. 2, pl. 1N [Japan: Ryukyus]; Wang and Liu 2003: 82, figs. 84–86 [Taiwan]; Shen and Jeng 2005: 166, 1 unnumbered fig. [Taiwan: Penghu]; Takeda and Ueshima 2006: 103 [Taiwan: Penghu; Japan: Okinawa; Palau]; Katsu 2007: 92, 5 unnumbered figs. [Japan: Amami, Ryukyus]; Naiyanetr 2007: 132 [Thailand]; Ng and Richer de Forges 2007: 326 [New Caledonia; list]; Juncker and Poupin 2009: 14, 75, pl. 5 (3 unnumbered figs.) [New Caledonia]; Shih et al. 2009: 376 [Taiwan]; Barnes 2010: 250, fig. 1 [Indonesia: Ambeuan, Sulawesi]; Liu and Wang 2010: 41, 3 unnumbered figs. [Taiwan]; Poupin 2010: 75 [part; New Caledonia]; Shih 2012: 66, figs. 94–96 [Taiwan: Dongsha]; Shih et al. 2013: 643 [Taiwan]; Fujita and Uyeno 2015: 95, fig. 2A, B [Japan: Ryukyus]; Kumaralingam et al. 2017: 121, 1 unnumbered fig. [India: Great Nicobar].

Uca annulipes subsp. *orientalis* – Tesch 1918: 37 [list].

Uca lactea – Boone 1934: 199, pl. 103 [New Caledonia]; Miyake 1936: 511 [Japan: Yaeyama, Ryukyus]; Sakai 1936: 171 [Palau]; Miyake 1938: 109 [Palau]; Miyake 1939: 222 [Palau]. (not *Ocypode (Gelasimus) lactea* De Haan, 1835).

Austruca orientalis – Bott 1973: 322 [list].

Uca (Minuca) lactea – Serène 1973a: 132, figs. 5–7, 23–29, pls. 5, 7A, C, D [New Caledonia]. (not *Ocypode (Gelasimus) lactea* De Haan, 1835).

Uca (Minuca) annulipes form *intermedia* – Serène 1973a: 138, figs. 19 (?), 20–22 [Thailand: Phuket; Singapore; Indonesia: Sulawesi]; Serène 1973b: 359 [key]. (not *Gelasimus annulipes* H. Milne Edwards, 1837).

Uca (Celuca) lactea perplexa – Crane 1975: 300, figs. 18D–F, 19C–H, 26D, 31E, 54K, KK, 69C [part; west of Samoa and Fiji]; Miyake 1983: 163, pl. 55(1) [Japan: Ryukyus]; Nagai and Nomura 1988: 55, 1 unnumbered fig. [Japan: Ryukyus]; Shih 1994: 103, fig. 69 [Taiwan].

Uca (Celuca) lactea lactea – Sakai 1976: 608 [part; Japan: Yaeyama, Ryukyus]; Wang 1984: 42 [Taiwan: Pingtung]. (not *Ocypode (Gelasimus) lactea* De Haan, 1835).

Uca lactea perplexa – Fukui et al. 1989: 227 [Taiwan: Pingtung]; Chen 2001: 208, 1 unnumbered fig. [Taiwan]; Jaroensutasinee et al. 2003: 1–2 [Thailand]; Nakasone and Irei 2003: 269, fig. 31F [Japan: Ryukyus]; Jaroensutasinee and Jaroensutasinee 2004: 536 [Thailand].

Uca annulipes – Ng and Sivasothi 1999: lower image on p. 76 [Singapore]; Ng et al. 2007: upper image on p. 75, lower image on p. 76 [Singapore]; Ng et al. 2008b: upper right image on p. 102 (Singapore). (not *Gelasimus annulipes* H. Milne Edwards, 1837).

Uca perplexa [sic] – Nhuong 2003: 8 [southern Vietnam].

Uca (Paraleptuca) perplexa – Beinlich and von Hagen 2006: 26 [list; part]; Ng et al. 2008a: 241 [list; part]; Rahayu and Setyadi 2009: 106, 1 unnumbered fig., 1 fig. on p. 104 [Indonesia: Papua]; Murniati and Pratiwi 2015: 71, 2 unnumbered figs., figs. 6.1, 8.12A, 8.13A [Indonesia].

Uca (Austruca) perplexa – Naderloo et al. 2010: 24, figs. 16a–g, 17a, b, 18c–f [part; west of Fiji]; Toyota and Seki 2014: 226, 4 unnumbered figs. [Japan: Ryukyus]; Shih et al. 2016a: 62, fig. 2C–E [Taiwan; Japan: Ryukyus].

Austruca perplexa – Shih et al. 2015a: 189, figs. 152–156 [Taiwan]; Shih et al. 2016b: 153, 168, fig. 8F [part; Taiwan; New

Caledonia]; Ng et al. 2017: 123 [list; Taiwan]; Fujita 2018: 72, fig. 5H [Japan: southern Ryukyus]; Trivedi et al. 2018: 54 [list; part; Andaman and Nicobar islands]; Sasaki 2019: 12436 [list; part]; Tanase and Wada 2019: 1 [Japan: Wakayama]; Wada 2019a: e142 [southern Vietnam]; Wada 2019b: e146 [Indonesia: Sumatra; Bali; Sulawesi; Halmahera; Ambon]; Shih 2020: 140, figs. 172–173 [Taiwan: Dongsha].
 ? *Uca perplexa* – Apreshgi et al. 2016: 102, fig. 1a, b [southwest India]. (see DISCUSSION).
 ? *Uca (Austruca) perplexa* – Patra et al. 2017: 209 [India: West Bengal]. (see DISCUSSION).
Austruca (Austruca) perplexa – Rosenberg 2019: 734 [list; part].
 Not *Gelasimus perplexus* – Heller 1865: 38, pl. 5(4) [India: Madras; Ceylon]; A. Milne-Edwards 1873: 274 [India]. (= *Gelasimus variegatus* Heller, 1862; see Shih et al. 2019).
 Not *Gelasimus annulipes* var. *orientalis* – Laurie 1906: 426, fig. 11 [Sri Lanka]. (= *Gelasimus annulipes* H. Milne Edwards, 1837).
 Not *Uca annulipes* var. *orientalis* – Stephensen 1946: 189 [Persian Gulf]. (= *Uca annulipes iranica* Pretzmann, 1971).
 Not *Uca annulipes* var. *orientalis* – Barnard 1950: 97 [Mozambique and South Africa]. (= *Uca occidentalis* Naderloo, Schubart & Shih, 2016).

Material examined: lectotype, ♂ (dry, CW 13.8 mm, PL 25.7 mm) (MNHN-IU-2008-10646 = MNHN-B.12005), M. Besukiil, Java, Indonesia. Paralectotype, 1 ♂ (rehydrated, broken, CW ~15–16 mm, PL 28.2 mm), same data as lectotype.

Others: **Ryukyus, Japan:** 1 ♂ (15.8 mm) (NCHUZOOOL 14652), Oura Bay, Okinawa, 13 Nov. 1975; 10 ♂♂ (11.6–14.7 mm) (NCHUZOOOL 15038), Oura Bay, Okinawa, 6 May 2012; 3 ♂♂ (9.6–15.1 mm), 1 ♀ (7.9 mm) (NCHUZOOOL 14654), Yuhi River (= R.), Okinawa, 19 Mar. 1992; 16 ♂♂ (11.2–17.5 mm) (NCHUZOOOL 14646), Manzamo, Okinawa, coll. P.-C. Tsai, 7 Jul. 2009; 4 ♂♂ (11.0–14.2 mm) (NCHUZOOOL 14642), Sashiki, Okinawa, 28 Dec. 2011; 1 ♂ (7.1 mm), 2 ♀♀ (6.5–10.6 mm) (NCHUZOOOL 14650), Okinawa, 9 Jul. 2009; 2 ♂♂ (13.4–16.2 mm) (NCHUZOOOL 14752), Nagura, Ishigaki, coll. T. Naruse, 23 Jun. 2004; 5 ♂♂ (13.5–15.6 mm), 2 ♀♀ (12.8–15.3 mm) (NCHUZOOOL 14648), Funaura Bay, Iriomote, coll. P.-C. Tsai, 8 Jul. 2011. **Taiwan:** 1 ♂ (13.5 mm) (NCHUZOOOL 14647), 1 ♀ (12.6 mm) (NCHUZOOOL 14674), Lanyang R. estuary, Yilan, 25 Jul. 2004; 4 ♂♂ (16.6–17.6 mm) (NCHUZOOOL 14677), 3 ♂♂ (12.2–13.0 mm), 2 ♀ (13.7–13.7 mm) (NCHUZOOOL 14643), Yanshuei R. estuary, Tainan, coll. J.-H. Lee et al., 4 Aug. 2009; 2 ♂♂ (14.4, 15.6 mm), 1 ♀ (14.5 mm) (NCHUZOOOL 14637), Dingtouer Shoal, Cigu, Tainan, coll. J.-H. Lee, 14 Aug. 2009; 2 ♂♂ (14.3–17.2 mm), 1 ♀ (15.7 mm) (NCHUZOOOL 14645), Gaoping R. estuary, Kaohsiung, coll. H.-T. Shih, 29 Apr. 1998; 1 ♂ (14.5 mm), 1 ♀ (12.0 mm) (NCHUZOOOL 14640), Dapengwan, Pingtung, 20 Jul. 2007; 2 ♂♂ (9.3–11.8 mm), 1 ♀ (12.9 mm) (NCHUZOOOL 13252), 1 ♂ (10.6 mm)

(NCHUZOOOL 13253), Baoli R. estuary, Pingtung, coll. H.-T. Shih, 7 Jul. 2001; 1 ♂ (14.0 mm), 1 ♀ (12.1 mm) (NCHUZOOOL 14641), Fengcueisha, Kenting, Pingtung, 18 May 2001; 3 ♂♂ (14.2–17.2 mm) (NTOU), Dulanwan, Taitung, coll. P.-H. Ho, 7 Apr. 2001; 1 ♂ (15.1 mm) (NCHUZOOOL 14675), Shihcuyuan, Penghu, 21 Jun. 2006; 2 ♂♂ (13.3–16.5 mm) (NCHUZOOOL 14639), Chihsia, Siyu, Penghu, 18 May 2007; 3 ♂♂ (15.8–16.4 mm) (NCHUZOOOL 14649), Chihsia, Siyu, Penghu, 19 May 2007; 3 ♂♂ (12.2–17.5 mm), 2 ♀♀ (10.4–15.1 mm) (NCHUZOOOL 14636), Dongsha Island, coll. C.-Y. Chung and Y.-H. Huang, 7 Jun. 2011; 1 ♂ (16.6 mm) (NCHUZOOOL 14651), Dongsha Island, 19 Nov. 2011; 1 ♀ (8.8 mm) (NCHUZOOOL 15039), Dongsha Island, 20 Nov. 2011; 1 ♂ (11.8 mm) (NCHUZOOOL 15066), Dongsha Island, 12 Feb. 2012; 1 ♂ (13.9 mm) (NCHUZOOOL 15039), Dongsha Island, 23 Mar. 2012; 1 ♂ (17.6 mm) (NCHUZOOOL 14644), 26 May 2012; 1 ♂ (11.0 mm) (NCHUZOOOL 15067), Dongsha Island, 18 Nov. 2012. **Philippines:** 6 ♂♂ (10.0–13.5 mm) (ZRC 2020.0284), Municipality of Santa Ana, Cagayan, coll. T. Naruse and J. C. E. Mendoza, 23 Apr. 2007; 2 ♂♂ (10.5–12.3 mm), 1 ♂ (broken) (NCHUZOOOL 15043), Puerto Galera, Mindoro, coll. K. Wong, 9 Jun. June 2009; 2 ♂♂ (12.7–15.2 mm) (RMNH.CRUS.D.35194), Tablas Island, 14 Sep. 1981; 3 ♂♂ (10.1–12.6 mm) (ZRC 2008.0721), Okoy R., Sibulan, Negros, coll. N. K. Ng et al., 5 Jul. 2002; 1 ♂ (13.1 mm) (ASIZ 74979), Kawasan, Cebu, coll. H.-C. Liu, 25 Nov. 2001; 9 ♂♂ (8.7–12.8 mm), 4 ♀♀ (9.1–11.7 mm) (NCHUZOOOL 15063), 2 ♀♀ (9.1–10.6 mm) (NCHUZOOOL 15062), Matutinao R. Badian, Cebu, coll. H.-T. Shih et al., 6 Sep. 2003; 2 ♂♂ (9.9–12.9 mm), 2 ♀♀ (11.1–12.3 mm) (NCHUZOOOL 15041), Blue Water Club, Cebu, coll. J.-D. Lee, 20 Feb. 1998; 6 ♂♂ (10.9–12.9 mm) (ASIZ 72886), Bohol, coll. H.-C. Liu, 20 Feb. 2003; 3 ♂♂ (12.0–13.3 mm) (NCHUZOOOL 15042), Bohol, coll. H.-T. Shih et al., 2 Sep. 2003; 1 ♀ (8.3 mm) (ASIZ CR 74975), Loboc R., Bohol, coll. H.-C. Liu, 21 Feb. 2003; 1 ♀ (8.4 mm) (ASIZCR), Loboc R., Bohol, coll. H.-C. Liu, 18 May 2004; 1 ♂ (14.8 mm) (ZRC 2020.0285), Panglao, Bohol, 4 Jun. 2004; 2 ♂♂ (12.2–16.1 mm), 1 ♂ (broken) (ZRC 2020.0286), Dumanhog, Siquijor, coll. N. K. Ng and J. L. Jozeph, 26 Jan. 2005; 1 ♀ (10.8 mm) (NCHUZOOOL 15044), Pago R., Mindanao, coll. H.-C. Liu, 13 Jul. 2007; 1 ♂ (11.5 mm), 1 ♀ (9.1 mm) (NCHUZOOOL 15045), Mindanao, coll. H.-C. Liu, 15 Jul. 2007; 4 ♂♂ (12.6–14.6 mm), 1 ♂ (broken) (NCHUZOOOL 15064), 1 ♂ (9.7 mm), 7 ♀♀ (8.4–11.8 mm) (NCHUZOOOL 15065), Zamboanga, Mindanao, coll. C. K. R. Ong, 10 Jun. 2006. **Palau:** 1 ♀ (10.9 mm) (ZRC 2020.0287), coll. B. Y. Lee, 13 Jan. 2019. **Malaysia:** 1 ♂ (17.3 mm) (NCHUZOOOL 15046),

Buntal, Kuching, Sarawak, coll. H.-T. Shih et al., 28 Jul. 2010; 1 ♂ (15.9 mm) (NCHUZOOL 15047), 7 ♀ ♀ (10.3–13.5 mm) (NCHUZOOL 15048), Petra Jaya, Kuching, Sarawak, coll. H.-T. Shih et al., 27 Jul. 2010; 1 ♂ (11.9 mm), 3 ♀ ♀ (9.6–9.8 mm) (NCHUZOOL 15050), Santubong, Kuching, Sarawak, coll. H.-T. Shih et al., 26 Jul. 2010; 5 ♂ ♂ (13.2–15.4 mm), 1 ♀ (11.3 mm) (NCHUZOOL 15052), Jeram, Selangor, coll. A. Sasekumar, 21 Mar. 2012; 11 ♂ ♂ (11.3–15.7 mm) (NCHUZOOL 15053), Port Dickson, Negeri Sembilan, coll. A. Sasekumar, 29 Feb. 2012; 1 ♂ (9.4 mm) (NTOU), Parit Jawa Lant, Muar, Johor, coll. P.-H. Ho, 19 Jul. 2001; 8 ♂ ♂ (8.7–12.2 mm), 1 ♀ (10.6 mm) (NCHUZOOL 15054), Tumpat, Kelantan, coll. A. Sasekumar, 28 Aug. 2013; 1 ♂ (11.6 mm) (NCHUZOOL 15055), Mersing, Johor, coll. H.-T. Shih et al., 19 Jul. 2010; 5 ♂ ♂ (7.9–14.4 mm) (NCHUZOOL 15056), Mersing, Johor, coll. H.-T. Shih et al., 20 Jul. 2010. **Singapore:** 2 ♂ ♂ (10.0–12.2 mm) (ZRC 1987.346–365), west coast, coll. S. Harminto, 18 Sep. 1986; 2 ♂ ♂ (12.0–15.3 mm) (ZRC 2006.0038), Pulau Hantu, Spore, coll. Z. Jaafar, 19 Apr. 2002; 1 ♂ (15.2 mm) (ZRC 2020.0288), Sultan Shoal, coll. P. K. L. Ng, Dec. 2008; 1 ♂ (14.9 mm) (NCHUZOOL 15057), 3 ♂ ♂ (14.0–14.1 mm) (NCHUZOOL 15058), Sarimbun, coll. H.-T. Shih, 4 Mar. 2012. **Indonesia:** 1 ♂ (13.1 mm) (ZRC 2000.1742), between Mapane and Poso mangroves, Sulawesi, coll. C. D. Schubart, 20 Jan. 2000; 1 ♂ (10.4 mm) (ZRC 2009.0928), Bunaken, Sulawesi, coll. N. K. Ng and C. Y. Lai, 18 Sep. 2003; 2 ♂ ♂ (11.2–12.7 mm) (ZRC 2020.0289), Bunaken, Sulawesi, coll. N. K. Ng and C. Y. Lai, 23 Sep. 2003; 2 ♂ ♂ (14.3–14.5 mm) (MZB Cru 3669), Belawan, Medan, Sumatra, coll. Arifin, 27 Dec. 2011; 1 ♂ (13.7 mm) (MZUF 4294), Nusa Dua, Bali, coll. Feb. 1987; 11 ♂ ♂ (8.4–11.0 mm), 4 ♀ ♀ (9.5–11.3 mm), 1 ovig. ♀ (9.1 mm) (NCHUZOOL 15059), Nusa Dua, Bali, coll. H.-T. Shih, 16 Jul. 2014; 4 ♂ ♂ (10.9–14.2 mm), 4 ♀ ♀ (8.7–11.9 mm) (NCHUZOOL 15060), Gerokgak, Bali, coll. H.-T. Shih, 18 Jul. 2014; 2 ♂ ♂ (13.3–13.4 mm) (ZRC 2017.0916), Tanjung Ringgit Temiak, Lombok, 13 Feb. 2002; 4 ♂ ♂ (10.4–16.3 mm), 1 ♂ (broken) (ZRC 2009.0933), Kuta, Lombok, coll. Z. Jaafar and A. Anker, 11 Feb. 2002; 5 ♂ ♂ (11.2–12.0 mm) (SMF 24578), Amboin Bay, Ambon, Maluku, coll. A. Ratraubun, 12 Oct. 1998; 4 ♂ ♂ (11.5–14.4 mm) (ZRC 2020.0290), Ambon, coll. H. H. Tan, 19 Aug. 2012; 2 ♂ ♂ (14.9–15.3 mm) (MZB Cru 1685), Warsamdin beach, Waigeo Island, Papua Barat, West Papua, coll. C. M. Sidabalok, 4 Jun. 2007; 2 ♂ ♂ (12.7–15.6 mm) (MZB Cru 3906), Kamora, Papua Barat, West Papua, coll. D. L. Rahayu, no date. **Papua New Guinea:** 1 ♂ (6.8 mm), 3 ♀ ♀ (8.1–9.5 mm) (UF 2333), Milne Bay, Louisiade Archipelago, coll. G.

Paulay, 4 Jun. 1998. **Australia:** 3 ♂ ♂ (11.4–15.0 mm) (SMF 17148), Tannum Sands 25 km from Gladstone, sand mangroves, coll. G. Hartmann and G. Hartmann-Schröder, 28 Jan. 1976; 2 ♂ ♂ (8.7–10.0 mm) (QM W18212), Starcke River mouth, Queensland, coll. P. Davie, J. Short and A. Humpherys, 13 Nov. 1992; 1 ♂ (12.5 mm) (QM W19270), Urangan boat harbor, Hervey Bay, Queensland, coll. P. Davie, J. Short and A. Humpherys, 25 Oct. 1993; 1 ♂ (12.0 mm) (ZRC 1995.966), Thomatis Creek mouth (16.49.8S, 145.43.8E), coll. P. Davie, J. Short and A. Humpherys, 30 Oct. 1993. **New Caledonia:** 4 ♂ ♂ (6.7–13.5 mm), 3 ♀ ♀ (7.1–9.5 mm) (MNHN-IU-2017-9118), CRISP 2009, st. 6, Koné Mangrove IFREMER, coll. J. Poupin and M. Juncker, 9 Mar. 2009; 1 ♂ (7.3 mm) (MNHN-IU-2017-9119), st. 8, Mangrove Oundjo Voh, coll. J. Poupin and M. Juncker, 11 Mar. 2009; 2 ♂ ♂ (8.9–10.2 mm), 2 ♀ ♀ (7.9–12.6 mm) (MNHN-IU-2017-9120), st. 9, Presqu'île Pindai, coll. J. Poupin and M. Juncker, 12 Mar. 2009; 1 ♂ (9.0 mm) (NCHUZOOL 13564), 2 ♂ ♂ (9.7–10.5 mm), 1 ♂ (broken) (NCHUZOOL 13573), Ouano Bay, coll. B. Richer de Forges, 30 Nov. 2008; 2 ♂ ♂ (11.0–11.9 mm) (NCHUZOOL 15061), coll. B. Richer de Forges, no date. **Solomon Islands:** 9 ♂ ♂ (10.5–15.5 mm), 1 chela, 2 ♀ ♀ (12.0–14.9 mm) (AM P98278), Guadalcanal, coll. R. T. Springthorpe, coll. McCoy Society, 7 Oct. 1991.

Diagnosis: Male. Carapace (Figs. 3D, 5A, 7A–C) subrectangular, smooth; front broad; anterolateral angles (= external orbital angles) triangular, directed anterolaterally; anterolateral margins moderately convergent, short; dorsolateral margins clear, long. Major cheliped (Figs. 2C, D, 3A, B, E, 5C, 8A–D) without groove on outer fingers; pollex narrower than dactylus for entire length, with moderate to large predistal triangular tooth; dactylus wider at base, narrower toward distal part, then arched and tapering in position of adjacent predistal pollex tooth. G1 (Fig. 6E–I) with strong torsion; thumb moderately long, reaching flange base, distal parts of both flanges broad, posterior flange longer, broader than anterior. Urocardiac ossicles of gastric mill (Fig. 9A–C) moderately complex, with 3 or 4 pairs of transverse ridges of median tooth, separated by gaps reached deeply near central ridge, on posterior tooth plate; 2 pairs of cusps on stem region.

Female: Carapace (Fig. 7F–G) with anterolateral region swollen, anterolateral angle sharper triangular, directed anterolaterally.

Size: Largest male CW 37.5 mm, CL 19.5 mm, PL 11.5 mm (Ryukyu); largest female CW 16.0 mm, CL 10.0 mm (Singapore) (Crane 1975).

Color in life: Adults with carapace marbled transversely with brown (or dark brown) and white;

entire major cheliped from pink, yellow to yellowish white, fingers white; walking legs marbled with brown and white; most females with carapace and legs with homogenous white or brownish yellow (Fig. 10).

Distribution: Indo-West Pacific: Nicobar Islands, Indonesia, Malay Peninsula, Borneo, Thailand, Cambodia, Vietnam, Taiwan, Japan, Philippines, Palau, New Guinea, Australia, Solomon and New Caledonia (Fig. 1).

Remarks: See Remarks under *Austruca citrus* for the differences between *A. perplexa* and the closely related *A. citrus* n. sp.

Austruca citrus n. sp.

(Figs. 4, 5B, D, E, 6A–D, J, 7D–E, H, 8E–H, 9D, 11, 12A, B)
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Gelasimus annulipes – Miers 1886: 244 [part; Fiji]; Ortmann 1894: 758 [Samoa].

Uca lactaea [sic] – Pesta 1913: 57 [Samoa].

Uca lactea – Balss 1938: 76 [Fiji].

Uca (Celuca) lactea perplexa – Crane 1975: 292, figs. 18D–F, 19B,

20A–C, 26D, 31E, 54K, KK, 69C, pl. 39E–F [part; Samoa; Fiji].
Uca (Paraleptuca) perplexa – Beinlich and von Hagen 2006: 26 [list; part]; Ng et al. 2008a: 241 [list; part].

Uca perplexa – Poupin and Juncker 2008: 35, fig. 9C [Wallis & Futuna]; Poupin 2010: 75 [part; Wallis & Futuna]; Weis and Weis 2013: fig. 1 [Fiji].

Uca (Austruca) perplexa – Naderloo et al. 2010: 24 [part; Fiji; Tonga; Samoa].

Austruca perplexa – Shih et al. 2016b: 153, 168 [part; Wallis & Futuna]; Sasaki 2019: 12436 [list; part].

Austruca (Austruca) perplexa – Rosenberg 2019: 734 [list; part].

Material examined: Holotype: ♂ (10.9 × 6.7 mm, PL 17.6 mm) (MNHN-IU-2017-9121), Wallis & Futuna, CRISP 2007, st. 24, coll. A. Malau, E. Liufau and C. Manry, Jan. 2010. Paratypes: Wallis & Futuna: 1 ♂ (11.1 mm), 2 ♀♀ (8.4–11.7 mm) (MNHN-IU-2017-9122), Halalo mangrove de Halalo, near gas terminal, coll. J. Poupin and M. Juncker, 23 Oct. 2007; 13 ♂♂ (8.5–12.7 mm), 1 ♀ (10.4 mm) (MNHN-IU-2017-9123), same data as holotype; 1 ♂ (11.3 mm) (NCHUZOOL 14912), CRISP 2007, st. 29, coll. J. Poupin and M. Juncker, 25 Oct. 2007; 3 ♂♂ (8.3–10.1 mm) (NCHUZOOL 15035), 3 ♂♂

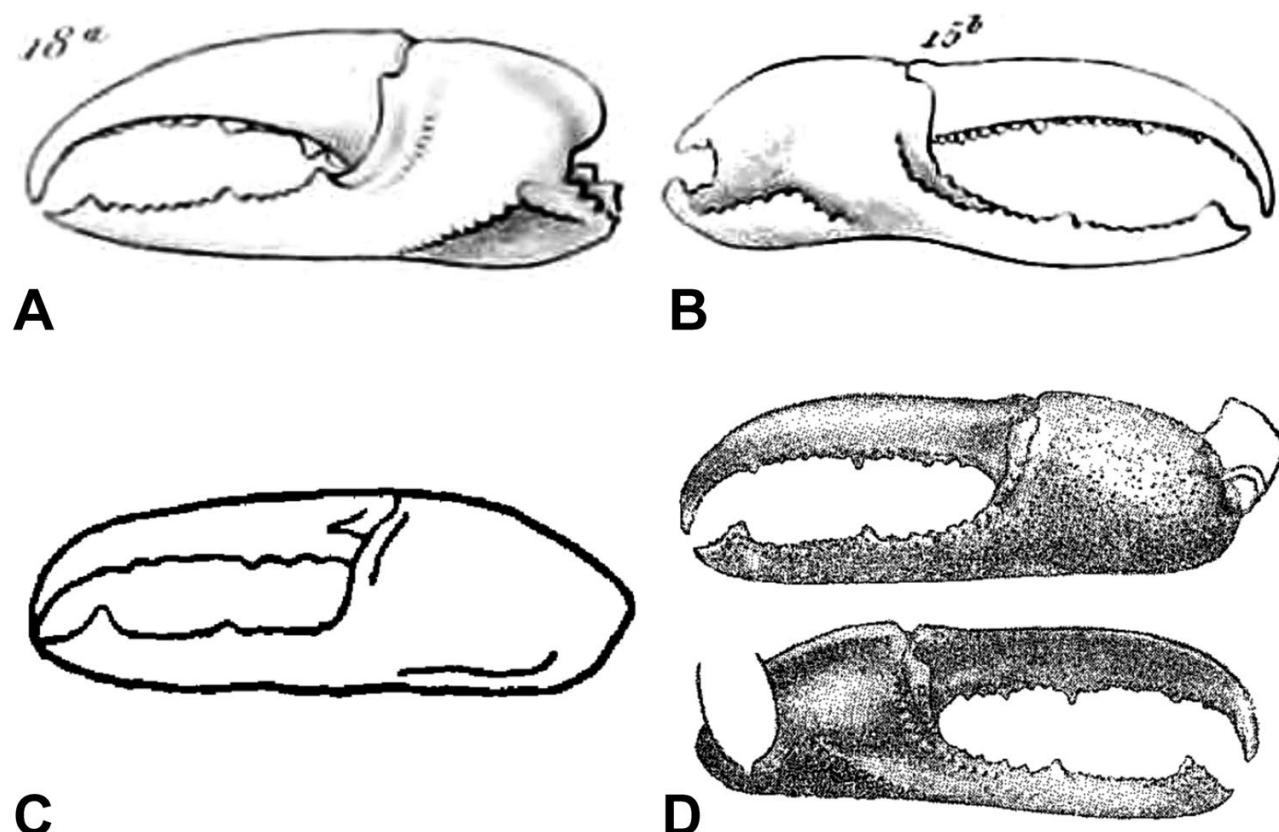


Fig. 2. Illustrations of syntypes of *Gelasimus perplexus*, *G. annulipes* and *Uca annulipes* var. *orientalis* (A–C), and specimen of *A. perplexa* from Borneo (D). A, *Gelasimus perplexus* H. Milne Edwards, 1852 (after H. Milne Edwards 1852: pl. 4(18a)); B, *Gelasimus annulipes* H. Milne Edwards, 1837 (after H. Milne Edwards 1852: pl. 4(15b)); C, *Uca annulipes* var. *orientalis* Nobili, 1901 (after Nobili 1901: fig. A); D, specimen from Buntal, Kuching, Sarawak, Malaysia (after Maccagno 1928: fig. 21).

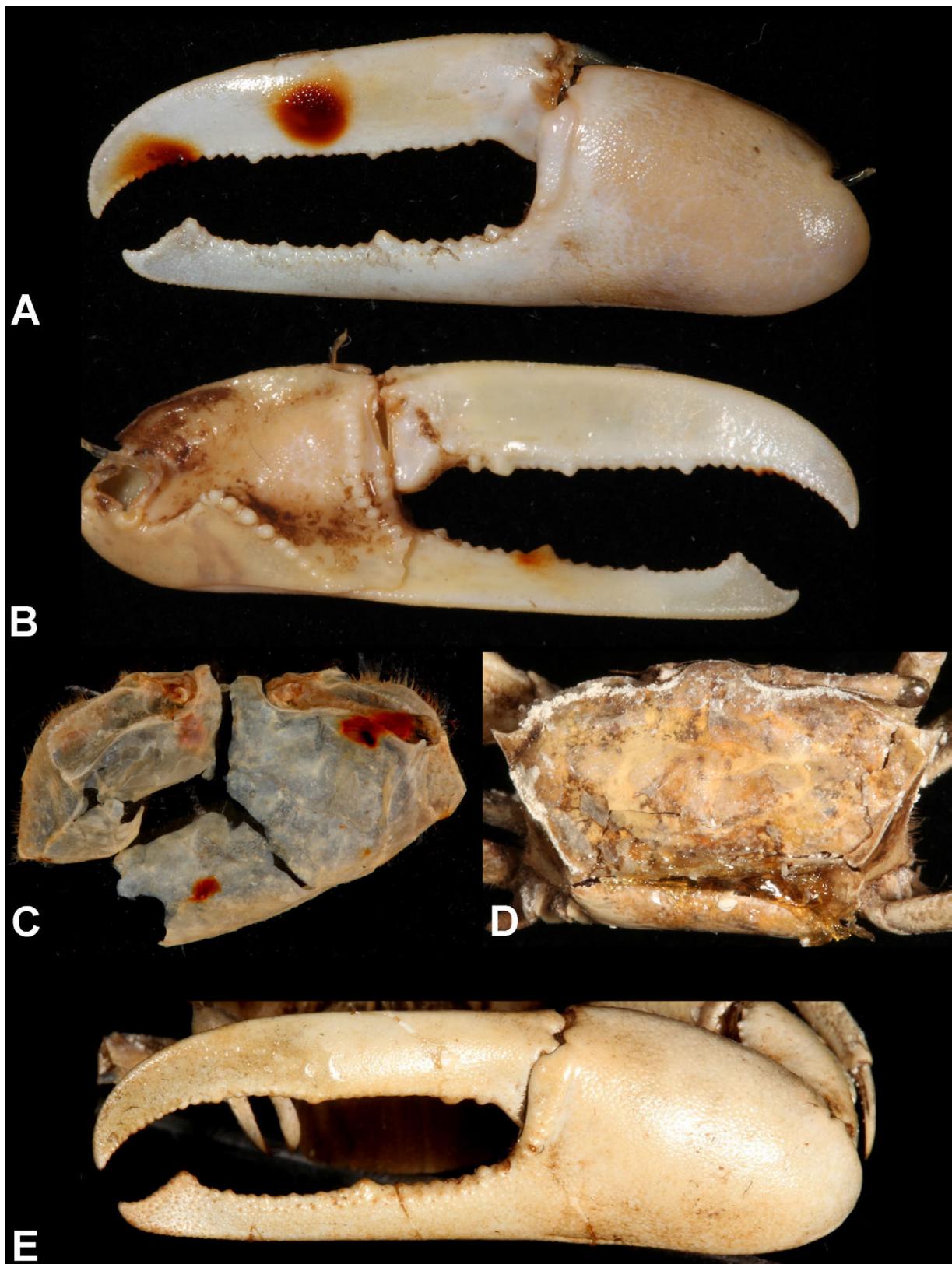


Fig. 3. The syntypes of *Gelasimus perplexus* H. Milne Edwards, 1852 (MNHN-IU-2008-10646). A–C, male paralectotype, rehydrated specimen; D–E, male lectotype, dry specimen. A, B, outer and inner surfaces of major cheliped (PL 17 mm); C, broken carapace, CW ~15–16 mm; D, carapace, CW 13.8 mm; E, outer surface of major cheliped, PL 25.7 mm.

(11.3–11.90 mm) (NCHUZOOL 15036), same data as holotype.

Others: **Fiji:** 1 ♂ (12.9 mm) (UF 3843), Viti Levu Island (= I.), coll. L. Kirkendale and V. Bonito, 18 Sep. 1982; 4 ♂♂ (9.6–11.0 mm) (UF 1488), 1 ♂ (11.6 mm) (NCHUZOOL 15037), Viti Levu I., coll. G. Paulay, 19 Oct. 2001; 1 ♂ (8.7 mm) (ZRC 2019.1320), Suva point beach, Suva, coll. B. Y. Lee and B. Rashni, 22 Jul. 2019; 1 ♂ (13.6 mm) (ZRC 2019.1316), 3 ♂♂ (8.6–11.9 mm) (ZRC 2019.1319), Nasoso mangroves, Nadi, coll. B. Y. Lee and B. Rashni, 28 Jul. 2019; 1 ♂ (14.6 mm) (ZRC 2019.1317), 6 ♂♂ (8.3–14.6 mm) (ZRC 2019.1321), Denarau mangroves, Nadi, coll. B. Y. Lee and B. Rashni, 28 Jul. 2019. **Samoa:** 1 ♂ (11.5 mm) (SMF 17153), Upolu, Samoa, coll. Museum Godeffroy, no date; 4 ♂♂ (10.4–12.7 mm) (SMF 5675), Samoa, coll. Hauck, 1904.

Diagnosis: Male. Carapace (Figs. 4A, 5B, 7D, E, 12A) subrectangular, smooth; front broad; anterolateral angles triangular, directed laterally; anterolateral margins moderately convergent, short; dorsolateral margins clear, long. Third maxillipeds (Fig. 4D) with merus about 1/3 length of ischium; longitudinal broad groove on outer surface of ischium and merus, close to inner margin. Male pleon (Fig. 4C) tapering from somites 2–5, somite 6 with lateral margin nearly straight. Major cheliped (Figs. 4B, 5D, E, 8E–H, 12B) without groove on outer fingers; pollex narrower than dactylus for entire length, with low, small to moderate predistal triangular tooth; dactylus with same width from base to position of adjacent predistal pollex tooth, then tapering and arched distally. Minor fingers without large tooth on occlusal margin, a large gap between fingers, about same width with adjacent fingers. G1 (Fig. 6A–D, J) with strong torsion; thumb moderately long, reaching flange base, distal parts of both flanges narrow, posterior flange longer, broader than anterior. Urocardiac ossicles of gastric mill (Fig. 9D) moderately complex, with 4 pairs of transverse ridges of median tooth, separated by gaps reached deeply near central ridge, on posterior tooth plate; 2 pairs of cusps on stem region.

Female: Carapace (Fig. 7H) with anterolateral angle more broadly triangular, directed laterally.

Size: Largest male CW 12.9 mm, CL 7.9 mm, PL 25.6 (Fiji); largest female CW 11.7 mm, CL 7.4 mm (Wallis & Futuna).

Color in life: Adults with carapace marbled with brown (or dark brown) and white; entire major cheliped chrome yellow, distal part of fingers white; walking legs, minor cheliped, third maxillipeds, orbital areas and pterygostomian regions always chrome yellow, sometimes deep pink; some females with carapace and legs with fine marbling of dark brown and gray (Figs.

11A–G, 12A, B).

Ecological and behavioral notes: High densities of individuals were found on middle and high intertidal zone of shelter shore, beside front mangroves with muddy sand substrate (Figs. 11G, H, 12C), as well as the interior flats along the tidal creek beside mangroves with about 1 km from the sea (B. Y. Lee, personal communication). The species has a unique aggressive behavior, a short, rapid and horizontal wave, toward the intruder which is different from the aggressive behavior with vertical wave of *A. perplexa* in Australia (Crane 1975; How et al. 2007; Weis and Weis 2013).

Distribution: Fiji, Wallis & Futuna, Samoa and probably Tonga (Fig. 1).

Etymology: The species name, *Citrus*, is from the Latin name for the lemon, alluding the lemon-colored major chela of the new species, which is very distinctive in the field. The name is used as a noun in apposition.

Remarks: *Austruca citrus* n. sp. is close to *A. perplexa*, but can be distinguished by the following characters, including the maximum adult size of males (CW 12.9 mm vs. CW 17.5 mm); the direction of the anterolateral angles of the male carapace (lateral vs. anterolateral) (Figs. 4A, 5B, 7D, E vs. Figs. 3D, 5A, 7A–C, 12A); the shape of anterolateral angles of the female carapace (relatively more broadly triangular vs. sharper triangular) (Fig. 7H vs. Fig. 7F–G); the ratios of major pollex length on carapace width (large vs. small; Fig. 13, see below); the major pollex (with a low, small to moderate predistal triangular tooth vs. with a moderate to large predistal triangular tooth) and the major dactylus (with the same width from the base to the position of the adjacent predistal pollex tooth vs. wider at the base and narrower toward the distal part) (Figs. 4B, 5D, E, 8E–H, 12B vs. Figs. 2C, D, 3A, B, E, 5C, 8A–D); the distal parts of both flanges of the G1 (narrow vs. broad) (Fig. 6A–D, J; Crane 1975: figs. 19B, 20A–C vs. Fig. 6E–I; Crane 1975: fig. 19C–H); and the coloration of major cheliped (chrome yellow vs. pink, yellow or yellowish white) (Figs. 11A–E, G, 12A, B vs. Fig. 10A–F).

Crane (1975: figs. 19, 20A–C) illustrated the G1 variation of *A. perplexa* s. l. from different regions. There is a pattern that the distal parts of both flanges are broad in specimens from the Gulf of Siam, Singapore and the Philippines; and narrow in those from Fiji and Samoa, which agree with our observations (Fig. 6). The distal part of the G1 from Australia in Crane (1975: fig. 19D) seems narrow, which might be caused by the specimens being small and/or figured from a different angle, because our specimens from Queensland (QM W19270) show this part as relatively broader (Fig. 6I). The distal parts of both flanges can be considered as a character to distinguish the two species, that is, it is

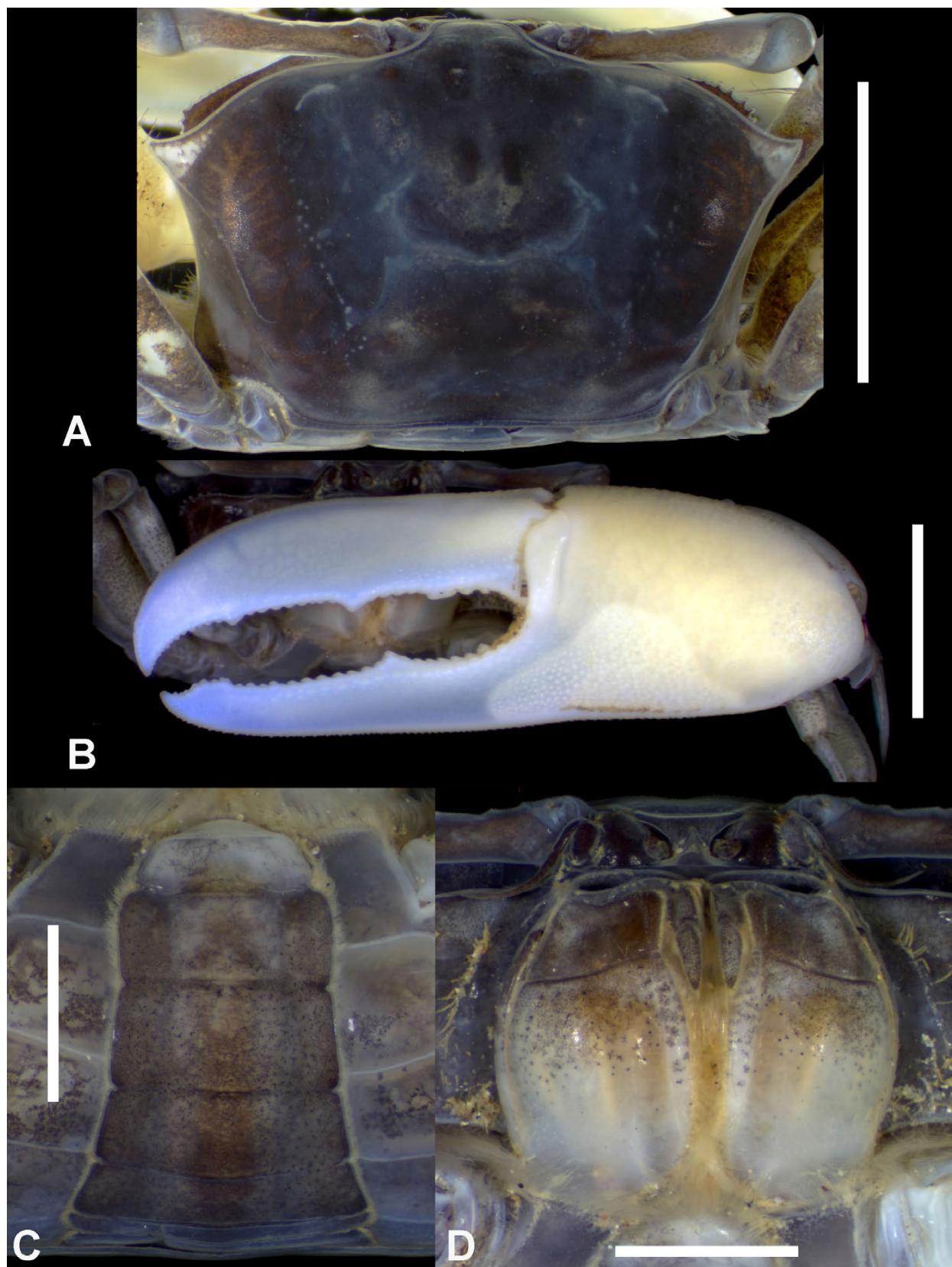


Fig. 4. Holotype of *Austruca citrus* n. sp. (MNHN-IU-2017-9121; CW 10.9 mm). A, dorsal view; B, major chela; C, pleon and telson; D, third maxillipeds. Scale bars: A, B = 5.0 mm; C, D = 2.0 mm.

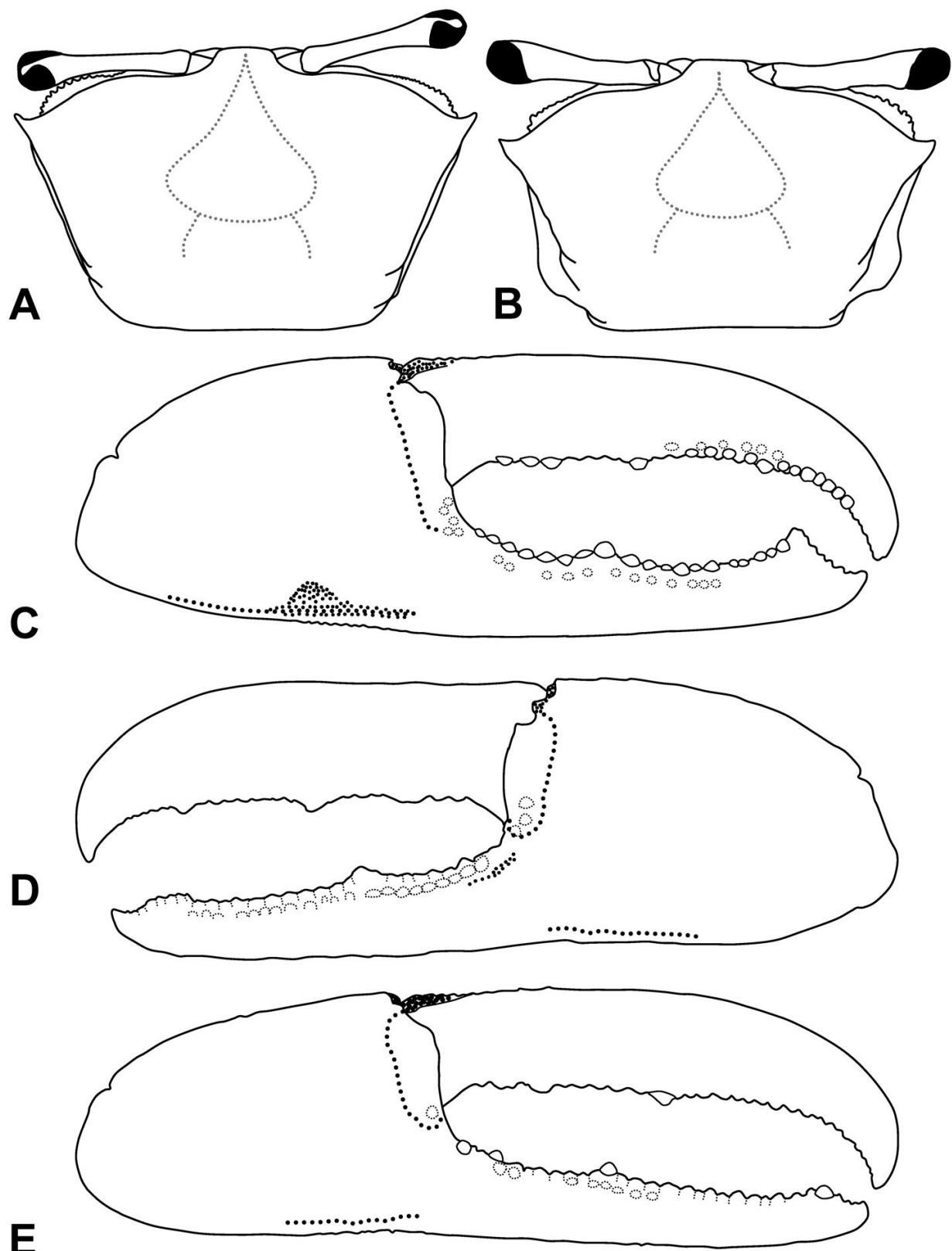


Fig. 5. *Austruca perplexa* (H. Milne Edwards, 1852) (A, C) and *A. citrus* n. sp. (B, D, E). A, B, carapace; C–E, major chela. A, C, male (NCHUZOOOL 15053; CW 15.6 mm, PL 25.6 mm; Negeri Sembilan, Malaysia); B, D, holotype of *A. citrus* (MNHN-IU-2017-9121; CW 10.9 mm, CL 6.7 mm, PL 17.6 mm; Wallis & Futuna); E, male (UF 3843; CW 12.9 mm, PL 25.6 mm; Fiji).

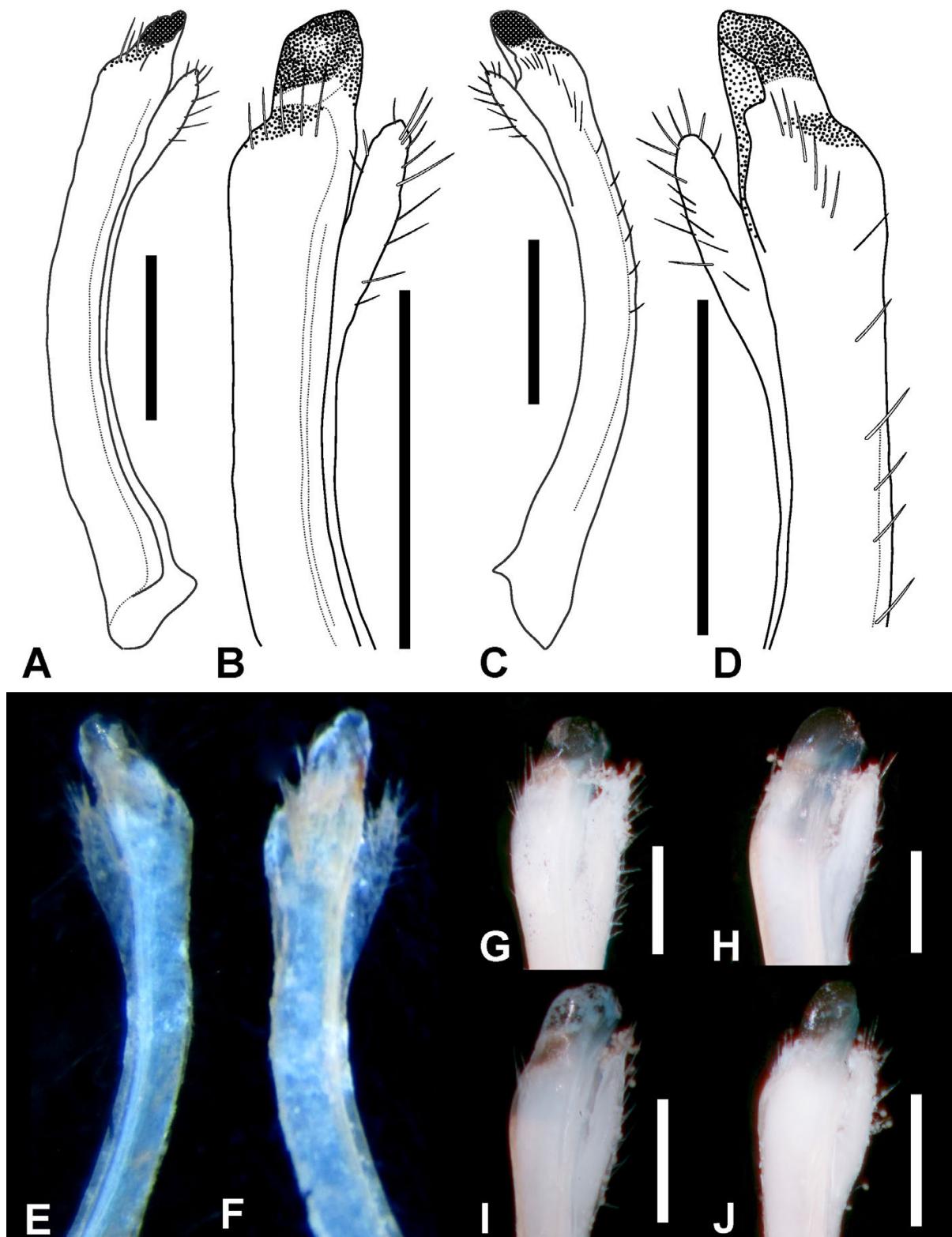


Fig. 6. G1s of *Austruca citrus* n. sp. (A–D, J) and *A. perplexa* (H. Milne Edwards, 1852) (E–I). A–D, G–J, right G1; E–F, left G1. A, E, mesial view; B, G–J, mesial view of distal part; C, F, lateral view; D, lateral view of distal part. A–D, holotype, CW 10.9 mm, MNHN-IU-2017-9121, Wallis & Futuna; J, paratype, CW 12.0 mm, MNHN IU-2017-9123, Wallis & Futuna; E–F, paralectotype, MNHN-IU-2008-10646, CW ~15–16 mm, Java; G, CW 15.2 mm, ZRC 2020.0288, Singapore; H, CW 17.5 mm, NCHUZOOL 14636; I, CW 12.5 mm, QM W19270. Scale bars: A–D = 2.0 mm; G–J = 0.5 mm.

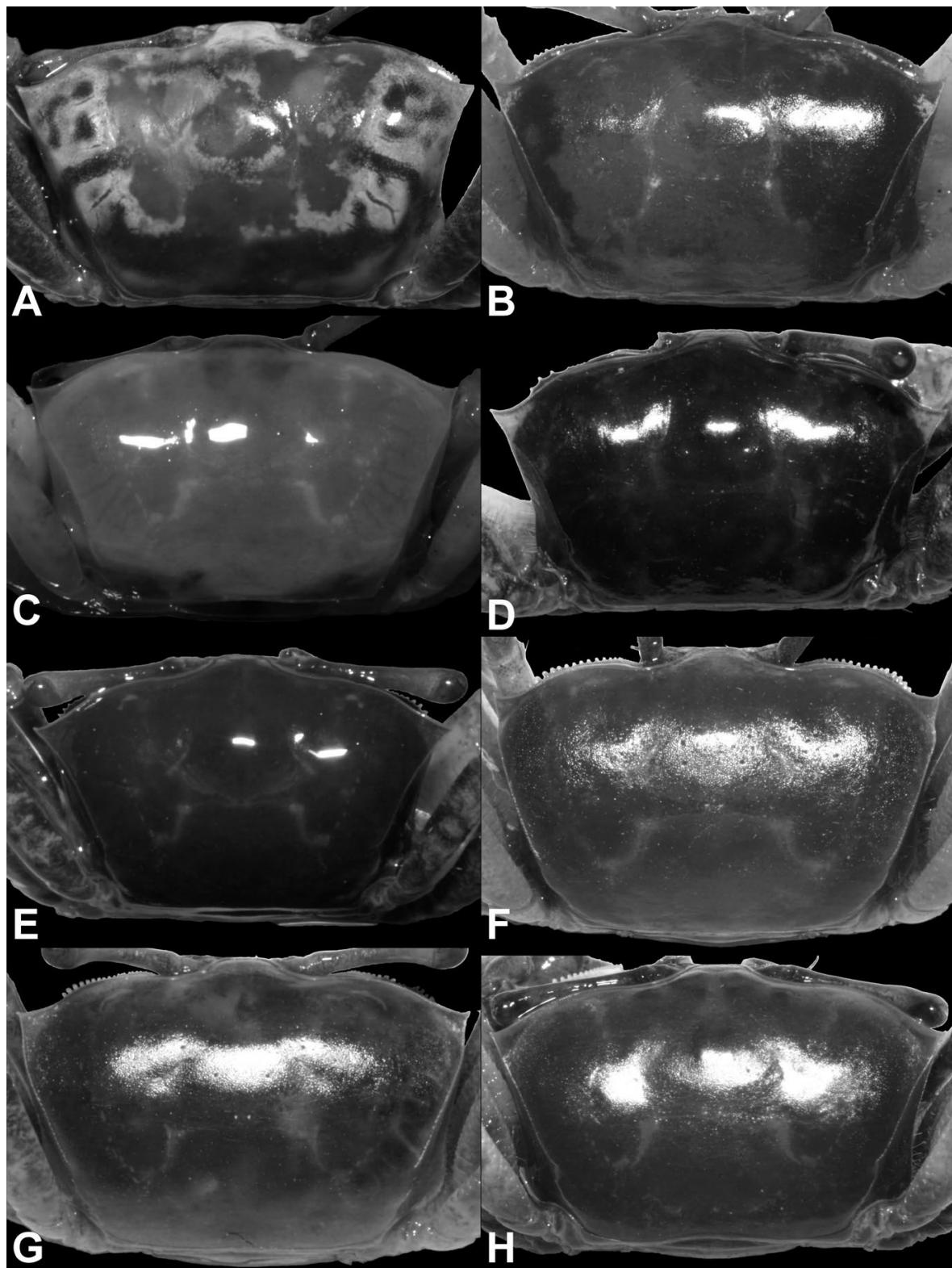


Fig. 7. Carapaces of male *Austruca perplexa* (H. Milne Edwards, 1852) (A–C, F, G) and *A. citrus* n. sp. (D, E, H). A, male, CW 17.3 mm (NCHUZOOL 15046), Kuching, Sarawak, Malaysia; B, male, CW 12.5 mm (QM W19270), Queensland, Australia; C, male, CW 12.0 mm (ZRC 1995.966), Queensland, Australia; D, male, CW 12.7 mm (MNHN-IU-2017-9123), Wallis & Futuna; E, male, CW 11.0 mm (UF 1488), Fiji; F, female, CW 13.7 mm (NCHUZOOL 14643), Tainan, Taiwan; G, female, CW 11.3 mm (NCHUZOOL 15052), Selangor, Malaysia; H, female, CW 11.7 mm (MNHN-IU-2017-9122), Wallis & Futuna.

broad for *A. perplexa* (Fig. 6A–D, J) and narrow for *A. citrus* (Fig. 6E–I).

The character of the urocardiac ossicles of the gastric mill is sometimes useful to separate species or genera of fiddler crabs (Naderloo et al. 2010; Shih 2015; Shih et al. 2015b 2016b 2019), but the three or four pairs of transverse ridges of the median tooth in both *A. perplexa* and *A. citrus* (Fig. 9) can only be considered as within the range of variation.

DNA analyses

A 567 bp segment (excluding the primer regions) of 16S rDNA from 70 specimens (excluding the outgroups) was amplified and aligned. Of these, 112 positions were variable and 85 parsimony informative, with 20 different haplotypes distinguished (Table 1). The studied segment of the 16S rRNA sequences was AT rich (71.1%) (T, 36.3%; A, 34.8%; G, 18.2%; C,

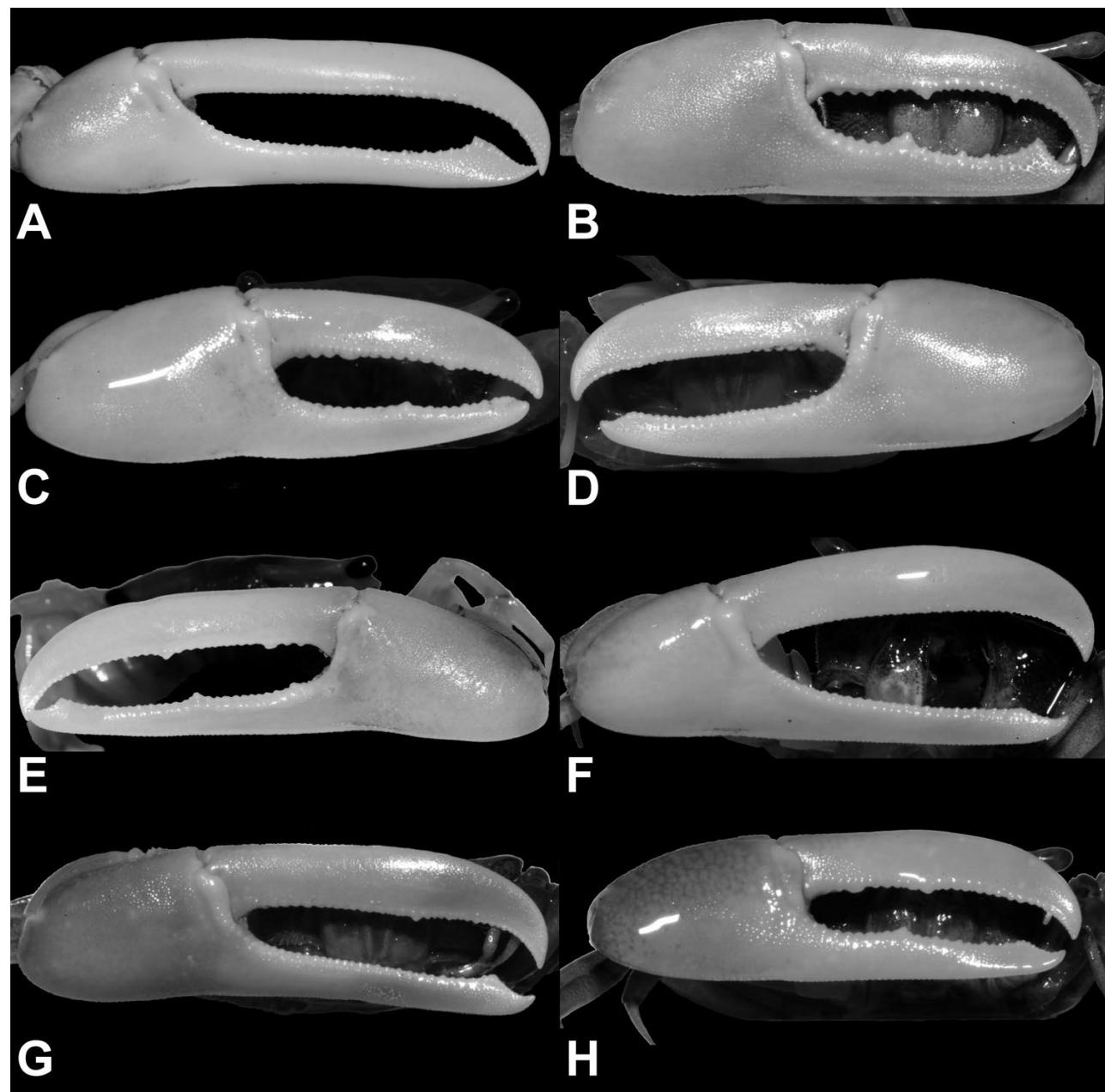


Fig. 8. Major chelae of *Austruca perplexa* (H. Milne Edwards, 1852) (A–D) and *A. citrus* n. sp. (E–H). A, CW 17.3 mm (NCHUZOOL 15046), Kuching, Sarawak, Malaysia; B, CW 14.9 mm (NCHUZOOL 15058), Singapore; C, CW 12.5 mm (QM W19270), Queensland, Australia; D, CW 12.0 mm (ZRC 1995.966), Queensland, Australia; E, CW 12.7 (SMF 5675), Samoa; F, CW 12.0 mm (MNHN-IU-2017-9123), Wallis & Futuna; G, CW 11.6 mm (UF 1488), Fiji; H, CW 11.0 mm (UF 1488), Fiji.

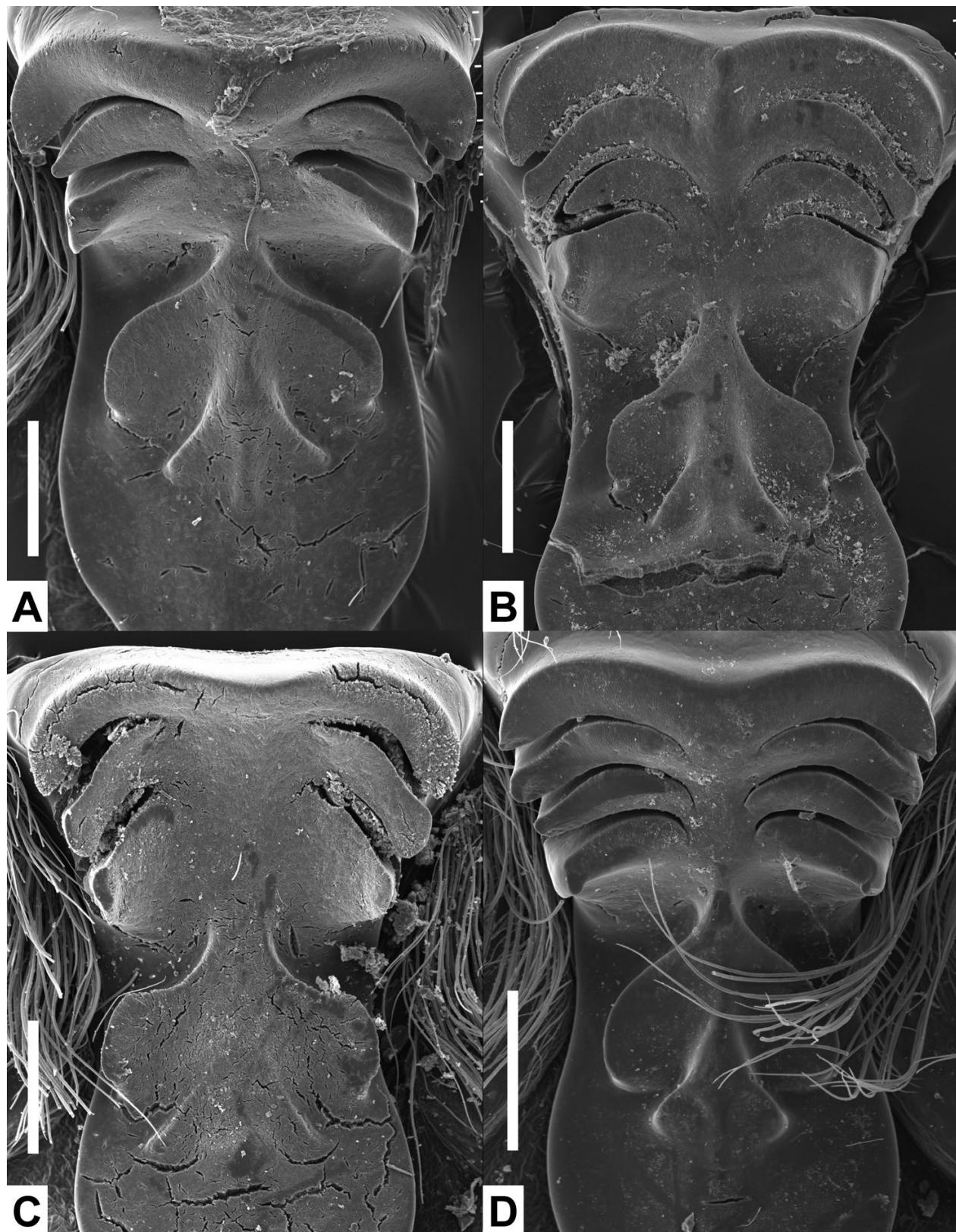


Fig. 9. Urocardiac ossicles of *Austruca perplexa* (H. Milne Edwards, 1852) (A–C) and *A. citrus* n. sp. (D). A, male, CW 13.6 mm (NCHUZOOL 15056), Mersing, Malaysia; B, male, CW 14.2 mm (NTOU), Taitung, Taiwan; C, male, CW 12.5 mm (QM W19270), Queensland, Australia; D, male, CW 11.1 mm (MNHN-IU-2017-9122), Wallis & Futuna. Scale bars = 0.2 mm.

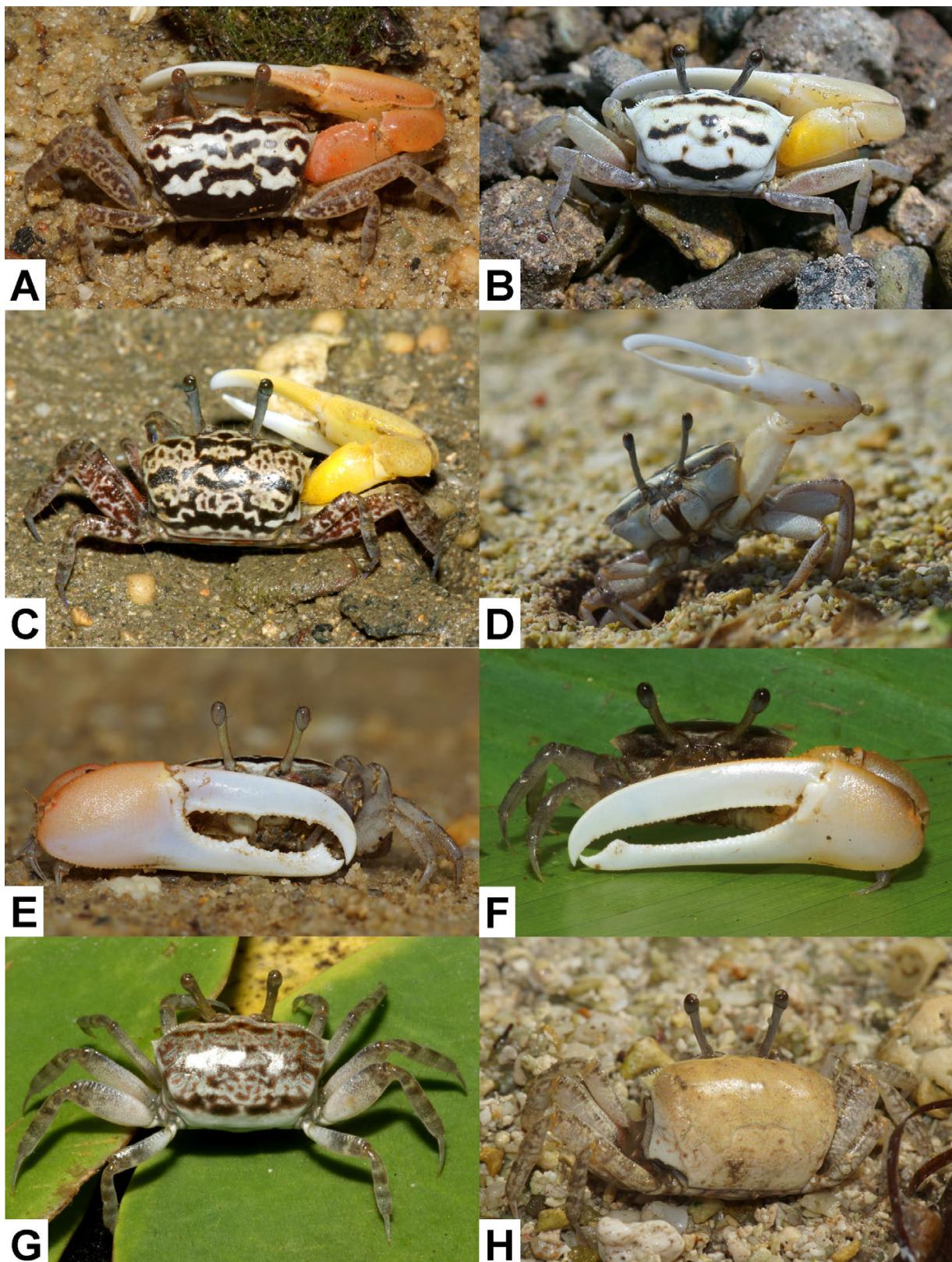


Fig. 10. *Austruca perplexa* (H. Milne Edwards, 1852). A–F, male; G–H, female. A, CW 14.9 mm (NCHUZOO!L 15057), Singapore; B, 12.0 mm (NCHUZOO!L 15042), Bohol, Philippines; C, specimen not collected, Penghu, Taiwan; D, H, specimens not collected, Dongsha, Taiwan; F, CW 12.0 mm (NCHUZOO!L 15060), Bali, Indonesia; G, CW 9.7 mm (NCHUZOO!L 15050), Kuching, Sarawak, Malaysia.



Fig. 11. *Austruca citrus* n. sp. A–E, male; F, female. A, CW 11.1 mm (MNHN-IU-2017-9122), Wallis & Futuna; B–F, specimens not collected, Fiji. G–H, a population with high density. B, G, courtesy of Mark Rosenstein; C–F, H, courtesy of Rocio Gajon Bunker.

10.7%). For the *COI* gene from 67 specimens (excluding the outgroups), a 658-bp segment was compared (except the haplotype “Ap-C2f” with 616 bp), resulting in 21 different haplotypes (Table 1). The studied segment of the *COI* sequences was also AT rich (63.2%) (T, 35.1%; A, 28.0%; G, 17.5%; C, 19.3%). In this gene fragment, 174 positions were variable and 133 were parsimoniously informative.

The best model selected for the *COI* dataset is the HKY + G model (TRatio = 6.3137, gamma distribution shape parameter = 0.123). The phylogenetic tree of *COI* from the BI analysis, with the posterior probability and bootstrap values from the BI and MP analyses on the main nodes, is shown in figure 14. Based on the tree, *Austruca perplexa* s. l. is monophyletic with high branch support, and sister to *A. lactea*, with two clades corresponding to *A. perplexa* s. s. and *A. citrus* n. sp.

The pairwise nucleotide divergences for 16S rDNA and *COI* (in parentheses) with K2P distance and differences in the total bp numbers (gaps considered in 16S) are shown in tables 2 and 3, respectively. The interspecific K2P distances of 16S rDNA and *COI* of

A. citrus n. sp. are 1.73% (1.29%–2.42%) and 4.59% (3.78%–5.28%) with the closest *A. perplexa*; and the numbers of bp differences between the two species are 11.08 (8–16) and 28.85 (24–33), respectively (Tables 2, 3).

Some specimens only have 16S rRNA sequences as the PCR of the *COI* failed. From the 16S sequences, specimens from the Samoa and Solomon Islands belong to the clades of *A. citrus* and *A. perplexa*, respectively (Table 1).

Morphometric analysis

The PLs were plotted against the CWs for the males of three groups. The ANCOVA results show that the regression lines of *A. citrus* and *A. perplexa*, as well as the lines of *A. citrus* and *A. perplexa* with CW between 8.3–14.6 mm, differ significantly both in intercept (*P*-values = 0.016 and 0.03, respectively) and slope (*P* = 0.039 and *P* = 0.037, respectively). It is clear that, for a given CW of *A. citrus* (about 10–14.6 mm), the PL is longer than that of *A. perplexa* (Fig. 13). The

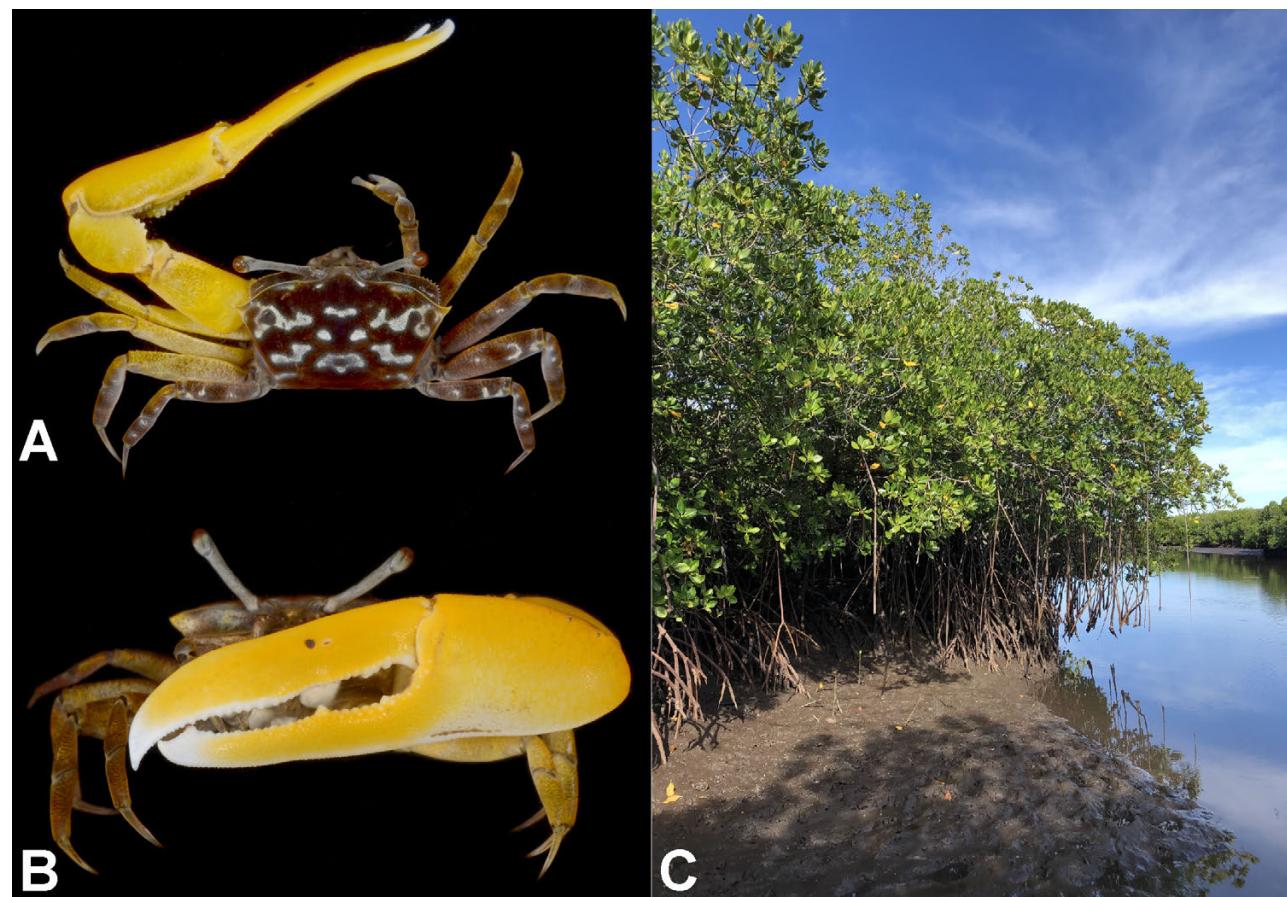


Fig. 12. Color in life of *Austruca citrus* n. sp. (male, CW 14.6 mm, ZRC 2019.1317) from Fiji (A, B) and its habitat in Denarau mangroves, Nadi, Fiji (C). A, dorsal view; B, frontal view. Courtesy of Bee Yan Lee.

largest specimen of *A. citrus* (Fiji, ZRC 2019.1317) is CW 14.6 mm, with PL 27.5 mm and the specimens with similar size (CW 14.4–14.7 mm) of *A. perplexa* have a PL of 20.8–26.9 mm ($n = 7$). The largest male of *A. perplexa* (CW 17.5 mm; Okinawa, Japan, NCHUZOOL 14646) has a PL of 34.6 mm.

DISCUSSION

Crane (1975) noted that the populations of *Austruca perplexa* s. l. in Samoa and Fiji differed from others in the western Pacific in several distinct features. These characters include the intense chrome yellow major cheliped (Crane 1975: 295), the wide major dactylus breadth and large predistal triangular tooth on major pollex (Crane 1975: fig. 41B and figure legend), some individuals with tuberculate ridge on major pollex (Crane 1975: 295), and the narrower distal parts of both posterior and anterior flanges of the G1 (Crane 1975: figs. 19B, 20A–C). The results of our study

support Crane's observations with additional anatomical characters and molecular data. As a result, *Austruca citrus* is here recognized as a new species from Fiji, Wallis & Futuna, and Samoa.

The characters distinguishing the two closely related species (see Remarks under *A. citrus*) include the maximum adult size of males, the direction of the anterolateral angles of male carapace, shape of anterolateral angles on the female carapace, the ratios of major pollex length on carapace width (also see below), the structures of the major pollex, major dactylus and distal parts of both flanges of the G1, as well as the life color of major cheliped.

The morphometric comparison of the major propodus length (PL) with the carapace width (Fig. 13) showed *A. citrus* has a longer PL than *A. perplexa* of similar sizes. For example, the largest specimen (CW 12.9 mm) of *A. citrus* (from Fiji) has a PL 25.6 mm (UF 3843), but a specimen (CW 13.0 mm) of *A. perplexa* (from Solomon) only has a PL 22.5 mm (AM P98278); and a specimen (CW 15.6 mm) (from Negeri Sembilan,

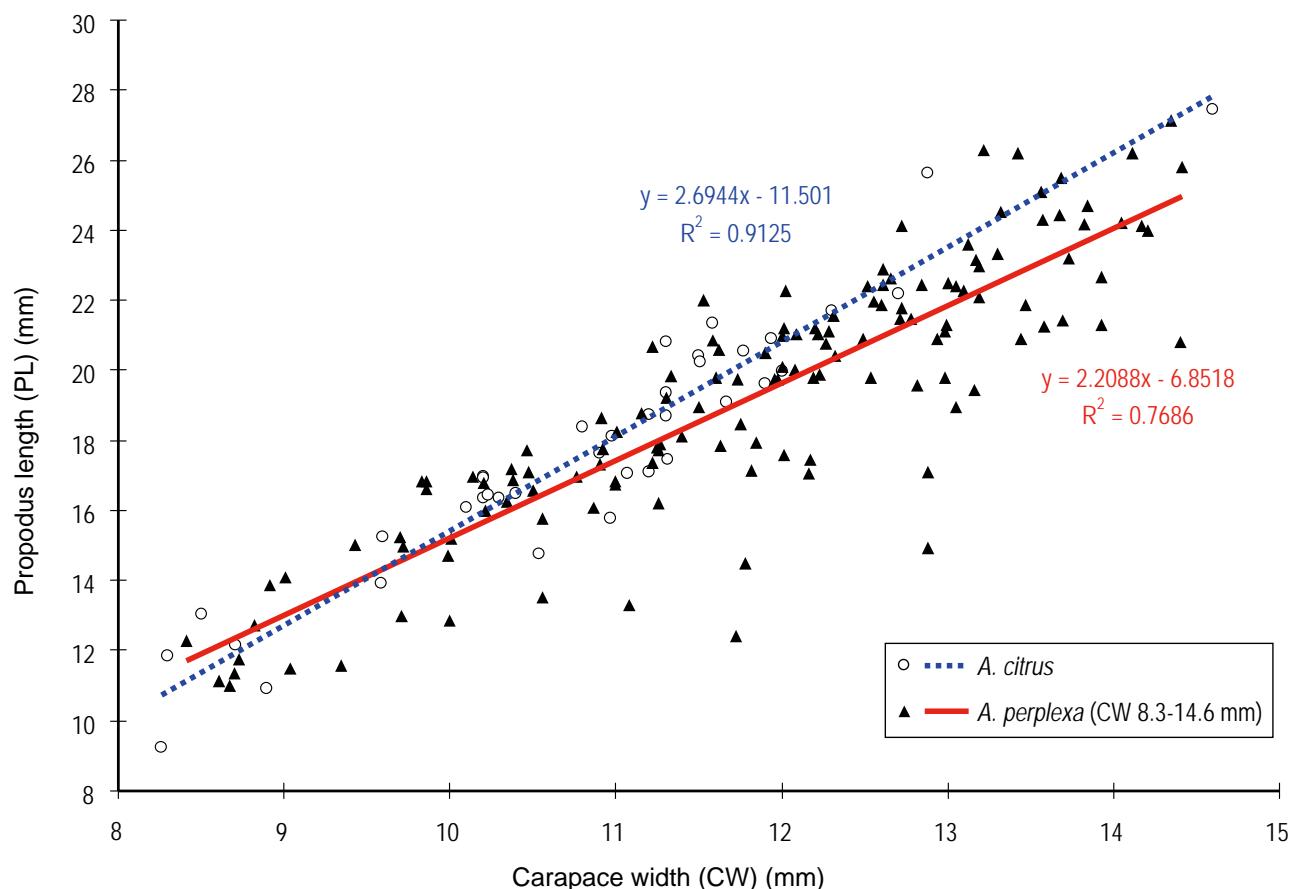


Fig. 13. Propodus length (PL) plotted as a function of carapace width (CW) of male *Austruca citrus* n. sp. and *A. perplexa* (H. Milne Edwards, 1852). CW ranged 8.3–14.6 mm: both intercepts and slopes of regression lines of *A. citrus* and *A. perplexa* with CW ranged 8.3–14.6 mm differ significantly (ANCOVA).

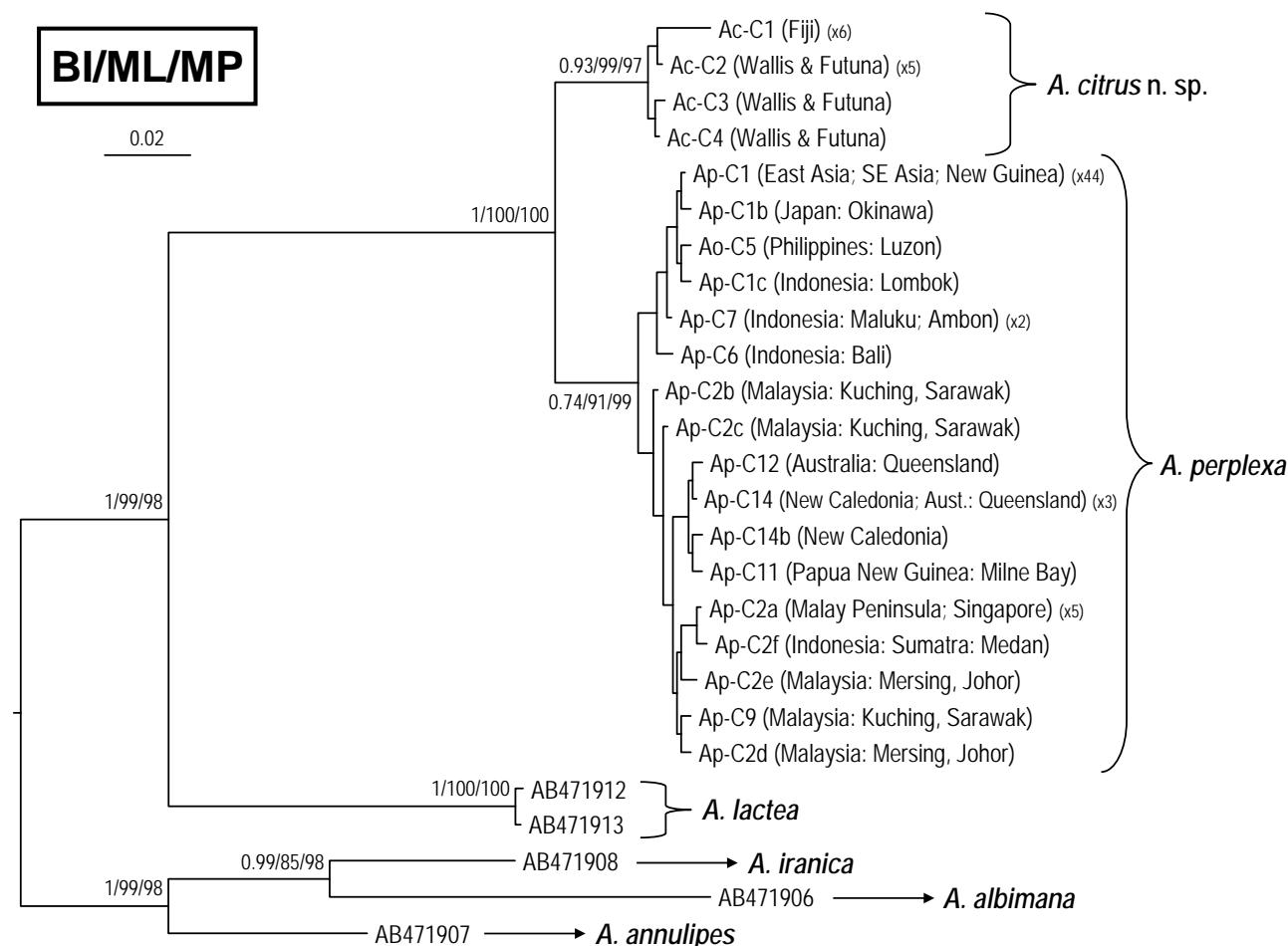


Fig. 14. A Bayesian inference (BI) tree for *Austruca citrus* n. sp. and *A. perplexa* (H. Milne Edwards, 1852), with outgroups of other congeneric species, based on cytochrome *c* oxidase subunit I (COI) gene. Probability values at nodes represent support values for BI, maximum likelihood (ML) and maximum parsimony (MP). For haplotype identities, see table 1.

Table 2. Matrix of percentage pairwise nucleotide divergences with K2P distance (lower left) and mean number of differences (upper right) based on 16S rDNA within and between species of *Austruca perplexa* (H. Milne Edwards, 1852), *A. citrus* n. sp., *A. lactea* (De Haan, 1835), *A. annulipes* (H. Milne Edwards, 1837), *A. iranica* (Pretzmann, 1971), and *A. albimana* (Kossmann, 1877). Range values are shown in parentheses

	Intraspecific		Interspecific					
	Nucleotide divergence	Mean nucleotide difference	<i>A. perplexa</i>	<i>A. citrus</i>	<i>A. lactea</i>	<i>A. annulipes</i>	<i>A. iranica</i>	<i>A. albimana</i>
<i>A. perplexa</i>	0.38 (0–1.11)	2.61 (0–8)		11.08 (8–16)	64.61 (62–66)	71.83 (69–73)	76.82 (74–78)	66.14 (64–67)
<i>A. citrus</i>	0.09 (0–0.18)	1.39 (0–3)		1.73 (1.29–2.42)	64.69 (64–66)	73.69 (73–75)	75.69 (75–77)	65.69 (65–67)
<i>A. lactea</i>	0.18	1		11.97 (11.53–12.42)	11.76 (11.55–11.97)	77	71	78
<i>A. annulipes</i>				11.38 (10.9–11.58)	11.57 (11.55–11.58)	11.89	48	41
<i>A. iranica</i>				12.84 (12.36–13.05)	12.37 (12.36–12.38)	10.91	10.91	36
<i>A. albimana</i>				10.74 (10.41–11.06)	10.42 (10.41–10.43)	12.64	12.64	7.28

Malaysia) has the same PL 25.6 mm (NCHUZOOL 15053).

Also, the recognition of the two species is supported by the phylogenetic tree using *COI* (Fig. 14) as well as the genetic divergence of *COI* and 16S rDNA among taxa (Tables 2, 3). The minimum interspecific divergence of *COI* between *A. citrus* and *A. perplexa* is 3.78%, which is similar to that between *Tubuca urvillei* (H. Milne Edwards, 1852) and *T. alcocki* Shih, Chan & Ng, 2018 (Shih et al. 2018) and higher than the 3.62% difference between *Gelasimus hesperia* (Crane, 1975) and the “Clade U” as well as the 2.79% difference between *Paraleptuca crassipes* (White, 1847) and *P. splendida* (Stimpson, 1858) (Shih et al. 2010 2012; Chu et al. 2015).

Biogeographically, the distribution of *A. citrus* in Fiji and eastwards is similar to that of *Gelasimus excisa* (Nobili, 1906) (= *G. neocultrrimana* (Bott, 1973), see Rosenberg 2019) (Shih et al. 2010). This implies there may be a marine barrier blocking the larval dispersal between the western margin of the Pacific and Fiji. This is worth investigating in the future with a number of other benthic species.

While the eastern boundary of *A. perplexa* is now in the Solomon Islands, Vanuatu and New Caledonia (Fig. 1), the western boundary of the species remains less clearly defined. Crane (1975: 612, map 21) included a “small series” of *A. perplexa* from Pondicherry in southeastern India. However, she considered this population to be a hybrid between *A. perplexa* and *A. annulipes*, and the predistal triangular tooth on the major pollex is sometimes small (Crane 1975: 294, table

6). In addition, Apreshgi et al. (2016) recently recorded “*A. perplexa*” from southwestern India. However, the coloration (Apreshgi et al. 2016: fig. 1a, b) agrees better with *A. annulipes* and its *COI* sequence (KJ535696) is problematic with 53 gaps, and aligned with other known sequences of fiddler crabs, indicating that it might be the result of contamination or a pseudogene (NUMT, nuclear mitochondrial DNA segment; Schubart 2009). The two records of *A. perplexa* from India are more likely to be *A. annulipes* and are here treated as such. Based on reliable records, the western boundary of *A. perplexa* is around the Andaman and Nicobar Islands (Naderloo et al. 2010; Kumaralingam et al. 2017; Trivedi et al. 2018).

CONCLUSIONS

In our study, a new species of fiddler crab, *Austruca citrus* n. sp., closely related to *A. perplexa*, is described from Fiji and eastwards in the South Pacific based on the evidence of morphology (adult size, carapace morphology, shape and coloration of the major chela, the ratio of major pollex length as a function of carapace width, and G1 form) and molecular data (mitochondrial 16S and *COI*). As a result, the distribution of *A. perplexa* is from the western boundary of the Andaman and Nicobar Islands to the eastern boundary of the Solomon Islands, Vanuatu and New Caledonia. In addition, the taxonomy of *Gelasimus perplexus* H. Milne Edwards, 1852 is discussed based on the available evidence from descriptions, figures,

Table 3. Matrix of percentage pairwise nucleotide divergences with K2P distance (lower left) and mean number of differences (upper right) based on *COI* within and between species of *Austruca perplexa* (H. Milne Edwards, 1852), *A. citrus* n. sp., *A. lactea* (De Haan, 1835), *A. annulipes* (H. Milne Edwards, 1837), *A. iranica* (Pretzmann, 1971), and *A. albimana* (Kossmann, 1877). Values of range are shown in parentheses

	Intraspecific		Interspecific					
	Nucleotide divergence	Mean nucleotide difference	<i>A. perplexa</i>	<i>A. citrus</i>	<i>A. lactea</i>	<i>A. annulipes</i>	<i>A. iranica</i>	<i>A. albimana</i>
<i>A. perplexa</i>	0.69 (0–1.98)	4.45 (0–12)		28.85 (24–33)	86.28 (84–89)	91.46 (89–95)	99.1 (96–101)	105.64 (102–107)
<i>A. citrus</i>	0.81 (0–1.7)	5.28 (0–11)		4.59 (3.78–5.28)	84.96 (83–87)	91.85 (91–93)	93.23 (91–96)	104.15 (103–106)
<i>A. lactea</i>	0.15	1		14.6 (14.15–15.44) (13.94–14.71)	14.32	86.5 (86–87)	98.5 (98–99)	103.5 (103–104)
<i>A. annulipes</i>				15.55 (15.05–16.83) (15.43–15.82)	15.59 (14.48–14.68)	14.58		70 82
<i>A. iranica</i>				17.08 (16.44–17.71) (15.44–16.43)	15.88 (16.86–17.06)	16.96	11.7	
<i>A. albimana</i>				18.35 (17.59–19.4)	18.01 (17.78–18.39)	17.82 (17.72–17.92)	13.84	11.64

labels and syntypes.

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Authors' contributions: HTS conceived this study, performed the morphological description and the molecular analysis, and drafted the manuscript. JP collected and processed the samples, performed the discussion and drafted the manuscript. Both authors read and approved the final manuscript.

Competing interests: The authors declare that they have no conflict of interests.

Availability of data and materials: Sequences generated in the study have been deposited in the DNA Data Bank of Japan (DDBJ) database (accession numbers in Table 1 in the manuscript).

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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