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Research Article

Revision of the Indo-West Pacific crab genus *Soliella* (Brachyura: Xanthidae: Etisinae): 'pseudocryptic species' and basinal speciation

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Etisine crabs are some of the most abundant cryptobionts in Indo-West Pacific coral reef systems. Despite their ecological importance and abundance in museum collections, several recent systematic studies have indicated family- to subspecies-level taxonomic problems. One such case involves the former chlorodielline genus *Soliella* Lasley, Klaus & Ng, 2015 (treated here as part of Etisinae), which currently comprises two valid species and three available names that have been in flux in recent literature. The validity of these taxa has only been cursorily discussed. To resolve species limits and distributions, a thorough morphological examination of hundreds of specimens was conducted, including scanning electron microscopy of male gonopods, along with analysis of sequence data of the mitochondrial marker cytochrome c oxidase subunit I (COI) from 84 exemplars across the distribution of the genus. The status of two species that have Indian Ocean versus Pacific Ocean distributions with overlap in the Indo-Australian Archipelago and adjacent regions is confirmed. While external morphology is not reliable for identification, a few discrete, although slight, differences in gonopod morphology were found, and these results are consistent with a 'pseudocryptic species' designation. Speciation conforms to a previously published etisine model of allopatric differentiation followed by subsequent divergence of gonopod morphology upon secondary sympatry. This pattern, the biogeography of the two species and the concept of 'pseudocryptic species' are discussed.

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Key words: Chlorodiellinae, coral reef, Crustacea, Decapoda, *Pilodius*, systematics, taxonomy, Xanthoidea

Introduction

The Indo-West Pacific (IWP) is the world's largest marine biogeographic region, characterized by many wide-ranging species that mostly disperse via long-lived, planktonic larvae (Briggs & Bowen, 2012; Forest & Guinot, 1961; Kay, 1984; Myers, 1994). Recent studies have indicated that many species previously thought to range across the IWP comprise mosaics of allo- or parapatric, cryptic lineages (e.g., Drew & Barber, 2009; Malay & Paulay, 2010; Meyer *et al.*, 2005; Titus *et al.*, 2018). One such study of the brachyuran crab clade 'Chlorodiellinae' (now Etisinae) found that while some species have IWP-wide distributions with little genetic structuring, others are complexes of deeply divergent allopatric lineages (Lasley et al., 2023). That study also uncovered a strong correlation between genetic distance (time), sympatry, and the divergence of genital morphology, highlighting the important roles of both allopatric genetic differentiation and genital divergence in the speciation process. Here the differentiation in one of these genera is examined in greater detail.

Members of the xanthid subfamily Etisinae Ortmann, 1893 are some of the most abundant crustacean cryptofauna in IWP coral reefs (Monteforte, 1987; Peyrot-Clausade, 1977, 1979, 1989). Despite their ecological importance, abundance and prevalence in museum collections, the taxonomy of this group has proved challenging and needs attention. The molecular phylogenetic study of the superfamily Xanthoidea Macleay, 1838, by Mendoza et al. (2022) greatly expanded the Etisinae, merging it with the subfamily Chlorodiellinae Ng and Holthuis, 2007 (sensu Ng et al., 2008). Mendoza et al. (2022) further included three xanthine genera, *Leptodius* A. Milne-Edwards, 1863, *Macromedaeus* Ward, 1942, and *Neoxanthops* Guinot, 1968. Although a

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formal morphological diagnosis for this grouping has yet to be proposed, its members commonly share spoon-tipped chelae and, to a lesser extent, a dactylopropodal lock and calcareous dactylar spines on the ambulatory legs. Nevertheless, most chlorodielline genera have been recovered in a subclade within Xanthidae with high support, and this lineage has been the subject of recent systematic studies (Lai et al., 2011; Lasley et al., 2013, 2015, 2022, 2023; Mendoza et al., 2022). Lasley et al. (2015) revised the genus-level taxonomy of 'Chlorodiellinae', particularly of *Pilodius* Dana, 1851, which was shown to be polyphyletic, and described two new genera: *Luniella* Lasley, Klaus & Ng, 2015 and *Soliella* Lasley, Klaus & Ng, 2015.

Three nominal species could be attributed to *Soliella*: *Pilodius flavus* Rathbun, 1893, *Chlorodopsis melanospinis* Rathbun, 1911, and *Chlorodopsis hawaiiensis* Edmondson, 1962 (see Clark & Galil, 1993; Ng et al., 2008). In their revision of the genus *Pilodius*, Clark and Galil (1993) considered all three to pertain to *P. flavus*. Lasley et al. (2015) also recognized *S. melanospinis* as valid based on morphology of the male gonopod (G1) and sequence data from two specimens but did not evaluate *C. hawaiiensis*. The differences between the species' G1s remain unclear, as do external morphological differences, historical literature, and geographic distributions of these species.

To stabilize the taxonomy of *Soliella* and investigate speciation in the genus, we conducted genus-level phylogenetic analyses using the DNA barcoding gene COI, and morphological examination, including scanning electron microscopy of male genital structures (first gonopod or 'G1'), of hundreds of specimens. Historical records were also reviewed especially to assess the geographic distributions of the two species.

Material and methods

Specimens for morphological and molecular analyses were obtained from the following institutions: Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore, Singapore (ZRC); Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA (UF); US National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM); and American Museum of Natural History, New York, New York, USA (AMNH). Historical literature and material examined are covered in SM1.

Morphological examination was conducted using a dissecting microscope (Leica MZ16, Leica Biosystems, Wetzlar, Germany) and a scanning electron microscope (SEM) (Leica Stereoscan 440 at the USNM Imaging Laboratory). The right first and second male gonopods (G1, G2) were removed for examination unless they were damaged, in which case the left one was removed. G1s were prepared for SEM as described by Felgenhauer (1987) and Lasley et al. (2022). Geographic ranges were compiled from locality information from material examined and literature. These data were checked against locality information associated with COI sequences when possible. Occurrence maps were generated with the R package ggplot2 (Wickham, 2016).

COI sequence data were obtained from Lasley et al. (2023), including sequences of *Pilodius maotieni* Serène, 1971, *Luniella spinipes* (Heller, 1860), and *Cyclodius granulatus* (Targioni Tozzetti, 1877) as outgroups (Lasley et al., 2015) (Supplemental Table S1). Maximum likelihood trees were generated using RAxML-HPC BlackBox 8.2.12 (Stamatakis, 2014) in the computer cluster of CIPRES (CyberInfrastructure for phylogenetic RESearch project) (http://www.phylo.org; Miller et al., 2011). The GTRGamma + I model of nucleotide substitution was selected and the analysis was conducted with 1000 bootstrap replicates. A Neighbour-Joining analysis using the Tamura–Nei genetic distance model was also performed in Geneious 8.1.9 with 1000 bootstrap replicates. Between group mean p-distance between species was calculated using Mega version 11.0.13.

Nomenclature and terminology follow Dana (1851), Serène (1984), Ng et al. (2008), and Davie et al. (2015). Measurements provided (in millimetres) are of the maximum carapace width and length, respectively. The following abbreviations are used: G1, male first gonopod; G2, male second gonopod; stn., station; and coll., collected by. Works by Raoul Serène's Vietnamese assistant, Nguyen Van Luom, have erroneously been referred to using one of his given names, 'Luom', rather than his surname 'Nguyen', in previous studies. Here the name is used in full, 'Nguyen Van Luom', e.g., Serène and Nguyen Van Luom (1958), for clarity (Waterman, 1953).

Results

Specimens grouped into two species based on G1 morphology and these corresponded to two reciprocally monophyletic COI clades separated by 11.3% p-distance (Fig. 1). The *S. melanospinis* clade comprises individuals from the Western Indian Ocean to the Indo-Australian Archipelago and adjacent areas: the Scattered Islands, Reunion Island, Chagos Archipelago, Indonesia (Aceh and Bali), Ningaloo Reef (W. Australia), Taiwan, Okinawa, Palau, Heron Island (Great Barrier Reef), the Solomon Islands, and Vanuatu. The *S. flava* clade comprises individuals from the Indo-Australian Archipelago and adjacent areas to the Eastern Pacific Barrier: Christmas Island (Indian Ocean), the Philippines, Indonesia (Bali and Sulawesi), Guam, New Caledonia, Line Islands, Society Islands, Tuamotu Islands, and Hawaiian Islands (Fig. 2).

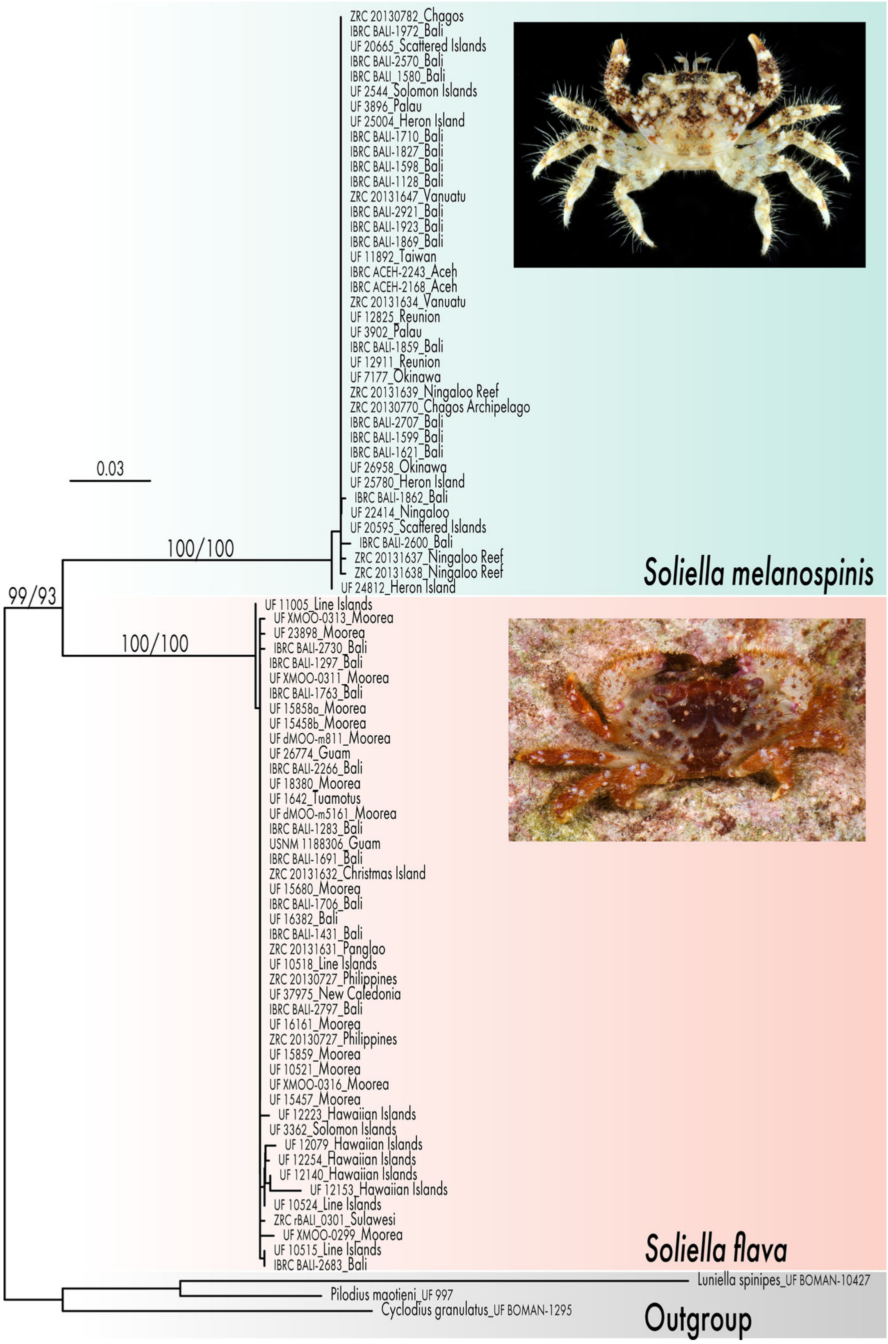

Fig. 1. Maximum likelihood phylogenetic tree of *Soliella* with bootstrap values from the RAxML analysis followed by bootstrap values from the Neighbour-Joining analysis.

Taxonomy

Superfamily Xanthoidea MacLeay, 1838

Family Xanthidae MacLeay, 1838

Subfamily Etisinae Ortmann, 1893

Soliella Lasley, Klaus & Ng, 2015

Chlorodopsis, Rathbun, 1911: 226.–Balss, 1938: 58.–Serène & Nguyen Van Luom, 1959: 88; 1959: 336.

Pilodius, Balss, 1938: 56.–Forest & Guinot, 1961: 81.–Serène, 1984: 233.–Clark & Galil, 1993: 1121.–Ng et al., 2008: 197.

Soliella Lasley et al., 2015: 173

Diagnosis. Carapace transversely subhexagonal, dorsal surface granular, covered with short and long, light-coloured setae, regions well defined. Front sinuous,

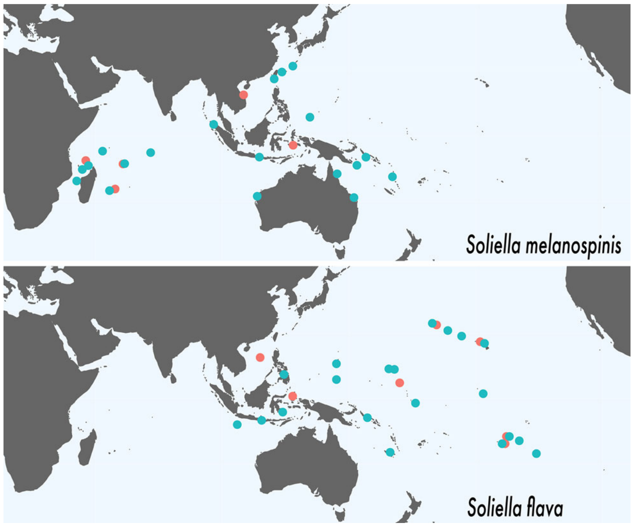

Fig. 2. Geographic distributions of *Soliella flava* and *S. melanospinis*. Turquoise dots represent material examined. Pink dots represent additional localities recorded in literature.

quadrilobate; submedian lobes broadly arched, separated by median, narrow, U-shaped notch, margins granular or spinose; lateral lobes distinct, narrow. Anterolateral margin with four lobes, each tipped with emergent, anteriorly directed spine surrounded by smaller accessory spines. Basal antennal article with distolateral extension reaching approximately halfway into orbital hiatus. Male thoracic sternum relatively broad; suture 3/4 distinct near lateral margins, interrupted medially; median line present on sternite 4 as short suture or shallow depression midway between anterior border of sternite and sterno-pleonal cavity, interrupted in exposed posterior part, reappearing in sterno-pleonal cavity on posterior surface of sternite 4; tubercle of press-button locking mechanism located on anterior half of sternite 5. External, superior surfaces of chelipeds spinose, granular, with numerous long, simple, yellow setae. Ambulatory legs relatively stout; dactylopropodal lock present, well developed; tip of dactylus terminating in long, curved, chitinous claw and two subdistal, small, calcareous spines. Pleon relatively long, slender, tip of telson reaching beyond imaginary transverse line connecting sternal condyles of P1 coxae; pleonites 3–5 functionally fused, with distinct furrows delineating 3/4 and 4/5; telson subtriangular, basal width slightly greater than median length. G1 narrow, sinuous but not drastically curved; distal tip tubular or spatulate with numerous subdistal, proximally directed, spiniform setae. G2 ca. one-third length of G1, sigmoidally curved, terminal segment ca. one-fourth length of subterminal segment. Penis emerging at anterior portion of sternal condyle of P5 coxa.

Remarks. Lasley et al. (2015) provided a diagnosis of the genus and compared it with four genera that were, along with *Soliella*, previously classified in the subfamily Chlorodiellinae (= Etisinae in part): *Chlorodiella* Rathbun, 1897, *Cyclodius* Dana, 1851, *Pilodius*, and *Luniella*. *Soliella* differs from these genera, most notably, in the morphology of its G1 (Fig. 3) (Serène 1984, figs 144–158, 163–165, 167–172, 173–177). *Soliella* also differs from all species in these genera with the exceptions of *Luniella pubescens* (Dana, 1852), *Luniella scabricula* (Dana, 1852), and *Cyclodius paumotensis* (Rathbun, 1907), by the presence of long and short, light-coloured setae on the carapace. Traditional characters, such as the shape and disposition of the basal antennal article and the form of the subterminal (bifid) spine of the ambulatory leg dactylus, that have been used to differentiate these genera are problematic and are not shared with the closest relatives of *Soliella*: *Cyclodius* and *Pilodius* (Ng & Yang, 1998; Clark & Ng, 1999; Lasley et al., 2015). The length of the distolateral extension of the basal antennal article varies in some genera (e.g., *Pilodius*) and with age (Lasley et al., 2015; Serène, 1984: 233, footnote by Crosnier). In *Soliella*, the basal antennal article has a distolateral extension that reaches approximately halfway the into orbital hiatus (vs no extension in *Cyclodius* and usually reaching the orbital hiatus in *Pilodius*). *Soliella* has small, calcareous subterminal spines on the flexor margin of the ambulatory leg dactylus, while the presence and length of subterminal spines vary in *Pilodius* and *Cyclodius* (Lasley et al., 2015). Relationships between *Soliella* and more distantly related genera that were previously assigned to Chlorodiellinae were reviewed in Lasley et al. (2015), e.g., *Tweedieia* Ward, 1935, *Vellodius* Ng & Yang, 1998, and *Sulcodius* Clark & Ng, 1999. All other etisine genera have been treated in Serène (1984). In view of the results from recent molecular phylogenetic studies on Xanthidae (Lai et al., 2011; Lasley et al., 2015; Mendoza et al., 2022), however, the diagnoses for the different genera in an expanded Etisinae will need to be re-evaluated and emended, with greater focus on thoracic sternal characters and other such non-traditional but informative characters.

Soliella flava (Rathbun, 1893)

Figs 3 A, C, 4, 5

Pilodius flavus Rathbun, 1893: 239; 1906: 860, fig. 21.–Edmondson, 1925: 43; 1933: 249; 1962: 275, fig. 22a, b.–Balss, 1938: 57.–Miyake, 1939: 215.–Forest & Guinot, 1961: 95.–Serène, 1968: 80; 1984: 235, 239 [key].–Peyrot-Clausade, 1989: 111.–Clark & Galil, 1993: 1130 (in part), figs 4A–G, 32B, 40D, 41 A.–DeFelice et al., 1998: 16; 2002: 30, 72.–Coles

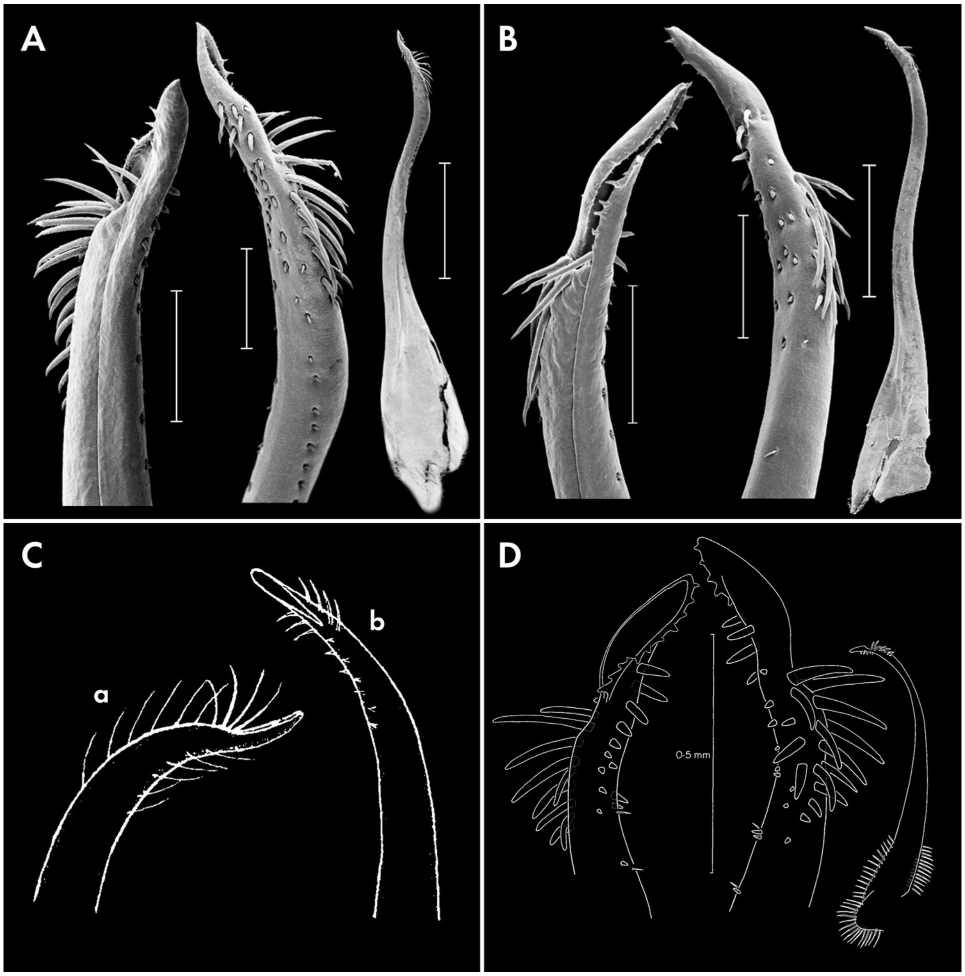

Fig. 3. First male gonopods (G1) of *Soliella* species; A, *Soliella flava* (Rathbun, 1893), G1, internal detail (scale = 200 µm), external detail (scale = 200 µm), and external full (scale = 1 mm) (UF 12254); B, *Soliella melanospinis* (Rathbun, 1911), G1, internal detail (scale = 200 µm), external detail (scale = 200 µm), and external full (scale = 1 mm) (ZRC 2013.1647); C, *S. flava* G1 (a) after Edmondson (1962: 21d) as *Chlorodopsis hawaiiensis*, (b) after Edmondson (1962: fig. 22b) as *Pilodius flavus*; D, *S. flava* G1 after Clark & Galil (1993: fig. 4E-G) as *Pilodius flavus*.

et al., 2002a: 271 (list); 2002b: 141, 194; 2008: 63 (list)–Ng et al., 2008: 197 (list).–Castro, 2011: 92. –Mendoza et al., 2014: 278.

Chlorodopsis flava, Serène & Nguyen Van Luom, 1959: 330, figs 2C, 5F, pl. 1 fig. B, pl. 3 fig. B.

Chlorodopsis hawaiiensis Edmondson, 1962: 273, fig. 21a–e.

Soliella flava, Lasley et al., 2015: 174, suppl. figs S1D, S3C, D, S5F.

Chlorodopsis melanodactylus, Miers, 1884: 531 (in part, from Etoile Island). Not *Pilodius melanodactylus* A. Milne-Edwards, 1873. [*fide* Clark & Galil, 1993].

Pilodius pubescens, De Man, 1902: 619. Not *Pilodius pubescens* Dana, 1852 [*fide* Balss, 1938].

?*Pilodius pubescens*, Nobili, 1907: 395. Not *Pilodius pubescens* Dana, 1852 [*fide* Balss, 1938].

Diagnosis. Carapace (Figs 4, 5A, B) transversely subhexagonal, ca. 1.5 times as broad as long; surface covered in short, stout and few long, light-coloured setae; regions well defined, separated by distinct, smooth furrows; 1 F indistinct; 2 F distinct; 1 M separated from 2 F and inner branch of 3 M by shallow furrow; 2 M entire or feebly divided anteriorly, 3 M entire; 4 M indistinct; 1 L indistinct; 1 L and 2 L partially confluent; 3 L-6L distinct; 1 P with defined anterior and posterior borders, lateral borders diffuse; 2 P with transverse row of granules. Submedian lobes of front (Fig. 5C) broadly convex, margin lined with granules, separated by median V- or U-shaped notch; lateral lobes triangular, granulate, separated from submedian lobes by deep, triangular notch, separated from orbits/supraorbital margin by rounded, L-shaped notch. Supraorbital margin lined dorsolaterally with short spines

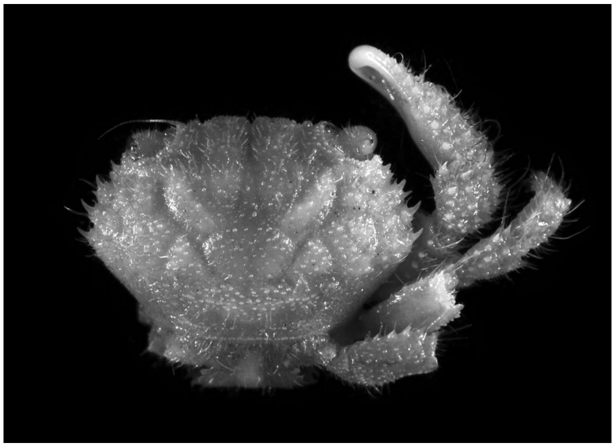

Fig. 4. *Soliella flava* (Rathbun, 1893), holotype female, 9 × 6 (USNM 17317), Hawaiian Islands, dorsal view.

or conical granules; infraorbital margin lined with conical granules. Anterolateral margin with four spinose lobes. Anterolateral angle of basal antennal article slightly expanded, entering less than halfway into orbital hiatus. Pterygostomial region minutely granulate, with plumose setae diagonally from posterior to lateral surface. Male thoracic sternum (Fig. 5D) relatively broad, minutely granulate, with few long, scattered setae; tubercle of press-button locking mechanism located on anterior half of sternite 5; suture 3/4 distinct near lateral margins, interrupted medially; median line present on sternite 4 as short suture midway between anterior border of sternite and sterno-pleonal cavity, interrupted in exposed posterior part, reappearing in sterno-pleonal cavity on posterior surface of sternite 4, absent at level of sternites 5 and 6, present and complete at level of sternites 7 and 8. Chelipeds (Fig. 5E, F) subequal, covered with long, simple, light-coloured setae, spinose; merus stout. Ambulatory legs (Fig. 5A) stout, setose; setae long, simple, light-coloured; extensor margin of merus lined with long spines; dactylo-propodal lock present, well developed; tip of dactylus terminating in long, curved, chitinous claw and two subdistal, small, calcareous spines. Male pleon (Fig. 5D) moderately stout, with few long posterior setae; pleonites 3–5 functionally fused, with distinct furrows delineating 3/4 and 4/5; pleonite 6 subquadrate, ca. as broad as long; telson subtriangular, ca. as broad as long. G1 (Fig. 3A, C) slender, sinuous, distal 1/4 curved ventrally; apex pointing anteroventrally with ca. 20 subdistal, perpendicular to proximally-directed, stout, spiniform setae on the anterior surface; apical lobe almost tubular, opening facing anteriorly. G2 ca. one-third length of G1, sigmoidally curved, terminal segment ca. one-fourth length of subterminal segment.

Female morphology. Females are similar to males, except in having nearly equal chelipeds and in sexual characters. Sternopleonal cavity wide, with the median line obscured completely by the pleon; sutures 2/3, 6/7, and 7/8 complete; suture 3/4 indicated only near lateral margin; sutures 4/5 and 5/6 interrupted medially. Vulvae crescent-shaped, positioned on sternite 6 near suture 5/6. Pleon long and wide relative to male; tip of telson reaching imaginary line between midpoint of cheliped coxae; all pleonites freely articulated.

Type status. The female holotype (USNM17317) from the Hawaiian Islands was examined for this study (SM1).

Remarks. *Soliella flava* and *S. melanospinis* are difficult to differentiate based on external morphology. Rathbun (1893, 1911) described both species. In her description of *S. melanospinis*, Rathbun (1911) stated that *S. flava* has a less deeply areolated carapace, a dorsum devoid of spines, and an upper margin of the orbit (supraorbital margin) without spines (vs. less deeply areolated regions, a spinose dorsum, and upper margin of the orbit in *P. melanospinis*). Serène (1984) stated that the spination on the supraorbital margin was a good character for differentiation, but that the difference in the areolation of the carapace was difficult to assess. He also stated that the G1s are similar, although he had provided figures of the two in his previous publications with Nguyen Van Luom (Serène & Nguyen Van Luom, 1958: pl. 4 fig. f; 1959: figs 2C, 2 *bis* M).

Edmondson (1962) described *Chlorodopsis hawaiiensis* without comparison with *S. flava* or *S. melanospinis*. He also provided illustrations of their G1s. Clark & Galil (1993) synonymized *S. melanospinis* and *S. hawaiiensis* with *S. flava*. However, Lasley *et al.* (2015, 2023) recovered two distinct, divergent species-level clades in *Soliella* in their molecular phylogenetic analyses, while there are three different G1 morphotypes illustrated in the literature. Edmondson (1962: figs 21d, 22b) provided figures of the ladle-like G1 of *Chlorodopsis hawaiiensis* and the tubular G1 of *S. flava*, illustrating them with distinct morphologies albeit in a simplistic, even schematic, style (Fig. 3C). Rathbun's (1893) Hawaiian holotype of *S. flava* is female. Examination of many Hawaiian specimens (SM1), however, including those previously identified as *Chlorodopsis hawaiiensis* and *S. flava* makes it clear that the G1s show only slight variation that had been exaggerated in the figures of Edmondson (1962). These gonopod morphotypes fall within the *S. flava* COI clade in the present analysis. The third G1 morphotype was illustrated by Clark & Galil (1993: fig. 4D–G) as *S. flava*, although their specimen is a paratype of *S. melanospinis* (Fig. 3D). This is the same morphotype as those illustrated by Serène and Nguyen Van Luom (1959: fig 2M) and Serène (1984:

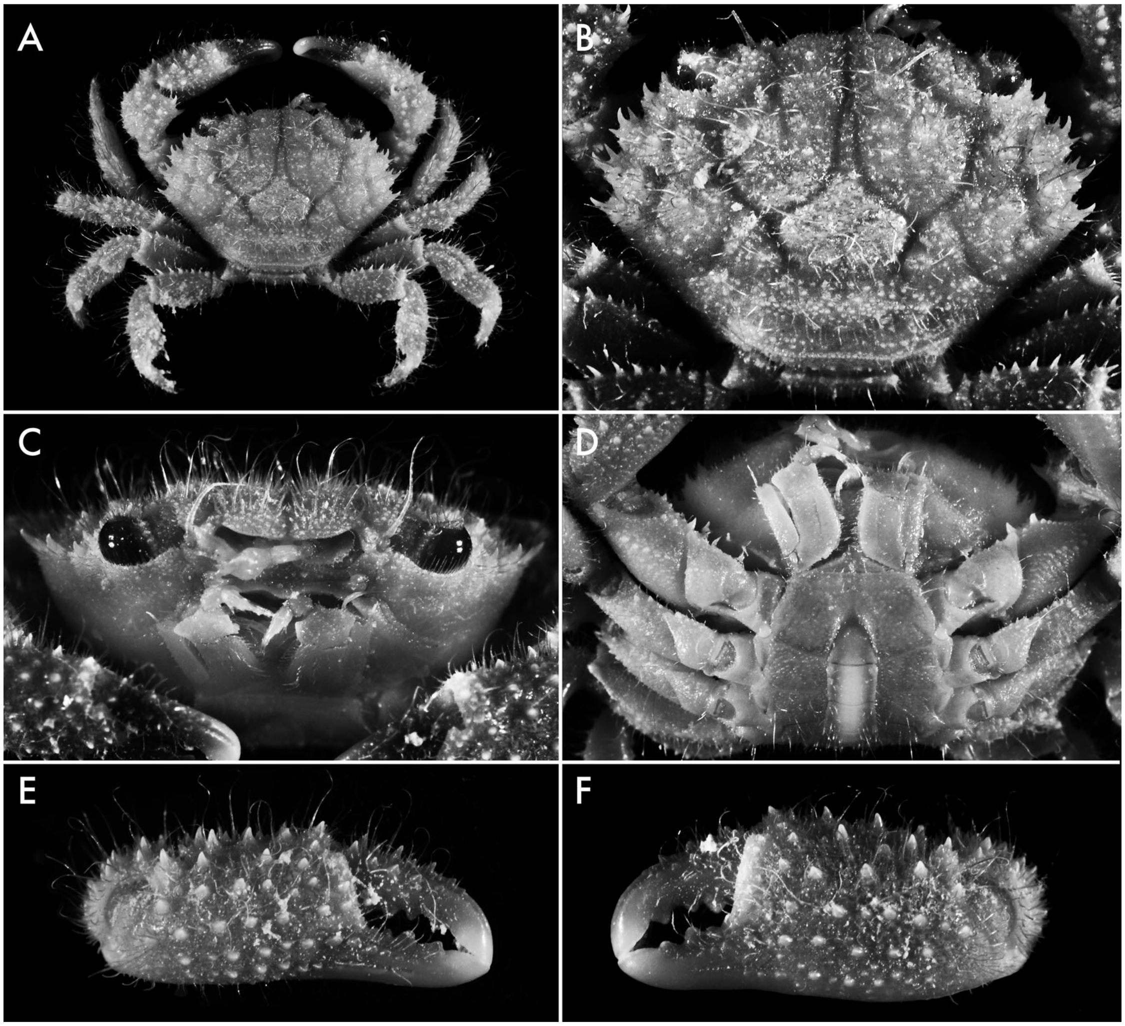

Fig. 5. *Soliella flava* (Rathbun, 1893), male, 10.2 × 6.9 (USNM 1181377), Marshall Islands; A, dorsal view; B, carapace, dorsal view; C, frontal view; D, thoracic sternum; E, minor chela, external view; F, major chela, external view.

fig. 146), but in these studies, they are identified as *S. melanospinis*.

In summary, the external morphological characters of Rathbun (1911) are difficult to appreciate, but G1 morphology and phylogenetic analyses indicate that there are clearly two species. Although the depth of the furrows separating the carapace regions and spination of the supraorbital margin vary, *S. flava* specimens do generally have less defined carapace regions and a supraorbital margin with shorter spines or conical granules (vs less relatively deeply defined regions and supraorbital margin with larger spines in *S. melanospinis*). These characters, however, display too much variation, especially in small individuals, to be used without caution. The form of the G1 appears to be the only reliable morphological character for identification. *Soliella flava* has a G1 pointing anteroventrally with an apical lobe opening anteriorly and ca. 20 spiniform subdistal setae on the anterior surface (vs apex pointing ventrally with an apical lobe that is longitudinally hollowed with a sinuous anterior margin and ca. 12 subdistal setae; Fig. 3). The two G1 morphotypes correspond with the well-supported clades in the phylogenetic analyses.

Distribution. *Soliella flava* is reported from Christmas Island (Indian Ocean) and the Indo-Australian Archipelago to the Hawaiian Islands and French Polynesia (Fig. 2).

Soliella melanospinis **(Rathbun, 1911)**

Figs 3B, D, 6

Chlorodopsis melanospinis Rathbun, 1911: 226, pl. 18 fig. 11.—Balss, 1938: 62.—Serène & Nguyen Van Luom, 1958: 108, pl. 1 fig. D, pl. 3 fig. b, pl. 4 fig. c; 1959: 302, fig. 2 *bis* M.

Pilodius melanospinis, Guinot, 1964: 67; 1967: 268.—Serène, 1968: 80; 1984: 242, figs 143e, 146, pl. 33 fig. E.

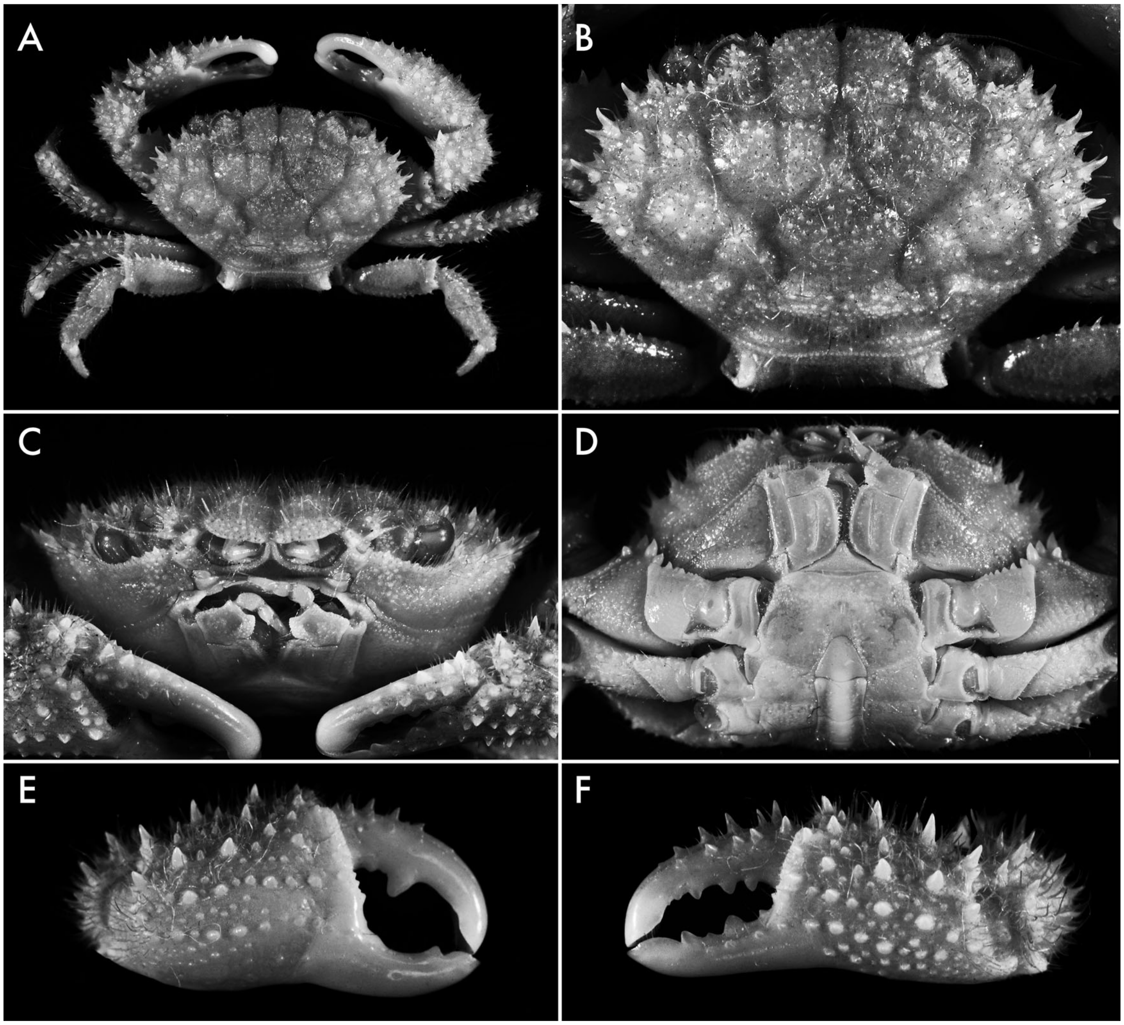

Fig. 6. *Soliella melanospinis* (Rathbun, 1911), holotype male, 17.0 × 11.4 (USNM 41268), Saya del Malha Bank; A, dorsal view; B, carapace, dorsal view; C, frontal view; D, thoracic sternum; E, major chela, external view; F, minor chela, external view.

Pilodius flavus, Clark & Galil, 1993: 1130 (in part).—Ng et al., 2008: 197 (list).

Chlorodopsis pilumnoides, Laurie, 1906: 406 (from Ceylon = Sri Lanka). Not *Pilodius pilumnoides* (White, 1848) [*fide* Clark & Galil, 1993].

Diagnosis. Carapace (Fig. 6A, B) transversely hexagonal, ca. 1.5 as broad as long; surface covered with short, stout light-coloured setae and few long, light-coloured setae; regions well defined, separated by wide, smooth, relatively deep furrows; 1 F indistinct; 2 F distinct; 1 M separated from 2 F and inner branch of 3 M by shallow furrow; 2 M entire or feebly divided anteriorly, 3 M entire; 4 M indistinct; 1 L indistinct; 1 L and 2 L partially confluent; 3 L–6L distinct; 1 P with defined anterior and posterior borders, lateral borders diffuse; 2 P with transverse row of granules. Submedian lobes of front (Fig. 6C) broadly convex, margin lined with granules, separated by median V- or U-shaped notch; lateral lobes triangular, separated from submedian lobes by deep, triangular notch, separated from orbits/supraorbital margin by rounded, L-shaped notch. Supraorbital margin generally lined dorsolaterally with relatively long spines or conical granules; infraorbital margin lined with conical granules. Anterolateral margin with four spinose lobes. Anterolateral angle of basal antennal segment slightly expanded, entering less than halfway into orbital hiatus. Pterygostomial region minutely granulate, with plumose setae diagonally from posterior to lateral surface. Male thoracic sternum (Fig. 4D) relatively broad, minutely granulate, with few long, scattered setae; tubercle of press-button locking mechanism located on anterior half of sternite 5; suture 3/4 distinct near lateral margins, interrupted medially; median line present on sternite 4 as short suture midway between anterior border of sternite and sterno-pleonal cavity, interrupted in exposed posterior part, reappearing in sterno-pleonal cavity on posterior surface of sternite 4, absent at level of sternites 5 and 6, present and complete at level of sternites 7 and 8. Chelipeds (Fig. 6E, F) subequal, covered with long, simple, light-coloured setae, spinose; merus stout. Ambulatory legs (Fig. 6A) stout, setose; setae long, simple, light-coloured; extensor margin of merus lined with long spines; dactylopropodal lock present, well developed; tip of dactylus terminating in long, curved, chitinous claw and two subdistal, small, calcareous spines. Male pleon (Fig. 6D) moderately stout, few long posterior setae; pleonites 3–5 functionally fused, with distinct furrows delineating 3/4 and 4/5; pleonite 6 subquadrate, ca. broad as long; telson subtriangular ca. as broad as long. G1 (Fig. 3B, D) slender, sinuous, distal 1/4 curved ventrally; apex pointing ventrally with ca. 12 subdistal, perpendicular to proximally directed, stout, spiniform setae on the anterior surface; apical lobe almost spatulate, longitudinally hollowed with sinuous anterior margin. G2 ca. one-third length of G1, sigmoidally curved, terminal segment ca. one-fourth length of subterminal segment.

Female morphology. Females are similar to males, except in having nearly equal chelipeds and in sexual characters. These characters are the same as those outlined for *Soliella flava* females (see above).

Remarks. See Remarks for *Soliella flava*.

Distribution. *Soliella melanospinis* occurs from the Western Indian Ocean to the Indo-Australian Archipelago and adjacent areas including Taiwan, Japan, Palau, the Solomon Islands, and Vanuatu (Fig. 2).

Type status. The male holotype (USNM 41268) from Saya del Malha Bank, Western Indian Ocean, was examined for this study (SM1).

Key to the species of *Soliella*:

- G1 ultimately pointing anteroventrally with apical lobe opening anteriorly. Carapace regions relatively less defined. Supraorbital margin with relatively low spines or conical granules .... *S. flava*
- G1 apex pointing ventrally with an apical lobe that is longitudinally hollowed with a sinuous anterior margin. Carapace regions relatively well defined. Supraorbital margin generally with longer spines *S. melanospinis*

Discussion

The synonymy of *S. melanospinis* with *S. flava* by Clark & Galil (1993) reflects the morphological similarity between the two species. The examination here further demonstrates this similarity: there are no external features that can reliably distinguish these two species. The two species, however, have discrete, although relatively slight, differences in G1 morphology (compare Fig. 3 with G1 figures of chlorodiellines in Serène 1984 and Lasley et al., 2023). Therefore, the term 'pseudocryptic' is used because: (1) molecular data guided the discovery of the species distinctions, and (2) there are minor but reliable morphological differences in a previously lumped species. The agreement between reciprocal monophyly in COI (here) and other markers (Lasley et al., 2023) with discrete differences in genital structures substantiates the use of the term 'species', especially considering their sympatric ranges and that genital divergence in arthropods is commonly used to infer reproductive isolation (Eberhard, 1985).

Lasley et al. (2023) showed a correlation between secondary sympatry and divergence of G1s among species in the clade Chlorodiellinae, which includes *Soliella*. The implication is that these crabs differentiate first in allopatry (or technically parapatry if some degree of homogenizing gene flow was present) and secondary contact is accompanied, or allowed, by G1 divergence. For analysis in the study, lineages were categorized as (a) sharing a G1 morphology with its sibling lineage or (b) possessing a unique G1; and geographic distribution was categorized as allopatric, narrowly sympatric, or sympatric. 'Narrowly sympatric' sibling lineages were defined as those having less than 10% overlap in total distribution. *Soliella melanospinis* and *S. flava* were coded as having unique G1s and sympatric distributions (Figs 2, 3). This differs from many sibling lineages in Chlorodiellinae that show less genetic divergence, are allopatric, and share the same G1 morphology. Although the ranges of the two *Soliella* broadly overlap in the West Pacific, *S. melanospinis* is the sole species through most of the Indian Ocean while only *S. flava* is known from remote Oceania in the central Pacific. Allopatric divergence between the Indian and Pacific Ocean basins is the most prevalent geographic differentiation in IWP marine taxa (Barber et al., 2000; Malay & Paulay, 2010, Ahti et al., 2016). The distribution of *Soliella* is suggestive of a similar history of allopatric divergence, followed by secondary range overlap in the West Pacific, likely allowed or facilitated by genital divergence, but accompanied by little other morphological differentiation.

Our limited COI dataset indicates panmixia in both species – not uncommon in marine organisms with long larval durations. Population genomic data could, however, indicate fine-scale divergence and/or directionality of gene flow. These data could shed more light on the geographic origins of, and processes that govern speciation in, these species.

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No potential conflict of interest was reported by the author(s).

Supplemental material

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