Revision of the coral reef crab genus *Tweedieia* Ward, 1935 (Decapoda, Brachyura, Xanthidae)

Robert M Lasley Jr.[1], Austin Smith[1], Gustav Paulay[1], and Peter K. L. Ng[2]

[1]Florida Museum of Natural History, University of Florida, Gainesville, FL, 32611-7800, USA

[2]Lee Kong Chian Natural History Museum, National University of Singapore, 2 Conservatory Drive, Singapore 117377

Correspondence: R. Lasley Jr.; rlasleyjr@gmail.com

ABSTRACT

Xanthid crabs of the genus *Tweedieia* Ward, 1935, are among the most charismatic decapod cryptofauna in Indo-West Pacific coral reefs. Ornamentation of granules and setae, in combination with color pattern, range from snowflake-like with purple spots to gem-like magenta. The genus and three recognised species (*T. odhneri* (Gordon, 1934); *T. laysani* (Rathbun, 1906) and *T. brevidactyla* Dai & Yang, 1998) are revised, and new diagnoses and figures are provided. The COI barcoding gene of 38 specimens was sequenced and used to generate maximum likelihood and neighbour-joining trees. *Tweeedieia brevidactyla* is here synonymized with *T. odhneri*. *Tweedieia* now comprises only two species, differentiated by morphological characters and sequence data. *Tweedieia odhneri* ranges from the western Indian Ocean to Hawai'i and French Polynesia, while the rare *T. laysani* is only recorded from the Hawaiian Islands. These crabs appear to favor clear, oligotrophic, oceanic waters and are common on oceanic islands and rare around continents and large islands of Australasia.

Key words: Crustacea, Chlorodiellinae, Continental Exclusion, Etisinae, Endemic, Hawai'i, Indo West-Pacific, Revision, Systematics, Taxonomy

INTRODUCTION

Crabs of the genus *Tweedieia* Ward, 1935 are chelate jewels of tropical, Indo-West Pacific reefs. The coloration—white and purple flecked, bright magenta, pale pink, or vibrant yellow and red—is striking, especially combined with the diagnostic, densely setose walking legs and strongly sculptured carapaces (see Poupin, 2018: fig. 17M). *Tweedieia* species live in reef interstices such as in dead branching coral, or under reef rocks. Although widespread, members of the genus are relatively uncommon in museum collections, probably because of

their preference for undersampled, cryptic habitats. The genus currently comprises three species: *T. laysani* (Rathbun, 1906), *T. odhneri* (Gordon, 1934), and *T. brevidactyla* Dai & Yang, 1998 (cf. Ng *et al*., 2008).

Ward (1935) described *Tweedieia* based on a new species, *T. noelensis*, from Christmas Island in the Indian Ocean. In his publication, Ward (1935) provided only a short description of *Tweedieia*, which focused mostly on the morphology of the front and orbits but did not make comparisons with other xanthid genera or species. *Tweedieia noelensis* was subsequently synonymized with *Phymodius odhneri* Gordon, 1934 (described from Macclesfield Bank in the South China Sea) by Balss (1938) without comment. Serène (1971) subsequently transferred *Phymodius laysani* Rathbun, 1906, to *Tweedieia*, with Dai & Yang (1998) describing a third species, *T. brevidactyla*, from the Nansha Islands (= Spratly Islands) in the South China Sea.

While the genus is generally accepted (see Serène, 1984), the taxonomy of the three species is not always clear as the identities of *T. odhneri* and *P. laysani* appear confused, at least on the basis of the literature. Additionally, the validity of *T. brevidactyla* is suspect as the authors did not compare it with *T. odhneri* even though both were described from the same area (South China Sea).

COI sequence data and examination of specimens throughout the Indo West-Pacific have shed light on the confusing taxonomy of the group. The present revision clarifies the identities of the three species, adding new morphological and genetic data, as well documenting variation. As a result, *Tweedieia* is now restricted to two species, with detailed figures and diagnoses provided for their identification. Hawaiian endemicity and continental exclusion are discussed in light of compiled range data of the two species.

MATERIAL AND METHODS

Specimens were examined from the collections of the Beijing Natural History Museum, Beijing (BNHM); Florida Museum of Natural History, Gainesville (UF); Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore (ZRC); Muséum National d'Histoire Naturelle, Paris (MNHN); Royal Belgian Institute of Natural Sciences (RBINS INV); The Natural History Museum, London (NHM); and U.S. National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM).

Morphological examination was done using a Leica MZ16 light microscope. The right first and second male gonopods (G1, G2) were removed for examination unless the specimen was damaged, in which case the left one was removed. Two specimens were selected for scanning electron microscopy of their G1s, including the holotype of *T. laysani*. Specimens were cleared of mucus and debris following Felgenhauer (1987) and dehydrated through a graded ethanol series followed by two changes in HMDS (hexamethyldisilazane). Dehydrated specimens were mounted on stubs using Elmer's glue and coated with 25 nm 60:40 gold:palladium using a Cressington Sputter Coater 108auto. Images were produced using a Leica Stereoscan 440 at the USNM Imaging Laboratory.

The DNA barcoding gene COI was sequenced to assess genetic variation across morphological variants and geographic populations, as this gene has been useful in delineating many crab species (Chu *et al*., 2015), including xanthoids (e.g., Lai *et al*., 2011; Lasley *et al.*, 2013; Thoma *et al*., 2014; Lasley *et al.*, 2015). The following species were selected as outgroups based on morphological diversity within Xanthidae and previous phylogenetic analyses (Lai *et al*., 2011; Lasley *et al.,* 2015): *Panopeus herbstii* H. Milne Edwards, 1834, *Etisus demani* Odhner, 1925, *Pilodius pilumnoides* (White, 1848), and *Cymo quadrilobatus* Miers, 1884. Outgroup and some ingroup taxa with published sequences from

previous taxonomic studies were culled from GenBank (https://www.ncbi.nlm.nih.gov/genbank/) (Table 1).

Various methods for amplification were used, with the majority of samples sequenced as described in Lasley *et al*. (2015). Sequences were checked for stop codons and aligned using MUSCLE, implemented in Geneious 8.1.9 (https://www.geneious.com). Specimens sequenced and GenBank accession numbers are provided in Table 1.

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*., 2010). The GTRGamma + I model of nucleotide substitution was selected and the analysis was conducted with 1,000 bootstrap replicates. A Neighbor-Joining analysis using the Tamura-Nei genetic distance model was also performed in Geneious 8.1.9 with 1,000 bootstrap replicates. Genetic distances were also calculated in Geneious 8.1.9.

The nomenclature and terminology used follows Ng *et al*. (2008) and Davie *et al*. (2015). The nomenclature for carapace regions follows Dana (1851) and Serène (1984). Measurements provided (in millimetres) are of the maximum carapace width and length, respectively. The following abbreviations are used: coll. = collected by; G1 = male first gonopod; G2 = male second gonopod; stn. = station.

RESULTS

Maximum likelihood (ML) and Neighbor-Joining (NJ) analyses resulted in phylogenetic trees with two well-supported, reciprocally monophyletic clades (Fig. 1). Clade 1 included two specimens that match the morphology of, and are topotypical with, *T. laysani*. Clade 2 included specimens from across the known range of *Tweedieia* (Western Indian Ocean to Hawaiian Islands and French Polynesia) and comprised specimens with morphological

features spanning *T. odhneri* and *T. brevidactylus*. The shortest interclade distance was 17.3%. Intraspecific distances were 0.6% (only two sequences) and 0–4.3% for *T. laysani* and *T. odhneri*, respectively.

TAXONOMY

Family Xanthidae MacLeay, 1838

***Tweedieia* Ward, 1935**

Tweedieia Ward, 1935: 22. — Balss, 1938: 61. — Serène, 1971: 911; 1984: 252. – Davie, 2002: 525. – Ng *et al.*, 2008: 197.

Type species: Tweedieia noelensis Ward, 1935, by monotypy; subjective junior synonym of *Phymodius odhneri* Gordon, 1934.

Diagnosis. Carapace transversely ovate to hexagonal, ca. 1.3–1.5 times broad as long; dorsal surface granular; regions defined by deep furrows, 2M and 3M prominent, well defined; front with wide medial lobes separated by notch, small lateral lobes merging with orbital angle. Anterolateral margin with 4 low, obtuse teeth apart from exorbital angle. Basal antennal article with elongated anterolateral angle extending partially into orbital hiatus, flagellum free to enter orbital hiatus. Adult chelipeds equal, short, edge of merus reaching just beyond edge of carapace in dorsal view; external surface of carpus granular; chela short, stout, fingers short, less than half length of palm, tips of fingers rounded, spatuliform, median part of occlusal margins with tuft of stiff setae. Ambulatory legs relatively short, covered with thick, plumose setae; merus length at most 2 times maximum width; dactylo–propodal locking mechanism well developed, formed by lamellar extension of distal margin of propodus that

slides beneath a bulbous flange on dactylus; tip of dactylus with chitinous, distal spine, without large secondary, downward directed calcareous spine. Male pleonal somites 3–5 completely fused, sutures not visible; anterior margin of male telson reaching beyond imaginary line between posterior margin of first ambulatory leg sternal condyles. Thoracic sternites 6, 7 delimited by sulcus. Pleonal somite 6 locking with round press-button on sternite 5, midway between sutures 4/5 and 5/6. G1 stout, tapering 3/4 distance to curved tip, with distal long, simple setae, numerous short spines, apex curved, long, open, tip rounded. G2 short, distally spatulate.

Remarks. Morphologically, *Tweedieia* is most similar to *Cyclodius* Dana, 1851 (a senior subjective synonym of *Phymodius* A. Milne-Edwards, 1863; cf. Davie, 2002: 520–521) in having spoon-tipped chelae and carapace regions that are well defined by deep furrows, with 2M and 3M distinct. The shape of the carapace in *Tweedieia*, however, is less transversely ovate, appearing more quadrate, with the dorsal surface covered in fine granules, often overlayed by scattered coarse granules (versus transversely ovate, with the exception of *Cyclodius nitidus* (Dana, 1852), and usually smooth in *Cyclodius*). *Tweedieia* also differs in having relatively shorter chelipeds, with the merus just extending beyond the anterolateral edge of the carapace in dorsal view; the chelae are distinctly shorter and stouter with the short fingers less than half the length of the palm; there are prominent brushes of stiff setae along the median parts of the occlusal margins of both fingers; and the G1 is diagnostic, with the structure curved and the tip open (versus proportionately longer chelipeds, longer chelae, longer fingers with the occlusal margins glabrous, and the G1 relatively straighter in *Cyclodius* (e.g., Serène, 1984: pl. 35, figs. 153–158).

The subfamilial placement of *Tweedieia* in the Xanthidae remains uncertain. Lai *et al*. (2011) did not treat the genus in their phylogenetic overview of the Xanthidae. Lasley *et al*.

(2015) regarded the genus as *incertae sedis* after excluding it from Chlorodiellinae Ng & Holthuis 2007. Despite its similarity to *Cyclodius*, genetic trees place *Tweedieia* outside the Chlorodiellinae as presently defined. That being said, the status of the Chlorodiellinae is also problematic, and some genera have already been transferred out (see Mendoza & Manuel-Santos, 2012; Lasley *et al*., 2013). Chlorodiellinae may just be a junior synonym of a redefined Etisinae Ortmann, 1893, but more work will need to be done to confirm this. For practical purposes and until the composition of these subfamilies can be clarified, we provisionally place *Tweedieia* in the Chlorodiellinae.

The type species of the genus is *Tweedieia noelensis* Ward, 1935, by original monotypy and designation. Balss (1938: 61) synonymised *Tweedieia noelensis* Ward, 1935, under *T. odhneri* (Gordon, 1934) without comment. Serène (1971) mistakenly gave priority to Ward's species name but later corrected this (Serène 1984: 252). Ward's (1935) description was published in a volume that was incorrectly dated as 1934 (Low *et al*., 2009). Serène (1971) was the first to transfer "*Phymodius laysani*" to *Tweedieia*.

The taxonomy of the two oldest species has been confusing, at least from the literature. In describing the first species, *Phymodius laysani*, Rathbun (1906: 858) commented that it was unusual and differed from other members of the genus "in the granulation of the (carapace) surface, in the union of the frontal and orbital angles, in the equal chelipeds, and indistinct spooning of the fingers". Gordon (1934: 33) agreed, treating her new species, *P. odhneri*, and the allied *P. laysani*, as "atypical species" of *Phymodius*. She suggested that the two species may need to be referred to a new subgenus or genus but did not take any formal action. Ward (1935), in describing *Tweedieia* and *T. noelensis*, did not realize his new genus and new species were close to *P. odhneri* and *P. laysani*, and made no mention of them. The concepts of *P. odhneri* and *P. laysani* were also unclear. In describing *P. odhneri*, Gordon (1934) was gifted a comparative specimen of "*P. laysani*"

from Balss which had belonged to Pesta. No locality was indicated for Pesta's specimen, but it probably was from Hawai'i as Pesta (1933) had earlier recorded the species from there. Gordon (1934: 47) listed three differences between *T. odhneri* and *T. laysani*: 1) "a deeper carapace with a wider frontal notch"; 2) "the anterior border of the buccal cavern is much less regular, being deeply concave on either side of the median line and the palatal ridges are much less pronounced"; and 3) "the fingers of the chela are considerably shorter and less hollowed at the tips". The problem here is that we do not believe Gordon's specimen of "*P. laysani*" is actually this species; her figures (Gordon, 1934: figs. 20c, d, 23b, c, 25a, b) indicate that it is actually morphologically closer to *P. odhneri*. Comparing figures of Gordon's specimen with Rathbun's (1906) holotype of *P. laysani*, we can discern clear differences in their chelar, G1, and buccal cavern morphology. This would explain why the three differentiating characters listed by Gordon are all minor ones.

Rathbun (1911) also reported a large specimen of "*P. laysani*" from the Chagos Archipelago in the western Indian Ocean that she said differed from her Hawaiian material in having a broadly U-shaped gap between the frontal lobes and in the pattern of grooves and lobules on the carapace. The commentary on variation in *P. laysani* was picked up by Guinot (1964: 85) in her report of another questionable specimen from the same area — this one from Aldabra — where she documented correspondence between herself and Gordon in which they both questioned the morphological limits of the two species, particularly *T. laysani*. The implication was that a third species might exist with her identifying the material as "*Phymodius* aff. *laysani*". However, Guinot (1964: 86) remarked, "seule la comparaison d'exemplaires des Hawai'i, des Chagos, du specimen determiné par PESTA, et enfin de celui récolté à l'île Aldabra permettra d'envisager la création d'une espèce nouvelle. L'étude de cette question fera l'objet d'une publication ultérieure." In short, these three authors were aware of significant variation but were wary of describing a third species without the

examination of more specimens. Interestingly, neither Guinot nor Gordon made the connection between the western Indian Ocean material to *P. odhneri* from Christmas Island and the South China Sea.

Key to the species of *Tweedieia*

- Carapace transversely hexagonal; anterolateral teeth anteriorly directed, relatively discrete with interdenticular clefts deeper; frontal notch narrow; carpus of cheliped without distinct, broad, transverse furrow on outer margin; dactyli of chelae slightly curved; external and superior surface of chelae evenly covered with numerous smaller granules…….. *T. laysani*

- Carapace transversely ovate; anterolateral teeth triangular, low with interdenticular clefts wide, shallow; frontal notch broad; carpus of cheliped with broad, transverse furrow on outer margin; dactyli of chelae strongly curved distally; external and superior surface of chelae with large, nodular granules, with one emergent nodular granule on propodus at superior junctions with dactylus and carpus……..*T. odhneri*

Tweedieia odhneri (Gordon, 1934)

(Figs. 2, 3B, 4)

Phymodius laysani, Rathbun, 1911: 226. – Pesta, 1933: 280. – Gordon, 1934: 47, fig. 23 c, 25 a. – Balss, 1938: 55. – Edmondson, 1946: 296, fig. 179d; 1962: 280, fig. 23c. – Holthuis, 1953: 24. – Guinot, 1964: 85, fig. 37 a, b.; 1967c: 267. – Serène, 1968: 81. – Dai *et al*., 1986: 311, pl. 44(5), fig. 167 A(2). – Chen and Lan, 1978: 275, fig. 8:1, pl. VI, fig. 23. – Dai & Yang, 1991: 335, pl. 44(5), fig. 167 A(2). Not *P. laysani* Rathbun, 1906.

Phymodius odhneri Gordon, 1934: 43, fig. 20 c, 22, 23 b, 24, 25 b, c [Type locality = Macclesfield Bank]. – Balss, 1938: 61. – Forest & Guinot, 1961: 104. – Guinot, 1964: 85. – Serène, 1968: 81 [list]; 1984: 253, fig. 164, pl. 37E.

Tweedieia noelensis Ward, 1935: 22, pl. 1, fig. 2 [Type locality = Christmas Island, Indian Ocean]. – Serène, 1971: 111.

Tweedieia odhneri, Balss, 1938: 61. – Serène *et al.,* 1976: 18. – Peyrot-Clausade, 1977a: 27; 1977b: 213. – Poupin, 1996: 57. – Guinot, 1985: 451. – Davie, 2002: 526. – Ng *et al*., 2008: 197.

Phymodius aff. *laysani,* Guinot, 1964: 85, pl. 10, fig. 3.

Tweedieia laysani, Serène, 1971: 112. – Takeda, 1972: 20, pl. I, fig. E. – Serène, 1984: 253–254, fig. 165, 166, pl. 37 F. – Dai *et al*., 1986: 311, pl. 44(5), fig. 167 A(2). – ?Peyrot-Clausade, 1989: 112. – Dai & Yang, 1991: 335, pl. 44(5), fig. 167 A(2). – ?Poupin, 1996: 57. Not *P. laysani* Rathbun, 1906.

Tweedieia brevidactyla Dai & Yang, 1998: 317, fig. 1(1–6) [Type locality = Zhubi Reef, Nansha Islands (= Subi Reef, Spratly Islands)]. – Ng *et al*., 2008: 197.

Tweedieа [sic] *odhneri*, Mendoza *et al*., 2014: 295.

Type material examined: 1 male, 10.3 × 7.3 (NHM 1935.5.21.12) (holotype of *Tweedieia noelensis* Ward, 1935), Christmas Island (Indian Ocean), coll. M. W. F. Tweedie [photographs examined]. – 1 holotype male, 9.8 × 7.1 mm, 1 paratype male, 9.6 × 6.7 mm, 1 paratype female, 8.1 × 6.1 mm (NHM 1935.1.28.19–21) (types of *Phymodius odhneri* Gordon, 1934), Macclesfield Bank, coll. P. Bassett-Smith, Esq., H. M. S. Penguin [photographs examined]. – 1 paratype female, 5.9 × 4.5 mm (RBINS INV 113725) (paratype of *Phymodius odhneri* Gordon, 1934), Macclesfield Bank, coll. P. Bassett-Smith, Esq., H. M. S. Penguin [photographs examined]. – 1 paratype female, 9.5 × 7.5 mm (BNHM CB 03297)

(paratype of *Tweedieia brevidactyla* Dai & Yang, 1998), Zhubi Reef, Nansha Islands (= Subi Reef, Spratly Islands), coll. Y. Cai, 9 April 1994 [photographs examined].

Other material examined: **Mozambique Channel:** 1 female, 6.5 × 5.0 mm (UF 20738), MEPA-00761, JDNO-17, 5 m, 17.0747° 42.7661°, from old dead *Pocillopora*, fore reef slope, Juan de Nova, coll. H. Bruggemann, 29 April 2009. – 1 female, 8.5 × 6.3 mm (UF 21130), stn. GLOR-2, -11.59088333° 47.2851333°, 7–14 m, reef platform and shallow canyons, Glorioso Islands, coll. H. Bruggemann, M. Malay, J. Rousse, G. Galves, 4 May 2009. – 2 males, 7.8 × 6.0 mm – 8.6 × 6.5 mm (UF 21143), stn. GLOR-2, -11.59088333° 47.2851333°, 7–14 m, reef platform and shallow canyons, Glorieuses Island, coll. H. Bruggemann, M. Malay, J. Rousse, G. Galves, 4 May 2009. – 1 male, 8.8 × 6.7 mm (MNHN IU-2009-2679), 15–20 m, Mayotte, coll. 2009.

Seychelles: 1 female, 9.2 × 6.6 mm (MNHN B. 6777), 40 m, entre Johny Channel et la Grande Passe, Aldabra, coll. Calypso Exp., 25 May 1954.

Chagos Archipelago: 1 male, 13.1 × 9.5 mm, 3 females, 7.8 × 5.8 mm – 10.5 × 7.6 mm, 1 juvenile (ZRC 2013.0781), CH0774, 10 m approx., dead branching coral heads, outer reef, Egmont Islands, coll. C. Head, H. Koldeway, 1 March 2013. – 1 male, 9.9 × 7.6 mm, 1 female, 9.7 × 7.3 mm, 1 juvenile (ZRC 2013.0783), CH0742, 10 m approx., dead branching coral heads, outer reef, Egmont Islands, coll. C. Head, H. Koldeway, 1 March 2013. – 1 male, 10.0 × 7.3 mm (ZRC 2013.0773), CH0853, 10 m approx., dead branching coral heads, outer reef, Diego Garcia, coll. C. Head, H. Koldeway, 5 March 2013. – 1 male, 12.2 × 8.6 mm (ZRC 2013.0785), CH0801, 10 m approx., dead branching coral heads, outer reef, Egmont Islands, coll. C. Head, H. Koldeway, 1 March 2013. – 1 male, 10.3 × 7.4 mm (ZRC 2013.0780), CH0223, 10 m approx., dead branching coral heads, outer reef, Salomon Island,

coll. C. Head, H. Koldeway, 20 February 2013. – 1 male, 11.3 × 7.9 mm (USNM 41260), near reef, Salomon Island, coll. J. Gardine, Sealark Expedition, Sealark R/V, 1905.

Maldives: 1 female, 11.9 × 6.8 mm (UF 39632), MALD-225, MG-20, 3.0613° 72.9311°, 10 m, forereef, E side of Dharanboodhoo Island, coll. J. Moore, 12 May 2014. – 1 female, 9.8 × 7.4 mm (UF 39693), MALD-348, MG-26, 3.077° 72.969°, 12 m, Magoodhoo Island, left of pass on outer reef, coll. Marco, 14 May 2014.

Cocos (Keeling) Islands: 1 female, 6.4 × 4.8 mm (ZRC 2013.1667), Stn. CK18, photo, 5.7 m, 12°05.675'S 96°53.175'E, daytime, diving, narrow channel connecting lagoon and ocean, the Rip, SW of Direction Island, coll. 22 March 2011.

Christmas Island (Indian Ocean): 1 male, 6.9 × 5.1 mm (ZRC 2013.1668), Stn. CI-D17-2011 (187), 3–16.6 m, S10° 27.906' E105° 36.465', submarine cave, afternoon, Thunderdome Cave, coll. 30 March 2011. – 1 male, 5.2 × 4.1 mm (ZRC 2013.1666), Stn. CI-D18-2011, 5–16 m, S10° 27.729' E105° 37.283', reef slope and crest, Rhoda Wall, off Rhoda Beach, coll. 30 March 2011. – 1 male, 7.4 × 5.5 mm (ZRC 2013.1669), Stn. CI-D16(139), photo DSC5647-5652, coll. 1 February 2010.

Indonesia: 1 male, 9.6 × 7.9 mm, 1 female, 7.3 × 5.8 mm (MNHN B. 6708), Île de Banda Neira, coll. Serène, Rumphius III, 30 January 1975. – 1 male, 4.0 × 3.1 mm (ZRC 2013.1597), Stn. BL11-013, BALI-0380, 22–24 m, rubble extraction, reef wall/steep slope, coral reef with sea grass and sand, Sombu, Wangi-Wangi Island, Sulawesi, coll. 24 June 2011. – 1 male, 6.3 × 4.7 mm (USNM 134579), coral head, Lembek Strait, Celebes Island, Greater Sunda Islands, Sulawesi, coll. A. Herre, 21 June 1929.

Mariana Islands: 1 female, 8.6 × 6.4 mm (UF 2567), stn. ZZZ-087046, 13.5° 144.8°, 50–100 m, among rocks, Orote Point, SE Side, Guam Island, coll. H. Conley, F. Schroeder, 30 December 2001. – 1 female, 8.0 × 6.0 mm (UF 763), stn. ZZZ-015453, 13.5° 144.8°, 20–25 m, under rock, reef slope, Orote Peninsula, SW side, Guam Island, coll. G. Paulay, 27

February 1998. – 1 female, 6.4 × 5.2 mm, 1 male, 5.9 × 4.6 mm, 2 juveniles (UF 56802), MAU-416, NOAA_MAU-09A, 20.030° 145.208°, 17 m, forereef, Maug Island, coll. 1 May 2009 – 20 April 2011. – 1 male, 6.4 × 4.9 mm, 1 female, 6.3 × 5.1 mm (UF 56566), MAU-004, NOAA_MAU-11B, 20.013° 145.209°, 12 m, forereef, Maug Island, coll. 30 April 2009 – 19 April 2011. – 1 male, 5.5 × 4.1 mm, 1 juvenile (UF 56825), PAG-611, NOAA_PAG-01A, 18.107° 145.786°, 11 m, forereef, Pagan Island, coll. 13 April 2011 – 20 April 2014.

Wake Island: 1 female, 8.4 × 6.3 mm (UF 8564), Bonito-Wake-09, 27–45 ft, 19.2712° 166.6512°, forereef, coll. V. Bonito, 31 November – 1 December 2005. – 1 female, 6.5 × 4.8 mm (UF 8561), stn. Bonito-Wake-04, 19.30782° 166.59378°, 45–59 m, forereef, coll. V. Bonito, 31 November 2005. – 1 male, 8.1 × 6.0 mm (UF 37042), stn. Kim-WAK-St-07, 50–70 m, in dead *Pocillopora*, ocean side of atoll, coll. S. Kim, 24 March 2009.

Marshall Islands: 1 male, 6.8 × 5.3 mm, 1 female, 7.0 × 5.3 mm (USNM 1181279), Bock Island, Rongerik Atoll, coll. F. M. Bayer, F. C. Zimmerman, 19 August 1947.

Kiribati: 1 male, 11.4 × 8.3 mm (USNM 93981), Onotoa Atoll, Gilbert Islands, coll. P. Cloud, 23 August 1951. – **1** male, 12.7 × 9.6 mm (UF 50873), PHOE-0287, PHX-018, -3.118° -171.093°, 40–58 feet, reef slope, rubble, coral, hard substrate with sand in valleys, NW corner of island, Lone Palm, Enderbury Island, Phoenix Islands, coll. R. Lasley, 9 September 2015. – 1 female, 7.5 × 6.9 mm (UF 51011), PHOE-0460, PHX-028, -3.579° -171.523°, 60 ft, steep reef slope, rubble, coral, Progathius Point, Bimie Island, Phoenix Islands, coll. R. Lasley, 12 September 2015. – 2 ovigerous females, 9.9 × 7.3 mm – 9.9 × 7.6 mm (UF 51406), PHOE-0934, PHX-052, -4.491° -172.137°, 40 ft, rubble, scattered corals, farside, Orona Island, Phoenix Islands, coll. R. Lasley, 20 September 2015. – 1 male, 11.3 × 8.4 (UF 51494), PHOE-1047, -3.60272° -174.12219°, 45 ft, hard substrate, coral rubble, southern point, McKean Island, Phoenix Islands, coll. R. Lasley, 22 September 2015.

American Samoa: 1 male, 7.0 × 5.8 mm (UF 56830), ROS-677, NOAA_ROS-04A, -14.560° -168.160°, 14 m, forereef, Rose Atoll, coll. 13 March 2008 – 4 March 2010. – 1 juvenile (UF 56829), ROS-670, NOAA_ROS-04C, -14.560° -168.160°, 13.7 m, forereef, Rose Atoll, coll. 13 March 2008 – 4 March 2010. – 1 male, 6.8 × 4.9 mm (UF 56799), TUT-401, NOAA_TUT-22B, -14.366° -170.763°, 12 m, forereef, Tutuila Island, coll. 24 February 2010 – 3 April 2012.

Cook Islands: 1 female, 9.6 × 7.1 mm (UF 1368), stn. EPASS, -21.233333° -159.766667°, 1–30 m, Avarua Pass, Rarotonga Island, coll. C. Meyer, 18 October 2001.

Johnston Atoll: 1 female, 9.6 × 6.7 mm (USNM 1181278), outer reef, NW side of island, coll. F. Bayer, 28 Aug 1947.

Hawaiian Islands: 1 female, 5.0 × 3.9 mm, 1 male 4.8 × 3.6 mm, 1 juvenile (UF 56812), KUR-372, NOAA_KUR-12B, 28.382° -178.324°, 9.8 m, forereef, Kure Atoll, coll. 30 September 2008 – 18 September 2010. – 1 male, 4.5 × 3.5 mm, 8 juveniles (UF 56811), KUR-341, NOAA_KUR12A, 28.382° -178.324°, 10 m, forereef, Kure Atoll, coll. 30 September 2008 – 18 September 2010. – 1 female, 11.2 × 8.1 mm (USNM 64184), Pearl and Hermes Reef, coll. P. Galtsoff, 23 July 1930 (identified as *T. laysani* by M. Rathbun). – 1 male, 6.9 × 5.4 mm (UF 56809), LIS-23B, NOAA_Lis-R10A, 25.945° -173.954°, 15 m, forereef, Lisiansky Atoll, coll. 5 October 2008 – 24 September 2010. – 1 male, 12.9 × 8.7 mm (UF 12047), BRRS-185, FFS-0025, 40 ft, 23.8617° -166.1852°, rubble extraction, fore reef, French Frigate Shoals, coll. G. Paulay *et al*., 12 October 2006. – 4 males, 13.2 × 8.9 mm – 4.8 × 3.7 mm, 5 females, 9.9 × 7.0 mm – 4.5 × 3.3 mm (UF 12342), stn. FFS-0091, 23.8733° -166.2347°, 15 m, back reef, French Frigate Shoals, coll. R. Brainard, B. Zgliczynski, 16 October 2006. – 1 male, 11.4 × 8.1 mm (UF 12116), stn. FFS-0088, 23.8733° -166.2347°, 15 m, under rocks, back reef, French Frigate Shoals, coll. G. Paulay, S. McKeon, J. Starmer, T. Lotufo, S. Godwin, J. Martin, J. Maragos, 16 October 2006. – 1 male, 13.3 ×

9.1 mm (UF 12343), stn. FFS-0091, 23.8733° -166.2347°, 15 m, back reef, French Frigate Shoals, coll. R. Brainard, B. Zgliczynski, 16 October 2006. – 1 ovigerous female, 13.2 × 9.1 mm (USNM 64185), Sta. 41, in coral, Bird Islands, coll., P. Galtsoff, 26 July 1930 (identified as *T. laysani* by M. Rathbun). – 1 juvenile (UF 56800), KAU-749, NOAA_KAU-08A, 22.167° -159.680°, 12.5 m, forereef, Kauai Island, coll. 5 November 2008 – 27 October 2010. – 1 male, 7.6 × 5.7 mm (ZRC 2000.0509), Moku Manu Island, north of Makapu Peninsula, Oahu, coll. R. De Felice & S. Coler, 26 January 2000. – 9 juveniles (UF 56819), HAW-495, NOAA_HAW-24B, 19.038° -155.883°, 14.6 m, Hawai'i Island, coll. 1 November 2008 – 12 October 2010.

Line Islands: I female, 10.7 × 7.6 mm (UF 10452), MSR-326, KINF20-DP, 6.3801° -162.4137°, 35 ft, outer reef slope, dead *Pocillopora* ?*verrucosa* head, S shore of atoll (W or KINB9), Kingman Reef, coll. M. Malay, 30 August 2005. – 1 female, 7.8 × 6.3 mm (UF 10595), MSR-155, KINF16-DP, 6.3796° -162.3648°, 40 ft, outer reef slope, from dead *Pocillopora* ?*verrucosa*, S shore of atoll, Kingman Reef, coll. M. Malay, 28 August 2005. – 1 male, 11.8 × 8.7 mm (UF 10836), stn. Clam Gardens-001-DP, 6.39079° -162.34189°, 13.5 m, from dead *Pocillopora* ?*verrucosa* head, lagoon?, W of Channel Buoy of La Paloma Pass, Kingman Reef, coll. M. Malay, 29 August 2005. – 1 male, 11.5 × 8.4 mm (UF 10505), stn. KINF20-DP, 6.3801° -162.4137°, 35 m, from dead *Pocillopora* ?*verrucosa* head, outer reef slope, S shore of atoll (w of Kinb9), Kingman Reef, coll. M. Malay, 30 August 2005. – 1 female, 7.5 × 4.9 mm (UF 10590), stn. KINF16-DP, 6.3796° -162.3648°, 40 m, from dead *Pocillopora* ?*verrucosa* head, outer reef slope, S shore of atoll, Kingman Reef, coll. M. Malay, 28 August 2005. – 1 female, 4.3 × 3.3 mm (UF 10527), stn. KINF16-DP, 6.3796° -162.3648°, 40 m, from dead *Pocillopora* ?*verrucosa* head, outer reef slope, S shore of atoll, Kingman Reef, coll. M. Malay, 28 August 2005. – 1 male, 11.1 × 8.0 mm (UF 13806), stn. PALB10-DP, 5.8663° -162.0581°, 0–16 m, in dead *Pocillopora* head, outer reef slope, S side

of atoll, Palmyra Atoll, coll. M. Malay, 22 August 2005. – 1 female, 6.1 × 4.5 mm (UF 10502), stn. GP-Loc-848-DP, 5.8693° -162.0757°, 9–15 m, from dead *Pocillopora* ?*verrucosa* head, outer reef slope, SSW side of Atoll, Palmyra Atoll, coll. G. Paulay, N. Knowlton, 18 August 2005. – 1 male, 11.2 × 8.1 mm, 1 female, 11.2 × 7.9 mm (UF 10504), stn. GP-Loc-841-DP, 3.8418° -159.3608°, 10–15 m, from dead *Pocillopora* ?*verrucosa* head, outer reef slope, W side, S of main reef pass, Tabuaeran Atoll, coll. G. Paulay, N. Knowlton, 12 August 2005. – 1 female, 8.4 × 6.4 mm (UF 10510), stn. GP-Loc-841-DP, 3.8418° -159.3608°, 10–15 m, from dead *Pocillopora* ?*verrucosa* head, outer reef slope, W side, S of main reef pass, Tabuaeran Atoll, coll. G. Paulay, N. Knowlton, 12 August 2005. – 1 juvenile (UF 10553), BTAB-704, TABB9-DP, 3.8681° -159.3742°, 35 ft, outer reef slope, from dead *Pocillopora* ?*verrucosa* head, W side of Atoll, N of Main Reef Pass, Tabuaeran Atoll, coll. G. Paulay, N. Knowlton, 15 August 2005. – 1 male, 9.6 × 7.1 mm, 2 ovigerous females, 9.2 × 6.9 mm – 10.2 × 7.6 mm (UF 10594), stn. GP-Loc-836-DP, 1.8563° -157.5539°, 10–20 m, from dead *Pocillopora* ?*verrucosa* head, outer reef slope, ca. 1 mile E of SW point, along S side of atoll, Kiritimati Atoll, coll. G. Paulay, N. Knowlton, 9 August 2005.

French Polynesia: 1 male, 7.3 × 5.8 mm (UF 16335), stn. MIB_200, -17.47638° -149.83266°, 4–7 m, extracted from large piece of dead *Acropora*, outer reef slope, spur & groove zone, between Cook's Bay and Sheraton, removal site 2 of SMc, Moorea Island, Society Islands, coll. S. McKeon, J. Moore, A. Anker, V. Ivanenko, 10 November 2008. – 1 female, 9.9 × 7.3 mm (UF 13861), stn. ZZZ-017503, -17.5° -149.8°, in dead *Pocillopora* head (#5), Moorea Island, Society Islands, coll. L. Plaisance, June 2006. – 1 female, 9.7 × 7.2 mm (UF 29165), stn. BIZ-623, -17.52192° -149.7622°, 15 m, broken rubble, forereef, N side of ferry channel, Moorea Island, Society Islands, coll. D. Uyeno, 22 November 2010. – 1 male, 8.2 × 6.3 mm, 1 juvenile, 3.6 × 2.7 mm (UF 29257), stn. BIZ-668, -17.52945° -149.76203°, 15–20 m, in/on rubble, Vaire Pass, S of ferry entrance, Moorea Island, Society

Islands, coll. C. Glasby, 30 November 2010. – 1 male, 10.0 × 7.3 mm (UF 35434), stn. GAMG-42, -23.1489° -134.846°, 14 m, leeward fore reef, Tauna Island, Gambier Islands, coll. J. Moore, 1 February 2013. – 1 male, 8.0 × 5.9 mm (UF 35518), stn. GATE-66, -23.329° -134.506°, 20 m, leeward fore reef, Temoe Atoll, Gambier Islands, coll. J. Moore, 9 February 2013.

Diagnosis: Carapace transversely ovate, ca. 1.3–1.4 times broad as long; dorsal surface granular; regions projecting, defined by deep furrows; anterolateral regions rounded, separated by deep broad depressions; region adjacent to tooth 3 large, confluent with tooth; posterolateral regions separated by broad furrows. Front sinuous; medial lobes subtriangular to convex, separated by wide, deep U-shaped notch; lateral lobes small, separated from medial lobes by concavity. Anterolateral margin with 4 low, obtuse, subtriangular teeth apart from exorbital angle with interdenticular clefts wide, shallow. Chelipeds equal, stout; external surface of carpus with nodules and distinct broad furrow near junction with propodus. Extensor margin of ambulatory meri lined with large conical granules. G1 stout, tapering abruptly 3/4 distance to recurved tip, distal anterodorsal surface covered with numerous long setae, numerous short spines on distal dorsal and ventral surfaces, twisting along long axis distally, apex recurved, pointing ventrally to ventromesially; long, hollowed, tip rounded.

Remarks: Gordon (1934) described *T. odhneri* from three males and two females collected from Macclesfield Bank in the South China Sea, the holotype male being 9.8 × 7.1 mm. Our material from nearby, Indonesia and Christmas Island, agree very well with the excellent description and figures by Gordon (1934), and we have no doubts of their conspecificity. As discussed above, we are confident that her specimen of "*P. laysani*" is almost certainly *T. odhneri* s. str. A comment on the proportions of the chelar fingers, which she used to separate

the two taxa (supposedly shorter in *T. odhneri*), however, is necessary. Several specimens in the *T. odhneri* clade we examined actually have conspicuously long chelar dactyli (e.g., UF 12047, UF 8564, UF 37042, UF 13861, and UF 1368), while other specimens in the same clade have significantly shorter chelar dactyli (e.g., UF 35518 and UF 12413). Furthermore, this clade contains individuals that show variations in the relative width of the frontal notch, Gordon's first distinguishing character. For example, several specimens have a wide notch and low submedian lobes (UF 10594 and UF 39693), whereas many others have a relatively narrow notch with more projecting submedian lobes (e.g., UF 10453 and UF 10452). The notch tends with be narrower in smaller individuals and most specimens have a frontal notch that is intermediate. That being said, and even accounting for variation, the median notch is always distinctly wider than that in *T. laysani*.

G1 morphology is relied upon heavily in distinguishing xanthid species (e.g., Serène 1984) and is thus worthy of comment. *Tweedieia odhneri* has a G1 that twists along the long axis at the distal one-fourth of its length, somewhat coincident with the narrowing of the G1's girth (versus without significant twisting in *T. laysani*). The degree of torsion varies in *T. odhneri*, which is mostly attributable to size. Small individuals generally lack the degree of torsion of large individuals. Specimens of the same size, however, can have different degrees of torsion (e.g., UF 12413 and UF 35518). This character does not correspond with other variable characters, such as the length the chelar dactyli. For example, the large male specimen, UF 40468, with short chelar dactyli has a twisted G1, whereas the small male specimen, UF 12413, with short chelar dactyli has a relatively flat G1. Variation in small specimens is displayed in Serène's (1984: fig. 164, 165) figures of *Tweedieia* G1s, the latter (fig. 165) of which is a reproduction of Guinot's (1964: 37a-b) figure and is incorrectly identified, in both publications, as *T. laysani*. Given the variation, identification of specimens based on G1 morphology should be done with caution.

The synonymy of *T. odhneri* (Gordon, 1934) with *T. noelensis* Ward, 1935, suggested by Balss (1938) is not in doubt. We have examined photographs of the holotype specimen of *T. noelensis* and four members of the type series, including the holotype, of *T. odhneri*. These photographs are sufficiently detailed as to leave no doubt about their conspecificity. Furthermore, high resolution photos of one of the female paratypes of *T. odhneri* (RBINS INV. 113725) at the Royal Belgian Institute of Natural Sciences are available to view online (http://virtualcollections.naturalsciences.be/) (Fig. 4C–D).

Tweedieia brevidactyla Dai & Yang, 1998, was described from one male (7.2 × 5.6 mm) and one paratype female (9.5 × 7.5 mm) from the Nansha Islands (= Spratly Islands) in the South China Sea. Their description was very brief, and they only compared it with *T. laysani*. On the basis of their figures (Dai & Yang, 1998: fig. 1–7) and our study of the photographs of the paratype female (BNHM CB 03297) (Fig. 4A–B) (the holotype male could not be found), we have no doubt that *T. brevidactyla* is a junior synonym of *T. odhneri*; all their diagnostic characters agree, including in the structure of the G1. It is also important to note that Macclesfield Bank, the type locality of *T. odhneri*, close to Subi Reef, the type locality of *T. brevidactyla*, with both sites in the center of the South China Sea; and it is therefore a bit surprising why the authors did not compare their new taxon with *T. odhneri*. Although no type or topotypic specimens of *T. brevidactyla* were available for examination or sequencing, a specimen from relatively nearby (Sulawesi, Indonesia) was recovered within the *T. odhneri* clade (Fig. 1).

The phylogeny comprised specimens from throughout the Indo-West Pacific, from the Hawaiian Islands and French Polynesia to the Western Indian Ocean, including important historical localities like the Glorioso Islands (near Aldabra), the Chagos Archipelago, Hawai'i, and Christmas Island. Specimens from these localities fall within the morphological variation of *T. odhneri* outlined above. Given these genetic and morphological data,

specimens, in addition to synonymies, that have been questioned based on morphological variation in the literature are assigned to *T. odhneri* including: 1) Gordon's (1934: figs. 20c, d, 23b, c, 25a, b) "*Phymodius laysani*" specimen, likely from the Hawaiian Islands, that was gifted to her by Balss and had previously belonged to Pesta; 2) Rathbun's (1911) "*Phymodius laysani*" specimen from the Chagos Archipelago; and 3) Guinot's (1964: 85) "*Phymodius* aff. *laysani*" specimen from Aldabra Island.

Distribution: Tweedieia odhneri occurs on reefs across the Indo-West Pacific from islands in the western Indian Ocean to the Hawaiian Islands and the Gambier Islands, but it is relatively rare around large islands and continents, including Australia, Southeast Asia, and the Coral Triangle. Some of the records in the coral triangle come from small oceanic islands or reefs, including the type specimens of *T. odhneri* and *T. brevidactyla*, both from the South China Sea (see Discussion).

Tweedieia laysani **(Rathbun, 1906)**

(Figs. 3A, 5)

Phymodius laysani Rathbun, 1906: 858, fig. 19, pl. 12, fig. 8 [Type locality: Laysan, Hawai'i]. – ?Edmondson, 1923: 1552; 1925: 44. – ?Amerson & Shelton, 1976: 76. – ?Titcomb *et al*., 1979: 364. – ?Coles *et al.*, 1999: 159. – ?Coles *et al*., 2001: 53. – ?DeFelice *et al.*, 2002: 30, 72. – Forest & Guinot, 1961: 104.

Tweedieia laysani, ?DeFelice *et al*., 1998: 16. – ?Coles *et al.*, 2002: 271, 334. – ?Godwin & Bolick, 2006: 39, 49. – Ng *et al*., 2008: 197. – Castro, 2011: 93 (in part).

Not *Phymodius laysani*, Gordon, 1934: 47, fig. 23 c, 25 a. – Balss, 1938: 55. – Edmondson, 1946: 289, fig. 179d; 1962: 280, fig. 23c. – Holthuis, 1953: 24. – Guinot, 1964 fig. 37 a,

b.; 1967c: 267. – Serène, 1968: 81. – Dai *et al*., 1986: 311, pl. 44(5), fig. 167 A(2). – Chen and Lan, 1978: 275, fig. 8:1, pl. VI, fig. 23. – Dai & Yang, 1991: 335, pl. 44(5), fig. 167 A(2). All *Tweedieia odhneri* (Gordon,1934).

Not *Tweedieia laysani*, Serène, 1971: 112. – Takeda, 1972: 20, pl. I, fig. E. – Serène, 1984: 253–254, fig. 165. – Dai *et al*., 1986: 311, pl. 44(5), fig. 167A(2). – Dai & Yang, 1991: 335, pl. 44(5), fig. 167 A(2). – Poupin, 1996: 57. All *Tweedieia odhneri* (Gordon, 1934).

Type material examined: holotype male, 8.2 × 5.8 mm (USNM 29530), Laysan, Hawaiian Islands, coll. U.S. Fish Commission, Steamer Albatross, May 1902.

Other material examined: **Hawaiian Islands:** 1 male, 10.2 × 7.4 mm, 1 female, 10.3 ×7.4 mm (UF 45738), BKON-113, KANI024C, 21.475° -157.799°, 1–2 m, in rubble, limestone bench, patch coral and rubble, S. of Kapapa Island, Kaneohe Bay, Honolulu, coll. IZ Team, 25 May 2017. – 1 juvenile, 5.4 × 4.4 mm (UF 45651), BKON-0737, KANI-022A, 21.477° -157.795°, 4–6 m, outer reef slope in rubble, NE side of Kapapa Island, Kaneohe Bay, Honolulu, coll. IZ Team, 25 May 2017.

Diagnosis: Carapace transversely hexagonal, ca. 1.5 times broad as long; dorsal surface granular; regions defined by deep furrows; anterolateral regions separated by deep, broad depressions, region adjacent to anterolateral tooth 3 small, separated from tooth by depression; posterolateral regions separated by narrow furrows. Medial lobes of front gently convex, separated by V- or narrow U-shaped notch; lateral lobes narrow. Anterolateral margin with 4 teeth, apart from exorbital angle, teeth discrete with interdenticular clefts relatively deep; tooth 1 low, obtuse; teeth 2, 3 projecting, anteriorly directed; tooth 4 small, triangular. Chelipeds equal, stout; external surface of carpus with large granules; external

surface of propodus granulate with few granules arranged in transverse rows externally; dactylus short, relatively straight, tip rounded. Extensor margin of ambulatory legs granulate. G1 stout, tapering gradually ¾ distance to curved tip, distal anterodorsal surface lined with long simple setae, numerous short spines on distal dorsal and ventral surfaces, without significant longitudinal torsion, apex pointing ventrally; long, hollowed, tip rounded.

Remarks: Tweedieia laysani s. str. is a rare species that is apparently restricted to the Hawaiian Islands. As discussed earlier, many early records of "*Phymodius laysani*" (or "*Tweedieia laysani*") are actually *T. odhneri*. *Tweedieia odhneri*, however, has a very wide Indo-Pacific range, occurring from the Hawaiian Islands and French Polynesia to the Western Indian Ocean, and varies in characters that have been used to diagnose the species. Accepting these precepts and applying them at critical stages in the literature resolves considerable confusion.

As stated above, Gordon's (1934) specimen of "*P. laysani*" from an unspecified location, as well as Rathbun's (1911) material from Chagos, is almost certainly *T. odhneri*. The wide U-shaped median frontal cleft is a reliable diagnostic character to distinguish *T. odhneri*, and this is supported by our extensive morphological examination combined with COI analyses (Fig. 1). The *T. laysani* holotype as well as three conspecific individuals (UF 45738, UF 45651) all have a narrow median notch of the front (Figs. 5A–C). All other specimens examined, including specimens from Chagos, have a relatively broad notch. This character, although it varies in degree in *T. odhneri*, is always relatively broad in the species and corresponds with a suite of characters that further distinguish it from *T. laysani* (see Remarks for *T. odhneri*). Guinot's (1964) specimen of "*Phymodius* aff. *laysani*", and likely the other specimen she obtained from Edmondson that was mentioned in the publication, fall within the range of morphological variation exhibited by *T. odhneri* (see Remarks for *T. odhneri*). Although it is possible that the Johnston Atoll specimen that Guinot obtained from

Edmondson is a true *T. laysani*, it is unlikely for two reasons: 1) the figure (Guinot, 1964: fig. 37a-b) provided of the Johnston Atoll specimen's G1 is much closer to that of *T. odhneri*; and 2) another specimen (USNM 1181278) examined from Johnston Atoll is *T. odhneri*. It is interesting that specimens previously reported by Edmondson (1946: 289, fig. 179d; 1962: 280, fig. 23c) from the Hawaiian Islands all appear to be *T. odhneri* as well, at least based on what we have examined, although *T. laysani* is also present in the islands. Furthermore, her correspondence with Gordon reported in the publication indicates that Guinot's understanding of the species was based, at least in part, on Gordon's understanding of the two species' morphological limits.

As discussed earlier, we believe Pesta's (1933) specimen of "*P. laysani*" from Hawai'i used by Gordon (1934) is probably *T. odhneri* instead. There are a number of records of "*T. laysani*" from the Hawaiian Islands by Amerson & Shelton (1976), Titcomb *et al*. (1979), DeFelice *et al*. (1998), Coles *et al*. (2001), DeFelice *et al.* (2002), Coles *et al.* (2002) and Godwin & Bolick (2006) which may all be *T. odhneri* instead. Their material will need to be re-examined to ascertain their identity. As such, we treat Castro's (2011) record of "*T. laysani*" as also a composite one as he included old reports of the species as well as the original description of the species by Rathbun (1906).

Guinot's (1964) restraint from describing a third species until more specimens could be examined was astute given what we now know about the species. Subsequent reports of *T. laysani* were probably also based on Gordon's perception of the two species—i.e., authors are most likely confusing *T. odhneri* with *T. laysani*. This is especially evident in Serène's (1984) monograph of Indian Ocean xanthids. In a footnote, Crosnier noted the difficulty in using Serène and other authors' diagnoses to identify specimens (Serène, 1984: 253). For variation within *T. odhneri*, see remarks for the species.

Only four specimens of *T. laysani* s. str. are known, the holotype and three other specimens from the Hawaiian Islands (UF 45651, UF 45738). *Tweedieia laysani* differs from *T. odhneri* in the following features: 1) frontal median notch shallow and narrow (versus relatively broad in *T. odhneri*) (Figs. 2A–C, 5A–C); 2) relatively broad, transversely hexagonal carapace with anterolateral margins more conventionally arcuate and a more angular border with the posterolateral margin, giving the anterior carapace a more fan-shaped aspect (versus relatively narrow, transversely ovate carapace with rounded lateral margins in *T. odhneri*) (Figs. 2B, 5B); 3) anterolateral teeth anteriorly directed and relatively discrete with interdenticular clefts relatively deep (versus triangular and low with interdenticular clefts wide, shallow in *T. odhneri*) (Figs. 2B, 5B); 4) carpus of cheliped with relatively narrow, shallow transverse furrow on outer margin (versus carpus of chelipeds with broad transverse furrow on outer margin in *T. odhneri*) (Figs. 2A, E–F; 5A, E–F); 5) movable fingers of the chelae relatively straight (versus curved movable fingers in *T. odhneri*) (Figs. 2E–F, 5E–F); and 6) external and superior surface of chelae evenly covered with smaller granules (versus external and superior surface of chelae with larger, nodular granules, with one emergent granule each at junctions of dactylus and carpus on superior margin) (Figs. 2A, E–F; 5A, E–F).

The rarity of *T. laysani* and ubiquity of *T. odhneri* is reaffirmed by the large metabarcode dataset assembled by the NOAA ARMS (Autonomous Reef Monitoring Structures) project (Timmers, 2021). This program placed ARMS at sites across the west and central Pacific, including throughout the Hawaiian Islands, on outer reef slope habitats around 15 m depths. ARMS were processed by identifying large mobile animals that colonized the structures and sequencing smaller mobile and sessile biomass from the units (see Leray & Knowlton, 2015). All *Tweedieia* specimens captured in these ARMS were *T. odhneri*, and a selection from across the localities are reported above. The metabarcode data

from these efforts also only have reads of *T. odhneri* COI sequences from all sites, specifically Timor, Mariana Islands (Guam, Pagan, Maug), Wake, Samoa (Rose Atoll, Tutuila), Line Islands (Kingman, Palmyra, Jarvis), and Hawaiian Islands (Kure, French Frigate Shoals, Pearl & Hermes, Lisianski, Kauai, Oahu, Hawai'i) (M. Timmers, pers. comm.). The lack of *T. laysani* in this record reaffirms the restriction and rarity of this species and suggests that the two species of *Tweedieia* may occur in different habitats in the Hawaiian Islands. Both recent samples of *T. laysani* come from shallow, nearshore waters, while collections of *T. odhneri* are typically from outer reef slopes at 10–30 m, the same habitat that the NOAA ARMS program sampled.

Distribution. Tweedieia laysani is only known from the Hawaiian Islands (see Discussion).

DISCUSSION

The revised taxonomy presented here underscores the importance of integrative taxonomy, utilizing historical literature and collections, and need for new, broadscale collections. *Tweedieia* now comprises two species, half the species previously described. Furthermore, understanding of the geographic distributions of *T. laysani* and *T. odhneri* has dramatically changed. *Tweedieia laysani* is a rare species only known from Laysan and Oahu, Hawaiian Islands. *Tweedieia odhneri*, on the other hand, is widespread from the Western Indian Ocean to French Polynesia and the Hawaiian Islands, where it co-occurs with *T. laysani*.

Relatively recent expeditions targeting reef cryptofauna, particularly those deploying ARMS or with intensive sampling of coral rubble, indicate that *T. odhneri* is abundant in oceanic reef systems in both the Pacific and Indian Oceans. Interestingly, similar expeditions in the Great Barrier Reef and Western Australia have produced no *T. odhneri* specimens. In addition to the type material of *T. brevidactyla* and *T. odhneri* from the South China Sea,

only four specimens are known from SE Asia, including the Coral Triangle: 3 specimens reported by Serene (1971, 1984) from the Philippines, Vietnam, and Indonesia, and one specimen collected by the first author in Sulawesi, Indonesia. The species is also represented in the ARMS metabarcode record from East Timor. No additional material from continental Asia or the Indo-Australian Archipelago (IAA) are known. These data indicate that the species is rare on continental reef systems. Most of the *Tweedieia* were collected on the outer reef slope, the part of the reef system directly exposed to clear, oceanic waters, and appear to be rare or absent from reef flats and lagoons, habitats more impacted by terrigenous influences, even though the latter are much better sampled habitats. This affirms the preference by these species for clear, oligotrophic, oceanic waters.

Continental exclusion and oceanic distributions straddling the IAA have been recorded in other decapod crustaceans, such as various sesarmids, ocypodids, the coconut crab, *Birgus latro*, various hermit crabs and lobsters (George, 1974; Lavery *et al.*, 1996; Malay & Paulay, 2010; Paulay & Starmer, 2011; Ma *et al.*, 2018; Schubart & Ng, 2020). Habitat preference for clear, oligotrophic waters or competition or predation in these highly diverse reefs are likely drivers of oceanic restriction (e.g., see Malay & Paulay, 2010, Paulay & Starmer, 2011), with the former more likely for *Tweedieia*.

ACKNOWLEDGEMENTS

We thank JC Mendoza and Dzaki Safaruan at the Lee Kong Chian Natural History Museum for sharing tissues of several specimens used in this study. We are also grateful to Paul Clark and Ashlie Hartigan, and Yves Samyn for supplying photos and measurements of type specimens at The Natural History Museum, UK, and the Royal Belgian Institute of Natural Sciences, respectively. We also thank R. Rotjan and S. Mangubhai for their leadership of the 2015 expedition to the Phoenix Islands Protected Area aboard the Hanse Explorer, supported

by the Republic of Kiribati, the New England Aquarium, Woods Hole Oceanographic Institution, Scripps Institution of Oceanography, and Fondation Prince Albert II of Monaco. Several specimens collected during the expedition were used in this study. Many of the specimens used in this study were taken during several other large-scale biodiversity surveys; we thank the funders and organizers of these efforts. These include the Kaneohe Bay Bioblitz in the Hawaiian Islands organized and funded in part by the Smithsonian and University of Hawaii, the Moorea Biocode project funded by the Gordon and Betty Moore Foundation, and the NOAA ARMS program. We also thank Molly Timmers for sharing metabarcode results from her dissertation research. We are also grateful for funding from NSF DBI-1756440 for student and curational support. This study began during the first author's predoctoral fellowship at the Smithsonian Institution's National Museum of Natural History.

REFERENCES

Amerson Jr, A.B. & Shelton, P.C. 1976. The natural history of Johnston Atoll, central Pacific Ocean. *Atoll Research Bulletin*, 192: i–xx, 1–479.

Balss, H. 1938. Ueber einige Xanthidae (Crustaea Dekapoda) von Singapore und Umgebung. *Bulletin of the Raffles Museum*, **14**: 48–63; Pls. II–III.

Castro, P. 2011. Catalog of the anomuran and brachyuran crabs (Crustacea: Decapoda: Anomura, Brachyura) of the Hawaiian Islands. *Zootaxa*, **2947**(1): 1–154.

Chen, H. & Lan, J. 1978. Preliminary studies on the Xanthidae (Brachyura, Crustacea) of the Xisha Islands, Guangdong Province China. In: *Report on the Scientific Results of Marine Biology of the Xisha Islands and Zhongsha Islands (South China Sea)*, pp. 261–286. South China Sea Institute of Oceanology, Academia Sinica, Guangzhou.

Chu, K.H., Schubart, C.D., Shih, H.T. & Tsang, L.M. 2015. Genetic diversity and evolution of Brachyura. In: *Treatise on Zoology-Anatomy, Taxonomy, Biology. The Crustacea, Volume 9 Part C* (2 vols) (P. Castro, P. Davie, D. Guinot, F. Schram, and C.V. Klein, eds.), pp. 775–820. Brill, Leiden.

Coles, S.L., DeFelice, R.C. & Eldredge, L.G. 1999. Nonindigenous marine species introductions in the harbors of the south and west shores of Oahu, Hawai'i. Report prepared for the David and Lucile Packard Foundation. *Bishop Museum Technical Report*, **15**: i–vii, 1–210.

Coles, S.L., DeFelice, R.C. & Minton D. 2001. Marine species survey of Johnston Atoll, Central Pacific Ocean, June 2000. Report to U.S. Fish & Wildlife Service, Honolulu. *Bishop Museum Technical Report*, **19**: i–v, 1–58.

Coles, S.L., DeFelice, R.C. & Eldredge, L.G. 2002. Nonindigenous marine species in Kane'ohe Bay, O'ahu, Hawai'i. Final report prepared for the David and Lucile Packard Foundation and the State of Hawai'i, Department of Land and Natural Resources, Division of Aquatic Resources. *Bishop Museum Technical Report*, **24**: i–vii, 1–353.

Dai, A.Y. & Yang, S.L. 1998. A new species of the genus *Tweedieia* from Nansha Islands (Crustacea: Decapoda: Brachyura: Xanthidae). *Studies on Marine Fauna and Flora and Biogeography of the Nansha Islands and Neighbouring Waters*, **3**: 317–320.

Dai, A.Y. & Yang, S.L. 1991. *Crabs of China Seas*. China Ocean Press, Beijing, pp 21+608.

Dai, A.Y., Yang, S.L., Song, Z.Y. & Chen, G.X. 1986. *Crabs of the China Seas*. China Ocean Press, Beijing, pp 11+642.

Dana, J.D. 1851. On the classification of the Cancroidea. *American Journal of Science and Arts, Series 2*, **12**: 121–131.

Davie, P.J.F. 2002. Crustacea: Malacostraca: Eucarida (Part 2): Decapoda-Anomura, Brachyura. In: *Zoological Catalogue of Australia* (A. Wells & W.W.K. Houston, eds.), Vol. 19.3B, pp. i–xiv, 1–641. CSIRO Publishing, Melbourne, Australia.

Davie, P.J.F., Guinot, D. & Ng, P.K.L. 2015. Anatomy and functional morphology of Brachyura. In: *Treatise on zoology – anatomy, taxonomy, biology, Decapoda: Brachyura* (P. Castro, P.J.F. Davie, D. Guinot, F.R. Schram & J.C. von Vaupel Klein, eds.), Vol. 9C-I, pp. 11–163. Brill, Leiden, The Netherlands.

DeFelice, R.C., Coles, S.L., Muir, D. & Eldredge, L.G. 1998. *Investigation of the Marine Communities of Midway Harbor and Adjacent Lagoon, Midway Atoll, Northwestern Hawaiian Islands. Report Prepared for U.S. Fish and Wildlife Service, Pacific Islands Area Office, Honolulu*. Hawaiian Biological Survey, Bishop Museum, Honolulu, 1–30.

DeFelice, R.C., Minton, D. & Godwin, S. 2002. Records of shallow-water marine invertebrates from French Frigate Shoals, Northwestern Hawaiian Islands, with a note on nonindigenous species. *Bishop Museum Technical Report*, **23**: 1–78.

Edmondson, C.H. 1923. A preliminary comparison between Hawaiian and Australian Crustacea. *Proceedings of the Pan-Pacific Science Congress, Australia 1923*, **2**: 1548–1553.

Edmondson, C.H. 1925. Crustacea. In: Marine Zoology of tropical central Pacific (Tanager Expedition, Publication 1). *Bulletin Bernice P. Bishop Museum*, **27**: 3–62.

Edmondson, C.H. 1946. *Reef and Shore Fauna of Hawai'i. Bernice P. Bishop Museum, Special Publication*, **22**: 1–381.

Edmondson, C.H. 1962. Xanthidae of Hawai'i. *Occasional Papers of Bernice P. Bishop Museum*, **22**(13): 215–309.

Felgenhauer, B.E. 1987. Techniques for preparing crustaceans for scanning electron microscopy. *Journal of Crustacean Biology*, **7**: 71–76.

Forest, J. & Guinot, D. 1961. Crustacés décapodes brachyoures de Tahiti et des Tuamotu. In: *Expédition française sur les Récifs coralliens de la Nouvelle-Calédonie. Volume préliminaire*. Fondation Singer-Polignac, Paris.

Forest, J. & Guinot, D. 1961. Crustacés Décapodes Brachyoures de Tahiti et des Tuamotu. In: *Expédition Français sur les Récifs Coralliens de la Nouvelle-Calédonie*, pp. 1–195. A. Lahure, Paris.

George, R.W. 1974. Coral reefs and rock lobster ecology in the Indo-West Pacific region. *Proceedings of the Second International Coral Reef Symposium, Brisbane*, **1**: 321–325.

Godwin, S. & Bolick, H. 2006. Inventory of intertidal and shallow subtidal marine invertebrates at Kalaupapa National Historic Park. Final report prepared for the U.S. Department of Interior, National Park Service, Pacific Islands Coral Reef Program, Honolulu. *Bishop Museum Technical Report*, 2006–003: 1–58.

Gordon, I. 1934. Résultats scientifiques du voyage aux Indes Orientales Néerlandaises de LL. AA. RR. le Prince et la Princesse Léopold de Belgique. Crustacea Brachyura. *Memoires du Musée Royal D'Histoire Naturelle de Belgique: Hors Série*, **3**: 3–78.

Guinot, D. 1985. Crustacea. French Polynesian coral reefs, reef knowledge and field guides. In: *Fifth international coral reef congress, Tahiti, 1985* (Richard, G., ed.), pp. 446–

455. Muséum National d'Histoire Naturelle and École Pratique des Hautes Études Antenne de Tahiti, Paris.

Guinot, D. 1964. Crustacés décapodes brachyoures (Xanthidae) des campagnes de la Calypso en Mer Rouge (1952), dans le golfe Persique et à l'île Aldabra (1954). *Mémoires du Muséum national d'Histoire naturelle (Paris), n.s., ser. A*, **32**(1): i–iii, 1–108, pls. 1–12.

Guinot, D. 1967. La faune carcinologique (Crustacea Brachyura) de l'océan Indien Occidental et de la Mer Rouge. Catalogue, remarques biogéographiques et bibliographie. Réunion de spécialistes C.S.A. sur les crustacés, Zanzibar 1964. *Mémoires de l'Institut Fondamentale d'Afrique Noire*, **72**(2): 237–352.

Guinot, D. 1985. Crustacea. *French Polynesian coral reefs, reef knowledge and field guides, Fifth international coral reef congress, Tahiti, 1985* (G. Richard, ed.), pp. 446–455. Muséum National d'Histoire Naturelle and École Pratique des Hautes Études Antenne de Tahiti, Paris.

Holthuis, L.B. 1953. Enumeration of the decapod and stomatopod Crustacea from Pacific coral islands. *Atoll Research Bulletin*, **24**: 1–66.

Lai, J.C., Mendoza, J.C.E., Guinot, D., Clark, P.F. & Ng, P.K. 2011. Xanthidae MacLeay, 1838 (Decapoda: Brachyura: Xanthoidea) systematics: a multi-gene approach with support from adult and zoeal morphology. *Zoologischer Anzeiger-A Journal of Comparative Zoology*, **250**(4): 407–448.

Lasley, R.M., Lai, J.C. & Thoma, B.P. 2013. A new genus for *Chlorodiella longimana* (H. Milne Edwards) supported by morphology and molecular data, with a preliminary

phylogeny of the Chlorodiellinae (Crustacea: Decapoda: Xanthidae). *Invertebrate Systematics*, **27**(4): 379–390.

Lasley Jr, R.M., Klaus, S. & Ng, P.K. 2015. Phylogenetic relationships of the ubiquitous coral reef crab subfamily Chlorodiellinae (Decapoda, Brachyura, Xanthidae). *Zoologica Scripta*, **44**(2): 165–178.

Lavery, S., Moritz, C. & Fielder, D.R. 1996. Indo-Pacific population structure and evolutionary history of the coconut crab *Birgus latro*. *Molecular Ecology*, **5**(4): 557–570.

Leray, M. & Knowlton, N. 2015. DNA barcoding and metabarcoding of standardized samples reveal patterns of marine benthic diversity. *Proceedings of the National Academy of Sciences*, **112**(7): 2076–2081.

Low, M.E. & Tan, S.H. 2009. Dates of publication of the Bulletin of the Raffles Museum and Bulletin of the National Museum, predecessors to the Raffles Bulletin of Zoology. *Raffles Bulletin of Zoology,* Supplement No. **22**: 283–294.

Ma, K.Y., Chow, L.H., Wong, K.J., Chen, H.N., Ip, B.H., Schubart, C.D., Tsang, L.M., Chan, B.K. & Chu, K.H. 2018. Speciation pattern of the horned ghost crab Ocypode ceratophthalmus (Pallas, 1772): An evaluation of the drivers of Indo-Pacific marine biodiversity using a widely distributed species. *Journal of Biogeography*, **45**(12): 2658–2668.

Malay, M.C.M.D. & Paulay, G. 2010. Peripatric speciation drives diversification and distributional pattern of reef hermit crabs (Decapoda: Diogenidae: *Calcinus*). *Evolution: International Journal of Organic Evolution*, **64**(3): 634–662.

Mendoza, J.C.E., Lasley Jr, R.M. & Ng, P.K.L. 2014. New rock crab records (Crustacea: Brachyura: Xanthidae) from Christmas and Cocos (Keeling) Islands, Eastern Indian Ocean. *Raffles Bulletin of Zoology*, **30**: 274–300.

Mendoza, J.C.E. & Manuel-Santos, M.R. 2012. Revision of *Garthiella* Titgen, 1986 (Crustacea: Decapoda: Brachyura: Xanthidae), with description of a new subfamily and a new species from the central Philippines. *Zootaxa*, **3446**: 32–48.

Miers, E.J. 1884. Crustacea, Part II, Collections from the Western Indian Ocean. In: *Report on the Zoological Collections Made in the Indo-Pacific Ocean During the Voyage of H.M.S. `Alert' 1881–2*, pp. 513–575, pls. 46–52. British Museum, London,

Miller, M.A., Pfeiffer, W. & Schwartz, T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov. 2010, New Orleans, LA 1 - 8.

Milne-Edwards, A. 1863. Monographie des Crustacés Fossiles de la Famille des Canceriens. *Annales des Sciences Naturelles, 4^{e} série,* **20**: 273–324.

Milne Edwards, H. 1834. *Histoire naturelle des Crustacés, Comprenant l'Anatomie, la Physiologie et la Classification des ces Animaux, vol. 1*. Librairie Encyclopédique de Roret, Paris.

Ng, P.K.L. & Holthuis, L.B. 2007. Case 3394. *Etisus* H. Milne Edwards, 1834 and *Chlorodiella* Rathbun, 1897 (Crustacea, Decapoda, Brachyura): proposed conservation of the generic names by suppression of the generic name *Clorodius* A.G. Desmarest, 1823. *Bulletin of Zoological Nomenclature*, **64**(1): 19.

Ng, P.K., Guinot, D. & Davie, P.J. 2008. Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology*, **17**(1): 1–286.

Odhner, T. 1925 Monographierte Gattungen der Krabbenfamilie Xanthidae. I. *Göteborgs Kungl. Vetenskaps- Och Vitterhets-Samhälles Handlingar, ser. 4 (Meddelanden från Göteborgs Musei Zoologiska Avdelning, Avd. 37)*, **29**(1): 1–92, pls. 1–5.

Ortmann, A.E. 1893. Abtheilung: Brachyura (Brachyura genuina Boas) 1. Unterabtheilung: Majoidea und Cancroidea, 1. Section: Portuninea. Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und z. Z. im Strassburger Museum aufbewahrten Formen, VI Theil. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Thiere*, **7**: 23–88, pl. 3.

Paulay, G. & Starmer, J. 2011. Evolution, insular restriction, and extinction of oceanic land crabs, exemplified by the loss of an endemic *Geograpsus* in the Hawaiian Islands. *PLoS One*, **6**(5): e19916 [https://doi.org/10.1371/journal.pone.0019916].

Pesta, O. 1933. Zoogeographische Berichte über Crustaceen. *Zoologisches Anzeiger*, **104**: 274–282.

Peyrot-Clausade, M. 1977a. *Faune cavitaire mobile des platiers coralliens de la region de Tulear (Madagascar).* PhD. thesis, Aix-Marseille University, Marseille, France.

Peyrot-Clausade, M. 1977b. Decapodes brachyoures et anomoures (à l, exception des Paguridae) de la cryptofaune de Tiahura Ile de Moorea. *Cahiers du Pacifique*, **20**: 211–221.

Peyrot-Clausade, M. 1989. Crab cryptofauna (Brachyura and Anomura) of Tikehau, Tuamotu Archipelago, French Polynesia. *Coral Reefs*, **8**(3):109-117.

Poupin, J. 1996. Crustacea Decapoda of French Polynesia (Astacidea, Palinuridea, Anomura, Brachyura). *Atoll Research Bulletin*, 144: 1–114.Poupin, J., Cleva, R., Bouchard, J.M., Dinhut, V. & Dumas, J. 2018. The crabs from Mayotte Island (Crustacea, Decapoda, Brachyura). *Atoll Research Bulletin*, **617**: 1–109.

Rathbun, M.J. 1906. The Brachyura and Macrura of the Hawaiian islands. *Bulletin of the United States Fish Commission*, **23**(3): 827–930, pls.1–24.

Rathbun, M.J. 1911. No. XI.—Marine Brachyura. *Transactions of the Linnean Society of London. 2nd Series: Zoology*, **14**(2): 191–261.

Schubart, C.D. & Ng, P.K.L. 2020. Revision of the intertidal and semiterrestrial crab genera *Chiromantes* Gistel, 1848, and *Pseudosesarma* Serène & Soh, 1970 (Crustacea: Brachyura: Sesarmidae), using morphology and molecular phylogenetics, with the establishment of nine new genera and two new species. *Raffles Bulletin of Zoology*, **68**: 891–994.

Serène, R. 1968. The Brachyura of the Indo Pacific Region. In: *Prodromus for a Check List of the Non-planctonic Marine Fauna of South East Asia. Special Publication of the Singapore National Academy of Science*, **1**: 33–120.

Serène, R. 1971. Observations préliminaires sur des Brachyoures nouveaux ou mal connus du Sud-Est Asiatique (Crustacea Decapoda). *Bulletin du Muséum national d'Histoire naturelle*, **42**: 903–918.

Serène, R. 1984. Crustacés décapodes brachyoures de l'océan Indien Occidental et de la mer Rouge. Xanthoidea: Xanthidae et Trapeziidae. Avec un addendum par Crosnier (A.): Carpiliidae et Menippidae. *Faune tropicale*, **24**: 1–400, pls. 1-48.

Serene, R., Romimohtarto, K. & Moosa, M.K. 1976. Hippidea, Brachyura and Stomatopoda of the Rumphius Expedition II. *Oseanologi Indonesia*, **6**: 15–21.

Stamatakis, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, **30**(9): 1312–1313.

Takeda, M. 1972. Further notes on the unrecorded xanthid crabs from the Rykyu Islands. *Biological Magazine, Okinawa*, **9**: 15–24.

Thoma, B.P., Guinot, D. & Felder, D.L. 2014. Evolutionary relationships among American mud crabs (Crustacea: Decapoda: Brachyura: Xanthoidea) inferred from nuclear and mitochondrial markers, with comments on adult morphology. *Zoological Journal of the Linnean Society*, **170**(1): 86–109.

Timmers, M.A. 2021. *DNA metabarcoding to examine the biodiversity of coral reef cryptobiota.* Ph.D. Dissertation, University of Hawai'i at Manoa, Honolulu, Hawai'i.

Titcomb, M., Fellows, D.B., Pukui, M.K. & Devaney, D.M. 1979. Native use of marine invertebrates in old Hawai'i. *Pacific Science*, **32**(4)[1978]: 325–391.

Ward, M. 1935. Notes on a collection of crabs from Christmas Island, Indian Ocean. *Bulletin of the Raffles Museum*, **9**:5–28.

White, A. 1848. Short descriptions of new or little-known decapod Crustacea. *Proceedings of the Zoological Society of London*, **15**: 222–228.

List of captions

Figure 1. Maximum likelihood tree inferred from COI sequences. Catalogue numbers are included. Numbers indicate maximum-likelihood and neighbour-joining bootstrap support, respectively.

Figure 2. *Tweedieia odhneri*, male, 11.3 × 7.9 mm (USNM 41260), Salomon Island. Dorsal view (A). Carapace, dorsal view (B). Frontal view (C). Thoracic sternum (D). Right chela, external view (E). Right chela, external view (F).

Figure 3. First male gonopods of *Tweedieia* species: internal detail, external detail, and external full. Scale bar measurements presented left to right. *Tweedieia laysani*, holotype male (USNM 29530), Laysan, Hawaiian Islands, right G1, 200um, 200um, 200um (A). *Tweedieia odhneri* male (ZRC 2013.0781), Chagos Archipelago, right G1, 200um, 200um, 1mm (B).

Figure 4. *Tweedieia brevidactyla*, paratype female, 9.5 × 7.5 mm (BNHM CB 03297), Nansha Islands (= Spratly Islands). Dorsal view (A). Ventral view (B). *Tweedieia odhneri*, paratype female, 5.8 × 4.5 mm (RBINS INV. 113725), Macclesfield Bank. Dorsal view (C). Ventral view (D). C-D downloaded from Royal Belgian Institute of Natural Sciences (http://virtualcollections.naturalsciences.be/virtual-collections/recent-invertebrates/crustacea/malacostraca/decapoda/phymodius-odhneri-gordon-1934).

Figure 5. *Tweedieia laysani*, holotype male, 8.2 × 5.8 mm (USNM 29530), Laysan, Hawaiian Islands. Dorsal view (A). Carapace, dorsal view (B). Frontal view (C). Thoracic sternum (D). Right chela, external view (E). Right chela, external view (F).