



Dividing the monopoly: the most broadly distributed *Actinopyga* is two species (Holothuroidea: Holothuriidae)

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Abstract

Actinopyga mauritiana stands as one of the most renowned sea cucumbers due to its size, conspicuousness, abundance in intertidal to shallow subtidal waters, and wide distribution. It is documented to range from East Africa to Hawaii and Panama. It is also among the most sought-after species for the bêche-de-mer fishery. However, color, anatomical, and genetic data indicate that it is a complex of two species: the nominal form that ranges across the Indian Ocean, and *Actinopyga varians*, distributed across the Pacific. Both species live on the outer margin of exposed reefs and prefer oceanic conditions, evident by their abundance on small reefs and islands, and their absence or rarity in protected continental shores and reefs. Despite the substantial separation between the two forms, each shows strong genetic connectivity across its broad range. This paper formally separates the two taxa.

Key words: Lectotype, Indo-West Pacific, speciation, biogeography, surf brownfish, surf redfish

Introduction

DNA sequence data are leading to a broad overhaul of species-level taxonomy because they reveal that many species thought to be well-understood are composites of more than one cryptic or semi-cryptic taxa. Cryptic complexes are especially common in the sea, as species recognition in marine animals tends to be by chemical or tactile, rather than visual or auditory means, thus at modalities not generally perused by systematists (Knowlton 1993). Uthicke *et al.* (2004) showed that teatfish (*Holothuria (Microthele)*), previously thought to be one or two species, can be differentiated into three. Massin *et al.* (2009) dissected the sandfish (*Holothuria (Metriatyla) scabra* Jaeger, 1833) complex morphologically, concluding that it included three species. Kim *et al.* (2013) resolved the *Bohadschia marmorata* Jaeger, 1833 complex, showing that the genus includes at least 12 species. Michonneau (2015) demonstrated that the circumtropical *Holothuria impatiens* (Forsskal, 1775) is a complex of at least 12 species. Samyn & Massin (2024) analyzed the *Holothuria (Thymiosycia) arenicola* Semper, 1868 complex, showing that this circumtropical species is a complex of 4 species.

Holothuriids of the genus *Actinopyga* Bronn, 1860 are among the most conspicuous sea cucumbers in the tropics because of their relatively large size and tendency to live epibenthically, exposed during the day, often in very shallow water. They are also among the most sought-after commercial species (aka bêche-de-mer), and their populations are heavily depleted (Purcell *et al.* 2012; Purcell *et al.* 2023). The species-level taxonomy of *Actinopyga* is not yet stable. The small, relatively simple ossicles defining the genus are taxonomically poor and have made species definitions challenging. As with other holothuriid genera such as *Bohadschia* Jaeger, 1833, anatomical diversity is rather limited. Color pattern is often of diagnostic value but rarely recorded in detail in older publications. At present 18 species are recognized as valid in this genus (WoRMS; accessed on 17 Sept. 2024), although several of these are suspected to be synonyms, and genetic data suggest that other, unrecognized species

may exist. At present 17 of these species are known from the Indo-West Pacific (IWP) and one, *Actinopyga agassizii* (Selenka, 1867) from the tropical Western Atlantic.

Actinopyga mauritiana (Quoy & Gaimard, 1834) is perhaps the best-known species in the genus, representing almost half of the *Actinopyga* records in GBIF, and two-thirds of them in *iNaturalist*¹. This species was thought to be well-understood, as it, together with *Actinopyga varians* (Selenka, 1867), is the only *Actinopyga* with 25 tentacles² other than the Atlantic *Actinopyga agassizii* (all other species have 20) and has distinctive ossicles. Field and genetic work, however, alerted us to the presence of two forms in this complex based on distinct color patterns, anatomy, ossicle characters, and genetics, with separate, parapatric ranges. Here, we describe these differences, assess their nomenclature, and recognize them as *Actinopyga mauritiana* (Quoy & Gaimard, 1834) from the Indian Ocean, and *Actinopyga varians* (Selenka, 1867) across the western and central Pacific.

Historical notes

Species of *Actinopyga* were among the earliest tropical Indo-West Pacific (IWP) holothuroids described, probably because of their large size and exposed habits. Lesson (1830) named the first species, *Holothuria monacaria*, also the oldest name for the *A. mauritiana* complex, but this name was suppressed (ICZN 1970, Opinion 914). Jaeger (1833) subsequently described two species: *Mülleria echinites* and *M. lecanora*, and established the genus *Mülleria*³ for these. Unlike many early generic concepts in holothuroids, Jaeger's *M. lecanora* included only members of what we still consider to be a single genus. Bronn (1860) noted that *Muelleria* Jaeger, 1833 was preoccupied by five earlier uses and provided the replacement name *Actinopyga*.

Quoy & Gaimard (1834) described four species that are presently placed in *Actinopyga*: *Holothuria lineolata*, *H. miliaris*, *H. mauritiana*, and *H. guamensis*. The first is considered a junior synonym of *Actinopyga lecanora* (Jaeger, 1833) and poses no problem. *Actinopyga miliaris* and *A. mauritiana* remain broadly recognized. The last had a confused nomenclatural history and was suppressed by the ICZN (1966), but clearly represents the second species in the *A. mauritiana* complex. Thus Quoy & Gaimard (1834) solved the problem we are addressing here almost 200 years ago, by recognizing the two species in this complex as different. However, history buried their conclusion, and the ICZN ruling prevents recognition of *H. guamensis*.

Selenka (1867) discussed species in the *Actinopyga mauritiana* complex next (*albeit* Brandt (1835) also mentioned them) and described *Mülleria varians*. He called attention to three species of *Muelleria* with 25 tentacles: *M. guamensis*, his new species *M. varians*, and *M. agassizii*. He also mentioned that the number of tentacles in *M. mauritiana* was not known. In the following year, Semper (1868) synonymized *M. varians* with *M. mauritiana* and mentioned *M. guamensis* passingly as another species attributed to the genus. From this point on, *A. varians* has been considered a synonym of *A. mauritiana* (e.g., Lampert 1885; Théel 1886; Pearson 1914; Panning 1929; Rowe & Doty 1977; Féral & Cherbonnier 1986; Massin 1996; Paulay 2003; Purcell *et al.* 2012), while *A. guamensis* was considered poorly understood (e.g., Lampert 1885; Théel 1886; Panning 1929).

Cherbonnier (1952) in his review of Quoy & Gaimard's species, published several plates intended for their original 1834 publication, but not printed. One of these shows Quoy & Gaimard's illustration of *Holothuria guamensis*. Cherbonnier concluded that this species was conspecific with *H. nobilis* (Selenka, 1867). Clark (1963) commented on the poor fit between *H. guamensis* and *H. nobilis*, including different numbers of tentacles, and because of the confusing nature of the evidence and lack of a surviving type, petitioned the ICZN to suppress the name *H. guamensis*, a request granted in Opinion 762 (ICZN 1966). Rowe & Doty (1977) in their review of Guam's holothuroid fauna revisited *H. guamensis* and concluded that it is conspecific with *A. mauritiana*, a conclusion also supported by Paulay (2003).

Michonneau *et al.* (2013) listed *Actinopyga varians* as valid for the first time since its original description, referring to Netchy & Paulay (in prep.). The present paper represents that manuscript. Based on Michonneau *et al.* (2013), the name *A. varians* was listed as valid in WoRMS and has now come into wider use (e.g., Purcell *et al.*, 2023).

¹ www.inaturalist.org (accessed May 2020).

² 24–26 tentacles were observed on vouchers examined in this study.

³ According to ICZN article 32.5.2, the name *Mülleria* is to be corrected to *Muelleria* as it is a justified emendation (Art. 33.2.2). From hereon we will therefore use *Muelleria* even though in the old literature (e.g. Bronn, 1860, Selenka, 1867) *Mülleria* was still in use.

The purpose of this paper is to formally raise *A. varians* from the synonymy of *A. mauritiana*, describe the differences between the two species on available type and non-type material, and detail their distribution.

Material and Methods

Animals were collected by snorkeling and diving at various locations across the Indo-West Pacific. Specimens were often photographed, anesthetized with $MgCl_2$, menthol, or chlorobutanol, and fixed/preserved in ethanol. Photographs and tissue subsamples were taken from many and preserved in 95% ethanol. Specimens studied were deposited at the Florida Museum of Natural History, University of Florida (UF). Additional photographs were also consulted, including those sent by N. Manickam and N. Marimuthu from a specimen collected at Lakshadweep, India. Additional specimens were examined from the US National Museum of Natural History (USNM); the Museum of Comparative Zoology, Harvard (MCZ), the Natural History Museum, London (BMNH/NHM), the Naturalis Biodiversity Center, Leiden (RMNH), the Zoological Museum of Hamburg (ZMH), the Muséum national d'Histoire naturelle (MNHN), the Royal Belgian Institute of Natural Sciences (RBINS), and the Ruykyu University Museum (RUMF). We visualize geographic information on specimens cited from these collections in Figure 7.

Ossicles were prepared for light and scanning electron microscopy by dissolving small pieces of dorsal and ventral body wall, tube feet, papillae, tentacle, longitudinal muscle, cloacal wall, gonad, and cloacal dilator muscle tissue in household bleach, and rinsing them carefully with distilled water (Samyn *et al.* 2006). For SEM, samples were dried and mounted on aluminum stubs, coated with gold in a sputter coater, and observed with a FEI/Philips XL30 ESEM TMP Scanning Electron Microscope. Stubs with ossicles from the lectotypes of *Actinopyga varians* and *A. mauritiana* have been deposited in the collection of the Royal Belgian Institute of Natural Sciences (I.G. 34271/HOL.1753/1-5 and I.G. 34272/HOL.1754/1-6, respectively).

DNA was isolated, amplified for COI and/or 16S, and sequenced as described in O'Loughlin *et al.* (2007) and Michonneau & Paulay (2014). PCR products were sequenced at the Interdisciplinary Center for Biotechnological Research at the University of Florida. The chromatograms were edited in Geneious 5.5 to 9.0.4 (Drummond *et al.* 2011), sequences aligned with Muscle (Edgar 2004), and the alignment checked by eye using MEGA software⁴. Sequences were translated to check for evidence of nonsense or stop codons, but none were detected. Sequences are deposited in Genbank (Table 1). We analyzed sequence data with RAxML 8.0.1 (Stamakis 2006) with 1000 bootstrap replicates, using the JTT+F model of molecular evolution as selected by the Akaike Information Criterion implemented in MEGA. We used *Actinopyga echinites* as an outgroup. Sequenced specimens are marked with an * under Materials Studied.

The distribution (Fig. 7) of both species is based on verified records from collections and iNaturalist images and displayed using ArcMap 10.8.

Results

Systematic Account

Order Holothuriida Miller *et al.*, 2017

Family Holothuriidae Burmeister, 1837

Genus *Actinopyga* Bronn, 1860

Actinopyga mauritiana (Quoy & Gaimard, 1834)

(Fig. 1A–F; Fig. 4B, Fig. 5B, 6, 7)

Holothuria mauritiana Quoy & Gaimard, 1834: 138.

On Official List of Specific Names in Zoology (name 2386): ICZN (1970) Opinion 914.

⁴ <https://www.megasoftware.net/>

lsid: zoobank.org:act: 6345B610-53F5-4EFC-B6B3-662A6C4F4254

Mülleria mauritiana—Brandt 1835: 74.—Selenka 1867: 315.—Selenka 1868: 116.—Lampert 1885: 98 (*partim*).—Ludwig 1887: 32. Koehler & Vaney 1908: 22.—Pearson 1910: 174, text fig. 16 A–C.

Holothuria (Actinopyga) mauritiana—Panning 1929 [1931]: 128.

Actinopyga mauritiana—Pearson 1903: 199.—Pearson 1914: 179–180, pl. 29, fig. 6.—Panning 1944: 55 (synonymy).—Cherbonnier 1952: 41, fig. 16A–J.—Cherbonnier 1955: 139.—Cherbonnier 1967: 55.—Clark & Rowe 1971: 176 (*partim*).—Price & Read: 8.—Cherbonnier 1988: 16, fig. 2 a–m.—Samyn 2003: 13 (*partim*).—Samyn *et al.* 2006: 52.

Material examined:

Lectotype (here designated)

Mauritius (Ile de France), Ile aux Cerfs • MNHN-IE-2013-17843 (formerly MNHN H3277).

2 Paralectotypes (specimens of *Actinopyga echinites* (Jaeger, 1833))

Mauritius (Ile de France), Ile aux Cerfs • MNHN-IE-2013-17842 (formerly MNHN H3276), MNHN-IE-2013-17845 (formerly MNHN H3279).

Red Sea: NHM 1991.11.15 (Stn. MB.A.); USNM E22420: Yemen, off South coast; UF 12185: Saudi Arabia, Jeddah; UF 13485*: Saudi Arabia, offshore of Farasan Banks, Dolphen Lagoon.

Oman: UF 22746, 22747: Mirbat, rocky intertidal inshore of Chinese Wreck, 0–2 m; UF 22848*: Mirbat, intertidal near military base, 0–1m.

Pakistan: NHM 1967.11.1.23: Karachi, Cape Mounze.

East Africa: USNM E23079: Kenya, Mombasa; USNM E.22885: Kenya, Mombasa; USNM E.23079: Kenya, Mombasa; NHM 1950.10.17.3: Zanzibar; NHM 82.10.16.38: Mozambique, between tide marks; USNM E.24530: Tanzania, Dar Es Salaam (Kendwa Island); USNM E.24497: Tanzania, Dar Es Salaam (Kendwa Island); RBINS, MOZ/2018.472 (tissue sample only): Mozambique, Inhambane Province, Zavora beach; RBINS, HOL.1716: Mozambique, Inhambane Province, Zavora beach; RBINS, MOZ/2018.56 (tissue sample only): Mozambique, Inhambane Province, Tofo beach;; RBINS, HOL.1639: Republic of South Africa, Sodwana Bay.

Seychelles: NHM 1969.5.1.273: Aldabra; NHM 1978.9.20.396 401: Aldabra; NHM 1972.1.13.5: Aldabra, 2.5m below mean tide level, off reef edge, outside settlement; NHM 1969.9.28.26: Seychelles, Anse aux Pins, algal ridge, sublittoral fringe, in sand; NHM 92.10.16 57 63: Amirante Islands, HMS Alert.

Madagascar: USNM E22882; RBINS, HOL. 787, 819, 867, 1486: Tulear.

Mozambique Channel: USNM E.22882; UF 9258*: Juan de Nova Island, Iles Esparses.

Mascarenes: NHM 76.5.5.31: Rodriguez; UF 7861: Mauritius, Flic en Flac Harbour; UF 3197: Mauritius, Cape Malheureux, Coin de Mire Island; UF 2066: Réunion Island, Saint Gilles Les Bains; UF 2069: Réunion Island, Saint Gilles Les Bains; UF 6332*: Réunion Island, Saint Gilles Chez Go; UF 6333*: Réunion Island, Saint Gilles Chez Go; UF 6558*: Réunion Island, La Possession, Banc des Lataniers; UF 6365*: Réunion Island, La Saline, Trou d'Eau; UF 6922: Réunion Island (exact locality not specified); UF 6985*: Réunion Island (exact locality not specified).

Lakshadweep & Maldives: NHM 1955.10.1. Mini Koi, between Laccadive & Maldiva Islands; USNM E24495: Maldives, 4°17'50"N, 73°33'40"E, 13 ft, RV Te Vega. 21.III.1964; NHM BMNH E/056/C/2: Maldives; Lakshadweep, pictures only, made by N. Marimuthu (exact locality not specified).

Chagos: NHM 1969.5.27.3: Diego Garcia; NHM 1969.5.27.4: Diego Garcia.

Indonesia: UF 4626*: Anak Krakatau; <https://www.inaturalist.org/observations/185730901>: Bali.

Cocos Keeling & Christmas Island: USNM E21591: Cocos Keeling Islands; <https://www.inaturalist.org/observations/162135465>: Cocos Keeling Islands; NHM 87.4.26.1 3: Christmas Island [possibly both *A. mauritiana* and *A. varians* in sample]; <https://www.inaturalist.org/observations/171501521>: Christmas Island; RUMF-ZE-00080*: Christmas Island.

Western Australia: UF 9602*: Ningaloo Reef, Black Rock; UF 9604: Ningaloo Reef, Black Rock; UF 9096: Ningaloo Reef, Black Rock; <https://www.inaturalist.org/observations/157516353>.

Description

Length to 35 cm, width to 10 cm; preserved specimens up to 30% smaller (Samyn 2003). Color variable (see “live coloration” below). Bivium clearly separated from flattened trivium that forms an adherent sole. Numerous, brown conical papillae scattered evenly over bivium. Trivium densely covered with long, light brown to green tube feet, scattered evenly across the ambulacral and interambulacral areas. Body wall up to 10 mm thick. Mouth ventral, with 20–26 brown, stout, peltate tentacles. Distinct collar of brown oral papillae. One to three Polian vesicles,

and 1–10 stone canals ending in egg-shaped madreporic plates. Anus terminal, guarded by five white anal teeth. Cuvierian tubules reported as a small pinkish tuft in live specimens (Samyn 2003, see also Vanden Spiegel and Jangoux 1993). Calcareous ring very stout, with radial pieces almost three time as wide as interradial elements, and interradials and radials of nearly the same height (*cf.* Cherbonnier 1988: 19, fig. 2H).

Ossicles: Tentacles with large, unbranched, rugose rods, 165–245 μm long (Fig. 1A). Dorsal body wall with simple rosettes, 20–45 μm long, and spiny, unbranched rods, 68–121 μm long (Fig. 1B). Ventral body wall with small grains, elongated grains, and smooth to spiny rods, 15–120 μm long (Fig. 1C). Gonad with slender, mostly unbranched, relatively smooth rods, 80–150 μm long (Fig. 1D). Cloacal wall with simple to complexly branched rods, 15–75 μm long (Fig. 1E). Longitudinal muscles with smooth, unbranched rods, 90–135 μm long (Fig. 1F).

Live coloration

The bivium of *Actinopyga mauritiana* is marked by a dense pattern of polygonal creases around papillae that are accentuated by dark lineation, giving the animal a breadfruit-like pattern (Figs 4B & 5B). Overall color ranges from solid light to dark brown across its extent, to a brown dorsal band bordered by cream-colored lateral bands. The brown and cream bands are abruptly delineated in some, broken up in other animals. Trivium white-grey to light-brown covered with numerous, densely-packed, light-brown to greenish tube feet.

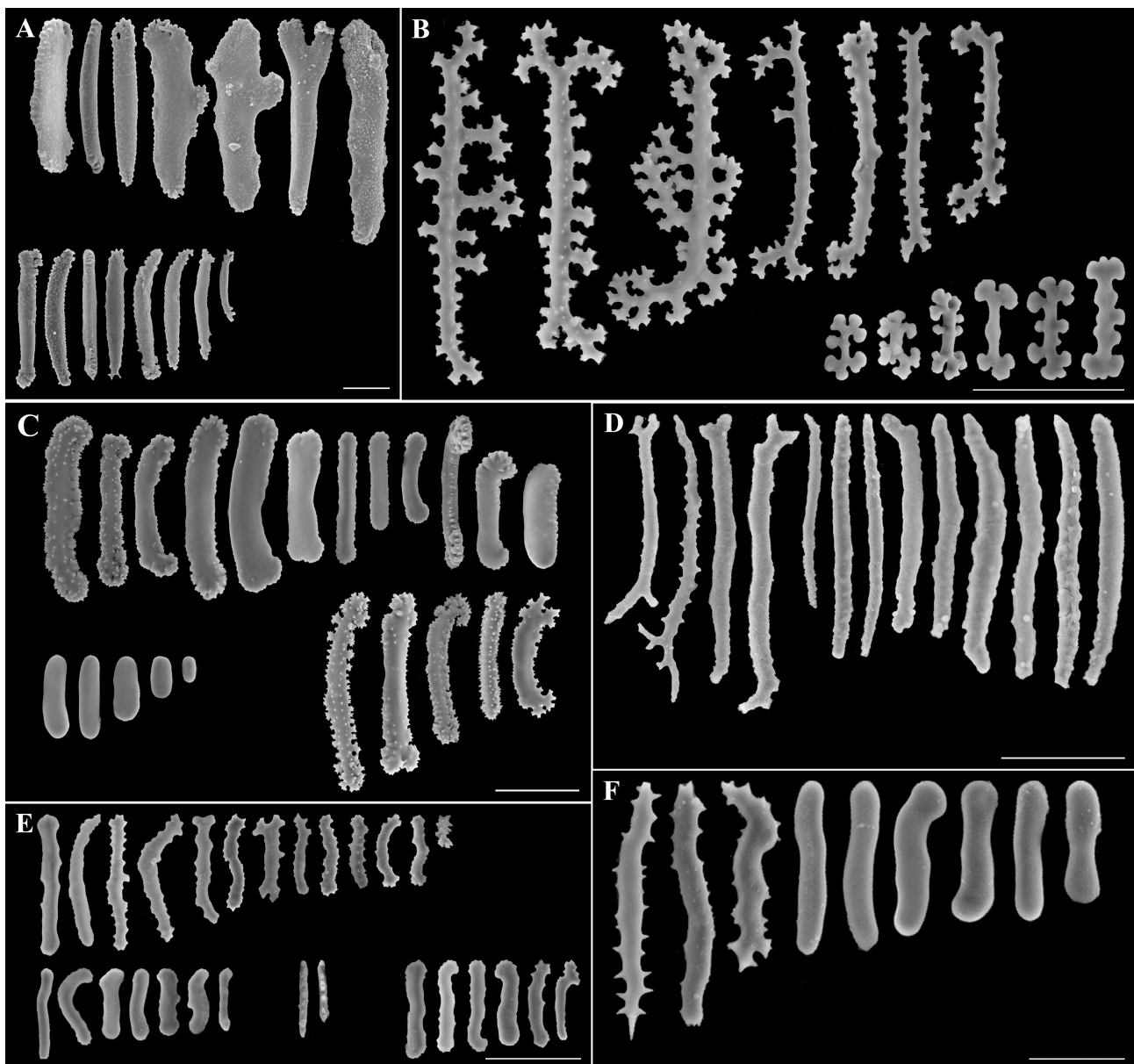


FIGURE 1. *Holothuria mauritiana* Quoy & Gaimard, 1834, Lectotype MNHN IE-2013-17843. (A) Rods from tentacles; (B) Rods and rosettes from the dorsal body wall; (C) Rods and grains from the ventral body wall; (D) Rods from the gonad; (E) Rods from the cloacal wall (F) Rods from the longitudinal muscle. Scale bar = 50 μm .

Distribution

Red Sea to South Africa, east to Christmas Island (Indian Ocean), Bali (Indonesia) and Western Australia (Fig. 7).

Remarks

Holothuria mauritiana Quoy & Gaimard, 1834 was described from an unknown number of specimens from Mauritius. Cherbonnier (1952) reported on four specimens attributed to Quoy & Gaimard at the MNHN and labeled ‘*Holothuria mauritiana* Quoy & Gaimard, Astr. Zooph., page. 138, de l’île de France, M.M. Quoy & Gaimard, 1829, expéd. D’Urville’. Cherbonnier regarded three specimens as syntypes of *H. mauritiana*; the fourth he considered to be *Actinopyga echinites* (Jaeger, 1833). He did not provide registration numbers for these. In 2019, one of us (GP) found three syntypes of *Holothuria mauritiana* in the MNHN type collection. Only these three were listed as type specimens in the MNHN collection database. Only one of these specimens matches *A. mauritiana*, the other two are specimens of *A. echinites*. We are not sure what happened to the other specimens mentioned by Cherbonnier (1952), and why he did not encounter the second *A. echinites* specimen. The single *A. mauritiana* found is in very good condition, with the internal anatomy, ossicles, and diagnostic color pattern all well preserved. It is here designated the lectotype of the species. Cherbonnier (1952) gave an excellent description of the syntypes, we complement it with SEM images of ossicles recovered from selected tissues of the here designated lectotype (Fig. 1).

Actinopyga varians (Selenka, 1867)

(Figs 2A–C, 3A–D, 4A, 5A, 6, 7)

Holothuria (Psolus) monacaria Lesson, 1830: 225, pl. 78.

Holothuria guamensis Quoy & Gaimard, 1834: 137, no figure; original artwork subsequently published in Cherbonnier 1952: pl. II, Fig. 1.

Holothuria (Psolus) monacaria—Selenka 1867: 331.—Cherbonnier 1951a: 295–298.—Clark & Rowe 1967: 126–128.—ICZN 1970: 31–32 (name suppressed, ICZN Opinion 914), not *Holothuria monacaria* of authors. lsid:zoobank.org:act:E7E66233-0BDA-400A-AE59-80FB89869154.

Mülleria mauritiana (non Quoy & Gaimard, 1834)—Semper 1868: 276.—Ludwig 1882: 134.—Théel 1886: 201.—Ludwig 1888: 812.—Mitsukuri 1912: 53, text fig. 11, pl. 3, figs 25–27.

Holothuria guamensis—Clark 1963: 383; ICZN 1966: 15 (name suppressed, ICZN Opinion 762). urn:lsid:zoobank.org:act:AA8E84AB-2375-4E67-8387-794FE7BFF575.

Mulleria guamensis—Brandt 1835: 74.—Théel 1886: 202.

Mülleria varians Selenka, 1867: 310, pl. 17, figs 4–9.—Selenka 1868: 116. urn:lsid:zoobank.org:act:6149D99C-81CE-47C2-AFE9-87E27BC76333.

Actinopyga mauritiana (non Quoy & Gaimard, 1834)—Fisher 1907: 648, pl. 67, fig 1a–d.—Panning 1944: 54–55, figs 23, 24 a–z.—Clark 1946: 440.—Cherbonnier 1951: 11.—Domantay 1954: 349.—Rowe & Doty 1977: 228, fig. 2f, pl. 6d (colour picture).—Féral & Cherbonnier 1986: 72 (colour picture).—Paulay 1989: 27.—Rowe & Gates 1995: 287.—Massin 1996: 11, fig. 5 A–B.—Paulay 2003: 577.

Actinopyga varians (Selenka, 1867)—Michonneau *et al.* 2013: 534–535.

Material examined:

Lectotype (here designated)

ZMH E.2497 (formerly MG.1165 ex Museum Godeffroy, Hamburg) Fidji.

Paralectotypes

Society Islands, Hawaii • MCZ:IZ: HOL-827 (4 specimens) • MCZ:IZ: HOL-828 (18 specimens) • Hawaii, MCZ:IZ: HOL-829 (12 specimens, not examined).

Indonesia: RMNH 5399: Indonesia (only photo of specimen seen); USNM E 24620: Borneo, Sangihe Islands, 1–18 m; USNM E 24613: Sulawesi.

Philippines: USNM E 16674: Luzon Island, Camarines Sur, Nato, anchorage; USNM E 45682: Negros Oriental, Apo Island, NW side; USNM E 27338: Zamboanga del Norte, Mindanao Island, SW side Silino Island; USNM E 2487: Luzon Island, near Mariveles; UF 4577: Batan.

Taiwan: USNM E 9152: Taiwan.

Japan: UF 10390: Ryukyu Islands, Okinawa Island, Okinawa, Cape Maeda; RUMF_ZE-00210*: Okinawa.

Papua New Guinea: RMNH 5405: Papua New Guinea (only photo of specimen seen); RBINS I.G. 26373/HOL.1539: Papua New Guinea; UF 14483: Madang Province, Sair Island; UF 14546*: Madang Province, Kranket Island, Cape Jantzen, 13 m.

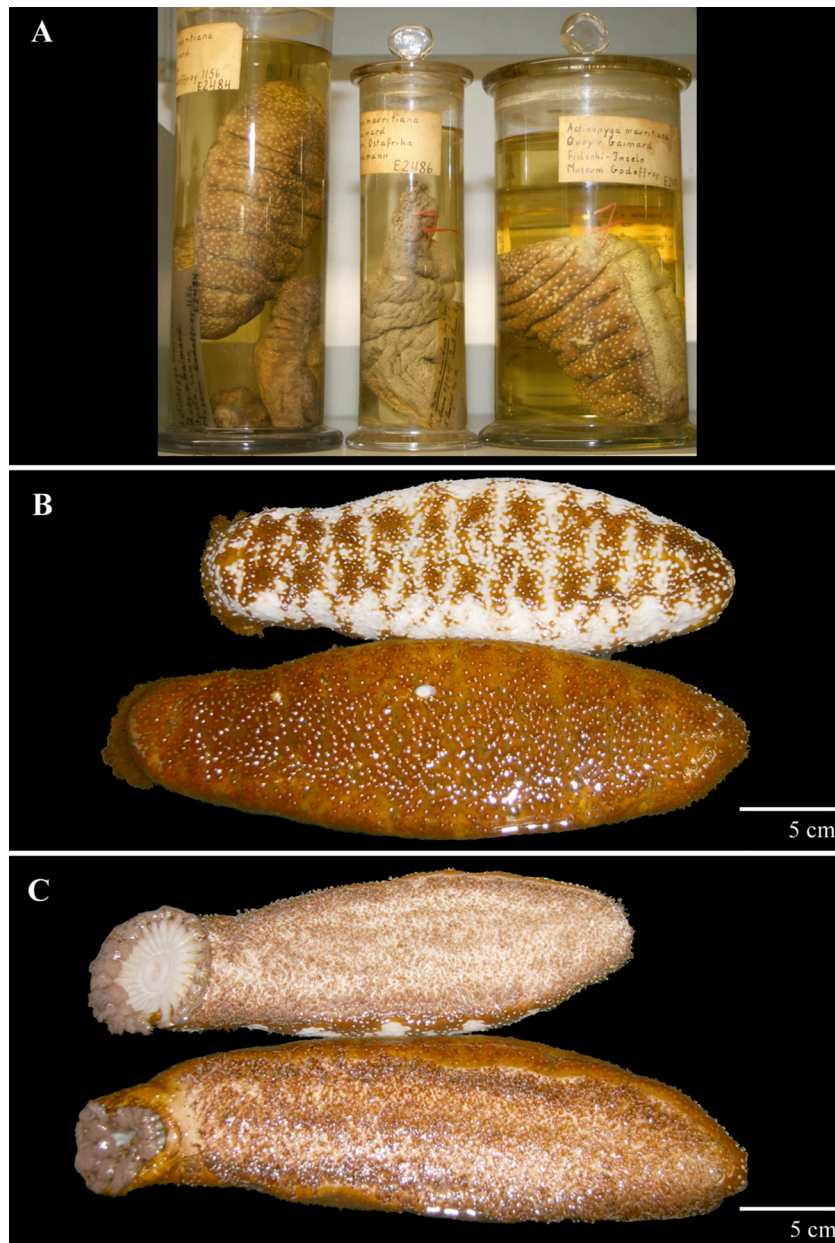


FIGURE 2. *Actinopyga varians* (Selenka, 1867). (A) Voucher specimens as pictured in the ZMH collection (ZMH.E.2484, 2486 & 2491); (B) Dorsal view of two freshly collected specimens from Guam (RBINS: I.G. 31558/HOL.1666); (C) Ventral view of the specimens depicted in (B) (pictures by Yves Samyn).

Mariana Islands: RBINS I.G.31558/HOL.1666: USA, Guam, Tanguisson; UF 4578, 4582, 4583*, 4584: Guam, Hagatna Bay, Oca Point, fore reef, 3–6 m; UF 4765: Guam, Gun Beach, north side of cable track, outer reef slope, 2–4 m; UF 1695: Guam, North Pago Bay, reef flat, 0–1 m; UF 6307: Guam, Cocos Island, ocean side, intertidal, 0–1 m; UF 6724: Guam, Hagatna, south of Adelup Island, fore reef, 0–1 m; UF 12215: Guam, Piti Bay, inner reef margin; UF 1222: Guam, Pago Bay, near marine lab, 50m from shore; UF 12222: Guam, Pago Bay, inner reef flat, in *Sargassum*; UF 12223: Guam, NCS Beach, outer reef flat, on wave washed rocks; UF 12224: Guam, Adelup Point, outer reef flat, rock. UF 12568: Agrihan Island, south tip of island, 12–13 m; UF 5009: Alamagan Island, surge, exposed coast, 6 m; UF 3228: Saipan Island; UF 3119: Saipan Island, just North of Banzai; UF 4413: Saipan Island, Garapan, patch reef in just south of Lighthouse Channel. 5–8 m; UF 4533, 4534, 4998: Saipan Island, Garapan Lagoon, in front of Dai Ichi Hotel, 2–3 m; USNM E 16720: Guam, Apra Harbor, outside breakwater; USNM E 16722: Guam, Oca Point; USNM E 22704: Guam, Oca Point; USNM E 31672: Guam; USNM E 51760: Guam, Tumon, Reef Flat at Tumon.

Federated States of Micronesia (FSM): UF 6953: Kosrae Island; UF 3194, 3299, 3300, 3302: Pohnpei Island; UF 13336: Pohnpei Island, around Temwen Island, reef flat; UF 11392: Yap Island, Colonia Channel, seagrass, sandflat, wreck, 0–3 m; UF 5881*: Yap Island, Colonia, S side of Woneeday Channel, outer reef flat, near reef crest, 0–6 m; USNM E 22723: Kapingamarangi Atoll, Touhou.

Marshall Islands: UF 6760*: Majuro Atoll, Eneko, channel (West side of the island), intertidal rocks and pools, 0 m; UF 6762: Majuro Atoll, Rita, channel (North end of main island) intertidal rocks and seagrass, 0 m; UF 7032: Majuro Atoll, Arrak, lagoon side, reef slope, relatively high coral cover, some sand, 2–4 m; USNM E 21369: Bikini Atoll, Enyu Island, lagoon side, tide pools; USNM E 21368: Marshall Islands: Bikini Atoll, Enyu Island, SE corner of, outer reef; USNM E 22681: Bikini Atoll, south end; USNM E 22701: Enewetak Atoll, Arambiru Island, ocean reef; USNM E 29495: Bikini Atoll, Bikini Island; USNM E 35418: Enewetak Atoll, Parry and Igurin Island; USNM E 35331: Enewetak Atoll, Parry Island, Elmer Reef.

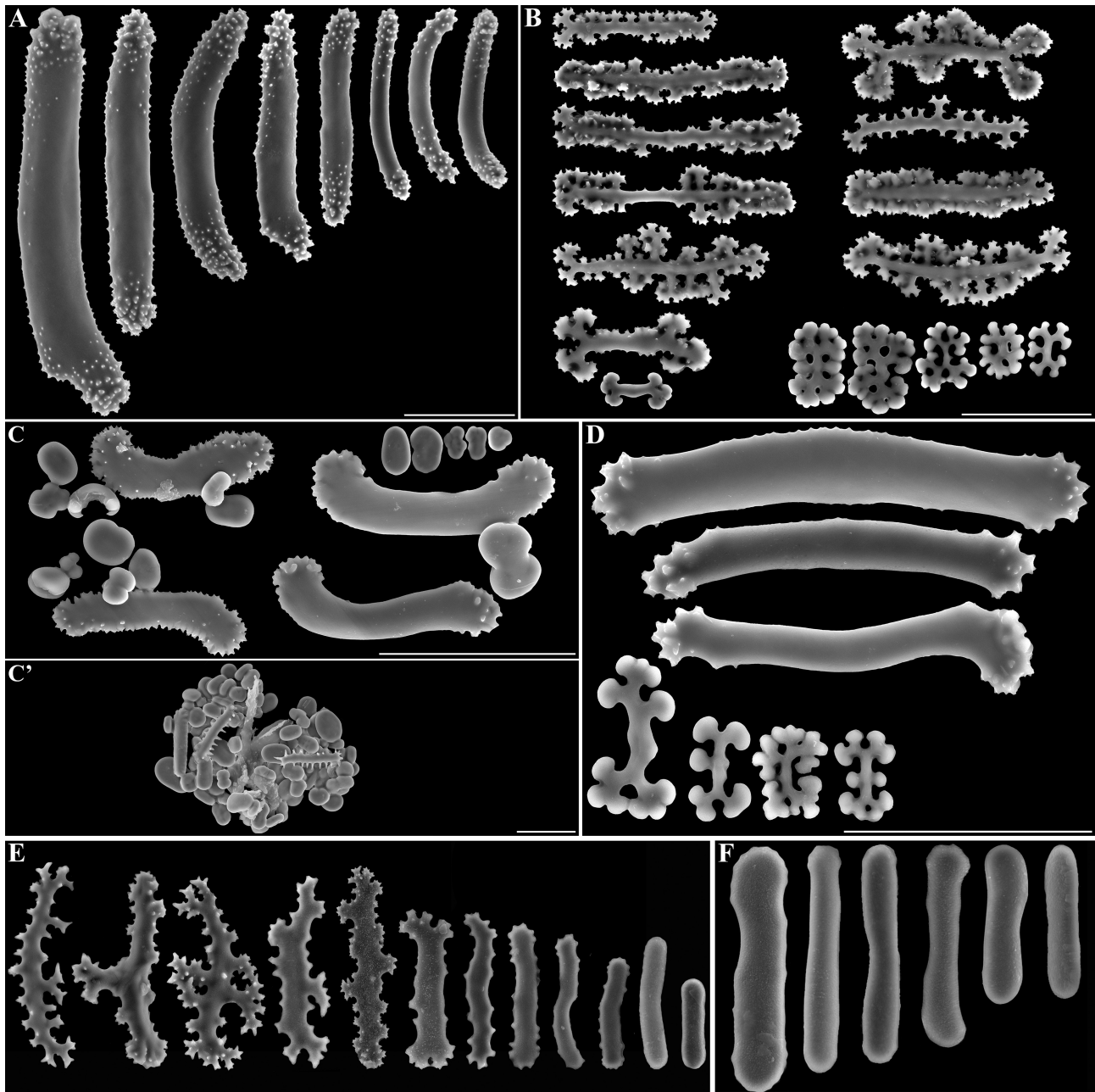


FIGURE 3. *Muelleria varians* Selenka, 1867, Lectotype: ZMH E.2497. (A) Rods from the tentacles; (B) Rods and rosettes from the dorsal body wall; (C & C') Grains and rods from the ventral body wall; (D) Rods and rosettes from the dorsal papillae (E) Smooth to spiny rods from the cloacal retractor muscles (and possibly cloacal wall); (F) Rods from the longitudinal muscles. Scale bar = 50 μm.

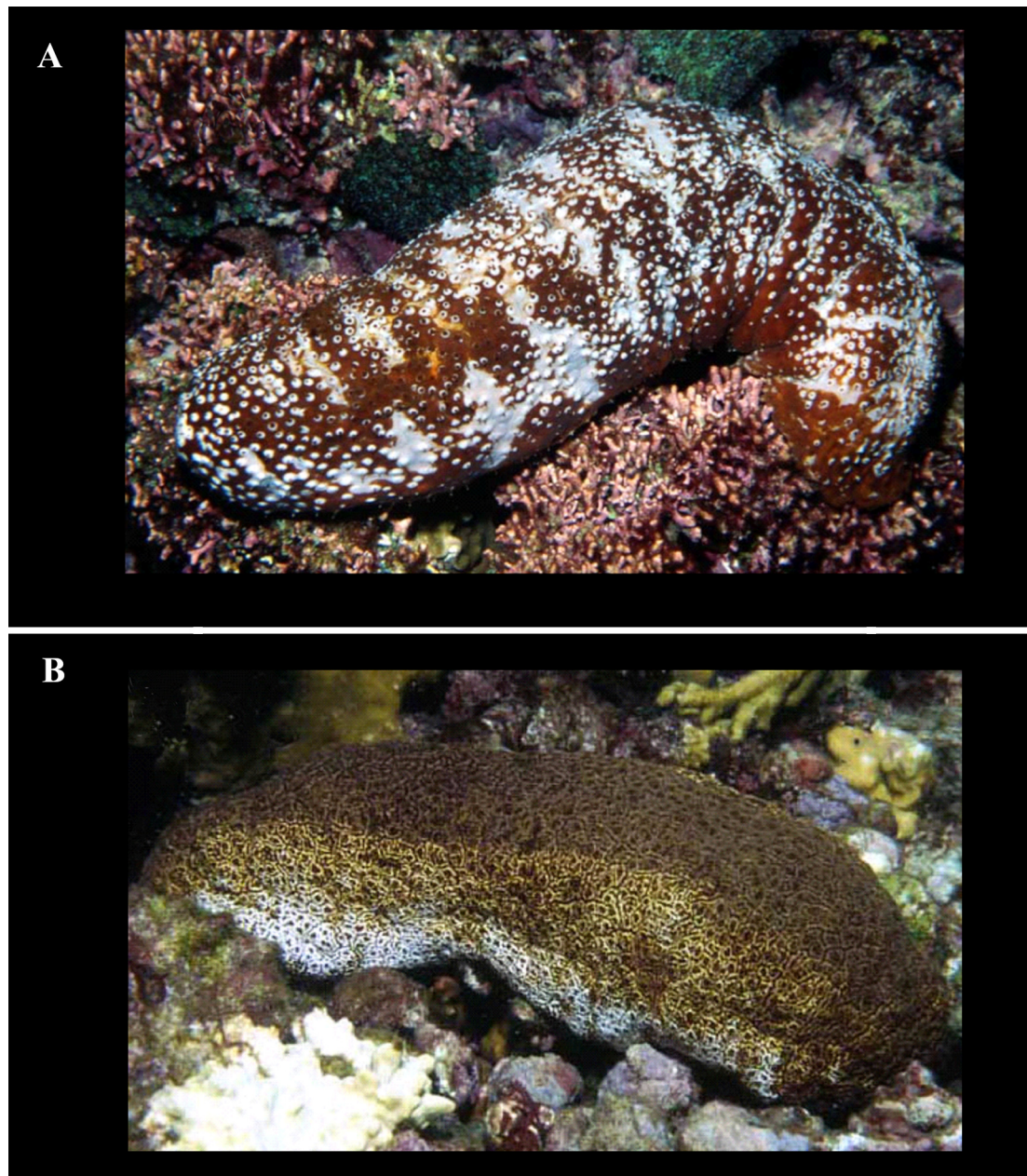


FIGURE 4. (A) *Actinopyga varians* in Guam (photo by Gustav Paulay); (B) *Actinopyga mauritiana* in Mauritius (photo courtesy of R.F. Myers).

Wake Island: UF 4490, 4491: forereef; UF 11516, 11524: ocean side of atoll.

Kiribati: Tungaru/Gilbert Islands: USNM E 16872: Onotoa Atoll USNM E 16807: Onotoa Atoll, About 7100 Ft S 50 Degrees West from Tekawa Church at Seaward Edge of Aon Te Baba Reef.

Line Islands: UF 5935*: Kingman Reef, NE/E of Atoll; UF 5759: Kiritimati Atoll, west side of atoll, N of passage; UF 5808*: Palmyra Atoll, South Atoll barrier reef rim seaward of sand islet.

Hawaiian Islands: UF 6156*: French Frigate Shoals; UF 1275: Maui Island, Hekili Point; UF 18329*: Oahu Island, Kaneohe Bay, Coconut Island, mammal pens; UF 18375*: Oahu Island, Kaneohe Bay, inshore (SW) of Kapapa Island; UF 1765: Oahu Island, Ala Moana Beach, Magic Island; UF 4592*: Oahu Island, Ko Olina, West of Harbor Channel; UF 4593: Oahu Island, Ko Olina, West of Harbor Channel; USNM 30366 Hawaii Island, Kealahakua Bay, Palemano Point; USNM 30451: Niihau Island, Kamalina Bay; USNM 30453: Hawaii Island, Puako Bay; USNM 30450: Hawaii Island, Puako Bay; USNM 30448: Molokai Island, Laau Point, South of; USNM 30452: Oahu Island, Waialua; USNM 30449: Niihau Island, Kamalina Bay; USNM E 16783, Oahu Island, Waimea;

USNM E 17049: Hawaii Island, Hilo Bay; USNM E 21295: Oahu Island, Kahuku, Pupukea Beach Park; USNM E 22630: Oahu Island, Near Waimea Bay; USNM E 22444: Oahu Island, Near Waimea Bay; USNM E 22449: Oahu Island, Near Waimea Bay; USNM E 25731: Oahu Island, Makapuu; USNM E 2691: Kailua; USNM E 45689: United States, Hawaii. USNM E 16733: United States, Hawaii; USNM 30479: United States Hawaii.

Australia: UF 10211*: Queensland, Heron Island; UF 13373: Australia, Queensland, Heron Island.

New Caledonia: UF 15777, 15746: Cook Reef; UF 15752: Huon Atoll, North tip; UF 15740: Portail Atoll.

Vanuatu: UF 4315: Sanma Province, Tutuba Island, south shore near “crossroads” dive site.

Niue Island: UF 1494: Avaiki at Tuapa; UF 1953: reef flat at Tuapa, near shore in pools; UF 1958: reef flat at Tuapa, near shore in pools.

Fiji: UF 1581: Lau Islands, Matuku Island.

Tonga: UF 3147: Tongatapu Island, Atata Island; USNM E 21301, 21396, 22688, 27488: Vava’u Group, Niuafo’ou Island.

Cook Islands: USNM E 35714: Rarotonga Island, just west of Ava Avaroa; UF 1330: Cook Islands, Mauke Island, west side, on reef; UF 1975: Cook Islands, Mauke Island, west side, on reef; UF 931: Cook Islands, Rarotonga Island, Arorangi, fringing reef.

French Polynesia: UF 13223: Gambier Islands, NE of Aukena Island; UF 13951: Marquesas Islands; UF 14026: Marquesas Islands, Nuku Hiva, Baie des Contrôleurs; UF 14055: Marquesas Islands, Haut fond Est de Motane—Point 18; UF 14071: Marquesas Islands, UaPou-Hakaheteau; UF 14080: Marquesas Islands, Hatu Iti; UF 14081: Marquesas Islands, Hatu Iti; UF 15739: Marquesas Islands, Nuku Hiva, Les 4 grottes; UF 11213: Marquesas Islands Eiao Island, Charner Bay, E side of bay, North side of island; UF 11296: Marquesas Islands, Fatu Hiva Island, Mahitoa Point, SW side of island; UF 11176: Marquesas Islands Nuku Hiva Island, Haahopu Bay, in front of the wharf, West side of island; UF 11220: Marquesas Islands Nuku Hiva Island, Baie du Contrôleur, East side of bay near exit; UF 11298: Marquesas Islands, Nuku, Hiva Island Haahopu Bay, in front of the wharf, West side of island; UF 13658: Marquesas Islands, Nuku Hiva Island, Haahopu Bay, in front of the wharf, West side of island; UF 11268: Marquesas Islands, Tahuata Island Namahana Point, exit of Anaete Bay, west side of island; UF 11231*: Marquesas Islands Ua Huka Island, south of Teaeopiki Point, between Motukeokoo and Hemeni islets, east coast of island; UF 9109: Society Islands, Moorea Island, reef front and very narrow reef flat off north end of airfield; UF 614: Tuamotu Islands, Tikehau Atoll, hoa at east end of Tuaherahera Motu and adjacent outer reef flat SE of hoa, just off Ohotu Motu; USNM E 22660: Tuamotu Archipelago, Mataiva Atoll, outer fringing reef north of main pass; USNM E 24489: Tuamotu Archipelago, Raroia Atoll; USNM E 8255: Tuamotu Archipelago, Tikahau Atoll, causeway south of Matiti Island; USNM E 9938: Society Islands, Tahiti, Papeete, reef; USNM E 9922: Gambier Islands, Mangareva Island; USNM E 9933: Society Islands, Tahiti, Papeete, reef; USNM E 9941: Tuamotu Archipelago, Rangiroa Atoll, Mohegan Reef; USNM E: 9939, Tuamotu Archipelago, Makatea Island; USNM E 21388: Society Islands, Bora Bora, Motu Tapin, west of outer leeward reef; USNM E 17091: Tuamotu Archipelago, Makemo Island.

Pitcairn Islands: USNM E: 37097, Pitcairn Islands (-24.37, -128.32).

Panama: USNM E 22543, 22637: Panama, Perlas Archipelago.

Description of ZMH.E.2497, lectotype from Fidji⁵. Specimen well-relaxed, fixed and preserved, with a ventral longitudinal dissection, not eviscerated. Body dorsally rounded and ventrally flattened, with rounded anterior and posterior extremities. Length 70 mm; width 30 mm. Mouth ventral. Anus terminal. Color of dorsal body wall beige, with distinct whitish circles surrounding the dark podia. Color of ventral body wall slightly lighter, podia beige, not circled by white rings. Bivium clearly separated from trivium. Tentacles beige. Anal teeth white. Body wall smooth to the touch, 2–3 mm thick. Tube feet of trivium predominantly in ambulacral areas, but with considerable spreading into the interambulacrae. Dorsal podia less numerous than ventral ones, dispersed regularly. The number of tentacles could not be determined without further dissection, 11 were observed⁶. Collar of papillae around the mouth missing. Anus surrounded by five anal teeth. 3 Polian vesicles (2 small, 2 mm long; 1 large, 10 mm long). About 10 stone canals. Cloaca 15 mm long. No Cuvierian tubules observed.

5 Féral & Cherbonnier (1986) provided an accurate description of a freshly collected specimen of this species (identified as *A. mauritiana* by them), and they noted that the ventral mouth is surrounded by a circle of papillae and 25 large, brown tentacles. Cherbonnier & Féral (1986) did not report Cuvierian tubules. Two specimens of *A. varians*, recently (2010) collected in Guam as present in the RBINS collection (I.G. 31558/HOL.1666) also have a collar of papillae and 25 large brown tentacles. No Cuvierian tubules were observed in the latter two specimens. These observations complement the description of *A. varians* as here provided through the description of the lectotype.

6 24–26 (rarely a few fewer) tentacles were counted in live and preserved non-type specimens (KN, pers. obs.).

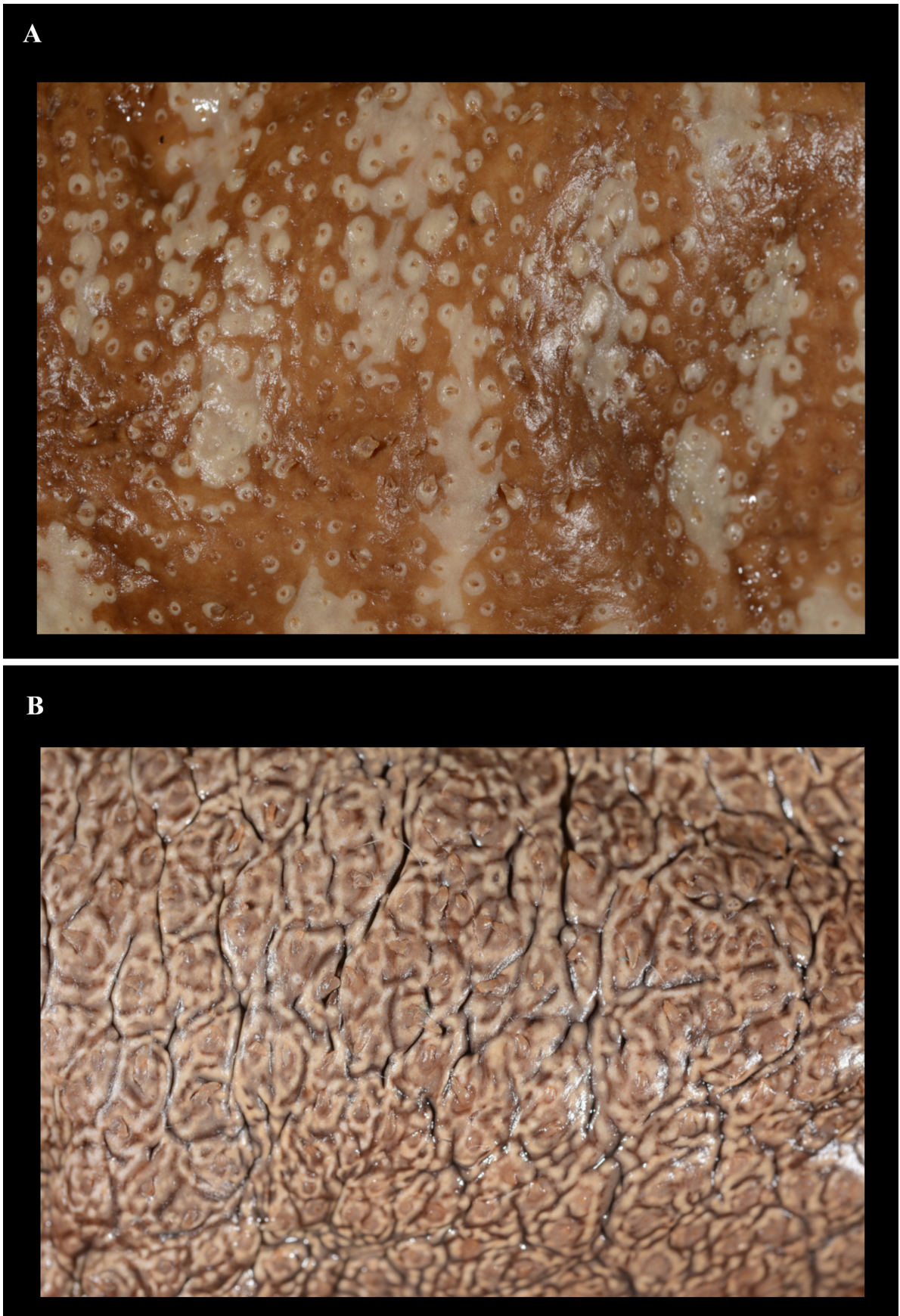


FIGURE 5. Detailed view of bivium in preserved specimens showing color pattern differences. (A) *Actinopyga varians*, UF 4578, about 6 cm long section; (B) *A. mauritiana*, UF 2069, about 5 cm long section.

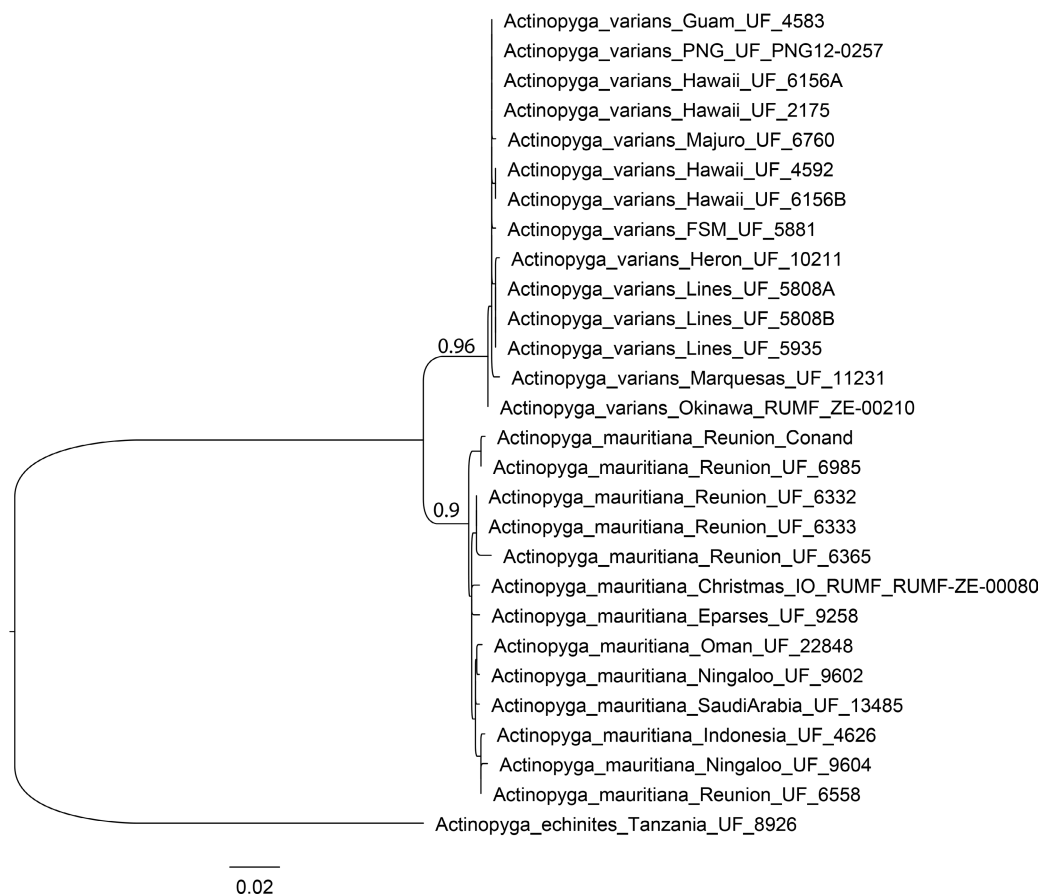


FIGURE 6. Maximum Likelihood phylogram of COI sequence data, with bootstrap values (1000 replicates); genetic distance scale at bottom. Specimens with UF and RUMF catalog numbers (marked with * in Materials examined).

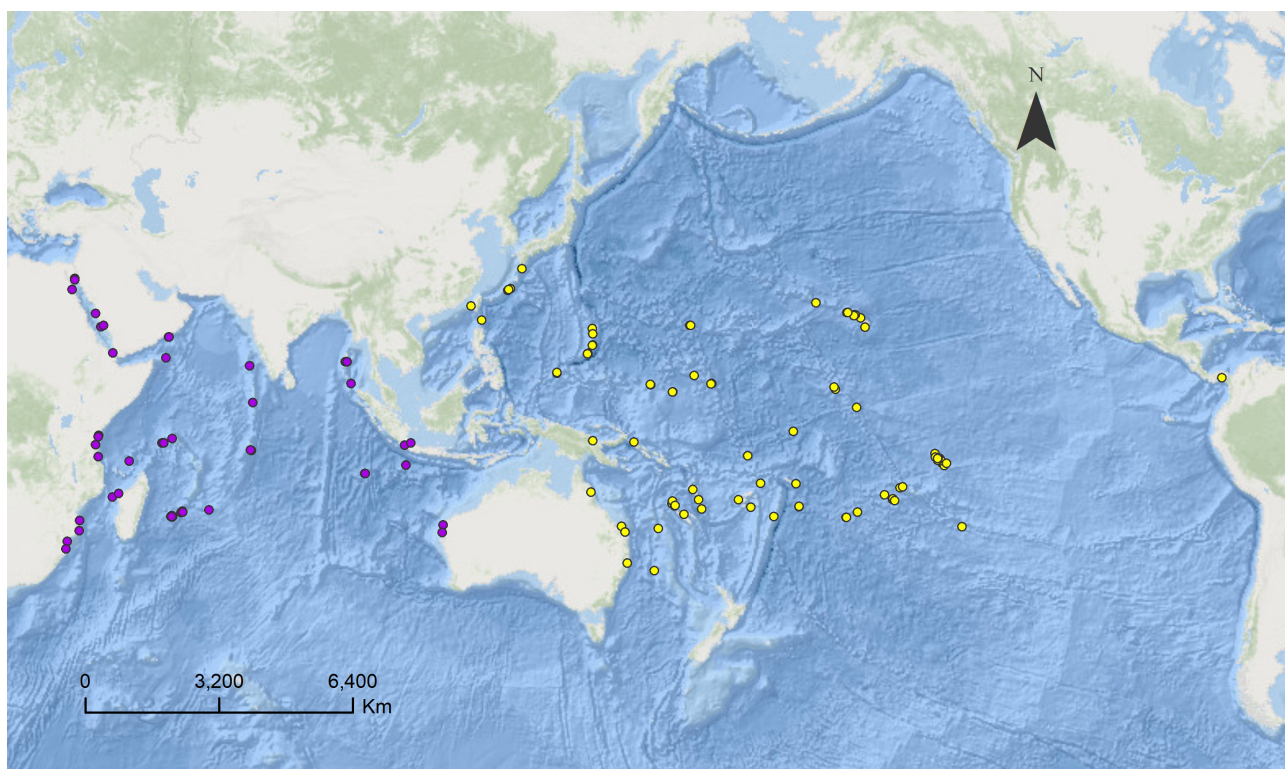


FIGURE 7. Distribution of *Actinopyga mauritiana* (purple symbols) and *A. varians* (yellow symbols).

Ossicles. Tentacles with straight to slightly curved rods, not bifurcating, rugose-spiny at ends, 100–190 μm long (Fig. 3A). Dorsal body wall with rosettes, 20–45 μm long, and spiny, sometimes bifurcating rods, 55–100 μm long (fig. 3B). Ventral body wall with grains, 7.5–20 μm long, and straight to slightly curved smooth rods with ends somewhat ragged, 50–65 μm long (Fig. 3C & C'). Dorsal papillae with simple rosettes, 20–35 μm long, and unbranched, straight rods with spiny ends, 75–100 μm long (Fig. 3D). Cloacal retractor muscles with straight, smooth, 30–50 μm long, spiny unbranched and branched rods, 30–80 μm long (Fig. 3E), but the branched spiky rods might be a contamination from the cloacal wall. Longitudinal muscles with smooth, straight rods, 30–55 μm long (Fig. 3F).

Live coloration

The bivium of *Actinopyga varians* is relatively smooth, “glossy”, with some lumpiness, but lacks the pronounced fine creasing seen in *A. mauritiana*. It is a mixture of vivid, slightly reddish brown intermixed with creamy white, giving a mottled appearance, with some irregular banding. In some individuals, brown, in others cream base color (e.g., type illustration of *A. guamensis*) predominates. Papillae are brown and tend to be surrounded by a whitish ring often even in the brown patches. The trivium is white-grey to pale reddish-brown covered with numerous, densely-packed, pale-brown tube feet.

Distribution

Indonesia to Hawaii and Pitcairn Islands, and Panama. Panama records are based on two specimens (USNM E22543 & E22637) from the Perlas Islands, so identified originally by Deichmann and reported on by Alvarado *et al.* (2010). These are two small specimens that fit the species, although they have not been sequenced. We are not aware of any other records and none have appeared in iNaturalist to date (18 Sept. 2024) that are attributable to *Actinopyga*.

Remarks

Muelleria varians is the first available name for the Pacific form in the *Actinopyga mauritiana* complex. This species was however first described as *Holothuria (Psolus) monacaria* by Lesson (1830) from Tahiti and Bora Bora in the Society Islands. Cherbonnier (1951a), in his review of Lesson's species, recognized that the excellent original figure and description in Lesson fits well with *A. mauritiana*. He noted that while the “holotype” from Tahiti is lost, several of Lesson's specimens from Bora Bora survived at the NMNH. As Lesson did not designate a holotype, all his specimens should be viewed as syntypes. No other species in the Society Islands can be confused with *A. varians*.

Holothuria monacaria Lesson, 1830 was however misinterpreted by most authors, beginning with Semper (1868) who put *H. gyrifer* Selenka, 1867 in its synonymy, thus effectively equating the concept of *H. monacaria* with the sea cucumber currently known as *Holothuria hilla* Lesson, 1830. This misinterpretation was consolidated by Théel (1886) and followed by most holothurian workers in the ensuing 50 years. Deichmann (1938) was the first to point out that *H. monacaria* did not fit the current concept of *H. hilla* and began using *H. gyrifer* for the latter. Cherbonnier (1951b) then showed that another of Lesson's species, *H. hilla*, is the oldest available name for *H. monacaria* auctorum, and the senior synonym of *H. gyrifer*. Clark & Rowe (1967) petitioned the ICZN to suppress *H. monacaria* to preserve the well-known *A. mauritiana*, and this was granted by ICZN (1970) opinion 914.

Holothuria guamensis Quoy & Gaimard, 1834, the next available name for *Actinopyga varians*, was also suppressed because of perceived confusion about its identity (Clark 1963) by ICZN (1966) Opinion 762. Paulay (2003) discussed the history of this species that has been interpreted as either *H. nobilis* (Cherbonnier 1952) or *A. mauritiana* (Rowe & Doty 1977). Quoy & Gaimard's (1834) figure, together with their description that describes 26 tentacles clearly match *A. varians*.

The next and only other available name for this species is *Muelleria varians* Selenka, 1867, name and identification that here we formally recognize.

Results & Discussion

Species delineation

DNA sequence data, coloration, and pattern of coloration consistently differentiate Indian and Pacific populations that have been attributed to the here discussed species. Classical ossicle-based delimitation on the other hand proved rather difficult given the little differences in the ossicle assemblage presented by both taxa.

The species differ in surface texture and color pattern. *Actinopyga mauritiana* has a dark to light, dirty brown dorsal surface that can transition to dirty tan to white sides and conspicuous polygonal patterning of creases and dark lines around the papillae. In contrast, *A. varians* has vivid, reddish-brown and creamy white dorsum and lacks the striking polygonal patterning.

Actinopyga mauritiana and *A. varians* are reciprocally monophyletic at COI and 16S, with 4.70+/-0.26% and 3.78% +/- 0.29% sequence divergence, respectively. The substantial interspecific divergence contrasts with small (0.33+/-0.28% and 0.19% +/-0.16%) intraspecific variation. This is especially striking given that both Indian and Pacific forms have been sampled across much of their range. We sequenced samples of *A. mauritiana* from the Red Sea, Mascarene Islands, Christmas Island (Indian Ocean), NW Australia and Anak Krakatau (Indonesia), and *A. varians* from the Ryukyus, Papua New Guinea, East Australia, Mariana, Line, Marquesas and Hawaiian Islands (Fig. 6). The low intraspecific variation in both species suggests high connectivity across their ranges.

TABLE 1. Genbank accession numbers for COI sequences.

Species	Locality	Repository	Cat #	GenBank
<i>A. echinites</i>	Tanzania	UF	8926	PV875067
<i>A. mauritiana</i>	Christmas Island	RUMF	ZE00080	PV875068
<i>A. mauritiana</i>	Scattered Islands	UF	9258	PV875069
<i>A. mauritiana</i>	Indonesia	UF	4626	PV875070
<i>A. mauritiana</i>	Australia: Ningaloo	UF	9602	PV875071
<i>A. mauritiana</i>	Australia: Ningaloo	UF	9604	PV875072
<i>A. mauritiana</i>	Oman	UF	22848	PV875073
<i>A. mauritiana</i>	Reunion Island		No voucher	PV875074
<i>A. mauritiana</i>	Reunion Island	UF	6332	PV875075
<i>A. mauritiana</i>	Reunion Island	UF	6333	PV875076
<i>A. mauritiana</i>	Reunion Island	UF	6365	PV875077
<i>A. mauritiana</i>	Reunion Island	UF	6558	PV875078
<i>A. mauritiana</i>	Reunion Island	UF	6985	PV875079
<i>A. mauritiana</i>	Saudi Arabia	UF	13485	PV875080
<i>A. varians</i>	Yap Island	UF	5881	PV875081
<i>A. varians</i>	Guam	UF	4583	PV875082
<i>A. varians</i>	Hawaii	UF	2175	PV875083
<i>A. varians</i>	Hawaii	UF	4592	PV875084
<i>A. varians</i>	Hawaii	UF	6156A	PV875085
<i>A. varians</i>	Hawaii	UF	6156B	PV875086
<i>A. varians</i>	Australia: Heron Island	UF	10211	PV875087
<i>A. varians</i>	Line Islands: Palmyra	UF	5808A	PV875088
<i>A. varians</i>	Line Islands: Palmyra	UF	5808B	PV875089
<i>A. varians</i>	Line Islands: Kingman	UF	5935	PV875090
<i>A. varians</i>	Marshall Islands: Majuro	UF	6760	PV875091
<i>A. varians</i>	Marquesas Islands	UF	11231	PV875092
<i>A. varians</i>	Okinawa	RUMF	ZE00210	PV875093
<i>A. varians</i>	Papua New Guinea	UF	14546	PV875094

Ecology and distribution

Both species are conspicuous, large sea cucumbers that prefer exposed reef margins. They live in a high-energy band where incoming oceanic waves hit and traverse reefs, from a depth of a few meters on the reef front, through the reef crest, to the outer part of the following barrier or fringing reef flat (Kerr *et al.* 1993; Purcell *et al.* 2012).

They hold on to reef rocks with a dense ventral cover of tube feet and withstand the force of ocean waves as they break across the reef front, surviving even through typhoons (Kerr *et al.* 1993).

Actinopyga mauritiana is known from the Red Sea, but has not been recorded from the Persian Gulf, and is rare in the Arabian Sea, where it is reported from Pakistan (Quratulain *et al* 2020) and from three specimens encountered in a single location in Oman during an extensive survey of the marine biota there (GP, pers. obs.). The Red Sea population is not divergent in COI. The species occurs throughout the oceanic island groups of the central and western Indian Ocean, including the Lakshadweeps, Maldives, Chagos, Seychelles, Comoros, and Mascarenes. It ranges on the East African coast from at least Kenya to Mozambique, occurs in southernmost India and Sri Lanka, and also in the Andaman, Cocos Keeling, and Christmas Island in the eastern Indian Ocean. It is further recorded from the western greater Sunda Islands east at least to Bali, and from West and Northwest Australia. Genetic samples show connectivity from the Red Sea to Christmas Island, Bali, and Northwest Australia.

Actinopyga varians is known from Indonesia (Borneo and Sulawesi), Philippines, Southern Japan through New Guinea to Eastern Australia, then eastward across all of Oceania to the Hawaiian, Line, and Pitcairn Islands. Two small specimens at the USNM from the Gulf of Panama tentatively identified as this species suggests that it has also traversed the East Pacific barrier. These species are rare in continental island setting of Indo-Malaya based on both collections surveyed and iNaturalists records. Fresh material and sequence data are needed to assess their distribution in this potential zone of transition.

Acknowledgments

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