

Enigmatic ophiuroids from the New Caledonian region

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Abstract

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Three new species are described from New Caledonia which have been provisionally placed in the genera *Ophiohamus* (Ophiacanthidae), *Ophionereis* (Ophionereididae) and *Ophiodaphne* (Amphiuridae) respectively, pending a comprehensive revision of the Ophiuroidea. In addition, new specimens and morphological variation is described for the species *Amphipholis linopneusti* (Amphiuridae). Our knowledge of the deep-sea fauna of New Caledonia remains incomplete.

Keywords

Brittle-stars, marine, continental slope, Pacific Ocean, *Ophiohamus*, *Ophionereis*, *Ophiodaphne*, *Amphipholis*.

Introduction

Our knowledge about deep-sea biodiversity is inadequate. Expeditions to even well-sampled regions continually turn up new species; many of which challenge our preconceived notions about the evolution of marine animals and their established taxonomy. One of the best sampled regions at bathyal depths is the New Caledonian Exclusive Economic Zone (EEZ). For the past 40 years, the Museum National d'Histoire Naturelle of Paris (MNHN) and the Institut de Recherche pour le Développement (IRD) have explored the diversity of the deep-sea benthos of the New Caledonian EEZ through the Tropical Deep-Sea Benthos program (TDSB). In all there have been 37 expeditions collecting approximately 3,800 samples, largely from the continental shelf and upper bathyal (200–1000 m) zones (S. Samadi *pers. comm.*).

This paper reports on four species from New Caledonia that stretch the limits of the existing generic classification of the Ophiuroidea (brittle-stars). Three are new species with clearly defined diagnostic characters; the fourth appears to be part of a morphological complex that possibly contains cryptic species. New comprehensive genetic data has shown that the existing classification of ophiuroids is flawed, from genus to order level (O'Hara et al. 2014, Hugall et al. 2015). Many morphological characters traditionally used to define genera and families have evolved multiple times. To date, only microscopic skeletal characters such as arm spine articulations have been successfully used to define higher-level taxa (Martynov 2010; Thuy & Stöhr 2011; O'Hara et al. 2014). A new classification of the Ophiuroidea is required.

The type material of the new species was dried after preservation. Given the fragile and rare nature of these

specimens we have not attempted dissection or SEM photography and the species descriptions are only of external features. The images were taken with a Visionary Digital Integrated System, using a Canon 5D Mark II camera with EF100mm and MP-E65mm macro-lenses, and montaged using Zerene Stacker v1.04 software.

Abbreviations include d.d. – disc diameter; stn – station; MNHN – Museum National d'Histoire Naturelle; MV – Museum Victoria; AM – Australian Museum; UF – Florida Natural History Museum.

Systematic Account

Family Ophiacanthidae

Ophiohamus georgemartini sp nov

Fig. 1

Zoobank LSID. <http://zoobank.org/urn:lsid:zoobank.org:act:11DC6E76-463D-42BE-AD04-25622254FB64>

Type material. – New Caledonia. SMIB5: stn DW94, Banc Alis, 22° 19.6'S, 168° 42.8'E, 275 m, 10 Sept 1989, holotype: 1 (MNHN IE.2013.16001).

Description. Disc 3.8 mm diameter, arms (all broken at tip) at least 10 times d.d., curved but not coiled. Disc circular, without interradial incisions, dominated by 5 pairs of large triangular radial shields, with rounded angles, 0.35 times d.d., contiguous for most of their length radially, separated at the distal and proximal ends by small scales, the former a small triangular

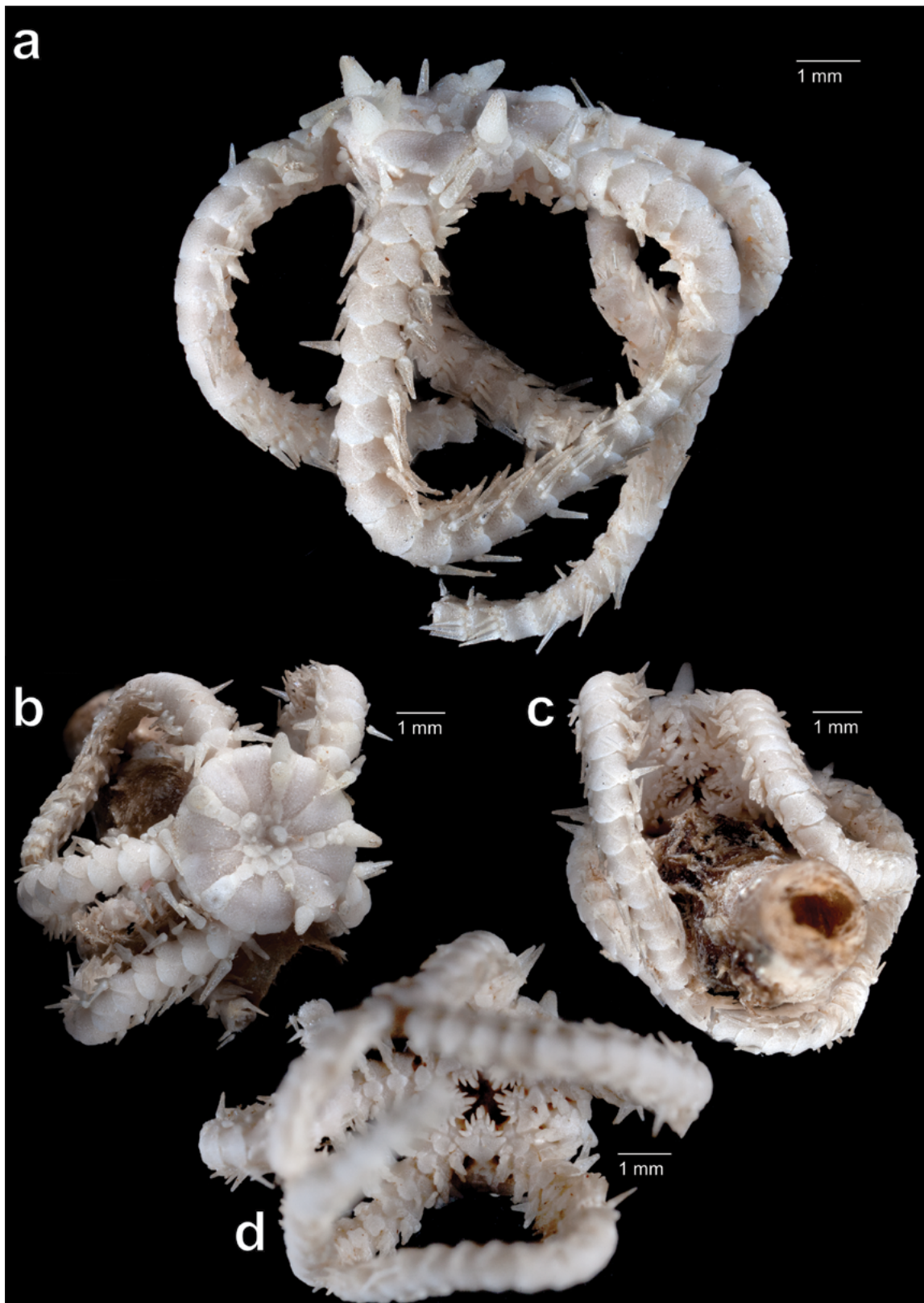


Figure 1. *Ophiohamus georgemartini* sp. nov., holotype MNHN IE.2013.16001, A, lateral view; B, dorsal view; C, ventral view; D ventral view (with glass sponge removed).

plate, possibly homologous to the dorsal arm plates. One row of 3-4 polygonal interradial plates separate the radial shields and a cluster of irregular rounded overlapping disc scales centrally. A large conical spine is present on the distalmost plate of each interradius, 0.7 mm high and 0.5 mm in diameter at the base. On one interradius, there is a second conical spine on the next proximal interradial plate, on another interradius there are two small round granules, 0.14 mm diameter; 1-2 similar granules are also present on some central plates.

Ventral disc covered in several rows of polygonal or rounded overlapping scales. Wide genital slits. Oral shields diamond shaped, two times as wide as long. Adoral shields thick, sausage-shaped, proximal to oral shields, contiguous interradially, twice as wide as long, extending beyond the lateral angles of the oral shields, beaded surface. Apical papilla conical, twice as high as wide; three slender subequal oral papillae borne on the oral shields, the distal papilla abutting the adoral shield and overlying the second oral tentacle pore.

Dorsal arm plates rounded triangular, with straight lateral edges and slightly convex distal edge, first two plates just contiguous, others separated widely by the lateral arm plates. First ventral arm plate small, projecting into jaw space, contiguous with the second plate. Succeeding ventral arm plates pentagonal at first, but from segment three becoming more rectangular or rounded, separate, without a proximal angle, longer than wide, lateral sides incurved to accommodate the pore, distal edge convex to truncate. Lateral arm plates with striated surface for much of the arm, with a large distal flange bearing up to four arm spines. Separated ventrally by a small uncalcified area basally. Basal arm spines conical with a blunt tip, three times as high as the basal diameter, 1.3 segments long, middle spines flattened and covered in minute thorns, restricted to the lateral side of the arm after the first two segments. Four arm spines persist to (near) arm tip, becoming slender and pointed, uppermost spine exceeding a segment in length, lowest half that length, becoming hooked (curved and rugose on the proximal side). Arm spine articulation, rounded volute-shape. A single oval tentacle scale covers the small tentacle pore, as long as one third of the ventral arm plate.

Colour (dry): white. Arms originally curved around a small hollow glass sponge.

Distribution. New Caledonia (275 m)

Remarks. The volute-shaped arm spine articulation surface and overall appearance indicates that this species is an Ophiacanthidae (Martynov 2010). Within this family, the new species is closest to the genera *Ophiomitrella* and *Ophiohamus*, having relatively large disc scales and radial shields, the former often bearing spines/granules, but lacking the deep interradial disc incisions characteristic of *Ophioplinthaca* or the enlarged ventral interradial disc scale characteristic of *Ophiurothamnus*. The new species bears a strong resemblance to *Ophiohamus nanus* O'Hara & Stöhr, 2006 in the shape of the disc plates, radial shields, arm plates and arm spines, adoral and oral shields. But *O. nanus* differs in having no disc spines or

granules; relatively small radial shields, 1/4 d.d.; several rows of disc scales interradially; only two oral papillae on most jaw sides, the outer being widened; and only three arm spines distally. The new species lacks the interradial incision present on the holotype of *O. nanus* but this was not consistently present on the paratypes. Some species of *Ophiomitrella* and *Ophiurothamnus* have large disc spines or tubercles, either cylindrical (*Ophiomitrella nugator* (Koehler, 1922a), *Ophiurothamnus excavatus* Koehler, 1922a) or capitate (*Ophiomitrella conferta* (Koehler, 1922b)) but they are never as robust and conical as the marginal spines in the new species.

The genus-level classification of the Ophiacanthidae is inadequate (O'Hara & Stöhr 2006), with the large genera *Ophiacantha* and *Ophiomitrella* being polyphyletic (O'Hara & Hugall unpublished genetic data). Until a new classification is proposed, we place the new species in *Ophiohamus*. However, this requires an amendment of the generic diagnosis to accommodate a species with no interradial disc incision, as follows: Disc covered with coarse overlapping disc plates and large contiguous radial shields that are integrated into the disc plating, spines may be present, a shallow interradial incision in disc margin may be present, 2-3 spiniform oral papillae, with a widened outer papillae replacing the distal two, small oral and adoral shields, oral shields contiguous with the lateral arm plate and lying distal to the adoral shields, oral tentacles enclosed within jaw slit. Arms can curve ventrally but don't coil, small mostly separate dorsal and ventral arm plates, 3-4 arm spines restricted to the lateral side of the arm, relatively short, up to, or just exceeding, a segment in length, lowest spine semi-hooked, small tentacle pore covered by a simple tentacle scale.

Etymology. Named after the author, George R.R. Martin, because the large marginal disc spines of the new species look similar to the crown on the cover of his second book in the 'Games of Thrones' series, 'A Clash of Kings'.

Family Ophionereididae

Ophionereis sykesi sp nov

Fig. 2

Zoobank LSID. <http://zoobank.org/urn:lsid:zoobank.org:act:F6388E19-397A-482A-90A8-1DA7BE551083>

Type material. -- *New Caledonia*. BIOCAL: stn CP110, Ride de Norfolk, 22° 12.38'S, 167° 6.43'E, 275-320 m, 9 Sept 1985, holotype (MNHN IE.2013.16002); paratypes, same locality: 26 (MNHN IE.2013.16003).

Other material examined. -- *New Caledonia*. -- Bathus 1: stn DW688, Côte est, 20° 33.17'S, 165° 0.37'E, 270-282 m, 1993: 14 (MNHN IE.2013.6536). -- Bathus 2: stn DW716, Sud-ouest, 22° 40.81'S, 167° 12.07'E, 290-308 m, 1993: 1 (MNHN IE.2013.6541). -- Bathus 2: stn DW717, Sud-ouest, 22° 44.02'S, 167° 16.58'E, 350-393 m, 1993: 1 (MNHN IE.2013.6542). -- EBISCO: stn DW2559, NW Bellona, 20° 28'S, 158° 41'E, 255-280 m, 2005: 1 (MNHN IE.2007.5401). -- EBISCO: stn CP2592, Plateau des Chesterfield, 19° 42'S, 158° 30'E, 273-281 m, 2005: 1 (MNHN IE.2007.5174). Musorstom 6: stn DW399, Ride des Loyauté, 20° 41.8'S, 167° 0.2'E, 282 m, 1989: 1 (MNHN IE.2013.6537). -- Musorstom 6: stn DW418,

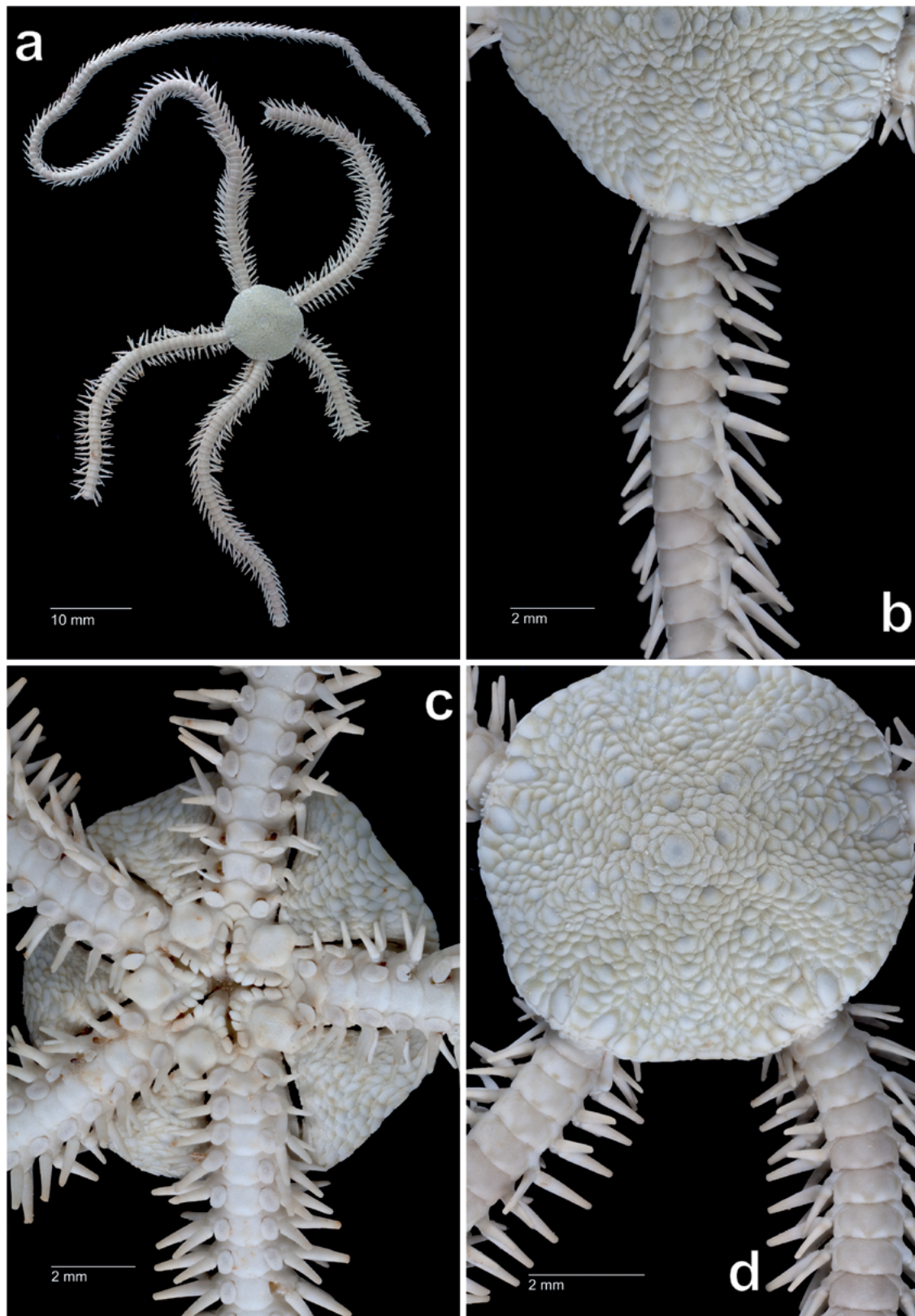


Figure 2. *Ophionereis sykesi* sp. nov., holotype MNHN IE.2013.16002, A, dorsal view of whole animal; B, oblique view of arm showing the supplementary dorsal arm plates dorsal view of disc and arm base; C, ventral view of disc and arm bases; D, dorsal view of disc and arm base.

Ride des Loyauté, 20° 41.75'S, 167° 3.35'E, 283 m, 1989: 1 (MNHN IE.2013.6538). -- Musorstom 6: stn DW422, Ride des Loyauté, 20° 26.2'S, 166° 40.31'E, 257 m, 1989: 1 (MNHN IE.2013.6539). -- Musorstom 6: stn DW423, Ride des Loyauté, 20° 25.85'S, 166° 40.5'E, 280 m, 1989: 9 (MNHN IE.2013.6540). -- SMIB5: stn DW95, 22° 59.7'S, 168° 19.8'E, 140-200 m, 1989: 1 (MNHN IE.2013.6544). -- SMIB5: stn DW96, 23° 0'S, 168° 18.7'E, 245 m, 1989: 1 (MNHN IE.2013.6545). -- **Vanuatu**. GEMINI: stn DW50, Mont Gemini, 20° 59.1'S, 170° 3.5'E, 425 m, 1989: 1 (MNHN IE.2013.6543).

Comparative Material. *Ophioneis degeneri* (A.H. Clark, 1949): FFS-0021, French Frigate Shoals, 23° 51.792'N, 166° 11.052'W, 85 m, 12/10/2006, UF 6679. FFS-0026, French Frigate Shoals, 23° 51.702'N, 166° 11.112'W, 12 m, 12/10/2006, UF 6039. *Ophioneis variegata* Duncan, 1879: BIOLUM/21, Lizard Is, Big Vicki, 14° 41.4'S, 145° 26.2'E, 2-4 m, 26/10/2005, MV F109863 (3). BIOLUM/30, Lizard Is, 7-14 m, 26/10/2005, MV F109864 (1). CReefs/GD.HI08-10, Heron Island, south side, 23° 28.4'S, 151° 57.83'E, 18 m, 6/9/2008, MV F211039 (4). HI09-011, Heron Island, Pinnacle, 23° 28.333'S, 151° 57.028'E, 9-10 m, 13/11/2009, UF 9963. HI09-018, Heron Island, Sykes Reef, 23° 25.943'S, 152° 2.025'E, 30 m, 14/11/2009, UF 9988. HI09-098, Heron Island, 23° 27.193'S, 151° 54.027'E, 24-26 m, 24/11/2009, UF 10115.

Description. Disc round, 10.4 mm diameter, arms at least 12 times d.d. (arm tips all broken). Disc covered in rounded overlapping scales, up to 0.35 mm diameter, primaries evident but small, centrodorsal 0.4 mm diameter, approximately 18 plates between centrodorsal and interradiar margin, marginal plates slightly larger than adjacent ones, forming a rim to the disc. Radial shields 1.0 mm long, twice as long as wide, roughly oval or triangular, with a truncate distal margin, convex lateral sides and an acute to rounded proximal angle, separated radially by 3 series of plates, the middle ones flanked by a row of smaller plates on either side. An irregular series of small papillae are present along the disc margin over the arm base, papillae conical with a blunt tip.

Ventral disc covered in similar overlapping plates as the dorsal surface, approximately 13 plates between oral shields and margin. Genital slits bordered interradiarially by an irregular series of rounded granules, obvious near the oral shield, becoming cuboid and contiguous from mid-radius to the disc margin (and often hidden within the slit), confluent with the papillae over the dorsal arm base. Oral shields rhomboid, just longer than wide, with rounded angles, and slightly concave sides. Adoral shields long and slender, tapering to a point proximally, rounded and widest distally, not contiguous with neighbouring plates, oral plates visible towards the jaw tip. Five oral papillae, inner papillae longest and orientated proximally so that they appear like infradental papillae on amphiuroids; next two papillae rhomboid to rectangular with flattened edge facing the jaw slit, fourth papillae 1.5 times as wide as high, rounded distally, touching the adoral shield, and finally a small recurved papilla at the end of the slit, sitting at the junction of the adoral plate and first ventral arm plate, protecting the second oral tube foot. Five teeth, dorsal three largest with thick enamelled tips, ventral one sits above the inner oral papillae.

Dorsal arm plates 0.75 mm wide, 1.8 times as wide as long, broadly contiguous throughout arm, hexagonal with a straight distal edge, straight distolateral sides that are contiguous with the supplementary arm plate, straight proximolateral sides

contiguous with the lateral arm plate, proximal edge overlaid by preceding plate. Basal supplementary dorsal arm plates small, roughly triangular, widest distally, extending proximally to the angle between the disto- and proximo-lateral sides of the dorsal arm plates, mostly lateral in position on the arm, appearing narrow and droplet-shaped from a dorsal projection. Dorsal arm plates become progressively more triangular in shape as the distolateral sides shorten and the proximolateral sides lengthen. Near the arm tip the distal side becomes convex and the proximolateral sides converge so that succeeding plates are only contiguous for 1/3 of their width. The supplementary plate becomes progressively smaller but persists as a tiny plate to (near) the arm tip. No accessory lateral arm plates, instead there is a decalcified gap between neighbouring lateral arm plates, the supplementary dorsal arm plate and the tentacle pore. First ventral arm plate diamond shaped, wider than long, the proximal sides contiguous with the adoral shields and distal oral papillae, the distal angle overlaps the second arm plate. Succeeding plates roughly quadrangular, as wide as long, with convex distal and proximal sides and concave lateral sides that border the tentacle pore, contiguous for 2/3 of their width. Second ventral arm plate with conspicuously convex distal edge. Plates becoming longer than wide near the arm tip, with convergent proximolateral sides, plates here contiguous for only 1/3 of their length.

Two arm spines on basal two segments, thereafter 3, slightly flattened to rounded, straight or slightly curved, blunt apex, on the first free segments the uppermost arm spine is 1.35 mm long, middle 1.5 mm long (to 1.7 segments long) and lowest 1.3 mm long. All 3 spines persist to the arm tip, slender, subequal to 1.2 segments in length. One thick ovoid tentacle scale, to 3/4 of a segment long, hinged on the ventral arm plate; a smaller rim-like scale on the ventral plate, usually overlain by the larger one. The ovoid scale persists to the arm tip.

Colour (dried). White with brown markings, notable on the proximal edge of large disc scales and around the interradiar rim of the radial shields. Dorsal arm plates with dark patch at the centre of the distal edge, with white markings on either side. Arm spines with faint brown bands near the base and around the tip, brown markings around the periphery of the oral shields and on some basal ventral arm plates.

Paratype variations. From 4 to 10 mm dd. Some dorsal arm plates are darker in colour, forming narrow bands of 1-2 segments on the arms, alternating with bands of 3-5 lighter segments.

Distribution. New Caledonia (140-393 m), Vanuatu (425 m).

Remarks. The new species is very similar in overall appearance to *Ophioneis novaezelandiae* Mortensen, 1936 known from the outer shelf and upper slope of southern Australia (formerly as *O. terba* Baker & Devaney, 1981) and the north-eastern coast of New Zealand to the Kermadec Islands (O'Hara 1998, Mills & O'Hara 2013). This species differs however, in lacking the papillae around the dorsal arm base, slightly narrower dorsal arm plates (generally less than 1.7 times as wide as long), and arms that form tight horizontal coils (see Mills & O'Hara 2013, fig. 13b). The colour scheme is also brighter on *O.*

novaezelandiae; the two white patches on either side of the distal midline of the dorsal arm plates are rimmed by a darker colour forming characteristic 'm' shaped markings. The differences between these species are slight but consistent. The dorsal papillae are always present on specimens of the new species, including small specimens of only 5 mm d.d..

Both *Ophionereis fusca* Brock, 1888 and *O. sasakii* A.M. Clark, 1953 have some genital papillae that extend around the arms until the dorsal surface. However, the papillae are restricted to the dorsolateral sides of the arm and are discontinuous radially, i.e. not present distal to the area between the radial shields. While the genital papillae on *O. fusca* are contiguous and blunt, like *O. sykesi*, they are separate, spiniform and pointed on *O. sasakii*. *Ophionereis fusca* is covered in prominent dots (see A.M. Clark 1953, fig. 5) and *O. sasakii* has thick bands of colour on the arms, the dark and light sections being both approximately 6 segments long. Dorsal papillae or spines are also characteristic of the genus *Ophiodoris*, however, the species in that genus do not have any supplementary arm plates.

There are specimens of another diminutive *Ophionereis* from northern Australia, with similarly patterned dorsal arm plates to *O. novaezelandiae*, which has been assigned by Rowe & Gates (1995) to the Korean species *O. variegata* Duncan, 1879. The dorsal arm plates of these specimens have a dark spot in the middle of the distal rim, surrounded by a 'V'-shaped patch of white, which in turn is bordered by two dark longitudinal lines. The arms are also banded, with 2 (rarely to 4) dark segments to every light segment. These specimens have been generally found from 5 to 100 m depth, often living in the small holes of dead coral pieces, and only observed by scuba divers at night (O'Hara, personal observations). *Ophionereis variegata* (including the Australian specimens) differs from other species in having small accessory lateral arm plates, wedged between the supplementary dorsal arm plate and the tentacle scale. It is unclear whether the Australian specimens are really conspecific with *O. variegata* as the arm length appears to be considerably longer (to eight times d.d.) than the four to five times disc diameter reported from Korea (Duncan 1879), Japan (Matsumoto 1917 as *O. porrecta*) and China (Liao & Clark 1995). Another similar species, *O. lineata* H.L. Clark, 1946, has been described from the southern Great Barrier Reef. We have seen unpublished photos of this species from the Great Barrier Reef Seabed Biodiversity Project (Pitcher et al. 2007) which confirm the type specimen's distinct colour pattern (figured by Clark & Rowe 1971 and Baker & Devaney 1981), having three to five light segments alternating with one to two darker ones, and a dark longitudinal line running down the centre of the dorsal arm surface bordered by two lighter lines, in turn bordered (on the lighter segments) by a dense pattern of small dots. Ventrally there are two faint longitudinal dark lines or series of dots. Two other species that can have two prominent white dots on each dorsal arm plate, *O. olivacea* H.L. Clark, 1901 and *O. squamulosa* Koehler, 1913 from the Caribbean (see Hendler 1995 fig. 51), may also be related. Finally, *O. degeneri* A.H. Clark, 1949 described from Hawaii, with similar specimens reported from New Caledonia (Stöhr 2011), differs from the other species in

having small circular disc scales and no prominent primary plates (see Stöhr 2011 fig. 15). Moreover, specimens from Hawaii (UF) do not have white markings on the dorsal arm plates. Thus, in conclusion, the Australian specimens of '*O. variegata*' possibly represent a new species, but this requires confirmation from a thorough morphological or molecular comparison with northern Pacific populations. None of these species have the marginal disc papillae running over the dorsal arm base that are found in *O. sykesi*.

A new genus-level revision of the Ophionereidae/Ophiochitonidae is required. The ophiuroid phylogenies of O'Hara et al. (2014) and Hugall et al. (2015) show that the Ophiochitonidae is paraphyletic with respect to the Ophionereidae. There is a morphological transition from *Ophiochiton*, *Ophioplax* and *Ophiodoris* with no supplementary dorsal arm plates, through *Ophionereis australis* (H.L. Clark, 1923) where they are restricted to a few basal segments, to *O. novaezelandiae* with small supplementary plates that persist down the arm, and finally to *O. annulata* (Le Conte, 1851) and *O. schayeri* (Müller & Troschel, 1844) where there are large persistent supplementary arm plates. The new species is assigned provisionally to *Ophionereis sensu lato* but we anticipate a future revision that recognises a clade including at least this species, *O. novaezelandiae*, *O. variegata*, *O. lineata* and *O. degeneri* at the genus or subgenus level of classification.

Etymology. Named after the wife of TOH, Deborah Sykes, who has had to put up with him rummaging around the world's museum collections for years.

Family Amphiuroidae

Ophiophane impellera sp nov

Fig. 3

Zoobank LSID. <http://zoobank.org/urn:lsid:zoobank.org:act:4F1FE97F-6B95-40AE-BDA1-092DED147E52>

Type material. -- New Caledonia. BIOCAL: stn CP23, Sud ouest, 22° 45.8'S, 166° 20.33'E, 2040 m, 28 Aug 1985, holotype (MNHN IE.2013.16004). -- paratype, same locality (MNHN IE.2013.16005)

Description. Disc 5.5 mm diameter, rounded pentagonal in outline; arms emerging from underneath the disc, at least 2.5 times d.d. (all broken). Disc completely covered in rugose scales. Radial shields 0.31 times d.d., D-shaped to pentagonal, with an acute proximal angle, straight to slightly convex adradial margin, convex abradial margin, and rounded distal edge, contiguous for distal half of length but separated proximally by 2 small disc plates, rugose surface. The centre of the disc is dominated by the primary plates with small intercalary plates at their corners, primary plates with thickened borders and tuberculate centre. Interradius with several overlapping plates, one or two plates wide proximally, then becoming more numerous near the margin, large plates with thickened distal edge, smaller marginal plates particularly rugose. A row of small plates border the radial shields distally over the arm. Ventral surface covered in thin flat, circular scales, persisting to oral shields.

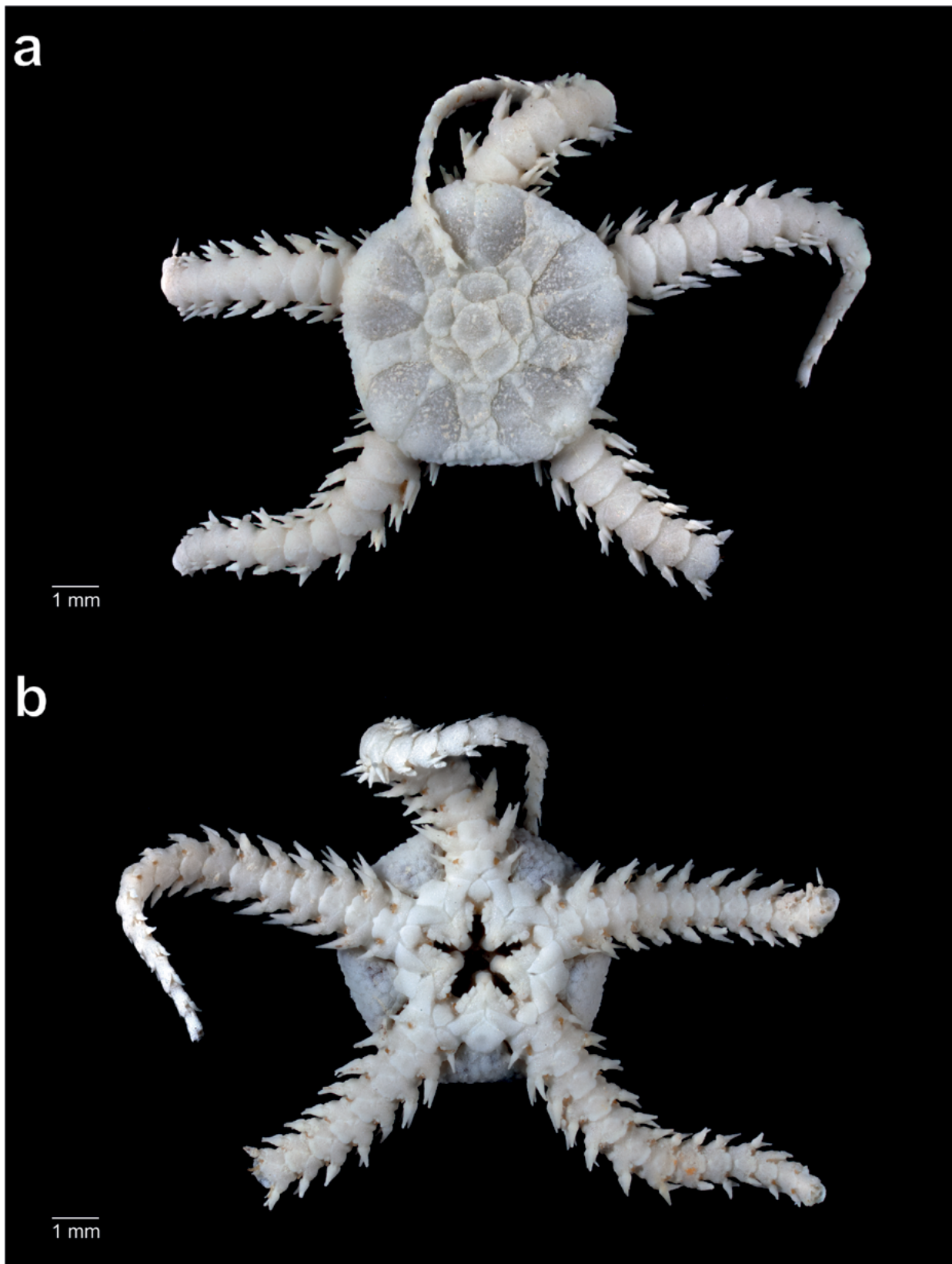


Figure 3. *Ophiodaphne impellera* sp. nov., holotype MNHN IE.2013.16004, A, dorsal view, B, ventral view.

A pair of pointed papillae at each jaw apex; 3-4 oral papillae on each jaw side, the proximal one wide and rim-like, pointed proximally (probably the first oral tentacle or buccal scale); the next 2 papillae squarish with rounded corners, the outer of the 2 slightly larger, sometimes a tiny scale is present either distally at the interstice of the oral and first ventral arm plate, protecting the second oral tentacle pore, or between the first and second oral papillae. Ventral surface of the oral plates triangular in shape, meeting broadly within, beaded surface, the pair of oral plates forming a wide obtuse shaped jaw. Teeth twice as wide as long with a broad enamelled margin. Oral shields roughly diamond-shaped, wide as long, with an obtuse proximal angle and rounded to lobed distal margin, acute lateral angles. Madreporite twice as large as other shields. Adoral shields tumid, wider than oral shield, trapezoid, widest radially, broadly contiguous interradially. Bursal slit extends to near disc margin, genital plates obscured.

Dorsal arm plates twice as wide as long, with an obtuse proximal angle, convex distal margin and rounded lateral angles, always separate, distal section of the plate with slightly tuberculate surface. Lateral arm plates beaded, meeting above and below arm, except basally where there is a small decalcified area between the ventral arm plates. Arm spine articulation formed from 2 parallel ridges, orientated radially. First ventral arm plate rounded triangular with a curved distal and obtuse proximal angle, forming distal margin to relatively wide oral cavity between jaws. Second to fourth plates twice as long as wide, roughly pentagonal with a straight to slightly convex distal edge, rounded distolateral angles, straight sides and convergent proximal edges that form an obtuse angle on the midline. The mid of the distal edge and the obtuse proximal angle can be produced into a small lobe that partially fills the decalcified area. Plates becoming progressively more triangular as the lateral edges shorten, becoming longer than wide distally, separate at first, becoming just contiguous distally. Three arm spines, rounded in cross section, tapering to a blunt tip, subequal, less than a segment in length basally, with middle spine slightly thickened. Uppermost spine reduced in size after basal segments, becoming absent after mid-arm. Lowermost spine becoming bottle-shaped with a narrow neck, which becomes curved, pseudo hook-shaped, on distal segments. Two small oval tentacle scales on first 4 segments, the one on the lateral arm plate larger than the one on the ventral arm plate, incompletely covering the pore. The smaller scale can be absent on the basal segments and is never present after the fourth.

Colour (dry): white.

Paratype 5.0 mm d.d. With similar morphology. Only 3 oral papillae, sometimes irregular in shape or position. Madreporite with rugose surface. Only 2 arm spines after the first few segments.

Distribution. New Caledonia (2040 m)

Remarks. These specimens have the two apical papillae and arm spine articulations characteristic of the Amphiuroidae (A.M. Clark 1970; Martynov 2010). Within that family we provisionally place them in the genus *Ophiophane* on the basis of similar oral frames, with oral shields smaller than the thick adoral shields which meet broadly within, arm plates and hooked distal arm

spines. The large female specimens of the type species, *Ophiophane formata* (Koehler, 1905), also have three oral papillae, but differ in having spiniform apical papillae and teeth, up to six cylindrical arm spines, narrow quadrangular radial shields, one oval tentacle scale and fine smooth disc plates (see Guille 1981). Large females of the second species, *Ophiophane scripta* (Koehler, 1904b) have a fused oral papilla with a minutely denticulate edge, fully contiguous D-shaped radial shields, small round disc plates marked by small grooves, a single wide tentacle scale, and several hook-shaped arm spines distally (see Cherbonnier & Guille 1978). In both previously-described species, the male is a dwarf that is frequently found clinging to the oral surface of the female, and they are generally found commensal with sand dollars (Tominaga et al. 2004) or (rarely) crinoids (Cherbonnier & Guille 1978). We refrained from dissecting the two known dry specimens of the new species and thus cannot determine their gender. Nor is there any information that these specimens were found in association with sea urchins or crinoids. In many ways the three species are quite morphologically diverse, and it is possible that the shared characters are convergent - perhaps adaptations to an epizoic lifestyle. The new species was found considerably deeper than the other two (0-630 m) which are widely distributed across the Indo-west Pacific Ocean. However, we see no advantage to assigning the new species to a separate genus until we have adequate molecular evidence. As discussed under the next species, further study is required to determine what characters are useful to define genera within the Amphiuroidae.

The mouth parts of *Ophiophane formata* and *O. scripta* are quite derived and there has been some debate whether they (and the similar sexually-dimorphic genus *Ophiophaera*) are better placed within the Amphiuroidae or Ophiactidae. Martynov (2010) however, found that both genera had arm spine articulations that are conclusively of the amphiuroid type.

Etymology. Named after the similar-looking impeller water pump that failed on TOH's attempted crossing of Bass Strait on the yacht Irene.

Amphipholis linopneusti Stöhr, 2001

Fig. 4

Amphiuroida crassa (in part)--Koehler, 1904a: 83-84, pl. 15(1-2) [Non *Amphiodia crassa* (Koehler, 1904); see Stöhr, 2001].

Amphiodia crassa--Koehler, 1922a: 167-168, pl. 69(11)--Clark, A.M., 1970: fig. 5c-d [Non *Amphiodia crassa* (Koehler, 1904); see Stöhr, 2001].

Amphipholis linopneusti Stöhr, 2001: 319-322, fig. 1a-h.

Material examined. -- *New Caledonia*. BIOCAL: stn DW44, Ride de Norfolk, 22° 47.3'S, 167° 14.3'E, 440-450 m, 30 Aug 1985: 10 (MNHN IE.2013.16006). -- EBISCO: stn DW2613, Plateau des Chesterfield, 19° 37'S, 158° 41.9998'E, 519-522 m, 2005: 7 (MNHN IE.2007.7480). -- *Australia*. FR0688: stn 01, east of Cape York, Queensland, Australia, 10° 29.82'S, 144° 0.38'E, 495-534 m, 1988: 14 (AM J23292). -- *Papua New Guinea*. BIOPAPUA: stn CP3692, Pointe Sud-Est Manus Island, 2° 10'S, 147° 19'E, 408-448 m, 2010: 1 (MNHN IE.2012.686). -- BIOPAPUA: stn CP3645, Tami Island, Golfe de Huon, 6° 44'S, 147° 50'E, 403-418 m, 2010: 20 (MNHN IE.2012.319). -- *Vanuatu*. Santo: stn AT122, SE Malékula Island, 16° 37'S, 168° 0'E, 567-580 m, 2006: 1 (MNHN IE.2009.1990).

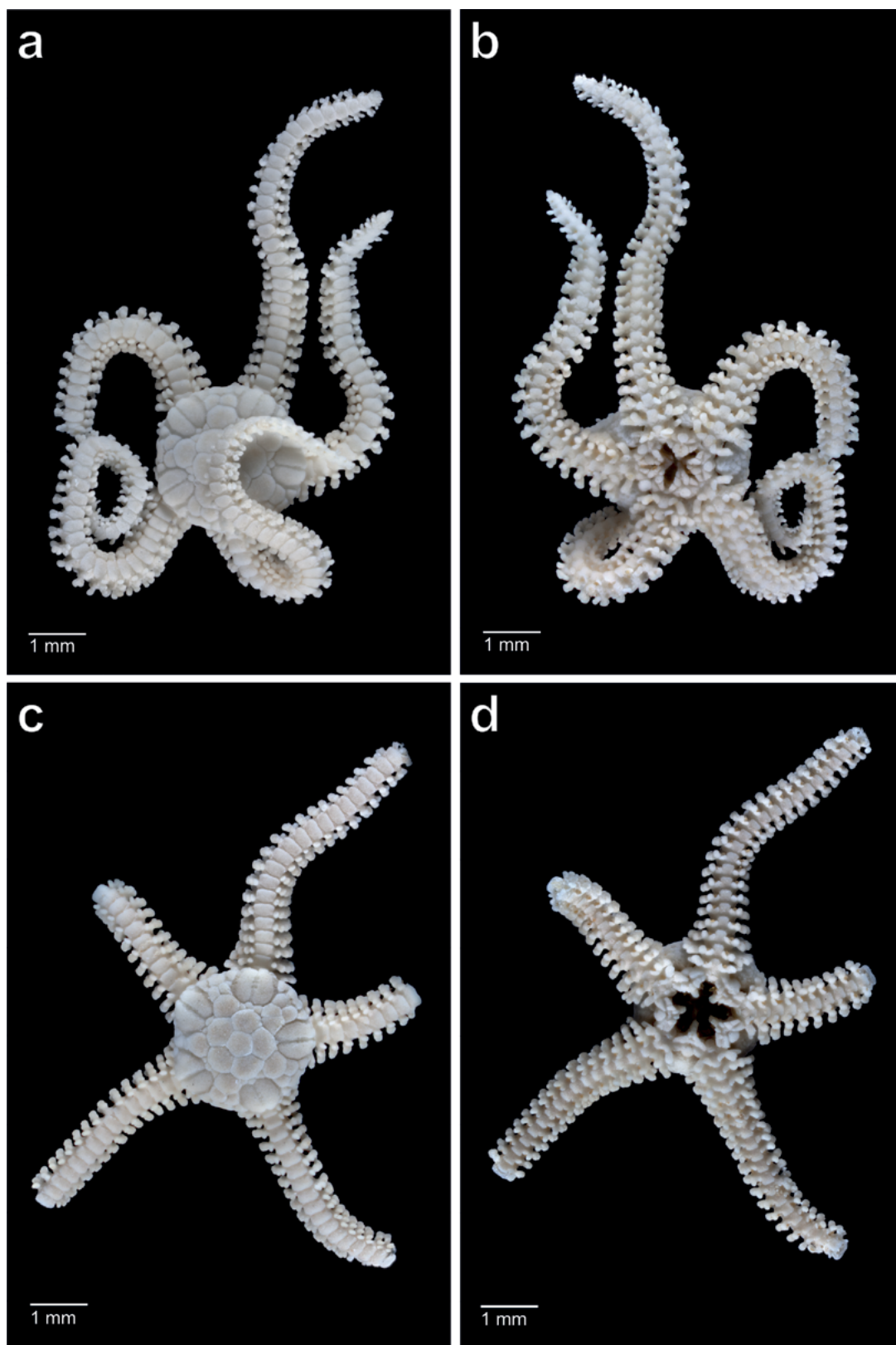


Figure 4. *Amphipholis linopneusti* Stöhr, 2001, MNHN IE.2013.16006, A, dorsal view of specimen 1, B, ventral view of specimen 1; C, dorsal view of specimen 2, B, ventral view of specimen 2.

Distribution. Fiji (260–651 m), New Caledonia and Vanuatu (440–580 m), NE Australia (495–534 m), Papua New Guinea (403–418 m), Indonesia (450–877 m), Philippines (242–454 m)

Remarks. This species is sexually dimorphic. The lowermost basal arm spines of males are enlarged, sometimes flattened and hour-glass-shaped, whereas on the females they are cylindrical with a blunt rounded apex (Fig. 4). In many ways, this species is very divergent from other *Amphipholis* species. The disc scales are raised, with the radial shields in particular being surrounded by sunken borders. The arm spines are thick and short, almost capitate in some specimens. The single tentacle scale is large, often erect (on preserved material), hinged on the lateral arm plate but angled outward away from the mid-radius. The two oral papillae on the side of each jaw can vary in size, sometimes the inner one is larger, although it is always longer than wide and pointed proximally. The distal one is square to rectangular, typically wider than long. Unusually, the species is also epizoic on sea urchins.

Most *Amphipholis* species have two small tentacle scales (A.M. Clark, 1970). Exceptions include *Amphipholis vitax* Koehler, 1904a, (which also has atypical long narrow divergent radial shields), *A. pentacantha* H.L. Clark, 1915, *A. murmanica* Djakonov, 1929 and *A. nudipora* Koehler, 1914 which have rudimentary tentacle scales on basal segments or not at all. *Amphipholis tuberosa* Stöhr, 2011 also has only a few small tentacle scales basally. This species has tuberculated disc plates and is very similar to *Amphistigma watsonae* Baker, 1979. Finally *Amphipholis loripes* Koehler, 1922a was recently transferred to *Amphiodia* (*Amphispina*) by Stöhr, 2011 after spinous plates were discovered distal to the radial shields. These species do not have a homogeneous morphology. Indeed, genetic evidence (Hugall & O'Hara unpublished data) indicates that many amphiuroid genera (*Amphiura*, *Amphipholis*, *Amphioplus*) are polyphyletic. We refrain from establishing a new genus for *A. linopneusti* until these genera are comprehensively revised.

There is also considerable morphological variation within *Amphipholis linopneusti*. As well as the sexual dimorphic characters, the number and shape of the other arm spines varies. There are up to seven arm spines in the BIOCAL stn DW44 lot (which contains only females). In the type series (Stöhr 2001), arm spines varied from being elongate (up to four times as long as wide) to small and stout (two times as long as wide). The shape of the oral shield also varies from round to triangular to oval (longer than wide). More research is required to determine whether this taxon includes one or more cryptic species. The taxon is distributed throughout the Indonesian-west-Pacific region at upper continental slope and rarely continental shelf (Koehler, 1922a) depths.

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