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Seamount ophiuroids from the High Seas of the western Indian Ocean

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Abstract

Twelve new species of Ophiuroid (brittle stars) are described, using both morphological and DNA evidence, from four seamounts (Atlantis, Melville, Coral and Walters Shoal) in the Area Beyond National Jurisdiction (High Seas) of the SW Indian Ocean, one in each of the genera: *Ophiocreas* (Euryalidae), *Ophiopyrgus*, *Amphiophiura*, *Glaciacantha*, *Ophiuroglypha*, *Stegophiura* (Ophiopyrgidae), *Ophiectodia*, *Ophiosabine*, *Ophiacantha*, *Ophiolimna* (Ophiacanthidae), *Ophiomyxa* (Ophiomyxidae) and *Ophionereis* (Ophionereididae). In addition, we resurrect several synonymised genus and species-level taxa, including the genera *Ophiopyrgoides* for a clade of *Ophiopyrgus* that includes *O. trispinosus* (type), *O. saccharatus*, and *O. depressus*; *Ophiectodia* for the clade containing *Ophiacantha enopla* (type), *O. imago* and *O. opulenta*; *Ophiodiplax* for *Ophiacantha antarctica*, and the subgenus *Ophiotriton* for the *Ophionereis* species *O. semoni* (type), *O. dubia*, *O. amoyensis*, *O. andamanensis*, *O. hexactis*, *O. intermedia*, *O. thryptica*, *O. tigris*, *O. vivipara* and *O. sexradia*. Resurrected species include: *Astrothamnus papillatus* and *Gorgonocephalus pectinatus* from South Africa; and *Ophiomyces peresi* for North Atlantic/Mediterranean specimens of *O. grandis*, and *Ophiotreta rufescens* for North Atlantic specimens of *O. valenciennesi*. The following species are transferred to different genera: *Asterostegus* (*Astroceras spinigerum*); *Ophiocreas* (*Asteroschema lissum*); *Ophiopyrgus* (*Amphiophiura solida*, *A. latro*, *A. bakeri*, *A. liberata* and *A. spatulifera*); *Ophiomastus* (*O. biocal*); *Glaciacantha* (*Ophiocten cryptum* and *O. banzarei*); *Stegophiura* (*Amphiophiura lapidaria*); and *Amphiophiura* (*Stegophiura sculpta*, *S. vivipara*, *Ophioplinthus inflatus*). Finally, we make two species-level synonymies: *Amphiophiura pertusa* is synonymised with *Ophiopyrgus latro* and *Ophiacantha veterna* with *Opiectodia enopla*. The biogeography of the fauna of each seamount depends on the location and summit depth. The remote Atlantis Seamount has a widespread bathyal seamount fauna, Coral Seamount has a temperate Southern Ocean bathyal fauna, and Walters Shoal has a continental SE African/Madagascar shelf and upper bathyal fauna, and a mixed temperate/tropical Indo-Pacific mid-bathyal fauna.

Introduction

The description of new species is a key aspect of biodiversity research. Taxonomic names are fundamental to linking studies in autecology, evolution, conservation, ecology, and biogeography together, in order to develop a deeper understanding of the natural world and how to protect it. One environment that has lacked taxonomic research effort is the marine area beyond national jurisdiction (ABNJ) or the "high seas". The International Seabed Authority has recognised this by setting up a Sustainable Seabed Knowledge Initiative, the "One Thousand Reasons Campaign", jointly financed by the European Maritime and Fisheries Fund of the European Union.

This paper describes new and existing species of brittle stars (ophiuroids) from seafloor habitats in the ABNJ of the south-western Indian Ocean (SWIO), a region recognised as lacking biological data (Ramiro-Sanchez *et al.* 2023). This region, however, is economically important. There is a contract area for the exploration of polymetallic sulphides (PMS) along the SWIO Ridge between Coral and Atlantis seamounts (International Seabed Authority 2023). From the 1970s, bottom fishing targeting alfonsino (*Beryx splendens*) and orange roughy (*Hoplostethus atlanticus*) was extensive on shallow banks and seamounts in the region, peaking in the 1990s (Marsac *et al.* 2020). Today, fishing vessels in the region typically use drifting longlines (International Seabed Authority 2023). Both the commercial Southern Indian Ocean Deepwater Fisheries Association (SIODFA) and the UN sanctioned Southern Indian Ocean Fisheries Agreement (SIOFA) have proposed benthic fishing protection areas around some key shallow water seamounts and banks including Atlantis, Middle of What (MOW), Coral, and Walters Shoal. In 2011, Madagascar formally submitted a proposal to the UN's Commission on the Limits of the Continental Shelf, to add the Madagascar Ridge, including Walters Shoal, to its extended continental shelf.

We focus on material from two expeditions (Fig. 1). The first is a voyage (JC066) of the UK research vessel James Cook to the SWIO Ridge in November–December 2011 led by Prof. Alex Rogers (then University of Oxford) (Rogers & Taylor 2012). This voyage surveyed five seamounts or banks along the ridge (Coral, Melville, Middle of What, Sapmer, and Atlantis) but collected ophiuroid specimens mainly from two seamounts (Coral and Atlantis, with one species lot of 3 specimens from the Melville seamount) using the RoV Kiel 6000. This expedition targeted vulnerable marine ecosystems and thus the ophiuroids were primarily collected as bycatch from off and around corals and other sessile invertebrates. The second voyage (MD208) was undertaken by the French research vessel Marion-Dufresne to the Walters Shoal seamount, about 400 nautical miles south of Madagascar, in April–May 2017, led by Prof. Philippe Bouchet (Muséum national d'Histoire naturelle Paris, MNHN). The collections were obtained by scuba-diving on the summit (26–47 m), and by the use of a beam-trawl and Warén dredge on the seamount flanks (199–2058 m).

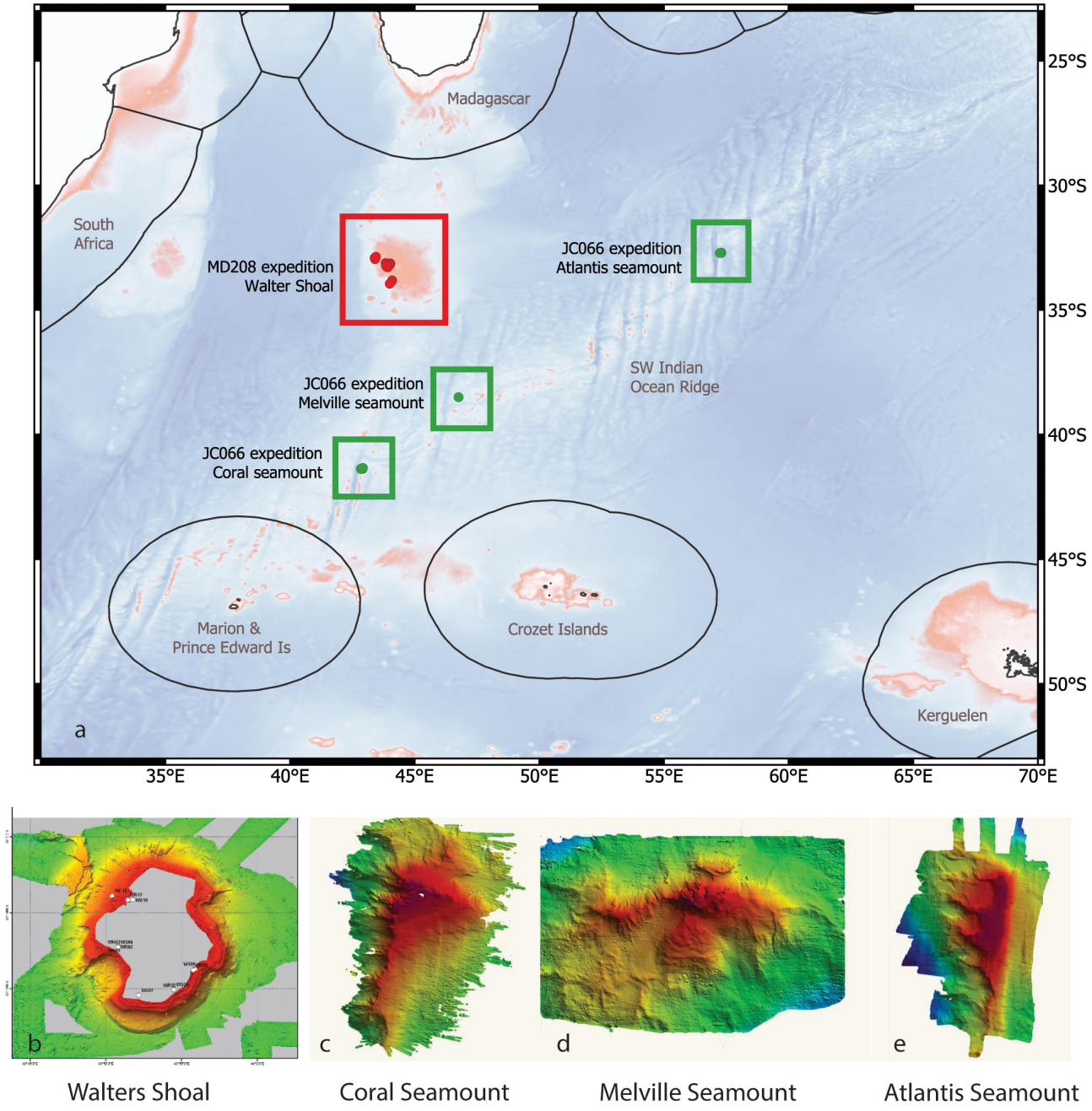

FIGURE 1. (a) Map of samples sites with ophiuroids from the MD208 (red) and JC066 (green) expeditions, (b) 3D terrain representations of Walters Shoal (MD208 expedition, courtesy of Philippe Bouchet), (c–e) 3D terrain representations of Coral, Melville and Atlantis seamounts (JC066 expedition, from Rogers & Taylor, 2012).

Atlantis, Melville and Coral are seamount features adjacent to the very slow-spreading SWIO ridge (Swanborn *et al.* 2023). Atlantis Bank (32° 45' S, 57° 16' E) is an oceanic mantle complex created through fault action (Dick *et al.* 2019). Rogers & Taylor (2012) describe Atlantis as having a flattened summit at 700 m depth, covered by a pavement of carbonate thinly draped in sediment punctured by steep outcrops of bedrock. The outcrops are covered in sessile invertebrates including stylasterids, octocorals and colonial scleractinians (*Madrepora oculata*), whereas the flat areas are dominated by echinoids. Two large mass-wasting events have occurred along the western flank, creating concave embayments between rocky spurs. While the floor of the embayments is relatively barren, the spurs are covered in dense communities of anemones, giant sponges and huge octocoral (*Paragorgia*) trees. Around 900 m, the sediment has been greatly disturbed by fishing trawl nets.

Melville Bank (38° 28’ S, 42° 44’ E) stretches over approximately 13.5 km from east to west with a small steep summit peaking at 100 m below sea level (Swanborn *et al.* 2023). The summit is dominated by steep rocky outcroppings covered by solitary corals (*Ballanophyllia*), fine black corals (Antipatharia), white and pink zoanthids, and colourful sponges, and surrounded by a tropical reef- fish assemblage (Rogers & Taylor 2012). Large lobsters of the genus *Jasus* occur just below the summit. The upper flanks of Melville are frequently steep and rocky with little obvious life, with sponges and corals at their base. The rocky spurs are covered in extensive growths of octocorals. *Projasus* lobsters occur in what appears to be old larva tubes. Flatter areas at 900 m are covered in fragments of stylasterids and sediment. Eels, pancake urchins, pencil urchins (Cidaridae), and Hexactinellida sponges occurred around boulders. Deep slopes are dominated by octocorals, large, stalked sponges and branching treelike sponges colonized by zoanthids.

Coral (41° 28’ S, 42° 53’ E) is the most southern seamount studied here, extending north to south for approximately 18 km and peaking at 200 m depth (Swanborn *et al.* 2023). The small summit area is covered in small boulders and sand and interspersed with dense carpets of zooanthids, sponge and scleractinian thickets. Tube worms, sea stars and brittlestars are present. The upper flanks (400 to 700 m) have bathymetric zones of calcareous polychaete tubes, gastropods and hermit crabs. There are large areas of dead coral framework (*Solenosmilia variabilis*, *Desmophyllum dianthus*) at 700–800 m depth that provide cryptic habitat for many invertebrates. Rogers & Taylor (2012) also observed several Patagonian Toothfish (*Dissostichus eleginoides*), a single Orange Roughy, and multiple instances of abandoned fishing trawl gear.

Walters Shoal (33°9–16’ S, 43°49–56’ E) is a large seamount at the southern end of the Madagascar Ridge that rises to 15–18 m below sea level. The rounded summit, extending over 400 km2 (at 500 m), is covered in bare rock and encrusting calcareous algae, with few large sessile or motile invertebrates (Bouchet pers. comm.). The coralline crust shelters smaller invertebrates (crustaceans, oysters, worms, hydroids, bryozoans, ophiuroids) and brown (*Lobophora*) and red algae. The flanks are relatively steep between 200–600 m, the flatter areas being covered in dead algal concretions and oyster shells. Below 600 m the slope is less steep, and there is more pelagic sedimentation, as well as some soft sea urchins (Asthenosomatidae), erect cnidarians (gorgonians, antipatharians) and ahermatypic corals, but no large holothurians. There was little evidence of demersal or lobster fishing.

Prior to the JC066 voyage, almost no benthic invertebrate collections were available to study from the SWIO Ridge. One exception is a dredge haul made by the South African research vessel Africana (station 1248, 36°48’S 52°8’E, 400–450 m, 9/7/1961) on what has subsequently been named the Sapmer seamount, from which four ophiuroid species were recorded (A.M. Clark 1974). Likewise, the MD208 expedition substantially increased the available benthic collections from Walters Shoal, which was previously represented from incidental catches. No ophiuroids had been previously reported from Walters Shoal.

Ophiuroids are ideal as a model group for the study of marine biogeography and the distinctiveness of regional faunas (O’Hara *et al.* 2019b). They occur in all marine habitats from the coastal zone to 8135 m in the hadal trenches, from the equator to polar regions, and on/within soft and hard benthic substrata. Many are epizoic on corals, sponges or other habitat-forming invertebrates. They exhibit a range of life history strategies including having feeding larvae, lecithotrophic (yolky) larvae, brooding of live young, and asexual reproduction by fission of larvae and adults (Hugall *et al.* 2024).

Methods and Materials

Morphological terms were derived largely from Stöhr *et al.* (2012) and the acronyms DAP, VAP, LAP derived from dorsal, ventral, and lateral arm plates. The nomenclature of ossicles around the mouth is derived from Hendler (2018), with the historical term “lateral oral papillae” used if the derivation of the ossicle could not be determined. The acronyms dd = disc diameter and x = multiplied by. Distribution regions were derived from Stöhr *et al.* (2012) with the exception that the North Atlantic and North Pacific have been both split into East and West regions, Southern Australia and New Zealand have been separated, and South Africa separated into temperate and subantarctic (Kerguelen, Marion, Crozet) regions. Depth ranges are derived from a global distributional database of validated museum and literature records (Woolley *et al.* 2016, O’Hara *et al.* 2019b).

Museum acronyms include: BAS—British Antarctic Survey, Oxford, UK; NHMUK—Natural History Museum, London, UK; CAS—Californian Academy of Sciences, San Francisco, USA; CNP-INV—CONICET/LABRIM Puerto Madryn, Argentina; DZMB-HH—Senckenberg Deutsches Zentrum für Marine Biodiversitätsforschung,

Hamburg, Germany; MNHN—Muséum national d'Histoire naturelle Paris, France; MTQ—Museum of Tropical Queensland, Townsville, Australia; MV—Museums Victoria, Melbourne, Australia; NHRM—Swedish Museum of Natural History, Stockholm, Sweden; NIWA—National Institute of Water and Atmosphere, Wellington, New Zealand; NSMT—National Museum of Nature and Science, Tsukuba, Japan; NUI—University of Galway, Ireland; RBCM—Royal British Columbia Museum, Victoria, Canada; SAMC—Iziko South African Museum, Cape Town, South Africa; SIO—Scripps Institute of Oceanology, San Diego, USA; UCN—Facultad de Ciencias del Mar, Universidad Católica del Norte, Coquimbo, Chile; UF—Florida Museum of Natural History, University of Florida, Gainesville, USA; USNM—United States National Museum (Smithsonian), Washington, USA; Vigo—University of Vigo, Spain; WAM—Western Australian Museum, Perth, Australia; ZMBN—Zoological Museum of the University of Bergen, Norway; ZMB—Zoological Museum of Berlin, Germany; ZSI—Zoological Survey of India, Calcutta.

Light images of holotypes were taken at Museums Victoria 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. Ossicles of the arm or disc skeleton were extracted from paratypes or other material, macerated in household bleach and rinsed in tap water, then mounted on aluminium stubs and gold-coated. Scanning electron microscope (SEM) images were taken with a JEOL Neoscope JCM-5000 at the National Museum of Natural History Luxembourg and a Hitachi TM 4000 Benchtop Electron microscope on general SEM settings, 15 kv and low vacuum (charge reduction) mode at Museums Victoria. We did not have permission to dissect all specimens for SEM analysis.

Our phylogeny was constructed from a next-generation exon-capture (targeted-enrichment) laboratory process (Hugall *et al.* 2016, O'Hara *et al.* 2017, 2019b, 2025). The majority of tissue samples were obtained from ethanol preserved museum specimens. Briefly, the laboratory methodology included 1) DNA extraction using Omega Bio-tek kits, 2) mechanical shearing to the target sequence length (~350bp) using a Covaris M220, 3) construction of libraries using Illumina TruSeq, XGen and NEBNext Ultra II kits with up to 192 barcodes, 4) hybridisation using a custom-designed myBaits (Daicel Arbor Biosciences) probe-set, and 5) sequencing on various Illumina © sequencers. Bioinformatics followed Hugall *et al.* (2016) and resulted in an aligned dataset of 263kb of nuclear DNA (across 1487 exons and 416 genes) and 1.4kb of the mitochondrial gene COI. This dataset was supplemented by several mitochondrial-only COI 'barcode of life' sequences (654 bp) harvested from NCBI and BOLD. The super-matrix phylogeny was developed in a three-step process. An all-compatible consensus topology was generated from the exon-capture dataset using a RAxML v.8.1.20 (Stamatakis, 2006) GTRCAT model fast-bootstrap (n=100) with 4 partitions (3 exon codon positions and COI). This topology was then used as a constraint tree in a second analysis using RAxML on the full dataset in a full search (4 partitions and GTR-gamma model) that both incorporated the COI-only samples and determined branch lengths. This tree was then converted into an ultrametric chronogram using TreePL v1.0 (Smith & O'Meara, 2012) using 11 fossil-based and one secondary root calibration points (O'Hara *et al.* 2014b) and visualised using Figtree v1.4.3 (Rambaut, 2010). Only a subset of these samples is displayed in the phylogeny in this paper (Fig. 2), consisting of the samples from the two focal surveys and closely related samples. The DNA sample data are given in the material examined under each species. Samples marked 'Not examined' include barcode COI sequences downloaded from NCBI or other sources without us validating the identifications.

There were not enough samples to perform DNA-based species-delimitation tests. Our DNA sampling was designed to identify the phylogenetic relationships of the samples not to resolve cryptic species complexes, which will require much greater sampling across their geographic and bathymetric ranges. Consequently, we have often erred on the side of caution and have tended to include clades of less than ~3 MY on our time calibrated phylogeny (Fig. 2) under a single species name (O'Hara *et al.* 2025), unless we have morphological or other evidence to the contrary.

Systematic Account

Family Euryalidae

Asterostegus sabineae Okanishi & Fujita, 2014

Asterostegus sp.—Okanishi & Fujita, 2013: 568.
Asterostegus sabineae Okanishi & Fujita, 2014: 4–9, fig. 2–5.

STUDY MATERIAL.—MD208: stn DW4885, Walters shoal, Pentes, 33° 16.68′S, 43° 54.18′E to 33° 16.61′S, 43° 54.9301′E, 272–380 m, 3/5/2017: 1 (MNHN IE.2016.1360) (**DNA code=IE.2016.1360**).—MD208: stn CP4901, Walters Shoal, Pentes, 33° 8.4′S, 44° 0.1199′E to 33° 9.36′S, 44° 1.2499′E, 647–672 m, 6/5/2017: 2 (MNHN IE.2013.17142) (**DNA code=IE.2013.17142**).

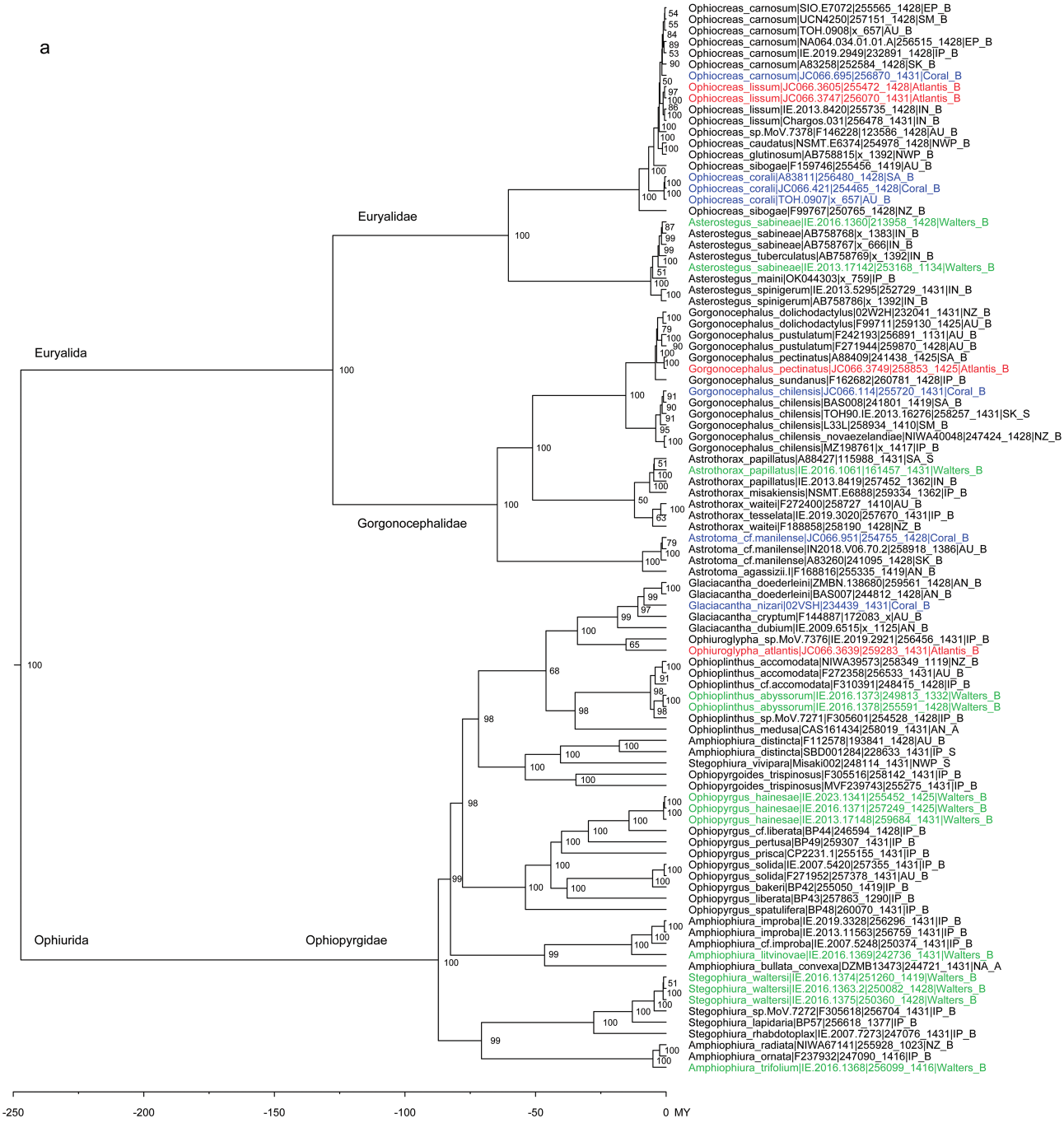

FIGURE 2. Maximum likelihood phylogeny of the ophiuroid samples from JC066 and MD208 expeditions and comparative specimens. The phylogeny was created from 275 kb of nuclear DNA and 1431 bp of mitochondrial COI using RAxML v.8.1.20 47 GTRCAT model with 4 partitions (3 exon codon positions and COI) and converted to a chronogram using TreePLv1.0 and 11 fossil-based calibration points. Green samples are from Walters Shoal, blue samples from Coral, purple from Melville, and red samples from Atlantis Bank. Node labels are RAxML fast-bootstrap values (n=100). The tip labels are composed of the species name, sample code, bp of nuclear (415 genes) and mitochondrial (COI) DNA, geographic and depth distribution. Geographic codes: AN=Antarctic, AR=Arctic, AU=S Australia, EA=E Atlantic, EP=E Pacific, IN=Indian, IP=Indo-Pacific, NA=N Atlantic, NEP=NE Pacific, NWP=NW Pacific, NZ=New Zealand, SA=S Africa, SK=Kerguelen, SM=S America, WA=W Atlantic; depth codes: S=Shelf, B=Bathyal, A=Abyssal. (a) the orders Euryalida and Ophiurida, (b) Ophiacanthida and Ophioscolecida, (c) Amphilepidida and Ophioleucida.

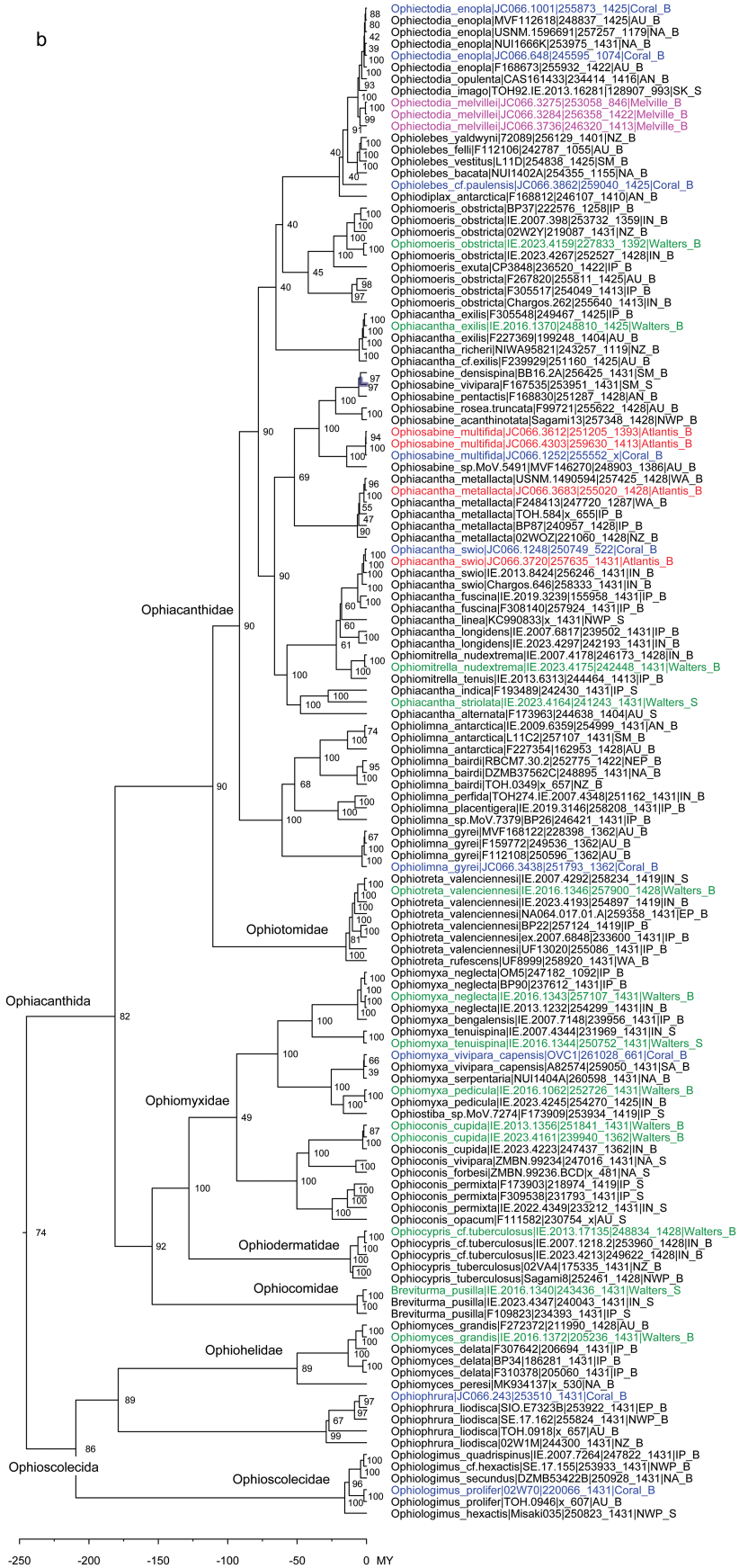

FIGURE 2. (Continued).

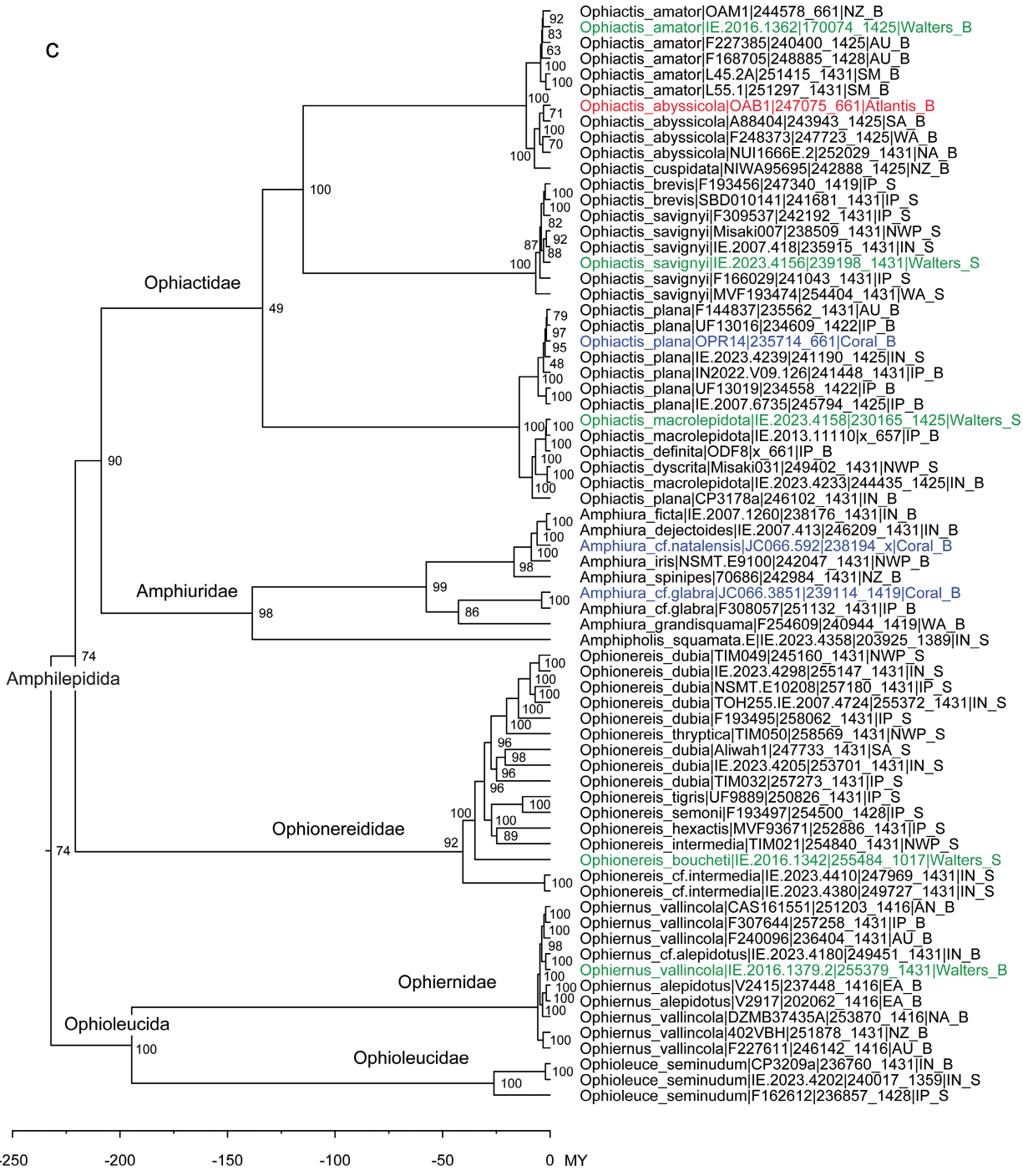

FIGURE 2. (Continued).

COMPARATIVE MATERIAL EXAMINED. ***Asterostegus spinigerum*** (Mortensen, 1933b): MD32/DC132, La Reunion, 20° 51.1′S, 55° 37.05′E, 510 m, 2/9/1982, MNHN IE.2013.8004 (**DNA code=AB758786**). MIRIKY/CP3182, entre Nosy-bé et Banc du Leven, 12° 35.32′S, 48° 17.0202′E to 12° 35.69′S, 48° 16.1598′E, 331–364 m, 26/6/2009, MNHN IE.2013.5295 (**DNA code=IE.2013.5295**).

COMPARATIVE MATERIAL NOT EXAMINED. ***Asterostegus maini*** McKnight, 2003b: Shenhalyongshi/SC009, South China Sea, near Xisha Islands archipelago, 16° 47.79′N, 113° 15.04′E, 602 m, 31/3/2020, identified by Nethupul *et al.* 2022b, CAS IDSSE-EEB-SW0076 (**DNA code=OK044303**). ***Asterostegus sabineae*** Okanishi & Fujita, 2014: ATIMO VATAE/CP3616, Sud Cap Sainte Marie, 26° 17′S, 45° 10′E, 409–473 m, 14/5/2010, holotype, MNHN IE.2018.8012 (**DNA code=AB758768**); identified by Okanishi & Fujita (2013) as *A. maini*, MNHN

IE.2013.8006 (**DNA code=AB758767**). off west coast of Madagascar, 500 m, 2009, identified by Okanishi & Fujita (2013) as *A. tuberculatus* Mortensen, 1933b, NHRM 123461 (**DNA code=AB758769**).

Distribution. W Indian Ocean (409–473 m), Walters Shoal (272–672 m).

Remarks. The COI from these specimens cluster with sequences of *O. sabineae* holotype deposited on NCBI (AB758768). They are also very similar to NCBI sequences (also from the SW Indian Ocean) named as *A. maini* (AB758767) and *A. tuberculatus* (AB758769) from a study by Okanishi & Fujita (2013). *Asterostegus maini* is a West Pacific species, and *A. tuberculatus* was described from NE South Africa (Mortensen 1933b). All three NCBI COI sequences should be regarded as coming from *O. sabineae*, although, without more data from type localities, is unclear whether this species can be distinguished from *A. tuberculatus* from South African.

Sequences of another species, *Astroceras spinigerum* Mortensen, 1933b also cluster with *Asterostegus*, including one of our samples from northern Madagascar (MNHN IE.2013.5295) and another NCBI sequence (AB758786) from off Reunion Island deposited by Okanishi & Fujita (2013). All other *Astroceras* samples form a monophyletic clade sister to *Astromorpha*, *Trichaster* and *Euryale*. On the basis of this evidence, we transfer *A. spinigerum* to *Asterostegus*.

***Ophiocreas corali* sp. nov.**

https://zoobank.org/urn:lsid:zoobank.org:act:24B96A8A-8FCE-4892-9818-190068B361E1
Fig. 3a–d, f–h

TYPE LOCALITY. Coral seamount, 41° 22.333′S, 42° 54.066′E to 41° 23′S, 42° 54.1′E, 730 m.

TYPE MATERIAL.—JC066: stn 4–12, Coral seamount, 41° 22.333′S, 42° 54.066′E to 41° 23′S, 42° 54.1′E, 730 m, 16/11/2011, holotype: 1 (NHMUK 2025.25); paratype: 1 (NHMUK 2025.24) (**DNA code=JC066-421**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiocreas caudatus*** Lyman, 1879: Toudai Motare, Off Katsuura, Japan, 34° 53′N, 140° 32.7′E, 330 m, 4/10/2008, NSMT E6374 (**DNA code=NSMT E6374**). ***Ophiocreas corali*** AND003/xx, 36° 8.47′S, 22° 22.73′E, 958 m, 1/5/2014, SAMC MB-A73811 (**DNA code=A83811**). TN228/J2-382-015, A1 Seamount, Huon, 44° 19.846′S, 146° 53.19′E, 1335 m, 16/12/2008, MV F168741 (**DNA code=TOH_0907**). TN228/J2-393-012, Tasman Fracture Zone, 45° 8.351′S, 145° 59.904′E, 1483 m, 12/1/2009, MV F168737 (**DNA code=TOH_0911**). ***Ophiocreas sibogae*** Koehler, 1904: SS03/2008/101, Great Australian Bight, 35° 3.24′S, 133° 57.384′E, 480 m, 9/3/2008, MV F159746 (**DNA code=F159746**). TAN0308/126, South Norfolk Ridge, 33° 23.41′S, 170° 11.58′E, 469–526 m, 31/5/2003, MV F99763 (**DNA code=AB758818**). TAN0308/133, South Norfolk Ridge, 33° 23.74′S, 170° 13.03′E to 33° 23.4′S, 170° 11.583′E, 465–490 m, 1/6/2003, MV F99767 (**DNA code=F99767**). ***Ophiocreas sp.MoV.7378*** SS02/2007/77, Cascade 1200m 5, 43° 55.406′S, 150° 27.889′E to 43° 55.778′S, 150° 28.352′E, 590–660 m, 10/4/2007, MV F146228 (**DNA code=F146228**).

COMPARATIVE MATERIAL NOT EXAMINED. ***Ophiocreas glutinosum*** Döderlein, 1911: Todai motare, off Katsuura, Chiba Prefecture, Japan, 34° 53′N, 140° 32.07′E, 500 m, 5/3/2009, identified by Okanishi & Fujita (2014), NSMT E6710 (**DNA code=AB758815**).

Diagnosis. Disc covered in thick skin that obscures the tiny (0.2 mm) embedded granules, no lateral oral papillae. Five arms, to 13x the disc diameter, VAPs are small oblong to sausage-shaped plates that are distal to the curved distal corners of the LAP pair, 2 arm spines after the 9th arm segment, inner larger (to 3 mm in length) with a few apical thorns, basal podia protected by a sheath of skin with a circular opening at the apex.

Description. Holotype 17 mm dd, disc petaloid, indented interradially, covered in thick papillate skin that obscure the underlying granules. Granules dense interradially but rarely touch each other, 0.2 mm wide, 16–25 per mm square, spherical to conical with minute thorns; radial shields can be seen as long bar-like raised plates under the skin, widely separate, slightly curved radially, 4.5x longer than wide, range from near the arm sides to ~2/5 dd; ventral disc also covered in thick skin that continues onto the oral/adoral shields and oral plates. Bursal slits vertical in a sunken section of the interradial disc margin. Jaw almost conical and smooth, teeth triangular, tapering to a blunt point, 1.3x as long as wide, no lateral oral papillae.

Arms 220 mm+ long, also covered in thick folded papillate skin with similar embedded granules to the disc, arms becoming wider and more robust after 50 mm from the base, basal dorsal surface forms a groove of skin that protects the underlying gonads, radial ribs of the arms formed from the laterodorsal flange of the vertebrae; LAPs are ventral in position, bar-like, meeting centrally, with a swollen outer section that supports the arm spine

articulations; there are one to several small circular superficial plates (possibly DAPs) between the LAP and the base of the vertebral flange; the VAPs are small oblong to sausage-shaped plates that are distal to the curved distal corners of the LAP pair, about 1/3 the length of the space between LAP pairs (rest is connective tissue); basal podia protected by a sheath of skin with a circular opening at the apex that the podia emerges from; first arm segment without spines, one arm spine for next 8 segments, thereafter 2 spines, the inner (up to 3 mm long) longer than the outer one (up to 2 mm long), with a clavate dark tip, smooth from the covering of skin; with sharp thorns facing proximally near the spine apex when skin is removed.

Paratype (NHMUK 2025.24) 12 mm dd, is broadly similar to the holotype, except the 2nd arm spine typically starts at the 25th segment. Parts of this animal were treated with bleach revealing the underlying plates. The adoral shields are massive and form part of the distal rim of the ventral disc, contiguous for 2/3 their length interradially, separated distally by the small triangular oral shield. The vertebrae have hourglass (streptospondylous) articulation surfaces (Fig. 3f).

Distribution. South Africa (958 m), S Australia (1335–1483 m), Coral Seamount (730 m).

Remarks. These specimens were originally named as *O. sibogae* Koehler, 1904. However, specimens of that species (at least as recorded from Australia and New Zealand) tend to have smaller VAPs, often a small oval plate that does not touch the LAPs, and longer, more thorny arm spines (see Mortensen, 1924, fig. 1–2). Furthermore, *O. sibogae* has been typically collected at shallower depths, the type locality being the Kei Islands, Indonesia, from 204 m. DNA evidence indicates that *O. corali* is distinct from Australian/New Zealand clades of *O. 'sibogae'* that also occur on shallower seafloor than *O. corali*, and that the distribution of *O. corali* extends from South Africa to Southern Australia.

Etymology. Named after Coral Seamount, the type locality.

Ophiocreas carnosum Lyman, 1879

Ophiocreas carnosus Lyman, 1879: 63, pl. 16(435–438).—Lyman, 1882: 281, pl. 31(1–4).—Seid *et al.*, 2025: 162, fig. 62d–f.
Ophiocreas carnosum.—Clark, H.L., 1915: 177.
Ophiocreas japonicus.—McKnight, 2000: 30–32, fig. 11, pl. 10.—Okanishi & Fujita, 2013: 568 [Non *Ophiocreas japonicus* Koehler R, 1907].

STUDY MATERIAL.—JC066: stn 4-37, Coral seamount, 41° 21.7673′S, 42° 54.9067′E to 41° 22.4′S, 42° 54.6′E, 740 m, 20/11/2011: 1 (NHMUK 2025.23) (**DNA code=JC066-695**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiocreas carnosum*** Lyman, 1879: Región de Ñuble, Treguaco, 36° 25.2336′S, 73° 42.16896′W, 624 m, 18/10/2010, UCN 4250 (**DNA code=UCN4250**). AT37-13/AD4923, Costa Rica Parrita Seep, 8° 58.555′N, 84° 37.4298′W, 1097 m, 6/6/2017, identified by Seid *et al.* (2025) as *Ophiocreas carnosus*, SIO E7072 (**DNA code=SIO E7072**). KANADEEP2/PL744_PBT-Q-1, Munida, 23° 5.17′S, 168° 15.048′E, 1093 m, 14/9/2019, MNHN IE.2019.2949 (**DNA code=IE.2019.2949**). Marion Toothfish Survey/T35, between Prince Edward and Marion Island, 46° 44.6′S, 38° 4′E to 46° 43.6′S, 37° 45.4′E, 298 m, 24/4/2001, SAMC MB-A83258 (**DNA code=A83258**). NA064/005, Galapagos Is marine park, 1° 12.825136′N, 91° 5.412714′W, 1154 m, 27/6/2015 (**DNA code=NA064-005-01-01-A**). NA064/034, Galapagos Is marine park, 1° 40.564′N, 91° 41.263′W, 974 m, 28/6/2015 (**DNA code=NA064-034-01-01-A**). TN228/J2-385-005, Z27 Seamount, Huon, 44° 14.715′S, 147° 7.276′E, 1060 m, 21/12/2008, MV F168738 (**DNA code=TOH_0908**).

COMPARATIVE MATERIAL NOT EXAMINED. ***Ophiocreas carnosum*** Lyman, 1879: NZOI/Z9592, 48° 33.06′S, 164° 57.03′E, 940–1180 m, 30/11/1998, identified by McKnight (2000) as *Ophiocreas japonicus*, NIWA 48407. TRIP2494/14, 47° 32.8′S, 177° 49.7′E to 47° 33.1′S, 177° 49.7′E, 867–915 m, 2/9/2007, identified by Okanishi & Fujita (2013) as *Ophiocreas japonicus*, NIWA 49793 (**DNA code=AB758816**).

Distribution. New Caledonia (1093 m), E Pacific (974–1886 m), S America (250–940 m), Marion Is (298 m), S Australia (810–1060 m), New Zealand (867–915 m), Coral Seamount (740 m).

Remarks. The large (19 mm dd) JC066 specimen is covered in thick fleshy skin without any hint of embedded granules or ossicles. DNA evidence indicates that this species occurs around the Southern Ocean, including on Marion Island and Southern Chile which are south of the Subtropical Front and as North as New Caledonia in the SW Pacific and Costa Rica in the East Pacific (Seid *et al.* 2025).

Okanishi & Fujita (2013) submitted a COI sequence to NCBI (AB758816) as *O. japonicus* collected off New Zealand, which appears to be a chimeric sequence, with the first section aligning with our *O. carnosum* sequences and the second half of unknown origin. McKnight (2000) also recorded a specimen of *O. japonicus* from New Zealand. This specimen was described as having thick wrinkled skin and is also likely to be *O. carnosum*.

Ophiocreas lissum (H.L. Clark, 1939)

Fig. 3e

Asteroschema lissum Clark, H.L., 1939: 37–41, fig. 1–3.
Non *Asteroschema cf lissum*.—Nethupul *et al.* 2022b: 198–201, fig. 16–17.

STUDY MATERIAL.—JC066: stn 8-3, Atlantis Bank, 32° 42.658′S, 57° 16.371′E to 32° 42.64′S, 57° 17.58′E, 707 m, 9/12/2011: 1 (NHMUK 2025.27) (**DNA code=JC066-3605**).—JC066: stn 8-22, Atlantis Bank, 32° 42.225′S, 57° 18.02′E to 32° 42.59′S, 57° 17.01′E, 1000 m, 13/12/2011: 1 (NHMUK 2025.26) (**DNA code=JC066-3747**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiocreas lissum*** (H.L. Clark, 1939): Chargos/18, Great Chargos Bank, Eagle Island, 6° 11.27326′S, 71° 19.10177′E, 488 m, 20/10/2022. Chargos/4, Peros Banhos, Ile de Pierre, 5° 18.633′S, 71° 43.447′E, 486–499 m, 16/10/2022 (**DNA code=Chargos.031**). PAMELA-MOZ01/DW1, Glorieuses, 11° 22.756′S, 47° 16.4097′E to 11° 22.749′S, 47° 17.2302′E, 753–824 m, 28/9/2014, MNHN IE.2013.8420 (**DNA code=IE.2013.8420**).

Distribution. Maldives and Chargos (486–797 m), Îles Glorieuses (753–824 m), Atlantis Seamount (707–1000 m).

Remarks. The two JC066 specimens measure 14 mm dd (NHMUK 2025.27) and 10 mm dd (NHMUK 2025.26) with arms at least 13x dd, and purple/brown/pink in colouration. The radial shields are covered in skin but can be seen as white radial markings that extend from the margin to centre of disc. There are tiny ossicles buried in the skin of the dorsal disc and arms, around 25–42 granules per square mm. The lateral arm plates do not extend across the dorsal midline of the first 9 or so segments, leaving a sunken groove of skin that lies on top of the gonads that extend along the arm. But these segments are not transversely expanded. There are 1–2 dental papillae at the tip of each jaw and sometimes a low domed lateral oral papilla to the side of the apex. The first 2 segments have no arm spines, the second 10–12 have one, and after that two. The inner arm spines become much longer and clavate by the 21–24th arm segment. Two Chargos specimens are similar except the larger one (Chargos 18) has 2 arm spines by segment two. The 17 mm dd specimen from Îles Glorieuses (IE.2013.8420) has 6 equal arms and arm spines that start on the 2nd segment. The epidermal granules are difficult to see.

We have identified these specimens as *Asteroschema lissum* on the basis of the small granules embedded in the thick skin covering the disc and arms, as well as the type location (Maldives, 797 m). But there are some differences from the unique 7.5 mm holotype, which has 2 arm spines on segment 2, 3-5 ill-defined lateral oral papillae on the sides of the jaw, and radial shields that don't extend to the centre of the disc. But this specimen is small and dry, and it is unclear if these differences are significant, given the morphological variation shown by our material.

Our phylogeny shows this species embedded within an *Ophiocreas* clade that includes *O. sibogae* Koehler, 1904, *O. carnosum* Lyman, 1879, and *O. caudatus* Lyman, 1879. We temporarily transfer this species to *Ophiocreas* pending a *Asteroschema-Ophiocreas* revision. The type of *Ophiocreas* (*O. oedipus* Lyman, 1879) is in a separate clade to *O. lissum*. Furthermore, our phylogeny shows that the type species of *Asteroschema*, *A. oligactes* (Pallas, 1788), is a long-branched taxa that is sister to all other species and is likely to be monotypic (at least at the subgenus level). The traditional character that distinguished *Asteroschema* and *Ophiocreas*, disc granules present in the former and absent in the latter, does not hold. Several species of *Ophiocreas* can have some small granules in the skin (e.g., *O. lissum*, and *O. corali*) and other species (*O. gilolense* Döderlein, 1927 and *O. spinulosum* (Lyman, 1883)) have small tubercles on the dorsal arm surface.

The specimens identified as *A.* cf. *lissum* by Nethupul *et al.* (2022b) cluster separately from our material on our phylogeny and likely represent a separate species. Three other species of *Asteroschema* recorded from the Indian Ocean, *A. flosulum* Alcock, 1893, *A.* cf. *arenosa* (see Baker *et al.* 2018), and *A.* cf. *igloo* Baker, 1980 (see O'Hara 2024), differ in having prominent globular granules on their dorsal surface.

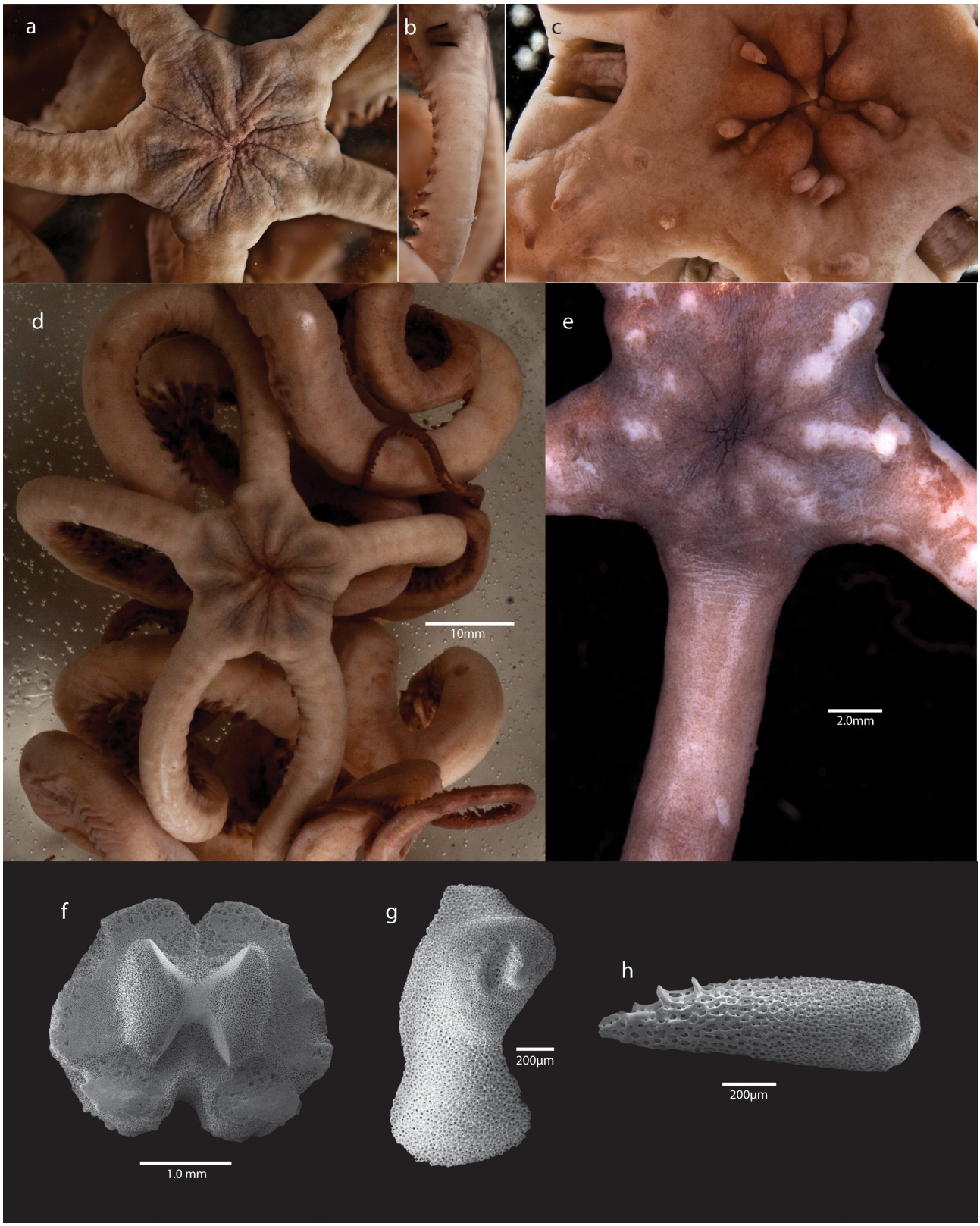

FIGURE 3. (a–c) *Ophiocreas corali* **sp. nov.** holotype NHMUK 2025.25 (a) dorsal disc, (b) arm, lateral view, (c) ventral disc, (d) dorsal view. (e) *Ophiocreas lissum* NHMUK 2025.26, dorsal view. (f–h) *Ophiocreas corali* **sp. nov.** paratype NHMUK 2025.24 (f) vertebra distal view, (g) lateral arm plate, (h) inner arm spine.

Family Gorgonocephalidae

***Astrothorax papillatus* (H.L. Clark, 1923)**

Astrothamnus papillatus Clark, H.L., 1923: 316–318, pl. 20(5–6).
Astrothorax papillata.—Mortensen, 1933b: 279–280, fig. 15.—Clark, A.M., 1951: 199.—Clark, A.M. & Courtman-Stock, 1976: 132.
Astrothorax waitei.—Baker, 1980: 30–32 (in part).
Astrothorax papillatus.—Olbers *et al.* 2019: 67–68, fig. 44–45.

STUDY MATERIAL.—MD208: stn CP4882, Walters shoal, Pentes, 33° 16.67′S, 43° 50.4899′E to 33° 16.03′S, 43° 49.84′E, 371–399 m, 2/5/2017: 1 (MNHN IE.2023.4160).—MD208: stn CP4902, Walters Shoal, Pentes, 33° 7.95′S, 44° 1.4001′E to 33° 8.44′S, 44° 1.7901′E, 700–711 m, 7/5/2017: 1 (MNHN IE.2016.1061) (**DNA code=IE.2016.1061**).

COMPARATIVE MATERIAL EXAMINED. ***Astrothorax misakiensis*** Döderlein, 1911: NW of Iejima Osl., Okinawa Pref. Japan, 26° 55.793′N, 127° 39.676′E, 650 m, 22/7/2007, NSMT E6888 (**DNA code=NSMT E6888**). ***Astrothorax papillatus*** (H.L. Clark, 1923): CCH009/D00749, 36° 33.32′S, 20° 36.79′E, 172 m, 2/5/2016, SAMC MB-A88427 (**DNA code=A88427**). PAMELA-MOZ01/CP2, Betsiboka, 15° 21.727′S, 45° 57.6521′E to 15° 21.515′S, 45° 55.9884′E, 719–1019 m, 8/10/2014, MNHN IE.2013.8419 (**DNA code=IE.2013.8419**). ***Astrothorax tesselata*** Mortensen, 1933c: KANADEEP2/PL743_PBT-I-6, Stylaster, 23° 36.815′S, 167° 43.935′E, 548 m, 12/9/2019, MNHN IE.2019.3020 (**DNA code=IE.2019.3020**). ***Astrothorax waitei*** (Benham, 1909): IN2018_V06/132, Andy's Hill, 44° 11.652′S, 146° 58.8′E to 44° 11.748′S, 146° 58.56′E, 727–877 m, 10/12/2018, MV F272400 (**DNA code=F272400**). TAN1206/95, Site SM3aa Clark Seamount, Southern Kermadec Ridge, 36° 27.072′S, 177° 50.388′E to 177° 50.382′N, 36° 26.928′W, 840–872 m, 24/4/2012, MV F188858 (**DNA code=F188858**).

Distribution. Madagascar (719–1019 m), S Africa (43–650 m), Walters Shoal (371–711 m).

Remarks. The three western Indian Ocean DNA samples (from South Africa, Madagascar and Walters Shoal) cluster separately from Southern Australian and New Zealand *A. waitei* samples and are closer to *A. misakiensis* from Japan. Consequently, we reject the synonymy of Baker (1980) and resurrect *A. papillatus* as a separate allopatric species to *A. waitei*. The largest of the Walters Shoal animals (IE.2016.1061) was 11 mm dd, an orange-red colour when alive, and was found wrapped around a cup coral.

Astrotoma* cf. *manilense
Fig. 4a–h

Astrotoma drachi.—McKnight, 2000: 68, fig. 33, pl. 32.—Okanishi & Fujita, 2013: 569.—Jossart *et al.*, 2019: 622–631 [Non *Astrotoma drachi* Guille A, 1979].
Astrotoma manilense.—O'Hara & Harding, 2014: 135–136.

STUDY MATERIAL.—JC066: stn 4-4, Coral seamount, 41° 22.8371′S, 42° 50.6024′E to 41° 22.85′S, 42° 51.99′E, 1186 m, 13/11/2011: 1 (NHMUK 2025.28) (**DNA code=JC066-951**).

COMPARATIVE MATERIAL EXAMINED. ***Astrotoma agassizii.I*** US AMLR-09/103-77, South Orkney Islands, 62° 35.23′S, 53° 46.37′W to 62° 33.8′S, 53° 49.19′W, 745–711 m, 5/3/2009, MV F168816 (**DNA codes=TOH_1054, F168816**). ***Astrotoma* cf. *manilense*** IN2018_V06/070, Flat Matsuyker, 44° 9.438′S, 146° 10.26′E to 44° 9.474′S, 146° 9′E, 1218–1223 m, 3/12/2018, MV F315387 (**DNA code=IN2018_V06_70_2**). Marion Toothfish Survey/T35, between Prince Edward and Marion Island, 46° 44.6′S, 38° 4′E to 46° 43.6′S, 37° 45.4′E, 298 m, 24/4/2001, SAMC MB-A83260 (**DNA code=A83260**).

Distribution. S America (201–309 m), Kerguelen (20–838 m), S Australia (391–1223 m), New Zealand (1036–1402 m), Antarctic (1559–1680 m), Coral Seamount (1186 m).

Remarks. COI for the 15 mm dd NHMUK 2025.28 sample clusters within the *Astrotoma agassizii* clade II of Jossart *et al.* (2019), within which they also included specimens from New Zealand identified by McKnight (2000) as *A. drachi*. O'Hara & Harding (2014) had previously placed New Zealand and Southern Australian specimens into *A. manilense* Döderlein, 1927 a name that has priority over *A. drachi*. However, without DNA from specimens around their type localities off the Philippines, it is unclear whether either of these poorly known tropical species

are really the same as Jossart *et al.*'s clade II that occurs across southern subpolar and temperate regions (but not Antarctica). In the interim, we use the unofficial name *Astrotoma* cf. *manilense* for this clade, which is genetically distinct from all other *Astrotoma agassizii* clades (Jossart *et al.*, 2019).

We isolated some internal arm ossicles for SEM. The vertebrae are streptospondylous (Fig. 4d). The LAPs (Fig. 4e–f) are ventrolateral in position, meeting mid-radially, enlarged abradially to support arm spines. There are 2–3 simple hollow arm spine articulations and 1–2 cylindrical pedicels that support the most ventral hooklets. A small oval VAP occurs distal to the LAP pair, not contiguous with succeeding LAPs. A row of quadrangular hooklet base plates (Fig. 4g) extend across the lateral and dorsal arm surfaces, with 5–8 ovoid-shaped hooklet pedicels on each plate. These are more regularly placed than in *A. agassizii* (see Turner *et al.* 2021, fig. 17f). Arm spines 2–3, flat, rising to 1–2 apices, often thorny at tip (Fig. 4h).

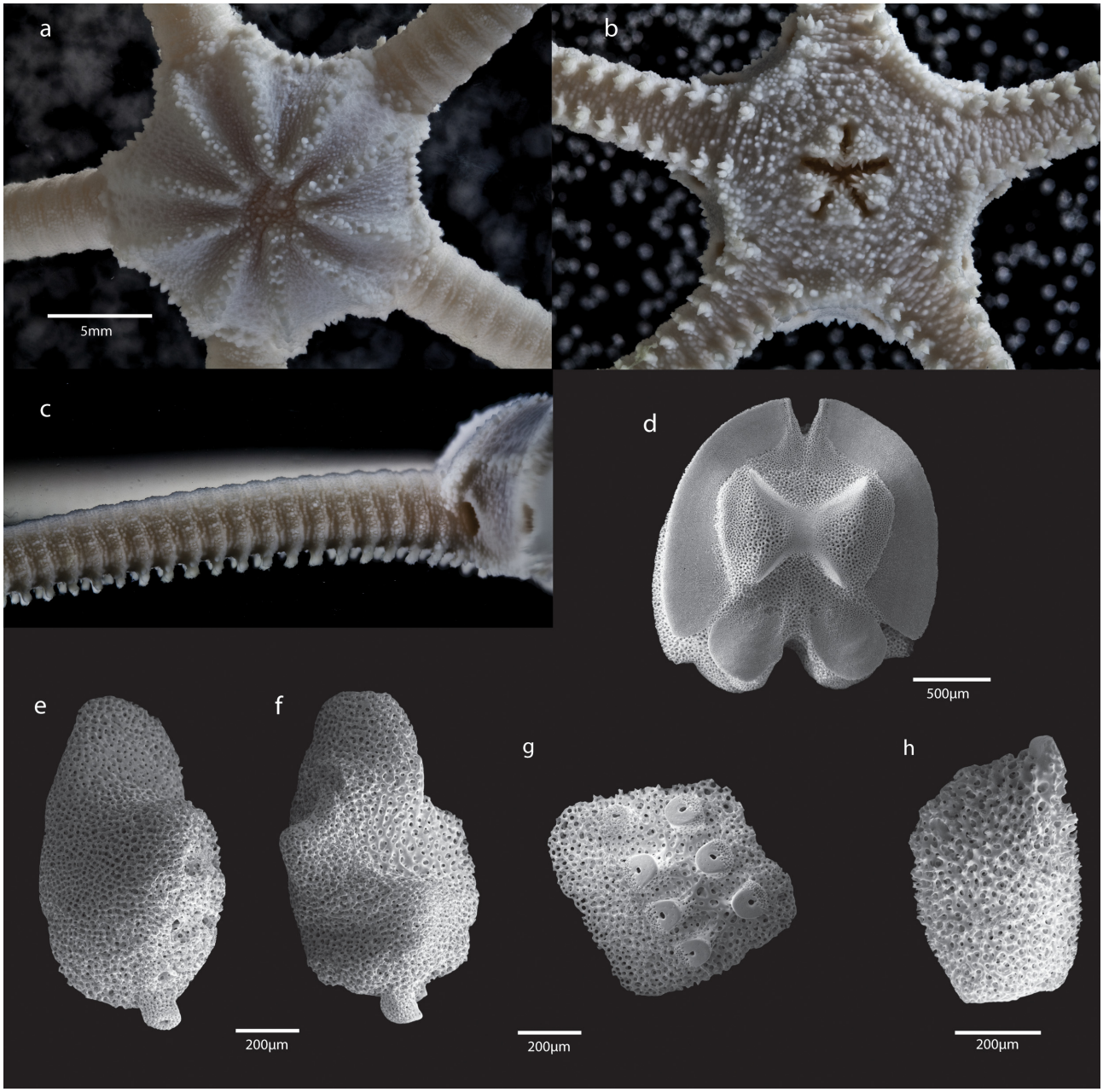

FIGURE 4. *Astrotoma* cf. *manilense* NHMUK 2025.28 (a) dorsal disc, (b) ventral disc, (c) arm base, lateral view, (d) vertebra distal view, (e) lateral arm plate from mid arm ventral view, the upper flatter section is orientated towards the ventral mid arm, the cylindrical boss supports the ventralmost hooklet (f) lateral arm plate interior view, (g) lateral arm hooklet plate, (h) arm spine.

Gorgonocephalus chilensis (Philippi, 1858)

Fig. 5d–n

Astrophyton chilense Philippi, 1858: 268.

Gorgonocephalus chilensis.—Lyman, 1882: 265.—Döderlein, 1927: 30–31.—Mortensen, 1936: 240–241.—Mortensen, 1952: 11–12.—Bernasconi & d'Agostino, 1977: 68–70, pl. 1(1–2).—Manso, 2010: 3, fig. 1a–c.—Olbers *et al.* 2019: 68–70, fig. 46–47.

STUDY MATERIAL.—JC066: stn 4-2, Coral seamount, 41° 20.708′S, 42° 55.292′E to 41° 20.99′S, 42° 55.12′E, 1300 m, 12/11/2011: 1 (NHMUK 2025.30) (**DNA code=JC066-114**); 1 (NHMUK 2025.29).

COMPARATIVE MATERIAL EXAMINED. ***Gorgonocephalus chilensis*** (Philippi, 1858): PROTEKER 2/CH06, Baie de l'Oiseau, 48° 40.759′S, 69° 7.42′E to 48° 40.792′S, 69° 7.361′E, 93–105 m, 27/11/2013, MNHN IE.2013.16276 (**DNA code=TOH90-IE.2013.16276**). Talud Continental 1/33, Mar del Plata Submarine Canyon, 37° 58.698′S, 55° 11.899′W, 308 m, 17/8/2012, CNP-INV (**DNA code=L33L**). TAN0803/53, Seamount 5 Eltanin, Macquarie Ridge. New Zealand EEZ, 51° 2.82′S, 162° 1.13′E to 51° 3.15′S, 162° 1.48′E, 398–489 m, 5/4/2008, NIWA 40048 (**DNA code=NIWA40048**).

COMPARATIVE MATERIAL NOT EXAMINED. ***Gorgonocephalus chilensis*** (Philippi, 1858): AV17-18/H116, Tristan da Cunha EEZ, Yakhont Sea Mount WEST, 39° 18.9′S, 8° 1.92′W, 327 m, 4/1/2018, BAS (**DNA code=BAS008**). Shenhalyongshi/SY013, Zhongsha Island complex seamount, 13° 58.68′N, 114° 52.09′E, 1550 m, 25/9/2020, identified by Nethupul *et al.* 2022a as *Gorgonocephalus chilensis novaezelandiae*, CAS IDSSE-EEB-SW0007 (**DNA code=MZ198761**).

Distribution. S America (6–1398 m), Kerguelen (60–943 m), Antarctic (40–1615 m), Tristan da Cunha (310–335 m), Coral Seamount (1300 m).

Remarks. The Coral Seamount specimens (40 and 55 mm dd) have tall tubercles on the disc, especially along the raised section over the radial shields, the dorsal arm surface is granular but with few tubercles, there are 3, rarely 4, arm spines, and girdle hooklets start after the 2nd arm branching. The DNA sequence of NHMUK 2025.30 is very similar to other *G. chilensis* specimens across the Southern Ocean, from South America to the Balleny seamounts. But it does not occur around the continent of Antarctica. The New Zealand-South China Sea specimens form a separate COI clade distinct from those of the Southern Ocean and are currently recognised as *G. chilensis novaezelandiae* Mortensen, 1924 (see Nethupul *et al.* 2022a).

Gorgonocephalus pectinatus Mortensen, 1933

Fig. 5a–c, o–t

Gorgonocephalus pectinatus Mortensen, 1933b: 281–285, fig. 16–17, pl. 18(1–2).

Gorgonocephalus pectinatus.—Clark, A.M. & Courtman-Stock, 1976: 133, fig. 86, 88.

Gorgonocephalus pustulatum.—Baker, 1980: 54–56, fig. 18b, 20, 30 (in part).—Olbers *et al.* 2019: 70–72, fig. 48–49 [Non *Gorgonocephalus pustulatum* (Clark H L, 1916)].

?*Gorgonocephalus pustulatum*.—Calero & Ramil, 2023: 67–68, figs 10–11.

STUDY MATERIAL.—JC066: stn 8-22, Atlantis Bank, 32° 42.225′S, 57° 18.02′E to 32° 42.59′S, 57° 17.01′E, 1000 m, 13/12/2011: 1 (NHMUK 2025.31) (**DNA code=JC066-3749**).

COMPARATIVE MATERIAL EXAMINED. ***Gorgonocephalus dolichodactylus*** Döderlein, 1911: TAN0308/90, Lord Howe plateau, 34° 12.17′S, 163° 21.36′E to 34° 12.617′S, 163° 16.783′E, 1090–1117 m, 26/5/2003, MV F99711 (**DNA code=F99711**). TAN1206/3, Site SL1a, slope, Bay of Plenty, 37° 10.158′S, 176° 39.522′E to 176° 39.762′N, 37° 9.96′W, 681–710 m, 15/4/2012, MV F188859 (**DNA code=02W2H**). ***Gorgonocephalus pectinatus*** Mortensen, 1933b: AFR246/A28872, 35° 8′S, 23° 9′E, 451 m, 11/9/2008, SAMC MB-A88409 (**DNA code=A88409**). ***Gorgonocephalus pustulatum*** (H.L. Clark, 1916): IN2018_V06/178, St Helens Seamount, 41° 13.584′S, 148° 45.72′E to 41° 13.536′S, 148° 45.72′E, 727–755 m, 16/12/2018, MV F271944 (**DNA code=F271944**). TN228/RD1, 2008, MV F242193 (**DNA code=F242193**). ***Gorgonocephalus sundanus*** Döderlein, 1927: SS05/2007/107, Northwestern Australia, Leveque L27 transect, 14° 49.026′S, 121° 27.552′E to 14° 48.533′S, 121° 29.567′E, 400.5-378.2 m, 27/6/2007, MV F162682 (**DNA code=F162682**).

Distribution. South Africa (78–580 m), ?E Atlantic (902–908 m), Atlantis Seamount (1000 m).

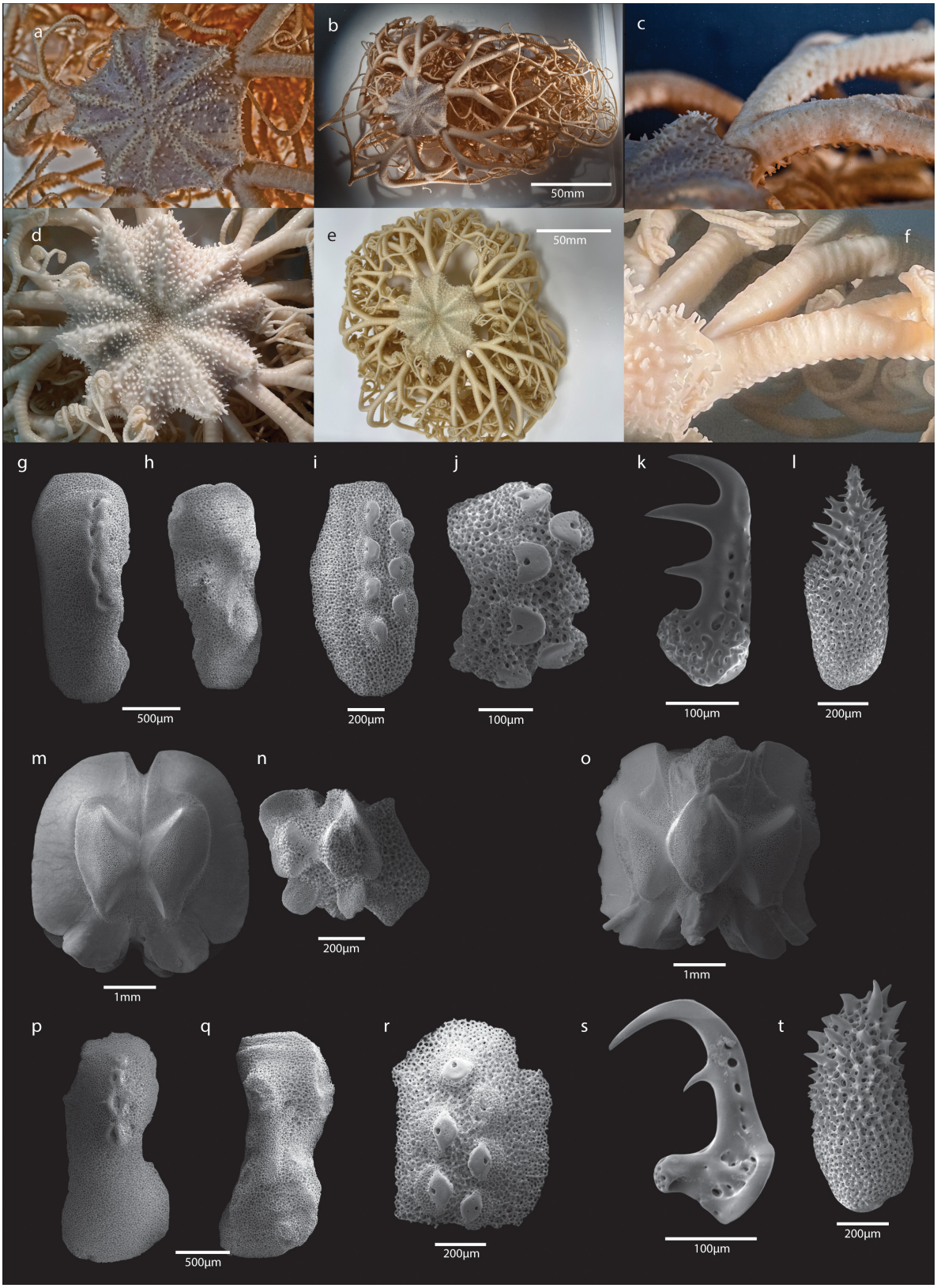

FIGURE 5. (a–c) *Gorgonocephalus pectinatus* NHMUK 2025.31 (a) dorsal disc, (b) dorsal (whole animal), (c) lateral arm; (d–n) *Gorgonocephalus chilensis* NHMUK 2025.30 (d) dorsal disc, (e) dorsal (whole animal), (f) lateral arm, (g) lateral arm plate, exterior view, (h) lateral arm plate, interior view, (i) lateral arm hooklet plate, (j) dorsal arm hooklet plate, (k) distal arm spine, (l) proximal arm spine; (m) vertebra of proximal segment, distal view, (n) vertebra of distal arm segment, distal view; (o–t) *Gorgonocephalus pectinatus* NHMUK 2025.31 (o) vertebra, distal view, last segment before branching, (p) lateral arm plate, exterior view), (q) lateral arm plate, interior view, (r) arm hooklet plate, (s) hooklet, (t) proximal arm spine.

Remarks. *Gorgonocephalus* forms 2 clades on our phylogeny, the subantarctic-boreal *G. chilensis-eucnemis* and the temperate-tropical *G. pustulatum-dolichodactylus-sundanus* clades. Both *Gorgonocephalus* clades occur on the SW Indian Ocean Ridge. Two specimens found on the southern Coral seamount fall into the *G. chilensis* clade and another from the more northern Atlantis Seamount into the *G. pustulatum* clade. They differ in the placement of girdle hooklets (which continue across the dorsal arm by the first arm branching in *G. pustulatum* and start at the 2nd fork in *G. chilensis*) and the greater tuberculation along the arms in *chilensis* (Baker 1980).

Within the *G. pustulatum* clade, the Atlantis specimen (38 mm dd) clusters with a specimen from South Africa (A88409), and both specimens are polyphyletic with respect to Australian-New Zealand *G. pustulatum* specimens (being separated by specimens of *G. dolichodactylus*, which lack a secondary tooth on girdle hooklets). Consequently, like for *Astrothorax*, we reject the trans-Indian Ocean synonymy of Baker (1980), recognise the SW Indian Ocean population as a separate allopatric species and resurrect the name *G. pectinatus* for this species. Calero & Ramil (2023) report a specimen of *G. pustulatum* from off Guinea-Bissau in the tropical eastern Atlantic. No DNA sequences are available; and it is unclear whether this represents a new lineage or a range extension of *G. pectinatus*.

The LAPs (Fig. 5g, p) differ slightly between *G. chilensis* and *G. pectinatus*, the muscle opening on the arm spine articulations is more slit-like in *G. chilensis* (similar to the Arctic *G. eucnemis*, see Martynov 2010a, pl. 1(2)) and the rim is less elevated than in *G. pectinatus*. More data from other species is required to see if this is diagnostic for the two clades discussed above. The hooklet base plates on the lateral side of the arm (Fig. 5i, r) are largely similar, both species having the hemispherical or rhomboid-shaped hooklet articulation surface and asymmetrical tubercle foramen that allow the hooklets to function as pedicellariae (Turner *et al.* 2021).

Family Ophiopyrgidae

Ophiopyrgus hainesae sp. nov.

https://zoobank.org/urn:lsid:zoobank.org:act:89E7073A-F21A-4E68-84DC-0E3935D8F19F
Fig. 6–7

TYPE LOCALITY. Walters shoal, Plaine Sud, 33° 48.82′S, 44° 5.9699′E to 33° 51.8′S, 44° 4.72′E, 1539–1615 m.

TYPE MATERIAL.—MD208: stn CP4913, Walters shoal, Plaine Sud, 33° 48.82′S, 44° 5.9699′E to 33° 51.8′S, 44° 4.72′E, 1539–1615 m, 11/5/2017, holotype: 1 (MNHN IE.2023.4001); paratypes: 4 (MNHN IE.2016.1341) (**DNA code=IE.2023.1341**); paratypes: 184 (MNHN IE.2016.1376).

OTHER STUDY MATERIAL.—MD208: stn CP4914, Walters shoal, Plaine Sud, 33° 51.1′S, 44° 4.8999′E to 33° 54.73′S, 44° 3.2199′E, 1598–1714 m, 11/5/2017: 194 (MNHN IE.2016.1371) (**DNA code=IE.2016.1371**).—MD208: stn CP4917, Walters Shoal, Plaine Nord-Ouest, 32° 54.9′S, 43° 23.8499′E to 32° 55.18′S, 43° 27.0001′E, 1375–1296 m, 13/5/2017: 49 (MNHN IE.2013.17148) (**DNA code=IE.2013.17148**).—MD208: stn CP4918, Walters Shoal, Plaine Nord-Ouest, 32° 57.8′S, 43° 24.7′E to 32° 57.86′S, 43° 27.0499′E, 1356–1295 m, 14/5/2017: 7 (MNHN IE.2013.17156).—MD208: stn CP4920, Walters Shoal, Plaine Nord-Ouest, 32° 52.01′S, 43° 26.6899′E to 32° 51.99′S, 43° 30.9599′E, 1293–1210 m, 14/5/2017: 1 (MNHN IE.2013.17162).

COMPARATIVE MATERIAL EXAMINED. ***Amphiophiura bullata*** (Lyman, 1878): ME 79- 1/554, Brasilian Basin, 26° 34.7′S, 35° 12.7896′W to 26° 34.87′S, 35° 12.7896′W, 4485 m, 22/7/2009, DZMB-HH 13473 (**DNA code=DZMB13473**). ***Ophiopyrgoides trispinosus*** (Koehler, 1904): IN2017_V03/128, Coral Sea CMR, 23° 37.872′S, 154° 39.582′E to 23° 39.54′S, 154° 38.628′E, 1770–1761 m, 13/6/2017, MV F239743 (**DNA code=MVF239743**). IN2021_V04/5, Christmas Island SE, 10° 34.22′S, 105° 41.376′E to 10° 33.791′S, 105° 41.6358′E, 643–997 m, 6/7/2021, identified by O'Hara (2024b), MV F305516 (**DNA code=F305516**). ***Ophiopyrgus bakeri*** (McKnight, 2003a): BIOPAPUA/CP3653, Ouest de la Nouvelle Hanovre, 2° 13′S, 150° 23′E, 680–700 m, 28/8/2010, MNHN IE.2023.4071 (**DNA code=BP42**). ***Ophiopyrgus* cf.*liberata*** BIOPAPUA/CP3672, Nord de Rabaul, 4° 4′S, 151° 50′E, 702–724 m, 24/9/2010, MNHN IE.2007.2873 (**DNA code=BP44**). ***Ophiopyrgus latro*** (Koehler, 1904): Siboga/251, Kapulauan Kai (Kei Islands), 5° 28.4′S, 132° 0.2′E, 204 m, 8/12/1899, holotype, ZMA E2403. BIOPAPUA/DW3732, Au large des îles et récifs Lancasay, 8° 16′S, 150° 29′E, 340–358 m, 9/10/2010, MNHN IE.2023.4072 (**DNA code=BP49**). ***Ophiopyrgus liberata*** (Koehler, 1904): BIOPAPUA/CP3653, Ouest de la Nouvelle Hanovre, 2° 13′S, 150° 23′E, 680–700 m, 28/8/2010, MNHN IE.2007.2820 (**DNA code=BP43**). ***Ophiopyrgus prisca***

(Koehler, 1904): SALOMON 2/CP2231, NW Choiseul, 6° 25′S, 156° 21′E, 1083–1100 m, 29/10/2004, MNHN (**DNA code=CP2231-1**). ***Ophiopyrgus solida*** (Lyman, 1878): Challenger/192, Ki (Kei) Is, 5° 42′S, 132° 25′E, 239 m, 26/9/1874, holotype, BMNH 1882.12.23.44. EBISCO/CP2628, S Lansdowne, 21° 6′S, 160° 48.0002′E, 672–678 m, 21/10/2005, MNHN IE.2007.5420 (**DNA code=IE.2007.5420**). IN2018_V06/094, Baseline_14, 44° 6.588′S, 146° 12.6′E to 44° 6.144′S, 146° 11.82′E, 965–941 m, 6/12/2018, MV F271952 (**DNA code=F271952**). ***Ophiopyrgus spatulifera*** (Koehler, 1922a): BIOPAPUA/CP3686, Monts sous-marins, sud de Manus Is., 3° 16′S, 147° 18′E, 964–1025 m, 28/9/2010, MNHN IE.2007.2817 (**DNA code=BP48**).

Diagnosis. Dome-shaped disc with a tubercle-like centrodorsal plate, 5 primary plates, 2 dorsal and 1 ventral scale in each interradius, and D-shaped radial shields; all plates delimited by V-shaped furrows. Spiniform arm comb and genital papillae present. Oral shields 2x as long as wide with a narrower proximal lobe and squarish distal margin. Oral frame (including oral plates and adoral shields) sunken. Short tapering arms (to 4x dd) with contiguous DAPs, VAPs separate after first few proximal plates, 2 arm spines.

Description. Holotype 12 mm dd, disc dome-shaped, covered in a few large disc scales including a centrodorsal with a round pedicel and a dome-like tubercle, five hexagonal longer than wide primary plates with a peaked central point and a low ridge that extends from this peak to the centrodorsal, two plates in each interradius, a pentagonal proximal one and a tumid hexagonal distal one that forms the lateral edge to the disc, D-shaped radial shields with a straight edge radially, 2x as long as wide, all plates contiguous with a v-shaped furrow along their suture lines; ventral disc area covered by a single large square to rhomboid scale; arm comb comprises a series of separate spiniform papillae that articulate with a series of bosses on the abradial genital plate; these papillae continue along the bursal slit ventrally to half the disc radius, becoming square or slightly pointed, a few opposing papillae arising from a LAP occur under the dorsalmost end of the main arm comb series.

Oral shields teat-shaped with a squarish distal section, with straight to concave sides, and a narrower convex proximal lobe, slightly longer than wide; adoral shields slender, 4x as long as wide, meeting interradially and extending distally to 4/5 of the proximal lobe of the oral shield; exterior section of the oral plates parallelogram-shaped, 4x as long as wide, contiguous interradially and extending to the end of the jaw slit; 8 conical oral papillae along each jaw side, interleaving with papillae on the opposing jaw; 2–3 abradial and 3–4 adradial tentacle scales around the 2nd oral tentacle pore, the distal adradial one enlarged.

Arms to 4x dd in length, rounded-triangular in cross section with a much narrower dorsal than ventral surface; first DAPs wider than long, elliptical, succeeding plates become smaller, kite-shaped to droplet-shaped, and separated by the 7th DAP; LAPs 2x as high as long, with a rounded dorsal angle, straight lateral sides and bent underneath to form the ventral surface; 1st VAP appears triangular in shape, with a bluntly rounded proximal edge and a straight to slightly convex distal edge, next plates 2x as wide as long, sometimes a small bare patch occurs between basal VAPs, becoming smaller and more separated by the 5th VAP, VAPs notably striated from the 2nd plate; 2 arm spines, 1/2 the length of a segment, situated lower down on the ventral section of the LAP, with the upper one occurring at the widest point of the arm and the lowest near the tentacle pore, the upper one developing a hook-like apex distally; 4–5 abradial and 2–3 adradial tentacle scales around basal arm pores, the distalmost adradial one much longer than wide, extending to midway of the abradial series, but which is not plate like nor confluent with the VAP (cf *Ophiuroglypha*), by the 6th VAP there are 3 abradial and 1 rim-like adradial scale, distally only one abradial scale persists. Colour (live) pinkish-grey disc and light pink arms (Fig. 6f), (preserved) pale.

Paratype variations. The smallest specimen (6 mm dd) has a disc that is almost as high as wide, with tumid primaries and proximal interradial plates, and a comparatively large centrodorsal tubercle, the other specimens (to 11 mm dd) can be brown or white, and generally have a less prominent ridge between the centrodorsal and primary plates.

Paratype ossicles (MNHN IE.2016.1376). Vertebrae zygospondylous (Fig. 7a–e) with prominent muscle fossae and podia basins, a long narrow zygosphene, and a prominent ventral groove; LAPs with dense stereom and simple arm spine-articulations with small circular pores for muscle attachment and nerve (Fig. 7f–g); dental plate 2.5 times as long as wide, with straight sides and 3 articulations for the teeth (Fig. 7k); centrodorsal tubercle with prominent perforations surrounded by small thorns (Fig. 7l); 1st VAP more complex that it appears from the external surface, with an extended rounded margin proximally and a squarish margin distally that sit underneath neighbouring plates (Fig. 7o); abradial genital plate nodulated along the dorsal edge, the nodules functioning as the base of the arm comb papillae (Fig. 7r); tentacle scales and arm spines with minute longitudinal grooves towards their apex (Fig. 7s–t).

Distribution. Walters Shoal (1210–1714 m).

Remarks. We have provisionally placed this new species in the genus *Ophiopyrgus* due to characters shared with the type species *O. wyvillethomsoni* Lyman, 1878, including the raised centrodorsal plate, the few disc plates composed of the centrodorsal, primaries, radial shields and a series of 3 interradial plates extending from the primaries around the lateral side of the disc to the teat-shaped oral shield, the sunken oral frame, large basal tentacle pores with numerous scales, and the presence of a spiniform arm comb. However, *O. wyvillethomsoni* also has paedomorphic arms that are short, slender and rapidly tapering, with reduced VAPs and DAPs, and only a single arm spine, which makes comparison problematic. Unfortunately, we lack DNA sequences from *O. wyvillethomsoni* or the similar *O. alcocki* Koehler, 1897 (without a centrodorsal tubercle) and *O. turritus* Litvinova, 1984 (with a very tall centrodorsal tubercle), and future research could separate these species into a separate lineage.

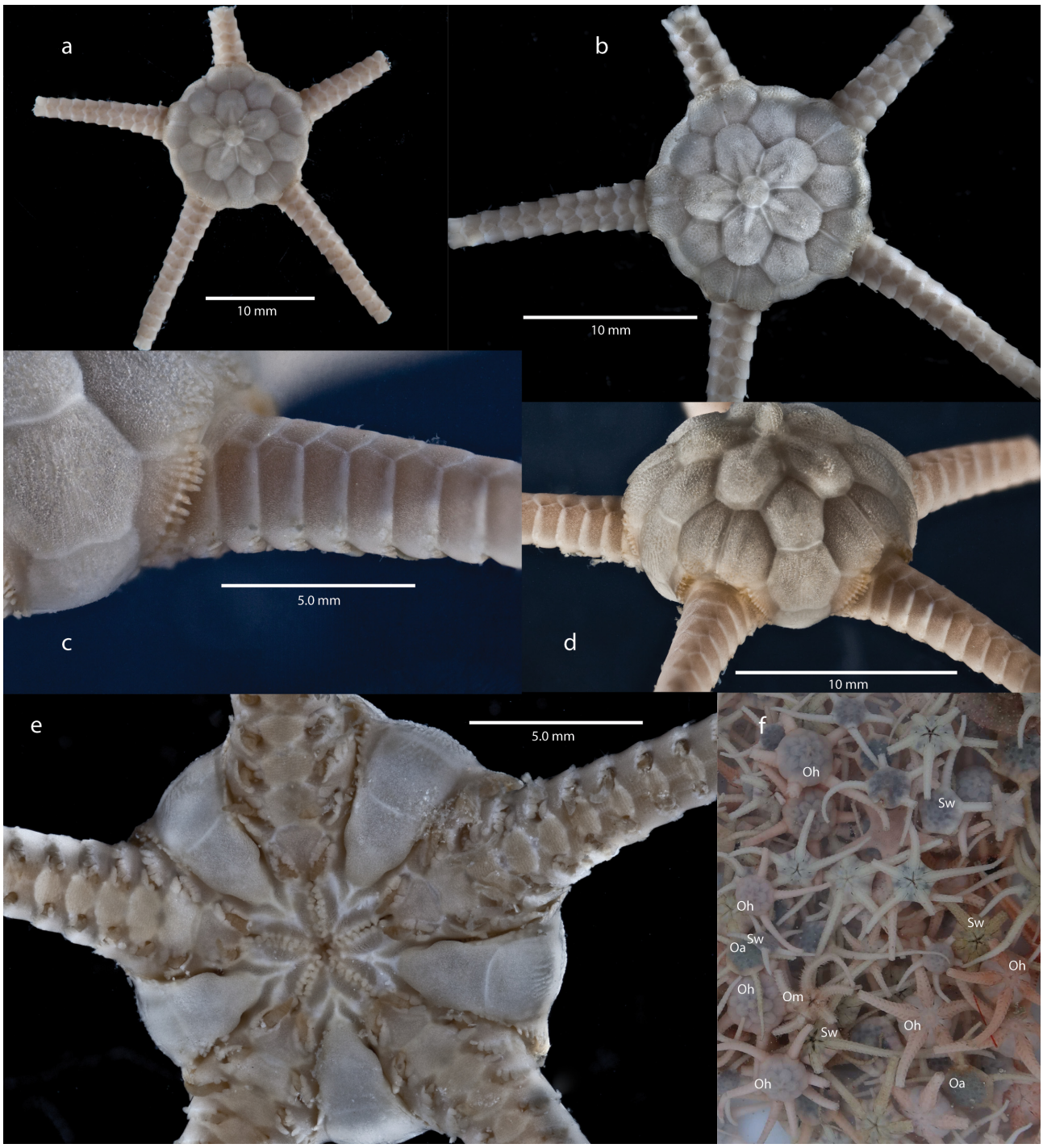

FIGURE 6. *Ophiopyrgus hainesae* **sp. nov.** holotype MNHN IE.2023.4001 (a) dorsal view, (b) dorsal view enlarged, (c) arm base, lateral view, (d) dorsolateral view, (e) ventral view. (f) Ship-board photo of MD208 catch CP4914, with the species: Oh = *Ophiopyrgus hainesae,* Oa = *Ophioplinthus abyssorum*, Om = *Ophiomyces delata*, Sw = *Stegophiura waltersi*.

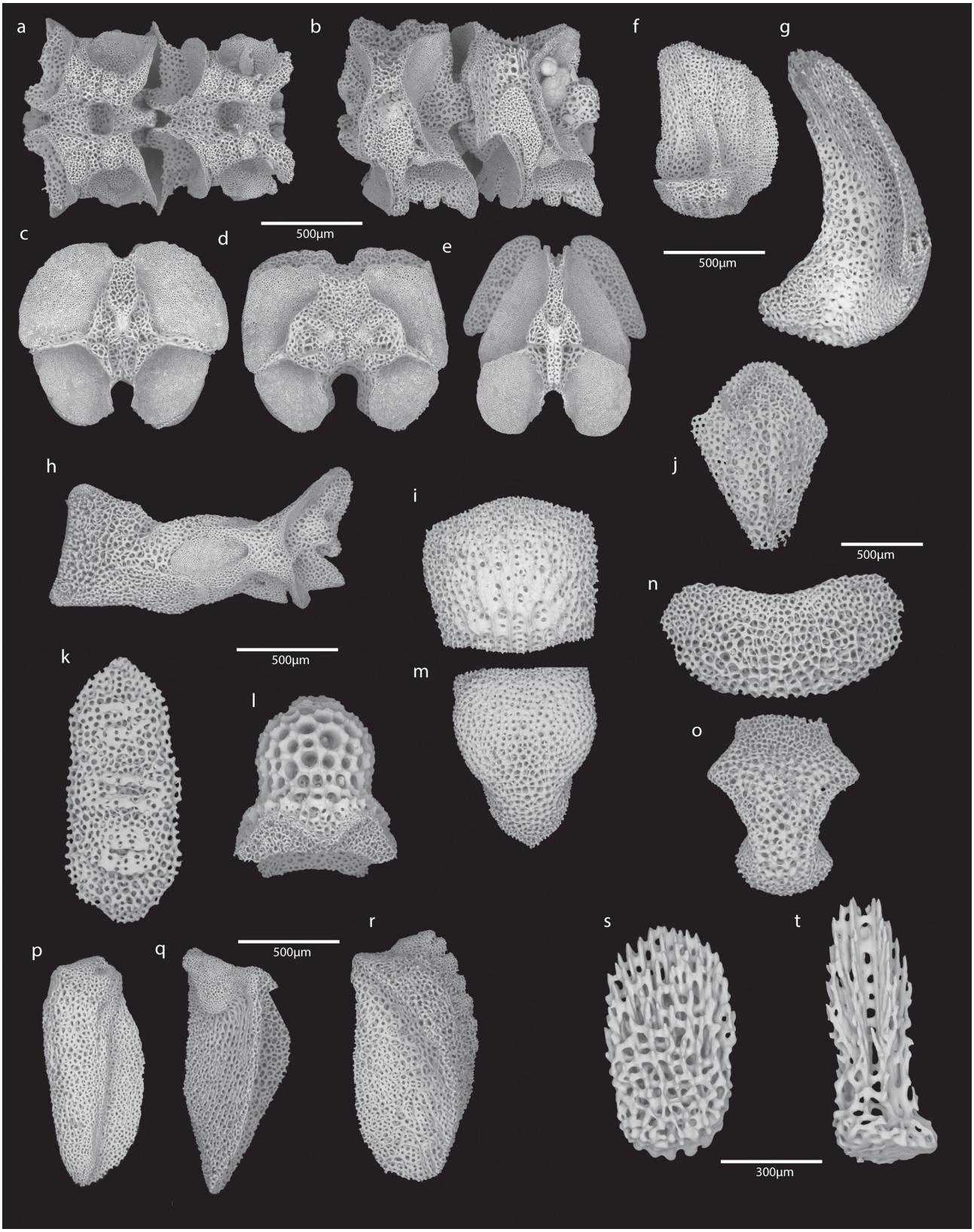

FIGURE 7. *Ophiopyrgus hainesae* **sp. nov.** paratype MNHN IE.2016.1376 (a) paired vertebrae, dorsal view, (b) paired vertebrae, lateral view, (c) vertebra, proximal view, (d) vertebra, distal view, (e) basal vertebra, proximal view, (f) lateral arm plate, ventral view, (g) lateral arm plate, lateral view, (h) oral plate, (i) ventral disc plate, (j) dorsal arm plate, (k) dental plate, (l) centrodorsal plate and tubercle, (m) oral shield, (n) second ventral arm plate, (o) first ventral arm plate, (p–q) opposite faces of adradial genital plate, (r) abradial plate with arm comb articulations on the upper right, (s) tentacle scale, (t) arm spine.

In our phylogeny, *O. hainesae* is in the same clade as several other species of '*Amphiophiura*', which are polyphyletic with respect to the type species of *Amphiophiura*, *A. bullata*. These include the species *A. bakeri* McKnight, 2003, *A. liberata* (Koehler, 1904), *A. latro* (Koehler, 1904), *A. prisca* (Koehler, 1904), *A. solida* (Lyman, 1878) and *A. spatulifera* Koehler, 1922a. All of these species share many of the characters of the genus *Ophiopyrgus* as outlined above and we transfer them all to his new genus.

Ophiopyrgus bakeri has a domed disc, with the same number of disc plates, but differs from our new species in lacking a centrodorsal tubercle and typically has 3 arm spines near the arm base. *Ophiopyrgus liberata* also has no centrodorsal tubercle but has very deep furrows between the dorsal disc plates, 4 arm spines, and oral shields that are 2x as long as wide with a square shaped distal section. Re-examination of the holotype of *O. latro* shows it has spinous or very granular disc scales that are deeply separated from neighbouring scales except for a ridge that connects the primary plates to each other and to the proximal interradial plates. This is different from the type description, which does not mention any spines or granules on the plates. In fact, Koehler (1930: 230) explicitly notes that the disc plates on *O. latro* have no trace of granules. Furthermore, there are only 2, basally 3 arm spines (not 4 as mentioned in the type description). However, the *O. latro* holotype is very similar to type description and figures of *Amphiophiura pertusa* Koehler, 1930, which consequently we consider a synonym. *Ophiopyrgus prisca* has a relatively flat disc, with slightly raised circular areas in the centre of the centrodorsal and primary plates. It also differs from *O. hainesae* in appearing to lack an arm comb (although there can be some small spines on the basal LAP that may function as a comb), having 2–3 transverse series of ventral disc plates, and three long arm spines, the uppermost being almost as long as a segment. *Ophiopyrgus solida* is similar to *O. bakeri* except it has two rhomboidal ventral interradial plates that are parallel to each other, 2x as long as wide, and separated by a deep groove. Koehler (1930) distinguished his new species *'Stegophiura' turgida* from *O. solida* on the basis of its shorter radial comb papillae, larger decalcified areas between basal VAPs and the lack of furrows between the disc plates. However, having compared the holotype of *O. solida* with the type photos of *S. turgida* we find no substantial difference in these characters, and also consider them to be synonyms. All the Challenger (Lyman 1882), Siboga (Koehler 1904) and Mortensen (Koehler 1930) material of *O. solida* and *O. turgida* were collected near each other, around the Kei Islands Indonesia in 196–348 m. Finally, *O. spatulifera* differs in having only two large interradial plates (only the proximal one is visible dorsally, the other is lateral), although it can have 1–2 smaller scales at the distolateral corners of the oral shield. The dorsal comb papillae are paddle-shaped, expanded near their apex.

There is also an undescribed species from Solomon Islands and Papua New Guinea (e.g., sample BP44) which is very similar to *O. hainesae* in having a tall tubercle on the centrodorsal, and similar patterns of disc plates, arm plates and arm spines. They differ from *O. hainesae* in having much deeper furrows around the disc plates (so that the plates appear like low tables), no connecting ridges, a raised central section on the lateral and ventral interradial disc plates, and concave margins to the distal section of the oral shields.

Other species referred to *Ophiopyrgus* do not seem related. *Ophiopyrgus biocalae* Vadon, 1991 has opposing rim-like tentacle scales similar to the type species of *Ophiomastus*, *O. tegulitus* Lyman, 1878. *Ophiopyrgus saccharatus* Studer, 1882, *O. depressus* Koehler, 1904, *O. trispinosus* Koehler, 1904 were placed by H.L. Clark in a separate genus *Ophiopyroides*, characterised by the very large oral shield that takes up most of the ventral disc surface. Our DNA evidence supports this decision, as our samples of *O. trispinosus* are divergent from both the *hainesae* and *bullata* clades.

Etymology. Named after Maggie Haines, who sequenced many of the ophiuroids for this project.

***Amphiophiura litvinovae* sp. nov.**

https://zoobank.org/urn:lsid:zoobank.org:act:DCC22461-646D-4B44-8A10-2EF066BBC8B4

Fig. 13a–h

TYPE LOCALITY. Walters shoal, Plaine Sud, 33° 56.85′S, 44° 0.07′E to 33° 58.8′S, 43° 55.3999′E, 1865–2058 m.

TYPE MATERIAL.—MD208: stn CP4915, Walters shoal, Plaine Sud, 33° 56.85′S, 44° 0.07′E to 33° 58.8′S, 43° 55.3999′E, 1865–2058 m, 12/5/2017: holotype (MNHN IE.2016.1369) (**DNA code=IE.2016.1369**).

COMPARATIVE MATERIAL EXAMINED. ***Amphiophiura* cf. *improba*** EBISCO/CP2652, SE Fairway, 21° 24′S, 162° 37.0001′E, 1019–1147 m, 23/10/2005, MNHN IE.2007.5248 (**DNA code=IE.2007.5248**).

Amphiophiura improba (Koehler, 1904): Siboga/226, Banda Sea, between Lucipara and Mai Islands, Mid channel between the Lacipara and Schildpad Islands, 5° 26.7′S, 127° 36.5′E, 1595 m, 11/11/1899, 2 syntypes, ZMA E2400. KANACONO/CP4751, N Mont Antigonia, 23° 19.3′S, 167° 56.77′E to 23° 21.42′S, 167° 57.4603′E, 946–998 m, 25/8/2016, MNHN IE.2013.11563 (**DNA code=IE.2013.11563**). KANADEEP2/CP5101, Stylaster, 23° 24′S, 168° 31.1′E, 1190–1194 m, 30/9/2019, MNHN IE.2019.3328 (**DNA code=IE.2019.3328**).

Diagnosis. Disc with large (1/6x dd) contiguous radial shields and smaller disc scales, primary plates not obvious. Spiniform to conical arm comb papillae. Ventral interradial area covered by a large oral shield and some smaller marginal scales. Arm carinate in cross-section. 3 sharply pointed arm spines on the ventral half of the LAP, to 2/5 segment in length.

Description. Holotype 6.5 mm dd, disc pentagonal, fully contiguous radials, 1/6x dd, disc plates small, no evident primaries, an enlarged marginal plate with small ones on either side, several transverse rows of disc plates laterally, arm comb conical to spiniform, genital papillae smaller with a sharp point, continuing along bursal slit 1/2 way to the oral shield; oral shield large, taking up the majority of the ventral disc surface, egg-shaped, tapered proximally into an acute point, not incised or trefoil, adoral shields small and narrow, 3.5x as long as wide, only extending along the proximal end of the oral shields, meet interradially; exposed section of oral plate larger than adorals, roughly rhomboid, contiguous for 1/2 their length interradially; bluntly pointed teeth, a little longer than wide, inner oral papillae similar but smaller, distal papillae becoming low and wide, all occurring on the oral plate; 2nd oral tentacle pore elliptical, adjacent to 1st VAP, with 2 adradial and 3 abradial rounded scales not enclosing pore.

Arms triangular in cross section, narrower dorsally than ventrally, first and 2nd DAP 2.5x as wide as long, succeeding plates longer, basal DAPs are rhomboid, then succeeding plates becoming ovoid, becoming separated by the 11th DAP; first VAP roughly triangular, tapering proximally, with a concave distal border and rounded proximodistal corners, a little wider than long; 2nd VAP rhomboid, also with a central concave margin to distal border, contiguous, subsequent plates more hourglass-shaped, with incised lateral sides, acute angle proximally and convex distal margin, separate from the 7th VAP; 3 arm spines on lower half of arms, 2/5 segment in length, terminate in a blunt to sharp point. Basal tentacle pores large elongate and open, with 4 semicircular to spatulate abradial scales and 2–3 smaller ones adradially (on VAP), by 6th VAP 2–3 abradial and one rim-like adradial scales, reduced to a single abradial scale by the 11th VAP. Colour (preserved) brown.

Ossicles. LAPs (Fig. 13d–e) quadrangular in lateral view, with a bent lower section that meets the opposite plate on the ventral midline, external stereom regularly perforated; arm spine articulations along the distal edge, slightly raised circular holes; VAPs (Fig. 13f) with low transverse ridges that are separated by rows of perforations; vertebrae (Fig. 13h) zygospondylous, with elongate zygosphene and reduced zygocondyles on distal face.

Distribution. Walters Shoal (1865–2058 m).

Remarks. This sample is morphologically similar to specimens of *Amphiophiura improba* (Koehler, 1904) from the Indo-Pacific region. Both have similar dorsal disc plating and carinate arms. The holotype of *A. improba* differs in having only 2 arm spines and smaller disc scales that are not observable from the ventral side. There is another undescribed species (*A.* cf. *improba*) from the SW Pacific with one large unbroken marginal ventral disc plate (rather than a number of smaller plates) and up to 4 arm spines. The DNA sequence of the Walters Shoal specimen is divergent from both these species, justifying the description of a new species.

Etymology. Named after Nina Litvinova, former ophiuroid specialist at the P.P. Shirshov Institute of Oceanography, Moscow, who worked extensively on deep-sea ophiuroids and *Amphiophiura* in particular.

Amphiophiura trifolium Hertz, 1927

Amphiophiura trifolium Hertz, 1927b: 78–79, fig. 3, pl. 6(14–15).—Clark, H.L., 1939: 108–109.—Clark, A.M., 1974: 476.—Clark, A.M. & Courtman-Stock, 1976: 187.—Guille & Vadon, 1986: 181.—Olbers *et al.* 2019: 94–95, fig. 72–73.

STUDY MATERIAL.—MD208: stn CP4915, Walters shoal, Plaine Sud, 33° 56.85′S, 44° 0.07′E to 33° 58.8′S, 43° 55.3999′E, 1865–2058 m, 12/5/2017: 4 (MNHN IE.2016.1368) (**DNA code=IE.2016.1368**).

COMPARATIVE MATERIAL EXAMINED. ***Amphiophiura ornata*** (Lyman, 1878): Challenger/216, 2° 56′N, 134° 11′E, 3720 m, 16/2/1875, holotype, NHMUK 1882.12.23.411. IN2017_V03/101, off Moreton Bay, 26° 56.748′S, 153° 56.7′E to 26° 58.272′S, 153° 57.072′E, 2520–2576 m, 9/6/2017, MV F237932 (**DNA**

code=F237932). ***Amphiophiura radiata*** (Lyman, 1878): Challenger/205, west of Luzon Is, 16° 42′N, 119° 22′E, 1953 m, 13/11/1874, holotype, NHMUK 1882.12.23.422. TAN0205/21, Ngatorirangi Seamount, 33° 42.082′S, 179° 51.294′E to 33° 42.469′S, 179° 50.751′E, 1627–1330 m, 14/4/2002, NIWA 67141 (**DNA code=NIWA67141**).

Description. Disc to 8 mm dd, radial shields 1/5 dd, contiguous over much of their length, large marginal interradial plate, other disc covered in numerous small overlapping scales, primaries larger; arm comb comprised of small spatulate papillae becoming a row of close set square genital papillae ventrally, some opposing spines on basal DAPs, DAPs ovoid at first become separate by 4th plate, with long tapering proximal borders and a convex distal border; tiny then 3 tiny arm spines, 10th segment long, middle one becoming hooked distally; oral shields trefoil as wide as long, numerous small ventral disc scales, oral frame a little sunken.

Distribution. W Indian Ocean (949–2727 m), Walters Shoal (1865–2058 m).

Remarks. These specimens conform to the description of *A. trifolium* known from the western Indian Ocean. However, they are also very similar to *A. radiata* (Lyman, 1878) from the Indo-Pacific and more research is required to test whether these species should remain distinct. *Amphiophiura ornata* (Lyman, 1878) is also related, differing in having contiguous DAPs. *Amphiophiura trifolium*, *A. radiata* and *A. ornata* form a distinct clade on our phylogeny but more work is required to determine morphological characters that could define this clade as a new genus.

Glaciacantha nizari **sp. nov.**

https://zoobank.org/urn:lsid:zoobank.org:act:150E1956-19A7-46B3-851C-D87E28FDCFBE

Fig. 8a–m

TYPE LOCALITY. Coral seamount, 41° 21.7673′S, 42° 54.9067′E to 41° 22.4′S, 42° 54.6′E, 740 m

TYPE MATERIAL.—JC066: stn 4-37, Coral seamount, 41° 21.7673′S, 42° 54.9067′E to 41° 22.4′S, 42° 54.6′E, 740 m, 20/11/2011, holotype: 1 (NHMUK 2025.62); paratype: 1 (NHMUK 2025.61); paratype: 1 (MV F321040) (**DNA code=02VSH**).

COMPARATIVE MATERIAL EXAMINED. ***Glaciacantha cryptum*** (McKnight, 2003a): SS02/2007/37, Mini Matt SSW, 44° 14.654′S, 146° 9.899′E to 44° 14.95′S, 146° 9.656′E, 1120–1380 m, 5/4/2007, MV F144887 (**DNA code=F144887**). ***Glaciacantha doederleini*** (Hertz, 1927): PS77/235-3, 65° 32.83′S, 61° 37.29′W, 300 m, 2/3/2011, BAS (**DNA code=BAS007**). SOMUB/73-BT-4, King Haakon VII Sea, 65° 12′S, 2° 38.76′E, 1210 m, 29/3/2019, ZMBN 138680 (**DNA code=ZMBN 138680**). ***Glaciacantha dubium*** (Koehler, 1901): CEAMARC/48EV194, Eastern Antarctica, 66° 56.366′S, 144° 41.148′E to 66° 56.322′S, 144° 37.245′E, 325–409 m, 29/12/2007, MNHN IE.2009.6515 (**DNA code=2009.6515**). ***Ophiocten banzarei*** Madsen, 1967: BANZARE/41, off Enderby Land, 65° 48′S, 53° 16′E, 193 m, 7 paratypes, SAM K1303. BANZARE/42, off Enderby Land, 65° 50′S, 54° 23′E, 220 m, 3 paratypes, SAM K1304.

Diagnosis. Disc with thickened rounded scales and triangular radial shields (1/6x dd), lacking disc granules or spines, and lacking arm comb papillae and genital granules. Oral shields 2x as wide as long. Arms with contiguous DAPs, separate VAPs with convex distal margins and a small point proximally, and 4 slender pointed arm spines to 1.5x as long as a segment, with the ventralmost one becoming hook-like distally.

Description. Holotype 6 mm dd, disc pentagonal, covered in round disc plates of various sizes, centrodorsal round and prominent, primary plates not as notable, 6 scales between centrodorsal and interradial margin, scales with fine perforations, covered in a thin epithelium with tiny ossicles in the centre of the disc; radial shields 1/6 dd, rounded triangular, a little longer than wide, divergent proximally, just separated distally, 5 marginal interradial scales between radial shields, centre one a little larger than the others; disc higher than arms but without comb. Ventral disc surface covered by 4–5 transverse rows of small scales, no genital papillae. Oral shield 2x as wide as long, pentagonal, with an obtuse angle proximally, straight distal edge and short lateral edges; adoral shields bar-like, 4x as long as wide, slightly separated interradially; visible portion of the oral plates thicker than adoral shields, meeting proximally separated distally by the 1st VAP. Spiniform teeth, 3x as long as wide, ventral tooth and infradental oral papillae pointed but smaller, 2x as long as wide, inner lateral oral papillae squarish and close together, distal one 2x as wide as long; 2nd oral tentacle pore opening outside of slit, small with 3 adradial and 3 abradial rounded scales that do not fully close the pore.

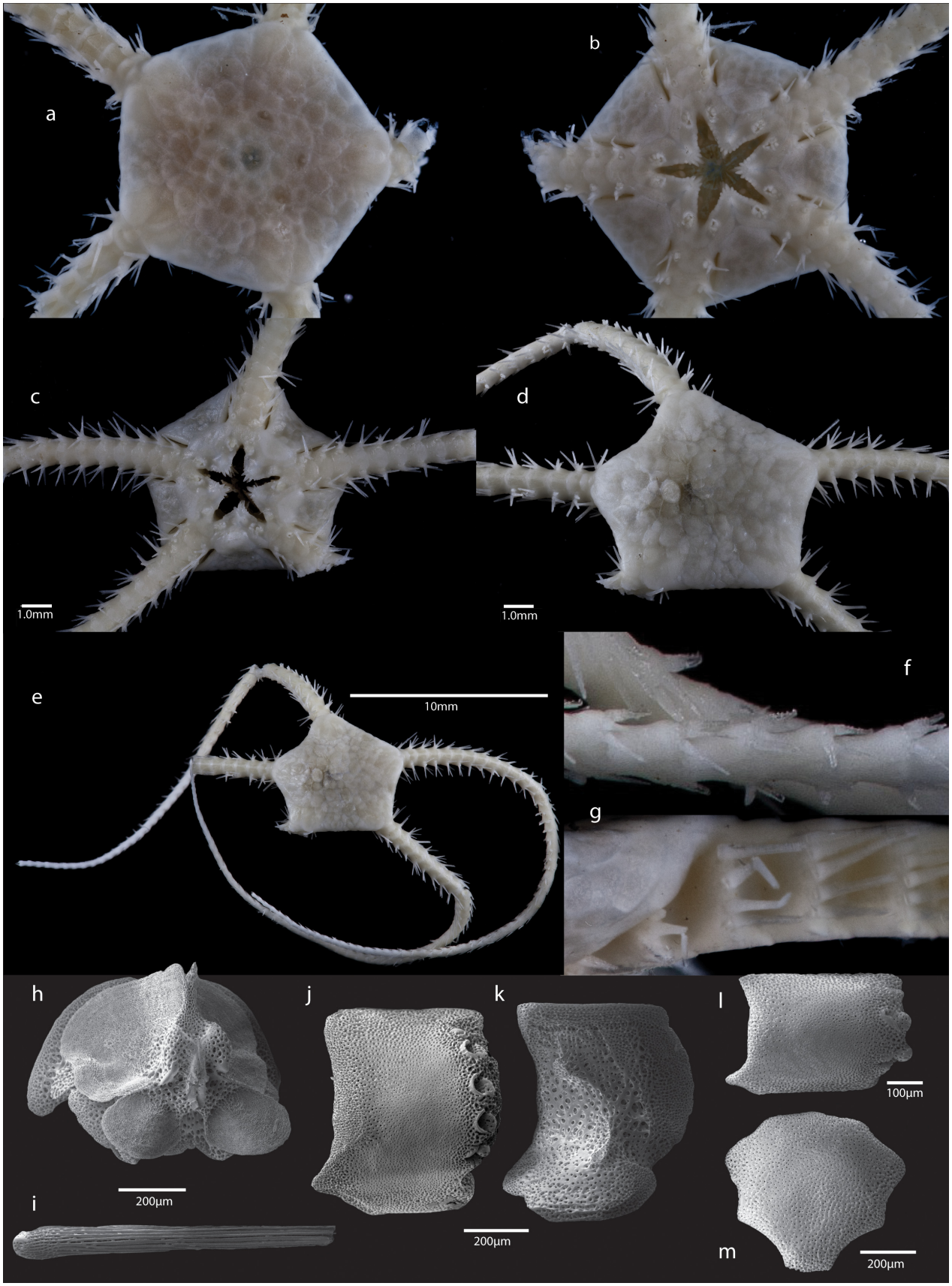

FIGURE 8. *Glaciacantha nizari* **sp. nov.** holotype NHMUK 2025.62 (a) dorsal view, (b) ventral view, (g) lateral arm base; paratype MV F321040 (c) ventral view, (d) dorsal view, (e) whole animal, (f) distal arm segments showing hooked dorsal arm spines; paratype MV F321040 (h) vertebra distal view, (i) arm spine (broken at tip), (j) proximal lateral arm plate exterior view, (k) proximal lateral arm plate interior view, (l) distal lateral arm plate exterior view, (m) ventral arm plate.

Arms 4.5x dd; DAPs rhomboidal, as wide as long, widest distally, with distal margin slightly convex, contiguous, becoming long triangular plates distally, 2.5x as long as wide, just contiguous, but separate near the arm tip; LAPs with a raised flange that bears the arm spines; 1st VAP elliptical to fan-shaped, wider than long, with a convex distal margin and straight lateroproximal sides meeting in a small furrow near the end of the jaw slit; 2nd VAP just wider than long, roughly oval, with a convex distal margin and tapered lateroproximal sides; succeeding plates almost semicircular but produced into a small point proximally, by the middle of the arm the plates are broadly oblong, 2x as wide as long, all VAPs separate, but the separation distance becoming progressively greater down the arm; arm spines slender with a sharp tip, 2 on first segment, 3 on 2nd, to 5 on next segments, upper spine longest to 1.5x segment in length, lower ones almost a segment in length; 4 then 3 spines distally, to 3/4 a segment in length, lower spine becomes hook like with a curved tip and ventrally directed thorns by the middle of the arm; tentacle pores small, one oval scale on the lateral arm plate, 1/4 the length of the VAP, opposed by 1–2 rim-like scales around the basal pores, becoming longer and more slender in the middle of the arm, 2x as long as wide and 1/2 the length of the associated VAP. Colour (preserved) dirty white.

Paratype variations. MV F321040 is a similar size and shape to the holotype, with more concave interradial disc margins; to 6 teeth in an irregular vertical series. NHMUK 2025.61 is 5 mm dd. Internal ossicles obtained from paratype MV F321040. LAPs (Fig. 8j–k) quadrangular in lateral view, higher than long, with a bent ventral section that meets the opposing plate on the ventral midline; stereom dense except around the arm spine articulations. Arm spine articulations spaced regularly in a row near the distal LAP border, upper 3 have a raised rim in an asymmetrically circular or spiral shape that do not meet dorsally; lower 2 articulations are sunken into the stereom; distal LAPs (Fig. 8l) 2x longer than high. Vertebrae (Fig. 8h) zygospondylous with a small zygosphene and wing like zygocondyles.

Distribution. Coral seamount (740 m).

Remarks. O'Hara *et al.* (2018) resurrected the genus *Glaciacantha* Fell, 1961 for two *Ophiocten*-like species *G. dubium* (Koehler, 1901) and *G. doederleini* (Hertz, 1927) that occur in the Ophioprygidae, having hook-like lower distal arm spines, thickened disc plates, disc granules or spines, and lacking an arm comb and genital papillae. In addition, our DNA data indicates *Ophiocten cryptum* McKnight, 2003a is also a member of this clade. Although it lacks disc granules or spines, it does have thickened disc plates, hook-like distal lower arm spines, and no arm comb or genital papillae. *Ophiocten banzarei* Madsen, 1967 is also very similar, with a similar disc and arms to *G. cryptum* and no arm comb or genital papillae, although we could not confirm the presence of hooked distal arm spines on the broken paratypes we have examined. Nevertheless, we consider both *O. cryptum* and *O. banzarei* are better placed in *Glaciacantha*. DNA evidence also supports the inclusion of *O. cryptum* within *Glaciacantha* (Fig. 2a).

The new species is most similar to *G. cryptum* in lacking disc granules and spines. It differs mainly in the shape of the oral shield, which is almost as long as wide, with a produced acute angle proximally. *Glaciacantha dubium* has a series of small spines that surround the larger disc plates, and up to 10 arm spines. *Glaciacantha doederleini* has larger conical spines on irregular bases that cover the disc.

Etymology. Named after Nishath Mohamed Nizar who photographed many of the specimens for this paper.

Ophioplinthus abyssorum (Lyman, 1883)

Fig. 9a–k

Ophioglypha abyssorum Lyman, 1883: 238, pl. 3(25–27).
Homalophiura abyssorum.—Clark, H.L., 1915: 326.—Clark, H.L., 1939: 112–113.—Clark, H.L., 1941: 92.—Litvinova, 1975: 199.
Ophiurolepis abyssorum.—Hertz, 1927b: 93–94, pl. 7(13).
Homalophiura aff abyssorum.—Vadon & Guille, 1984: 596, pl. 2(1–2).
Homophiura abyssorum.—Paterson, 1985: 138, fig. 52.—Guille & Vadon, 1986: 169.
Ophioplinthus abyssorum.—Martynov & Litvinova, 2008: 88, fig. 6b.
?*Ophiurolepis mordax*.—Guille & Vadon, 1986: 184–185, pl. 1(1–2).

STUDY MATERIAL.—MD208: stn CP4913, Walters shoal, Plaine Sud, 33° 48.82′S, 44° 5.9699′E to 33° 51.8′S, 44° 4.72′E, 1539–1615 m, 11/5/2017: 2 (MNHN IE.2016.1378) (**DNA code=IE.2016.1378**).—MD208: stn CP4914, Walters shoal, Plaine Sud, 33° 51.1′S, 44° 4.8999′E to 33° 54.73′S, 44° 3.2199′E, 1598–1714 m, 11/5/2017: 1 (MNHN IE.20234002); 21 (MNHN IE.2016.1373) (**DNA code=IE.2016.1373**).

COMPARATIVE MATERIAL EXAMINED. ***Ophioplinthus accomodata*** (Koehler, 1922b): IN2018_V06/169, Flat area south of Brians, 44° 14.364′S, 147° 17.58′E to 44° 13.938′S, 147° 18.12′E, 1443–1422 m, 14/12/2018, MV F272358 (**DNA code=F272358**). TAN0803/17, Seamount 1 Spastic Spider, Macquarie Ridge. New Zealand EEZ, 48° 32.93′S, 164° 57.75′E to 48° 32.66′S, 164° 58.04′E, 1318–1327 m, 30/3/2008, NIWA 39573 (**DNA code=NIWA39573**). ***Ophioplinthus* cf. *accomodata***: IN2022_V09/071, Gascoyne Marine Park. Site:024, 20° 49.689′S, 111° 36.2038′E to 20° 51.295′S, 111° 35.522′E, 1990–2057 m, 4/12/2022, MV F310391 (**DNA code=F310391**). ***Ophioplinthus inflata*** (Koehler, 1897): off Colombo, 6° 29′N, 79° 34′E, 1110 m, holotype, ZSI 5190/7. ***Ophioplinthus medusa*** Lyman, 1878: PS61 ANT-XIX/4 (ANDEEP)/138-4, 62° 57.8′S, 27° 52.14′W to 62° 57.77′S, 27° 51.1′W, 4544–4545 m, 16/3/2002, CASIZ 161434 (**DNA code=CAS161434**). ***Ophioplinthus* sp.MoV.7271** IN2021_V04/28, Karma Seamount, 12° 49.551′S, 107° 2.7912′E to 12° 50.03′S, 107° 3.6′E, 2760–2850 m, 11/7/2021, identified by O'Hara (2024b), MV F305601 (**DNA code=F305601**).

Description. Disc 7 to 11 mm dd, arms 1.5 to 2 times dd, relatively longer on smallest specimens, pentagonal, rounded edges, dorsal side (Fig. 9a) with prominent round centrodorsal and separated primary plates at mid-radius, some secondary larger plates radially and interradially, 2–3 rows of smaller scales between centrodorsal and primary plates, large marginal plate laterally, radial shields 1/6 dd, just touching or separate radially; hydroid tracks meander across the disc between plates; visible arm comb consists of a few low inconspicuous square papillae (Fig. 9c). Oral shield pentagonal, with straight or slightly convex lateral and distal edges, opposed by a large ventral plate; can be fragmented by hydroid tracks (Fig. 9b). Genital slit is half the disc radius in length, bordered by low square papillae, becoming more separate and plate or granule like near the margin. Oral tentacle pore with 4 scales on either side.

DAPs usually separate, except between 1st and 2nd plate, diamond shaped with rounded corners, hydroid tracks can obscure plate outlines (Fig. 9a). LAPs squarish, overlapping neighbouring plates, penetrated by the tentacle pore (Fig. 9e–f), arm spine articulations obscure. VAPs separate, enlarged proximally, becoming broadly triangular distally. Tentacle pores obvious for only the first 2–3 segments, thereafter they penetrate the LAP, opening near the lowest arm spine (Fig. 9c). Three small simple arm spines, 1/10 segment in length, lowest longest. 1–2 tentacle scales on either side of the basal pores, hereafter one small pointed scale, next to the lowest arm spine. Colour (live, Fig. 6f): light grey dorsal disc, disc rim and arms pale.

Distribution. W Atlantic (1956–3442 m), E Atlantic (2100–3200 m), S Africa (1539–2700 m), W Indian Ocean (1880–3645 m).

Remarks. Following previous authors, these specimens have been named as *O. abyssorum*, whose type locality is in the West Indies at 1997 m. This species resembles *O. tessellata* (Verrill, 1894) from the temperate bathyal North Atlantic, *O. pseudotessellata* Martynov & Litvinova, 2008 from off the Azores, and *O. mordax* (Koehler, 1922b) from off eastern Antarctica. Distinguishing these species is difficult as they are often infested with a hydroid (named as *Hydractinia ingolfi* (Kramp) on *O. tessellata*, see Mortensen, 1933d: 92) that creates variation in the shape and distribution of dorsal and central disc plates, oral shields and dorsal arm plates. On the dorsal disc these hydroid tracks can have the appearance of heart-urchin fascioles (Fig. 9a). However, *O. tessellata* is perhaps distinguished by its contiguous DAPs on the basal part of the arm, *O. pseudotessellata* has elongated radial shields, and *O. mordax* appears to lack a larger ventral plate distally to the oral shield (although this could be due to fragmentation from the hydroid infestation). Guille & Vadon (1986) identified a specimen from off northern Madagascar (2300–2500 m) as *O. mordax* based on a comparison with two Antarctic syntypes of *O. mordax* in the MNHN.

DNA data is required to satisfactorily separate these forms. Unfortunately, we have failed to obtain DNA sequence data from any of the North Atlantic *Ophioplinthus* species, nor an Antarctic *O. mordax*. The DNA data we do have indicates that the MD208 specimens form a sister clade to an undescribed species (*Ophioplinthus* sp.MoV.7271, see O'Hara 2024b) from the eastern Indian Ocean seamounts (1915–3172 m), which together are sister to *O. accommodata* (Koehler, 1922b) from off southern Australia and New Zealand (1000–2902 m).

The two species of *Ophioplinthus* described from the western Indian Ocean are not closely related. *Ophioplinthus inconveniens* (Hertz, 1927b) is known from the unique 4 mm holotype found off East Africa (1668 m) and resembles an *Ophiomastus* or *Anthophiura*. There are very few disc plates, with the primaries contiguous with each other and the radial shields. *Ophioplinthus inflata* from off Sri Lanka (1110 m) appears from the type figures to be more like an *Ophiuroglypha* with pronounced arm comb granules, large triangular oral shield, small ventral disc plates, radials that are contiguous over their distal half, and appearing to lack a hydroid infestation. The unique type of *O. inflata* in the ZSI has disintegrated (O'Hara pers. obs.).

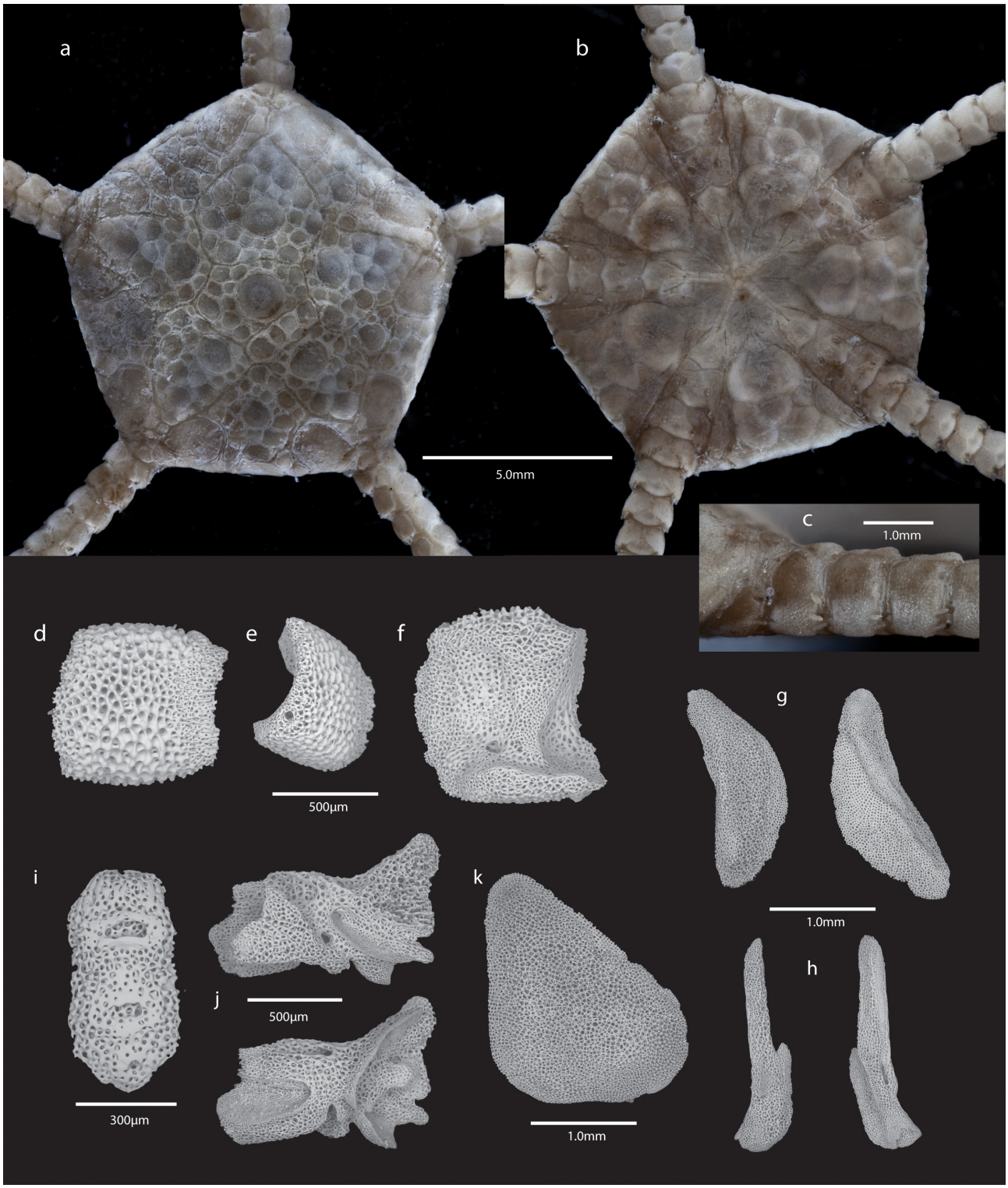

FIGURE 9. *Ophioplinthus abyssorum* MNHN IE.2023.4002 (a) dorsal view, (b) ventral view, (c) arm base, lateral view; MNHN IE.2016.1373 (d) SEM lateral arm plate, external view, (e) lateral arm plate, distal view, (f) lateral arm plate, internal view, (g) adradial genital plate, ventral and dorsal view, (h) abradial genital plate, ventral and dorsal view, (i) dental plate, (j) oral plate, interradial and radial views, (k) radial shield.

***Ophiuroglypha atlantis* sp. nov.**

https://zoobank.org/urn:lsid:zoobank.org:act:B8507B22-881A-493D-ACFB-9F6DCF9DEBE6

Fig. 10a–l

TYPE LOCALITY. Atlantis Bank, 32° 42.658′S, 57° 16.371′E to 32° 42.64′S, 57° 17.58′E, 707 m

TYPE MATERIAL.—JC066: stn 8-3, Atlantis Bank, 32° 42.658′S, 57° 16.371′E to 32° 42.64′S, 57° 17.58′E, 707 m, 9/12/2011, holotype: 1 (NHMUK 2025.64); paratype: 1 (MV F321045) (**DNA code=JC066-3639**).

OTHER STUDY MATERIAL. ***Ophiuroglypha* sp**: JC066/4-20, Coral seamount, 41° 22.35′S, 42° 54.64′E, 732 m, 17/11/2011, NHMUK.2025.63 (1).

COMPARATIVE MATERIAL EXAMINED. ***Ophiuroglypha* sp.MoV.7376** KANADEEP2/PL740_ASPI-6, Mont D, 23° 34.417′S, 169° 36.953′E, 667 m, 6/9/2019, MNHN IE.2019.2921 (**DNA code=IE.2019.2921**).

Diagnosis. Radial shields contiguous for distal half of plates. Disc plates polygonal, variable in size. Arm comb with conical to hemispherical papillae, continue along genital slit until mid-radius. Oral shield longer than wide, concave laterally. DAPs rhomboid, contiguous. VAPs contiguous for basal 5 plates, 1st and 2nd VAPs contiguous for over half their width. 3 short peg-like arm spines, to 1/4 segment in length, middle one becoming upturned and hook-like distally.

Description. Holotype 12 mm dd, disc indented interradially, thick rounded margin, covered in round to polygonal imbricating scales, centrodorsal pentagonal, primary and secondary plates larger and surrounded by smaller scales, marginal interradial plate not particularly enlarged, 6–7 plates between centrodorsal and radial shields; radial shields 1/5 dd, egg-shaped, with flattened distal edge, tapering proximally, contiguous radially for 1/2 plate, separated interradially by 3 scales; 5–6 rows of smaller disc scales ventrally; arm comb consists of hemispherical to conical papillae, not contiguous over dorsal arm base, becoming granule-like ventrally, persisting 1/2 way down bursal silt towards oral shield. Oral shield pentagonal, just longer than wide, with slightly convex distal margin, slightly concave distolateral sides and tapered proximally to a rounded angle; adoral shields narrow, 5.5 times longer than wide, extending to 1/2 way down oral shield, contiguous (or sometime sunken) interradially, contiguous with the first LAP distally; visible section of the oral plate sausage-shaped, leaving a small triangular decalcified area between them and the oral shields; 4–5 oral papillae along jaw edge, inner ones pointed, outer ones wide and rectangular; teeth conical to triangular, 4 in the main series, in addition a smaller apical tooth sits ventral to the oral papillae; 2nd oral tentacle pore opens outside the jaw slit with 5–6 abradial and 4 adradial scales, the outer adradial scales are larger and sit on the lateroproximal edge of the first VAP, the inner 2 arise from the ventral tentacle compartment which form the distal edge of the jaw slit.

First 1–2 DAPs rhomboid, visible underneath the arm combs, next DAP 3 times as wide as long with a convex distal edge and straight proximal one, succeeding plates becoming rhomboid then rounded triangular, with a straight proximal edge, divergent lateral sides and convex distal edge, distally 2x longer than wide, contiguous until near arm tip; LAP with an obtuse distal angle, straight lateral sides, and ventral part that is curved under the arm; 1st VAP 2x wider than long, hexagonal, a small gap between the first VAP and LAP, 2nd VAP more rhomboid, as wide as long, becoming a wide triangular shape by 5th segment with rounded angles (Fig. 10k), separate from the 5th VAP, developing notched proximolateral edges by the 8th VAP (Fig. 10g), 4x as wide as long distally and widely separated; 3 spaced spindle-like to cylindrical arm spines on the ventral half of the LAP, 1/4x segment length, middle one develops a rudimentary hook-tip distally; tentacle pore adjacent to the 2nd VAP with 6 abradial (on LAP) and 5 adradial (on VAP) tentacle scales, the distal adradial one is much wider than the others, forming the distal edge to the pore, appears like an accessory plate that separates the VAP and LAP; only a smaller version of this plate and 2–3 abradial ones persist by the 12th VAP, and only 1 pointed abradial scale distally. Colour (preserved) white.

Paratype 10 mm dd, similar to holotype. LAP (Fig. 10h–j) with dense stereom, transversely striated where it sits under its proximal neighbour, arm spine articulation very simple with small holes for both the muscle attachment and nerve (Fig. 10j); vertebrae with tall dorsal muscle fossae and well-developed ventral podia basins, strongly grooved ventrally, with tall narrow zygosphene (Fig. 10d).

Distribution. Atlantis Bank, SW Indian Ridge (707 m).

Remarks. This species possesses the enlarged plate-like adradial tentacle scale and separate arm combs that are characteristic of the *Ophiuroglypha irrorata* complex of species. This complex has been treated as a single morpho-species by many taxonomists, with an extensive list of synonyms (e.g. Madsen 1967). However, DNA evidence indicates that it is an extensive complex of many sibling species (see tree in Christodoulou *et al.* 2020),

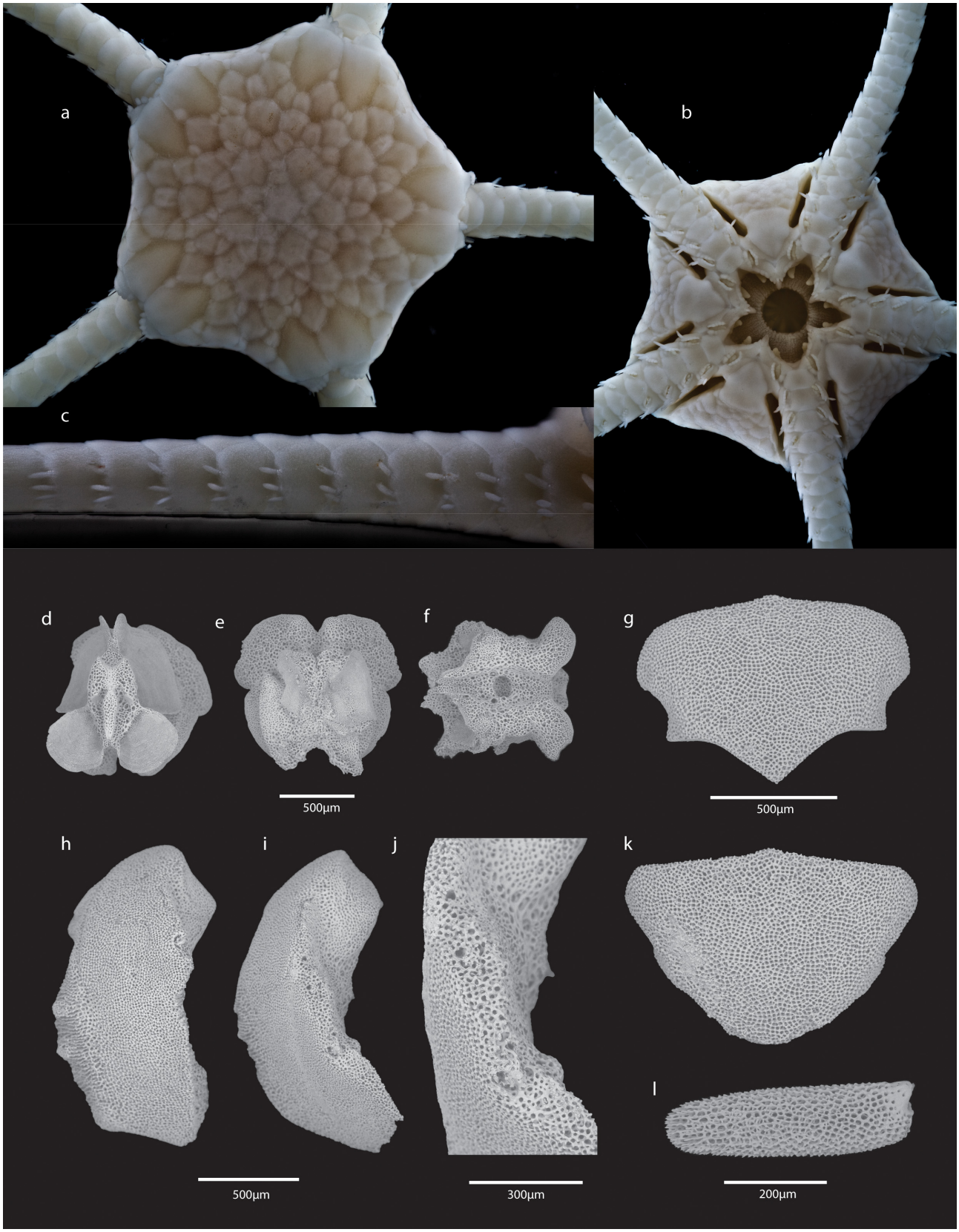

FIGURE 10. *Ophiuroglypha atlantis* **sp. nov.** holotype NHMUK 2025.64 (a) Dorsal view, (b) Ventral view, (c) arm, lateral view; paratype MV F321045, proximal vertebra from (d) proximal, (e) distal, and (f) ventral views, (g) ventral arm plate from mid arm, (h–j) lateral arm plate, from (h) lateral, (i) distal views, and (j) closeup of arm spine articulations, (k) basal ventral arm plate, and (l) arm spine.

and characters such as the nature of the adradial tentacle scale (hinged vs flat), disc margin (sharp vs rounded), the size and position of the radial shields, the extent of the arm comb (limited to the disc margin or extending dorsally), and number (3 to many) and position (spaced or bunched on the lower portion of the LAP) of the arm spines may provide species-level diagnoses (see also Paterson 1985). Assigning names to the DNA clades requires further research. In particular, we require DNA samples from near the type locality of *O. irrorata* off western South Africa in 3534 m.

The new species appears to differ from existing species in having a combination of contiguous radial shields, separate dorsal arm combs, an oral shield that is longer than wide, a persistent enlarged adradial tentacle scale, and 3 widely separated arm spines. It is closest genetically to an upper bathyal specimen from New Caledonia (IE.2019.2921) which also appears to be a new species (*O.* sp.MoV.7376).

A smaller 6 mm dd specimen from the Coral Seamount (NHMUK 2025.63, Fig. 13i–k) is probably a distinct species. It has large irregular radial shields, arm spines that can reach a segment in length, and lacks the plate-like adradial tentacle scale. Better material is required to understand its relationships.

Etymology. Named after Atlantis seamount, the type locality.

***Stegophiura waltersi* sp. nov.**

https://zoobank.org/urn:lsid:zoobank.org:act:468F1E3F-FBC8-47B1-878A-8A0B1C792EBC

Fig. 11–12

TYPE LOCALITY. Walters shoal, Plaine Sud, 33° 48.82′S, 44° 5.9699′E to 33° 51.8′S, 44° 4.72′E, 1539–1615 m

TYPE MATERIAL.—MD208: stn CP4913, Walters shoal, Plaine Sud, 33° 48.82′S, 44° 5.9699′E to 33° 51.8′S, 44° 4.72′E, 1539–1615 m, 11/5/2017, holotype: 1 (MNHN IE.2023.4069); paratypes: 27 (MNHN IE.2016.1375) (**DNA code=IE.2016.1375**).

OTHER STUDY MATERIAL.—MD208: stn CP4914, Walters shoal, Plaine Sud, 33° 51.1′S, 44° 4.8999′E to 33° 54.73′S, 44° 3.2199′E, 1598–1714 m, 11/5/2017: 258 (MNHN IE.2016.1374) (**DNA code=IE.2016.1374**).—MD208: stn CP4915, Walters shoal, Plaine Sud, 33° 56.85′S, 44° 0.07′E to 33° 58.8′S, 43° 55.3999′E, 1865–2058 m, 12/5/2017: 191 (MNHN IE.2016.1363) (**DNA code=IE.2016.1363-2**).

COMPARATIVE MATERIAL EXAMINED. ***Amphiophiura distincta*** (Koehler, 1904): SBD/825S, Great Barrier Reef Seabed Survey, 18° 22.033′S, 147° 16.8289′E to 18° 22.107′S, 147° 17.0129′E, 74.4–73.7 m, 19/9/2003, MTQ SBD001284 (**DNA code=SBD001284**). SS10/2005/26, Albany, 35° 20.382′S, 118° 20.46′E to 35° 20.682′S, 118° 19.74′E, 212–213 m, 23/11/2005, MV F112578 (**DNA code=F112578**). ***Stegophiura lapidaria*** (Lyman, 1878): Challenger/235, off Hamamatsu, 34° 7′N, 138° 0′E, 1050 m, 4/6/1875, holotype, NHMUK 1882.12.23.412. BIOPAPUA/CP3759, Au large de Feni Islands, 4° 0′S, 153° 36′E, 287–352 m, 14/10/2010, MNHN IE.2007.2942 (**DNA code=BP57**). ***Stegophiura rhabdotoplax*** Murakami, 1942: EXBODI/DW3876, Ile Matthew-Volcan nord, 22° 17.2′S, 171° 17.6′E, 518–833 m, 17/9/2011, MNHN IE.2007.7273 (**DNA code=IE.2007.7273**). ***Stegophiura* sp.MoV.7272** IN2021_V04/26, Max Seamount, 11° 42.608′S, 107° 1.9122′E to 11° 42.92′S, 107° 3.459′E, 1915–1990 m, 10/7/2021, identified by O'Hara (2024b), MV F305618 (**DNA code=F305618**). ***Stegophiura vivipara*** Matsumoto, 1915: Sagami Bay, off Misaki, 35° 7.746′N, 139° 34.255′E to 35° 8.033′N, 139° 34.057′E, 94.5–96.6 m, 31/5/2018, MV F248380 (**DNA code=Misaki002**).

Diagnosis. Disc with rounded imbricating disc scales and polygonal radial shields that are contiguous for their distal half. Genital granules hemispherical near the oral shield, becoming conical near margin and spiniform as arm comb papillae. Oral shields wider than long, trilobed. Arms rounded, DAPs and VAPs becoming separate after basal 5 plates, lacking mid-ventral ridge on basal VAPs. 3 conical arm spines, to 0.5 segments in length, no accessory plate-like arm spines.

Description. Holotype 12 mm dd, disc pentagonal, thick; largest arm fragment 30 mm long. Disc covered with rounded imbricating scales, with radiating patterns of stereom, primary plates and interradial scales largest, surrounded by smaller plates, 3 plates between radial shields interradially, marginal interradial plate not larger than other scales; radial shields longer than wide, irregularly hexagonal, with an acute to rounded angle proximally, an obtuse angle distally, and contiguous radially for half their length; scales smaller ventrally, 3 transverse and 6–7 longitudinal rows; hemispherical papillae along genital slit from oral shield, becoming cone-shaped to spine-like and separate near margin and onto the dorsolateral surface; an opposing comb of small spines occurs along the outer

edge of the first DAP and first free LAP. Oral shields bilobed, with a large rounded distal lobe, 2x wider than long, and smaller inner lobe, just wider than long, with an obtuse inner angle and straight to slightly concave lateral sides; adoral shields narrow, curve around the inner lobe of the oral shields and slightly expanded distally, contiguous interradially and separated radially by the first VAP; visible section of the oral plates parallelogram in shape, 2x as wide as long, contiguous interradially, and slightly concave distally where it is incised by the 2nd oral tentacle pore; 5 lateral oral papillae, rounded and taller than wide proximally becoming low and wide distally; ventral tooth ovoid with a blunt terminal edge; 2nd oral tentacle pore with 5 abradial scales (adoral shield spines) which are widest distally, and 4 adradial scales, the distal two arise from the first VAP and inner two from the triangular ventral compartment plate that borders the distal section of the jaw slit.

Arms oblong-shaped in cross-section; first DAP very thin triangular just visible distal to the radial shields, 2nd DAP 2.3x as wide as long, hexagonal, 2nd DAP 1.75x as wide as long, becoming narrower from the 3rd, kite-shaped from the 5th, and separate from the 8th DAP, with minute spinous processes distally; LAPs higher than long, obtusely pointed dorsally, beaded/perforated. First VAP irregular hexagonal, 2x as wide as long, widest distally, with a truncate proximal edge and a slightly concave distal edge, contiguous with succeeding plate, 2nd VAP as long as wide, gradually attenuating proximally, 3rd similar except it has notable transverse striations, becoming kite-shaped by the 5th VAP, smaller and separated from the 6th, wider than long by the 8th VAP. Three cone-shaped to spiniform arm spines, to 1/2 segment in length near arm base, widely separated, with the middle spine slightly closer to the ventral than dorsal spine, middle spine shorter and hooklet-shaped on distal segments with an abradially bent apex and no secondary teeth; no smaller accessory arm spines (except opposing arm comb on first free LAP). Tentacle pore adjacent to 2nd and 3rd VAP with 4–5 abradial (on LAP) and 3–4 adradial (on VAP) scales, the inner adradial scale enlarged, 4 abradial and 4 adradial ones by the 5th VAP; adradial scales cease by 8–9th VAP. Colour (live and preserved) light brown (Fig. 6f).

Paratypes 5–12 mm dd, sometimes lower arm spine duplicated, preserved colour on some specimens notably darker brown than the holotype. Vertebrae (Fig. 12a–d) zygospondylous, with high dorsal and well-developed ventral fossae, narrow ventral groove and tall narrow zygosphene; LAPs (Fig. 12e–f) with densely perforated exterior stereom, simple round arm spine articulations for muscle attachment and small adjacent neural perforations; DAPs (Fig. 12j) kite-shaped with denticulate distal edge; oral plates (Fig. 12g–h) long, distal and proximal sections fused, 2nd oral tentacle pore exiting outside of jaw slit; dental plate (Fig. 12i) 2x as tall and wide; teeth and infradental papillae perforations small; five teeth in vertical series (Fig. 11e), 3rd to 4th (from ventral) chisel like, widened at tip, dorsal tooth spine-like; tentacle scales (Fig. 12l) with angled spinous apical edge; arm spines (Fig. 12m) with longitudinal grooves in the stereom on the apical section; abradial genital scale smaller and wider than adradial plate (Fig. 12n–p).

Distribution. Walters Shoal (1539–2058 m).

Remarks. Molecular evidence places this species within the genus *Stegophiura*. Two characters tend to characterise *Stegophiura* species, the presence of small scale-like accessory arm spines between the longer pointed ones, and/or the presence of a swollen mid-radial ridge on basal VAPs. The following species possess accessory arm spines: *S. nodosa* type species (see Djakonov 1954, fig. 28), *S. brachyactis* (H.L. Clark, 1911), *S. carinata* Djakonov, 1954, *S. hainensis* Liao, 1995, *S. ponderosa* (Lyman, 1878), *S. rhabdotoplax*, *S. sladeni* (Duncan, 1879), *S. sterea* H.L. Clark, 1908, *S. sterilis* Koehler, 1922a and *S.wilhelmi* Manso, 2010. In addition, re-examination of the unique holotype of *Amphiophiura lapidaria* revealed a series of flat rounded papilla-like accessory arm spines on the LAPs, 7 between the dorsal and middle arm spine, and 2 between the middle and ventral spine, and on this basis (confirmed by DNA evidence, Fig. 2a) this species is transferred to the genus *Stegophiura*. It is unclear from Duncan's (1879) type description of *S. striata* whether it has dimorphic arm spines or not. Species that have swollen ridges on the basal VAPs include *S. nodosa* (Lütken, 1855), *S. carinata*, *S. elevata* (Lyman, 1878), *S. hainensis*, *S. macrantha* H.L. Clark, 1915, *S. singletoni* McKnight, 1975, *S. sladeni*, and *S. stuwitzii* (Lütken, 1857). Only two existing species appear to lack both of these characters: *S. sculpta* from Korea-Japan and *S. vivipara* from Japan. These are very similar and possibly synonymous. Both are reported to be viviparous (Murakami 1941, Matsumoto 1917 respectively). Our DNA sample of *S. vivipara* from Japan was phylogenetically placed in a separate evolutionary lineage that also contains *Amphiophiura distincta*. All three species are characterised by the very short arms (to 2x dd) and few disc plates. Consequently, we consider *S. sculpta* and *S. vivipara* to be *Amphiophiura* species, pending a revision of that genus.

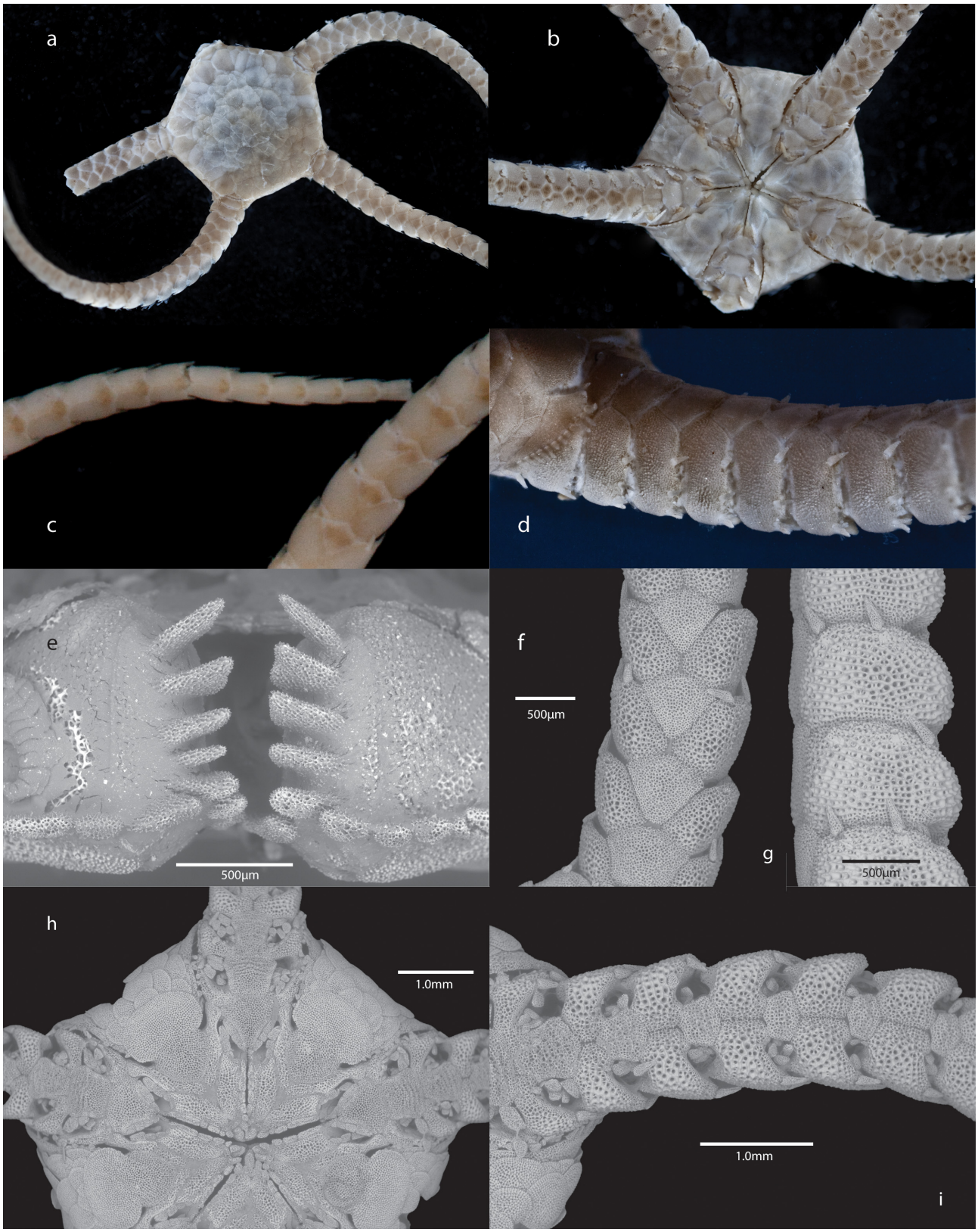

FIGURE 11. *Stegophiura waltersi* **sp. nov.** holotype MNHN IE.2023.4069 (a) dorsal view, (b) ventral view, (c) dorsal arm tips, (d) arm base, lateral view; paratype MNHN IE.2016.1375 (e) two jaws, lateral view (SEM), (f) arm, dorsal view (SEM), (g) arm, lateral view (SEM, some arm spines missing), (h) ventral disc (SEM), (i) arm, ventral view (SEM).

FIGURE 12. *Stegophiura waltersi* **sp. nov.** paratype MNHN IE.2016.1375 (a) vertebra, proximal view, (b) vertebra, distal view, (c) vertebra, proximal view, (d) vertebra, ventral view, (e) lateral arm plate, distal view, (f) lateral arm plate, lateral view, (g) oral plate, interradial view, (h) oral plate, radial view, (i) dental plate, (j) dorsal arm plate, (k) ventral arm plate, (l) tentacle scale, (m) arm spine, (n–o) opposite faces of adradial genital plate, (p) abradial plate, (q) radial shield, (r) centrodorsal plate.

Stegophiura waltersi **sp. nov.** also does not have accessory arm spines nor swollen ventral arm plates. However, it is otherwise morphologically and genetically very close to *S. lapidaria*, sharing the same oral frame, arm plates, and radial shields. *Stegophiura lapidaria* differs in having a pentagonal centrodorsal plate, no smaller plates around the primaries, and the accessory arm spines. We consider the lack of accessory arm spines on our new species as a derived character. A related undescribed lineage (*Stegophiura* sp.MoV.7272) that also lacks accessory arm spines occurs on seamounts in the eastern Indian Ocean (O'Hara 2024b).

Amphiophiura radiata is superficially similar but can be distinguished by its square genital papillae and an enlarged plate at the interradial margin.

Etymology. Named after the Walters Shoal seamount.

Family Ophiohelidae

Ophiomyces grandis Lyman, 1879

Fig. 19g–k, 21i

Ophiomyces grandis Lyman, 1879: 46–47, pl. 14(383–385).—Lyman, 1882: 241–242, pl. 19(13–15).—Paterson, 1985: 75–76, fig. 31 (in part).—O'Hara, 1990: 302–303, fig. 2k.

Non *Ophiomyces grandis*.—Cherbonnier, 1965: 846, fig g–k.—Paterson, 1985: 75–76 (in part).—Litvinova, 2001: 147–148, fig. 2–3.—Ordines *et al.* 2019: 1819–1821, fig. 2 [= *Ophiomyces peresi* Reys, 1961].

STUDY MATERIAL.—MD208: stn CP4913, Walters shoal, Plaine Sud, 33° 48.82′S, 44° 5.9699′E to 33° 51.8′S, 44° 4.72′E, 1539–1615 m, 11/5/2017: 1 (MNHN IE.2016.1377).—MD208: stn CP4914, Walters shoal, Plaine Sud, 33° 51.1′S, 44° 4.8999′E to 33° 54.73′S, 44° 3.2199′E, 1598–1714 m, 11/5/2017: 4 (MNHN IE.2016.1372) (**DNA code=IE.2016.1372**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiomyces delata*** Koehler, 1904: BIOPAPUA/CP3639, Sud de Lae, Golfe de Huon, 7° 23′S, 147° 35′E, 900–932 m, 23/8/2010, MNHN IE.2023.4070 (**DNA code=BP34**). in2022_v08/143, Cocos (Keeling), 12° 13.526′S, 96° 57.5957′E to 12° 14.351′S, 96° 58.2647′E, 1113–1343 m, 17/10/2022, identified by O'Hara (2024b), MV F307642 (**DNA code=F307642**). IN2022_V09/116, Site:038, 23° 9.354′S, 112° 48.3609′E, 992 m, 9/12/2022, MV F310378 (**DNA code=F310378**). ***Ophiomyces grandis*** Lyman, 1879: Challenger/135E, Tristan d'Acunha, 37° 21′S, 12° 22.5′W, 1828 m, 18/10/1873, holotype, NHMUK 1882.12.23.291. IN2018_V06/007, Deep west of Pedra, 44° 20.844′S, 146° 56.82′E to 44° 22.596′S, 146° 56.76′E, 1745 m, 24/11/2018, MV F272372 (**DNA code=F272372**). TAN0307/31, Campbell Plateau, 49° 19.56′S, 176° 33.12′E to 49° 19.62′S, 176° 32.32′E, 1522–1552 m, 21/4/2003, NIWA 48457 (14). TAN0307/85, Bollons Seamount, 49° 48.69′S, 176° 33.5′W, 1266 m, 2/5/2003, NIWA 48621.

COMPARATIVE MATERIAL NOT EXAMINED. ***Ophiomyces peresi*** Reys, 1961: INTEMARES-A22B_0718/20, Ses Olives seamount, 38° 56.1′N, 1° 57.97′E, 275 m, 7/2018, identified by Ordines *et al.* 2019 as *Ophiomyces grandis*, CFM 7020-7022 (**DNA code=MK934137**).

Distribution. SE Australia (1000–1840 m); Campbell Plateau/Bollons Seamount (1266–1522 m); Tristan da Cunha (1828 m), Walters Shoal (1539–1714).

Remarks. *Ophiomyces grandis* (type locality Tristan da Cunha) is a southern hemisphere mid-bathyal (1000–1840 m) species, found on seamounts, and is characterised by having only the most distal oral papillae widened at the tip like hockey sticks and up to 3 tentacle scales on the ventral arm plates and several on the lateral arm plates (O'Hara 1990). The MD208 specimens measure up to 7 mm dd, and have dimorphic arm spines, with the 4 lowest pointed and as long as the segment and the upper 5–6 short and needle-like. Unlike in the genera *Ophiotholia* and *Ophiohelus*, there are no parasol-shaped arm spines. The vertebrae (Fig. 19k) have pronounced vertical zygocondyles and a small reduced zygosphene. The LAPs (Fig. 19g–h) have a long ventral extension that meets on the mid-radius and separates the VAPs (Fig. 19j). The arm spine articulations consist of two convex lips orientated vertically, the arm spines themselves (Fig. 19i) have a pronounced groove along their length. The living colour is an off-white (Fig. 6f).

Ophiomyces grandis has also been reported from the North Atlantic in 124–802 m (Cherbonnier 1965; Paterson 1985; Ordines *et al.* 2019). The latter study supplies the only DNA sequence (MK934137, COI) available from this region, which is distinct from the southern hemisphere *O. grandis*. This, and the shallower bathymetric distribution

of the North Atlantic specimens (124–802 m), suggests that it represents a separate species for which the name *Ophiomyces peresi* Reys, 1961 (Type locality: Gorringe Bank, North of Madeira, 200 m) is available.

Family Ophioscolecidae

Ophiologimus prolifer (Studer, 1882)

Ophioscolex prolifer Studer, 1882: 28, pl. 3(13a–e).
Ophiologimus prolifer.—Martynov, 2010b: 70.

STUDY MATERIAL.—JC066: stn 4-12, Coral seamount, 41° 22.333′S, 42° 54.066′E to 41° 23′S, 42° 54.1′E, 730 m, 16/11/2011: 1 (NHMUK 2025.) (**DNA code=02W70**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiologimus* cf. *hexactis*** SE-1722/10DR, Kumano-nada, 33° 59.72′N, 136° 56.67′E to 33° 59.72′N, 136° 56.68′E, 796–768 m, 10/11/2017, NSMT E11571 (**DNA code=SE-17-155**). ***Ophiologimus hexactis*** H.L. Clark, 1911: Sagami Bay, off Misaki, stn1, 35° 8.415′N, 139° 32.944′E to 35° 8.262′N, 139° 32.746′E, 109–160 m, 4/6/2018 (**DNA code=Misaki035**). ***Ophiologimus prolifer*** (Studer, 1882): Gazelle/Barrier Island, off Barrier Island, 35° 21′S, 175° 40′E, 1092.5 m, 12/11/1875, syntype, ZMB Ech2535. SS02/2007/8, Huon Margin, 44° 1.837′S, 147° 34.776′E to 44° 2.135′S, 147° 34.912′E, 830–1030 m, 31/3/2007, MV F146329 (**DNA code=TOH_0946**). TAN0803/69, Macquarie Ridge, Seamount 6, 52° 23.85′S, 160° 39.4′E to 52° 23.91′S, 160° 40.13′E, 451–438 m, 9/4/2008, NIWA 43108 (**DNA code=TOH_0425**). ***Ophiologimus quadrispinus*** H.L. Clark, 1925: EXBODI/DW3918, Récifs de l'Astrolabe- Mont sous-marin Est, 19° 51.9′S, 165° 55.2′E, 748–922 m, 24/9/2011, MNHN IE.2007.7264 (**DNA code=IE.2007.7264**). ***Ophiologimus secundus*** Koehler, 1914: ME 85- 3/1069, South Iceland, Irminger Basin, 62° 59.33′N, 28° 5.7′W to 62° 59.81′N, 28° 5.01′W, 1588 m, 8/9/2011, DZMB-HH 58752 (**DNA code=DZMB53422B**).

Distribution. New Zealand (170–1110 m), Macquarie Ridge (438–451 m), SE Australia (830–1640 m), Coral Seamount (730 m).

Remarks. The JC066 specimen was preserved in RNALater. An RNA transcriptome was successfully sequenced (O'Hara *et al.* 2014b), but the remaining specimen was subsequently destroyed through a freezer failure. The COI of this specimen is similar to that from Australian specimens of *O. prolifer*. The specimens here have 6 arms. They also have one elongated tentacle scale, and three arm spines, the upper being flatter, wider and longer than the others. The upper arm spines are modified into hooks distally. The type of this species (ZMB Ech 2535) is similar, but has 7 arms, but one arm is smaller than the others and may have originated from an injury. It has one lanceolate tentacle scale, 3 arm spines (middle shortest), the DAPs are longer than wide, rounded triangular, and the distal tips of the radial shields are exposed.

Two other 6-armed *Ophiologimus* species have been described: the type species *O. hexactis* H.L. Clark, 1911 from Japan and *O. secundus* Koehler, 1904 from the North Atlantic. The former is distinguished from *O. prolifer* by the presence of 2 oval tentacle scales. Martynov (2010b) separated *O. secundus* from *O. prolifer* by the shape of the oral shield (with a dorsal lobe in *O. secundus*) and DAPs (contiguous and polygonal in *O. prolifer*). However, the latter character does not hold good in the present material and may be influenced by size. However, a specimen of *O. secundus* from Iceland is clearly separated from *O. prolifer* on our phylogeny (Fig. 2b). Another similar genus is *Ophiolycus* which appears to differ in having more spine-like inner oral papillae, a 2nd oral tentacle that emerges outside of the slit, and distal oral tentacle scales that are not confluent with the inner ones.

Ophiophrura sp.

Fig. 13l–o

STUDY MATERIAL.—JC066: stn 4-2, Coral seamount, 41° 20.708′S, 42° 55.292′E to 41° 20.99′S, 42° 55.12′E, 1300 m, 12/11/2011: 1 (NHMUK 2025.65) (**DNA code=JC066-243**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiophrura liodisca*** H.L. Clark, 1911: FK190106/S0219-S3, Costa Rica Rio Bongo Scar, 9° 17.5527′N, 84° 17.1487′W, 606 m, 13/1/2019, identified by Seid *et al.* (2025), SIO E7980 (**DNA code=SIO E7323B**). SE-1722/10DR, Kumano-nada, 33° 59.72′N, 136° 56.67′E to 33° 59.72′N, 136°

56.68′E, 796–768 m, 10/11/2017, NSMT E11516 (**DNA code=SE-17-162**). SS01/2008/40, Tasmanian fracture zone, 45° 8.5848′S, 146° 2.052′E to 45° 9.0552′S, 146° 0.1866′E, 1610–1640 m, 24/1/2008, MV F162603 (**DNA code=TOH_0918**). TAN1206/32, Site SM4d, NE flank, Tangaroa Seamount, Kermadec Ridge, 36° 19.218′S, 178° 3.39′E to 178° 3.318′N, 36° 19.152′W, 1421–1412 m, 18/4/2012, MV F188883 (**DNA code=02W1M**).

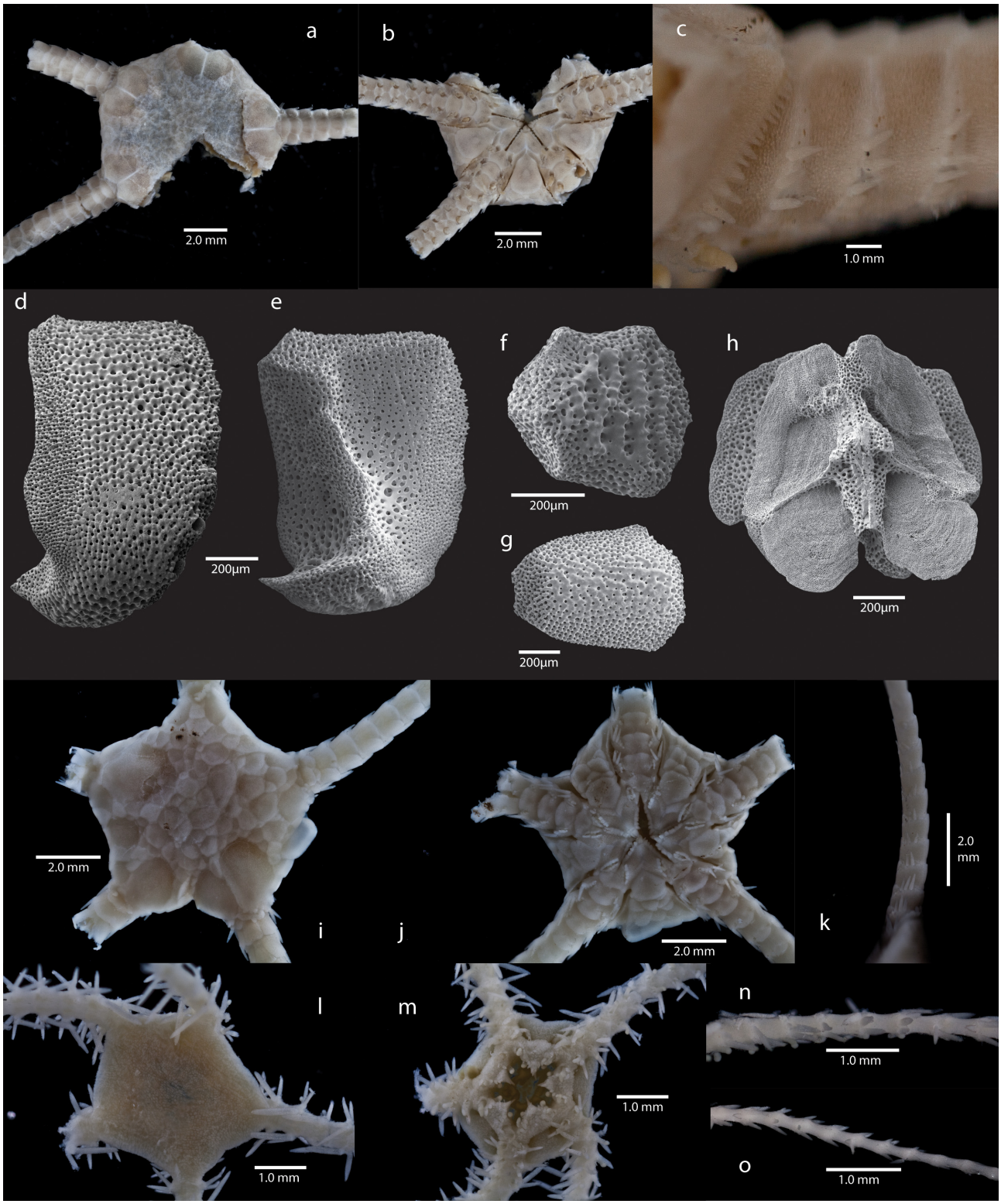

FIGURE 13. (a–h) *Amphiophiura litvinovae* **sp. nov.** MNHN IE.2016.1369 (a) dorsal, (b) ventral, (c) lateral view of arm base, (d) lateral arm plate, exterior view, (e) lateral arm plate, interior view,, (f) ventral arm plate, (g) dorsal arm plate, (h) vertebra, distal view; (i–k) *Ophiuroglypha* sp NHMUK 2025.63 (i) dorsal, (j) ventral, (k) lateral arm base; (l–o) *Ophiophrura* sp NHMUK 2025.65 (l) dorsal, (m) ventral, (n) lateral mid-arm, (o) arm tip.

Remarks. The disc (3 mm dd) is covered with skin that hides the underlying thin imbricating disc scales, no spines or granules, radial shields not evident; oral shields 2x wider than long with a slightly convex distal border; 3–5 blunt lateral oral papillae, outer longest, adoral shield spine present; 4 arm spines after the disc, falling to 3, uppermost longest, slightly flattened, distally they are not hooked; triangular DAPs, 2–3 tentacle scales,

Martynov (2010) diagnosed 3 species within this genus based mainly on the shape of the oral shield, but O'Hara & Thuy (2022) found this to be variable, even on the same specimen. O'Hara & Thuy (2022) identified a specimen from the St Paul and Amsterdam Islands as *O. tripapillata* on the basis that it had a cluster of ventral tooth papillae at the jaw apex and a maximum of 4 arm spines. All other specimens from the bathyal of the Indo-Pacific have been referred to as *O. liodisca*. The current specimen is too juvenile to be clearly identifiable using the above criteria and we do not have any DNA sequences from the Atlantic as a comparison. However, the 4 DNA samples of *Ophiophrura* we have from the Indo-Pacific are genetically divergent, indicating the probability of cryptic speciation.

Family Ophiacanthidae

Ophiectodia Verrill, 1899

Ophiacantha (Ophiectodia) Verrill, 1899: 42 [type *Ophiacantha enopla* Verrill, 1885 designated herein].

TYPE SPECIES. *Ophiectodia enopla*

COMPARATIVE MATERIAL EXAMINED. ***Ophiodiplax antarctica*** (Koehler, 1901): US AMLR-09/40-29, South Orkney Islands, 61° 0.78′S, 44° 53.73′W to 60° 59.89′S, 44° 52.44′W, 265–254 m, 17/2/2009, MV F168812 (**DNA code=F168812**). ***Ophiolebes bacata*** Koehler, 1921: CE13008/36, Rockall Trough, 'North' Canyon, 54° 3.19′N, 12° 32.45′W, 1361 m, 6/2013, NUI (**DNA code=NUI1402A**). ***Ophiolebes felli*** O'Hara & Thuy, 2022: SS10/2005/44, Albany, 35° 26.046′S, 118° 21′E to 35° 26.244′S, 118° 21.06′E, 900–915 m, 25/11/2005, MV F112106 (**DNA code=F112106**). ***Ophiolebes vestitus*** Lyman, 1878: Talud Continental 1/11, Mar del Plata Submarine Canyon, 37° 59.258′S, 54° 41.436′W, 854 m, 11/8/2012, CNP-INV (**DNA code=L11D**). ***Ophiolebes yaldwyni*** Fell, 1958: TAN1104/9, Clark Seamount, south flank, 36° 30.252′S, 177° 52.62′E to 36° 30.108′S, 177° 52.392′E, 1583–1576 m, 3/3/2011, NIWA 72089 (**DNA code=72089**).

Remarks. *Ophiacantha* is a polyphyletic taxon. The type species is *O. bidentata* but most *Ophiacantha* species are not closely related to this species, and they are separated from the type species on our phylogeny by other genera. This includes a clade of species related to *O. enopla* and *O. veterna* with a disc covering of minute granules, minute tentacle scales, and 3–4 oral papillae. We resurrect the genus-level name *Ophiectodia* Verrill, 1899 for this clade of species. Verrill never nominated a type species but included 3 species (*O. enopla*, *O. rosea* and *O. spectabilis*) in his genus. The only specimens he had to hand were *O. enopla*, which we designate as the type species. The species *O. rosea* and *O. spectabilis* are now considered to belong to *Ophiosabine* and *Ophiotreta* respectively. Other described species in our DNA clade include *O. imago* Lyman, 1878 from Kerguelen and the 6–7 armed *O. opulenta* Koehler, 1908 from the Antarctic lower bathyal.

The sister clade to *Ophiectodia* is *Ophiolebes*. The sister lineage to these two clades is *O. antarctica* Koehler, 1901 for which we further resurrect the available genus-level name *Ophiodiplax* Koehler, 1911.

Ophiectodia enopla (Verrill, 1885)

Fig. 14a–g

Ophiacantha enopla Verrill, 1885: 153.
Ophiacantha (Ophiectodia) enopla.—Verrill, 1899: 37, 42.
Ophiacantha veterna Koehler, 1907: 41–43.—Koehler, 1909: 189–190, pl. 29(3–4).—Martynov & Litvinova, 2008: 96–97, fig. 11d.—O'Hara & Thuy, 2022: 16–17, fig. 6a–b [new synonymy].
Ophiacantha enopla enopla.—Paterson, 1985: 36–37, fig. 16.
Ophiacantha enopla veterna.—Paterson, 1985: 37, fig. 16.—Stöhr & Segonzac, 2005: 392.

STUDY MATERIAL.—JC066: stn 4-4, Coral seamount, 41° 22.8371′S, 42° 50.6024′E to 41° 22.85′S, 42° 51.99′E, 1186 m, 13/11/2011: 1 (NHMUK 2025.37) (**DNA code=JC066-648**).—JC066: stn 4-9, Coral seamount, 41°

21.0283′S, 42° 55.145′E to 41° 21.7′S, 42° 54.8′E, 1100 m, 14/11/2011: 1 (NHMUK 2025.38) (**DNA code=JC066-1001**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiectodia enopla*** (Verrill, 1885): CE13008/91, Whittard Canyon, 48° 38.15′N, 10° 41.4′W, 2400 m, 6/2013, NUI (**DNA code=NUI1666K**). EX1905L2/D12-04B, small canyon between Block and Alvin canyons, 39° 49.12′N, 70° 51.2′w, 1138 m, 14/9/2019, USNM 1596691 (**DNA code=USNM 1596691**). SS10/2005/54, Pt Hillier, 35° 31.362′S, 117° 12.66′E to 35° 31.566′S, 117° 13.8′E, 1075–1110 m, 27/11/2005, MV F112618 (**DNA code=MVF112618**). TN228/J2-389-008, Hill offshore of St. Helens, 41° 14.369′S, 148° 49.325′E, 1286 m, 1/1/2009, MV F168673 (**DNA code=F168673**). TAN1402/14, Forde Seamount, Stratum 1, 35° 19.57′S, 170° 26.32′W to 35° 19.42′S, 170° 26.14′W, 1137–1154 m, 9/2/2014, NIWA 94074.

Description. Large specimen (NHMUK 2025.37, 8 mm dd, arms 46+ mm), disc covered in tiny granules, with naked region triangular regions indicating the distal end of the radial shields; oral shields 2x as wide as long, lozenge-shaped, with a small distal lobe; adoral shields thick, almost as long as the oral shields, 2x as wide as long, fully contiguous interradially; 4–5 oral papillae, 3rd & 4th stoutest, almost as wide as long, minutely thorny; arm plates not striated or glassy, separate throughout (except for a few basal DAPs); DAPs triangular to bell-shaped; VAPs 2x as wide as long; to 8 arm spines, uppermost to 2 segments in length, lower ones minutely thorny, becoming hook-shaped distally; tiny spine-like tentacle scale, visible until near the arm tip. Small specimen (NHMUK 2025.38, 4 mm dd), disc spines, arm spines and oral papillae spinier than the adult; disc granules with numerous thorns; 3–5 oral papillae, some suboral in position; tentacle scale visible until arm tip.

Distribution. Arctic (1992–1995 m), NW Atlantic (457–1421 m), NE Atlantic (1350–2669 m), E Atlantic (1004–1679 m), Amsterdam & St Paul (940–1680 m), S Australia (900–1650 m), Louisville Ridge (1075–1448 m), Coral Seamount (1100–1186 m)

Remarks. Paterson (1985) and Martynov & Litvinova (2008) separated *O. veterna* from *O. enopla* on the basis of the smaller tentacle scales that are absent near the arm tip, and the smaller disc granules with less pronounced thorns. *Ophiectodia veterna* was recorded from the NE and central N Atlantic and *O. enopla* from the NW Atlantic Ocean. We have sequenced DNA from specimens on both sides of the Atlantic and throughout the cool temperate Southern Ocean, including from the Coral seamount, and find no bathymetric or geographic structure. This dataset includes a juvenile (Fig. 14a–d) and adult (Fig. 14e–g) from the Coral Seamount that show ontogenetic variations in morphology. The juvenile differs in having relatively larger disc granules with numerous thorns, and more thorny arm spines and oral papillae. Consequently, we consider *O. veterna* a synonym of *O. enopla*.

Ophiectodia melvillei **sp. nov.**

https://zoobank.org/urn:lsid:zoobank.org:act:739A07F7-F437-459E-95EB-6EE7DF93C160
Fig. 14h–k, 15

TYPE LOCALITY. Melville Bank, 38° 30.081′S, 46° 45.78′E to 38° 29.77′S, 46° 45.58′E, 1364 m

TYPE MATERIAL.—JC066: stn 5-24, Melville Bank, 38° 30.081′S, 46° 45.78′E to 38° 29.77′S, 46° 45.58′E, 1364 m, 26/11/2011, holotype: 1 (NHMUK 2025.40); paratype: 1 (MV F321044) (**DNA code=JC066-3284**); paratype: 1 (NHMUK 2025.39) (**DNA code=JC066-3275**).

OTHER STUDY MATERIAL. ***Ophiectodia*** **cf** ***melvillei***: JC066: stn 8-22, Atlantis Bank, 32° 42.225′S, 57° 18.02′E to 32° 42.59′S, 57° 17.01′E, 1000 m, 13/12/2011: 1 (NHMUK 2025.41) (**DNA code=JC066-3736**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiectodia imago*** (Lyman, 1878): PROTEKER 1/trois bergers, Ilot des 3 Bergers, 49° 17.382′S, 69° 42.666′E, 5–20 m, 28/12/2011, MNHN IE.2013.16281 (**DNA code=TOH92-IE.2013.16281**). ***Ophiectodia opulenta*** (Koehler, 1908): PS61 ANT-XIX/4 (ANDEEP)/132-3, 65° 17.88′S, 53° 22.88′W to 65° 17.35′S, 53° 22.89′W, 2087–2084 m, 6/3/2002, CASIZ 161433 (**DNA code=CAS161433**).

Diagnosis. Disc covered in small conical granules terminating in a few thorns, middle surface of bar-like radial shields naked, some granules on distal edge of basal DAPs. Oral shields wider than long. 4–7 spiniform oral papillae. Five arms with to 9 arm spines on each side, less than a segment in length, minutely thorny, 1 tiny, pointed tentacle scale, absent basally.

Description. Holotype 8 mm dd, disc pentagonal to round, covered in thin round perforated disc scales with dense (but separate) tiny conical disc granules with a few short thorns at the apex, 0.10–0.15 mm wide, 1–2x as high as wide, a small narrow naked area over the mid-part of the radial shield, granules extend onto the dorsal arm;

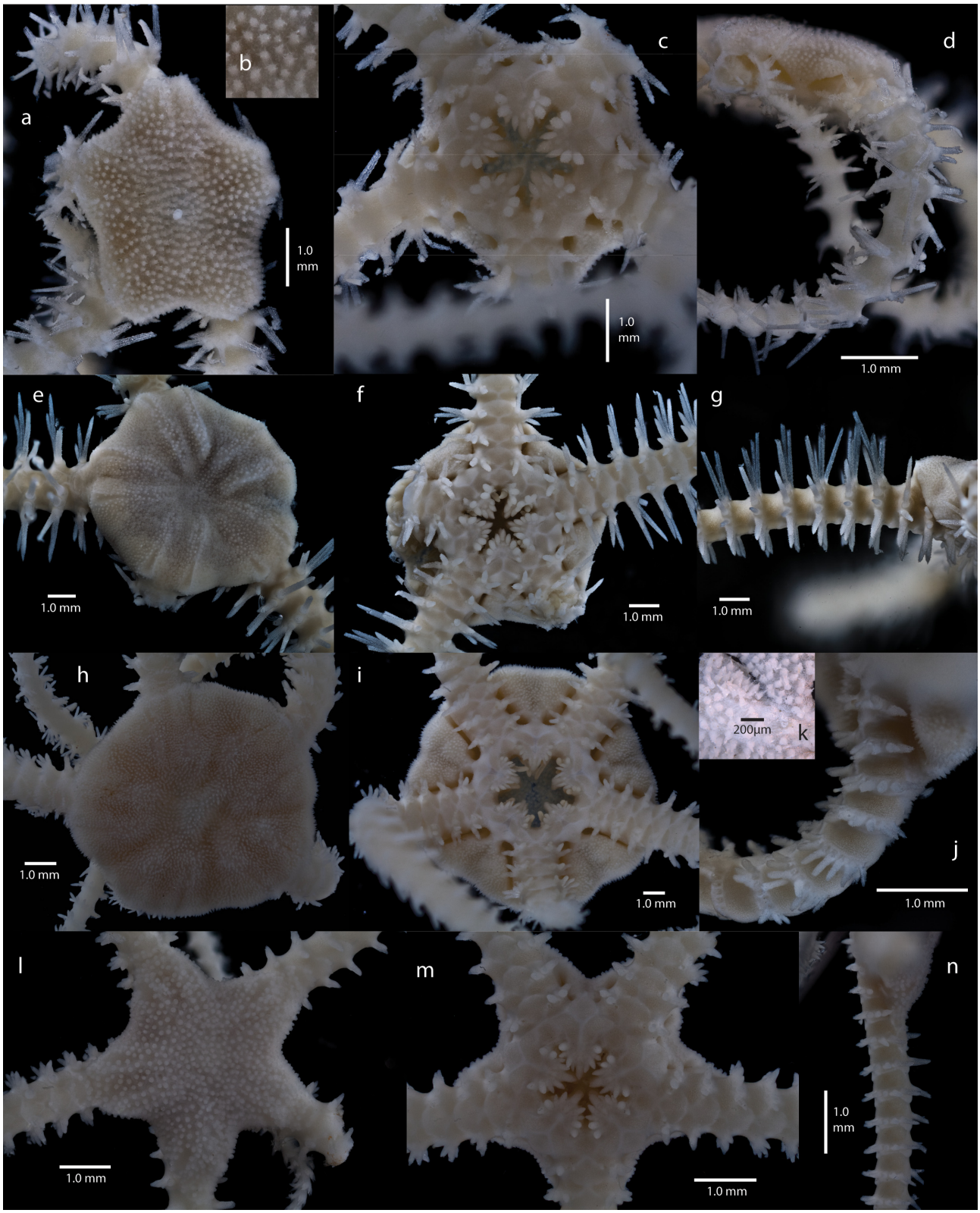

FIGURE 14. (a–d) *Ophiectodia enopla* NHMUK 2025.38 (a) dorsal, (b) dorsal view enlarged, (c) ventral, (d) lateral view of arm base; (e–g) NHMUK 2025.37 (e) dorsal, (f) ventral view, (g) lateral view of arm base; (h–k) *Ophiectodia melvillei* **sp. nov.** holotype NHMUK 2025.40 (h) dorsal, (i) ventral, (j) lateral view of arm base, inset (k) dorsal disc spines; (l–n) *Ophiectodia* cf *melvillei* NHMUK 2025.41 (l) dorsal, (m) ventral, (n) lateral view of arm base.

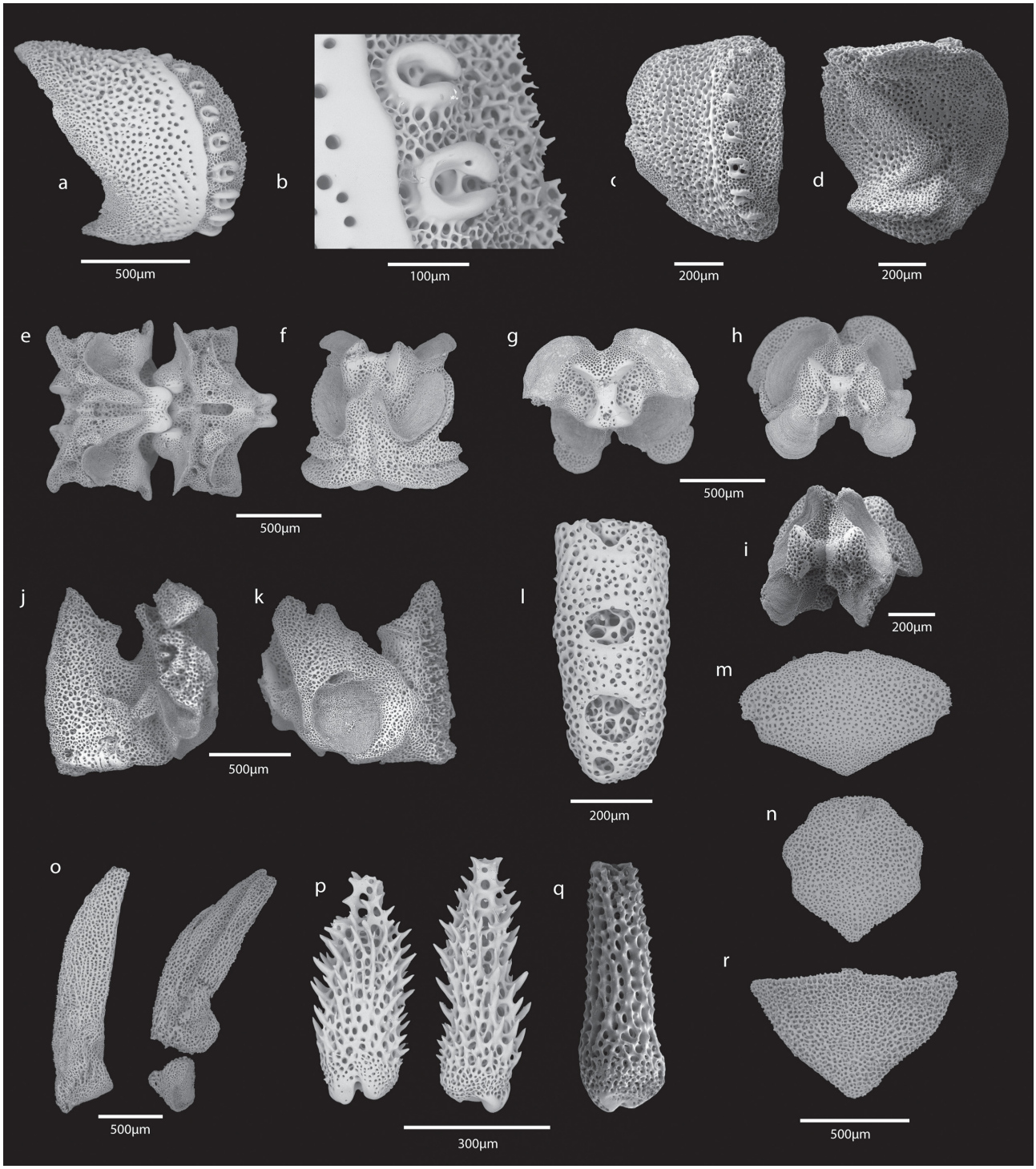

FIGURE 15. *Ophiectodia melvillei* **sp. nov.** paratype NHMUK 2025.39 (a) lateral arm plate, proximolateral view, (b) inset of arm spine articulations, (c) lateral arm plate, exterior view, (d) lateral arm plate, interior view, (e–f) proximal vertebra in (e) pair in ventral view, (f) dorso-distal view, (g) proximal view, (h) distal view, (i) ventrodistal view, (j) oral plate, radial view (k) oral plate, interradial view, (l) dental plate (broken), (m) proximal ventral arm plate, (n) ventral arm plate from the middle of the arm, (o) genital plate, (p) ventral arm spine, (q) middle arm spine (tip broken), (r) dorsal arm plate.

granules covering entire ventral disc surface, but smaller and conical to hemispherical near the genital slit and oral shields; oral shield lozenge-shaped with rounded angles, proximal and distal angle a little lobed, 2x as wide as long; adoral shields 2x as wide as long, separated interradially by a small decalcified area, do not continue distally around the lateral edges of the oral shields; jaws wider than long, bearing 4–7 spiniform oral papillae, some suboral in

position, 2–3x as long as wide, inner ones pointed, distal ones more rounded, minutely thorny; 4 teeth, 3 ventralmost with a wide truncate distal edge, dorsal one thinner, more spine like; 2nd oral tentacle opening within the jaw slit.

Arms five, exceeding 37 mm in length; DAPs wider than long, fan-shaped to triangular, with an obtuse proximal angle and convex distal margin, separate, with 1–2 rows of disc granules occurring around the edge of the 3 basal DAPs, then just on the distal edge of the succeeding 3 plates; VAP1 heart-shaped with proximolateral lobes, narrow distal edge that is contiguous with VAP2, succeeding VAPs broadly triangular, 2x as wide as long, with an obtuse proximal angle and rounded distal edge, slightly notched laterally for the podial pores, just contiguous, becoming as wide as long by the 8th segment and then longer than wide; to 9 short minutely-thorny arm spines, middle one longest but less than a segment in length, 3x as long as wide, blunt apex, 2 spines on the first arm segment, 3 on the 2nd and 5 on the 3rd, distally the lowest arm spine has ventral thorns that give it a hook-shape; one tiny pointed tentacle scale about 1/5 the segment in length with 1–2 terminal thorns, absent for the first 14 segments or so (the lower arm spine bent over the pore), but then persisting until end of arm.

Paratypes MV F321044 (6 mm dd) and 6.5 mm dd) are similar but differ in having fewer arm spines (up to 7) that typically extend to less than 1/2 the segment in length, the number of granules along the distal DAP edge reduced to 1 by the 4th segment. Paratype (NHMUK 2025.39) vertebrae (Fig. 15e–i) with streptospondylous hour-glass articulations, ventral fossae positioned near distal margin and the whole vertebra appears attenuated proximally. LAPs (Fig. 15a–d) longer dorsally than ventrally, with dense perforated but not striated stereom, and a clear demarcation to the ridge of spine articulations which has a more open stereom network, articulations horse-shoe-shaped with a distal opening, slightly more thickened dorsally, enclosing muscle and nerve pores that are separated by a vertical septum. Dental plate (Fig. 15l) oblong shaped with at least 4 sunken tooth articulation points, ventrally smallest. Oral plates (Fig. 15j–k) short, only as wide as long.

Distribution. Melville Bank (1364 m), ?Coral Seamount (1000 m).

Remarks. Our genetic evidence places this species within *Ophiectodia*, sister to all the other described species. Its morphology is also consistent with *Ophiectodia* by having small dense disc spines, more than 3 oral papillae, numerous arm spines and a tiny tentacle scale. The new species differs from the other described species (*O. enopla, O. imago, O. opulenta*) by having very short arm spines that do not exceed a segment in length. The upper arm spine on the other species exceeds 2 segments in length. *Ophiectodia enopla* further differs in having granule-shaped disc spines (in adults) covered in multiple tiny points, and *O. opulenta* has 6–7 arms, although it does not appear to be fissiparous.

We have also included a small specimen (NHMUK 2025.41, 4 mm dd) from the Atlantis Bank (Fig 14l–n) in this species. Its DNA is divergent from the two Melville Bank samples, and it differs morphologically in having granule-shaped disc spines with some tiny terminal thorns, a larger section of the radial shield that is exposed, to 6 short arm spines, and a smaller oral shield, only as wide as long. With only one small specimen it is unclear whether this represents a distinct species or a juvenile of *O. melvillei*. Ophiacanthid disc spines are known to alter shape with growth from juvenile to adult (see *O. enopla*).

Etymology. Named after Melville Bank, the type locality.

Ophiacantha exilis **(Koehler, 1922)**

Fig 16d–g

Ophiomitrella exilis Koehler, 1922a: 110–111, pl. 22(9,10).
Ophiacantha exilis.—O'Hara & Stöhr, 2006: 49, 89.—O'Hara, 2024b: 39, fig. 39.

STUDY MATERIAL.—MD208: stn CP4915, Walters shoal, Plaine Sud, 33° 56.85′S, 44° 0.07′E to 33° 58.8′S, 43° 55.3999′E, 1865–2058 m, 12/5/2017: 1 (MNHN IE.2016.1370) (**DNA code=IE.2016.1370**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiacantha exilis*** (Koehler, 1922a): IN2015_E02/021, Huon Commonwealth Marine Reserve, 44° 19.35′S, 147° 19′E to 44° 19.17′S, 147° 18.47′E, 2028 m, 11/4/2015, MV F227369 (**DNA code=F227369**). IN2017_V03/069, Hunter CMR, 32° 28.74′S, 152° 59.64′E to 32° 30.42′S, 152° 59.46′E, 1006–1036 m, 3/6/2017, MV F239929 (**DNA code=F239929**). IN2021_V04/40, Shcherbakov Seamount, 10° 55.475′S, 104° 36.687′E to 10° 55.441′S, 104° 38.0688′E, 1608–1663 m, 14/7/2021, identified by O'Hara (2024b), MV F305548 (**DNA code=F305548**). TN228/RD2, A1 Seamount, Huon, 44° 19.667′S, 147° 16.48458′E, 1253–1273 m, 20/12/2008, MV F168108. ***Ophiacantha richeri*** O'Hara & Stöhr, 2006: TAN1402/31, Forde

Seamount, Stratum 1, 35° 19.01′S, 170° 27.09′W to 35° 18.48′S, 170° 27.53′W, 1205–1600 m, 11/2/2014, NIWA 95821 (**DNA code=NIWA95821**).

Distribution. E Indo-W Pacific (1280–1663 m), S Australia (1006–2518 m), Walters Shoal (1865–2058 m).

Remarks. The single MD208 specimen measures 2 mm dd. It has the characters of *O. exilis* including a petaloid disc that is indented interradially; moniliform arms that curl under the disc; small slender disc spinelets, pedicel with 3–5 terminal thorns, sometimes smaller thorns on major ones; thorny arm spines that are short except the uppermost one near the arm base; one tentacle scale that is acute and thorny, to half the VAP in length; 3 oral papillae, the outer one pointed; and adoral shields that extend around the lateral tip of the oral shields. It differs a little from the type and specimens reported by O'Hara (2024b) in having lozenge-shaped oral shields that are only a little extended proximally. On specimens from Australia, the oral shields have a long pointed proximal extension that can separate the adoral shields, and the oral papillae are more spiniform. DNA evidence indicates that this species ranges across the Indian Ocean to SE Australia.

Ophiacantha metallacta H.L. Clark, 1915

Fig 16a–c, 19a–f

Ophiacantha vepratica.—Koehler, 1914: 94–95, pl. 13(6) [Non *Ophiacantha vepratica* Lyman T, 1878; see Clark, H.L., 1915].

Ophiacantha metallacta Clark, H.L., 1915: 202–203.—Mortensen, 1933d: fig. 18b,d.—Paterson, 1985: 44, fig. 19.

STUDY MATERIAL.—JC066: stn 8-5, Atlantis Bank, 32° 42.862′S, 57° 14.666′E to 32° 43.3′S, 57° 15.2′E, 828–994 m, 10/12/2011: 1 (NHMUK 2025.32) (**DNA code=JC066-3683**); 1 (NHMUK 2025.33).

COMPARATIVE MATERIAL EXAMINED. ***Ophiacantha metallacta*** H.L. Clark, 1915: BIOPAPUA/DW3719, Vitiaz strait, 6° 3′S, 147° 36′E, 410 m, 7/10/2010, MNHN IE.2023.4074 (**DNA code=BP87**). EX1806/D07_01B, Richardson Ridge, 31° 46.2′N, 77° 21.6′W, 1753 m, 21/6/2018, USNM 1490594 (**DNA code=USNM 1490594**). Kraken2/2-2, 24° 14.3322′N, 80° 55.0169′W, 513 m, 29/11/2011, MV F248413 (**DNA code=F248413**). SS05/2007/156, Northwestern Australia, Leveque L27 transect, 14° 33.432′S, 121° 20.388′E to 14° 32.767′S, 121° 19.65′E, 1100 m, 3/7/2007, MV F167998 (**DNA code=TOH_584**). TAN1206/34, Site SM3a, summit of Clark Seamount, Kermadec Ridge, 36° 26.832′S, 177° 50.31′E to 177° 50.508′N, 36° 26.982′W, 850–980 m, 18/4/2012, MV F188863 (**DNA code=02WOZ**).

Description. Disc 6 mm dd, covered in small disc spines (Fig. 19e), typically 0.20 mm high, with a slightly waisted pedicel and a convex crown bearing short divergent points, 0.18 mm across, absent from the radial shields, becoming smaller and conical to spherical in shape ventrally, extend to the oral shields; oral shields 1.5x wider than long, widest proximally with a rounded distal lobe; 3 oral papillae along the jaw sides in addition to 3–8 suboral papillae that can also occur around the adoral shields, tapered apical teeth. Arms not moniliform, vertebrae (Fig. 19f) with a pronounced distal zygosphene and zygocondyles further back. DAPs wide and triangular, over 2x wider than long, widely separated. LAPs quadrangular in lateral view (Fig. 19a–b) with a notable vertical wavy ridge that separates the proximal part of the plate from the arm spine articulation area, arm spine articulations typical *Ophiacantha* in form. VAPs 1.5x as wide as long, contiguous, with a glassy striated convex distal margin and obtuse angle proximally (Fig 19c); to 9 finely-rugose arm spines forming a fan across the dorsal arm proximally, uppermost just over 2 segments in length (Fig. 19d); one oval tentacle scale, sometimes thorny at the tip, 1/3 the VAP in length.

Distribution. W Atlantic (305–1753 m), Indo-Pacific (410–1100 m), New Zealand (850–980 m), Atlantis Bank (828–994 m).

Remarks. The Atlantis Bank specimens differ from previous descriptions in having suboral as well as the 3 oral papillae. These are only rarely present on the other specimens examined. More specimens are required to determine whether this difference is significant or not. The DNA evidence (Fig. 2b), however, suggests that it is a widespread species complex occurring from Western Atlantic to northern New Zealand.

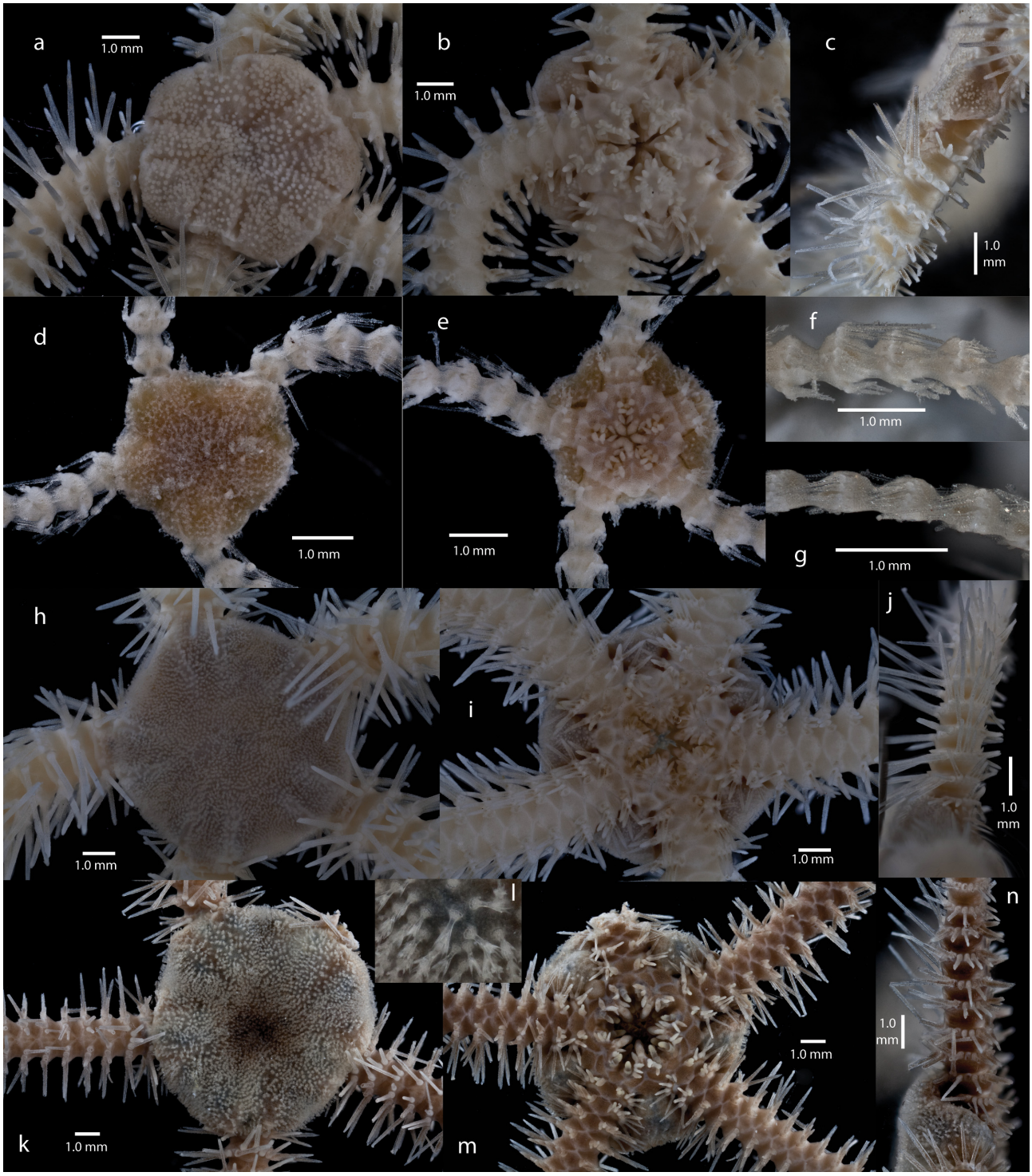

FIGURE 16. (a–c) *Ophiacantha metallacta* NHMUK 2025.33 (a) dorsal, (b) ventral, (c) lateral view of arm base. (d–g) *Ophiacantha exilis* MNHN IE.2016.1370 (d) dorsal, (e) ventral, (f) lateral view of arm base, (g) lateral view of arm tip. (h–j) *Ophiosabine multifida* **sp. nov.** holotype NHMUK 2025.50 (h) dorsal, (i) ventral, (j) lateral view of arm base. (k–n) *Ophiacantha swio* **sp. nov.** holotype NHMUK 2025.34 (k) dorsal, (l) disc spines, (m) ventral, (n) lateral view of arm base.

Ophiacantha striolata Mortensen, 1933

Ophiacantha striolata Mortensen, 1933b: 322–324, fig. 42–43.—Clark, A.M. & Courtman-Stock, 1976: 168–169, figs 169, 175, 180.—Clark, A.M., 1977: 135.—Olbers *et al.* 2019: 122–123, fig. 106–107.

STUDY MATERIAL.—MD208: stn WB05, Walters shoal, Zone sommitale Sud, 33° 15.12′S, 43° 54.514′E, 26–30 m, 1/5/2017: 1 (MNHN IE.2023.4164) (**DNA code=IE.2023.4164**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiacantha alternata*** A.M. Clark, 1966: MRG/797, Flinders, bay side of West Head, 38° 29′S, 145° 2′E, 0–1 m, 7/3/2014, MV F173963 (**DNA code=F173963**). ***Ophiacantha indica*** Ljungman, 1867: KGR/Sled12, King George River region, 13° 53.933′S, 127° 20.6148′E, 41 m, 7/6/2013, MV F193489 (**DNA code=F193489**).

Distribution. South Africa to Southern Mozambique (84–412m), Walters Shoal (26–30 m)

Remarks. The single Walters Shoal specimen (3 mm dd) has short arms, barely 3x dd; the disc is covered in trifid disc spinelets with numerous thorns (see Mortensen 1933b) on thin perforated overlapping plates, including a few on the distal ends of radial shields, sparser ventrally; to 8 arm spines meeting dorsally, middle to lower ones with numerous thorns, upper more smooth, up to 2 segments in length, distally the lowest spine is a little curved; narrow jaw, 3 erect oral papillae, triangular oral shields, adoral shields extended radially, but separated by the first VAP; LAPs very striated; the single tentacle scale is 1/2 as long as segment, 2x as long as wide, striated with pointed or thorny tip, VAPs thin glassy and beaded. This specimen matches Mortensen's type description and figures of *O. striolata* from eastern South Africa, especially the form of the disc spines, however, the tentacle scale is larger than the minute scale figured for the type. On our phylogeny (Fig. 2b) this specimen is sister to *Ophiacantha indica* and *O. alternata* both shallow water species from the East Indo-West Pacific and Southern Australia respectively.

Ophiacantha swio **sp. nov.**

https://zoobank.org/urn:lsid:zoobank.org:act:EB5F3CF4-6A8A-488E-A7D2-CB2DA40F8320
Fig. 16k–n, 18

TYPE LOCALITY. Coral seamount, 41° 21.7673′S, 42° 54.9067′E to 41° 22.4′S, 42° 54.6′E, 740 m

TYPE MATERIAL.—JC066: stn 4-37, Coral seamount, 41° 21.7673′S, 42° 54.9067′E to 41° 22.4′S, 42° 54.6′E, 740 m, 20/11/2011, holotype: 1 (NHMUK 2025.34); paratype: 1 (MV F321042) (**DNA code=JC066-1248**); paratype: 1 (NHMUK 2025.35).

OTHER STUDY MATERIAL.—JC066: stn 8-5, Atlantis Bank, 32° 42.862′S, 57° 14.666′E to 32° 43.3′S, 57° 15.2′E, 828–994 m, 10/12/2011: 1 (NHMUK 2025.36) (**DNA code=JC066-3720**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiacantha fuscina*** O'Hara & Stöhr, 2006: in2022_v08/126, Cocos (Keeling), 11° 47.492′S, 96° 50.4342′E to 11° 47.504′S, 96° 51.5463′E, 820–822 m, 14/10/2022, identified by O'Hara (2024b), MV F308140 (**DNA code=F308140**). KANADEEP2/CP5074, Mont J, 750–901 m, 25/9/2019, MNHN IE.2019.3239 (**DNA code=IE.2019.3239**). ***Ophiacantha longidens*** Lyman, 1878: EXBODI/DW3938, Récif Pétrie, 18° 36.2′S, 164° 24′E, 505–761 m, 27/9/2011, MNHN IE.2007.6817 (**DNA code=IE.2007.6817**). SAYA/DW5429, SE Seamount, 11° 52.331′S, 62° 22.833′E, 554 m, 14/11/2022, MNHN IE.2023.4297 (**DNA code=IE.2023.4297**). ***Ophiacantha swio*** Chargos/25, Great Chargos Bank, Eagle Island, 6° 10.45369′S, 71° 18.9175′E, 483 m, 22/10/2022 (**DNA code=Chargos.646**). PAMELA-MOZ01/DW1, Glorieuses, 11° 22.756′S, 47° 16.4097′E to 11° 22.749′S, 47° 17.2302′E, 753–824 m, 28/9/2014, MNHN IE.2013.8424 (**DNA code=IE.2013.8424**). PAMELA-MOZ01/DW2, Betsiboka, 15° 21.786′S, 45° 57.4619′E to 15° 20.907′S, 45° 56.5654′E, 727–1179 m, 5/10/2014, MNHN IE.2023.4012.

COMPARATIVE MATERIAL NOT EXAMINED. ***Ophiacantha linea*** Shin & Rho, 1986: Sogwip'o, Cheju, 34° 14′N, 126° 34′E, 50–60 m (**DNA code=KC990833**).

Diagnosis. Disc covered in spinelets with a rounded pedicel, waisted stalk, and 3–7 apical thorns diverging at 2/3 spinelet height. Oral shield wide than long, smaller than adoral shields, 3–4 oral papillae. Five arms, bell-shaped DAPs, glassy VAPs, striated LAPs, up to 12 hollow arm spines, upper smooth to 3 segments in length, lower ones with some thorns, one flat rounded tentacle scale to half a segment in length.

Description. Holotype 9.5 mm dd, disc covered in separate to overlapping thin circular perforated scales that bear a multifid spinelet, with an expanded base, a long smooth pedicel and 3–7 divergent apical thorns that arise about 1/3 from the top of the spinelet; radial shields mostly hidden by plates and spinelets, only the distal tip exposed; disc spinelets continue onto lateral disc surface but sparse ventrally, reduced to a conical-shape without thorns near oral shield; oral shield lozenge-shaped, 2x as wide as long with obtuse proximal and distal angles and acute lateral ones; adoral shields smaller than oral shields, sausage-shaped with concave proximal and convex

distal sides, not meeting interradially and separated radially by the 1st VAP, both oral and adoral shields covered in speckled epidermis; exposed section of the oral plate is small triangular, contiguous, bearing 3 sometimes 4 spiniform to leaf-shaped lateral oral papillae, 2–3x as long as wide, 5 leaf-shaped teeth, larger than the oral papillae with a rounded apex; 2nd oral tentacle pore opens within jaw slit.

Arms five, to 38 mm, not moniliform, DAPs kite to bell-shaped with a convex margin and convergent latero-proximal sides, separate, distally the DAPs are more triangular, wider than long, with a slightly convex distal edge; LAPs striated with a raised distal edge proximal to the arm spines; First VAP lozenge-shaped, 2x as wide as long, 2nd–3rd VAPs pentagonal with an obtuse proximal angle, convergent laterodistal sides and a truncate distal edge, wider than long, contiguous, succeeding VAPs separate, as wide as long, with an obtuse proximal angle, concave lateral sides and convex distal margin, glassy; up to 12 arm spines, meeting dorsally on basal segments, upper ones smooth hollow, slender, tapering to a sharp point, to 3 segments in length, middle and lower spines develop small sparse thorns, particularly near the spine base, lowest ones slightly bent, bluntly pointed, as long as a segment, distally 6 arm spines, the lowermost 2 are only 1/2 as long as the segment, becoming hook-like with ventrally directed thorns only at the arm tip; one flat rounded tentacle scale, basal ones oval to slightly bent, 2x as long as wide, 1/2 as long as the VAP, becoming leaf-shaped with a pointed thorny tip, 2/3 as long as the VAP. Colour (preserved) disc grey with light brown arms and oral frame, arm and disc spines white, glassy.

Paratype and other material variations. The largest paratype (NHMUK 2025.35, 7.5 mm dd) has 10 arm spines and little spherical nodules at the end of some of the thorns on the disc spines. A second paratype (MV F321042, 6 mm dd) and the (5–6 mm) Madagascar specimens are similar. On smaller specimens (Atlantis specimen, 4.5 mm dd, and Chargos 3.5 mm), the pedicel and thorns of the disc spinelets are very slender, often trifid, or with these primary thorns bifurcated, the oral papillae number 3 and there are only 8 arm spines basally.

Paratype ossicles (MV F321042). The DAPs, VAPs and LAPs (Fig 18a–d) can have some distal transverse striations. The ear-like arm spine articulations have a larger ventral and smaller dorsal lobe joined by a central flange. The muscle and neural pores are round and easily distinguished from the surrounding stereom (Fig. 18e). The dental plate (Fig. 18g) is 2.5x as long as wide, with 5 obvious articulations for teeth, the largest ventrally; the teeth are minutely thorny (Fig. 18h); vertebrae zygospondylous, basal vertebrae are as wide as tall (Fig. 18i) with distally orientated ventral muscle attachment surfaces and the distal articulation surface with a triangular shaped epanapophysis sitting dorsal to the wing-like zygapophysis; middle arm vertebrae almost semi-circular with ventrally orientated ventral muscle attachment surfaces and a cruciform distal articulation surface (Fig. 18l), and a proximal articulation surface that looks like ‘scales of justice’ with a long zygosphene and lateral zygocondyles (Fig. 18k); tentacle scales are minute thorny at the tip and can be slightly bent on basal segments (Fig. 18o); lower arm spines are also terminally thorny, middle arm spines can have sparse thorns along their margins (Fig. 18p).

Distribution. Coral (740 m) and Atlantis (828–994 m) Seamounts, Chargos (483 m), Madagascar (727–1179 m).

Remarks. The new species is morphologically and genetically similar to *Ophiacantha longidens*, *O. fuscina*, and *O. linea*. They all have thin glassy arm plates, multifid disc spinelets, bell-shaped DAPs, and numerous arm spines. *Ophiacantha longidens* differs in having shorter simpler disc spinelets, typically with 3 short terminal thorns. *Ophiacantha fuscina* has 2–4 long slender upwardly curved thorns on the disc spinelets, often webbed at their base. *Ophiacantha linea* is the most similar to *O. swio* but differs in having shorter arms, only 3x dd, and strong striations on the LAPs and basal VAPs. It also occurs in much shallower water (50–60 m) off Korea.

Etymology. Named after the acronym of the South-West Indian Ocean (SWIO).

Ophiosabine multifida sp. nov.

https://zoobank.org/urn:lsid:zoobank.org:act:3856120E-E062-47A4-9C4C-8D46B2930B04
Fig. 16h–j, 17

TYPE LOCALITY. Atlantis Bank, 32° 42.658′S, 57° 16.371′E to 32° 42.64′S, 57° 17.58′E, 707 m

TYPE MATERIAL.—JC066: stn 8-3, Atlantis Bank, 32° 42.658′S, 57° 16.371′E to 32° 42.64′S, 57° 17.58′E, 707 m, 9/12/2011, holotype: 1 (NHMUK 2025.50); paratype: 1 (MV F321041) (**DNA code=JC066-3612**); paratype: 1 (NHMUK 2025.49); paratype: 1 (NHMUK 2025.48); paratype: 1 (NHMUK 2025.47); paratype: 1 (NHMUK 2025.51); paratype: 1 (NHMUK 2025.52).

OTHER STUDY MATERIAL.—JC066: stn 4-37, Coral seamount, 41° 21.7673′S, 42° 54.9067′E to 41° 22.4′S, 42° 54.6′E, 740 m, 20/11/2011: 1 (NHMUK 2025.46) (**DNA code=JC066-1252**).—JC066: stn 8-4, Atlantis Bank, 32° 42.43′S, 57° 16.48′E to 32° 42.17′S, 57° 14.42′E, 800 m, 10/12/2011: 1 (NHMUK 2025.53) (**DNA code=JC066-4303**).—JC066: stn 8-5, Atlantis Bank, 32° 42.862′S, 57° 14.666′E to 32° 43.3′S, 57° 15.2′E, 828–994 m, 10/12/2011: 1 (NHMUK 2025.54).

COMPARATIVE MATERIAL EXAMINED. ***Ophiosabine acanthinotata*** (H.L. Clark, 1911): Rinkai/120110(D-105)st1, Sagami Bay, 35° 6.101′N, 139° 34.284′E to 35° 6.684′N, 139° 34.061′E, 218–318 m, 10/11/2012, NSMT E11758 (**DNA code=Sagami13**). ***Ophiosabine densispina*** (Mortensen, 1936): PBBB/L84, Burwood Bank, 54° 48.468′S, 59° 40.945′W to 54° 48.618′S, 59° 41.357′W, 694–727 m, 27/8/2018, CNP-INV (**DNA code=BB16-2A**). ***Ophiosabine pentactis*** (Mortensen, 1936): US AMLR-09/101-76, South Orkney Islands, 63° 1.09′S, 52° 21.94′W to 63° 1.07′S, 52° 26.74′W, 628–627 m, 4/3/2009, MV F168830 (**DNA code=F168830**). ***Ophiosabine rosea truncata*** (Koehler, 1930): TAN0308/85, Lord Howe plateau, 34° 13.89′S, 162° 40.59′E, 515–700 m, 26/5/2003, MV F99721 (**DNA code=F99721**). ***Ophiosabine* sp.MoV.5491** SS02/2007/77, Cascade 1200m 5, 43° 55.406′S, 150° 27.889′E to 43° 55.778′S, 150° 28.352′E, 590–660 m, 10/4/2007, MV F146270 (**DNA code=MVF146270**). ***Ophiosabine vivipara*** (Ljungman, 1870): ICEFISH/18-OT14, Falkland Islands, 52° 7.07′S, 58° 4.37′W to 52° 9′S, 58° 6.07′W, 82–104 m, 28/5/2004, MV F167535 (**DNA code=F167535**).

Diagnosis. Disc covered in dense multifid spinelets with a round pedicel, waisted stalk and >10 divergent apical thorns. Oral shields wider than long but with rounded distal margin, trapezoid adoral shields occur proximal to oral shields, 4–5 oral papillae. Arms 5, DAPs triangular separate, VAPs wider than long, separate, to 10 arm spines, uppermost to smooth to 4 segments in length, lower ones with a few basal thorns, one ovate tentacle scale, to ½ the segment in length.

Description. Holotype 7.5 mm dd, disc pentagonal, covered in dense multifid spinelets that obscure the underlying scales, radial shields to 1/4 dd, distal section naked (without spinelets), spinelets with a round pedicel, waisted stalk and >10 divergent apical thorns, spinelets reduced to a conical stump near oral shield. Bursal slit open, extending from oral shield to near disc margin. Oral shields wider than long, with an obtuse angle proximally, straight laterodistal edges and a rounded to truncate distal side. Adoral shields proximal to oral shield, 2x wider than long, trapezoid, with shorter distal edge, contiguous interradially with neighbouring adoral, and radially with first ventral arm plate. Jaw as wide as long, bearing 4–5 oral papillae along each side, inner papillae spiniform to narrowly lanceolate, distal ones more thickened mid-height with a constricted base and bluntly pointed apex, 2nd papillae often the largest. Teeth 2x as long as wide, with a rounded proximal edge, up to 8 in a vertical series, the dorsalmost one often narrower.

Arms five, 7x dd (55+ mm), broadly triangular in cross section, with a narrow rounded dorsal surface and flat widened ventral surface. DAPs 1/2 as wide as arm, triangular-shaped with straight to slightly convex distal edge, glassy, separate. LAPS widened under arm ridge (arms not moniliform), meet dorsally and ventrally after the 3rd arm segment. 1st VAP wider than long but much smaller than succeeding plates, succeeding VAPs 1.5x as wide as long, 1/2 width of the arm segment, with obtuse proximal sides, incised lateral edges (around pore), and convex distal edge, glass-like or transversely striated, just separated. Up to 10 arm spines, that almost meet dorsally on proximal segments, upper spine longest, to 4 segments (2.5 mm) long, smooth, hollow, bluntly pointed; middle ones 1/2 as long as upper spines, with a few thorns at their base; lowest spines narrow to sabre-shaped, to one segment (0.7 mm) long, distally developing a terminal proximal-orientated hook-like thorn. Tentacle scale single, elliptical to ovate, 1/2 as long as the ventral arm plate, becoming narrower distally. Colour (preserved): white with pale-grey disc, some brown shading on oral/adoral shields, oral papillae, and around the base of lower proximal arm spines.

Non type variations. Disc to 9 mm dd (NHMUK 2025.46), arms 6+ times dd. Radial shields can be prominent white lines on disc, naked for their entire extent. Some distal oral papillae have a longitudinal groove and/or a truncate tip (MV F321041). Oral shields can be depressed in the centre (NHMUK 2025.53) or almost as long as wide with a minor distal lobe.

Paratype ossicles MV F321041. Vertebrae zygospondylous with a long narrow zygosphene (Fig. 17a). The external stereom of the LAP is dense proximally, with fine perforations orientated into vertical striations; distally (around the spine articulations) it is more open and regularly perforated (Fig. 17f). Spine articulations (Fig. 17g) are freestanding in a continuous vertical row on a raised distal portion of the LAP, ear-shaped, composed of a thicker dorsal and thinner ventral lobe, just merged proximally, enclosing a large round muscle opening and a smaller slit-like nerve opening. Disc plates irregular with flat perforated sections and peripheral thorny extensions (Fig. 17h).

Disc spinelets with a perforated pedicel, constricted shank and >=10 divergent apical thorns, 1/3 as long as the spinelet (Fig. 17i). Oral plate almost as high as long, proximal and distal sections strongly fused together (Fig. 17j). Radial shield hockey-stick shaped, with a distal lobe (Fig. 17m).

Distribution. SW Indian Ridge (707–994 m).

FIGURE 17. *Ophiosabine multifida* **sp. nov.** paratype MV F321041 (a–d) proximal vertebra in (a) proximal, (b) distal, (c) dorsal, and (d) ventral views, (e) lateral arm plate, proximal view, (f) lateral arm plate, lateral view, (g) inset of arm spine articulations, (h) disc plates, (i) disc spines, (j) oral plate, (k) ventral arm plate, (l) abradial genital plate, (m) radial shield, (n) tentacle scale, and (o) arm spines.

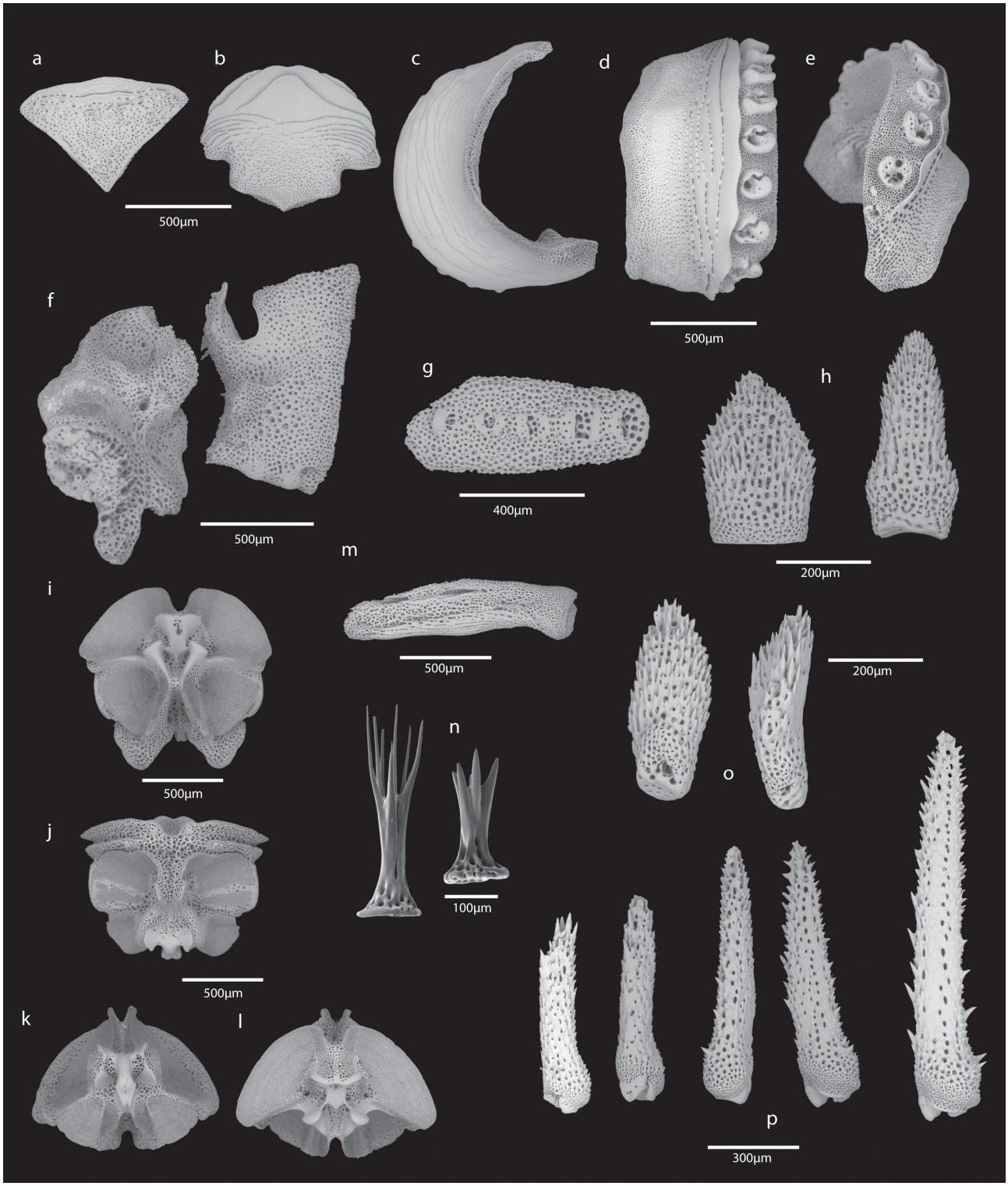

FIGURE 18. *Ophiacantha swio* **sp. nov.** paratype MV F321042 (a) dorsal arm plate, (b) ventral arm plate, (c) lateral arm plate, proximal view, (d) Lateral arm plate, lateral view, (e) lateral arm plate, ventrolateral view, (f) oral plate, separated into proximal and distal halves, (g) dental plate, (h) teeth, (i) proximal vertebra from distal angle, (j–l) middle arm vertebra from (j) dorsal, (k) proximal, (l) distal views, (m) genital scale, (n) central and smaller marginal disc spines, (o) tentacle scale, and (p) arm spines.

Remarks. This species is reminiscent of the holotype of *Ophiacantha parcita* Koehler, 1906 found off Cape Verde Islands in the equatorial Atlantic Ocean at 633–598 m depth. Both have dense spinelets with a smooth shank and multiple divergent thorns, adoral shields that are situated proximal to the oral shields, striated VAPs, blunt

hollow arm spines, the lowermost slightly curved, and oval tentacle scales. But *O. parcita* differs in having shorter fewer thorns on disc spinelets, longer oral shields with a distinct distal lobe, thicker adoral shields, and only 3 oral papillae. O'Hara & Thuy (2022) included *O. parcita* and the similar *O. notata* (Koehler, 1906) in their new genus *Ophiosabine*. We do not have DNA sequences of *O. parcita* or *O. notata*, however, genetic sequences of this new species are sister to the main *Ophiosabine* clade. *Ophiosabine multifida* and *O. parcita* have oral shields that are as wide or wider than long (especially proximally), whereas they are notably longer than wide in other species.

All three DNA samples of *O. multifida* are very similar, indicating the same species occurs on both Coral Seamount and Atlantis Bank on the SW Indian Ocean Ridge.

Etymology. Meaning multiply-divided (Latin, feminine), in reference to the numerous divergent thorns on the disc spines.

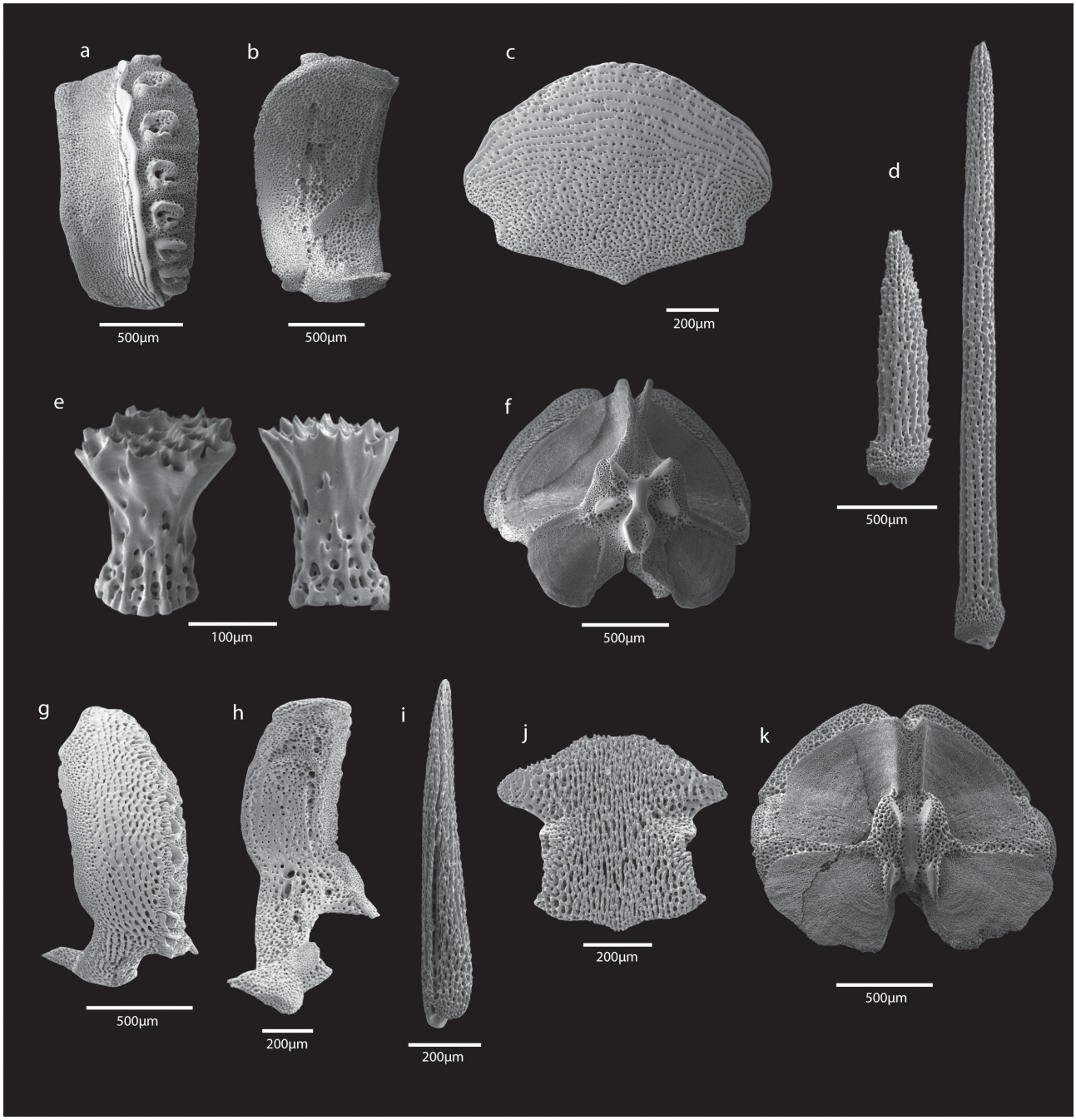

FIGURE 19. *Ophiacantha metallacta* NHMUK 2025.32 (a) lateral arm plate, exterior view, (b) Lateral arm plate, interior view, (c) ventral arm plate, (d) arm spines, (e) disc spines, (f) proximal vertebra distal view; *Ophiomyces grandis* MNHN IE.2016.1377 (g) lateral arm plate, exterior view, (h) Lateral arm plate, interior view, (i) arm spine (j) ventral arm plate, (k) proximal vertebra distal view,.

***Ophiolimna gyrei* sp. nov.**

https://zoobank.org/urn:lsid:zoobank.org:act:96E04FAF-011A-4873-B889-0D21FDB8CC2A

Fig. 21a–f, 22

? *Ophiolimna bairdii*.—O'Hara & Thuy, 2022: 28, fig. 6g–h.

TYPE LOCALITY. Coral seamount, 41° 20.708′S, 42° 55.292′E to 41° 20.99′S, 42° 55.12′E, 1300 m

TYPE MATERIAL.—JC066: stn 4-2, Coral seamount, 41° 20.708′S, 42° 55.292′E to 41° 20.99′S, 42° 55.12′E, 1300 m, 12/11/2011, holotype: 1 (NHMUK 2025.43); paratypes: 6 (NHMUK 2025.44) (**DNA code=JC066-3438**); paratype: 1 (MV F321043).

OTHER STUDY MATERIAL.—JC066: stn 4-9, Coral seamount, 41° 21.0283′S, 42° 55.145′E to 41° 21.7′S, 42° 54.8′E, 1100 m, 14/11/2011: 1 (NHMUK 2025.45).

COMPARATIVE MATERIAL EXAMINED. ***Ophiolimna gyrei*** SS01/2008/25, Huon seamounts, 44° 16.6296′S, 147° 15.9498′E, 900 m, 17/1/2008, MV F159772 (**DNA code=F159772**). SS10/2005/44, Albany, 35° 26.046′S, 118° 21′E to 35° 26.244′S, 118° 21.06′E, 900–915 m, 25/11/2005, MV F112108 (**DNA code=F112108**). TN228/J2-385-002, Z27 Seamount, Huon, 44° 14.623′S, 147° 7.339′E, 1184 m, 21/12/2008, MV F168122 (**DNA code=MVF168122**). ***Ophiolimna antarctica*** (Lyman, 1879): CEAMARC/29EV59, Eastern Antarctica, 66° 0.478′S, 143° 18.915′E to 65° 58.594′S, 143° 23.255′E, 452–480 m, 24/12/2007, MNHN IE.2009.6359 (**DNA code=IE.2009.6359**). IN2015_E02/021, Huon Commonwealth Marine Reserve, 44° 19.35′S, 147° 19′E to 44° 19.17′S, 147° 18.47′E, 2028 m, 11/4/2015, MV F227354 (**DNA code=F227354**). Talud Continental 1/11, Mar del Plata Submarine Canyon, 37° 59.258′S, 54° 41.436′W, 854 m, 11/8/2012, CNP-INV (**DNA code=L11C2**). ***Ophiolimna bairdi*** (Lyman, 1883): ME 85- 3/967, South Iceland, Iceland Basin, 60° 2.77′N, 21° 28.5396′W to 60° 2.78′N, 21° 30.0696′W, 2750 m, 29/8/2011, DZMB-HH 58721 (**DNA code=DZMB37562C**). Ricker/TC2006-012, Cape Scott; West of Cape Scott, 50° 36.45′N, 129° 4.37′W to 50° 35.9′N, 129° 2.3′W, 1847–1867 m, 11/10/2006, RBCM 007-00030-002 (**DNA code=RBCM7-30-2**). TAN0803/17, Seamount 1 Spastic Spider, Macquarie Ridge. New Zealand EEZ, 48° 32.93′S, 164° 57.75′E to 48° 32.66′S, 164° 58.04′E, 1318–1327 m, 30/3/2008, NIWA 43081 (**DNA code=TOH_0349**). ***Ophiolimna perfida*** (Koehler, 1904): ATIMO VATAE/CP3595, Sud Pointe Barrow, 25° 35′S, 44° 15′E, 821–910 m, 12/5/2010, MNHN IE.2007.4348 (**DNA code=TOH274-IE.2007.4348**). IN2022_V09/106, Gascoyne Marine Park. Site:031, 22° 11.766′S, 113° 38.9403′E to 22° 12.608′S, 113° 38.4044′E, 712–730 m, 7/12/2022, MV F309523 (**DNA code=F309523**). ***Ophiolimna placentigera*** (Lyman, 1880): KANADEEP2/CP5060, Slope, 22° 15.6432′S, 167° 37.5174′E, 2018–2065 m, 22/9/2019, MNHN IE.2019.3146 (**DNA code=IE.2019.3146**). ***Ophiolimna sp.MoV.7379*** BIOPAPUA/CP3672, Nord de Rabaul, 4° 4′S, 151° 50′E, 702–724 m, 24/9/2010, MNHN IE.2023.4067 (**DNA code=BP26**).

Diagnosis. Disc covered in dense spherical to conical granules with a few longer spines in the centre of the disc, radial shields hidden. Disc granules present on oral frame, 4 oral papillae, distal papilla small and round, oral shields triangular. Five arms, DAPs triangular and separated, LAPs striated but arms not moniliform, VAPs axe-head shaped, separate, striated, 4 smooth hollow arm spines, upper to 2 segments in length, with a flattened ventral side, one oval tentacle scale.

Description. Holotype 4 mm dd, disc covered in very thin irregular scales which are in turn covered by dense round to conical granules, interspersed with taller sharp spines on the central part of the dorsal disc, 4x as high as wide, radial shields hidden by granules, 4x as long as wide, bar-like with slightly expanded distal section, separate; ventral granules smaller than dorsal, genital slits wide, extending from the oral shields to disc margin, disc granules also covering the oral frame except for a small naked patch in the centre of the oral shields; 4 round oral papillae, inner 2x higher than wide, some pointed, distal ones as high as wide, round, separate; 3 pointed teeth, upper two can be horizontally offset from each other, widest at mid-height, 2x as large as oral papillae, 2nd oral tentacle pore opening inside of slit between the distal two oral papillae.

Arms five, DAPs triangular, 2x as wide as long, widely separated, a few disc granules on the basal plate; LAPs with a notable spine flange, but arms not moniliform, vertically striated, widely contiguous dorsally and ventrally, ventral side constricted thus forming the proximal angle of the VAPs; first VAP obscured by granules, 2nd VAP roughly rhomboid, with wider straight to slightly convex distal edge, incised lateral sides (for pore) and with a very obtuse angle proximally, 3rd VAP axe-head shaped, wider than 2nd, all VAPs widely separate, transversely striated; 4 arm spines, hollow, semi-circular in cross section, with a tapering bluntly pointed apex, microscopically

perforated and furrowed near tip, basal dorsalmost one to 2 segments in length, lower ones 1–1.5 segments long, distal arm spines not hooked; one oval tentacle scale, 2x as long as wide, just shorter than the VAP, thin and glassy, longitudinally striated, orientated distolaterally, becoming more pointed after the first few segments. Colour (preserved) pale brown, arm spines with dark patch near base.

Paratypes 2–4 mm dd, disc spines continue to near margin one some specimens, one paratype has 5 arm spines on 2nd free arm segment. Ventral granules were removed from one paratype which revealed triangular oral shields, as wide as long, roughly triangular adoral shields, expanded distally, meeting proximally at interradius, and small rhomboid first VAP, widest proximally at end of jaw slit. Other material: F112108 (5 mm dd) has 5 arm spines on the first 2 free segments, the upper one is thickened as well as longer; lacking tall disc spines, but having elongated granules, distal oral papilla can be a little widened but not scale-like.

Paratype ossicles, LAPs (Fig. 22a–c) squarish in lateral view and curved over and under arm to meet centrally, with external vertical striations, often bordered by a row of minute thorns, wavy distal margin, more open stereom near arm spines, with large prominent ear-shaped arm spine articulations, with expanded curved distal lobe and smaller ridge-like ventral lobe, with large central muscle attachment and smaller distal nerve pore; vertebrae semi-circular in cross section (Fig. 22h–i) with spindle-shaped ventral groove outlined by ridges, vertebrae wider proximally than distally, zygospondylous articulation, v-shaped processes on the dorsal surface; DAPs (Fig. 22d) and VAPs (Fig. 22e) with similar transverse striations to LAPs, arm spines semi-cylindrical with ventral side flattened perforated and grooved apically (Fig. 22r, left), and the curved side transversely striated (Fig. 22r, right), a few thorns apically; disc spines conical with thorny striations and relatively few perforations; oral plate complex 2x as long as tall; dental plate small and oblong, with 3 tooth articulations.

Distribution. S Australia (900–1184 m), Coral seamount (1100–1300 m)

Remarks. DNA evidence (Fig. 2b) indicates the Coral seamount specimens are part of a lineage that is divergent from other *Ophiolimna* species known from the Southern Ocean including *O. antarctica* and *O. bairdi*. This new lineage also occurs off Southern Australia, and possibly around the Amsterdam and St Paul Islands (O'Hara & Thuy 2022). The Coral seamount specimens appear to differ from *O. antarctica* and *O. bairdi* by having asymmetrical arm spines that have a flattened ventral edge, being more densely granulated on oral and adoral shields, and having small rounded distal oral papillae. *Ophiolimna antarctica* is further differentiated by lacking spines on the disc surface. Larger specimens (to 10 mm dd) of *O. antarctica* and *O. bairdi* can have up to 7 arm spines. Specimens from the tropical Indo-Pacific (e.g. BP26, and O'Hara & Stöhr 2006) are another undescribed species (*Ophiolimna* sp.MoV.7379, see O'Hara & Thuy 2022).

Etymology. Named after the South Indian Gyre that transports ophiuroid larvae eastward across the Indian Ocean.

Ophiomitrella nudextrema (H.L. Clark, 1939)

Ophiacantha nudextrema Clark, H.L., 1939: 44–45, fig. 6.
Ophiomitrella nudextrema.—O'Hara & Stöhr, 2006: 126, fig. 18q.

STUDY MATERIAL.—MD208: stn DW4881, Walters shoal, Pentes, 33° 16.87′S, 43° 50.69′E to 33° 16.24′S, 43° 50.0599′E, 377–382 m, 2/5/2017: 1 (MNHN IE.2023.4175) (**DNA code=IE.2023.4175**).—MD208: stn DW4890, Walters Shoal, Pentes, 33° 8.7′S, 43° 58.16′E to 33° 8.77′S, 43° 59.13′E, 492–588 m, 4/5/2017: 1 (MNHN IE.2016.1357).

COMPARATIVE MATERIAL EXAMINED. ***Ophiomitrella nudextrema*** (H.L. Clark, 1939): John Murray/157, Maldive Is, 4° 43.48′N, 72° 55.24′E to 4° 44′N, 72° 54.18′E, 229 m, 6/4/1934, holotype, NHMUK 1948.5.26.32. ATIMO VATAE/CP3614, Sud Cap Sainte Marie, 26° 14′S, 45° 9′E, 250–300 m, 14/5/2010, MNHN IE.2007.4178 (**DNA code=IE.2007.4178**). ***Ophiomitrella tenuis*** (Koehler, 1904): EBISCO/DW2607, Plateau des Chesterfield, 19° 33′S, 158° 40.0003′E, 400–413 m, 18/10/2005, MNHN IE.2013.6313 (**DNA code=IE.2013.6313**).

Distribution. Maldives (229 m); Madagascar (250–333 m); Walters Shoal (377–588 m).

Remarks. The 3 mm dd holotype of this species is characterised by a pentagonal disc; separate broadly-triangular radial shields, with slightly concave sides, naked; disc granules small stumps, centrally becoming trilobed with minute terminal thorns, disc stumps near the marginal interradial midline become lengthened; to 8 short slender arm spines, uppermost to 2 segments in length, lowermost with some thorns; LAPs striated; 3–4 lateral oral papillae; oral shields 2x as wide as long; one oval tentacle scale with a rough tip, to 1/2 segment in length. The MD208 (2–3.5

mm dd) specimens are similar, except the smallest (IE.2016.1357, 2 mm dd) has only one elongated disc stump on the interradial slide of the radial shields. The ATIMO VATAE specimen has some taller disc stumps near the centre of the disc also. This species is sister to *Ophiomitrella tenuis* from the East Indo-West Pacific.

Ophiolebes* cf. *paulensis

Fig. 20a–c

STUDY MATERIAL.—JC066: stn 4-9, Coral seamount, 41° 21.0283′S, 42° 55.145′E to 41° 21.7′S, 42° 54.8′E, 1100 m, 14/11/2011: 1 (NHMUK 2025.42) (**DNA code=JC066-3862**).

Description. Disc petaloid, incised interradially, 7 mm dd, disc scales round, thin and perforated, obscured by a layer of skin and spines; disc spines robust sparse, central spines to 0.6 mm long, 3x as long as wide, slightly capitate (due to thicker skin at tip), lateral spines more like slightly elongated granules, absent for most of ventral disc; disc is distorted but triangular distal end to the radial shields appear to be naked,

Oral shields as long as wide, widest proximally with an obtuse angle, and acute proximolateral angles, rounded distally; adoral shields short and thick, positioned proximal to oral shields, rectangular to rhomboid, 2x as wide as long, fully contiguous interradially, separated radially by VAP1, beaded surface; jaw short and wide, bearing spiniform bluntly pointed teeth and 2 similar-shaped lateral oral papillae, the outer with a slightly roughened tip, 3x as long as wide. Genital slits open from oral shield to disc margin.

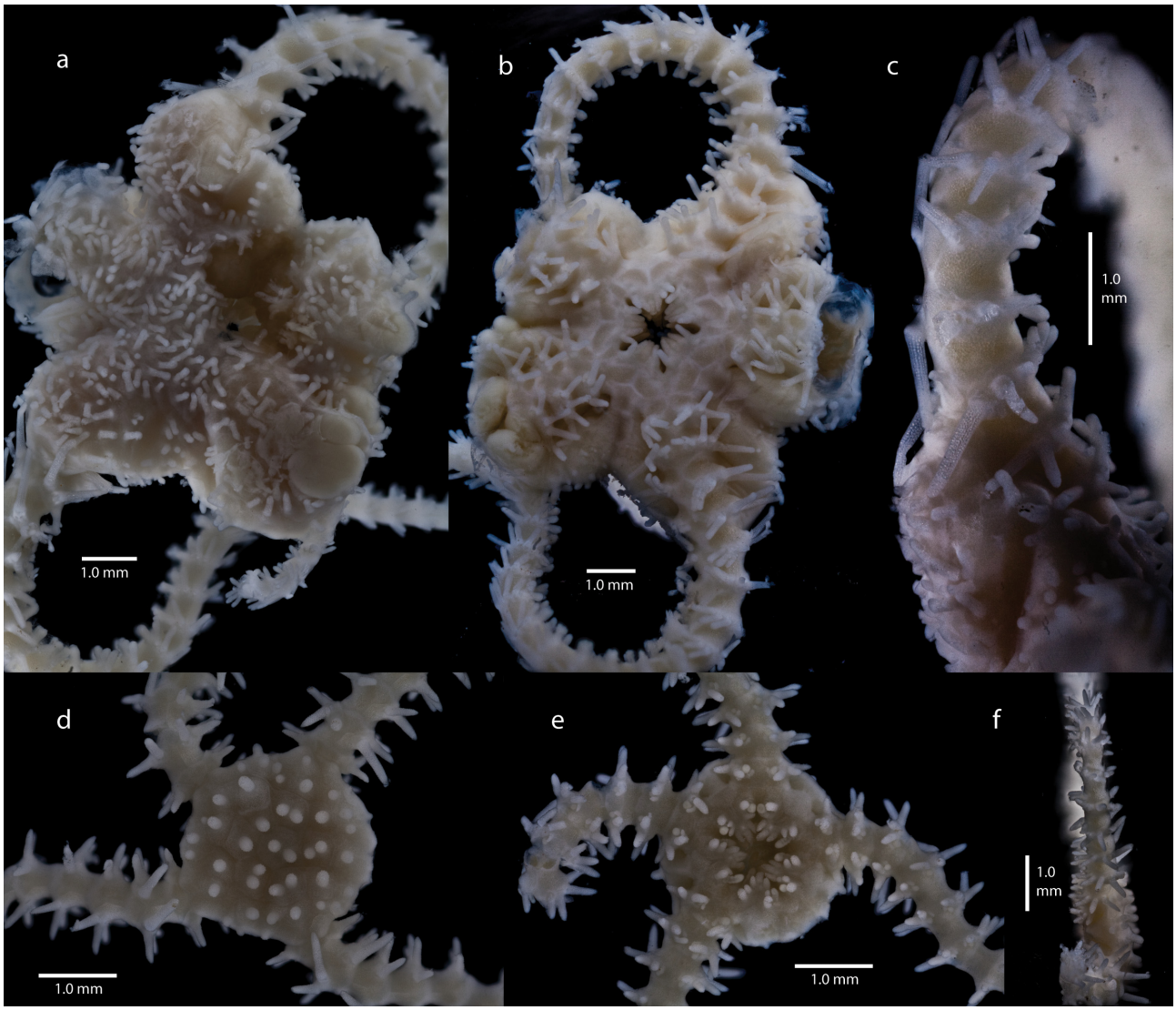

FIGURE 20. (a–c) *Ophiolebes* cf *paulensis* NHMUK 2025.42 (a) dorsal, (b) ventral, (c) lateral view of arm base; (d–f) *Ophiosemnotes conferta* NHMUK 2025.55 (d) dorsal, (e) ventral, (f) arm base.

Arms curled under disc, 2x dd; DAPs ovoid, 1.5x longer than wide, widest distally, with rounded margins, separated by a small decalcified section; VAP1 2x as long as wide, slightly widened proximally, separated from VAP2 by LAP1s that meet on the ventral midline, VAP2-5 as long as wide, with a rounded distal margin and acute proximal angle, separated; 3 arm spines on first arm segment, 4 on next 2 segments under the disc, 5 arm spines at beginning of free arm, uppermost longest to 1.5 segments in length, upper 3 spines slightly tapering to a blunt tip, lowest 2 spines slightly capitate (due to thick skin at tip). 0.7x segment in length, distally can be 6 arm spines, all less than a segment long, upper one a little longer, lower arm spines with some thorns but generally hidden by a layer of thick skin; tentacle scales apparently absent (the small basal podia can look like tentacle scales). Colour: pale brown.

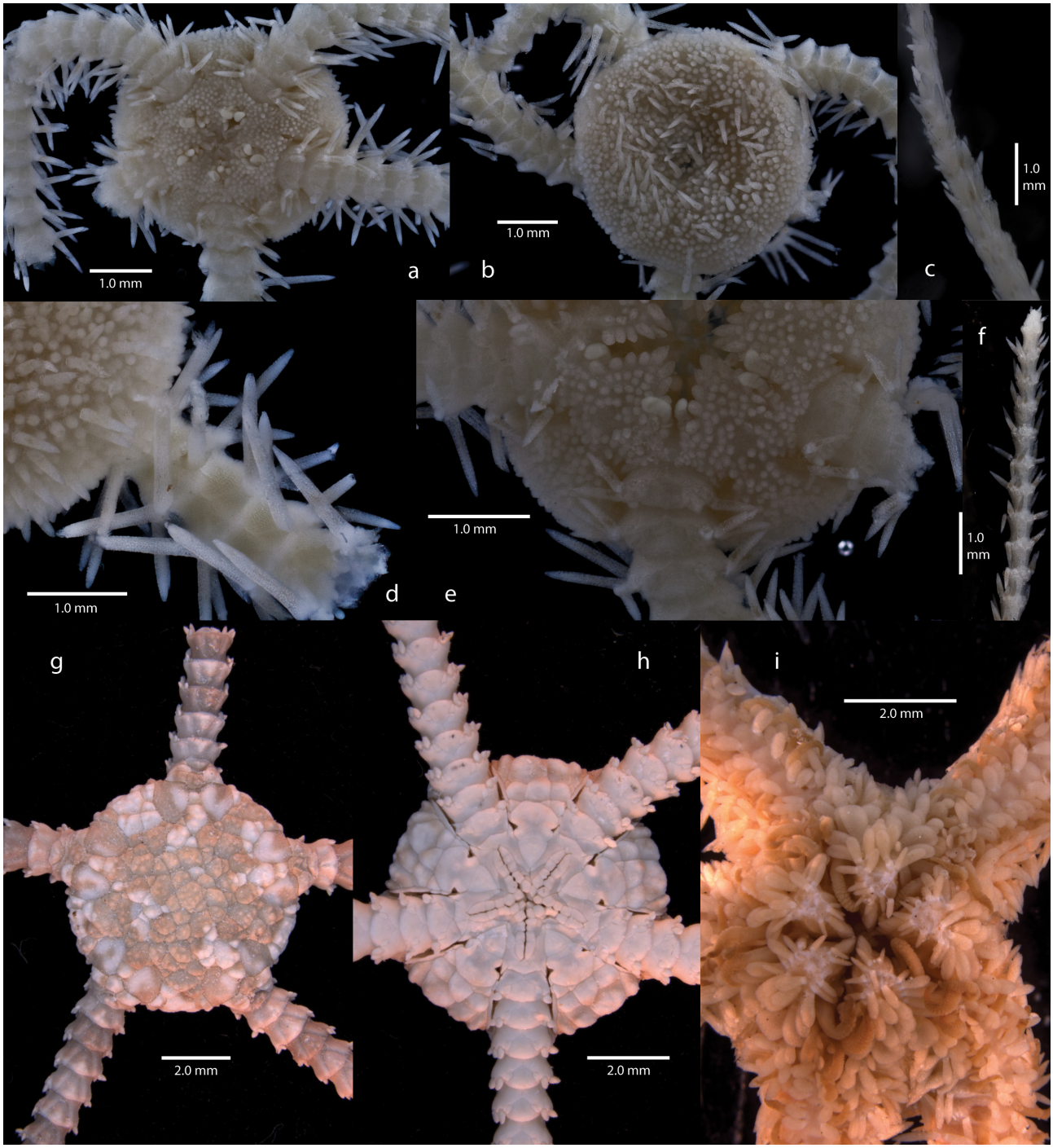

FIGURE 21. (a–c) *Ophiolimna gyrei* **sp. nov.** holotype NHMUK 2025.43 (a) dorsal, (b) ventral, (c) lateral view of mid arm; (d–f) paratype NHMUK 2025.44 (d) dorsal, (e) ventral, (f) arm tip. (g–h) *Ophiocypris* cf *tuberculosus* MNHN IE.2016.1365 (g) dorsal disc, (h) ventral disc. (i) *Ophiomyces grandis* MNHN IE.2016.1372, ventral disc (some abrasion damage on proximal jaws).

Distribution. Coral Seamount (1100 m).

Remarks. This species is very similar to *O. paulensis* O'Hara & Thuy, 2022 from the St Paul/Amsterdam islands. Many of the features that look different are due to preservation (the types were dried). In particular, the capitate disc and lower arm spines on the JC066 specimen is due to thickened skin at the spine tip. However, there are some real differences as well. The types had 3 oral papillae on longer jaws and longer sausage-shaped adoral shields. More material is required to assess the importance of these variations. The South African species *Ophiosemnotes corynephora* (H.L. Clark, 1923) has superficially similar disc spines but differs in having wide exposed radial shields.

Ophiomoeris obstricta (Lyman, 1878)

Ophioceramis (?) obstricta Lyman, 1878: 124–125, pl. 6(164–166).—Lyman, 1882: 26–27, pl. 11(1–3).
Ophiomoeris obstricta.—Koehler, 1904: 17.—Koehler, 1922a: 38–39, pl. 5(3–4).—O'Hara & Stöhr, 2006: 120–123, fig. 16a–g.—Martynov, 2010b: 124, fig. 7g–h, 13k, 16q, 36e–h.—O'Hara, 2024b: 48, fig. 48.
Ophiurases obstrictus.—Clark, H.L., 1911: 250–252, fig. 122.
Ophiomoeris parva Clark, H.L., 1939: 39–41, fig. 4–5 [according to O'Hara & Stöhr, 2006].
Ophiomoeris cf obstricta.—Stöhr, 2011: 23–24, fig. 8c–e.

STUDY MATERIAL.—MD208: stn CP4882, Walters shoal, Pentes, 33° 16.67′S, 43° 50.4899′E to 33° 16.03′S, 43° 49.84′E, 371–399 m, 2/5/2017: 6 (MNHN IE.2023.4159) (**DNA code=IE.2023.4159**).—MD208: stn DW4885, Walters shoal, Pentes, 33° 16.68′S, 43° 54.18′E to 33° 16.61′S, 43° 54.9301′E, 272–380 m, 3/5/2017: 1 (MNHN IE.2016.1361).—MD208: stn DW4887, Walters Shoal, Pentes, 33° 17.23′S, 43° 55.44′E to 33° 16.98′S, 43° 56.6899′E, 599–640 m, 3/5/2017: 1 (MNHN IE.2016.1366).—MD208: stn DW4896, Walters Shoal, Pentes, 33° 7.24′S, 43° 50.3199′E to 33° 6.71′S, 43° 50.8099′E, 325–357 m, 5/5/2017: 1 (MNHN IE.2013.17158).

COMPARATIVE MATERIAL EXAMINED. ***Ophiomoeris exuta*** Stöhr, 2011: EXBODI/CP3848, Banc Durand, 22° 3.5′S, 168° 41.6′E, 430–440 m, 13/9/2011, MNHN IE.2023.4007 (**DNA code=CP3848**). ***Ophiomoeris obstricta*** (Lyman, 1878): BIOPAPUA/CP3737, Au large des îles et récifs Lancasay, 8° 15′S, 150° 45′E, 587 m, 9/10/2010, MNHN IE.2007.2936 (**DNA code=BP37**). Chargos/10, Peros Banhos, Ile de Pierre, 5° 19.118′S, 71° 43.502′E, 250 m, 18/10/2022 (**DNA code=Chargos.262**). IN2018_V06/105, Baseline_29, 44° 5.622′S, 146° 41.298′E to 44° 5.922′S, 146° 40.26′E, 541–560 m, 8/12/2018, MV F267820 (**DNA code=F267820**). IN2021_V04/5, Christmas Island SE, 10° 34.22′S, 105° 41.376′E to 10° 33.791′S, 105° 41.6358′E, 643–997 m, 6/7/2021, identified by O'Hara (2024b), MV F305517 (**DNA code=F305517**). MIRIKY/CP3251, au large de Majumga, 15° 23.16′S, 45° 57.75′E to 15° 24.55′S, 45° 56.5602′E, 609–620 m, 8/7/2009, MNHN IE.2007.398 (**DNA code=IE.2007.398**). SAYA/CP5436, SW Saya de Malha, 11° 49.972′S, 60° 55.632′E to 11° 49.802′S, 60° 56.275′E, 312–300 m, 16/11/2022, MNHN IE.2023.4267 (**DNA code=IE.2023.4267**). TAN1206/99, Site SM3b, NE of summit, Clark Seamount, Southern Kermadec Ridge, 36° 26.718′S, 177° 50.352′E to 177° 50.418′N, 36° 26.568′W, 850–927 m, 24/4/2012, MV F188867 (**DNA code=02W2Y**).

Distribution. NW Pacific (50–470 m), W Indian Ocean (202–1206 m), E Indo-W Pacific (35–1901 m), S America (180–471 m), S Africa (272–640 m), S Australia (145–877 m), New Zealand (146–1190 m), Walters Shoal (272–640 m).

Remarks. O'Hara & Stöhr (2006) synonymised several Indo-Pacific species of *Ophiomoeris* as their diagnostic characters overlapped. However, subsequent DNA data has revealed much sequence variation within this complex and it is likely that cryptic species are present. The sequenced MD208 sample clusters with a sample from the Saya de Malha Bank, however, specimens from Madagascar and Chargos are distinct and the geographic and bathymetric range of these lineages are unclear. In the interim we continue to use the name *Ophiomoeris obstricta* for the complex.

The current specimens (to 3.2 mm dd) can have rounded granules on the disc, between the proximal ends of the radial shields and sometimes in the centre of the disc. There are 5–6 arm spines, the upper longest, to longer than a segment, and meet dorsally on the first free segment. The radial shields are separated distally by a triangular plate. Although, the upper arm spine is longer than the others on these specimens, they do not reach the length (3x segment length) shown in the type series of *O. parva* H.L. Clark, 1939 from the Maldives, which also lacked disc granules.

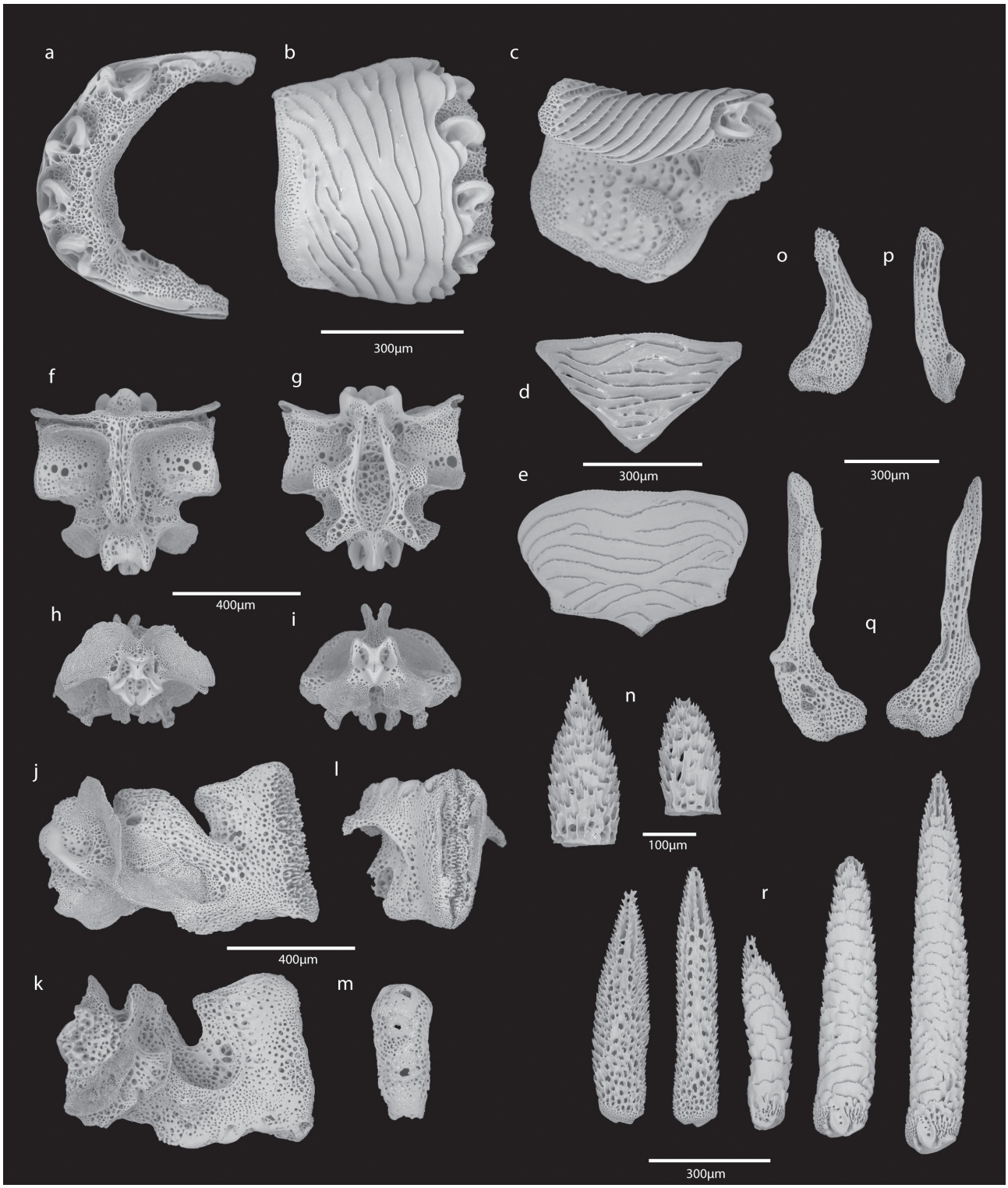

FIGURE 22. *Ophiolimna gyrei* **sp. nov.** paratype MV F321043 (a–c) lateral arm plate from (a) distal, (b) lateral and (c) dorsal views, (d) dorsal arm plate, (e) ventral arm plate, (f–i) proximal vertebra from (f) dorsal, (g) ventral, (h) proximal, (i) distal views, (j–l) oral plate from (j) interradial, (k) radial and (l) proximal views, (m) dental plate, (n) disc spines, (o) abradial genital plate, (p) radial shield, (q) adradial genital plate, (r) arm spines.

Ophiosemnotes conferta **(Koehler, 1922)**
Fig. 20d–f

Ophioripa conferta Koehler, 1922b: 19–21, pl. 85(9–13).—Rowe & Pawson, 1977: 350.
Ophiomitrella falklandica Mortensen, 1936: 256–259, figs 8c–d, pl. 7(5) [according to O'Hara, 1990].
Ophiomitrella conferta.—Madsen, 1967: 127.—O'Hara, 1990: 299–300, fig. 2c–d, f–g.—O'Hara & Stöhr, 2006: 90–92, fig. 10f–h, 18n–o.
Ophiosemnotes conferta.—O'Hara & Thuy, 2022: 20, fig. 7a–b.

STUDY MATERIAL.—JC066: stn 4-2, Coral seamount, 41° 20.708′S, 42° 55.292′E to 41° 20.99′S, 42° 55.12′E, 1300 m, 12/11/2011: 1 (NHMUK 2025.55).

Distribution. E Indo-W Pacific (480–1019 m), S America (79–1738 m), Kerguelen (247–247 m), S Australia (640–2340 m), New Zealand (27–1365 m), Antarctica (74–835 m), St Paul/Amsterdam Is (420–1680 m), Coral seamount (1300 m).

Remarks. This specimen is small (2.5 mm dd) and we were unable to obtain a DNA sequence. The radial shields are contiguous distally, it has the classic robust stumps of this species, 4 arm spines, the upper longest, and 3–4 oral papillae. *Ophiosemnotes conferta* is a brooder and it is likely to contain cryptic species (O'Hara & Thuy 2022).

Family Ophiocomidae

Breviturma pusilla **(Brock, 1888)**
Fig. 23

Ophiomastix pusilla Brock, 1888: 499–500.—Koehler, 1905: 65, pl. 6(6–10), 13(3).
Ophiocoma pusilla.—Clark, H.L., 1921: 131.—Devaney, 1970: 25–28, fig. 26, 29.—Clark, A.M. & Rowe, 1971: 86–87,.—Clark, A.M. & Courtman-Stock, 1976: 174, fig. 190.—Clark, A.M., 1976: 259–260.—Cherbonnier & Guille, 1978: 173–174, pl. 11(3–4).—Sloan, Clark & Taylor, 1979: 106.—Clark, A.M., 1980: 544.—Price & Rowe, 1996: 77.—Stöhr, 2011: 36–38, fig. 17l–m.
Ophiocoma aegyptica Soliman, 1991: 81–86, fig. 2–6 [according to Olbers & Samyn, 2012].
Breviturma pusilla.—O'Hara *et al.*, 2019a: 74.—Olbers *et al.* 2019: 169–171, fig. 162–163.

STUDY MATERIAL.—MD208: stn WS03, Walters shoal, Zone sommitale Sud-Ouest, 33° 12.25′S, 43° 50.818′E, 40 m, 30/4/2017: 1 (MNHN IE.2016.1340) (**DNA code=IE.2016.1340**).—MD208: stn WB05, Walters shoal, Zone sommitale Sud, 33° 15.12′S, 43° 54.514′E, 26–30 m, 1/5/2017: 1 (MNHN IE.2023.4162).—MD208: stn WB09, Walters shoal, Zone Sommitale Nord Ouest, 33° 13.767′S, 43° 55.7751′E, 27–30 m, 4/5/2017: 8 (MNHN IE.2023.4165), 1 (MNHN IE.2016.1351).—MD208: stn WB10, Walters shoal, Zone Sommitale Nord Ouest, 33° 9.131′S, 43° 51.7939′E, 30 m, 6/5/2017: 2 (MNHN IE.2016.1352).

COMPARATIVE MATERIAL EXAMINED. ***Breviturma pusilla*** (Brock, 1888): BIOLUM/18, Lizard Is, Coconut Beach, 14° 40.8′S, 145° 28.5′E, 2–5 m, 25/10/2005, MV F109823 (**DNA code=F109823**). SAYA/YB01, NE Saya de Malha, 10° 22.75′S, 62° 7.75′E, 24 m, 10/11/2022, MNHN IE.2023.4347 (**DNA code=IE.2023.4347**).

Distribution. W Indian Ocean (0–70 m), E Indo-W Pacific (0–120 m), S Africa (11–20 m), Lord Howe Island (4–21 m), Walters Shoal (26–40 m).

Remarks. These diminutive specimens (maximum 7 mm dd) are identifiable as *B. pusilla*, having relatively narrow dorsal arm plates, hollow non-alternating arm spines, 3–4 oral papillae and lacking granules near the radial shields (Devaney 1970). The single Indo-Pacific DNA sample we have sequenced is sister to both Indian Ocean samples. Sibling species are common across the Indian Ocean, including in the Ophiocomidae (Boissin *et al.* 2017; O'Hara *et al.* 2019a), but more samples are required before species boundaries can be defined in this instance. The name *B. aegyptica* (type locality Red Sea) is available if all Indian Ocean specimens prove to be conspecific. *Breviturma pusilla* is a shallow water species and historical records below 100 m need to be verified.

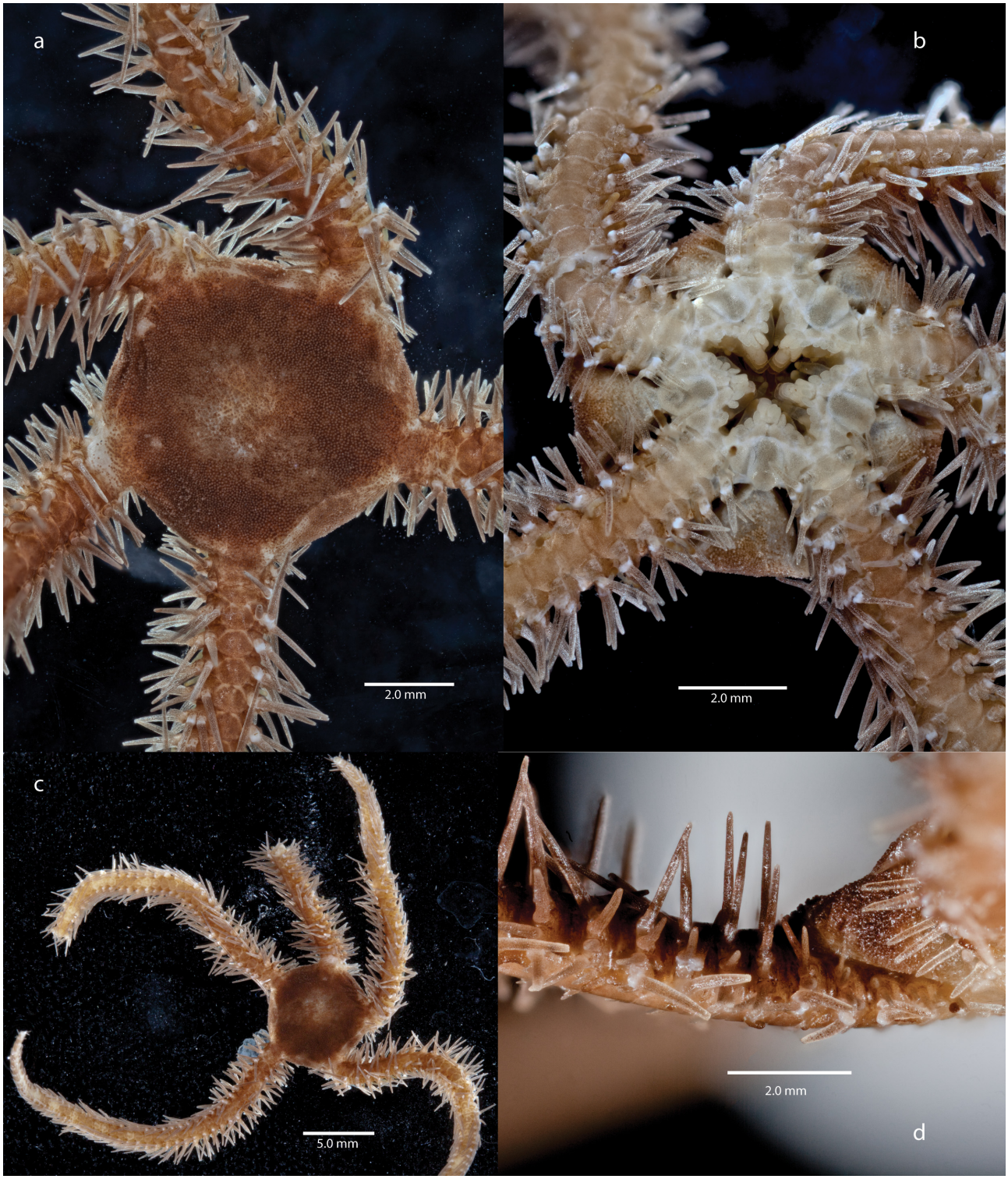

FIGURE 23. *Breviturma* cf. *pusilla* MNHN IE.2023.4165 (a) dorsal, (b) ventral, (c) whole body, (d) lateral arm base.

Family Ophiodermatidae

Ophiocypris cf. *tuberculosus*

Fig. 21g–h

Ophiocypris sp.—Guille & Vadon, 1986: 175, pl. 1(5–6).

STUDY MATERIAL.—MD208: stn DW4887, Walters Shoal, Pentes, 33° 17.23′S, 43° 55.44′E to 33° 16.98′S, 43° 56.6899′E, 599–640 m, 3/5/2017: 1 (MNHN IE.2016.1365).—MD208: stn DW4891, Walters shoal, Pentes, 33° 10.8′S, 44° 0.97′E to 33° 11.59′S, 44° 0.97′E, 650–653 m, 4/5/2017: 1 (MNHN IE.2016.1354).—MD208: stn CP4903, Walters Shoal, Pentes, 33° 10.78′S, 44° 0.1499′E to 33° 11.44′S, 44° 0.6601′E, 620–642 m, 7/5/2017: 1 (MNHN IE.2013.17135) (**DNA code=IE.2013.17135**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiocypris* cf. *tuberculosus*** MIRIKY/DW3179, entre Nosy-bé et Banc du Leven, 12° 57.96′S, 48° 9.4302′E to 12° 59.09′S, 48° 9.4698′E, 362–220 m, 25/6/2009, MNHN IE.2007.1218 (**DNA code=IE.2007.1218-2**). SAYA/DW5430, SW Saya de Malha, 11° 46.521′S, 61° 9.254′E to 11° 46.359′S, 61° 9.558′E, 267–265 m, 15/11/2022, MNHN IE.2023.4213 (**DNA code=IE.2023.4213**). ***Ophiocypris megaloplax*** (Mortensen, 1936): TAN0308/154, West Norfolk Ridge, Wanganella Bank, 34° 37.2′S, 168° 57.03′E to 34° 37.683′S, 168° 58.1′E, 521–539 m, 3/6/2003, MV F101790. ***Ophiocypris tuberculosus*** Koehler, 1930: Rinkai/120110(D-105)st1, Sagami Bay, 35° 6.101′N, 139° 34.284′E to 35° 6.684′N, 139° 34.061′E, 218–318 m, 10/11/2012, NSMT E11798 (**DNA code=Sagami8**). TAN0308/43, North Norfolk Ridge, 26° 25.94′S, 167° 10.87′E to 26° 26′S, 167° 9.63′E, 750–774 m, 18/5/2003, MV F99771. TAN1206/90, Site SM2ac, Whakatane Seamount, Southern Kermadec Ridge, 36° 47.37′S, 177° 27.252′E to 177° 27.36′N, 36° 47.4′W, 1160–1155 m, 23/4/2012, MV F193426 (**DNA code=02VA4**).

Distribution. W Indian Ocean (220–362 m), S Africa (599–653 m), Walters Shoal (599–653 m).

Remarks. The size of the MD208 specimens is 3.3 (IE.2016.1354), 8.5 (IE.2016.1365) and 10 mm dd (IE.2013.17135). The arms on specimen IE.2016.1365 are almost entire, extending 3.5x dd. The oral shields are broken into proximal and distal halves (Fig. 21h), characteristic of the genus *Ophiocypris*. There are 3, rarely 4, very short arm spines. The disc is covered with coarse polygonal multicoloured plates that are covered in some nodules (Fig. 21g). This is characteristic of the species *O. tuberculosus*. However, as Guille & Vadon (1986) have observed, SWIO specimens differ a little from the Indonesian types. On the figured 9 mm holotype, the disc tubercles are small and quite dense, with up to 20 on larger plates. There are even more on the radial shields, where the outer ones form 1–2 regular rings of granules. This is similar to specimens from the Tasman Sea (MV F99771), where they measure 0.1 mm in diameter. On the SWIO specimens they are much fewer (to 8) and larger (to 0.2 mm) on the disc plates, although smaller on the radial shields. The SWIO specimens have only one elongate tentacle scale that sits in a notch between the LAP and VAP, whereas the type is described as having two. However, that is possibly a mistake, as the Tasman Sea animals also have one. Unfortunately, the photo of the type is unclear here and we have not physically examined any types. Until specimens from Indonesia are examined or sequenced, we refrain from describing the SWIO specimens as a new species.

The disc plates nodules are less obvious on the smallest SWIO specimens which also have only 2 arm spines on many segments. This approximates the other *Ophiocrypis* species *O. megaloplax* which has flat disc plates, 2 arm spines and one tentacle scale. The type of this New Zealand species is also small (3 mm dd), and this opens up the possibility that *O. megaloplax* is the juvenile stage of *O. tuberculosus*. However, the arms are also very short, up to 2x dd, whereas *O. tuberculatus* has much longer arms, over 3x dd, and we maintain them here as separate species.

Family Ophiomyxidae

Ophioconis cupida Koehler, 1905

Ophioconis cupida Koehler, 1905: 15–16, pl. 1(19–20).—Clark, A.M. & Rowe, 1971: 88–89, 127, pl. 21(4).—Cherbonnier & Guille, 1978: 222–223, pl. 16(3–4).—Stöhr *et al.*, 2008: 556.—Olbers *et al.*, 2015: 105–107, pl. 7C–D.—Olbers *et al.* 2019: 157–158, fig. 148–149.
Ophiurodon cupida.—Matsumoto, 1915: 85.—Matsumoto, 1917: 315.—Clark, H.L., 1918: 332–333.
Ophiurodon cupidum.—Clark, H.L., 1939: 95–96.

STUDY MATERIAL.—MD208: stn DW4881, Walters shoal, Pentes, 33° 16.87′S, 43° 50.69′E to 33° 16.24′S, 43° 50.0599′E, 377–382 m, 2/5/2017: 1 (MNHN IE.2023.4169).—MD208: stn DW4885, Walters shoal, Pentes, 33° 16.68′S, 43° 54.18′E to 33° 16.61′S, 43° 54.9301′E, 272–380 m, 3/5/2017: 1 (MNHN IE.2023.4161) (**DNA code=IE.2023.4161**).—MD208: stn DW4889, Walters shoal, Pentes, 33° 9.7′S, 43° 57.1099′E to 33° 9.12′S, 43° 57.9899′E, 353–465 m, 3/5/2017: 1 (MNHN IE.2023.4008).—MD208: stn DW4890, Walters Shoal, Pentes, 33° 8.7′S, 43° 58.16′E to 33° 8.77′S, 43° 59.13′E, 492–588 m, 4/5/2017: 1 (MNHN IE.2016.1356) (**DNA**

code=IE.2013.1356).—MD208: stn DW4896, Walters Shoal, Pentes, 33° 7.24′S, 43° 50.3199′E to 33° 6.71′S, 43° 50.8099′E, 325–357 m, 5/5/2017: 1 (MNHN IE.2016.1063).

COMPARATIVE MATERIAL EXAMINED. ***Ophioconis cupida*** Koehler, 1905: SAYA/DW5423, SE Saya de Malha, 11° 26.777′S, 62° 0.864′E to 11° 27.116′S, 62° 0.771′E, 210–198 m, 12/11/2022, MNHN IE.2023.4223 (**DNA code=IE.2023.4223**). ***Ophioconis forbesi*** (Heller, 1862): MIWA/2012404-SL34, 25° 41.436′N, 15° 10.944′W, 111 m, 20/6/2012, ZMBN 99236 (**DNA code=ZMBN_99236**). ***Ophioconis opacum*** (H.L. Clark, 1928): SS10/2005/35, Bald Island, 35° 11.442′S, 118° 38.7′E to 35° 11.25′S, 118° 39′E, 157–147 m, 24/11/2005, MV F111582 (**DNA code=F111582**). ***Ophioconis permixta*** Koehler, 1905: IN2022_V09/150, Site:044, 23° 54.934′S, 113° 5.7412′E to 23° 55.346′S, 113° 5.6486′E, 105–104 m, 13/12/2022, MV F309538 (**DNA code=F309538**). SAYA/YB01, NE Saya de Malha, 10° 22.75′S, 62° 7.75′E, 24 m, 10/11/2022, MNHN IE.2023.4349 (**DNA code=IE.2022.4349**). SOL5117/025BS020, Bonaparte Gulf, 10° 25.762′S, 129° 40.023′E to 10° 25.793′S, 129° 40.028′E, 74.8–75.1 m, 8/8/2010, MV F173903 (**DNA code=F173903**). ***Ophioconis vivipara*** Mortensen, 1925: MIWA/2011410-SL33, 22° 5.508′N, 17° 23.358′W, 106 m, 20/11/2011, ZMBN 99234 (**DNA code=ZMBN 99234**).

Distribution. NW Pacific (140 m), W Indian Ocean (10–310 m), E Indo-W Pacific (2–485 m), Walters Shoal (272–588 m)

Remarks. The five Walters Shoal specimens measure 1.5 to 5 mm dd. They are characterised by an even covering of granules over the disc, including over the oral and adoral shields, and oral plates; up to 6 flattened spatulate arm spines, the uppermost to just longer than a segment in length; 3–4 small tentacle scales around the basal pores, reducing to 2 rounded glassy scales on most of the arm, the inner being largest; widened glassy denticulate teeth, with 4–5 lateral oral papillae; VAPs that are longer than wide, transversely striated LAPs, and broadly rhomboid DAPs with a convex outer edge, and covered in small dark spots.

Ophioconis species are hard to distinguish. *Ophioconis vivipara* differs in having short arm spines, limited to half a segment in length. *Ophioconis grandisquama* Koehler, 1904 has an elongated inner tentacle scale that exceeds the VAP in length. *Ophioconis permixta* and *O. cincta* Brock, 1888 have some disc granules that are extended into small spines, and thinner more pointed arm spines. *Ophioconis forbesi*, *O. opacum*, and *O. cupida* are morphologically similar to the SWIO specimens, but DNA sequences of the first two species are divergent from the SWIO samples. Consequently, material from the Western Indian Ocean is tentatively referred to *O. cupida* until these DNA sequences can be compared to samples obtained from near the type locality in Indonesia.

Ophiomyxa pedicula **sp. nov.**

https://zoobank.org/urn:lsid:zoobank.org:act:D2498578-F5D3-473E-B1AF-48EBA3AAC7D9
Fig. 24d–g, 25f–j

TYPE LOCALITY. Walters Shoal, Pentes, 33° 8.7′S, 43° 58.16′E to 33° 8.77′S, 43° 59.13′E, 492–588 m

TYPE MATERIAL.—MD208: stn DW4890, Walters Shoal, Pentes, 33° 8.7′S, 43° 58.16′E to 33° 8.77′S, 43° 59.13′E, 492–588 m, 4/5/2017, holotype: 1 (MNHN IE.2016.1062) (**DNA code=IE.2016.1062**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiomyxa pedicula*** SAYA/DW5411, N Saya de Malha, 9° 49.812′S, 60° 45.455′E to 9° 49.759′S, 60° 45.569′E, 216–192 m, 7/11/2022, MNHN IE.2023.4245 (**DNA code=IE.2023.4245**). ***Ophiostiba*** **sp.MoV.7274** SOL5117/044BS026, Bonaparte Gulf, 10° 27.123′S, 129° 31.439′E to 10° 27.144′S, 129° 31.476′E, 55.2–55.7 m, 16/8/2010, MV F173909 (**DNA code=F173909**).

Diagnosis. Disc covered in a thick pulpy skin, no marginal row of disc plates, short (2 arm segments long) genital slits, 3 flattened oral papillae with a denticulate margin, Five arms, arms and spines covered in thick skin, 1 (sometimes 2) thin ovoid fenestrated DAPs on each segment, VAPs longer than wide, with prominent distal notch and distolateral ‘wings’, 2–3 arm spines on each side, alternating on different segments, less than a segment in length, with lateral thorns, no tentacle scale, but tube feet strengthened by a pair of elongate plates.

Description. Holotype 10 mm dd, arms 40+ mm long; disc pentagonal, covered in a thick pulpy skin that obscures any embedded plates, radial shields apparently bar-like widely separate, no discernible series of margin plates between radial shields; genital slits short, 2 arm segments long; Oral shields rounded triangular, with a slightly convex distal edge and rounded angles, wider than long, adoral shields long and thin, extending around the lateral angles of the oral shields, meeting interradially, separated radially by the small 1st VAP; 5 teeth, thin with a denticulate glassy edge, ventral 4 are rounded, dorsalmost (inner) tooth longer and spatulate; 3 oral papillae, wide, with a rounded to truncate outer edge, also finely denticulate and glassy; both pairs of oral tentacles emerge within slit.

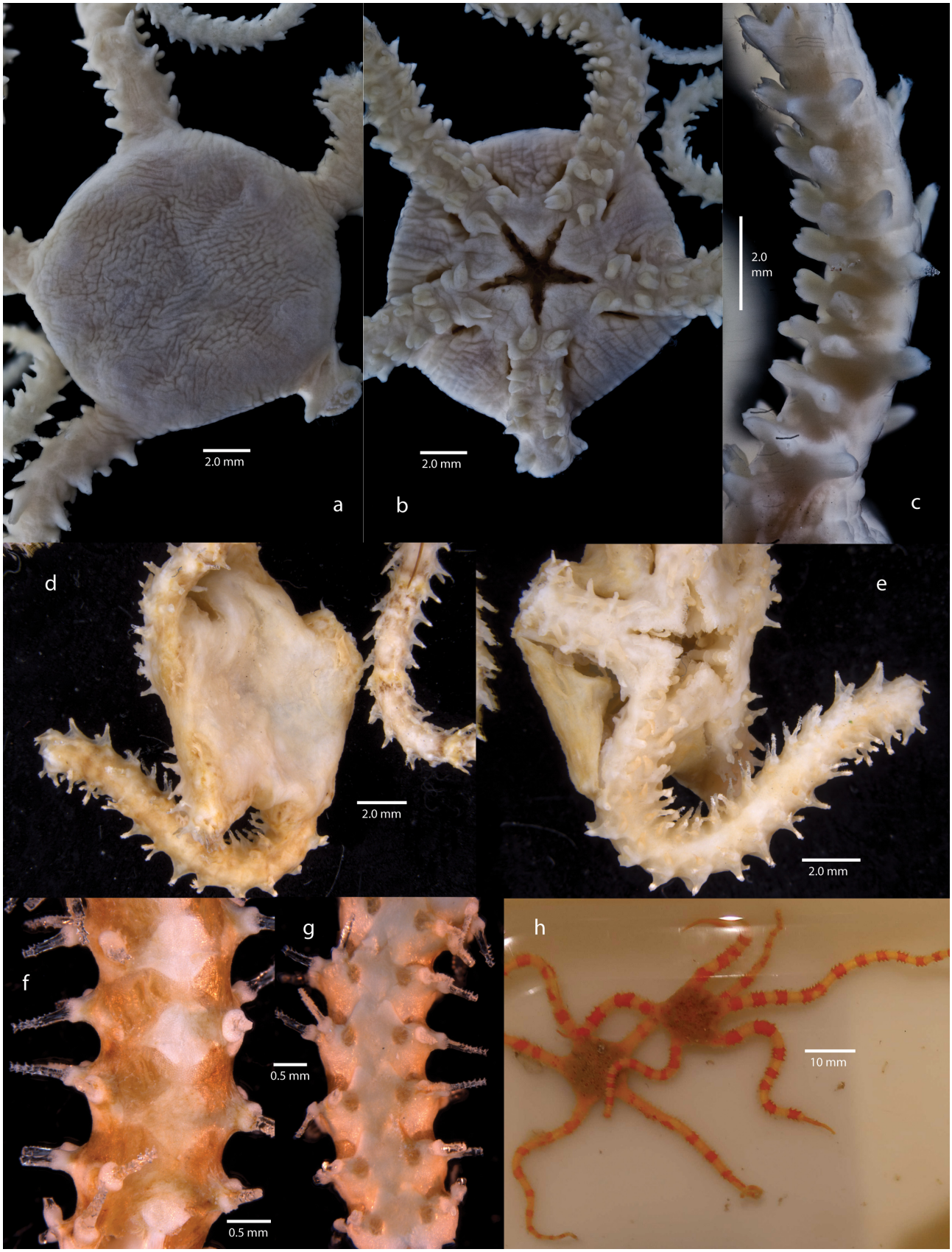

FIGURE 24. (a–c) *Ophiomyxa vivipara* NHMUK 2025.59: (a) dorsal, (b) ventral, (c) lateral view of mid arm. (d–g) *Ophiomyxa pedicula* **sp. nov.** holotype MNHN IE.2016.1062: (d) dorsal, (e) ventral, (f) dorsal view of (dried) arm piece showing the thin perforated DAPs overlying the vertebrae, (g) ventral view of (dried) arm piece. (h) *Ophiomyxa neglecta* MNHN IE.2016.1343, live colour (shipboard).

Five arms, arms and spines covered in thick skin, DAPs thin and fenestrated, in 1–2 pieces, ovoid to irregular in shape, just separated, sometimes appear to be split at mid-length (but this could be an artefact), do not hide the dorsal wings of the underlying vertebrae; LAPs ventrolateral, ventral flanges meet on the midline, plate longer where the arm spines articulations are present; overlain and separated longitudinally by the VAPs; VAPs longer than wide, with prominent distolateral 'wings' with pointed distal angles, distal margin deeply v-shaped, rounded proximolaterally around the tube foot, with an obtuse angle proximally, widest just distal to the tentacle pores; one arm spine on first 2 segments, 2 on next 2 segments, 2–3 arm spines on succeeding proximal segments, alternating on successive segments, then becoming regularly 3 spines from mid-arm, uppermost longest, less than a segment in length, proximal arm spines with thorns, distal arm spines more hook-like with 2 teeth and a wide opaque pedicel; no tentacle scales, but tube feet strengthened by a pair of elongate plates on either side. Colour pale with some remnant darker markings on the dorsal side of the arm, perhaps indicating some banding when alive.

Ossicles. Arm spine articulations round to oval with a central muscle perforation and a smaller ventrodistal nerve opening; arm spines when stripped of skin have a large vase-shaped opaque basal pedicel, supporting a glassy ridged spine, with notable denticulations on the ventral and to a lesser extent dorsal side of the upper half of the spine. Vertebrae zygospondylous, with large muscle fossae dorsolaterally, and a groove along the dorsal midline that can be seen under the DAPs.

Distribution. Walters Shoal (492–588 m), Saya de Malha Bank (192–216 m)

Remarks. The denticulate oral papillae and teeth clearly identify this species as an *Ophiomyxa*. The unfragmented DAPs indicate a relationship to the *O. vivipara-serpentaria* complex, as DAPs are present as numerous fragmented pieces in most species. Also, both *O. vivipara* and *O. serpentaria* have elongated ossicles in the sheaf around the tube feet similar to the new species. Our phylogeny also places the new species close to the *O. vivipara-serpentaria* complex. However, the new species appears to lack the row of disc scales that connect the radial shields in *O. vivipara-serpentaria* (see Mortensen, 1933d) as well as many other *Ophiomyxa* species. *Ophiohyalus gotoi* Matsumoto, 1915 from Japan also has unfragmented DAPs, and may be related. The type differs in having DAPs that are figured as being separate from each other, a row of disc scales that border the disc, and curved arm spines (Matsumoto, 1917).

A specimen from Saya de Malha Bank is molecularly and morphologically similar to the MD208 specimen and is referred to the new species. It measures 9 mm dd, the long arms have slender tips, the arms covered in thick skin around the vertebrae, especially distally, three pointed skeletal arm spines (in thick skin) upper one hook-like at very arm tip, the row of marginal disc plates appears to be lacking, there are 3–4 small serrated oral papillae.

The next nearest specimen on our phylogeny is a 6-armed specimen from Western Australia. It also has DAPs that are entire, and the wide rounded oral papillae and teeth have denticulations. The 3 arm spines have thorns in annulations around the spine flank. The only described ophiomyxid species with 6-arms is *Ophiostiba hidekii* Matsumoto, 1915 also from Japan. The type is small (3.5 mm dd) but differs from the new species in having 6 arms, being fissiparous, lacking DAPs and having 4–5 oral papillae are simple and triangular, lacking denticulations, and having a marginal row of disc scales (Matsumoto, 1917). More research is needed to clarify the relationships of these species.

The other SWIO species can be distinguished from *O. pedicula* as follows: *O. tenuispina* has fragmented DAPs, *O. neglecta* has 4 oral papillae, and *O. vivipara* has a row of disc scales around the margin. The arm ossicles also differ: the VAPs are typically wider in other species with a less pronounced distal notch, and the arm spines have a less widened base with smaller thorns near the tip (Fig. 25).

Etymology. Named after the large vase-shaped pedicel on the arm spines.

Ophiomyxa tenuispina Mortensen, 1933

Fig. 25k–n

Ophiomyxa tenuispina Mortensen, 1933b: 304–306. fig. 30, pl. 19(27).—Clark, A.M. & Courtman-Stock, 1976: 134, fig. 97, 99–100.—Olbers *et al.* 2019: 154–155, fig. 144–145.

STUDY MATERIAL.—MD208: stn WCAS11, Walters shoal, Zone Sommitale Nord Ouest, 33° 8.88′S, 43° 50.43′E, 125 m, 7/5/2017 to 8/5/2017: 1 (MNHN IE.2016.1344) (**DNA code=IE.2016.1344**).—MD208: stn WR12, Walters shoal, Zone Sommitale Nord Ouest, 33° 9.158′S, 43° 51.4538′E, 43–47 m, 8/5/2017: 1 (MNHN IE.2016.1359).—

MD208: stn DW4894, Walters shoal, Pentes, 33° 8.19′S, 43° 50.3101′E to 33° 8.59′S, 43° 49.75′E, 199–261 m, 5/5/2017: 1 (MNHN IE.2016.1347).

COMPARATIVE MATERIAL EXAMINED. ***Ophiomyxa tenuispina*** Mortensen, 1933b: ATIMO VATAE/DW3600, SW Cap Sainte Marie, 25° 59′S, 44° 42′E, 143 m, 13/5/2010, MNHN IE.2007.4344 (**DNA code=IE.2007.4344**).

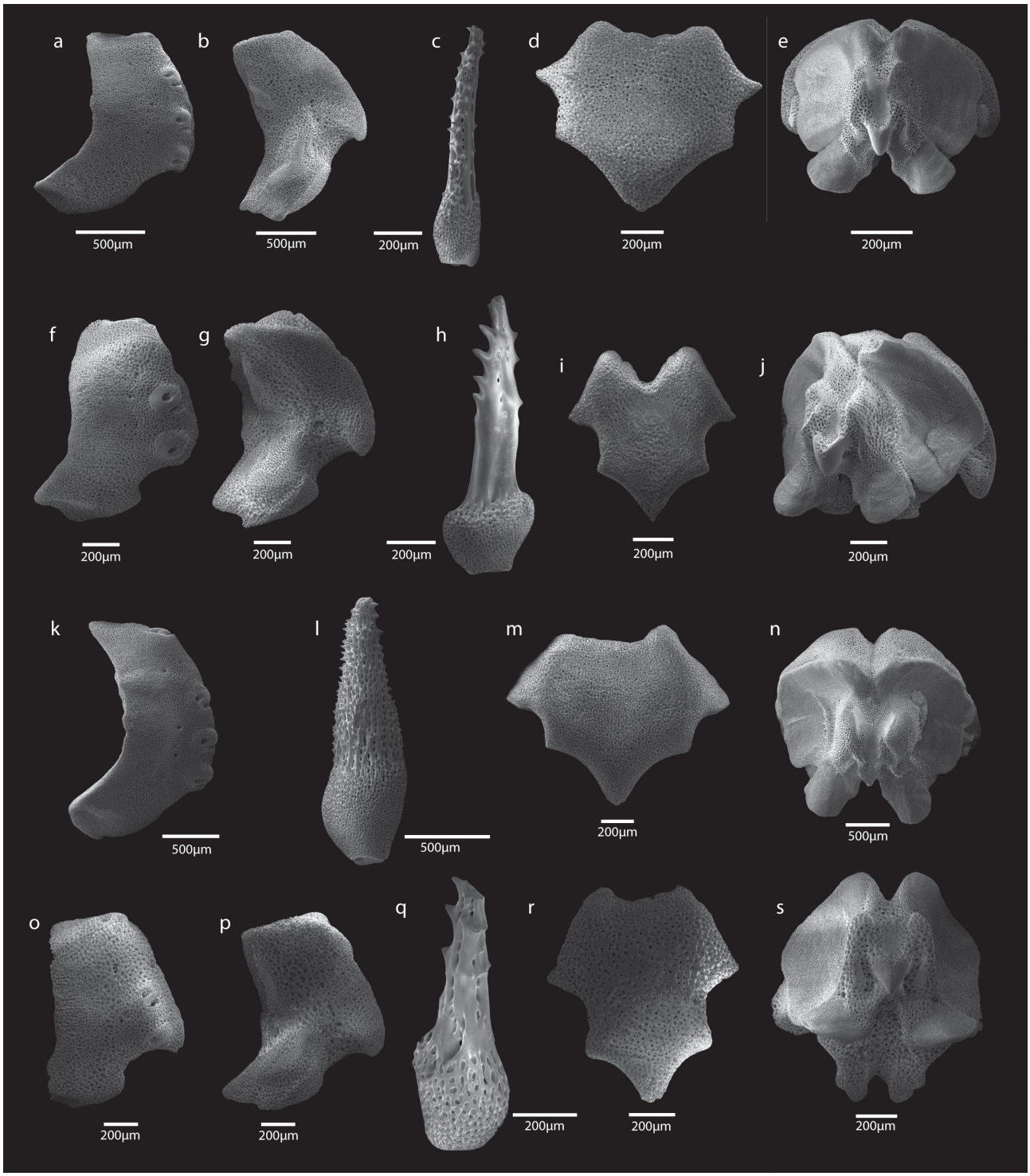

FIGURE 25. (a–e) *Ophiomyxa neglecta* MNHN IE.2016.1343, (a) lateral arm plate, exterior view, (b) lateral arm plate, interior view, (c) arm spine, (d) ventral arm plate, (e) vertebra, distal view; (f–j) *Ophiomyxa pedicula* **sp. nov.** holotype MNHN IE.2016.1062, (f) lateral arm plate, exterior view, (g) lateral arm plate, interior view, (h) arm spine, (i) ventral arm plate, (j) vertebra, distal view; (k–n) *Ophiomyxa tenuispina* MNHN IE.2016.1344, (k) lateral arm plate, exterior view, (l) arm spine, (m) ventral arm plate, (n) vertebra, distal view; (o–s) *Ophiomyxa vivipara* NHMUK 2025.60, (o) lateral arm plate, exterior view, (p) lateral arm plate, interior view, (q) arm spine, (r) ventral arm plate, (s) vertebra, distal view.

Distribution. South Africa (174 m)

Remarks. The Walters Shoal specimens (to 18.5 mm dd) are (preserved) brownish-yellow, without obvious colour patterns. They have rounded oral papillae and upper teeth with a glassy serrated border, up to 5 arm spines (typically 4) that are swollen at the base and small thorns over the upper shaft and apex (Fig. 25i). The DAPs are fragmented into pieces that sit above the vertebrae. They are similar to the type drawings and description of *O. tenuispina* Mortensen, 1933b from South Africa, except the smaller (12 mm dd) type had only 4 arm spines. Another similar species is *O. irregularis* Koehler, 1922a from the Philippines (up to 15 mm dd) which also was reported to have only 4 arm spines. Additional DNA samples are required before we can successfully determine whether these form one or more species.

Ophiomyxa neglecta (Koehler, 1904)

Fig. 24h, 25a–e

Ophiodera neglecta Koehler, 1904: 153–154, pl. 28(6–7).—Koehler, 1922a: 20–22, pl. 6(3,7–8).—Liao & Clark, A.M. 1995: 154–155, fig. 63.

Ophiomyxa neglecta.—Clark, H.L., 1915: 170.

STUDY MATERIAL.—MD208: stn DW4887, Walters Shoal, Pentes, 33° 17.23′S, 43° 55.44′E to 33° 16.98′S, 43° 56.6899′E, 599–640 m, 3/5/2017: 1 (MNHN IE.2016.1064); 8 (MNHN IE.2016.1364).—MD208: stn DW4888, Walters shoal, Pentes, 33° 9.7′S, 43° 56.8199′E to 33° 10.33′S, 43° 57.32′E, 299–311 m, 3/5/2017: 2 (MNHN IE.2016.1343) (**DNA code=IE.2016.1343**).—MD208: stn DW4889, Walters shoal, Pentes, 33° 9.7′S, 43° 57.1099′E to 33° 9.12′S, 43° 57.9899′E, 353–465 m, 3/5/2017: 1 (MNHN IE.2016.1348).—MD208: stn DW4892, Walters shoal, Pentes, 33° 10.92′S, 44° 0.025′E to 33° 11.63′S, 44° 0.8201′E, 624–646 m, 4/5/2017: 1 (MNHN IE.2016.1349).

COMPARATIVE MATERIAL EXAMINED. ***Ophiomyxa bengalensis*** Koehler, 1897: EXBODI/CP3883, Volcan-Mont Vauban, 22° 21.3′S, 171° 38.9′E, 433–516 m, 18/9/2011, MNHN IE.2007.7148 (**DNA code=IE.2007.7148**). ***Ophiomyxa neglecta*** (Koehler, 1904): BIOPAPUA/DW3732, Au large des îles et récifs Lancasay, 8° 16′S, 150° 29′E, 340–358 m, 9/10/2010, MNHN IE.2012.677 (**DNA code= OM5**); MNHN IE.2023.4073 (**DNA code=BP90**). MIRIKY/DW3197, Ouest du Cap d'Ambre, 12° 7.04′S, 48° 56.9298′E to 12° 6.63′S, 48° 58.0398′E, 362–431 m, 28/6/2009, MNHN IE.2013.1232 (**DNA code=IE.2013.1232**).

Distribution. W Indian Ocean (362–431 m), E Indo-W Pacific (76–1418 m), Walters Shoal (299–646 m).

Remarks. These specimens of *Ophiomyxa neglecta* (up to 18 mm dd) differ from other SWIO species in having to 4 triangular to truncate oral papillae that have a glassy edge, but without notable serrations, and tend to be separate and not overlapping. There are typically only 3 (rarely 4) pointed arm spines that do not exceed the segment in length, and there is not a continuous row of scales along the disc margin. Live photos (Fig. 24h) show a greyish disc with arms that are brightly banded yellow/red every 3 or so segments. Genetically, the Walters Shoal sample is most similar to an upper bathyal sample collected from the North of Madagascar (IE.2013.1232) and then to specimens from Papua New Guinea. *Ophiomyxa bengalensis* Koehler, 1897 differs in having notable white calcareous bodies in the skin of the disc. Similar ossicles can be observed in the smallest (up to 7 mm dd) of the Walters Shoal *O. neglecta* specimens.

Ophiomyxa vivipara Studer, 1876

Fig. 24a–c, 25o–s

Ophiomyxa vivipara Studer, 1876: 462.—Mortensen, 1924: 114, fig. 6b.—Mortensen, 1936: 241–242.—Mortensen, 1941: 6–7.—Mortensen, 1952: 12.—Manso, 2010: 5, fig. 5a–b.—Lyman, 1882: 246.—Clark, H.L., 1923: 313.—Mortensen, 1933b: 301–304, fig. 27–29.

Ophiomyxa vivipara var capensis Mortensen, 1936: 242.

Ophiomyxa vivipara capensis.—Clark, A.M., 1974: 482.—Clark, A.M. & Courtman-Stock, 1976: 134–135, fig. 101–102.—Alva & Vadon, 1989: 832.—Olbers *et al.* 2019: 155–156, fig. 146–147.

STUDY MATERIAL.—JC066: stn 4-37, Coral seamount, 41° 21.7673′S, 42° 54.9067′E to 41° 22.4′S, 42° 54.6′E, 740 m, 20/11/2011: 1 (NHMUK 2025.59) (**DNA code=OVC1**); 1 (NHMUK 2025.60) (**DNA code=OVC2**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiomyxa serpentaria*** Lyman, 1883: CE13008/36, Rockall Trough, 'North' Canyon, 54° 3.19′N, 12° 32.45′W, 1361 m, 6/2013, NUI (**DNA code=NUI1404A**). ***Ophiomyxa vivipara*** Mortensen, 1936: Lara/86, South Africa, 30° 56.31′S, 16° 37.998′E, 337 m, 2/2/2013, SAMC MB-A82574 (**DNA code=A82574**).

Distribution. S America (6–507 m), S Africa (80–755 m), SW Indian Ocean (373–1179 m), E Indo-W Pacific (385–888 m), S Australia (522–2170 m), New Zealand (150–1408 m), St Paul/Amsterdam Is (460–1680 m), Coral Seamount (740 m).

Remarks. The 2 specimens measure 11.5 (NHMUK 2025.60) and 12 mm dd (NHMUK 2025.59). They both have one thin perforated ovoid to rhomboid DAP, similar to that illustrated by Mortensen (1933d, fig. 2) for the very similar species *O. serpentaria* Lyman, 1883. There are 2–3 alternating arm spines, the uppermost longest on segments with 3, spine-like in nature with some notable thorns, generally obscured by thick skin. The oral papillae are rounded and wide with denticulate glassy edges. The tube feet have two elongated plates that reinforce the sides (see also Mortensen, 1933d, fig. 3e–f). Neither specimen has any obvious brooded juveniles.

Ophiomyxa vivipara occurs through the temperate Southern Ocean as evidenced by mitochondrial DNA but populations appear to vary in reproduction (O'Hara *et al.* 2014a). Specimens from around South America have large, brooded juveniles, whilst other populations do not.

Family Ophiotomidae

Ophiotreta valenciennesi (Lyman, 1879)

Ophiacantha Valenciennesi Lyman, 1879: 57–58, pl. 15(408–410).—Lyman, 1882: 183–184, pl. 26(7–8).—Koehler, 1904: 110–111.—Clark, H.L., 1917: 434.

Ophiotreta valenciennesi.—Koehler, 1922a: 84, pl. 16(4), 93(6).—Mortensen, 1933d: fig. 19b, 21i.—O'Hara & Stöhr, 2006: 62–63, fig. 5a–d, 17p.

STUDY MATERIAL.—MD208: stn DW4894, Walters shoal, Pentes, 33° 8.19′S, 43° 50.3101′E to 33° 8.59′S, 43° 49.75′E, 199–261 m, 5/5/2017: 2 (MNHN IE.2016.1346) (**DNA code=IE.2016.1346**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiotreta rufescens*** (Koehler, 1896): UF/IZ-2009-06-10, S of Florida Keys, 24° 13.452′N, 81° 29.004′W, 457 m, 8/6/2009, UF 8999 (**DNA code=UF8999**). ***Ophiotreta valenciennesi*** (Lyman, 1879): ATIMO VATAE/DW3522, secteur de Manantenina, 24° 23′S, 47° 32′E, 154–168 m, 1/5/2010, MNHN IE.2007.4292 (**DNA code=IE.2007.4292**). BIOPAPUA/DW3719, Vitiaz strait, 6° 3′S, 147° 36′E, 410 m, 7/10/2010, MNHN IE.2023.4066 (**DNA code=BP22**). EXBODI/DW3940, Récif Pétrie, 18° 35.9′S, 164° 23.9′E, 380–430 m, 27/9/2011, MNHN IE.2023.4075 (**DNA code=ex 2007.6848**). NA064/017, Galapagos Is marine park, 1° 13.879064′N, 91° 6.803404′W, 354 m, 27/6/2015 (**DNA code=NA064-017-01-A**). SAYA/DW5434, SW Saya de Malha, 11° 47.436′S, 61° 5.361′E to 11° 47.436′S, 61° 5.435′E, 268–270 m, 15/11/2022, MNHN IE.2023.4193 (**DNA code=IE.2023.4193**). TARASOC/CP3464, Moorea Island, 17° 34′S, 149° 54′W, 460 m, 20/10/2009, UF 13020 (**DNA code=UF13020**).

Distribution. NW Pacific (228–512 m), W Indian (133–554 m), E Indo-W Pacific (73–1901 m), E Pacific (332–549 m), S America (370–748 m), S Africa (199–261 m), S Australia (132–700 m), New Zealand (88–883 m).

Remarks. *Ophiotreta valenciennesi* is a species complex, with considerable genetic divergence between lineages. The most recent common ancestor on our tree dated to approximately 15 MY. The DNA sequence from the Walters Shoal specimen (16 mm dd) is closest to that obtained from a specimen from Madagascar (IE.2007.4292). Both have some slightly elongated granules but not as spine-like as figured for the type of related species *O. durbanensis* Mortensen, 1933b from eastern South Africa. More samples are required to resolve whether this character is diagnostic. The radial shields are mostly covered by granules (except at their distal tip) and there are spines along the distal edge of the dorsal arm plates. *Ophiotreta valenciennesi rufescens* (Koehler, 1896) samples are phylogenetically sister to all our Indo-Pacific *O. valenciennesi* samples and deserves recognition as a separate species, *Ophiotreta rufescens*.

Family Ophiernidae

Ophiernus vallincola Lyman, 1878

Ophiernus vallincola Lyman, 1878: 122–123, pl. 6(170–172).—Lyman, 1882: 32–33, pl. 24(16–18), 38(6–9).—Clark, H.L., 1923: 365.—Clark, H.L., 1939: 134.—Clark, A.M. & Courtman-Stock, 1976: 185, fig. 201.—Madsen, 1977: 112–114, fig. 2.—Paterson, 1985: 98–99, fig. 40.—Guille & Vadon, 1986: 169.—Olbers *et al.* 2019: 185–186, fig. 178–179.—O'Hara, 2024b: 64, fig. 63

STUDY MATERIAL.—MD208: stn CP4913, Walters shoal, Plaine Sud, 33° 48.82′S, 44° 5.9699′E to 33° 51.8′S, 44° 4.72′E, 1539–1615 m, 11/5/2017: 1 (MNHN IE.2016.1379) (**DNA code=IE.2016.1379-2**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiernus alepidotus*** Madsen, 1977: CCLME-1205/BT327, Bissau, 11° 31.08′N, 17° 24.27′W to 11° 32.08′N, 17° 24.22′W, 738–730 m, 19/5/2012, Vigo 2719 (**DNA code=V2917**). Maurit-1011/MU256, Mauritania, 19° 35′N, 17° 16.03′W to 19° 36.67′N, 17° 18.72′W, 1160 m, 25/11/2010, Vigo 2415 (**DNA code=V2415**). ***Ophiernus* cf. *alepidotus*** SAYA/CP5412, N Saya de Malha, 9° 44.192′S, 60° 48.05′E to 9° 44.561′S, 60° 48.435′E, 1441–1396 m, 7/11/2022, MNHN IE.2023.4180 (**DNA code=IE.2023.4180**). ***Ophiernus vallincola*** Lyman, 1878: IN2015_C01/117, Great Australian Bight, SZ03Area22, 34° 40.458′S, 132° 28.7635′E to 34° 39.618′S, 132° 27.2761′E, 1017–1014 m, 24/11/2015, MV F227611 (**DNA code=F227611**). IN2017_V03/056, Jervis CMR, 35° 19.98′S, 151° 15.48′E to 35° 19.92′S, 151° 12.84′E, 2650–2636 m, 29/5/2017, MV F240096 (**DNA code=F240096**). in2022_v08/145, Cocos (Keeling), 12° 7.593′S, 96° 40.9921′E to 12° 7.82′S, 96° 40.6418′E, 3078–3002 m, 17/10/2022, identified by O'Hara (2024b), MV F307644 (**DNA code=F307644**). ME 85- 3/1072, South Iceland, Irminger Basin, 63° 0.46′N, 28° 4.0896′W to 63° 1.1′N, 28° 3.15′W, 1594 m, 8/9/2011, DZMB-HH 37435 (**DNA code=DZMB37435A**). PS61 ANT-XIX/3 (ANDEEP)/044-1, Elephant Island, 60° 58.08′S, 55° 6.85′W to 60° 58.09′S, 55° 4.05′W, 308–399 m, 29/1/2002, CASIZ 161551 (**DNA code= CAS161551**). TAN1206/15, Site SL1d, slope, Bay of Plenty, 36° 55.44′S, 176° 58.782′E to 176° 58.752′N, 36° 55.152′W, 1502-1493 m, 16/4/2012, MV F188877 (**DNA code=402VBH**).

Distribution. Arctic (1643–1648 m), NE Atlantic (619–4000 m), W Indian Ocean (1000–2312 m), E Indo-W Pacific (300–3078 m), S Africa (1097–3255 m), Kerguelen (2557–2557 m), S Australia (439–2821 m), New Zealand (1139–3391 m), Antarctic (308–3673 m).

Remarks. *Ophiernus vallincola* is a worldwide complex of bathyal species that also includes the weakly calcified *O. alepidotus* from off western Africa. More DNA samples are required across its geographic and bathymetric range to establish species boundaries. The Walters Shoal specimen is 7 mm dd, with the wide radial shields, disc scales limited to a row that surrounds the radial shields and a few in the centre of disc. Arm bristles are present.

Family Ophioleucidae

Ophioleuce seminudum Koehler, 1904

Ophioleuce seminudum Koehler, 1904: 33–34, pl. 2(7–10).—Madsen, 1983: 36–45, figs 2–4, 5a–b, 6.—Guille & Vadon, 1986: 169.
Ophiocirce inutilis Koehler, 1904: 13–14, pl. 3(4–5).—Clark, H.L., 1939: 131–132.—Clark, A.M., 1974: 476–477, fig. 14.—Clark, A.M. & Courtman-Stock, 1976: 185–186, figs 198, 202 [according to Madsen, 1983].
Ophiocten charischema Clark, H.L., 1911: 97–98, fig. 35 [according to Madsen, 1983].
Ophioleuce charischema.—Clark, H.L., 1915: 345.—Hertz, 1927b: 109, pl. 9(4).
Ophiocirce mabahithae Mortensen, 1939: 42, figs 3–4, pl. 3(7–8) [according to Madsen, 1983].

STUDY MATERIAL.—MD208: stn DW4886, Walters shoal, Pentes, 33° 17.25′S, 43° 54.89′E to 33° 16.63′S, 43° 55.9401′E, 582–573 m, 3/5/2017: 2 (MNHN IE.2023.4155) (**DNA code=IE.2023.4155**).—MD208: stn DW4891, Walters shoal, Pentes, 33° 10.8′S, 44° 0.97′E to 33° 11.59′S, 44° 0.97′E, 650–653 m, 4/5/2017: 1 (MNHN IE.2016.1355).

COMPARATIVE MATERIAL EXAMINED. ***Ophioleuce seminudum*** Koehler, 1904: MIRIKY/CP3209, entre Nosy-bé et Banc du Leven, 12° 41.87′S, 48° 15.36′E to 12° 42.87′S, 48° 14.22′E, 291–353 m, 29/6/2009, MNHN IE.2023.4004 (**DNA code=CP3209a**). SAYA/DW5424, SE Saya de Malha, 11° 27.684′S, 62° 0.602′E to 11°

28.02′S, 62° 0.546′E, 171–150 m, 12/11/2022, MNHN IE.2023.4202 (**DNA code=IE.2023.4202**). SS05/2007/129, Northwestern Australia, Lacepede L26 transect, 15° 47.568′S, 121° 3.504′E to 15° 48.5′S, 121° 2.883′E, 117–109 m, 1/7/2007, MV F162612 (**DNA code=F162612**).

Distribution. NW Pacific (94–1250 m), W Indian Ocean (73–1073 m), E Indo-W Pacific (50–2084 m), S Africa (573–653 m), S Australia (194–256 m), New Zealand (376–380 m).

Remarks. The discs are 9 (IE.2023.4155) and 5.5 (IE.2016.1355) mm dd. We were unsuccessful in obtaining DNA from these samples. However, two samples from Madagascar (IE.2023.4004) and Saya de Malha (IE.2023.4202) cluster separately from East Indo-West Pacific specimens and possibly represent a cryptic species. If this western Indian Ocean clade is found to extend northwards to the Red Sea, then the name *O. mabahithae* (Mortensen, 1939) is available.

Family Amphiuridae

Amphipholis squamata (Delle Chiaje, 1828)

Asteria squamata Delle Chiaje, 1828: 74.
Amphipholis squamata.—Clark, H.L., 1923: 330.—Mortensen, 1933b: 364–365.—Clark, A.M. & Rowe, 1971: 80–81, 99, fig. 27b, pl. 13(5).—Clark, A.M. & Courtman-Stock, 1976: 151–152, fig. 138.—Clark, A.M., 1976: 258.—Clark, A.M., 1977: 135.—Cherbonnier & Guille, 1978: 105–106, fig. 48(A–B).—Sloan, Clark & Taylor, 1979: 101.—Stöhr *et al.*, 2008: 552–553, fig. 4d–e.—Olbers *et al.* 2019: 217–218, fig. 214–215.—O'Hara & Thuy, 2022: 38–39.
Ophiactis minor Döderlein, 1910: 253, pl. 5(3–3a) [according to Mortensen, 1933b].
Amphipholis minor.—Clark, H.L., 1923: 329.—Hertz, 1927a: 35.

STUDY MATERIAL.—MD208: stn WS07, Walters shoal, Zone sommitale Sud, 33° 15.435′S, 43° 52.1851′E, 30–33 m, 2/5/2017: 1 (MNHN IE.2016.1367).

COMPARATIVE MATERIAL EXAMINED. ***Amphipholis squamata.E*** SAYA/YR03, NW Saya de Malha, 9° 52.3′S, 60° 11.82′E, 43 m, 5/11/2022, MNHN IE.2023.4358 (**DNA code=IE.2023.4358**).

Distribution. Arctic (29–2369 m), NW Atlantic (0–1962 m), NE Atlantic (0–1560 m), NW Pacific (0–413 m), NE Pacific (0–933 m), W Atlantic (0–353 m), E Atlantic (0–741 m), W Indian Ocean (0–750 m), E Indo-W Pacific (0–694 m), E Pacific (0–46 m), S America (0–134 m), S Africa (0–1600 m), S Australia (0–841 m), New Zealand (2–1059 m). SPA (3–1600 m).

Remarks. *Amphipholis squamata* is an allopatric hybrid swarm with at least 4 major mitochondrial maternal lineages (Hugall *et al.* 2024). This complex is a successful coloniser of isolated habitats (Mortensen 1941); all individuals bear live young (or clones) and it is known to use macroalgal holdfasts to raft across oceans. DNA was not obtained from this tiny Walters Shoal specimen, however, other shallow water records from the Western Indian Ocean have proved to belong to the widespread tropical "clade E" (O'Hara unpublished data). Only synonyms relevant to the western Indian Ocean are listed above.

Amphiura cf. *glabra*

Fig. 26a–c

STUDY MATERIAL.—JC066: stn 4-4, Coral seamount, 41° 22.8371′S, 42° 50.6024′E to 41° 22.85′S, 42° 51.99′E, 1186 m, 13/11/2011: 1 (NHMUK 2025.20) (**DNA code=JC066-3851**).

COMPARATIVE MATERIAL EXAMINED. ***Amphiura* cf. *glabra*** in2022_v08/141, Cocos (Keeling), 12° 7.677′S, 96° 58.8014′E to 12° 7.98′S, 96° 59.35′E, 1139–1110 m, 16/10/2022, identified by O'Hara (2024b), MV F308057 (**DNA code=F308057**).

Description. Disc 5 mm dd, petaloid, covered dorsally in scales, no primary plates evident, radial shields large, 1/5 dd in length, D-shaped, proximally divergent; disc scales become sparse around the oral shields; oral shields rounded triangular, 1.5x as wide as long, distally widest with a slightly convex distal side; adoral shields narrow with wide lateral wings, just separated interradially and separated radially by the VAP1; distal oral papillae small and conical; DAPs ovoid, slightly wider than long; VAPs longer than wide, with a tapered angle proximally, a

convex distal edge and incised lateral sides, contiguous; to 6 arm spines, lowest longer, especially around mid-arm, to 1.5 segments; one oval tentacle scale, 1/2 to 1/3 the length of the VAP. Colour (preserved): light brown, with a darker spot at the base of the arm spines.

Distribution. tropical Indian Ocean—bathyal

Remarks. This specimen is similar to a 3 mm dd specimen described from off the Cocos (Keeling) islands in the eastern Indian Ocean (O'Hara, 2024b), differing only in having slightly smaller radial shields, smaller distal oral papillae, and an additional arm spine, all of which may be due to its larger size. The holotype of *A. glabra* Lyman, 1879 from the Philippines (930 m) is not described as having longer ventral arm spines, and we defer considering these three specimens the same species until the holotype has been re-examined.

Amphiura cf. *natalensis*

Fig. 26d–g

STUDY MATERIAL.—JC066: stn 4-12, Coral seamount, 41° 22.333′S, 42° 54.066′E to 41° 23′S, 42° 54.1′E, 730 m, 16/11/2011: 1 (NHMUK 2025.22) (**DNA code=JC066-592**); 1 (NHMUK 2025.21).

COMPARATIVE MATERIAL EXAMINED. ***Amphiura dejectoides*** H.L. Clark, 1939: MIRIKY/CP3247, au large de la Baie Mahajamba, 14° 50.39′S, 46° 59.1498′E to 14° 49.86′S, 47° 0.0198′E, 349–442 m, 7/7/2009, MNHN IE.2007.413 (**DNA code=IE.2007.413**). ***Amphiura ficta*** Koehler, 1910: MIRIKY/CP3223, entre Nosy-bé et Banc du Leven, 12° 47.94′S, 48° 11.28′E to 12° 46.26′S, 48° 11.2602′E, 430–488 m, 2/7/2009, MNHN IE.2007.1260 (**DNA code=IE.2007.1260**). ***Amphiura grandisquama*** Lyman, 1869: Johnson Sea Link II/JSL-II-3665, Miami Terrace, 26° 3.8757′N, 79° 50.9349′W, 329–343 m, 22/9/2004, MV F254609 (**DNA code=F254609**). ***Amphiura iris*** Lyman, 1879: SE-1518/14, Kumano Sea, S of Shirna Peninsula, Mie Pref, 34° 2.8′N, 136° 53.2′E, 725 m, 9/10/2015, NSMT E9100 (**DNA code=NSMT E9100**). ***Amphiura spinipes*** Mortensen, 1924: TAN1007/104, Rumble II West seamount, 35° 21.732′S, 178° 31.548′E to 35° 21.582′S, 178° 31.848′E, 1287–1378 m, 6/6/2010, NIWA 70686 (**DNA code=70686**).

Description. Disc to 3.8 mm dd, disc covered in tiny disc scales, primaries distinct, a little larger than others, widely separated, disc scales near the centre of the disc becoming isolated, not contiguous with neighbours, radial shields 1/6–1/7 dd, divergent proximally, 3x as long as wide; disc scales persist ventrally until the oral shield; oral shield round triangular, 1.5x as wide as long, no distal lobe; adoral shields triangular, proximolateral to the oral shields, just meeting or separate interradially; distal oral papillae leaf-shaped, 1.5–2.0x as high as wide; DAPs ovoid, as wide as long, contiguous; VAPs 1.5x longer than wide, with convergent proximal sides, incised lateral ones (around pores) and a straight lateral edge with rounded corners; basally 6 arm spines, upper and lowest longest, bluntly pointed, no apical thorns, by the centre of the arm the lowest is 1.5x segment in length, almost 2x the size of the 2nd ventralmost, capitate, upper is 2nd longest, 3 middle spines becoming 2 middle spines by the end of the arm; one large flat oval tentacle scale. The LAPs (Fig. 26d–e) are curved with extensions meeting on the dorsal and ventral radial midline; the stereom is densest just proximal to the line of arm spine articulations, articulations with two horizontal raised lips with gaps at each lateral end. Vertebrae (Fig. 26f) with pronounced distal articulation, with a small heart-shaped zygosphene, and a deep furrow ventrally.

Distribution. Coral Seamount (730 m)

Remarks. The Coral Seamount specimens have the distinctive long ventral arm spines and single oval tentacle scale typical of the *A. magellanica-A. grandisquama* group of *Amphiura*. They are closest to the descriptions of *A. grandisquama natalensis* Mortensen, 1933b known from off the Indian Ocean coastline of South Africa. The South African specimens (<4 mm dd) have been described as having up to 5 rather than 6 arm spines, no primary plates (although they appear to be present in photos in Olbers *et al.* 2019 fig. 229), and longer ventral arm spines (to 3 segments in length). More specimens from the region are required to determine species boundaries.

Other similar bathyal species from the Indo-Pacific include *A. iris* Lyman, 1879 from off Japan which has only 4 arm spines. It was synonymised by Paterson (1985) with the Atlantic species *A. grandisquama* Lyman, 1869, however, our DNA evidence indicates that specimens from Japan are polyphyletic with respect to Atlantic specimens and should be retained as a separate species pending a larger revision. *Amphiura iridoides* Matsumoto, 1917 from off Japan (580 m) has much larger disc scales and radial shields. *Amphiura dejecta* Koehler, 1922a from off Borneo (558 m) has larger disc plates and radial shields and prominent, sometimes contiguous) primary plates.

Amphiura glabra Lyman, 1879 (see below) from the Philippines (930 m) has much larger radial shields and a naked ventral disc. In shallower waters, *A. dejectoides* from the Western Indian Ocean has arm spines with squared-off minutely thorny tips.

Family Ophiactidae

Ophiactis abyssicola (M. Sars, 1861)

Fig. 26h–j

Amphiura abyssicola Sars, 1861: 18 pl. 2(7–12).
Ophiactis poa Lyman, 1879: 40, pl. 13(356–358).—Lyman, 1882: 119, pl. 20(13–15) [according to Clark, H.L., 1918].
Ophiactis abyssicola.—Lyman, 1882: 122.—Clark, H.L., 1923: 334–335.—Mortensen, 1933b: 347.—Clark, A.M. & Courtman-Stock, 1976: 161.—Olbers *et al.* 2019: 247–249, fig. 250–251.—O'Hara & Thuy, 2022: 33, fig. 13(c–d).
Ophiactis corallicola Koehler, 1895: 460–461, fig. 5 [according to Clark, H.L., 1918].
Ophiactis echinata Koehler, 1898: 48–49, pl. 5(15–16) [according to Clark, H.L., 1918].

STUDY MATERIAL.—JC066: stn 8-5, Atlantis Bank, 32° 42.862′S, 57° 14.666′E to 32° 43.3′S, 57° 15.2′E, 828–994 m, 10/12/2011: 2 (NHMUK 2025.56) (**DNA code=OAB1**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiactis abyssicola*** (M. Sars, 1861): AFR239/A28266, West coast, 33° 9.6′S, 17° 12′E, 455 m, 1/2008, SAMC MB-A88404 (**DNA code=A88404**). CE13008/91, Whittard Canyon, 48° 38.15′N, 10° 41.4′W, 2400 m, 6/2013, NUI (**DNA code=NUI1666E-2**). GB903/2, Gulf of Mexico, central slope, 27° 4.794′N, 92° 48.996′W, 1066–1067 m, 16/7/2016, MV F248373 (**DNA code=F248373**). ***Ophiactis cuspidata*** Lyman, 1879: TAN1402/31, Forde Seamount, Stratum 1, 35° 19.01′S, 170° 27.09′W to 35° 18.48′S, 170° 27.53′W, 1205–1600 m, 11/2/2014, NIWA 95695 (**DNA code=NIWA95695**).

Distribution. Arctic (127–1838 m), NE Atlantic (27–2400 [?4813] m), W Atlantic (1054–3465 m), E Atlantic (425–1642 m), S Africa (311–2000 m).

Remarks. The COI sequences from these SWIO Ridge specimens fall into the "abyssicola" clade of this complex, similar to specimens from the Atlantic and South Africa at bathyal depths (O'Hara *et al.* 2014). The type series of *O. corallicola* (Gulf of Gascoyne, 950–1700 m) and *O. echinata* (Azores, 800 m) and *O. poa* (Tristan da Cunha, 914–1005 m) fall within the geographic and depth range of this species (as known from COI barcodes) and are here regarded as synonyms. However, Paterson (1985) has also recorded lower bathyal/abyssal specimens from the North Atlantic under this name, which would give it a very extensive bathymetric range. These deeper animals deserve further investigation. Off Australia and New Zealand, the sister species *O. cuspidata* Lyman, 1879 is restricted to upper bathyal depths and another species *O. amator* Koehler, 1922b inhabits mid-lower bathyal depths (O'Hara *et al.* 2014a).

Ophiactis amator Koehler, 1922

Ophiactis amator Koehler, 1922b: 34–36, pl. 81(1–6).—Rowe & Pawson, 1977: 349.—Rowe & Gates, 1995: 377–378.
Non *Ophiactis amator*.—Bernasconi & d'Agostino, 1974: 129–130, pl. 11(3–4) [see Brogger & O'Hara, 2015].

STUDY MATERIAL.—MD208: stn CP4915, Walters shoal, Plaine Sud, 33° 56.85′S, 44° 0.07′E to 33° 58.8′S, 43° 55.3999′E, 1865–2058 m, 12/5/2017: 2 (MNHN IE.2016.1362) (**DNA code=IE.2016.1362**).

COMPARATIVE MATERIAL EXAMINED. ***Ophiactis amator*** Koehler, 1922b: IN2015_C01/064, Great Australian Bight, OR13Area05, 34° 4.438′S, 129° 10.924′E to 34° 3.557′S, 129° 8.6852′E, 2649–2805 m, 13/11/2015, MV F227385 (**DNA code=F227385**). Talud Continental 3/45, Mar del Plata Submarine Canyon, 38° 1.913′S, 53° 39.268′W, 2934 m, 5/9/2013, CNP-INV (**DNA code=L45-2A**). Talud Continental 3/55, Mar del Plata Submarine Canyon, 37° 52.154′S, 53° 51.582′W, 1712 m, 8/9/2013, CNP-INV (**DNA code=L55-1**). TAN1007/114, Kermadec deep, 35° 29.76′S, 178° 31.23′E to 35° 29.53′S, 178° 30.59′E, 3036–3034 m, 7/6/2010, NIWA 64929 (**DNA code=OAM1**). TN228/J2-387-004, Z39 Seamount, Huon, 44° 23.345′S, 147° 16.277′E, 2004–1990 m, 25/12/2008, MV F168705 (**DNA code=F168705**).

Distribution. S America (1712–3447 m), S Africa (2707–3036 m), S Australia (1688–4052 m), New Zealand (1473–3580 m), Walters Shoal (1865–2058 m).

Remarks. The specimens measure up to 6.5 mm dd, with relatively thin arms, and long spines and rounded plates on the disc. Genetic sequences from these animals cluster with other *O. amator* specimens from across the Southern Ocean from off Argentina to New Zealand. Mid bathyal specimens (e.g., NUI1666.2, 2400 m) from the North Atlantic cluster with *O. abyssicola* (see above).

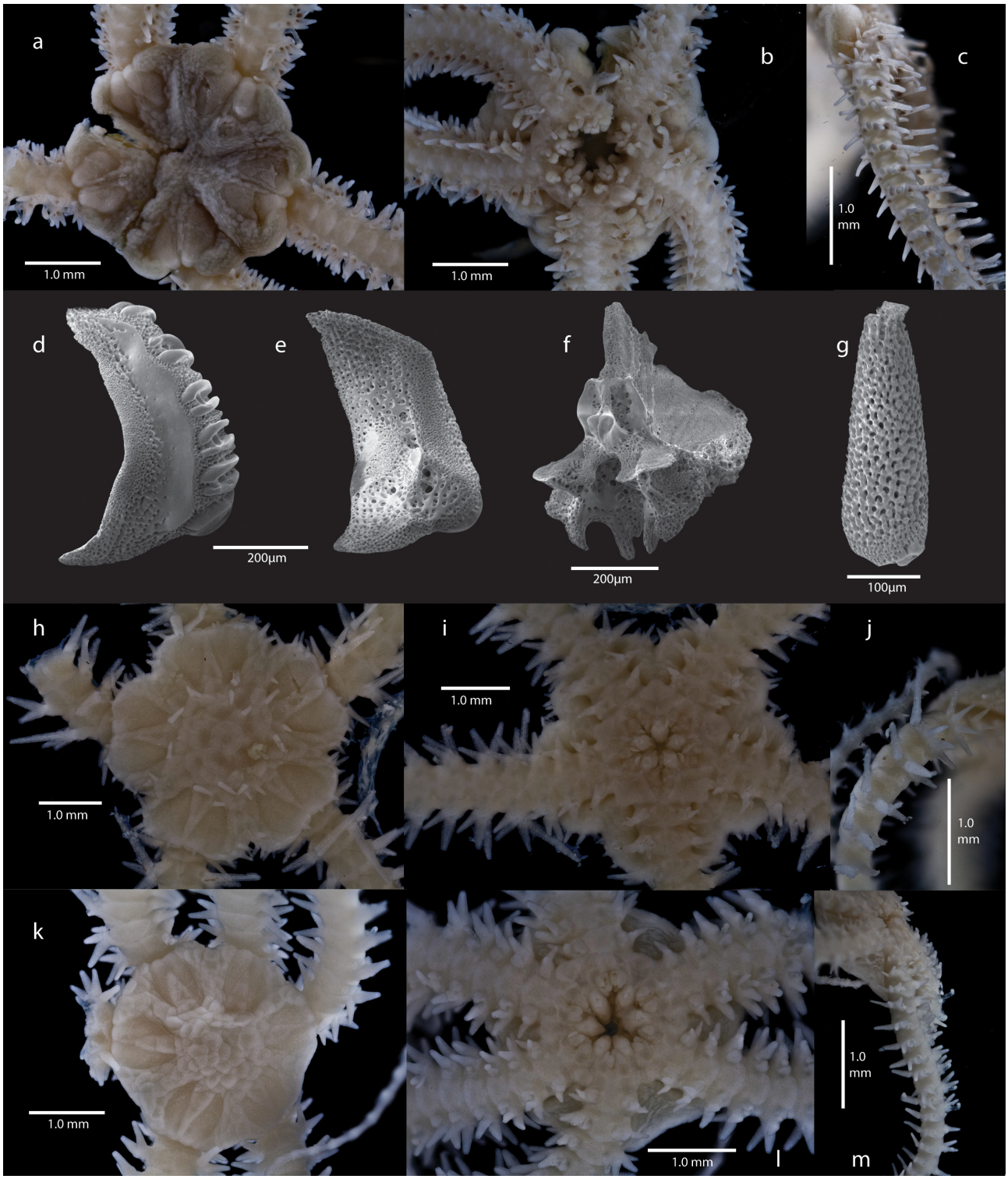

FIGURE 26. (a–c) *Amphiura* cf. *glabra* NHMUK 2025.20 (a) dorsal, (b) ventral, (c) lateral view of arm base; (d–g) *Amphiura* cf. *natalensis* NHMUK 2025.22 (d) basal lateral arm plate exterior view, (e) lateral arm plate, interior view, (f) vertebra ventrodistal view, (g) arm spine (tip broken); (h–j) *Ophiactis abyssicola* NHMUK 2025.56 (h) dorsal, (i) ventral, (j) lateral view of arm base; (k–m) *Ophiactis plana* NHMUK 2025.58 (k) dorsal, (l) ventral, (m) lateral view of arm base.

Ophiactis macrolepidota Marktanner-Turneretscher, 1887

Ophiactis macrolepidota Marktanner-Turneretscher, 1887: 298, pl. 12(12–13).—Matsumoto, 1917: 155–156, fig. 37.—Clark, A.M. & Rowe, 1971: 104.—Rowe & Gates, 1995: 379.
Ophiactis delicata Clark, H.L., 1915: 260–261, pl. 11(9–10).—Clark, A.M. & Rowe, 1971: 82–83, [according to Rowe & Gates, 1995].
Ophiactis parva Mortensen, 1926: 123.—Mortensen, 1940: 70–71, fig. 5.—Clark, A.M. & Rowe, 1971: 82–83, 105, fig. 31d [according to Rowe & Gates, 1995].
Ophiactis acosmeta Clark, H.L., 1938: 262–264.—Clark, A.M. & Rowe, 1971: 82–83, 104 [according to Rowe & Gates, 1995].

STUDY MATERIAL.—MD208: stn WB05, Walters shoal, Zone sommitale Sud, 33° 15.12′S, 43° 54.514′E, 26–30 m, 1/5/2017: 2 (MNHN IE.2023.4158) (**DNA code=IE.2023.4158**).—MD208: stn WS08, Walters shoal, Zone sommitale, Sud-Est, 33° 13.722′S, 43° 55.8861′E, 30–33 m, 3/5/2017: 2 (MNHN IE.2023.4172).—MD208: stn WB09, Walters shoal, Zone Sommitale Nord Ouest, 33° 13.767′S, 43° 55.7751′E, 27–30 m, 4/5/2017: 1 (MNHN IE.2023.4168).—MD208: stn WB10, Walters shoal, Zone Sommitale Nord Ouest, 33° 9.131′S, 43° 51.7939′E, 30 m, 6/5/2017: 1 (MNHN IE.2023.4173).

COMPARATIVE MATERIAL EXAMINED. ***Ophiactis definita*** Koehler, 1922a: BIOPAPUA/DW3770, Jacquinot Bay (Nouvelle-Bretagne), 5° 34′S, 151° 32′E, 220–294 m, 16/10/2010, MNHN IE.2012.222 (**DNA code=ODF2**). ***Ophiactis dyscrita*** H.L. Clark, 1911: Sagami Bay, off Misaki, stn1, 35° 8.415′N, 139° 32.944′E to 35° 8.262′N, 139° 32.746′E, 109–160 m, 4/6/2018, MV F248398 (**DNA code=Misaki031**). ***Ophiactis macrolepidota*** Marktanner-Turneretscher, 1887: KANACONO/DW4724, W Ile des Pins, 22° 39.6′S, 167° 8.3002′E to 22° 39.5′S, 167° 7.1795′E, 260–255 m, 20/8/2016, MNHN IE.2013.11110 (**DNA code=IE.2013.11110**). SAYA/CP5433, SW Saya de Malha, 11° 41.947′S, 61° 11.853′E to 11° 42′S, 61° 12.327′E, 234–235 m, 15/11/2022, MNHN IE.2023.4233 (**DNA code=IE.2023.4233**). ***Ophiactis plana*** Lyman, 1869: MIRIKY/CP3178, entre Nosy-bé et Banc du Leven, 12° 58.88′S, 48° 9.09′E to 12° 59.01′S, 48° 9.0402′E, 378–380 m, 25/6/2009, MNHN IE.2023.4013 (**DNA code=CP3178a**).

Description. Disc to 1.6 mm dd; typically 6 arms (one 1 mm dd specimen MNHN IE.2023.4168 with only 5 arms), 3 arms thinner so fissiparous, 3 times dd; disc scales rounded, small, overlapping, primary plates not prominent, few to no disc spines; radial shields small, 2x l/w, separated; ventral scales present; oral shields spear-head shaped with a sharp proximal angle and a slightly lobed distal margin, as long as wide; adoral shields separated radially; 1 small distal oral papilla; basal dorsal arm plates almost oval, tapered proximally, 1.5–2 times as wide as long, subsequent plates more triangular, separated or just contiguous throughout; 3 short, blunt arm spines, middle spine largest; tentacle scale half as long as ventral arm plate. Colour: dorsal arm surface pinkish/brown; disc brownish-yellow.

Distribution. NW Pacific (0–67 m), W Indian Ocean (3–235 m), E Indo-W Pacific (0–294 m), S Africa (26–33 m), S Australia (1–196 m), New Zealand (0–27 m).

Remarks. Clark & Rowe (1971) remarked on the difficulty of separating small *Ophiactis* species that have 6 arms, one distal oral papilla, and divide by fission. Characters used to separate these species, such as the shape of the oral/adoral/radial shields, arm spines and the presence of disc spines, are morphologically variable, and Rowe & Gates (1995) proceeded to synonymise *O. parva*, *O. delicata*, *O. acosmeta* with *O. macrolepidota*. The Indonesian *O. brachyura* Döderlein, 1898 and the Japanese *O. dyscrita* could also be added to this list. In contrast, our DNA evidence suggests that there are multiple clades of such species, with overlapping species ranges, that may contain both 5- and 6-armed individuals. The COI sequence of the MD208 specimen clusters with a 6-armed specimen from New Caledonia (IE.2013.11110) and two 5-armed specimens from Papua New Guinea (IE.2012.222). The latter specimens are larger, have purple arms, a bulbous pale disc, tiny radial shields and 4 arm spines at the base. Until type material (or neotypes from the type locality) are sequenced, it remains problematic to determine whether this clade is a new species or can be associated with an existing available name.

Ophiactis plana Lyman, 1869

Fig. 26k–m

Ophiactis plana Lyman, 1869: 330–331.—Clark, H.L., 1915: 265, pl. 10(1–2).—Clark, H.L., 1918: 301–302.—Clark, H.L., 1923: 333.—Mortensen, 1933b: 345–346, fig. 57.—Clark, H.L., 1939: 76–77.—Clark, A.M., 1974: 464–465.—Clark,

A.M. & Courtman-Stock, 1976: 163–164, figs 157, 162.—Alva & Vadon, 1989: 839.—Glück *et al.* 2012: 10, fig. 4a–b.—Olbers *et al.* 2019: 254–255, fig. 258–259.—O'Hara, 2024b: 77, fig. 75.

Ophiactis flexuosa.—Lyman, 1882: 116–117, pl. 20(1–3) (in part).—Studer, 1882: 17 [Non *Ophiactis flexuosa* Lyman T, 1879; see Clark, H.L., 1923].

Ophiactis profundi Lütken & Mortensen, 1899: 140–142, pl. 6(4–6).—Koehler, 1922a: 192–193, pl. 63(8).—Nethupul *et al.* 2022a: 68, fig. 38–39.

Ophiactis pteropoma Clark, H.L., 1911: 134–135, fig. 50.—Matsumoto, 1917: 154, pl. 3(9) [according to Koehler, 1922a].

Ophiactis profundi var. novaezelandiae Mortensen, 1924: 128–131, fig. 13.

STUDY MATERIAL.—JC066: stn 4-12, Coral seamount, 41° 22.333′S, 42° 54.066′E to 41° 23′S, 42° 54.1′E, 730 m, 16/11/2011: 1 (NHMUK 2025.58) (**DNA code=OPR14**); 1 (NHMUK 2025.57).

COMPARATIVE MATERIAL EXAMINED. ***Ophiactis plana*** Lyman, 1869: EXBODI/CP3852, Banc Sud Durand, 22° 16.6′S, 168° 43.2′E, 582 m, 14/9/2011, MNHN IE.2007.6735 (**DNA code=IE.2007.6735**). IN2022_V09/126, Site:039, 23° 17.75′S, 113° 5.1391′E to 23° 17.992′S, 113° 4.9411′E, 425–375 m, 10/12/2022, WAM (**DNA code=IN2022_V09_126**). MIRIKY/CP3178, entre Nosy-bé et Banc du Leven, 12° 58.88′S, 48° 9.09′E to 12° 59.01′S, 48° 9.0402′E, 378–380 m, 25/6/2009, MNHN IE.2023.4013 (**DNA code=CP3178a**). SAYA/DW5407, W Saya de Malha, 10° 59.357′S, 60° 18.914′E to 10° 59.649′S, 60° 19.103′E, 193–198 m, 6/11/2022, MNHN IE.2023.4239 (**DNA code=IE.2023.4239**). SS02/2007/77, Cascade 1200m 5, 43° 55.406′S, 150° 27.889′E to 43° 55.778′S, 150° 28.352′E, 590–660 m, 10/4/2007, MV F144837 (**DNA code=F144837**). TARASOC/DW3481, Moorea Island, 17° 29′S, 149° 45′W, 610 m, 22/10/2009, UF 13016 (**DNA code=UF13016**). TARASOC/DW3502, Tahiti Island, 17° 35′S, 149° 17′W, 430–580 m, 25/10/2009, UF 13019 (**DNA code=UF13019**).

Distribution. NE Atlantic (650–914 m), NW Pacific (88–1702 m), W Atlantic (48–800 m), E Atlantic (41–41 m), W Indian Ocean (22–1441 m), E Indo-W Pacific (55–1618 m), E Pacific (850–1644 m), S America (748–748 m), S Africa (0–730 m), S Australia (25–1443 m), New Zealand (55–1583 m).

Remarks. The taxonomy of many *Ophiactis* species is very confused. The incidence of specimens with 6 arms is high and many of these can divide by fission (A.M. Clark 1967). However, multi-armed and fissiparous forms do not always form separate clades on a phylogeny (see tree in Christodoulou *et al.* 2019) and can be similar genetically to 5 armed forms. Morphology is often variable, especially in fissiparous forms. Location is not necessarily a good guide to identity as some species are evidently very widespread, occurring throughout the Indo-Pacific and sometimes into the Atlantic as well. In some regions, notably the Western Atlantic, there are numerous small ill-defined fissiparous species that need to be delimited.

A multi-armed bathyal species called *O. plana* (type locality Florida), *O. profundi* (type locality eastern Pacific) or *O. pteropoma* (type locality: Japan) is evidently one of the widespread species. It has a single oral papilla on the side of each jaw, fan-shaped dorsal arm plates with a straight to slightly convex distal border, large radial shields (typically 1/5 dd), 3–4 arm spines, and rarely has disc spines. It typically has 6 arms (rarely 5 or 7) and small specimens are regularly found with 3 large and 3 small arms indicating that they are regenerating after having previously divided by fission. However, specimens identified as this species prove to be polyphyletic on a phylogeny. The majority, including the 2 specimens from Coral Seamount (2.5–3 mm dd), do form a monophyletic clade that occurs from the SW Indian Ocean to Moorea, South China Sea to New Zealand. But other 6-armed specimens cluster with either 5-armed species such as *O. definita* and *O. perplexa* or shallow water fissiparous species such as *O. macrolepidota* and are probably mis-identified atypical members of those species.

Unfortunately, we do not have genetic sequences from the Atlantic or eastern Pacific that may guide the nomenclature of this species. In the interim, we follow Mortensen (1933b) in regarding *O. plana* and *O. profundi* as conspecific.

Ophiactis savignyi (J. Müller & Troschel, 1842)

Ophiolepis savignyi Müller & Troschel, 1842: 95.

Ophiactis savignyi.—Clark, H.L., 1918: 305–306.—Koehler, 1922a: 193–195, pl. 64(5–6), 96(2).—Mortensen, 1933b: 348, fig. 58b.—Mortensen, 1936: 264.—Clark, H.L., 1939: 77.—Mortensen, 1940: 70.—Clark, A.M. & Rowe, 1971: 82–83, fig. 22e, 23d, 31b, pl. 14(4).—Clark, A.M. & Courtman-Stock, 1976: 164, figs 156, 161.—Cherbonnier & Guille, 1978: 125–128, fig. 57(A–I) (in part).

Ophiactis sp probably O. savignyi.—Clark, A.M., 1976: 259.

STUDY MATERIAL.—MD208: stn WR02, Walters shoal, Zone sommitale Sud-Ouest, 33° 12.25′S, 43° 50.818′E, 40 m, 30/4/2017: 1 (MNHN IE.2023.4156) (**DNA code=IE.2023.4156**).—MD208: stn WB05, Walters shoal, Zone sommitale Sud, 33° 15.12′S, 43° 54.514′E, 26–30 m, 1/5/2017: 3 (MNHN IE.2016.1345); 1 (MNHN IE.2023.4163).—MD208: stn WB09, Walters shoal, Zone Sommitale Nord Ouest, 33° 13.767′S, 43° 55.7751′E, 27–30 m, 4/5/2017: 1 (MNHN IE.2023.4167).—MD208: stn WB10, Walters shoal, Zone Sommitale Nord Ouest, 33° 9.131′S, 43° 51.7939′E, 30 m, 6/5/2017: 1 (MNHN IE.2016.1353); 2 (MNHN IE.2023.4174).

COMPARATIVE MATERIAL EXAMINED. ***Ophiactis brevis*** H.L. Clark, 1938: SBD/1554S, Great Barrier Reef Seabed Survey, 22° 3.224′S, 150° 21.2078′E to 22° 3.25′S, 150° 21.2861′E, 28.4–27.5 m, 10/5/2004, MTQ SBD010141 (**DNA code=SBD010141**). SS2012t07/8, 11° 13.324′S, 134° 45.12′E to 11° 13.378′S, 134° 45.12′E, 27.7–27.9 m, 18/10/2012, MV F193456 (**DNA code=F193456**). ***Ophiactis savignyi*** (J. Müller & Troschel, 1842): Blue Heron Bridge, Palm Beach, 26° 46.962′N, 80° 2.664′W, 1–5 m, 3/2/2013, MV F193474 (**DNA code=TOH12**). Misaki marine station, rocky shore, 35° 9.52′N, 139° 36.65′E, 0–1 m, 3/6/2018 (**DNA code=Misaki007**). IN2022_V09/133, Gascoyne Marine Park. Site:040, 23° 22.963′S, 113° 25.4141′E to 23° 24.154′S, 113° 24.9746′E, 114–104 m, 11/12/2022, MV F309537 (**DNA code=F309537**). MIRIKY/CP3257, Nord du Cap Saint André, 15° 47.52′S, 44° 44.9598′E to 15° 46.74′S, 44° 45.5202′E, 48 m, 9/7/2009, MNHN IE.2007.418 (**DNA code=IE.2007.418**). SS05/2007/140, Northwestern Australia, Leveque L27 transect, 15° 5.67′S, 121° 47.184′E to 15° 5.5′S, 121° 47.417′E, 77 m, 2/7/2007, MV F166029 (**DNA code=F166029**).

Distribution. NW Atlantic (1–12 m), NE Atlantic (0–43 m), NW Pacific (0–130 m), NE Pacific (0–70 m), W Atlantic (0–211 m), E Atlantic (0–50 m), W Indian Ocean (0–144 m), E Indo-W Pacific (0–206 m), E Pacific (0–33 m), S America (1–153 m), S Africa (0–77 m), S Australia (0–60 m).

Remarks. *Ophiactis savignyi* is a species complex that includes several mitochondrial DNA clades that are widespread in tropical waters (Roy & Sponer 2001, 2022). The sequenced MD208 specimen belongs to Clade 2 of Roy & Sponer (2001), which also includes sequences from the closely related five-armed species *O. brevis*. Further work is required to determine whether these clades can be distinguished as separate species. *Ophiactis savignyi* is a shallow water species and any historical record deeper than 200 m requires re-examination.

Family Ophionereididae

Ophionereis (*Ophiotriton*) *boucheti* sp. nov.

https://zoobank.org/urn:lsid:zoobank.org:act:AD90A98A-774C-4160-A88F-55FC5376642F
Fig. 27

TYPE LOCALITY. Walters shoal, Zone sommitale Sud, 33° 15.053′S, 43° 54.4771′E, 26 m

TYPE MATERIAL.—MD208: stn WS06, Walters shoal, Zone sommitale Sud, 33° 15.053′S, 43° 54.4771′E, 26 m, 1/5/2017, holotype: 1 (MNHN IE.2016.1342); paratypes: 2 (MNHN IE.2023.4170) (**DNA code=IE.2016.1342**).

OTHER STUDY MATERIAL.—MD208: stn WR01, Walters shoal, Zone sommitale Sud-Ouest, 33° 12.18′S, 43° 50.828′E, 36 m, 30/4/2017: 1 (MNHN IE.2016.1350).—MD208: stn WB05, Walters shoal, Zone sommitale Sud, 33° 15.12′S, 43° 54.514′E, 26–30 m, 1/5/2017: 2 (MNHN IE.2023.4157).—MD208: stn WS07, Walters shoal, Zone sommitale Sud, 33° 15.435′S, 43° 52.1851′E, 30–33 m, 2/5/2017: 1 (MNHN IE.2016.1358).—MD208: stn WS08, Walters shoal, Zone sommitale, Sud-Est, 33° 13.722′S, 43° 55.8861′E, 30–33 m, 3/5/2017: 1 (MNHN IE.2023.4171).—MD208: stn WB09, Walters shoal, Zone Sommitale Nord Ouest, 33° 13.767′S, 43° 55.7751′E, 27–30 m, 4/5/2017: 4 (MNHN IE.2023.4166).

COMPARATIVE MATERIAL EXAMINED. ***Ophionereis* cf. *intermedia*** Mayotte, Recif Nord, 12° 35.964′S, 45° 5.994′E, 0–2 m, 9/1959, identified by Cherbonnier & Guille (1978) as *Ophionereis hexactis,* MNHN EcOs21707. SAYA/YB05, Saint Brandon, 16° 28.97′S, 59° 42.66′E, 12 m, 19/11/2022, MNHN IE.2023.4380 (**DNA code=IE.2023.4380**). SAYA/YS12, NE Saya de Malha, 10° 22.75′S, 62° 7.75′E, 26 m, 9/11/2022, MNHN IE.2023.4410 (**DNA code=IE.2023.4410**). ***Ophionereis* cf. *variegata*** Ilot Tanikely, near Nosy Be, 17/3/1960, identified by Cherbonnier & Guille (1978) as *Ophionereis degeneri*, MNHN EcOs21706; identified by Cherbonnier & Guille (1978) as *Ophionereis degeneri*, MNHN EcOs21705. ***Ophionereis dubia*** (J. Müller & Troschel, 1842): Pulau Pinang, Malaysia, 5° 22.7′N, 100° 6.9′E, 13.6 m, 12/9/2005, NSMT E5543 (**DNA code=TIM032**). Scottburgh, Aliwah Shoal, 30° 16.034′S, 30° 49.07′E, 12–17 m, 15/11/2016, MV F237926 (**DNA code=Aliwah1**). ATIMO

VATAE/TR02, 25° 1.3′S, 47° 0.5′E, 17 m, 29/4/2010, MNHN IE.2007.4724 (**DNA code=TOH255-IE.2007.4724**). KGR/Sled11, King George River region, 13° 54.291′S, 127° 19.7315′E, 11 m, 7/6/2013, MV F193495 (**DNA code=F193495**). Koyo2014/16, E of Mago-jima Island, Ogasawara, 27° 11.878′N, 142° 12.843′E to 27° 12.346′N, 142° 12.625′E, 126.5–128.9 m, 25/6/2014, NSMT E10208 (**DNA code=NSMT E10208**). SAYA/YB07, Saint Brandon, 16° 48.622′S, 59° 29.88′E, 7 m, 20/11/2022, MNHN IE.2023.4205 (**DNA code=IE.2023.4205**). SAYA/YR05, NW Saya de Malha, 10° 37.2′S, 60° 10.3′E, 39 m, 6/11/2022, MNHN IE.2023.4298 (**DNA code=IE.2023.4298**). ***Ophionereis hexactis*** (H.L. Clark, 1938): Ashmore/18, Ashmore Reef, Blue Grotto, SW of Middle Island, 12° 16.42′S, 123° 0.71′E, 2–6 m, 7/10/2002, MV F93671 (**DNA code=MVF93671**). ***Ophionereis semoni*** Döderlein, 1896: KGR/AS03, King George River region, 13° 48.957′S, 127° 19.2864′E, 73 m, 12/6/2013, MV F193497 (**DNA code=F193497**). ***Ophionereis tigris*** H.L. Clark, 1938: UF/HI09-003, Heron Island, Wistari Reef, 23° 27.113′S, 151° 52.027′E, 11–13 m, 11/11/2009, UF 9889 (**DNA code=UF9889**).

COMPARATIVE MATERIAL NOT EXAMINED. ***Ophionereis intermedia*** (A.M. Clark, 1953): Magari, Notojima Island, Ishikawa Pref., Japan, 37° 9′N, 136° 59′E, 1.5–2 m, 4/3/2003, NSMT E5055 (**DNA code=TIM021**). ***Ophionereis thryptica*** (Murakami, 1943): 2008, NSMT E-2172-p01 (**DNA code=TIM050**).

Diagnosis. Small body size (to 2.2. mm dd). Disc covered in minute overlapping scales, without enlarged scales around the margin, small widely separate radial shields not covered by scales. No genital papillae. Five arms, supplementary DAPs 2/3 as long as the primary DAP, 3 rounded arm spines with blunt tip, middle one only slightly longer than the others. Thin brown bands across the distal end of white radial shields.

Description. Holotype 2.2 mm dd, arms 13 mm long, disc covered in minute overlapping scales, 0.05–0.08 mm wide, no obvious primaries, marginal disc scales not enlarged, exposed section of radial shields 0.2 mm long, 2x as long as wide, widely separate, aligned to each side of the arm base, continuing proximately under the disc for another 0.2 mm; disc scales not continuing onto dorsal arm; ventral scales similar size, obscured by skin near oral shields; no granules or spines along wide genital slit; oral shields broadly triangular with rounded angles, widest distally, adoral shields narrowly triangular, with an acute proximal angle and a widened concave distal edge, just touching or separate interradially, radially separated by the small 1st VAP, oral and adoral shields minutely beaded; 4 broad teeth with convex or obtusely-angled hyaline edges, ventralmost smallest; 4 oral papillae, the inner three (infradental, buccal shield, and 2nd adoral shield spine) are oval, often pointing proximally, adoral shield spine is plate like, a little separate, and larger than the others, the thin Lyman's ossicle forms the distal rim of the 2nd oral tentacle pore, which opens into the jaw slit.

Arms five, thin, DAPs hexagonal, basal plates as wide as long, widest proximally (almost triangular), becoming thinner and widest near the mid-length of the plate, contiguous; supplementary plates not contiguous, start at the widest point of the main DAP, and widen into a triangular plate distally confluent with the main DAP; first VAP much smaller than the rest, triangular to rhomboid, widest distally, succeeding VAPs contiguous, 1.5x as long as wide, with convex distal edge, rounded distolateral corners, concave lateral sides and an obtuse angle proximally, minutely beaded, becoming wider distally than proximally, 3 arm spines, round in cross-section, slightly tapering towards a blunt apex, subequal and as long as a segment near the arm base, middle one becomes a little longer than the others at mid-arm; single oval tentacle scale, 1.5x as long as wide, 1/2 the VAP in length.

Colour (preserved): disc light yellow-brown, with darker patches near the arm base and sometimes around the lateral disc area, radial shields lighter colour, so that the dark patch appears to be divided into 3 sections, ventral disc surface also darker, which continues to a variable extent across the oral shields, first dorsal arm segment light, rest of the arm greenish-brown with thin dark transverse lines every 3–6 segments, these lines are often wider near the edge of the arm than the centre; arms also banded ventrally, 1–2 dark segments alternating with 3–6 light segments, base of arm spines also dark adjacent to dark segments.

Paratypes and other material (1.5–3 mm dd), smallest specimens with thin brown bands across the distal end of radial shields, some specimens with pale patches in the centre of the ventral disc area, and darker colours on the oral plates, others with pale areas next to the genital slits, some with the bases of all arm spines coloured. Paratype (IE.2023.4170) ossicles: LAPs higher proximally then distally, with nodulated surface, arm spine articulations composed of two straight parallel lobes, with a smaller knob proximally between them, muscle and neural perforation sit between the lobes; arm spine minutely thorny with vertical grooves near the spine apex; vertebrae zygospondylous.

Distribution. Walters shoal (26–36 m).

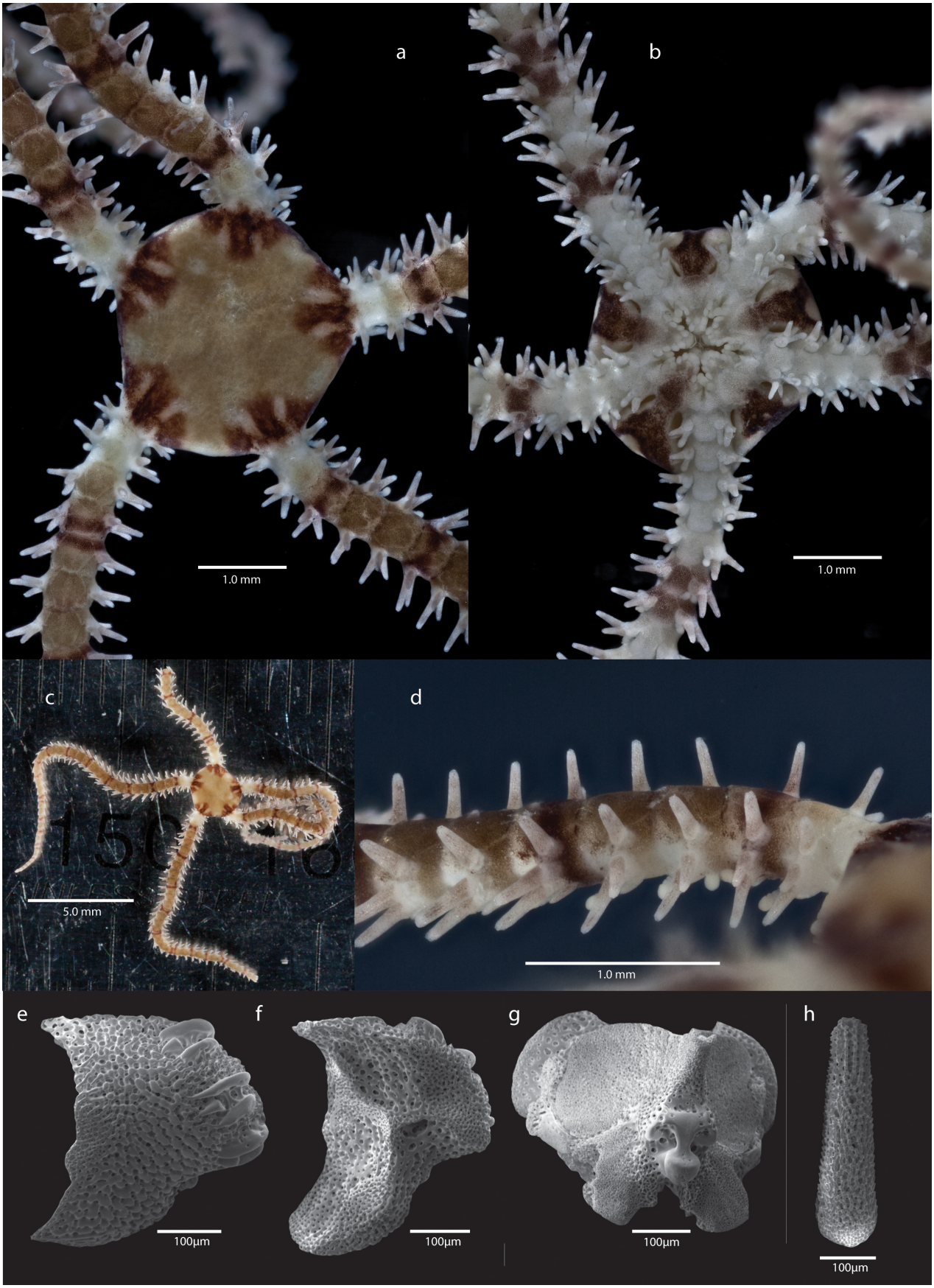

FIGURE 27. (a–d) *Ophionereis* (*Ophiotriton*) *boucheti* **sp. nov.** holotype MNHN IE.2016.1342 (a) dorsal, (b) ventral, (c) whole body, (d) lateral view of arm base; (e–h) paratype MNHN IE.2023.4170 (e) exterior view of lateral arm plate, (f) interior view of lateral arm plate, (g) distal view of vertebra, (h) arm spine.

Remarks. There are a group of *Ophionereis* species which have discs covered with very fine plates or skin, large supplementary DAPs that are typically as long as the primary DAP, and (excepting *O. intermedia*) lack granules/spines along the genital slits. We propose to utilise the subgenus name *Ophiotriton* Döderlein, 1896 for this group of species. Döderlein (1896) created this taxon for his new species *O. semoni* and defined it by the presence of skin rather than plates covering the disc. However, we expand this narrow definition to include all *Ophionereis* species with very fine disc plating and no genital granules, including *O. dubia* (Müller & Troschel, 1842), *O. hexactis* H.L. Clark, 1938, *O. thryptica* Murakami, 1943, and *O. tigris* H.L. Clark, 1938. We have representatives of all these species in this clade on our phylogeny. To this list could be added *O. amoyensis* A.M. Clark, 1953, *O. andamanensis* James, 1982, *O. vivipara* Mortensen, 1933a and *O. sexradia* Mortensen, 1936, although we have not examined specimens of these species. *Ophionereis sexradia* from the Canary Islands is fissiparous, as are some small specimens from Japan (H.L. Clark 1911, fig. 79g) that possibly represent undescribed species. In addition, the *Ophiotriton* clade with these species on our tree also contains a sample from a small Japanese specimen of *O. intermedia* A.M. Clark, 1953 that differs in having a row of small sharp separated spines running along the genital slit. Similar 5-armed specimens also occur in the Indian Ocean (erroneously reported as *O. hexactis* by Cherbonnier & Guille, 1978), which are divergent from the Japanese *O. intermedia* in our phylogeny, and which we designate as *O.* cf. *intermedia* pending formal description. The widespread 'species' *O. dubia* is also polyphyletic on our tree and appears to contain cryptic species. There are numerous synonyms (A.M. Clark 1953, Irimura 1982). More DNA samples are required to sort out species boundaries and nomenclature in this taxon, including from the Red Sea, type locality for *O. dubia*.

The new species *O. boucheti* is distinguished by its small size, 5 arms, covering of tiny disc plates except over the small radial shields, lack of genital granules, and colour scheme. It is closest in form to *O. dubia* and *O. vivipara*. Small specimens of *O. dubia* (at least a small Australian specimen, MV F109865, that has the colour scheme of synonym *O. stigma* H.L. Clark, 1938) have DAPs as wide as long, with large glassy supplementary DAPs that are contiguous along the arm. The VAPs are hourglass-shaped, 2x as long as wide, incised laterally around the tentacle pores. The dark colour across the radial shields is a thin 'Y'-shaped band that forks proximally. *Ophionereis vivipara*, a brooding species from the intertidal of Mauritius, is also a small species (to 3 mm dd) that has non-contiguous supplementary DAPs, but differs in having characteristic star-shaped markings on the centre of the disc. The type figures also show extremely small scales on the dorsal and ventral disc surfaces (Mortensen 1933a).

Specimens from Madagascar and the Comoro Islands, referred by Cherbonnier & Guille (1978) to the species *O. degeneri* A.H. Clark, 1949, are mis-identified. An examination revealed enlarged marginal plates adjacent to the radial shields and a small accessory LAP between the arm segments laterally, a characteristic of the species *Ophionereis variegata* Duncan, 1879 not *O. degeneri* (see Matsumoto 1917 fig 79, A.M. Clark 1953).

Etymology. Named after Dr Philippe Bouchet (Muséum National d'Histoire Naturelle, Paris) a principal investigator of the MD208 expedition.

Discussion

This paper focuses on the Ophiuroid fauna from 3 seamounts in the SW Indian Ocean, Walters Shoal on the MD208 expedition, and Atlantis and Coral Seamounts on the JC066 expedition. However, a macro-ecological analysis of these samples is problematic as the collection gear and targeted habitats differ between the 2 surveys. MD208 was principally a sledge/beam trawl survey targeted soft sediment species with some scuba collected hard substratum samples from shallow water, and JC066 was an ROV survey that targeted species epizoic on corals and sponges. Furthermore, the depths of the collected ophiuroids differ. On Walters Shoal ophiuroids were sampled from 26–711 and 1210–2058 m, compared with 707–1364 m from Atlantis and Coral seamounts. Consequently, the following biogeographic discussion uses phylogenetic information to relate the collected ophiuroids to those found in surrounding regions.

Walters Shoal

The shallow water (26–200 m) fauna from Walters Shoal consists of 6 species, *Ophiactis savignyi*, *O. macrolepidota*, *Breviturma pusilla*, *Ophionereis boucheti*, *Amphipholis squamata*, *Ophiacantha striolata*, and *Ophiomyxa tenuispina*.

The first three represent widespread Indo-Pacific clades. The Indian Ocean population of *B. pusilla* may represent a cryptic species that ranges (at least) from Walters Shoal north to the Saya de Malha bank. *Ophionereis boucheti* is an endemic species, related most closely to an undescribed species found off Oman. *Amphipholis squamata* is a worldwide allopolyploid complex (Hugall *et al.* 2024). The mitochondrial clade found in the western Indian Ocean is the tropical clade 'E', distinct from the temperate clade 'A' found off South Africa and Southern Australia. The last 2 species of the 6 were described from eastern South Africa. However, our data also suggests they range northward from there to at least Madagascar. In summary, the relationships of the shallow water fauna are primarily with the tropical western Indian Ocean. Some species have a distribution that extends southwards to eastern South Africa.

These relationships are broadly similar to those reported for other taxonomic groups, with the exception that, unlike for fish, there are no species endemic to a proposed "West Wind Drift" faunal province (i.e. Gough Island, Tristan da Cuhna, Vema seamount, Amsterdam & St Paul Islands, see Collette & Parin 1991). The fish fauna from the summit of Walters Shoal (20 species) consists of 20–25% species that are endemic to Walters Shoal, 15% endemic to the islands of the "West Wind Drift", 25–30% to a temperate/subtropical fauna, and 30% tropical-Indo-Pacific species. The sponges (23 species) consist of 74% with tropical Indian Ocean affinities and 26% with temperate South Africa (Payne 2015). Most of the larger molluscs have Madagascan affinities (Bouchet pers. comm.). The endemic lobster species *Palinus barbarae* is closest to the species *P. delagoae* that occurs from eastern South Africa to Mozambique (Groeneveld *et al.* 2006). The endemic summit crinoid *Comanthus walhbergi tenuibrachia* is a subspecies of a widespread Indo-Pacific species complex (Clark A.M., 1972).

We further report 9 ophiuroid species from upper bathyal depths (200–700 m) at Walters Shoal, including *Asterostegus sabinae*, *Astrothorax papillatus*, *Ophioconis cupida*, *Ophiocypris tuberculatus*, *Ophioleuce seminudum*, *Ophiomitrella nudextrema*, *Ophiomoeris obstricta*, *Ophiomyxa neglecta*, and *Ophiotreta valenciennesi*. All these species form regional clades with other SW Indian Ocean samples, that are sister to the Indo-Pacific clades (or more rarely to NW Pacific or E Pacific clades). One species (*A. papillatus*) has a distribution that extends to South Africa. Interestingly, there are no species at these depths that have a distribution that includes the Amsterdam/St Paul Islands (cf. O'Hara & Thuy 2022).

The 9 species found at mid-bathyal (1200–2100 m) depths around Walters Shoal have a different pattern, with 5 species (*Amphiophiura litvinovae*, *A. trifolium*, *Ophiopyrgus hainesae*, *Stegophiura waltersi* and *Ophiacantha exilis*) belonging to tropical Indo-Pacific species complexes, and 2 belonging to temperate complexes (*Ophiactis amator*, *Ophiomyces grandis*). *Ophioplinthus abyssorum* is also reported from the North Atlantic (although we have no DNA sequences to confirm this). *Ophiernus vallincola* belongs to a global species complex, with the sequenced Walters Shoal specimen being sister to a SW Indian Ocean sample from the Saya de Malha bank. Again, none of these species has been reported with certainty from around the Amsterdam/St Paul Islands (although small specimens of *Ophiomyces* and *Ophioplinthus* found there, see O'Hara & Thuy, 2022, may belong to *O. grandis* and *O. abyssorum* respectively).

Atlantis Bank

Eight ophiuroid species were collected from Atlantis Bank between 707 and 1000 m deep. Of these, the distribution of *Gorgonocephalus pectinatus* ranges to South Africa and possibly into the East Atlantic. *Ophiactis abyssicola* and *Ophiacantha metallacta* are widespread species, the former occurring in South Africa up to the East and North Atlantic, and the latter in the West Atlantic and East Indo-West Pacific. Two species (*Ophiocreas lissum* and *Ophiacantha swio* are widespread in the West Indian Ocean from the SWIO Ridge to Chargos, and 3 others (*Ophiectodia melvillei*, *Ophiosabine multifida* and *Ophiuroglypha atlantis*) have been found only on the SWIO Ridge. Two species are shared with Coral Seamount, one with Melville Seamount, and only one *O. abyssicola* with the Amsterdam/St Paul Islands. Thus, Atlantis has a mixed tropical/temperate summit fauna, unsurprising for a seamount located at 32°S.

Coral Seamount

Eighteen ophiuroid species were collected from Coral Seamount in depths of 730–1300 m. However, unlike Atlantis, the affinities of this fauna at 41°S lie much more with the temperate to subpolar Southern Ocean. DNA

confirms that *Gorgonocephalus chilensis*, *Astrotoma* cf. *manilense*, *Ophiocreas carnosum* and *Ophiomyxa vivipara* occur throughout the Southern Ocean on either side of the subtropical front. *Glaciacantha nizari*, *Ophiosemnotes conferta*, *Ophiolimna gyrei*, *Ophiolebes* cf. *paulensis*, *Ophiologimus prolifer* and *Ophectodia enopla* belong to species complexes that are also widespread in the temperate Southern Ocean and the latter up into the Atlantic. *Ophiocreas corali*, and *Amphiura* cf. *natalensis* are similar to animals found off South Africa. Two species are endemic to the SWIO Ridge (*Ophiacantha swio* and *Ophiosabine multifida*). The relationships of *Ophiuroglypha* sp are unknown. Only *Ophiophrura* sp. and *Amphiura* cf. *glabra* appear to have tropical affinities, but sampling is sparse and their true relationships are uncertain. A number of species also occur at Amsterdam/St Paul Islands including *O. vivipara*, *O. conferta*, *O. enopla*, *O. gyrei* and possibly the *Ophiophrura* and *Ophiolebes* species.

Another published phylogeny arising from the JC066 expedition materials for the octocoral family Primnoidae also shows mixed faunal relationships (Taylor & Rogers 2017). They found that six species (from Coral, Atlantis and Sapmer) were placed in a Pacific Ocean clade, two species (Melville) in a subantarctic clade, and one (unknown locality) in a predominantly Atlantic clade.

Distinctiveness, connectivity and endemicity of the SWIO seamount ophiuroid faunas

We report a distinct fauna on each of the three seamounts studied (Walters, Atlantis and Coral). Coral (at 42°S) has a strong relationship to temperate/subpolar faunas, with only a few species indicative of a tropical origin. Walters (33.2°) has shelf to upper bathyal (26–700 m) fauna with close affinities to a Western Indian Ocean fauna, including around the African continental margin, Madagascar and Mascarene Plateau, whereas the fauna of Atlantis (32.7°S) is more a widespread tropical/temperate seamount fauna. These patterns match expectations of dispersal probabilities derived from modelled oceanic currents (Crochelet *et al.* 2020), where Coral Seamount was associated with the longest estimated mean distance of larval dispersal of any seamount in the region due to its location within the strong eastward flowing Agulhas Return Current. Walters was included in a bilateral connectivity network that includes Madagascar, the Madagascar Ridge, the southern Mascarene Plateau and the Mozambique Channel. Conversely, Atlantis was connected to other seamounts on the SWIO Ridge. Modelled dispersal from Walters and Atlantis was quite limited and they are only connected at the longest estimates of pelagic larval duration (>360 days). Walters and Atlantis are at roughly the same latitude, but, although we lack samples from the same depth for a direct faunal comparison, the physical structure of the seamounts is distinct. The flattened Atlantis summit (around 700 m) has rocky outcrops and thin sediment. The rocky summit of Walters is at 18 m, with steep flanks to 600 m, and less steep sediment draped areas below that. These habitat differences would be enough to expect a distinct ophiuroid fauna (O'Hara 2024a, b). The ophiuroid fauna of the Amsterdam/St Paul Islands is also distinct (O'Hara & Thuy, 2022). The fauna of Walters also varies with depth, with different shallow (0–200 m), upper bathyal (200–700) and mid bathyal (1300–2100 m) assemblages. The faunas on Walters, Atlantis, Coral, Amsterdam/St Paul are distinct and require separate conservation management arrangements that acknowledge depth and location as key drivers of assemblage structure.

We report several new species that are currently known from a single seamount. However, this may alter with increased sampling. Historical reports of elevated species endemism on seamounts have proven to be overstated for ophiuroids (O'Hara 2007). Life on seamounts is precarious. Firstly, because seamount biotas are vulnerable to local extinction from changes to water temperature and other oceanographic conditions through climate change. Unlike biotas on continental margins, seamount populations cannot always shift distribution to different latitudes to escape changing conditions. Oceanographic fronts and water masses are known to change position over time, including for the SW Indian Ocean (Trend-Staid & Prell, 2002; McKay *et al.* 2012). Fluctuating water masses are known to induce local extinction of deep-sea faunas (Yasuhara *et al.*, 2008). Secondly, many seamounts are formed through volcanic eruptions and can eventually rise for kilometres above the seafloor. Like on Walters Shoal, the biota that eventually colonises this new habitat is typically related to other shallow water faunas, not the surrounding fauna of the abyssal plains. Seamount faunas are largely structured by dispersal with similar communities appearing on neighbouring seamounts at the same depths (Clark *et al.* 2010). This process continues over time, a constant supply of new evolutionary lineages would compete with any existing fauna. Finally, seamounts are typically composed of heavy basalt rock which gradually sinks into the softer oceanic crust over millions of years once volcanism ceases. Shallower benthic habitats and their specialised biota disappear with this process. All these processes must reduce the likelihood of endemic species forming on seamounts.

The placement of a seamount in regard to ocean currents is critical for dispersal. Unlike Walters and Atlantis, Coral Seamount sits within the strong eastward flow of the South Indian Gyre that originates off SE Africa. Thus. dispersal to Coral is more likely for a range of species with shorter pelagic larval durations, which may partly explain the elevated higher species richness.

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