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Primnoidae (Cnidaria: Octocorallia) of the SW Indian Ocean: new species, genus revisions and systematics

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The Indian Ocean is one of the least-studied areas of the world's largest biome, the deep sea. On an expedition to five seamounts along the SW Indian Ocean Ridge in 2011, thousands of specimens from deep-sea habitats were procured. We propose five new species of Primnoidae, a predominantly deep-sea octocoral family. The new species include three from the genus *Narella*, and one new species each from *Primnoa* and *Primnoeides*; the latter genus is revised and we propose *Digitogorgia* as its junior synonym. We support the new species placement within Primnoidae through taxonomic descriptions and the most comprehensive molecular phylogenetic analysis of any deep-sea coral family (81 species across 29 genera). We also present a rare example of polar submergence (from the Antarctic shelf into deeper more Northern waters).

ADDITIONAL KEYWORDS: deep-sea – octocoral – phylogenetic – polar submergence.

INTRODUCTION

Although often viewed as remote, the deep ocean plays a major role in the Earth's biogeochemical cycles, particularly in terms of carbon cycling and storage (Armstrong *et al.*, 2012). As potentially the largest habitat on the planet, the deep sea is also home to a dizzying array of animals and ecosystems, from hydrothermal vents to cold-water coral reefs (Rogers, 2015).

The large topographic elevations of seamounts provide (relatively) shallow habitat and thus a higher food supply compared to the surrounding deep ocean (Rowden *et al.*, 2010). Furthermore, complex hydrographic conditions that focus nutrients, as well as physical and biological interactions with overlying zooplankton and micronekton communities, may also lead to enhanced food supplies on seamounts creating hotspots of biodiversity in the deep sea (reviewed in Rowden *et al.*, 2010). Distinct species-rich benthic habitats have been found on many seamounts worldwide (Clark *et al.*, 2010). Cold-water coral reefs formed by stony corals (Scleractinia) and/or gardens of octocorals (Octocorallia), hydrocorals (Stylasteridae) and black corals (Antipatharia) (Rogers, 1994) are common. Globally, seamounts cover an area about the size of Europe (Kvile *et al.*, 2014) making them an important, and understudied, ecosystem.

The Indian Ocean, unlike other oceans, was little studied in the 'heroic age' of deep-sea exploration (Rogers & Taylor, 2012). There are an estimated 24 000 seamounts and/or knolls in the Indian Ocean, consisting of over 4000 large seamounts (1000+ m tall) and almost 20 000 knolls (200–1000 m tall) (Yesson *et al.*, 2011) – yet few have even been named and any known biological sampling has tended to be linked with exploratory fisheries (e.g. Romanov, 2003). The exception is Walter's Shoal, a relatively shallow seamount that is therefore more accessible for study, although most biological collections there have been shallow (under 50 m) or pelagic in nature with few investigations done into deep-sea areas.

The southern Indian Ocean is the meeting point of a number of different water masses. The Aghulas Current to the west, the sub-tropical front to the south of this, and further south is the Antarctic Circumpolar current (ACC; Read *et al.*, 2000). Below the surface there is sub-Antarctic Mode Water down to 500 m depth, and Antarctic Intermediate Water flowing below this to around 1500 m depth. And under this is Upper Deep Water to around 2000 m depth, which is

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mainly Indian deep water flowing south (McDonagh *et al.*, 2008). This complex current system could create barriers to gene flow and species migration into and out of Antarctica. Placing species from this area into wider phylogenetic contexts, to investigate their evolutionary history and biogeographical origins, is therefore important. Are species from the southern Indian Ocean part of Antarctic fauna that have submerged into the deep sea of the Indian Ocean, so-called 'polar submergence' (discussed in Brandt *et al.*, 2007)? If not, what is the origin of Indian Ocean deep-sea fauna?

A 51-day expedition on the RRS *James Cook* in 2011 (JC066) visited five seamounts on the southwest Indian Ocean ridge (SWIOR, see Fig. 1). The expedition collected ~2500 specimens using the remotely operated vehicle, *Kiel 6000*. The limited deep-sea sampling in the Indian Ocean makes the specimens presented here very rare. The rate of species discovery from JC066 specimens has been high with three new species of holothurians from the families Synallactidae, Laetmogonidae and Psolidae (O'Loughlin, Mackenzie & VandenSpiegel, 2013), a new species of squat lobster from the Munidopsidae family (Macpherson, Amon & Clark, 2014) and many new species of ophiuroids (T.D. O'Hara, Victoria Museum, personal communication).

Octocorals are common and prominent components of many deep-sea habitats and communities (Watling *et al.*, 2011), including seamounts (Henry *et al.*, 2014; Davies *et al.*, 2015). The seamounts of the SW Indian Ocean are no exception. Here we propose five new species of the octocoral family Primnoidae, a family of corals that often dominated habitats seen on the SWIOR and a family described as the 'quintessential deep-water octocoral family' (Cairns & Bayer, 2009). The new species include three from the genus *Narella*, and one new species each from *Primnoa* and *Primnoeides*; the latter genus is revised and we propose *Digitogorgia* is synonymized within it. Biogeographically, through phylogenetic analysis, we also present rare examples of cold-adapted species moving to warmer waters and one example of 'polar submergence'.

MATERIAL AND METHODS

Samples were collected on a 2011 expedition on the RRS *James Cook* to the SW Indian Ocean Ridge (Fig. 1) using the remotely operated vehicle, *Kiel 6000*. Primnoidae were frequent members of the deep-sea communities on surveyed seamounts (see Primnoidae *in situ*, Fig. 2).

Samples were grabbed using a robotic arm and placed into bioboxes before being brought to the surface. On ship they were processed in a temperature-controlled cold room at 4 °C, photographed and genetic subsamples of a few centimetres of branchlets were taken and placed in ~99% ethanol and then put into a –20 °C freezer; the remainders of colonies were preserved in 70% ethanol.

All specimens have been catalogued at the Natural History Museum, London, UK (Abbreviation: NHMUK).

TAXONOMIC METHODOLOGY

Several polyps from each specimen were examined under a light microscope (specific details in Taylor *et al.*, 2013). Polyps were dissolved in sodium hypochlorite (bleach), washed and mounted on SEM stubs using methods discussed in Taylor *et al.* (2013). All images within this publication were taken from stubs coated in a gold:palladium 60:40 alloy, to a thickness of between 30 and 40 μm, on a JEOL JSM 5510 in the SEM Facility, Department of Plant Sciences, University of Oxford.

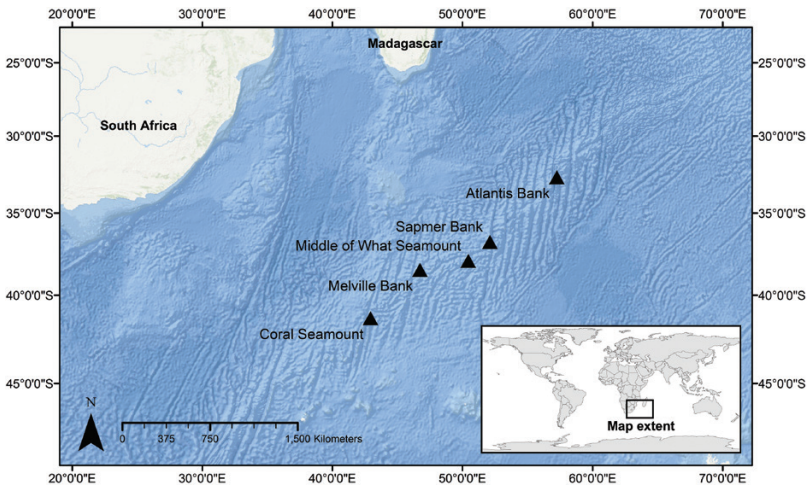

Figure 1. Southwest Indian Ocean ridge seamounts (inset – boxed area shows global position of map).

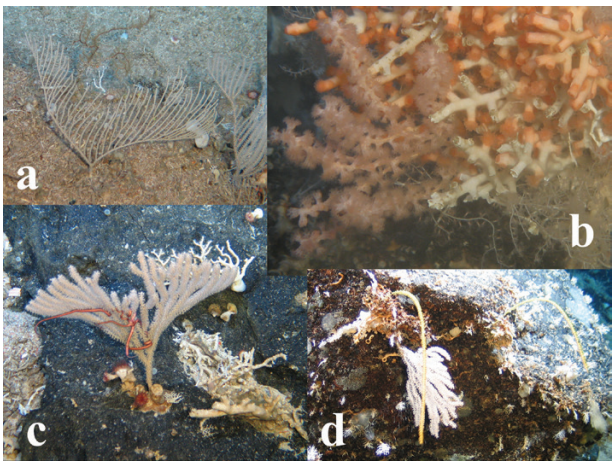

Figure 2. New species *in situ*. (a) ***Narella valentine* sp. nov.**; (b) ***Primnoa bisquama* sp. nov.**, pink colony within *Goniocorella dumosa* framework; (c) ***Narella candidae* sp. nov.**; (d) yellow whip colony, ***Primnoeides flagellum* sp. nov.** Images taken by the *Kiel 6000* on JC066.

PHYLOGENETIC METHODOLOGY

Extractions were undertaken using Qiagen Blood and Tissue Kit (Qiagen Ltd. Crawley, East Sussex, UK). Five gene regions were targeted: *cox1* (subunit I of cytochrome c oxidase; mitochondrial), *mtMutS* (also mitochondrial; often written in octocoral research as *msh1*; however, the name *mtMutS* makes fewer assumptions about gene origins; Bilewitch & Degnan, 2011), *16S* ribosomal RNA (mitochondrial), *18S* ribosomal RNA (nuclear) and *28S* ribosomal RNA (nuclear). PCR reactions were conducted using 8 μL of Master mix with HotStarTaq (Qiagen), 2 μL of template DNA and 1 μL of each primer (2 μM): total volume 12 μL. PCR conditions, primers and PCR clean-up followed methods in Taylor & Rogers (2015). Initial alignments were undertaken using ClustalW with default settings in Geneious 6.1.7 (Biomatters Ltd.). Alignments were checked and edited by eye. Model selection was the same as in Taylor & Rogers (2015), using PartitionFinder to evaluate the best partition scheme and associated substitution model (Lanfear *et al.*, 2012). The major differences between that paper and the phylogenetic analyses presented here are as follows: (1) a reduced selection of some samples is presented (duplicates of many species were removed) with a higher overall number of species; (2) phylogenies were inferred using MrBayes v.3.2 (Ronquist *et al.*, 2012), where Metropolis-coupled Monte Carlo Markov Chains were run for 10 million generations (8 chains, temp = 0.05) with trees sampled every 1000 generations; (3) the *coxI* intergenic region and *cox II* were removed from *coxI*, making this alignment 813 bp long and (4) as a wider array of genes (*ND2* and *ND6*) was available for three of the new *Narella* species presented here, these genes were initially included (marked with * in Appendix 1); preliminary analyses were run both with and without *ND2* and *ND6* – however, this made no difference to results so just the five-gene alignment (which had higher percentage of sequence coverage) is presented here. Eighty-one species of Primnoidae from 29 genera were represented in this analysis (Table S1). Outgroups were designated as Chrysogorgiidae (JC066-0714) and *Chrysogorgia chryseis* (CR106-2) as these are sister species to Primnoidae (Pante *et al.*, 2012).

RESULTS

Out of 96 partitioning schemes and nucleotide substitution models and two user-defined alternative models (linking the first two codons of protein-coding genes in one partition), a four-partition scheme retained the highest score in PartitionFinder (Lanfear *et al.*, 2012) for the five-gene (*cox1*, *MutS*, *16S*, *18S* and *28S*) alignment (Table 1).

MrBayes ran for 10 million generations and resulted in an effective sample size of over 2000 and standard deviation of split frequencies of 0.004; traces were viewed in Tracer v1.6 (Rambaut & Drummond, 2015) and had converged. The resulting 50% majority-rule consensus phylogenetic tree of Bayesian inference is presented in Figure 3.

Broad groupings of genera and species seen in Taylor & Rogers (2015) are maintained here with Pacific samples (from New Caledonia) in a sister clade to groups of mostly Atlantic and sub-Antarctic specimens, albeit weakly supported. The new SW Indian Ocean species of *Narella* and *Primnoa* fall within the Pacific group (Fig. 3). Along with New Genus B (Indian Ocean, 4500–4612 m depth) and *Thouarella laxa* Versluys, 1906 from New Caledonia (455–650 m; known from 290–660 m depth), *Primnoiedes flagellum* sp. nov., from the SW Indian Ocean (1020–1339 m depth), is embedded within the 'sub-Antarctic' clade (Fig. 3). *Primnoeides flagellum* sp. nov. is sister to the only other species of this genus previously described, *Primnoeides sertularoides* Wright & Studer, 1889. The genus *Primnoeides* falls within a clade alongside *Digitogorgia kuekenthali* Zapata-Guardiola & López-González, 2010. We propose that this species and *Digitogorgia brochi* Zapata-Guardiola & López-González, 2010 (the only other member of *Digitogorgia*), are transferred to *Primnoeides* (see below).

Narella is paraphyletic, clustering together with *Parastenella* and *Primnoa*. To ensure the placement of *Narella* that fall within a clade with *Parastenella* and *Primnoa* (*N. abyssalis*, *N. bayeri*, *N. cristata* – all from the Gulf of Alaska) was not an artefact of data gaps (as we do not have *28S* or *18S* sequences for these specimens), we ran a three-gene tree (as above except with

Table 1. Gene alignments, coverage and partitions

Gene/gene codon position (pos)	Gene sequence positions within concatenated alignment	Partition no. and model of nucleotide substitution	Percent of sequences with missing data
cox1 pos1	1–813\3	1 – GTR+I+R	–
cox1 pos2	2–813\3	2 – F81+I	–
cox1 pos3	3–813\3	1 – GTR+I+R	0.99
MutS pos1	814–1596\3	1 – GTR+I+R	–
MutS pos2	815–1596\3	1 – GTR+I+R	–
MutS pos3	816–1596\3	1 – GTR+I+R	2.97
16S	1597–1922	1 – GTR+I+R	21
18S	1923–3688	3 – K80+I+G	34
28S	3689–4472	4 – SYM+I+G	34

2 million generations) of remaining genes; the resulting tree is identical.

TAXONOMIC DESCRIPTIONS

PHYLUM CNIDARIA VERRILL, 1865
CLASS ANTHOZOA EHRENBERG, 1834
ORDER ALCYONACEA LAMOUROUX, 1812
FAMILY PRIMNOIDAE MILNE EDWARDS, 1857

NARELLA GRAY, 1870

Narella Gray, 1870: 49. – Bayer, 1956: F222, fig. 159(5). – 1961: 295 [illustrated key to genus]. – Bayer, 1981: 937 [key to genus]. –Bayer & Stefani, 1989: 455 [key to genus]. – Williams, 1992: 272. – Cairns & Bayer, 2003: 618–619; 2007: 84–86 [list of species]; 2008: 85–86 [key to Hawaiian species]; 2009: 43, figs. 14A–G [revision, list of species]. – Cairns & Baco, 2007: 392–393 [list of species]. – Cairns, 2012: 14 [key to New Zealand species].
Not *Stachyodes* Bargatzky, 1881 [a stromatoporoid].
Stachyodes Wright & Studer, 1889: 49. – Versluys, 1906: 86–88. – Kinoshita, 1908: 45–47. – Kükenthal, 1912: 325–328. – 1919: 452–456 [key to genus and species]. – 1924: 308–309 [key to genus and species].
Calypterinus Wright & Studer in Studer, 1887: 49–60. – Wright & Studer, 1889: 53.

Type species: *Primnoa regularis* Duchassaing & Michelotti, 1860, by monotypy.

Diagnosis (from Cairns, 2012 *– changes in bold)*: Colonies **lyrate**, dichotomously branched, pinnate or unbranched (flagelliform). Polyps arranged in whorls, with polyps always facing downwards. Polyps covered by three (rarely four) pairs of abaxial body-wall scales (1 pair of basals, 1–2 pairs of medials and 1 pair of buccals), 1–3 pairs of much smaller adaxial body-wall scales, and sometimes additional scattered adaxial scales, nonetheless resulting in a partially naked adaxial face; **two** species also have unpaired infrabasal scales. Distal margins of body-wall scales often spinose, toothed or lobate, sometimes extending as a protective buccal cowl. Opercular scales usually prominently keeled. Coenenchymal scales arranged in one **or two** layers, often quite thick and often ridged. Flattened, curved tentacular platelets often present.

Known distribution: Global, 129–4594 m depth.

Discussion: Narella is the most species-rich genus within Primnoidae. The history of this globally occurring genus has been well summarized in a number of publications (Cairns & Bayer, 2003, 2008; Cairns & Baco, 2007; Cairns, 2012). Just one species has been previously described from the Indian Ocean, *N. gilchristi* (Thomson, 1911), of which we present new specimens. Three new species from the SW Indian Ocean are described here: *N. speighti* sp. nov., *N. valentine* sp. nov. and *N. candidae* sp. nov., bringing the total number of species in this genus to 46. A new species list for *Narella* is presented in Table 2 and SW Indian Ocean species are compared in Table 3.

NARELLA GILCHRISTI (THOMSON, 1911) (FIGS 4, 5)

Stachyodes gilchristi Thomson, 1911: 885, pl. 44, fig. 1, pl. 45, fig. 2a,b; – Stiasny, 1940: 34, text-fig. H, pl. 1, fig. 8.
Stachyodes gilberti Kükenthal, 1919: 468 (?misspelling of *S. gilchristi*); – 1924: 316.
Stachyodes capensis Thomson, 1917: 25, text-fig. 5, pl. 3.
Narella gilchristi – Williams, 1992: 272–276, figs. 1G, 63–65.

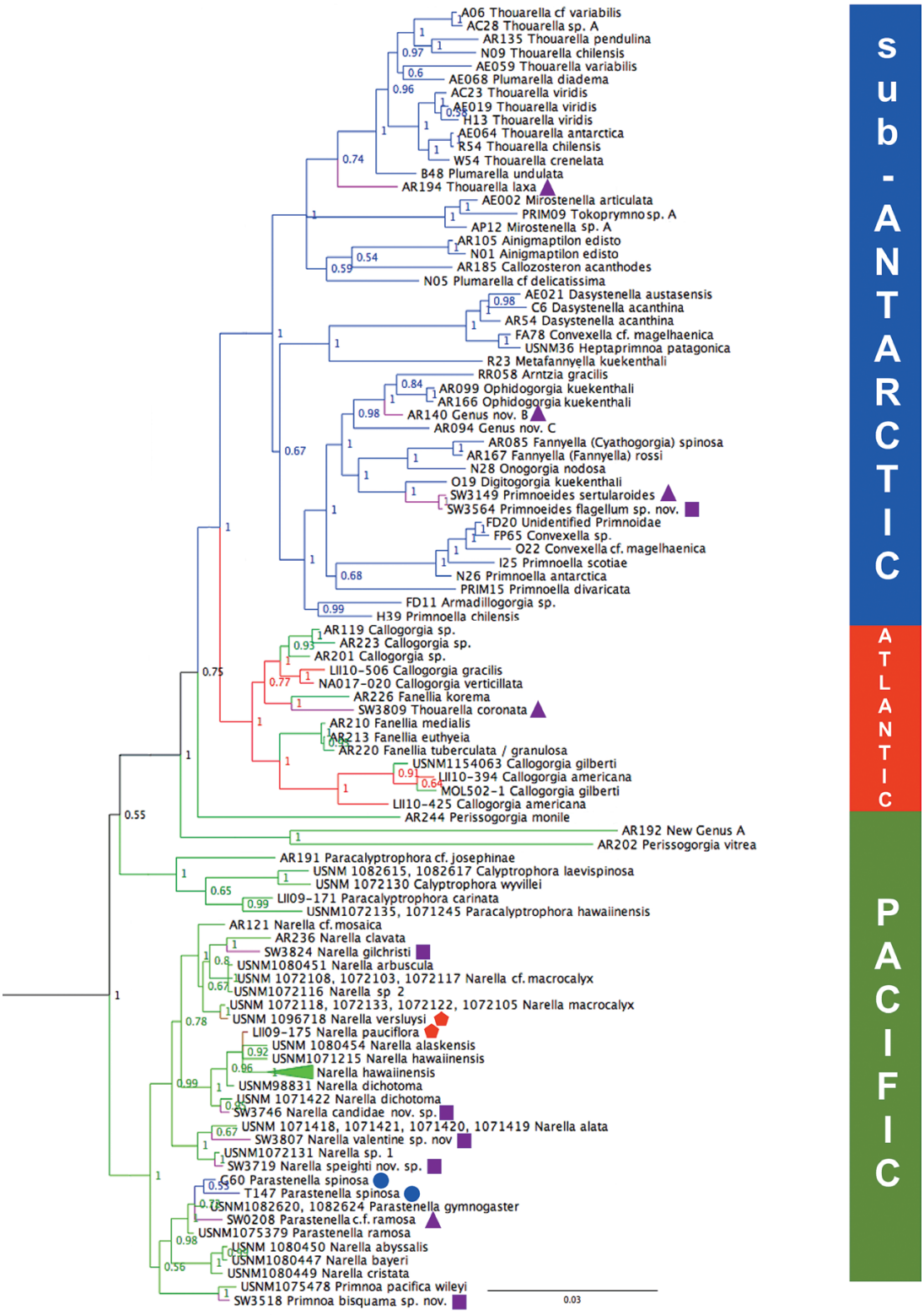

Figure 3. Fifty-percent majority rule consensus Bayesian Inference phylogenetic tree from five-gene concatenated alignment. Purple represents samples from the SW Indian Ocean (triangles are previously described species and squares are new specimens presented here), red pentagons are specimens from the Atlantic and blue circles are specimens from the sub-Antarctic. Outgroups were Chrysogorgiidae (JC066-0714) and *Chrysogorgia chryseis* (CR106-2).

Table 2. List of all *Narella* species arranged by ocean or region. New species in bold.

Species name	Range	Depth
N. megalepis (Kinoshita, 1908)	Japan	Unknown (probably 300–400 m)
N. irregularis (Kinoshita, 1907)	Japan	137 m
N. compressa (Kinoshita, 1908)	Japan	Unknown
N. biannulata (Kinoshita, 1907)	Japan	Unknown
N. japonensis (Aurivillius, 1931)	Japan	731 m
N. bayeri Cairns & Baco, 2007	Gulf of Alaska	3291–4091 m
N. cristata Cairns & Baco, 2007	Gulf of Alaska	3385 m
N. abyssalis Cairns & Baco, 2007	Gulf of Alaska	4594 m
N. arbuscula Cairns & Baco, 2007	Gulf of Alaska	2775–3465 m
N. alaskensis Cairns & Baco, 2007	Gulf of Alaska	2377–3075 m
N. leilae Bayer, 1951	Indonesia	740 m
N. clavata (Versluys, 1906)	Indonesia, Philippines, Japan, New Zealand	128–335 m
N. horrida (Versluys, 1906)	Indonesia	204 m
N. obscura (Versluys, 1906)	Indonesia	984 m
N. orientalis (Versluys, 1906)	Indonesia	520 m
N. parva (Versluys, 1906)	Indonesia	920–2400 m
N. grandiflora (Kukenthal, 1907)	Sumatra	805 m
N. studeri (Versluys, 1906) (*nom. nov*. for *S. regularis* Wright & Studer, 1889)	Kermadec and Indonesia	732–1392 m
N. allmani (Wright & Studer, 1889)	Fiji	'deep'
N. dichotoma (Versluys, 1906)	Indonesia	204–1264 m
= *N. nuttingi* Bayer, 1997	Hawaiian Islands	743–1448 m
N. gigas, Cairns & Bayer, 2008	Hawaiian Islands	302–399 m
N. alata, Cairns & Bayer, 2008	Hawaiian Islands	477–750 m
N. vermifera, Cairns & Bayer, 2008	Hawaiian Islands	275–527 m
N. macrocalyx, Cairns & Bayer, 2008	Hawaiian Islands	1206–1807 m
N. ornata Bayer, 1995	Hawaiian Islands	748–1007 m
N. bowersi (Nutting, 1908)	Hawaiian Islands	1218–1758 m
N. muzikae, Cairns & Bayer, 2008	Hawaiian Islands	326–381 m
N. hawaiinensis, Cairns & Bayer, 2008	Hawaiian Islands	1492–1921 m
N. ambigua (Studer, 1894)	Galapagos	691 m
N. gaussi (Kukenthal, 1912)	Antarctic	2450 m
N. bellissima (Kukenthal, 1915)	Amphi-Atlantic	225–1968 m
N. versluysi (Hickson, 1909)	Amphi-Atlantic	550–3100 m
= *?N. elegans* Tixier-Durivault &Lafargue, 1968		
N. regularis (Duchassaing & Michelotti, 1860)	Lesser Antilles	366–792 m
N. laxa Deichmann, 1936	New England seamounts	3186 m
N. pauciflora Deichmann, 1936	Lesser Antilles	738–1446 m
N. spectabilis Cairns & Bayer, 2003	Bahamas	1485 m
N. alvinae Cairns & Bayer, 2003	Bermuda	3419 m
N. mesolepis Cairns, 2012	New Zealand	157–1246 m
N. hypsocalyx Cairns, 2012	New Zealand	510–1118 m
N. vulgaris Cairns, 2012	New Zealand	335–1165 m
N. mosaica Cairns, 2012	New Zealand	278–294 m
N. dampieri Cairns, 2012	New Zealand	342 m
N. gilchristi (Thomson, 1911)	SW Indian Ocean	90–1365 m
= *S. capensis* Thomson, 1917		141–173 m
= *Stachyodes* '*gilberti*' Kukenthal, 315:1918 *nom. nud*. (misspelling of *gilchristi*)		
***N. speighti* sp. nov.**	**SW Indian Ocean**	**870 m**
***N. valentine* sp. nov.**	**SW Indian Ocean**	**383–444 m**
***N. candidae* sp. nov.**	**SW Indian Ocean**	**763 m**

Table 3. Comparison of morphological characters of all known Indian Ocean species of *Narella*. New species are in bold. bw, body wall. H:W, height:width ratio.

Species name	Location	Depth	Branching	Calyces/whorl; whorls/3 cm; whorl diameter (mm)	Calyx length (and width)	Basal body-wall scale: height; dorsolateral edge; distal edge; closed adaxial basal ring?	Basal body-wall scale modified to form worm tube - no = not recorded	Medial body-wall scale: % length of the buccal; dorsolateral edge; distal edge	Abaxial buccal body-wall scale: length; dorsolateral edge; distal edge; closed adaxial ring	Adaxial buccal scale: additional adaxial scales?; shape	Opercular scales: H:W of abaxials; inner keel	Coenenchymal scales	Other distinctive characteristics
N. gilchristi (Thomson, 1911)	SW Indian Ocean	90–1365 m	Lyrate with secondary dichotomous branching	4–8 (mostly 6–7); 7–15; 4–9	2.0–3.0 mm (1.0–1.5 mm)	1.6–3 mm; basolateral edge with small ridges; lobate, flared; yes	Yes	87%; rounded smooth; rounded, smooth, thin	1.5–1.6 mm; flared, rounded; thin, sometimes broken; no	1 pair; square	1:1; large keel	'Cobblestone-like appearance' (Williams, 1992), thin, irregular shape, upturned edges	Axis brown basally, yellow to the apex
***N. speighti* sp. nov.**	SW Indian Ocean	870 m	Equal dichotomous branching (possibly bushy)	3–4; 9–12; 2.5–3.6	2–2.2 mm	1.4 mm; wide, rounded; rounded; yes	No	93%; rounded, smooth; rounded smooth, thin	1.5–1.6 mm; outwardly curved; smooth rounded; yes	1 pair; square to oblong	1:1; large keel	Mostly long thin shape, edges upturned, one layer	
***N. valentine* sp. nov.**	SW Indian Ocean	383–444 m	Uniplanar, lyrate, some secondary dichotomous branching	4–5 (sometimes 8); 15–16; 2.4–2.8 mm	1.5–1.8 mm	1.25–1.45 mm; right angle with lateral ridge; peaked; yes	No	90%; ridged; pointed	0.8 mm; straight; rounded; yes	1 pair; squarish	1:0.7; large keel	Mostly long, thin shape, outer surface ridged, inner granular	
***N. candidae* sp. nov.**	SW Indian Ocean	763 m	Uniplanar, equal dichotomous branching	4–6; 9–10; 4–5 mm	2.0–2.4 mm	1.4 mm; smooth; rounded lobes; yes	No	75%; rounded, smooth; rounded	1.5 mm; rounded; rounded; no	2 pairs: squarish; rarely one extra in second row	1:0.45; keeled	Elongate with rounded edges forming a mosaic	Green iridescent striated axis

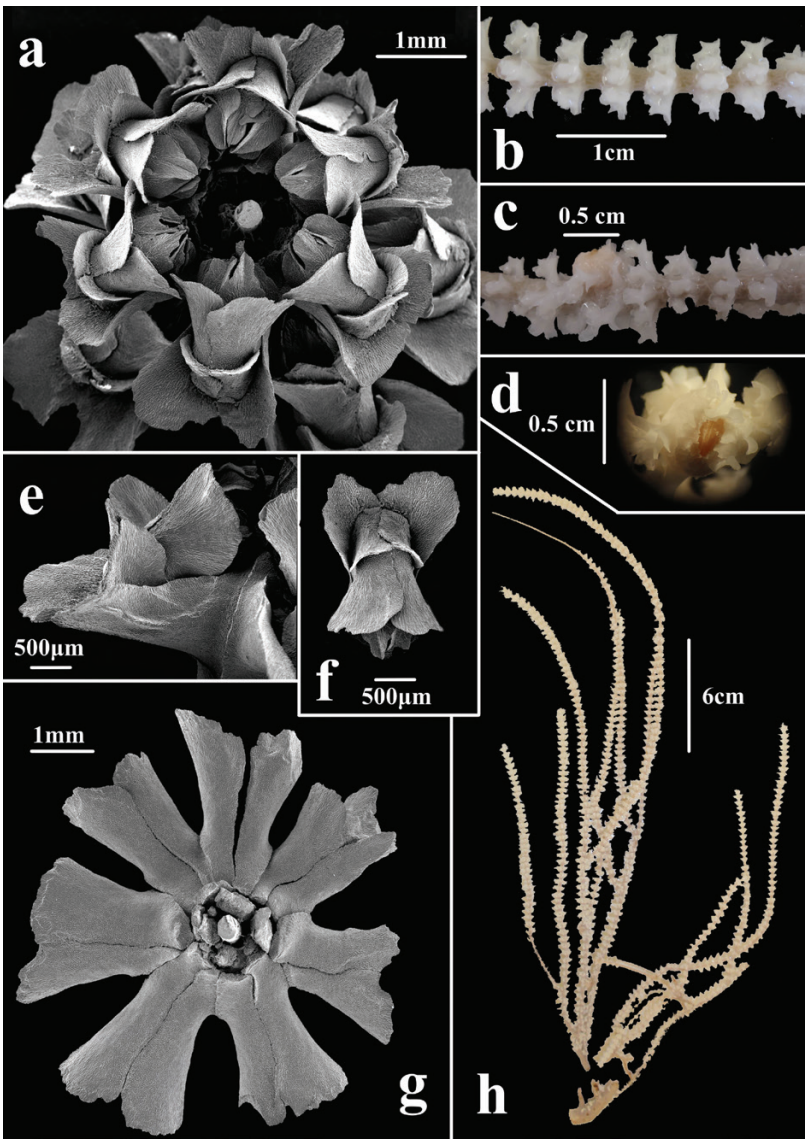

Figure 4. Colony, whorls and polyps of *Narella gilchristi*, NHMUK 2016.19, JC066-3824: (a) anterior view of polyp whorl; (b) section of branchlet; (c) section of branchlet with parasite ball; (d) close-up of parasite ball; (e) lateral view of polyp; (f) view of polyp cowl; (g) underside of polyp whorl; (h) colony.

Material examined: NHMUK 2016.19 (JC066-3824), RRS *James Cook*, sta. 7, ev. 10, Sapmer Bank, 36°47.798′S, 052°6.315′E, 300–700 m, 7 December 2011; NHMUK 2016.20 (JC066-216), NHMUK 2016.21 (JC066-217), NHMUK 2016.22 (JC066-212), RRS *James Cook*, sta. 4., ev. 2, Coral Seamount, 41°20.708′S, 42°55.2922′E, 1365 m, 12 November 2011; NHMUK 2016.23 (JC066-640), NHMUK 2016.24 (JC066-641), NHMUK 2016.25 (JC066-643), NHMUK 2016.26 (JC066-644), NHMUK 2016.27 (JC066-645), NHMUK 2016.28 (JC066-647), sta. 4, ev. 4, 41°22′48.780′S, 42°51′09.109′E, 1332 m, 13 November 2011; NHMUK 2016.29 (JC066-716), NHMUK 2016.30 (JC066-717), NHMUK 2016.31 (JC066-718), NHMUK 2016.32 (JC066-719), sta. 4, ev. 4, Coral seamount, 41°22′48.780′S, 42°51′09.109′E, 800–1332 m, 13 November 2011. SEM stubs – T146-148.

Description: Largest colony (NHMUK 2016.19, JC066-3824) 40 cm tall, ~14 cm wide, lyrate branching (remainder are mostly fragments), some secondary dichotomous branching (Fig. 4h). Branching sometimes in more than one plane with different planes interconnected by thin branchlets. Branches thick, up to 8.0 mm diameter, rigid. Axis smooth, gold. No holdfast.

Calyces mostly in whorls of 6–7 (Fig. 4a, g), whorls modestly spaced, ~7 whorls per 3 cm of branchlet,

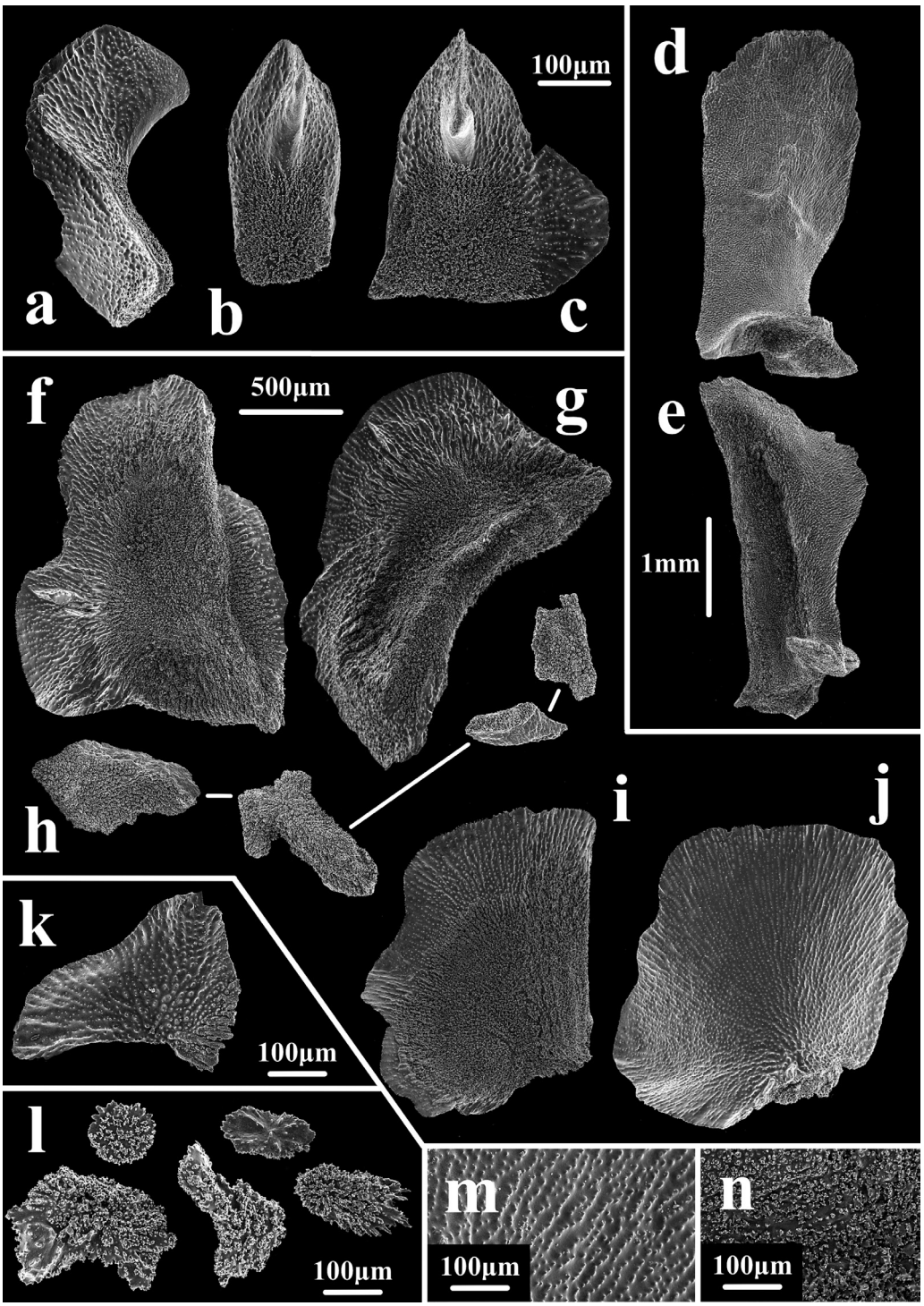

Figure 5. Sclerites of *Narella gilchristi*, NHMUK 2016.19, JC066-3824: (a) side view of opercular keel; (b, c) inner surface of opercular; (d, e) basal scales; (f,g) buccal scales; (h) scales basal to basal scales; (i, j) medial scales; (k) outer surface of coenenchymal scale; (l) coenenchymal scales of inner layer; (m) close up of outer surface of scales; (n) close up of inner surface of scales.

rarely 8 (Fig. 4b, c). Whorl diameter ~5.0–6.0 mm. Calyces 2.5–3.0 mm tall (Fig. 4e), each with three pairs of abaxial (Fig. 4a, e) and one pair of square adaxial body-wall scales.

Basal scales (Fig. 5d, e) tall, 2.5–3.0 mm, slender, 1.0–1.5 mm wide, standing almost perpendicular to branchlet, forming a closed ring, distal quarter to third is a projecting lobe (Figs 4e, f, 5d, e). One pair of adaxial

body-wall scales. Two to three small, thick, irregular sclerites (Fig. 5h) at base of basal scales, could be described as infrabasal. Medial scales (Fig. 5i, j) slightly shorter than buccal scales, 1.3–1.4 mm long, 1.1–1.3 mm wide, squarish in shape. Buccal scales (Fig. 5f, g) 1.5–1.6 mm long, 1.3–1.4 mm wide, flared distally, with fine ridging along inner distal edge; lateral edges curve around side of polyp, extending to form cowl around operculum; distal inner edges also finely ridged. Distal edge of medial and buccal scales thin, therefore sometimes broken and jagged.

In lateral view operculum mostly hidden by cowl (Fig. 4b, c, e). Opercular scales (330–400 μm tall, 150–325 μm wide) with large keel (side view – Fig. 5a). Like congenerics, opercular size decreases progressively from ab- to adaxial. Opercular scale shape ranges from lanceolate (Fig. 5b) to ones bearing one wide lobe laterally (Fig. 5c). Opercular scale outer surface often deeply concave, mirroring inner, keeled surface. No tentacular scales observed.

Outer surface of all above scales smooth; close-up with fine, low granular lines (Fig. 5m). Inner surfaces vary, tending to be covered with dense granular markings basally (Fig. 5n), with a smooth or finely ridged distal area.

Coenenchymal scales (300–400 μm) irregular in shape with upturned edges, forming thick mosaic of cover over axis (Fig. 5k). Secondary inner layer of small irregular coenenchymal scales present (Fig. 5l).

Known distribution: SW Indian Ocean, 90–1365 m depth.

Remarks: Four gall-forming mesoparasites from the Infraclass Ascothoracida, Subphylum Crustacea, were found on specimen NHMUK 2016.19, JC066-3824. Colony, or many polyps of the colony, is brooding. Basal scales can be modified and attached to adjacent sclerites to form tubes for commensal polychaete worms.

Comparisons: The sclerites of *N. gilchristi* presented here are near identical to those of holotype material held at the Smithsonian National Museum of Natural History (NMNH, S. Cairns, personal communication). Specimens examined here appear to have thinner scales than those described in Williams (1992). They have sparser whorl placement and the basal scales are taller. However, polyp structure and other sclerite sizes and shapes are very similar to those described in Williams (1992). Taking both these sources into account we thus consider these specimens to be *N. gilchristi*.

Lyrate colony shape is confirmed only in four species of *Narella*: *N. gilchristi*, *N. valentine* sp. nov., *N. compressa* and *N. bellissima*.

On first glance *N. bellissima* is very similar to *N. gilchristi*, with smooth outer surfaces on scales and basal scales departing branchlets at 90°; however, the former has smaller polyps, whorls much more densely placed than the latter, and tentacular scales. Calyces of *N. valentine* sp. nov. are far smaller than those of *N. gilchristi*. Polyps of the former have a peaked basal cowl whereas those of the latter have two basal scales with rounded lobate projections. The species also differ in number of polyps per whorl and whorl density. The holotype of *N. compressa* would appear to be half of what may well be a lyrate colony (Kinoshita, 1908; plate 3, image 25). Polyps also have a tall basal scale rising perpendicular from the branchlet, similar to *N. gilchristi*. The polyps of *N. compressa* are smaller and there are 11–12 whorls per 3 cm of branchlet; far more than are found in *N. gilchristi* presented here. A fresh assessment of Kinoshita's material is required to confirm that *N. compressa* is not conspecific with *N. gilchristi*.

Thick mosaic-like coenenchymal scales are found on *N. clavata*, *N. mosaica*, *N. compressa* and *N. gilchristi*. Although basal scales of *N. gilchristi* can be as tall as *N. clavata*, they are not laterally fused and the coenenchymal layer is not as thick in *N. gilchristi*. *Narella mosaica* has shorter basal scales than those found in *N. gilchristi* and thus does not have the large cowl formed by the basal scales (seen in Fig. 4f).

There are three species where branching pattern is unknown: *N. ornata*, *N. hawaiinensis* and *N. ambigua*. *Narella gilchristi* differs from *N. ornata* in having more polyps per whorl and taller basal body-wall scales that are rounded and lacking ridges. There is little detail in the original description of *N. ambigua*; the few details of polyp size and number of calyces per whorl are similar to *N. gilchristi*; however, until examined these species should remain separate and valid. *Narella hawaiiensis* has fewer calyces per whorl than *N. gilchristi*, shorter, less robust basal scales that have ridges (something lacking in the latter), sclerites that are thinner, and more brittle, and ridged coenenchymal scales; very different characters to that found in the latter.

NARELLA SPEIGHTI SP. NOV.

(FIGS 6, 7)

Material examined: Holotype – NHMUK 2016.33 (JC066-3719), RRS *James Cook*, sta. 8, ev. 5, Atlantis Bank, 32°42.862′S, 57°14.666′E, 870 m, 10 December 2011. SEM stubs – T165-166.

Description: Holotype has equal dichotomous branching, 11 cm tall. Holdfast has multiple main branches indicating, speculatively, branching may be bushy. Axis straw coloured. Polyps 3–4 per whorl (Fig. 6d), 6–9 whorls (usually 6–7) per 2 cm of axis (Fig. 6e), whorl diameter 2.5–3.6 mm. Polyps 2.0–2.2 mm tall (Fig. 6c).

Basal scales ~1.4 mm tall (Fig. 7n, o), curved away from polyp body, closed ring adaxially, free distal edge tall and rounded, thin and often broken, sometimes

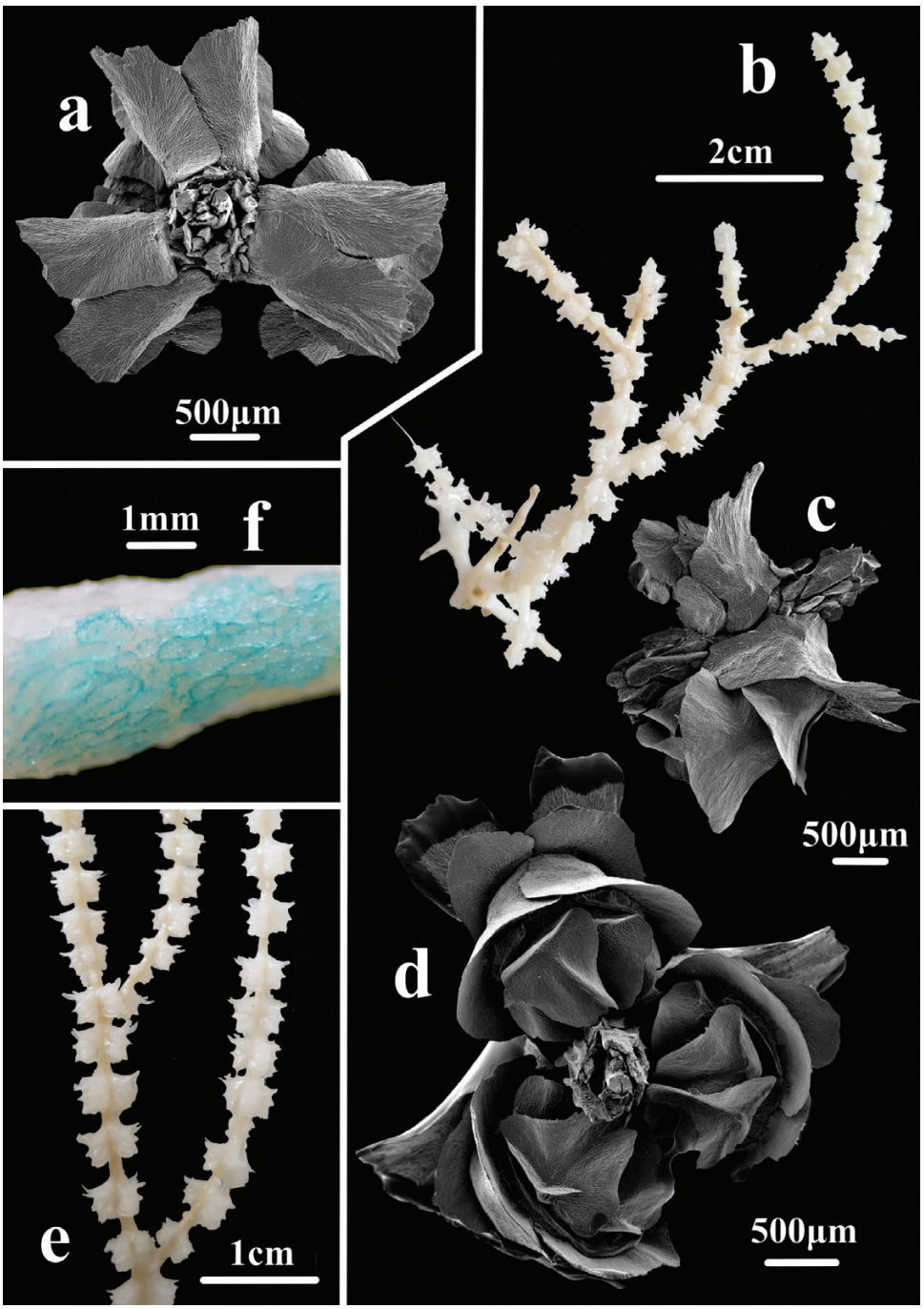

Figure 6. Colony, whorls and polyps of ***Narella speighti* sp. nov.**: (a) base of whorl; (b) colony; (c) lateral polyp view; (d) anterior whorl view; (e) close up of branchlet; (f) close up of coenenchyme.

jagged, so is not a smooth cowl. One pair of square to oblong body-wall scales placed adaxially.

Medial scales curved outwards, smooth rounded distal edge (Fig. 7j, m), ~1.5 mm wide and 1.1–1.5 mm tall; inner surface with smooth band across distal third, dense granules basally (Fig. 7j).

Buccal scales outwardly curved with round, smooth distal edge (Fig. 7k, l), 1.5–1.6 mm tall and wide; outer surface smooth, inner with smooth band across distal third, dense tubercles basally (Fig. 7k, l).

Opercular scales reduce in size from abaxial to adaxial side. Abaxial opercular scales (Fig. 7f, g) large, up to 0.86 mm wide, 0.8–0.86 mm tall. Abaxial opercular scales symmetrical (Fig. 7g, f); asymmetrical on either side (Fig. 7h, i), with just one wide lateral wing. Adaxial scales smaller, 0.3–0.5 mm wide, 0.55–0.7 mm tall (Fig. 7a–e),

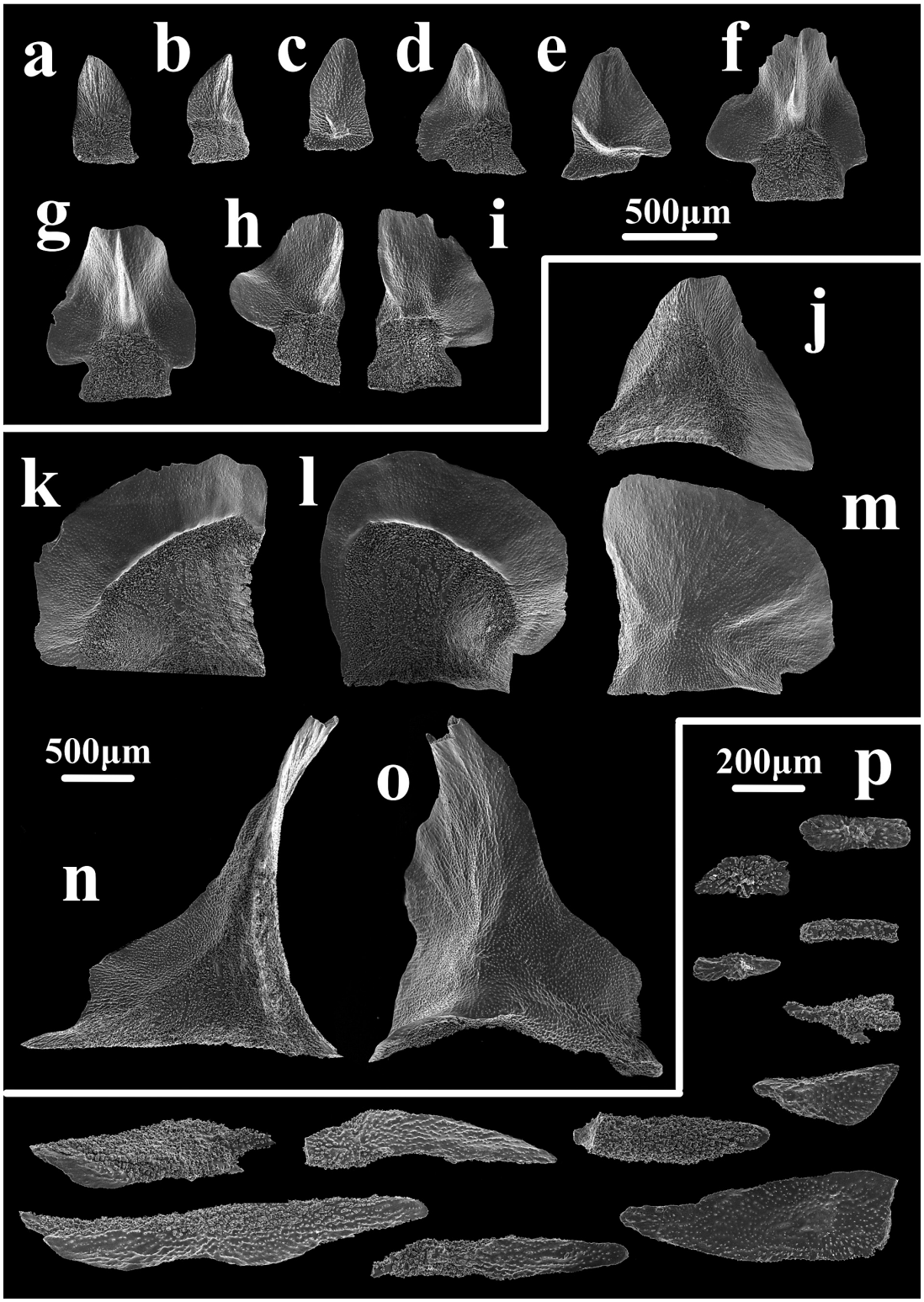

Figure 7. Sclerites of ***Narella speighti*** **sp. nov.**: (a, c, e) inner surface; (b, d, f–i) outer surface of opercular scales; (j, m) medial scales; (k, l) buccal scales; (n, o) basal scales; (p) coenenchymal scales.

lanceolate shape. Opercular scales with highly concaved outer surface (mirroring keeled inner surface), distal edge appears notched. No tentacular scales.

Branchlet axis surface uneven as coenenchymal scale edges curve away from branchlet. Coenenchymal scales long, thin, 0.3–1.0 mm length (Fig. 7p) relatively smooth outer surface, dense tubercles on inner surface, and mosaicked when *in situ* (Fig. 6f). One layer of coenenchymal scales.

Known distribution: Atlantis Bank, SE Indian Ocean. 870 m depth.

Etymology: Named after Prof. Martin Speight for his mentorship and support of generations of marine biologists.

Comparisons: Most species of *Narella* have dichotomous branching. As many species are described from specimens lacking a holdfast or colony fragments, some described as uniplanar may well be bushy so all dichotomously branched species and those with unknown branching patterns were considered if they had polyps ≤2.5 mm tall. *Narella gilchristi*, *N. megalepis*, *N. biannulata*, *N. horrida*, *N. bayeri* and *N. dampieri* all have more than four polyps per whorl so were disregarded. *Narella clavata* has thick mosaic-like coenenchymal scales, very different to those of *N. speighti* sp. nov. *Narella laxa* was not considered as it has four pairs of body-wall scales. The outer surface of sclerites of *N. speighti* are relatively smooth, whereas those of *N. parva*, *N. regularis*, *N. cristata* and *N. abyssalis* have distinct ridges. *Narella leilae* has basal scales that form a large, flared cone; unlike the projecting, lobate edges of the basal scales seen in *N. speighti*. Polyp and sclerite size, structure and orientation look very similar to those of *N. obscura*. We separate them based on their coenenchymal scales, which are not elongate in *N. obscura*, as they are in *N. speighti*. Basal and buccal scales of *N. japonensis* are more modest than those of *N. speighti* and the colony branching does not appear to be bushy from the fragment described. The basal scales of *N. vulgaris* do not have lobate projections; they are more rounded and the sclerites are not as smooth as those of *N. speighti*. There is also no clear separation of the dense tubercle-covered base on the inner surface of sclerites, something clearly seen in *N. speighti*. With the above comparisons considered we recommend this specimen as a new species.

NARELLA VALENTINE SP. NOV.

(FIGS 2A, 8, 9)

Material examined: Holotype – NHMUK 2016.34 (JC66-3807), RRS *James Cook*, sta. 7, ev. 10, Sapmer Bank, 36°48′10.284′S, 52°06′55.706′E, 383–444 m, December 2011. Paratypes: NHMUK 2016.35 (JC066-3808), NHMUK 2016.36 (JC066-3813), same details as holotype. SEM stubs – T149-150.

Description: Holotype uniplanar, 32 cm tall, 17 cm wide, with true lyrate branching and rare secondary dichotomous branching, terminal branches generally long (*in situ*, Figs 2a, 8b), no holdfast. Polyps 1.5–1.8 mm tall (Fig. 8d), 4–5 polyps per whorl on branchlets, main branches ~8 polyps per whorl, 15–16 whorls per 3 cm of branchlet (Fig. 8a), whorl diameter 2.4–2.8 mm.

Basal scales (Fig. 9n–p) modest size (1.25–1.45 mm tall) in comparison to medial scales (Fig. 9j–m); 1:0.8:0.8 ratio of major body-wall scales. Basal scale distal edge peaked, joined to adjacent basal scale forming a sculpted cowl (Fig. 8c). Outer basal scale surfaces have lateral crest or ridge. Basal scales form closed ring. No infrabasal scales.

Medial scales square-shaped (Fig. 9j–m), with peaked distal edge, rounded dorso-lateral edge, very slight curve to outer surface, 0.64–0.74 mm tall.

Buccal scales ~0.8 mm tall with rounded distal edge, scale base and lateral edges straight (Fig. 9h, i). One pair of square-to-oblong adaxial buccal scales cover adaxial side of polyp.

Operculum visible from lateral view, forming one-third of polyp height. Opercular scales reduce in size from abaxial to adaxial; generally 0.3–0.66 mm tall. Opercular scales wide with a lateral wing (0.5 mm, Fig. 9c) or lanceolate-shaped (Fig. 9a, d, f, g), strongly keeled (lateral keel view, Fig. 9b).

Little coenenchyme visible as polyp whorls closely placed. One layer of long, thin coenenchymal scales (Fig. 9q), some smaller sclerites arranged around them (Fig. 9r); outer surfaces ridged, inner granular (Fig. 9s). No tentacular scales noted.

Known distribution: Sapmer Bank, SW Indian Ocean, 383–444 m depth.

Etymology: Named in honour of Dr Taylor's mother, Valerie, after her secret spy name, Valentine. And in honour of Dr Taylor's sister, Claire, who was born on Valentine's Day. As a non-Latin word, 'valentine', is treated as indeclinable under 31.2.3 of the International Code of Zoological Nomenclature (ICZN).

Comparisons: As described in comparisons of *N. gilchristi*, lyrate branching occurs in just four species of *Narella*. Calyces of *Narella valentine* sp. nov. are smaller than those of *N. gilchristi*. Polyps of the former have a peaked basal cowl, whereas those of the latter have two rounded lobate projections, and they differ in number of polyps per whorl and whorl density.

Polyps of *N. compressa* are of a similar size to those of *N. valentine* sp. nov. However, the basal scale of the

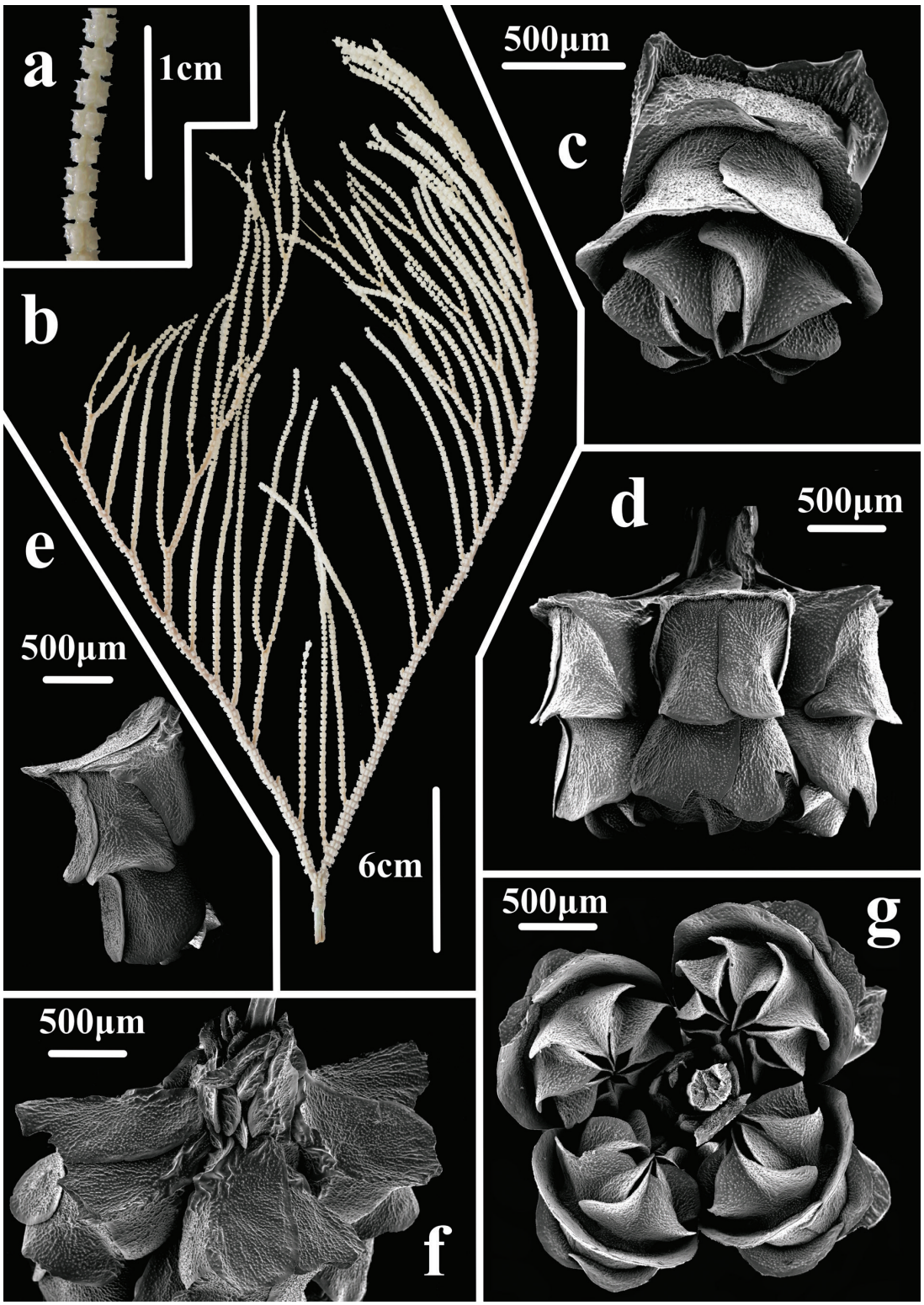

Figure 8. Colony, whorls and polyps of ***Narella valentine*** **sp. nov.**: (a) close-up of branchlet; (b) colony; (c) cowl view of polyp; (d) lateral view of whorl; (e) lateral view of polyp; (f) posterior view of whorl and *in situ* coenenchymal scales; (g) anterior view of whorl.

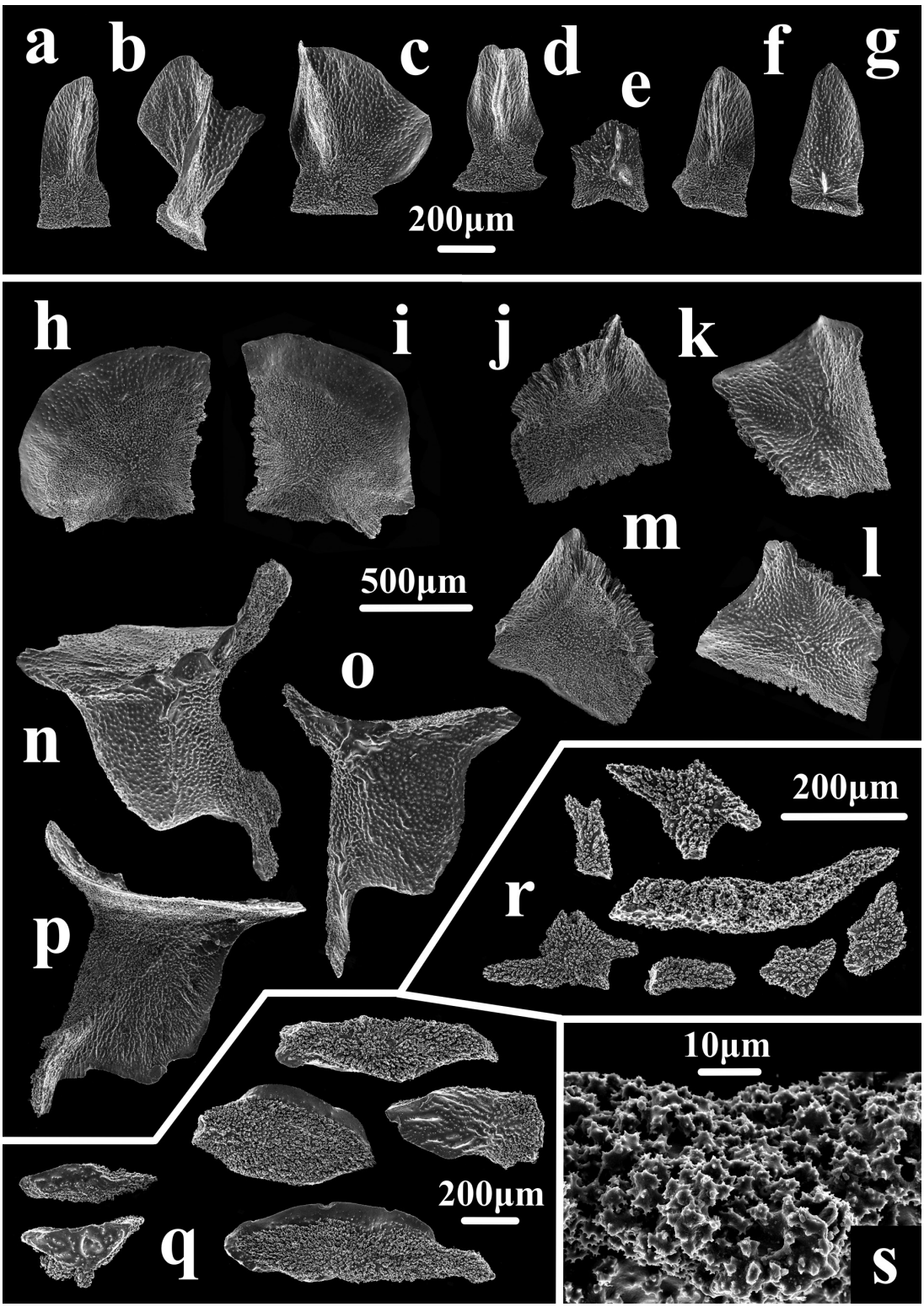

Figure 9. Sclerites of ***Narella valentine*** **sp. nov.**: (a, c–f) inner surface of opercular; (g) outer surface of opercular; (b) side view of opercular keel; (h, i) buccal scales; (j–m) medial scales; (n–p) basal scales; (q) coenenchymal scales; (r) smaller coenenchymal scales; (s) close-up of inner surface of a coenenchymal scale.

former is larger and there is no mention of a crest or ridge, as is found in the latter. The basal scales of *N. bellissima* have a rounded lobate distal edge whereas those of *N. valentine* have a short point. Opercular of the former are thicker and more rounded than the more delicate opercular of the latter. The basal scales of polyps of *N. gilchristi* are rounded distally, unlike the peaked edges seen in *N. valentine*.

There are three species of *Narella* where branching patterns are unknown: *N. ornata*, *N. hawaiinensis* and *N. ambigua*. The largest polyps found on *N. valentine* are ~2 mm tall. Polyps of the three species mentioned are much larger, all over 3 mm tall. With little further information about *N. ambigua* it is hard to make further comparisons. Both *N. ornata* and *N. hawaiiensis*, although with similar ridged basal scales as *N. valentine*, have far fewer polyps per whorl and basal scales that do not form a closed ring.

NARELLA CANDIDAE SP. NOV.

(FIGS 2C, 10, 11)

Material examined: Holotype – NHMUK 2016.37 (JC066-3746), sta. 8, ev. 22, Atlantis Bank, 32°41′55.177′S, 57°17′40.325′E, 763 m, 13 December 2011. SEM stubs – T170-172.

Description: Holotype uniplanar with equal dichotomous branching, 31 cm high, 18 cm wide (Fig. 10a; wider *in situ*, Fig. 2c), base diameter 4 mm. No holdfast. Axis striated, iridescent green (Fig. 10g) with darker brown to green nodes which are slightly thickened; axis light gold distally (Fig. 11l), where just nodes are darkened. Polyps ~2.5 mm tall, whorls of 4–6 (higher number on larger-diameter branches), 9–10 whorls per 3 cm of branch (Fig. 10b), whorl diameter 4.0–5.0 mm.

Polyps with thick, robust sclerites. Basal scales ~1.4 mm tall (Fig. 11f) with rounded distal margin; generally two pairs of adaxial body-wall scales (Fig. 10d, i) that together do not form a closed basal ring. Sometimes a third smaller scale in centre of basal row (Fig. 10d, ii). Exterior basal scale surface covered in thick layer of flesh. Medial scales smaller (1.1 mm tall, 0.8 mm wide, Fig. 11g, h), similar shape to buccal scales (1.5 mm tall, 1.4 mm wide), with rounded distal and lateral edges (Fig. 11g, h). Inner surface of basal, medial and buccal scales have a large sparsely granular area; basally there is a large smooth distal margin (Fig. 11f, i, j).

Tall operculum, easily seen in lateral view (Fig. 10c, f). Opercular scales (0.95–1.5 mm tall, 0.4–0.7 mm wide) progressively smaller from adaxial to abaxial. Larger opercular scales with large keel (Fig. 11b, lateral keel view) and corresponding concaved abaxial surface; smaller opercular less concaved bearing modest keel (Fig. 11c–e). All opercular scales robust, thick, with a smooth surface; granules to posterior of inner opercular surface small and evenly spread. No tentacular scales noted.

Coenenchymal scales elongate (up to 2.5 mm long), rounded edges forming a mosaic, slab-like coenenchyme (Fig. 11m) on larger branches; branchlet coenenchymal scales are longer and thinner.

Known distribution: Atlantis Bank, SW Indian Ocean, 763 m depth.

Etymology: Named after Dr Candida Rogers, wife of Prof. Alex Rogers, and suitably also Latin for 'white' and 'radiant'. We present '*candidae*' as a noun in the genitive form as per article 31.1.2 of the ICZN.

Remarks: Colony, or many polyps of the colony, is brooding. No other *Narella* has been noted as having dark gorgonin nodes or internodes. This phenomenon has evolved independently at least twice in Primnoidae – *Mirostenella* and *Narella* (see Fig. 3); and four times in Octocorallia – the above and Isididae (bamboo corals) and Melithaeidae (McFadden *et al.*, 2006).

The colony had a resident snake star (Ophiuroidea: Euryalidae) attached when collected (see Fig. 2c).

Comparisons: Similar to comparisons of *Narella speighti* sp. nov., it is here necessary to make comparisons to a number of species which have dichotomous colony branching, or species of unknown branching structure which have polyps that are under 2.5 mm in length. Again, *N. cristata*, *N. parva* and *N. regularis* are not compared as they have lateral crests or ridges on their basal scales which are lacking in *N. candidae* sp. nov. Basal scales of *N. horrida* have a pointed distal edge so are also not considered further.

Polyps of *N. laxa* tend to have four pairs of body-wall scales and a pointed tall operculum with opercular scales that are not concaved. Polyps of *N. speighti* sp. nov., *N. leilae*, *N. vulgaris*, *N. obscura*, *N. clavata* and *N. japonensis* are flared with thin distal edges on medial and buccal scales; this is unlike the rounded, thick, and slight inward curve of these scales in *N. candidae* sp. nov.

The species most similar to *Narella candidae* sp. nov. is *N. biannulata*. Described by Kinoshita in 1907 (a paper we were unable to locate) and re-described, with drawings, in 1908, this species has similar branching structure, polyp size, polyp and whorl density, and scale orientation and ornamentation as *N. candidae*; it even has an unusual greenish metallic tinge to its axis. The 1908 description indicates that *N. biannulata* has coenenchymal scales with outer surfaces that are wrinkly or creased ('Runzeln'). The specimen presented here as

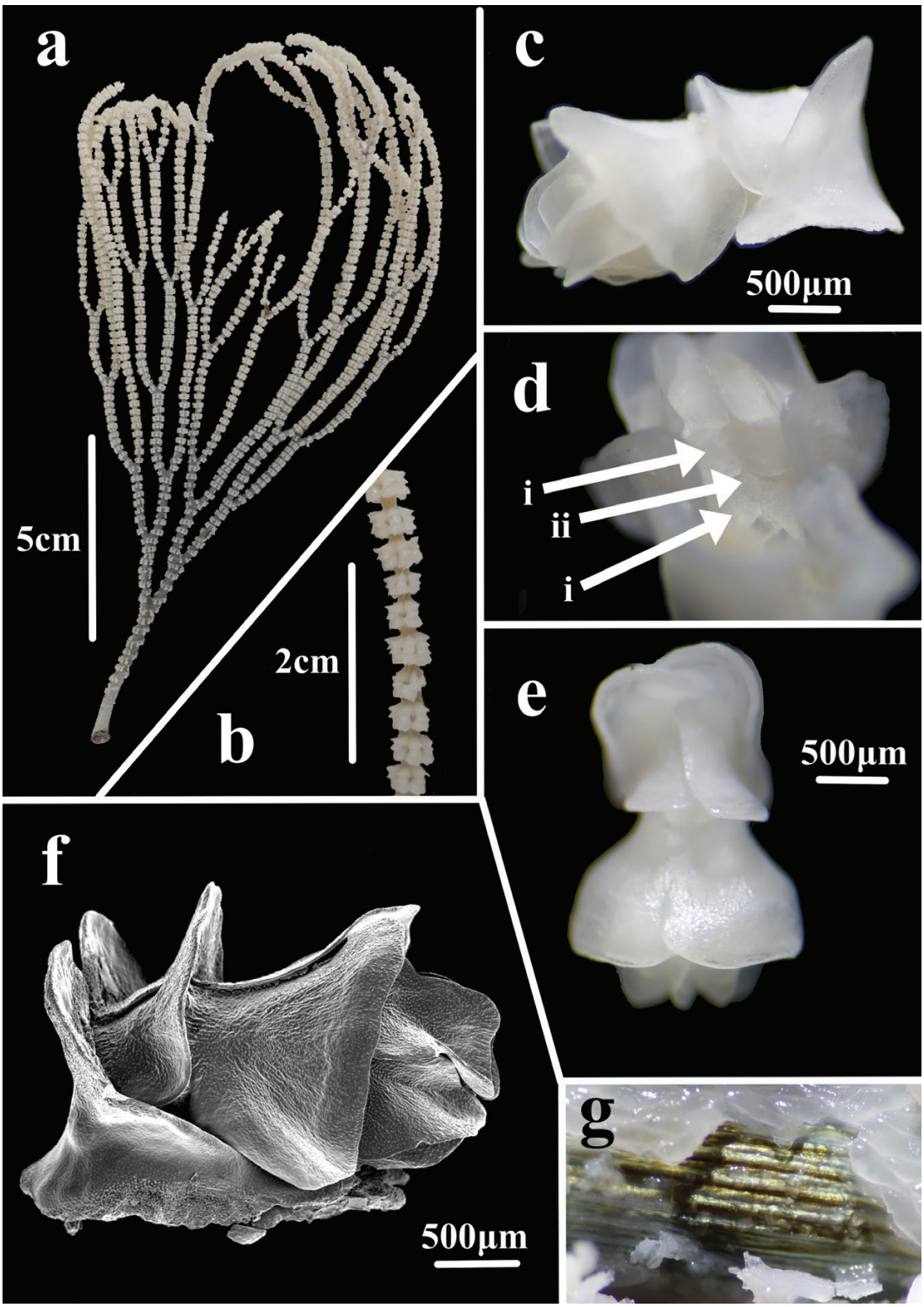

Figure 10. Colony, whorls and polyps of ***Narella candidae* sp. nov.**: (a) colony; (b) close-up of branchlet; (c) lateral view of polyp; (d) adaxial polyp view showing two pairs of adaxial body-wall scales (i), with a third minor scale (ii); (e) abaxial polyp view; (f) lateral polyp view; (g) main axis.

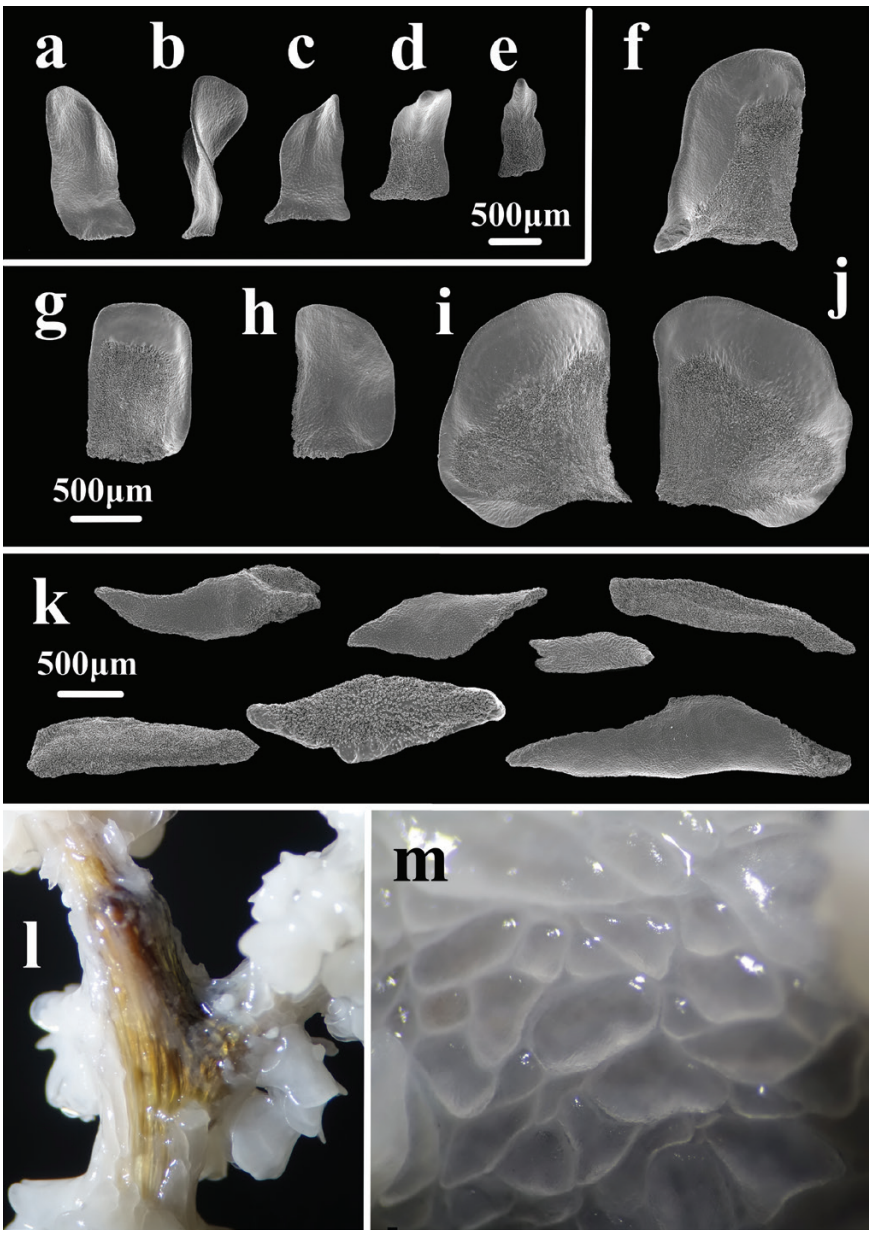

Figure 11. Sclerites and axis of ***Narella candidae* sp. nov.** (a–e) Opercular scales; (f) basal scale; (g, h) medial scales; (i, j) buccal scales; (k) coenenchymal scales; (l) close up of branchlet axis; (m) close-up of coenenchymal scales *in situ*.

N. candidae has coenenchyme with smooth, rounded outer surfaces. And *N. biannulata* is described as lacking adaxial buccal or basal scales; *N. candidae* commonly has two pairs of adaxial buccal scales. For these reasons we propose *N. candidae* as a new species.

Narella canididae was placed as sister to *Narella dichotoma* in the phylogenetic analysis. The latter differs in having larger polyps than the former and just one pair of adaxial buccal scales as well as having a bushy, flabellate colony shape.

PRIMNOA LAMOUROUX, 1812

Primnoa Lamouroux, 1812: 188. – Studer, 1887: 49. – Wright & Studer, 1889: xlviii. – Versluys, 1906: 84–85. – Kükenthal, 1915: 143 [key to genus]; – 1919: 357–360 [key to genus]; – 1924: 265–266 [key to genus and species]. – Bayer, 1956: F220; 1961: 294 [illustrated key to genus]; – 1981: 937 [key to genus]. – Bayer & Stefani, 1989: 454 [key to genus]. – Cairns & Bayer, 2005: 226–228 [revision and key to species]. – Cairns & Bayer, 2009: 41–42.

Lithoprimnoa Grube, 1861: 174–175.

Diagnosis (from Cairns & Bayer, 2009, edits in bold): Colonies dichotomously branched and usually bushy. Calyces closely spaced and randomly arranged on all branch surfaces, the appressed calyces facing downwards. Well-developed operculum present, opercular scales keeled on inner surface. Polyps large and fleshy, each polyp protected by two rows of **three** or more large abaxial scales, sometimes arranged in an irregular manner, two short inner lateral rows of two or three smaller scales (including the marginals), and two even shorter rows of two (including the marginals) adaxial scales, resulting in six longitudinal rows, but four of them composed of few **variable-sized** scales; adaxial side of body-wall predominantly bare. There is also a crown of eight large, concave marginals, the adaxial marginals usually smaller than other marginals. Coenenchymal scales arranged in one layer. Tentacular rods often present.

Type species: *Gorgonia lepadifera* Linneaus, 1767 (= *Gorgonia resedaeformis* Gunnerus, 1763), by monotypy. Type not found.

Known distribution: Global, 9–1339 m depth.

PRIMNOA BISQUAMA SP. NOV.

(FIGS 2B, 12, 13)

Material examined: Holotype – NHMUK 2016.38 (JC066-960), RRS *James Cook*, sta. 4, ev. 9, Coral seamount, 41°21′20.103′S, 42°55′8.423′E, 952 m, 14 November 2011; Paratype: NHMUK 2016.39 (JC066-3518), sta. 6, ev. 7, Middle of What seamount, 37°56′37.200′S, 50°27′06.450′E, 1339 m, 2 December 2011; NHMUK 2016.40 (JC066-3568), sta. 6, ev. 7, Middle of What seamount, 37°56′36.986′S, 50°26′46.044′E, 1309 m, 2 December 2011; NHMUK 2016.41 (JC066-3569), likely a fragment of NHMUK 2016.40 (JC066-3568). SEM stubs – T154-156.

Description: Holotype is a 15 cm tall colony, light pink *in vivo* (*in situ* Fig. 2b), white once preserved (Fig. 12a). Colony uniplanar with infrequent dichotomous branching. Axis near black in colour towards base with gold iridescent hue towards branchlet tips.

Polyps isolated, downward facing (as is typical of this genus; Fig. 12b), slightly flared (Fig. 12c), appressed against branchlets, 2.0–4.0 mm tall (usually around 3.0–4.0 mm, Fig. 12b). Polyps placed 3–5 per centimetre.

Operculum well-developed, low in height (Fig. 12c). Opercular scales tongue-shaped with small, modest keel (Fig. 13a); some nearly flat (Fig. 13c). Adaxial opercular scales slightly smaller than abaxial. Outer surfaces smooth (Fig. 13b, d). Small tentacular rods abundant, 100–300 μm in length, 50 μm wide (Fig. 13e, same scale as surrounding scales; Fig. 13s close up).

Majority of polyp body covered by three pairs of large abaxial scales (Fig. 13j, k; two being marginal scales, Fig. 13f–i); basal pair of scales (Fig. 13m, l) slightly smaller than marginal scales (Fig. 13f–i) and separated by a number of small irregular-shaped sclerites (Fig. 13n, p). No clear adaxial rows of body-wall scales as polyp appressed against branchlet, meaning adaxial marginal scales are often mistaken for coenenchyme.

Marginals near square in shape with rounded distal edge (no marginal spine) and irregular basal edge (most pronounced in Fig. 13h). Four large marginal scales (Fig. 13f–i) surround 270° of opercular opening (Fig. 12d); remaining diameter with 2–4 smaller (usually 4, although they are sometimes missing) marginal scales of similar shape. Body-wall scales held together by flesh embedded with small irregularly shaped body-wall scales (Fig. 13r).

All above sclerites have a smooth to granular outer surface and are tuberculate across majority of inner surface. Marginal scales have wide smooth band across distal edge of inner surface (Fig. 13h). Basal edges of sclerites finely serrate; distal edges relatively smooth.

Elongated, irregularly shaped coenenchyme of variable length, commonly up to 800 μm (Fig. 13o, *in situ* at base of Fig. 13p,q).

Known distribution: SW Indian Ocean: Coral and Middle of What seamounts, 952–1339 m depth.

Etymology: The name is formed from a combination of the Latin for 'double', *bi-*, and 'scale', *squama* – in reference to the two pairs of body-wall scales that distinguish this species from other *Primnoa*. We treat *squama* as a noun in the apposition and it therefore retains the feminine gender.

Remarks: Previous species of *Primnoa* have been found from the northern boreal Atlantic, North and East Pacific, Japan and sub-Antarctic areas of the south Pacific.

Comparisons: Primnoa bisquama sp. nov. is distinguished from the remaining four species and one variety of *Primnoa* (see Cairns & Bayer, 2005) in its low-rise operculum, infrequent polyp placement and relatively modest polyp size. Lacking a marginal spine and having a squat polyp means this species is most similar to *P. notalis* and *P. resedaeformis*. *Primnoa bisquama* differs from both these species in having fewer pairs of body-wall scales: just two pairs of large body-wall scales (in addition to a large pair of abaxial marginal scales) with a variable number of smaller scales in the basal abaxial polyp area, rather than four (or more) pairs of body-wall scales.

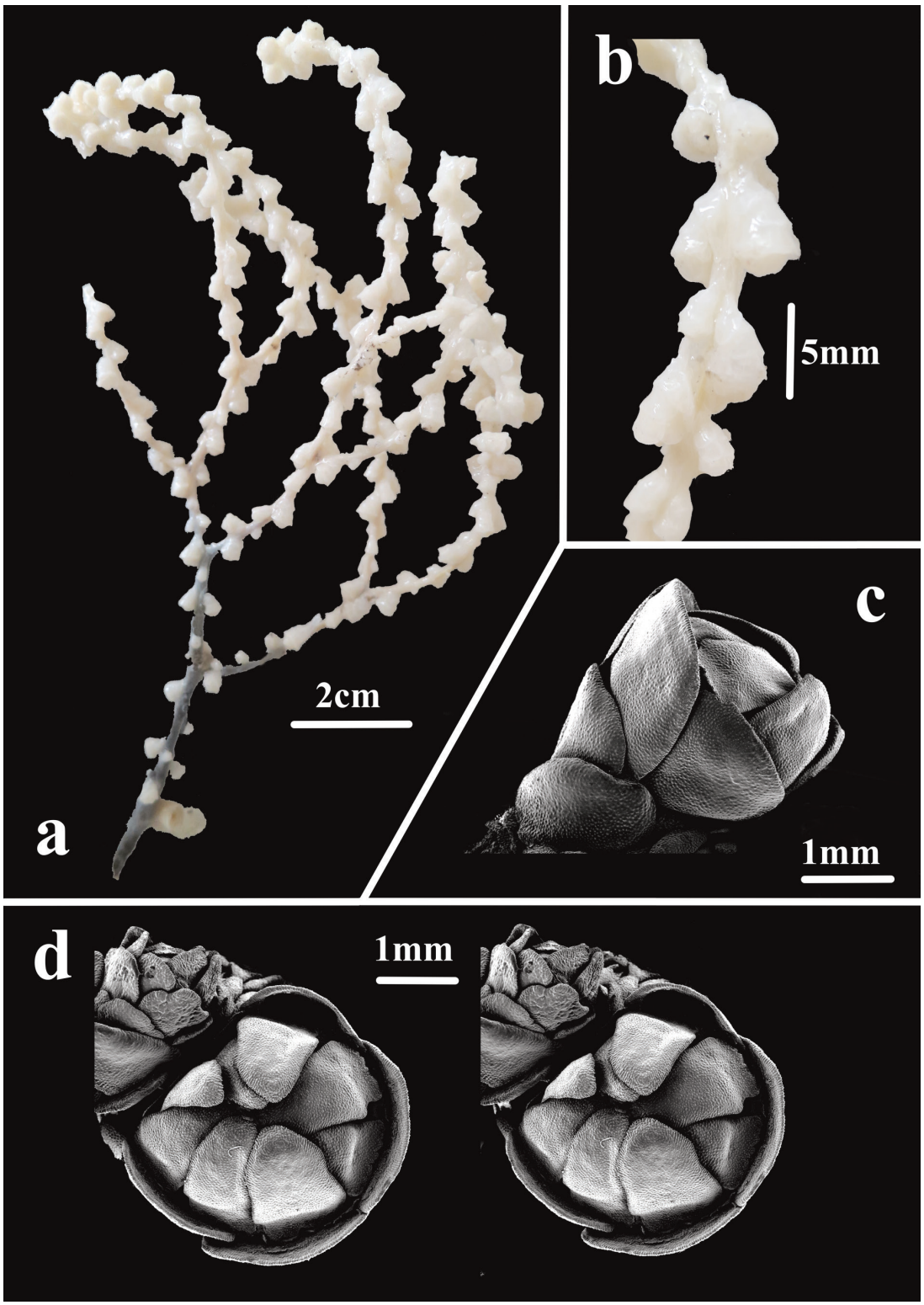

Figure 12. Colony, branchlet and polyps of ***Primnoa bisquama*** **sp. nov.** holotype: (a) colony; (b) close-up of branchlet; (c) lateral view of polyp; (d) stereo image of polyp operculum.

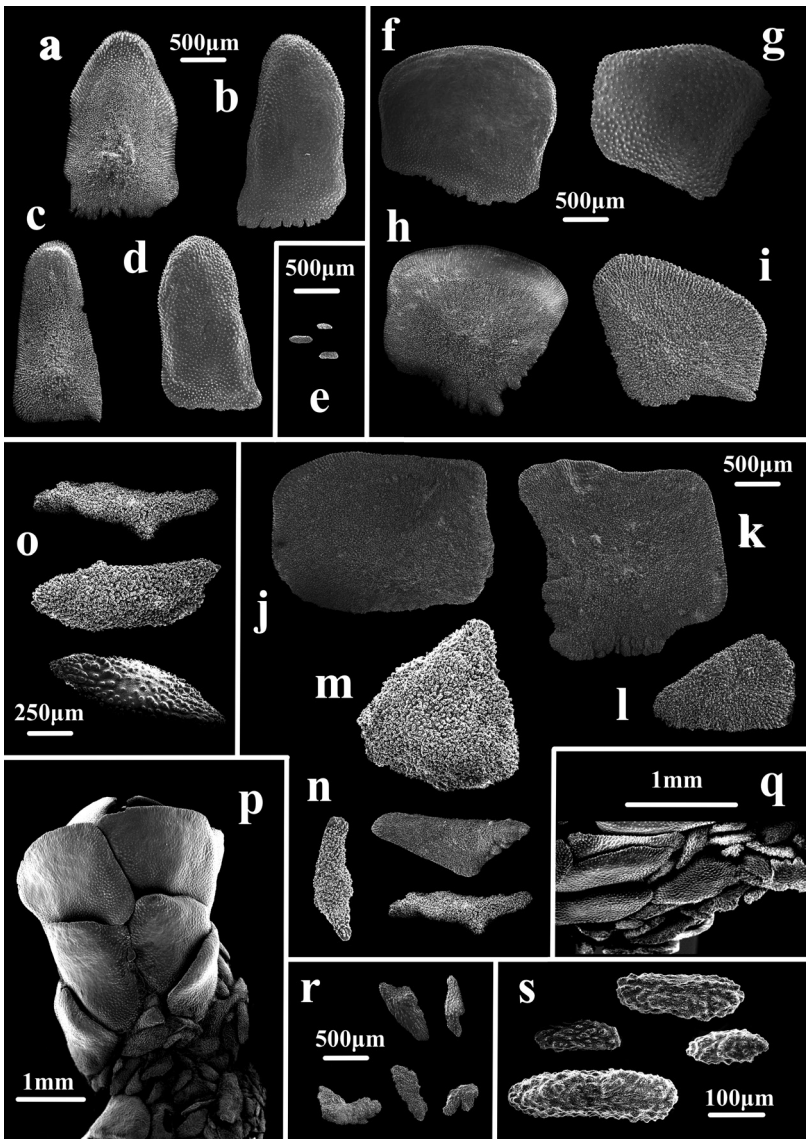

Figure 13. Sclerites, polyp and axis images of ***Primnoa bisquama*** **sp. nov.** holotype: (a–d) opercular; (e, s) tentacular rods; (f–i) marginal scales; (j–n) body-wall scales; (o) coenenchymal scales; (p) abaxial polyp view; (q) axis, showing coenenchyme *in situ*; (r) inter-body wall scales.

Primnoides Studer & Wright in Studer, 1887

Primnoides Studer & Wright in Studer, 1887: 52. – Bayer, 1956: F220; 1961: 292 [illustrated key to genus]; – 1981: 934 [key to genus]. – Bayer & Stefani, 1989: 455 [key to genus]. – Williams, 1992: 276. – Cairns & Bayer, 2009: 23, fig. 3A–F.

Primnoides Wright & Studer, 1889: 90 [incorrect subsequent spelling]. – Versluys, 1906: 9. – Kükenthal, 1915: 142, 144 [key to genus]; 1919: 339; 1924: 253.

Digitogorgia Zapata-Guardiola & López-González, 2010a: 317–320, figs. 2c, d, 7–10). – Zapata-Guardiola & López-González, 2010b: 56–63 (figs. 8–12). – Taylor & Rogers, 2015: 189 (listed).

Diagnosis (from Cairns & Bayer, 2009*, changes in bold)*: Colonies uniplanar, branching in an opposite pinnate manner, **flagelliform or bottlebrush**. Calyces arranged in pairs or whorls of three, calyces inclined upwards. Rudimentary operculum composed of small round, **tongue-shaped or elongate triangular** scales that bear no keel on the inner surface. Body-wall and marginal scales similar in shape, becoming progressively smaller distally. Small calyces completely covered with eight longitudinal rows of body-wall scales, with larger calyces **sometimes** having additional basal scales placed in an irregular manner, resulting in non-linear arrangement of body-wall scales. Broadly, outer surface of scales smooth, inner

surface with only sparse tubercles. Coenenchymal scales in two layers: outer layer consists of smooth, flat, circular to elliptical scales; inner layer of small tuberculate spheroids.

Type species: *P. sertularoides* Wright & Studer, 1889, by subsequent monotypy.

Known distribution: Southern tip of South America, Southern Africa to the SW Indian Ocean, 111.5–2468 m.

Remarks: With the addition of a species to the genus *Primnoeides* that has a layer of inner coenenchymal tuberculate scales, and regularly has whorls of three polyps (see *P. flagellum* sp. nov.), there is need to reassess the taxonomic classification of *Digitogorgia*, which also has these morphological characters and was placed in a well-supported clade alongside *Primnoeides* in phylogenetic analysis (Fig. 3). These genera share many common characters: cylindrical polyp shape, flat, round scales, a rudimentary operculum and similar scale orientation (both have eight regular rows at the polyp base, which becomes more haphazard towards the polyp anterior in *Primnoeides*). *Digitogorgia* is seemingly only differentiated from *Primnoeides* by having species with a bottlebrush colony shape. And, with the expansion of *Primnoeides* to include a second colony shape (fan and now flagelliform as well), colony shape seems a weak reason for their continued separation. We hereby propose *Digitogorgia* as a junior synonym of *Primnoeides*, with the latter taking precedence according to the Principle of Priority, article 23.1 of the ICZN.

Primnoeides sertularoides Wright & Studer, 1889

(Fig. 14)

Material examined: NHMUK 2016.42 (JC066-3149), NHMUK 2016.43 (JC066-3165), NHMUK 2016.44 (JC066-3174), NHMUK 2016.45 (JC066-3181), RRS *James Cook*, sta. 5, ev. 14, Melville Bank, 38°27′47.014′S, 46°45′28.880′E, 572 m, 24 November 2011; NHMUK 2016.46 (JC066-3202), RRS *James Cook*, sta. 5, ev. 14, Melville Bank, 38°27′35.8′S, 46°45′16.03′E, 693 m, 24 November 2011.

Additional description details: *In vivo* species is light yellow in colour (Fig. 14b). Two layers of coenenchymal scales: outer layer of coenenchyme is similar to the original description, that is small rounded sclerites with a smooth outer surface and granular patch on the inner surface; the inner layer are small spheroid tuberculate sclerites, as seen in *Primnoeides flagellum* sp. nov. (Fig. 16g, i).

Known distribution: Prince Edward Island, sub-Antarctic, to Melville Bank in the SW Indian Ocean, 400–693 m.

Remarks: NHMUK 2016.43 (JC066-3165) had two different species of associated arcturid (an isopod). One is shown in Fig. 14a.

Primnoeides flagellum sp. nov.

(Figs 2D, 15, 16)

Material examined: Holotype – NHMUK 2016.47 (JC066-3297), RRS *James Cook*, sta. 5, ev.24, Melville Bank, 38°29′35.476′S, 46°45′36.036′E, 1020 m, 26 November 2011. Paratypes: NHMUK 2016.49 (JC66-3291), sta. 5, ev. 24, 38°29′58.220′S, 46°45′37.531′E, 1087 m, 26 November 2011; NHMUK 2017.1, (JC66-3527, 29 cm tall colony), NHMUK 2016.48 (JC66-3564, 28 cm tall colony), sta. 6, ev. 7, Middle of What seamount, 37°56′37.360′S, 50°27′06.37′E, 1339 m, 2 December 2011. SEM stubs – T152-153, 157–159.

Description: Holotype is a 35 cm tall flagelliform colony complete with calcareous holdfast (*in situ* Figs 2d, 15). Alive colony light yellow, preserved white. Axis light yellow and smooth.

Polyps inclined upwards, whorls of three (Fig. 15a; towards tip of colony sometimes paired), three whorls per cm (Fig. 16h). Polyps 3 mm tall, 1.6 mm wide. Polyp abaxial surface covered with 3–4 longitudinal rows of body-wall scales although pattern obscured as body-wall scales are irregularly placed (Fig. 16f). Operculum mostly hidden beneath marginal scales (Fig. 16e). Opercular scales tongue-shaped (Fig. 16a) with smooth outer surface and small patch of tubercles on inner proximal surface.

Marginal and body-wall scales (Fig. 16b) non-differentiated, circular to wide-elliptical in shape with smooth outer surfaces. Inner scale surface has small area of tubercles proximally and smooth band following scale's distal edge.

Two layers of coenenchymal scales: outer layer circular, very similar to body-wall and marginal scales (Fig. 16c, d); inner layer spheroid-shaped sclerites covered in tubercles (Fig. 16g, i).

Known distribution: Specimens collected from Melville Bank and Middle of What seamounts on the SW Indian Ocean Ridge at 1020–1339 m depth.

Etymology: Named after the Latin for 'whip', as this species has a whip-like colony form.

Remarks: The 0.2% genetic variability across five genes (most variation found within *18S* and *28S*) that separates *P. sertularoides* from *P. flagellum*

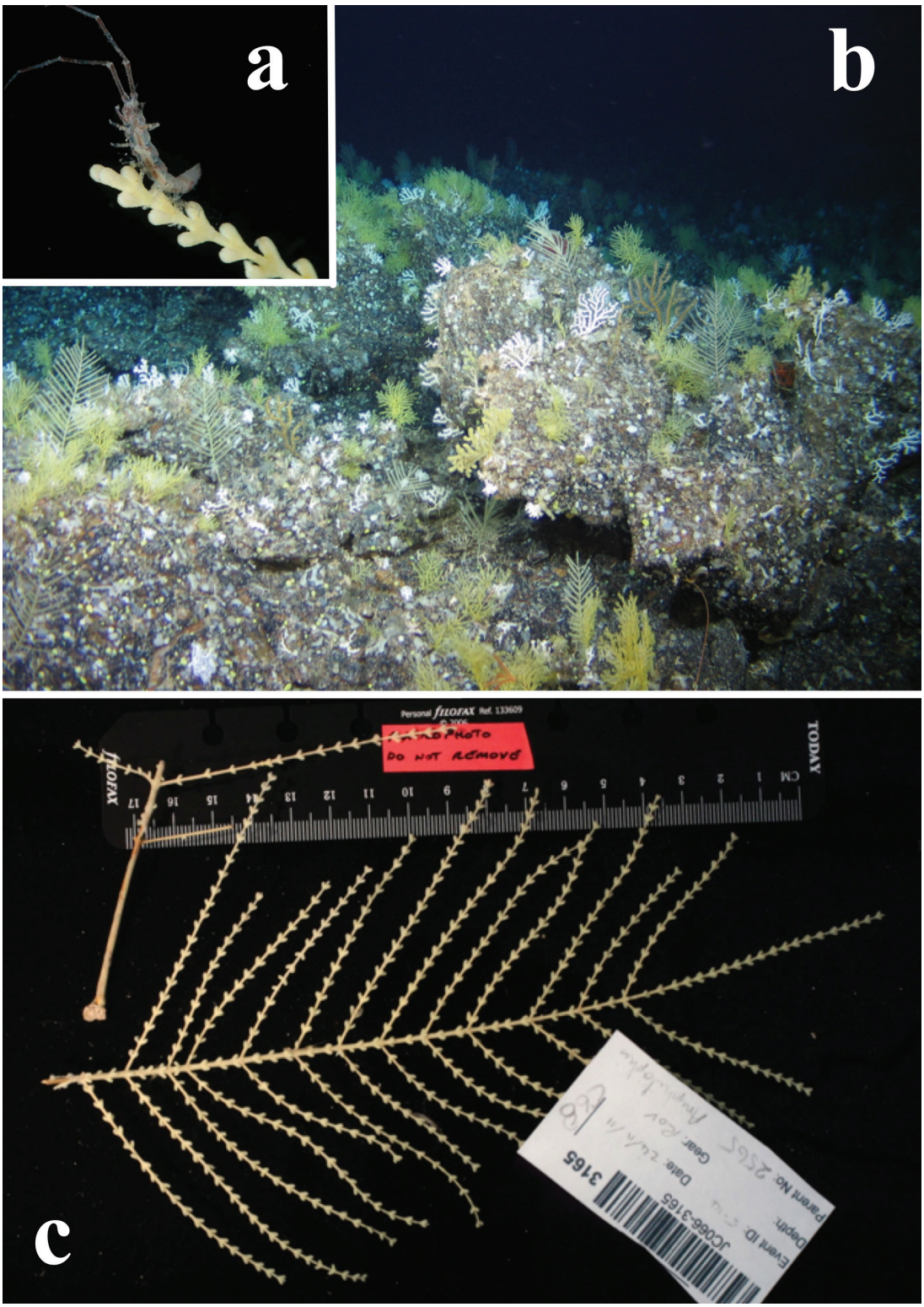

Figure 14. (a) Arcturid isopod on colony of *Primnoides sertularoides* (NHMUK 2016.44, JC066-3174); (b) many colonies of *P. sertularoides in situ*, in a mixed octocoral garden; (c) colony of *P. sertularoides*, NHMUK 2016.43 (JC066-3165). (a) Taken by David Shale.

Figure 15. ***Primnoeides flagellum*** **sp. nov.** holotype. (a) Close up of section of branchlet; (b) whole colony.

would not be considered enough for many barcoding or species definition studies. However, given the acknowledged low rate of genetic variation in coral mitochondrial DNA (Shearer *et al.*, 2002) and low genetic variability between other octocoral species (McFadden *et al.*, 2011), alongside the clear differentiation in colony shape, we believe this distinction is valid.

This species could be the same as that occurring 400–450 m depth off the east coast of Africa, alluded to, but not described, in Williams (1992). Observation of those specimens is required for confirmation.

Comparisons: Primnoeides was a monotypic genus before this description and genus revision. *Primnoeides sertularoides* has a uniplanar colony with opposite branching, very distinct from the flagelliform colony of *P. flagellum*. sp. nov. and distinct from both species formerly within *Digitogorgia* – *Primnoeides kuekenthali* and *P. brochi* – which both have a bottlebrush colony branching pattern. In addition, opercular scales of *P. flagellum* are differentiated from marginal and body-wall scales as they are tongue-shaped; this is not the case in specimens of *P. sertularoides*.

DISCUSSION

INTEGRATIVE TAXONOMIC RESULTS

We present the most comprehensive phylogenetic analysis of any deep-sea coral family. It is fitting, being a widely spread, common, deep-sea family, that Primnoidae is the target of these efforts.

The clear placement of *Digitogorgia* species next to *Primnoeides* in phylogenetic analysis drew attention to the striking similarities between these two genera. The broadening of *Primnoeides* generic description makes it discordant for *Digitogorgia* to remain distinct from these species, resulting in the suggested synonymization presented here.

The three new species descriptions of *Narella* bring the total number of species within this genus to 46; the highest number for any Primnoidae. Morphologically, the genera *Parastenella*, *Narella,* and *Primnoa* (which clustered together) all have relatively large, fleshy

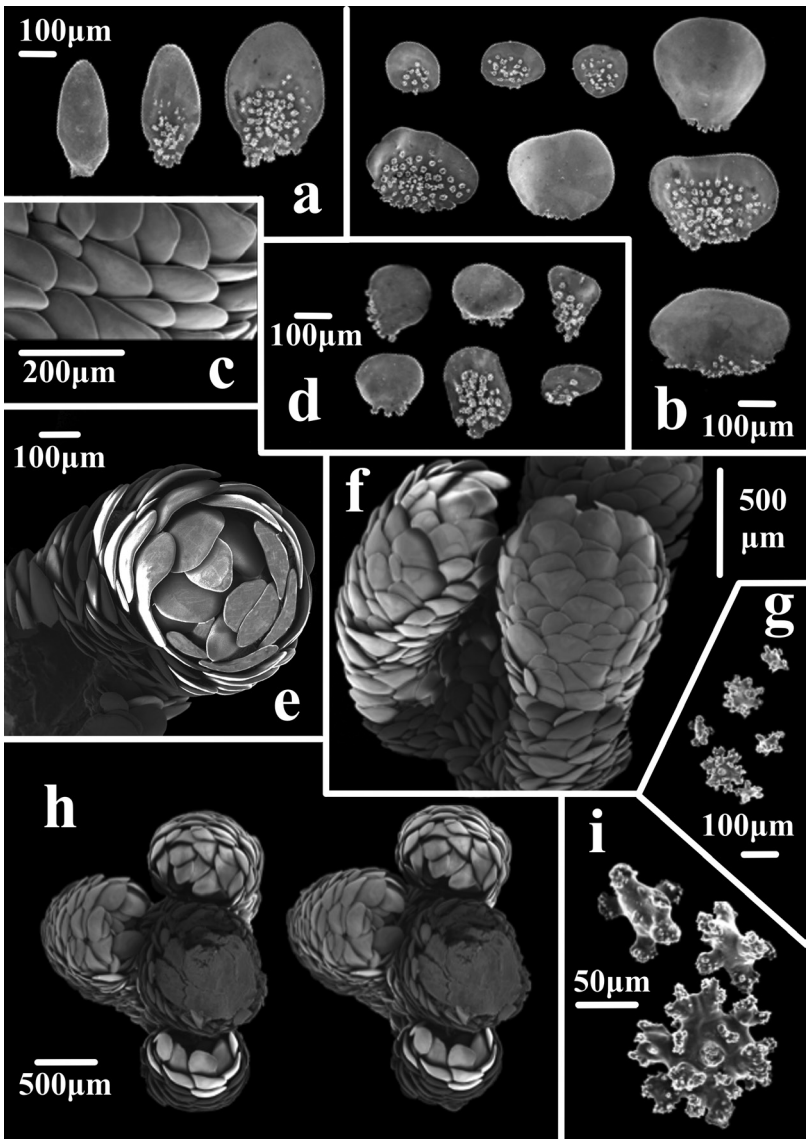

Figure 16. ***Primnoeides flagellum*** **sp. nov.** holotype: (a) opercular scales; (b) marginal and body-wall scales; (c) close-up of coenenchymal scales *in situ*; (d) outer layer of flat coenenchymal scales; (e) anterior view of polyp showing operculum below encroaching marginal scales; (f) side and abaxial view of polyps; (g, i) inner layer of tuberculate spheroid coenenchyme; (h) stereo anterior view of a whorl of polyps.

polyps with *Parastenella* being differentiated by having opercular scales that alternate in alignment to marginals and marginals that are distinctively fluted; and *Primnoa* having polyps protected by two rows of three or more large abaxial scales. *Parastenella* also has polyps that are perpendicular to the axis; polyps of *Narella* and *Primnoa* are mostly downward facing. Although genetic analysis would suggest that *Parastenella*, *Primnoa* and some *Narella* species may in fact be within the same genus, until wider sampling and genetic analysis is possible (although we do present 17 species of 47 in *Narella* plus two undescribed species; Cairns & Bayer, 2008), and for ease of identification, we suggest these genera remain separate.

The large fleshy polyps and the relatively few scales found on polyps unite the Pacific Primnoidae, within which most of the SW Indian Ocean specimens originate (Fig. 3). More specific morphological characters are not, however, obvious. More sampling and improved genetic tools (discussed below) are required for phylogenetic and species delimitation analyses.

BIOGEOGRAPHY

In the Watling *et al.* (2013) proposed biogeography of the deep-ocean floor, the SWIO ridge areas sampled here are within the lower bathyal, 801–3500 m, biogeographic classification of the Indian Ocean; with waters of 2–3 °C. In phylogenetic analysis, most Indian Ocean specimens presented here (labelled in purple in Fig. 3) were embedded within a clade of Pacific samples (as seen in Taylor & Rogers, 2015). The depth ranges of *P. sertularoides* and *P. flagellum*, whose geographical ranges span into the cooler sub-Antarctic Indian Ocean, fall well within the lower bathyal. As they are embedded in a clade of sub-Antarctic species (Fig. 3), this is likely a geographical emigration from similar depths around Antarctica, into the slightly warmer waters of the Indian Ocean. The same could be said for *Thouarella laxa* (Fig. 3, top purple triangle in sub-Antarctic clade), which was collected at 290–1339 m depth. These are perhaps examples of cold-adapted species, from colder waters around Antarctica, moving into warmer waters; an important possibility in the sub-Antarctic, an area where species are potentially threatened by warming waters (Peck, 2005) and where warming is causing species range shifts towards the poles (Thomas, 2010).

At abyssal depths, 3501–6500 m in Watling *et al.* (2013), the SWIO ridge area was considered within the Antarctica East biogeographic region, defined by cold seafloor waters. The undescribed Genus B specimen was found at 4500–4612 m depth in the SW Indian Ocean yet is embedded within the sub-Antarctic clade (Fig. 3) of mostly much shallower lower bathyal (801–3500 m) depth samples; this is an example of the 'polar submergence' (discussed in Brandt *et al.*, 2007), where species from Antarctic, from cold waters, have submerged into the deep sea elsewhere where there are also cold waters; in this case species have submerged into the southern Indian Ocean.

Conversely, *Parastenella spinosa* from South Georgia (Fig. 3, blue circles, from 1010 to 1539 m) is embedded in a clade of mostly Pacific specimens (from a range of depths), suggesting that this species has emigrated from the Pacific into Antarctica. This is perhaps unsurprising given the large influence of Antarctic Intermediate water at that depth in the Pacific (Watling *et al.*, 2013).

GENE UTILITY

The quest for informative genetic markers has been a long time pursuit of octocoral researchers (France *et al.*, 1996; Sánchez, Lasker & Taylor, 2003; McFadden *et al.*, 2006; McFadden, Sanchez & France, 2010). The restricted phylogenetic utility of *ND2* and *ND6* resulted in limited impact on the phylogenetic tree in terms of node supports and structure, hence results were not presented. Perhaps this is unsurprising given their very low variability, for example *ND6* has just three base pair variation across five species of *Narella* from Alaska (Cairns & Baco, 2007). Although, in this analysis, their limited utility was most likely due to low sequence coverage for most of the specimens investigated (79% of sequences with missing data for *ND2* and *ND6*).

Given that the five-gene phylogenetic tree presented here (covering both mitochondrial and nuclear genes) only weakly supported the separation of Pacific specimens from those originating in the Atlantic and sub-Antarctic, it is highly recommended that novel techniques are now utilized to elucidate the octocoral phylogeny. Research in this field is already underway and looks very promising (Pante *et al.*, 2015).

CONCLUSIONS

Octocorals are a common and essential component of deep-sea communities yet we know little about how they have evolved, their biogeography, reproduction, and connectivity. Global warming and ocean acidification may well have impacts in the deep-sea, impacts that will affect octocorals (Yesson *et al.*, 2012). Species-level designations and biogeographical knowledge are the first steps necessary to understand the broader octocoral community dynamics, drivers, and bottlenecks; important considerations for survival in a changing world.

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REFERENCES

Armstrong CW, Foley NS, Tinch R, van den Hove S. 2012. Services from the deep: steps towards valuation of deep sea goods and services. *Ecosystem Services* **2:** 2–13.

Bayer FM. 1956. Octocorallia. In: Moore RC, ed. *Treatise on Invertebrate Palaeontology*. Lawrence, Kansas: University of Kansas Press. F166–F189, F192–F231.

Bayer FM. 1961. The shallow-water Octocorallia of the West Indian region - A manual for marine biologists. *Studies on the Fauna Curacao and other Caribbean Islands* **12:** 1–373.

Bayer FM. 1981. Key to genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa), with diagnosis of new taxa. *Proceedings of the Biological Society of Washington* **94:** 902–947.

Bayer FM, Stefani J. 1989. Primnoidae (Gorgonacea) De Nouvelle-Calédonie. *Bulletin de Muséum national d'Histoire naturelle, Paris, Serie 4* **10:** 449–518.

Bilewitch JP, Degnan SM. 2011. A unique horizontal gene transfer event has provided the octocoral mitochondrial genome with an active mismatch repair gene that has potential for an unusual self-contained function. *BMC Evolutionary Biology* **11:** 228.

Brandt A, Gooday AJ, Brandão SN, Brix S, Brökeland W, Cedhagen T, Choudhury M, Cornelius N, Danis B, De Mesel I, Diaz RJ, Gillan DC, Ebbe B, Howe JA, Janussen D, Kaiser S, Linse K, Malyutina M, Pawlowski J, Raupach M, Vanreusel A. 2007. First insights into the biodiversity and biogeography of the Southern Ocean deep sea. *Nature* **447:** 307–311.

Cairns SD. 2012. *The Marine Fauna of New Zealand: New Zealand Primnoidae (Anthozoa: Alcyonacea). Part 1. Genera Narella, Narelloides, Metanarella, Calyptrophora, and Helicoprimnoa NIWA Biodiversity Memoir*. Wellington: NIWA (National Institute of Water and Atmospheric Research Ltd), 1–126.

Cairns SD, Baco A. 2007. Review and five new Alaskan species of the deep-water octocoral *Narella* (Octocorallia: Primnoidae). *Systematics and Biodiversity* **5:** 391–407.

Cairns SD, Bayer FM. 2003. Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 3: the genus *Narella* Gray, 1870. *Proceedings of the Biological Society of Washington* **116:** 617–648.

Cairns SD, Bayer FM. 2005. A review of the genus *Primnoa* (Octocorallia: Gorgonacea: Primnoidae), with the description of two new species. *Bulletin of Marine Science* **77:** 225–256.

Cairns SD, Bayer FM. 2008. A review of the Octocorallia (Cnidaria: Anthozoa) from Hawai'i and adjacent seamounts: the genus *Narella*. *Pacific Science* **62:** 83–115.

Cairns SD, Bayer FM. 2009. A generic revision and phylogenetic analysis of the Primnoidae (Cnidaria: Octocorallia). *Smithsonian Contributions to Zoology* **629:** 1–79.

Clark MR, Rowden AA, Schlacher T, Williams A, Consalvey M, Stocks KI, Rogers AD, O'Hara TD, White M, Shank TM, et al. 2010. The ecology of seamounts: structure, function, and human impacts. *Annual Review of Marine Science* **2:** 253–278.

Davies JS, Stewart HA, Narayanaswamy BE, Jacobs C, Spicer J, Golding N, Howell KL. 2015. Benthic assemblages of the Anton Dohrn Seamount (NE Atlantic): defining deep-sea biotopes to support habitat mapping and management efforts with a focus on vulnerable marine ecosystems. *PLoS One* **10:** e0124815.

France SC, Rosel PE, Agenbroad JE, Mullineaux LS, Kocher TD. 1996. DNA sequence variation of mitochondrial large-subunit rRNA provides support for a two-subclass organization of the Anthozoa (Cnidaria). *Molecular Marine Biology and Biotechnology* **5:** 15–28.

Henry L-A, Vad J, Findlay HS, Murillo J, Milligan R, Roberts JM. 2014. Environmental variability and biodiversity of megabenthos on the Hebrides Terrace Seamount (Northeast Atlantic). *Scientific Reports* **4**. Article no 5589:1-10

Kinoshita K. 1908. Primnoidae von Japan. *Journal of the College of Science, Imperial University, Tokyo, Japan* **23:** 1–74.

Kükenthal W. 1912. Die Alcyonaria Der Deutschen Südpolar, Expedition 1901–1903 *Deutsche Südpolar Expedition* 1901–1903, *Zoologie*. 289–349.

Kükenthal W. 1915. System und Stammesgeschichte der Primnoidae. *Zoologischrn Anzeiger* **46:** 142–158.

Kükenthal W. 1919. *Gorgonaria Wissenschaftliche Ergebnisse der deutschen Tiefsee–Expedition auf dem Dampfer "Valdivia" 1898–1899*. 1–946.

Kükenthal W. 1924. Coelenterata: Gorgonaria Das Tierreich: Walter de Gruyter & Co., Berlin. 478.

Kvile KØ, Taranto GH, Pitcher TJ, Morato T. 2014. A global assessment of seamount ecosystems knowledge using an ecosystem evaluation framework. *Biological Conservation* **173:** 108–120.

Lanfear R, Calcott B, Ho SY, Guindon S. 2012. Partitionfinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* **29:** 1695–1701.

Macpherson E, Amon D, Clark PF. 2014. A new species of *Munidopsis* from a seamount of the Southwest Indian Ocean Ridge (Decapoda: Munidopsidae). *Zootaxa* **3753:** 291–296.

McDonagh EL., Bryden HL, King BA, Sanders RJ. 2008. The circulation of the Indian Ocean at 32 degrees S, *Progress in Oceanography* **79:** 20–36.

McFadden CS, Benayahu Y, Pante E, Thoma JN, Nevarez A, P., France SC. 2011. Limitations of mitochondrial gene barcoding in Octocorallia. *Molecular Ecology Resources* **11**: 19–31.

McFadden CS, France SC, Sánchez JA, Alderslade P. 2006. A molecular phylogenetic analysis of the Octocorallia (Cnidaria: Anthozoa) based on mitochondrial protein-coding sequences. *Molecular Phylogenetics and Evolution* **41:** 513–527.

McFadden CS, Sánchez JA, France SC. 2010. Molecular phylogenetic insights into the evolution of Octocorallia: a review. *Integrative and Comparative Biology* **50:** 389–410.

O'Loughlin MP, Mackenzie M, VandenSpiegel D. 2013. New sea cucumber species from the seamounts on the Southwest Indian Ocean Ridge (Echinodermata: Holothuroidea: Aspidochirotida, Elasipodida, Dendrochirotida). *Memoirs of Museum Victoria* **70:** 37–50.

Pante E, Abdelkrim J, Viricel A, Gey D, France SC, Boisselier MC, Samadi S. 2015. Use of RAD sequencing for delimiting species. *Heredity* **114:** 450–459.

Pante E, France SC, Couloux A, Cruaud C, McFadden CS, Samadi S, Watling L. 2012. Deep-sea origin and *in-situ* diversification of chrysogorgiid octocorals. *PLoS One* **7:** e38357.

Peck LS. 2005. Prospects for surviving climate change in Antarctic aquatic species. *Frontiers in Zoology* **2:** 9.

Rambaut A, Drummond A. 2015. *Tracer v1.6. http://tree.bio.ed.ac.uk/software/tracer/*

Read JF, Lucas MI, Holley SE, Pollard RT. 2000. Phytoplankton, nutrients and hydrography in the frontal zone between the Southwest Indian Subtropical gyre and the Southern Ocean. *Deep-Sea Research I* **47:** 2341–2368.

Rogers AD. 1994. The biology of seamounts. *Advances in Marine Biology* **30:** 305–350.

Rogers AD. 2015. Environmental change in the deep ocean. *Annual Review of Environment and Resources* **40:** 1–38.

Rogers AD, Taylor ML. 2012. *Benthic biodiversity of seamounts in the southwest Indian Ocean Cruise report–R/V James Cook 066.* Report for NERC. 235 pp. Available at: http://www.asclme.org/reports2013/Cruise%20reports/56%20Seamounts%20cruise%20report%202011%20-%20James%20Cook%20066.pdf

Romanov EV. 2003. *Summary and review of Soviet and Ukrainian scientific and commercial fishing operations on the deepwater ridges of the southern Indian Ocean FAO Fisheries Circular*. Rome: FAO, 84.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61:** 539–542.

Rowden AA, Dower JF, Schlacher TA, Consalvey M, Clark MR. 2010. Paradigms in seamount ecology: fact, fiction and future. *Marine Ecology* **31:** 226–241.

Sánchez JA, Lasker HR, Taylor DJ. 2003. Phylogenetic analyses among octocorals (Cnidaria): mitochondrial and nuclear DNA sequences (lsu-rRNA, 16S and ssu-rRNA, 18S) support two convergent clades of branching gorgonians. *Molecular Phylogenetics and Evolution* **29:** 31–42.

Shearer TL, Van Oppen MJ, Romano SL, Wörheide G. 2002. Slow mitochondrial DNA sequence evolution in the Anthozoa (Cnidaria). *Molecular Ecology* **11:** 2475–2487.

Stiasny G. 1940. Alcyonaria und Gorgonaria von Dud Afrika aus der Sammlung ds South African Museum, Cape Town. *Verhandelingen der K. Nederlandsche akademie van wetenschappen, Afdeeling Natuurkunde, Tweede Sectie* **39:** 1–37.

Studer T. 1887. Versuch Eines Systemes der Alcyonaria. *Archiv für Naturgeschichte* **53:** 1–74.

Taylor ML, Cairns SD, Agnew DJ, Rogers AD. 2013. A revision of the genus *Thouarella* Gray, 1870 (Octocorallia: Primnoidae), including an illustrated dichotomous key, a new species description, and comments on *Plumarella* Gray, 1870 and *Dasystenella*, Versluys, 1906. *Zootaxa* **3602:** 1–105.

Taylor ML, Rogers AD. 2015. Evolutionary dynamics of a common sub-Antarctic octocoral family. *Molecular Phylogenetics and Evolution* **84:** 185–204.

Thomas CD. 2010. Climate, climate change and range boundaries. *Diversity and Distributions* **16:** 488–495.

Thomson JS. 1911. The Alcyonaria of the Cape of Good Hope and Natal. Gorgonacea. *Proceedings of the Zoological Society of London* **1911:** 870–893.

Versluys J. 1906. Die Gorgoniden Der *Siboga*-Expedition *Siboga-Expeditie*. 1–187.

Watling L, France SC, Pante E, Simpson A. 2011. Biology of deep-water octocorals. *Advances in Marine Biology* **60:** 41–122.

Watling L, Guinotte J, Clark MR, Smith CR. 2013. A proposed biogeography of the deep ocean floor. *Progress in Oceanography* **111:** 91–112.

Williams GC. 1992. The Alcyonacea of Southern Africa. Gorgonian corals. *Annals of the South African Museum* **101:** 181–296.

Wright EP, Studer T. 1889. Report on the Alcyonaria Collected by H.M.S. Challenger during the Years 1873–76 *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–76*, *Zoology*. 1–314.

Yesson C, Clark MR, Taylor ML, Rogers AD. 2011. The global distribution of seamounts based on 30 arc seconds bathymetry data. *Deep Sea Research Part I: Oceanographic Research Papers* **58:** 442–453.

Yesson C, Taylor ML, Tittensor DP, Davies AJ, Guinotte J, Baco A, Black J, Hall-Spencer JM, Rogers AD. 2012. Global habitat suitability of cold-water octocorals. *Journal of Biogeography* **39:** 1278–1292.

Zapata-Guardiola R, Lopez-Gonzalez PJ. 2010b. Redescription of *Thouarella brucei* Thomson and Ritchie, 1906 (Cnidaria: Octocorallia: Primnoidae) and description of two new Antarctic primnoid species. *Zootaxa:* 48–68.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix 1. List of specimens included in phylogenetic analysis.