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).


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 Agulas 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...
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 (OLoughlin, 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).
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 Primnoidea from 29 genera were represented in this analysis (Table S1). Outgroups were designated as Chrysogorgiidae (JC066-0714) and Chrysorgia chryseis (CR106-2) as these are sister species to Primnoidea (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), Primnoeides 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
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


Not *Stachyodes* Bargatzky, 1881 [a stromatoporoid].


*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.

**Table 1. Gene alignments, coverage and partitions**

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

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.

<table>
<thead>
<tr>
<th>Species name</th>
<th>Range</th>
<th>Depth</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>N. megalepis</em> (Kinoshita, 1908)</td>
<td>Japan</td>
<td>Unknown (probably 300–400 m)</td>
</tr>
<tr>
<td><em>N. irregularis</em> (Kinoshita, 1907)</td>
<td>Japan</td>
<td>137 m</td>
</tr>
<tr>
<td><em>N. compressa</em> (Kinoshita, 1908)</td>
<td>Japan</td>
<td>Unknown</td>
</tr>
<tr>
<td><em>N. biannulata</em> (Kinoshita, 1907)</td>
<td>Japan</td>
<td>Unknown</td>
</tr>
<tr>
<td><em>N. japonensis</em> (Aurivillius, 1931)</td>
<td>Japan</td>
<td>731 m</td>
</tr>
<tr>
<td><em>N. bayeri</em> Cairns &amp; Baco, 2007</td>
<td>Gulf of Alaska</td>
<td>3291–4091 m</td>
</tr>
<tr>
<td><em>N. cristata</em> Cairns &amp; Baco, 2007</td>
<td>Gulf of Alaska</td>
<td>3385 m</td>
</tr>
<tr>
<td><em>N. abyssalis</em> Cairns &amp; Baco, 2007</td>
<td>Gulf of Alaska</td>
<td>4594 m</td>
</tr>
<tr>
<td><em>N. arbuscula</em> Cairns &amp; Baco, 2007</td>
<td>Gulf of Alaska</td>
<td>2775–3465 m</td>
</tr>
<tr>
<td><em>N. alakensis</em> Cairns &amp; Baco, 2007</td>
<td>Gulf of Alaska</td>
<td>2377–3075 m</td>
</tr>
<tr>
<td><em>N. leilae</em> Bayer, 1951</td>
<td>Indonesia</td>
<td>740 m</td>
</tr>
<tr>
<td><em>N. clavata</em> (Versluys, 1906)</td>
<td>Indonesia, Philippines, Japan, New Zealand</td>
<td>128–335 m</td>
</tr>
<tr>
<td><em>N. horrida</em> (Versluys, 1906)</td>
<td>Indonesia</td>
<td>204 m</td>
</tr>
<tr>
<td><em>N. obscura</em> (Versluys, 1906)</td>
<td>Indonesia</td>
<td>984 m</td>
</tr>
<tr>
<td><em>N. orientalis</em> (Versluys, 1906)</td>
<td>Indonesia</td>
<td>520 m</td>
</tr>
<tr>
<td><em>N. parva</em> (Versluys, 1906)</td>
<td>Indonesia</td>
<td>920–2400 m</td>
</tr>
<tr>
<td><em>N. grandiflora</em> (Kukenthal, 1907)</td>
<td>Sumatra</td>
<td>805 m</td>
</tr>
<tr>
<td><em>N. studeri</em> (Versluys, 1906) (nom. nov. for <em>S. regularis</em>) Wright &amp; Studer, 1889</td>
<td>Kermadec and Indonesia</td>
<td>732–1392 m</td>
</tr>
<tr>
<td><em>N. allmani</em> (Wright &amp; Studer, 1889)</td>
<td>Fiji</td>
<td>‘deep’</td>
</tr>
<tr>
<td><em>N. dichotoma</em> (Versluys, 1906)</td>
<td>Indonesia</td>
<td>204–1264 m</td>
</tr>
<tr>
<td>= <em>N. nuttingi</em> Bayer, 1997</td>
<td>Hawaiian Islands</td>
<td>743–1448 m</td>
</tr>
<tr>
<td><em>N. gigas</em>, Cairns &amp; Bayer, 2008</td>
<td>Hawaiian Islands</td>
<td>302–399 m</td>
</tr>
<tr>
<td><em>N. alata</em>, Cairns &amp; Bayer, 2008</td>
<td>Hawaiian Islands</td>
<td>477–750 m</td>
</tr>
<tr>
<td><em>N. vernifera</em>, Cairns &amp; Bayer, 2008</td>
<td>Hawaiian Islands</td>
<td>275–527 m</td>
</tr>
<tr>
<td><em>N. macrocalyx</em>, Cairns &amp; Bayer, 2008</td>
<td>Hawaiian Islands</td>
<td>1206–1807 m</td>
</tr>
<tr>
<td><em>N. ornata</em> Bayer, 1995</td>
<td>Hawaiian Islands</td>
<td>748–1007 m</td>
</tr>
<tr>
<td><em>N. bowersi</em> (Nutting, 1908)</td>
<td>Hawaiian Islands</td>
<td>1218–1758 m</td>
</tr>
<tr>
<td><em>N. muzikae</em>, Cairns &amp; Bayer, 2008</td>
<td>Hawaiian Islands</td>
<td>326–381 m</td>
</tr>
<tr>
<td><em>N. hawaiinensis</em>, Cairns &amp; Bayer, 2008</td>
<td>Hawaiian Islands</td>
<td>1492–1921 m</td>
</tr>
<tr>
<td><em>N. ambiguus</em> (Studer, 1894)</td>
<td>Galapagos</td>
<td>691 m</td>
</tr>
<tr>
<td><em>N. gaussii</em> (Kukenthal, 1912)</td>
<td>Antarctic</td>
<td>2450 m</td>
</tr>
<tr>
<td><em>N. bellissima</em> (Kukenthal, 1915)</td>
<td>Amphi-Atlantic</td>
<td>225–1968 m</td>
</tr>
<tr>
<td><em>N. versluysi</em> (Hickson, 1909)</td>
<td>Amphi-Atlantic</td>
<td>550–3100 m</td>
</tr>
<tr>
<td>= ?<em>N. elegans</em> Tixier-Durivault &amp; Lafargue, 1968</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>N. regularis</em> (Duchassaing &amp; Michelotti, 1860)</td>
<td>Lesser Antilles</td>
<td>366–792 m</td>
</tr>
<tr>
<td><em>N. laxa</em> Deichmann, 1936</td>
<td>New England seamounts</td>
<td>3186 m</td>
</tr>
<tr>
<td><em>N. pauciflora</em> Deichmann, 1936</td>
<td>Lesser Antilles</td>
<td>738–1446 m</td>
</tr>
<tr>
<td><em>N. spectabilis</em> Cairns &amp; Bayer, 2003</td>
<td>Bahamas</td>
<td>1485 m</td>
</tr>
<tr>
<td><em>N. alvinae</em> Cairns &amp; Bayer, 2003</td>
<td>Bermuda</td>
<td>3419 m</td>
</tr>
<tr>
<td><em>N. mesolepis</em> Cairns, 2012</td>
<td>New Zealand</td>
<td>157–1246 m</td>
</tr>
<tr>
<td><em>N. hypsocalyx</em> Cairns, 2012</td>
<td>New Zealand</td>
<td>510–1118 m</td>
</tr>
<tr>
<td><em>N. vulgaris</em> Cairns, 2012</td>
<td>New Zealand</td>
<td>335–1165 m</td>
</tr>
<tr>
<td><em>N. mosaica</em> Cairns, 2012</td>
<td>New Zealand</td>
<td>278–294 m</td>
</tr>
<tr>
<td><em>N. dampieri</em> Cairns, 2012</td>
<td>New Zealand</td>
<td>342 m</td>
</tr>
<tr>
<td><em>N. gigilchristi</em> (Thomson, 1911)</td>
<td>SW Indian Ocean</td>
<td>90–1365 m</td>
</tr>
<tr>
<td>= <em>S. capensis</em> Thomson, 1917</td>
<td>SW Indian Ocean</td>
<td>141–173 m</td>
</tr>
<tr>
<td>= <em>Stachyodes</em> ‘gilberti’ Kukenthal, 315:1918 nom. nud. (misspelling of <em>gilchristi</em>)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>N. speighti</em> sp. nov.</td>
<td>SW Indian Ocean</td>
<td>870 m</td>
</tr>
<tr>
<td><em>N. valentine</em> sp. nov.</td>
<td>SW Indian Ocean</td>
<td>383–444 m</td>
</tr>
<tr>
<td><em>N. candidae</em> sp. nov.</td>
<td>SW Indian Ocean</td>
<td>763 m</td>
</tr>
</tbody>
</table>
### 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; whorl diameter (mm) | Calyx length (and width) | Basal body-wall scale height; dorso-lateral 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; distal edge | Abaxial buccal body-wall scale: length; dorso-lateral edge; distal edge; closed adaxial ring | Adaxial buccal scale: additional adaxial bw scales?; shape | Opercular scales: H:W of abaxials; inner keel | Coenenchymal 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 | 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’ basally, (Williams, 1992), yellow to the thin, irregular apex shape, upturned edges | Axis brown basally, |
| *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 | 1.25–1.45 mm; right angle with lateral ridge; peaked; yes | No 90%; ridged; 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 green iridescent striated round edges forming a mosaic axis |

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,
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.
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 Ascothoracica, Subphylum Crustacea, were found on specimen NHMUK 2016.19, JCO66-3824. 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 (NMMH, 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 perpendicularly 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 hawaiinensis* 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 (JCO66-3719), 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

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. bianculus*, *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.


**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-obleng 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. Operculars 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. ambiguа*. 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. ambiguа* it is hard to make further comparisons. Both *N. ornata* and *N. hawaiinensis*, although with similar ridged basal scales as *N. valentine*, have fewer polyps per whorl and basal scales that do not form a closed ring.

**NARELLA CANDIDAЕ 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 widened; axis light gold distally (Fig. 10g) and ‘radiant’. We present ‘candidae’ as a noun in the genitive form as per article 31.1.2 of the ICZN.

**Etymology:** Named after Dr Candida Rogers, wife of Prof. Alex Rogers, and suitably also Latin for ‘white’ and ‘radiant’.

**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. laxа* 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.
**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**


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**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.
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 opercular 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 Linnaeus, 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, 12°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 (JC066-3518), likely a fragment of NHMUK 2016.40 (JC066-3568), 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.

Opercular 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.
**Primnoeides Studer & Wright in Studer, 1887**


**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

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**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.
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)


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).

PRIMNOEIDES FLAGELLUM SP. NOV.
(FIGS 2D, 15, 16)


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). Polype 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 Primnoeides 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.
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 bottle-brush 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 synonymy 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
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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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.