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New Insights into the Biodiversity of Benthic Hydroids (Cnidaria, Hydrozoa) from Seamounts in the Remote Macquarie Ridge, with the Description of Three New Species

Álvaro Luis Peña Cantero*

*Instituto Cavanilles de Biodiversidad y Biología Evolutiva / Departamento de Zoología, Universidad de Valencia, Valencia, Spain, Apdo. Correos 22085, 46071 Valencia, Spain. *Correspondence: E-mail: alvaro.l.pena@uv.es (Peña Cantero)*

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The Macquarie Ridge is a major seafloor feature in the Southern Hemisphere between New Zealand and the Antarctic continent, and its marine communities have been poorly explored. During the MacRidge 2 TAN0803 survey conducted on board the R/V *Tangaroa*, several seamounts of the Macquarie Ridge were sampled. Among the benthic samples obtained, a collection of hydroids was present. Eleven species were recorded, including *Acryptolaria seamountensis* sp. nov., *Filellum liberum* sp. nov. and *Nemertesia macquariensis* sp. nov. Anthoathecata is represented only by *Eudendrium* sp. The collection is essentially dominated by Leptothecata, with ten species, belonging to the families Campanulariidae, Lafoeidae, Phylactothecidae, Plumulariidae and Sertularellidae. Lafoeidae is by far the most diversified family, accounting for half of the leptothecate species. At the generic level, the collection is dominated by the deep-water genus *Acryptolaria*, with four species; all the remaining genera are represented by a single species. Seven species represent new records for the area and *Calamphora quadrispinosa* Watson, 2003 is recorded for the second time.

Key words: Hydrozoans, New species, New records, Biodiversity, Sub-Antarctic

BACKGROUND

The Macquarie Ridge is a prominent elevation on the southern hemisphere seafloor between New Zealand and the Antarctic continent, extending from the Antarctic Balleny Islands region northwards through Macquarie Island towards New Zealand (Brodie and Dawson 1965). It is a rather continuous feature, forming an important boundary between the deep waters of the Pacific and Indian Oceans and also interrupting the flow of the Antarctic Circumpolar Current (ACC), the world′s largest current and the dominant feature of the Southern Ocean circulation.

In 2008, the MacRidge 2 TAN0803 scientific survey was carried out to study the Macquarie Ridge and its adjacent sediment basins. One of the cruise objectives was to investigate the biodiversity and habitat of the seamounts associated with the ridge. These distinctly elevated features of the ridge have rarely been sampled and there is great interest in assessing their biodiversity (Samadi et al. 2007; Stocks and Hart 2007).

As far as benthic hydroids are concerned, only one study has so far dealt with this zoological group from this large seafloor feature. Watson (2003) reported 27 species of hydrozoans, including six new to science, from a collection obtained during a survey of sub-Antarctic areas north, south, east and west of Macquarie Island (Fig. 1), between latitudes 53°0'S and 56°17'S and longitudes 158°30'E and 159°25'E.

The aim of this study is to increase scientific

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knowledge of the biodiversity of benthic hydroids inhabiting the Macquarie Ridge through the study of the collection of benthic hydrozoans collected during the MacRidge 2 TAN0803 survey, hosted by the National Institute of Water and Atmospheric Research (NIWA). The results of this study are presented here.

MATERIALS AND METHODS

The material studied was collected during the New Zealand-Australia MacRidge 2 TAN0803 scientific survey conducted on board the R/V *Tangaroa*, from 26 March to 26 April 2008. Samples studied here were gathered using an epibenthic sledge in two seamounts of the Macquarie Ridge, north and south of Macquarie Island (Fig. 1), at depths between 119 and 750 m (Table 1). Hydrozoans were preserved in 70% ethanol.

The materials studied here are deposited in the National Institute of Water and Atmospheric Research Invertebrate Collection at Wellington (NIWA), New Zealand.

A reference publication, for both specialist and non-specialist readers, with valuable descriptions and figures of the characters used in the identification of hydrozoans, together with diagnoses and keys of the families and genera, is *An introduction to Hydrozoa* by Bouillon et al. (2006). I have included below a key for the identification of the species studied, and a figure illustrating the diversity of hydrothecal shapes and the main morphological characters used in their identification (Fig. 2).

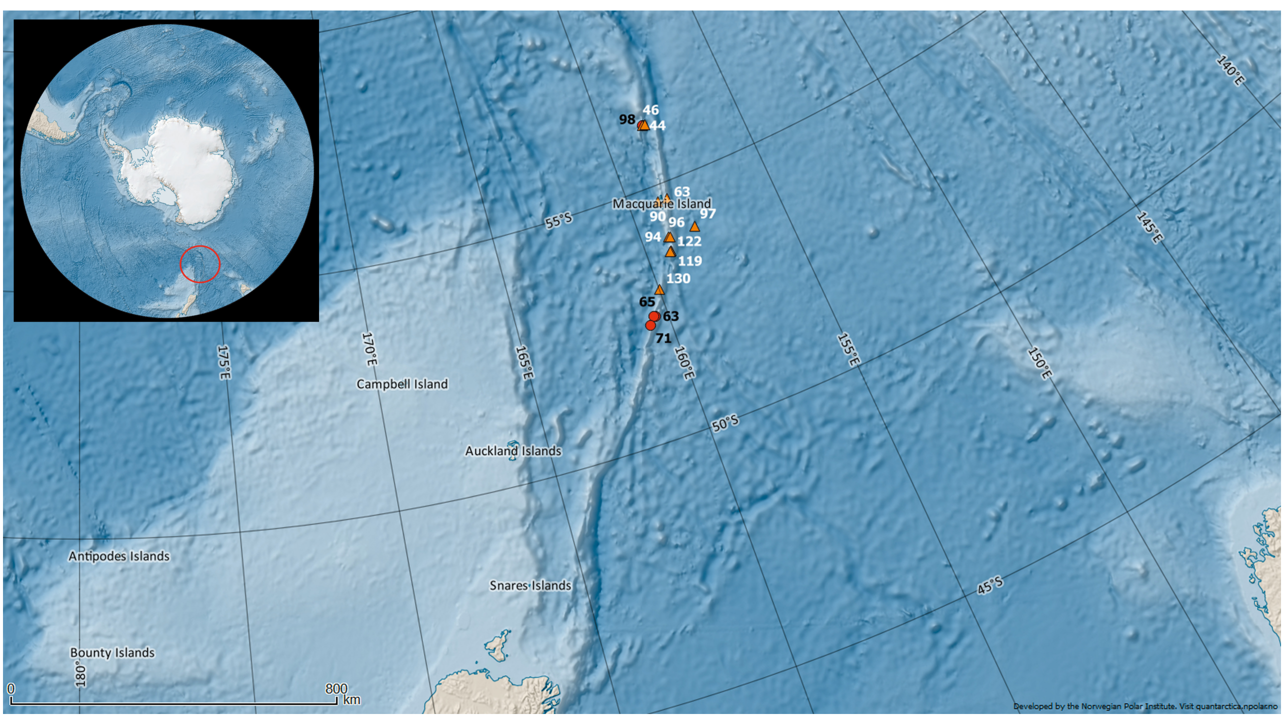

Fig. 1. Area of study and location of the sampling stations of the present study (see Table 1 for more details), represented with circles, and those surveyed by Watson (2003), indicated with triangles and white numbers.

Table 1. Station data

Station	Date	Latitude (S)	Longitude (E)	Depth (m)	Locality
63	09/04/2008	52.48733–52.48383	160.415–160.40916	350–560	Seamount 6
65	09/04/2008	52.497–52.49916	160.48916–160.49183	119–125	Seamount 6
71	09/04/2008	52.34416–52.344	160.68133–160.68766	488–542	Seamount 6
98	16/04/2008	56.24633–56.2415	158.50566–158.515	676–750	Seamount 9 Hjort

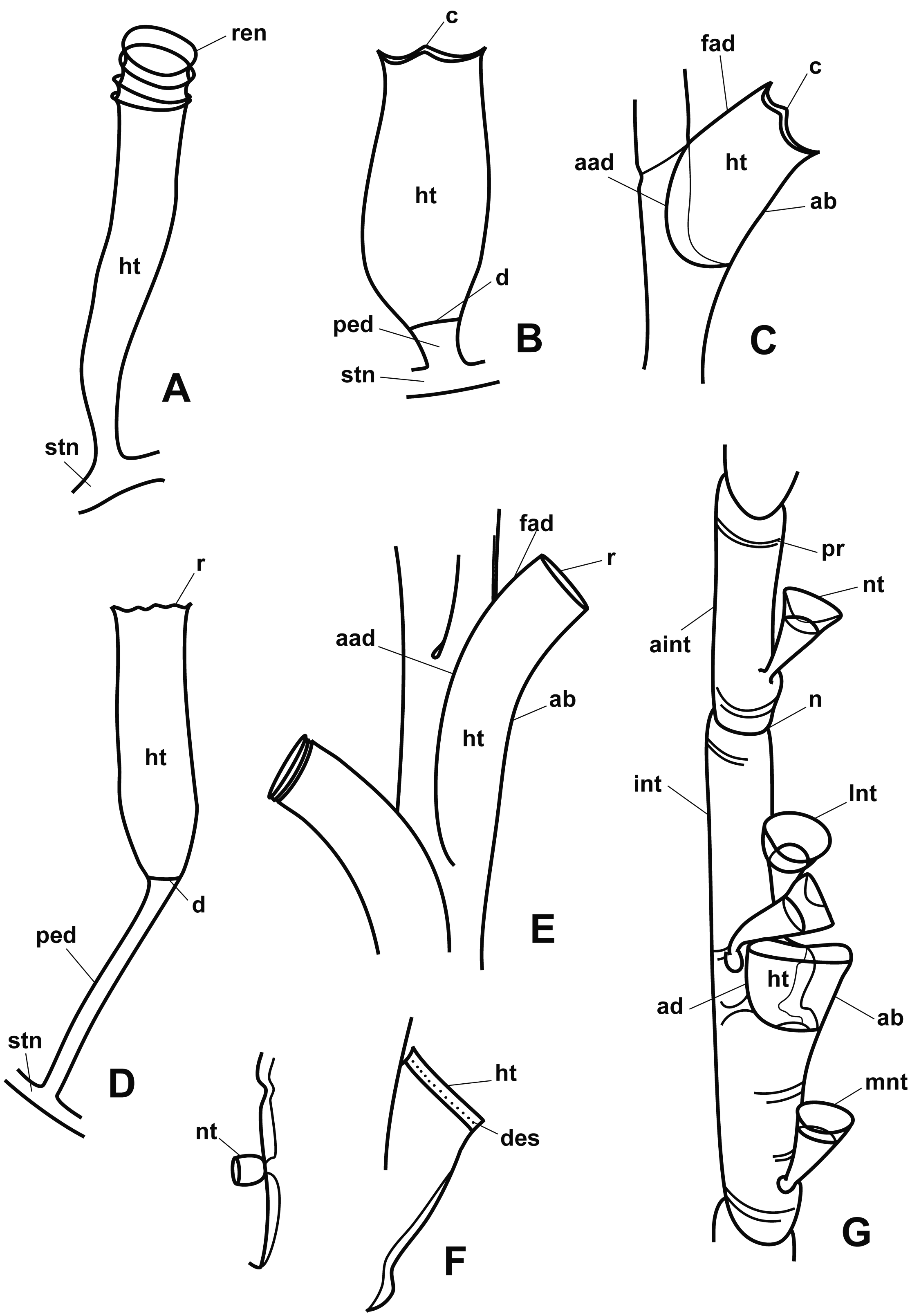

Fig. 2. Types of hydrothecae found in the collection studied and their main morphological characters. Abbreviations: aad, adnate adcauline wall; ab, abcauline wall; ad, adcauline wall; aint, ahydrothecate intermediate internode; c, cusp; d, diaphragm; des, desmocytes; fad, free adcauline wall; ht, hydrotheca; int, internode; lnt, lateral nematotheca; mnt, medial infrahydrothecal nematotheca; n, node; nt, nematotheca; ped, pedicel; pr, perisarc ridge; r, rim; ren, renovation; stn, stolon.

RESULTS

TAXONOMY

Key for the identification of the species found in the studied collection

1. Definite hydrothecae present (Leptothecata) (Fig. 2) 2
- Definite hydrothecae absent (Anthoathecata) ..... *Eudendrium* sp.
2. Colony exclusively stolonal (Fig. 2A–B) 3
- Colony with erect stems 4
3. Without hydrothecal pedicel, rim of hydrothecal aperture even ... . *Filellum liberum* sp. nov. (Fig. 2A)
- With hydrothecal pedicel, rim of hydrothecal aperture with 4 cusps .... *Calamphora quadrispinosa* (Fig. 2B)
4. Without nematothecae (Fig. 2A–E) 5
- With nematothecae (Fig. 2F–G) 10
5. Rim of hydrothecal aperture with cusps (Fig. 2C) 6
- Rim without cusps, tubiform hydrotheca (Fig. 2E) 7
6. Rim with 4 cusps .... *Sertularella* sp. (Fig. 2C)
- Rim with 12 weakly marked cusps, tulip-shaped hydrotheca .... *Tulpa tulipifera* (Fig. 2D)
7. Hydrotheca relatively small, diameter at aperture less than 150 µm .... *Acryptolaria minuta*
- Diameter of hydrothecal aperture larger than 150 µm 8
8. Hydrothecae in a marked zigzag pattern, horn-shaped .... *Acryptolaria* sp.
- Hydrotheca arranged approximately in a straight line (Fig. 2E) 9
9. Hydrothecae cylindrical at free part, diameter decreasing basally at basal third, diameter at aperture 330–340 µm, nematocysts 14–15 × 4.5–6 µm .... *Acryptolaria operculata*
- Hydrotheca distinctly cylindrical, diameter constant, only slightly narrowing at basal end, diameter at aperture 160–210 µm, nematocysts 22–26 × 10.5–13 µm .... *Acryptolaria seamountensis* sp. nov. (Fig. 2E)
10. Hydrotheca much reduced, saucer-shaped, arranged alternately along branch .... *Hydrodendron* sp. (Fig. 2F)
- Well-developed hydrothecae, unilaterally arranged on one side of branch .... *Nemertesia macquariensis* sp. nov. (Fig. 2G)

Family Eudendriidae L. Agassiz, 1862
Eudendrium sp.

Material examined: Stn 98, numerous monosiphonic stems up to 70 mm high, with gonophores, in very poor condition, growing on the axis of a gorgonian (NIWA 114752).

Description: Monosiphonic stems up to 70 mm high, scarcely branched (up to second-order branches present). Perisarc dark brown, fading to light brown distally, and smooth, except for a few rings at origin of stems, branches and pedicels. No polyps present, but remnants of a few mature female gonophores observed.

Remarks: The material is unidentifiable, as it is in very poor condition, devoid of polyps and with only remnants of a few mature female gonophores. Regarding the cnidome, only a few empty capsules could be observed, some 9–10 × 3–3.5 µm and one 20 × 10 µm.

Watson (2003) reported four species of *Eudendrium* Ehrenberg from the area, only two of which have monosiphonic stems, *Eudendrium deforme* Hartlaub, 1905, with stems up to 70 mm high, and *Eudendrium macquariensis* Watson, 2003, with stems up to 7 mm high. According to this, the present material would be closer to the former.

Ecology and distribution: The material was collected from Seamount 9 Hjort, south of Macquarie Island, at a depth of 676–750 m.

Family Lafoeidae Hincks, 1868
Acryptolaria minuta Watson, 2003
(Fig. 3A)

Acryptolaria minuta Watson, 2003: 163–164, fig. 13A–C; Peña Cantero and Vervoort, 2010: 302–304, figs. 18, 30; Peña Cantero, 2020: 288, figs. 1D, 3E–F, 5G.

Material examined: Stn 98, one stem fragment 9 mm long with several hydrothecae, without coppinia (NIWA 114754).

Description: Stem fragment 9 mm long, with hydrothecae arranged alternately in two planes forming a very open angle. Hydrotheca markedly curved outwards, tubular, free part cylindrical, diameter barely dwindling basally at adnate part. Hydrotheca adnate to internode for about two-thirds of its length. Free adcauline wall strongly convex; adnate part much less so. Abcauline wall concave, but nearly straight at basal part. Hydrothecal aperture circular, directed outwards, often parallel to longitudinal axis of branch; rim even, with up to four renovations.

Measurements (in µm): *Hydrothecae*: abcauline wall 680–700, free part of adcauline wall 230–350, adnate part of adcauline wall 550–570, adcauline wall 850–860, diameter at aperture 110–130, diameter at base 80. *Cnidome* (taken with × 40): putative macrobasic mastigophores, range 17.5–20 × 7.5.

Remarks: The material consists of a single stem fragment, 9 mm long; however, the specimen corresponds well to recent descriptions of the species by Peña Cantero and Vervoort (2010) and Peña Cantero (2020). The species is well characterised by the shape and size of the hydrotheca and the size of the larger nematocysts (*e.g.*, 17–19 × 7–8 µm in Peña Cantero and Vervoort 2010).

Ecology and distribution: *Acryptolaria minuta* has been collected from depths of 300 (Peña Cantero and Vervoort 2010) to 1422 m (Watson 2003); present material from 676 to 750 m.

This species has been previously recorded north

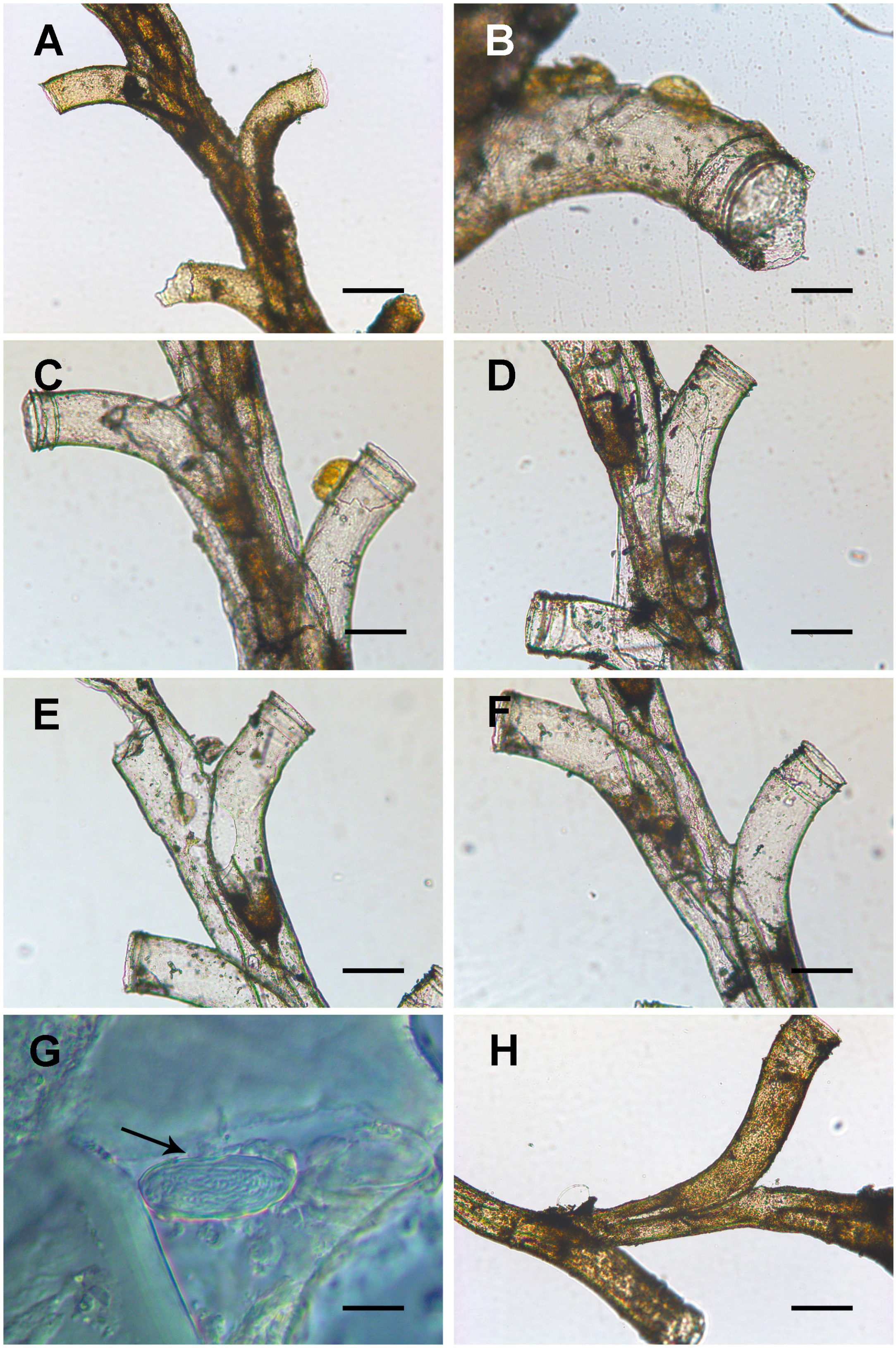

Fig. 3. *Acryptolaria minuta* Watson, 2003: A, hydrothecae. *Acryptolaria operculata* Stepanjants, 1979; B, distal part of hydrotheca. *Acryptolaria seamountensis* sp. nov.: C−F, hydrothecae and hydrothecal disposition; G, putative macrobasic mastigophore (arrow). *Acryptolaria* sp.: H, hydrothecae and hydrothecal disposition. Scale bars: A−F, H = 200 µm; G = 10 µm.

of Macquarie Island (Watson 2003), from the Loyalty Islands and Norfolk Ridge areas (Peña Cantero and Vervoort 2010) and off Antipodes Island, southeast of New Zealand (Peña Cantero 2020). The material studied here was collected from Seamount 9 Hjort, south of Macquarie Island.

Acryptolaria operculata Stepanjants, 1979
(Fig. 3B)

Acryptolaria operculata – Peña Cantero et al., 2007: 258–261, figs. 12, 16D, 18D, 19E; Peña Cantero, 2020: 288−291, figs. 1E, 6B, 7E.
Acryptolaria patagonica – Watson, 2003: 162−163, fig. 12A–C.

Material examined: Stn 71, one stem fragment 11 mm long with several hydrothecae, without coppinia, in bad condition (NIWA 114754).

Description: Stem fragment 11 mm long, with two short lateral branches. Hydrothecae arranged alternately in two planes forming an obtuse angle. Hydrotheca markedly curved outwards, fusiform, largest diameter at the middle; diameter barely decreasing toward aperture, more noticeably basally at adnate part. Hydrotheca adnate to internode for around half its length. Adcauline wall convex. Abcauline wall concave. Hydrothecal aperture circular, directed up- and outwards; rim even, with a few short renovations.

Measurements (in µm): *Hydrothecae*: abcauline wall 1400, free part of adcauline wall 900−950, adnate part of adcauline wall 700−1050, adcauline wall 1650−1970, diameter at aperture 330−340, diameter at base 180−190. *Cnidome* (taken with × 40): putative macrobasic mastigophores, 15 × 6.

Remarks: Although scarce, the material examined undoubtedly corresponds to *A. operculata* (for recent descriptions, see Peña Cantero et al. 2007; Peña Cantero 2020). This species is well characterised by the shape and large size of the hydrotheca and the small size of the nematocysts (*e.g.*, 14–15 × 4.5–5.5 µm in Peña Cantero 2020). In terms of hydrotheca size, the material studied here is closer to that of Peña Cantero (2020) from the Tasman Sea, with hydrothecae significantly smaller than his material from the southwest Atlantic.

Ecology and distribution: The species has been collected at depths between 98 (El Beshbeeshy 2011) and 4740 m (Peña Cantero 2020); present material was gathered from depths of 488 to 542 m.

Acryptolaria operculata is mainly distributed in sub-Antarctic waters, although it penetrates into Antarctic waters along part of the Scotia Arc (Peña Cantero 2020). It has been reported in sub-Antarctic waters of the southwest Atlantic: the Patagonian shelf (Stepanjants 1979; El Beshbeeshy 2011), the Burdwood Bank (Soto Àngel and Peña Cantero 2015), and the area between Staten Island (Tierra del Fuego), the Falkland Islands and South Georgia (Peña Cantero 2020). In the sub-Antarctic waters of the Pacific it has been documented in the Macquarie region (Watson 2003), New Zealand waters (Vervoort and Watson 2003) and the Tasman Sea (Peña Cantero 2020). It is also known from Antarctic waters of the Scotia Arc, from Shag Rocks to Discovery Bank (Soto Àngel and Peña Cantero 2015). Present material was collected from Seamount 6, north of Macquarie Island.

Acryptolaria seamountensis sp. nov.
(Figs. 3C−G, 4A, 5A−C)
urn:lsid:zoobank.org:act:795B3DE1-6785-4708-8C7D-3B72F08ACD79

Material examined: Stn 63, a complete stem 65 mm high, without coppinia (Holotype, NIWA 40133) and several stem fragments up to 50 mm long (Paratype, NIWA 126561).

Etymology: The specific name *seamountensis* is formed with the Latin adjectival suffix *–ensis* to indicate that the species originates from a seamount on the Macquarie Ridge.

Diagnosis: Stem polysiphonic, frequently branched. Branches practically straight. Hydrotheca cylindrical, smoothly curved outwards; adcauline wall convex, adnate over three-fourths of its length; abcauline wall concave towards the middle, practically straight at basal and distal thirds. Aperture directed outwards and upwards. Cnidome consisting of large macrobasic mastigophores and small microbasic mastigophores.

Description: Stem up to 65 mm high. Branching frequent, at least of fifth order. In some parts of the colony, mainly distal, branches alternate every third hydrotheca (*i.e.*, there are two hydrothecae between branches) and slightly disposed in two planes. Branching more irregular at basal parts (probably due to loss of branches). Branches practically straight.

Hydrothecae alternate, in one or two planes forming a very obtuse angle. Hydrotheca cylindrical; diameter constant, slightly narrowing in basal part. Hydrotheca smoothly curved outwards; adcauline wall convex throughout, adnate to internode over three-fourths of its length (adnate/free ratio 2.6−3.6); abcauline wall concave towards the middle, practically straight at basal and distal thirds. Hydrothecal aperture circular, directed upwards and outwards. Rim even, often with a few short renovations.

Measurements (in µm): *Hydrothecae*: abcauline wall 740−900, free part of adcauline wall 160−420, adnate part of adcauline wall 630−820, adcauline wall

900−1150, diameter at aperture 160−210, diameter at base 80−120. *Cnidome*: large putative macrobasic mastigophores, 23.8 ± 1.0 × 11.7 ± 0.7 (n = 12), range 22−26 × 10.5−13, small putative microbasic mastigophores 8 × 4.

Remarks: The present material cannot be assigned to any of the known species of the genus and it is therefore considered a new species to science.

Acryptolaria seamountensis sp. nov. is similar to *Acryptolaria minima* Totton, 1930 in the shape of the hydrotheca, almost completely cylindrical, with its diameter only slightly decreasing at the basal part, and with the aperture directed outwards and upwards. However, the hydrotheca is much smaller in *A. minima*, about half the size of the present species (*e.g.*, abcauline length 392–480 µm or diameter at aperture 120−136 µm, in the holotype of *A. minima*, in Peña Cantero et al. 2007). On the contrary, nematocysts are slightly longer and thinner (25.8 ± 0.8 × 9.8 ± 0.4, 25−27 × 9−10). Furthermore, in *A. minima* the abcauline wall is slightly convex at the basal part, with a clear discontinuity with the previous internode (Fig. 6A−B in Vervoort and Watson 2003 and Fig. 16B in Peña Cantero et al. 2007), whereas in *Acryptolaria seamountensis* sp. nov. the abcauline wall is straight, and essentially a prolongation of the preceding internode. Finally, Totton's species is characterized by having hydrothecae almost completely adnate to the branch (about four-fifths of their adcauline length are adnate to the internode), whereas in the present species a greater proportion of the adcauline wall is free. Vervoort and Watson (2003) assigned to *A. minima* material from Sta. BS 756 that differed from their remaining material, including type material, by "the slightly longer hydrothecae, the greater length being principally due to the longer free hydrothecal portion" (Vervoort and Watson 2003: 48). Their figures and measurements are in agreement with the present species. However, without information about the cnidome it is not possible to assign it to *Acryptolaria seamountensis* sp. nov.

The present species is also morphologically close to *Acryptolaria bathyalis* Peña Cantero and Vervoort, 2010 in the general shape of the hydrotheca: cylindrical, with a constant diameter throughout, decreasing only at its base. However, the species are clearly distinguishable because in *A. bathyalis*, the hydrotheca is markedly curved outwards and, therefore, the hydrothecal aperture is roughly parallel to the long axis of the branch, whereas in *Acryptolaria seamountensis* sp. nov., the hydrotheca is less bent and, consequently, the aperture is clearly directed upwards. In addition, the hydrothecae in *A. bathyalis* are smaller (*e.g.*, abcauline length 680−770 µm) and the nematocysts are shorter and thinner (21.6 ± 0.8 × 8.5 ± 0.4 µm) (Peña Cantero and Vervoort 2010).

Finally, *Acryptolaria seamountensis* sp. nov.

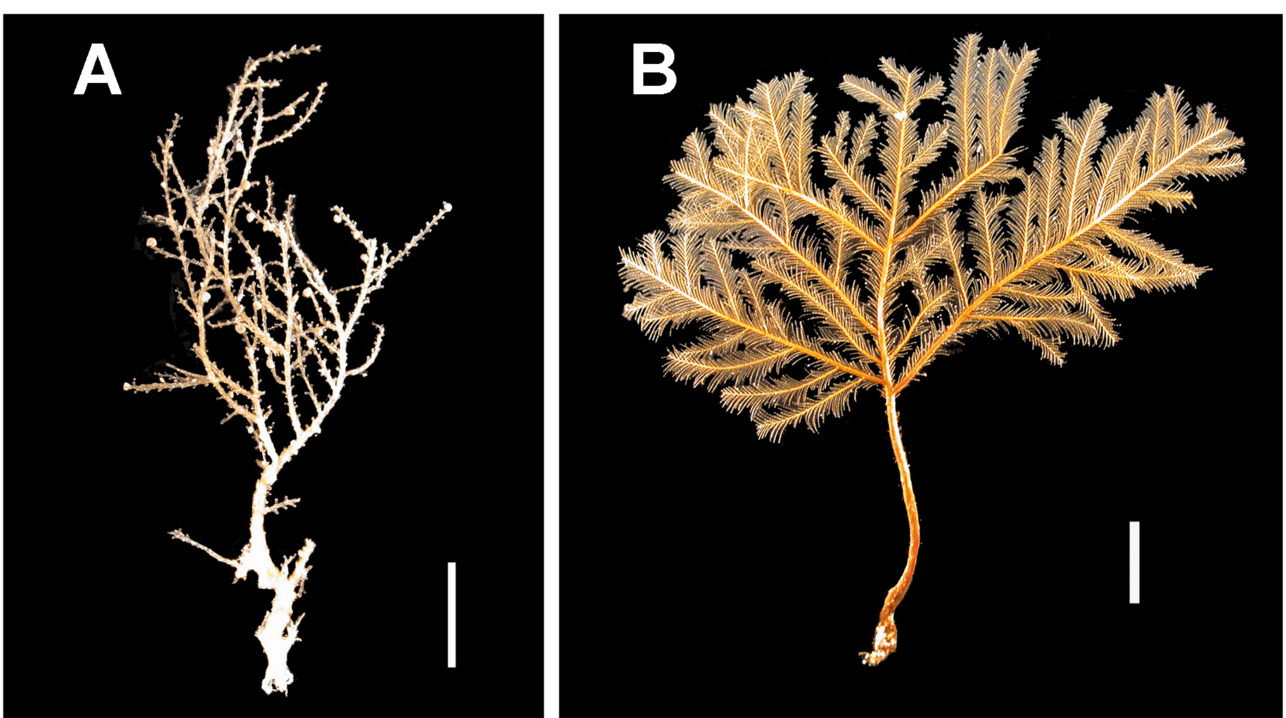

Fig. 4. Holotypes: A, *Acryptolaria seamountensis* sp. nov. (NIWA 40133); B, *Nemertesia macquariensis* sp. nov. (NIWA 40094). Scale bar = 10 mm.

agrees with the holotype of *Acryptolaria gracilis* (Allman, 1888) in the size of hydrothecae and nematocysts (23.5–26 × 9 µm), although Peña Cantero et al. (2007) were able to take measurements of only two nematocysts from the holotype. However, the shape of the hydrotheca is clearly different due to the absence in the present species of the characteristic basal bottleneck described from the holotype of *A. gracilis*. According to Peña Cantero et al. (2007: 250) "Hydrotheca tubular, cylindrical at distal half, diameter approximately constant from hydrothecal aperture to the middle of hydrothecal length, then slightly decreasing up to become more or less constant, forming a kind of bottleneck at the most basal part."

Ecology and distribution: *Acryptolaria seamountensis* sp. nov. was collected from Seamount 6, north of Macquarie Island, at depths between 350 and 560 m.

Acryptolaria sp.

(Fig. 3H, 5D–E)

Material examined: Stn 98, one stem 5 mm high with a few hydrothecae, without coppinia, on the axis of a dead gorgonian (NIWA 130063).

Description: Monosiphonic, incipient stem, 5 mm high, with six hydrothecae in a marked zigzag, arranged alternately in two planes forming an obtuse angle. Hydrotheca tubular, free part almost cylindrical, its diameter only slightly narrowing from aperture to where adcauline wall becomes adnate; more pronounced afterwards. Hydrotheca gently curved outwards. Hydrotheca adnate to internode for more than half its length. Free adcauline wall straight or slightly convex; adnate part initially convex, becoming roughly straight basally, forming a sort of bottleneck. Abcauline wall concave by the middle, practically straight at basal and distal thirds. Hydrothecal aperture circular, directed up- and outwards. Rim even, with up to four renovations.

Measurements (in µm): *Hydrothecae*: abcauline wall 770–850, free part of adcauline wall 310–450, adnate part of adcauline wall 510–530, adcauline wall 840–930, diameter at aperture 160–200, diameter at base 60–70. *Cnidome* (taken with × 40): large putative macrobasic mastigophores, range 14–17.5 × 7.5.

Remarks: The diameter of most hydrothecae gradually decreases in their adnate part until about the basal fourth, from where it remains approximately constant, forming a sort of basal bottleneck, much like that found in *A. gracilis*.

The present material agrees with *Acryptolaria corniformis* Naumov and Stepanjants, 1962 in having internodes in zigzag, in the general shape of the hydrotheca and in the size of the nematocysts. However, it differs in the size of the hydrotheca, which is significantly smaller in the present material (*e.g.*, abcauline length 1600–1900 µm and diameter at aperture 320–400 µm in the holotype of *A. corniformis*, in Peña Cantero et al. 2007), although this could be related to the fact that the material studied here consists of an incipient stem with only six hydrothecae. All previously described material of *A. corniformis* consists of four stem fragments up to 20 mm long, and therefore knowledge of this species is incomplete (Peña Cantero 2020). For example, in the material studied by Peña Cantero (2020), the smallest diameter at the hydrothecal aperture reached 270 µm, closer to that found in the present material. On the other hand, considerable variation in the size of the hydrotheca has been reported in some species of *Acryptolaria*, like *Acryptolaria angulata* (Bale, 1914) and *Acryptolaria bulbosa* (Stechow, 1932) (Peña Cantero and Vervoort 2010). However, it is important to highlight that the present material differs from the holotype of *A. corniformis* in other details. In the holotype, the branches are slightly zigzagged, whereas in the present specimen the zigzagging is more pronounced; the hydrotheca is smoothly curved outwards and the hydrothecal aperture is strongly directed upwards in *A. corniformis*, whereas in the present species the hydrotheca is more curved outwards and the aperture is less directed upwards. The scarcity of the available material and the differences indicated do not allow me to assign the present material with certainty to *A. corniformis*.

The present material is also similar to *Acryptolaria gemini* Peña Cantero and Vervoort, 2010 in the size and general shape of the hydrotheca. They differ because in *A. gemini* the branches are approximately straight, the adcauline wall of the hydrotheca is free for more than half its length and there is a sharp reduction in the hydrothecal diameter at the point where the hydrotheca becomes adnate.

The other species with a similar hydrothecal shape is *Acryptolaria longitheca* (Allman, 1877), but it has distinctly larger hydrothecae and nematocysts.

Ecology and distribution: *Acryptolaria* sp. was collected from Seamount 9 Hjort, south of Macquarie Island, at depths between 676 and 750 m.

Filellum liberum sp. nov.

(Figs. 6–8)
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Lafoea tenellula – Watson, 2003: 156–157, fig. 6A–C.

Material examined: Stn 98, numerous hydrothecae and several coppiniae, growing on *Eudendrium* sp.

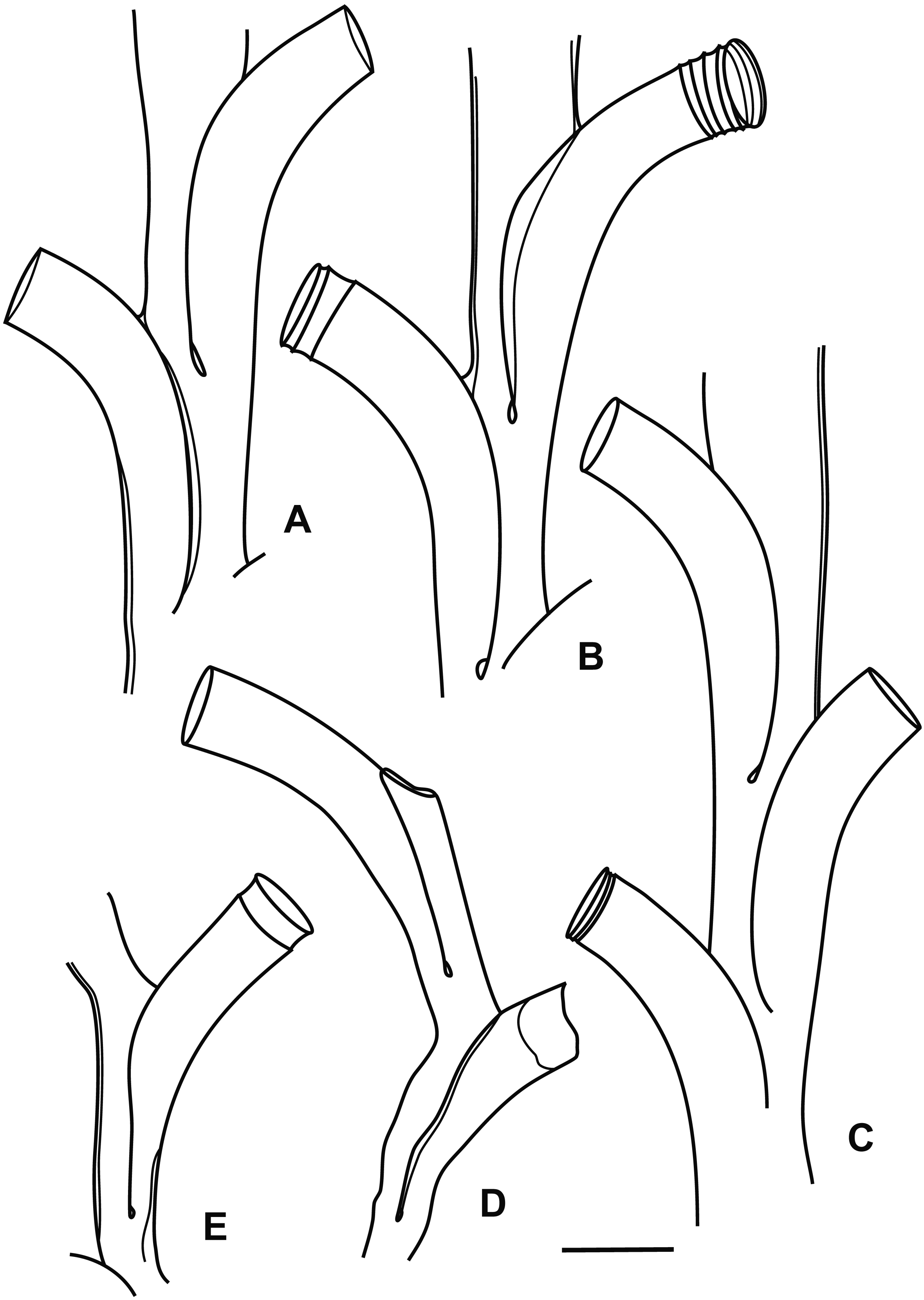

Fig. 5. *Acryptolaria seamountensis* sp. nov.: A−C, hydrothecae and hydrothecal disposition. *Acryptolaria* sp.: D−E, hydrothecal arrangement and shape of hydrothecae. Scale bar = 250 µm.

(Holotype, NIWA 40962).

Etymology: The specific name *liberum* comes from the Latin adjective 'liberum' and refers to the fact that the hydrothecae of this species are completely free from the substrate.

Diagnosis: Hydrothecae erect, tubiform, straight, curved or winding, completely free; height highly variable and diameter distinctly increasing distally; a wide band of desmocytes present at their basal part. Aperture circular; rim even, flared, often with renovations. Coppinia a fence of unforked, distally open, protective tubes surrounding and arching over closely packed gonothecae. Gonotheca flask-shaped; aperture circular, on a short distal neck markedly widening distally. Cnidome consisting of microbasic euryteles.

Description: Stolonal colony growing on *Eudendrium* sp. Stolons giving rise to erect, tubiform, straight, curved or winding, completely free hydrothecae; height highly variable and diameter distinctly increasing distally. Hydrothecal aperture circular; rim even, flared, often with renovations, increasing in diameter distally. A wide band of desmocytes present at basal portion of hydrotheca.

Coppinia with a fence of protective tubes surrounding the closely packed gonothecae and arching over them, creating a protective chamber. Defensive tubes unforked, distally open, relatively large compared to gonothecae; adjacent protective tubes coalescent with each other for part of their basal length. Gonothecae tightly packed, flask-shaped; aperture circular, on a short distal neck markedly widening distally; gonothecal shape becoming irregular towards the vicinity of protective tubes.

Measurements (in µm): *Hydrothecae*: height 490–1170, height with renovations up to 1700, diameter at origin 50−100, diameter at aperture 150−190 (primary hydrotheca), diameter at aperture of lower-order hydrothecae 180−200. *Gonothecae*: height c. 200, diameter at aperture 30−50. *Cnidome*: microbasic euryteles, range 5.5−6.5 × 2.5−3.

Remarks: Coppinia forms a kind of nest, similar to that found in other species of the genus, with gonothecae surrounded by a fence of protective tubes arching over them. It can even form a disk-shaped structure around the stem of *Eudendrium* sp., much like that described for *Filellum antarcticum* (Hartlaub, 1904) (Fig. 3A in Peña Cantero et al. 2004).

The position of the band of desmocytes at the base of the hydrotheca is quite variable; in the hydrothecae examined it started at a height between 170 and 300 µm from the origin of the hydrotheca. It is important to note that the desmocytes do not form a single narrow ring, but rather a band, with a width of 100 to 250 µm.

The presence of desmocytes, which might initially be thought to be related to the free condition of the hydrotheca, is not unique to the present species. I have re-examined material of *Filellum magnificum* Peña Cantero, Svoboda and Vervoort, 2004 from Peter I Island and found that desmocytes are also present, even in hydrothecae with an adnate part, occupying a wide area of the wall in contact with the substrate.

The hydrothecae show a wide variety of shapes, with some being completely straight, others gradually curved at the distal part and still others winding along their length. As mentioned above, the diameter of the hydrotheca increases significantly distally; for example, in one of the hydrothecae the diameter was 100 µm at the origin and 160 µm at the aperture, reaching even 200 µm at the aperture of a secondary hydrotheca.

The present material seems to be conspecific with the material, also from the area of Macquarie Island, assigned to *Lafoea tenellula* Allman, 1877 by Watson (2003). *Filellum liberum* sp. nov. is, however, different from *L. tenellula*. According to Allman (1877: 12) “Hydrothecae very minute, slightly curved, contracted below into a short thick peduncle”. In the present species there is no pedicel, and instead there is a continuum along the whole structure and the basal part is very variable, being quite wide in some hydrothecae, but very narrow in others. In addition, whereas Allman indicated that the hydrothecae in *L. tenellula* are slightly curved, their shape is very variable, from straight to sinuous, in *Filellum liberum* sp. nov. It is likely that Allman’s species was actually a stolonal form of *Lafoea* Lamouroux, probably *Lafoea dumosa* (Fleming, 1820). In fact, Allman himself stated that “the form of the hydrothecae resembles that of the hydrothecae of *L. dumosa*, but the whole hydroid is more minute and delicate.” The material ascribed to *L. tenellula* by Hirohito (1995) is clearly a *Lafoea* and differs markedly from both Watson’s and the present material. According to Hirohito (1995), the hydrotheca is similar to that of *Hebella* Allman but is distinguishable by the absence of a diaphragm.

In my opinion, the present species is conspecific with Watson’s material and clearly belongs to *Filellum* Hincks. Even when the genus *Filellum* is generally characterised by having hydrothecae partially adnate to the substrate, there are species with hydrothecae with a much reduced or even absent adnate part. *Filellum bouvetensis* Marques, Peña Cantero, Miranda and Migotto, 2011 has erect and almost completely free hydrothecae and *Filellum magnificum* Peña Cantero, Svoboda and Vervoort, 2004 is characterised by hydrothecae adnate to the substrate for only a tiny part; Peña Cantero (2010), for example, studied material with hydrothecae with a much reduced, or even absent, adnate part. Completely free hydrothecae have even been observed in *Filellum antarcticum* (Hartlaub, 1904) (Fig. 2D in Peña Cantero et al. 2004).

The characteristics of the new species, *Filellum liberum* sp. nov., make it necessary to propose the following diagnosis for the genus *Filellum*, with slight modifications from that presented by Marques et al. (2011).

Lafoeidae with young and adult colonies stolonal; hydrorhiza filiform, branched, creeping on substratum. Hydrorhizal stolons giving rise directly to hydrothecae. Hydrothecae tubular, either completely free from substrate or partially sessile; hydrotheca or distal free part directed upward to varying degrees and extension. Desmocytes present. Hydranth long, a distal whorl of filiform tentacles; hypostome short, dome-shaped. Hydrothecal diaphragm, hydrothecal operculum, nematothecae and nematophores absent. Gonophores as fixed sporosacs, in gonothecae forming coppiniae. Gonothecae either closely set, with lateral walls juxtaposed, or weakly aggregated, with gonothecae isolated. Coppinia with or without defensive tubes (modified hydrothecae). Cnidome consisting mainly of heterotrichous microbasic mastigophores and/or microbasic euryteles.

The presence of completely free hydrothecae in *Filellum liberum* sp. nov. may raise questions about the differences between *Filellum* and *Lafoea*, as stolonal colonies have also been described in *Lafoea*. In my opinion, there are enough differences between the two genera to distinguish them. In *Filellum*, both juvenile and adult colonies have an exclusive stolonal structure (Marques et al. 2011), with coppiniae developing on the substrate on which the colony is growing. In *Lafoea*, colonies typically consist of erect, branched, polysiphonic stems, although occasionally juvenile colonies with a stolonal structure exist (Millard 1975). Coppiniae are specifically associated with the erect, polysiphonic stems. It appears that stolonal colonies in *Lafoea* represent the initial stages in the formation of a typical colony with erect stems. According to Schuchert (2001), erect stems are simply older. This seems to be the case in other genera of the family (Millard 1975), such as *Acryptolaria* Norman, where stolonal and pedicellate hydrothecae have been reported in several species, including *Acryptolaria conferta* (Allman, 1877) (Calder 1991) or *Acryptolaria infinita* Peña Cantero and Vervoort, 2010 and *A. operculata* (Peña Cantero and Vervoort 2010).

Filellum and *Lafoea* also differ in the presence of a pedicel. Hydrothecae in *Lafoea* are typically pedicellate, although the pedicel is sometimes absent in *L. dumosa*, in which case the hydrothecae are directly joined to the branch. In *Filellum* the hydrothecae are either partially sessile or completely free, but without a pedicel. Schuchert (2001: 69) stated about *L. dumosa*: "Even among colonies from the same locality, there are often very distinct morphotypes, mostly differing in size and shape of the hydrothecae, and presence or absence of a hydrothecal pedicel (comp. Fig. 54C). However, comparing enough material, all forms will ultimately intergrade and they are not objectively identifiable." In *Filellum* there are no intergrading morphologies; the hydrothecae never show a pedicel. In fact, in *L. dumosa*, when the hydrothecae are sessile, it is because the pedicel is absent, as shown by the position of the desmocytes, located at the origin of the hydrothecae (see Fig. 3G in Peña Cantero and Horton 2017). In contrast, in *Filellum liberum* sp. nov. desmocytes are always far above the origin of the hydrothecae (Fig. 6H), even in hydrothecae that are relatively short and could be confused with sessile hydrothecae of *Lafoea* (Fig. 6D). Furthermore, as mentioned above, desmocytes form a broad band in *Filellum liberum* sp. nov., but a narrow ring in *Lafoea*.

There are also differences concerning the cnidome. The nematocysts of *Lafoea* species include small microbasic mastigophores (Calder 2013; personal observations) and large isorhizas (Schuchert 2001; Calder 2013; Peña Cantero and Horton 2017); the latter type is absent in *Filellum* species, where only microbasic mastigophores and/or microbasic euryteles are present (Marques et al. 2011; Soto Àngel and Peña Cantero 2019). In *Filellum liberum* sp. nov. only microbasic euryteles were observed (Fig. 7E–F).

Ecology and distribution: *Filellum liberum* sp. nov. has been collected at depths from 500 to 1064 m (Watson 2003); present material between 676 and 750 m. Coppiniae in January (Watson 2003) and April (present material).

Filellum liberum sp. nov. has been found north, west and south of Macquarie Island (Watson 2003). Present material was collected from Seamount 9 Hjort, south of Macquarie Island.

Family Campanulariidae Johnston, 1836
Tulpa tulipifera (Allman, 1888)
(Fig. 9A–C)

Tulpa diverticula – Watson, 2003: 173–174, fig. 24A–D.

Material examined: Stn 98, several hydrothecae and stems up to 20 mm high, with incomplete gonothecae, growing on *Eudendrium* sp. and on the axis of a gorgonian (NIWA 131357).

Description: Stolons on substrate giving rise to long pedicels with a single distal hydrotheca or

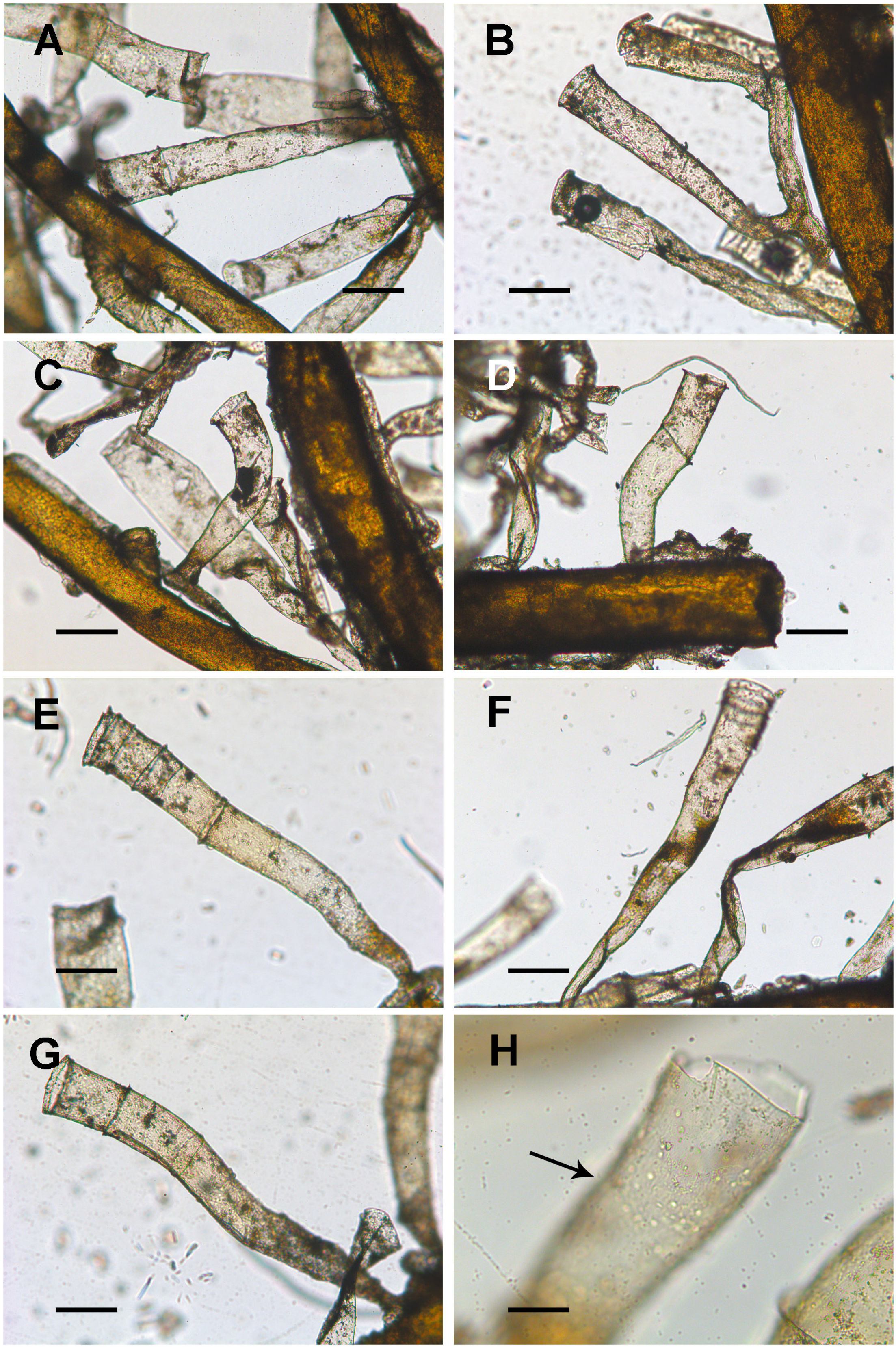

Fig. 6. *Filellum liberum* sp. nov.: A–G, different shapes of hydrothecae; H, broken hydrotheca showing desmocytes (arrow). Scale bars: A–G = 200 µm; H = 100 µm.

unbranched monosiphonic stems up to 20 mm high. Stems with one distal hydrotheca and a series of up to six hydrothecae, on short pedicels, arranged in an alternate, almost unilateral pattern; some pedicels with regeneration joints. Hydrothecae tubular, almost cylindrical, diameter increasing markedly at diaphragm, then roughly constant and finally widening at distal part; maximum diameter at aperture. Hydrothecal wall with a series of longitudinal facets fading basally. Inner hydrothecal wall with marked perisarc keels running

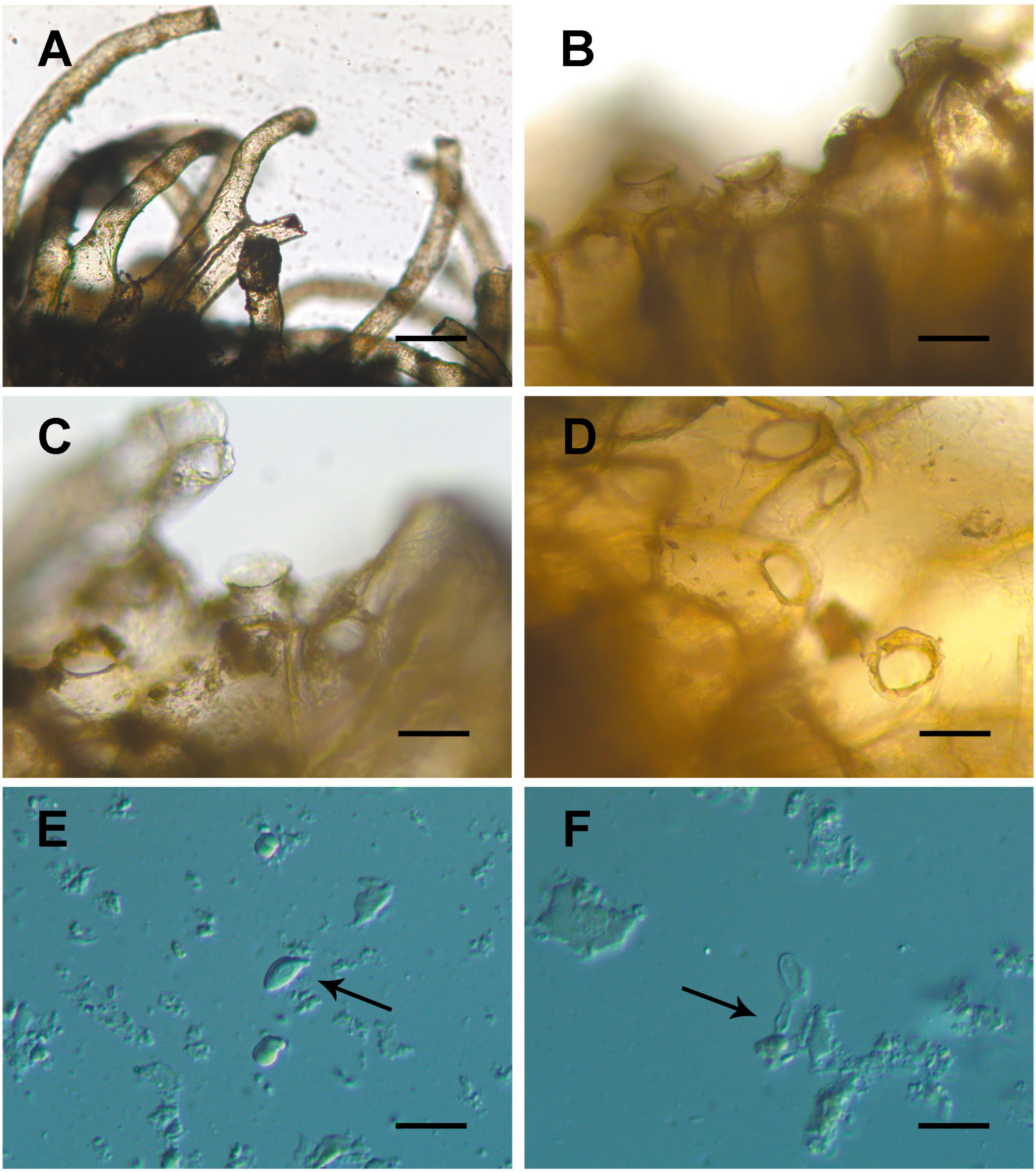

Fig. 7. *Filellum liberum* sp. nov.: A, defensive tubes of coppinia; B−D, gonothecae; E, microbasic eurytele (arrow); F, discharged microbasic eurytele (arrow). Scale bars: A = 200 µm; B−D = 100 µm; E−F = 10 µm.

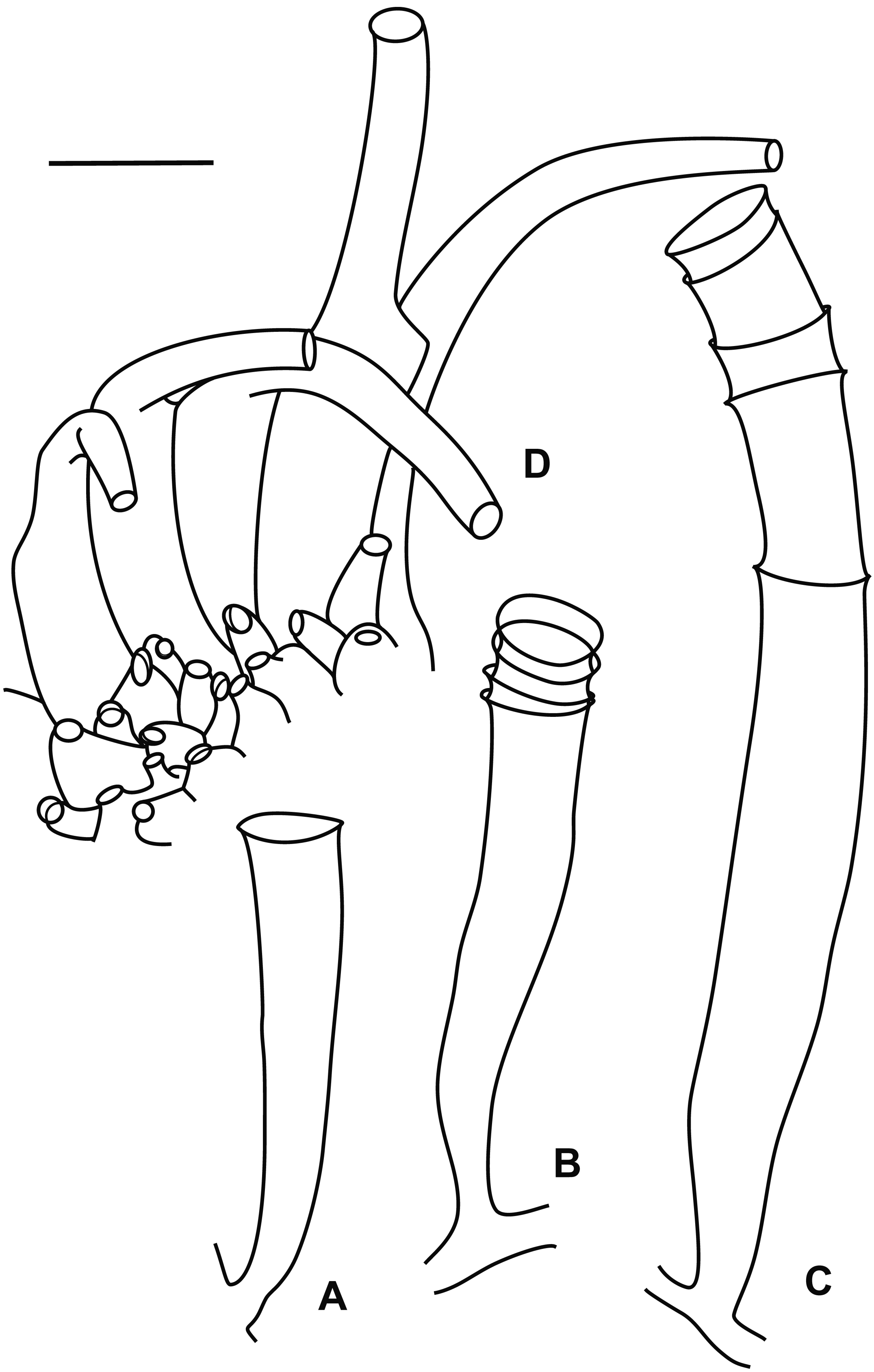

Fig. 8. *Filellum liberum* sp. nov.: A−C, hydrothecae; D, part of a coppinia showing gonothecae and defensive tubes. Scale bar = 250 µm.

down from rim. Hydrothecal aperture uneven, with 12 weakly marked cusps.

Gonothecae incomplete, conical, on both stems and stolons growing on substrate.

Measurements (in µm): *Stolon*: diameter 400. *Pedicel*: length 1200. *Hydrotheca*: height 2900–3800, diameter at aperture 960–1200, diameter at diaphragm 280–300. *Gonothecae* (incomplete): height 1300–1400, maximum diameter 700–900.

Remarks: It is my opinion that the material assigned to *Tulpa diverticulata* Totton, 1930 by Watson (2003) does not belong to Totton's species as it lacks the characteristic diverticula described by Totton (1930). Instead, it appears to be conspecific with the present material, with which it agrees in the shape and size of the hydrotheca and the presence of internal keels; according to Watson (2003: 174) "usually six to eight faint pleats extending partially or completely down into hydrotheca from embayments between crenulations."

Present material is assigned to *T. tulipifera* due to the presence of stems, the absence of diverticula, and the shape and size of the hydrotheca.

According to Bouillon et al. (2006), the classification of the Campanulariidae is unsatisfactory, and the generic divisions are not well defined, with many genera very close to each other, such as *Tulpa* Stechow and *Campanularia* Lamarck. Although they indicated that these genera, among other pairs, could be treated as synonyms without great difficulty, they kept both separate, as has been done traditionally (Totton 1930; Stepanjants 1979; Calder 1991) or more recently (Soto Àngel and Peña Cantero 2015; Oliveira et al. 2016; Cunha et al. 2017). In my opinion, *Tulpa* and *Campanularia* are easily distinguishable by the absence of a sub-hydrothecal spherule in the former. Additionally, hydrothecae of *Tulpa* species are very deep and large, typically much larger than those of *Campanularia*, and the rim of the hydrothecal aperture is undulating and turned outward, giving the hydrotheca a tulip-shaped appearance. Finally, while colonies are typically stolonal in *Campanularia*, seldom erect and branched, they are stolonal or erect and branched in *Tulpa* (Bouillon et al. 2006).

Ecology and distribution: In the area of study, *Tulpa tulipifera* has been collected at depths from 453 to 1064 m (Watson 2003, as *T. diverticulata*); present material between 676 and 750 m.

Watson (2003) reported the species north and south of Macquarie Island. Present material was collected from Seamount 9 Hjort, south of Macquarie Island.

Family Sertularellidae Maronna, Miranda, Peña Cantero, Barbeitos and Marques, 2016
Calamphora quadrispinosa Watson, 2003
(Fig. 9D–F)

Calamphora quadrispinosa Watson, 2003: 168, fig. 18.
Sertularella quadrispinosa – Galea et al. 2017: 297, fig. 15H.

Material examined: Stn 98, several hydrothecae and three gonothecae, growing on *Eudendrium* sp. (NIWA 144256).

Description: Stolonal colony with several hydrothecae and three gonothecae. Hydrothecae erect, entirely free, resting on pedicels originating from stolons. Hydrotheca tubular, sometimes slightly asymmetrical, and markedly separated from pedicel by a diaphragm. Diameter markedly increasing from diaphragm to basal third, then smoothly decreasing toward aperture, distinctly increasing again at distal end. Some hydrothecae with three to four little marked undulations. Rim of hydrothecal aperture with four little-developed cusps separated by shallow embayments.

Gonothecae on short pedicels arising directly from stolon. Gonotheca ovoid, with seven to eight marked rings and with a distal crown of four or five spines slightly curved inwards at their distal end.

Measurements (in µm): *Hydrotheca*: height 1230–1260, maximum diameter 600–680, diameter at aperture 500–520, diameter at diaphragm 240–260. *Pedicel*: length 200–400. *Gonotheca*: height 950–1000, maximum diameter 550–640.

Remarks: This study represents the second record of the species. The material examined is scarce and there was little to add to the original description (Watson 2003).

Galea et al. (2017: 297), based on Watson's (2003) description, considered this species to belong to *Sertularella* Gray "because its colonies, besides the commonest stolonal hydrothecae, comprise short, unbranched or sparingly-branched, erect stems," which is reasonable taking into account that Watson (2003) wrote "stolons … becoming free at intervals as monosiphonic stems, sometimes sparingly branched." However, Watson (2003) clearly stated that this species has stolonal colonies. I believe that the species has stolonal colonies and that the "monosiphonic stems" mentioned by Watson are simply detached stolons. Watson (2003: 169), discussing on the genera she considered, indicated that as her "material is stolonal, *Thyroscyphus* was rejected." It is therefore clear that she did not consider those free stolons as true stems. In addition, Watson (2003) herself rejected *Sertularella* because her material had no clear abcauline

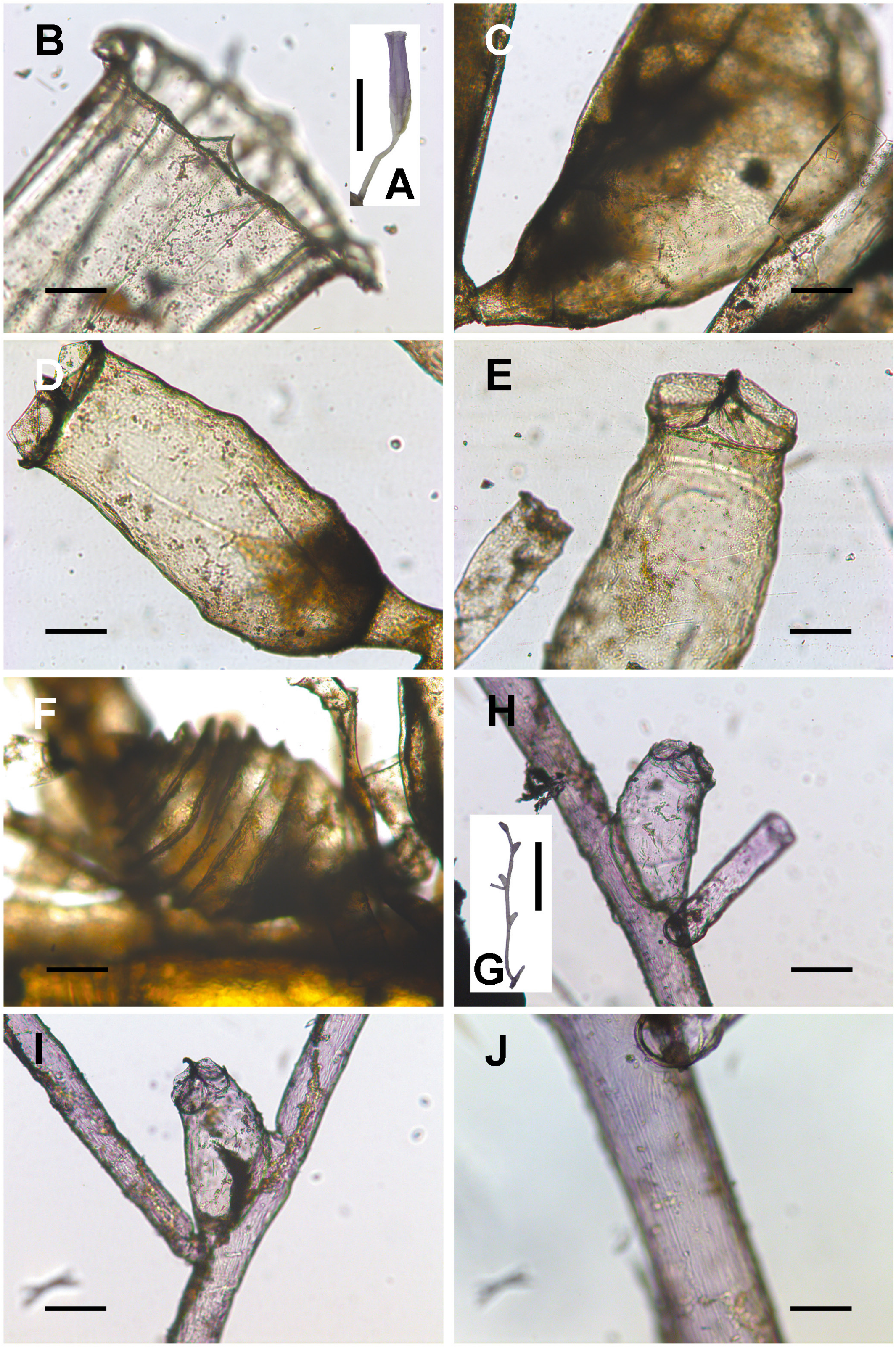

Fig. 9. *Tulpa tulipifera* (Allman, 1888): A, hydrotheca and pedicel; B, distal part of hydrotheca showing aperture; C, incomplete gonotheca. *Calamphora quadrispinosa* Watson, 2003: D, hydrotheca; E, distal part of hydrotheca showing aperture; F, gonotheca. *Sertularella* sp.: G, stem; H−I, stem fragments showing hydrothecae and origin of branch; J, fragment of stem showing longitudinal striation. Scale bars: A, G = 3 mm; B−F, H−I = 200 μm; J = 100 μm.

diverticulum. As a result, I am retaining the species in *Calamphora*, pending molecular studies to establish its precise taxonomic position.

Ecology and distribution: *Calamphora quadrispinosa* had been found at depths from 453 to 1422 m (Watson 2003); present material between 676 and 750 m. Gonothecae are known in January (Watson 2003) and April (present material).

The species has been reported from north and south of Macquarie Island (Watson 2003); present material was collected from Seamount 9 Hjort, south of Macquarie Island.

Sertularella sp.

(Fig. 9G–J)

Material examined: Stn 63, five stems up to 8 mm high, without gonothecae, growing on *Nemertesia macquariensis* sp. nov. (NIWA 144258).

Description: Monosiphonic stems with up to six hydrothecae. Stems unbranched or with only one lateral branch with up to two hydrothecae. Stems divided into long internodes by slightly marked oblique nodes; stem internodes linear, branch internodes in zigzag. Perisarc of internodes finely longitudinally striate.

Hydrothecae arranged alternately in one plane, flask-shaped, outwardly curved. Adcauline wall adnate to internode for about half its length; free part slightly convex, with two slightly marked undulations; adnate part straight or slightly convex. Abcauline wall straight, but outwardly curved in distal part. Rim of hydrothecal aperture with four equal cusps separated by shallow embayments.

Measurements (in μm): *Internodes*: length 1240–1600, diameter at hydrothecal base 180–220. *Hydrotheca*: abcauline length 370–410, free adcauline length 250–270, adnate adcauline length 250–330, adcauline length 500–580, diameter at aperture 200–220, diameter at diaphragm 100–120, maximum diameter 250–270.

Remarks: The present species differs from all the species of *Sertularella* Gray considered by Galea et al. (2017) in their revision of the genus from southern South American and sub-Antarctic waters. It belongs to the group of species with hydrothecae bent outwards, but it differs from all of them primarily by the size of the hydrotheca, which is smaller in the present material, but also by having long stem internodes arranged in a straight line. Some species in this group have polysiphonic stems and unique branching patterns. However, making direct comparisons could be misleading because the material studied here (monosiphonic stems, unbranched, or with only one lateral branch with up to two hydrothecae) may represent incipient, rather than well-developed stems. Further distinctions involve the precise shape of the hydrotheca, the adnate/free proportions of the adcauline hydrothecal wall, and the presence of internal hydrothecal cusps. Consequently, even when the material studied differs from those species in one or a combination of these characteristics, the scarcity of the available material and its infertile condition make it more reasonable not to assign a specific name to this material.

Ecology and distribution: *Sertularella* sp. was collected from Seamount 6, north of Macquarie Island, at depths between 350 and 560 m.

Family Phylactothecidae Stechow, 1921

Hydrodendron sp.

(Fig. 10)

Material examined: Stn 65, a few stem fragments up to 40 mm long, without gonothecae (NIWA 40219).

Description: Stem and branches strongly polysiphonic, with anastomoses. Only a few short hydrocladia left, with only a few hydrothecae visible. Hydrothecae on a short, usually adnate hydrophore (some with a short free part). Hydrothecae completely free, low, with a ring of desmocytes between diaphragm and aperture; abcauline wall straight, adcauline wall slightly adcaudally directed. Hydrothecal aperture circular, strongly tilted abcaudally. Secondary hydrothecae usually present, on a short hydrophore, also with ring of desmocytes, aperture circular, rim slightly everted. No nematothecae left, but their positions clearly visible. One nematophore per internode, on opposite side of hydrotheca (some internodes seem to have another on hydrothecal side). With accessory hydrothecae arising from accompanying stolons, short and completely free, with diaphragm and desmocytes.

Measurements (in μm): *Internodes*: length 480, diameter at distal node 310. *Hydrophore*: adnate part 230–260, free part 20–40. *Hydrothecae*: height 30–50, diameter at aperture 230–250, diameter at diaphragm 230–260. *Accessory hydrothecae*: height 40–50, diameter at aperture 220–230, diameter at diaphragm 210.

Remarks: Although there are no nematothecae left, their positions are clearly visible, indicating that this material belongs to *Hydrodendron* Hincks.

As mentioned above, there are short and completely free hydrothecae, provided with diaphragm and desmocytes, arising from accessory stolons, which are also present in *Hydrodendron arboreum* (Allman, 1888) (see Fig. 2A in Peña Cantero and García Carrascosa 1995).

It is not possible to assign the present material to any species of the genus. It could belong to either *H. arboreum* or *Hydrodendron tottoni* Rees and Vervoort, 1987, but the difference between these two species is not clearly established. According to Vervoort and Watson (2003), *H. tottoni* is characterised by the slanting hydrothecal rim, although the degree of tilt varies within and between colonies. They kept it separate from *H. arboreum*, suggesting that in Allman's species the hydrophore appears to be considerably elongated, with the hydrothecal diaphragm a considerable distance above the node. Vervoort and Watson (2003) also noted that in *H. tottoni* the hydrothecal rim is not perfectly flat, but is laterally curved downward to varying degrees, and that desmocytes were not observed. In the present material, the hydrotheca is clearly tilted abcaudally and the hydrophore does not project the hydrotheca beyond the distal node, bringing it closer to *H. tottoni*. However, the hydrotheca is approximately straight and desmocytes are present, which would place it closer to *H. arboreum*. Apparently, *H. arboreum* and *H. tottoni* also differ in the size of the nematotheca, as it is larger in the former. Unfortunately, this character cannot be considered here, as nematothecae are missing in the present material.

The species described by Watson (2003) as *Halecium* sp. may actually be a species of *Hydrodendron* and be conspecific with the present material. In my opinion, it is plausible that the "gonothecae" she describes are actually nematothecae. They are "on proximal part of internode opposite a hydrophore" (Watson 2003: 167), a typical position of nematothecae in *Hydrodendron* species (*e.g.*, *H. arboreum*). Watson herself described the "gonothecae" as "minute to small, base subspherical, perisarc very thin" and "arising without pedicel" (Watson 2003: 167). These features are consistent with what could be the description of a nematotheca of *Hydrodendron*. Furthermore, the width of the "gonothecae" reported by Watson, around 120 μm, is similar to that of nematothecae in *Hydrodendron* species; for instance, Peña Cantero

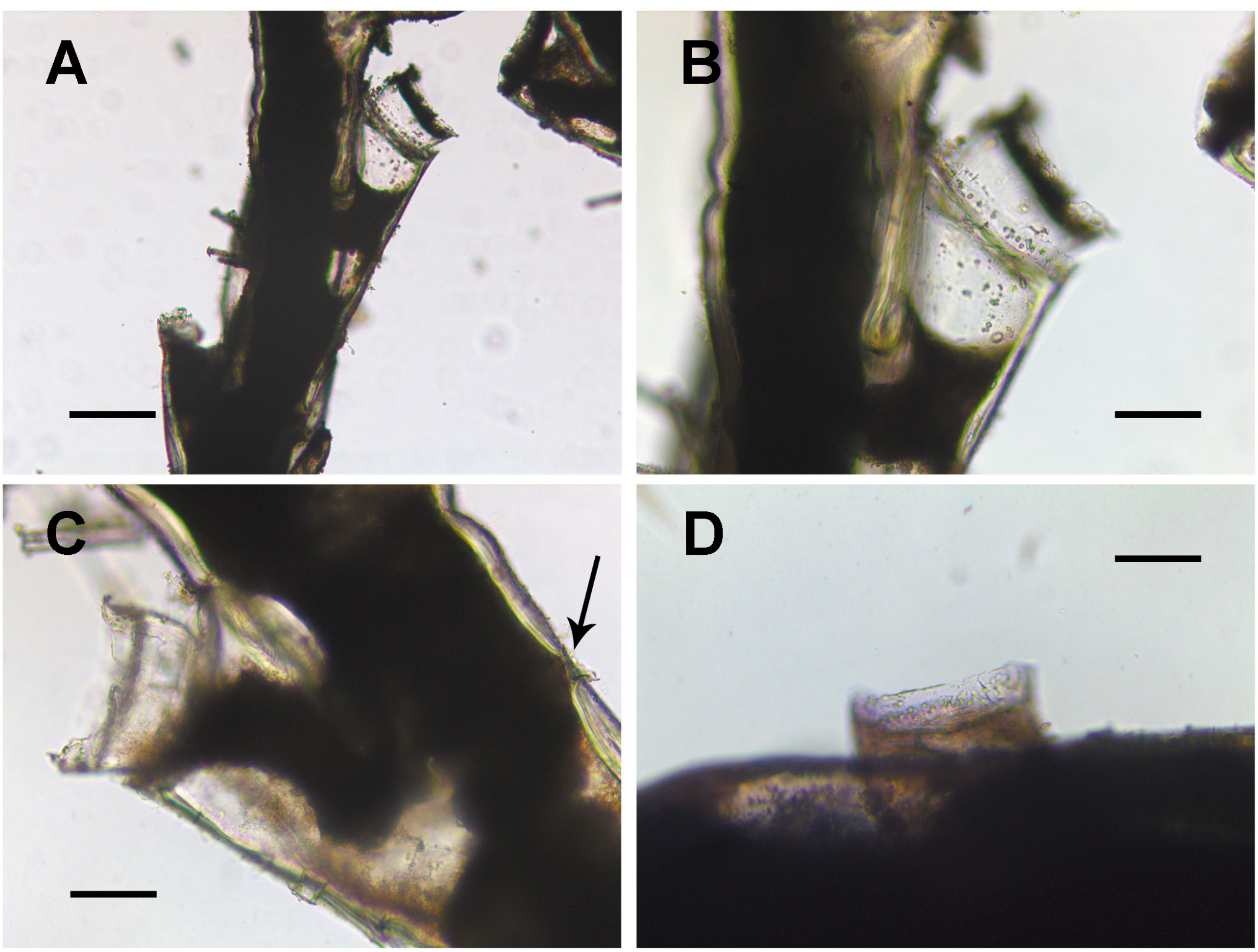

Fig. 10. *Hydrodendron* sp.: A, internode with hydrotheca; B, detail of primary and secondary hydrothecae; C, internode showing hydrothecae and position of missing nematothecae (arrows); D, accessory hydrotheca. Scale bars: A = 200 μm; B−D = 100 μm.

and García Carrascosa (1995) reported nematothecae 60−110 µm high and 50−80 µm in diameter at aperture in *H. arboreum*. Watson's material also appears to have hydrothecae originating from accessory tubes; according to her description, "hydrocladium issuing from inside a hydrotheca on peripheral tube of stem or polysiphonic tube of branch" (Watson 2003: 167).

Watson's material is similar to the present species in having hydrophores with a short free part, but differs in that they are longer and have a larger free part (304−416 µm and 56−100 µm adnate and free part, respectively) and in that the hydrotheca, opposite or just above the node, slightly widens to a weakly everted rim. In addition, Watson's material was collected at depths between 818 and 1158 m, significantly deeper than the present material (see below).

Ecology and distribution: *Hydrodendron* sp. was collected from Seamount 6, north off Macquarie Island, at depths between 119 and 125 m.

Family Plumulariidae McCrady, 1859
Nemertesia macquariensis sp. nov.

(Figs. 4B, 11−12)
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Material examined: Stn 63, one stem 120 mm high, without gonothecae (Holotype, NIWA 40094) and four stems up to 170 mm high, without gonothecae (Paratype, NIWA 144254); Stn 71, two stems, 180 and 130 mm high, without gonothecae (NIWA 40351).

Etymology: The specific name *macquariensis* is formed with the Latin adjectival suffix *–ensis* to indicate that the species originates from the Macquarie Ridge.

Diagnosis: Stems polysiphonic, planar, frequently branched. Hydrocladia on cauline apophyses arranged in decussate pairs, not at right angles, resulting in four longitudinal rows; apophyses with one mamelon (two also observed), two axial nematothecae and another pair more above mamelon. Hydrocladia divided into alternating hydrothecate and ahydrothecate internodes, starting with a hydrothecate internode. Ahydrothecate internode with a basal nematotheca. Hydrothecate internode with one hydrotheca in the middle and three nematothecae: two flanking hydrothecal aperture, and one mesial infrahydrothecal nematotheca not reaching hydrothecal base. Internode with strongly developed perisarc ridges. Hydrotheca low, about as high as wide; abcauline wall straight, directed outwards. Hydrothecal aperture circular, slightly tilted adcaudally; rim even. Nematothecae with scooped rim. Paired nematothecae of hydrothecate internodes similar to infrahydrothecal ones.

Description: Stems strongly polysiphonic, branched, up to 180 mm high and 5 mm in diameter at base. Hydrorhiza disc-shaped or rhizoidal. Stems deprived of branches for a large basal part. Branching in one plane, rather irregular, alternate in some places, sub-opposite in others; branches up to sixth order, arising from accessory tubes. Hydrocladia originating from cauline apophyses arranged in decussate pairs in X (*i.e.*, not at right angles), giving rise to four longitudinal rows. Branches divided into internodes by straight transverse nodes, with variable number of hydrocladia per internode. Hydrocladia with up to fourteen hydrothecae. Cauline apophyses with one mamelon (two also observed), two axial nematothecae and another pair more above mamelon.

Hydrocladia divided into internodes by oblique nodes, alternately hydrothecate and ahydrothecate, starting with a hydrothecate internode. Ahydrothecate internode with a basal nematotheca resting on upper side of basal swelling of internode.

Hydrothecate internode with one hydrotheca resting approximately in the middle of internode and three nematothecae: two lateral, flanking hydrothecal aperture, and one mesial infrahydrothecal resting on basal swelling of internode and not reaching hydrothecal base. Internode with strongly developed perisarc ridges: one before mesial nematotheca, one in the middle between mesial nematotheca and hydrotheca, one at base of hydrotheca, one just above hydrothecal aperture and a fifth before distal node (a sixth ridge present in some internodes just above mesial nematotheca). Ahydrothecate internodes typically with two perisarc ridges, one basal and one distal.

Hydrotheca low, about as high as wide. Abcauline wall straight, directed outwards. Hydrothecal aperture circular, slightly tilted adcaudally; rim even.

Nematothecae bithalamic; distal chamber with scooped rim. Paired nematothecae of hydrothecate internodes similar to infrahydrothecal nematothecae.

Measurements (in µm): *Cauline apophyses*: length 300–350. *Hydrothecate hydrocladial internodes*: length 330−350, diameter at hydrothecal base 75–105. *Ahydrothecate hydrocladial internodes*: length 180−200. *Hydrotheca*: abcauline length 60–90, adcauline length 50–65, diameter at aperture (frontal view) 70–90. *Lateral nematotheca*: height 80−85, diameter at aperture 50−60, diameter at diaphragm 30, height of distal chamber 20. *Mesial nematotheca*: height 70, diameter at aperture 45−50, diameter at diaphragm 30, height of distal chamber 20−25.

Remarks: The colonies are strongly polysiphonic, except for the most distal, lowest-order branches.

The internodes of stems and branches are very variable in length (some have only one pair of hydrocladia, but others up to five pairs), probably

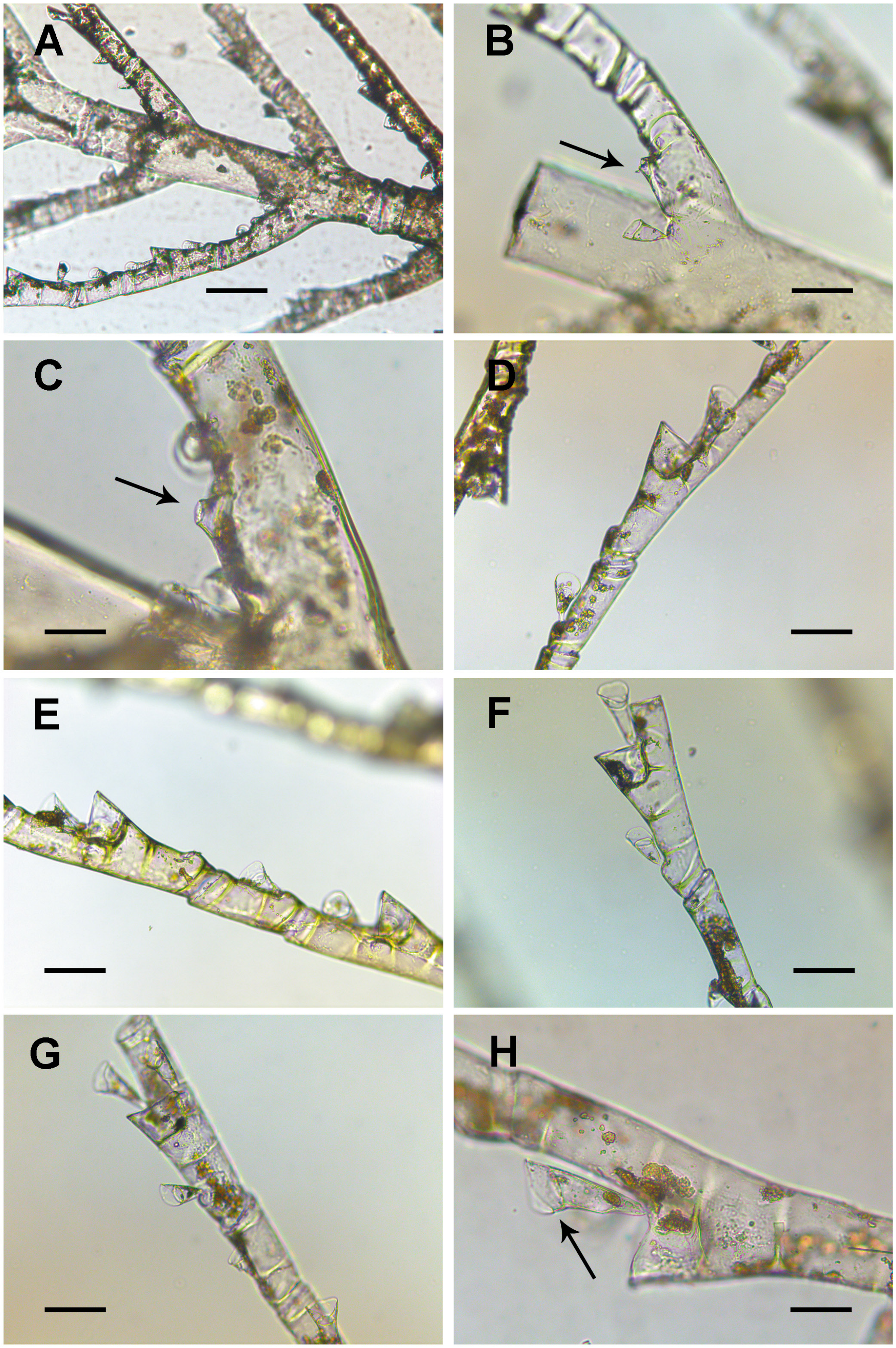

Fig. 11. *Nemertesia macquariensis* sp. nov.: A, stem fragment showing hydrocladial arrangement; B, stem fragment with cauline apophysis showing mamelon (arrow) and one axillary nematotheca; C, detail of cauline apophysis showing mamelon (arrow); D−G, hydrocladial internodes showing hydrothecae and nematothecae; H, detail of hydrotheca and nematotheca with scooped rim (arrow). Scale bars: A = 200 µm; B, D−G = 100 µm; C, H = 50 µm.

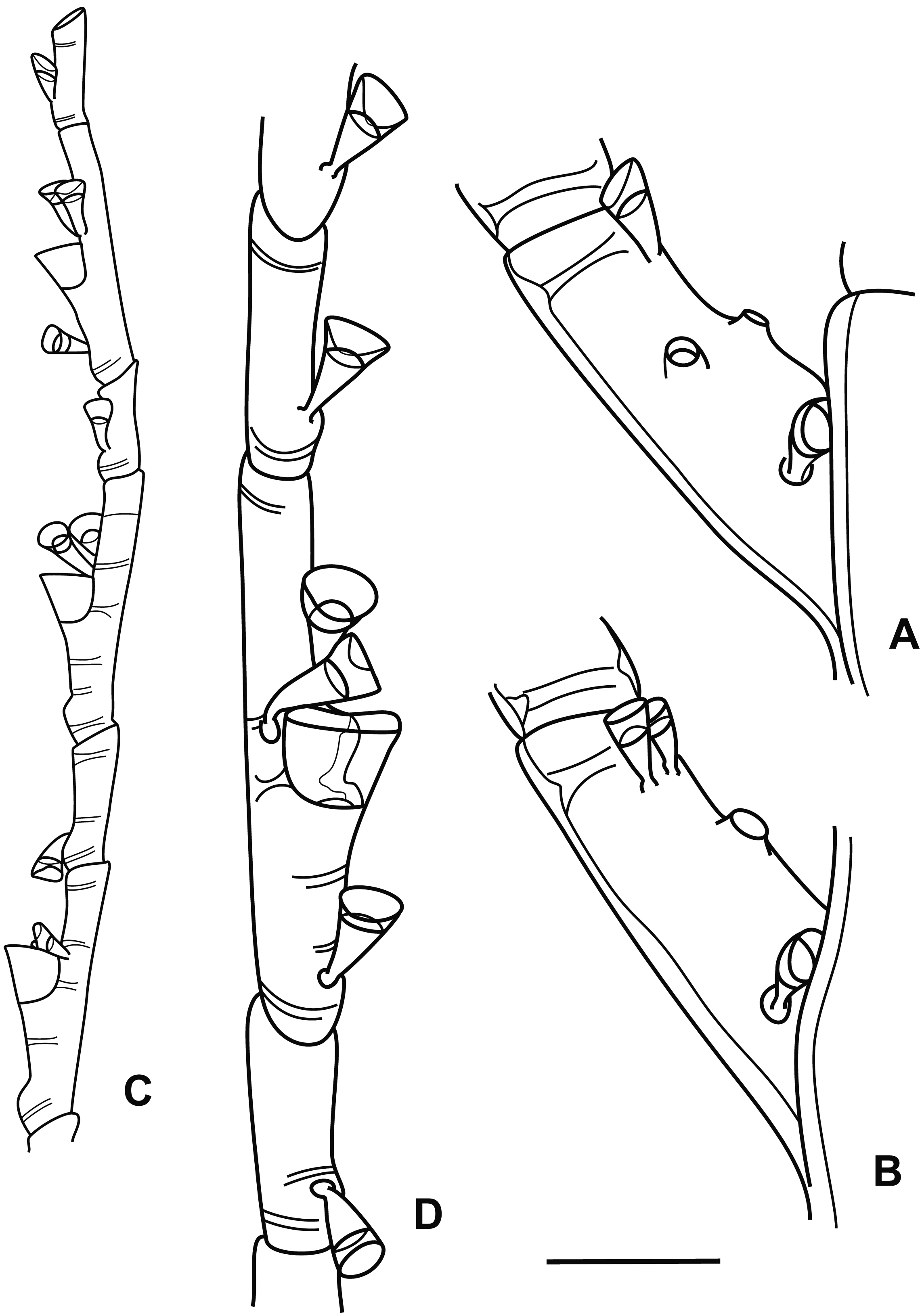

Fig. 12. *Nemertesia macquariensis* sp. nov. A−B, cauline apophyses showing mamelon and nematothecae (A with two mamelons); C−D, fragments of hydrocladia showing division into hydrothecate and ahydrothecate internodes, hydrothecae and nematothecae. Scale bars: A−B, D = 250 µm; C = 500 µm.

because they are just the result of growth interruptions, as is also indicated by the decrease in diameter (*e.g.*, from 200–210 µm at the first internode to 170–180 µm at distal one).

As mentioned above, hydrocladia originate from cauline apophyses arranged in decussate pairs which are not at right angles. Lower-order branches typically originate in the narrower sides of the X and, as a result, it is possible to observe a bilateral symmetry in the colonies, with the hydrocladia and branches confined to the laterals, and the anterior and posterior parts devoid of them, giving rise to the final planar structure of the colony.

As previously stated, branching is in one plane, but is quite irregular. In some parts of the colony it appears to be alternate, with branches widely separated, but in other parts the branches are close together and then appear to form sub-opposite pairs, yet in other parts the alternate order is reversed.

Branches, or lower-order stems, arise from accessory stolons and start with an apophysis, which may be followed by an intermediate athecate internode, and a first internode with hydrocladia at different levels and positions. The following internode already has apophyses with more or less the typical arrangement.

In the general colony shape, *Nemertesia macquariensis* sp. nov. is allied to *Nemertesia pinnatifida* Vervoort and Watson, 2003, which has a fan-shaped colony with all branches and the main stem in one plane. They also share the heteromerous division of the hydrocladia, starting with a hydrothecate internode. However, they differ in several aspects.

In *N. pinnatifida* the secondary or lower-order branches are quite short (10–20 mm long) and pinnately arranged in close opposite or sub-opposite pairs, whereas in the present species branches are longer (30 mm long) and, as mentioned above, branching is quite irregular. In *N. pinnatifida*, the number of longitudinal rows of apophyses is quite irregular, whereas in *Nemertesia macquariensis* sp. nov. the apophyses are arranged in decussate pairs in X and, consequently, the number of longitudinal rows is always four.

The number of associated nematothecae on the cauline apophyses is higher in *N. pinnatifida* (5 to 6). According to Vervoort and Watson (2003: 284), "1 or a pair may occur in the axil, 1 halfway mamelon, 1 or a pair above mamelon, and 1 on slight elevation almost at end of apophysis". In *Nemertesia macquariensis* sp. nov. there are four nematothecae, one pair at the axil and another pair above the mamelon.

The nematothecae in *N. pinnatifida* are significantly longer (height 67–100 µm) than in the present species, whereas the hydrothecae are smaller (abcauline length 34–45 µm, in Vervoort and Watson 2003). As a result, the nematothecae are very long compared to the hydrothecae in *N. pinnatifida*. In addition, the hydrotheca is located in the middle of the internode in the present species, whereas it is clearly below the middle in *N. pinnatifida*.

The species also differ in the development and number of the perisarc ridges of the hydrothecate internodes. In *N. pinnatifida*, there are incomplete septa at both ends of the internode, just above the insertion of the median inferior nematotheca and at the base of the hydrotheca. In *Nemertesia macquariensis* sp. nov., the perisarc ridges are more developed and more numerous.

Nemertesia macquariensis sp. nov. shares with *Nemertesia cymodocea* (Busk, 1851), the polysiphonic, branched stems, and the structure of the hydrocladial apophyses. They differ because in *N. cymodocea* the cauline apophyses are usually arranged in decussate verticils of three or four apophyses, although decussate pairs are also found in younger parts of the colony (Ramil and Vervoort 2006); in *Nemertesia macquariensis* sp. nov., however, there are only decussate pairs arranged in X. They also share the heteromerous division of the hydrocladia into internodes with alternating hydrothecate and ahydrothecate internodes. However, they differ because in *N. cymodocea* the first hydrocladial internode is ahydrothecate, whereas in the present species it is hydrothecate. The colony structure is also completely different, with the stem provided with long branches arising just above the base and the branches re-branching basally into long upwardly directed shoots in *N. cymodocea* (Vervoort and Watson 2003). Finally, there are biogeographical reasons, as *N. cymodocea* seems to be restricted to temperate waters.

Nemertesia macquariensis sp. nov. shares with *Nemertesia ciliata* Bale, 1914, the presence of branched and polysiphonic stems and the heteromerous division of the hydrocladia into internodes. However, in Bale's species the hydrocladia start with an ahydrothecate internode. They also differ because in *N. ciliata* the cauline apophyses are typically arranged in verticils of three or four, although decussate or even alternate pairs are also present in younger parts (Ramil and Vervoort 2006). Finally, the hydrotheca is well below the middle of the internode. The geographically closer records of *N. ciliata* are from Tasmania, New Zealand and waters around South Africa.

Ecology and distribution: *Nemertesia macquariensis* sp. nov. was collected from Seamount 6, north of Macquarie Island, at depths between 350 and 560 m.

DISCUSSION

The only previous study dealing with benthic hydroids from the Macquarie Ridge is by Watson (2003). She studied a collection gathered north, south, east and west of Macquarie Island (Fig. 1), between latitudes 53°0'S and 56°17'S and longitudes 158°30'E and 159°25'E, at depths ranging from 364 to 1422 m. In the present study, the collection was obtained between 52.34−52.49'S and 160.40−160.68'E, south of Macquarie Island, and at 56.24'S and 158.50−158.51'E, north of the island, at depths between 119 and 750 m.

Watson (2003) reported 27 species, six of which are new to science. In the present studied collection, I found 11 species, three of them new to science. Since the material assigned by Watson to *L. tenellula* is considered to be conspecific with *Filellum liberum* sp. nov., and the material assigned to *T. diverticulata* is considered to correspond to *T. tulipifera*, the number of known species in the region is increased to 32.

The occurrence of hydroids in this study was very low. With the exception of *Nemertesia macquariensis* sp. nov., which was found at two stations, all species were found at only one station. The station with the highest species diversity was Stn 98 with six species, followed by Stn 63 with three, Stn 71 with two and Stn 65 with only one species. It is worth mentioning that the last, the station with the lowest biodiversity, is the shallowest (119−125 m), while Stn 98, the station with the highest species diversity and the only station north of Macquarie Island, is the deepest (676−750 m). In Watson’s (2003) study, the station with the highest number of species (14) was also north of Macquarie Island and at a similar depth (500–600 m).

As shown above, Anthoathecata has a very low representation in the collection studied, with only one species present (*Eudendrium* sp.), representing 9.1% of the total. Leptothecata is clearly the dominant group and accounts for the remaining species diversity. In Watson’s (2003) study, Leptothecata was also dominant, but she found a greater presence of Anthoathecata (four species of *Eudendrium* and one species of *Hydractinia* Van Beneden), representing 18.5% of the total.

As seen above, Lafoeidae is by far the most diverse family in the collection studied, accounting for half of the leptothecate species. In Watson’s (2003) study, Lafoeidae was also the dominant family, with seven species (31.8% of Leptothecata). *Acryptolaria*, a genus of deep-water species, is clearly the dominant genus in the present study with four species. Watson (2003) also reported a relatively high number of species in this genus (three), but *Halecium* Oken was the dominant genus in her study with five species.

The Macquarie Ridge benthic hydroid fauna has a great originality in its species composition. Four of the six new species described by Watson (2003) are known only from this area. With the three new species described here, there are now seven species endemic to this important seafloor feature of the sub-Antarctic region.

CONCLUSIONS

The results of this study have provided new information for a better understanding of the diversity of benthic hydroids inhabiting the under-explored Macquarie Ridge. Despite the small size of the collection studied, the known species diversity of the area significantly increased, with six new records, including three species new to science, showing that the area is still very poorly known. The relatively high number of endemism also indicates the great originality of its hydrozoan fauna. Further studies are needed to better assess its benthic hydrozoan diversity and to establish its position within the framework of Southern Hemisphere marine biogeography and its role as a potential bridge between the Southern Ocean and sub-Antarctic New Zealand.

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