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Hydroids (Cnidaria, Hydrozoa) from the Vema and Valdivia seamounts (SE Atlantic)

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Abstract. In this report, we analyse the benthic hydroids collected on the Vema and Valdivia seamounts during a survey conducted in 2015 in the SEAFO Convention Area, focused on mapping and analysing the occurrence and abundance of benthopelagic fish and vulnerable marine ecosystem (VMEs) indicators on selected Southeast Atlantic seamounts. A total of 27 hydroid species were identified, of which 22 belong to Leptothecata and only five to Anthoathecata. *Monostaechoides* gen. nov. was erected within the family Halopterididae to accommodate *Plumularia providentiae* Jarvis, 1922, and a new species, *Monotheca bergstadi* sp. nov., is also described. *Campanularia africana* is recorded for the first time from the Atlantic Ocean, and the Northeast Atlantic species *Amphinema biscayana*, *Stegopoma giganteum* and *Clytia gigantea* are also recorded from the South Atlantic. Three species were identified to the genus level only, due to the absence of their gonosomes. None of the reported species are endemic, and the hydroid community is clearly dominated by species with a wide geographical distribution in the three major oceans. Only *Monotheca bergstadi* sp. nov. presently has its distribution restricted to the Vema Seamount and the South African coast.

Keywords. *Monostaechoides* gen. nov., *Monotheca bergstadi* sp. nov., new species, Hydroidolina-SEAFO.

Introduction

Seamounts are one of the most ubiquitous components and major biomes of the world oceans (Wessel 2007; Rogers 2018). Nevertheless, there is no universal definition of the term 'seamount' and, in many cases, different definitions are linked to different disciplines (Staudigel *et al.* 2010). In this way, for geologists, seamounts are seabed elevations exceeding 1000 m (Rogers 1994; Wessel 2007; Clark *et al.* 2011), but Pitcher *et al.* (2007), in a more ecological or functional approach, includes any topographically

distinct formation elevated at least 100 m above the seafloor in this concept, a definition widely accepted in recent literature (Hillier & Watts 2007; Consalvey *et al.* 2010; Yesson *et al.* 2011; Rogers 2018). Linked to these different interpretations, the estimated number of seamounts is also highly variable, ranging from around 10 200 (Harris *et al.* 2014) to 68 700 (Costello *et al.* 2010) large seamounts, and up to 25 million in the global ocean when elevations of ≤ 100 m are taken into account (Wessel *et al.* 2010).

Some historical seamount paradigms, such as the concept of isolated submarine islands, hotspots of biodiversity and endemism centres, were challenged by the information discovered over the last few years by the CenSam program (The Census of Marine Life on Seamounts) (Clark *et al.* 2012; Stocks *et al.* 2012). Nevertheless, seamounts represent unique environments for the deep-sea megabenthos (Samadi *et al.* 2007; Rowden *et al.* 2010; Clark *et al.* 2012) and host resident populations of demersal fish. They also attract top-predators such as sharks, pelagic fish, marine mammals and seabirds (Roberts 2018 and references therein). In addition, despite the fact that seamount biodiversity still remains unknown or poorly understood (Rowden *et al.* 2010; Clark *et al.* 2012), it is well documented that many seamounts are inhabited by vulnerable marine ecosystems (VMEs) that can easily be impacted by human activities (Bergstad *et al.* 2019b).

Taking into account that seamounts are increasingly exploited and continue to be fished globally (Clark *et al.* 2012), the protection and conservation of seamount ecosystems became an international concern over the last few years, especially for international organisations, such as the United Nations General Assembly and RFMOs (Regional Fisheries Management Organisations). In this way, and supported by the FAO (Food and Agriculture Organisation of the United Nations) and SEAFO (South East Atlantic Fisheries Organisation), a 29-day research cruise on board R/V *Dr Fridtjof Nansen* was conducted in January–February 2015, which aimed at mapping and analysing the occurrence and abundance of benthopelagic fish and sessile epibenthos on selected Southeast Atlantic seamounts. This region harbours hundreds of nearly unstudied seamounts with little available data, which is mainly focused on fisheries resources but lacks information on benthic communities (Bergstad *et al.* 2019b). The only exceptions are the Vema Seamount, where detailed benthic research was conducted in 1964 (Simpson & Heydorn 1965; Mallory 1966; Berrisford 1969), and the Walvis ridge area, where several Spanish fisheries surveys were also conducted, including the study of some benthic taxa (Macpherson 1984; Alvà & Vadon 1989; Gili *et al.* 1989; Zibrowius & Gili 1990; López Abellán & Holtzhausen 2011).

Benthic hydroids are a common and ubiquitous representative of the sessile epibenthos, even within the seamount communities. Nevertheless, there are few research studies focusing specifically on seamount hydroids other than stylasterids (Calder 2000). These include those conducted on the Vema Seamount (Millard 1966), the Lusitanian banks (Ramil *et al.* 1988), three seamounts near Bermuda (Calder 2000), the Tasmanian seamounts (Watson & Vervoort 2001), and the peaks of Ormonde and Gettysburg at the Gorringe Bank (NE Atlantic) (Moura 2015).

In this paper, we provide new information on the Southeast Atlantic hydroid fauna, based on the study of samples collected from the Vema and Valdivia seamounts during the cruise of the R/V *Dr Fridtjof Nansen*, carried out in 2015 in the SEAFO Convention Area. Data on bathymetry, substrate and fishing areas (Bergstad *et al.* 2019a) and megabenthos and benthopelagic fish (Bergstad *et al.* 2019b) obtained in the same cruise are already available.

Material and methods

A total of five southeastern Atlantic seamounts, namely Schmitt-Ott, Wüst, Vema, Valdivia and Ewing, were explored during the cruise (Fig. 1). The sampling program included, at each seamount, multibeam echosounder mapping, hydrographic surveys with a CTD profiler, visual observations of benthic megafauna using a 'CAMPOD' towed video rig, and biological sampling activities using bottom and

midwater trawls for fish and other megafauna, and a van Veen grab for benthic invertebrates in soft bottoms. A more detailed description of sampling methodology can be found in Bergstad *et al.* (2019a, 2019b). Hydroid samples were obtained from 11 stations located at Vema and Valdivia seamounts during trawl and grab operations. In addition, some colonies were also collected from the CAMPOD video rig at three diving stations, after accidental encounters with old pot ropes. In each case, hydroids were carefully sorted onboard and preserved in 70% ethanol for further studies. Taxonomical identification was performed at the University of Cape Town during an FAO Expert Workshop on the identification of SEAFO's research cruise biological samples, and at the Marine Zoology Laboratory of the University of Vigo (Spain), following standard methodology (see Ansín Agís *et al.* 2001; Gil 2017). Measurements were always obtained from the same colony, and the range of variation for each item was based on 15 measurements. Nematocysts were studied in temporary preparations. Drawings were made with a camera lucida mounted on a Nikon Labophot compound microscope.

The samples collected during the cruise were labeled (SEAFO-2015-XXXX) and sent to the IZIKO South African Museum in Cape Town, South Africa, including type material (SAMC), for conservation and curation. Some colonies, mostly as microslide preparations, are housed in the zoological collections of the University of Vigo (LZM-UV).
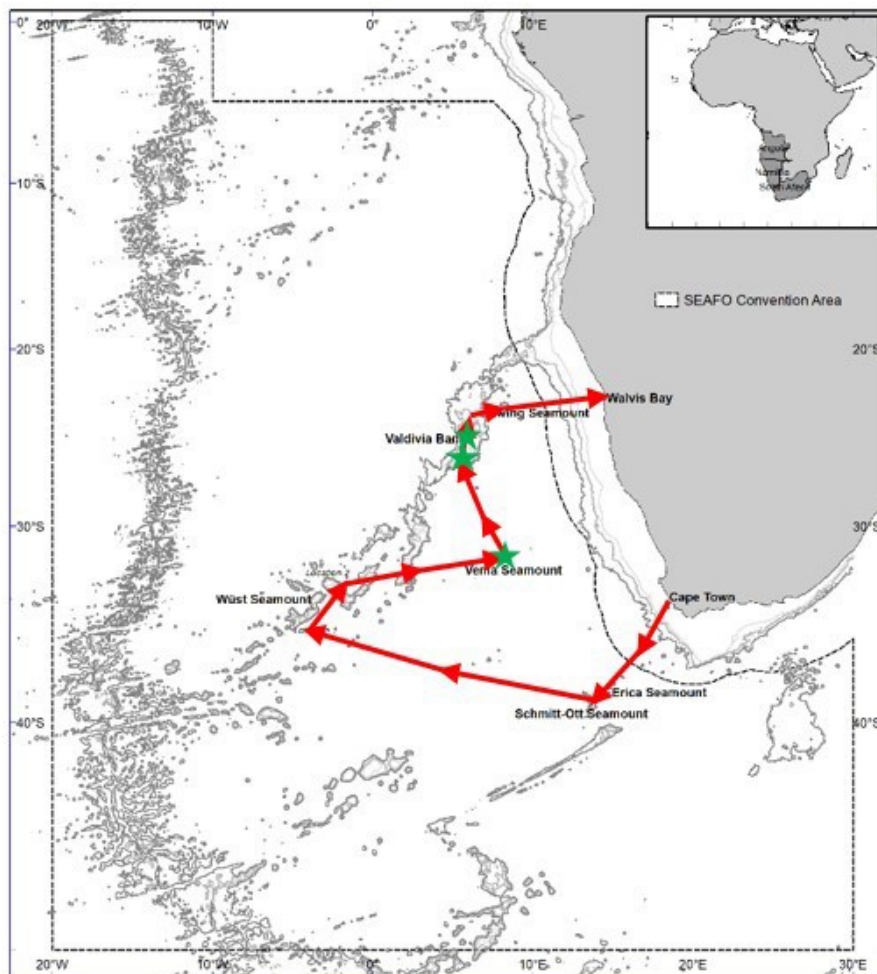

Fig. 1. Trajectory of the R/V *Dr Fridtjof Nansen* during the cruise SEAFO-2015 (in red) and the seamounts where hydroids were collected (in green).

Abbreviations

BT   =   bottom trawl
PT   =   pelagic trawl
GRAB   =   van Veen grab
LZM-UV =   Laboratorio de Zooloxía Mariña, Universidade de Vigo, Spain
Stn   =   station
SAMC   =   Iziko South African Museum Collection

Results

<div align="center">

Phylum Cnidaria Hatschek, 1888
Class Hydrozoa Owen, 1843
Subclass Hydroidolina Collins, 2000
Order Anthoathecata Cornelius, 1992
Suborder Capitata Kühn, 1913
Family Corynidae Johnston, 1836
Genus *Coryne* Gaertner, 1774

Coryne pusilla Gaertner, 1774

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Coryne pusilla Gaertner, 1774: 40–41, pl. 4 fig. 8.

Coryne pusilla – Millard 1975: 51–52, fig. 19f–g. — Schuchert 2001b: 776–780, fig. 14a–b; 2012: 134–135, fig. 142.

Material examined

SOUTH ATLANTIC OCEAN • 1 colony, with sporosacs; Vema Seamount, stn BT5; 31°37′16″– 31°36′58″ S, 8°22′37″–8°23′06″ E; 71–94 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40942 • 1 colony, with sporosacs, growing on sponge; Vema Seamount, stn Dive 5; 91–42 m depth; 1 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40191.

Remarks

Molecular studies carried out by Schuchert (2005) to explore species boundaries within the genus *Coryne* found that populations identified as *Coryne pusilla* from the Mediterranean, Japan and Korea are genetically different from the Northeast Atlantic ones. Based on these results, Schuchert (2005, 2010) indicated that *C. pusilla* appears to be a species complex, an opinion also shared by Calder (2017).

The material examined here is scarce and prevents us from giving a detailed description of the species. Nevertheless, we want to highlight that we found two size-classes of stenoteles: small (8.2–10.3 × 4.1– 5.5 µm) and large (15.1–17.6 × 10.3–11.8 µm) ones. These measurements concur with those obtained by Millard (1975) from South African material, but they are clearly inferior to those reported from East and West Atlantic populations (see Schuchert 2001b and Calder 2017, respectively). These data suggest that the Southeast Atlantic populations of *C. pusilla* could also represent a different species.

Distribution

Coryne pusilla is considered as a circumglobal species, although the records from Madagascar and Kerguelen Islands (Millard 1975) and those from the Pacific Ocean (Millard 1975; Schuchert 2005, 2012) are considered as uncertain. It was reported from South Africa by Millard (1975). Its bathymetric range extends from the intertidal level to 100 m depth (Hirohito 1988).

Family Oceaniidae Eschscholtz, 1829
Genus *Turritopsis* McCrady, 1857

Turritopsis sp.

Turritopsis sp. – Gil 2017: 37–41, fig. 6a. — Gil *et al*. 2020: 7–8, fig. 2a.

Material examined

SOUTH ATLANTIC OCEAN • 3 colonies, up to 6 mm high, without gonophores; Vema Seamount, stn PT4; 31°39′43″–31°38′10″ S, 8°22′37″–8°23′42″ E; 50–108 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40072; SEAFO-2015-40093, SEAFO-2015-40273 • 2 colonies, without gonophores (1 growing on ascidian and 1 on a gorgonian); Vema Seamount, stn Dive 4; 91–95 m depth; 1 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40134, SEAFO-2015-40631.

Distribution

Turritopsis sp. was collected from depths of 18 to 1581 m at several localities stretching from Western Sahara to Gabon (Gil 2017).

Family Pandeidae Haeckel, 1879
Genus *Amphinema* Haeckel, 1879

Amphinema biscayana (Browne, 1907)
Fig. 2A–E

Bimeria biscayana Browne, 1907: 21–23, pl. 1 figs 4–5.

Amphinema biscayana – Schuchert 2000: 415–417, fig. 3a–e; 2001a: 21–22, fig. 11a–d; 2007: 317–319, fig. 51.

Material examined

SOUTH ATLANTIC OCEAN • 3 colonies, 23–30 mm high (1 with medusa buds); Valdivia Seamount, stn BT12; 24°49′01″–24°47′38″ S, 6°24′40″–6°25′26″ E; 887–886 m depth; 7 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40162, SEAFO-2015-40522.

Description

Colonies up to 20 mm high, polysiphonic in their basal parts, grading to monosiphonic distally; ramified, with thick main stem and branches; axial tube surrounded by numerous, comparatively thinner, auxiliary tubes running parallel to one another (Fig. 2B, D). Branches originating from auxiliary tubes, and not from the main tube. Polyps scattered along the main stem and branches, placed at the distal end of short pedicels originating from both the main and auxiliary tubes (Fig. 2C–E); basal parts of the polyps covered by a pseudohydrotheca, ending below the tentacles; column cylindrical, with an apical, conical hypostome, surrounded by a whorl of 15–16 filiform tentacles. Nematocysts: desmonemes ($5.5–6 \times 3.5–5$ µm) and asymmetric microbasic euryteles ($6–8 \times 3.5–4$ µm).

Medusa buds given off from auxiliary tubes, far away from hydranths; almost rounded and enclosed in thin perisarcal envelope; four small bulbs are clearly differentiated distally (Fig. 2D).

Remarks

In our material, we have not observed the distal ramification of the main axis with lateral branches, as described by Schuchert (2001a). Nevertheless, other features, such as the origin of lateral branches
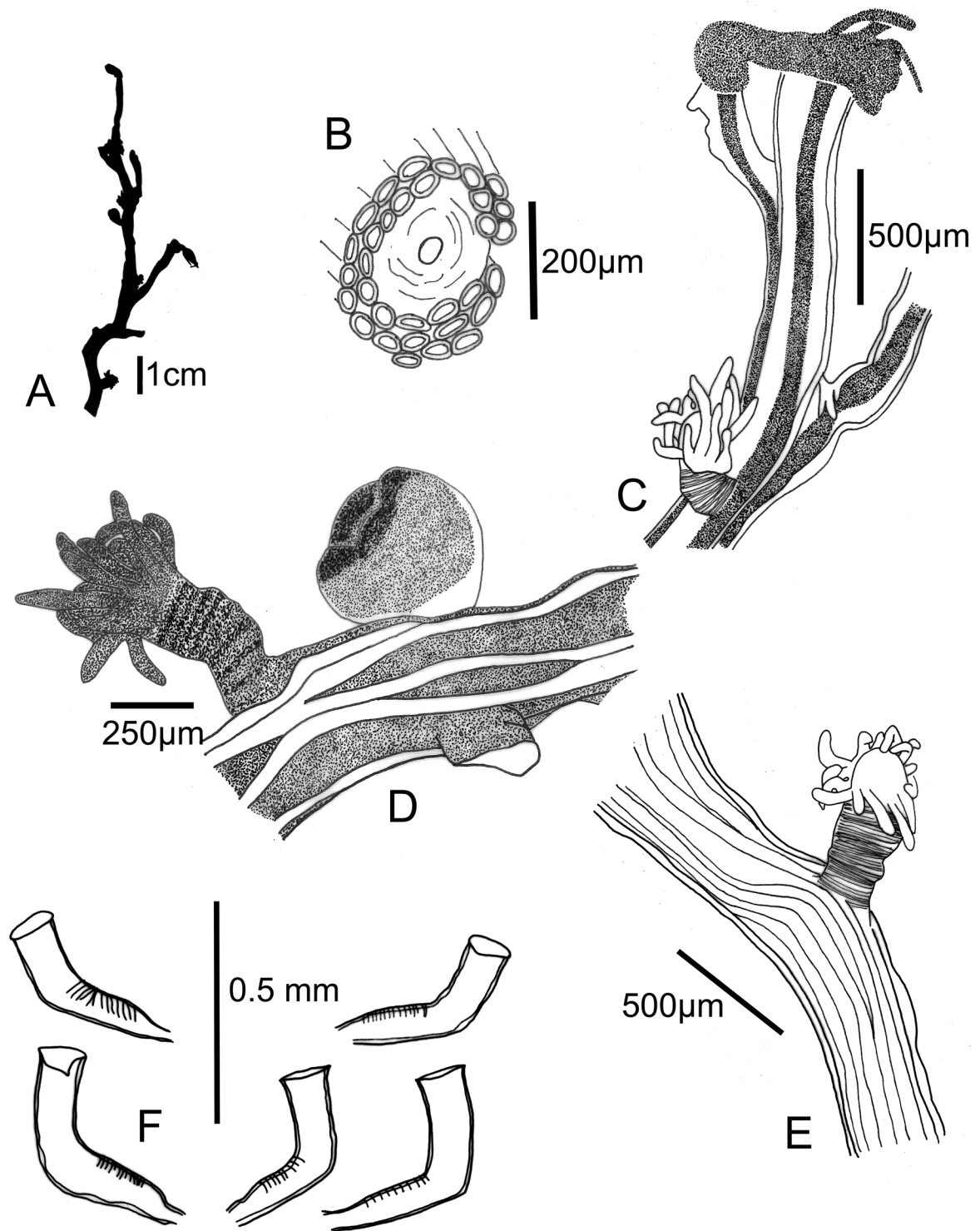
Fig. 2. **A–E**. *Amphinema biscayana* (Browne, 1907). **A**. Colony. **B**. Cross-section of the main stem. **C**. Part of branch with polyps. **D**. Part of branch with polyp and medusa bud. **E**. Part of main stem with polyp. — **F**. *Filellum* sp., several hydrothecae.

from auxiliary tubes, the morphology and type of nematocysts, as well as their measurements, concur with observations made by Schuchert (2000, 2001a) and, consequently, we identified our material as *A. biscayana*.

Distribution

Amphinema biscayana has previously been reported from South Iceland (Schuchert 2000) and the Bay of Biscay (Browne 1907, as *Bimeria biscayana*). Its bathymetric distribution ranges from depths of 20 to 2076 m (Schuchert 2000, 2001b).

Our discovery is the first record of this species for South Atlantic waters.

Genus *Leuckartiara* Hartlaub, 1914

Leuckartiara octona (Fleming, 1823)

Geryonia octona Fleming, 1823: 298.

Leuckartiara octona – Millard 1975: 123–125, fig. 41a–d. — Schuchert 2012: 251–252, fig. 232.

Material examined

SOUTH ATLANTIC OCEAN • 1 colony, without gonophores; Valdivia Seamount, stn GRAB14B; 26°15′38″ S, 6°16′37″ E; 451 m depth; 5 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40452.

Distribution

Circumglobal in subtropical and temperate waters. In the eastern Atlantic, it has been reported from the Arctic Seas (Kramp 1938) to South Africa (Millard 1975). Its bathymetric range extends from the intertidal (Millard 1975) to depths of 418 m (Gil & Ramil 2017) and 451 m (this paper).

Family Eudendriidae Agassiz, 1862
Genus *Eudendrium* Ehrenberg, 1834

Eudendrium ramosum (Linnaeus, 1758)

Tabularia ramosum Linnaeus, 1758: 804.

Eudendrium ramosum – Marques *et al.* 2000: 104, figs 75–78. — Schuchert 2012: 322–323, fig. 281.

Material examined

SOUTH ATLANTIC OCEAN • 9 colonies, 7–44 mm high (2 growing on ghost fishing net), 8 of them with gonophores; Valdivia Seamount, stn BT12; 24°49′01″–24°47′38″ S, 6°24′40″–6°25′26″ E; 887–886 m depth; 7 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40252, SEAFO-2015-40402, SEAFO-2015-40737, SEAFO-2015-40811, SEAFO-2015-40852.

Distribution

Eudendrium ramosum is considered as a cosmopolitan species by Bouillon *et al.* (2006), but many records are likely doubtful (Ramil & Vervoort 1992; Marques *et al.* 2000). Schuchert (2012) indicated that all records outside the East Atlantic (Arctic to South Africa, including the Mediterranean) need confirmation. The bathymetrical distribution of the species extends from intertidal areas (Ansín Agís 1992) to a depth of 1870 m (Ramil & Vervoort 1992).

Table 1. Measurements of *Filellum* sp., in µm.

	Filellum sp. SEAFO-2015 Stn PT4	*Filellum serratum* (in Peña Cantero *et al.* 2004)	*Filellum magnificum* (in Peña Cantero *et al.* 2004)	*Filellum antarcticum* (in Peña Cantero *et al.* 2004) Neotype
Hydrothecae, diameter aperture	100–110	ca 125	169–208	104–130
abcauline wall	340–480	ca 460	553–800	550–630
adnate adcauline wall	250–290	ca 320	208–300	240–350
free adcauline wall	180–280	ca 264	436–670	300–350
Nematocysts				
large size group	15–17.5×7.5–10	9.5–10×2–2.5	18.2×5.2	10.4–12.4×4.2–5.2
small size group	10–12.5×5–7.5	6–6.5×2.5	5.9–7.2×2.6–3.3	5.5–6.5×2.6

Order Leptothecata Cornelius, 1992
Family Lafoeidae Hincks, 1869
Genus *Filellum* Hincks, 1869

Filellum sp.
Fig. 2F; Table 1

Material examined

SOUTH ATLANTIC OCEAN • 2 colonies (1 growing on an antipatharian, 1 on *Sertularella patagonica*), no coppinia; Vema Seamount, stn PT4; 31°39′43″–31°38′10″ S, 8°22′37″–8°23′42″ E; 50–108 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40003, SEAFO-2015-40033 • 4 colonies (3 growing on *Campanularia hincksii*, 1 on a bryozoan), no coppinia; Vema Seamount, stn Dive 3; 71–935 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40132, SEAFO-2015-40257, SEAFO-2015-40921 • 1 colony, growing on *Amphisbetia distans*, no coppinia; Vema Seamount, stn Dive 4; 91–95 m depth; 1 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40661.

Description

Stolonal colonies arising from a filiform hydrorhiza creeping on other hydroids and a bryozoan. Hydrorhizal stolons give rise to small, tubular hydrothecae adnate for ca half their length; adnate part parallel to hydrorhiza, upper, free part provided with numerous and very faint striations on abcaulinar side, and bent upwards from hydrorhiza at an angle between 45° and 90°, although only occasionally perpendicular to the adnate part; aperture circular, rim even, only slightly everted; renovations have not been observed. Cnidome: two size classes of nematocysts, with small (10–12.5×5–7.5 µm) and large (15–17.5×7.5–10 µm).

Coppinia absent.

Remarks

The shape of the hydrothecae in the colonies studied herein resembles those of *Filellum serratum* (Clarke, 1879), *Filellum antarcticum* (Hartlaub, 1904) and *Filellum magnificum* Peña Cantero, Svoboda & Vervoort, 2004, due to the presence of numerous transversal striations of the adnate part. Nevertheless, the measurements of both hydrothecae and nematocysts do not match with those of the species mentioned above. In our material, the hydrothecae are smaller and the nematocysts larger than those of *F. serratum*, *F. antarcticum* and *F. magnificum*. Based on these differences, we considered this material to be a different species, but the absence of coppinia prevents us from establishing a more accurate identification.

Family Zygophylacidae Quelch, 1885
Genus *Zygophylax* Quelch, 1885

***Zygophylax* sp.**
Fig. 3A–C; Table 2

Zygophylax ? *biarmata* – Millard 1958: 176–177, fig. 4a; 1975: 193, fig. 63c.

Material examined

SOUTH ATLANTIC OCEAN • 29 colonies, 16–61 mm high (1 growing on ghost fishing net), without coppiniae; Valdivia Seamount, stn BT12; 24°49′01″–24°47′38″ S, 6°24′40″–6°25′26″ E; 887–886 m depth; 7 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40192, SEAFO-2015-40282, SEAFO-2015-40432, SEAFO-2015-40492, SEAFO-2015-40767, SEAFO-2015-40811, SEAFO-2015-40827, LZM-UV slide R. 580.

Description

Colonies branched, stems erect, with a main primary tube surrounded by many secondary tubes, grading to monosiphonic distally. Lateral hydrocladia, originating from the primary tube, monosiphonic, forming an angle of 45° in all directions around the stem, always with an axillary hydrotheca. Some branches are occasionally branched once (secondary hydrocladia). The existence of internodes in both the stem and branches was not observed. Main stem and branches with the same structure and provided with alternately disposed hydrothecal apophyses, slightly directed to the 'frontal' side of the colony (Fig. 3B). Some isolated apophyses and hydrothecae were also observed arising from secondary tubes.

Hydrothecae slightly shifted frontally, long, tubular, with the adcauline wall convex and the abcauline wall almost straight; basal part tapering below into a short pedicel, separated from hydrotheca by a slightly oblique, thin diaphragm; rim smooth, circular and slightly everted; renovations of the hydrothecal rim common and usually multiple; diaphragm occasionally renovated as well. Nematothecae inserting on small apophyses, usually one on each side of hydrotheca, but when lost, only a circular depression, corresponding to their origin, could be observed; tubular, with short, spherical pedicel; rim smooth, circular, slightly everted; renovations absent (Fig. 3C).

Variabillity

In one colony we found one hydrocladium that was polysiphonic at its basal part and distally monosiphonic.

Remarks

Our material clearly resembles *Zygophylax biarmata* Billard, 1905, but the hydrothecae are larger and, in addition, the arrangement of branches in all directions around the stem makes it easy to differentiate between species, as *Z. biarmata* presents branches that are arranged in the same plane as the main stem.

Among all species of *Zygophylax* reported from West Africa, only one, *Z. parabiarmata* Vervoort, 2006, shows the lateral branches arranged in several planes, but in this case hydrothecae are arranged in different planes as well, whereas in *Zygophylax* sp. hydrothecae are almost in the same plane. Moreover, in *Zygophylax* sp. hydrothecae are longer and narrower than in *Z. parabiarmata*.

Nevertheless, the material studied here agrees with that described by Millard (1958, 1975) as *Zygophylax* ? *biarmata* (not *Z. biarmata* Billard, 1905, see Ramil & Vervoort 1992: 60–65) in both measurements and the irregular disposition of the lateral branches around the stem, and the occasional presence of
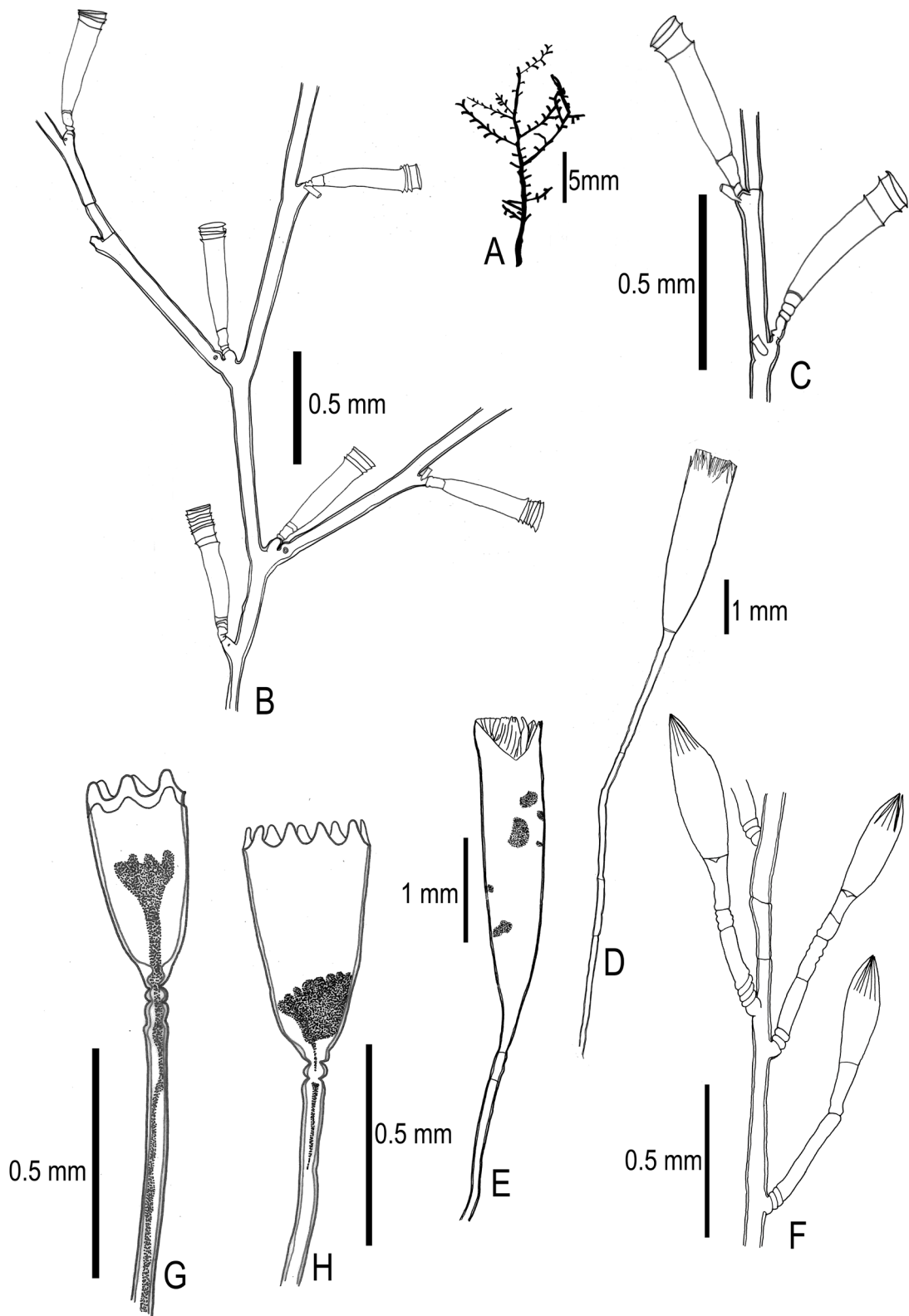
Fig. 3. A–C. *Zygophylax* sp. **A**. Colony. **B**. Distal part of colony with hydrocladia. **C**. Part of hydrocladia with two hydrothecae. — **D–E**. *Stegopoma giganteum* Ramil & Vervoort, 1992. **D**. Hydrotheca on pedicel. **E**. Gonotheca. — **F**. *Campanulina denticulata* Clarke, 1907, part of colony ramified with hydrothecae. — **G–H**. *Campanularia africana* Stechow, 1923, detail of hydrotheca, lateral view.

Table 2. Measurements of *Zygophylax* sp., in µm.

	SEAFO-2015 Stn BT12	***Zygophylax* ?*biarmata** (in Millard 1958)
Axis, distance between two consecutive hydrothecae	430–650	420–580
diameter at 'node'	40–60	70–80
Hydrothecal pedicel, length of adcauline wall	40–80	60–110
diameter of hydrothecal pedicel	40–55	–
Hydrotheca, length adcauline wall from diaphragm onwards, without renovations	375–475	310–410
Hydrotheca, length adcauline wall from diaphragm onwards, with renovations	425–500	–
Hydrotheca, length abcauline wall from diaphragm onwards, without renovations	330–425	270–350
Hydrotheca, length abcauline wall from diaphragm onwards, with renovations	400–475	–
Diameter at diaphragm	50–70	60–70
Diameter at rim	125–145	130–160
Nematotheca, length without renovations	65–85	80–140
diameter at rim	25–35	35–50

hydrothecae on secondary tubes. Consequently, we consider that all belong to the same species, but the absence of coppinia prevents us from assigning this material to a new species.

Distribution

This species has previously been recorded from off Natal, South Africa (Millard 1958, 1975, as *Zygophylax* ? *biarmata*), at depths of 164 to 333 m.

Family Tiarannidae Russell, 1940
Genus *Modeeria* Forbes, 1848

Modeeria rotunda (Quoy & Gaimard, 1827)

Dianeae rotunda Quoy & Gaimard, 1827: 181–182, pl. 6a figs 1–2.

Modeeria rotunda – Millard 1975: 137–138, fig. 45a. — Ramil & Vervoort 1992: 29–32, fig. 4a–b.

Material examined

SOUTH ATLANTIC OCEAN • 1 colony, growing on *Eudendrium ramosum*, without gonothecae; Vema Seamount, stn Dive 3; 71–935 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40708.

Distribution

Modeeria rotunda is a cosmopolitan species (Ramil & Vervoort 1992; Vervoort 2006). In the Southeast Atlantic, it was reported from Namibia (Gili *et al.* 1989) and also from the east coast of South Africa to Mozambique (Millard 1975). Its bathymetric distribution extends from 0.5 to 1575 m (Gil 2017).

Genus *Stegolaria* Stechow, 1913

Stegolaria geniculata (Allman, 1888)

Cryptolaria geniculata Allman, 1888: 41, pl. 20 figs 1, 1a–b.

Stegolaria geniculata – Ramil & Vervoort 1992: 32–34, fig. 4c–e. — Watson & Vervoort 2001: 154, fig. 2a–d.

Material examined

SOUTH ATLANTIC OCEAN • 1 colony, 10 mm high, without gonothecae; Vema Seamount, stn Dive 3; 71–935 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40648 • 54 colonies, 15–62 mm high (2 colonies growing on bivalves, 2 on ghost fishing net and 2 on ropes), 21 colonies, with gonothecae; Valdivia Seamount, stn BT12; 24°49′01″–24°47′38″ S, 6°24′40″–6°25′26″ E; 887–886 m depth; 7 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40220, SEAFO-2015-40342, SEAFO-2015-40462, SEAFO-2015-40582, SEAFO-2015-40707, SEAFO-2015-40792, SEAFO-2015-40811, SEAFO-2015-40822, SEAFO-2015-40850, SEAFO-2015-40852.

Distribution

A circumglobal species (Ramil & Vervoort 1992), widely distributed in deep waters of the Atlantic Ocean (Vervoort 2006). Its bathymetric distribution extends between 300 and 1727 m (Stepanjants 2012; Gil 2017).

Genus *Stegopoma* Levinsen, 1893

Stegopoma giganteum Ramil & Vervoort, 1992
Fig. 3D–E; Table 3

Stegopoma giganteum Ramil & Vervoort, 1992: 36–38, fig. 5e–f.

Material examined

SOUTH ATLANTIC OCEAN • 5 colonies, up to 15 mm high (1 growing on *Zygophylax* sp., 1 on bivalve shell, 1 on ghost fishing net with a gonotheca); Valdivia Seamount, stn BT12; 24°49′01″–24°47′38″ S, 6°24′40″–6°25′26″ E; 887–886 m depth; 7 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40222, SEAFO-2015-40612, SEAFO-2015-40811, SEAFO-2015-40827, SEAFO-2015-40852, LZM-UV slide R. 587.

Description

Colony composed of a thin and ramified stolon, growing attached on the hydrocaulus and branches of *Zygophylax* sp., from which arise pedicellate hydrothecae and gonothecae. Hydrothecae placed at the end of long, slender, smooth-walled and unbranched pedicels with some transversal scars due to regeneration after damage. Hydrothecae large, tubular, with smooth walls, almost bilaterally symmetrical, and slightly widening distally (Fig. 3D). Aperture closed by a triangular operculum adopting the shape of a gabled roof, formed by two opposite, semicircular sections on the distal part of the hydrothecal wall; opercular apparatus provided with longitudinal strips running downwards from top to basis. Hydranths are damaged or absent, and their description is not possible, but we can confirm that they are attached to the inner side of the hydrothecal base by means of a hyaline membranous ring, identical to the description given by Ramil & Vervoort (1992); this membranous ring indicates the boundary between the pedicel and the hydrotheca.

60

Table 3. Measurements of *Stegopoma giganteum* Ramil & Vervoort, 1992, in µm.

	SEAFO-2015 Stn BT12
Hydrotheca, length 'diaphragm-rim'	2000–3300
max. diameter	412–550
Pedicel, length	5000–10 000
diameter	110–130
Gonotheca, length	3100
max. diameter	725

The gonotheca shows similar morphology to that described for the hydrotheca, including the closing apparatus, but it is supported by a shorter pedicel (Fig. 3E).

Remarks

This is the first record of *S. giganteum* after its original description. The large size of the hydrothecae (2–3 mm long), with long and narrow pedicels, are distinctive features of this species. In addition, the opercular apparatus, the presence of a hyaline membranous ring at the attachment site of the hydrant to the hydrothecal base, and the gonothecal shape fit well with the original description of this species. Consequently, despite the wide geographical distance between the type locality and the present record, we include this material in *S. giganteum*.

Distribution

This species is only known from off Cape São Vicente (Portugal; type locality) where it was collected at a depth of 1523 m (Ramil & Vervoort 1992). This is the first record for the South Atlantic.

Family Campanulinidae Hincks, 1868
Genus *Campanulina* Van Beneden, 1847

Campanulina denticulata Clarke, 1907
Fig. 3F; Table 4

Campanulina denticulata Clarke, 1907: 12–13, pl. 8.

Campanulina denticulata – Stechow 1913: 122–123, fig. 92.
Opercularella denticulata – Vervoort 1966: 104–106, figs 4–5.

Material examined

SOUTH ATLANTIC OCEAN • 2 colonies, up to 10 mm high (1 growing on ghost fishing net) and with gonothecae; Valdivia Seamount, stn BT12, 24°49′01″–24°47′38″ S , 6°24′40″–6°25′26″ E; 887–886 m depth; 7 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40811, SEAFO-2015-40887.

Remarks

Campanulina denticulata was considered a synonym of *Earleria panicula* (G.O. Sars, 1874) by several authors (Leloup 1974; Schuchert 2003), but Calder (2012) suggested that the Atlantic *E. panicula* is a different species from the Indo-Pacific *C. denticulata*. The comparison of the material from the Valdivia Seamount with colonies of *E. panicula* collected in NW Africa showed some morphological differences, and agrees with descriptions of *C. denticulata* given by Clarke (1907) and Vervoort (1966).

Table 4. Measurements of *Campanulina denticulata* Clarke, 1907, in µm.

	SEAFO-2015 Stn BT12
Diameter of hydrocaulus	110
Length of hydrothecal pedicel	520–980
diameter of hydrothecal pedicel	40–60
Length of hydrotheca	370–480
diameter of hydrotheca	60–90

Distribution

Campanulina denticulata has an Indo-Pacific distribution (Calder 2012). Its bathymetric distribution extends from more than 500 m (Clarke 1970, as *Opercularella denticulata*) to 4040 m deep (Vervoort 1966, as *O. denticulata*).

Family Campanulariidae Johnston, 1836
Genus *Campanularia* Lamarck, 1816

Campanularia africana Stechow, 1923
Fig. 3G–H; Table 5

Campanularia africana Stechow, 1923: 104.

Campanularia africana – Leloup 1938: 13–14, fig. 9. — Millard 1975: 204, fig. 67a.

Material examined

SOUTH ATLANTIC OCEAN • 2 colonies, growing on algae, without gonothecae; Vema Seamount, stn BT5; 31°37′16″–31°36′58″ S, 8°22′37″–8°23′06″ E; 71–94 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40437, SEAFO-2015-40768, LZM-UV slide R. 577.

Distribution

Campanularia africana has previously been reported from Australia (Watson 1990), Japan (Stechow 1923; Leloup 1938; Hirohito 1995) and Natal, South Africa (Millard 1975). Its bathymetric distribution extends from the littoral area to a depth of 102 m (Millard 1975; Stechow 1925). Our finding of *C. africana* at Vema Seamount represents the first record of this species for the Atlantic Ocean.

Campanularia hincksii Alder, 1856

Campanularia hincksii Alder, 1856: 360–361, pl. 13 fig. 9.

Campanularia hincksii – Ramil & Vervoort 1992: 233–235, fig. 66. — Cornelius 1995: 229–231, fig. 52.

Material examined

SOUTH ATLANTIC OCEAN • 9 colonies, 0.5–17 mm high (2 growing on antipatharians, 1 on sponge, 1 on *Sertularella arbuscula*, 1 on *Sertularella striata*, 1 on *Turritopsis* sp.), all without gonothecae; Vema Seamount, stn PT4; 31°39′43″–31°38′10″ S, 8°22′37″–8°23′42″ E; 50–108 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40003, SEAFO-2015-40093, SEAFO-2015-40123, SEAFO-2015-40153, SEAFO-2015-40213, SEAFO-2015-40243, SEAFO-2015-40273, SEAFO-2015-

Table 5. Measurements of *Campanularia africana* Stechow, 1923, in µm.

	SEAFO-2015 Stn BT5
Hydrothecal pedicel, length	1220–1240
diameter	40–45
Hydrotheca, total depth	460–600
diameter at rim	210–310

40444, SEAFO-2015-40972 • 5 colonies, 8–12 mm high (2 with gonothecae); stn Dive 3; 71–935 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40132, SEAFO-2015-40257, SEAFO-2015-40678 • 2 colonies, without gonothecae (1 growing on *Amphisbetia distans*); Vema Seamount, stn Dive 4; 91–95 m depth; 1 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40131, SEAFO-2015-40977 • 1 colony, growing on ghost fishing net, without gonothecae; Valdivia Seamount, stn BT12; 24°49′01″–24°47′38″ S, 6°24′40″–6°25′26″ E; 887–886 m depth, 7 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40850.

Distribution

Campanularia hincksii is a circumglobal species, recorded in the eastern Atlantic from Iceland to South Africa (Peña Cantero & García Carrascosa 2002). Its bathymetric distribution extends from the tidal level to a depth of 1200 m (Peña Cantero & García Carrascosa 2002; Leloup 1940).

Family Clytiidae Cockerell, 1911
Genus *Clytia* Lamouroux, 1812

Clytia gigantea (Hincks, 1866)
Fig. 4A; Table 6

Campanularia gigantea Hincks, 1866: 297.

Clytia gigantea – Calder 2012: 46–47, figs 46–47. — Peña Cantero & Horton 2017: 13, fig. 5a–b.
Clytia sp. – Ramil 1988: 254–256, pl. XVII.

Material examined

SOUTH ATLANTIC OCEAN • 5 colonies, up to 13 mm high (2 growing on a ghost fishing net, 1 on *Stegolaria geniculata*), no gonothecae; Valdivia Seamount, stn BT12; 24°49′01″–24°47′38″ S, 6°24′40″–6°25′26″ E; 887–886 m depth; 7 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40552, SEAFO-2015-40582, SEAFO-2015-40811, SEAFO-2015-40852, SEAFO-2015-40857, LZM-UV slide R. 579.

Remarks

Despite the fact that this species is currently included in the synonymy of *Clytia hemisphaerica* (Linnaeus, 1767) (Schuchert 2020), we agree with Calder (2012) who considers *C. gigantea* as a valid species, due to the comparatively larger size of its hydrothecae, provided with linguiform cusps, an opinion that was also later shared by Peña Cantero & Horton (2017). Moreover, Ramil (1988), in his study of the hydroids of Galicia (NW Spain), described this species as *Clytia* sp., apart from *C. hemisphaerica*, based on the same features highlighted by Calder (2012). Therefore, considering that both morphological features and measurements of our colonies coincide with those given by Ramil (1988), Calder (2012) and Peña Cantero & Horton (2017), we identify this material as *C. gigantea*.
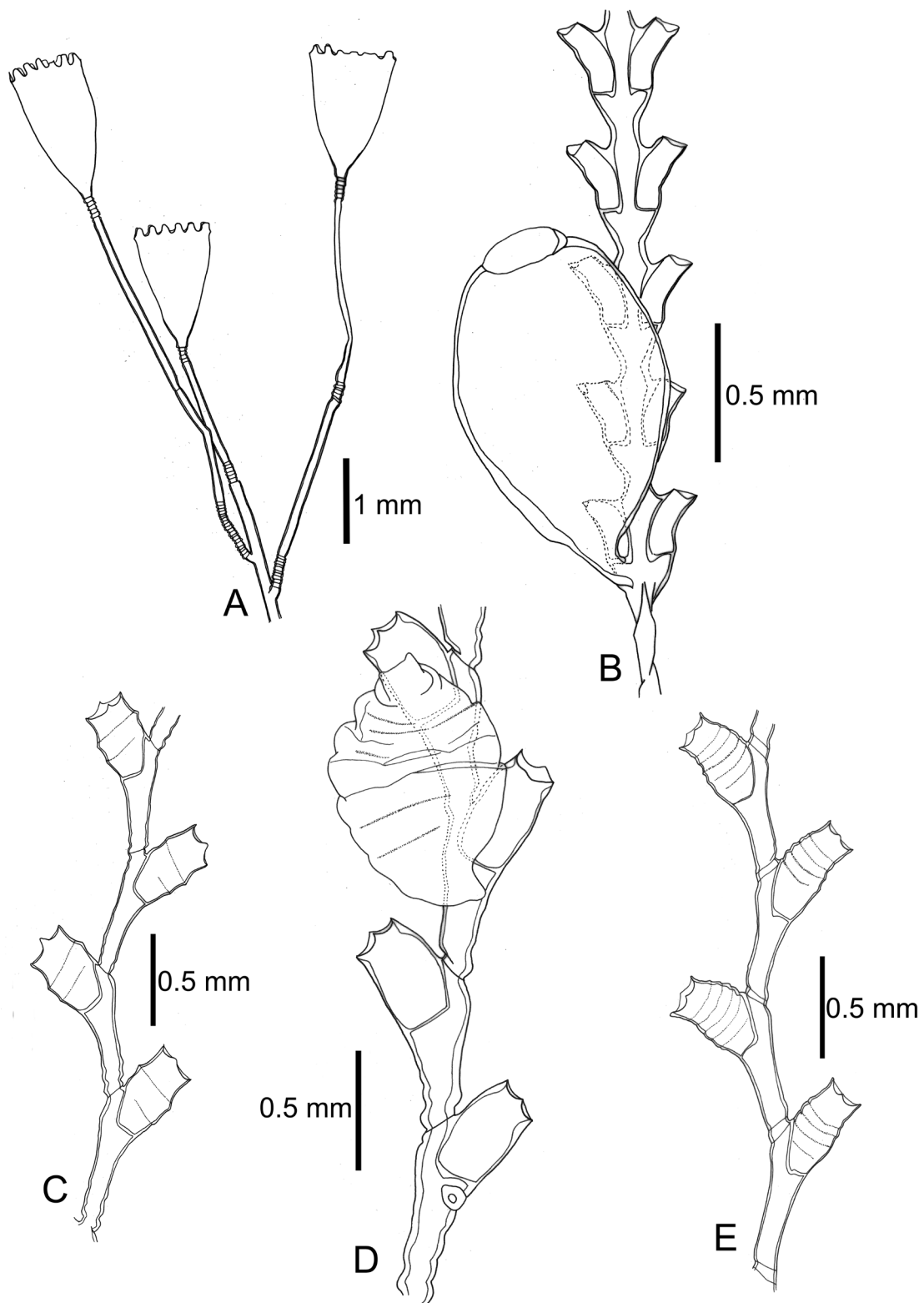
Fig. 4. A. *Clytia gigantea* (Hincks, 1866), portion of colony with three hydrothecae. **B**. *Amphisbetia minima* (Thompson, 1879), portion of hydrocladia with hydrothecae and basal gonotheca. **C**. *Sertularella areyi* Nutting, 1904, part of hydrocladia with hydrothecae. **D**. *Sertularella polyzonias* (Linnaeus, 1758), part of hydrocladia with hydrotheca and one gonotheca. **E**. *Sertularella patagonica* (d' Orbigny, 1846), part of hydrocladia with hydrothecae.

Table 6. Measurements of *Clytia gigantea* (Hincks, 1866), in μm.

	SEAFO-2015 Stn BT12
Hydrothecal pedicel, length	3200–5200
diameter	40–50
Hydrotheca, total depth	1475–1700
diameter at rim	340–390

The material studied here also resembles *C. joycei* Calder, 2019 in the hydrothecal shape; however, *C. joycei* is a shallow-water species, growing on the seagrass *Thalassia testudinum* K.D. Koening, 1805 and develops minute, stolonal colonies with comparatively smaller hydrothecae. These features typically separate *C. joycei* from *C. gigantea* (Calder 2019).

Distribution

This species has been recorded from the boreal waters of the Northeast Atlantic (Calder 2012) to Galicia, NW Spain (Ramil 1988, as *Clytia* sp.) and also from Newfoundland to Cape Cod in the West Atlantic (Calder 2012). Its presence outside the Atlantic Ocean, including the Mediterranean Sea, is considered as doubtful by Calder (2012). The records from Chile (Leloup 1974; Galea *et al.* 2009) are based on misidentifications (Galea & Schories 2012). Its bathymetric distribution extends from 20 (Calder 2012) to 950 m (Peña Cantero & Horton 2017). *Clytia gigantea* is reported here for the first time from the South Atlantic, at Valdivia Seamount.

Clytia gracilis (Sars, 1850)

Laomedea gracilis Sars, 1851: 138.

Clytia gracilis – Ramil & Vervoort 1992: 235–238, fig. 67a. — Cornelius 1995: 246–248, fig. 56.

Material examined

SOUTH ATLANTIC OCEAN • 1 colony, growing on *Campanularia hincksii*, without gonothecae; Vema Seamount, stn Dive 3; 71–935 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40132.

Distribution

Clytia gracilis is a circumglobal species in temperate and tropical waters, widely distributed in the East Atlantic, from England to South Africa (Gil 2017). Its bathymetric distribution ranges from 0 (Peña Cantero & García Carrascosa 2002) to 1443 m (Schuchert 2001a).

Family Obeliidae Haeckel, 1879
Genus *Obelia* Péron & Lesueur, 1810

Obelia dichotoma (Linnaeus, 1758)

Sertularia dichotoma Linnaeus, 1758: 812.

Laomedea (*Obelia*) *dichotoma* – Vervoort 1959: 315– 316.
Obelia dichotoma – Millard 1975: 229–230, fig. 75a–b. — Ramil & Vervoort 1992: 243–244, fig. 68c. — Cornelius 1995: 296–300, fig. 69.

Material examined

SOUTH ATLANTIC OCEAN • 2 colonies, up to 19 mm high, without gonothecae; Vema Seamount, stn Dive 4; 91–95 m depth; 1 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40020, SEAFO-2015-40131.

Distribution

Obelia dichotoma is a well-known species with a nearly cosmopolitan distribution (Cornelius 1995); it is absent from Arctic and Antarctic waters (Peña Cantero & García Carrascosa 2002). In the Southeast Atlantic, it was reported from Angola (Vervoort 1959, as *Laomedea* (*Obelia*) *dichotoma*) and South Africa (Millard 1975). Its bathymetric distribution ranges from the intertidal (Cornelius 1995) to 540 m (Vervoort 2006).

Obelia geniculata (Linnaeus, 1758)

Sertularia geniculata Linnaeus, 1758: 812.

Laomedea geniculata – Broch 1914: 37.
Obelia geniculata – Millard 1975: 229–230, fig. 75a–b. — Cornelius 1995: 301–303, fig. 70. — Calder 2012: 50–51, fig. 53.

Material examined

SOUTH ATLANTIC OCEAN • 3 colonies, up to 5 mm high (all growing on brown algae, 2 colonies, with gonothecae); Vema Seamount, stn BT5; 31°37′16″–31°36′58″ S, 8°22′37″–8°23′06″ E; 71–94 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40317, SEAFO-2015-40327, SEAFO-2015-40768.

Distribution

Usually considered as a cosmopolitan species, with records from all oceans (Peña Cantero & García Carrascosa 2002), although absent from Antarctic waters (Peña Cantero 2004). In the Southeast Atlantic, it was recorded from Namibia (Broch 1914, as *Laomedea geniculata* (Linnaeus, 1758)), Vema Seamount (Millard 1966) and South Africa (Millard 1975). Its bathymetric distribution extends from the intertidal (Cornelius 1995) to 381 m (Gili *et al.* 1989).

Family Haleciidae Hincks, 1868
Genus *Halecium* Oken, 1815

Halecium tenellum Hincks, 1861

Halecium tenellum Hincks, 1861: 252, pl. 6 figs 1–4.

Halecium tenellum – Cornelius 1975: 409–411, fig. 12. — Ramil & Vervoort 1992: 90–91, fig. 21f–g.

Material examined

SOUTH ATLANTIC OCEAN • 7 colonies, without gonothecae (1 growing on *Zygophylax* sp., 1 on bivalve shell, and 5 on ghost fishing net); Valdivia Seamount, stn BT12; 24°49′01″–24°47′38″ S, 6°24′40″–6°25′26″ E; 887–886 m depth; 7 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40282, SEAFO-2015-40402, SEAFO-2015-40762, SEAFO-2015-40797, SEAFO-2015-40811, SEAFO-2015-40850, SEAFO-2015-40852.

Distribution

Halecium tenellum is a nearly cosmopolitan species (Cornelius 1975), with records from all oceans, including polar waters, although some identifications from high latitudes in the North Atlantic proved to be erroneous (Calder 1991; Schuchert 2005). Reported from South Africa by Millard (1975). Its bathymetric range extends from the intertidal zone to 1200 m (Peña Cantero & García Carrascosa 2002).

Family Sertulariidae Lamouroux, 1812
Genus *Amphisbetia* Agassiz, 1862

Amphisbetia distans (Lamouroux, 1816)

Dynamena distans Lamouroux, 1816: 180, pl. 5 fig. 1.

Sertularia distans – Broch 1914: 34.
Sertularia distans – Millard 1975: 306–307, fig. 99e–h. — Ramil & Vervoort 1992: 227–228, fig. 63c.
Tridentata distans – Calder 1991: 105–107, fig. 55. — Cornelius 1995: 108–111, fig. 27.

Material examined

SOUTH ATLANTIC OCEAN • 4 colonies, 4–5 mm high (3 growing on algae, 1 of them with gonothecae); Vema Seamount, stn BT5; 31°37′16″–31°36′58″ S, 8°22′37″–8°23′06″ E; 71–94 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40377, SEAFO-2015-40437, SEAFO-2015-40768, SEAFO-2015-40912, LZM-UV slide R. 578 • 1 colony, without gonothecae; Vema Seamount, stn GRAB11A; 31°37′55″ S, 8°21′48″ E; 64 m depth; 1 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40853 • 1 colony, without gonothecae; Vema Seamount, stn Dive 4; 91–95 m depth; 1 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40661.

Distribution

Amphisbetia distans was considered as a circumtropical species by Ramil & Vervoort (1992, as *Sertularia distans*), and circumglobal by Calder (1991, as *Tridentata distans*). In the southeastern Atlantic, it is known from Angola (Broch 1914, as *S. distans*), Vema Seamount (Millard 1966, as *S. distans gracilis*) and South Africa (Millard 1975, as *S. distans*). Its bathymetric distribution ranges from 0 (Millard 1975; Cornelius 1995, as *Tridentata distans*) to 826 m (Ramil & Vervoort 1992).

Amphisbetia minima (Thompson, 1879)
Fig. 4B; Table 7

Sertularia minima Thompson, 1879: 104–105, pl. 17 fig. 3.

Amphisbetia minima – Millard 1975: 250, fig. 82h–k. — Galea & Schories 2012: 36, fig. 3n–o.

Material examined

SOUTH ATLANTIC OCEAN • 2 colonies, growing on algae (1 with gonothecae); Vema Seamount, stn BT5; 31°37′16″–31°36′58″ S, 8°22′37″–8°23′06″ E; 71–94 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40617, SEAFO-2015-40768, LZM-UV slide R. 584.

Remarks

The presence of "pores" or "holes" surrounded by a low perisarcal collar below various hydrothecae and usually located at the proximal internodes of the colonies was described by Ralph (1961), Millard (1975)

Table 7. Measurements of *Amphisbetia minima* (Thompson, 1879), in µm.

	SEAFO-2015 Stn BT5
Internode length	380–440
diameter at node	60–100
Hydrotheca, length adnate wall	210–260
length abcauline wall	240–290
diameter aperture	90–120
Gonothecae, length	1200–1350
max. diameter	700–750
diameter aperture	260–270

and Vervoort & Watson (2003), but we have not observed any "pores" in our colonies. Nevertheless, these pores seem to be a variable feature in this species, as Vervoort & Watson (2003), after reviewing a large amount of material from New Zealand, stated that in some cases there is a pair of holes in the basalmost internode, but other colonies have a single pore or none at all. This structure has been interpreted as nematothecae (Ralph 1961), comparable to the mamelon of Plumularidae (Millard 1975), or glandular pores (Vervoort & Watson 2003), but their true significance remains unknown.

Distribution

Amphisbetia minima is considered as a circumglobal species, without records from Arctic and Antarctic waters (Millard 1975; Vervoort & Watson 2003). In the South Atlantic, it was reported from Vema Seamount (Millard 1966), the west coast of South Africa (Millard 1975) and the Tristan da Cunha group of islands (Galea 2010, 2015). Its bathymetric distribution extends from the littoral zone to 664 m depth (Vervoort & Watson 2003).

Genus *Sertularella* Gray, 1848

Sertularella areyi Nutting, 1904
Fig. 4C; Table 8

Sertularella areyi Nutting, 1904: 83, pl. 17 fig. 6.
Sertularella annulaventricosa Millard, 1975: 279 –281, fig 91F –H.

Sertularella areyi – Vervoort 1993: 201–203, fig. 41c–g. — Vervoort & Watson 2003: 156–158, fig. 35f–i.
— Calder 2013: 28–29, fig. 8h.

Material examined

SOUTH ATLANTIC OCEAN • 5 colonies, up to 5 mm high (2 growing on algae), all without gonothecae; Vema Seamount, stn BT5; 31°37′16″–31°36′58″ S, 8°22′37″–8°23′06″ E; 71–94 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40407, SEAFO-2015-40513, SEAFO-2015-40768, SEAFO-2015-40798, SEAFO-2015-40882, LZM-UV slide R. 585.

Distribution

Sertularella areyi is considered as a circumtropical species (Calder 2013). It was reported from the east coast of South Africa by Millard (1975, as *Sertularella annulaventricosa* Mulder & Trebilcock, 1915), but not from the west coast. Our record from Vema Seamount is the first one in the South Atlantic Ocean. The bathymetric distribution ranges from 47 (Millard 1975, as *S. annulaventricosa*) to a depth of 480 m (Vervoort 1993).

Table 8. Measurements of *Sertularella areyi* Nutting, 1904, in µm.

	SEAFO-2015 Stn BT5
Primary internode, length	800
diameter	120
Secondary and following internodes, length	640–1000
diameter	90–140
Hydrotheca, length abcauline wall	410–470
length adnate part, adcauline wall	150–220
length adnate part, free part, adcauline wall	320–400
diameter at rim	210–300
max. diameter	300–350

Sertularella arbuscula (Lamouroux, 1816)
Table 9

Sertularia arbuscula Lamouroux, 1816: 191–192, pl. 5 fig. 4.
Sertularella crassipes Allman, 1886: 133–134, pl. 8 figs 4–5.

Sertularella arbuscula – Millard 1975: 281–282, fig. 91j–l.

Material examined

SOUTH ATLANTIC OCEAN • 2 colonies, up to 31 mm high, without gonothecae; Vema Seamount, stn PT4; 31°39′43″–31°38′10″ S, 8°22′37″–8°23′42″ E; 50–108 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40093, SEAFO-2015-40123 • 2 colonies, up to 40 mm high growing on algae, without gonothecae; Vema Seamount, stn BT5; 31°37′16″–31°36′58″ S, 8°22′37″–8°23′06″ E; 71–94 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40527, SEAFO-2015-40768, LZM-UV slide R. 588 • 1 colony, 30 mm high, growing on bryozoan, with gonothecae; Valdivia Seamount, stn PT10; 25°36′54″–25°37′26″ S, 6°12′40″–6°11′31″ E; 476–707 m depth; 5 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40414.

Distribution

This species has been previously recorded from the Australasian Seas, Indian Ocean, South Africa and Vema Seamount, from the littoral zone to a depth of 219 m (Millard 1966, 1975). Our records from Valdivia Bank, between 476 and 707 m, represent the deepest known localities for this species.

Table 9. Measurements of *Sertularella arbuscula* (Lamouroux, 1816), in µm.

	SEAFO-2015 Stn BT5
Internode, length	600–790
diameter	340–410
Hydrothecae, length adcauline wall, adnate part	390–450
length adcauline wall, free part	260–340
length abcauline wall	450–540
diameter at rim	200–290

Sertularella patagonica (d' Orbigny, 1846)
Fig. 4E; Table 10

Sertularia patagonica d' Orbigny, 1846: 25–26, pl. 11 figs 3–5.

Sertularella striata – Millard 1975: 304–305, fig. 97e–f. — Gili *et al*. 1989: 104–105, fig. 29a.
Sertularella patagonica – Galea *et al*. 2017: 294–295, fig. 15a–e.

Material examined

SOUTH ATLANTIC OCEAN • 11 colonies, up to 24 mm high (1 growing on antipatharian), all devoid of gonothecae; Vema Seamount, stn PT4; 31°39′43″–31°38′10″ S, 8°22′37″–8°23′42″ E; 50–108 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40003, SEAFO-2015-40033, SEAFO-2015-40077, SEAFO-2015-40093, SEAFO-2015-40107, SEAFO-2015-40183, SEAFO-2015-40213, SEAFO-2015-40474, LZM-UV slide R. 586 • 4 colonies, without gonothecae (1 growing on algae and 1 on a bryozoan); Vema Seamount, stn BT5; 31°37′16″–31°36′58″ S, 8°22′37″–8°23′06″ E; 71–94 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40387, SEAFO-2015-40467, SEAFO-2015-40723, SEAFO-2015-40768 • 3 colonies, without gonothecae; Vema Seamount, stn Dive 4; 91–95 m depth; 1 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40131, SEAFO-2015-40917, SEAFO-2015-40977.

Remarks

Our material coincides in both morphology and measurements with those given for *S. patagonica* by Galea *et al.* (2017), who synonymized *Sertularella striata* Stechow, 1923 with *S. patagonica* after a literature review. It also fits well with the colonies described by Gili *et al.* (1989, as *S. striata*) from the Namibian coast, but this record was considered as doubtful by Galea *et al.* (2017) due to the hydrothecal measurements being larger than those reported for *S. patagonica* in the literature. However, there are some contradictions between the measurements given by Gili *et al.* (1989) in the text and those that we have obtained from their figure 29a; indeed, the latter fall within the size range given for *S. patagonica*, and Namibian colonies prove identical with those collected at Vema Seamount. Consequently, we consider our Namibian material as conspecific with *S. patagonica*.

Distribution

In the Atlantic, *Sertularella patagonica* was recorded from the Argentinean coast (Galea *et al.* 2017) and off Namibia (Gili *et al.* 1989, as *S. striata*), and from the east coast of South Africa, Mozambique (Millard 1975) and India (Nagale & Apte 2014, as *S. striata*) in the Indian Ocean. Its bathymetric distribution ranges from the intertidal (Nagale & Apte 2014, as *S. striata*) to 429 m (Gili *et al.* 1989, as *S. striata*).

Table 10. Measurements of *Sertularella patagonica* (d' Orbigny, 1842), in μm.

	SEAFO-2015 Stn PT4
Internode, length	550–850
diameter	100–140
Hydrothecae, length adcauline wall, adnate part	200–260
length adcauline wall, free part	250–360
length abcauline wall	400–470
diameter at rim	190–220

Sertularella polyzonias (Linnaeus, 1758)
Fig. 4D

Sertularia polyzonias Linnaeus, 1758: 813.

Sertularella polyzonias – Ramil & Vervoort 1992: 225–227, fig. 63a–b. — Cornelius 1995: 74–76, fig. 17.

Material examined

SOUTH ATLANTIC OCEAN • 5 colonies, 6–13 mm high (2 growing on algae and 2 on bryozoan), 3 of them bear gonothecae; Vema Seamount, stn BT5; 31°37′16″–31°36′58″ S, 8°22′37″–8°23′06″ E; 71–94 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40197, SEAFO-2015-40347, SEAFO-2015-40387, SEAFO-2015-40602, SEAFO-2015-40768, LZM-UV slide R. 583.

Distribution

Sertularella polyzonias is a circumglobal species (Gil 2017). In the Southeast Atlantic, it was reported from Angola by Broch (1914). Its bathymetric distribution ranges from 2 (Peña Cantero & García Carrascosa 2002) to 2500 m (Fraser 1944).

Family Halopterididae Millard, 1962

Genus *Monostaechoides* gen. nov.
urn:lsid:zoobank.org:act:E7E0F40E-8573-4EDF-98F5-D3CD4EAA3ED2

Type species

Plumularia providentiae Jarvis, 1922, designated herein.

Additional species

Monostaechoides bertoti (Galea & Ferry, 2015) gen. et comb. nov. (= *Monostaechas bertoti* Galea & Ferry, 2015).

Diagnosis

Halopteridids with monosiphonic hydrocladia arising directly from creeping stolons. Hydrocladia branched, with several cladia originating dorsally from the distal parts of its ahydrothecate internodes. All cladia directed towards the same side or arranged either alternately or irregularly left and right along the stem. Branches of second and third order frequent in, at least, one species. Hydrothecate internodes with one hydrotheca, two pairs of lateral nematothecae and one mesial inferior nematotheca. Ahydrothecate internodes with a variable number of nematothecae. Hydrotheca partly adnate to its corresponding internode, cup-shaped, with untoothed rim. All nematothecae conical, bithalamic and movable. Gonothecae provided with nematothecae on the basal part.

Etymology

The generic name *Monostaechoides* is derived from a combination of the generic name *Monostaechas* Allman, 1877, and the latinized form of the Greek word-forming element '*-eidés*', meaning 'like, resembling' and referring to the affinities of the new taxon with the genus *Monostaechas*. The gender of the name is masculine.

Remarks

The presence of hydrothecae on the hydrocaulus is the main defining character of the family Halopterididae Millard, 1962 (Millard 1962, 1975; Schuchert 1997), and the generic limits within the family are largely based on the shape of the colonies and their ramification patterns (Schuchert 1997).

The new genus described herein is characterized by having monosiphonic stems or primary hydrocladia arising from hydrorhiza and supporting irregularly pinnate or unilaterally-arranged secondary hydrocladia that, in turn, can originate hydrocladia of second and third order, in at least the type species. Another distinctive feature is the origin of the subsidiary hydrocladia from the postero-distal parts of ahydrothecate internodes, on the backside of an oblique distal node.

The general habit of the colonies, with single monosiphonic stems carrying laterally-placed hydrocladia, resembles those of *Halopteris* Allman, 1877, *Monostaechas* Allman, 1877 and the recently described *Thamnopteros* Galea, 2020.

Resemblances with *Halopteris* are found in the ramified nature of the colonies belonging to both genera, but in *Halopteris* the hydrocladia are routinely arranged in either alternate or opposite pairs, and originate from the hydrothecate internodes of the stem, laterally to the hydrothecae. *Thamnopteros* builds polysiphonic colonies giving rise to monosiphonic branchlets bearing pinnate hydrocladia with the same origin as in *Halopteris* (Galea & Maggioni 2020).

The new genus shows more affinities with *Monostaechas* Allman, 1877 in both the origin of subsidiary hydrocladia on the postero-distal part of ahydrothecate internodes, just behind the distal oblique node, and the tendency to a unilateral disposition of subsidiary hydrocladia. Nevertheless, in *Monostaechas* the ramification pattern is a helicoid or scorpioid sympodium, in which each subsidiary hydrocladium originates from the postero-distal part of the first ahydrothecate internode of the previous hydrocladium (Billard 1913; Millard 1975; Schuchert 1997), resulting in a false axis composed of the basal parts of successive hydrocladia (Billard 1913; Millard 1975). In *Monostaechoides* gen. nov., there is a 'true axis' represented by a stem or primary hydrocladium bearing several secondary hydrocladia irregularly disposed along the same axis. This branching pattern is clearly different from that displayed by *Monostaechas*, supporting the creation of a new genus.

The colonies of *Monostaechas fisheri* Nutting, 1906, recently redescribed by Galea & Maggioni (2020), show another ramification pattern, different from that met with in *Monostaechoides* gen. nov. In this case, the stem is devoid of hydrothecae and the lateral ramification builds a true sympodium (see Billard 1913: fig. 7).

The same type of ramification found in *Monostaechoides* gen. nov. was also described in specimens of *Antennella secundaria* (Gmelin, 1791) collected from Indonesia (Billard 1913: 8, pl. 1 figs 2–3), the Seychelles (Millard & Bouillon 1973: 78) and South Africa (Millard 1975: 334), suggesting the existence of other undescribed species within this genus. Both Billard (1913) and Millard (1975) pointed out that, in these colonies, the main axis is formed by the first hydrocladium, and does not originate from the basal part of successive hydrocladia, excluding these materials from *Monostaechas*. Ramified colonies assigned to *A. secundaria* were also described by Vervoort & Vasseur (1977: 66, fig. 28b), Ryland & Gibbons (1991: 526, fig. 1a) and Calder (1997: 30, fig. 7a), but, in all cases, the ramification fits well with a sympodial pattern and was clearly different from that in *Monostaechoides* gen. nov.

Monostaechoides providentiae (Jarvis, 1922) gen. et comb. nov.
Figs 5–6, 7A–B; Table 11

Plumularia providentiae Jarvis, 1922: 347–348, pl. 26 fig. 21.

Antennella quadriaurita – Millard 1966: 492–493. — Calder 1997: 27–29, fig. 6 (not *Antennella quadriaurita* Ritchie, 1909).

Material examined

SOUTH ATLANTIC OCEAN • 3 colonies, 19–23 mm high, on sponge (1 with gonothecae); Vema Seamount, stn PT4; 31°39′43″–31°38′10″ S, 8°22′37″–8°23′42″ E; 50–108 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40063, LZM-UV slide R. 576 • 4 colonies, 5–7 mm high (1 colony, growing on algae, with gonothecae); Vema Seamount, stn BT5; 31°37′16″–31°36′58″ S, 8°22′37″–8°23′06″ E; 71–94 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40227, SEAFO-2015-40497, SEAFO-2015-40768, LZM-UV slide R. 581.

Description

Hydrorhiza composed of a cluster of perisarcal tubes covered by a sponge growing on old gorgonian axis. In some cases, isolated hydrocladia are born directly on the hydrorhiza but, in most cases, several monosiphonic primary hydrocladia arise in tufts from a short, polysiphonic axis composed by several entangled stolons protruding from the sponge. The basal part of the primary hydrocladium is composed of one to five internodes separated by straight nodes, provided with a variable number of scattered nematothecae separated from the remainder of hydrocladium by an oblique node. This part is formed by a regular succession of hydrothecate and ahydrothecate internodes, delimited by alternating oblique and straight nodes; hydrothecate internodes with proximally oblique and distally straight nodes; ahydrothecate internodes with a reversed position of nodes (Figs 5E, 6C, 7B). Almost all primary hydrocladia carry lateral ramifications randomly disposed, always originating from their posterior side. In most cases, the subsidiary hydrocladia arise from the distal end of ahydrothecate internodes, just on the back side of the oblique nodes within the heteromerous part of the colony (Fig. 6A); occasionally, some ramifications are found on the basal part of primary hydrocladia (Figs 5F–G, 7A). All subsidiary hydrocladia (i.e., of the second, third and even fourth order) are born on small apophyses and are composed of a basal ahydrothecate internode of varied length carrying between one and four nematothecae (Figs 6A, D, 7A), followed by a regular succession of hydrothecate and ahydrothecate internodes with the same structure as the primary hydrocladia. Usually, all subsidiary hydrocladia originating from the same hydrocladium are directed to the same side in a linear succession, but irregularities also occur.

Hydrothecate internodes with one hydrotheca and five nematothecae: one mesial inferior and two pairs of laterals. Hydrotheca cup-shaped, widening towards rim; adcauline wall adnate for about half its length; abcauline wall straight; hydrothecal rim circular, even and slightly everted. Mesial nematothecae not reaching hydrothecal base. Two pairs of lateral nematothecae; first pair borne on well-developed apophyses adpressed to the hydrothecal wall, and as long as the nematothecae proper, the latter reaching the hydrothecal rim; second pair small, inserted on bases of apophyses (Fig. 5D). Ahydrothecate internodes usually with two frontal nematothecae in a row, although the number may vary between one and three. All nematothecae bithalamic, movable and conical, with adcauline wall of distal chamber scooped.

Colonies monoecious; gonothecae of both sexes found on same hydrocladia, arising from below the hydrothecal bases, just above the mesial nematothecae (Figs 6A–B, 7B). Male gonotheca small, sack-shaped, with small and circular aperture located at the rounded top, basal part slightly curved and carrying one nematotheca, and narrowing into a short pedicel composed of one internode. Female gonotheca
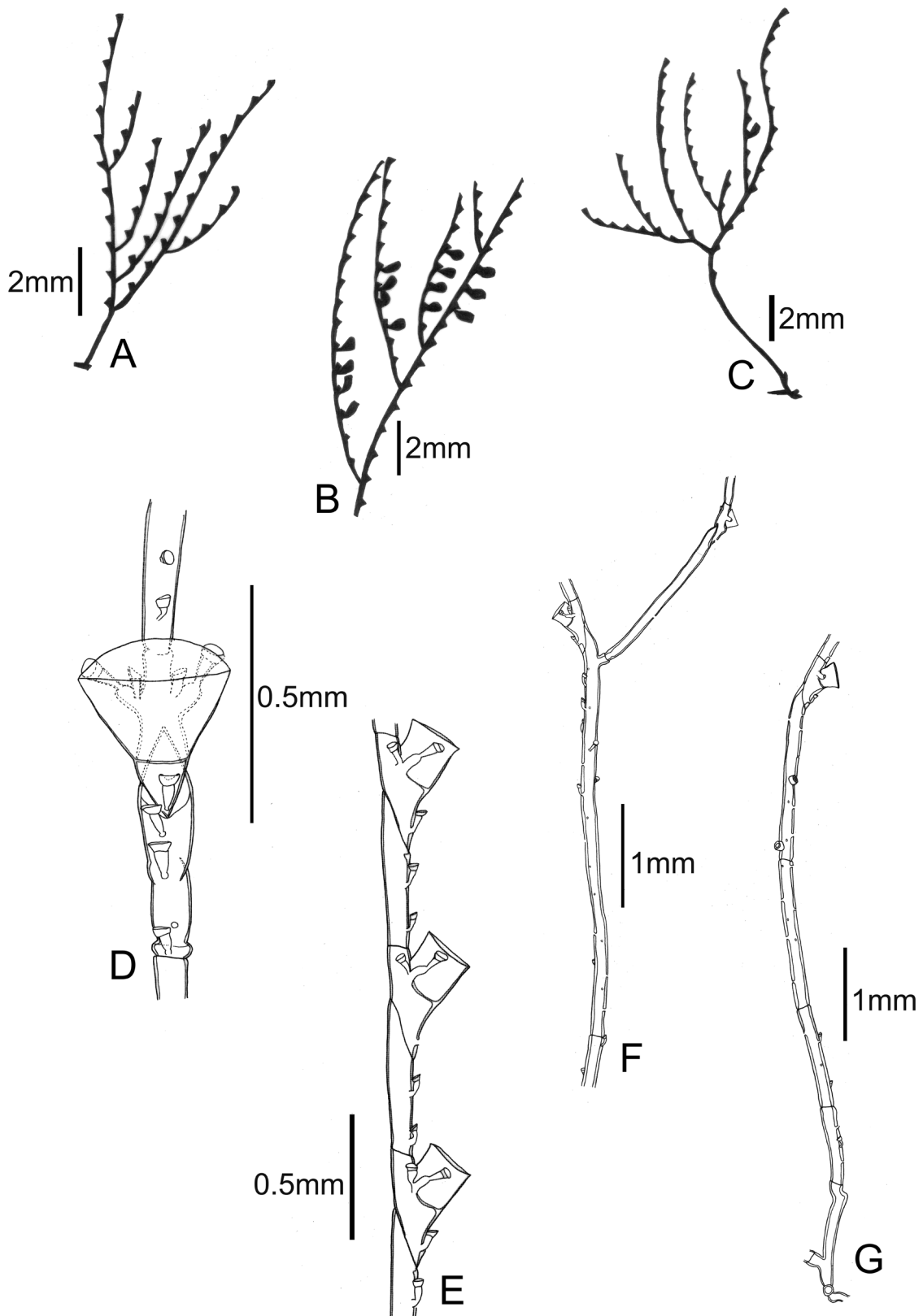
Fig. 5. *Monostaechoides providentiae* (Jarvis, 1922) gen. et comb. nov., stn PT4. **A–C**. Three distinct colonies showing their distinctive ramification. **D**. Detail of hydrotheca, frontal view. **E**. Detail of hydrocladia with hydrothecae, lateral view. **F–G**. Details of the basal part of several hydrocladia.
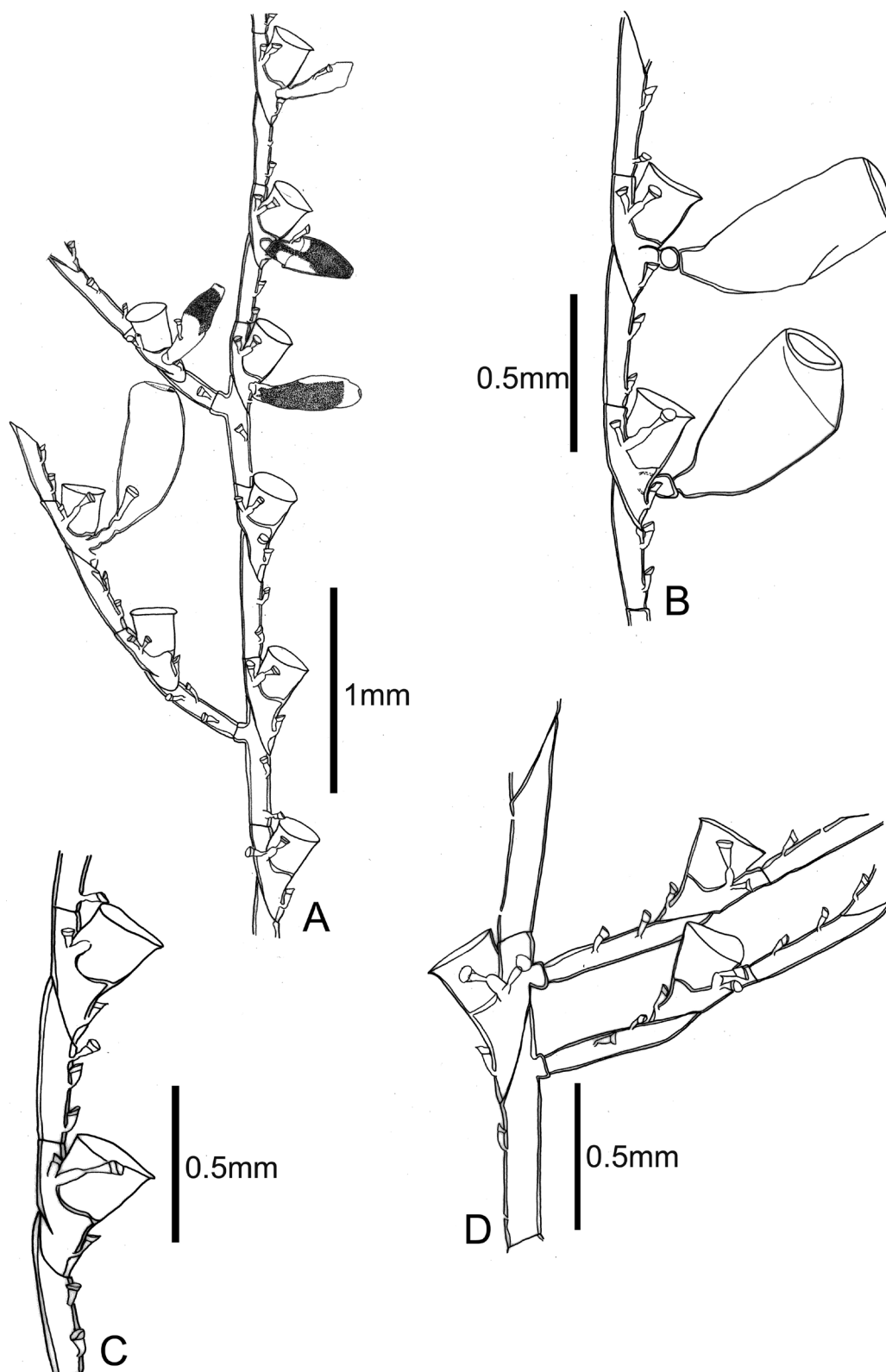
Fig. 6. *Monostaechoides providentiae* (Jarvis, 1922) gen. et comb. nov., stn PT4. **A**. Part of colony with hydrocladia, and male and female gonothecae. **B**. Detail of hydrocladia with hydrothecae and two female gonothecae, lateral view. **C**. Part of hydrocladia, lateral view. **D**. Portion of hydrocladia with two consecutives ramifications.
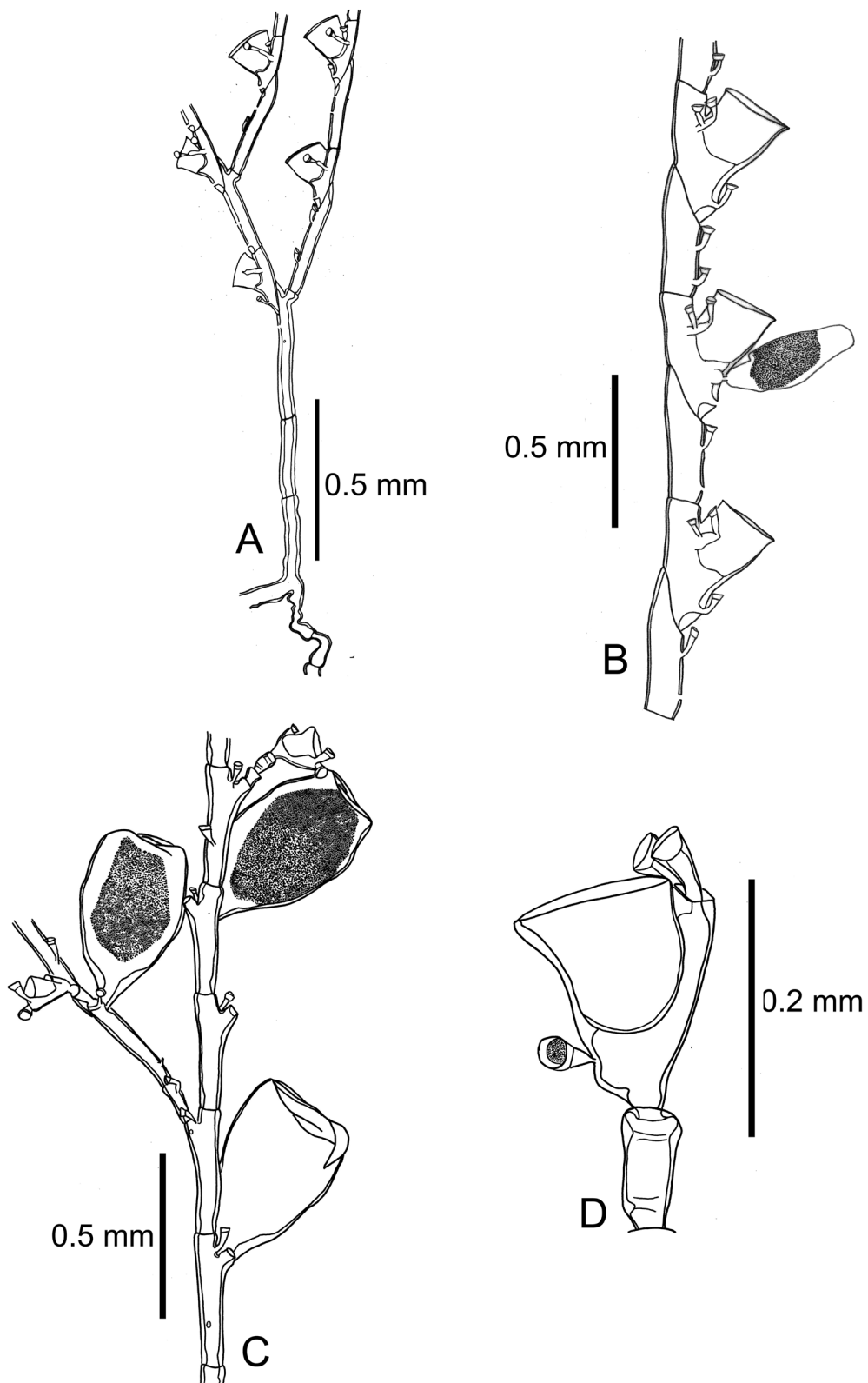
Fig. 7. A–B. *Monostaechoides providentiae* (Jarvis, 1922) gen. et comb. nov. **A**. Stn PT4, detail of basal part of hydrocladia. **B**. Stn BT5, part of hydrocladium with hydrothecae and a male gonotheca. **C–D**. *Monotheca bergstadi* sp. nov. **C**. Hydrocladia ramified and with gonothecae. **D**. Detail of hydrotheca, lateral view.

Table 11. Measurements of *Monostaechoides providentiae* (Jarvis, 1922), in µm.

	SEAFO-2015 Stn PT4	*Antennella quadriaurita* (Calder, 1997)
Length hydrothecate internodes	400–470	294–820
length ahydrothecate internodes	300–370	168–503
diameter at node	60–80	–
Hydrotheca, length abcauline wall	200–260	163–256
length free part adcauline wall	120–170	–
diameter at rim	210–260	140–168
Male gonotheca, length	415–475	–
max diameter	140–180	–
length pedicel	50–60	–
Female gonothecae, length	630–750	515
max. diameter	270–390	195
length pedicel	90–160	80

pear-shaped, rather curved, with a distal, slightly tilted, circular aperture, closed by lid; basally provided with two nematothecae and narrowing into a two-segmented pedicel.

Variability

In some hydrocladia, the regeneration processes when ahydrothecate internodes are damaged result in two ahydrothecate internodes, each one with one or two nematothecae, between two consecutive hydrothecate internodes. We have also observed a subsidiary hydrocladium originating from the back side of a hydrothecate internode (Fig. 6D), but this type of ramification is exceptional and probably related to regeneration processes.

Remarks

Our material agrees with the main features described by Jarvis (1922) as *Plumularia providentiae*. In both cases the colonies are ramified, with the subsidiary hydrocladia originating from the back side of a true axis (or hydrocladia) shifted on to one side, but that does not adopt the shape of a scorpioid sympodium. Moreover, the morphology of hydrothecae and the number and arrangement of the nematothecae are also similar.

The main difference is found in the presence, in our colonies, of subsidiary hydrocladia originating from the basal part of some primary hydrocladia; however, this is an occasional feature and not the norm. Moreover, Jarvis (1922) described *P. providentiae* with homomerously segmented hydrocladia, but in our colonies the segmentation is heteromerous. Nevertheless, the existence of intermediate ahydrothecate internodes is clearly visible only in subsidiary and younger hydrocladia. In older parts of the colony, and mainly in primary hydrocladia, the perisarc of the wall is thick, masking the heteromerous segmentation.

In our opinion, these differences do not justify the description of a new species and, therefore, we identify our material as *Monostaechoides providentiae* (Jarvis, 1922) gen. et comb. nov.

In addition, the material described from the Vema Seamount by Millard (1966) as *Antennella quadriaurita* (Ritchie, 1909), with hydrocladia clustered together basally and ramified following the same pattern as our colonies, also belongs to this species.

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Colonies found in Bermuda with a similar morphology and with the same ramification pattern were described by Calder (1997) as *A. quadriaurita* (see Calder 1997: 28, fig. 6a). That material, excluded from *A. quadriaurita* by Galea & Ferry (2015), is also included here in *M. providentiae* gen. et comb. nov.

Differences between *M. providentiae* gen. et comb. nov. and *M. bertoti* gen. et comb. nov. were discussed by Galea & Ferry (2015), and refer to the ramification pattern, with hydrocladia more or less alternately arranged in *M. bertoti* gen. et comb. nov., and a different number of nematothecae on both cauline and cladial internodes.

Distribution

This species has been reported from Providence Atoll, the Seychelles (Jarvis 1922, as *Plumularia providentiae*), Vema Seamount (Millard 1966; Berrisford 1969, both as *A. quadriaurita*) and Bermuda (Calder 1997, as *A. quadriaurita*) in depths from 42 to 85 m.

Family Plumulariidae Agassiz, 1862
Genus *Monotheca* Nutting, 1900

***Monotheca bergstadi* sp. nov.**
urn:lsid:zoobank.org:act:3BFDE359-6A4B-4910-9AB5-226193B6584E
Figs 7C–D, 8; Table 12

Plumularia pulchella – Millard 1957: 232; 1962: 300; 1966: 493; 1975: 398–399, fig. 125c–d [not *Monotheca pulchella* (Bale, 1882)].

Diagnosis

Colonies monosiphonic, mostly unbranched. Hydrocaulus divided into internodes by straight nodes, each internode bearing one apophysis and three nematothecae. Hydrocladia composed of two internodes: one athecate proximal without nematothecae, with two internal perisarcal rings, and one thecate distal bearing a hydrotheca and three nematothecae. Hydrotheca deep campanulate and abcauline wall concave. Mesial inferior nematotheca long and lateral nematothecae short. Gonothecae arising frontally, large, barrel-shaped and smooth-walled.

Etymology

The specific name *bergstadi* honours Dr. Odd Aksel Bergstad, Institute of Marine Research (IMR), Bergen, Norway, leader of the SEAFO 2015 cruise, in recognition of his wide contribution to deep-sea research.

Material examined

Holotype
SOUTH ATLANTIC OCEAN • colony, 10 mm high, with gonothecae; Vema Seamount, stn BT5; 31°37′16″–31°36′58″ S, 8°22′37″–8°23′06″ E; 71–94 m depth; 31 Jan. 2015; SEAFO-2015 leg.; LZM-UV slide R. 582; SAMC-A092083.

Paratypes
SOUTH ATLANTIC OCEAN • 7 colonies, 8–13 mm high (2 growing on algae), 3 colonies, with gonothecae; same collection data as for holotype; SEAFO-2015-40042, SEAFO-2015-40167, SEAFO-2015-40572, SEAFO-2015-40768.

Additional material
SOUTH ATLANTIC OCEAN • 1 colony, 10 mm high growing on algae, with gonothecae; Vema Seamount, stn PT4; 31°39′43″–31°38′10″ S, 8°22′37″–8°23′42″ E; 50–108 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40137 • 1 colony, growing on bryozoan, without gonothecae; Vema Seamount, stn GRAB9C; 31°36′09″ S, 8°22′29″ E; 84 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40080 • 1 colony, without gonothecae; Vema Seamount, stn GRAB12B; 31°37′56″ S, 8°23′12″ E; 89 m depth; 1 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40245.

Description

Colonies composed of a reticulate hydrorhiza growing on algae and a bryozoan, supporting erect, monosiphonic and mostly unbranched, occasionally branched once, hydrocauli (Fig. 7C). Stem regularly divided into internodes by straight nodes, each bearing a latero-distal apophysis and three nematothecae: two axillar, flanking the apophysis and one on the basal half on the opposite side. Apophyses alternately directed left and right and disposed almost in the same plane (Fig. 8A). Hydrocladia inserted on apophyses and composed of two internodes: one athecate basal and one thecate distal. Basal internode short, without nematothecae and with two internal perisarcal rings, one basal and the other distal. Thecate internode slightly longer than athecate, with one hydrotheca and three nematothecae: one mesial inferior and a pair of laterals (Figs 7D, 8A).

Hydrotheca deep campanulate, adcauline wall fully adnate to internode, abcauline wall concave, margin straight, smooth and slightly flared. Mesial nematotheca long, reaching or even surpassing the middle of the abcauline wall of hydrotheca. Lateral nematothecae comparatively shorter and placed on small, yet distinct apophyses reaching the hydrothecal rim (Fig. 7D). All nematothecae two-chambered and movable; rim of upper chamber even throughout.

Gonothecae arising frontally from apophyses of hydrocladia; large, barrel-shaped, smooth-walled, truncated apically; aperture wide and circular; operculum not observed (Figs 7C, 8B–C).

Remarks

The validity of the genus *Monotheca* or its synonymy with *Plumularia* Lamarck, 1816 has been widely discussed during the last few years in the literature. Watson (2011) and Calder (2019) indicated that, despite the traditional interpretation of the genus, *Monotheca* might involve a polyphyletic group. Indeed, some molecular analyses (Leclère *et al.* 2007, 2009; Moura *et al.* 2008; Maronna *et al.* 2016) revealed that the type species of both genera, *Monotheca margaretta* Nutting, 1900 and *Plumularia setacea* (Linnaeus, 1758), respectively, did not cluster together. In addition, the latest molecular study of the superfamily Plumularioidea (Moura *et al.* 2018) supports the validity of *Monotheca*. Taking into account that the new species is closely allied to *M. margaretta*, we have decided to assign it to this genus, under the name *Monotheca bergstadi* sp. nov.

Our material is closely related to four nominal species of *Monotheca*, namely *M. margaretta* Nutting, 1900, *M. pulchella* (Bale, 1882), *M. flexuosa* (Bale, 1894) and *M. femina* (García, Aguirre & González, 1978). The latter is currently accepted as a junior synonym of *M. margaretta* (Calder 1977; Ansín Agís *et al.* 2001; Schuchert 2020; as *Plumularia margaretta*), and we agree.

The remaining valid species are easily recognizable by the morphology of their gonothecae. In *M. margaretta*, they are barrel-shaped, with well-developed transverse ridges and a broad, apical aperture (Calder 1997; Ansín Agís *et al.* 2001); in *M. pulchella* the gonothecae are ovate, with an obliquely truncate aperture with a submarginal row of large, internal teeth surrounded by large, internal teeth (Bale 1882; Ralph 1961; Watson 1973, 2011); finally, in *M. flexuosa*, the gonothecae are fusiform, with
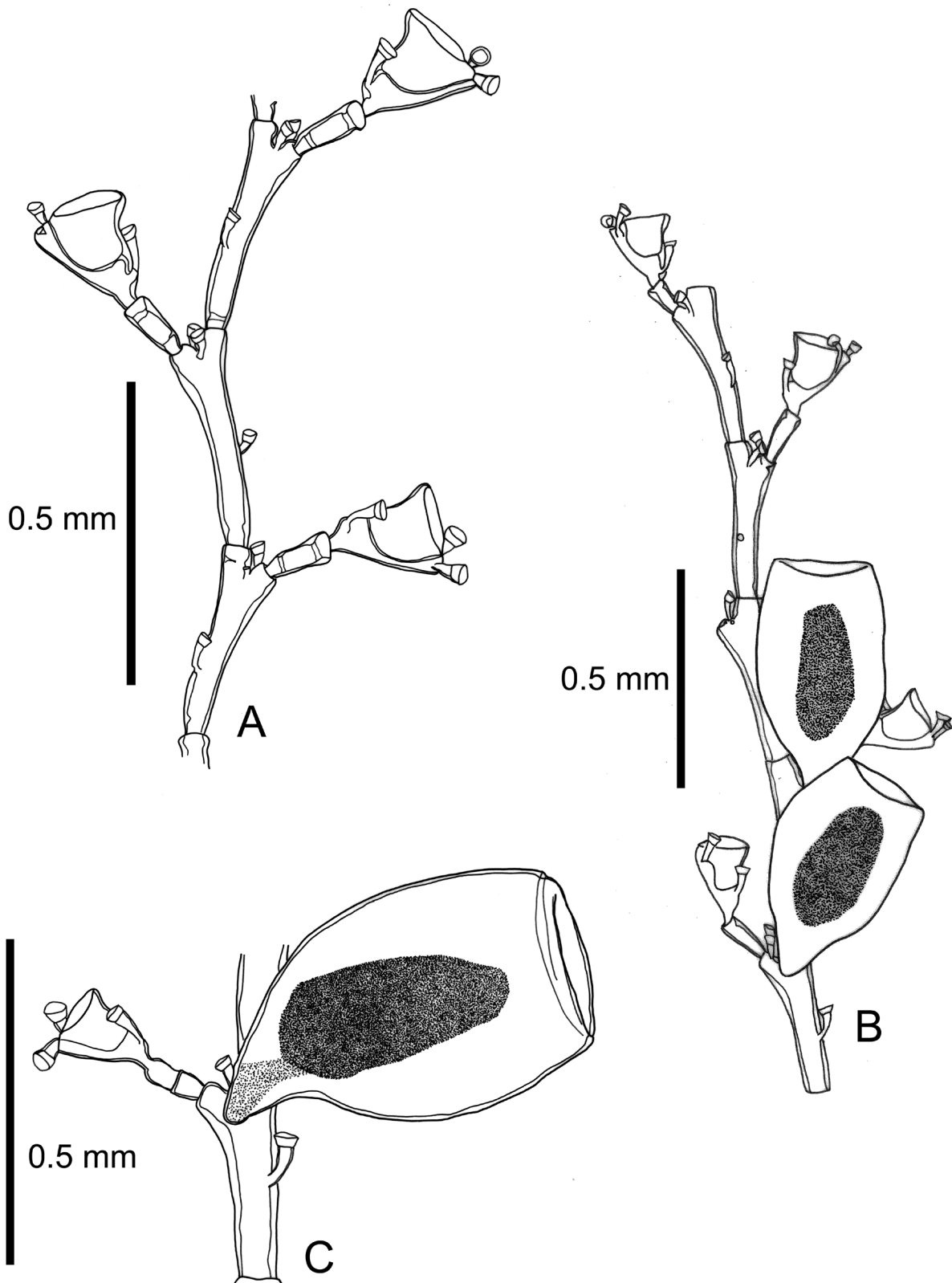
Fig. 8. *Monotheca bergstadi* sp. nov. **A**. Portion of colony with hydrocladia. **B**. Part of colony with hydrocladium and gonothecae. **C**. Detail of hydrocladia and gonotheca.

Table 12. Measurements of *Monotheca bergstadi* sp. nov., in µm.

	SEAFO-2015 Stn BT5
Stem internode, length	320–400
diameter at node	50–70
First hydrocladial internode ahydrothecate, length	85–120
diameter at node	40–45
Following hydrocladial internode hydrothecate, length	140–180
Hydrotheca length abcauline wall	90–110
length adcauline wall	90–110
diameter at rim	90–140
Lateral nematotheca, length	80–116
diameter at rim	44–64
Mesial nematotheca, legth	80–140
diameter at rim	48–60
Gonotheca, length	470–590
maximum diameter	260–420
diameter at rim	170–280

slightly undulated walls and a rather small, apical aperture produced into a neck of variable height (Bale 1894; Watson 2011).

In addition, *M. margaretta* is an amphi-Atlantic species, whereas *M. pulchella* and *M. flexuosa* are predominately Indo-Pacific.

Nevertheless, *M. pulchella* was reported several times from the Atlantic Ocean and Mediterranean Sea (for a review, see Calder 1997 and Ansín Agís *et al.* 2001), and the actual status of these records have been subjected to different interpretations in the literature. The records from the Northeast Atlantic and the Mediterranean Sea, all with annulated and barrel-shaped gonothecae, were included in *M. margaretta* by Calder (1997) and Ansín Agís *et al.* (2001), and we agree with this conclusion, despite the fact that Watson (2011) considers that they are conspecific with *M. flexuosa*. The records of *M. pulchella* from the Mediterranean (Bouillon *et al.* 2004) are based on the material studied by García Corrales *et al.* (1978, as *Plumularia femina*) and Medel & Vervoort (1995), and belong to *M. margaretta*, despite some figures (Bouillon *et al*. 2004: fig. 92h, j) being based on Millard (1975: fig. 125c–d) and representing a different species (see below). The records of *M. pulchella* from the Argentinian coast (Blanco 1973, 1994; Genzano 1990, 1994; all as *Plumularia pulchela*), were provisionally placed under *M. margaretta* by Ansín Agís *et al.* (2001) because the involved colonies were sterile.

The morphology of the colonies collected at the Vema Seamount studied in this report, with respect to their tropho- and gonosome, completely coincides with those described by Millard (1975) as *M. pulchella* from South Africa and the Vema Seamount. This material, characterized by its barrel-shaped, smooth-walled gonothecae, is clearly distinct from the current concept of *M. pulchella*, and also from other previously discussed species.

In fact, Watson (2011) excluded the South African records from the synonymy of *M. pulchella*, but did not assign them to any known species of *Monotheca*. Consequently, we consider that this material represents a new species, for which we propose the name *M. bergstadi* sp. nov.

Distribution

Monotheca bergstadi sp. nov. has previously been reported from Vema Seamount (Millard 1966, as *Plumularia pulchella*) and South Africa, from the west coast of Cape Peninsula to Natal (Millard 1957, 1962, 1975; all as *P. pulchella*). Its bathymetric distribution extends from the littoral zone to a depth of 100 m (Millard 1975, as *P. pulchella*).

Genus *Plumularia* Lamarck, 1816

Plumularia setacea (Linnaeus, 1758)

Sertularia setacea Linnaeus, 1758: 813.

Plumularia setacea – Ramil & Vervoort 1992: 191–193, fig. 47f–i. — Ansín Agís *et al*. 2001: 238–245, fig. 91.

Material examined

SOUTH ATLANTIC OCEAN • 1 colony, without gonothecae; Vema Seamount, stn PT4; 31°39′43″–31°38′10″ S, 8°22′37″–8°23′42″ E; 50–108 m depth; 31 Jan. 2015; SEAFO-2015 leg.; SEAFO-2015-40924 • 2 colonies (1 with gonothecae); Vema Seamount, stn Dive 4; 91–95 m depth; 1 Feb. 2015; SEAFO-2015 leg.; SEAFO-2015-40050, SEAFO-2015-40131.

Distribution

Circumglobal, with a bathymetric range of 0 to 1517 m (Ansín Agís *et al.* 2001; Gil 2017). In the Southeast Atlantic, it was reported from Angola (Broch 1914; Bouillon *et al.* 1995), Namibia (Broch 1914; Gili *et al.* 1989), Vema Seamount (Millard 1966) and South Africa (Millard 1975).

Discussion

A total of 27 species belonging to 15 families were identified in this study. The most specious families were Sertulariidae (6 species), followed by Tiarannidae (3 species) and Pandeidae, Plumulariidae, Campanulariidae, Clytiidae, and Obeliidae (each with 2 species). The remaining eight families were represented by only one species. In terms of availability, Tiarannidae was the most abundant family (59 colonies), followed by Sertulariidae (39 colonies), Zygophylacidae (29 colonies), Campanulariidae (19 colonies) and Plumulariidae (14 colonies). The remaining families accounted for less than 10 colonies each.

The hydroid collection includes two new taxa for science, the genus *Monostaechoides* gen. nov. (described to accommodate both *Plumularia providentiae* Jarvis, 1922 (formerly included in *Monostaechas* Allman, 1877) and *Monostaechas bertoti* Galea & Feery, 2015), and the plumulariid *Monotheca bergsatdi* sp. nov. (also based, beyond the type designated herein, on material assigned to *Plumularia pulchella* (Bale, 1882) by Millard (1966, 1975)). In addition, *Campanularia africana*, a species with an Indo-Pacific distribution, is reported for the first time from the Atlantic Ocean, while the previously known Northeast Atlantic species *Amphinema biscayana*, *Stegopoma giganteum* and *Clytia gigantea* were found for the first time in the South Atlantic Ocean. Moreover, *S. giganteum* was recorded for the first time since its original description. Three taxa, *Turritopsis* sp., *Filellum* sp. and *Zygophylax* sp., were identified to genus level only, as the absence of fertile material prevented us from providing a reliable specific identification. The morphology of the colonies reported here as *Turritopsis* sp. fits well with that described by Gil (2017) and Gil *et al.* (2020), but its taxonomical status in West Africa remains unresolved (see Gil 2017; Gil *et al.* 2020). *Filellum* sp. shows some affinities with *Filellum antarcticum* (Hartlaub, 1904) and *Filellum magnificum* Peña Cantero, Svoboda & Vervoort, 2004, but exhibits some

differences in measurements of hydrothecae and nematocysts. *Zygophylax* sp. is conspecific with the material assigned by Millard (1958, 1968, 1975) to *Zygophylax ? biarmata* Billard, 1905, but its specific identity was questioned by Ramil & Vervoort (1992), and could represent a new species.

Of the 27 species studied in this report, 11 were collected from Valdivia and 19 from Vema, while three species, *Stegolaria geniculata*, *Sertularella arbuscula* and *Campanularia hincksii*, were common to both seamounts. Although this strong difference between hydroid communities is biased by the low number of samples examined, the environmental conditions clearly contribute to differentiate both seamount communities. The Vema Seamount, despite its isolated location in the middle of a deep abyssal plain at ca 450 nautical miles from the West African coast (Simpson & Heydorn 1965; Berrisford 1969; Bergstad *et al.* 2019a), its summit reaches the euphotic zone, with a depth oscillating from 100 to 21.5 m at its shallowest peak (Bergstad *et al*. 2019a, 2019b), and its benthic community is characterized by the abundance of coralline algae and prominent kelp forests (Simpson & Heydorn 1965; Berrisford 1969; Bergstad *et al*. 2019b) (Fig. 9), with recorded temperatures of 16–18°C and a salinity of 35.6 psu at the summit of the seamount (Bergstad *et al.* 2019b) (Fig. 9). At the Valdivia Bank and its associated seamount complex, the summits of the sampled areas were located at depths from 227–235 to ca 500 m, deeper than the euphotic zone. There, the benthic communities were characterized by corals, mainly alcyonarians, but also scleractinians at Valdivia Middle, although more or less extensive areas of bare
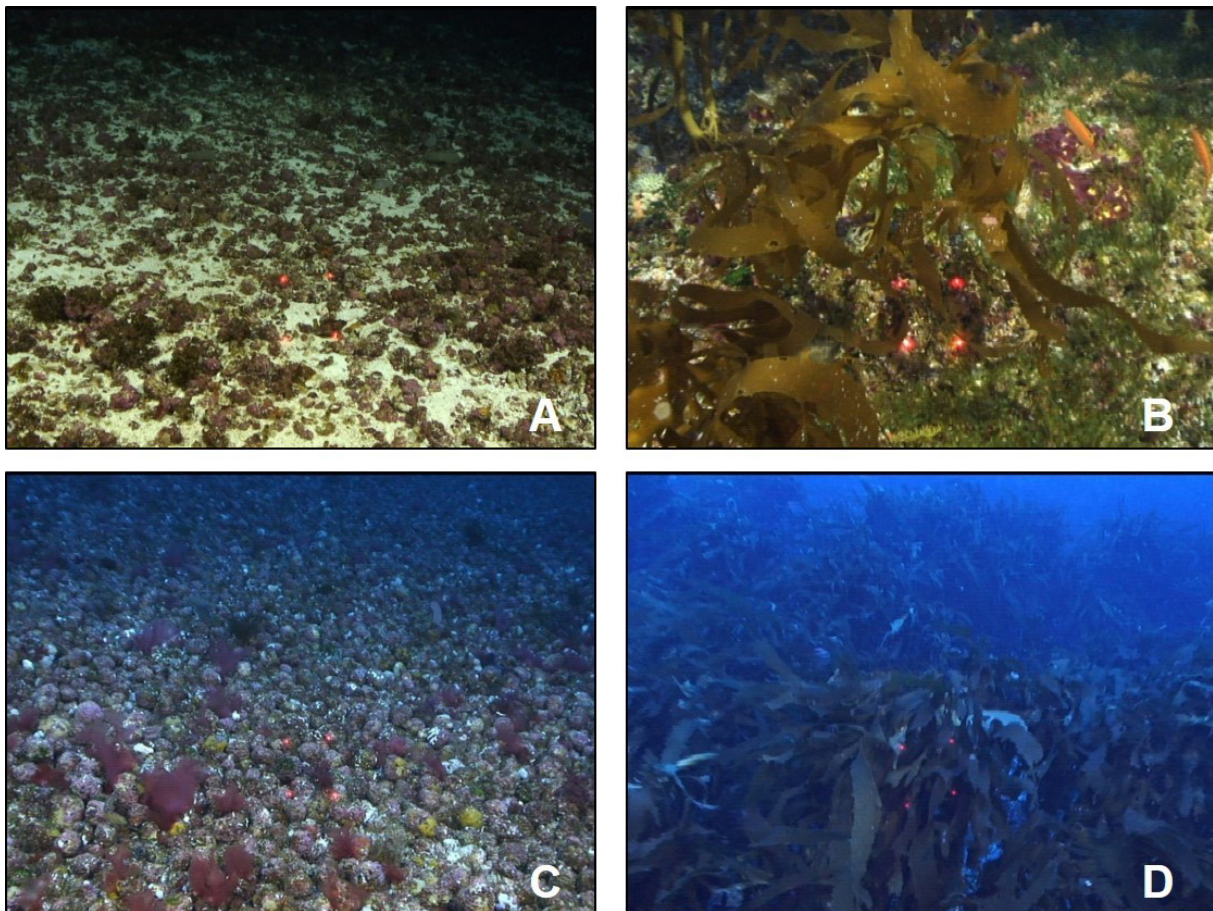

Fig. 9. Vema Seamount summit. Images obtained from video footage taken during the cruise of the R/V *Dr Fridtjof Nansen* in the SE Atlantic. **A**. Dive 4 (95–91 m depth). **B**. Dive 5 (91–42 m depth). **C–D**. Dive 6 (72–43 m).

rocks were also reported (Bergstad *et al.* 2019b); summit temperatures and salinity were 12–13°C and 34.9 psu, respectively.

The current number of benthic hydroids described from the Vema Seamount reaches 35 species and rises to 45 when those reported from Valdivia are included. A similar number was found by Calder (2000) at three semounts near Bermuda (48 species), which is clearly higher that those provided by Watson & Vervoort (2001) from the Tasmanian seamounts (13 species) and Moura (2015) from the Gorringe Bank (27 species). Ramil *et al.* (1998) reported on 21 species of haleciids and plumularioid hydroids collected on Lusitanian seamounts during the French SEAMOUNT 1 Expedition, but the total number of species collected during that survey totals ca 60 species (Ramil, unpublished data). The specific richness at the Vema Seamount seems to be related to the more heterogeneous habitats found at the summit, and mainly to the presence of kelp forests (*Ecklonia* sp.), providing suitable secondary substrates for hydroids. The settlement on kelps avoids the negative effects of sedimentation and improves the water exchange around the colonies, enhancing their trophic capabilities (Boero 1984). The importance of algal communities on seamounts to promote hydroid diversity was also pointed out by Calder (2000) and Moura (2015). The Valdivia Bank was also studied during several Spanish fisheries surveys, but Gili *et al.* (1989) reported on only two hydroid species, while González-Porto (2011), although highlighting the importance of the hydroids among the benthic invertebrates, did not provide a species list, and his material remains as yet unidentified.

Endemism and connectivity are two of the main concerns in seamount research, and their role in ecology has not yet been fully understood. Wilson & Kaufmann (1987), after an extensive review of the seamount literature, estimated the endemism of the invertebrates at 15.4%, and highlighted the affinity of the seamount biota with that of the nearest continental shelf as well as the importance of widespread and cosmopolitan species. High endemism rates at seamounts also seem to be supported by the results of Richer de Forges *et al.* (2000) and Koslow *et al.* (2001), who reported on up to 43% of new species and 33% of potential endemics on the Tasmanian and Southeast Coral Sea seamounts. At the Vema Seamount, Berrisford (1969) reported 28% of endemics, mainly based on sponges and ascidians (see Millar 1968 and Levi 1969).

Nevertheless, Samadi *et al.* (2006) indicated that at the Norfolk ridge seamounts, despite the fact that they can represent hotspots of biodiversity linked to the high productivity of these areas, local endemism was never noted, and a low genetic connectivity between seamounts was detected only for species with limited dispersal capabilities. In the same way, O'Hara *et al.* (2007) showed that for ophiuroid assemblages, the specific richness and rates of endemism are similar at seamount and non-seamount habitats. These and other evidence accumulated over the last few years revealed that the paradigms on endemicity and isolation of seamount faunas are not well supported (Rowden *et al.* 2010; Clark *et al.* 2012), and only the species with poor dispersal capabilities show narrow-range endemism and low genetic connectivity between populations (Samadi *et al.* 2006; O'Hara 2007; Rogers 2018).

When analyzing the biogeographic patterns at the Vema and Valdivia seamounts, we found that most of the identified species are widely distributed in the three major oceans: eleven are circumtropical, four cosmopolitans, two circumglobal, two Indo-Pacific, and three are eastern Atlantic, previously reported from the European coasts. Moreover, none of the new taxa described herein are restricted to these seamounts. The genus *Monostaechoides* gen. nov. currently includes two species, *Monostaechoides providentiae* gen. et comb. nov. (reported from its type locality, Providence Island, West Indian Ocean (Jarvis 1922) and Bermuda (Calder 1997, as *Antennella quadriaurita*)) and *Monostaechoides bertoti* (Galea & Ferry 2015) gen. et comb. nov. (from Martinique, Western Atlantic). *Monotheca bergstadi* sp. nov. represents the species with the most restricted geographical distribution, only reported from the Vema and the south and east coasts of South Africa (Millard 1966, 1975, both as *Plumularia*

pulchella). These results are consistent with those obtained at the Vema Seamount by Millard (1966), who indicated that 19 out of the 23 identified hydroids were widely distributed species (cosmopolitan and Indo-Pacific); in both cases, the affinity with the South African fauna is very high (91% according to Millard (1966) and 94% resulting from our research). Despite the affinity of the fish fauna with that of the Tristan da Cunha Islands (Penrith 1967; Berrisford 1969) and the presence of the rock-lobster *Jasus tristani* Holthuis, 1963 (= *Jasus paulensis* (Heller, 1862)) at the Vema Seamount, the affinity of the hydroid fauna is lower, sharing only six species, all of them with wide geographical distributions (five circumglobal and one cosmopolitan) (for a list of the hydroids from Tristan da Cunha, see Galea (2015: table 2). Lutjeharms & Heydorn (1981) suggested that the colonization of the Vema Seamount by *J. paulensis* could have occurred by drift, but our results seem to indicate that this way of dispersal is not suitable for hydroids despite rafting being an effective dispersal mechanism for benthic hydroids (Cornelius 1981, 1992a, 1992b; Calder 2000).

The dominance of widely distributed species within the hydroid seamount fauna is also consistent with the results obtained for other Atlantic seamounts. Ramil *et al.* (1998) reported on 21 species from six Lusitanian seamounts, and only one seems to be restricted to the seamounts; of the remaining species, six are cosmopolitan, ten Atlantic-Mediterranean, and four Northeast Atlantic. Calder (2000) identified 48 species from three Bermuda seamounts, of which 43 were reported elsewhere in the Western Atlantic Tropical region. Moura (2015) indicated that all of the 17 species identified at a specific level from the Gorringe Bank are also present in the Mediterranean Sea, and show a high affinity with the Lusitanian fauna. Only the study carried out by Watson & Vervoort (2001) on the hydroids collected from 14 Tasmanian seamounts reported a relevant rate of endemism among the group, accounting for ca 29% (four out of 14 species). This rate seems consistent with those reported for other major phyla, suggesting a high level of endemism on the Tasmanian seamounts (Watson & Vervoort 2001).

The analysis of the life cycles of the hydroid species collected in this study reveals that fixed gonophores occur in 17 species (63%) and free medusae in only 9 species (33%). The dominance of species with fixed gonophores vs free medusae in their life histories was also highlighted by Calder (2000) and Moura (2015) while focusing on other Atlantic seamounts. Ramil *et al.* (1988) studied only families without a medusa stage and, consequently, comparisons are not possible in this case. The same reproduction pattern is shared by the hydroid fauna of Tasmanian seamounts studied by Watson & Vervoort (2001): all genera except *Tasmanaria* Watson & Vervoort, 2001 were reported as having fixed sporosacs in their life cycles (Bouillon *et al.* 2006).

Short-lived meroplanktonic stages in the life cycles, associated with particular water circulation patterns found on seamounts (e.g., Taylor column, eddy formation, rectified flows) that enhance the local larval retention are considered as a biological advantage, once the species have been introduced (Rogers 1994, 2018; Johannesson 1988; Calder 2000). Nevertheless, this advantage also represents an impediment in colonizing remote seamounts. It is broadly assumed that species with long-lived planktonic larvae can disperse over long distances, while those with short-lived larvae and low adult mobility show restricted geographical distributions (Samadi *et al.* 2006; Rogers 2018). For South African hydroids, Gibbons *et al.* (2010) found that holoplanktonic taxa display less biogeographic structure that meroplanktonic ones, and these, in turn, less than the strictly benthic taxa. Nevertheless, the seamount hydroid fauna is dominated by species with suppressed medusa stages and short-lived planula larvae, but with wide (in many cases near-cosmopolitan) distribution patterns. This paradox ("The paradox of Rockall", see Johannesson 1988) was also pointed out by Boero & Bouillon (1993), who indicated that, in Mediterranean hydroids, the cosmopolitan species show a prevalence of life cycles with fixed sporosacs, which further suggests that the distribution of hydroids does not depend on their modes of dispersal, but on their limits of environmental tolerance. In our opinion, the tolerance to different environmental conditions is the key to understanding the current species distribution in marine ecosystems, but their dispersive abilities, not

only those linked to their life histories, drive the distribution patterns, at least in hydroids. In addition to the medusa and planula stages, the benthic hydroids show a remarkable capability to disperse over long distances by rafting on algae and other substrata, by fouling on ships (Cornelius 1981, 1992a, 1992b; Calder 2000; Ronowicz *et al.* 2015), and also through detached living colonies drifted by both surface and bottom currents. Invertebrate dispersion by rafting after either transoceanic dispersal events, such as tsunamis (Carlton *et al.* 2017), or floating marine litter (Kiessling *et al.* 2015), were recently highlighted and, in both cases, benthic hydroids benefit from this 'new' dispersal possibility. In this context, Calder *et al.* (2014) recorded 14 hydroid species on debris washed ashore on the west coast of North America after the tsunami that struck Japan on March 2011, while Kiessling *et al.* (2015) summarized 21 hydroid taxa as marine litter rafters. In addition, free-living colonies of *Amphisbetia operculata* (Linnaeus, 1758) were sampled by Ramil (1988) and Genzano *et al.* (2008) at several littoral areas, but more recently 'rolling tufts' of *A. operculata* (Ramil, unpublished data) and mats of *Aglaophenia parvula* Bale, 1882 (Gil 2017) were reported living on the deep shelf and bathyal muddy bottoms off Northwest Africa; this unusual dispersal mechanism through 'rolling colonies' could possibly be shared by other benthic hydroids. Pagliara *et al.* (2000) documented, under laboratory conditions, the existence of long-lived photosynthetic planulae in *Halecium nanun* Alder, 1859 and the capacity of some planulae of *Clytia viridicans* (Leuckart, 1856) to settle on the underside of air-water interfaces, producing floating colonies that could also represent new dispersal ways for hydroids, but there is no evidence whether this can really occur in the sea. Consequently, the dispersal abilities of benthic hydroids by rafting and drifting support their capabilities to colonize remote habitats, such as seamounts, and explain, at least in part, the wide distributions displayed by species without a medusa stage in their life cycles. As Johannesson (1988) pointed out, the transport of benthic invertebrates over long distances may be more effective than the larval dispersal, even when these events are rare or isolated.

Given the significant number of colonies and varied species found on ghost fishing nets (e.g., *Eudendrium ramosum*, *Zygophylax* sp., *Stegolaria geniculata*, *Stegopoma giganteum*, *Campanulina denticulata*, *Campanularia hincksii*, *Clytia gigantea*, *Halecium tenellum*), these ghost nets could also represent another dispersal possibility for benthic hydroids, at least when hydroids colonize near-surface or midwater driftnets. However, all fishing devices that we observed at the Vema and Valdivia seamounts during the video surveys were demersal fishing gear, entangled on coral mounds or on rocky bottoms. In this case, the ghost nets offer suitable secondary substrates for hydroid settlement but probably do not represent a dispersal pathway for seamount species.

To summarize, the hydroid community at the Vema and Valdivia seamounts lacks endemic species and is dominated by widely distributed taxa (mainly circumtropical, cosmopolite and circumglobal) with life histories with the medusa stage suppressed. The capacity of hydroids to colonize remote seamounts seems driven by a high plasticity of their dispersal mechanisms, but also by their tolerance to different environmental conditions. At the same time, the absence of long-lived planktonic stages contributes to maintain the hydroid populations on seamounts.

Acknowledgements

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