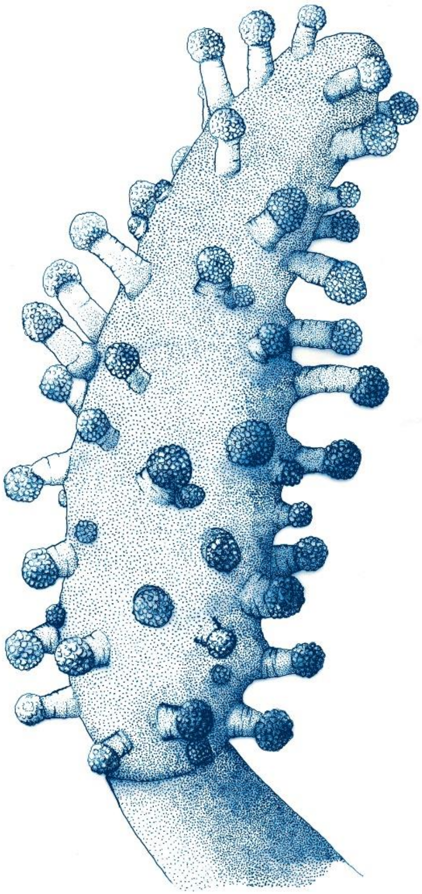
Diversity, ecology and biogeography of Antarctic benthic hydrozoans: the Weddell Sea and the Scotia Arc as study cases.

Joan J. Soto Àngel



PhD in Biodiversity (3001)

Advisor: Álvaro L. Peña Cantero

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Diversity, ecology and biogeography of Antarctic benthic hydrozoans: the Weddell Sea and the Scotia Arc as study cases.

MEMÒRIA PRESENTADA PER JOAN JOSEP SOTO ÀNGEL, CANDIDAT AL GRAU
DE DOCTOR
PER LA UNIVERSITAT DE VALÈNCIA

DIRECTOR:

DR. ÁLVARO LUIS PEÑA CANTERO

VALÈNCIA, MAIG DE 2017

El Dr. ÁLVARO LUIS PEÑA CANTERO, Professor Titular del Departament de Zoologia de la Facultat de Ciències Biològiques:

AUTORITZA la presentació de la memòria titulada "Diversity, ecology and biogeography of Antarctic benthic hydrozoans: the Weddell Sea and the Scotia Arc as study cases" en compliment de la normativa vigent, i CERTIFICA que els resultats inclossos van ser obtinguts sota la seua direcció a l'Institut Cavanilles de Biodiversitat i Biologia Evolutiva per JOAN JOSEP SOTO ÀNGEL, i constitueixen la seua tesi per optar al grau de Doctor per la Universitat de València.

I perquè així conste, signa el següent certificat.

Dr. Álvaro Luis Peña Cantero

València, 29 de maig de 2017

Si són colonials,
acrobàticament,
embranquen l'art contemporani dels seus cossos
i codifiquen la repartició d'oficis
de les seues societats ancestrals.
Si són solitaris,
dansen sofisticadament a la deriva,
vestits amb tela de paraigua,
amb dramatisme agestual.
Però tots senyalitzen el seu contacte
amb jeroglífics urticants.

Laia Fontana i Bria. Novembre 2015

Els nostres veïns submarins.
Bestiari contemporani de la Mediterrània.

The tree of life should perhaps be called the coral of life, base of branches dead;
so that passages cannot be seen.

Charles Darwin. 1837-1838

Notebook on transmutation of species.

On ne voit bien qu'avec le cœur;
l'essentiel est invisible pour les yeux.

Antoine de Saint-Exupéry. Abril 1943

Le Petit Prince.

Agraïments

Ho reconec: he deixat aquesta secció per al final i molt probablement no manifeste del tot com d'agraït estic a qui, d'una manera o d'altra, ha compartit amb mi aquesta (llarga) temporada de ma vida. Allà vaig:

En primer lloc, el meu més profund agraïment a Álvaro Peña: infinites gràcies per oferir-me l'oportunitat de fer aquesta tesi doctoral i per guiar-me durant el procés. Gràcies pel teu consell expert; pels colpets a l'esquena i pels tocs d'atenció (sí, gràcies també per això); per la paciència amb les *deadlines*, els *sprints* i amb totes-les-coses paral·leles. I sobretot gràcies per deixar-me recórrer camins desconeguts, i per confiar que aquest dia, finalment, arribaria.

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I per últim a tu, Luis. M'has fet retrobar el nord, fins acabar convertint-te en ell. Aquesta tesi va dedicada a tu. Gràcies per fer-me coneixedor del vertader significat de felicitat.

Contents

Abstract

Benthic hydrozoans are one of the most speciose and characteristic taxa living in Antarctic waters, with highly diverse genera, such as *Antarctoscyphus*, *Halecium*, *Oswaldella*, *Schizotricha*, *Staurotheca*, and *Symplectoscyphus*, being common in the area. Our knowledge of these and other Antarctic hydrozoans has recently increased thanks to several studies, but much remains to be done in some areas of the Southern Ocean and with some particular taxa. In the present dissertation, traditional morphology, cnidome determination, multivariate analyses, and comprehensive literature searches were employed to improve our current understanding of the group, with a strong focus in the relevant regions of the Scotia Arc and Weddell Sea, providing novel data on the reproductive phenology, distribution, use of substrate, and epibionts of the studied species. A complete inventory of benthic hydrozoans from the Patagonian and Antarctic regions was produced, allowing the analysis of faunal affinities, endemism, and trends in the relevant scientific literature in the area. In the Scotia Arc and surrounding waters, 45 species belonging to 9 families and 20 genera were found, including the new species *Halecium stoloniferum* and *Schizotricha discovery*. Leptothecata was the dominant taxon. Multivariate analysis based on two similarity indexes showed that the Scotia Arc has greater affinity with Antarctica than Patagonia, also highlighting the effectiveness of the Polar Front as a major oceanographic barrier, and strongly supporting the placement of the Scotia Arc within the Antarctic region. In the Weddell Sea, 77 species belonging to 21 families and 28 genera were found in what constitutes the most prolific collection of Antarctic benthic hydroids hitherto analyzed. Leptothecata was again the dominant taxon, but there was a higher percentage of Anthoathecata species than in other collections from Antarctic waters. A new species, *Aglaophenia baggins*, was collected in the Weddell Sea, representing the first evidence of this genus in any polar region, and the first record of any member of the family Aglaopheniidae in Antarctic waters. The most likely explanations for this unexpected finding include the potential recent arrival of the species (either by its own means or by human mediation), or the existence of a previously overlooked natural population. In conclusion, the present dissertation increased our knowledge of taxonomic, ecological, and biogeographical aspects of 102 different species, besides presenting evidence for the placement of the Scotia Arc as part of the Antarctic region, updating the inventory of Antarctic hydrozoans to 227 species, describing three new species to science, extending the known bathymetric range and reproductive phenology of many species, and providing 11 new records for the Scotia Arc, 27 for the Weddell Sea, and 10 for the entire Antarctic region.

Introduction

1. The Antarctic benthos: a song of ice and forest

The Antarctic is a polar region situated in the South Pole that includes a huge continent named Antarctica, the ice shelves, and the surrounding waters and islands situated south of the Antarctic Convergence or Polar Front. This oceanographic barrier results from the encounter of Antarctic waters with sub-Antarctic ones (Moore et al. 1999 and references therein), and contributes to the isolation of the fauna inhabiting the Southern Ocean by forming strong latitudinal gradients of temperature and salinity (i.e. density). This cold ring has been considered as ''one of the strongest natural boundaries in the world ocean'' (Crame 1999), and delimit one of the most discrete and zoogeographically isolated marine ecosystems (Dayton 1990; Arntz et al. 1994).

A major oceanographic current, the Antarctic Circumpolar Current (ACC), surrounds the entire Antarctic continent in a non-interrupted flux of clockwise direction (Orsi et al. 1995). Within the ACC, two major cyclonic cells of recirculating waters, the Weddell and Ross gyres, contribute to the upwelling of cold, nutrient rich water (Deacon 1979). Unlike the Arctic, the Antarctic includes a true continent isolated from others, and has no influence of river flow (Orejas and Jiménez 2017 and literature therein). Within High Antarctic waters, marine benthic habitats are subjected to relatively constant physical parameters such as temperature, salinity and substrata, with few remarkable barriers (Orejas et al. 2000, Gutt et al. 2015).

The Antarctic shelf, which is deeper than any other around the globe, averaging about 500 m (but sometimes deeper, Dayton 1990), mainly consists of soft bottoms dominated by benthic suspension feeders that develop complex epifaunal assemblages (Teixidó et al. 2004 and references therein). These communities (Fig. 0.1), which have been considered among the richest in terms of sessile fauna (Dayton 1990) and macroinvertebrate diversity (Clarke 2008) in the global ocean, cover large sections of the Antarctic continental shelf around the whole continent (Gili et al. 2006 and literature cited), a unique phenomenon in marine biogeography (Orejas et al. 2000). This probably results from the oceanographic conditions propitiated by the ACC (Clarke and Johnston 2003). Biomass, complexity and species richness of some Antarctic benthic assemblages are comparable to other mega-benthic communities in the tropics and temperate seas (Thomas et al. 2008, Orejas and Jiménez 2017 and references therein). Ascidians, bryozoans and sponges dominate many of the Antarctic shelf benthic communities (Galerón et al. 1992), and cnidarians are, in many cases, one of the main contributors to the tridimensional structure of these communities (Orejas et al. 2000), functioning as ecosystem engineers (Orejas et al. 2002 and references therein), increasing the stability of the substratum, acting as nursery, providing a broad range of habitats and enhancing bentho-pelagic coupling (Gili and Coma 1998, Artnz et al. 1994, Orejas and Jiménez 2017). In this animal forest inhabit a wide spectrum of taxa, including opisthobranchs, asteroids, pycnogonids, amphipods and isopods among many others (Grebmeier and Barry 1991; Clark et al. 2015), some of them reaching large sizes, probably due to high oxygen availability and low metabolism (Chapelle and Peck 1999, and references cited). In contrast, top predators are generally restricted to slow-moving invertebrates (i.e. echinoderms and nemerteans), whereas there is an almost complete lack of skeleton-crushing predators (i.e. fish and decapodes) (Aronson et al. 2007 and literature cited), although they are rather well represented in the deep shelf and slope (Arntz et al. 1994). It is estimated that the number of macrozoobenthic species inhabiting the Antarctic shelf range between 11.000 and 17.000, though the real species richness is probably much higher (Gutt et al. 2004). The degree of endemism in the Antarctic benthic fauna is, in general, distinctly high when compared with other regions, and it varies considerably between different zoological groups, from a 50% as mean value (Griffiths et al. 2009) up to a 97% in some marine taxa (Gili et al. 2016).

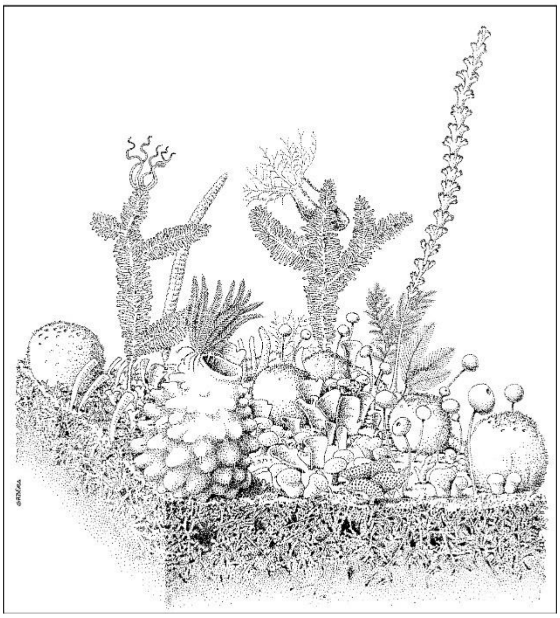

Figure 0.1 Representation of an Antarctic community of benthic suspension feeders (author: Jordi Corbera; originally published in Orejas et al. 2000)

Antarctic benthic fauna has multiple origins: relict species, taxa that arrived from somewhere else, and taxa that have evolved *in situ* (Clarke and Crame 1989). Antarctic benthos present ecological characteristics reminiscent of paleozooic marine communities (Aronson and Blake, 2001; Gili et al. 2006 and literature cited), as a result of a long isolation, coupled to the effects of reduced terrestrial input and favorable conditions due to resuspension processes (Orejas et al. 2000, Gili et al. 2006). Nowadays, and despite the stability of the factors mentioned above, the distribution of benthic communities at small scale is highly patchy, and responds to both historic and ecological features (Gili et al. 2001). The main factors affecting the structure and distribution of these communities are the variations in ice cover and ice scouring by grounding icebergs, sediment dynamics, local hydrodynamic, and trophic factors (Clarke and Crame, 1989; Gutt and Piepenburg 2003, Barnes and Conlan 2007). The advective supply of phytodetritus has been considered as the main and constant food source supporting these communities (Thrush et al. 2006).

The High Antarctic has been considered as the least anthropogenically disturbed placed on Earth, but vulnerable to large-scale climatic changes (see Gutt and Piepenburg 2003 and references therein). The ecological and evolutionary adaptations of the Antarctic fauna to the coldest marine temperatures and most intense seasonality of primary production on Earth (see Peck et al. 2006) make the Antarctic communities particularly vulnerable to global warming and the concomitant invasion of species from lower latitudes (Barnes et al. 2006 and references therein). Indeed, a short-term increase in temperature in the shallow waters surrounding the Antarctic Peninsula is already known for the last decades (Meredith and King 2005). Despite some evidence of non-indigenous species in terrestrial Antarctic environments (Rogan-Finnemore 2008 and cited literature), neither changes in marine benthic communities nor alien species have been reliably documented from the Southern Ocean so far (Griffiths et al. 2013, but see Aronson et al. 2007 for a contrasting opinion).

2. Introducing the hydrozoans

Hydrozoa Owen 1843 is a class of the *Phylum* Cnidaria Verrill, 1865. With ca. 3709 species described to date (Schuchert 2017), hydrozoans constitute a well-defined taxon, sharing a set of characters: Symmetry either tetramerous, polymerous or, exceptionally, biradial; gastrovascular system simple, without stomodeum, septa or gastric tentacles; acellular mesoglea; sexes (commonly) separated; gametes ectodermal in origin (with few exceptions), usually ripening in the ectoderm and shed directly to the outside; medusae with velum (except in *Obelia*); polyps solitary or (more often) colonial, modular, with interconnected coelenterons, often polymorphic, with chitinous and/or calcium carbonate exoskeleton; cnidocysts of about 24 major types, generally restricted to the ectoderm, being atrichous isorhizas the only common type found throughout the whole class) (Bouillon et al. 2006).

This group of animals has high plasticity in terms of life cycle strategies, which, in turn, translates into a wide array of morphologies, habitat use, trophic strategies and ecological adaptations (cf. Cartwright and Nawrocki 2010). The typical hydrozoan life cycle includes a benthic, usually colonial stage (the polyp) from which a planktonic medusa is produced; male and female medusae release gametes that combine in the water; fertilized egg later develops into a ciliated larva (the planula); finally, the planula settles and gives rise to a new polyp, completing the cycle (Bouillon and Boero, 2000).

Nevertheless, there are exceptions to the general pattern: the medusa stage may be reduced to various degrees or even suppressed entirely (fixed sporosacs); the reduced medusae (= medusoids, swimming gonophores) can be released only as temporary, non-eating, short-lived planktonic forms that function strictly as gamete-carriers; the planktonic planula may develop directly into a medusa or other planktonic stage, leading to the suppression of the benthic polyp stage from the life cycle; some representatives lack the planula stage.

Benthic hydroids are one of the major components of hard and soft bottom biocenoses in shallow coastal waters (Boero 1984, Morri et al. 1991; Gili and Hughes, 1995), where they often act as key regulators of zooplankton abundance (Gili et al. 1998), and even may compete with algae during some periods (Bianchi et al. 2004) or may persist throughout the year (Bellan-Santini et al. 2002). Especially, but not exclusively, species with a medusa stage have a relevant role in the benthic-pelagic coupling (Boero et al. 1996; Marcus and Boero, 1998). Benthic hydroids constitute the food supply of several organisms (MacLeod and Valiela 1975, Folino 1993, Stachowicz and Lindquist 2000, Martin 2003) and provide substrate and refuge for others, positively affecting the recruitment of larvae of merobenthic species (Di Camillo et al. 2013 and literature within). Some species may even be considered as habitat former, increasing spatial complexity, which positively affects biodiversity and enhances interspecific interactions, being an important but neglected component of the so-called marine animal forest (Di Camillo et al. 2017).

The ubiquity and abundance of some hydrozoans contribute to their considerable economic and ecological importance in marine environments. In the plankton, some hydromedusae may appear in large numbers, consuming significant amounts of zooplankton, and competing with other species for the same food resources (Zelickman et al. 1969; Matsakis and Conover 1991; Rees and Gershwin 2000; Purcell and Arai 2001; Boero et al. 2008), while others are involved in the transmission of parasites (Marcogliese 1995; Martorelli 2001) and bacterial diseases (Ferguson et al. 2010) to fish. They also affect aquaculture negatively by killing fish in net-pens, tourism by stinging swimmers, fisheries by clogging nets, and operation of power plants by clogging intake systems (Purcell et al. 2007).

The sensitivity of hydrozoans to environmental variations makes them a potential ecological and climate change indicators, since it is known that an increase in temperature has profound effects on both hydroids (Puce et al. 2009) and hydromedusae (Purcell 2005; Purcell et al. 2007). Some species are of medical importance (Burnett and Gable 1989; Moats 1992; Burnett et al. 1994), while others have become a nuisance in the parts of the world where they have been introduced (Meek et al. 2012, 2013; Govindarajan and Carman 2016). Indeed, hydrozoans are one of the animal groups most frequently relocated by human-mediation, as noted by their ubiquity in fouling communities in harbours (Megina et al. 2013), ship hulls and ballast waters (Morri and Boero 1986). Certain aspects of their life cycles improve their invasiveness, such as the occurrence of encysted stages or their ability to reverse development (Boero and Bouillon 1993; Piraino et al. 2004), which allows them to surpass hard environmental conditions.

3. The study of Antarctic benthic hydroids: past and present

In the Antarctic benthos, hydrozoans are one of the most diversified and characteristic zoological groups (Peña Cantero 2014c), ubiquitous and widely represented in the different epibenthic communities (Clarke and Johnston 2003). The study of benthic hydroids in the Southern Ocean began simultaneously with that of other taxa through several expeditions carried out at late nineteenth and early twentieth centuries (Fig. 0.2). During the British *Challenger* Expedition aboard the homonymous HMS *Challenger* (1872-1876), a great number of benthic hydroids from different sub-Antarctic Islands (Marion Island, Kerguélen region and Falkland Island) were collected and subsequently studied by Allman (1876, 1883, 1888). The genus *Staurotheca* was established from sub-Antarctic specimens sampled from Marion Island (Allman 1888). However, a single species, *Eudendrium rameum*, was reported within the limits of the Antarctic convergence, from South Georgia. Soon after, Pfeffer (1889) studied a small-unlabored collection from the transit of Venus German Expedition to South Georgia during the first international Polar Year (1882-1883) collected by Karl Von de Steinen from shallow-waters around *Moltke* station. The first evidence of the genus *Symplectoscyphus* was then reported from Antarctic waters. In the meantime, the Belgian Antarctic expedition aboard RV *Belgica* (1897-1899) collected samples from South Shetland and from off High Antarctica (Antarctic Peninsula and the Bellingshausen Sea) for the first time. The hydroids obtained were studied by

Hartlaub (1904), who contributed with nine new records for the Antarctic hydrozoan fauna, seven of which new to science, including the first report of both *Staurotheca* and *Oswaldella* from Antarctic waters. A year later, Hartlaub (1905) performed the first review of the current knowledge of Antarctic and sub-Antarctic benthic hydroids, including the description of a new species from Von de Steinen's material unnoticed by Pfeffer (1889). Almost contemporary, Jäderholm (1904, 1905) noticed 23 species, 16 new, among the abundant material collected by the Swedish Antarctic Expedition with the *Antarctic* (1901-1904) from South Georgia and the east coast of Graham Land (Antarctic Peninsula). The first Antarctic species of the genera *Halecium* and *Schizotricha* were described in Jäderholm's contributions, and the first specimen of *Antarctoscyphus* was found, although its generic name would not be ascribed until nearly a century later.

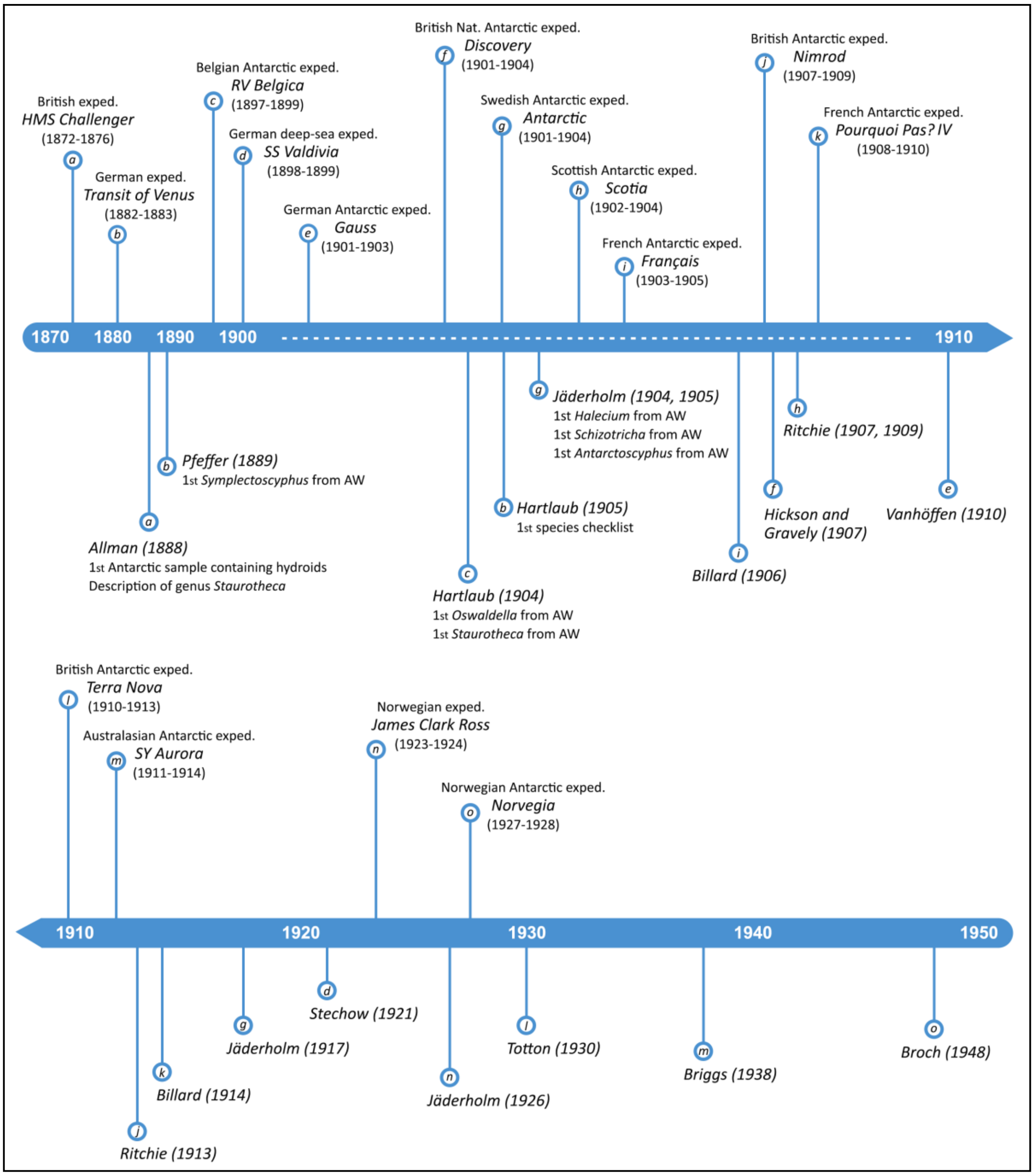

Figure 0.2 Timeline showing early Antarctic expeditions (above) and scientific contributions (below)

Billard (1906) studied the benthic hydroids collected during the French Antarctic expedition (1903-1905) aboard the ship the *Français* off the west coast of Graham Land. A collection of benthic hydroids from the Ross Sea obtained during the British National Antarctic Expedition on the RRS *Discovery* (1901-1904) was examined by Hickson and Gravely (1907). These authors reported and described 17 species, of which 16 were previously unknown from Antarctic waters, and ten of them were new to science. Benthic hydroids from the Weddell sector and Orkney Islands collected during the Scottish National Antarctic Expedition aboard the *Scotia* (1902-1904) were studied by Ritchie (1907, 1909), whose contributions allow to increase in seven representatives the number of species known from Antarctic waters, four of which were new to science. Vanhöffen (1910) studied a prolific collection of benthic hydroids from the Davis Sea obtained during the German Antarctic Expedition aboard the *Gauss* (1901-1903). Twenty-four species were inventoried by Vanhöffen, of which fourteen new reports for the Antarctic region, and six new species. The same year, Jäderholm (1910) studied a collection obtained by Carl Johan Frederik Skottsberg during Swedish Magellan Expeditions (1907-1909) aboard the *Cachalote*. Among the material studied, a shallow-water sample from South Georgia containing *Abietinaria abietina* (Linnaeus, 1758) was documented. At the same time, the British Antarctic Expedition (1907-1909) aboard the *Nimrod* was taking place in the Ross Sea and surrounding waters. Ritchie (1913) examined the hydroid collection and reported 11 species, only one constituting a new record from Antarctic waters. Billard (1914) was in charge of studying the benthic hydroids collected by French Antarctic Expedition (1908-1910) aboard the *Pourquoi-Pas? IV* off the west coast of the Antarctic Peninsula and from the Bellingshausen Sea. Twelve species were reported, four of which were evidenced from Antarctic waters for the first time, and three were new to science. By means of the examination of additional material from the Swedish expedition (1901-1904), deposited in the University of Lunds, Jäderholm (1917) described two new *Symplectoscyphus* from Graham Land. Shortly after, Stechow (1921) studied a collection of benthic hydroids obtained during the German deep-sea expedition aboard the SS *Valdivia* (1898-1889). Antarctic material included three species from Bouvet Island, two of them new. A few years later, Jäderholm (1926) studied a small collection of hydroids from the Norwegian expedition to the Ross Sea aboard the ship *James Clark Ross* (1923–1924), including one new species. Totton (1930) studied the hydroid fauna from the Ross Sea and nearby waters obtained by the British Antarctic Expedition aboard the *Terra Nova* (1910-1913). Twenty-two species were documented, thought only two were previously unknown from Antarctic waters. The benthic hydroids obtained by the Australasian Antarctic Expedition aboard the SY *Aurora* (1911-1914) were documented by Briggs (1938), who reported fifteen species from off George V Coast (East Antarctica), three of them new to science.

The geopolitical events that occurred during and after the Second World War restrained the scientific production in many fields of knowledge, and the study of Antarctic hydrozoans was no exception. Very few contributions dealing with benthic hydroids (excluding Stylasteridae) were produced during the 1940s, 1950s and 1960s. Broch (1948) examined several specimens obtained by the Norwegian Antarctic Expedition aboard the *Norvegia* (1927-1928) from the Antarctic Peninsula, Bouvet Island, Peter I Island, South Georgia and the South Shetland Islands. Ten species were reported in Broch's contribution, four of them previously unknown from Antarctic waters, including a new species. Some years later, the benthic hydroids obtained by the Soviet Antarctic Expedition (1955-1959) were documented by Naumov and Stepanjants (1962). Among the fourteen species documented, five were unknown from Antarctic waters, and two of them were described as new.

From the beginning of the seventies, the study of the Antarctic hydrozoans underwent a strong acceleration. Naumov and Stepanjants (1972) studied the collections of benthic hydroids obtained off Adélie Coast during the XIIth and XVth French Antarctic Expeditions (1961-1965). Twenty species were found, but a single species was previously unknown from Antarctic waters. These authors provided additional notes on the vertical distribution of the species inventoried, constituting the first non-taxonomic approach to the knowledge of Antarctic benthic hydroids. The same year, Stepanjants (1972) documented the benthic hydroids from the Davis Sea collected by the XIth Soviet Antarctic Expedition (1965-1966), with the description of a new species. Vervoort (1972a) studied shallow-water benthic hydroids collected in the vicinity of Arthur Harbor, in Palmer Archipelago. Nine species were documented, one previously unknown from Antarctic waters. That same year, Vervoort (1972b) documented the benthic hydroids obtained during the US expeditions aboard the RV *Theta* (1956), RV *Vema* (1957-1962) and RV *Yelcho* (1962). Although these cruises centered the sampling effort on sub-Antarctic Patagonia, a few samples from off Graham Land and the South Shetland Islands region, containing three species, were reported. At the end of the same decade, Stepanjants (1979) reviewed the current knowledge of Antarctic and sub-Antarctic hydroid fauna, described five new species and compiled the available information of the 38 species inventoried in previous Soviet and French expeditions. Furthermore, this major contribution put in order the existing information, and shed light to a better understanding of patterns of reproduction, and vertical distribution from Antarctic benthic hydroids. For the first time, biogeographic patterns were defined based on the existing information about the distribution of the taxa surveyed.

From the late 1960s to the early 1990s, a new key contributor and a new type of scientific contributions entered the scene. Some papers based on specific morphological characters, specific taxa (new or already known) or genera were produced by Olga Blanco. She contributed to knowledge of the genera *Antarctoscyphus* (Blanco 1968), *Filellum* and *Halisiphonia* (Blanco 1984a), *Oswaldella* (Blanco and Bellusci de Miralles 1972a; Blanco and Lunaschi de Redolatti 1977), *Staurotheca* (Blanco 1971, 1992a), and predominantly *Symplectoscyphus* (Blanco 1969, 1977a, 1977b, 1982, 1985, 1991, 1992b; Blanco and Bellusci de Miralles 1970), with the description of several new species from the re-examination of museum specimens and new material collected by the Argentinian Antarctic Institute in Low Island. Additionally, some collections obtained by the same institution from Peter I Island (Blanco and Bellusci de Miralles 1972b) and the Antarctic Peninsula (Blanco 1984b) were documented by these authors. The latter reported 21 different species already known from Antarctic waters.

In the mid-1990s, the most prolific contemporary author began its work with Antarctic benthic hydroids by studying the material obtained during the Spanish Antarctic Expedition *Antártida 8611* (Peña

Cantero and García Carrascosa 1995). Among the many species reported, 10 species would be described as new in upcoming contributions, and seven were unknown from Antarctic waters. Similarly to Blanco's contributions, his early production was centered (in part) on a better taxonomic delimitation of some taxa such as *Abietinella* (Peña Cantero and García Carrascosa 1993); *Staurotheca* (Peña Cantero et al. 1996a, Peña Cantero et al. 1999b), with the description of two new species; *Oswaldella* (Peña Cantero and Vervoort, 1995, 1996, 1997, 1998; Peña Cantero and García Carrascosa 1998; Peña Cantero et al. 1995), with the description of seven new species; *Schizotricha* (Peña Cantero 1998; Peña Cantero and Vervoort 1999), with the description of two new species; and the establishment of the new genus *Antarctoscyphus* (Peña Cantero et al. 1997a). From mid-1990s to the early 2000s, many specimens of the most widespread Antarctic genera obtained by several German Antarctic Expeditions aboard the RV *Polarstern* were studied, and 21 new species were described (Peña Cantero et al. 1996b, 1997b, 1997c, 1999a, 2002). At the end of the 1990s, a comprehensive contribution compiled the available information about the distribution of Antarctic and Patagonian Leptothecata, provided a check list of the species known, compared the faunistic differences between these regions, and established biogeographic patterns for the species inventoried (Peña Cantero and García Carrascosa 1999).

In the meantime, a new kind of contribution, based on ecological, and/or evolutionary aspects with specific experimental design began to appear: the trophic strategies of *Silicularia rosea*, *Hydractinia angusta*, *Tubularia ralphii* and *Zyzzyzus parvula* were studied by Gili et al. (1996), Cerrano et al. (2000), Gili et al. (1999) and Orejas et al. (2000), and Gili et al. (2001) respectively. Gili et al. (2001) explored the reproductive output of selected species of *Schizotricha* and *Oswaldella*. Other authors presented evidences for the bipolarity of some genera such as *Bouillonia* (Svoboda et al. 2006), *Corymorpha* (as *Monocaulus*; Svoboda and Stepanjants 2001), *Monocoryne* (Stepanjants et al. 2003), as well as of ecological strategies (i.e. epibiosis of *Hydractinia* on brittle stars; Svoboda et al. 1997). On the other hand, taxonomic studies continued with Puce et al. (2002), who reviewed the genus *Eudendrium* from Antarctic waters by examining museum specimens and the new material obtained by the XV Italian Antarctic Expedition (1999-2000) from shallow waters from Tethys Bay, and described two new species to science.

In the mid-2000s, material from US Antarctic expeditions aboard RV *Eltanin*, *Hero*, *Islas Orcadas* and *Pr Siedlecki* was examined and documented by Peña Cantero and Vervoort (2003, 2004a, 2004b, 2005a, 2005b), with the description of 11 new species, including the new genus *Myxoscyphus*. The new family Clathrozoellidae and three new species were described by Peña Cantero et al. (2003). The following year, Peña Cantero et al. (2004) examined the Antarctic material of Campanularidae, Campanulinidae and Lafoeidae from German Antarctic Expeditions, with the description of a new species. Marques et al. (2005) reviewed the systematic status of the genus *Abietinella*. A few contributions on new Antarctic associations involving hydroids were published during those years: Piraino et al. (2003) reported larval necrophilia between pandeid polyps (previously unknown from Antarctic waters) and dead polychaetes in the Weddell Sea; Gili et al. (2006) evidenced, for the first time from the Southern Ocean, an association between

Corynidae and gorgonians, and therefore described a new species.

Later, many collections from a wide range of different geographic entities were studied. Benthic hydroids from off Livingston Island obtained during the Spanish expedition Bentart 94 aboard the BIO *Hesperides* were studied by Peña Cantero (2006). In the same year, Peña Cantero and Gili (2006) studied a hydroid collection from the remote Bouvet Island from material collected by the German Antarctic Expedition ANT XXI/2; and the benthic hydroids collected by the Spanish Antarctic expedition GEBRAP96 from the Bransfield Strait (Antarctica), associated to volcanic structures, were studied by Peña Cantero and Ramil (2006). The hydroid collection from the Spanish Antarctic expedition Bentart 95 from the South Shetland Islands region and the Antarctic Peninsula was documented by Peña Cantero (2008): to date, the largest collection dealing with Antarctic hydroids, with 51 species documented, though only two were new records for Antarctic waters. The following year, the benthic hydroids obtained in the Balleny Islands during the BioRoss expedition with the NIWA RV *Tangaroa* in 2004 was studied by Peña Cantero (2009). Brazilian expeditions PROANTAR (III and IV) to the Bransfield Strait area obtained a total of 36 hydroid species, which were studied by Peña Cantero and Vervoort (2009): two new reports for Antarctic waters were given, one of them a new species. The hydroid collections collected by Spanish Antarctic Expeditions *Bentart 2003* and *Bentart 2006* from off Peter I Island, the Bellingshausen Sea and off Low Island were later studied by Peña Cantero (2010a, 2012 and 2013, respectively), reporting for the first time from Antarctic waters five species, three of which were new to science. Galea and Schories (2012) studied a collection obtained by scuba diving from King George Island (Shetland sector), with one new record for Antarctic waters. A collection also obtained by scuba diving from Tethys Bay (the Ross Sea) was documented by Peña Cantero et al. (2013). Finally, benthic hydroids obtained by an Australian Antarctic expedition with the RV *Aurora Australis* in 2009–2010 were studied by Peña Cantero (2014b), and included the description of a new species.

New approaches concerning historical biogeography of Antarctic benthic hydroids saw the light at the beginning of the current decade: Marques and Peña Cantero (2010) defined areas of endemism in the Southern Ocean based on known distribution of representatives of *Oswaldella*; Miranda et al. (2013) repeated the analysis also including the records from species of *Antarctoscyphus* and *Staurotheca*. Furthermore, the existence of spirit-preserved specimens allow gathering molecular information. The first contributions on phylogenetic systematics and character evolution based on morphological and/or genetic evidences were produced for Antarctic hydroids in general (Peña Cantero et al. 2010) and for the genera *Oswaldella* (Peña Cantero and Marques 1999) and *Staurotheca* (Peña Cantero and Sentandreu 2017). Peña Cantero and Manjón Cabeza (2014) shed light on the environmental factors conditioning the spatial distribution of benthic hydroids, which constitutes the only contribution on the topic.

In parallel, more taxonomic effort and the subsequent description of new species was produced by dealing with material from several taxa such as *Oswaldella* (Peña Cantero 2007; González Molinero and Peña Cantero 2015), *Acryptolaria* (Peña Cantero et al. 2007), *Symplectoscyphus* (Peña Cantero 2010), *Halecium* (Watson 2008, Peña Cantero 2014a), and some little known anthoathecatae species (Peña Cantero 2015).

For the moment, according to the last revision by Peña Cantero (2014c), a total of 177 species of benthic hydrozoans belonging to Leptothecata and Anthoathecata (excluding Stylasteridae) are known from Antarctic waters. As a group, Antarctic benthic hydroids are characterized by their low diversity at the genus level, a few presumably monophyletic speciose genera that harbour ca. 75% of the species known (*Antarctoscyphus, Halecium, Oswaldella, Schizotricha, Staurotheca* and *Symplectoscyphus*), and the high level of endemism at the species level (ca. 80%), among the highest of all the different Antarctic zoological taxa (Peña Cantero and García Carrascosa 1999; Peña Cantero 2014c, and literature cited). However, at a genus level, a single endemism is known (i.e. *Myxoscyphus*).

Bathymetric and biogeographic patterns, as well as life cycle strategies of Antarctic benthic hydroids are unevenly distributed (Peña Cantero 2014c and references therein). In regards to biogeographic distribution, many species (29%) are considered circum-Antarctic. Other many species are for now restricted either to West or East Antarctica, but most of them are probably also circum-Antarctic. Some species are known exclusively from very small geographic areas, especially South Georgia and the Balleny Islands. Finally, a few species inhabiting Antarctic waters are found, besides, in sub-Antarctic waters. In relation to the bathymetric distribution, most species are eurybathic. Approximately 93% of the species are present in the shelf, though ca. 33% are shelf species absent from shallow (< 30 m) and deeper (>500 m) waters. Concerning life cycle strategies, most hydroid species have fixed sporosacs, and only few representatives have a free medusa stage, which could partially explain the high levels of endemism according to Peña Cantero (2014c).

In brief, the aforementioned scientific effort dealing with Antarctic benthic hydroid fauna has shed some light on the knowledge of the patterns and processes that explain their diversity, ecology and distribution. However, despite the recent increase in sampling and taxonomic contributions, there are still some regions, topics and taxa which knowledge are still limited or almost non-existent. We have only just begun to understand the true complexity of this speciose Cnidarians' class, but much remains to be done, and much remains to be understood.

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Objectives

The main objective of this thesis is to improve current knowledge of the Antarctic benthic hydroid fauna in three complementary aspects: diversity, ecology and biogeography. The term diversity here refers to several subjects, including species richness (i.e. number of representatives) through the different taxonomic ranks and geographic entities, and taxonomic analyses (description, identification, character evaluation, nomenclature, and/or classification) of selected taxa. Ecology is used in a wide sense, and includes basic biological aspects (see below). Finally, biogeography refers to patterns of distribution and faunistic affinities.

Within this broad framework, the specific objectives of the thesis are:

- Taxonomic study and cataloguing of the unpublished benthic hydroid collections ANT XV/3, ANT XVII/3, ANT XIX/5, ANT XXI/2 from the Scotia Arc and the Weddell Sea; including a better characterization of some taxa and, if applicable, the description of new species to science.
- Contributing to knowledge of the reproductive phenology, bathymetric range, use of substrate, and distribution of the species inventoried.
- Providing a complete and updated catalogue of the benthic hydrozoans known from the Antarctic and Patagonian regions.
- Analysing faunistic affinities, species richness and endemism of the benthic hydrozoans from the Scotia Arc in relation to High Antarctica and the Patagonian region.
- Studying trends and patterns in the production of scientific literature dealing with benthic hydroids from Antarctic waters.

Structure of the thesis

Present thesis is structured following the regulation for the deposit of doctoral dissertation of the Universitat de València (*Reial decret 99/2011 Modificat pel Consell de Govern 28-VI-2016*) for theses presented as compendium of scientific articles.

Thus, the thesis includes a general introduction, four chapters each corresponding to a different scientific article, a general discussion, and the conclusions. The **introduction** contextualizes both the region and the zoological group studied, and provides a brief but complete account on the scientific production regarding benthic hydroids from the Antarctic region since the early expeditions to the current day. In **Chapter I**, the benthic hydroids collected during the expedition ANT XIX/5 to the Scotia Arc are studied, including the description of two new species, as well as taxonomic, ecological and biogeographic notes of the species inventoried. In **Chapter II**, faunistic affinities of the benthic hydrozoans from the Scotia Arc with those from surrounding waters are studied after an exhaustive literature revision including all historical records of benthic hydroids from Antarctic, Scotia Arc, and Patagonian waters. The results are compared with those of other benthic taxa. Species richness and endemism for Antarctic benthic hydrozoans are provided. The complete and updated catalogue of hydrozoan species categorized by different regions, produced within the framework of this chapter, is annexed. **Chapter III** deals with a new species to science from the Weddell Sea, which constitutes the first evidence of the family Aglaopheniidae from the Southern Ocean, accompanied with a discussion about its putative origin. In **Chapter IV**, benthic hydroids collected by the expeditions ANT XV/3, ANT XVII/3 and ANT XXI/2 to the eastern end of the Weddell Sea are studied, including taxonomic notes on selected taxa, and ecological and biogeographic remarks on the species inventoried.

In the **general discussion**, the results from chapters I and IV are compared to each other and with the general pattern for the whole Antarctic region obtained in Chapter II. Additionally, an analysis of the trends in the production of the scientific literature concerning benthic hydroid species, in regards to new records, frequency of records, and number of species reported per contribution, has been included in this section. The findings belonging to chapters I and IV are incorporated within the analysis in order to determine the weight of the contributions found through this thesis.

CHAPTER I

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On the benthic hydroids from the Scotia Arc (Southern Ocean): new insights into their biodiversity, ecology and biogeography.

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Abstract

The Scotia Arc, located between the Antarctic Peninsula and the southern tip of South America, is an important zone from the biogeographic point of view. Its benthic biodiversity has been extensively documented with a few exceptions, among others, the hydroid fauna, which constitutes one of the major components of the benthic Antarctic communities. With the aim of increasing the data in three different but complementary fields of knowledge (namely biodiversity, ecology and biogeography), an unpublished collection obtained during the German Antarctic expedition ANTARKTIS XIX/5 (LAMPOS) with the *RV Polarstern* in 2002 has been studied. A total of 45 species of benthic hydroids, belonging to nine families and 20 genera was found. Forty of them, including *Halecium stoloniferum* sp. nov. and *Schizotricha discovery* sp. nov., were identified to species level. Leptothecata was by far the most dominant order with 42 species, while Anthoathecata are only represented by three species. Fifteen species (38%) are endemic to the Antarctic region and 31 (78%) are restricted to Antarctic and/or sub-Antarctic waters. *Schizotricha southgeorgiae*, *Halecium elegantulum* and *Sertularella argentinica* are reported for the second time, whereas *Schizotricha jaederholmi*, *Antarctoscyphus gruzovi* and *Sertularella jorgensis*, for the third time. New original autoecological data concerning the use of substrate, reproductive phenology and bathymetric range of the inventoried species are provided.

Introduction

The Scotia Arc is an island arc with a volcanic origin, located in the Southern Ocean, between Tierra del Fuego and the Antarctic Peninsula. It comprises an island arc system which surrounds the so-called Scotia Sea. The arc includes submarine ridges and the islands of Isla de los Estados, Shag Rocks, South Georgia, South Sandwich Islands, South Orkney Islands, Elephant Island and South Shetland Islands. The region is completely encompassed by the Antarctic convergence, unlike the neighbour sub-Antarctic Patagonian shelf, although South Georgia and Shag Rocks are north of the Antarctic Circumpolar Current (Orsi et al. 1995). The mentioned oceanographic particularities make the Scotia Arc an interesting biogeographic transition zone due to its position among High Antarctica and the Magellan region, as it has been underlined by many authors (e.g. Arntz and Rios 1999; Arntz 2005).

The benthic hydroids from the entire Scotia Arc were previously studied as a whole by Peña Cantero and García Carrascosa (1995), who studied as well their distribution patterns (Peña Cantero and García Carrascosa 1999). However, there are only a few punctual records on some areas such as South Georgia (Jaederholm 1904, 1905; Broch 1948; Naumov and Stepanjants 1962) and the South Orkney Islands (Billard 1906; Ritchie 1907), and the South Shetland Islands (Hartlaub 1904; Broch 1948; Galea and Schories 2012). The Discovery Bank, located between South Sandwich Islands and South Orkney Islands, constitutes a previously unknown area for hydrozoans.

In addition, some of the hydroids studied were collected outside the Scotia Arc, specifically in Burdwood Bank and nearby waters (previously studied by Billard 1906; Ritchie 1907; Vervoort 1972 and El Besbeeshy 2011).

Materials and methods

The material studied was collected by the *RV Polarstern* during the German expedition ANT XIX/5 (LAMPOS) in April 2002. The 14 samples studied here (see Tab. 1.1 and Fig. 1.1) were obtained using an Agassiz trawl and a bottom trawl at depths between 249 and 647 meters. Samples were sorted on board into main zoological groups. Hydrozoans were first fixed in 10% formalin, later transferred to 70% ethanol and finally studied at the laboratory. Holotypes have been deposited in the collections of the Museo Nacional de Ciencias Naturales (MNCN) of Madrid, Spain. The remaining material is kept in the Hydrozoan collection of the Zoology Department of the University of Valencia, Spain.

Data regarding the ecology (bathymetric range, reproductive phenology and use of substrate) and distribution (within the Scotia Arc and nearby waters) of the species inventoried are incorporated, but

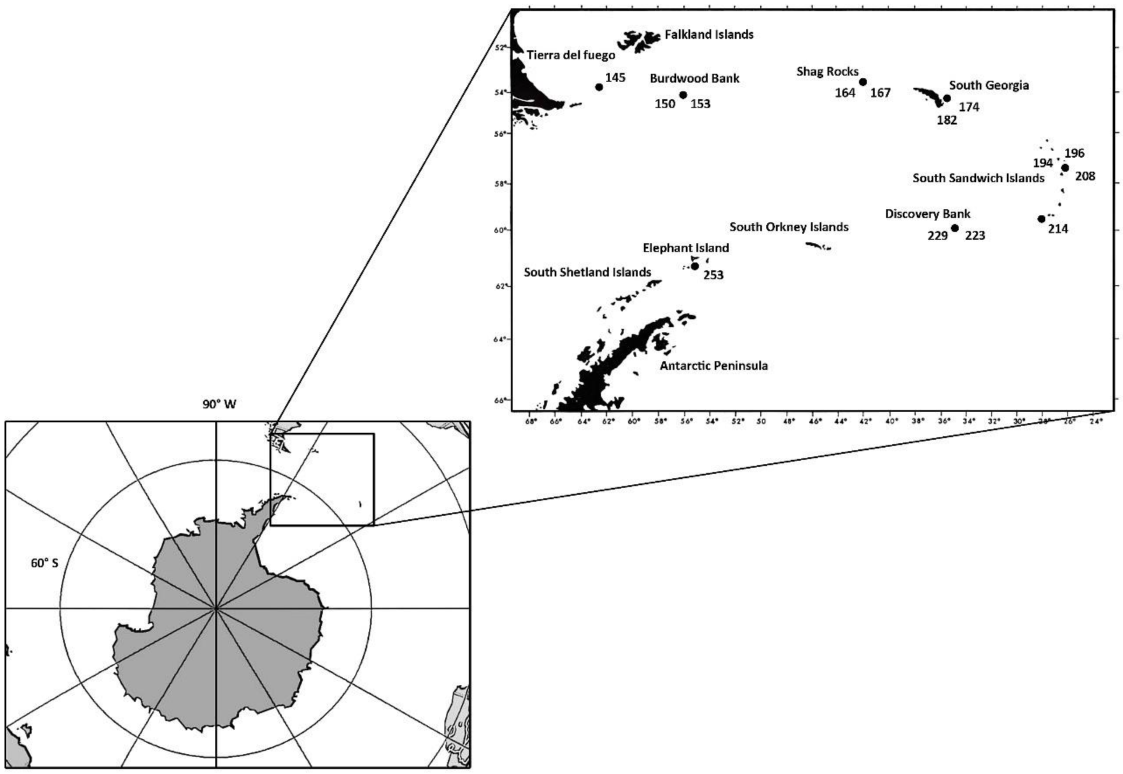

Figure 1.1 Study area and location of the stations in the Scotia Arc and Patagonian shelf

Table 1.1 Sampling stations containing hydroids

Station	Date	Latitude (S)	Longitude (W)	Locality	Sampling gear	Depth (m)
145	5 April 2002	54° 01,11'	62° 01,63'	Burdwood Bank	Agassiz trawl	272
150	6 April 2002	54° 29,64'	56° 08,13'	Burdwood Bank	Agassiz trawl	286-290
153	6 April 2002	54° 30,04'	56° 08,33'	Burdwood Bank	Bottom trawl	277-296
164	9 April 2002	53° 23,82'	42° 42,46'	South Georgia	Agassiz trawl	313-322
167	9 April 2002	53° 22,93'	42° 43,75'	South Georgia	Bottom trawl	306-343
174	11 April 2002	54° 25,30'	35° 38,50'	South Georgia	Bottom trawl	278-280
182	12 April 2002	54° 27,44'	35° 41,76'	South Georgia	Agassiz trawl	249-256
194	15 April 2002	57° 40,70'	26° 26,09'	South Sandwich	Agassiz trawl	278-309
196	15 April 2002	57° 40,95'	26° 27,85'	South Sandwich Islands	Bottom trawl	286-301
208	16 April 2002	57° 40,62'	26° 29,18'	South Sandwich Islands	Bottom trawl	630-647
214	17 April 2002	59° 42,62'	27° 57,68'	South Sandwich Islands	Agassiz trawl	332-340
223	21 April 2002	60° 08,39'	34° 54,96'	Discovery Bank	Agassiz trawl	374-379
229	21 April 2002	60° 07,81'	34° 56,17'	Discovery Bank	Bottom trawl	362-371
253	25 April 2002	61° 24,03'	55° 24,72'	Elephant Island	Bottom trawl	276-282

only significant new contributions are discussed. A comprehensive table summarizing that information is included.

Results and discussion

Taxonomic account

Anthoathecata Cornelius, 1992

Bougainvilliidae Allman, 1863

Bougainvilliidae undetermined

(Fig. 1.2a-b)

Material examined. **St. 153**, a few polyps, c. 2 mm high, on *Sertularella vervoorti* and *Tulpa tulipifera.*

Description. Stolonal, unbranched colony. Polyp at the end of a perisarc covered pedicel *ca*. 1.5 mm long. Pseudohydrotheca located at the basal part of the polyp and reaching the base of the tentacles. Polyp *ca*. 500 μm high, provided with 18-20 tentacles scattered in 2-3 crowns, rounded hypostome. Gonophores located on pedicels, globiform, and covered with perisarc.

Remarks. The scarcity and state of the material precludes a proper identification.

Ecology and distribution. The material examined was collected at depths between 277 and 296 m, at Burdwood Bank.

Eudendriidae L. Agassiz, 1862

Eudendrium Ehrenberg, 1834

Eudendrium generale von Lendenfeld, 1885

(Fig. 1.2c-e)

Material examined. **Stn 214**, one colony, c. 55 mm high, with male gonophores, on polychaete tube; **Stn 223**, one colony, c. 50 mm high, on sponge.

Remarks. Cnidome composed of microbasic euryteles in two size classes: 14.4 ± 0.7 x 7.8 ± 0.5 μm (n=26) and 7.9 ± 0.5 x 3.3 ± 0.3 μm (n=11), in agreement with the measurements given by Peña Cantero (2009). Larger euryteles forming a ring at the basal part of the polyp, what allows to distinguish the species from its congenerics.

Ecology and distribution. Previously recorded at depths between 10 (Puce et al. 2002) and 702 m (Peña Cantero 2009); present material from 332 to 379 m. The presence of gonophores on Antarctic waters is only known in January (Puce et al. 2002) and December (Peña Cantero et al.

2013); our fertile material was found in April. Reported from south-Australian (Watson 1985) and Antarctic waters: Terra Nova Bay (Puce et al. 2002; Peña Cantero et al. 2013) and the Balleny Island (Peña Cantero 2009). This constitutes the first record from both the South Sandwich Islands and the Scotia Arc.

Eudendrium sp.

(Fig. 1.2f)

Material examined. **Stn 167**, a few stems, c. 2 mm high, on *Symplectoscyphus bathyalis*; **Stn 214**, one colony, c. 15 mm, on octocoral; **Stn 253**, a few stems, c. 2 mm high, on *Symplectoscyphus glacialis.*

Remarks. The scarcity of material and the lack of reproductive structures prevent us from providing a proper identification.

Ecology and distribution. The material was collected at depths from 276 to 343 m, epibiotic on *S. bathyalis*, *S. glacialis* and an octocoral.

Leptothecata Cornelius, 1992

Campanulinidae Hincks, 1868

Stegella lobata (Vanhöffen, 1910)

(Fig. 1.2g)

Material examined. **Stn 194**, one stem, c. 30 mm high.

Ecology and distribution. Circum-Antarctic species (Peña Cantero et al. 2004), collected at depths from 10 (Naumov and Stepanjants 1972) to 700 m (Naumov and Stepanjants 1962); present material from 278 to 309 m. This constitutes the first record from the South Sandwich Islands.

Tiarannidae Russell, 1940

Modeeria rotunda (Quoy & Gaimard, 1827)

(Fig. 1.2h)

Material examined. **Stn 223**, stolonal, c. 18 mm, on *Billardia subrufa.*

Ecology and distribution. Cosmopolitan species (Boero and Bouillon 1993), reported on Antarctic waters at a depth of 365-377 m (Peña Cantero and Gili 2006); our material comes from 374-379 m. This constitutes the first record from the Scotia Arc.

Stegopoma plicatile (M. Sars, 1863)

(Fig. 1.2i)

Material examined. **Stn 214**, one fragmented colony, c. 25 mm, on gravel and pebbles.

Ecology and distribution. Species with a bipolar distribution (Peña Cantero and García Carrascosa 1999), reported in Antarctic waters at depths between 385 (Vanhöffen 1910) and 1019 m (Peña Cantero 2008); present material from 332 to 340 m. The present contribution constitutes the first record from the South Sandwich Islands.

Lafoeidae Hincks, 1868

Abietinella Levinsen, 1913

Abietinella operculata (Jäderholm, 1903)

(Fig. 1.3a)

Material examined. **Stn 194**, one colony, c. 90 mm high, on stone; **Stn 196**, one fragmented colony, c. 170 mm high; **Stn 208**, one colony, c. 150 mm high, on stone; **Stn 229**, one colony, c. 95 mm high.

Ecology and distribution. Patagonian-Antarctic species (cf. Peña Cantero and García Carrascosa 1999), reported at depths from 63 (Peña Cantero and García Carrascosa 1995) to 1500 m depth (Stepanjants 1979), present material between 287 and 647 m. This constitutes the first evidence from South Sandwich Islands.

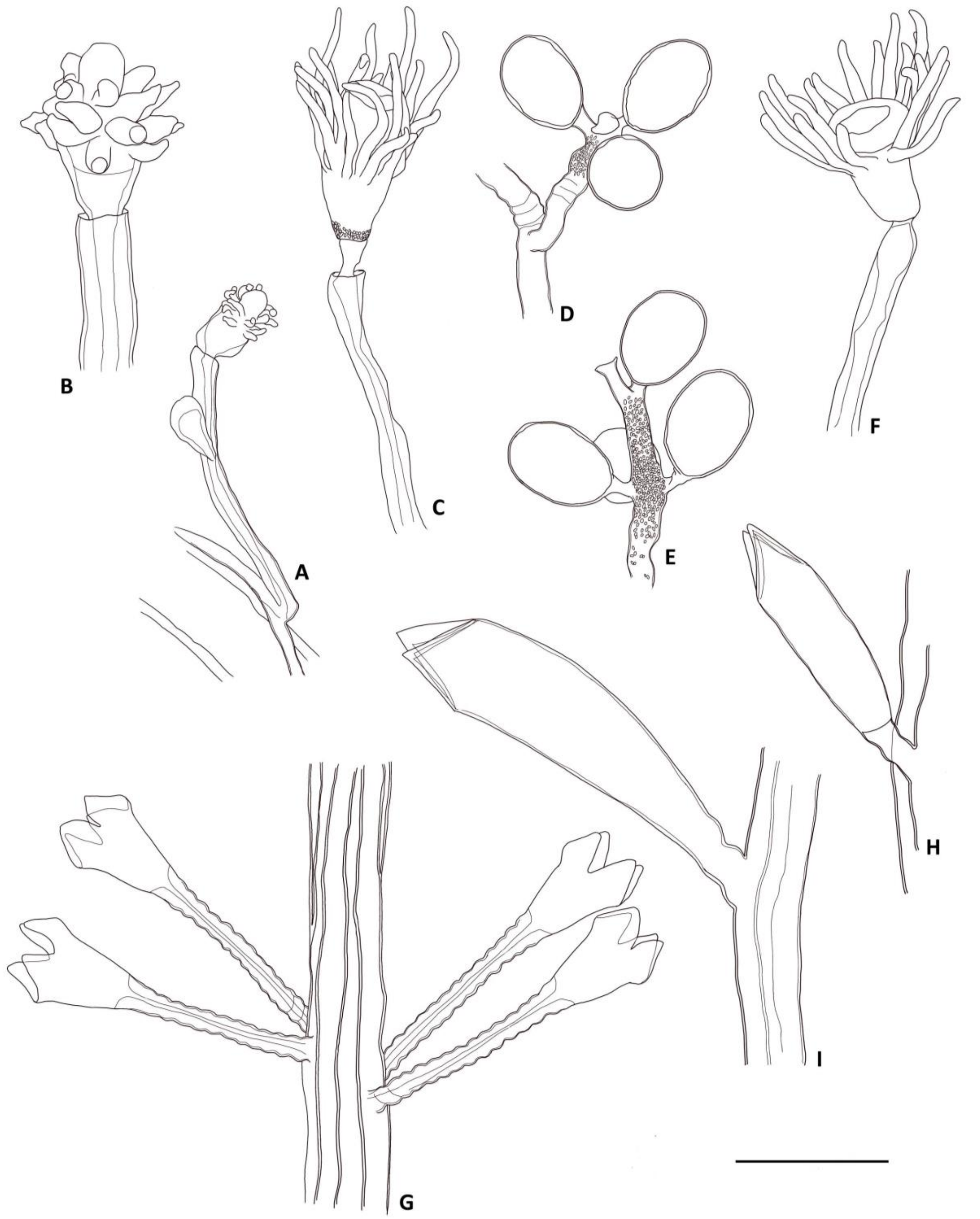

Figure 1.2 a-b Bougainvilliidae undetermined: **a** polyp with gonophore; **b** polyp. **c-e** *Eudendrium generale*: **c** polyp; **d-e** male gonophores. **f** *Eudendrium* sp.: polyp. **g** *Stegella lobata*: hydrothecal shape and arrangement. **h** *Modeeria rotunda*: hydrotheca. **i** *Stegopoma plicatile*: hydrotheca. *Scale bar*: 500 µm (**b**-**f**, **h**-**i**); 1 mm (**a**, **g**)

Acryptolaria Norman, 1875
Acryptolaria conferta (Allman, 1877)
(Fig. 1.3c-d)

Material examined. **Stn 153**, one stem fragment, c. 14 mm high.

Remarks. The systematic of the genus *Acryptolaria* was a complicated issue until the studies carried out by Peña Cantero et al. (2007) and Peña Cantero and Vervoort (2010), who specifically shed light on the morphometry and cnidome of the species of the genus. Our material perfectly coincides with the measurements of the type material obtained by Peña Cantero et al. (2007), although it is slightly larger than the material studied by Peña Cantero and Vervoort (2010) as *Acryptolaria* cf. *conferta*. Cnidome composed of large macrobasic mastigophores 19.9 ± 1.1 x 8.5 ± 0.3 µm (n=12) and small microbasic mastigophores 6.5-7 x 2.5-3 µm (n=5).

Ecology and distribution. Species with an allegedly wide distribution, including Patagonian waters (cf. Vervoort 1972; El Beshbeeshy and Jarms 2011), although most of the records have to be considered as doubtful, and only the type material from Cuba and material from New Caledonia are unambiguously referable to this species (see Peña Cantero et al. 2007 and Peña Cantero and Vervoort 2010). Our material was collected at depths from 277 to 296 m in Burdwood Bank, and it constitutes the first valid report from Patagonian waters.

Acryptolaria operculata Stepanjants, 1979

(Fig. 1.3b)

Material examined. **Stn 150**, one colony, c. 130 mm high, **Stn 164**, one stem, c. 95 mm high, on dead octocoral; **Stn 167**, one stem fragment, c. 10 mm high; **Stn 182**, one colony, c. 50 mm high, on dead octocoral; **Stn 208**, one colony, c. 135 mm high; **Stn 229**, one stem fragment, c. 45 mm high.

Remarks. This species is easily distinguishable from its congenerics by the shape and great size of the hydrotheca and its cnidome (see Peña Cantero and Vervoort 2010). We found the cnidome composed of large putative macrobasic mastigophores [13.8 ± 0.5 x 5.2 ± 0.5 µm (n=16)] and small putative microbasic mastigophores 7-8 x 3.5 µm, in agreement with the data obtained by Peña Cantero and Vervoort (2010).

Ecology and distribution. Previously ascribed as a Patagonian species (cf. Peña Cantero and García Carrascosa 1999), found from 98 to 980 m (El Beshbeeshy and Jarms 2011); present material from 249-647 m. This constitutes the first record from both the Scotia Arc and Antarctic waters. Therefore, *A. operculata* could be considered as a species with a tendency to penetrate into Antarctic waters via the Scotia Arc, although we need more evidence regarding this statement due to the scarcity of records.

Filellum Hincks, 1868

Filellum cf. *magnificum* Peña Cantero, Svoboda & Vervoort, 2004

(Fig. 1.3e-f)

Material examined. **Stn 167**, stolonal colony with a few hydrothecae, on *Sertularella* sp.

Remarks. Despite of the absence of coppinia, we tentatively assign the material studied to *Filellum magnificum* based on the great size of the hydrotheca (650-700 µm at abcauline wall, and 160-220 µm at aperture), and the cnidome (17 x 4.5 µm and 7 x 3 µm), coinciding with Peña Cantero et al. (2004).

Ecology and distribution. Antarctic species, reported from depths between 85 (Peña Cantero 2010) and 640 m (Peña Cantero et al. 2004). *Filellum magnificum* is only known from Peter I Island (Peña Cantero 2010) and the Weddell Sea (Peña Cantero et al. 2004). This constitutes the first record from the Scotia Arc and also the third record worldwide.

Filellum sp.

(Fig. 1.3g)

Material examined. **Stn 164**, stolonal colony with several hydrothecae, on *A. operculata*; **Stn 167**, stolonal colony with a few hydrothecae, on *S. bathyalis*; **Stn 253**, stolonal colony, with a few hydrothecae, on *S. glacialis.*

Remarks. The scarcity of material and lack of reproductive structures prevented us from identifying the species properly.

Ecology and distribution. Material collected off Shag Rocks and Elephant Island, at depths from 276 to 322 m.

Halisiphonia Allman, 1888

Halisiphonia megalotheca Allman, 1888

(Fig. 1.3i)

Material examined. **Stn 223**, a single hydrotheca, c. 3 mm high.

Remarks. Despite the scarcity of material, the great size of the hydrotheca (3.5 mm long and 450 µm of diameter at the aperture) allowed us to assign our material to this species.

Ecology and distribution. Previously reported at depths between 672 (Stechow 1925) and 4961 m (Vervoort 1972); present material between 374-379 m. Recorded from Oman (Rees and Vervoort 1987); South-Australia (Allman 1888), Saint Paul Island (Stechow 1925), New Zealand (Kramp 1956, as *Halisiphonia galatheae*) and South Africa (Vervoort 1972). This constitutes both the first evidence from the Scotia Arc, and also from Antarctic waters.

Halisiphonia nana Stechow, 1921

(Fig. 1.3h)

Material examined. **Stn 194**, stolonal colony with several hydrothecae, on *Billardia subrufa*.

Remarks. Marques et al. (2006) pointed out that *Halisiphonia nana* had a single category of nematocyst (6-7 x 2 µm). However, a second larger class has been found in the studied material [9 ± 0.5 x 3.8 ± 0.3 µm (n=10)].

Ecology and distribution. *Halisiphonia nana* has been found at depths from 180 (Blanco 1984) to 457 m (Stechow 1921), our material at 278-309 m. It is known from Bouvet Island (Stechow 1921; Peña Cantero and Gili 2006), South Georgia (Blanco 1984) and the Kerguélen area (Millard 1977), although the last record seems doubtful (cf. Marques et al. 2006). The present finding constitutes the first record from South Sandwich Island.

Lafoea Lamouroux, 1821

Lafoea benthophila Ritchie, 1909

(Fig. 1.3j)

Material examined. **Stn 167**, stolonal colony with a few hydrothecae, on *Sertularella* sp.; **Stn 194**, a few stems, up to 6 mm high, on *Staurotheca frigida*; **Stn 196**, a few stems, up to 7 mm high, on *Staurotheca dichotoma*, and stolonal colony with a few hydrothecae, on dead octocoral.

Remarks. The cnidome consists of microbasic mastigophores in two size classes: 21.8 ± 0.8 x 9.8 ± 0,9 µm (n=15) and 6.5 ± 0.6 x 3.7 ± 0.4 µm (n=15).

Ecology and distribution. Outside Antarctic waters, it has been reported from depths between 90 (Hirohito 1995) and 1040 m (Antsulevich and Vervoort 1993), whereas in Antarctic waters it has been found at greater depth, 3246 m (Ritchie 1909); our material comes from 278 to 343 m. The present contribution constitutes the first record from the Shag Rocks and the South Sandwich Islands.

Lafoea dumosa (Fleming, 1820)

(Fig. 1.3k)

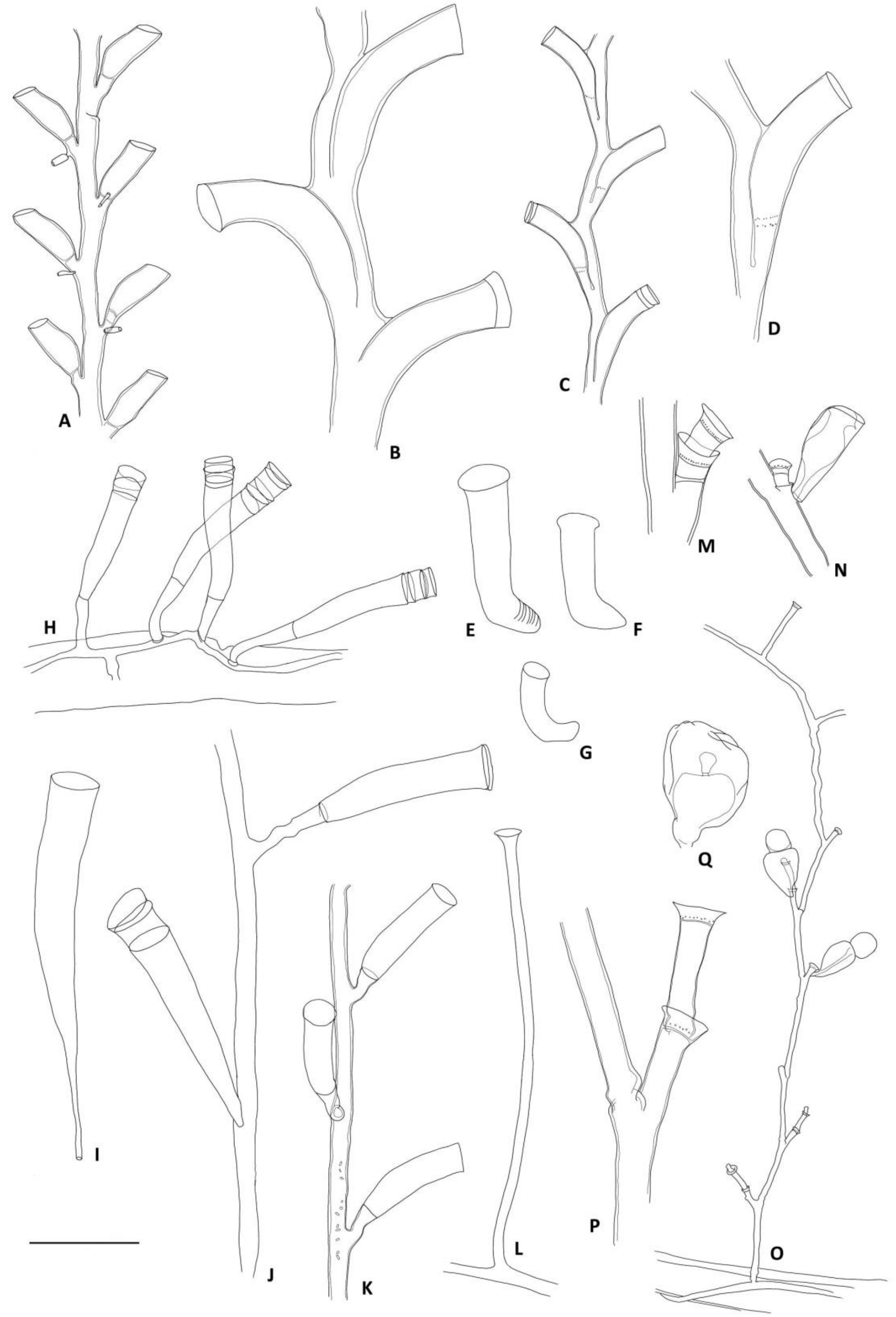

Figure 1.3 **a** *Abietinella operculata*: hydrothecal shape and arrangement. **b** *Acryptolaria operculata*: hydrothecal shape and arrangement. **c-d** *A. conferta*: **c** hydrothecal shape and arrangement; **d** hydrotheca. **e-f** *Filellum* cf. *magnificum*: hydrothecae. **g** *Filellum* sp.: hydrotheca. **h** *Halisiphonia nana*: stolon with hydrothecae. **i** *H. megalotheca*: hydrotheca. **j** *Lafoea benthophila*: hydrothecal shape and arrangement. **k** *L. dumosa*: hydrothecal shape and arrangement. **l** *Halecium elegantulum*: hydrophore. **m-n** *H. incertus*: **m** hydrophore with hydrothecae; **n** gonotheca. **o-q** *Halecium stoloniferum* sp. nov.: **o** stem showing stolonal, distal structure; **p** hydrophore and renovations; **q** gonotheca. **Scale bar**: 250 µm (**p**); 500 µm (**d-h**, **j-k**, **m**, **q**); 1 mm (**a-c**, **i**, **l**, **n**); 1.4 mm (**o**)

Material examined. **Stn 145**, one colony, c. 8 mm high, on bryozoan; **Stn 167**, one colony, c. 3 mm high, on bryozoan; **Stn 194**, one colony, c. 9 mm high; **Stn 196**, some stems, up to 12 mm high, on *Schizotricha* cf. *turqueti*; stolonal colony, on *Halecium incertus*.

Remarks. Cnidome consisting of microbasic mastigophores in two size categories: 20.3 ± 0.8 x 9.8 ± 0.8 µm (n=13) and 6.1 ± 0.4 x 3.5 ± 0.4 µm (n=14).

Ecology and distribution. Cosmopolitan species (cf. Peña Cantero and García Carrascosa 1999), reported in Antarctic waters at depths from 12 to 520 m (Stepanjants 1979); our material was collected between 272 and 343 m.

Haleciidae Hincks, 1868

Halecium Oken, 1815

Halecium elegantulum Watson, 2008

(Fig. 1.3l)

Material examined. **Stn 223**, stolonal colony with a few hydrants, up to 2 mm high, on *B. subrufa*.

Remarks. *Halecium elegantulum* is a recently described species, characterized by its tiny, monosiphonic, unbranched stems, formed by a series of hydrothecae, each emerging from the previous one (cf. Watson 2008; Peña Cantero 2014). There are no more known species of *Halecium* with this peculiar trait. The cnidome was previously unknown. It is composed of two size classes: large microbasic euryteles 10.9 ± 0.5 x 2.9 ± 0.2 µm (n=8) and putative microbasic mastigophores 4.9 ± 0.2 x 1.5 µm (n=7).

Ecology and distribution. *Halecium elegantulum* is only known from Prydz Bay, in East Antarctica, where it was collected at a depth of 437 m (Watson 2008); the present material constitutes the second record for the species, at 374-379 m from the South Sandwich Islands, consequently pointing to a circum-Antarctic distribution.

Halecium incertus Naumov & Stepanjants, 1962

(Fig. 1.3m-n)

Material examined. **Stn 194**, fragmented colony, c. 130 mm high; **Stn 196**, fragmented colony, c. 110 mm high.

Ecology and distribution. *Halecium incertus* has been previously reported at depths from 15 (Stepanjants 1979) to 693 m (Branch and Williams 1993); our material comes from 278-309 m. Antarctic-Kerguélen distribution (Peña Cantero and Gili 2006).

Halecium stoloniferum sp. nov.

(Fig. 1.3o-q, 1.9i-o)

Material examined. **Stn 153**, stolonal colony with several stems, up to 3 mm high, with female gonothecae, on *Tulpa tulipifera*. (Holotype, MNCN 2.03/446).

Description. Creeping stolon giving rise to tiny, monosiphonic, unbranched stems, up to 3 mm high (Fig. 1.9i). Internodes arranged in a distinct zigzag pattern, with hydrophores alternately arranged in more or less one plane (Fig. 1.9i-j). Sometimes, stems with a stolonal, distal structure that attaches to substrate and continues growing on it, even when hydrothecae and gonothecae are fully developed, giving rise to new stems (Fig. 1.3o).

Internodes relatively long, separated by thin, oblique nodes, smooth with the exception of a slight swelling at the basal part (Fig. 1.9k). Hydrophores very elongated, from 180 to 220 µm long, considerably exceeding the distal node of internode, and gently diverging from internode. Ratio between adcauline length of hydrophore and diameter at diaphragm c. 2.2-3.0 (Fig. 1.3p, 1.9k-l).

Hydrotheca low, 30-40 µm high, distinctly widening distally, rim strongly everted, 110-135 µm in diameter at rim and 65-85 µm at diaphragm (Fig. 1.9l). With a ring of desmocytes above the diaphragm (Fig. 1.3p, 1.9l). Without pseudodiaphragm. Hydrothecal renovations present, but scarce (up to five, usually no more than two). Hydrants absent due to bad preservation.

Female gonothecae pear-shaped, emerging from hydrophore of primary hydrothecae, slightly flattened in lateral view; 520-620 µm high and 250-270 and 400-450 µm wide in lateral and frontal views respectively. Aperture inconspicuous, circular and narrow. With acrocyst (Fig. 1.3q, 1.9n), with about 3-4 eggs. Male gonothecae unknown.

Cnidome composed of large microbasic euryteles 9.0 ± 0.3 x 3.7 ± 0.2 µm (n=21) and microbasic mastigophores c. 6.7 ± 0.3 x 1.8 ± 0.2 µm (n=15).

Remarks. Despite its tiny stems, the colony of *Halecium stoloniferum* sp. nov. had reached maturity, being provided with fully-developed female gonothecae. The species is characterized by the tiny stems, the relatively long stem internodes and hydrophores, the distally widening hydrotheca and strongly everted rim, the size of the microbasic euryteles, and the presence of acrocysts.

Halecium stoloniferum sp. nov. belongs to a group of species characterized by having elongated hydrophores (cf. *H. antarcticum* Vanhöffen, 1910, *H. banzare* Watson, 2008, *H. delicatulum* Coughtrey, 1876, *H. exaggeratum* Peña Cantero, Boero and Piraino, 2013, *H. fraseri* Ralph, 1958, *H. frigidum* Peña Cantero, 2010, *H. mediterraneum* Weismann 1883, *H. pallens* Jäderholm, 1904 and *H. pseudodelicatulum* Peña Cantero, 2014). However, these species (apart from *H. exaggeratum*) form erect colonies with large and branched stems, and the hydrophores and the internodes are comparatively shorter. In addition, *H. antarcticum*, *H. banzare*, *H. delicatulum*, *H. fraseri*, *H. mediterraneum* and *H. pseudodelicatulum* are provided with a pseudodiaphragm.

Halecium stoloniferum sp. nov. closely resembles the Antarctic *H. frigidum* Peña Cantero, 2010 and *H. exaggeratum* Peña Cantero, Boero and Piraino, 2013 due to the very long hydrophores and internodes, the general shape of the hydrothecae and the absence of pseudodiaphragm. However, it differs from those species by forming tiny, unbranched stems and the absence of paired branches. *Halecium stoloniferum* sp. nov. is also distinguishable from *H. exaggeratum* by the size of the hydrothecae, distinctly larger in the latter (200-215 µm in diameter at the aperture and 120-130 µm at diaphragm), and by the size of the larger nematocysts, distinctly smaller in *H. exaggeratum* [7.2 ± 0.3 x 3.9 ± 0.3 (n=10), see Peña Cantero et al. (2013)]. On the other hand, although *Halecium stoloniferum* sp. nov. is closer to *H. frigidum* in the size of the larger nematocysts [9.4 ± 0.3 x 4.7 ± 0.2 (n=6) see Peña Cantero (2014)] and by the size of the hydrothecae [115 µm in diameter at the aperture and 90 µm at diaphragm in *H. frigidum*, see Peña Cantero (2010)], the latter forms large, polysiphonic stems giving rise to paired branches, the internodes are straight, the hydrothecal diameter only slightly increases distally and the hydrothecal rim is not everted.

Another peculiar feature that allows distinguishing *Halecium stoloniferum* sp. nov. from other species of the genus is the presence of the acrocyst. According to Millard (1977) the presence of an external acrocyst is an important diagnostic character. This structure is only known from a few species of *Halecium*, namely *H. antarcticum*, *H. dyssymetrum* Billard, 1929, *H. incertus* Naumov and Stepanjants 1962, *H. marsupiale* Bergh, 1887, *H. pallens* and *H. reduplicatum* (Fraser, 1935). The very long hydrophores of *Halecium stoloniferum* sp. nov allow the distinction from those species.

Ecology and distribution. *Halecium stoloniferum* sp. nov. was collected at a depth of 277-296 m, growing on *T. tulipifera.* Provided with gonothecae when it was sampled (April). It is only known from the type locality: Burdwood Bank, in the Patagonian shelf. Being so, it constitutes a new species for the Magellanic hydroid fauna.

Etymology. The specific epithet *stoloniferum* is given by its stolonal, distal structures that grow horizontally, creeping on the substrate and giving rise to new stems.

Halecium sp.

Material examined. **Stn 167**, stolonal colony with a few hydrants, on *Sertularella* sp.

Remarks. Probably conspecific with *Halecium interpolatum*. The scarcity of material and the absence of gonothecae prevent us from a proper identification.

Ecology and distribution. *Halecium* sp. was collected from Shag Rocks, at a depth between 306-343 m, epibiotic on *Sertularella* sp.

Schizotrichidae Peña Cantero, Sentandreu & Latorre, 2010

Schizotricha Allman, 1883

Schizotricha jaederholmi Peña Cantero & Vervoort, 1996

(Fig. 1.4a-d)

Material examined. **Stn 182**, one fragmented colony, up to 120 mm, with female gonothecae.

Remarks. There is a decrease in the length of the internodes along the hydrocladia (from 1050 to 960 µm) whereas the hydrothecae become longer (from 340 to 400 µm). The cnidome consists of microbasic mastigophores of two size classes, the larger ones 19.0 ± 1.0 x 4.2 ± 0.4 µm (n=12), and the smaller ones 6-7 x 2 µm (n=8). The gonothecae were unknown. We found female gonothecae. They are fusiform, with a large, subterminal aperture, a basal diaphragm delimiting a basal chamber, and two nematothecae (Fig. 1.4c-d).

Ecology and distribution. Previously reported at depths between 252 and 310 m (Peña Cantero and Vervoort 1996); our material from 249-256 m. Reproductive state previously unreported, so it is only known carrying gonothecae in April. Considered as a South Georgia endemism, our material, which constitutes the third record for the species, comes from the same area.

Schizotricha southgeorgiae Peña Cantero & Vervoort, 2004

(Fig. 1.4k-m)

Material examined. **Stn 167**, one colony, c. 100 mm high.

Remarks. As it occurs in other species of the genus, the internode length gradually decreases towards the end of the hydrocladia (from 1120 to 850 µm) whereas the hydrothecae become longer (from 310 to 370 µm). Cnidome composed of microbasic mastigophores of two size classes: the larger ones 19.5 ± 1.2 x 4.4 ± 0.5 µm (n=12) and the smaller ones 5.4 ± 0.5 x 2 ± 0.6 µm (n=5), similar as those obtained by Peña Cantero et al. (1996).

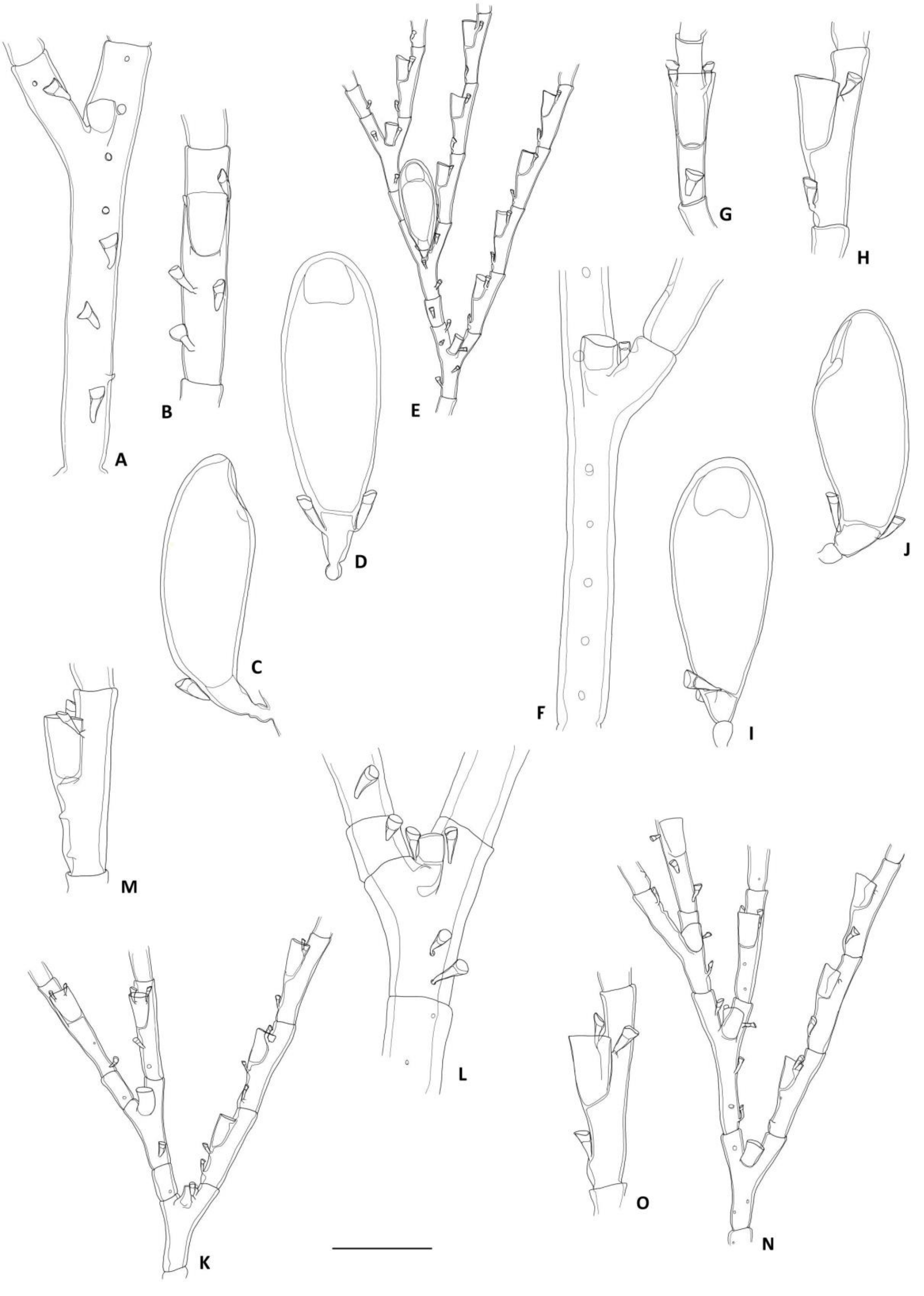

Figure 1.4 a-d *Schizotricha jaederholmi*: **a** cauline internode; **b** unforked hydrocladial internode; **c-d** gonothecae. **e-j** *Schizotricha discovery* sp. nov.: **e** hydrocladia with ahydrothecate intermediate internodes; **f** cauline internode; **g-h** unforked hydrocladial internode; **i-j** gonothecae. **k-m** *S. southgeorgiae*: **k** hydrocladia with ahydrothecate intermediate internodes; **l** cauline internode; **m** unforked hydrocladial internode. **n-o** *Schizotricha* cf. *turqueti*: **n** hydrocladia; **o** unforked hydrocladial internode. *Scale bar*: 500 µm (**a**-**d**, **f-j**, **l-m, o**); 1 mm (**k**, **n**); 1.4 mm (**e**)

Ecology and distribution. This species is known only from the South Georgia area, where it was reported at depths between 659 and 686 m by Peña Cantero and Vervoort (2004b); our material was collected between 306-343 m depths, from Shag Rocks. This constitutes the second record of the species.

Schizotricha cf. *turqueti* Billard, 1906

(Fig. 1.4n-o)

Material examined. **Stn 194**, one fragmented colony, c. 80 mm high, on gravel; **Stn 196**, one fragmented colony, c. 190 mm high, on gravel.

Remarks. *Schizotricha turqueti* is typically provided with 1-2 infrathecal nematothecae in the cauline internodes, and one, rarely two, infrathecal one in the hydrocladia. Our specimens, however, have 3-5 and 1-3, respectively. On the other hand, the larger microbasic mastigophores are slightly smaller [20.3 ± 1.6 x 4.4 ± 0.5 µm (n=12)], than those found in the type material studied by Peña Cantero et al. (1996) (namely 23.7 ± 1 x 4.8 ± 0.1 µm). These differences prevent us from assigning the material unequivocally. As observed in other species (see above), the internode length gradually decreases towards the end of the hydrocladium (from 1120 to 850 µm) and the hydrothecae become longer (from 310 to 370 µm).

Ecology and distribution. Circum-Antarctic species (cf. Peña Cantero and Vervoort 2005), previously found from the tidal level (Billard 1906) to a depth of 1890 m (Peña Cantero and Vervoort 2005); our material comes from 278 to 309 m.

Schizotricha discovery sp. nov.

(Fig. 1.4e-j, 1.9a-h)

Material examined. **Stn 223**, six colonies, c. 110, 120, 150, 210, 250 and 300 mm high, on stone (Holotype, MNCN 2.03/447, one stem, c. 300 mm high, with gonothecae; remaining material paratype); **Stn 229**, one fragmented colony, c. 110 mm high, on pebbles.

Description. Colonies composed of polysiphonic stems, up to 300 mm high, provided with disc shaped hydrorhiza. Diameter at base c. 3 mm. Stems usually unbranched (Fig. 1.9a, c); occasionally with some secondary hydrocauli (Fig. 1.9b).

Stem composed of a main axial tube and several secondary tubes growing upwards around the main tube. The former homomerously divided into hydrothecate internodes, bearing hydrothecae and nematothecae. Without cauline ahydrothecate intermediate internodes (Fig. 1.4f). Accessory tubes only provided with nematothecae. Secondary tubes decreasing in number distally, leaving the main tube alone at distal part of stem.

Cauline internodes with a short apophysis, provided with a nematotheca, near distal end. Cauline apophyses alternately arranged in two planes, forming an angle of c. 90° at basal part of the stem, but smaller at distal part. Cauline internodes with a small hydrotheca located at axil between apophysis and internode; 4-5 infrathecal nematothecae (Fig. 1.4f), two nematothecae flanking hydrothecal aperture and one (rarely two) suprathecal ones.

Cauline apophyses giving rise to hydrocladia, forming an acute angle with stem (Fig. 1.9d), and provided with a single nematotheca. Hydrocladia heteromerously divided into internodes, due to the presence of intermediate ahydrothecate internodes, provided with one or two nematothecae, following hydrocladial apophyses (Fig. 1.4e). These with one or two nematothecae.

Hydrocladia repeatedly branched (up to fifth-order observed). Forked hydrocladial internodes following intermediate ahydrothecate internodes (Fig. 1.4e). Hydrocladial apophyses provided with one or two nematothecae and forming an acute angle with internode, kept constant along the hydrocladia, resulting in an elongated and stylized hydrocladium. Hydrocladia long, with up to 27 internodes. Length of hydrocladial internodes quite constant along hydrocladia.

Forked hydrocladial internodes provided with a small hydrotheca at axil of branching, one or two infrathecal nematothecae (Fig. 1.4e) and a pair flanking the hydrothecal aperture.

Unforked hydrothecate hydrocladial internodes with a hydrotheca located at half its length, one, rarely two, infrathecal nematothecae (Fig. 1.4g-h) and the typical pair flanking hydrothecal aperture. Occasionally, a suprathecal nematotheca present.

Hydrotheca deep, cup-shaped, adcauline wall completely adnate to internode, 350 to 400 μm in length (Fig. 1.4g-h); length increasing distally along hydrocladium.

Gonothecae on small apophyses, inserted between hydrotheca and infrathecal nematothecae, usually on forked hydrocladial internodes (Fig. 1.4i-j). Gonotheca fusiform, with a circular, basal diaphragm delimiting a basal chamber with two opposite nematothecae, one near the level of the gonothecal aperture, and the other one on the opposite side. Sub-terminal, kidney-shaped aperture.

Cnidome composed of microbasic mastigophores of two size categories: 20.2 ± 2 x 4.3 ± 0.4 μm (n=12) and 5.7 ± 0.9 x 2.5 ± 0.7 μm (n=17).

Remarks. *Schizotricha discovery* sp. nov. belongs to the group of species provided with intermediate ahydrothecate internodes (i.e. *Schizotricha anderssoni*, *S. multifurcata*, *S. nana*, *S. southgeorgiae* and *S. unifurcata*). It is easily recognizable from those species by the absence of ahydrothecate intermediate internodes after the cauline apophyses; they are only present after the hydrocladial apophyses. Hitherto this feature had been only documented for a single species among the antarctic representatives of the genus, namely *Schizotricha anderssoni* (cf. Peña Cantero and Vervoort 2005). Despite sharing this characteristic, *Schizotricha discovery* sp. nov differs from *S. anderssoni* in having 1-2 infrathecal nematothecae in the unforked hydrocladial internodes and 1-2 infrathecal nematothecae in the forked hydrocladial internodes, (there are 3-6 and 3-4 respectively, in *S. anderssoni*) and unbranched, or very little branched stems (*S. anderssoni* has densely branched stems).

When comparing other diagnostic features, *Schizotricha discovery* sp. nov. and *S. turqueti* share the number and arrangement of the nematothecae, with the exception of the presence of 1-2 cauline infrathecal nematothecae in *S. turqueti* (4-5 in *Schizotricha discovery* sp. nov.). However, *S. turqueti* forms stems with a great density of hydrocladia arranged in one plane. The hydrocladial internodes becomes shorter distally along the hydrocladia, unlike present material and there is no intermediate ahydrothecate internode (see Peña Cantero et al. 1996).

Ecology. *Schizotricha discovery* sp. nov. has been found at depths from 362 to 379 m, epilithic on stones or with gravel attached to the hydrorrhizal stolons. Fertile specimens were collected in April.

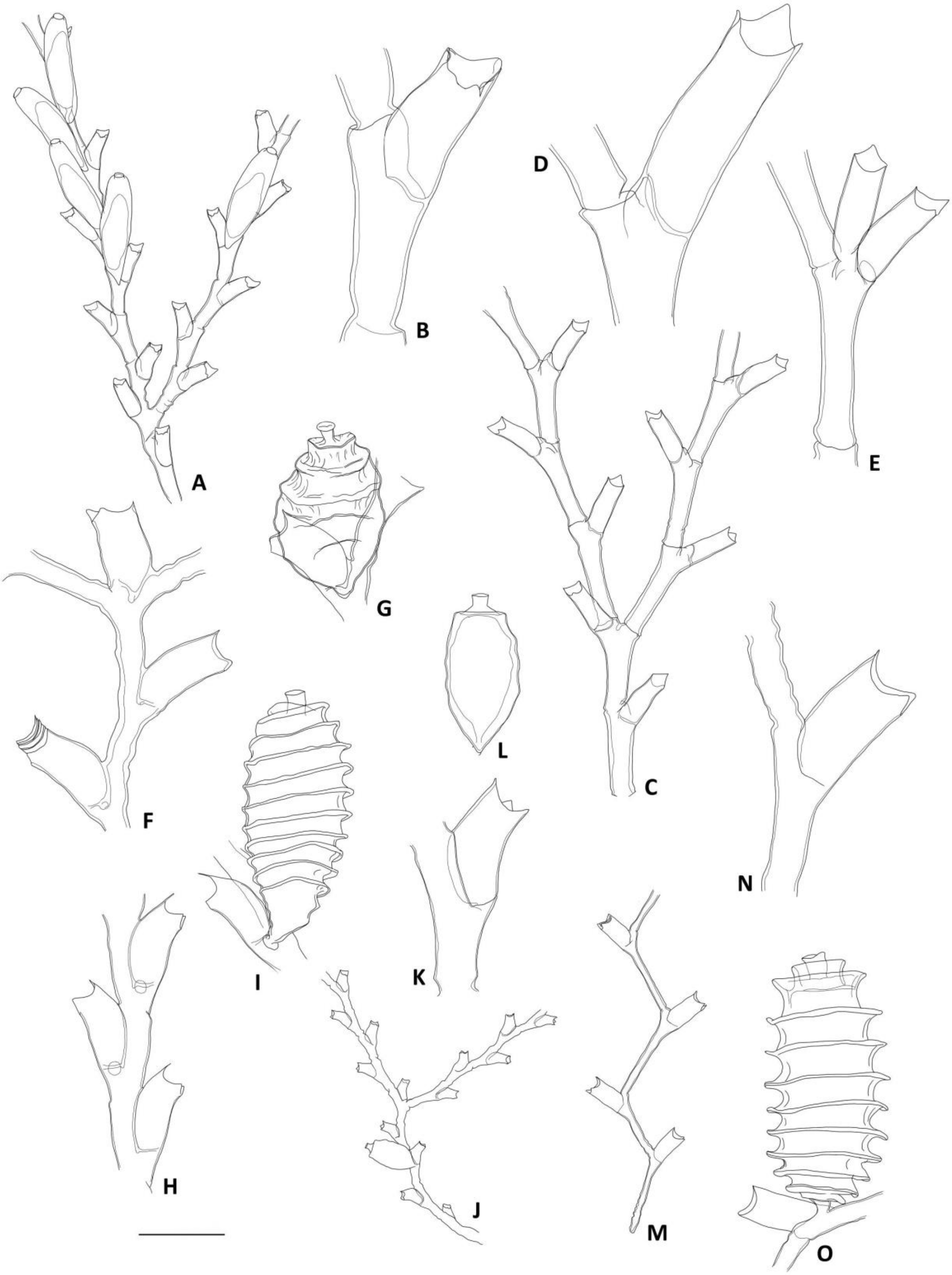

Figure 1.5 a-**b** *Antarctoscyphus spiralis*: **a** fragment of a branch showing branching and hydrothecal arrangement; **b** hydrotheca. **c**-**e** *A. gruzovi*: **c** fragment of a branch showing branching and hydrothecal arrangement; **d** hydrotheca; **e** internode forming a branching. **f**-**g** *Symplectoscyphus bathyalis*: **f** hydrothecal shape and arrangement; **g** gonotheca. **h**-**i** *S. cumberlandicus*: **h** hydrothecal shape and arrangement; **i** gonotheca. **j**-**l** *S. glacialis*: **j** stem; **k** hydrotheca; **l** gonotheca. **m**-**o** *S. nesioticus*: **m** hydrothecal shape and arrangement; **n** hydrotheca; **o** gonotheca. *Scale bar*: 1 mm (**a**, **c**, **f**-**g**, **m**); 500 µm (**e**, **h**-**i**, **l**, **o**); 1 mm (**b**, **d**, **k**, **n**); 1.4 mm (**j**)

Distribution. *Schizotricha discovery* sp. nov. comes from the Discovery Bank, located midway between the South Sandwich Islands and the South Orkney Islands, a previously unsampled area concerning benthic hydroids. It is tentatively considered endemic to Discovery Bank, given its absence from outer waters.

Etymology. The specific name *discovery* refers to Discovery Bank, where it has been found.

Sertulariidae Hincks, 1868
Antarctoscyphus Peña Cantero, García Carrascosa & Vervoort, 1997
Antarctoscyphus gruzovi (Stepanjants, 1979)

(Fig. 1.5c-e)

Material examined. **Stn 253**, one colony, c. 65 mm high.

Ecology and distribution. Previously reported at depths from 350 (Stepanjants 1979) to 414 m (Peña Cantero et al. 1999b); our material comes from 262-282 m. Endemic to the Scotia Arc, where it has been found from off Elephant Island (Stepanjants 1979) and the South Shetland Islands (Peña Cantero et al. 1999b); the present material, which also comes from off Elephant Island, constitutes the third record of the species.

Antarctoscyphus spiralis (Hickson & Gravely, 1907)

(Fig. 1.5a-b)

Material examined. **Stn 253**, one colony, c. 80 mm high.

Ecology and distribution. Circum-Antarctic species, previously reported from six (Naumov and Stepanjants 1972) to 1958 m (Peña Cantero 2011); present material between 276-282 m. The present contribution constitutes the first evidence from Elephant Island.

Sertularella Gray, 1848
Sertularella argentinica El Beshbeeshy, 2011

(Fig. 1.6a-b)

Material examined. **Stn 145**, one colony, c. 50 mm high.

Remarks. Since the original description, *Sertularella argentinica* has been found only once, off the Chilean Patagonian Coast (Galea 2007). However, as El Beshbeeshy and Jarms (2011) stated, *Sertularella argentinica* forms bush-like colonies, with monosiphonic stems, coinciding with the specimens found in present study, but differing from the material described by Galea (2007), which forms erect and polysiphonic colonies. Furthermore, our material perfectly match the measurements given by El Besbeeshy (2011), unlike those by Galea (2007), who found specimens with larger hydrothecae than those from the original description and the material described here (see Tab. 1.2). For these reasons, we consider Galea's (2007) record as doubtful.

Ecology and distribution. Reported at depths from 30 to 1200 m (El Beshbeeshy and Jarms 2011); present material at 272 m. It has been collected off the Patagonian Atlantic coast, Falkland Island and Burdwood Bank (El Beshbeeshy and Jarms 2011); the present contribution constitutes the second record for the species.

Sertularella jorgensis El Beshbeeshy, 2011

(Fig. 1.6e-f)

Material examined. **Stn 196**, one fragmented colony, up to 17 mm high, on

Table 1.2 Morphometric account of *Sertularella argentinica*

	Galea 2007	El Beshbeeshy and Jarms 2011	Sta. 145
Abcauline wall	477–573	394–440	400–450
Free part adcauline wall	337–393	232–301	255–280
Adnate part adcauline wall	356–477	301–359	290–330
Diaphragm	253–303	185–255	160–200
Aperture	337–376	208–255	220–240
Maximum diameter	399–444	–	280–310

Table 1.3 Morphometric account of *Sertularella jorgensis*

	Galea 2007	El Beshbeeshy and Jarms 2011	Sta. 196
Abcauline wall	546–632	434–469	490–550
Free part adcauline wall	391–460	295–353	290–340
Adnate part adcauline wall	270–345	203–237	220–260
Diaphragm	153–180	133–145	120–140
Aperture	289–312	203–214	200–210
Maximum diameter	316–362	-	290–300

octocoral; **Stn 253**, one colony, up to 30 mm high, on *Staurotheca compressa*.

Remarks. Present specimens, as well the material studied by Galea (2007) coincide with data from original description by El Beshbeeshy and Jarms (2011) (Tab. 1.3).

Ecology and distribution. Reported at depths from 32 (Galea 2007) to 620 m (El Beshbeeshy and Jarms 2011); present material from 276 to 301 m. It was only known from off the Chilean Patagonian coast (Galea 2007), and off Argentinean Patagonian coast (El Besbeeshy 2011). This is the third record for the species and constitutes the first evidence of its presence in Antarctic waters, having been collected from the the South Sandwich Islands and the South Shetland Islands. It can be considered as a Patagonian species with a tendency to enter Antarctic waters via the Scotia Arc.

Sertularella robusta Coughtrey, 1876

(Fig. 1.6g)

Material examined. **Stn 153**, one stem, c. 10 mm high, on *Tulpa tulipifera*; **Stn 194**, one colony, c. 12 mm high, on *B. subrufa*.

Ecology and distribution. Reported in Patagonian waters at depths from 40 to 520 m (El Beshbeeshy and Jarms 2011); present material from 277 to 309 m. Species with a wide distribution, previously reported from Patagonian waters (Leloup 1974; Galea 2007; El Beshbeeshy and Jarms 2011) and Burdwood Bank (El Beshbeeshy and Jarms 2011; present study). This study constitutes the first evidence from South Sandwich Islands, and as a result, from Antarctic waters. Consequently, it can be considered as a widely distributed species with a tendency to enter Antarctic waters via the Scotia Arc.

Sertularella sanmatiasensis El Beshbeeshy, 2011

(Fig. 1.6h-i)

Material examined. **Stn 194**, one colony, c. 28 mm high, on stone; **Stn 208**, one colony, c. 35 mm high.

Ecology and distribution. West-Antarctic-Patagonian species (Peña Cantero 2006), previously found at depths from 30 to 1801 m (Peña Cantero 2011); present material from 278 to 647 m.

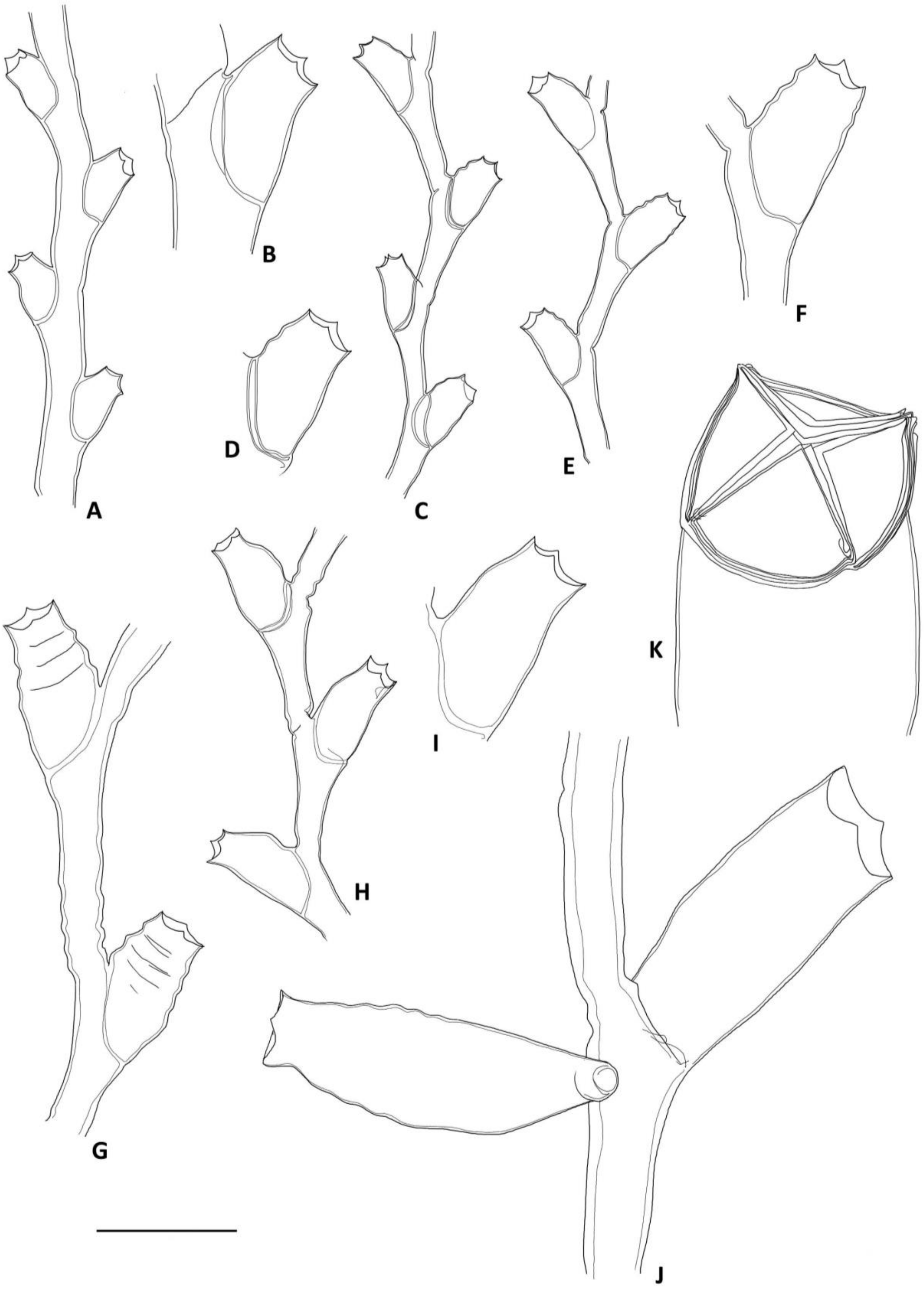

Figure 1.6 a-**b** *Sertularella argentinica*: **a** hydrothecal shape and arrangement; **b** hydrotheca. **c**-**d** *Sertularella* sp.: **c** hydrothecal shape and arrangement; **d** hydrotheca. **e**-**f** *S. jorgensis*: **e** hydrothecal shape and arrangement; **f** hydrotheca. **g** *S. robusta*: hydrothecal shape and arrangement. **h**-**i** *S. sanmatiasensis*: **h** hydrothecal shape and arrangement; **i** hydrotheca. **j**-**k** *S. vervoorti*: **j** hydrothecal and gonothecal shape and arrangement; **k** detail of opercular flaps. *Scale bar*: 500 μm (**b**, **d**, **f**-**g**, **i**, **k**); 1 mm (**a**, **c**, **e**, **h**, **j**)

Sertularella vervoorti El Beshbeeshy, 2011

(Fig. 1.6j-k)

Material examined. **Stn 153**, stolonal colony, on *T. tulipifera*; **Stn 167**, stolonal colony, c. 21 mm long.

Ecology and distribution. Reported at depths from 80 to 960 m (El Beshbeeshy and Jarms 2011); material examined from 277 to 343 m. Previously considered as a Patagonian species (Peña Cantero and García Carrascosa 1999), its presence on Tasmanian waters (Watson and Vervoort 2001) points to a sub-Antarctic distribution. This finding constitutes the first evidence for Shag Rocks.

Sertularella sp.

(Fig. 1.6c-d)

Material examined. **Stn 153**, stolonal colony, up to 3 mm high, on *S. vervoorti*; stolonal colony, up to 7 mm high, on octocoral; **Stn 167**, fragmented stems, c. 55 mm high, on octocoral.

Remarks. Probably conspecific with Sertularella sp.1 described by El Beshbeeshy and Jarms (2011) from the same region, but further information is needed. A critical revision of the genus would be very helpful to clarify the systematic position of the Patagonian species of *Sertularella*.

Ecology and distribution. The material comes from the Patagonian shelf and off Shag Rocks, at a depth of 277-343 meters.

Staurotheca Allman, 1888

Staurotheca amphorophora Naumov & Stepanjants, 1962

(Fig. 1.7a)

Material examined. **Stn 153**, one stem, c. 160 mm high.

Ecology and distribution. Previously found at depths from 111 (Peña Cantero and Vervoort 2003) to 370 m (Stepanjants 1979); present material from 277-296 m. It had been considered an endemism of West Antarctica (Stepanjants 1979; Peña Cantero and García Carrascosa 1999), where it had been reported from the South Shetland and off South Georgia (Peña Cantero and Vervoort 2003; Stepanjants 1979). Nevertheless, our material comes from the sub-Antarctic Burdwood Bank, being the first evidence of its presence outside truly Antarctic waters.

Staurotheca compressa Briggs, 1938

(Fig. 1.7b-c)

Material examined. **Stn 253**, one colony, c. 70 mm high, with female gonothecae.

Ecology and distribution. Previously found at depths from 45 (Briggs 1938) to 1042 m (Peña Cantero and Vervoort 2003); present material from 276-282 m. Circum-Antarctic species (Stepanjants 1979), known from the area of study off Elephant Island, the South Sandwich Island and the South Shetland Islands (Peña Cantero and Vervoort 2003).

Staurotheca dichotoma Allman, 1888

(Fig. 1.7d-e)

Material examined. **Stn 167**, one fragmented stem, c. 6 mm, on sponge. **Stn 196**, one colony, c. 75 mm, on gravel of a polychaete tube; **Stn 229**, one colony, up to 90 mm high.

Ecology and distribution. Previously found at depths between 82 (Totton, 1930) and 799 m (Peña Cantero et al. 1997b); present material from 286-371 m. Antarctic-Kerguélen species (Peña Cantero and Vervoort 2003), reported from the Scotia Arc from off South Georgia, the

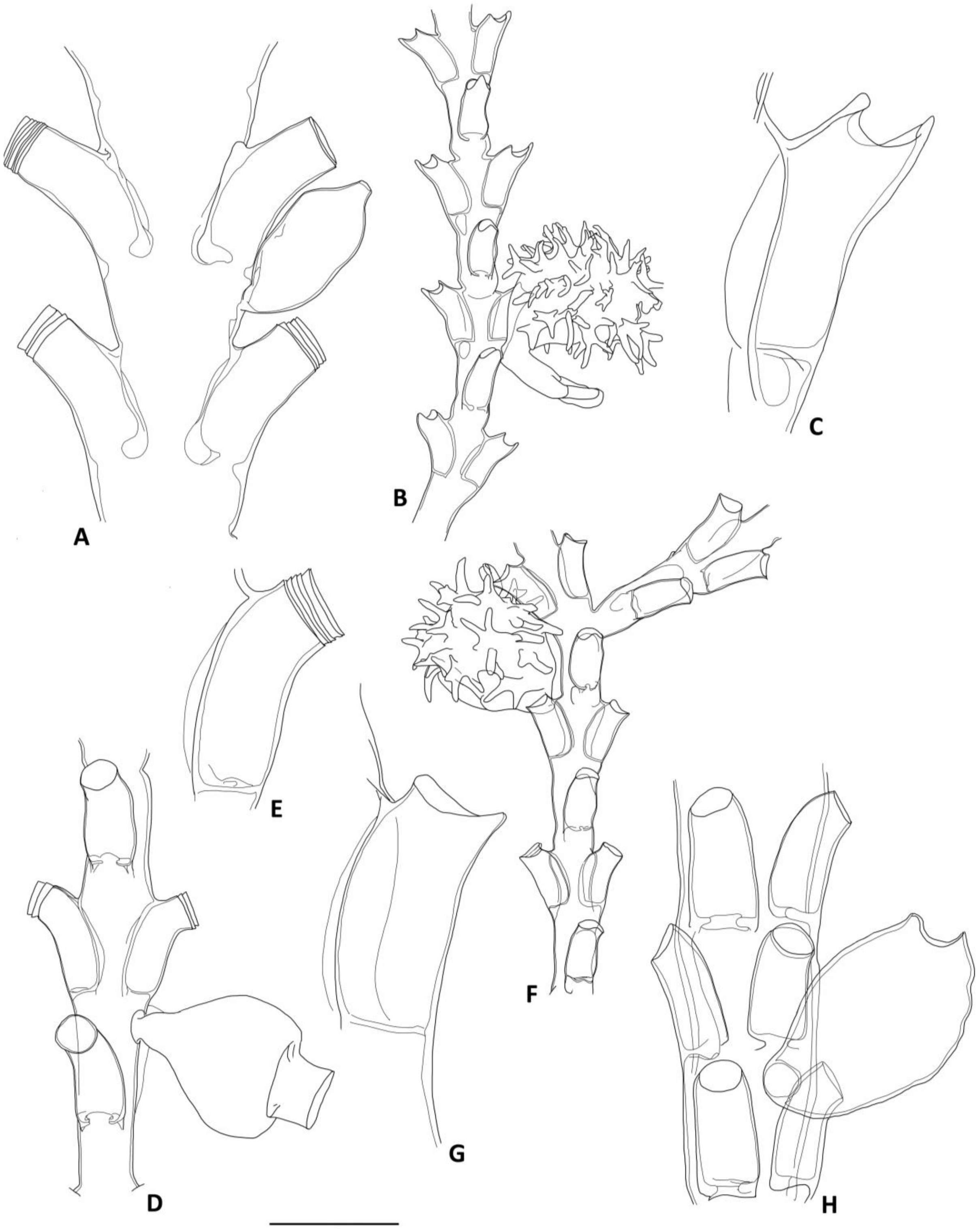

Figure 1.7 **a** *Staurotheca amphorophora*: fragment of a branch showing hydrothecal arrangement and gonotheca. **b**-**c** *S. compressa*: **b** fragment of a branch showing hydrothecal arrangement and gonotheca; **c** hydrotheca. **d**-**e** *S. dichotoma*: **d** fragment of a branch showing hydrothecal arrangement and gonotheca; **e** hydrotheca. **f**-**g** *S. frigida*: **f** fragment of a branch showing hydrothecal arrangement and gonotheca; **g** hydrotheca. **h** *S. undosiparietina*: fragment of a branch showing hydrothecal arrangement and gonotheca. *Scale bar*: 250 μm (**c**, **g**); 500 μm (**e**); 1 mm (**b**, **d**, **f**, **h**); 1.4 mm (**a**)

South Sandwich Islands and the South Shetland Islands (Peña Cantero and Vervoort 2003). Present material examined collected from off South Georgia and the South Sandwich Islands.

Staurotheca frigida Peña Cantero, Svoboda & Vervoort, 1997

(Fig. 1.7f-g)

Material examined. **Stn 194**, two colonies, c. 65 and 80 mm high, on stone; **Stn 196**, one colony, c. 80 mm high; **Stn 208**, one colony, c. 64 mm, on gravel.

Ecology and distribution. Species reported at depths from 86 (Peña Cantero and García Carrascosa 1995) to 550 m (Peña Cantero and Vervoort 2003); present material collected between 278 and 647 m. Antarctic-Kerguélen species (Peña Cantero and Vervoort 2003), found in all the Scotia Arc islands with the exception of Elephant Island (Peña Cantero and Vervoort 2003); the present material comes from the South Sandwich Islands.

Staurotheca undosiparietina (Stepanjants, 1979)

(Fig. 1.7h)

Material examined. **Stn 164**, one colony, c. 50 mm high. **Stn 174**, one colony, c. 70 mm high.

Ecology and distribution. Previously found at depths between 74 (Peña Cantero and García Carrascosa 1995) and 700 m (Stepanjants 1979); present material at 278-322 m. Although Peña Cantero and Vervoort (2003) assigned to it a West Antarctic distribution, due to its absence outside the Scotia Sea, it could be better considered as a Scotia Arc endemism. It has been found in the whole Scotia Arc, with the exception of South Sandwich Islands. The material examined comes from off Shag Rocks and South Georgia.

Symplectoscyphus Marktanner-Turneretscher, 1890

Symplectoscyphus bathyalis Vervoort, 1972

(Fig. 1.5f-g)

Material examined. **Stn 167**, one colony, c. 70 mm high, on bryozoan; **Stn 182**, one colony, up to 42 mm high, on bryozoans.

Remarks. Some authors (cf. Calder and Vervoort 2003; Altuna 2012) have pointed out the great resemblance between *Symplectoscyphus paulensis* and *S. bathyalis*, highlighting the need of a revision of both species to check the validity of the latter, which could be a junior synonym of the former. Cnidome consisting of nematocysts of two size classes: larger group 10.9 ± 0.3 x 3 μm (n=9) and smaller one 6.7 ± 0.3 x 1.9 ± 0.2 (n=11).

Ecology and distribution. In Patagonian waters, it has been reported at depths from 2450 to 2657 m (Vervoort 1972); our material was collected at Shag Rocks and South Georgia, from 249 to 343 m. This rare species has been reported a few times worldwide: in the Bay of Biscay (Vervoort, 1972; Altuna 2012), Iceland (Broch 1918; Schuchert 2001), Mauritania (Medel and Vervoort 1998), the Mid-Atlantic ridge (Calder and Vervoort 2003), New Scotland (Henry et al. 2006), Chilean waters (Vervoort, 1972) and New Caledonia (Vervoort 1993). Present study constitutes the first report from off Shag Rocks and South Georgia, and, consequently, from Antarctic waters.

Symplectoscyphus cumberlandicus (Jäderholm, 1905)

(Fig. 1.5h-i)

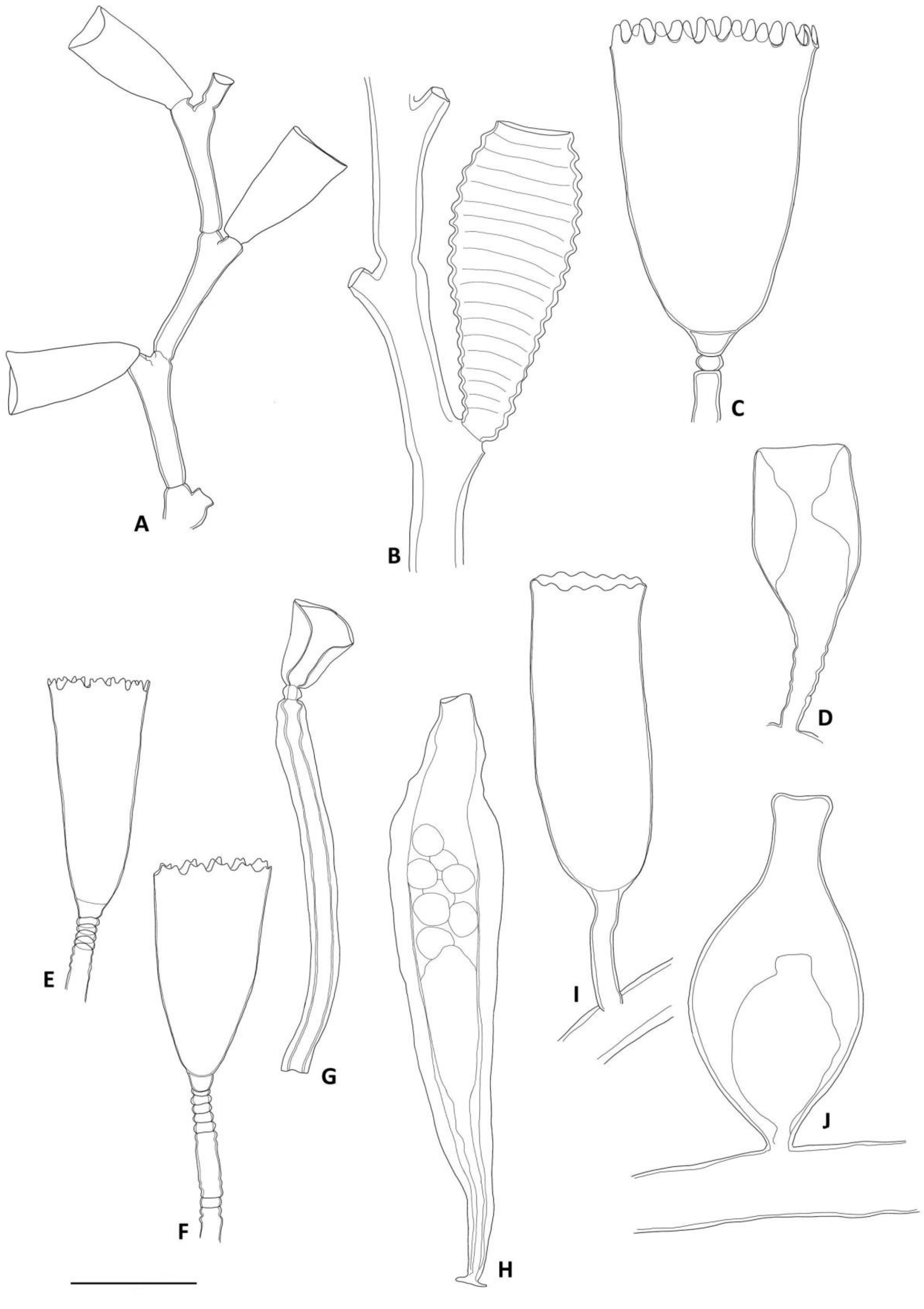

Figure 1.8 **a**-**b** *Billardia subrufa*: **a** hydrothecal shape and arrangement; **b** branch with gonotheca. **c**-**d** *Campanularia hicksoni*: **c** hydrotheca; **d** gonotheca. **e**-**f** *Obelia bidentata*: hydrothecae. **g**-**h** *Silicularia rosea*: **g** hydrotheca and pedicel; **h** gonotheca. **i**-**j** *Tulpa tulipifera*: **i** hydrotheca and pedicel; **j** gonotheca. *Scale bar*: 500 µm (**e**-**f**); 1 mm (**a**-**d**, **j**); 1.4 mm (**g**-**i**)

Material examined. **Stn 229**, one colony, c. 30 mm high, with gonothecae.

Ecology and distribution. Previously found at depths from eight (Naumov and Stepanjants 1972) to 540 m (Peña Cantero 2011); present material at 362-371 m. Circum-Antarctic species (Peña Cantero et al. 2002), reported in the area from off South Georgia (Jaederholm 1905) and the South Shetland Islands (Peña Cantero 2006, 2008). Our material comes from Discovery Bank.

Symplectoscyphus glacialis (Jäderholm, 1904)

(Fig. 1.5j-l)

Material examined. **Stn 153**, one fragmented stem, c. 11 mm high, on stone; **Stn 194**, one fragmented colony, up to 15 mm high; **Stn 253**, one colony, c. 40 mm high, on *S. compressa*; one colony, c. 55 mm high, plus one colony, c. 9 mm high, on bryozoan.

Ecology and distribution. Reported at depths from 5 (Naumov and Stepanjants 1972) to 922 m (Peña Cantero and Ramil 2006); present material at 276-296 m. *Symplectoscyphus glacialis* had been considered an Antarctic-Kerguélen species (Peña Cantero et al. 2002). We found it, however, at Burdwood Bank, suggesting a Pan-Antarctic distribution. In the Scotia Arc it is known from all the archipelagos except from the South Sandwich Islands.

Symplectoscyphus nesioticus Blanco, 1977

(Fig. 1.5m-o)

Material examined. **Stn 196**, one colony, c. 7 mm high, on polychaete tube; **Stn 223**, one colony, c. 22 mm high, on *B. subrufa.*

Ecology and distribution. Previously found at depths from 56 (Peña Cantero 2006) to 522 m (Peña Cantero et al. 2002); present material from 286 to 379 m. Species endemic from the West Antarctica (Peña Cantero 2010). In the Scotia Arc only known from the South Shetland Islands. The present record constitutes the first evidence from the South Sandwich Islands and Discovery Bank.

Campanulariidae Hincks, 1868

Billardia Totton, 1930

Billardia subrufa (Jäderholm, 1904)

(Fig. 1.8a-b)

Material examined. **Stn 194**, one colony, c. 85 mm high; **Stn 196**, one colony, c. 20 mm high, on *S. dichotoma*; **Stn 208**, one colony, c. 42 mm high, on polychaete tube; **Stn 223**, one fragmented colony, up to 90 mm high.

Ecology and distribution. Previously reported at depths between 25 (Stepanjants 1972) and 1030 m (Peña Cantero et al. 2004); present material from 287 to 647 m. Antarctic-Patagonian species (Peña Cantero et al. 2004). In the Scotia Arc it had been reported from off Shag Rocks, South Georgia, the South Orkney Islands and the South Shetland Islands; the present study constitutes the first evidence from the South Sandwich Islands and Discovery Bank.

Campanularia Lamarck, 1816

Campanularia hicksoni Totton, 1930

(Fig. 1.8c-d)

Material examined. **Stn 194**, a few hydrothecae, up to 14 mm high, on *S. frigida;* **Stn 196**, a few hydrothecae, up to 13 mm high, on *S. dichotoma.*

Ecology and distribution. Species reported at depths from 10 to 385 m (Peña Cantero et al. 2004); present material from 278 to 309 meters. Circum-Antarctic species (Peña Cantero et al. 2004), previously reported in the Scotia Arc from the South Shetland

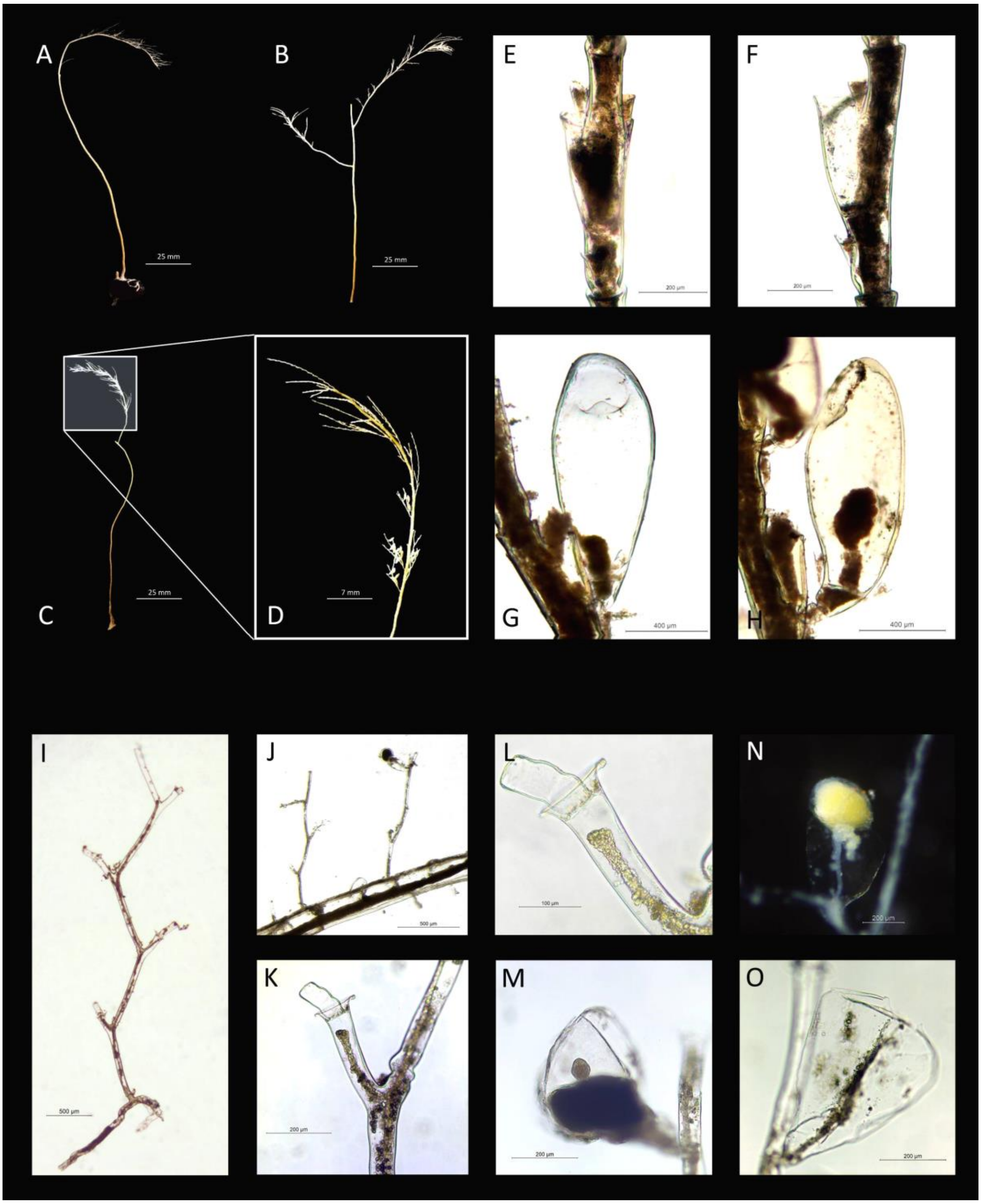

Figure 1.9 **a**-**h** *Schizotricha discovery* sp. nov.: **a**-**c** colonies; **d** detail of stem showing hidrocladia; **e**-**f** unforked hydrocladial internode; **g**-**h** gonotheca. **i**-**o** *Halecium stoloniferum* sp. nov.: **i** stem; **j** stems jointed by stolon; **k** hydrophore; **l** detail of hydrotheca; **m** gonotheca with developing gonophore; **n** gonotheca with acrocyst; **o** gonotheca after releasing acrocyst

Islands (Stepanjants 1979; Peña Cantero 2008); material studied here collected at the South Sandwich Islands, constituting the first record for this archipelago.

Obelia Péron and Lesueur, 1810

Obelia bidentata Clark, 1875

(Fig. 1.8e-f)

Material examined. **Stn 145**, a fragment, c. 1 mm high, with two hydrotheacae, on *S. argentinica*; **Stn 253**, one colony, up to 14 mm high, on *S. compressa*, plus one colony, c. 6 mm high, on bryozoan.

Ecology and distribution. Cosmopolitan species (cf. Galea et al. 2009), present in Antarctic and sub-Antarctic waters, where it has been reported at depths from three (Stepanjants 1979) to 377 m (Peña Cantero and Gili 2006); present material at 272-282 m. In the Scotia Arc it was only known from off South Georgia (Jaederholm 1905) and South Shetland (Peña Cantero 2008); the present contribution constitutes the first evidence from off Elephant Island.

Silicularia Meyen, 1834

Silicularia rosea Meyen, 1834

(Fig. 1.8g-h)

Material examined. **Stn 182**, two hydrothecae and several gonothecae, on laminarial alga.

Ecology and distribution. Species found from the tidal level (Gili et al. 1996) to a depth of 110 m (Millard 1977); present material from 249-256 meters, but its photophilic substrate suggests an accidental presence at those depths, and prevents us from assigning a new bathymetric range. It was considered as a sub-Antarctic species (Peña Cantero and García Carrascosa 1999); however, due to the presence in South Georgia (Hartlaub, 1905; present study), and the South Shetland Islands (Gili et al. 1996), it could be better considered as a sub-Antarctic species penetrating into Antarctic waters along the Scotia Arc.

Tulpa Stechow, 1921

Tulpa tulipifera (Allman, 1888)

(Fig. 1.8i-j)

Material examined. **Stn 153**, a few hydrothecae, on dead octocoral.

Ecology and distribution. Species known from depths between 10 and 1200 m (El Beshbeeshy and Jarms 2011); present material was found at 277-296 m. Originally described by Allman (1888) from material from Heard Island, it has been later reported from the Patagonian shelf (Jaederholm 1905; Vervoort 1972; El Beshbeeshy and Jarms 2011; Stepanjants 1979), Falkland Islands (El Beshbeeshy 2011), Burdwood Bank (El Beshbeeshy and Jarms 2011; present study) and off Kerguélen (Millard 1977, Stepanjants 1979). *Tulpa tulipifera* has, therefore, a Kerguélen-Patagonian distribution (Peña Cantero and García Carrascosa 1999).

General remarks

As mentioned above, the 45 species studied belong to nine families and 20 genera. Most of the species documented in the present study are representatives of the order Leptothecata Cornelius, 1992, with a scant representation of the order Anthoathecata Cornelius, 1992, of which only two species of *Eudendrium* and an undetermined Bougainvillidae were found. As previously stated by Peña Cantero (2004), these faunistic asymmetries could be ascribed to intrinsic bias of the sampling procedures, that fragment and destroy tiny and soft specimens, mainly members of the order Anthoathecata (see also Bouillon et al. 2006). Sertulariidae with 17 species (38%) is the dominant family, as it would be expected when examining any Antarctic hydroid collection (e.g. Peña Cantero 2008). It is followed by Lafoeidae with nine species (20%) and Campanulariidae with five (11%). At the generic level, *Sertularella* and *Staurotheca* are the most diverse genera, with six (14%) and five (11%) species respectively, followed by *Halecium, Schizotricha* and *Symplectoscyphus* with four (9%) species each. It is worth to mention that 23 species (52%) belong to these five genera, which only represent 25% of the whole genus diversity, whereas nine genera (45%) are represented by a single species. At a species level, *Acryptolaria operculata* is the species with the highest occurrence, being present in six (43%) stations, followed by *Abietinella operculata* and *B. subrufa*, found in four (29%).

When comparing our results with the single previous report on benthic hydroids from the Scotia Arc (Peña Cantero and García Carrascosa 1995), some similarities and differences can be highlighted. Those authors also found that Sertulariidae was the dominant family with 45% of the species diversity; however, *Staurotheca* was the most diverse genus with 31% of the species.

The high number of unusual species found in the collection is remarkable. Hitherto, 11 species (24%) had been reported less than five times worldwide (*A. gruzovi*, *Filellum* cf. *magnificum*, *H. elegantulum*, *H. nana*, *S. jaederholmi*, *S. southgeorgiae*, *S. argentinica*, *S. jorgensis*, *S. vervoorti*, *S. amphorophora* and *S. nesioticus*). In addition, two new species to science have been found: *Halecium stoloniferum* sp. nov and *Schizotricha discovery* sp. nov. This is not an isolated trait. In fact Peña Cantero and García Carrascosa (1995) found, in their material from the Scotia Arc, up to ten putative new species that were described in subsequent papers (Peña Cantero et al. 1995, 1997a, 1999a, b, 2002, Peña Cantero, 1998). This put into evidence the need to continue inventorying the hydroid fauna from the Scotia Arc region, where new species could still be awaiting to be discovered. Conversely to the results by Peña Cantero and García Carrascosa (1995) it is worth mentioning the complete absence of species of *Oswaldella*, one of the most characteristic and diversified genera in Antarctic waters (cf. Peña Cantero and Vervoort 2004a), what could be related to sampling effort on the different areas of the Scotia Arc (see below).

Regarding the updated bathymetric distribution range of the 40 species inventoried (excluding those undetermined), and following the bathymetric patterns established by Peña Cantero (2004), four different groups could be assigned. The dominant group is that formed by species exclusively found on the continental shelf, but absent in the shallowest sublittoral zone, with 14 (35%) representatives. The eurybathic species and those species extending from below the shallowest levels of the continental shelf to beyond the continental shelf-break are well represented groups, with 11 (28%) species each. The less represented contingent is the group of species inhabiting exclusively in the whole continental shelf, with only five (13%) species. Remarkably, as it could be noted in Tab. 1.4, 11 species extended their previously known bathymetric range, from a few meters (e.g *S. plicatile* and *A. gruzovi*) to some hundreds (e.g *S. southgeorgiae*, *H. megalotheca*, *L. benthophila* and *S. bathyalis*). Furthermore, two species are allocated into a different group and two species previously unnoticed from Antarctic waters are assigned to a group for the first time. Being so, *L. benthophila* and *S. southgeorgiae,* previously considered as a deep sea species (cf. Peña Cantero 2004), are reported at less than 500 m for the first time. Consequently, they could be ascribed to the group of species extending from below the shallowest levels of the continental shelf to beyond the continental shelf-break, but absent in shallow waters. On the other hand, the deep-sea and widely distributed species *S. bathyalis* and *H. megalotheca,* are reported in the Antarctic continental shelf for the first time, at a shallower depth than previous reports. We

Table 1.4. Main ecological characteristics of the species inventoried (*in Patagonian waters, **worldwide; numbers in bold are new bathymetric range or new reproductive period ascribed; species in bold are new records for the Scotia Arc)

	Depth		**Substrate**	**Epibionts**		**Reproduction**	
	Known	**Obtained**		**Hydroids**	**Other fauna**	**Fertile**	**Reproductive phenology**
Bougainvilliidae indet.	-	277-296*	*S. vervoorti*, *T. tulipifera*			Yes	IV
Eudendrium generale	10-702	332-379	Polychaete tube, sponge			Yes	I, **IV**, XII
Eudendrium sp.	-	306-343	*S. bathyalis*, *S. glacialis*, octocoral			No	-
Stegella lobata	10-700	278-309				No	I, II
Modeeria rotunda	365-377	**374-379**	*B. subrufa*			No	0
Stegopoma plicatile	385-1019	**332-340**	Graves, pebbles		Polychaetae	No	0
Abietinella operculata	63-1500	278-647	Pebbles		Protozoa	No	I, II
Acryptolaria conferta	-	**277-296***				No	0
Acryptolaria operculata	98-980*	**249-647**	Dead octocoral	*Filellum* sp.		No	0
Filellum cf. *magnificum*	85-640	306-343	*Sertularella* sp.				II
Filellum sp.	-	276-322	*Acryptolaria operculata*, *S. bathyalis*, *S. glacialis*			No	-
Halisiphonia megalotheca	672-4961**	**374-379**				No	III
H. nana	180-457	278-309	*B. subrufa*			No	0
Lafoea benthophila	3246	**278-343**	*Sertularella* sp., *S. dichotoma*, *S. frigida*, Dead octocoral			No	X
L. dumosa	12-520	272-309	*H. incertus*, *Schizotricha* cf. *turqueti*, bryozoan			No	V, XII
Halecium elegantulum	437	**374-379**	*B. subrufa*			No	0
H. incertus	15-1019	278-309		*L. dumosa*		Yes	I-IV, XI-XII
Halecium stoloniferum sp. nov.	-	277-296*	*T. tulipifera*			Yes	IV
Halecium sp.	-	306-343	*Sertularella* sp.			No	-
Schizotricha jaederholmi	252-310	**249-256**				Yes	**IV**
S. southgeorgiae	659-686	**306-343**				No	II
Schizotricha cf. turqueti	0-1890	278-309	Gravel	*L. dumosa*		Yes	I, II, III, **IV**, V, XII
***Schizotricha discovery* sp. nov.**	-	362-379	Pebbles			Yes	IV
Antarctoscyphus gruzovi	350-414	**276-282**			Bryozoan	No	II
A. spiralis	6-1958	276-282			Bryozoan	Yes	I, II, **IV**, VI, VII, XII
Sertularella argentinica	30-1200*	272*		*O. bidentata*		No	VI
S. jorgensis	32-620*	276-301	*S. compressa*, octocoral			No	0
S. robusta	40-520*	277-309	*T. tulipifera*, *B. subrufa*			No	III*
S. sanmatiasensis	30-1801	278-647	Stone			No	I, II, IV, XII
S. vervoorti	80-960*	277-343	*T. tulipifera*	Bougainvilliidae		Yes	I**, **IV***

Table 1.4 continued

	Depth		Substrate	Epibionts		Reproduction	
	Known	Obtained		Hydroids	Other fauna	Fertile	Reproductive phenology
***Sertularella* sp.**	-	277-343	*S. vervoorti*, octocoral	*Filellum cf. magnificum*, *Halecium* sp., *L. benthophila*		No	0
Staurotheca amphorophora	111-370	277-296*			Bryozoan	Yes	II, **IV**, VI, XI
S. compressa	45-1042	276-282		*O. bidentata*, *S. jorgensis*, *S. glacialis*		Yes	I, II, III, **IV**, V, VI, XII
S. dichotoma	82-799	286-371	Sponge, Polychaete tube	*B. subrufa*, *C. hicksoni*, *L. benthophila*		Yes	I, II, IV, V, VI, X, XI, XII
S. frigida	86-550	278-647	Pebbles, Gravel	*C. hicksoni*, *L. benthophila*	Acari, bivalves, barnacles, polychaetae	Yes	I, II, III, IV, V, VI, X, XI, XII
S. undosiparietina	74-700	278-322			Barnacles	Yes	I, II, III, IV, V, VI, X, XI, XII
Symplectoscyphus bathyalis	2450-2657*	**249-343**	Bryozoan	*Eudendrium* sp., *Filellum* sp.		Yes	**IV**, VI
S. cumberlandicus	8-540	362-371				Yes	II, **IV**, V, VIII
S. glacialis	5-922	276-296	Pebbles, bryozoan, *S. compressa*	*Eudendrium* sp., *Filellum* sp.,		Yes	I, II, III, **IV**, IX, XII
S. nesioticus	56-522	286-379	Polychaete tube, *B. subrufa*			Yes	II, **IV**
Billardia subrufa	25-1030	278-647	Polychaete tube, *S. dichotoma*	*H. nana*, *H. elegantulum*, *S. robusta*, *M. rotunda*, *S. nesioticus*		Yes	I, II, III, IV, V, X, XI, XII
Campanularia hicksoni	10-385	278-309	*S. frigida*, *S. dichotoma*			Yes	I, II, **IV**
Obelia bidentata	3-377	272-282	*S. argentinica*, *S. compresa*, bryozoan			No	0
Silicularia rosea	0-110	**249-256**	Laminarial algae			Yes	I, IV, VII, IX, XI, XII
Tulpa tulipifera	50-1200	277-296*	Dead octocoral	Bougainvilliidae indet, *Halecium stoloniferum* sp. nov, *Sertularella* sp., *S. robusta*, *S. vervoorti*	Caprellids, crinoids, ophiuroids, gammarids, polychaetae, pycnogonids	Yes	IV

tentatively ascribed these two new findings for the Antarctic hydroid fauna to the group of species present in the continental shelf excluding shallow waters.

Concerning the use of substratum, and knowing the limitations of indirect sampling (cf. Peña Cantero 2008) some interesting data have been obtained (cf. Tab. 1.4). In one hand, 17 species (38%) were found growing exclusively on biotic substrate (strict epibionts), some of them (7 species, 41%) exclusively on other hydroids. On the other hand, 17 species (38%) were found on both abiotic and biotic substrates (facultative epibionts) and the remaining 11 species (24%) were attached to abiotic substrates (epilithic species). Focusing on hydroids as a source of substrate, it is worth noting the high abundance of epibiotic fauna that are found attached or associated with them, specially the larger ones (e. g. *Tulpa tulipifera* and *B. subrufa* harboured five different species of hydroids, and other several marine invertebrates such as barnacles, caprellids, echinoids, ophiuroids, polychaetes and pycnogonids among others). It is necessary to undertake studies that allow us to understand how the hydroids may function as a trophic source and substrate, harbouring a rich microcosmos with high biodiversity [cf. Soto Àngel and Peña Cantero (2013); Di Camillo et al. (2013)].

In relation to the reproductive patterns, specimens of 12 species (26%) are provided with reproductive structures in a period previously undocumented, with the subsequent extension of their known reproductive period (see Tab. 1.4). This also highlights the first evidence of *S. jaederholmi* in a reproductive status, which has been found with fully-grown gonothecae for the first time.

Regarding the geographic data of the material inventoried, the study of the 45 species present in the collection has led to an increase in our knowledge of their distribution. Moreover, some interesting contributions have been drawn from our results: at archipelago and seamount scale, the present work provides with six new records to Burdwood Bank, six for Shag Rocks, two for South Georgia, 17 for the South Sandwich Islands, ten for Discovery Bank (previously unsampled), and three for Elephant Island. At a broader scale, three new records are added to Patagonian waters, ten to the Scotia Arc and eight to Antarctic waters (considering the whole Scotia Arc as part of the latter).

When assigning and applying the models established by Peña Cantero and García Carrascosa (1999), the dominant observed group is that formed by strictly Antarctic species, with 15 representatives (38%). Among them, seven species (47%) show a circum-Antarctic distribution, five species (33%) are restricted to West Antarctica, and the remaining three are tentatively endemic from the Scotia Arc. The next contingent in terms of dominance is the group of species present in both Antarctic and Sub-Antarctic waters, with ten representatives (25%), five of them with an Antarctic-Kerguélen distribution, three with a West Antarctic-Patagonian distribution, and finally two of them present in both, Antarctic and Patagonian waters. It is notorious the presence of six Sub-Antarctic species (15%), three distributed across Sub-Antarctic waters, two of them restricted to the Patagonian region, and the remaining last one present in both Patagonian waters and the Kerguélen region. The remaining species (9 species, 22%) have wider distributions.

If we compare these results with those obtained in previous analyses of the hydroids from the Scotia Arc (i.e. Peña

Cantero and García Carrascosa, 1999) obtained from the Spanish Antarctic Expedition *Antártida 8611*, it is evident a great difference in terms of the contingents of Antarctic species (67% in Peña Cantero and García Carrascosa, 1999; 38% in our study) and Sub-Antarctic species (3% in Peña Cantero and García Carrascosa, 1999; 15% in our study). This is probably due to differences in the sampling effort in the different regions of the Scotia Arc: whereas part of our collection contains material from Patagonian waters (i.e. Burdwood Bank and surrounding waters), most of the sampling during the *Antártida 8611* expedition was carried out in the southern part of the Scotia Arc, mainly in the South Shetland Islands, a region not sampled in the present study.

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CHAPTER II

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A new piece in the puzzle of the Antarctic Biogeography: what do benthic hydroids tell us about the Scotia Arc affinities?

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Abstract

The biogeography of the Southern Ocean and its subdivisions has attracted the interest of the scientific community for many years, especially for those border regions with great sub-Antarctic influence. The Scotia Arc, located between the Antarctic Peninsula and the Magellan region, has been considered as a biogeographic bridge and hence widely discussed, but there are still gaps in the knowledge of some zoological groups and its inclusion in truly Antarctic waters still constitutes an unresolved topic. The faunistic affinities between the benthic hydroids from the Scotia Arc and those from nearby regions (i.e. High Antarctica, Patagonian region and Bouvet Island) were evaluated with different similarity index and hierarchical analyses in order to put into evidence the biogeographical connectivity among those regions. The results show that the Scotia Arc archipelagos have greater affinity with continental Antarctica than with the Patagonian region, with an increasing similarity while approaching to High Antarctica, highlighting their importance as a biogeographic bridge and the effectiveness of the Polar Front as a major oceanographic barrier. Evidences from the present study on benthic hydroids supports the placement of the whole Scotia Arc within of the Antarctic region. Present data were compared with those from other benthic invertebrates groups to contribute to a better understanding of the biogeography of the Scotia Arc as a whole.

Introduction

The Antarctic region has a well-defined northern limit due to a major oceanographic barrier, the Antarctic Convergence (Crame 1999), also known (although without consensus) as the Antarctic Polar Front. This oceanographic feature remains in a remarkably constant position (Thomas et al. 2008; but see also Moore et al. 1999) and contributes to the isolation of the fauna inhabiting Antarctic waters. As a barrier, it signals the location where Antarctic surface waters sink below sub-Antarctic waters (Deacon 1933), with the subsequent development of strong latitudinal gradients of temperature and salinity (i.e. density), thus constituting "one of the strongest natural boundaries in the world ocean" (Crame 1999). Despite this well-established delimitation, however, the subdivision of the Antarctic region and nearby areas into biogeographic provinces and the biogeographic affinity of the bordering regions are still a matter of controversy.

In this regard, the Scotia Arc, with its intermediate position between the Magellan region and the Antarctic Peninsula, has greatly attracted the interest of the scientific community in recent times. The origin of the different sectors included in the Scotia Arc (i. e. Shag Rocks, South Georgia, South Sandwich Islands, South Orkney Islands, Elephant Island and South Shetland Islands) dates back to the late Cenozoic, after the geographic separation of South America and Antarctica (Dalziel and Eliot 1971) and the establishment of the Antarctic Circumpolar Current (Scher and Martin 2006). The region is located south of the Antarctic Convergence, although South Georgia and Shag Rocks lie north of the Antarctic Circumpolar Current (Orsi et al. 1995). The deep waters between the Magellan and the Antarctic regions, coupled with the oceanographic peculiarities stated above, constitute an open-ocean barrier for larval and adult dispersal and genetic flow (see Thornhill et al. 2008; Thatje 2012 and references therein), and therefore the region represents an excellent framework for the study of biogeographic bridges, as highlighted in several recent scientific contributions (e.g. Arntz and Rios 1999; Arntz 2005, Linse et al. 2007).

The biogeographic affinities of the benthos of the Scotia Arc have been discussed by many authors based on data from several marine taxa, leading to the existence of three different approaches among researchers: (i) the 'joiners' see the whole of the Scotia Arc as part of the Antarctic region, although different authors do not fully agree about further regionalization of this area (cf. Carcelles 1953; Ekman 1953; Hedgpeth 1969; Kott 1969; Briggs 1974; Cairns 1983; Knox 1994; Mülhenhardt-Siegel 1999; Gorny 1999, Moyano 2005, Zelaya 2005 and Munilla and Membrives 2008, among others); (ii) the 'cautious' are in formal agreement with (i), but their view highlights the lack of strong evidence for the subdivision of the Scotia Arc and the need to keep inventorying its biota (cf. Dell 1972; Arntz et al. 1999); finally, (iii) the 'splitters' argue that either part or all the Scotia Arc do not belong to the Antarctic region, although every author differs in the "sub-antarcticity" of the composing islands. In the latter view the whole Scotia Arc can be considered sub-Antarctic (Casteló 1999) or part of it (most often South Georgia) is regarded either as transitional between Antarctic and Magellan regions (Millar 1971; Monniot and Monniot 1983; Linse et al. 2003; Schröld 2003; Lovrich et al. 2005; Ramos-Esplà et al. 2005; Tatiàn et al. 2005; Linse et al. 2006; Barboza et al. 2011), a distinctive biogeographic unit (Powell 1951; Linse 2002; De Broyer and Jazdzewski 1993, Clarke et al. 2007), or as an area related to Kerguélen and Crozet Islands (Canteras and Arnaud 1985) or to the Magellan region (Fortes and Absalão 2011).

The Antarctic benthos is dominated by suspension feeders with complex epifaunal assemblages (Teixidó et al. 2004), and is considered as one of the richest in terms of sessile fauna in the global ocean (Dayton, 1990). Hydrozoans play an important role in the ecological structure of these communities, increasing the stability of the substratum, providing a broad range of habitats and enhancing the bentho-pelagic coupling (see Gili and Coma 1998). Furthermore, they constitute one of the most diversified and characteristic groups in the Antarctic benthos, with low diversity at genus level but reaching high levels (c. 80%) of endemism at species level (Peña Cantero 2014b). Despite this, only two studies focusing exclusively on benthic hydroids from the Scotia Arc have been published (Peña Cantero and García Carrascosa 1995; Soto Àngel and Peña

Cantero 2015) and there has been only one previous attempt to understand the geographic distribution of the hydroids from this area (Peña Cantero and García Carrascosa 1999). Furthermore, few contributions have dealt with hydrozoan biogeographic patterns around the world (e. g. Boero and Bouillon, 1993; Watson 1996; Peña Cantero and García Carrascosa 1999; Boero et al. 2003; Henry 2011), including two historical biogeography studies that employ Parsimony Analysis of Endemicity and Endemicity Analysis using selected hydrozoan groups (Miranda et al. 2013 and Miranda et al. 2015, respectively). Conversely, the present study aims to explore the faunistic affinities of the benthic hydroids from the Scotia Arc in relation to the Patagonian and Antarctic regions, explicitly addressing the question of whether its hydroid fauna can be considered as Antarctic or sub-Antarctic. The selected methodological approach, recently applied to elucidate patterns of distribution and diversity in Arctic hydrozoans (Ronowicz et al. 2015), is for the first time followed here for the benthic hydrozoans of the Scotia Arc, therefore constituting another step towards a better understanding of the Antarctic biogeography.

Material and methods

A comprehensive review of the literature concerning benthic hydroids from the Patagonian region, the Scotia Arc, and continental Antarctica has been carried out in order to create a complete presence/absence data matrix with all the species reported from those regions. The selection of Operative Geographic Units (OGUs) for the analysis was based mainly on natural geographic entities (islands, archipelagos, and submarine banks) surrounded by deep waters that constitute a potential barrier for dispersal. The Antarctic and Patagonian regions were subdivided into western and eastern sectors in order to reflect current hypothesis about the biogeographic provinces comprising these regions (e.g. Miloslavich et al. 2011; Convey et al. 2012). The following fourteen OGUs were selected (Fig. 2.1): western Patagonia Chilean Patagonia), eastern Patagonia (Argentinian Patagonia), Falkland Islands, Burdwood Bank, Shag Rocks, South Georgia, South Sandwich Islands, Discovery Bank, South Orkney Islands, Elephant Island, South Shetland Island, West Antarctica (including the Ross Sea), East Antarctica and Bouvet Island. The northern limits of the Patagonian region established by Briggs (1974) and later used by Peña Cantero and García Carrascosa (1999) have been followed: 42° latitude in the eastern sector and 35° latitude in the western one.

Some of the most comprehensive papers published in the area of study include relevant taxonomic work carried out in Antarctic waters by Allman (1883; 1888), Hartlaub (1904, 1905), Jäderholm (1904, 1905), Billard (1906, 1914), Hickson and Gravely (1907), Ritchie (1907), Totton (1930), Broch (1948), Naumov and Stepanjants (1965), Stepanjants (1979), Blanco and De Miralles (1972), Blanco (1977, 1978, 1984), Vervoort (1972a), Cairns (1983), Puce et al. (2002), Galea and Schories (2012b), and many recent contributions by Peña Cantero that have led to an increase in the knowledge of species richness and the distribution of many Antarctic taxa (see Xavier et al. 2013). Likewise, our understanding of Patagonian benthic hydrozoan diversity has been greatly expanded by the work of Vervoort (1972b), Stepanjants (1979), Blanco (1967a, 1967b, 1974, 1976, 1984), Cairns 1983, Genzano (1990, 1994, 1995), Genzano and Zamponi (1997), Galea (2007), Galea et al. (2007, 2009, 2014), Galea and Schories (2012a), and El Beshbeeshy and Jarms (2011).

The criteria employed for the elaboration of the matrix aim to minimize the bias inherent to the comparison of results from different sources. We excluded from the matrix any material not identified at species level, as well as that concerning doubtful identifications or specimens tentatively assigned to a species without strong confidence by the author. Additionally, we updated the distributional information of each taxon based on the most recent findings confirming or dismissing the presence of some species in the studied area [e.g. species of *Halecium* recently reviewed by Peña Cantero (2014a)]. Furthermore, not only the polyp stage, but also benthic medusae (e.g. members of genus *Staurocladia*) were included in the analysis (e.g. Galea and Schories 2012a).

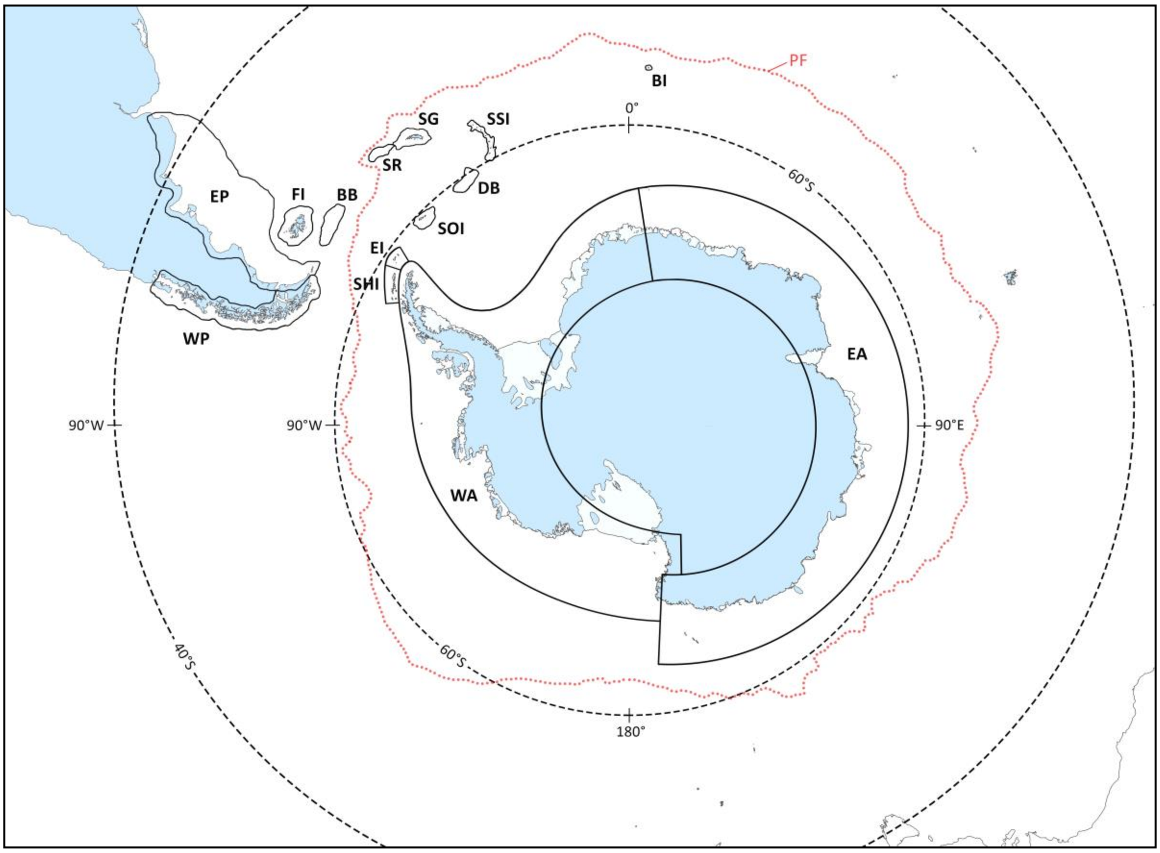


Figure 2.1 Map of the study area with selected Operational Geographic Units (OGUs). *Dotted line* indicates the mean position of the Antarctic Polar Front (PF) according to Moore et al. (1999) [Western Patagonia (WP), Eastern Patagonia (EP), Falkland Islands (FI), Burdwood Bank (BB), Shag Rocks (SR), South Georgia (SG), South Sandwich Islands (SSI), Discovery Bank (DB), South Orkney Islands (SOI), Elephant Island (EI), South Shetland Island (SHI), West Antarctica (WA), East Antarctica (EA) and Bouvet Island (BI)]

A similarity matrix was built from the presence/absence data using two different similarity indexes: Jaccard and Sørensen. They were selected due to both their wide use in the literature, which allows direct comparison of our results, and their known adequacy to run this kind of biogeographic analyses through the generation of large percentages of highly informative structures (Murguía and Villaseñor 2003). Jaccard similarity index gives the same importance to each presence/absence combination, while Sørensen Index minimizes the effect of double absence by adding double value to shared presence between OGUs, making it "one of the most effective presence/absence dissimilarity measures" (Vavrek 2016 and references therein). To avoid the effect of cumulative absences (see John and Birks 1987), we excluded from the analyses those regions with less than 20 species reported (in our case Discovery Bank, with only 13 species known to date). A cluster analysis (hierarchical agglomerative linkage by group average) was performed on both matrices in order to determine the relationship among OGUs. A non-metric multidimensional scaling analysis (*nMDS*) was also conducted to represent graphically the distance among OGUs. We performed an Analysis of Similarity test (*ANOSIM*) in order to evaluate the statistical support of *a priori* established groups of OGUs. The PRIMER 6 (v.6.1.6) software package was used to run all statistical analysis.

Results

A total of 375 species of benthic hydroids has been inventoried from the reviewed literature from the Patagonian Region, Continental Antarctica and the Scotia Arc waters (Supplementary Tab. S1). The Patagonian waters include 217 species, whereas those from continental Antarctica total 170 species. The latter number increases to 226 species when continental Antarctica and the Scotia Arc are considered together. Among the 226 Antarctic + Scotia Arc species of benthic hydroids recorded in present study, 142 (63%) are presumably endemic. Out of the 144 species of benthic hydroids known to date in the Scotia Arc, 56 (39%) are also present in Patagonian waters and 89 (62%) are also present in continental Antarctica (Fig. 2.2). Conversely, 29 (20%) species of the Scotia Arc are absent from both the Patagonian region and continental Antarctica, and 24 (17%) of them are presumably endemic to this region, most (18 species) being present exclusively in South Georgia and/or the South Shetland Islands, coinciding with the highest species richness in the whole Scotia Arc.

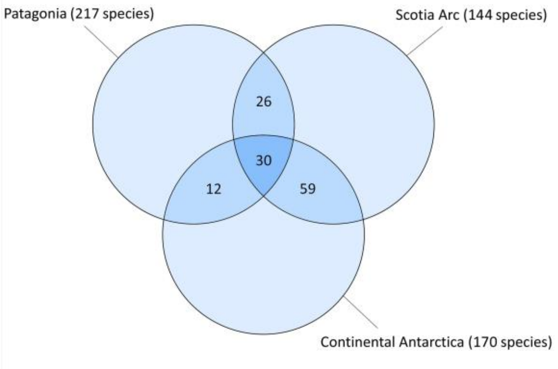


Figure 2.2 Number of species shared among sectors

The cluster analyses with Jaccard and Sørensen indexes have identical arrangement but different similarity values (Fig. 2.3), these being higher in the latter. The hierarchical aggregation of the considered OGUs shows two major groups: the Patagonian region, including the Falkland Islands and Burdwood Bank, and the Antarctic Region, which includes South Georgia and the rest of archipelagos from the Scotia Arc, as well as Bouvet Island. Within the Patagonian group, both eastern and western Patagonian regions fall together, while the Falkland Islands are clustered with Burdwood Bank.

All the OGUs comprising the Scotia Arc are invariably clustered with continental Antarctica, but with different similarities. Shag Rocks and South Georgia fall together in a group having low similarity with the rest of the Antarctic Region, but in any case with higher affinity than with the Patagonian Region. These patterns can also

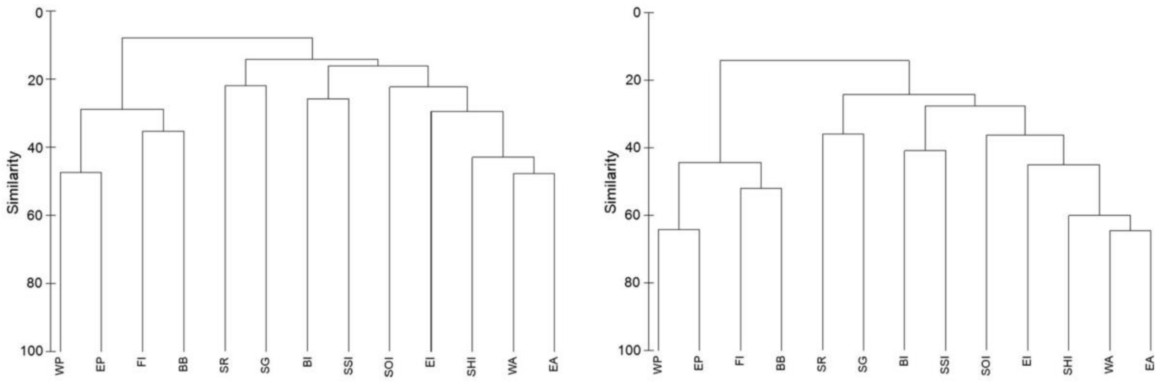
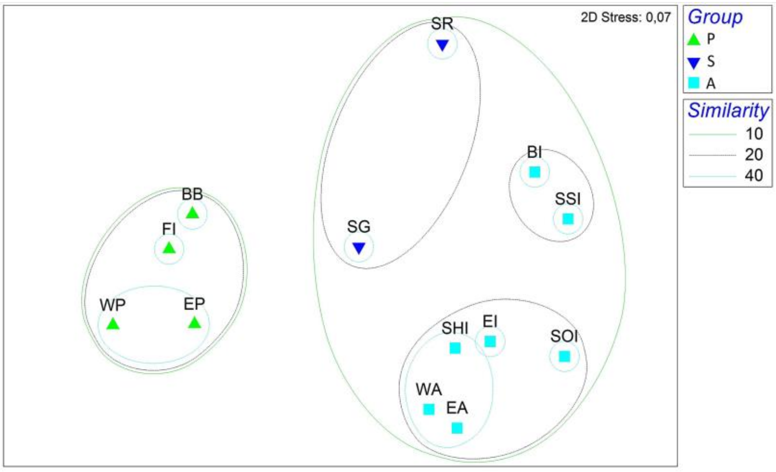


Figure 2.3 Cluster analysis of the studied OGUs based on Jaccard (left) and Sørensen (right) Similarity Indexes [same legend as Fig. 2.1]

be observed in the *nMDS* (Fig. 2.4, identical for both similarity indexes), where those Scotia Arc OGUs geographically close to continental Antarctica show the highest similarity with this region. Further analysis of the similarity matrix obtained (supplementary Tab. S2) reveals that the highest similarity values are found between Western and Eastern Patagonia, the South Shetland Islands and West Antarctica, and West and East Antarctica. On the contrary, Shag Rocks presents low affinity with continental Antarctica and the rest of the Scotia Arc, with the exception of South Georgia, with which it clusters.

Figure 2.4 Non-metric multidimensional scaling (*nMDS*) of the studied OGUs based on Sørensen Similarity Index [same legend as Fig. 2.1; Groups: Patagonian region (P); South Georgia and Shag Rocks (S); Continental Antarctica and South Sandwich, South Orkney, Elephant, South Shetland and Bouvet Islands (A)]



The *ANOSIM* test performed with only two *a priori* groups (Patagonian region and continental Antarctica + Scotia Arc) shows the separation between these areas with a robust statistical support (Tab. 2.1). The division between the Patagonian region (including Falkland and Burwood Bank), South Georgia group (Shag Rocks and South Georgia), and continental Antarctica and nearby archipelagos (South Sandwich Islands, South Orkney Islands, Elephant Island, South Shetland Islands, and Bouvet) is also well supported, although there is not strong support in pairwise comparisons. Despite the great statistical significance and R-value observed between the Patagonian and South Georgia regions, the number of permutations is low. The R-statistic between the South Georgia group and the continental Antarctica and nearby archipelagos is considerably lower than in the other combinations.

Discussion

Species richness and endemism

Data from the present study contrast sharply with those obtained by Peña Cantero and García Carrascosa (1999).

Table 2.1 Results of the *ANOSIM* test with the different grouped regions

Groups	*R*-Statistic	Significance level %	Possible permutations	Actual permutations	Number >= observed
P, S+A	0.84	0.1	715	715	1
P, S, A	0.866	0.008	25740	25740	2
P, S	1	6.7	15	15	1
P, A	0.995	0.3	330	330	1
S, A	0.578	5.6	36	36	2

[Groups: Patagonian region (P); South Georgia and Shag Rocks (S); Continental Antarctica and South Sandwich, South Orkney, Elephant, South Shetland and Bouvet Islands (A)]

These authors found 126 and 104 species in the Patagonian and Antarctica + Scotia Arc regions, respectively, representing only 58% and 46% of the species found in the present contribution. The exclusion of the members of the subclass Anthoathecata from their study surely contributes to the observed discrepancies, but this is not the only explanation. The recent large taxonomic effort (Peña Cantero 1998; Peña Cantero et al. 1995, 1997a, 1997b, 1999a, 1999b, 2002; Galea 2007; Galea and Schories 2012a, 2012b; Galea et al. 2007, 2009, 2014) has largely increased the number of species observed in both regions, especially after the description of many endemic taxa. On the other hand, it is worth noting that 68 species are shared between Antarctica + Scotia Arc and the Patagonia (Fig. 2.2), which represents three times the number of shared species (23) found by Peña Cantero and García Carrascosa (1999). Recent contributions about the Scotia Arc hydroid fauna (cf. Galea and Schories 2012b, Soto Àngel and Peña Cantero 2015) have led to an increase in the knowledge of this region, reporting species previously unnoticed in the Scotia Arc, but present in nearby waters. These 68 shared species constitute *ca*. 30% of the total species known from each region, slightly above the 18-22% obtained by Peña Cantero and García Carrascosa (1999). The Scotia Arc alone accounts for the majority of these shared species (56 out of 68, 82%), and in fact 26 of them are not found elsewhere in continental Antarctica, highlighting once again the importance of the Scotia Arc in terms of hydroid diversity. Among the 42 species shared by the Patagonian region and continental Antarctica, 30 of them are potentially shared by means of the Scotia Arc (Fig. 2.2).

As previously stated by Soto Àngel and Peña Cantero (2015), some Patagonian hydrozoan species could reach Antarctic waters via the Scotia Arc. In fact, these authors reported five species (*Acryptolaria operculata, Sertularella jorguensis, Sertularella robusta, Symplectoscyphus bathyalis* and *Silicularia rosea*) present in Patagonian waters but previously unnoticed from the Scotia Arc. Likewise, they also recorded *Staurotheca amphorophora* from Patagonian waters, a species previously considered restricted to Antarctic waters. Moreover, in our results, a high percentage (71%) of the species shared by continental Antarctica and Patagonia are also present in the Scotia Arc, while only 12 species (29%) are absent (see Fig. 2.2), strengthening the hypothesis of a potential role of this area as a biogeographic bridge. These findings could also be suggesting recent changes in species distribution due to global climate change, though this hypothesis should be taken with caution until it can be evaluated with further research.

The observed percentage of hydroid endemics in Antarctic waters (63%) is lower than the 69% recorded by Peña Cantero and García Carrascosa (1999) and the 80% recently stated by Peña Cantero

(2014b). These discrepancies are mostly attributed to the inclusion of the family Stylasteridae in the present database, with 21 Antarctic taxa but only three endemic species. In any case, the obtained endemism constitutes one of the highest among the different groups of the Antarctic fauna (see Peña Cantero 2014b). Higher taxonomic efforts and the subsequent description of several species (see Xavier et al. 2013) are surely contributing to the increase of this number.

Table 2.2 Number and percentage of endemic species of Bryozoa (Cyclostomata and Cheilostomata), Mollusca (Bivalvia and Gastropoda) and Hydrozoa within different sectors from the Scotia Arc and Bouvet Island. Bryozoa and Mollusca data have been calculated from Griffiths et al. (2009)

	Cyclostomata		Cheilostomata		Bivalvia		Gastropoda		Hydrozoa	
	Species	%	Species	%	Species	%	Species	%	Species	%
South Georgia	1	4.8	16	15.2	7	13.2	53	36.3	9	13.4
South Sandwich Islands	0	0	0	0	2	6.7	8	26.7	1	3.6
South Orkney Islands	0	0	2	2.0	0	0	21	25.0	1	3.0
South Shetland Islands	2	7.1	7	5	2	3.2	4	4.0	7	7.6
Bouvet Island	0	0	1	5.0	2	14.3	11	50.0	1	4.8

The percentage of species endemic to the Scotia Arc found in the present contribution (17%) contrasts with lower values of endemism in ascidians (Ramos-Esplà et al. 2005; Tatiàn et al. 2005) and higher ones in other groups [22% in Pycnogonida (Munilla and Membrives 2008); 36% in bivalves (Zelaya 2005) and 40% in mollusks in general (Fortes and Absalão 2011)]. When considering the OGUs from the Scotia Arc separately (Tab. 2.2), the highest levels of endemism are those for South Georgia (13%), the South Shetland Islands (8%) and Discovery Bank (8%), the latter with only 13 species known to date and a single endemic taxon. This pattern is very similar to that observed by Griffiths et al. (2009) in other invertebrates (Tab. 2.2); they also noted a positive correlation between levels of endemism and species richness. Thus, the Scotia Arc contributes with ca. 17% of the total endemism in Antarctic hydroids, highlighting the relevance of this region as an area of endemism, in concordance with the results obtained by Miranda et al. (2013) in their Parsimony Analysis of Endemicity of benthic hydroids from the Southern Ocean.

Faunistic affinities

In general, the similarity between OGUs is low (with a few exemptions stated below), presumably due to the high number of double absence rather than to real distinctness between sectors. This is partially, but not fully corrected by the Sørensen index (see Fig. 2.3). The isolated position of Shag Rocks in the *nMDS* (Fig. 2.4), located farther away from areas with more Antarctic affinity, even farther than Bouvet, could be due to its peripheral position in the Antarctic region, its proximity to the Polar Front, or more probably to the lack of knowledge on its hydroid diversity (only 22 species are known in the area). In contrast, Bouvet is clustered with the South Sandwich Islands, having greater similarity with continental Antarctica than the group of South Georgia and Shag Rocks (Fig. 2.3). Conversely, South Georgia as a separate unit has higher affinity with continental Antarctica OGUs than Bouvet Island (see Tab. S2). Recent contributions dealing with areas of endemism in the Southern Ocean also showed greater affinity of the hydroid fauna between Bouvet Island and continental Antarctica (Peña Cantero and Marques 2010; Miranda et al. 2013).

Nevertheless, as stated above, only 21 species are known from Bouvet, which could be creating an artefact within the results. In parallel, the results of the *ANOSIM* test (Tab. 2.1) show that there is not enough evidence to consider the South Georgia cluster as a proper group (i.e. an independent province), in terms of benthic hydroid diversity. East and West Antarctica show one of the highest similarity values between OGUs (see Fig. 2.3 and supplementary Tab. S2 and S3). Based on marine benthos data, previous authors have suggested that these sectors are clearly distinct, although this difference may simply reflect the asymmetries in the sampling effort (see Clarke 2008 and references therein). Further sampling and inventorying taxa, especially in East Antarctica, as well as new studies implementing other approaches and/or methodologies, will surely shed light on these issues.

In general terms, and without neglecting the heterogeneity of both the data used and the results obtained with different methodologies and approaches, some similarities/discrepancies with previous studies dealing with other benthic invertebrates are found.

In agreement with the results obtained by Zelaya (2005) with bivalves (using the Simpson Coefficient of faunal similarity), a strong increase in similarity is observed from Burdwood Bank to South Georgia (Tab. S2), constituting another evidence of the strong effect of the Polar Front. Similarly, other authors using presence/absence data and the Bray Curtis dissimilarity index [Barboza et al. (2011) with benthic echinoderms; Moyano (2005) with benthic bryozoans; Munilla and Membrives (2008) with pycnogonids, and Griffiths et al. (2009) with cheilostome bryozoans, bivalves and gastropods] obtained results grouping all the Scotia Arc archipelagos with other Antarctic areas (i.e. the Antarctic Peninsula, Weddell Sea, Bellingshausen Sea, and Ross Sea), supporting the inclusion of the Scotia Arc within the Antarctic region. Noteworthy, the comparison of our results from the Sørensen index with those obtained by other authors from Bray-Curtis is straightforward, since the Sørensen coefficient is identical to Bray-Curtis coefficient when the latter is calculated from presence/absence data (Clarke and Warwick 2001).

In contrast, other authors obtained differing results using presence/absence data and several similarity indexes. Fortes and Absalão (2011), analyzing mollusk data with the Jaccard Index, observed a much higher affinity between South Georgia and the Magellan region than with the other archipelagos from the Scotia Arc. Griffiths et al. (2009) grouped the cyclostome bryozoans from South Georgia, South Sandwich Islands and South Orkney Islands with those of the Magellan region based on Bray-Curtis similarity values. The results obtained by Lovrich et al. (2005) with crustacean decapods distribution (without performing statistics analyses), and Ramos-Esplà et al. (2005) with ascidians (Bray-Curtis index), allowed them to suggest that the fauna from South Georgia should be considered intermediate between the Antarctic and Magellan ones. Tatiàn et al. (2005), also working with ascidians (Kulczynski-2 index), concluded that South Georgia shows similar affinities to both regions, although in their analysis South Georgia is clustered with the South Sandwich Islands and not with the Magellan region. Finally, in his monograph of the Stylasteridae (Hydrozoa: Anthoathecata) from sub-Antarctic and Antarctic waters, Cairns (1983) considered South Georgia as a transition district between the Patagonian and the Antarctic regions in terms of faunistics, while the same area is regarded as Antarctic in terms of its biogeography (no statistical tests were performed). When analyzing exclusively the records of the Stylasteridae, our results show that South Georgia is more similar to the Magellan region (supplementary Fig. S1 and S2). This pattern could reflect differences in the dispersal capabilities of the Stylasteridae compared with other benthic hydroids. This assumption would imply an ecological strategy to cross the Polar front (as hypothesized by Cairns 1983) not displayed by most hydrozoans from the region. Alternatively, it could also be explained by the large gap in knowledge of Stylasteridae from the Scotia Arc (see Bax and Cairns 2014).

In summary, our results, in agreement with those obtained by Moyano (2005), Zelaya (2005) Munilla and Membrives (2008) and Barboza et al. (2011) among others, suggest the biogeographic placement of the Scotia Arc, including South Georgia, within the Antarctic region, without neglecting its peculiar faunal composition, as noted unambiguously by previous authors. This highlights the important role of the Scotia Arc system as a biogeographic bridge. Additionally, our results and previous studies underline the strong effect of the Polar Front in delimiting the biogeographic regions, at least for some groups of invertebrates. However, as noted by Tatiàn et al. (2005), and documented by Moore et al. (1999), the position of the Polar Front is subjected to oscillation, which may cause some succession in the faunistic assemblages from the closest regions (specially South Georgia and Bouvet Islands). This phenomenon could explain part of the discrepancies among the different authors who have dealt with the present topic. In future approaches, it would also be desirable to include the "z" axis (i.e. bathymetrical information) coupled with species abundance data in the different sectors to explore more comprehensive interpretations. Certainly, further efforts in taxonomic calibration will play an important role in future biogeographic contributions by eliminating duplicates (i.e. synonyms) and recovering lost information due to missing values (i.e. cryptic species). These questions require further research and it would be necessary to include in the analysis other sub-Antarctic zones, such as the Kerguélen region (including Crozet and Prince Edward Islands), with the aim of testing the affinity of Bouvet with other potential similar areas. Furthermore, future studies with other clustering methods such as K-means, UPGMA or NERC (see Vavrek 2016) as well as historic biogeography approaches (e. g. Endemicity Analysis, as Miranda et al. 2015) will shed more light on the topic, allowing us to understand the biogeography of the Antarctic region in a holistic and multidisciplinary manner.

As stated by Clarke (2008), there are several factors that constrain the analyses of this kind of pragmatic approaches, and the faunal similarity should be taken with caution, not only because the gaps in knowledge cause the clustering of under-sampled regions (see Griffiths et al. 2009), but also due to the fact that these approaches do not differentiate between biogeographic units and more or less discrete evolutionary units. Moreover, each faunistic group has its own dispersal capabilities and ecological constraints (see Thatje 2012 and references therein), frequently resulting in important differences in the distributional patterns exhibited (see Barnes and De Grave 2000, 2001), even within the same group (Griffiths et al. 2009, present contribution). For these reasons, it would be necessary to undertake meta-analyses with all the available information from all different taxa with the aim of understanding the biogeography of the Southern Ocean as a whole.

Supplementary material (Appendix B)

Table S1: Presence/absence data matrix and species richness for Antarctic, Scotia Arc and Patagonian benthic hydrozoans.

Table S2 and S3: Similarity matrixes obtained with Jaccard and Sørensen indexes.

Figure S1 and S2: Cluster analysis and *nMDS* from Sørensen Similarity for the Stylasteridae.

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CHAPTER III

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Inhabitant or visitor? Unexpected finding of *Aglaophenia* (Cnidaria, Hydrozoa) in Antarctic waters

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Abstract

Benthic hydrozoans are one of the most speciose and characteristic taxa from the Antarctic region, with a high number of endemic species, low diversity at the genus level and some worldwide-distributed families unrepresented. This is the case of the family Aglaopheniidae. A new species to science of the genus *Aglaophenia* Lamouroux, 1812 has been found in the eastern end of the Weddell Sea, at depths between 65 and 116 meters, within the material obtained by the German Antarctic expedition ANT XV/3. This finding constitutes a new record for the Weddell Sea fauna, the first evidence of the genus for polar regions, and even the family Aglaopheniidae from Antarctic waters. The material has been accurately examined and described. Literature concerning the species of *Aglaophenia* from sub-Antarctic and other close areas has been reviewed and, as a result, a checklist of 20 species, with their corresponding distribution, is given. The material examined does not agree with any of the species and therefore it is described as a new species. Some possible scenarios for the presence of an aglaopheniid in Antarctic waters are contemplated and discussed (e.g. alien species, relict, global climate change, microhabitat).

Introduction

Aglaopheniidae Marktanner - Turneretscher, 1890 constitutes one of the most diverse and well-known families of benthic hydroids, comprising ca. 250 known species (Bouillon et al. 2006). The distinction at the genus level is based mainly on the gonosome typology, as the trophosome is relatively constant among genera. Its representatives are widely distributed from temperate to tropical waters and from shallow to deep bottoms. Within the family, there are some differences in the general distribution of different genera: *Macrorhynchia* is more common in tropical and subtropical waters, *Aglaophenia* in tropical, subtropical and temperate waters, *Cladocarpus* in Arctic and deep sea waters and *Lytocarpia* in temperate, Arctic and sub-Antarctic waters. Nevertheless, despite their wide distribution, aglaopheniids have never been reported from Antarctic waters, i.e. south of the Polar Front.

Members of the genus *Aglaophenia* are characterized by feather-like, branched or unbranched, monosiphonic or polysiphonic stems (cormoids);

unbranched, pinnately arranged hydrocladia, arising from alternate apophyses provided with two lateral nematothecae and a median inferior one; hydrothecae only on hydrocladia, from cone to sac-shaped; each hydrotheca typically flanked by a pair of adnate, lateral nematothecae, and with a, partly to wholly adnate, median inferior nematotheca; reproductive structure, named corbula, enclosing gonophores within modified hydrocladia, bearing alternately inserted secondary ribs with nematothecae; corbula ribs from completely free to totally fused; fixed sporosacs or released swimming gonophores (modified from Bouillon et al. 2006).

The effects of global climate change (anthropogenic impacts coupled with global warming) are pushing some species to change their distribution to maintain their thermal optimum. Thus, some species with warm affinity are extending their geographical distribution to areas where it would have been impossible for them to live (due to low temperatures) just a few decades ago (Hughes 2000). In general, most contributions concerning changes in fauna composition and distribution in marine ecosystems (within a perspective of global climate change) have been focused on plankton or nekton, while benthic communities have been practically neglected, above all those inconspicuous groups without commercial value (see González Duarte et al. 2014 and references therein). With a few exemptions [i.e. Puce et al. (2009) and González Duarte et al. (2014)], long-term changes in the distribution of benthic hydroids are not well documented, and there is still a need to establish a comprehensive baseline database to enable future comparisons among benthic hydroid assemblages.

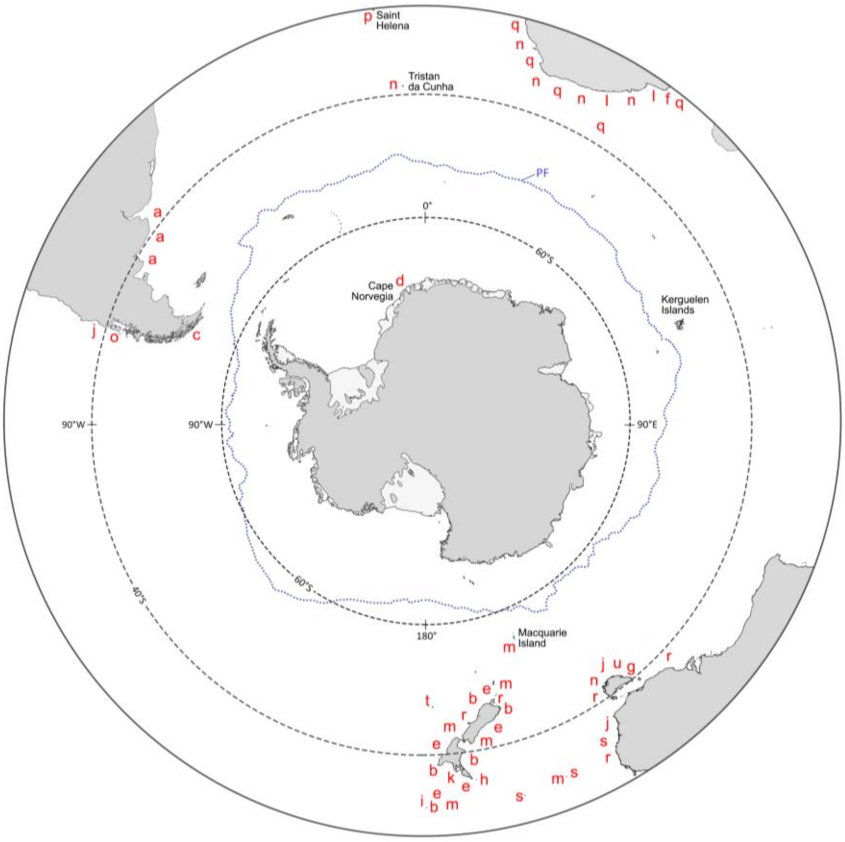

Figure 3.1 Distribution of the *Aglaophenia* species in the Antarctic, sub-Antarctic and nearby regions:
a *Aglaophenia acacia*;
b *A. acanthocarpa*;
c *A. antarctica*;
d *A. baggins* sp. nov;
e *A. ctenata*; **f** *A. cupressina*;
g *A. decumbens*;
h *A. difficilis*; **i** *A. digitulus*;
j *A. divaricata*; **k** *A. hystrix*;
l *A. latecarinata*; **m** *A. laxa*;
n *A. parvula*;
o *A. patagonica*;
p *A. picardi*; **q** *A. pluma*;
r *A. plumosa*; **s** *A. sinuosa*;
t *A. subspiralis*;
u *A. tasmanica*.
[Dotted line indicates the mean position of the Antarctic Polar Front according to Moore et al. (1999)]

The Antarctic shelf benthic communities are dominated by benthic suspension feeders. The top-predators are generally restricted to slow-moving invertebrates (i.e asteroids and nemerteans), whereas there is an almost complete lack of skeleton-crushing predators (i.e. fish and decapods). Their absence is explained by physiological constrains rather than to oceanographic barriers (Aronson et al. 2007 and literature cited). They are however well-known in the deep shelf and slope (Arntz et al. 1994).

Some evidence of non-indigenous species in terrestrial Antarctic environments is known (Rogan-Finnemore 2008 and literature cited), but neither truly alien species nor changes in Antarctic benthic communities have been documented from the Southern Ocean. In the last years, some authors have hypothesized that the recent findings of some decapod crustaceans species in the Antarctic continental slope could be pointing out recent invasions (e.g. Aronson et al. 2007 and references therein). However, as stated by the authors, some species could correspond to unreported endemics and the time they have been present in the Antarctica remains an unresolved question [Aronson et al. (2007) p. 143].

Despite being a widespread and speciose family, the representatives of Aglaopheniidae were completely unknown from the Antarctic region (see Fig. 3.1). Consequently, the present contribution represents the first evidence of the occurrence of the family Aglaopheniidae in this huge region, and the first report of the genus for any polar region.

Material and methods

The specimens were obtained during the German Antarctic expedition ANT XV/3 off Cape Norvegia, in the eastern end of the Weddell Sea in January 1998. The samples were collected with a Photo Sled and a TV Grab, at depths between 65 and 112 m, from two nearby sampling stations. Material was fixed on board with 4% formalin and later transferred to 70% ethanol. Holotype and paratypes are deposited in Museo Nacional de Ciencias Naturales (MNCN), Madrid, Spain. Remaining material is kept in the Hydrozoan collection of the Department of Zoology, University of Valencia (HCUV), Spain.

The material has been examined in detail, identified and illustrated by the authors, and a full description, including the reproductive structures, is provided. To assign a specific epithet to the specimens found, an exhaustive literature search of the species of *Aglaophenia* reported from the sub-Antarctic region and other close areas (i.e. South Africa, New Zealand and Tasmania) has been done. As a result, a checklist of the species reported in those waters, their distribution and the corresponding contributor is provided (Tab. 3. 1).

Material examined:

Holotype, MNCN 2.03/448: *ANT XV/3*: 48-33, 29-01-1998, 71° 07.3' S 11° 28.3' W, 65 m, one cormoid, 42 mm high, with corbulae; substrate unknown.

Paratype, MNCN 2.03/449: *ANT XV/3*: 48-34, 29-01-1998, 71° 07.2' S 11° 28.3' W, 68-116 m, two cormoids, 43 and 45 mm high, with corbulae; substrate unknown.

Additional material (HCUV): *ANT XV/3*: 48-34, 29-01-1998, 71° 07.2' S 11° 28.3' W, 68-116 m, one cormoid, 36 mm high; substrate unknown.

Results

Aglaophenia baggins sp. nov.

Diagnosis. Stems erect, delicate, dichotomously branched, with short hydrocladia not very conspicuous (Fig. 3.2a). Hydrorhiza unknown. Presence of prosegment unknown. Hydrocauli monosiphonic, divided into short internodes, separated by inconspicuous nodes, more visible at basal portions of stems or after branching. Nodes straight and transversal, with the exception of those from basal part of the secondary stems, which remain parallel to those from the primary stem, and therefore resembling oblique, but gradually inclined along the stem until becoming perpendicular to long axis of those second-order stems (Fig. 3.3b). Cauline apophyses, one per internode, alternately arranged in two rows along the hydrocauli, making an angle of c. 30°, giving rise to alternate hydrocladia (Fig. 3.3a). Each cauline internode provided with an apophysis with a 'mamelon' (also named pseudonematotheca), and three nematotheca (Fig. 3.3a). Mamelons facing to the inner space delimited by the two rows of apophyses (Fig. 3.3a). Two of the nematothecae flanking the apophysis and, the third one separated from the apophysis at the basal third of the segment (Fig. 3.3a).

Branching bifid and symmetrical (Fig. 3.2a, 3.3b), taking place between apophysis and inferior nematotheca, the former supporting a normal hydrocladia. No prosegments observed after branching.

Hydrocladia with transversal nodes delimiting short hydrothecate internodes, each with three nematothecae: one mesial inferior and two lateral (Fig. 3.3c). Cladial internodes, 259-289 μm in length, provided with two conspicuous perisarcal thickening, one at the level of lateral nematothecae, the other as a continuation of the intrathecal septum (Fig. 3.3d-f).

Hydrotheca sac-shaped, short and broad, 299-362 μm in length and 181-219 μm in diameter at aperture (Fig. 3.2b-c, 3.3d-e). Length/diameter ratio 1.52-1.77. Free part of abcauline wall slightly concave, with thick perisarc, 78-138 μm in length (including adcaulinar cusp), part adnate to nematotheca convex, located more outwards than distal free part, and forming a sort of swelling (Fig. 3.2b, 3.3e). Hydrothecal rim directed downwards, provided with nine marginal cusps: four pairs of blunt, well-developed, lateral cusps, becoming shorter towards internode, and a single abcauline one, slightly pointed outwards. Intrathecal septum thick but incomplete, located adcaudally at the basal fourth of the hydrotheca. Lateral nematotheca strongly bent upwards in the middle of its length, distally rounded and projecting outwards, reaching and slightly surpassing hydrothecal rim. Mesial nematotheca tubular, adnate to hydrotheca for c. two thirds of its length, and distinctly bent outwards at distal part. Protruding part located in the middle of abcauline wall or slightly above. Mesial nematotheca with gutter-shaped aperture, never reaching hydrothecal rim, connected to hydrothecal cavity distally.

Corbulae growing in substitution of hydrocladia. Male corbula ovoid, 1875-2270 μm in length and 825-923 μm in maximal diameter, and provided with six to seven corbulacostae, from mostly to completely unfused nematocladia. The former only fused in the middle of the nematocladium (i.e. unfused near the raquis and distally from its origin). The completely unfused are centrally located along the axis of the corbula. Without secondary free ribs. Female corbula not seen.

Cnidome composed of microbasic mastigophores in two size classes: the larger ones 30.1 ± 0.8 x 3.5 ± 0.2 µm (n=18) and the smaller ones [5.4 ± 0.4 x 1.5 µm ± 0.1 (n=17)].

Discussion

Identity of the species

Taxonomic remarks. Despite the new species reported here being ascribed to the genus *Aglaophenia* with confidence, it is worth mentioning that recent studies (i.e. Moura et al. 2012, Postaire et al. 2016) have shown the genus as polyphyletic and thus its systematics is in need of revision utilizing multi-locus molecular examination. Although the colonies were devoid of the basal section and the presence of prosegment cannot be completely validated, a prosegment-like internode was observed following a stem breakage, with oblique distal node and ca. transversal basal one (Fig. 3.2j). A single cormoid was observed bearing stolon-like structures (thickened hydrocaulus) developing from distal part of stem, and

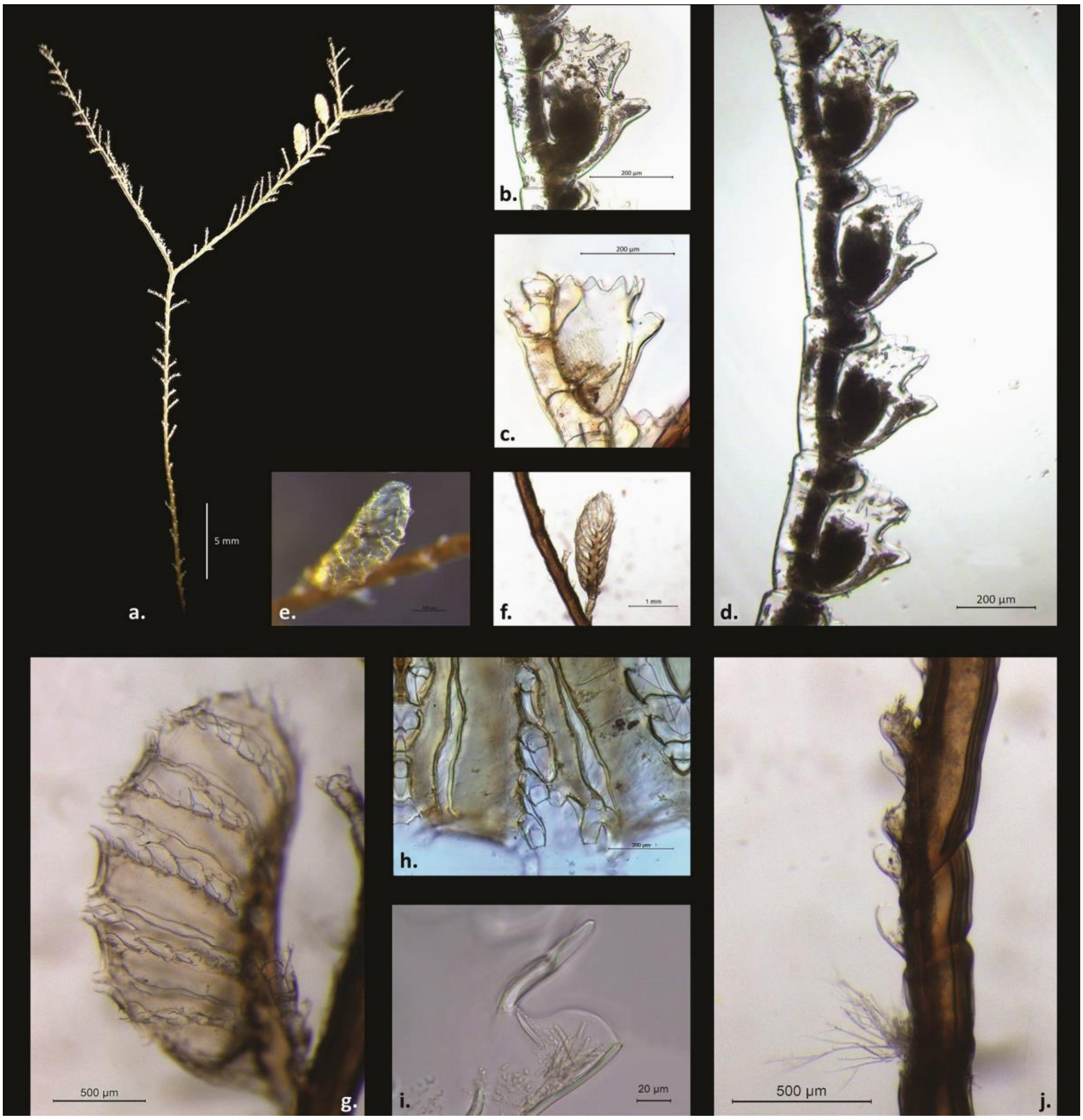

Figure 3.2 *Aglaophenia baggins* sp. nov.: **a** cormoid showing dichotomous branching; **b-c** hydrothecae; **d** fragment of hydrocladium; **e-g** different views of the corbulae: **e** top, **f** underneath, **g** lateral; **h** detail of the corbulacostae; **i** detail of a mesial nematotheca carrying nematocysts; **j** prosegment

giving rise to new cormoids [a similar structure was described in the seagrass epizooic *Aglaophenia harpago* and *Aglaophenica picardi* (Svoboda and Cornelius 1991)]. A developing corbula was located replacing the first hydrocladia of the secondary branch, in a stem bifurcation (Fig. 3.3b), but not replacing a branch itself as described in *Aglaophenia acacia* (Svoboda and Cornelius 1991).

Aglaophenia baggins sp. nov. shares the general appearance of the colony and the shape of the hydrotheca with both the cosmopolitan species *Aglaophenia pluma* and the Atlantic-Mediterranean *Aglaophenia tubiformis*, the latter considered conspecific with the former by Moura et al. (2012). *Aglaophenia baggins* sp. nov., however, differs from both by the larger size of the hydrotheca, the presence of incompletely fused corbulacostae in the male corbula, and the size of the nematocysts (pers. observ.). Furthermore, *Aglaophenia tubiformis* differs by the presence of symbiotic zooxanthellae. On

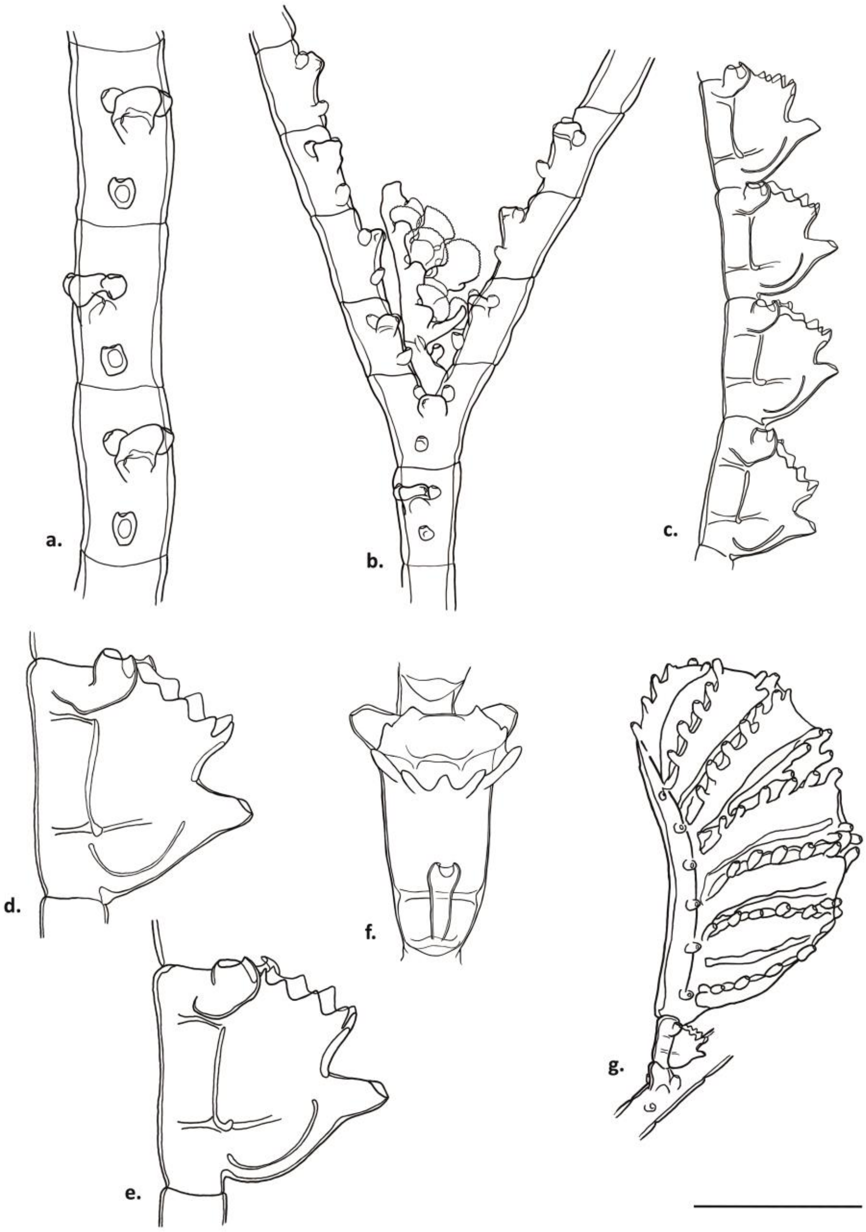

Figure 3.3 *Aglaophenia baggins* sp. nov: **a** cauline internodes; **b** branching stem with developing corbula (hydrocladia not shown); **c** portion of hydrocladium; **d-e** hydrothecae in lateral view; **f** hydrotheca in frontal view; **g** corbula. *Scale bars*: 200 μm (**d**–**f**), 400 μm (**c**), 500 μm (**a**), 1 mm (**b**, **g**)

the other hand, bifid colonies of *Aglaophenia pluma* have been referred to other species of the genus lately (see Thorpe et al. 1992 and Ansín Agís et al. 2001) and there is a general trend that considers *Aglaophenia pluma* as an unbranched species. The presence of some incompletely fused corbulacostae have only been reported for *Aglaophenia lophocarpa* [as abnormal morphology by Svoboda and Cornelius (1991), but as a character variation by Ansín Agís et al. (2001)] and *Aglaophenia tubulifera*, a species with a remarkably long mesial nematotheca, which allows distinguishing it easily from *Aglaophenia baggins* sp. nov.

In relation with the species reported in nearby areas (see Tab. 3.1), *Aglaophenia acacia* is easily distinguishable by the trifid branching pattern, deeper hydrothecae and larger corbulae. *Aglaophenia antarctica* (despite its name, a Patagonian species), has tubular hydrotheca, with the median nematotheca located distally, and elongate lateral nematothecae. The other species are quickly discarded by some distinctive diagnostic traits: *Aglaophenia latecarinata* by the presence of a keel at the abcauline hydrothecal wall, *Aglaophenia ctenata* by its strong intrathecal septae, and *Aglaophenia difficilis* and *Aglaophenia hystrix* by the inconspicuous lateral cusps of the hydrotheca.

Even when *Aglaophenia baggins* sp. nov. could be superficially considered closed to the group of *A. pluma*-like species, the morphological peculiarities discussed above, as well as its location, in an unexpected biogeographic region, allow us to describe it as a new species to science.

Ecology. The known bathymetric range of *Aglaophenia baggins* sp. nov. extends from 65 to 116 m. In the absence of further information, and following the bathymetric groups established by Peña Cantero (2004), it could be considered for now as a species that inhabits the continental shelf excluding shallow waters, and therefore avoids anchor ice (see Picken 1985). Even when the frequency of ice scour disturbances decreases with depth (cf. Smale et al. 2008), living ca. one hundred meters deep does not prevent ice abrasion at all. Modern ice scour reaches depths up to 500 meters at least once every 230 years (Gutt et al. 1996). Furthermore, the eastern Weddell Sea is being strongly disturbed by grounding icebergs (Gutt and Piepenburg 2003). Therefore, if the species described here is well established, either the actual bathymetric or geographic range could be considerably larger. Future sampling will allow a better understanding on its bathymetric distribution. Regarding the reproductive phenology, the colonies, which are provided with corbulae, were collected in January, coinciding with the austral summer.

Distribution. *Aglaophenia baggins* sp. nov. is only known from its type locality, off the north of Cape Norvegia, in the eastern end of the Weddell Sea. It constitutes not only a new record for the Weddell Sea fauna, but also the first report of the genus and the family for the entire Antarctic region.

Etimology. The specific epithet "*baggins*" is dedicated to the hobbit characters of the Baggins family created by Prof. J.R.R. Tolkien in his fiction, in reference to their tendency, unusual among hobbits, to venture away from their known habitat.

The presence of an *Aglaophenia* species in the Antarctic:

The ecological and evolutionary adaptations of the Antarctic fauna to the coldest marine temperatures and most intense seasonality of food supply on Earth (see Peck et al. 2006), make the Antarctic communities particularly vulnerable to global warming and the concomitant invasion of species from lower latitudes (Barnes et al. 2006 and references therein). This fact constitutes an excellent framework for understanding the impacts of climate change on marine systems (Aronson et al. 2007). In this sense, shallow-water benthic hydrozoans, which are particularly sensitive to climatic changes (see Puce et al. 2009), constitute a potential candidate to detect long-term changes in the community structure of benthic assemblages (e.g. Gonzalez-Duarte et al. 2014).

The high Antarctic has been considered as the least anthropogenically perturbed placed on Earth, but it is vulnerable to large-scale climatic changes (see Gutt and Piepenburg 2003 and references therein). Recent studies report a considerable short-term increase of shallow-water temperature in the Antarctic Peninsula and nearby waters over the last decades (Meredith and King 2005). Nevertheless, this increase dilutes with depth: the water temperature at 100 m was almost constant in the period studied by these authors. The great depth reached by the Antarctic continental shelf and the subsequent massive energy input necessary to warm this water volume, coupled with the Antarctic Circumpolar Current circulation, could explain this stability. In this sense, very few reports assuming changes in the benthic communities are known from Antarctic waters. However, those putative drifts are zoologically restricted to some species of litholid crustaceans and geographically limited to the continental slope of the Bellingshausen sea, the Balleny Islands, and the Antarctic Peninsula (García Raso et al. 2005 and literatured cited), the latter with higher warming threat (see Kidawa and Janecki 2011, and references therein). A similar situation occurred for litholids from the sub-Antarctic Kerguélen region (Macpherson 2004) and Arctic waters (Starikov et al. 2015 and literature cited). As stated above, some authors (e.g. Griffiths et al. 2013) consider there is no real evidence for current "crab re-invasion" [but see Basher and Costello (2016) for a contrasting opinion]. Therefore, no truly non-indigenous metazoan species have been documented from Antarctic marine waters.

The Antarctic benthic hydroid assemblages are rather peculiar in the sense that the diversity of genera that are otherwise distributed world wide and of speciose members of the superfamily Plumularioidea is low. Among the five families included in the taxon (*viz.* Aglaopheniidae, Halopterididae, Kirchenpaueriidae, Plumulariidae and Schizotrichidae), only Kirchenpaueriidae and Schizotrichidae are well known from Antarctic waters, each represented by a single but speciose genus (*Oswaldella* and *Schizotricha*, respectively). Therefore, despite that the material of *Aglaophenia baggins* sp. nov. is scarce and the real *in situ* abundance still has to be determined, the finding of an aglaopheniid in Antarctic waters was unexpected. A similar situation happened to the genus *Nemertesia* and the family Plumulariidae, unknown from Antarctic waters until Peña Cantero (2008) reported a badly preserved specimen of *Nemertesia* from off Deception and Livingston islands, in the South Shetland Islands area. The present finding is even more remarkable, as the material comes from High Antarctica and was reproductive when sampled. Unlike the Arctic waters, where some species of *Cladocarpus*, *Aglaophenopsis* and *Lytocarpia* are known (Ronowicz et al. 2015), the aglaopheniids were previously unnoticed from the whole Antarctic region (i.e. south of Polar front), either from the Kerguélen region (Fig. 3.1). In addition, the genus *Aglaophenia* has never been reported from polar waters. Thus, our knowledge about the distribution of its representatives should be re-evaluated.

The presence of this species of *Aglaophenia* in Antarctic waters may be explained by several factors that can be grouped into three broad scenarios: (i) the material studied is a sampling artefact (i.e. contamination from previous samples), (ii) *Aglaophenia baggins* sp. nov. is a non-indigenous species that arrived to Antarctica either by its own means or by anthropogenic ways [i.e. global change (associated or not to global warming)], or (iii) it was already there, but had gone unnoticed.

Cape Norvegia was the first area studied during the cruise ANT XV/3 and, therefore no possible contamination from previous areas sampled by that Polarstern cruise can be attributed. Furthermore, some of the material came from a TV Grab, a very accurate sampling gear (Eleftheriou and Moore 2005). In addition, the presence of well-preserved colonies (with coenosarc and even with reproductive structures) allow us to discard the sampling artefact hypothesis.

There is limited knowledge on the anthropogenic disturbance of marine benthic communities by research stations in Antarctica (see Stark et al. 2014 and literature cited). The nearest inhabited research station is located ca. hundred miles away from the area where *Aglaophenia baggins* sp. nov. was collected (see COMNAP 2016), which permits us to dismiss the hypothesis of the presence of a human-induced microhabitat that may enhance its settlement and survival. Fauna translocation by fouling is prevented by ice scrapping, and ballast water exchanges are only allowed by the Antarctic Treaty north of the continental shelf, although re-ballasting at sea could be an upcoming issue (Barnes and Conlan 2007). Dispersion through plastic marine debris have also been considered as vectors of colonization for the Antarctic benthos (Barnes and Conlan 2007 and references therein).

There are already some evidences of benthic hydrozoans extending its geographical distribution, although their transmission vector is unknown. This is the case of the campanulariid *Clytia hummelincki* (Gravili et al. 2008) and the sertulariid *Sertularia marginata* (González Duarte et al. 2013) in Mediterranean waters. Additionally, the aglaopheniid *Macrorhynchia philippina*, which entered the Mediterranean via the Suez Channel, is now a common species in the eastern Mediterranean waters (See Morri et al. 2009). Recently, Galea (2015) reported *Aglaophenia parvula* and *A. picardi* from Tristan da Cunha and Saint Helena (south Atlantic) respectively (see Fig. 3.1). Whereas the former species is known from South Africa (see Fig. 3.1 and Tab 3.1), *Aglaophenia picardi* was previously unknown from the Southern Hemisphere, pointing to great dispersal capability, human-mediated translocation, or lack of knowledge on the taxonomy and/or distribution of some benthic hydrozoans. If considering the first case, a significant number of shared species between different sub-Antarctic and nearby waters (ca. 35°–45°S) would be expected, but this is not the case: 17 of the 19 species are not shared between the major regions analysed (see Fig. 3.1 and Tab. 3.1).

Some similar and unexpected findings have been recently reported from Mediterranean waters with the description of two new pelagic cnidarians: *Marivagia stellata* Galil & Gershwin and *Pelagia benovici* Piraino, Aglieri, Scorrano & Boero (Galil et al. 2010, Piraino et al. 2014). The authors suggested that it is highly unlikely that those species remained unnoticed until their recent description due to their bloom potential and the great number of observers (scientist or not) in that region. None of these premises can be applied to *Aglaophenia baggins* sp. nov and the Weddell Sea.

Assuming that the real distribution and dispersal capabilities of most benthic hydroid species are still far to be completely understood, the presence of *Aglaophenia baggins* sp. nov could simply be explained by "it was already there, but never found". Being a relict species of a warmer (i.e. interglacial) period that survived the last glaciation in an *in situ* refugium (see Barnes and Kuklinski 2010), coupled with the low dispersal capability of pioneer species (Potthoff et al. 2006), would partially explain its putative low frequency and restricted distribution. Nonetheless, the previous complete absence of representatives of the family in Antarctic waters, the warmer-water affinity of the genus (cf. Nutting 1900), the pronounced sampling effort in the eastern

Table 3.1 Species of *Aglaophenia* reported from Patagonia, South Atlantic, South Africa, Tasmania and New Zealand [Locations marked with * slighly northern to Patagonian region (i.e. 40° S in the western sector)]. Only the last and/or major contributions per locality are given

	Patagonia	**South Atlantic**	**South Africa**	**Tasmania**	**New Zealand**	**Source (respectively)**
A. acacia Allman, 1883	x					El Beshbeeshy and Jarms (2011)
A. acanthocarpa Allman, 1876					x	Vervoort and Watson (2003), Alfaro et al. (2004)
A. antarctica Jäderholm, 1903	x					Jäderholm (1903)
A. ctenata (Totton, 1930)					x	Vervoort and Watson (2003)
A. cupressina Lamouroux, 1816			x			Millard (1975)
A. decumbens Bale, 1914				x		Hodgson (1950)
A. difficilis Vervoort & Watson, 2003					x	Vervoort and Watson (2003)
A. digitulus Vervoort & Watson, 2003					x	Vervoort and Watson (2003)
A. divaricata (Busk, 1852)	x*			x		Galea et al. (2014); Watson (1975)
A. hystrix Vervoort & Watson, 2003					x	Vervoort and Watson (2003)
A. latecarinata Allman, 1877			x			Millard (1975)
A. laxa Allman, 1876					x	Vervoort and Watson (2003)
A. parvula Bale, 1882		x	x	x		Galea (2015); Millard (1975) (as *Aglaophenia pluma parvula*), Gili et al. (1989); Hodgson (1950)
A. patagonica d'Orbigny, 1839	x					Leloup (1974)
A. picardi Svoboda, 1979		x				Galea (2015)
A. pluma (Linnaeus, 1758)			x			Millard (1975) (as *A. pluma pluma* and *A. pluma dichotoma*)
A. plumosa Bale, 1882				x	x	Watson (1975); Vervoort and Watson (2003)
A. sinuosa Bale, 1888					x	Vervoort and Watson (2003)
A. subspiralis Vervoort & Watson, 2003					x	Vervoort and Watson (2003)
A. tasmanica Bale, 1914				x		Hodgson (1950)

Weddell Sea, and the great taxonomic effort regarding Antarctic benthic hydrozoans [resulting in the description of many new species in recent years (see Xavier et al. 2013)], prevent us from unequivocally considering the new species as an endemism from the Antarctic region that has gone unnoticed until now. Therefore, it cannot be completely dismissed that *Aglaophenia baggins* sp. nov. could be a non-indigenous species that has recently reached the Antarctica, and whose native distribution remains unknown.

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CHAPTER IV

in prep

Benthic hydroids from the Weddell Sea collected by German Antarctic expeditions: do we know enough?

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Abstract

Hydrozoans are a conspicuous component of Antarctic benthic communitites. The recent taxonomic effort has led to a substantial increase in knowledge of the diversity of benthic hydroids from some areas of the Southern Ocean, such as the Weddell Sea, the largest sea in the Antarctic continent. However, the study of many taxons are still pending, and the diversity in this huge region is expected to be higher than currently known. In order to increase our knowledge of taxonomy, ecology and distribution of these organisms, a study of unpublished material collected by several German Antarctic expeditions aboard the RV *Polarstern* in the eastern sector of the Weddell Sea has been conducted. A total of 77 species belonging to 21 families and 28 genera of benthic hydroids have been inventoried, constituting the most prolific collection hitherto analyzed. Most species (81%) belong to Leptothecata, but the observed share of Anthoathecata (19%) is higher than in previous Antarctic hydrozoan studies. Symplectoscyphidae was the most speciose family with 16 representatives (22%), followed by Haleciidae with 11 (15%) and Staurothecidae with 8 (11%). The number of species known in the area was increased with 27 new recods, including several species rarely documented. As a result, the Weddell Sea becomes the second Antarctic region in terms of hydrozoan diversity, with 91 species known to date. Novel data on the use of substrate, reproductive phenology, and bathymetric range are provided for the inventoried species.

Introduction

The Weddell Sea is an embayment of the Southern Ocean, nestled between the Antarctic Peninsula and Larsen Ice Shelf on the west, Cape Norvegia and Riiser-Larsen Ice Shelf on the east, South Atlantic to the north, and Filchner and Ronne ice shelves to the south. With up to 2000 km from side to side in its widest length, a deep shelf (ca. 500 m depth), and 6000 m of maximum depth, the Weddell Sea is the largest sea from the Antarctic continent, with a continental shelf of c. 1.3 million km^2 (cf. Douglass et al. 2014).

The oceanographic features in the Weddell Sea are highly dominated by the northward flowing current of a cyclonic gyre named Weddell Gyre: a cold, low salinity surface layer. Below this, after a weak pycnocline, there is a saltier and warmer layer, the Weddell Deep Water. Finally a cold layer dominates the Weddell Sea bottom (Gordon et al. 1993). The ocean/ice shelf interaction by the sinking of the dense Ice Shelf Water (a process known as "Ice pump") is also an important factor in the formation of deep and bottom water (Rodehacke et al. 2007). In this sense, the Weddell Sea constitutes a key piece in the thermohaline ocean circulation by ocean water modification and deep water formation by cabbeling (Muench and Gordon 1995 and literature cited), and a main source of the dense water that fills the global ocean basins (Orsi et al. 1999 and references therein). These peculiarities, linked to the huge water volume and the isolation of the Antarctic continent, make the Weddell Sea one of the most pristine ecosystems in the world (Halpern et al. 2008) and a region being considered as potential candidate to be the next Antarctic Marine Protected Area (MPA), following the recently accepted MPAs of the South Orkney Islands and the Ross Sea (CCAMLR 2016).

The state of knowledge in regards to benthic hydroid diversity was rather scarce until the late 1990s and early 2000s (cf. Gili et al. 1999; Peña Cantero et al. 2002). In fact, early records are restricted to a few taxa reported by Ritchie (1907), Hickson and Gravely (1907), Jäderholm (1917) and Broch (1948). The most speciose collections of Antarctic benthic hydrozoans were obtained by different French and German Antarctic expeditions aboard the *RV Polarstern* between the years 1983 and 1991. As a result, the number of species known from the Weddell Sea rised considerably, with many new records, including the description of several new species (Peña Cantero et al. 1996, 1997b, 1997c, 1999, 2002). However, the effort was centered in the most common and speciose Leptothecata genera (*viz. Antarctoscyphus, Oswaldella, Schizotricha, Staurotheca* and *Symplectoscyphus*), while other taxa, especially Anthoathecata, remained mostly unknown. Gili et al. (1999) provided a preliminar account on part of the material collected from the expedition ANT XV/3. Subsequent publications were centered in some specific taxa, mainly Tubulariidae Goldfuss, 1818 and Corymorphidae Allman, 1872, studied by Svoboda and Stepanjants (2001), and Svoboda et al. (2006), and the description of a new species of *Sarsia* Lesson, 1843 in association with gorgonians by Gili et al. (2006).

Present study aims to contribute to knowledge of diversity, taxonomy, ecology and distribution of benthic hydroids from the Weddell Sea through the study of unpublished material collected by the *RV Polarstern* in the eastern sector of this key Antarctic region.

Material and methods

The material examined here was collected with the RV *Polarstern* during the German Antarctic expeditions ANT XV/3 (EASIZ II), ANT XVII/3 (EASIZ III) and ANT XXI/2 (BENDEX), which took place in January-March 1998, April 2000 and December-January 2003-2004, respectively. Samples were obtained from a large area of study, including two stations from the South Shetland Islands region, although sampling effort was mainly focused on Cape Norvegia (see Fig. 4.1; Tab. 4.1). The bathymetric range surveyed extends from the upper shelf (60 m) to the upper slope (750 m). Samples were sorted on board into main zoological groups and hydrozoans were selected and fixed in 10% formalin. In the laboratory, hydroids were sorted at a genus level and transferred to 70% ethanol. The material examined was subsequently identified to the lowest taxonomic level possible and a numerical identifier code was assigned for each specimen. In order to facilitate the visualization and taking of microphotographs, some specimens or fragments were exposed to small sonication pulses, in some cases after a small immersion in sodium hypochlorite, to eliminate debris, bubbles, and/or organic matter. Mayer's hemalum solution has been used to increase the contrast of tiny translucent structures. Multifocal

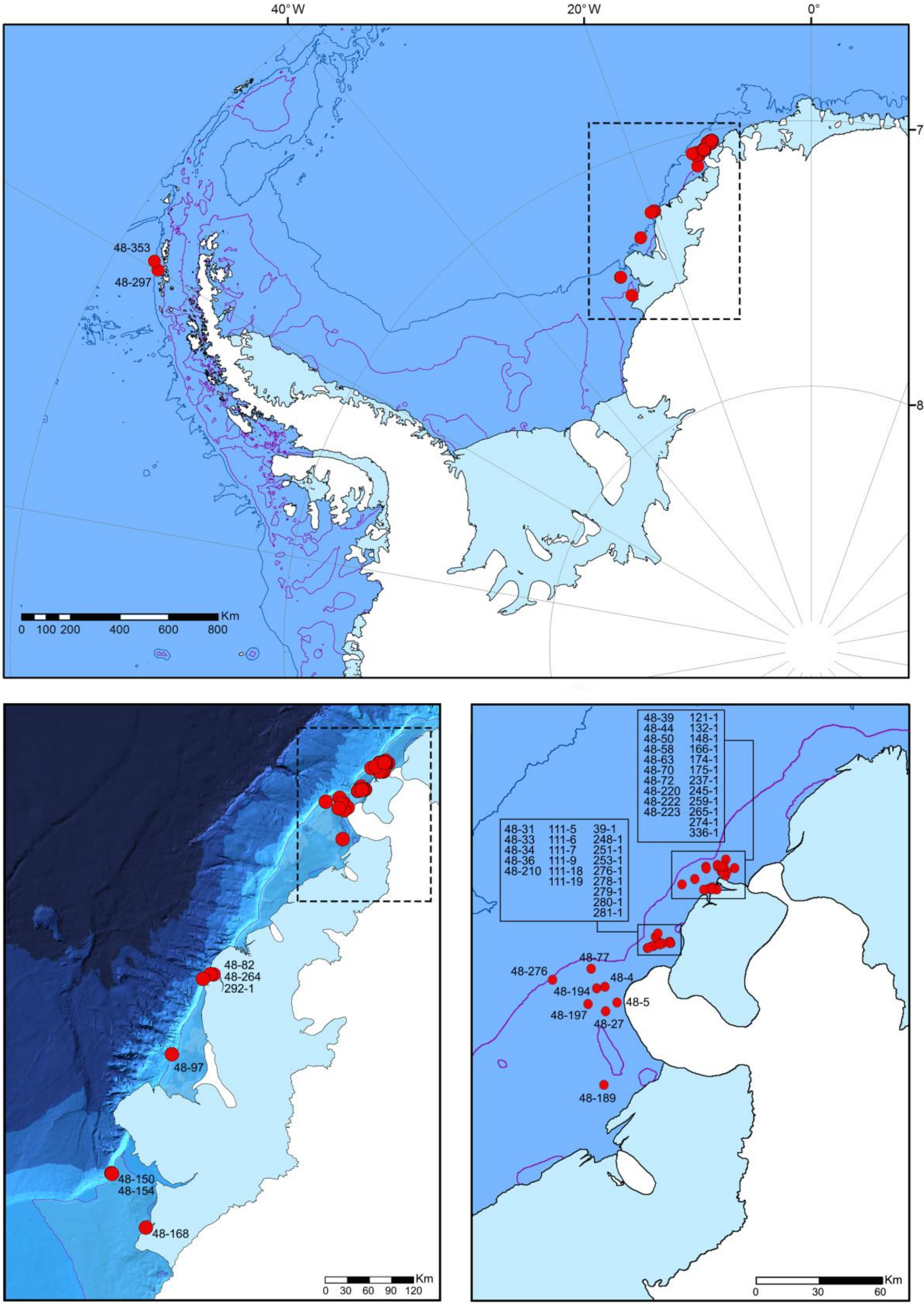

Figure 4.1 Study area showing the location of stations within the Weddell Sea and South Shetland Islands

Table 4.1 Sampling stations [Areas: Drescher Inlet (DI); Drake Passage (DP); Halley Bay (HB); King George Island (KG); Kape Norvegia (KN); North of Kape Norvegia (N/KN); South of Kape Norvegia (S/KN); South of Vestkapp (S/VK). Sampling gears: Agassiz trawl (AGT); Photo sled (FTS); Bottom trawl (GSN); Multigrab/Multibox corer (MG); Rauschert dredge (RD); Remotely operated vehicle (ROV); TV grab (TVG)]

Expedition	Station	Date	Latitude (S)	Longitude (W)	Area	Sampling gear	Depth (m)
XV/3	48-4	25 Jan 1998	71°14.2'	12°21.7'	KN	TVG	241
XV/3	48-5	25 Jan 1998	71°18.1'	12°16.0'	KN	TVG	177
XV/3	48-27	28 Jan 1998	71°19.4'	12°25.2'	KN	TVG	191
XV/3	48-31	29 Jan 1998	71°07.3'	11°28.3'	N/KN	TVG	64
XV/3	48-33	29 Jan 1998	71°07.3'	11°28.3'	N/KN	TVG	65
XV/3	48-34	29 Jan 1998	71°07.2'	11°28.3'	N/KN	FTS	68-116
XV/3	48-36	29 Jan 1998	71°07.2'	11°28.2'	N/KN	TVG	68
XV/3	48-39	29 Jan 1998	70°52.8'	10°31.4'	N/KN	AGT	237-244
XV/3	48-44	30 Jan 1998	70°51.8'	10°34.0'	N/KN	AGT	227-229
XV/3	48-50	30 Jan 1998	70°51.6'	10°24.3'	N/KN	RD	282-283
XV/3	48-58	31 Jan 1998	70°52.1'	10°29.8'	N/KN	AGT	243-247
XV/3	48-63	31 Jan 1998	70°52.1'	10°32.4'	N/KN	MG	234
XV/3	48-70	01 Feb 1998	70°49.4'	10°28.9'	N/KN	ROV	275-288
XV/3	48-72	01 Feb 1998	70°50.8'	10°31.4'	N/KN	FTS	230-232
XV/3	48-77	02 Feb 1998	71°09.7'	12°28.7'	N/KN	AGT	341-360
XV/3	48-82	03 Feb 1998	72°50.8'	19°18.8'	DI	GSN	395-417
XV/3	48-97	05 Feb 1998	73°35.8'	22°12.9'	S/VK	GSN	629-659
XV/3	48-150	11 Feb 1998	74°38.0'	27°00.2'	HB	GSN	710-758
XV/3	48-154	11 Feb 1998	74°38.7'	26°59.3'	HB	GSN	569-583
XV/3	48-168	12 Feb 1998	75°26.3'	26°41.7'	HB	GSN	228-233
XV/3	48-189	15 Feb 1998	71°40.2'	12°43.3'	KN	AGT	244-248
XV/3	48-194	16 Feb 1998	71°14.1'	12°27.7'	KN	AGT	244-246
XV/3	48-197	16 Feb 1998	71°17.0'	12°36.3'	KN	AGT	415-416
XV/3	48-210	18 Feb 1998	71°07.2'	11°28.4'	KN	TVG	67
XV/3	48-220	19 Feb 1998	70°50.4'	10°35.4'	KN	GSN	236-272
XV/3	48-222	19 Feb 1998	70°50.6'	10°35.5'	KN	GSN	234-267
XV/3	48-223	19 Feb 1998	70°50.2'	10°35.5'	KN	MG	276
XV/3	48-264	25 Feb 1998	72°49.9'	19°26.5'	DI	AGT	470-473
XV/3	48-276	27 Feb 1998	71°10.2'	13°01.7'	S/KN	AGT	417
XV/3	48-297	14 Mar 1998	62°15.8'	58°42.7'	KG	AGT	211-232
XV/3	48-353	20 Mar 1998	61°59.4'	59°14.4'	DP	AGT	129-132
XVII/3	111-5	05 Apr 2000	71°07.5'	11°27.7'	KN	TVG	65-66
XVII/3	111-6	05 Apr 2000	71°07.5'	11°27.8'	KN	TVG	68
XVII/3	111-7	05 Apr 2000	71°07.5'	11°27.7'	KN	TVG	67
XVII/3	111-9	05 Apr 2000	71°07.5'	11°27.8'	KN	RD	62
XVII/3	111-18	05 Apr 2000	71°07.5'	11°28.0'	KN	TVG	105
XVII/3	111-19	05 Apr 2000	71°07.48'	11°28.3'	KN	TVG	112
XXI/2	PS65/39	05 Dec 2003	71°06.47'	11°32.29'	N/KN	AGT	166-175
XXI/2	PS65/121	11 Dec 2003	70°50.08'	10°35.54'	N/KN	AGT	268-274
XXI/2	PS65/132	12 Dec 2003	70°56.42'	10°31.61'	N/KN	GSN	244-284
XXI/2	PS65/148	13 Dec 2003	70°56.56'	10°31.75'	N/KN	GSN	256-290
XXI/2	PS65/166	15 Dec 2003	70°56.83'	10°32.61'	N/KN	GSN	253-338
XXI/2	PS65/174	16 Dec 2003	70°56.82'	10°32.57'	N/KN	GSN	321-352
XXI/2	PS65/175	16 Dec 2003	70°57.11'	10°33.32'	N/KN	GSN	261-337
XXI/2	PS65/237	22 Dec 2003	70°50.50'	10°35.54'	N/KN	GSN	254-264
XXI/2	PS65/245	22 Dec 2003	70°56.74'	10°32.60'	N/KN	GSN	318-337
XXI/2	PS65/248	23 Dec 2003	71°05.51'	11°30.46'	N/KN	GSN	286-287
XXI/2	PS65/251	23 Dec 2003	71°07.34'	11°27.80'	N/KN	RD	125-146
XXI/2	PS65/253	23 Dec 2003	71°04.89'	11°32.21'	N/KN	GSN	295-309
XXI/2	PS65/259	24 Dec 2003	70°56.57'	10°31.98'	N/KN	GSN	300-333
XXI/2	PS65/265	27 Dec 2003	70°52.74'	10°52.72'	N/KN	GSN	286-295
XXI/2	PS65/274	28 Dec 2003	70°52.16'	10°43.69'	N/KN	GSN	288-291
XXI/2	PS65/276	28 Dec 2003	71°07.30'	11°27.85'	N/KN	AGT	268-277
XXI/2	PS65/278	29 Dec 2003	71°07.51'	11°29.94'	N/KN	AGT	119-120
XXI/2	PS65/279	29 Dec 2003	71°07.48'	11°29.91'	N/KN	AGT	120
XXI/2	PS65/280	29 Dec 2003	71°07.20'	11°26.47'	N/KN	AGT	191-228
XXI/2	PS65/281	29 Dec 2003	71°07.32'	11°28.45'	N/KN	RD	82
XXI/2	PS65/292	31 Dec 2003	72°51.43'	19°38.62'	DI	GSN	596-598
XXI/2	PS65/336	05 Jan 2004	70°50.70'	10°28.32'	N/KN	AGT	276-281

microphotographs have been obtained for most of the species inventoried with the aid of a motorized focus coupled to a microscope (Leica DM 3000) and stereomicroscope (Leica DMS 1000), and image software (Leica Application Suite). The material is kept in the Hydrozoan collection of the Department of Zoology (University of Valencia).

Additionally, complementary data were obtained in regards to the ecology (reproductive phenology, presence of epibionts, bathymetric range and substrate used) and distribution (within the Antarctic region and nearby waters) of the species inventoried, but only significant new contributions are discussed. Biogeographic and bathymetric patterns established by Peña Cantero and García Carrascosa (1999) and Peña Cantero (2004) respectively have been followed. Much of the material examined was fragmented, and only measurements of the largest fragment per specimen are specified. If not indicated otherwise, the specimens were not reproductive when sampled. Comprehensive tables summarizing all the information concerning use of substrate, presence of epibionts, reproductive phenology and bathymetric distribution in Antarctic waters are included.

With the aim of evaluating the state of knowledge concerning the hydrozoan diversity in the Weddell Sea and enabling future studies of ecology and distribution, a comprehensive database including all previous records from the region has been compiled (supplementary Table S5).

Results and discussion

Taxonomic account

Anthoathecata Cornelius, 1992
Bougainvilliidae Allman, 1863

Bougainvilliidae undetermined
(Fig. 4.2d-e)

Material examined. *ANT XVII/3*: **111-9**, one stem, c. 5 mm high, with gonophores; some stems, up to 8 mm high, on *Schizotricha unifurcata* Allman, 1883 and *Symplectoscyphus weddelli* Peña Cantero, Svoboda & Vervoort, 2002, with gonophores; *ANT XXI/2*: **PS65/39**, some stems, up to 3 mm high, on *Symplectoscyphus exochus* Blanco, 1982; **PS65/248**, some stems, up to 10 mm high, on *Halecium incertus* Naumov & Stepanjants, 1962, with gonophores; **PS65/248**, few stems, up to 8 mm high, on *Stegella lobata* (Vanhöffen, 1910) and *Symplectoscyphus curvatus* (Jäderholm, 1917); **PS65/280**, few stems, up to 3 mm high; **PS65/336**, one stem, c. 3 mm high, on *Symplectoscyphus glacialis* (Jäderholm, 1904).

Remarks. Despite being abundant and fertile, the material examined does not agree with any of the bougainvillids reported from Antarctic waters. It has great resemblance with the syntypes of *Bougainvillia macloviana* Lesson, 1830 re-described by Peña Cantero (2015), in colony and polyp shapes, presence of pseudohydrotheca (Fig. 4.2d), and type and size of cnidome (see below). However, the present material has clearly identifiable fixed sporosacs (Fig. 4.2e), with up to seven eggs, that arise from a large perisarc cup which rim is not well-defined. In contrast, *B. macloviana* produces free medusae, and the gonophores originate from a well-defined, smaller, cup-shaped pedicel of perisarc (Peña Cantero 2015, p. 373).

Cnidome composed by heteronemes [range 5.5–7.0 x 3.5–4.0 μm, mean 6.2±0.4 x 3.6±0.2 μm (n=29)] and desmonemes [range 3.0–3.5 x 2.0–2.5 μm, mean 3.3±0.3 x 2.3±0.3 μm (n=24)].

Figure 4.2 a-c *Bimeria corynopsis*: **a** stem showing branching; **b** stem showing annulation; **c** detail of polyp and slightly capitate tentacles. **d-e** Bougainvillidae undetermined: **d** polyp; **e** gonophore. **f-i** *Rhizorhagium antarcticum*: **f** colony shape; **g** extended (left) and contracted (right) polyps; **h** shape (left) and developing eggs (right) of female gonophores; **i** male gonophore. **j** ?*Sarsia* sp.: polyp

Ecology and distribution. Material examined collected at depths from 62 to 287 m off Cape Norvegia.

Bimeria Wright, 1859

Bimeria corynopsis Vanhöffen, 1910

(Fig. 4.2a-c)

Material examined. *ANT XV/3*: **48-150**, stolonal colony up to 1 mm high, two polyps, on *Eudendrium scotti* Puce, Cerrano & Bavestrello, 2002.

Remarks. In spite of being scarce, our material perfectly agrees with the description of the syntypes examined by Peña Cantero (2015), including the slightly-capitate appearance of tentacles (Fig. 4.2c), which has been considered as the diagnostic trait of the species (see Schuchert 2007).

Cnidome consisting in microbasic euryteles [range 7.5–9 x 5.0–5.5 µm, mean 8.6±0.5 x 5.2±0.3 µm (n=21)] and desmonemes [range 4.5–5.0 x 3.0–3.5 µm, mean 4.7±0.4 x 3.3±0.3 µm (n=16)].

Ecology and distribution. Previously found at depths between 385 (Vanhöffen 1910) and 527 m (Peña Cantero 2014a); present material at 710-758 m. Hitherto considered as endemic of East Antarctica (Peña Cantero 2014a); present finding, the third report of the species, and the first for both the Weddell Sea and West Antarctica, points to a circum-Antarctic distribution.

***Rhizorhagium* M. Sars, 1874**
***Rhizorhagium antarcticum* (Hickson & Gravely, 1907)**

(Fig. 4.2f-i)

Material examined. *ANT XV/3:* **48-31**, some polyps, up to 3 mm high, on *Oswaldella stepanjantsae* Peña Cantero, Svoboda & Vervoort, 1997; few polyps, up to 4 mm high, on *Antarctoscyphus grandis* (Blanco, 1977); **48-33**, several polyps, up to 7 mm high, on *S. unifurcata*, with gonophores; few polyps, up to 4 mm high, on *O. stepanjantsae*; some polyps, up to 4 mm high, on *Tubularia* sp.2; **48-36**, some polyps, up to 3 mm high, on *O. stepanjantsae*, with gonophores; **48-50**, several polyps, up to 10 mm high, on *Schizotricha nana* Peña Cantero, Svoboda & Vervoort, 1996 and *Campanularia hicksoni* Totton, 1930; **48-194**, a few polyps, up to 2 mm high, on *C. hicksoni*; some polyps, up to 3 mm high, on *S. nana*, with gonophores; **48-220**, some polyps, up to 3 mm high, on *S. nana*; some polyps, up to 5 mm high, on *S. exochus*, with gonophores; a few polyps, up to 3 mm high, on *Symplectoscyphus anae* Peña Cantero, Svoboda & Vervoort, 2002, with gonophores; **48-222**, several polyps, up to 4 mm high, on *Eudendrium generale* von Lendenfeld, 1885, with gonophores; **48-223**, some polyps, up to 3mm high, on *S. nana*; *ANT XVII/3:* **111-5**, some polyps, up to 5 mm high, on *O. stepanjantsae*, with gonophores; **111-6**, some polyps, up to 5 mm high, on *S. exochus* and *C. hicksoni*, with gonophores; **111-7**, few polyps, up to 6 mm high, on *Tubularia longstaffi* Hickson & Gravely, 1907, with gonophores; **111-9**, some polyps, up to 4 mm high, on polychaete tube; few polyps, up to 3 mm high, on *S. weddelli*, with gonophores; few polyps, up to 2 mm high, on *Zyzzyzus parvula* (Hickson & Gravely, 1907), with gonophores; some polyps, up to 10 mm high, on *S. unifurcata*, with gonophores; several polyps, up to 10 mm high, on *O. stepanjantsae* with gonophores; several polyps, up to 15 mm high, on *T. longstaffi* and *E. generale*, with gonophores; several polyps, up to 4 mm high, on *A. grandis*, with gonophores; **111-18**, some polyps, up to 5 mm high, on *S. nana*, with gonophores; some polyps, up to 6 mm high, on *O. stepanjantsae* and *C. hicksoni*, with gonophores; few polyps, up to 3 mm high, on *Billardia subrufa* (Jäderholm, 1904); few polyps, up to 3 mm high, on *S. weddelli*; few polyps, up to 3 mm high, on *Halecium interpolatum* Ritchie, 1907; several polyps, up to 5 mm high, on *Tubularia* sp.1, with gonophores; *ANT XXI/2*: **PS65/39**, few polyps, up to 6 mm high, on *S. exochus*, with gonophores; **PS65/248**, some polyps, up to 2 mm high, on *S. curvatus* and octocoral; **PS65/276**, few polyps, up to 3 mm high, on bryozoan; few polyps, up to 3 mm high, on *Symplectoscyphus vanhoeffeni* Totton, 1930, with gonophores; few polyps, up to 3 mm high, on *Staurotheca vanhoeffeni* (Peña Cantero & García Carrascosa, 1994); few polyps, up to 5 mm high, on *Staurotheca glomulosa* Peña Cantero, Svoboda & Vervoort, 1997; **PS65/278**, some polyps, up to 5 mm high, on *Antarctoscyphus elongatus* (Jäderholm, 1904); some polyps, up to 6 mm high, on *Halecium secundum* Jäderholm, 1904 and sponge; **PS65/279**, few polyps, up to 3 mm high, on *B. subrufa*; **PS65/280**, some polyps, up to 3 mm high, on bryozoan; **PS65/281**, few polyps, up to 3 mm high, on *O. stepanjantsae.*

Remarks. The presence of some extraordinarily preserved reproductive colonies allowed us to confirm the presence of a distinct pseudohydrotheca, as a thin layer of perisarc, reaching the base of tentacles, but not covering them (Fig. 4.2g), as noticed by Hickson and Gravely (1907) in the original description, and by other authors (Naumov and Stepanjants 1972). In contrast, according to Peña Cantero (2015: 378), "the perisarc sheet covering the polyp body is totally inconspicuous" in the type material he examined. Sampling procedures could strongly damage or even remove this sensitive structure, and this could be the reason, in this specific case, of discrepancies among different authors' observations.

Hickson and Gravely (1907) provided a detailed description of the gonophores of *R. antarcticum.* However, these authors employed a terminology commonly used with reduced medusae (i.e. criptomedusoids or eumedusoids), therefore causing some misperception about the nature of the gonophore. According to the figures by Hickson and Gravely (1907) and our own observations while dissecting the gonophores (Fig 4.2h), the gonosome of *R. antarcticum* can be recognized as fixed sporosacs with confidence, in agreement with the diagnosis of the genus (Bouillon et al. 2006).

Cnidome comoposed by microbasic euryteles [range 6.5–8.0 x 4.0–4.5 μm, mean 7.4±0.5 x 4.4±0.2 μm (n=22)] and desmonemes [range 5.0–6.0 x 3.0–3.5 μm, mean 5.7±0.3 x 3.3±0.3 μm (n=16)].

Ecology and distribution. Previously found between the tidal level (Hickson and Gravely 1907) and 450 m (Totton 1930); present material was collected from 62 to 287 m. In agreement with Peña Cantero et al. (2013) and Peña Cantero (2014a), a careful re-examination of the abundant records is needed in order to assign a pattern of distribution; for now, *R. antarcticum* can be tentatively considered as a species with an Antarctic-Kerguélen distribution. In spite of being a widely reported species in the whole Southern Ocean, its presence in the Weddell Sea sector had not been confirmed yet; therefore, the first evidence comes from the present study.

Eudendriidae L. Agassiz, 1862

Eudendrium Ehrenberg, 1834

Eudendrium antarcticum Stechow, 1921

(Fig. 4.3g)

Material examined. *ANT XV/3*: **48-31**, one colony, c. 15 mm high, on *Tubularia* sp.1; **48-77**, one colony, c. 15 mm high, with female gonophores; **48-197**, one colony, c. 50 mm high; **48-276**, one colony, 20 mm high, on *B. subrufa*; *ANT XVII/3*: **111-19**, one colony, c. 4 mm high, on *H. interpolatum*; *ANT XXI/2*: **PS65/292**, one colony, c. 7 mm high.

Remarks. Non-reproductive material was attributed based on the cnidome, consisting of microbasic euryteles of only one size category [range 7.0–8.0 x 1.5–2.5 μm, mean 7.8±0.3 x 2.3±0.3 μm (n=23)], in agreement with previous material examined by Peña Cantero and Gili (2006) and Peña Cantero and Vervoort (2009). In the material examined here, unlike previous reports of the species (e.g. Puce et al. 2002), the female gonophores originated from partially atrophied hydranths with a reduced number of tentacles (Fig. 4.3g), probably due to the complete maturation of the gonozooid, as known to occur in other species of the genus, a process known

Figure 4.3 **a-f** *Hydractinia dendritica*: **a-b** general view of the colony; **c** detail of spines; **d** gastrozooids and dactylozooid; **e** gonozooid with gonophores; **f** dactylozooid. **g** *Eudendrium antarcticum*: female gonophore. **h** *Eudendrium generale*: female gonophore. **i, k** *Eudendrium scotti*: **i** gonozooid with male gonophores; **k** colony. **j** *Eudendrium* sp.2: gonozooid with male gonophores

as reproductive exhaustion (see Schuchert 2008b).

Ecology and distribution. In Antarctic waters, the species is known from depths between 240 (Peña Cantero and Vervoort 2009) and 260 m (Peña Cantero and Gili 2006); material examined collected at depths between 64 and 598 m, considerably extending its bathymetric range. Species previously reported from off South Africa, Bouvet, the Bransfield Strait area and doubtfully from Peter I Island [cf. Peña Cantero and Vervoort (2009) and literature therein]. Present contribution constitutes the first evidence of *E. antarcticum* from the Weddell Sea.

Eudendrium generale von Lendenfeld, 1885

(Fig. 4.3h)

Material examined. *ANT XV/3*: **48-4**, one colony, c. 35 mm high; **48-27**, one colony, c. 40 mm high, on sponge; **48-31**, some stems, up to 20 mm high, on *Tubularia* sp.2 and *O. stepanjantsae*, with female gonophores; **48-33**, some stems, up to 10 mm high, on *S. nana*; several polyps, up to 3 mm high, on *O. stepanjantsae*; *ANT XVII/3*: **111-9**, one colony, 20 m high, on *T. longstaffi*, with female gonophores; *ANT XXI/2*: **PS65/251**, one colony, 10 mm high; **PS65/281**, some stems, up to 40 mm high, on *Symplectoscyphus cumberlandicus* (Jädherholm, 1905), with female gonophores; few stems, up to 2 mm high, on *S. nana*.

Cnidome composed by microbasic euryteles in two size classes: large [range 13.0–16.0 x 5.5–6.5 µm, mean 14.3±1.2 x 6.1±0.3 µm (n=21)] and small ones [range 6.5–7.5 x 2.0–3.0 µm, mean 6.8±0.4 x 2.5±0.4 µm (n=17)].

Ecology and distribution. Previously reported at depths between 10 (Puce et al. 2002) and 702 m (Peña Cantero 2009); present material from 62 to 241 m. Australian-Antarctic species reported from East Antarctic (Peña Cantero 2009) and the Scotia Arc (Soto Àngel and Peña Cantero 2015); present finding constitutes the first evidence of *E. generale* from the Weddell Sea.

Eudendrium scotti Puce, Cerrano & Bavestrello, 2002

(Fig. 4.3i, k)

Material examined. *ANT XV/3*: **48-150**, one colony, c. 80 mm high, on sponge, with male gonophores; **48-222**, c. 25 mm, on *S. weddelli*, with female gonophores; *ANT XXI/2*: **PS65/276**, c. 6 mm, on *St. vanhoeffeni*.

Remarks. Cnidome comprising large macrobasic euryteles [range 22.0–24.5 x 9.0–10.0 µm, mean 23.3±1.1 x 9.2±0.4 µm (n=20)] and small microbasic euryteles [range 8.0–10.5 x 3.5–4.5 µm, mean 8.9±0.8 x 4.2±0.4 µm (n=18)].

Ecology and distribution. Species previously reported from depths between 10 (Puce et al. 2002) and 135 m (Peña Cantero and Vervoort 2009); present material between 234 and 758 m depth, considerable extending its bathymetric range. Circum-Antarctic species (Peña Cantero 2009), previously unreported from the Weddell Sea.

Eudendrium sp.1

Material examined. *ANT XV/3*: **48-197**, one colony, 60 mm high; *ANT XVII/3*: **111-7**, one colony, c. 55 mm high, on *O. stepanjantsae*; *ANT XXI/2*: **PS65/174**, one colony, c. 6 mm high, on *Oswaldella erratum* Peña Cantero & Vervoort, 1997; **PS65/175**, one colony, c. 5 mm high, on *S. lobata*; one colony, c. 5 mm high, on *B. subrufa*; **PS65/251**, one colony, c. 2 mm high, on *O. stepanjantsae;* **PS65/253**, one colony, c. 5 mm high, on *S. lobata;* **PS65/259**, one colony, c. 40 mm high.

Remarks. The bad state of preservation and the infertile condition precludes a proper identification.

Ecology and distribution. Material collected at depths from 62 to 417 m off Cape Norvegia.

Eudendrium sp.2

(Fig. 4.3j)

Material examined. *ANT XXI/2*: **PS65/248**, one colony, c. 80 mm high, with male gonophores.

Remarks. This species is characterized by having a strongly polysiphonic stem, up to 80 mm high, with smooth perisarc. Only 8-9 polyps remain in the material examined. Male gonophores are mono- or bichambered, up to nine per polyp (Fig. 4.3j) The cnidome consists of microbasic euryteles of two size classes: the smaller [range 10.5–12.0 x 5.0–5.5 µm, mean 11.3±0.5 x 5.1±0.2 µm (n=15)], abundant on tentacles, and the larger [range 32.0–35.5 x 16–18.0 µm, mean 33.5±1.4 x 17.1±0.6 µm (n=16)] are scarce on the hypostome. The present material agrees, in the shape of the colony and the size of the nematocysts, with the material described as *Eudendrium* sp.1 by Peña Cantero (2009) and reported anew by Peña Cantero (2014a). As stated by the author, the material could be conspecific with *Eudendrium cyathiferum* Jäderholm, 1904, but the cnidome of Jäderholm's species remains unknown and further investigations are needed regarding this issue.

Ecology and distribution. Previously found at depths between 103 (Peña Cantero 2009) and 699 m (Peña Cantero 2014a); present material at 286-287 m. Previously known from the Balleny Islands (Peña Cantero 2009) and Queen Mary Coast (Peña Cantero 2014a), in East Antarctica. Subsequently, present contribution constitutes the first evidence from both the Weddell Sea and West Antarctica, pointing to circum-Antarctic distribution.

Hydractiniidae L. Agassiz, 1862

Hydractinia Van Beneden, 1844

Hydractinia dendritica Hickson & Gravely, 1907

(Fig. 4.3a-f)

Material examined. *ANT XV/3*: **48-33**, some polyps, on *H. interpolatum*; with developing gonophores; **48-36**, several polyps, on *O. stepanjantsae*, with developing gonophores; **48-39**, several polyps, on dead octocoral, with developing gonophores; **48-210**, several polyps, on *O. stepanjantsae*, with developing gonophores; **48-220**, several polyps, on *S. nana*, with developing gonophores; **48-264**, several polyps, on dead octocoral, with developing gonophores; *ANT XVII/3*: **111-5**, several polyps, on *O. stepanjantsae*, with mature gonophores; **111-7**, several polyps, on dead octocoral, with mature gonophores; several polyps, on *O. stepanjantsae*, with mature gonophores; few polyps, on *T. longstaffi*, with developing gonophores; **111-9**, several polyps, on *T. longstaffi*, with mature gonophores; several polyps, on *S. unifurcata*, with developing gonophores; **111-18**, several polyps, on *O. stepanjantsae*, with mature gonophores; *ANT XXI/2*: **PS65/248**, few polyps, on *Eudendrium* sp.2, with developing gonophores; **PS65/281**, several polyps, on *O. stepanjantsae*, with developing gonophores.

Remarks. The material examined here entirely coincides with the re-description of the type-series of *H. dendritica* provided by Peña Cantero (2015), including the presence of erect stems, dwarf gonophores (Fig. 4.3e), and dactylozooids (Fig. 4.3f). *H. dendritica* seems to have different growing strategies depending on the substrate on which it develops, as it has already been reported for other congeneric (Schuchert 2008a). In the material examined, some sections of the same colony (or whole colonies) develop sharp spines when gastrozooids and dactyolozooids are not yet developed or are proportionally less abundant (Fig. 4.3c), while other portions (or colonies) are almost deprived of spines but have abundant gastrozooids, and some dactylozooids (c. one dactylozooid per 10-20 gastrozooids). The fully mature colony, where gonozooids carrying gonophores are found, have a sort of perisarcal wall joining spines, as a kind of "room divider", which could act as an extra-protection for the reproductive polyps (Fig. 4.3b, e). All this different growing morphologies can be observed in the same colony, and we suggest they correspond either to differences in the substrate used or to ontogenetic changes.

Ecology and distribution. The species had been found once, in McMurdo Sound (Ross Sea), at a depth of 9–18 m (Hickson and Gravely 1907); our material was collected from several locations in the Weddell Sea, at depths between 62 and 473 m, growing on different substrates (see Tab. S4). Present contribution constitutes the second report of the species, and the first evidence from both the Weddell Sea and West Antarctica, pointing to a circum-Antarctic distribution.

Hydractinia sp.

Material examined. *ANT XV/3*: **48-34**, few polyps, on *O. stepanjantsae*; *ANT XVII/3*: **111-9**, few polyps, on *Z. parvula*; *ANT XXI/2*: **PS65/251**, few polyps, on *S. lobata*.

Remarks. The scarce and non-reproductive state of the material examined prevents us from attributing a specific epithet.

Ecology and distribution. Material collected at depths from 62 to 146 m, in the vicinity of Cape Norvegia.

Tubulariidae Goldfuss, 1818

Tubularia Linnaeus, 1758

Tubularia longstaffi Hickson & Gravely, 1907

(Fig. 4.4a-i)

Material examined. *ANT XVII/3*: **111-5**, few stems, up to 45 mm high, on *O. stepanjantsae*; **111-7**, some stems, up to 40 mm high, with developing gonophores; **111-9**, some stems, up to 110 mm, with mature gonophores.

Remarks. The material examined here has all the diagnostic features mentioned in the re-description of the type of *T. longstaffi* by Peña Cantero (*in press*): yellow stems, in entwined clusters, tube diameter increasing distally (Fig. 4.4a), with transversal ridges; polyps large, up to 5 x 5 mm, with an oral crown of 29-37 tentacles and an aboral one of 12-19 tentacles; type and size of nematocysts, and gonophores as cryptomedusoids (Fig. 4.4d, g-h). Additional knowledge regarding sexual dimorphism and early developmental stages is drawn from the present study. Male styloids elongate, c. 4 mm long and with up to 17 stalked gonophores as cryptomedusoids (Fig. 4.4c). Gonophores, maturity increasing distally: recently formed gonophores located proximally, spherical, c. 300 μm in diameter, and completely filled with spermatogenic tissue (reddish in preserved specimens); mid-term gonophores, c. 600 μm in diameter, filled for 2/3 to 3/4 with spermatogenic tissue, with 4-5 rudimentary tentacular bulbs and slightly protruded aperture (Fig. 4.4c); fully grown male gonophores located distally, spherical, c. 1 mm in diameter, almost completely filled with whitish sperm cells between aperture and spermatogenic tissue, rudimentary tentacular bulbs difficult to appreciate at this stage (Fig. 4.4d). Female styloids elongate, up to 7 mm long, and with up to 11 stalked gonophores as cryptomedusoids, fully matured ones scattered along the styloid (Fig. 4.4f). Developing gonophores sphaerical, c. 250-600 μm; fully grown female gonophores oblong in lateral view, c. 1.5 mm wide x 1 mm high, with a digitiform process running on proximal section, with 4-5 rudimentary tentacular bulbs, and with up to four actinulae, of which 2-3 developing and 1-2 mature (Fig. 4.4g-h). Actinula resembling a *Tubularia* polyp, with 10 elongate aboral tentacles and four short oral ones. Basal section dense, with two constrictions, one at the base of aboral tentacles, the other at the basal fourth, delimiting a disc. Basal disc with radial grooves, probably with adhesive function (Fig. 4.4i).

Ecology and distribution. *Tubularia longstaffi* was only known from the Ross

Figure 4.4 a-i *Tubularia longstaffi*: **a** polyp-carrying tube; **b** male polyp; **c** styloid with developing male gonophores; **d** styloid with fully-grown male gonophores; **e** female polyp; **f** styloid with fully-grown female gonophores; **g-h** detail of female gonophores carrying actinulae; **i** actinulae in different stages of development. **j-m** *Zanclea hicksoni*: different polyp morphologies (**j** showing hydrorhizal filaments and **m** showing tentacle arrangement in linear clusters)

Sea (Hickson and Gravely 1907; Peña Cantero *in press*), reported at depths between 222 and 630 m (Peña Cantero *in press*); present material was collected at 62-67 m depth, in the vicinity of Cape Norvegia. This constitutes the second record of the species, and the first evidence from both the Weddell Sea and West Antarctica. We tentatively assign a circum-Antarctic distribution to *T. longstaffi*.

Cnidome comoposed by small stenoteles [range 9.0–11.0 x 7.0–8.5 µm, mean 10.1±0.7 x 7.8±0.6 µm (n=18)], large stenoteles [range 14.0–15.5 x 10.0–12.5 µm, mean 14.4±0.4 x 10.7±0.7 µm (n=17)], tear-shaped haplonemes [range 13.5–16.5 x 4.0–5.5 µm, mean 14.9±1.1 x 4.9±0.6 µm (n=16)], rounded haplonemes [range 15.5–16.5 x 10.0–11.5 µm, mean 16.0±0.5 x 10.9±0.5 µm (n=15)] and desmonemes [range 5.5–7.0 x 4.0–6.0 µm, mean 6.4±0.6 x 4.8±0.6 µm (n=16)].

Tubularia sp.1

Material examined. *ANT XVII/3*: **111-18**, few stems, without polyps; **111-19**, some stems, without polyps.

Remarks. The bad preservation of the specimens precludes a proper identification.

Ecology and distribution. Material collected from off Cape Norvegia, at 105-112 m depth.

Tubularia sp.2

Material examined. *ANT XV/3*: **48-31**, few stems, up to 65 mm high, on stone, with developing gonophores; **48-33**, some stems, up to 40 mm high.

Remarks. The scarcity of the material does not allow us to assign a specific epithet. The general shape of the stems, and the cnidome are similar to those of *Tubularia hodgsoni* Hickson & Gravely, 1907 (cf. Peña Cantero *in press*). However, lack of mature specimens precludes a proper identification.

Cnidome comprising stenoteles [range 9.0–11.0 x 7.5–9.0 µm, mean 10.1±0.7 x 8.4±0.5 µm (n=16)], tear-shaped haplonemes [range 13.0–15.5 x 4.0–5.0 µm, mean 14.6±0.7 x 4.8±0.3 µm (n=14)], rounded haplonemes [range 13.0–15.0 x 9.5–11.0 µm, mean 14.0±0.8 x 10.1±0.6 µm (n=14)] and desmonemes [range 5.5–7.0 x 4.0–5.5 µm, mean 6.3±0.4 x 5.1±0.6 µm (n=14)].

Ecology and distribution. Material examined comes from 64-65 m off Cape Norvegia.

Zyzzyzus Stechow, 1921

Zyzzyzus parvula (Hickson & Gravely, 1907)

(Fig. 4.5a-h)

Material examined. *ANT XVII/3*: **111-9**, several polyps, up to 45 mm high, with mature gonophores; a single polyp, c. 10 mm high, on *S. unifurcata*; few polyps, up to 12 mm high, on *T. longstaffi* and *E. generale;* few polyps, up to 3 mm high, on *H. interpolatum*; **111-18**, a single polyp, c. 1 mm high, on *Lafoea dumosa* (Fleming, 1820).

Remarks. As also mentioned by Svoboda and Stepanjants (2001), many juveniles have been observed sharing substrate with adults, pointing to a gregarious habit, and putatively restricted dispersal capabilities. Juvenile specimens, especially the youngest ones, have slightly capitate aboral tentacles (Fig. 4.5a), which is in agreement with the genus diagnoses by Campos et al. (2007).

Originally described from the Ross Sea as *Lampra parvula* Hickson & Gravely, 1907, the species has had a complicated taxonomical history, being re-allocated in several genera, even belonging to different families. It was considered as *Corymorpha* by Stepanjants (1972), and later re-allocated in *Lampra* by Stepanjants and Svoboda (1999). Svoboda and Stepanjants (2001) included it in the reestablished genus *Monocaulus*. Nowadays, after the revision of the genus *Zyzzyzus* by Campos et al. (2007), included within Tubulariidae, the species is considered as a member of this genus (Schuchert 2017).

Svoboda and Stepanjants (2001) re-described the syntypes of *Z. parvula* and provided a detailed account on new material from the Weddell Sea. However, the authors pointed out, based on *in situ* photographs from the Weddell Sea (Svoboda and Stepanjants 2001:57), that living specimens are white, but reddish-orange after preservation. We disagree with that assumption. *In situ* photographs by Brueggeman (1998) referable to *Z. parvula* show deep-red to brown polyps, with a pale-orange basal section, coloration similar to that found in preserved specimens. Therefore, those white specimens mentioned by Svoboda and Stepanjants (2001) could actually correspond to an undescribed species. Material examined here entirely agrees with the description given by Svoboda and Stepanjants (2001), as well as with the original description by Hickson and Gravely (1907). However, unfortunately previous authors did not provide any information about the type and size of the nematocysts. Given that present study constitutes the first account on the cnidome, it would be necessary to compare present data with the type series and the material studied by Svoboda and Stepanjants (2001) to put in order the existent information on the species.

Cnidome comprising small stenoteles [range 10.0–11.5 x 8.0–9.5 μm, mean 10.9±0.4 x 8.8±0.4 μm (n=19)], large stenoteles [range 15.0–16.0 x 10.0–10.5 μm, mean 15.4±0.4 x 10.1±0.2 μm (n=14)] and desmonemes [range 6.0–6.5 x 5.0–6.0 μm, mean 6.2±0.2 x 5.9±0.3 μm (n=15)].

Ecology and distribution. Previously reported at depths from 5 (Stepanjants 1979) to 440 m (Svoboda and Stepanjants 2001); present material from 62 to 105 m. Species with circum-Antarctic distribution (Stepanjants 1979).

Corymorphidae Allman, 1872

Corymorpha M. Sars, 1835

Corymorpha microrhiza (Hickson & Gravely, 1907)

(Fig. 4.5i-l)

Material examined. *ANT XVII/3*: **111-9**, few polyps, up to 80 mm high, on gravel, with mature gonophores; *ANT XXI/2*: **PS65/253**, few polyps, up to 80 mm high, with developing gonophores; **PS65/280**, few polyps, up to 140 mm high, with mature gonophores.

Remarks. Similarly to *Z. parvula*, *C. microrhiza* was first described as *Lampra microrhiza* (Hickson & Gravely, 1907), and then allocated within *Corymorpha* by Stepanjants (1972), re-allocated within *Lampra* by Stepanjants and Svoboda (1999), and in *Monocaulus* by Svoboda and Stepanjants (2001). However, the species is now considered to belong to *Corymorpha* (Vervoort 2009).

Svoboda and Stepanjants (2001) provided a detailed description of the syntypes and additional material from the Weddell Sea. Specimens examined here concur in every aspect, but for the presence of branched blastostyles, although exclusively observed in large and mature specimens (Fig. 4.5j). The original description by Hickson and Gravely (1907) refers branched blastostyles, but Svoboda and Stepanjants were not able to determine this character in the type material. This discrepancy could be attributed either to putative sexual dimorphism or to the fact that the material examined by Svoboda and Stepanjants was not completely developed. Cnidome information was not given in previous descriptions. Therefore, until the analysis of the cnidome in the type

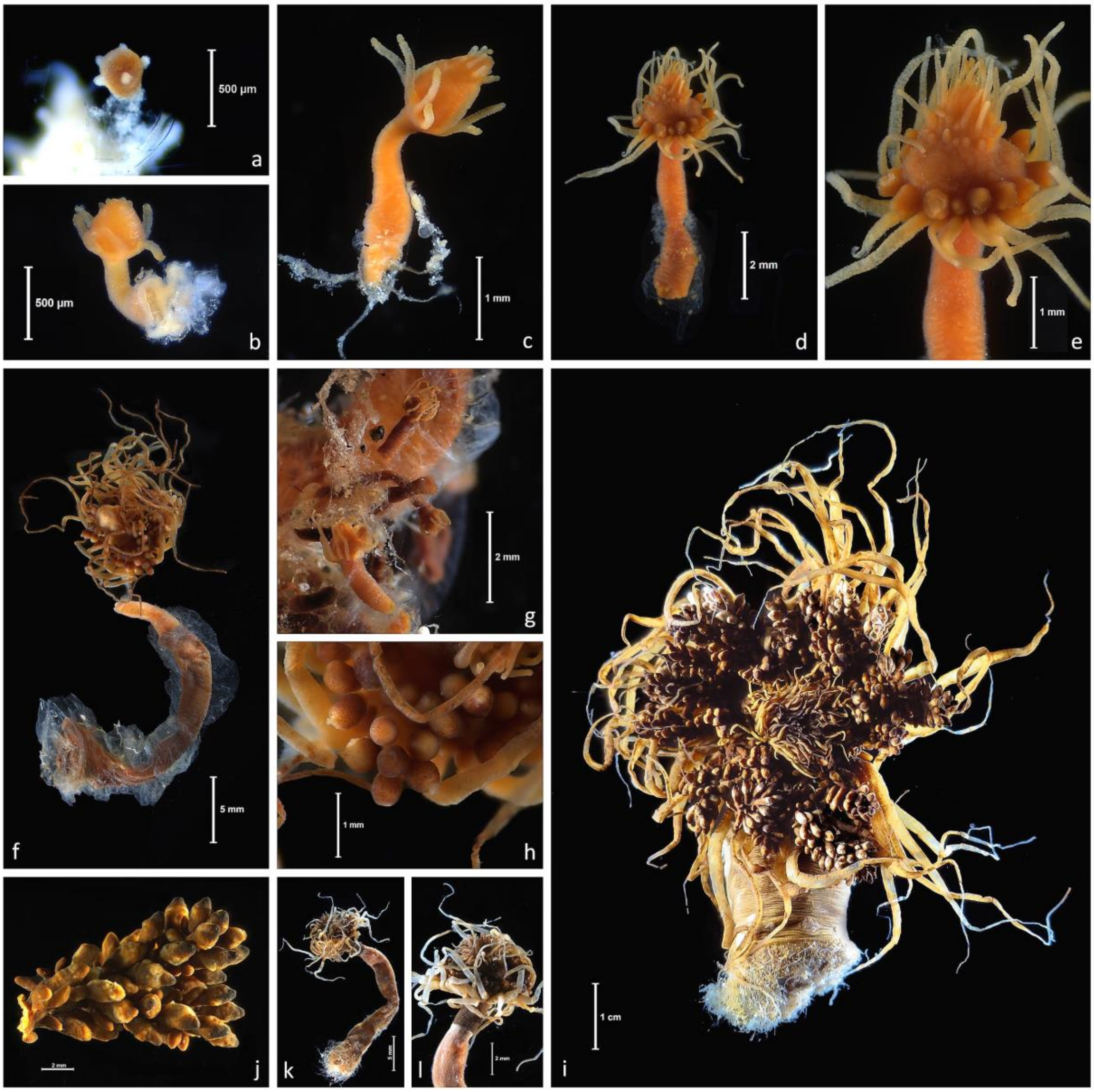

Figure 4.5 a-h *Zyzzyzus parvula*: **a-f** polyps in different developmental stages; **g** detail of juvenile polyps in the basal portion of a mature specimen; **h** styloid with developing gonophores. **i-l** *Corymorpha microrhiza*: **i** mature polyp; **j** styloid with gonophores; **k-l** juvenile polyps

series, none of the previous records can be ascribed with confidence to *C. microrhiza.*

Cnidome consisting in stenoteles [range 11.0–13.0 x 8.0–11.0 µm, mean 11.9±0.8 x 9.9±0.9 µm (n=15)], rounded haplonemes [range 16.0–17.5 x 13.5–14.5 µm, mean 17.0±0.5 x 14.1±0.3 µm (n=15)] and desmonemes [range 7.0–7.5 x 6.5–7.5 µm, mean 7.3±0.3 x 7.1±0.3 µm (n=15)].

Ecology and distribution. Species previously known from 237 to 629 m (Svoboda and Stepanjants 2001); present material collected from 62 to 309 m. Little-recorded species, only known from the Ross Sea (Hickson and Gravely 1907) and the Weddell Sea (Svoboda and Stepanjants 2001). Probably circum-Antarctic distribution (Svoboda and Stepanjants 2001). Present contribution represents the third record of the species.

Corynidae Johnston, 1836

Sarsia Lesson, 1843

?Sarsia sp.

(Fig. 4.2j)

Material examined. *ANT XV/3*: **48-210**, a single polyp, c. 3 mm high; *ANT XXI/2*: **PS65/248**, a single polyp, c. 2 mm high, on *H. incertus.*

Remarks. Aside from *Sarsia medelae* Gili, López-González & Bouillon, 2006, a non-parasitic mesobiont inhabiting calcaxonian gorgonians in the Weddell Sea (Gili et al. 2006), very few reports of the family Corynidae exist for Antarctic waters, most of which could not be assigned to species level with enough solid grounds. Hickson and Gravely (1907) mentioned an undeterminable immature Corynidae from the McMurdo Sound (Ross Sea). Later, Stepanjants (1979) reported *Sarsia tubulosa* (M. Sars, 1835) (as *Coryne tubulosa*) from the Davis Sea, although her Antarctic material was infertile. Recently, Peña Cantero et al. (2013) described the early formation of tetraradial canals on reared polyps under laboratory conditions, which let them to assign their material to genus *Sarsia* with confidence, although no species could be attributed. These authors pointed out that their material might be conspecific with those previous records mentioned above. Material examined here might be also conspecific, but the absence of gonophores precludes a proper assignment even at genus level. Further research is needed regarding the corynids from the Southern Ocean.

Ecology and distribution. Similar specimens were found at depths between 3 (Stepanjants 1979) and 40 m (Peña Cantero et al. 2013); present material collected from 67-287 m. All the previous records of *Sarsia* sp. originate from East Antarctica (see Peña Cantero et al. 2013). Present finding constitutes the first evidence of this undetermined corynid from West Antarctica and the Weddell Sea.

Zancleidae Russell, 1953

Zanclea Gegenbaur, 1856

Zanclea hicksoni (Stepanjants, 1972)

(Fig. 4.4j-n)

Material examined. *ANT XV/3*: **48-31**, a single polyp, c. 3 mm high, on *O. stepanjantsae*; *ANT XVII/3*: **111-9**, several polyps, up to 5 mm high, on *T. longstaffi* and *E. generale.*

Remarks. According to Peña Cantero et al. (2013), *Z. hicksoni* is conspecific with Corynidae Species B Hickson & Gravely, 1907. However, it was not until years later when it was described as *Gemmaria hicksoni* Stepanjants, 1972. As previously noted by Hickson and Gravely (1907), polyps examined here are provided with hydrorhizal filaments which anchor them to the substrate (Fig. 4.4j). Additionally, we have observed some large specimens with linear clusters of 3-5 tentacles, being the central one larger (Fig. 4.4m-n). These two characteristics are diagnostic features of the genus *Monocoryne* Broch, 1910 (Fam. Candelabridae Stechow, 1921) according to Stepanjants et al. (2003). Conversely, there are no *Zanclea* species with those characters (cf. Bouillon et al. 2006). According to Stepanjants et al. (2003), the tentacles of *Monocoryne* sp. Stepanjants, 1979 are irregularly distributed, and can be either solitary or arranged in groups of three, being one larger (Stepanjants et al. 2003: 104). Among the several polyps observed, the smallest ones certainly resemble a zancleid (Fig. 4.4k), however, while the largest ones have more affinities with *Monocoryne*, and intermediate medium-sized specimens are also present in material examined (Fig. 4.4j, l). The great morphological variability observed here (Fig. 4.4j), the very few available polyps examined by previous authors, and the lack of medium-sized specimens could be the reason why Stepanjants (1979) described two different species (i.e. *Gemmaria hicksoni* and *Monocoryne* sp.).

Finally, the type and size of the nematocysts of *Z. hicksoni* obtained by Peña Cantero et al. (2013), of *Monocoryne* sp. by Stepanjants et al. (2003), and of the present material are almost identical. Therefore, *Z. hicksoni* might be conspecific with *Monocoryne* sp. described by Stepanjants (1979) and Stepanjants et al. (2003), with subsequent family and genus re-allocation. However, due to the reproductive structures of *Z. hicksoni* are still unknown, further evidence is needed to confirm its true identity.

Cnidome composed by small stenoteles [range 8.5–11.0 x 6.5–8.0 μm, mean 9.6±0.8 x 7.1±0.4 μm (n=15)], large stenoteles [range 13.0–17.0 x 11.0–14.0 μm, mean 14.9±1.0 x 12.7±0.7 μm (n=15)], haplonemes (isorhiza) [range 14.0–18.0 x 4.5–7.0 μm, mean 16.7±1.4 x 5.7±0.7 μm (n=14)] and desmonemes [range 5.0–8.5 x 4.5–5.5 μm, mean 6.9±0.8 x 5.1±0.3 μm (n=17)].

Ecology and distribution. Previously found at depths from 12 (Peña Cantero et al. 2013) to 183 m (Hickson and Gravely 1907); present material was collected at 62-64 m. All previous records were restricted to East Antarctica (see Peña Cantero et al. 2013); present contribution confirms its presence in West Antarctica and constitutes the first record from the Weddell Sea, and pointing to a circum-Antarctic distribution.

Leptothecata Cornelius, 1992

Lafoeidae Hincks, 1868

Acryptolaria Norman, 1875

Acryptolaria frigida Peña Cantero, 2014

(Fig. 4.6a-b)

Material examined. *ANT XV/3*: **48-77**, two stems, up to 110 mm high, on sponge and octocoral; **48-197**, one colony, c. 60 mm high.

Ecology and distribution. Reported from 85 (Peña Cantero 2010) to 728 m (Peña Cantero 2014a); present material collected between 341 and 416 m. Circum-Antarctic species (Peña Cantero 2014a).

Filellum Hincks, 1869

Filellum antarcticum (Hartlaub, 1904)

(Fig. 4.6c-f)

Material examined. *ANT XV/3*: **48-5**, several hydrothecae, on *S. lobata*, with coppinia; *ANT XVII/3*: **111-9**, several hydrothecae, on *S. lobata*, with coppinia; *ANT XXI/2*: **PS65/276**, several hydrothecae, on *St. vanhoeffeni*, with coppinia.

Remarks. Cnidome comprising large microbasic mastigophores [range 10.0–12.0 x 4.0–4.5 μm, mean 10.9±0.8 x 4.1±0.2 μm (n=11)] and small microbasic euryteles [range 5.5–6.5 x 2.5–3.0 μm, mean 6.1±0.3 x 2.8±0.3 μm (n=18)].

Ecology and distribution. Species previously reported at depths from 14 (Millard 1964) to 552 m (Peña Cantero 2014a); present material from 62 to 277 m. Species known from all over Antarctic waters (Peña Cantero et al. 2004) and South Africa (Millard 1964, 1975).

Filellum cf. *magnificum*

(Fig. 4.6g)

Material examined. *ANT XV/3*: **48-150**, some hydrothecae, on *E. scotti*; **48-220**, some hydrothecae, on *S. exochus*; **48-276**, several hydrothecae, on *S. nana*; *ANT XXI/2*: **PS65/166**, several hydrothecae, on *O. erratum*; **PS65/274**, several hydrothecae, on *Staurotheca nonscripta* Peña Cantero, Svoboda & Vervoort, 1997.

Remarks. In spite of the absence of coppinia, the size of the hydrotheca and the size of the nematocysts perfectly agree with previous reports (Peña Cantero 2010,

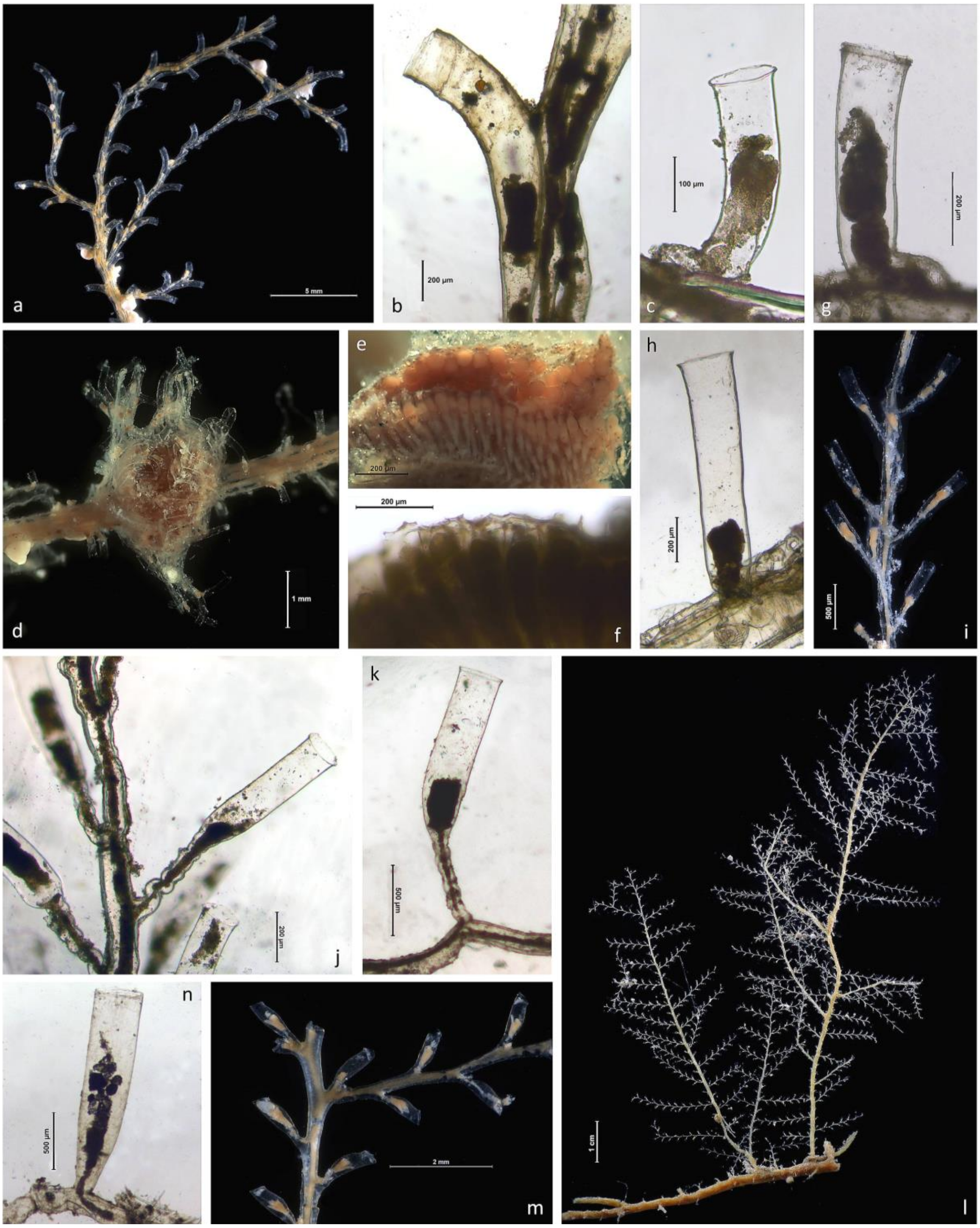

Figure 4.6 a-b *Acryptolaria frigida*: **a** stem; **b** hydrotheca. **c-f** *Filellum antarcticum*: **c** hydrotheca; **d** coppinia; **e** section of a coppinia showing gonothecae and eggs; **f** detail of gonothecal aperture. **g** *Filellum* cf. *magnificum*: hydrotheca. **h** *Filellum* cf. *bouvetensis*: hydrotheca. **i-j** *Lafoea dumosa*: **i** stem; **j** detail of the stem showing hydrothecal arrangement. **k** *Lafoea gaussica*: hydrotheca. **l-m** *Abietinella operculata*: **l** stems; **m** detail of the stem showing hydrothecal arrangement

Peña Cantero et al. 2004, Soto Àngel and Peña Cantero 2015). However, in agreement with Peña Cantero et al. (1998), the identification of infertile material of *Filellum* is pointless.

Cnidome consisting in large microbasic mastigophores [range 17.5–19.0 x 4.5–6.0 µm, mean 18.1±0.6 x 5.4±0.8 µm (n=4)] and small microbasic euryteles [range 6.0–7.5 x

2.5–3.5 μm, mean 6.9±0.4 x 2.8±0.3 μm (n=13)].

Ecology and distribution. Previously known from 85 (Peña Cantero 2010) to 640 m (Peña Cantero et al. 2004); present material collected at depths from 236 to 758 m. Only known from Peter I Island (Peña Cantero 2010) and the Weddell Sea (Peña Cantero et al. 2004; material examined).

Filellum cf. *bouvetensis* Marques, Peña Cantero, Miranda & Migotto, 2011

(Fig. 4.6h)

Material examined. *ANT XXI/2*: **PS65/39**, some hydrothecae, on *S. nana*; **PS65/121**, several hydrothecae, on *S. nana* and *B. subrufa*; **PS65/278**, some hydrothecae, on *A. elongatus*.

Remarks. The size of the hydrotheca (measurements) and the size of the nematocysts are in agreement with the description of the species (cf. Marques et al. 2011). However, the absence of coppinia precludes a proper identification.

Cnidome composed exclusively by microbasic mastigophores [range 6.5–9.0 x 3.0–3.5 μm, mean 7.4±0.7 x 3.2±0.3 μm (n=21)].

Ecology and distribution. Previously reported in Antarctic waters at 122-134 m depth (Peña Cantero and Gili 2006, as *Filellum contortum* (Nutting, 1906)). Rare species only reported twice: from its type locality at Bouvet Island (Peña Cantero and Gili 2006) and from Gough Island, Tristan da Cunha archipelago, in the South Atlantic (Galea 2015). If confirmed, present record would constitute the first evidence of the species from both the Weddell Sea and High Antarctica.

Filellum sp.

Material examined. *ANT XV/3*: **48-4**, some hydrothecae, on *E. generale*; **48-5**, some hydrothecae, on sponge; **48-27**, some hydrothecae, on *E. generale*; some hydrothecae, on *S. lobata* and *Halecium exaggeratum* Peña Cantero, Boero & Piraino, 2013; **48-44**, few hydrothecae, on *S. lobata*; several hydrothecae, on *S. exochus*; several hydrothecae, on *Halecium banzare* Watson, 2008; **48-50**, several hydrothecae, on *S. nana* and *C. hicksoni*; **48-77**, several hydrothecae, on *Halecium jaederholmi* Vervoort, 1972; **48-168**, some hydrothecae, on *S. exochus*; **48-194**, several hydrothecae, on *S. nana*; **48-220**, few hydrothecae, on *Symplectoscyphus liouvillei* (Billard, 1914); few hydrothecae, on *C. hicksoni*; some hydrothecae, on *H. interpolatum*; **48-222**, few hydrothecae, on *S. weddelli*; several hydrothecae, on *S. nana*; **48-276**, few hydrothecae, on *S. weddelli*; some hydrothecae, on *Halecium* cf. *antarcticum*; *ANT XVII/3*: **111-9**, few hydrothecae, on *R. antarcticum*; **111-19**, several hydrothecae on *S. unifurcata* and *Symplectoscyphus naumovi* Blanco, 1969; several hydrothecae, on *L. dumosa*; some hydrothecae, on *S. exochus*; few hydrothecae, on *S. weddelli*; some hydrothecae, on *R. antarcticum*; some hydrothecae, on *H. interpolatum*; some hydrothecae, on *S. weddelli*; *ANT XXI/2*: **PS65/39**, several hydrothecae, on *S. lobata*; several hydrothecae, on *Sy. glacialis*; several hydrothecae, on *S. exochus*; several hydrothecae, on *S.* nana, *C. hicksoni* and *Symplectoscyphus plectilis* (Hickson & Gravely, 1907); some hydrothecae, on *S. glomulosa*; several hydrothecae, on *S. plectilis*; **PS65/121**, some hydrothecae, on *Sy. glacialis*; some hydrothecae, on *S. plectilis*; some hydrothecae, on hydrorrhiza of undetermined hydroid; **PS65/166**, several hydrothecae, on *S. exochus*; **PS65/174**, several hydrothecae, on *S. exochus*; **PS65/175**, several hydrothecae, on *S. lobata* and *S. naumovi*; **PS65/237**, several hydrothecae, on *Sy. glacialis*; several hydrothecae, on *S. exochus*; some hydrothecae, on *S. weddelli*; **PS65/248**, some hydrothecae, on *S. plectilis*; several hydrothecae, on *S. curvatus*; several hydrothecae, on *H. incertus*; **PS65/253**, several hydrothecae, on *S. lobata*; **PS65/265**, several hydrothecae, on *Sy. glacialis*; **PS65/274**, some hydrothecae, on *S. plectilis*; several hydrothecae, on *S. nonscripta*; **PS65/276**, some hydrotheca on *Sy. vanhoeffeni*; several hydrothecae, on *S. exochus*; **PS65/278**, several hydrothecae, on *L. dumosa*; several hydrothecae, on *H. secundum*; some hydrothecae, on sponge; **PS65/292**, several hydrothecae, on *Staurotheca antarctica* Hartlaub, 1904; several hydrothecae, on *S. nonscripta.*

Remarks. Material included here comprises a huge amount of small-sized hydrothecae, with 100-150 µm in diameter of aperture, and provided with striae. The material could correspond, at least in part, to *F. antarcticum*. However, in agreement with Peña Cantero et al. (2004) and Marques et al. (2011), the small-sized *Filellum* from Antarctic waters are not identifiable in the absence of coppinia, and therefore it precludes a proper identification of material examined here.

Ecology and distribution. Material examined was collected at depths between 62 and 598 m.

Lafoea Lamouroux, 1821

Lafoea dumosa (Fleming, 1820)

(Fig. 4.6i-j)

Material examined. *ANT XV/3*: **48-50**, one colony, up to 55 mm high; **48-194**, one colony, up to 50 mm high; **48-276**, one colony, up to 10 mm high, on *S. nana*; **48-297**, one colony, up to 15 mm high, on *B. subrufa* and ascidian; *ANT XVII/3*: **111-5**, one colony, up to 35 mm high, on *O. stepanjantsae*; **111-6**, one colony, up to 40 mm high; **111-18**, one colony, up to 40 mm high, on *O. stepanjantsae*; one colony, up to 20 mm high, on polychaete tube; **111-19**, one colony, up to 20 mm high, on *S. unifurcata*; *ANT XXI/2*: **PS65/121**, some stems, up to 40 mm high, on *S. nana* and *S. curvatus*; **PS65/278**, one colony, up to 40 mm high; **PS65/279**, one colony, up to 10 mm high, on sponge.

Ecology and distribution. In Antarctic waters, reported from 12 (Stepanjants 1979) to 1157 m depth (Peña Cantero 2014a); present material was collected between 65-417 m. Worldwide distributed, known from both East and West Antarctica (Peña Cantero et al. 2004), as well as the Scotia Arc (Soto Àngel and Peña Cantero 2015).

Lafoea gaussica Vanhöffen, 1910

(Fig. 4.6k)

Material examined. *ANT XXI/2*: **PS65/280**, stolonal colony, few hydrothecae, on bryozoan.

Ecology and distribution. Previously found at depths from 40 (Stepanjants, 1979) to 460 m (Peña Cantero et al. 2004); present material collected at 191-228 m. Species with circum-Antarctic distribution (Peña Cantero et al. 2004).

Hebellidae Fraser, 1912

Hebella Allman, 1888

Hebella cf. *plana*

(Fig. 4.6n)

Material examined. *ANT XV/3*: **PS65/77**, few hydrothecae, on *A. frigida*.

Remarks. In our material, the length of the hydrotheca is 1440–1600 µm, the diameter at the aperture is 411–431 mm, and the diameter at diaphragm 280–312 µm. The length of the pedicel is 115 µm. These measurements are considerably larger than those given by Peña Cantero et al. (2004), and therefore we are not entirely confident with its specific assignation.

Ecology and distribution. Previously known from depths between 92 (Peña Cantero 2008) and 722 m (Peña Cantero et al. 2004); present material came from depths between 340 and 360 m. Species with Antarctic-Patagonian distribution (Peña Cantero et al. 2004).

Campanulinidae Hincks, 1868

Lafoeina Sars, 1874

Lafoeina longitheca Jäderholm, 1904

(Fig. 4.7a)

Material examined. *ANT XV/3*: **48-77**, few hydrothecae, on *Halecium pseudodelicatulum* Peña Cantero, 2014; *ANT XVII/3*: **111-5**, several hydrothecae, on *O. stepanjantsae*, with gonothecae; **111-9**, some hydrothecae, on polychaete tube; some hydrothecae, on *T. longstaffi*; several hydrothecae, on *O. stepanjantsae*; **111-18**, some hydrothecae, on *S. nana*; some hydrothecae, on undeterminate hydrorhiza; some hydrothecae, on *O. stepanjantsae*, with gonothecae; few hydrothecae, on *C. hicksoni*; several hydrothecae, on *H. interpolatum*; *ANT XXI/2*: **PS65/251**, several hydrothecae, on *O. stepanjantsae*; **PS65/281**, some hydrothecae, on *B. subrufa*; few hydrothecae, on *L. dumosa*; some hydrothecae, on *S. cumberlandicus*.

Ecology and distribution. Species reported at depths from five (Stepanjants 1979) to 701 m (Peña Cantero 2014a); present material comes from 62 to 360 m. Pan Antarctic species (Peña Cantero and Vervoort 2009).

Stegella Stechow, 1919

Stegella lobata (Vanhöffen, 1910)

(Fig. 4.7b-c)

Material examined. *ANT XV/3*: **48-4**, few hydrothecae, c. 4 mm high, on dead octocoral; **48-5**, a few hydrothecae, up to 3 mm high, on *S. unifurcata*; one colony, c. 90 mm high, with gonothecae; **48-27**, one colony, c. 60 mm high; **48-36**, some stems, up to 20 mm high, on *O. stepanjantsae*; **48-44**, some stems, up to 40 mm high, on polychaete tube; **48-44**, one colony, c. 75 mm high, with gonothecae; **48-50**, one colony, c. 60 mm high, on dead octocoral; **48-63**, one colony, c. 60 mm high, with gonothecae; **48-77**, one colony, c. 80 mm high; two hydrothecae, c. 3 mm high, on *S. weddelli*; **48-194**, one hydrotheca, c. 5 mm high; **48-197**, some stems, up to 20 mm high, on *B. subrufa*; **48-220**, some stems, up to 120 mm high, on gravel and dead octocoral, with gonothecae; **48-276**, few hydrothecae, up to 3 mm high, on *S. nana*; *ANT XVII/3*: **111-9**, one colony, c. 130 mm high, with gonothecae; **111-18**, few hydrothecae, c. 2 mm high, on *O. stepanjantsae*; few hydrothecae, c. 6 mm high, on *S. nana*; *ANT XXI/2*: **PS65/39**, one colony, c. 110 mm high, with gonothecae; one colony, c. 55 mm high, on *S. nana*, with gonothecae; **PS65/121**, one colony, c. 70 mm high, with gonothecae; one colony, c. 15 mm high, on bryozoan; **PS65/132**, one colony, c. 75 mm high; **PS65/166**, one hydrotheca, c. 2 mm high, on *S. nonscripta*; **PS65/175**, few stems, up to 6 mm high, on *B. subrufa*; one colony, c. 40 mm high, on dead *Oswaldella*; **PS65/237**, one colony, c. 110 mm high, on *S. nana*, with gonothecae; two hydrothecae, c. 2 mm high, on *S. exochus*; **PS65/248**, one colony, c. 40 mm high, on octocoral; two hydrothecae, c. 2 mm high, on *H. incertus*; **PS65/253**, one colony, c. 60 mm high, on polychaete tube, with gonothecae; **PS65/265**, few stems, up to 5 mm high, on *H. pseudodelicatulum*; **PS65/276**, one colony, c. 75 mm high, with gonothecae; **PS65/281**, one colony, c. 90 mm high, on sponge, with developing gonothecae; **PS65/336**, some stems, up to 30 mm high, on *S. nana.*

Remarks. Specimens analyzed have been observed using a wide range of basibionts as substrate (see above). Large colonies are seen in many cases overgrowing the basibiont almost completely. *S. lobata* seems to behave as an aggressive epibiont species that uses its host to reach large size. This relationship can be described as parasitism *sensu lato*, in which the epibiont is detrimental to the host but is not metabolically dependent upon it (see Gili et al. 2006 and literature cited).

Ecology and distribution. Previously collected at depths from 10 (Naumov and Stepanjants 1972) to 700 m (Naumov and Stepanjants 1962); present material was obtained from 62 to 417 m. Circum-Antarctic species (Peña Cantero et al. 2004).

Phialellidae Russell, 1953
Phialella belgicae (Hartlaub, 1904)
(Fig. 4.7d)

Material examined. *ANT XV/3*: **48-27**, some hydrothecae, on *S. lobata* and *H. exaggeratum*; two hydrothecae, on *S. anae*; three hydrothecae, on *Sy. glacialis*; few hydrothecae, on *E. generale*; **48-33**, several hydrothecae, on *O. stepanjantsae* and *C. hicksoni*; **48-36**, some hydrothecae, on *O. stepanjantsae*; **48-39**, several hydrothecae, on dead octocoral; **48-44**, two hydrothecae, on *S. naumovi*; three hydrothecae, on *A. elongatus*; some hydrothecae, on bryozoan; **48-50**, several hydrothecae, on *S. nana* and *C. hicksoni*; some hydrothecae, on *H. secundum*; several hydrothecae, on bryozoan; **48-63**, some hydrothecae, on *Staurotheca frigida* Peña Cantero, Svoboda & Vervoort, 1997; **48-77**, several hydrothecae, on *H. jaederholmi*; **48-82**, several hydrothecae, on *Staurotheca polarsterni* Peña Cantero, Svoboda & Vervoort, 1997; several hydrothecae, on *B. subrufa*; some hydrothecae, on *Sy. glacialis*; **48-168**, two hydrothecae, on *S. weddelli*; **48-220**, some hydrothecae and few erect stems, up to 2.5 mm high, on *S. plectilis*; several hydrothecae, on *S. nana*; several hydrothecae, on *S. nana* and *C. hicksoni*; few hydrothecae, on *S. exochus*; few hydrothecae, on *S. anae*; some hydrothecae, on *S. exochus*; few hydrothecae, on *H. interpolatum*; **48-276**, several hydrothecae, on *S. nana* and *C. hicksoni*; few hydrothecae, on *Halecium* cf. *antarcticum*; *ANT XVII/3*: **111-7**, some hydrothecae, on *O. stepanjantsae*; some hydrothecae, on *S. cumberlandicus*; **111-9**, several hydrothecae, on *T. longstaffi*, *R. antarcticum* and *E. generale*; several hydrothecae, on *A. grandis*; **111-19**, two hydrothecae, on *H. interpolatum*; few hydrothecae, on *Tubularia* sp.1; *ANT XXI/2*: **PS65/39**, some hydrothecae, on *S. nana*, with gonothecae; one hydrotheca, on *S. exochus*; few hydrothecae, on polychaete tube; **PS65/121**, few hydrothecae, on *Antarctoscyphus spiralis* (Hickson & Gravely, 1907); **PS65/132**, some hydrothecae, on *B. subrufa*; **PS65/175**, three hydrothecae, on *A. elongatus*; **PS65/237**, few hydrothecae, on *Sy. glacialis*; some hydrothecae, on *S. nana* and *Halecium* cf. *antarcticum*; **PS65/248**, one hydrotheca, on indeterminate hydrorhiza; **PS65/274**, several hydrothecae, on *S. nonscripta*; **PS65/278**, few hydrothecae, on *H. secundum* and sponge; **PS65/281**, some hydrothecae, on *S. curvatus*; **PS65/336**, some hydrothecae, on *Staurotheca pachyclada* (Jäderholm, 1904).

Ecology and distribution. Species previously reported from the low tide (Billard 1914) to 779 m depth (Peña Cantero 2014a); present material was collected from 62 to 417 m. Probably a Pan-Antarctic species (Peña Cantero et al. 2013).

Figure 4.7 **a** *Lafoeina longitheca*: hydrotheca. **b-c** *Stegella lobata*: **b** stem showing hydrothecal arrangement; **c** gonotheca. **d** *Phialella belgicae*: hydrotheca. **e-h** *Campanularia hicksoni*: **e** general view of the colony; **f** hydrotheca; **g** pioneer polyp showing planula attachment; **h** gonotheca. **i-j** *Campanularia* sp.: **i** hydrotheca; **j** developing gonotheca. **k-m** *Billardia subrufa*: **k** general view of a colony growing on *Oswaldella erratum*; **l** stem showing hydrothecal arrangement; **m** gonothecae

Campanulariidae Johnston, 1836
Campanularia Lamarck, 1816
Campanularia hicksoni Totton, 1930
(Fig. 4.7e-h)

Material examined. *ANT XV/3*: **48-33**, several hydrothecae, up to 20 mm high, on *O. stepanjantsae*, with developing gonothecae; **48-36**, several hydrothecae, up to 25 mm high, on *O. stepanjantsae*, with developing gonothecae; **48-50**, several hydrothecae, up to 20 mm high, on *S. nana*, with developing gonothecae; **48-72**, few hydrothecae, up to 15 mm high, on *S. polarsterni*; **48-210**, several hydrothecae, up to 25 mm high, on *O. stepanjantsae*, with developing gonothecae; **48-220**, few hydrothecae, up to 25 mm high, on *S. nana*; few hydrothecae, up to 25 mm high, with developing gonothecae; **48-276**, few hydrothecae, up to 5 mm high, on *S. nana*; *ANT XVII/3*: **111-5**, several hydrothecae, up to 15 mm high, on *O. stepanjantsae*, with gonothecae; **111-6**, some hydrothecae, up to 15 mm high, on *Hydrodendron arboreum* (Allman, 1888), with gonothecae; few hydrothecae, up to 15 mm high, on *S. exochus*, with gonothecae; several hydrothecae, up to 15 mm high, on *O. stepanjantsae*; **111-7**, several hydrothecae, up to 15 mm high, on *O. stepanjantsae*, with gonothecae; **111-9**, few hydrothecae, up to 15 mm high, on *O. stepanjantsae*; few hydrothecae, up to 20 mm high, on *T. longstaffi*; several hydrothecae, up to 30 mm high, on *O. stepanjantsae*, with gonothecae; **111-18**, few hydrothecae, up to 15 mm high, on *S. nana*; **111-19**, few hydrothecae, up to 20 mm high, on *S. glomulosa*; few hydrothecae, up to 5 mm high, on *Tubularia* sp.1; *ANT XXI/2*: **PS65/39**, few hydrothecae, up to 20 mm high, on *S. glomulosa*, with gonothecae; some hydrothecae, up to 20 mm high, on *S. nana*, with gonothecae; **PS65/166**, few hydrothecae, up to 20 mm high, on *A. elongatus*; **PS65/237**, several hydrothecae, up to 15 mm high, on *S. nana*; few hydrothecae, up to 10 mm high, on *S. exochus*; **PS65/248**, few hydrothecae, up to 15 mm high, on *S. curvatus*; **PS65/276**, few hydrothecae, up to 25 mm high, on *S. glomulosa*; **PS65/281**, few hydrothecae, up to 15 mm high, on *O. stepanjantsae*; few hydrothecae, up to 7 mm high, on *S. cumberlandicus*; few hydrothecae, up to 30 mm high, on *S. nonscripta.*

Remarks. According to Peña Cantero et al. (2004), *C. hicksoni* forms large hydrothecae (2335–2946 mm in length and 902–1417 mm in diameter at aperture). However, among the abundant material examined, some smaller hydrothecae (1000-1800 µm) have been observed. In this regard, Totton (1930) and Blanco (1984) already noted a great variability in the size of the hydrotheca, but in opinion of Peña Cantero et al. (2004), Totton’s material could be composed of two different species. A detailed examination of the stolonal hydrorhiza let us confirm that some polyps with small hydrothecae are joined through the same stolon to slightly larger ones (c. 1400-1500 µm), which in turn are united to medium-sized ones (c. 2000 µm), and so on. Furthermore, in a few occasions we observed the pioneer polyp with remanents of the planula attachment (see Fig. 4.7g), and thus, the first polyp of the colony, confirming the smaller size of the hydrotheca (c. 950 µm in length). Centering the focus on the size of the nematocysts, previous studies reported nematocysts of 17–18.5 x 4–4.5 µm (Peña Cantero 2013), slightly larger in Peña Cantero (2014a): 19–20 x 4.5–5 µm. The size distribution of large microbasic mastigophores suggests a positive correlation between length of hydrotheca and mean size of these nematocysts (Fig. 4.8). We consider that the small polyps (accordingly provided with small hydrothecae) studied here also belong to *C. hicksoni,* based on the following reasons: in some occasions, small polyps have been noticed joined to larger ones; most small polyps were recorded from the same basibiont than larger ones, although the connection could not be seen; the large microbasic mastigophores of the smallest polyps always included at least a few large nematocysts, regardless of the mean size (see Fig. 4.8). We hypothesized that this ontogenetic drift could be attributed to changes in the trophic ecology of the species: larger polyps probably eat larger preys, and could need larger nematocysts. This is similar to previous findings relating prey and cnidome size, but they are restricted to various planktonic cnidarians. Purcell (1984) observed that siphonophores species with larger nematocyst capture larger prey. She subsequently suggested that the presence of longer threads in larger nematocysts could make them more effective in entangling prey. On the other hand, Carrette et al. (2002) evidenced profound changes in the ratio of different types of nematocysts between small and large specimens of the cubomedusa *Chironex fleckeri* Southcott, 1956 that are, in turn, correlated with ontogenetic drifts in its diet. Further research is needed regarding this finding, and specific future experimental design will shed more light on this issue.

Cnidome (in polyps within large hydrothecae) composed by large microbasic mastigophores [range 13.5–20.5 x 3.5–4.5 µm, mean 19.3±1.4 x 4.5±0.2 µm (n=56)] and small microbasic mastigohpores [range 7.5–9.0 x 1.5–2.0 µm, mean 8.2±0.4 x 1.6±0.1 µm (n=27)].

Ecology and distribution. Species previously reported at depths between 10 (Peña Cantero et al. 2004) and 779 m (Peña Cantero 2014a); material examined collected from 62 to 598 m. Species with circum-Antarctic distribution (Peña Cantero et al. 2004).

Campanularia sp.
(Fig. 4.7i-j)

Material examined. *ANT XV/3:* **48-27**, few hydrothecae, up to 6 mm high, on *S. anae*; **48-36**, several hydrothecae, up to 5 mm high, on *O. stepanjantsae*; **48-220**, several hydrothecae, up to 6 mm high, on *S. nana*, with developing gonothecae; single

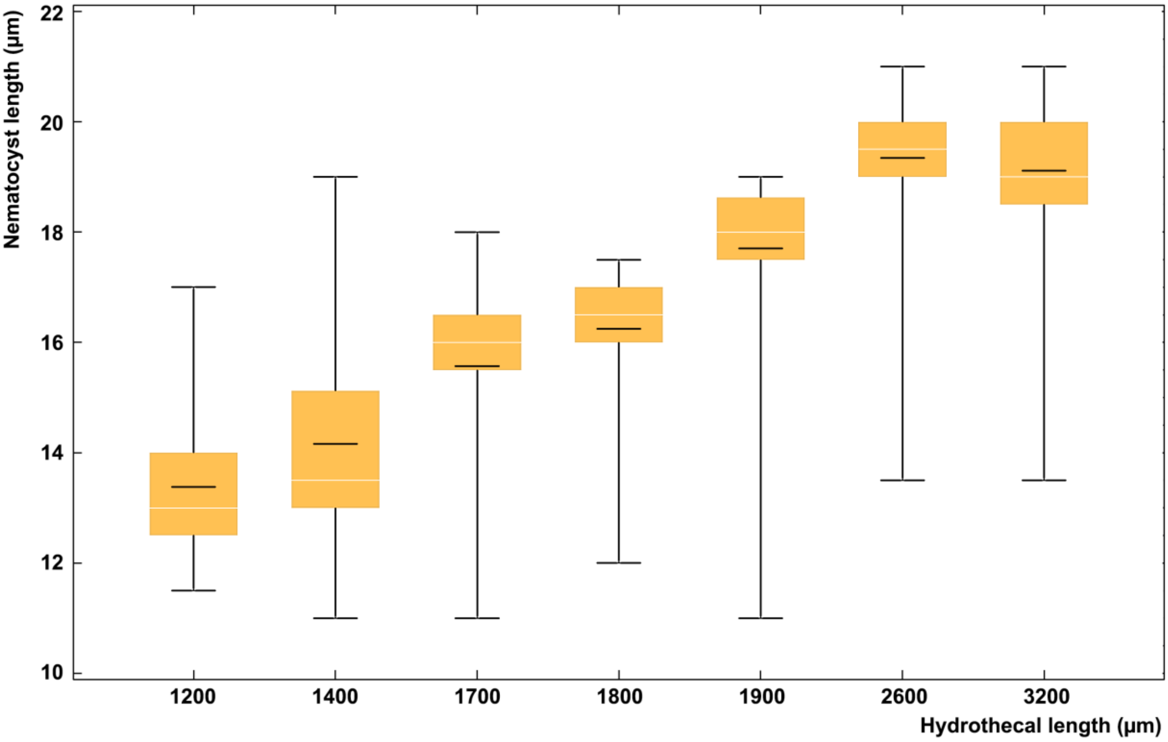

Figure 4.8 Box and whiskers chart showing variation in length of large microbasic mastigophores of *Campanularia hicksoni* according to hydrothecal length (black line = mean; white line = median)

hydrothecae, c. 4 mm high, on *S. exochus*; few hydrothecae, up to 6 mm high, on *H. interpolatum*; few hydrothecae, up to 5 mm high, on *S. glomulosa*; **48-222**, few hydrothecae, up to 6 mm high, on *S. nana*; **48-223**, few hydrothecae, up to 6 mm high, on *S. nana*; *ANT XVII/3*: **111-6**, few hydrothecae, up to 6 mm high, on *B. subrufa*; *ANT XXI/2*: **PS65/39**, few hydrothecae, up to 5 mm high, on *S. nana* and *Sy. glacialis*; **PS65/174**, few hydrothecae, up to 4 mm high, on *O. erratum*; **PS65/175**, few hydrothecae, up to 5 mm high, on *Sy. glacialis*; **PS65/248**, few hydrothecae, up to 6 mm high; single hydrotheca, c. 2 mm, on *H. incertus*; few hydrothecae, up to 5 mm high, on *S. nonscripta*; **PS65/274**, few hydrothecae, up to 5 mm high, on *S. nonscripta*; **PS65/278**, few hydrothecae, up to 5 mm high, on *H. secundum*; **PS65/280**, some hydrothecae, up to 7 mm high, on *Sy. glacialis*; **PS65/281**, few hydrothecae, up to 7 mm high, on *O. stepanjantsae*.

Remarks. Material studied here is probably conspecific with *Campanularia* sp. reported from several localities in the Southern Ocean by Peña Cantero (2006, 2013, 2014a); Peña Cantero and Gili (2006) and Peña Cantero et al. (2004, 2013). The material agrees in the shape and size of hydrothecae (850-950 µm in length and 350-450 µm in diameter at aperture) as well as in the size of the nematocysts. The species, however, has never been found with gonothecae. Material examined from XV/3 48-220 has developing gonothecae (Fig. 4.7j), but unfortunately they cannot be completely characterized given its uncomplete maturation. In contradistinction to the young specimens of *C. hicksoni*, whose hydrotheca is quite similar in shape and size to that of *Campanularia* sp., the range of the nematocyst size obtained for the latter is narrower, and the largest nematocysts do not reach more than 10.5 µm in length (see below). For these reasons, we prefer keeping both species as separated entities until further evidence is known.

Cnidome composed by large microbasic mastigophores [range 9.0–10.5 x 1.5–2.0 µm, mean 9.8±0.5 x 1.7±0.2 µm (n=56)] and small microbasic mastigohpores [range 6.5–7.5 x 1.5–2.0 µm, mean 7.0±0.4 x 1.5±0.1 µm (n=22)].

Ecology and distribution. Previously known from 15 (Peña Cantero et al. 2013) to 728 m (Peña Cantero 2014a); present material comes from depths between 68 to 291 m.

Staurothecidae Maronna, Miranda, Peña Cantero, Barbeitos & Marques, 2016

Staurotheca Allman, 1888

Staurotheca antarctica Hartlaub, 1904

(Fig. 4.9a)

Material examined. *ANT XV/3*: **48-168**, mass of stems, c. 20 mm high; *ANT XXI/2*: **PS65/292**, one colony, c. 30 mm high, with male gonothecae.

Ecology and distribution. Species collected at depths between 55 (Peña Cantero and Vervoort 2003) and 708 m (Peña Cantero 2014a); present material from 228 to 598 m. Circum-Antarctic species (Peña Cantero and Vervoort 2003).

Staurotheca dichotoma Allman, 1888

(Fig. 4.9b)

Material examined. *ANT XV/3*: **48-276**, several stems, c. 30 mm high, on gravel; *ANT XXI/2*: **PS65/121**, mass of stems, c. 120 mm high.

Ecology and distribution. Species reported at depths from 82 (Totton 1930) to 799 m (Peña Cantero et al. 1997c); present material collected between 268 and 417 m. Antarctic-Kerguélen distribution (Peña Cantero and Vervoort 2003).

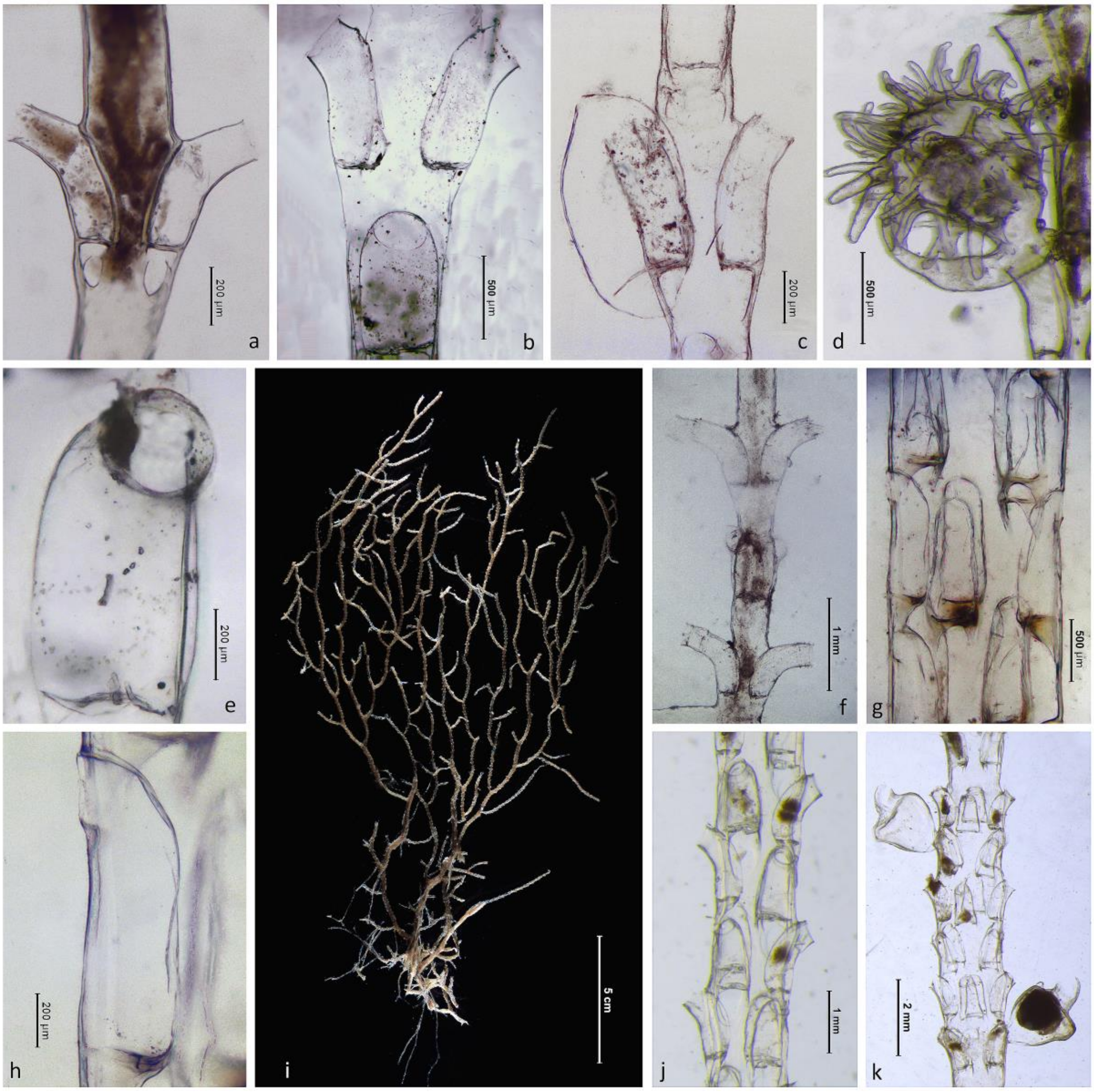

Figure 4.9 **a** *Staurotheca antarctica*: stem showing hydrothecal arrangement. **b** *S. dichotoma*: stem showing hydrothecal arrangement. **c-d** *S. frigida*: **c** stem with male gonothecae; **d** stem with female gonotheca. **e** *S. glomulosa*: hydrotheca. **f** *S. nonscripta*: stem showing hydrothecal arrangement. **g-h** *S. pachyclada*: **g** stem showing hydrothecal arrangement; **h** hydrotheca. **i-j** *St. vanhoeffeni*: **i** colony; **j** stem showing hydrothecal arrangement. **k** *S. polarsterni*: stem showing hydrothecal arrangement and female gonothecae

Staurotheca frigida Peña Cantero, Svoboda & Vervoort, 1997

(Fig. 4.9c-d)

Material examined. *ANT XV/3*: **48-50**, mass of stems, c. 40 mm high, with male gonothecae; **48-63**, mass of stems, c. 25 mm high, with male gonothecae; **48-77**, mass of stems, c. 20 mm high, with female gonothecae; **48-189**, mass of stems, c. 25 mm high, with male gonothecae; **48-194**, mass of stems, c. 30 mm high, with male gonothecae; **48-220**, mass of stems, c. 30 mm high, with female gonothecae; **48-222**, mass of stems, c. 40 mm high, with male gonothecae; *ANT XXI/2*: **PS65/121**, mass of stems, c. 35 mm high, with female gonothecae; **PS65/166**, mass of stems, c. 25 mm high, with male gonothecae; **PS65/248**, mass of stems, c. 40 mm high, with female gonothecae; **PS65/274**, mass of stems, c. 40 mm high, with male gonothecae.

Ecology and distribution. Species known from depths between 86 (Peña Cantero and García Carrascosa 1995) and 647 m (Soto Àngel and Peña Cantero 2015); present material collected from 234 to 360 m. Antarctic-Kerguélen species (Peña Cantero and Vervoort 2003).

Staurotheca glomulosa Peña Cantero, Svoboda & Vervoort, 1997

(Fig. 4.9e)

Material examined. *ANT XV/3*: **48-70**, mass of stems, c. 80 mm high; **48-77**, mass of stems, c. 75 mm high; **48-150**, mass of stems, c. 60 mm high, on gravel, with female gonothecae; **48-189**, mass of stems, c. 35 mm high, with female gonothecae; **48-220**, mass of stems, c. 65 mm high, on gravel, with female gonothecae; *ANT XVII/3*: **111-19**, two colonies, c. 30 and 60 mm high, with male and female gonothecae respectively; *ANT XXI/2*: **PS65/39**, mass of stems, c. 80 mm high, with male gonothecae; **PS65/245**, some stems, up to 40 mm high; **PS65/253**, some stems, up to 20 mm high; **PS65/274**, one colony, c.18 mm high, on bryozoan; **PS65/276**, few stems, c. 20 mm high, with female gonothecae.

Ecology and distribution. Species collected at depths between 55 (Peña Cantero and Vervoort 2003) and 1157 (Peña Cantero 2014a); present material from 112 to 758 m. Species with circum-Antarctic distribution (Peña Cantero and Vervoort 2003).

Staurotheca nonscripta Peña Cantero, Svoboda & Vervoort, 1997

(Fig. 4.9f)

Material examined. *ANT XV/3*: **48-58**, few stems, c. 15 mm high; **48-77**, some stems, up to 30 mm high; *ANT XXI/2*: **PS65/166**, some stems, up to 35 mm high; **PS65/248**, mass of stems, c. 140 mm high, with male gonothecae; **PS65/265**, some stems, up to 40 mm high; **PS65/274**, some stems, up to 45 mm high; **PS65/280**, some stems, up to 40 mm high; **PS65/292** mass of stems, c. 75 mm high, with male gonothecae.

Ecology and distribution. Species reported at depths between 15 (Peña Cantero and Vervoort 2003) and 728 m (Peña Cantero 2014a); material examined collected from 191 to 598 m. Antarctic-Patagonian species (Peña Cantero and Vervoort 2003).

Staurotheca pachyclada (Jäderholm, 1904)

(Fig. 4.9g-h)

Material examined. *ANT XV/3*: **48-77**, one colony, c. 50 mm high, with female gonothecae; **48-154**, one colony, c. 45 mm high; **48-220**, one colony, c. 25 mm high, with female gonothecae; **48-222**, one colony, c. 25 mm high; *ANT XXI/2*: **PS65/237**, several stems, c. 130 mm high; **PS65/265**, several stems, c. 125 mm high, on gravel, with female gonothecae; **PS65/336**, one colony, c. 85 mm high.

Ecology and distribution. Previously found at depths from 42 (Stepanjants 1979) to 1405 m (Peña Cantero and Vervoort 2003); present material at 267-583 m. Species with a circum-Antarctic distribution (Peña Cantero and Vervoort 2003).

Staurotheca polarsterni Peña Cantero, Svoboda & Vervoort, 1997

(Fig. 4.9k)

Material examined. *ANT XV/3*: **48-63**, one colony, c. 40 mm high; **48-70**, one colony, c. 90 mm high; **48-72**, several stems, c. 130 mm high; **48-77**, one colony, c. 40 mm high; **48-82**, one colony, c. 75 mm high, on stone; **48-97**, several stems, up to 110 mm high; **48-150**, several stems, up to 120 mm high, on gravel, with male gonothecae; **48-154**, several stems, up to 140 mm high, with female gonothecae; **48-197**, several stems, up to 100 mm high; *ANT XXI/2*: **PS65/248**, several stems, up to 80 mm high; **PS65/253**, one colony, c. 75 mm high; **PS65/265**, one colony, c. 130 mm high, with female gonothecae; **PS65/274**, one colony, c. 85 mm high.

Ecology and distribution. Previously collected at depths between 181 and 1030 m (Peña Cantero et al. 1997c); present material from 230 to 758 m. Circum-Antarctic species (Peña Cantero et al. 1997c).

Staurotheca vanhoeffeni (Peña Cantero & García Carrascosa, 1994)

(Fig. 4.9i-j)

Material examined. *ANT XV/3*: **48-220**, one colony, c. 65 mm high, on gravel; *ANT XXI/2*: **PS65/248**, one colony, c. 120 mm high; **PS65/259**, one colony, c. 100 mm high, on gravel, with female gonothecae; **PS65/265**, one colony, c. 230 mm high; **PS65/276**, one colony, c. 110 mm high, on stone, with female gonothecae; **PS65/278**, one colony, c. 70 mm high.

Ecology and distribution. Species collected at depths from 92 (Peña Cantero 2008) to 527 m (Peña Cantero 2014a); present material at depths between 119 and 333 m. Circum-Antarctic distribution (Peña Cantero and García Carrascosa 1995).

Symplectoscyphidae Maronna, Miranda, Peña Cantero, Barbeitos & Marques, 2016

Antarctoscyphus Peña Cantero, García Carrascosa & Vervoort, 1997

Antarctoscyphus asymmetricus Peña Cantero, García Carrascosa & Vervoort, 1997

(Fig. 4.10a)

Material examined. *ANT XV/3*: **48-72**, one colony, c. 65 mm high, with developing gonothecae; *ANT XXI/2*: **PS65/121**, one colony, c. 50 mm high; **PS65/237**, one colony, 11 mm high.

Ecology and distribution. Previously reported at depths from 70 to 429 m (Peña Cantero 2008); material examined comes from 230 to 274 m. West-Antarctic species, only known from the Scotia Arc (Peña Cantero 2006 and references therein); subsequently, present contribution reports the species from the Weddell Sea as well as from High Antarctica for the first time.

Antarctoscyphus elongatus (Jäderholm, 1904)

(Fig. 4.10b-d)

Material examined. *ANT XV/3*: **48-44**, one colony, c. 50 mm high; **48-63**, one colony, c. 70 mm high; **48-72**, one colony, c. 15 mm high; **48-77**, one colony, c. 75 mm high; *ANT XVII/3*: **111-18**, one colony, c. 35 mm high, on *O. stepanjantsae*; *ANT XXI/2*: **PS65/132**, one colony, c. 85 mm high; **PS65/148**, one colony, c. 55 mm high; **PS65/166**, one colony, c. 65 mm high; **PS65/174**, one colony, c. 105 mm high; **PS65/175**, some stems, c. 60, 75 and 80 mm high; **PS65/237**, one colony, c. 95 mm high, with developing gonothecae; **PS65/278**, one colony, c. 65 mm high; **PS65/279**, one colony, c. 100 mm high; **PS65/280**, one colony, c. 10 mm high; **PS65/281**, one colony, c. 15 mm high.

Ecology and distribution. Species reported at depths between 10 (Naumov and Stepanjants 1972) and 1958 m (Peña Cantero 2012); present material collected from 82 to 360 m. Antarctic-Kerguélen species (Peña Cantero 2012).

Antarctoscyphus grandis (Blanco, 1977)

(Fig. 4.10e-g)

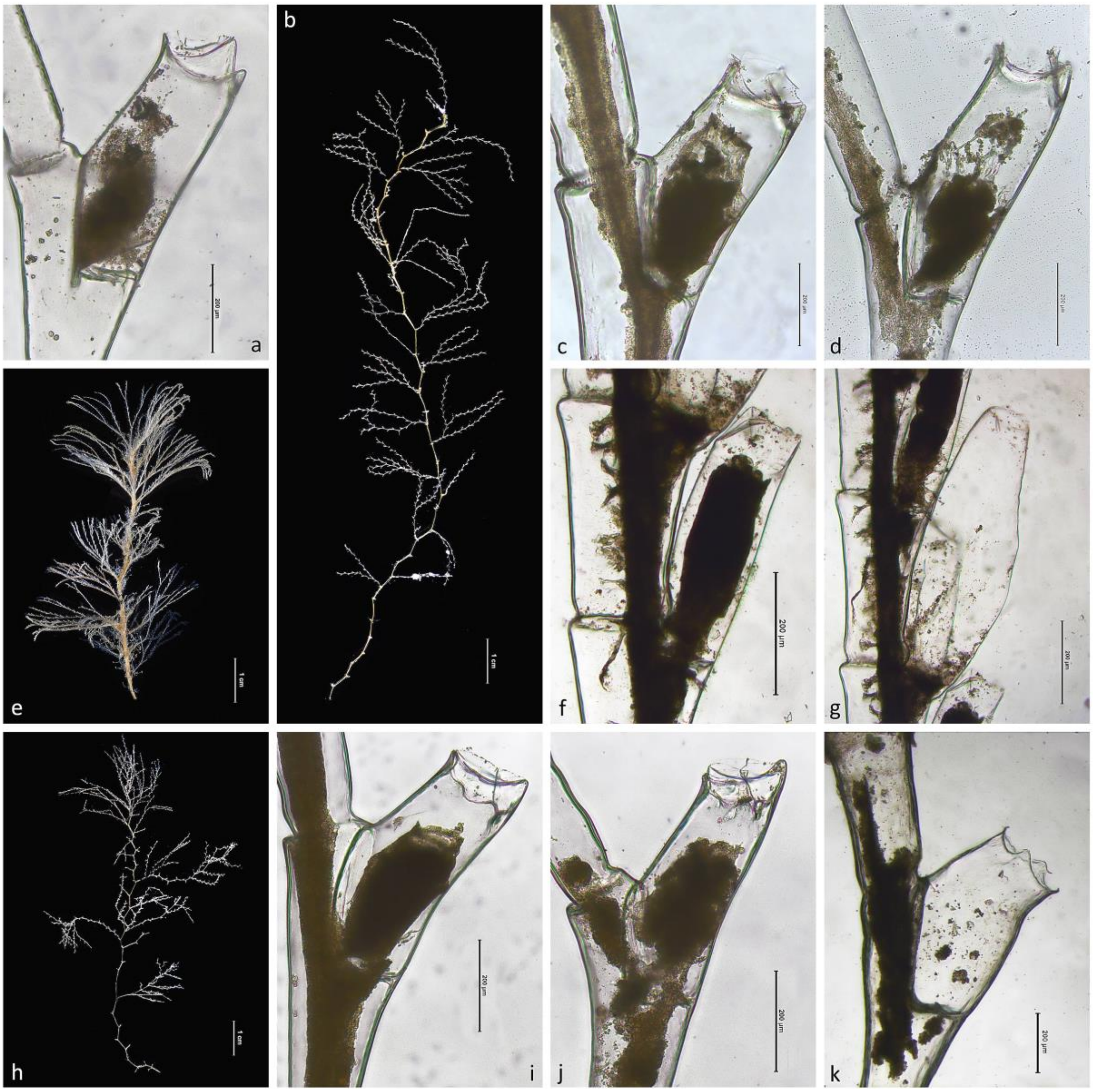

Figure 4.10 a *Antarctoscyphus asymmetricus*: hydrotheca. **b-d** *A. elongatus*: **b** colony; **c-d** hydrothecae. **e-g** *A. grandis*: **e** colony; **f** hydrotheca; **g** gonotheca. **h-j** *A. spiralis*: **h** colony; **i-j** hydrothecae. **k** *Sertularella* sp.: hydrotheca

Material examined. *ANT XV/3*: **48-31**, one colony, c. 50 mm high, with developing gonothecae; *ANT XVII/3*: **111-5**, one colony, c. 45 mm high; **111-9**, one colony, c. 60 mm high, with gonothecae; *ANT XXI/2*: **PS65/121**, one colony, c. 40 mm high, with gonothecae; **PS65/248**, one colony, c. 35 mm high.

Ecology and distribution. Previously reported at depths from 15 m (Naumov and Stepanjants 1972) to 380 m (Peña Cantero et al. 1999); present material was collected between 62 and 287 m. Circum-Antarctic distribution (Peña Cantero et al. 1997a).

Antarctoscyphus spiralis (Hickson & Gravely, 1907)

(Fig. 4.10h-j)

Material examined. *ANT XV/3*: **48-77**, one colony, c. 45 mm high; **48-274**, one colony, c. 75 mm high; **48-276**, one colony, c. 25 mm high; **48-297**, one colony, c. 20 mm high; *ANT XXI/2*: **PS65/121**, one colony, c. 80 mm high; **PS65/132**, one colony, c. 65 mm high; **PS65/166**, one colony, c. 10 mm high, on *S.*

nonscripta; **PS65/253**, three stems, c. 60, 70, 75 mm high; **PS65/265**, one colony, c. 65 mm high; one colony, c. 20 mm high, on *S. polarsterni*; **PS65/274**, one colony, c. 75 mm high; **PS65/278**, one colony, c. 30 mm high.

Ecology and distribution. Previously reported at depths from 6 (Naumov and Stepanjants 1972) to 1958 m (Peña Cantero 2010); our material comes from depths between 119 and 417 m. Species with a circum-Antarctic distribution (Stepanjants 1979).

Symplectoscyphus Marktanner-Turneretscher, 1890

Symplectoscyphus anae Peña Cantero, Svoboda & Vervoort, 2002

(Fig. 4.11a, 4.12a)

Material examined. *ANT XV/3*: **48-27**, several stems, up to 30 mm high, on dead octocoral; **48-77**, several stems, up to 30 mm high, on octocoral, with gonothecae; several stems, up to 40 mm high, with gonothecae; one colony, up to 12 mm high, on *A. frigida*; **48-197**, one colony, up to 10 mm high, on *S. polarsterni*; **48-220**, several stems, c. 40 mm high, with gonothecae; *ANT XVII/3*: **111-18**, several stems, up to 30 mm high, on an undetermined hydroid hydrorhiza, with gonothecae; *ANT XXI/2*: **PS65/174**, one colony, up to 14 mm high, on *A. elongatus*; **PS65/237**, one colony, up to 10 mm high, on *S. lobata*; **PS65/265**, several stems, up to 35 mm high, on *S. polarsterni*; **PS65/276**, few stems, up to 15 mm high; **PS65/278**, few stems, up to 15 mm high; one colony, up to 8 mm high, on *H. secundum*; one colony, up to 18 mm high, on *B. subrufa;* **PS65/280**, few stems, up to 8 mm high; **PS65/281**, several, up to 35 mm high.

Ecology and distribution. Previously reported at depths between 20 (Naumov and Stepanjants 1972) and 640 m (Peña Cantero et al. 2002); material examined collected from 82 to 416 m. Species with circum-Antarctic distribution (Peña Cantero et al. 2002).

Symplectoscyphus cumberlandicus (Jädherholm, 1905)

(Fig. 4.11b, 4.12b)

Material examined. *ANT XVII/3*: **111-7**, several stems, up to 25 mm high; one colony, up to 35 mm high, on *O. stepanjantsae*, with gonothecae; *ANT XXI/2*: **PS65/281**, some stems, up to 20 mm high, on *O. stepanjantsae*; several stems, up to 60 mm high, on gravel, with developing gonothecae.

Ecology and distribution. Reported at depths from 8 (Naumov and Stepanjants 1972) to 540 m (Peña Cantero 2012); present material collected at 67-82 m. Species widely distributed in Antarctic waters, with circum-Antarctic distribution (Peña Cantero et al. 2002), but previously not documented from the Weddell Sea.

Symplectoscyphus curvatus (Jäderholm, 1917)

(Fig. 4.11c, 4.12c)

Material examined. *ANT XV/3*: **48-44**, several stems, up to 30 mm high, with gonothecae; **48-77**, one colony, up to 5 mm high, on *H. jaederholmi*; **48-168**, few stems, up to 66 mm high, with gonothecae; **48-222**; several stems, up to 25 mm high, with gonothecae; *ANT XXI/2*: **PS65/121**, few stems, up to 30 mm high, on *S. nana;* **PS65/237**, few stems, up to 9 mm high; **PS65/248**, one colony, up to 45 mm high, on octocoral, with developing gonothecae; **PS65/281**, few stems, up to 15 mm high.

Ecology and distribution. Previously known from 49 (Peña Cantero 2008) to 2043 m (Peña Cantero 2012); present material

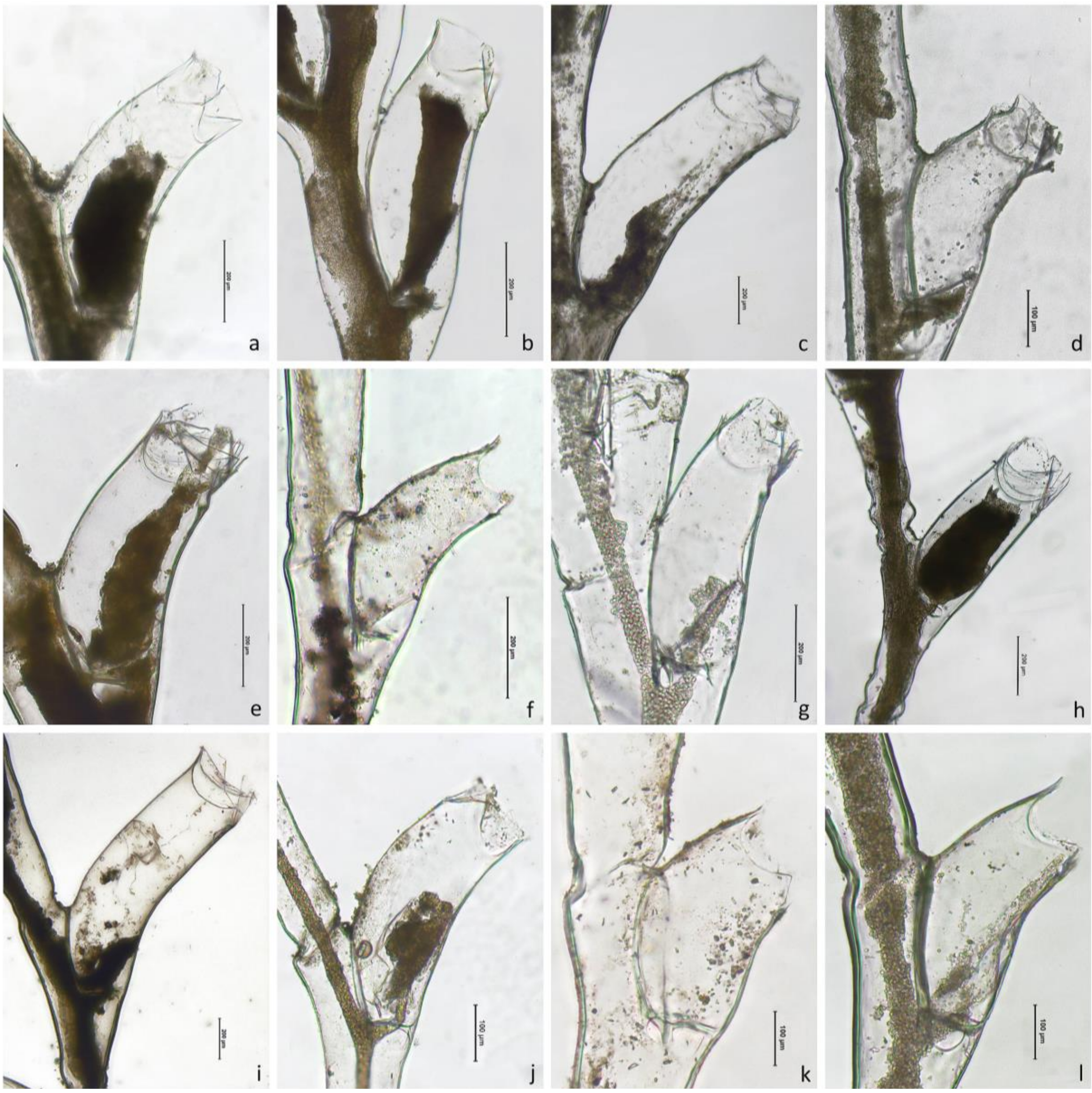

Figure 4.11 **a** *Symplectoscyphus anae*: hydrotheca. **b** *S. cumberlandicus*: hydrotheca. **c** *S. curvatus*: hydrotheca. **d** *S. exochus*: hydrotheca. **e** *S. frigidus*: hydrotheca. **f** *S. glacialis*: hydrotheca. **g** *S. liouvillei*: hydrotheca. **h** *S. naumovi*: hydrotheca. **i** *S. paulensis*: hydrotheca. **j** *S. plectilis*: hydrotheca. **k** *S. vanhoeffeni*: hydrotheca. **l** *S. weddelli*: hydrotheca

found between 82 and 360 m. Circum-Antarctic species (Stepanjants 1979).

Symplectoscyphus exochus Blanco, 1982

(Fig. 4.11d, 4.12d)

Material examined. *ANT XV/3*: **48-4**, few stems, c. 9 mm high; **48-44**, few stems, up to 14 mm high, on bryozoan; mass of stems, c. 40 mm high, with gonothecae; **48-58**, mass of stems, c. 40 mm high, with developing gonothecae; **48-72**, some stems, up to 10 mm high; **48-168**, some stems, up to 25 mm high; one colony, up to 10 mm high, on *S. liouvillei*; **48-189**, some stems, up to 15 mm high; **48-220**, several stems, up to 30 mm high; mass of stems, c. 40 mm high, with gonothecae; one colony, up to 15 mm high, on *S. nana*; *ANT XVII/3*: **111-6**, mass of stems, c. 30 mm high; **111-9**, some stems, up to 10 mm high, on *T. longstaffi*; some stems, up to 20 mm high, with developing gonothecae; *ANT XXI/2*: **PS65/39**, mass of stems, c. 65 mm high, with gonothecae; some stems, up to 15 mm high, on *S. nana*, with gonothecae; **PS65/121**, several stems, up to 35 mm high; few stems, up to 11 mm high, on *S. dichotoma;* **PS65/132**, several stems, up to 20 mm high; few stems, up to 15 mm high, on *B. subrufa*; **PS65/166**, mass of stems, c. 40 mm high, with developing gonothecae; **PS65/174**, several stems, up to 30 mm high, with gonothecae; some stems, up to 30 mm high, on *B. subrufa,* with developing gonothecae; **PS65/237**, some stems, up to 25 mm high, on *S. nana* and *S. lobata*; mass of stems, c. 40 mm high, with gonothecae; **PS65/248**, few stems, up to 6 mm high; **PS65/253**, mass stems, up to 60 mm high, with gonothecae; **PS65/265**, mass stems, up to 30 mm high; **PS65/276**, mass stems, up to 40 mm high, with developing gonothecae; **PS65/278**, few stems, up to 12 mm high; **PS65/279**, mass of stems, c. 30 mm high, with developing gonothecae.

Ecology and distribution. Species reported at depths between 15 (Vervoort 1972b) and 1958 m (Peña Cantero 2012); present material collected from 62 to 352 m. Species with circum-Antarctic distribution (Peña Cantero 2014a).

Symplectoscyphus frigidus Peña Cantero, Svoboda & Vervoort, 2002

(Fig. 4.11e)

Material examined. *ANT XXI/2*: **PS65/166**, few stems, up to 15 mm high.

Ecology and distribution. Previously documented at depths from 86 (Broch 1948) to 402 m (Peña Cantero et al. 2002); present material collected between 253 and 338 m. West-Antarctic distribution (Peña Cantero et al. 2002).

Symplectoscyphus glacialis (Jäderholm, 1904)

(Fig. 4.11f, 4.12e)

Material examined. *ANT XV/3*: **48-27**, few stems, up to 15 mm high; **48-44**, few stems, up to 6 mm high; some stems, up to 10 mm high, on polychaete tube; **48-50**, one colony, c. 50 mm high; **48-58**, some stems, up to 20 mm high, on *S. frigida*; **48-63**, one colony, c. 30 mm high; **48-70**, few stems, up to 6 mm high, on *S. polarsterni*; **48-77**, several stems, up to 20 mm high; some stems, up to 15 mm high, on octocoral; some stems, up to 10 mm high, on *H. jaederholmi*; **48-82**, several stems, up to 30 mm high; few stems, up to 10 mm high, on *S. polarsterni*; **48-97**, few stems, up to 8 mm high, on *S. polarsterni*; **48-154**, some stems, up to 17 mm high, on *S. polarsterni*; **48-189**, some stems, up to 16 mm high; **48-194**, few stems, up to 25 mm high, on *S. nana*; **48-197**, few stems, up to 3 mm high, on *A. frigida*; **48-220**, some stems, up to 10 mm high, on *S. glomulosa*; some stems, up to 20 mm high, on *S. nana*; **48-222**, few stems, up to 9 mm high; some stems, up to 10 mm high, on *S. nana*; *ANT XXI/2*: **PS65/39**, some stems, up to 15 mm high, on *S. lobata*; few stems, up to 8 mm high, on *S. lobata*; some stems, up to 30 mm high, on *S. glomulosa*, with gonothecae; few stems, up to 5 mm high, on *S. exochus*; **PS65/121**, few stems, up to 2 mm high, on *S. lobata*; some stems, up to 20 mm high; **PS65/174**, some stems, up to 17 mm high, on *O. erratum*; few stems, up to 3 mm high, on *A. elongatus*; few stems, up to 2 mm high, on *S. weddelli*; **PS65/175**, few stems, up to 2 mm high, on *B. subrufa*; **PS65/237**, several stems, up to 65 mm high; **PS65/248**, some stems, up to 40 mm high, on dead octocoral; some stems, up to 15 mm high, on *H. incertus*; **PS65/253**, few stems, up to 4 mm high, on *S. polarsterni*; **PS65/265**, few stems, up to 8 mm high, on *St. vanhoeffeni*; some stems, up to 35 mm high; some stems, up to 20 mm high, on *S. polarsterni*; **PS65/274**, mass of stems, c. 40 mm high, with gonothecae; few stems, up to 10 mm high, on *S. polarsterni*; few stems, up to 8 mm high, on *S. nonscripta*; **PS65/276**, few stems, up to 8 mm high, on *S. lobata*; few stems, up to 2 mm high, on *Sy. vanhoeffeni*; few stems, up to 10 mm high; **PS65/278**, mass of stems, c. 20 mm high; few stems, up to 5 mm high, on *A. elongatus*; few stems, up to 10 mm high, on *H. secundum*; **PS65/279**, some stems, up to 13 mm high, on *B. subrufa*; **PS65/280**, mass of stems, c. 30 mm high, with developing gonothecae; few stems, up to 7 mm high, on *C. microrhiza*; **PS65/292**, some stems, c. 15 mm high; **PS65/336**, some stems, c. 20 mm high, on bryozoan.

Ecology and distribution. Previously collected from 5 (Naumov and Stepanjants 1972) to 1157 m (Peña Cantero 2014a); material examined collected between 120 and 659 m. Pan-Antarctic distribution (Soto Àngel and Peña Cantero 2015).

Symplectoscyphus liouvillei **(Billard, 1914)**

(Fig. 4.11g, 4.12f-g)

Material examined. *ANT XV/3*: **48-168**, one colony, c. 105 mm high, with gonothecae; **48-197**, one colony, c. 20 mm high; **48-220**, one colony, c. 45 mm high, with gonothecae; *ANT XXI/2*: **PS65/174**, one colony, c. 280 mm high, on gravel, with developing gonothecae.

Ecology and distribution. Previously reported at depths between 65 (Peña Cantero 2008) and 443 m (Peña Cantero 2006); present material collected from 228 to 416 m. West Antarctic-Patagonian distribution (Peña Cantero et al. 2002).

Symplectoscyphus naumovi **Blanco, 1969**

(Fig. 4.11h, 4.12h)

Material examined. *ANT XV/3*: **48-31**, few stems, up to 9 mm high, on *O. stepanjantsae*; some stems, up to 17 mm high, on *Tubularia* sp.2, with gonothecae; **48-44**, some stems, up to 18 mm high, on *S. lobata*, with gonothecae; some stems, up to 40 mm high, with gonothecae; **48-194**, one colony, c. 10 mm high; some stems, up to 40 mm high, on *Oswaldella tottoni* Peña Cantero & Vervoort, 1996, with gonothecae; **48-220**, one colony, c. 13 mm high; some stems, up to 15 mm high, on *S. nana*; **48-276**, some stems, up to 10 mm high, on *S. nana*; *ANT XVII/3*: **111-5**, some stems, up to 10 mm high, on *O. stepanjantsae*, with gonothecae; **111-9**, some stems, up to 13 mm high, on *S. lobata*; **111-19**, some stems, up to 15 mm high, on *S. unifurcata*; some stems, up to 2 mm high, on *Tubularia* sp.1; *ANT XXI/2*: **PS65/39**, some stems, up to 20 mm high, on *S. nana* and *S. lobata*, with gonothecae; **PS65/121**, one colony, c. 10 mm high, with developing gonothecae; **PS65/175**, some stems, up to 12 mm high, on *O. erratum*; some stems, up to 10 mm high, on *Eudendrium* sp.1; **PS65/237**, some stems, up to 20 mm high, on *S. unifurcata*; **PS65/276**, some stems, up to 10 mm high, on *S. lobata*; **PS65/281**, some stems, up to 13 mm high, on *S. nana*.

Ecology and distribution. Species known from the tidal level (Blanco 1984) to 1379 m (Peña Cantero and Ramil 2006); present material collected between 62 and 417 m. Circum-Antarctic distribution (Peña Cantero and Ramil 2006).

Symplectoscyphus paulensis **Stechow, 1923**

(Fig. 4.11i)

Material examined. *ANT XXI/2*: **PS65/259**, few stems, c. 10 mm high; **PS65/276**, few stems, c. 15 mm high.

Ecology and distribution. Species reported in Antarctic waters in only one occasion at a depth of 603 m in the Bellingshausen Sea, although it is widely distributed in the Southern Hemisphere (Peña Cantero 2012 and literature therein); material examined

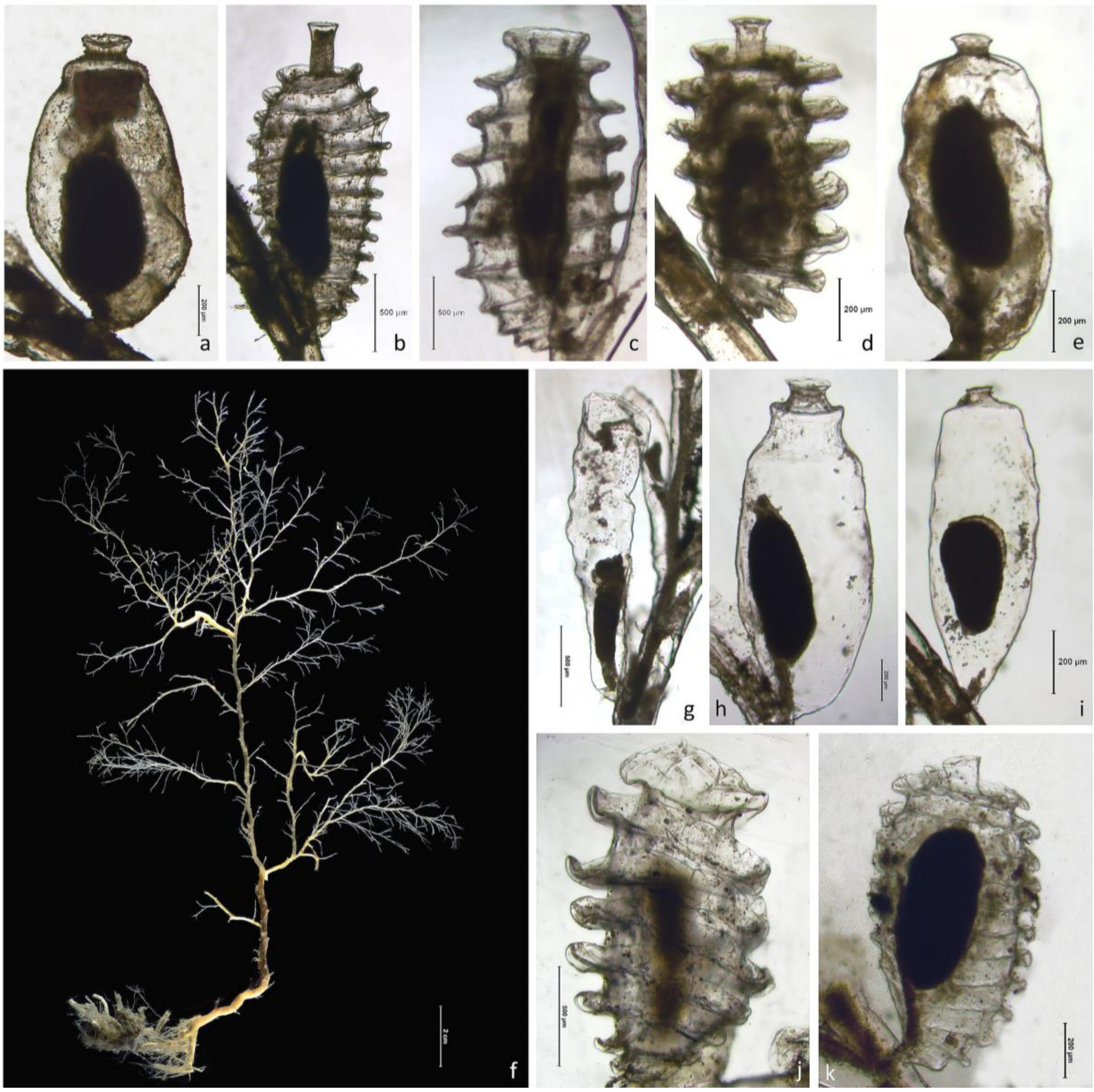

Figure 4.12 **a** *Symplectoscyphus anae*: gonotheca. **b** *S. cumberlandicus*: gonotheca. **c** *S. curvatus*: gonotheca. **d** *S. exochus*: gonotheca. **e** *Sy. glacialis*: gonotheca. **f-g** *S. liouvillei*: **f** colony; **g** gonotheca. **h** *S. naumovi*: gonotheca. **i** *S. plectilis*: gonotheca. **j** *Sy. vanhoeffeni*: gonotheca. **k** *S. weddelli*: gonotheca

was collected at depths from 268 to 333 m. This finding constitutes the second report of the species in Antarctic waters and the first evidence for the Weddell Sea.

Symplectoscyphus plectilis (Hickson & Gravely, 1907)

(Fig. 4.11j, 4.12i)

Material examined. *ANT XV/3*: **48-4**, some stems, up to 12 mm high; **48-189**, some stems, up to 20 mm high; **48-220**, several stems, up to 25 mm high, on *S. exochus*, with gonothecae; **48-223**, some stems, up to 12 mm high, on *S. nana*; *ANT XVII/3*: **111-6**, some stems, up to 6 mm high, on *O. stepanjantsae*; *ANT XXI/2*: **PS65/39**, mass of stems, c. 30 mm high, with gonothecae; some stems, up to 20 mm high, on *S. lobata*, with gonothecae; some stems, up to 15 mm high, on *S. lobata*; several stems, up to 60 mm high, on *S. nana*, *S. naumovi* and *C. hicksoni*, with gonothecae; **PS65/121**, some stems, up to 35 mm high, on *S. nana*; mass of stems, c. 25 mm high; **PS65/245**, mass of stems, c. 20 mm high, with developing gonothecae; **PS65/248**, mass of stems, c. 50 mm high; **PS65/253**, mass of stems, c. 30

mm high; **PS65/274**, few stems, up to 10 mm high, on *S. glomulosa* and bryozoan; **PS65/276**, mass of stems, c. 30 mm high, with gonothecae; **PS65/281**, one stem, c. 3 mm high, on gravel.

Ecology and distribution. Species collected from 7 (Vervoort 1972b) to 1958 m (Peña Cantero 2012); present material between 68 and 337 m. Circum-Antarctic distribution (Stepanjants 1979).

Symplectoscyphus vanhoeffeni Totton, 1930

(Fig. 4.11k, 4.12j)

Material examined. *ANT XV/3*: **48-5**, one colony, c. 18 mm high, on sponge; **48-222**, one colony, c. 16 mm high, with gonothecae; *ANT XXI/2*: **PS65/276**, one colony, c. 25 mm high.

Ecology and distribution. Previously reported from depths between 6 (Naumov and Stepanjants 1972) and 964 m (Peña Cantero 2014a); material examined collected at 177-277 m. Species with circum-Antarctic distribution (Peña Cantero and García Carrascosa 1995).

Symplectoscyphus weddelli Peña Cantero, Svoboda & Vervoort, 2002

(Fig. 4.11l, 4.12k)

Material examined. *ANT XV/3*: **48-168**, mass of stems, c. 40 mm high, with developing gonothecae; **48-222**, mass of stems, c. 50 mm high, with gonothecae; **48-276**, few stems, up to 13 mm high, on *S. nana*; *ANT XVII/3*: **111-7**, some stems, up to 11 mm high, with gonothecae; **111-9**, some stems, up to 13 mm high, with gonothecae; **111-18**, some stems, up to 10 mm high, on *O. stepanjantsae*; **111-19**, some stems, up to 20 mm high, with gonothecae; few stems, up to 12 mm high, on *S. unifurcata*; *ANT XXI/2*: **PS65/39**, some stems, up to 10 mm high; **PS65/121** few stems, up to 10 mm high, on *O. tottoni*; **PS65/174**, some stems, up to 35 mm high, with gonothecae; **PS65/237**, some stems, up to 10 mm high, on sponge; some stems, up to 40 mm high, on *S. nana*; **PS65/276**, mass of stems, c. 50 mm high, with developing gonothecae; **PS65/278**, some stems, up to 15 mm high; **PS65/281**, some stems, up to 15 mm high, on *O. stepanjantsae*.

Ecology and distribution. Species only known so far from the Weddell Sea, at depths from 119 to 390 m (Peña Cantero et al. 2002); present material, which constitutes the second report of the species, was collected from 62 to 417 m depth.

Zygophylacidae Quelch, 1885

Abietinella Levinsen, 1913

Abietinella operculata (Jäderholm, 1903)

(Fig. 4.6l-m)

Material examined. *ANT XV/3*: **48-197**, one colony, c. 45 mm high; **48-220**, one colony, c. 65 mm high; *ANT XXI/2*: **PS65/174**, one colony, c. 60 mm high, **PS65/175**, one colony, c. 130 mm high.

Ecology and distribution. Species reported at depths from 63 (Peña Cantero and García Carrascosa 1993) to 1500 m (Stepanjants 1979); present material from 236 to 416 m. Species with Antarctic-Patagonian distribution (Stepanjants 1979).

Haleciidae Hincks, 1868

Halecium Oken, 1815

Halecium cf. *antarcticum* Vanhöffen, 1910

(Fig. 4.13a)

Material examined. *ANT XV/3*: **48-150**, three stems, c. 70, 75 and 110 mm high; **48-237**, some stems, up to 25 mm high, on *S. nana*; **48-276**, two stems, 40 and 60 mm high.

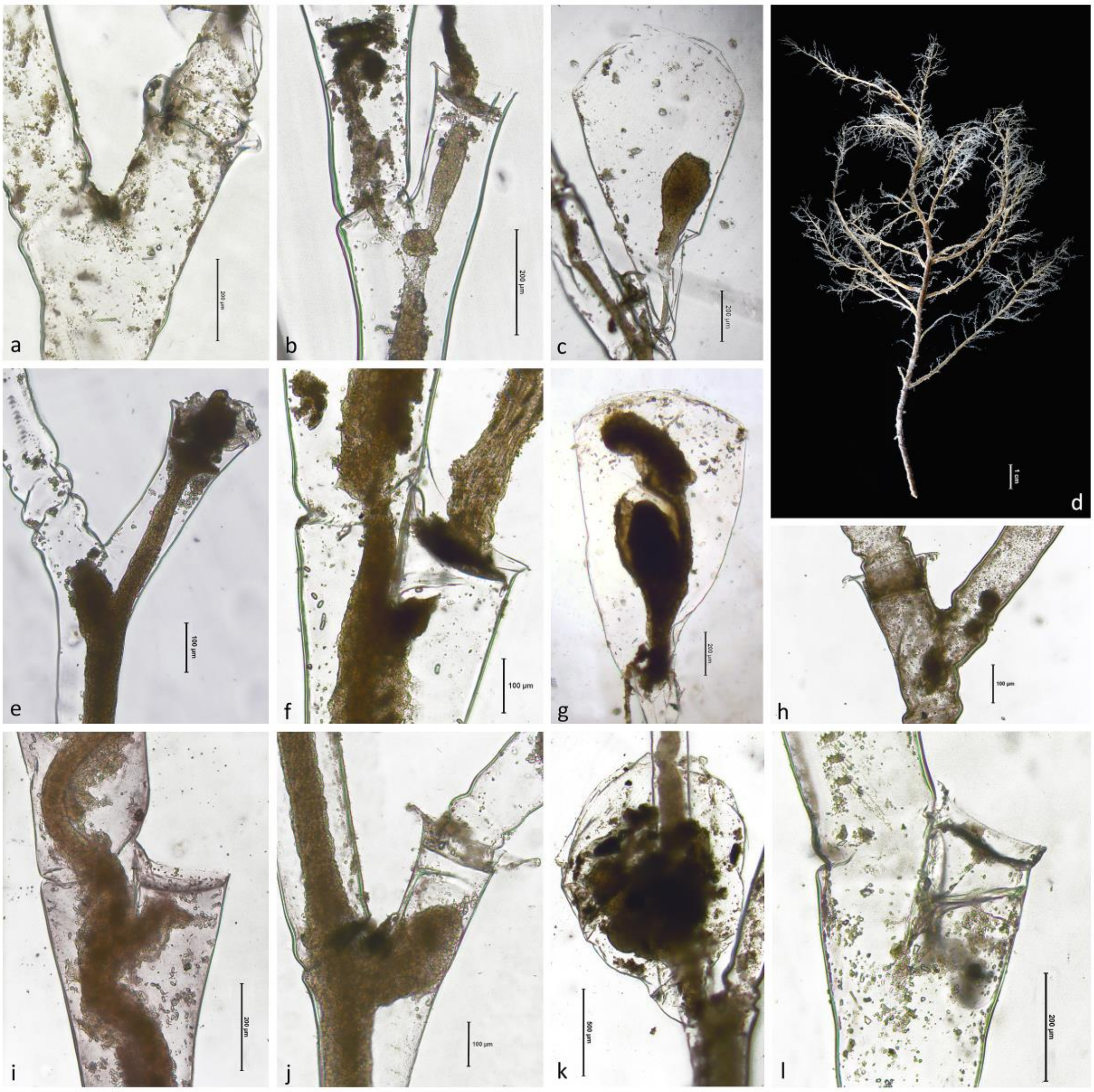

Figure 4.13 a *Halecium* cf. *antarcticum*: hydrophore. **b-d** *H. banzare*: **b** hydrophore; **c** male gonotheca; **d** colony. **e** *H. exaggeratum*: hydrophore. **f-g** *H. incertus*: **f** hydrophore; **g** gonotheca. **h** *H. interpolatum*: hydrophore. **i** *H. jaederholmi*: hydrophore. **j-k** *H. pseudodelicatulum*: **j** hydrophore; **k** female gonotheca. **i** *H. pseudoincertus*: hydrophore

Remarks. The great resemblance between *Halecium antarcticum* and *H. pseudodelicatulum* makes both species almost indistinguishable in the absence of gonothecae (see Peña Cantero 2014b). The material examined here has been tentatively assigned to *H. antarcticum* based on the disposition of the hydrophore, pointing more outwards than in *H. pseudodelicatulum* (Fig. 4.13a, j).

Ecology and distribution. Species reported from 45 (Watson 2008) to 1157 m (Peña Cantero 2014a); present material was collected between 254 and 758 m. Species reported exclusively from East Antarctica (Peña Cantero 2014b). Thus, if confirmed, present record will constitute the first evidence from the Weddell Sea as well as for West Antarctica, pointing out a circum-Antarctic distribution.

Halecium banzare Watson, 2008

(Fig. 4.13b-d)

Material examined. *ANT XV/3*: **48-44**, one colony, c. 230 mm high, with male gonothecae; **48-50**, one colony, c. 220 mm high, with male gonothecae; **48-70**, few stems, up to 5 mm high, on *B. subrufa*; **48-222**, one colony, c. 270 mm high, with gonothecae; *ANT XXI/2*: **PS65/276**, one colony, c. 18 mm high.

Ecology and distribution. Species known from depths between 200 (Broch 1948) and 708 m (Peña Cantero 2014a); material examined from 227 to 288 m. Species with circum-Antarctic distribution (Peña Cantero 2014b), reported here for the Weddell Sea for the first time.

Halecium exaggeratum Peña Cantero, Boero & Piraino, 2013

(Fig. 4.13e)

Material examined. *ANT XV/3*: **48-27**, few stems, up to 20 mm high, on *S. lobata*; **48-77**, few stems, up to 15 mm high, on sponge spicule.

Ecology and distribution. Species reported from 22 (Vervoort 1972b) to 350 m (Hartlaub 1904); present material at 191-360 m. Circum-Antarctic species (Peña Cantero et al. 2013). Present finding constitutes the first evidence for the Weddell Sea.

Halecium incertus Naumov & Stepanjants, 1962

(Fig. 4.13f-g, 4.14a)

Material examined. *ANT XXI/2*: **PS65/121**, one colony, c. 220 mm high, on gravel, with female gonothecae; **PS65/248**, one colony, c. 260 mm high, on stone, with female gonothecae.

Ecology and distribution. Reported at depths from 15 (Stepanjants 1979) to 693 m (Branch and Williams 1993); present material at 268-287 m. Species with Antarctic–Kerguélen distribution (Peña Cantero and Gili 2006). This new report constitutes the first evidence from both the Weddell Sea and West Antarctica.

Halecium interpolatum Ritchie, 1907

(Fig. 4.13h)

Material examined. *ANT XV/3*: **48-5**, few stems, up to 2 mm high, on sponge; **48-27**, few stems, up to 2 mm high, on *Sy. glacialis*; **48-31**, few stems, up to 5 mm high, on *O. stepanjantsae*; **48-33**, few stems, up to 10 mm high, on *O. stepanjantsae*; **48-36**, several stems, up to 25 mm high, on *O. stepanjantsae*, with male gonothecae; **48-77**, some stems, up to 15 mm high, on *S. polarsterni*; **48-150**, few stems, up to 3 mm high, on *E. scotti*; some stems, up to 10 mm high, on *S. polarsterni*; **48-220**, few stems, up to 6 mm high, on *S. naumovi*; several stems, up to 60 mm high, on *S. nana*, with female gonothecae; some stems, up to 6 mm high, on *S. exochus*, with male gonothecae; some stems, up to 20 mm high, on *S. anae*; some stems, up to 10 mm high, on *S. anae*; **48-222**, few stems, up to 2 mm high, on *S. nana*; **48-276**, some stems, up to 10 mm high, on *S. nana*; *ANT XVII/3*: **111-5**, several stems, up to 30 mm high, on *O. stepanjantsae*, with female gonothecae; some stems, up to 10 mm high, on polychaete tube; **111-7**, several stems, up to 20 mm high, on *O. stepanjantsae*; **111-9**, few stems, up to 3 mm high, on polychaete tube; several stems, up to 40 mm high, on *T. longstaffi*, with gonothecae; few stems, up to 15 mm high, on *H. arboreum*, with gonothecae; some stems, up to 15 mm high, on *O. stepanjantsae*; **111-18**, several stems, up to 20 mm high, on *O. stepanjantsae*, with gonothecae; some stems, up to 10 mm high, on *S. nana*; one colony, c. 15 mm high, with gonothecae; some stems, up to 15 mm high, on *S. nana*; **111-19**, one colony, c. 20 mm high, with gonothecae; some stems, up to

20 mm high, on *S. weddelli*; few stems, up to 15 mm high, on *Tubularia* sp.1 *ANT XXI/2*: **PS65/39**, one colony, c. 30 mm high; few stems, up to 10 mm high, on *S. exochus*; several stems, up to 3 mm high, on *C. hicksoni*, *S. nana*, *S. plectilis*, with gonothecae; **PS65/121**, few stems, up to 3 mm high, on *S. lobata*; **PS65/248**, few stems, up to 2 mm high, on *S. curvatus*; some stems, up to 10 mm high, on *S. plectilis*; **PS65/253**, some stems, up to 10 mm high, on *S. polarsterni*; **PS65/265**, some stems, up to 10 mm high, on *S. polarsterni*; some stems, up to 15 mm high, on *H. pseudodelicatulum*; **PS65/276**, one colony, c. 15 mm high; **PS65/278**, several stems, up to 20 mm high, on *O. stepanjantsae*; **PS65/281**, few stems, up to 3 mm high, on *O. stepanjantsae*; few stems, up to 3 mm high, on *S. cumberlandicus*.

Ecology and distribution. Reported from three (Stepanjants 1979) to 728 m (Peña Cantero 2014a); examined material from 62 to 758 m. Circum-Antarctic species (Peña Cantero 2014b), reported here in the Weddell Sea for the first time.

Halecium jaederholmi Vervoort, 1972

(Fig. 4.13i)

Material examined. *ANT XV/3*: **48-77**, one colony, c. 100 mm high; *ANT XVII/3*: **111-5**, one colony, c. 45 mm high; *ANT XXI/2*: **PS65/248**, one colony, c. 40 mm high, on bryozoan.

Ecology and distribution. Previously reported at depths between 24 (Vervoort 1972a) and 945 m (Peña Cantero 2014a); present material from 65 to 360 m. A probable Pan-Antarctic species (Peña Cantero 2014b).

Halecium pseudodelicatulum
Peña Cantero, 2014

(Fig. 4.13j-k)

Material examined. *ANT XV/3*: **48-77**, one colony, c. 70 mm high; **48-168**, one colony, c. 25 mm high, on dead octocoral; **48-194**, one colony, c. 35 mm high, with gonothecae; **48-222**, some stems, up to 7 mm high, on *S. nana*; *ANT XXI/2*: **PS65/237**, one colony, c. 20 mm high; **PS65/265**, one colony, c. 35 mm high, with female gonothecae; **PS65/274**, one colony, c. 80 mm high, on dead octocoral; **PS65/278**, one colony, c. 35 mm high.

Ecology and distribution. Previously collected at depths from 82 (Peña Cantero 2013) to 240 m (Peña Cantero and Vervoort 2009); present material from 119 to 360 m. Until now, valid records are restricted to West Antarctica (Peña Cantero 2014b); reported here from the Weddell Sea for the first time.

Halecium pseudoincertus
Peña Cantero, 2014

(Fig. 4.13l)

Material examined. *ANT XV/3*: **48-154**, one colony, c. 150 mm high.

Ecology and distribution. Reported at depths from 96 (Peña Cantero 2009) to 1019 m (Peña Cantero 2008); material examined at 569-583 m. Circum-Antarctic species (Peña Cantero 2014b) found in rare occasions; present finding constitutes a new addition for the Weddell Sea fauna.

Halecium secundum Jäderholm, 1904

(Fig. 4.14b-c)

Material examined. *ANT XV/3*: **48-50**, one colony, c. 70 mm high, with gonothecae; **48-58**, one colony, c. 65 mm high; *ANT XXI/2*: **PS65/278**, mass of stems, c. 140 mm high, with male gonothecae.

Remarks. The species had not been found with gonothecae since its original description (Jäderholm 1904), and only male ones are known. Our material is provided with male gonothecae: 1.3-1.5 mm high, 380 µm in maximum diameter; very delicate, easily collapsible; cylindrical, truncated distally; with terminal, circular aperture (Fig. 4.14c). Jäderholm (1904) mentioned a shallow distal furrow and a proximal sharp keel in the gonothecae. However, given the delicate consistence, we regard Jäderholm's observations as probable artefact occurred when mounting the microslides.

Peña Cantero (2014b) revised the holotype of *Halecium brevithecum* Watson, 2008, discussed the few differences between *H. secundum* and *H. brevithecum*, and noted that the latter was described from scarce, infertile material mounted in microslides, and that therefore cannot be completely characterized (Peña Cantero 2014b: 253). According to him, the hydrothecal adcauline wall of *H. brevithecum* is completely adnate to the internode in the holotype. In the original description, Watson (2008) aslo indicated that the adcauline hydrothecal wall is adnate to the internode. However, she also pointed out that the adcauline wall of the hydrophore becomes free just below the hydrotheca. This imply that the hydrothecae might also be free. In this sense, a figure provided by her (Watson 2008: Fig. 4c) apparently shows a free adcauline hydrothecal wall. It seems, therefore, that this character may vary between hydrothecae, as it has been documented for *H. secundum* (cf. Peña Cantero 2014b). Apart from the aforementioned, Peña Cantero (2014b) indicated that *H. brevithecum* can be distinguished from *H. secundum* by the distinctly longer first hydrothecate internode of the branches, the presence of reddish stems, and the perpendicular arrangement of the lower-order branches compared to previous ones. All these features have been clearly observed from the reproductive material of *H. secundum*. Being so, we consider *Halecium brevithecum* as a junior synonym of Jäderholm's species.

Ecology and distribution. Previously reported at depths between 40 (Peña Cantero et al. 2013) and 150 m (Jäderholm 1904); present material at 119-283 m. Circum-Antarctic species (Peña Cantero et al. 2013), with only two validated records and a third pending one (see Peña Cantero 2014b), present finding constitutes the first evidence from the Weddell Sea.

Halecium tubatum Watson, 2008
(Fig. 4.14d-g)

Material examined. *ANT XV/3*: **48-276**, several hydrothecae, on *S. nana*; *ANT XXI/2*: **PS65/278**, few hydrothecae, on *S. weddelli*; several polyps, on sponge; **PS65/280**, few hydrothecae, on undetermined anthoathecata.

Remarks. *Halecium tubatum* has been previously considered as a *species inquirenda* by Peña Cantero (2014b), pointing out that the species could correspond to incipient stems of other haleciids such as *H. interpolatum*. However, the analyses of the cnidome has contribute to a better characterization of the species (see below), proving to be different from other congenerics previously documented in Antarctic waters (cf. Peña Cantero 2014b). The species is considered here as valid, although mature specimens have not been found yet. We consider the two-three basal rings followed by wavy internode (Fig. 4.14e), the absence of diaphragm (Fig. 4.14f), the presence of desmocytes (Fig. 4.14f), and the greatly recurved hydrotheca (Fig. 4.14f-g), coupled with the size of the nematocysts, as unequivocal diagnostic characters of the species.

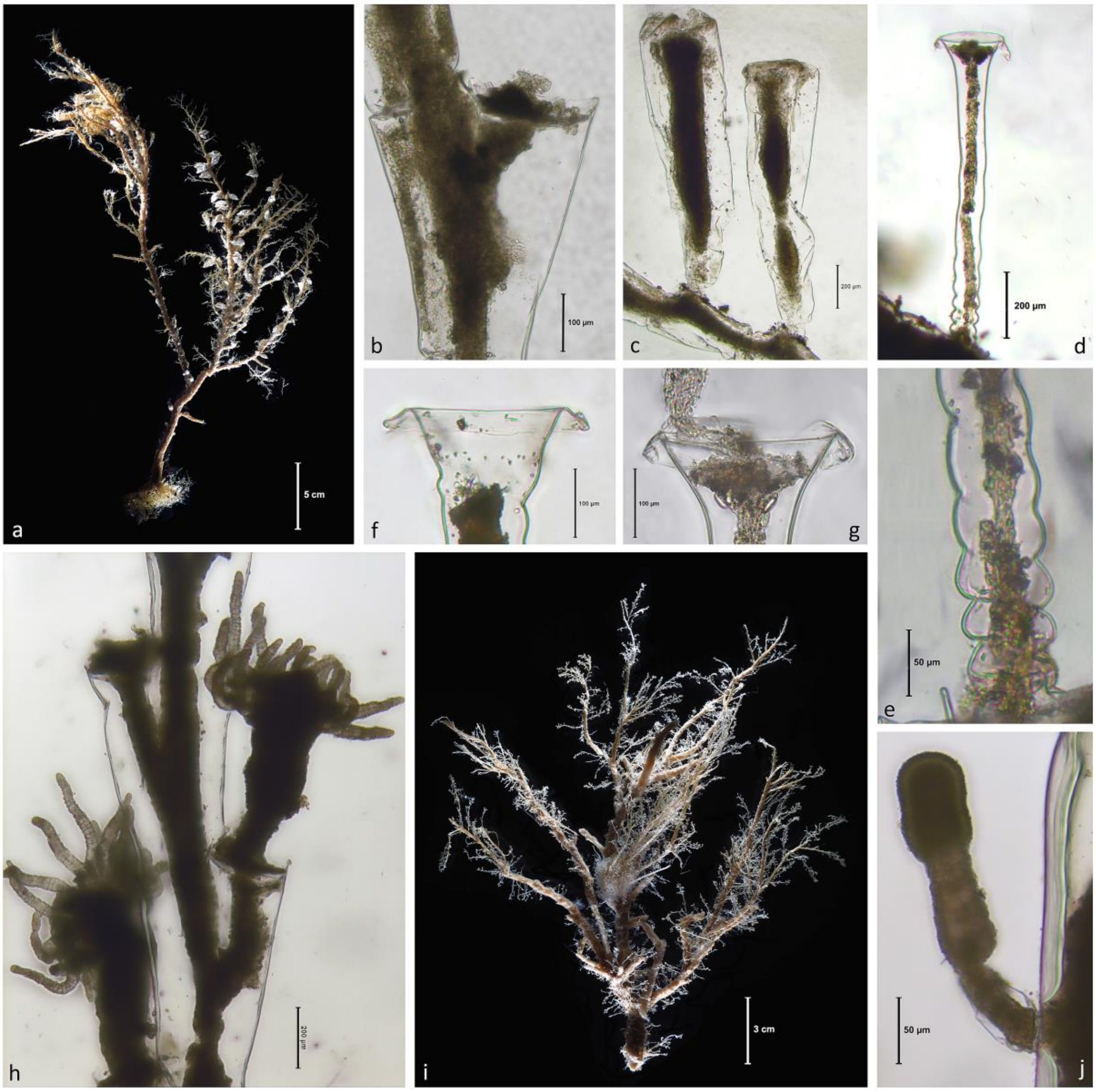

Figure 4.14 a *Halecium incertus*: colony. **b-c** *H. secundum*: **b** hydrophore; **c** gonothecae. **d-g** *H. tubatum*: **d** stem; **e** detail of the basal rings of the stem; **f-g** hydrothecae. **h-j** *Hydrodendron arboreum*: **h** stem showing hydrophores arrangement; **i** colony; **j** nematophore

Cnidome composed by microbasic euryteles? [range 17.0–19.5 x 6.0–8.0 µm, mean 18.7±0.6 x 7.2±0.6 µm (n=19)] and microbasic mastigophores [range 8.0–8.5 x 1.5–2.0 µm, mean 8.2±0.2 x 1.6±0.2 µm (n=17)].

Ecology and distribution. Valid records of the species are restricted to the holotype, which was collected off Wilkes Land (East Antarctica) at a depth of 163 m (Watson 2008). Material examined here was found between 119 and 417 m depth. Present finding constitutes the first evidence of the species from both the Weddell Sea and West Antarctica, pointing to a circum-Antarctic distribution.

Hydrodendron Hincks, 1874

Hydrodendron arboreum (Allman, 1888)

(Fig. 4.14h-j)

Material examined. *ANT XV/3*: **48-36**, one colony, up to 80 mm high; *ANT XVII/3*: **111-5**, one colony, c. 40 mm high; **111-6**, several stems, c. 140 mm high, on stone, with gonothecae; **111-7**, several stems, up to 120 mm high; few stems, up to 6 mm high, on *O. stepanjantsae*; **111-9**, several stems, up to 110 mm high, with gonothecae; **111-18**, one colony, c. 135 mm high, with gonothecae; **111-19**, one colony, c. 20 mm high; *ANT XXI/2*: **PS65/39**, a few stems, up to 33 mm high; **PS65/278**, one colony, c. 50 mm high; **PS65/279**, one colony, c. 20 mm high; one colony, c. 31 mm high, on sponge; **PS65/281**, some stems c. 80 mm high.

Ecology and distribution. Species collected between 18 (Hickson and Gravely 1907) and 1370 m depth (Peña Cantero and Ramil 2006); present material at 62-175 m. Pan-Antarctic species widely distributed in Antarctic and sub-Antarctic waters (Peña Cantero and Ramil 2006). Documented in the Weddell Sea by means of remote operate vehicle (Dimmler et al. 2001), present contribution constitutes the first verifiable record from this Antarctic region.

Sertularellidae Maronna, Miranda, Peña Cantero, Barbeitos & Marques, 2016
Sertularella Gray, 1848
Sertularella sp.
(Fig. 4.10k)

Material examined. *ANT XV/3*: **48-5**, one stem, c. 12 mm high.

Remarks. The material examined does not agree with any other species of genus previously reported from Antarctic waters. It shares with the material described as *Sertularella* sp. by Peña Cantero (2008) the size of the hydrotheca, but differs in the shape and length of free part of adcauline wall. By the shape and great size of the hydrotheca, the material examined closely resembles to *Sertularella gayi* (Lamouroux, 1821), previously known from South Africa (Ritchie 1909) and the Patagonian region (Blanco 1982 and literature cited), and *Sertularella blanconae* El Beshbeeshy, 2011, known from the Patagonian region (El Beshbeeshy and Jarms 2011). However, the scarcity of the available material and the lack of gonosome prevent us for providing a proper identification.

Ecology and distribution. Material examined comes from a depth of 177 m. Species previously unknown from Antarctic waters.

Aglaopheniidae Marktanner-Turneretscher, 1890
Aglaophenia Lamouroux, 1812
Aglaophenia baggins Soto Àngel & Peña Cantero, 2017
(Fig. 4.15a)

Material examined. *ANT XV/3*: **48-33**, one cormoid, c. 42 mm high, with corbulae; **48-34**, three cormoids, up to 45 mm high, with corbulae.

Remarks. Recently described species, whose finding constituted the first evidence of the genus for any polar region and the first report of the family Aglaopheniidae from Antarctic waters (see Soto Àngel and Peña Cantero 2017b).

Ecology and distribution. Reported at depths from 62 to 116 m. Only known for now for the Cape Norvegia region, in the Weddell Sea.

Schizotrichidae Peña Cantero, Sentandreu and Latorre, 2010
Schizotricha Allman, 1883
Schizotricha glacialis (Hickson & Gravely, 1907)
(Fig. 4.15b-c)

Material examined. *ANT XV/3*: **48-353**, one colony, c. 90 mm high, with gonothecae.

Ecology and distribution. Rare species, only reported twice: from its type locality in the Ross Sea at a depth of 180 m

Figure 4.15 a *Aglaophenia baggins*: hydrotheca. **b-c** *Schizotricha glacialis*: **b** forked hydrocladial internode; **c** unforked hydrocladial internode. **d-f** *S. nana*: **d** stem; **e** forked hydrocladial internode; **f** unforked hydrocladial internode. **g-j** *S. unifurcata*: **g** stem; **h** forked hydrocladial internode; **i** unforked hydrocladial internode; **j** internode with two hydrothecae

(Hickson and Gravely 1907), and from the eastern part of the Weddell Sea, at a depth of 620-640 m (Peña Cantero et al. 1996); present material collected at 129-132 m. Probably a circum-Antarctic species. Thus, present finding constitutes the third record of the species and the first evidence from the South Shetland Islands.

Schizotricha nana Peña Cantero, Svoboda & Vervoort, 1996

(Fig. 4.15d-f)

Material examined. *ANT XV/3*: **48-50**, several stems, up to 270 mm high, on gravel, with developing gonothecae; **48-194**, several stems, up to 160 mm high, on gravel, with developing gonothecae; **48-220**, several stems, up to 210 mm high, on gravel, with developing gonothecae; **48-222**, few stems, up to 100 mm high, with developing gonothecae; **48-223**, several stems, up to 130 mm high, with gonothecae; **48-276**, several stems, up to 320 mm high, with gonothecae; *ANT*

XVII/3: **111-9**, few stems, up to 125 mm high, with gonothecae; **111-18**, few stems, up to 90 mm high, with gonothecae; *ANT XXI/2*: **PS65/39**, several stems, up to 200 mm high, with gonothecae; **PS65/121**, several stems, up to 280 mm high, with gonothecae; **PS65/237**, few stems, up to 140 mm high, on gravel, with gonothecae; **PS65/280**, few stems, up to 80 mm high, with gonothecae; **PS65/281**, few stems, up to 85 mm high; **PS65/336**, few stems, up to 90 mm high.

Ecology and distribution. Species collected at depths between 43 (Stepanjants 1972) and 1890 m (Peña Cantero and Vervoort 2005); present material from 62 to 417 m. Circum-Antarctic species (Peña Cantero et al. 1996).

Schizotricha unifurcata Allman, 1883

(Fig. 4.15g-j)

Material examined. *ANT XV/3*: **48-5**, one stem, c. 30 mm high; **48-33**, few stems, up to 80 mm high, with developing gonothecae; **48-197**, few stems, up to 50 mm high; **48-220**, few stems, up to 60 mm high, with developing gonothecae; **48-276**, several stems, up to 80 mm high, with gonothecae; *ANT XVII/3*: **111-9**, one stem, c. 30 mm high; **111-19**, several stems, up to 330 mm high, some on sponge, with gonothecae; *ANT XXI/2*: **PS65/121**, several stems, up to 100 mm high, with gonothecae; **PS65/132**, few stems, up to 95 mm high; **PS65/274**, few stems, up to 80 mm high.

Remarks. Some specimens differ from the re-description of the species provided by Peña Cantero et al. (1996) and the diagnoses of the species by Peña Cantero and Vervoort (2005). The materials from the stations XV/3 48-5, 48-63, 48-220, ANT XXI/2 PS65/121, PS65-132 are unbranched, unlike our current knowledge of the species (see Peña Cantero and Vervoort 2005). However, according to the drawings provided by Allman (1883), the branching takes place in the very basal region of the colony. The fragmented condition of the material examined here could be masking this character. In the specimens mentioned above, there is a single nematotheca in the hydrocladial intermediate internode (Fig. 4.15h) (but two in the caulinar intermediate internodes), unlike previous descriptions of the species, which reported two nematotheca in the intermediate internode. However, no differences among caulinar and cladial ones are mentioned by previous authors. Additionally, some hydrocladial internodes are provided with two consecutive hydrothecae (Fig. 4.15j), while a single one has been mentioned by previous contributions (e.g. Peña Cantero et al. 1996). This character variation has also been reported for *Schizotricha turqueti* Billard, 1906 (see Peña Cantero and Vervoort 2005). We have considered these observations as minor variations, and we assign all the material examined to *S. unifurcata* with confidence.

Ecology and distribution. Previously reported at depths from 15 (Millard 1977) to 567 m (Stechow 1925); present material between 62 to 417 m. Antarctic-Kerguélen distribution (Peña Cantero 1998).

Kirchenpaueriidae Stechow, 1921

Oswaldella Stechow, 1919

Oswaldella delicata Peña Cantero, Svoboda & Vervoort, 1997

(Fig. 4.16k-l)

Material examined. *ANT XXI/2*: **PS65/278**, one stem, c. 10 mm high, on *H. arboreum.*

Ecology and distribution. Previously found at depths between 126 (Peña Cantero 2008) and 440 m (Peña Cantero et al. 1997b); present material at 119-120 m. West Antarctic distribution (Peña Cantero and Vervoort 2004).

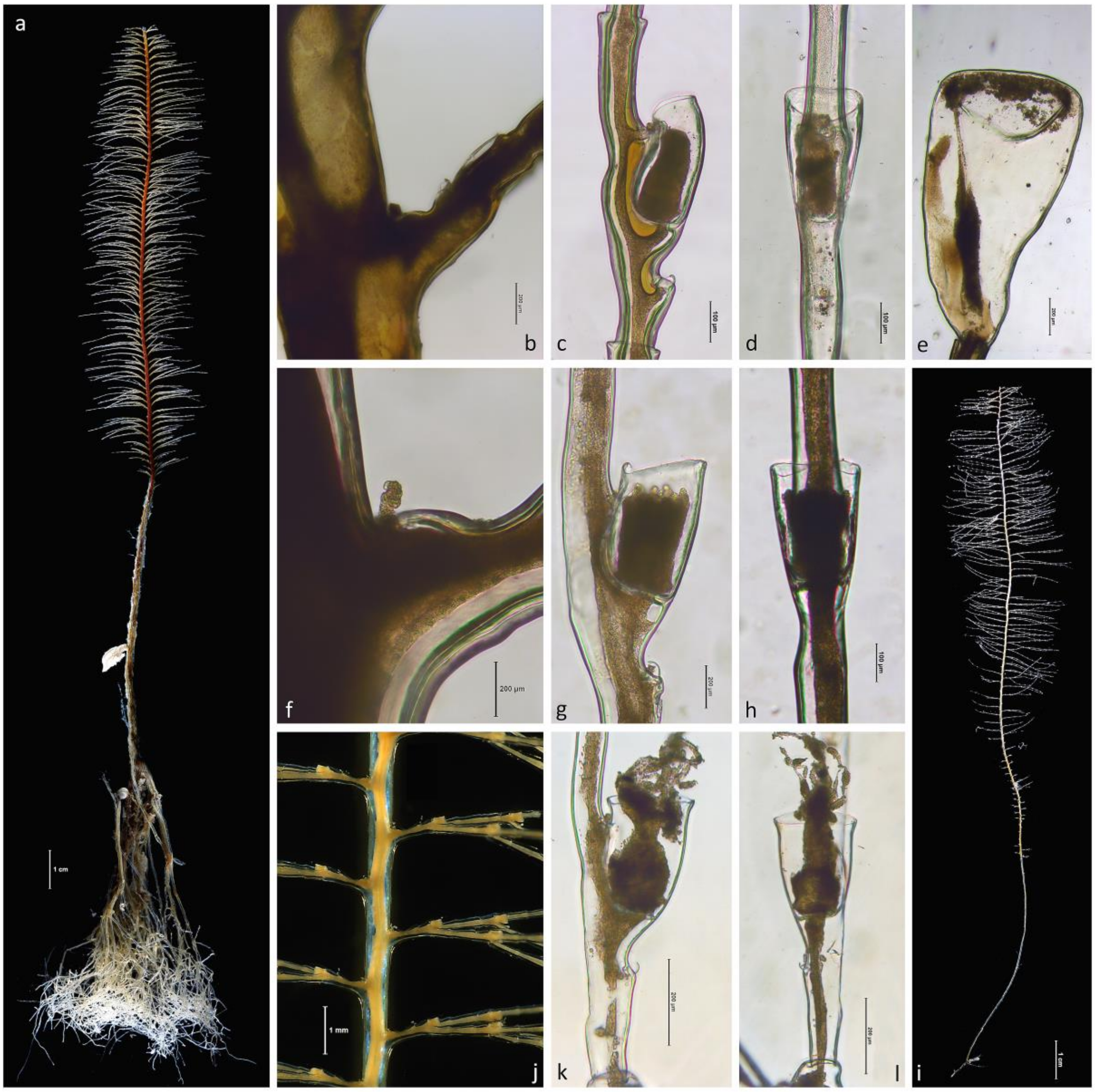

Figure 4.16 a-e *Oswaldella erratum*: **a** stem; **b** cauline apophysis showing nematophore; **c** hydrotheca in lateral view; **d** hydrotheca in frontal view; **e** female gonotheca. **f-j** *O. rigida*: **f** cauline apophysis showing nematophore; **g** hydrotheca in lateral view; **h** hydrotheca in frontal view; **i** stem; **j** detail of the stem showing hydrocladial arrangement. **k-l** *O. delicata*: **k** hydrotheca in lateral view; **l** hydrotheca in frontal view

Oswaldella erratum Peña Cantero & Vervoort, 1997

(Fig. 4.16a-e)

Material examined. *ANT XV/3*: **48-4**, few stems, up to 80 mm high, on gravel, with developing gonothecae; **48-50**, few stems, up to 100 mm high, with developing gonothecae; **48-58**, few stems, up to 90 mm high, with developing gonothecae; **48-168**, few stems, up to 60 mm high, with developing gonothecae; **48-197**, few stems, up to 45 mm high; **48-222**, few stems, up to 55 mm high, with developing gonothecae; **48-276**, few stems, up to 95 mm high, with developing gonothecae; *ANT XXI/2*: **PS65/39**, few stems, up to 70 mm high, with gonothecae; **PS65/121**, several stems, up to 100 mm high, with developing gonothecae; **PS65/132**, several stems, up to 205 mm high, some on polychaete tube; **PS65/148**, few stems, up to 75 mm high, on gravel; **PS65/166**, several stems, up to 160 mm high; **PS65/174**, several stems, up to 170 mm high; **PS65/175**, several stems, up to

120 mm high; **PS65/237**, several stems, up to 120 mm high, with gonothecae; **PS65/274**, several stems, up to 150 mm high; **PS65/280**, several stems, up to 140 mm high; **PS65/336**, one stem, c. 20 mm high.

Ecology and distribution. Species previously found at depths between 55 (Peña Cantero and Vervoort 2004) and 696 m (Peña Cantero et al. 1997b); present material between 166 and 417 m. West Antarctic distribution (Peña Cantero and Vervoort 2004).

Oswaldella rigida Peña Cantero, Svoboda & Vervoort, 1997

(Fig. 4.16f-j)

Material examined. *ANT XV/3*: **48-27**, few stems, up to 55 mm high; **48-72**, few stems, up to 50 mm high; **48-168**, few stems, up to 60 mm high; **48-189**, few stems, up to 55 mm high; **48-276**, few stems, up to 20 mm high; *ANT XXI/2*: **PS65/148**, few stems, up to 75 mm high; **PS65/237**, few stems, up to 30 mm high; **PS65/278**, few stems, up to 70 mm high.

Ecology and distribution. Species collected at depths between 80 (Peña Cantero et al. 1997b) and 1157 m (Peña Cantero 2014a); present material was collected at depths between 119 and 417 m. Circum-Antarctic distribution (Peña Cantero et al. 1997b).

Oswaldella stepanjantsae Peña Cantero, Svoboda & Vervoort, 1997

(Fig. 4.17a-f)

Material examined. *ANT XV/3*: **48-27**, several stems, up to 110 mm high; **48-31**, few colonies, up to 80 mm high, some on stone; **48-33**, several colonies, up to 170 mm high, some on stone; **48-34**, one colony, up to 150 mm high, on sponge, with developing gonothecae; **48-36**, few colonies, up to 120 mm high, with gonothecae; **48-50**, several stems, up to 100 mm high; **48-63**, several stems, up to 170 mm high; **48-210**, several stems, up to 70 mm high, on stone and gravel, with developing gonothecae; **48-276**, several stems, up to 110 mm high; *ANT XVII/3*: **111-5**, several stems, up to 130 mm high, on gravel, with gonothecae; **111-6**, several stems, up to 100 mm high; **111-7**, several stems, up to 120 mm high, with developing gonothecae; **111-9**, few stems, up to 60 mm high, with gonothecae; **111-18**, few colonies, up to 210 mm high, with gonothecae; *ANT XXI/2*: **PS65/251**, few colonies, up to 115 mm high, on gravel and stone; **PS65/278**, few stems, up to 130 mm high; **PS65/281**, few colonies, up to 110 mm high, with gonothecae.

Remarks. Among the abundant material examined, we found some small fragments with caulinar apophyses in spiral arrangement forming three longitudinal rows (Fig. 4.17e). In one case, a transition between triseriate and biseriate arrangement has been observed. Till the date, triseriate apophyses were only known from a single representative of the genus, *Oswaldella laertesi* Peña Cantero, 2007, in which the triseriate disposition is a constant. The fragments studied are clearly referable to *O. stepanjantsae* because up to six axillary nematophores have been observed on the caulinar apophyses, and the abcauline length of the hydrotheca is clearly higher than its aperture (cf. Peña Cantero and Vervoort 2004). *Oswaldella laertesi* has low hydrothecae, and up to four axillary nematophore (González Molinero and Peña Cantero 2015). Present finding evidence that at least two species of genus *Oswaldella* present apophyses in a triseriate arrangement, although in *O. stepanjantsae* the biseriate disposition is the rule, and could point to a putative phylogenetic relationship between the two species.

Figure 4.17 a-f *Oswaldella stepanjantsae*: **a** hydrotheca in lateral view; **b** hydrotheca in frontal view; **c-d** cauline apophysis showing nematophores; **e** hydrocaule with apophyses in triseriate arrangement; **f** male gonotheca. **g-m** *O. tottoni*: **g** hydrotheca in lateral view; **f** hydrotheca in frontal view; **i** colony; **j** detail of the stem showing hydrocladial arrangement; **k** female gonootheca in lateral view; **l** male gonotheca in frontal view; **m** female gonotheca in frontal view (left) and male gonotheca in frontal view (right)

Ecology and distribution. Species collected at depths between 36 and 1890 m (Peña Cantero and Vervoort 2004); present material between 62 and 417 m. As pointed out by Peña Cantero (2013, 2014a), and evidenced here, this species serve as basibiont for a great diversity of epibiotic hydrozoans, as well as other several taxa (cf. supplementary Tab. S4), thus constituting an important habitat former. Species with a circum-Antarctic distribution (Peña Cantero and Vervoort 1998).

Oswaldella tottoni Peña Cantero & Vervoort, 1996

(Fig. 4.17g-m)

Material examined. *ANT XV/3*: **48-194**, few stems, up to 120 mm high, with gonothecae; *ANT XXI/2*: **PS65/121**, several stems, up to 150 mm high, with gonothecae; **PS65/276**, few stems, up to 120 mm high, with gonothecae.

Remarks: Only known with female gonothecae from its type locality in the Ross Sea (Peña Cantero and Vervoort 1996), although no sex was attributed by the authors. Material examined here let us confirm a patent sexual dimorphism (Fig. 4.17m). Male gonotheca, 1.3-1.7 mm high x 0.7-0.8 mm maximum width, cylindrical with rounded end, fusiform in lateral view, with distal, circular aperture. Female gonotheca larger, 2.4-3.0 mm high x 1.2 mm maximum width, inverted cone-shaped, flattened in lateral view, with subterminal, oval aperture.

Ecology and distribution. Species reported from depths between 256 (Peña Cantero and Vervoort 1996) and 400 m (Peña Cantero et al. 1997b); present material from 244 to 277 m. Circum-Antarctic species (Peña Cantero and Vervoort 2004).

Incertae saedis
Billardia subrufa (Jäderholm, 1904)

(Fig. 4.7k-m)

Material examined. *ANT XV/3*: **48-4**, one colony, c. 50 mm high; **48-5**, some stems, up to 50 mm high, on sponge, with gonothecae; some stems, up to 10 mm high, on *S. lobata*; **48-27**, one colony, c. 40 mm high; some stems, up to 5 mm high, on *E. generale*; **48-44**, some stems, up to 25 mm high, on *S. lobata*, with gonothecae; several stems, up to 60 mm high, on polychaete tube, with gonothecae; **48-63**, one colony, c. 10 mm high; **48-70**, one colony, c. 90 mm high, with gonothecae; **48-72**, several stems, up to 30 mm high, on sponge, with gonothecae; **48-82**, few stems, up to 20 mm high, on *S. polarsterni*; one colony, c. 110 mm high, with developing gonothecae; **48-154**, one colony, c. 60 mm high; **48-168**, one colony, c. 130 mm high, with gonothecae; **48-194**, one colony, c. 50 mm high; **48-197**, some stems, up to 11 mm high, on *Eudendrium* sp.1; one colony, c. 60 mm high, with gonothecae; one colony, c. 90 mm high, on dead octocoral, with gonothecae; **48-222**, one colony, c. 150 mm high; **48-276**, one colony, c. 190 mm high, with gonothecae, on *S. nana*; **48-297**, several stems, up to 45 mm high, on ascidian, with gonothecae; *ANT XVII/3*: **111-5**, some stems, up to 13 mm high, on *O. stepanjantsae*; **111-6**, one colony, c. 55 mm high, with gonothecae; **111-9**, few stems, up to 10 mm high, on *O. stepanjantsae*; some stems, up to 35 mm high, on *S. lobata*; **111-18**, some stems, up to 30 mm high, on *O. stepanjantsae*, with gonothecae; few stems, up to 13 mm high, on *S. nana*; one colony, c. 65 mm high, on polychaete tube, with gonothecae; one colony, c. 65 mm high, with gonothecae; *ANT XXI/2*: **PS65/39**, one colony, c. 20 mm high; **PS65/121**, one colony, c. 30 mm high; few stems, up to 10 mm high, on *S. nana*; **PS65/132**, one colony, c. 82 mm high, on bryozoan, with gonothecae; **PS65/166**, one colony, c. 110 mm high, with gonothecae; **PS65/174**, one colony, c. 90 mm high, on *O. erratum*, with gonothecae; one colony, c. 90 mm high, with developing gonothecae; **PS65/175**, some stems, up to 15 mm high, on *O. erratum*; one colony, c. 80 mm high; one colony, c. 110 mm high, on octocoral and bryozoan, with gonothecae; several stems, up to 40 mm high, on polychaete tube, with gonothecae; **PS65/237**, some stems, up to 60 mm high, on *S. nana*, with gonothecae; some stems, up to 50 mm high, on *S. lobata*; one colony, c. 30 mm high, on sponge, with gonothecae; **PS65/245**, one colony, c. 50 mm high; **PS65/253**, one colony, c. 40 mm high; **PS65/259**, one colony, c. 75 mm high; **PS65/265**, one colony, c. 120 mm high, with gonothecae; few stems, up to 15 mm high, on *S. polarsterni*; **PS65/274**, few stems, up to 10 mm high, on *S. polarsterni*; **PS65/276**, few stems, up to 6 mm high, on *S. lobata*; **PS65/278**, one colony, c. 60 mm high; few stems, up to 10 mm high, on sponge; **PS65/279**, one colony, c. 60 mm; **PS65/280**, one colony, c. 20 mm high; **PS65/281**, one colony, c. 140 mm high, on gravel and sponge, with gonothecae; some stems, up to 25 mm high, on *O. stepanjantsae*; **PS65/336**, few stems, up to 10 mm high, on *S. nana*.

Remarks. Similarly to the process described for *S. lobata*, several specimens have been observed using a wide range of basibionts as substrate (octocorals, hydroids or polychaete tubes, among others). Large colonies are seen in many cases growing on the basibiont until completely overgrow the host colony, which is completely indiscernible unless a cross section is done. We suggest that *B. subrufa* behaves as an aggressive epibiont species that needs a basibiont to reach large size, as it is known from the zoantharian *Savalia savaglia* (Bertoloni, 1819) (Zibrowius 1985). As mentioned above, the relationship can be categorized as parasitism *sensu lato*, in which the epibiont is detrimental to the host but is not metabolically dependent upon it (see Gili et al. 2006 and references therein). That assumption implies that *B. subrufa* should have a quicker growth rate than its host. The presence of horizontal growing by polysiphonic stems could enhance its colonizing efficiency. Further *in vivo* experiments are needed to test this hypothesis.

Ecology and distribution. Species collected at depths between 25 (Stepanjants 1972) and 1030 m (Peña Cantero et al. 2004); present material from 62-583 m depth. Antarctic-Patagonian species (Peña Cantero et al. 2004).

General remarks

A total of 77 species belonging to 21 families and 28 genera has been inventoried, of which 67 have been identified to species level, and six more are unequivocally considered different from the other representatives found in the collection. It is, therefore, the most prolific collection of Antarctic benthic hydroids ever analyzed in terms of number of species, followed by the work by Peña Cantero (2008) who reported 61 species from the Antarctic expedition *Bentart 95* in the South Shetland Islands sector. Among these 73 species, 59 (81%) are members of Leptothecata, while 14 (19%) are representatives of Anthoathecata. Despite being a fifth of the collection, the number of athecate species are is higher than usual. With a few exceptions mentioned below, the proportion of athecates usually does not exceed 10% of the total species reported from a single Antarctic collection (e.g. Galea and Schories 2012; Peña Cantero 2006, 2008, 2010, 2015; Peña Cantero and Gili 2006; Peña Cantero and Vervoort 2009, Soto Àngel and Peña Cantero 2015). Some authors have argued that sampling procedures strongly determine the absence of representatives of Anthoathecata, given that soft tissues are usually damaged when sampled with indirect gears (e.g. Peña Cantero 2004). Other hypothesis were explored by Stepanjants (1972) who reported a high number of athecates from shallow waters in the David Sea, and later suggested that they are better represented in shallow depths, probably due to a higher tolerance to low salinity (Stepanjants 1979). Peña Cantero et al. (2013) found several athecates in a collection obtained by scuba-diving from Tethys Bay (Ross Sea), and underlined the idea of the effectiveness and carefulness of sampling gear as the major reason of lopsided athecate/thecate ratios. In fact, most of the anthoathecatecontaining samples studied here were obtained by TV grab, and were exceptionally well preserved, regardless of the depth sampled. Hydroid assemblages, as part of benthic communities, are strongly influenced by ice scouring (Teixidó et al. 2004 and references therein), which is especially intense in the Cape Norvegia area (Gutt and Piepenburg 2003). Under a scenario of recent scouring, some particular taxa (i.e. pioneer species) are favored by their quick development and reproduction rates, and low dispersal capabilities (Potthoff et al. 2006). This is probably the case of some athecates reported here, such as *C. microrhiza*, *T. longstaffi*, *C. hicksoni*, and *Z. parvula*, which are observed in high numbers, especially juveniles and new recruits (cf. Gili et al. 2001, Dimmler et al. 2001; Orejas et al. 2000; Gut and Piepenburg 2003; Svoboda and Stepanjants 2001; Teixidó et al. 2004). In the same way that ice scouring does not happen exclusively in shallow waters (i.e. below 150 m) but it is more intense there, some species of athecates, which have also been found deeper, could be especially abundant in shallow waters regularly subjected to ice-scouring, which are frequently in early stages of recolonization (cf. Teixidó et al. 2004). Indeed, some of the species mentioned above were also reported in the shallow-water collections studied by Stepanjants (1972) and Peña Cantero et al. (2013). Specific experimental designs and forthcoming research will shed more light on this interesting topic.

Symplectoscyphidae with 16 representatives (22%) is the most speciose family, followed by Haleciidae with 11 representatives (16%) and Staurothecidae with 8 (11%). In contradistinction to most contributions dealing with benthic hydroids from different Antarctic regions, the family Sertulariidae is not represented. This is due to recent profound changes in the systematic of Leptothecata (Maronna et al. 2016), which have shown the polyphyly of several taxa, including Sertulariidae, now splitted into several monophyletic families. Being so, although Sertulariidae *sensu novo* is not represented, Sertulariidae *sensu lato* includes 24 representatives, a third of the total species found, in agreement with previous studies (e.g. Peña Cantero 2008, 2010). Likewise, a few but speciose genera (i.e. *Antarctoscyphus*, *Halecium*, *Oswaldella*, *Schizotricha*, *Staurotheca*, and *Symplectoscyphus*) concentrate 42 (58%) of the species found, in spite of representing one fifth of the number of genera, a feature shared with the whole Antarctic regions in terms of benthic hydroid diversity (cf. Peña Cantero 2014a, Soto Àngel and Peña Cantero 2017a). At the generic level, *Symplectoscyphus* with 12 (16%) species and *Halecium* with 10 (14%) are the most diverse genera, followed by *Staurotheca* and *Oswaldella* with eight (11%) and five (7%) species, respectively. It is worth to mention that the collection includes almost all the species of *Halecium* known from Antarctic waters (10 of 13) (according to Peña Cantero 2014a), but excluding *H. brevithecum*, which is considered here conspecific with *H. secundum.* Similarly, 12 of the 23 species of *Symplectoscyphus* known from Antarctic waters are reported. At the species level, *B. subrufa* is the species with the highest occurrence, being present in 37 (63%) stations, followed by *Sy. glacialis* present in 29 (49%), and *P. belgicae* and *S. lobata*, found in 25 (42%).

Halecium banzare, *H. incertus*, *H. arboreum*, *O. stepanjantsae*, *S. nana*, *S. unifurcata*, *S. polarsterni*, and *St. vanhoeffeni* are the largest representatives, surely reaching sizes much greater than those presented here, since the material examined was strongly fragmented. Among them, *H. arboreum*, *S. nana*, *O. stepanjantsae* and *S.*

polarsterni are the dominant species in the collection studied here, and frequently documented in previous reports (e.g. Peña Cantero and García Carrascosa 1995; Peña Cantero and Vervoort 2004; Peña Cantero et al. 1997b, 1997c). Indeed, during the expedition ANT XVII/3, whose hydroid material is studied here, Dimmler et al. (2001) studied shallow epibenthic communities from Cape Norvegia by remote operate vehicles and reported high abundances of *H. arboreum* at a depth around 50 m, *Oswaldella antarctica* (Jäderholm, 1904) at 55-65 m (but probably a mix of *O. erratum* and *O. stepanjantsae*), and *S. unifurcata* (probably a mix of *S. nana and S. unifurcata)* at 65-75 m. *S. polarsterni* is found in deeper waters, probably associated to undisturbed assemblages, in final stages of succession. Despite the lack of comprehensive quantitative sampling, and *in situ* abundance not yet determined, these four species are potential candidates to be considered as habitat formers, harbouring a wide array of taxa (see below and Tab. S4). In this sense, hydroids are an important component of animal forests that have been usually neglected (see Di Camillo et al. 2017 and references therein), and their diversity is often underestimated in studies of benthic ecology, particularly in Antarctic waters (e.g. Gutt and Piepenburg 2003, Teixidó et al. 2004).

Concerning the use of substrate, *S. nana* is the basibiont harbouring the highest diversity of hydroids on it, with 23 species. *Oswaldella stepanjantsae* is next, with 22 species. *B. subrufa* harbours 13 hydroid epibionts, while 12 were growing on *S. lobata* and 10 on *T. longstaffi*. Many additional epibionts belonging to several zoological groups have been observed during the examination of the material (Tab. S4). Focusing on epibionts, *P. belgicae* is the species with the largest array of hydroids as substrate with 28 species, followed by *R. antarcticum* with 20 different hydroid basibionts, *Sy. glacialis* with 18, *H. interpolatum* with 17, and *B. subrufa* with six (Tab. S4).

Following the bathymetric distribution patterns established by Peña Cantero (2004), four different groups are recognized in the collection (Tab. 4.2). Eurybathic species dominate with 26 (36%) representatives. Twenty-two species (30%) extend from below the shallowest levels of the continental shelf to beyond the continental shelf-break. The group of species exclusively found on the continental shelf, but absent from the shallowest sublittoral zone, is also well represented (19 species, 26%). The less-represented contingent is the group of species inhabiting exclusively on the continental shelf (including the shallowest waters), with six (8%) members. The bathymetric range of 19 species has been extended (Tab 4.2), in some of them for some hundred meters (e.g. *E. antarcticum, E. scotti*, *H. dendritica*, *H. tubatum*, and *S. paulensis*). Five of the species are translocated to a different bathymetric group (Tab. 4.2): *S. paulensis* is reported here for the first time on the Antarctic continental shelf; *H. dendritica* are reported much deeper than the shallowest waters; and finally, *B. corynopsis*, *E. antarcticum* and *E. scotti* are found beyond the continental shelf-break. The remaining two groups (exclusive deep-sea species and shallow-water species) established by Peña Cantero (2004) are absent from the collection examined. The lack of samples shallower than 30 m depth, and the very few ones deeper than 500 m explain the absence of these bathymetric groups.

Regarding the reproductive phenology, the period has been extended for 32 species (45%), including *Campanularia* sp., never found with gonothecae before (Tab 4.2). No specific pattern has been detected in relation to the production of reproductive structures for the species analyzed, and environmental factors triggering sexual reproduction of Antarctic benthic hydrozoans are still unknown.

Table 4.2 Main ecological characteristics and distribution of the species inventoried. In bold are marked new bathymetric range, bathymetric pattern, reproductive period or pattern of distribution; species in bold are new records for the Weddell Sea. [Continental shelf (CS); shallow waters (SW); deep waters (DW); eurybathic (EU). Antarctic-Kerguélen (AK); Antarctic-Patagonian (AP); Circum-Antarctic (CA); pan-Antarctic (PA); west-Antarctic (WA); west-Antarctic Patagonian (WAP); Weddell Sea (WED); widely distributed (W)]

	Depth (m)					Reproduction			Distribution
	Known		Obtained		Group	Fertile	Reproductive phenology	References	
B. corynopsis	385	527	710	**758**	**CS-SW+DW**	No	Unknown	-	**CA**
Bougainvillidae undet	-	-	62	287	CS-SW	XII, IV	-	-	-
R. antarcticum	0	450	62	287	CS+SW	I, II, **IV**, XII	I, II, V, VI, VII, VIII, XII	Peña Cantero (2015)	AK
E. antarcticum	240	260	**64**	**598**	**CS-SW+DW**	**I**, II	II	Peña Cantero and Vervoort (2009)	W
E. generale	10	702	62	241	EU	IV, XII	I, IV, XII	Soto Àngel and Peña Cantero (2015)	W
E. scotti	10	135	234	**758**	**EU**	II	II, XII	Peña Cantero (2008), Peña Cantero and Vervoort (2009), Peña Cantero et al. (2013)	CA
Eudendrium sp.1	-	-	67	416	CS-SW	No	-	-	-
***Eudendrium* sp.2**	103	699	286	287	CS-SW+DW	**XII**	I, III	Peña Cantero (2009, 2014a)	**CA**
H. dendritica	9	18	62	**473**	**CS+SW**	**IV**	III	Peña Cantero (2015)	**CA**
Hydractinia sp.	-	-	62	146	CS-SW	No	-		-
T. longstaffi	222	630	**62**	67	CS-SW	IV	II, IV	Peña Cantero (*in press*)	**CA**
Tubularia sp.1	-	-	105	112	CS-SW	No	-		-
Tubularia sp.2	-	-	64	65	CS-SW	I	-		-
Z. parvula	5	440	62	105	CS-SW	**IV**	I, II, IX, XII	Svoboda and Stepanjants (2001)	CA
C. microrhiza	237	629	**62**	309	CS-SW+DW	**IV**	I, II	Svoboda and Stepanjants (2001)	CA
Sarsia sp.	3	40	67	**287**	CS+SW	No	XII	Peña Cantero et al. (2013)	-
Z. hicksoni	12	183	62	64	CS+SW	No	Unknown		**CA**
A. frigida	85	728	341	416	CS+DW	No	III	Peña Cantero et al. (2004)	CA
F. antarcticum	14	552	62	277	EU	I, **IV**, XII	I, II, VI, XII	Peña Cantero et al. (2004)	W
F. cf. magnificum	85	640	236	**758**	CS-SW+DW	No	II	Peña Cantero et al. (2004), Peña Cantero (2010)	WA
F. cf. bouvetensis	122	134	**120**	**274**	CS-SW	No	XI	Marques et al. (2011)	W
Filellum sp.	-	-				-	-	-	-
L. dumosa	12	1157	65	417	EU	No	V, XII	Peña Cantero et al. (2004)	W
L. gaussica	40	460	191	228	CS-SW	No	II	Peña Cantero et al. (2004)	CA
Hebella cf. plana	92	722	341	360	CS-SW+DW	No	I	Peña Cantero (2014a)	AP
L. longitheca	5	701	62	360	EU	**IV**	I, III, XII	Peña Cantero (2009); Peña Cantero et al. (2013)	PA
S. lobata	10	700	62	417	EU	I, **IV, XII**	I, II	Peña Cantero et al. (2004)	CA
P. belgicae	0	779	62	417	EU	**XII**	I, II	Peña Cantero et al. (2013)	PA
C. hicksoni	10	779	62	598	EU	I, II, IV, **XII**	I, II, IV	Soto Àngel and Peña Cantero (2015)	CA
Campanularia sp.	15	728	68	291	EU	**II**	Unknown	Peña Cantero et al. (2004)	CA
S. antarctica	55	708	228	598	CS-SW+DW	**XII**	I, II, XI	Peña Cantero and Vervoort (2003)	CA
S. dichotoma	82	799	268	417	CS-SW+DW		I, II, IV, V, VI, X, XI, XII	Soto Àngel and Peña Cantero (2015)	AK
S. frigida	86	647	234	360	CS-SW+DW	I, II, XII	I , II, III, IV, V, VI, X, XI, XII	Soto Àngel and Peña Cantero (2015)	AK
S. glomulosa	55	1157	112	758	CS-SW+DW	I, **IV**, XII	I, II, III, XII	Peña Cantero and Vervoort (2003)	CA
S. nonscripta	15	728	191	598	EU	**XII**	I, II, XI	Peña Cantero and Vervoort (2003)	AP
S. pachyclada	42	1405	267	583	CS-SW+DW	II, XII	I, II, III, XII	Peña Cantero (2006, 2009)	CA
S. polarsterni	181	1030	230	758	CS-SW+DW	II, XII	II, X, XII	Peña Cantero and Vervoort (2003), Peña Cantero (2014a)	CA
St. vanhoeffeni	92	527	119	333	CS-SW	**XII**	I, II, III	Peña Cantero and Vervoort (2003)	CA
A. asymmetricus	70	429	230	274	CS-SW	No	I	Peña Cantero (2006)	WA
A. elongatus	10	1958	82	360	EU	No	I, II, XII	Peña Cantero (2006)	AK

Table 4.2 continued

	Depth (m)					Reproduction			Distribution
	Known		Obtained		Group	Fertile	Reproductive phenology	References	
A. grandis	15	360	62	287	CS+SW	**IV, XII**	I, II	Peña Cantero (2008)	CA
A. spiralis	6	1958	119	417	EU	No	I, II, IV, VI, VII, XII	Soto Àngel and Peña Cantero (2015)	CA
S. anae	20	640	82	416	EU	II, **IV**	II	Peña Cantero et al. (2002)	CA
S. cumberlandicus	8	540	67	82	EU	IV	II, IV, V, VIII	Soto Àngel and Peña Cantero (2015)	CA
S. curvatus	49	2043	82	360	CS-SW+DW	I, II	I, II, XII	Peña Cantero et al. (2002)	CA
S. exochus	19	1958	62	352	EU	I, II, III, **XII**	I, II, III	Peña Cantero et al. (2002)	CA
S. frigidus	86	402	253	338	CS-SW	No	I, II	Peña Cantero et al. (2002)	WA
Sy. glacialis	5	1157	120	659	EU	XII	I, II, III, IV, IX, XII	Soto Àngel and Peña Cantero (2015)	PA
S. liouvillei	65	443	228	416	CS-SW	II, **XII**	I, II, III	Peña Cantero et al. (2002)	WAP
S. naumovi	0	1379	62	417	EU	I, II, **IV**, **XII**	I, II, III	Peña Cantero et al. (2002)	CA
S. paulensis	603	603	**268**	333	**CS-SW+DW**	No	-		W
S. plectilis	7	1958	68	337	EU	II, XII	The whole year	Peña Cantero et al. (2002)	CA
Sy. vanhoeffeni	6	964	177	277	EU	II	I, II	Peña Cantero et al. (2002)	CA
S. weddelli	119	390	**62**	**417**	CS-SW	II, **IV**, **XII**	I, II	Peña Cantero et al. (2002)	WED
A. operculata	63	1500	236	416	CS-SW+DW	No	I, II	Peña Cantero et al. (2004)	AP
H. cf. antarcticum	45	1157	254	758	CS-SW+DW	No	I	Peña Cantero (2014b)	**CA**
H. banzare	200	708	227	288	CS-SW+DW	I, **II**	I	Peña Cantero (2014b)	CA
H. exaggeratum	22	350	191	**360**	CS+SW	No	I	Vervoort (1972b)	CA
H. incertus	15	693	268	287	EU	XII	I, II, IV, XI, XII	Peña Cantero (2014b)	AK
H. interpolatum	3	728	62	**758**	EU	I, II, **IV**, XII	I, II, XII	Peña Cantero (2014b)	CA
H. jaederholmi	24	945	65	360	EU	No	I, IV, VI	Peña Cantero (2014a, 2014b)	PA
H. pseudodelicatulum	82	240	119	**360**	CS-SW	II, **XII**	II	Peña Cantero and Vervoort (2009), Peña Cantero (2013)	WA
H. pseudoincertus	96	1019	569	583	CS-SW+DW	No	Unknown	-	CA
H. secundum	40	150	119	**283**	CS-SW	I, **XII**	I	Jäderholm (1904)	CA
H. tubatum	163	163	**119**	**417**	CS-SW	No	Unknown	-	**CA**
H. arboreum	18	1370	62	175	EU	IV	I, II, IV, VI, VII, VIII, XI, XII	Peña Cantero and Ramil (2006)	PA
Sertularella sp.	-	-	177	177	**CS-SW**	-	-	-	-
A. baggins	-	-	65	116	**CS-SW**	I	I	Soto Àngel and Peña Cantero (2017a)	**WED**
Sc. glacialis	180	640	**129**	132	CS-SW+DW	**III**	I	Peña Cantero and Vervoort (1999)	CA
S. nana	43	1890	62	417	CS-SW+DW	I, II, **IV, XII**	I, II, III, V, VI	Peña Cantero and Vervoort (2005)	CA
S. unifurcata	15	567	62	417	EU	I, II, IV, **XII**	I, II, IV, XI	Peña Cantero and Vervoort (2005)	AK
O. delicata	126	440	**119**	120	CS-SW	No	II	Peña Cantero et al. (1997b)	WA
O. erratum	55	596	166	417	CS-SW+DW	I, II, **XII**	I, II, III, XI	González Molinero and Peña Cantero 2015	WA
O. rigida	80	1157	119	417	CS-SW+DW	No	I, II	Peña Cantero (2014a), González Molinero and Peña Cantero (2015)	CA
O. stepanjantsae	36	1890	62	417	EU	I, II, **IV**, XII	I, II, XII	González Molinero and Peña Cantero (2015)	CA
O. tottoni	256	400	**244**	277	CS-SW	**II, XII**	I	Peña Cantero and Vervoort (1996)	CA
B. subrufa	25	1030	62	583	EU	I, II, III, IV, XII	I, II, III, IV, V, X, XI, XII	Soto Àngel and Peña Cantero (2015)	AP

In terms of number of records, 333 previous historical records of 64 hydroid species from a total of 86 different stations have been compiled from previous studies in the Weddell Sea (cf. Tab. S5). We provide 560 additional records of 73 species collected from 57 different stations. In this sense, the geographic distribution pattern of several species has been changed thanks to the new findings reported here. Seven species are reported from West Antarctica for the first time, and they are tentatively considered as circum-Antarctic (Tab 4.2). Additionally, the present study has allowed us to report 13 rare species, i.e. found less than five times worldwide (*B. corynopsis*, *C. microrhiza*, *H. dendritica*, *H. exaggeratum*, *H. pseudoincertus*, *H. secundum*, *O. delicata*, *Sc. glacialis*, *S. frigidus*, *S. weddelli*, *T. longstaffi*, *Z. parvula*, *Z. hicksoni*). This study also represents the second Antarctic record for *S. paulensis*. According to Mercado Casares et al. (2017), and following the Antarctic regionalization by Douglass et al. (2014), the Weddell Shelf is the third Antarctic region in terms of hydrozoan diversity, with 64 known species of benthic hydroids (excluding Stylasteridae). In our study, 27 species are reported for the first time from the Weddell Sea, therefore increasing substantially the knowledge of the benthic hydroid fauna from this huge region. Thus, present contribution increases in 42% the number of hydroid species previously known from the Weddell Sea, becoming the second Antarctic area in terms of species richness, with a total of 91 species, only surpassed by the Antarctic Peninsula with 104 (cf. Mercado Casares et al. 2017).

The analysis of distribution patterns according to Peña Cantero and García Carrascosa (1999) reveals the dominance of species with circum-Antarctic distribution (39 species, 56%) (Tab 4.2). Eight species (12%) are only known from West Antarctica, two of which exclusively from the Weddell Sea. These two groups form the contingent of Antarctic endemisms, representing 68% of the species, a percentage slightly higher than the 63% reported by Soto Àngel and Peña Cantero (2017a) for the whole Antarctic region. Sixteen (23%) species are known from Antarctic and sub-Antarctic waters: six (9%) have an Antarctic-Kerguélen distribution, five (7%) species are considered Pan-Antarctic (i.e. Patagonia, Kerguélen and Antarctic waters), four (6%) Antarctic-Patagonian, and one is considered to have a West Antarctic-Patagonian distribution. Among the total species found, only six (9%) have wider distribution (i.e. reported outside Antarctic and sub-Antarctic waters).

Supplementary material (Appendix B)

Table S4: Substrate and epibionts of the species inventoried.

Table S5: Previous records of benthic hydroids from the Weddell Shelf.

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General discussion

Throughout this thesis, a total of 102 different species of benthic hydroids have been inventoried, 96 from Antarctic waters (59 from the Weddell Sea, 24 from the Scotia Arc and 13 from both regions) and six from the Patagonian region. On the whole, 10 species are first reported from Antarctic waters, unevenly distributed between the Scotia Arc (eight species, one new) and the Weddell Sea (two species, one new). In Patagonian waters, three species are evidenced for the first time for the region, including one new (Tab. 5.1).

Table 5.1 Main contributions and comparison among different sections of this thesis

	Contribution		**Source**
	Scotia Arc (Chapter I)	Weddell Sea (Chapter IV)	
Total species found/total species known (%)	37/127 (29%)	72/91 (79%)	Chapter I, II & IV / Chapter IV
New records for the Antarctic (new species)	8 (1)	2 (1)	Chapter I / Chapter III & IV
New records for the Patagonia (new species)	3 (1)	-	Chapter I
Species richness in the Patagonia (before/after)	195/198	-	Chapter I & II
Species richness in the Scotia Arc (before/after)	116/126	126/127	Chapter I & II / Chapter III & IV
Species richness in the Weddell Sea (before/after)	-	64/91	Mercado Casares et al. 2017, Chapter IV (Tab S5)
Endemic Antarctic species	38%	68%	Chapter I / Chapter IV
Sub-Antarctic + Antarctic species	25%	23%	Chapter I / Chapter IV
Wide distribution	23%	9%	Chapter I / Chapter IV

At a smaller scale, 11 representatives have been added to the inventory of Antarctic benthic hydroid species (ABHS from now on) for the Scotia Arc, and 27 to for the Weddell Sea, increasing in c. 10% and c. 42%, respectively, the number of species previously known from those regions (excluding Stylasteridae). On the other hand, 29% of the species known from the Scotia Arc has been reported (Chapter I), and 79% of those known to date from the Weddell Sea (Chapter IV). These differences are attributable to both unequal previous sampling effort between the regions, resulting in very different starting numbers (cf. Mercado Casares et al. 2017), and the amount of samples analyzed, much more numerous in the material from the Weddell Sea.

The contingent of endemic ABHS differs significantly between contributions: whereas the Scotia Arc collection harbors 38% of exclusively Antarctic species, it rises to 68% in the Weddell Sea collection. According to data provided in Chapter II, the endemism of the whole Antarctic region (c. 63%) is intermediate between those values, but closer to that from the Weddell Sea. Conversely, the species with a wide distribution (i.e. also known outside the Antarctic and sub-Antarctic regions) are distinctly higher in the Scotia Arc collection (Chapter I) than in the one from the Weddell Sea (Chapter II), with 23% and 9% respectively (Tab 5.1). The proportion of species present in both Antarctic and sub-Antarctic are quite similar between both collections, but slightly higher in the Scotia Arc (Tab 5.1). The multiple-origin (mainly sub-Antarctic) influence that receives the Scotia Arc, especially South Georgia (evidenced in Chapter II), is probably the reason of the differences observed. In other words, the Scotia Arc fauna promotes a decrease in the endemism rate of ABHS by its rich, widely distributed, hydroid diversity (Chapter I). However, as underlined in Chapter II, some unique endemisms are known from that region, which also contributes to the total number of endemisms from the Southern Ocean.

Regarding the species richness of ABHS, the catalogue provided by Soto Àngel and Peña Cantero (2017a) (Chapter II and Tab. S1) updates the current knowledge on the diversity and distribution of this zoological group, calibrated with the newest taxonomical contributions (e.g. Peña Cantero 2014a). In this sense, the inventory also includes benthic hydroids from the Patagonian region and, for the first time, species of Stylasteridae and benthic hydromedusae known from both Antarctic and Patagonian waters. Compared with the latest available data on species richness offered by Peña Cantero (2014b), who named 177 ABHS, the present inventory provides 49 new entries [including 21 species of Stylasteridae, and the eight new records from Soto Àngel and Peña Cantero (2015) among others], resulting in a total of 226 ABHS. To this number it should be added the new species *Aglaophenia baggins* described here (Chapter III). Thus, a total of 227 benthic hydroids (including Stylasteridae) are presently known in the Antarctic region.

In relation to the scientific literature dealing with ABHS, and excluding specific taxonomic references in which no new material was considered, some issues are discussed below in order to adequately contextualize the contributions derived from this monograph.

When analyzing the new records of ABHS per contribution and per year, several periods can be distinguished. An early phase, with a logical clear acceleration is observed (Fig. 5.1a-b). The first five references (6% of the total) yielded a total of 36 different species (c. one fifth of the total) between 1888 and 1905, highlighting the collections reported by Hartlaub (1904) and Jäderholm (1904, 1905). Approximately half of the known ABHS had already been found within the first quarter of the contributions, in the period between 1888 and 1930, with special relevance of the works by Hickson and Gravely (1907) and Vanhöffen (1910) (i.e. the two highest points in Fig. 5.1c). After this period, between 1930 and 1970, the number of contributions reached minimum levels, with just five references in 40 years (Fig. 5.1a). They were, however, relatively rich in number of new records (Fig. 5.1c, standing out the work by Naumov and Stepanjants (1962). From the early 1970s to mid-1990s, there were three times more references than in the previous period (Fig. 5.1a), but little prolific in terms of number of new records for the Antarctic region, with the exception of Stepanjants (1979) (Fig. 5.1c). At this point, in the history of the study of Antarctic benthic hydroids, 118 species (61% of the total) had been found in the first 35 (46% of the total) contributions (Fig. 5.1a), though most of these taxa would be described in the following decades. From mid-1990s to nowadays, 40 references (54%) reported 77 (39%) new records of ABHS in just two decades, at a similar rate than early discoveries (Fig. 5.1a). Several of these contributions reported a large number of species (usually more than 15, Fig. 5.1d), but few new records of ABHS per reference were provided (Fig. 5.1c). This is virtually the opposite of early scientific literature, which evidenced many new records each (Fig. 5.1c). Among the contributions in this last period, Peña Cantero and García Carrascosa (1995), and Soto Àngel and Peña Cantero (2015) (i.e. Chapter I) were those with more new records for Antarctic waters, with seven new records each (excluding taxa not determined at species

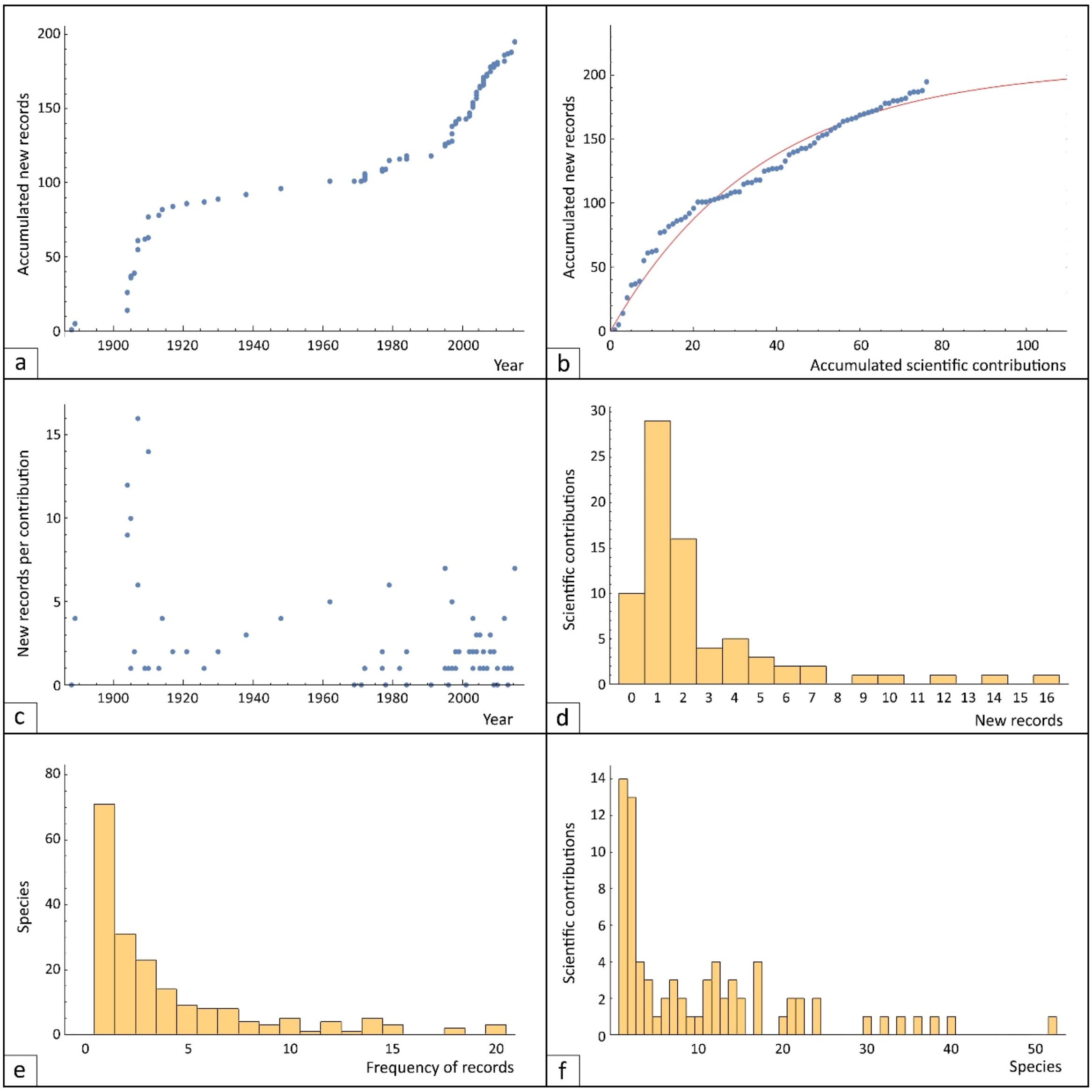

Figure 5.1 **a** Accumulated new records per year. **b** Accumulated new records per accumulated contributions. **c** Number of new records per contribution per year. **d** Number of contributions per number of new records. **e** Number of species per frequency of records. **f** Number of contributions per number of species

level). Both studies were focused on the same region: the Scotia Arc. Considering all the publications together, the vast majority (55 out of 76, 72%) reported zero, one, or two new records (Fig. 5.1d). The mean is located around 2.5 new records per reference. Finally, the contribution by Hickson and Gravely (1907) is, until now, the most prolific reference in terms of new records of benthic hydroids from the Southern Ocean.

Concerning the frequency of records of ABHS in the scientific literature (Fig. 5.1e), 71 species (36%) have been found in a single occasion, 125 species (64%) three times or less, and most (148 species, 76%) five times or less. These species can be regarded as rare, although it is worth mentioning that several of them (e.g. *Filellum magnificum*) have been described in the last decade (see Xavier et al. 2013). Other species, such as *Hydractinia dendritica*, reported here for the second time (Chapter IV), had not been found since their original description, more than a hundred years ago (Hickson and Gravely

1907). On the other hand, very few species are cited more than 20 times (Fig 5.1e): *Billardia subrufa*, *Symplectoscyphus glacialis* and *Symplectoscyphus plectilis*. These species are widely distributed through Antarctic waters and can be considered very common; findings presented in Chapter I and IV concur.

The analysis in reverse reveals that 14 contributions (18% of the total) dealt with a single ABHS, and 13 (17%) focused on two taxa each (Fig. 5.1f). Only in seven cases (9%) more than 30 species were cited, and only in four (5%) more than 35. Among them, Soto Àngel and Peña Cantero (2015) (Chapter I), with 36 species from the Scotia Arc. The study dealing with more ABHS reported 51 species from the South Shetland Islands and nearby waters (Peña Cantero 2008). In this sense, it is noteworthy that 73 species are documented in Chapter IV, dealing with the Weddell Sea collection, making it the largest contribution to date in terms of number of ABHS recorded.

In light of the information presented here, it could be deduced that the number of the known ABHS, whose increment decreases over time, is close to reach the asymptote (Fig. 5.1b). However, the inclusion of many references reporting a single species (not excludable because they deal with a new record) strongly forces the curve towards the asymptote. Indeed, as aforementioned, the study of ABHS has gone through periods of much acceleration, and others in which the activity slowed down (the latter situated under the curve in Fig. 5.1b). In this sense, the heterogeneity of the data, and the uneven sampling effort in space and time, prevent from considering the accumulation curve (i.e. Fig. 5.1b) as reliable (see Pardo et al. 2013 and literature cited). Therefore, we are still in process of understanding the true species richness of the ABHS. As an example, the Mediterranean Sea includes 400 hydrozoan species, excluding siphonophora (Gravili et al. 2013), while in the Weddell Sea, of relatively similar surface area but of larger volume, less than one fourth are known. The recent record of the family Aglaopheniidae in the Southern Ocean (Soto Àngel and Peña Cantero 2017b, Chapter III) constitutes another example showing that our knowledge of the species richness and diversity of benthic hydroids from Antarctic waters is far from being complete. This assumption is particularly evident for some regions (principally East Antarctica) where the hydrozoan fauna is almost completely unknown (see Peña Cantero 2014b and literature therein), and for some taxa, especially within Anthoathecatae, whose diversity has not been evaluated in detail.

Present thesis has contributed to increase knowledge of several aspects of the benthic hydroids from Antarctic waters. However, a great array of topics with ABHS as a subject of study is still scarcely developed. Few contributions exist dealing with trophic ecology (e.g. Orejas et al. 2000), environmental factors affecting distribution (e.g. Peña Cantero and Manjón Cabeza 2014), recolonization processes (e.g. Teixidó et al. 2004) and symbiotic associations (e.g. Piraino et al. 2003; Gili et al. 2006). Multidisciplinary approaches and collaborative teamwork will undoubtedly be the framework that will enable to reach a greater, wider and better understanding of this group of amazing, extraordinarily diverse Antarctic inhabitants.

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Conclusions

Through this thesis, several aspects concerning benthic hydrozoans from the Antarctic region have been analyzed, contributing to a better understanding of their diversity, ecology and biogeography. The conclusions reached for each topic are described in detail in the corresponding chapters. The general conclusions emerging from the study are:

- The complete catalogue of Antarctic benthic Hydrozoa known to date includes 227 species, of which 63% are Antarctic endemisms.
- The collections analyzed contained a total of 102 species of benthic hydroids, 96 of which from Antarctic waters and six species from the Patagonian region.
- Ten new records from Antarctic waters are provided: eight from the Scotia Arc, and two from the Weddell Sea.
- Twenty-seven new records of benthic hydroids for the Weddell Sea, and eleven from the Scotia Arc have increased in c. 42% and 10%, respectively, the number of species known in these regions.
- The Weddell Sea collection is mainly composed of Antarctic endemisms (68%), while the collection from the Scotia Arc contained 38% of exclusively-Antarctic species.
- Three new species to science have been described, one from the Scotia Arc (*Schizotricha discovery* sp. nov), one from the Weddell Sea (*Aglaophenia baggins* sp. nov), and one from the Patagonian region (*Halecium stoloniferum* sp. nov).
- The finding of *Aglaophenia baggins* sp. nov constitutes the first evidence of the family Aglaopheniidae from Antarctic waters, and the first report of the genus for any polar region.
- *Oswaldella stepanjantsae* is the second species in the genus in which a triseriate arrangement of the cauline apophyses has been documented.
- *Halecium brevithecum* is considered as a junior synonym of *Halecium secundum*.
- *Halecium tubatum* is considered a valid species based mainly on cnidome characteristics.
- *Campanularia hicksoni* displays differences in the size of the nematocysts as a function of hydrothecal size (i.e. polyp size).
- *Zanclea hicksoni* (Fam. Zancleidae) presents morphological characteristics that bring it closer to the genus *Monocoryne* (Fam. Candelabridae).
- The known bathymetric range has been extended for 30 species, 11 from the Scotia Arc and 19 from the Weddell Sea; and seven species, two from the Scotia Arc and five from the Weddell Sea, are re-allocated into a new bathymetric group.
- The reproductive phenology has been extended for a total of 44 species: 12 from the Scotia Arc and 32 from the Weddell Sea.

- A new biogeographic pattern has been assigned to eleven species: four from the Scotia Arc collection and seven from the Weddell Sea.
- A considerable change in the faunistic affinities of benthic hydroids between Burdwood Bank and South Georgia has been detected, probably evidencing the strong effect of the Polar Front as a barrier for dispersal.
- The benthic hydroids from the Scotia Arc (including South Georgia) present higher affinity with High Antarctica than with the Patagonian region. Consequently, the whole Scotia Arc can be regarded as part of the Antarctic region.

Resum en valencià

Introducció:

Les comunitats bentòniques que es desenvolupen a les aigües antàrtiques són altament singulars com a resultat d'un ambient relativament estable i aïllat. Tal aïllament és degut, entre altres factors, a la presència de la convergència Antàrtica, una forta barrera (o filtre) de temperatura i salinitat, que circumscriu de forma efectiva un dels ecosistemes marins més discrets i isolats geogràficament.

Els factors abans esmentats han jugat un paper important en el desenvolupament d'un dels ecosistemes més rics del món pel que respecta a diversitat de fauna marina sèssil. Així doncs, la plataforma Antàrtica, més profunda que qualsevol altra plataforma continental, està constituïda principalment per fons tous que alberguen comunitats d'animals suspensívors bentònics, i dins d'aquestes, els representants del fílum Cnidaria són un dels principals contribuents a l'estructura tridimensional del medi, actuant com a formadors d'habitat. A més, són estabilitzadors de substrat, proporcionen zones d'alevinatge i intervenen en els processos d'acoblament bentopelàgic.

Els hidrozous, un dels principals grups de cnidaris amb vora 3700 espècies descrites fins a la data, són un taxó ben definit amb una enorme plasticitat de cicles de vida, que al seu torn es tradueix en una gran varietat de morfologies, d'ús de l'hàbitat, d'estratègies tròfiques i d'adaptacions ecològiques. Els seus representants bentònics són un dels components més conspicus del bentos antàrtic, i un dels grups zoològics més diversificats i característics de la regió, amb un baix nombre de gèneres, sis dels quals (*Antarctoscyphus*, *Halecium*, *Oswaldella*, *Schizotricha*, *Staurotheca*, *Symplectoscyphus*) presenten una elevada diversitat. L'estudi dels hidrozous bentònics a l'oceà Antàrtic va començar simultàniament amb el d'altres grups taxonòmics a través de diverses expedicions realitzades a la fi del segle XIX i principis del XX. En els darrers anys, la producció científica amb hidrozous bentònics antàrtics s'ha accelerat considerablement, fet que ha contribuït enormement a reduir els buits d'informació en diferents vessants. No obstant això, el coneixement dels hidrozous bentònics antàrtics és encara ben limitat en algunes zones de l'oceà Antàrtic i en alguns taxons concrets.

Objectius:

El principal objectiu d'aquesta tesi és millorar el coneixement actual dels hidrozous bentònics antàrtics en tres aspectes complementaris. Per tal d'assolir-ho, es plantegen els objectius que figuren a continuació:

1) Estudi taxonòmic i catalogació de les col·leccions inèdites ANT XV/3, ANT XVII/3, ANT XIX/5, ANT XXI/2 esdevingudes a l'Arc de Scotia i al mar de Weddell, incloent una millor caracterització d'alguns taxons i, si escau, la descripció de noves espècies.

2) Incrementar el coneixement de la fenologia reproductiva, la distribució batimètrica i geogràfica, i l'ús del substrat de les espècies inventariades.

3) Realització d'un inventari complet dels hidrozous bentònics de les regions antàrtica i patagònica.

4) Anàlisi de les afinitats faunístiques, la riquesa específica i el nivell d'endemisme dels hidrozous bentònics de l'Arc de Scotia.

5) Estudi de les tendències i els patrons en la producció de la literatura científica sobre els hidrozous bentònics antàrtics.

Metodologia:

1) Estudi taxonòmic i catalogació.

Es procedeix al triatge a nivell de gènere, i posterior identificació a nivell d'espècie/morfoespècie de la totalitat del material procedent de les col·leccions inèdites d'hidrozous bentònics recollides durant les campanyes oceanogràfiques alemanyes ANT XV/3, ANT XVII/3, ANT XIX/5 i ANT XXI/2 realitzades a bord del *RV Polarstern*. Les campanyes ANT XV/3, ANT XVII/3 i ANT XXI/2 es van dur a terme a l'àrea més oriental del mar de Weddell (Antàrtida occidental), a la plataforma de gel Riiser-Larsen, majoritàriament a les immediacions del cap Norvegia, a la costa Princesa Martha. La campanya ANT XIX/5 s'esdevingué a l'Arc de Scotia (oceà Antàrtic) i al banc Burdwood (Patagònia). Si escau, es descriuen espècies noves per a la ciència. El material examinat s'ha il·lustrat mitjançant càmera clara acoblada a microscopi òptic i s'han obtingut imatges digitals mitjançant captura d'imatge acoblada tant a estereomicroscopi com a microscopi òptic. El material s'ha catalogat mitjançant l'ús d'un identificador distintiu i la informació obtinguda s'ha desat en una base de dades que inclou, addicionalment, dades accessòries del material inventariat: presència d'estructures reproductores, substrat, localitat i profunditat de la mostra, i presència d'epibionts.

2) Actualització de l'ecologia i la distribució.

Es realitza una revisió bibliogràfica de la totalitat de cites de les espècies inventariades per redefinir, i ampliar si escau, els períodes de reproducció, el rang batimètric, el llistat d'espècies per localitat, així com els patrons de distribució prèviament coneguts. Per a cada regió d'estudi, s'analitzen els patrons de distribució biogeogràfica de les espècies registrades, es comparen amb estudis previs i es discuteixen les diferències observades.

3) Inventari complet dels hidrozous bentònics antàrtics.

S'ha revisat la totalitat de la literatura científica que inclou cites d'hidrozous bentònics de les regions antàrtica i patagònica per produir el primer catàleg complet d'hidrozous bentònics de les regions esmentades. El llistat s'ha confeccionat i calibrat tenint en compte les més recents contribucions científiques per tal d'evitar la duplicació d'entrades (sinonímies), o la inclusió d'espècies la presència de les quals no està fidedignament contrastada en aigües antàrtiques.

4) Afinitats faunístiques dels hidrozous bentònics de l'Arc de Scotia.

S'ha elaborat una taula de presència/absència amb la totalitat d'espècies citades per a les diferents regions d'estudi. A partir d'aquestes dades s'han obtingut matrius de similitud amb diferents índexs (Jaccard i Sørensen) i s'han agrupat mitjançant tècniques d'aglomeració jeràrquica (Cluster). Paral·lelament es representa gràficament la distància entre entitats geogràfiques mitjançant *non-Metric Multidimensional Scaling* (*nMDS*). S'analitzen conjuntament el percentatge d'endemismes per a cada àrea de l'Arc de Scotia i per a la regió antàrtica. Els resultats obtinguts es discuteixen en el marc conceptual de la biogeografia global de l'oceà Antàrtic, mitjançant la comparació amb estudis previs amb altres grups d'invertebrats bentònics.

5) Estudi de la tendència en la producció científica sobre hidrozous bentònics antàrtics.

S'han recopilat els primers registres per a l'Antàrtida de totes les espècies inventariades d'hidrozous bentònics antàrtics (excloent Stylasteridae), així com el nombre d'espècies tractades en cada article. S'han contextualitzat, en diferents aspectes, les contribucions derivades de la present tesi amb el conjunt d'articles publicats des de l'inici de les investigacions sobre el grup en aigües antàrtiques.

Resultats i discussió:

S'han inventariat un total de 45 espècies d'hidrozous bentònics a la col·lecció de l'Arc de Scotia, pertanyents a nou famílies i 20 gèneres. Quaranta espècies han sigut identificades a nivell d'espècie, de les quals dues són noves espècies per a la ciència: *Halecium stoloniferum* sp. nov i *Schizotricha discovery* sp. nov. Leptothecata va ser el taxó més dominant amb 42 espècies, mentre que Anthoathecata només fou representat per tres espècies. Quinze de les espècies observades (38%) són endèmiques de la regió antàrtica, mentre que 31 (78%) estan restringides a les aigües antàrtiques i/o subantàrtiques. Els registres de *Schizotricha southgeorgiae*, *Halecium elegantulum* i *Sertularella argentinica* suposen la segona menció a nivell mundial d'aquestes espècies, mentre que els registres de *Schizotricha jaederholmi*, *Antarctoscyphus gruzovi* i *Sertularella jorgensis* constitueixen la tercera menció a nivell mundial. S'ha estés el rang batimètric prèviament conegut per a 11 espècies, i la fenologia reproductiva de 12 espècies. A 11 espècies se'ls ha assignat un nou patró de distribució biogeogràfica.

Els resultats de l'anàlisi de les afinitats faunístiques dels arxipèlags de l'Arc de Scotia mostren una major afinitat entre aquests i l'Antàrtida continental que amb la regió de la Patagònia. S'observa, a més, un augment de similitud a mesura que augmenta la proximitat amb l'alta Antàrtida. Aquests resultats destaquen la importància de l'Arc de Scotia com un pont biogeogràfic, i evidencien l'eficàcia del front polar com a barrera (o filtre) per a la dispersió. Aquest estudi dóna suport a la inclusió de tot l'Arc de Scotia dins de la regió antàrtica. Addicionalment, s'ha inventariat un total de 226 espècies d'hidrozous bentònics antàrtics, amb 49 entrades més que l'últim recompte, i s'ha actualitzat el nivell d'endemisme per a hidrozous antàrtics, resultant en un 63%. Es tracta, a més, del primer catàleg que inclou els hidrocoralls i les hidromeduses bentòniques.

Una nova espècie pertanyent al gènere *Aglaophenia* s'ha descrit a partir de material recollit en l'extrem est del mar de Weddell, entre els 65 i 116 m. Aquesta troballa constitueix un nou registre per a la fauna del mar de Weddell, però també és la primera evidència de la presència d'aquest gènere en qualsevol regió polar, i el primer registre per a la família Aglaopheniidae a les aigües antàrtiques. A través d'un examen exhaustiu s'ha descrit el material examinat com a *Aglaophenia baggins* sp. nov. S'ha tractat d'aportar llum sobre el possible origen d’aquest grup prèviament desconegut a la regió antàrtica. Les dues explicacions més probables inclouen la possible arribada d’*Aglaophenia baggins* a l'Antàrtida (ja siga pels seus propis mitjans o mitjançant formes antropogèniques) o més probablement l'existència d'una població natural al mar de Weddell prèviament desconeguda.

Respecte de la col·lecció d’hidrozous de la mar de Weddell, s’han trobat 77 espècies pertanyents a 21 famílies i 28 gèneres, convertint-se així en la col·lecció més prolífica d’hidrozous bentònics antàrtics en termes de nombre d'espècies. El 81% de les espècies pertanyen a Leptothecata, mentre que el 19% són representants d’Anthoathecata. Tot i que menys nombrosos, els atecats representen un increment sensible en el nombre d'espècies reportades en altres col·leccions similars. Symplectoscyphidae va ser la família amb més espècies, seguida per Haleciidae i Staurothecidae. Al contrari que en la majoria de contribucions anteriors, la família Sertulariidae no va estar representada, sent això conseqüència de profunds canvis recents en la sistemàtica de Leptothecata. S’ha contribuït, a més, a una millor coneixença taxonòmica d’algunes espècies, com ara *Campanularia hicksoni*, *Oswaldella stepanjantsae* i *Zanclea hicksoni*. Les espècies euribàtiques dominen en la col·lecció. *Schizotricha nana* va ser l'espècie que albergava el major nombre d’espècies d’hidrozous, amb 23 espècies diferents. D’altra banda, *Phialella belgicae* va ser l'espècie amb l'ús més estès d'altres hidrozous com a basibionts. La col·lecció està composta majoritàriament per endemismes antàrtics, amb 47 representants (68%), seguit del grup d’espècies presents en aigües subantàrtiques amb 16 espècies (23%), i sis espècies (9%) d’ampla distribució. S’evidencia per primera vegada a l’Antàrtida occidental un total de set espècies, essent considerades temptativament com a espècies de distribució circumantàrtica. A més, el present estudi aporta una nova cita en tretze espècies rares (trobades en menys de cinc ocasions a nivell mundial). Notablement, 27 espècies es registren per primera vegada al mar de Weddell, augmentant substancialment el coneixement de la fauna bentònica d’hidrozous d'aquesta regió. Per tant, la plataforma de Weddell es destaca com a la segona regió antàrtica en termes de diversitat d’hidrozous bentònics, amb 91 espècies conegudes (excloent Stylasteridae). El rang batimètric prèviament conegut s’ha ampliat per a 19 espècies, i a cinc d’elles se’ls ha assignat un patró de distribució batimètric diferent. La fenologia reproductiva s’ha estés per a 32 espècies.

Conclusions:

A través d’aquesta tesi, s’ha contribuït a un millor coneixement dels hidrozous bentònics antàrtics pel que fa a la seua diversitat, ecologia i biogeografia. S’ha inventariat un total de 102 espècies, 96 d’elles antàrtiques, i sis patagòniques. S’ha contribuït a una millor coneixença taxonòmica d’algunes espècies. S’ha esclarit l’afinitat faunística dels hidrozous bentònics de l’Arc de Scotia, podent ésser considerat com a part de la regió antàrtica. S’ha actualitzat el catàleg d’espècies d’hidrozous antàrtics, amb un total de 227 espècies, i el percentatge d’endemismes, un 63%, incloent la descripció de tres espècies noves per a la ciència, i el primer registre de la família Aglaopheniidae en aigües antàrtiques. S’han aportat nombroses noves cites per a l’Arc de Scotia (11 espècies) i el mar de Weddell (27 espècies) en concret, i per a l’Antàrtida en general (10 espècies). S’ha actualitzat, en nombrosos taxons, el rang batimètric, la fenologia reproductiva i la distribució prèviament coneguda.

Appendix A

Original publication reprints

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ORIGINAL PAPER

On the benthic hydroids from the Scotia Arc (Southern Ocean): new insights into their biodiversity, ecology and biogeography

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Abstract The Scotia Arc, located between the Antarctic Peninsula and the southern tip of South America, is an important zone from the biogeographic point of view. Its benthic biodiversity has been extensively documented with a few exceptions, among others, the hydroid fauna, which constitutes one of the major components of the benthic Antarctic communities. With the aim of increasing the data in three different but complementary fields of knowledge (namely biodiversity, ecology and biogeography), an unpublished collection obtained during the German Antarctic expedition ANTARKTIS XIX/5 (LAMPOS) with the *RV Polarstern* in 2002 has been studied. A total of 45 species of benthic hydroids, belonging to 9 families and 20 genera, was found. Forty of them, including *Halecium stoloniferum* sp. nov. and *Schizotricha discovery* sp. nov., were identified to the species level. Leptothecata was by far the most dominant order with 42 species, while Anthoathecata was only represented by 3 species. Fifteen species (38 %) are endemic to the Antarctic region and 31 (78 %) restricted to Antarctic and/or sub-Antarctic waters. *Schizotricha southgeorgiae*, *Halecium elegantulum* and *Sertularella argentinica* are reported for the second time, whereas *Schizotricha jaederholmi*, *Antarctoscyphus gruzovi* and *Sertularella jorgensis* for the third time. New original autoecological data concerning the use of the substrate, reproductive phenology and bathymetric range of the inventoried species are provided.

Keywords Biodiversity · Biogeography · Hydrozoa · New records · New species · Scotia Arc

Introduction

The Scotia Arc is an island arc with a volcanic origin, located in the Southern Ocean between Tierra del Fuego and the Antarctic Peninsula. It comprises an island arc system that surrounds the so-called Scotia Sea. The arc includes submarine ridges and the islands of Isla de los Estados, Shag Rocks, South Georgia, South Sandwich Islands, South Orkney Islands, Elephant Island and South Shetland Islands. The region is completely encompassed by the Antarctic convergence, unlike the neighbor sub-Antarctic Patagonian shelf, although South Georgia and Shag Rocks are north of the Antarctic Circumpolar Current (Orsi et al. 1995). The mentioned oceanographic particularities make the Scotia Arc an interesting biogeographic transition zone because of its position among High Antarctica and the Magellan region, as has been underlined by many authors (e.g., Arntz and Ríos 1999; Arntz 2005).

The benthic hydroids from the entire Scotia Arc were previously studied as a whole by Peña Cantero and García Carrascosa (1995), who also studied their distribution patterns (Peña Cantero and García Carrascosa 1999). However, there are only a few punctual records on some areas such as South Georgia (Jäderholm 1904, 1905; Broch 1948; Naumov and Stepanjants 1962), the South Orkney Islands (Billard 1906; Ritchie 1907) and the South Shetland Islands (Hartlaub 1904; Broch 1948; Galea and Schories 2012). The Discovery Bank, located between the South Sandwich Islands and South Orkney Islands, constitutes a previously unknown area for hydrozoans.

In addition, some of the hydroids studied were collected outside the Scotia Arc, specifically in Burdwood Bank and

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ORIGINAL PAPER

A new piece in the puzzle of the Antarctic Biogeography: What do benthic hydroids tell us about the Scotia Arc affinities?

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Abstract The biogeography of the Southern Ocean and its subdivisions has attracted the interest of the scientific community for many years, especially for those border regions with great sub-Antarctic influence. The Scotia Arc, located between the Antarctic Peninsula and the Magellan region, has been considered as a biogeographic bridge and hence widely discussed, but there are still gaps in the knowledge of some zoological groups and its inclusion in truly Antarctic waters still constitutes an unresolved topic. The faunistic affinities between the benthic hydroids from the Scotia Arc and those from nearby regions (i.e., High Antarctica, Patagonian region and Bouvet Island) were evaluated with different similarity index and hierarchical analyses in order to put into evidence the biogeographic connectivity among those regions. The results show that the Scotia Arc archipelagos have greater affinity with continental Antarctica than with the Patagonian region, with an increasing similarity while approaching to High Antarctica, highlighting their importance as a biogeographic bridge and the effectiveness of the Polar Front as a major oceanographic barrier. Evidences from the present study on benthic hydroids supports the placement of the whole Scotia Arc within of the Antarctic region. Present data were compared with those from other benthic invertebrates groups to contribute to a better understanding of the biogeography of the Scotia Arc as a whole.

Keywords Hydrozoa · Scotia Arc · Biogeography · Endemism · Species richness

Introduction

The Antarctic region has a well-defined northern limit due to a major oceanographic barrier, the Antarctic Convergence (Crame 1999), also known (although without consensus) as the Antarctic Polar Front. This oceanographic feature remains in a remarkably constant position (Thomas et al. 2008; but see also Moore et al. 1999) and contributes to the isolation of the fauna inhabiting Antarctic waters. As a barrier, it signals the location where Antarctic surface waters sink below sub-Antarctic waters (Deacon 1933), with the subsequent development of strong latitudinal gradients of temperature and salinity (i.e., density), thus constituting "one of the strongest natural boundaries in the world ocean" (Crame 1999). Despite this well-established delimitation, however, the subdivision of the Antarctic region and nearby areas into biogeographic provinces and the biogeographic affinity of the bordering regions are still a matter of controversy.

In this regard, the Scotia Arc, with its intermediate position between the Magellan region and the Antarctic Peninsula, has greatly attracted the interest of the scientific community in recent times. The origin of the different sectors included in the Scotia Arc (i.e., Shag Rocks, South Georgia, South Sandwich Islands, South Orkney Islands, Elephant Island and South Shetland Islands) dates back to

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Inhabitant or visitor? Unexpected finding of *Aglaophenia* (Cnidaria, Hydrozoa) in Antarctic waters

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Abstract: Benthic hydrozoans are one of the most speciose and characteristic taxa from the Antarctic region, with a high number of endemic species, but diversity at the genus level is low and some families with world wide distribution are unrepresented. This is the case of the family Aglaopheniidae. A new species to science of the genus *Aglaophenia* Lamouroux has been found in the eastern end of the Weddell Sea, at depths of 65–116 m, within the material obtained by the German Antarctic expedition ANT XV/3. This finding constitutes a new record for the Weddell Sea fauna, the first evidence of the genus for the Polar Regions, and even the family Aglaopheniidae from Antarctic waters. The material has been accurately examined and described. Literature concerning the species of *Aglaophenia* from the sub-Antarctic and other close areas has been reviewed and, as a result, a checklist of 20 species, with their corresponding distribution, is given. The material examined does not agree with any of the species and therefore it is described as a new species. Some possible scenarios for the presence of an aglaopheniid in Antarctic waters are discussed (e.g. alien species, relict, global climate change, microhabitat).

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Key words: *Aglaophenia baggins*, global climate change, new records, new species, Weddell Sea

Introduction

Aglaopheniidae Marktanner-Turneretscher constitutes one of the most diverse and well-known families of benthic hydroids, comprising *c.* 250 known species (Bouillon *et al.* 2006). The distinction at the genus level is based mainly on the gonosome typology, as the trophosome is relatively constant among genera. Its representatives are widely distributed from temperate to tropical waters and from shallow to deep regions. Within the family, there are some differences in the general distribution of different genera: *Macrorhynchia* is more common in tropical and subtropical waters, *Aglaophenia* in tropical, subtropical and temperate waters, *Cladocarpus* in Arctic and deep sea waters, and *Lytocarpia* in temperate, Arctic and sub-Antarctic waters. Nevertheless, despite their wide distribution, aglaopheniids have never been reported south of the Polar Front.

Members of the genus *Aglaophenia* are characterized by feather-like, branched or unbranched, monosiphonic or polysiphonic stems (cormoids); unbranched, pinnately arranged hydrocladia, arising from alternate apophyses provided with two lateral nematothecae and a median inferior one; hydrothecae only on hydrocladia, from cone to sac-shaped; each hydrotheca typically flanked by a pair of adnate, lateral nematothecae and with a partly to wholly adnate, median inferior nematotheca; reproductive structure, named corbula, enclosing gonophores within modified hydrocladia, bearing alternately inserted secondary ribs with nematothecae; corbula ribs from completely free to totally fused; fixed sporosacs or released swimming gonophores (modified from Bouillon *et al.* 2006).

The effects of global climate change (anthropogenic impacts coupled with global warming) are pushing some species to change their distribution to maintain their thermal optimum. Thus, some species with warm affinity are extending their geographical distribution to areas where it would have been impossible for them to live (due to low temperatures) just a few decades ago (Hughes 2000). In general, most contributions concerning changes in fauna composition and distribution in marine ecosystems (within a perspective of global climate change) have been focused on plankton or nekton, while benthic communities have been practically neglected, above all those inconspicuous groups without commercial value (see González-Duarte *et al.* 2014 and references therein). With a few exceptions (i.e. Puce *et al.* 2009, González-Duarte *et al.* 2014), long-term changes in the distribution of benthic hydroids are not well documented and there is still a need to establish a comprehensive baseline database to enable future comparisons among benthic hydroid assemblages.

The Antarctic shelf benthic communities are dominated by benthic suspension feeders. The top predators are

Appendix B

Supplementary tables and figures

Table S1 Presence/absence data matrix and species richness for Antarctic, Scotia Arc and Patagonian benthic hydrozoans [Western Patagonia (WP), Eastern Patagonia (EP), Falkland Islands (FI), Burdwood Bank (BB), Shag Rocks (SR), South Georgia (SG), South Sandwich Islands (SSI), Discovery Bank (DB), South Orkney Islands (SO), Elephant Island (EI), South Shetland Islands (SHI), West Antarctica (WA), East Antarctica (EA) and Bouvet Island (BI)]

Family	**Species**	**WP**	**EP**	**FI**	**BB**	**SR**	**SG**	**SSI**	**DB**	**SO**	**EI**	**SHI**	**WA**	**EA**	**BI**
Bougainvilliidae Lütken, 1850															
	Bimeria vestita Wright, 1859	1	1												
	Bimeria corynopsis Vanhöffen, 1910													1	
	Bougainvillia macloviana Lesson, 1836													1	
	Bougainvillia muscoides (M. Sars, 1846)	1													
	Bougainvillia muscus (Allman, 1863)	1	1												
	Bougainvillia pyramidata (Forbes & Goodsir, 1851)	1													
	?Koellekerina belgicae (Vanhöffen, 1910)												1	1	
	Rhizorhagium antarcticum (Hickson & Gravely, 1907)												1	1	
Family Clathrozoellidae Peña Cantero, Vervoort & Watson, 2003															
	Clathrozoella abyssalis Peña Cantero, Vervoort & Watson 2003													1	
	Clathrozoella drygalskii (Vanhöffen 1910)													1	
	Clathrozoella medeae Peña Cantero, Vervoort & Watson 2003									1	1	1		1	
Cordylophoridae von Lendenfeld, 1885															
	Cordylophora caspia (Pallas, 1771)	1													
Oceaniidae Eschscholtz, 1829															
	Rhizogeton nudus Broch, 1910		1												
Pandeidae Haeckel, 1879															
	Leuckartiara octona (Fleming, 1823)	1	1	1											
	Neoturris cf. *pileata* (Forsskål, 1775)												1		
Cytaeididae L. Agassiz, 1862															
	Perarella clavata (Jäderholm, 1905)											1	1		
Hydractiniidae L. Agassiz, 1862															
	Hydractinia angusta Hartlaub, 1904											1	1	1	
	Hydractinia dendritica Hickson & Gravely, 1907												1		
	Hydractinia humilis Hartlaub, 1905	1	1												
	Hydractinia pacifica Hartlaub, 1905	1												1	
	Hydractinia parvispina Hartlaub, 1905	1	1	1			1						1	1	
	Hydractinia vallini Jäderholm, 1926													1	
	Podocoryna borealis (Mayer, 1900)	1													
Corymorphidae Allman, 1872															
	Branchiocerianthus norvegicus Brattström, 1956		1												
	Corymorpha microrrhiza (Hickson & Gravely, 1907)												1	1	
	Gymnogonos ameriensis (Stepanjants, 1979)													1	
	Gymnogonos antarcticus (Pfeffer, 1889)						1								
	Gymnogonos cingulatus (Vanhöffen, 1910)													1	

Family	Species	WP	EP	FI	BB	SR	SG	SSI	DB	SO	EI	SHI	WA	EA	BI
Cladonematidae Gegenbaur, 1857															
	Staurocladia vallentini (Browne, 1902)	1		1											
	Staurocladia charcoti (Bedot, 1908)						1					1	1		
Eudendriidae L. Agassiz, 1862															
	Eudendrium antarcticum Stechow, 1921						1				1	1	1	1	
	Eudendrium arbuscula Wright, 1859	1	1												
	Eudendrium bentart Peña Cantero, 2013											1			
	Eudendrium capillare Alder, 1856												1		
	Eudendrium cyathiferum Jäderholm, 1904						1								
	Eudendrium deforme Hartlaub, 1905	1													
	Eudendrium generale von Lendenfeld, 1885							1	1				1	1	
	Eudendrium jaederholmi Puce, Cerrano & Bavestrello, 2002						1								
	Eudendrium laxum Allman, 1877		1												
	Eudendrium cf. *nambuccense* Watson, 1985	1													
	Eudendrium rameum (Pallas, 1766)	1	1	1	1									1	
	Eudendrium ramosum (Linnaeus, 1758)		1				1						1	1	
	Eudendrium scotti Puce, Cerrano & Bavestrello, 2002											1	1	1	
	Eudendrium tottoni Stechow, 1932													1	
Corynidae Johnston, 1836															
	Coryne eximia Allman, 1859	1													
	Coryne gracilis (Browne, 1902)	1													
	Sarsia medelae Gili, Lopez-Gonzalez & Bouillon, 2006												1	1	
	Sarsia tubulosa (M. Sars, 1835)		1											1	
Zancleidae Russell, 1953															
	Zanclea hicksoni (Stepanjants, 1972)												1	1	
Tubulariidae Allman, 1864															
	Bouillonia denhartogi Svoboda, Stepanjants & Ljubenkov, 2006												1		
	Ectopleura antarctica (Billard, 1914)											1		1	
	Ectopleura crocea (Agassiz, 1862)		1							1		1		1	
	Ectopleura dumortierii (Van Beneden, 1844)	1													
	Hybocodon chilensis Hartlaub, 1905	1													
	Tubularia antarctica (Hartlaub, 1905)						1								
	Tubularia hodgsoni Hickson & Gravely 1907												1		
	Tubularia longstaffi Hickson & Gravely 1907												1		
	Tubularia formosa Hartlaub, 1905	1	1												
	Zyzzyzus parvula (Hickson & Gravely, 1907)												1	1	
Rhysiidae (Hickson & Gravely 1907)															
	Rhysia halecii (Hickson & Gravely, 1907)												1		
Stylasteridae Gray, 1847															
	Adelopora pseudothyron Cairns, 1982				1										
	Cheiloporidion pulvinatum Cairns 1983	1	1		1	1									

Family	Species	WP	EP	FI	BB	SR	SG	SSI	DB	SO	EI	SHI	WA	EA	BI
	Conopora verrucosa (Studer, 1878)	1	1	1	1		1			1	1	1	1		
	Crypthelia formosa Cairns, 1983	1			1		1								
	Errina antarctica (Gray, 1872)	1	1	1	1										
	Errina boschmai Cairns, 1983					1	1				1	1	1	1	
	Errina cyclopora Cairns, 1983				1										
	Errina fissurata Gray, 1872										1	1	1	1	
	Errina gracilis von Marenzeller, 1903				1		1			1	1	1	1	1	
	Errina kerguelensis Broch, 1942													1	
	Errina laterorifa Eguchi, 1964										1	1	1	1	
	Errina reticulata Cairns, 1991					1									
	Errinopora cestoporina Cairns, 1983		1		1										
	Errinopsis fenestrata Cairns, 1983		1		1	1	1		1				1		
	Errinopsis reticulum Broch, 1951		1	1	1										
	Inferolabiata labiata (Moseley, 1879)	1	1	1	1		1		1	1	1	1	1	1	
	Inferolabiata lowei (Cairns, 1983)	1	1		1		1								
	Lepidopora acrolophos Cairns, 1983	1					1								
	Lepidopora granulosa (Cairns, 1983)	1	1	1	1	1									
	Lepidopora sarmentosa Boschma, 1968												1		
	Lepidotheca fascicularis (Cairns, 1983)	1	1		1		1								
	Sporadopora dichotoma (Moseley, 1876)	1	1	1	1		1				1				
	Stellapora echinata (Moseley, 1879)	1	1		1										
	Stylaster densicaulis Moseley, 1879	1	1		1		1								
	Stylaster eguchii (Boschma, 1966)													1	
	Stylaster profundus (Moseley, 1879)	1	1				1								
	Stylaster robustus (Cairns, 1983)						1			1	1	1			
Candelabriidae Stechow, 1921															
	Candelabrum austrogeorgiae (Jäderholm, 1904)						1			1			1	1	
	Candelabrum penola (Manton, 1940)											1	1		
Campanulinidae Hincks, 1868															
	Calycella syringa (Linnaeus, 1767)	1	1		1										
	Campanulina pumila (Clark, 1875)	1													
	Egmundella gracilis Stechow, 1921	1													
	Lafoeina longitheca Jäderholm, 1904	1					1					1	1	1	
	Stegella lobata (Vanhöffen 1910)		1					1		1		1	1	1	
Mitrocomidae Haeckel, 1879															
	Mitrocomella polydiademata (Romanes, 1876)		1												
Phialellidae Russell, 1953															
	Phialella belgicae (Hartlaub, 1904)	1	1									1	1	1	
	Phialella chilensis (Hartlaub, 1905)	1	1	1	1								1		
	Phialella quadrata (Forbes, 1848)	1													

Family	Species	WP	EP	FI	BB	SR	SG	SSI	DB	SO	EI	SHI	WA	EA	BI
Tiarannidae Russell, 1940															
	Modeeria rotunda (Quoy & Gaimard, 1827)	1	1		1				1						1
	Stegolaria irregularis Totton, 1930	1	1	1										1	
	Stegopoma plicatile (M. Sars, 1863)		1					1		1		1	1	1	
Lafoeidae Hincks, 1868															
	Abietinella operculata (Jäderholm, 1903)		1	1	1		1	1	1	1	1	1	1	1	1
	Acryptolaria conferta (Allman, 1877)	1	1	1	1										
	Acryptolaria corniformis Naumov & Stepanjants, 1962													1	
	Acryptolaria crassicaulis (Allman, 1888)	1	1												
	Acryptolaria frigida (Peña Cantero, 2015)												1	1	
	Acryptolaria operculata Stepanjants, 1979	1	1		1	1	1	1	1						
	Filellum antarcticum (Hartlaub, 1904)	1	1	1	1		1					1	1	1	
	Filellum bouventesis Marques, Peña Cantero, Miranda & Migotto 2011														1
	Filellum magnificum Peña Cantero, Svoboda & Vervoort, 2004												1	1	
	Filellum serpens (Hassall, 1848)	1	1		1										
	Filellum serratum (Clarke, 1879)	1	1												
	Grammaria abietina (M. Sars, 1850)	1	1	1	1		1								
	Lafoea annulata Watson, 2003													1	
	Lafoea benthophila Ritchie 1909					1		1		1					
	Lafoea dumosa (Fleming, 1820)	1	1	1	1	1	1	1			1	1	1	1	1
	Lafoea gaussica Vanhöffen, 1910												1	1	
Hebellidae Fraser, 1912															
	Halisiphonia megalotheca Allman, 1888								1						
	Halisiphonia nana Stechow, 1921						1	1							1
	Halisiphonia prolifica Peña Cantero, 2014													1	
	Hebella plana (Ritchie, 1907)		1									1	1	1	
	Hebella scandens (Bale, 1888)	1	1										1		
	Hebella striata Allman, 1888	1	1	1	1						1	1	1	1	
Haleciidae Hincks, 1868															
	Halecium annulatum Torrey, 1902		1												
	Halecium annuliforme Galea & Schories, 2012	1	1												
	Halecium antarcticum Vanhöffen, 1910												1	1	
	Halecium banzare Watson, 2008											1	1	1	
	Halecium beanii (Johnston, 1838)	1	1		1										
	Halecium brevithecum Watson, 2008													1	
	Halecium chilense Galea & Schories, 2014	1													
	Halecium cymiforme Allman, 1888	1													
	Halecium delicatulum Coughtrey, 1876	1	1												
	Halecium elegantulum Watson, 2008								1					1	
	Halecium erratum Galea, Försterra, Häussermann & Schories, 2014	1													
	Halecium exaggeratum Peña Cantero, Boero & Piraino, 2013									1		1	1	1	

Family	Species	WP	EP	FI	BB	SR	SG	SSI	DB	SO	EI	SHI	WA	EA	BI
	Halecium fjordlandicum Galea, 2007	1													
	Halecium flexile Allman 1888	1													
	Halecium frigidum Peña Cantero, 2010									1			1	1	
	Halecium humeriformis Galea & Schories, 2014	1													
	Halecium incertus Naumov & Stepanjants, 1962							1				1	1	1	1
	Halecium interpolatum Ritchie, 1907		1							1	1	1	1	1	
	Halecium jaederholmi Vervoort, 1972	1	1	1	1		1					1	1	1	
	Halecium pallens Jäderholm, 1904					1	1								
	Halecium platythecum Galea, Försterra & Häussermann 2014	1													
	Halecium pseudodelicatulum Peña Cantero 2014										1	1			
	Halecium pseudoincertus Peña Cantero 2014												1	1	
	Halecium secundum Jäderholm, 1904												1	1	
	Halecium stoloniferum Soto Àngel & Peña Cantero 2015				1										
	Halecium tehuelchum d'Orbigny 1842	1													
	Halecium tenellum Hincks, 1861	1	1		1										
	Hydrodendron arboreum (Allman, 1888)		1			1	1				1	1	1	1	1
Aglaopheniidae Broch, 1918															
	Aglaophenia acacia Allman, 1883		1												
	Aglaophenia antarctica Jäderholm, 1903	1													
	Aglaophenopsis cornuta (Verrill, 1879)		1												
	Lytocarpia canepa (Blanco & Bellusci De Miralles, 1971)		1	1	1										
	Lytocarpia distans (Allman, 1877)	1	1												
	Lytocarpia myriophyllum (Linnaeus, 1758)	1	1		1										
Halopterididae Millard, 1962															
	Halopteris catharina (Johnston, 1833)	1													
	Halopteris minuta (Trebilcock, 1928)	1	1												
	Halopteris diaphana (Heller, 1868)	1													
	Halopteris enersis Galea, 2006	1													
	Halopteris schucherti Galea, 2006	1													
Schizotrichidae Peña Cantero, Sentandreu & Latorre, 2010															
	Schizotricha anderssoni Jäderholm, 1904						1							1	1
	Schizotricha crassa Peña Cantero & Vervoort, 2004							1		1		1	1		
	Schizotricha discovery Soto Angel & Peña Cantero 2015								1						
	Schizotricha falcata Peña Cantero, 1998											1	1		
	Schizotricha glacialis (Hickson & Gravely, 1907)												1	1	
	Schizotricha heteromera Peña Cantero & Vervoort, 2005							1							
	Schizotricha jaederholmi Peña Cantero & Vervoort, 1996						1								
	Schizotricha multifurcata Allman, 1883	1	1					1						1	1
	Schizotricha nana Peña Cantero, Svoboda & Vervoort, 1996							1			1	1	1	1	
	Schizotricha southgeorgiae Peña Cantero & Vervoort, 2004					1	1								
	Schizotricha trinematotheca Peña Cantero & Vervoort, 2005													1	

Family	Species	WP	EP	FI	BB	SR	SG	SSI	DB	SO	EI	SHI	WA	EA	BI
	Schizotricha turqueti Billard, 1906							1		1	1	1	1	1	
	Schizotricha unifurcata Allman, 1883					1	1						1	1	1
	Schizotricha vervoorti Peña Cantero, 1998									1		1	1	1	
Kirchenpaueriidae Millard, 1962															
	Kirchenpaueria curvata (Jäderholm, 1904)	1		1											
	Kirchenpaueria pinnata (Linnaeus, 1758)		1												
	Kirchenpaueria magellanica (Hartlaub, 1905)	1													
	Oswaldella antarctica (Jäderholm, 1904)												1		
	Oswaldella bifurca (Hartlaub, 1904)												1	1	
	Oswaldella billardi Briggs, 1938													1	
	Oswaldella blanconae El Beshbeeshy, 2011											1	1	1	
	Oswaldella crassa Peña Cantero & Vervoort, 1998												1		
	Oswaldella curiosa Peña Cantero & Vervoort, 1998												1		
	Oswaldella delicata Peña Cantero, Svoboda & Vervoort, 1997											1	1	1	
	Oswaldella elongata Peña Cantero, García Carrascosa & Vervoort, 1995						1								
	Oswaldella encarnae Peña Cantero, Svoboda & Vervoort, 1997												1		
	Oswaldella erratum Peña Cantero & Vervoort, 1997							1		1	1	1	1		1
	Oswaldella frigida Peña Cantero & Vervoort, 2004											1		1	
	Oswaldella garciacarrascosai Peña Cantero, Svoboda & Vervoort, 1997												1		
	Oswaldella gracilis Peña Cantero, Svoboda & Vervoort, 1997												1		
	Oswaldella grandis Peña Cantero, Svoboda & Vervoort, 1997										1	1	1		
	Oswaldella herwigi El Beshbeeshy, 2011	1	1	1	1										
	Oswaldella incognita Peña Cantero, Svoboda & Vervoort, 1997									1	1	1	1	1	
	Oswaldella laertesi Peña Cantero, 2007													1	
	Oswaldella medeae Peña Cantero & Vervoort, 2004												1	1	
	Oswaldella monomammillata Peña Cantero & Vervoort, 2004										1				
	Oswaldella niobae Peña Cantero & Ramil, 2006											1	1		
	Oswaldella obscura Peña Cantero, Svoboda & Vervoort, 1997												1		
	Oswaldella rigida Peña Cantero, Svoboda & Vervoort, 1997												1	1	
	Oswaldella shetlandica Stepanjants, 1979									1		1	1		
	Oswaldella stepanjantsae El Beshbeeshy, 2011										1	1	1	1	
	Oswaldella terranovae Peña Cantero & Vervoort, 1996													1	
	Oswaldella tottoni Peña Cantero & Vervoort, 1996												1	1	
	Oswaldella vervoorti Peña Cantero & García Carrascosa, 1998									1		1	1	1	1
Plumulariidae Hincks, 1868															
	Nemertesia cymodocea (Busk, 1851)	1	1												
	Nemertesia ramosa (Lamarck, 1816)		1		1										
	Nemertesia vervoorti El Beshbeeshy, 2011		1	1	1										
	Plumularia duseni Jäderholm, 1904	1													
	Plumularia insignis Allman, 1883		1												

Family	Species	WP	EP	FI	BB	SR	SG	SSI	DB	SO	EI	SHI	WA	EA	BI
	Plumularia leloupi Blanco & Bellusci De Miralles, 1971		1		1										
	Plumularia pulchella Bale, 1882	1													
	Plumularia setacea (Linnaeus, 1758)	1	1												
	Plumularia vervoorti El Beshbeeshy, 2011	1													
Sertulariidae Hincks, 1868															
	Abietinaria abietina (Linnaeus, 1758)	1	1				1								
	Amphisbetia bispinosa (Gray, 1843)	1													
	Amphisbetia episcopus (Allman, 1876)	1													
	Amphisbetia minima (Thompson, 1879)	1	1												
	Amphisbetia norte El Beshbeeshy, 2011		1												
	Amphisbetia operculata (Linnaeus, 1758)	1	1	1	1								1		
	Amphisbetia rectitheca (Ritchie, 1907)									1					
	Amphisbetia trispinosa (Coughtrey, 1875)	1													
	Antarctoscyphus admirabilis Peña Cantero, Svoboda & Vervoort, 1999												1		
	Antarctoscyphus asymmetricus Peña Cantero, García Carrascosa & Vervoort, 1997						1	1			1	1	1		
	Antarctoscyphus biformis (Jäderholm, 1905)												1		
	Antarctoscyphus elongatus (Jäderholm, 1904)						1				1	1	1	1	1
	Antarctoscyphus encarnae Peña Cantero, García Carrascosa & Vervoort, 1997											1			
	Antarctoscyphus fragilis Peña Cantero, Svoboda & Vervoort, 1999												1		
	Antarctoscyphus grandis (Blanco, 1977)										1	1	1	1	
	Antarctoscyphus gruzovi (Stepanjants, 1979)										1	1			
	Antarctoscyphus mawsoni (Briggs, 1938)													1	
	Antarctoscyphus spiralis (Hickson & Gravely, 1907)							1		1	1	1	1	1	1
	Dynamena pumilla (Linnaeus, 1758)		1												
	Mixoscyphus antarcticus Peña Cantero & Vervoort, 2005											1			
	Sertularella antarctica Hartlaub, 1901	1	1	1											
	Sertularella argentinica El Beshbeeshy, 2011	1	1	1	1										
	Sertularella blanconae El Beshbeeshy, 2011	1	1	1											
	Sertularella conica Allman, 1877	1	1	1			1								
	Sertularella contorta Kirchenpauer, 1884	1		1			1								
	Sertularella cruzensis El Beshbeeshy, 2011		1												
	Sertularella fuegonensis El Beshbeeshy, 2011	1	1												
	Sertularella gaudichaudi (Lamoroux, 1824)	1	1	1								1			
	Sertularella gayi (Lamouroux, 1821)	1	1												
	Sertularella geodiae Totton, 1930	1	1	1	1										
	Sertularella grandensis El Beshbeeshy, 2011	1													
	Sertularella hermanosensis El Beshbeeshy, 2011		1	1	1										
	Sertularella implexa (Allman, 1888)	1	1	1											
	Sertularella jorgensis El Beshbeeshy, 2011	1	1	1				1			1				
	Sertularella cf. *lagena* (Allman, 1876)	1													
	Sertularella mogotensis El Beshbeeshy, 2011	1													

Family	Species	WP	EP	FI	BB	SR	SG	SSI	DB	SO	EI	SHI	WA	EA	BI
	Sertularella nuttingi Billard, 1914												1		
	Sertularella paessleri Hartlaub, 1901	1	1												
	Sertularella patagonica (D'Orbigny, 1839)	1	1												
	Sertularella paessleri Hartlaub, 1901			1											
	Sertularella polyzonias (Linnaeus, 1758)	1	1	1	1		1								
	Sertularella quadrifida Hartlaub, 1901		1												
	Sertularella robusta Coughtrey, 1876	1	1		1			1							
	Sertularella sanmatiasensis El Beshbeeshy, 2011	1	1				1	1			1	1	1		1
	Sertularella simplex (Hutton, 1873)	1													
	Sertularella stepanyantsae El Beshbeeshy, 2011	1													
	Sertularella striata Stechow, 1923		1		1										
	Sertularella tenella (Alder, 1857)		1		1										
	Sertularella vervoorti El Beshbeeshy, 2011		1	1	1	1									
	Sertularia tongensis (Stechow, 1919)	1													
	Staurotheca abyssalis Peña Cantero & Vervoort, 2003												1		
	Staurotheca affinis (Jäderholm, 1904)						1								
	Staurotheca amphorophora Naumov & Stepanjants, 1962				1	1	1					1			
	Staurotheca antarctica Hartlaub, 1904		1				1					1	1	1	
	Staurotheca australis Peña Cantero, Svoboda & Vervoort, 1997												1		
	Staurotheca compressa Briggs, 1938							1			1	1	1	1	
	Staurotheca cornuta Peña Cantero, García Carrascosa & Vervoort, 1999									1	1	1			
	Staurotheca densa Peña Cantero & Vervoort, 2003										1	1	1	1	
	Staurotheca dichotoma Allman, 1888					1	1	1	1		1	1	1	1	1
	Staurotheca echinocarpa (Allman, 1888)		1												
	Staurotheca frigida Peña Cantero, Svoboda & Vervoort, 1997					1	1	1		1		1	1	1	
	Staurotheca glomulosa Peña Cantero, Svoboda & Vervoort, 1997						1	1		1	1	1	1	1	
	Staurotheca jaederholmi Stechow, 1920	1	1										1	1	
	Staurotheca juncea (Vanhöffen, 1910)										1	1	1	1	
	Staurotheca multifurcata Peña Cantero, García Carrascosa & Vervoort, 1999					1	1	1				1			
	Staurotheca nonscripta Peña Cantero, Svoboda & Vervoort, 1997		1								1		1	1	
	Staurotheca pachyclada (Jäderholm, 1904)						1				1	1	1	1	
	Staurotheca plana Peña Cantero, Svoboda & Vervoort, 1997												1		
	Staurotheca polarsterni Peña Cantero, Svoboda & Vervoort, 1997											1	1	1	
	Staurotheca profunda Peña Cantero & Vervoort, 2003				1										
	Staurotheca stolonifera (Hartlaub, 1904)												1	1	
	Staurotheca undosiparietina (Stepanjants, 1979)					1	1				1	1	1		
	Staurotheca vanhoeffeni (Peña Cantero & García Carrascosa, 1993)										1	1	1	1	
	Staurotheca vervoorti (El Beshbeeshy, 2011)	1	1	1	1		1								
	Symplectoscyphus aggregatus (Jäderholm, 1917)												1		
	Symplectoscyphus anae Peña Cantero, Svoboda & Vervoort, 2002										1	1	1	1	
	Symplectoscyphus bathyalis Vervoort, 1972	1				1	1								

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	Symplectoscyphus bellingshauseni Peña Cantero, 2012												1		
	Symplectoscyphus chubuticus El Beshbeeshy, 2011		1												
	Symplectoscyphus cumberlandicus (Jäderholm, 1905)						1		1			1	1	1	
	Symplectoscyphus curvatus (Jäderholm, 1917)									1		1	1	1	
	Symplectoscyphus exochus Blanco, 1982											1	1		
	Symplectoscyphus filiformis (Allman, 1888)	1	1	1	1										
	Symplectoscyphus flexilis (Hartlaub, 1901)	1	1												
	Symplectoscyphus frigidus Peña Cantero, Svoboda & Vervoort, 2002					1						1	1		
	Symplectoscyphus frondosus Peña Cantero, 2010													1	
	Symplectoscyphus glacialis (Jäderholm, 1904)		1		1		1			1	1	1	1	1	1
	Symplectoscyphus hero Blanco, 1977											1			
	Symplectoscyphus hesperides Peña Cantero, 2012												1		
	Symplectoscyphus interruptus (Pfeffer, 1889)	1					1								
	Symplectoscyphus johnstoni (Gray, 1843)	1													
	Symplectoscyphus leloupi El Beshbeeshy, 2011	1	1	1											
	Symplectoscyphus liouvillei (Billard, 1914)			1						1		1	1		1
	Symplectoscyphus magellanicus (Marktanner-Turneretscher, 1890)	1	1	1											
	Symplectoscyphus magnificus Peña Cantero & Vervoort, 2009												1		
	Symplectoscyphus margaritaceus (Allman, 1885)	1	1												
	Symplectoscyphus marionensis Millard, 1971	1	1												
	Symplectoscyphus meriodionalis Nutting, 1904		1												
	Symplectoscyphus milneanus (D'Orbigny, 1842)	1	1	1											
	Symplectoscyphus modestus (Hartlaub, 1901)	1	1												
	Symplectoscyphus naumovi Blanco, 1969											1	1	1	
	Symplectoscyphus nesioticus Blanco, 1977							1	1			1	1		
	Symplectoscyphus paraglacialis El Beshbeeshy, 2011	1	1												
	Symplectoscyphus patagonicus Galea & Schories 2012	1													
	Symplectoscyphus paulensis Stechow, 1923		1										1		
	Symplectoscyphus pinnatus (Clark, 1877)		1												
	Symplectoscyphus plectilis (Hinckson & Gravley, 1907)					1	1					1	1	1	1
	Symplectoscyphus pulchellus (Jäderholm, 1904)	1													
	Symplectoscyphus pygmaeus (Bale, 1882)	1													
	Symplectoscyphus salvadorensis El Beshbeeshy, 2011		1	1											
	Symplectoscyphus singularis El Beshbeeshy, 2011		1												
	Symplectoscyphus sofiae Peña Cantero, Svoboda & Vervoort, 2002												1		
	Symplectoscyphus subarticulatus (Coughtrey, 1875)	1													
	Symplectoscyphus subdichotomous (Kirchenpauer, 1884)	1	1	1	1		1			1		1	1		
	Symplectoscyphus unilateralis (Lamoroux, 1824)			1											
	Symplectoscyphus tricuspidatus (Alder, 1856)				1										
	Symplectoscyphus valdesicus El Beshbeeshy, 2011		1												
	Symplectoscyphus vanhoeffeni Totton, 1930	1								1		1	1	1	

Family	Species	WP	EP	FI	BB	SR	SG	SSI	DB	SO	EI	SHI	WA	EA	BI
	Symplectoscyphus vervoorti El Beshbeeshy, 2011		1	1	1										
	Symplectoscyphus weddelli Peña Cantero, Svoboda & Vervoort, 2002												1		
	Tasmanaria edentula (Bale, 1924)				1										
	Thuiaria thuja (Linnaeus, 1758)	1	1												
	Thuiaria polycarpa Kirchenpauer, 1884	1	1												
Thyroscyphidae Stechow, 1920															
	Parascyphus repens (Jäderholm, 1904)	1	1												
	Parascyphus simplex (Lamoroux, 1816)												1		
Syntheciidae Marktanner-Turneretscher, 1890															
	Synthecium protectum Jäderholm, 1903	1	1	1	1										
Campanulariidae Hincks, 1868															
	Billardia intermedia Blanco, 1967												1		
	Billardia subrufa (Jäderholm, 1904)		1	1		1	1	1	1	1		1	1	1	1
	Campanularia agas Cornelius, 1982	1	1		1								1		
	Campanularia antarctica Ritchie 1913												1	1	
	Campanularia clytioides (Lamouroux, 1824)	1													
	Campanularia hicksoni Totton, 1930							1				1	1	1	
	Campanularia hincksii Alder, 1856	1	1												
	Campanularia lennoxensis Jäderholm, 1903	1	1	1											
	Clytia gracilis (M. Sars, 1850)	1	1												
	Clytia hemisphaerica (Linnaeus, 1767)	1	1												
	Clytia linearis (Thornely, 1900)	1													
	Clytia noliformis (McCrady, 1859)	1	1												
	Clytia paulensis (Vanhöffen, 1910)	1													
	Clytia cf. *gigantea* (Hincks, 1866)	1													
	Gonothyraea loveni (Allman, 1859)	1													
	Hartlaubella gelatinosa (Pallas, 1766)	1													
	Laomedea angulata Hincks, 1861			1											
	Obelia austrogeorgiae Jäderholm, 1904						1						1		
	Obelia bidentata Clarke, 1875	1	1		1		1				1	1	1	1	1
	Obelia dichotoma (Linnaeus, 1758)	1	1												
	Obelia geniculata (Linnaeus, 1758)	1	1	1			1								
	Obelia longissima (Pallas, 1766)	1	1							1		1	1		
	Orthopyxis clytoides (Lamouroux, 1824)	1		1											
	Orthopyxis crenata (Hartlaub, 1901)	1	1												
	Orthopyxis curiosa Peña Cantero, 2013											1			
	Orthopyxis everta (Clarke, 1876)	1	1										1		
	Orthopyxis hartlaubi El Beshbeeshy, 2011	1	1	1	1										
	Orthopyxis integra (MacGillivray, 1842)	1	1												
	Orthopyxis mollis (Stechow, 1919)	1													
	Orthopyxis norvegiae (Broch, 1948)						1					1			

Family	Species	WP	EP	FI	BB	SR	SG	SSI	DB	SO	EI	SHI	WA	EA	BI
	Orthopyxis tincta Hincks, 1861	1	1	1										1	
	Silicularia pedunculata (Jäderholm 1904)						1					1			
	Silicularia rosea Meyen, 1834	1	1	1			1					1			
	Tulpa tulipifera (Allman, 1888)	1	1	1	1										
Total		**159**	**143**	**57**	**62**	**22**	**67**	**28**	**13**	**33**	**43**	**92**	**138**	**113**	**21**

Table S2 Similarity matrix from Jaccard Index (same legend as Tab. S1)

	WP	EP	FI	BB	SR	SG	SSI	SO	EI	SHI	WA	EA
WP												
EP	47.317											
FI	25.581	32.450										
BB	22.099	34.868	35.227									
SR	2.841	5.096	5.333	9.091								
SG	14.141	16.022	15.888	19.444	21.918							
SSI	3.315	6.211	4.938	4.651	16.279	13.095						
SO	2.674	6.667	7.143	6.742	5.769	12.360	22.000					
EI	4.124	7.514	7.527	9.375	8.333	20.879	20.339	22.581				
SHI	6.356	10.849	8.759	8.451	10.680	26.190	20.000	30.208	40.625			
WA	7.220	12.400	7.143	8.108	7.383	19.186	13.699	18.750	23.973	46.497		
EA	6.250	11.304	6.918	6.061	6.299	16.883	12.800	17.742	23.810	39.456	47.647	
BI	2.857	5.806	5.405	6.410	16.216	17.333	25.641	14.894	18.519	15.306	11.189	12.605

Table S3 Similarity matrix from Sørensen Index (same legend as Tab. S1)

	WP	EP	FI	BB	SR	SG	SSI	SO	EI	SHI	WA	EA
WP												
EP	64.238											
FI	40.741	49.000										
BB	36.199	51.707	52.101									
SR	5.525	9.697	10.127	16.667								
SG	24.779	27.619	27.419	32.558	35.955							
SSI	6.417	11.696	9.412	8.889	28.000	23.158						
SO	5.208	12.500	13.333	12.632	10.909	22.000	36.066					
EI	7.921	13.978	14.000	17.143	15.385	34.545	33.803	36.842				
SHI	11.952	19.574	16.107	15.584	19.298	41.509	33.333	46.400	57.778			
WA	13.468	22.064	13.333	15.000	13.750	32.195	24.096	31.579	38.674	63.478		
EA	11.765	20.313	12.941	11.429	11.852	28.889	22.695	30.137	38.462	56.585	64.542	
BI	5.556	10.976	10.256	12.048	27.907	29.545	40.816	25.926	31.250	26.549	20.126	22.388

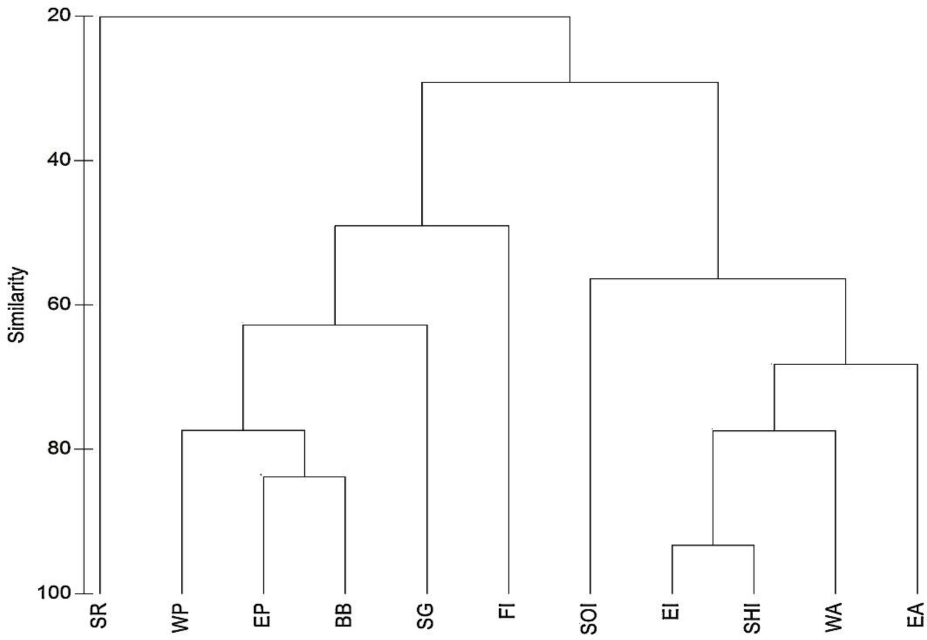

Figure S1 Cluster analysis from Sørensen Similarity for the Stylasteridae [Western Patagonia (WP), Eastern Patagonia (EP), Falkland Islands (FI), Burdwood Bank (BB), Shag Rocks (SR), South Georgia (SG), South Orkney Islands (SOI), Elephant Island (EI), South Shetland Islands (SHI), West Antarctica (WA) and East Antarctica (EA)]

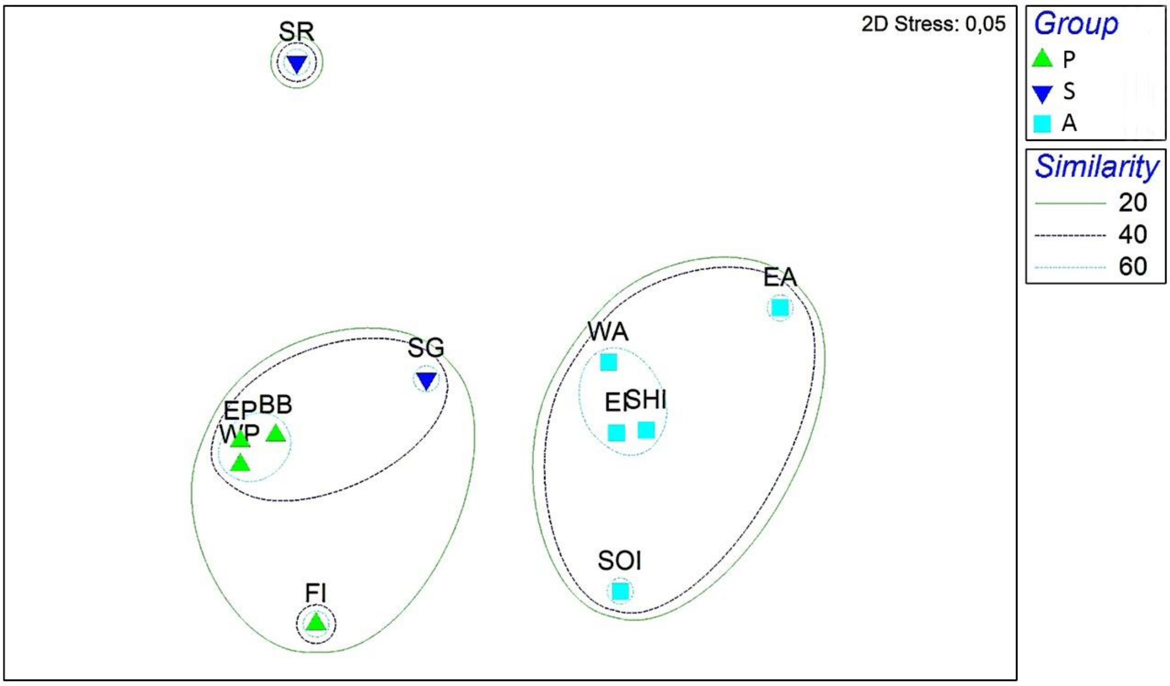

Figure S2 Non-metric multidimensional scaling (*nMDS*) from Sørensen Similarity for the Stylasteridae. [Groups: Patagonian region (P); South Georgia and Shag Rocks (S); Continental Antarctica and South Sandwich, South Orkney, Elephant and South Shetland Islands (A). Regions: as in Fig. S1]

Table S4 Substrate and epibionts of the species inventoried

	Substrate		**Epibionts**	
	Hydroids	**Other**	**Hydroids**	**Other**
B. corynopsis	*E. scotti*			
Bougainvillidae undet	*H. incertus, S. unifurcata, S. lobata, S. curvatus, S. exochus, Sy. glacialis, S. weddelli*			
R. antarcticum	*A. elongatus, A. grandis, B. subrufa, C. hicksoni, E. generale, H. interpolatum, H. secundum, O. stepanjantsae, S. nana, S. unifurcata, S. glomulosa, St. vanhoeffeni, S. anae, S. exochus, Sy. vanhoeffeni, S. weddelli, T. longstaffi, Tubularia* sp.1, *Tubularia* sp.2	bryozoan, octocoral, polychaete tube	*P. belgicae*	
E. antarcticum	*B. subrufa, H. interpolatum, Tubularia* sp.1			Acari, polychaete
E. generale	*O. stepanjantsae, S. nana, S. cumberlandicus, T. longstaffi, Tubularia* sp.2	sponge	*B. subrufa, R. antarcticum, P. belgicae, Z. hicksoni, Z. parvula*	bryozoan, pycnogonid, protozan
E. scotti	*St. vanhoeffeni, S. weddelli*	sponge	*B. corynopsis, F.* cf. *magnificum, H. interpolatum*	pycnogonid
Eudendrium sp.1	*O. erratum, O. stepanjantsae, S. lobata*		*Billardia subrufa, S. naumovi*	
Eudendrium sp.2			*H. dendritica*	pirripede
H. dendritica	*Eudendrium* sp.2, *H. interpolatum, O. stepanjantsae, S. nana, S. unifurcata, T. longstaffi*	dead octocoral		
Hydractinia sp.	*O. stepanjantsae, S. lobata, Z. parvula*			
T. longstaffi	*O. stepanjantsae*		*C. hicksoni, E. generale, H. interpolatum, H. dendritica, L. longitheca, P. belgicae, R. antarcticum, S. exochus, Z. hicksoni, Z. parvula*	octocoral, polychaete, protozoan, pygnogonid, sponge
Tubularia sp.1			*C. hicksoni, E. antarcticum, H. interpolatum, P. belgicae, R. antarcticum, S. naumovi*	
Tubularia sp.2			*E. generale, R. antarcticum, S. naumovi*	
Z. parvula	*E. generale, H. interpolatum, L. dumosa, S. unifurcata, T. longstaffi*		*Hydractinia* sp.	
C. microrhiza		gravel	*Sy. glacialis*	bryozoan
Sarsia sp.	*H. incertus*			
Z. hicksoni	*E. generale, O. stepanjantsae, T. longstaffi*			
A. frigida		octocoral, sponge	*H.* cf. *plana, S. anae, Sy. glacialis*	
F. antarcticum	*St. vanhoeffeni, S. lobata*			
F. cf. *magnificum*	*E. scotti, O. erratum, S. nana, S. nonscripta, S. exochus*			
F. cf. *bouvetensis*	*A. elongatus, B. subrufa, S. nana*			
Filellum sp.	Several species			
L. dumosa	*B. subrufa, O, stepanjantsae, S. nana, S. unifurcata, S. curvatus*	ascidian, sponge	*L. longitheca, Z. parvula*	bryozoan, protozoan
L. gaussica		bryozoan		
Hebella cf. *plana*	*A. frigida*			
L. longitheca	*B. subrufa, C. hicksoni, H. interpolatum, H. pseudodelicatulum, L. dumosa, O. stepanjantsae, S. cumberlandicus, T. longstaffi*			

	Substrate		**Epibionts**	
	Hydroids	**Other**	**Hydroids**	**Other**
S. lobata	*B. subrufa, H. incertus, H. pseudodelicatulum, O. stepanjantsae, S. nana, S. unifurcata, S. nonscripta, S. exochus, S. weddelli*	gravel, dead octocoral, octocoral, polychaete tube, sponge, bryozoan, dead octocoral	*B. subrufa*, Bougainvillidae undet, *Eudendrium* sp.1, *F. antarcticum, H. exaggeratum, H. interpolatum, Hydractinia* sp., *P. belgicae, S. anae, S. exochus, S. glacialis, S. naumovi, S. plectilis*	bryozoan, polychaete, pycnogonida, sponge
P. belgicae	*A. elongatus, A. grandis, A. spiralis, B. subrufa, C. hicksoni, E. generale, H.* cf. *antarcticum, H. exaggeratum, H. interpolatum, H. jaederholmi, H. secundum, O. stepanjantsae, R. antarcticum, S. nana, S. frigida, S. nonscripta, S. pachyclada, S. polarsterni, S. lobata, S. anae, S. cumberlandicus, S. curvatus, S. exochus, Sy. glacialis, S. naumovi, S. plectilis, S. weddelli, Tubularia* sp.1, *T. longstaffi*	bryozoan, sponge, dead octocoral, polychaete tube		
C. hicksoni	*A. elongatus, H. arboreum, O. stepanjantsae, S. nana, S. glomulosa, S. nonscripta, S. polarsterni, S. cumberlandicus, S. curvatus, S. exochus, T. longstaffi, Tubularia* sp.1		*H. interpolatum, L. longitheca, P. belgicae, R. antarcticum, S. plectilis*	diatoms
Campanularia sp.	*B. subrufa, H. incertus, H. interpolatum, H. secundum, O. erratum, O. stepanjantsae, S. nana, S. glomulosa, S. nonscripta, S. anae, S. exochus, Sy. glacialis*			
S. antarctica				
S. dichotoma		gravel	*S. exochus*	bryozoan, protozoan
S. frigida			*P. belgicae, Sy. glacialis*	polychaete
S. glomulosa		gravel	*C. hicksoni, Campanularia* sp., *R. antarcticum Sy. glacialis, S. plectilis*	bryozoan, polychaete, pycnogonid
S. nonscripta			*A. spiralis, C. hicksoni, Campanularia* sp. *F.* cf. *magnificum, P. belgicae, S. lobata*	bryozoan
S. pachyclada		gravel	*P. belgicae*	cirripede
S. polarsterni		gravel, stone	*A. spiralis, B. subrufa, C. hicksoni, H. interpolatum, P. belgicae, S. anae, Sy. glacialis*	cirripede, bryozoan, sponge
St. vanhoeffeni		gravel, stone	*E. scotti, F. antarcticum, R. antarcticum*	bryozoan, protozoan
A. asymmetricus				
A. elongatus	*O. stepanjantsae*		*C. hicksoni, F.* cf. *bouvetensis, P. belgicae, R. antarcticum, S. anae, Sy. glacialis*	protozoan
A. grandis			*P. belgicae, R. antarcticum*	
A. spiralis	*S. nonscripta, S. polarsterni*		*P. belgicae*	bryozoan
S. anae	*A. frigida, A. elongatus, B. subrufa, H. secundum, S. polarsterni, S. lobata*	octocoral, dead octocoral	*Campanularia* sp., *H. interpolatum, P. belgicae, R. antarcticum*	
S. cumberlandicus	*O. stepanjantsae*	gravel	*C. hicksoni, E. generale, H. interpolatum, L. longitheca, P. belgicae*	protozoan
S. curvatus	*H. jaederholmi, S. nana*	octocoral	Bougainvillidae undet, *C. hicksoni, H. interpolatum, L. dumosa, P. belgicae*	bryozoan

	Substrate		Epibionts	
	Hydroids	**Other**	**Hydroids**	**Other**
S. exochus	*B. subrufa, S. nana, S. dichotoma, S. lobata, S. liouvillei, T. longstaffi*	bryozoan	Bougainvillidae undet, *Campanularia* sp., *C. hicksoni, F.* cf. *magnificum, H. interpolatum, P. belgicae, R. antarcticum, S. lobata, Sy. glacialis, S. plectilis*	caprellidae, nematode, pycnogonid
S. frigidus				protozoan
Sy. glacialis	*A. elongatus, A. frigida, B. subrufa, C. microrhiza, H. incertus, H. jaederholmi, H. secundum, O. erratum, S. nana, S. frigida, S. glomulosa, S. polarsterni, S. vanhoeffeni, S. lobata, S. exochus, S. weddelli*	polychaete tube, bryozoan, dead octocoral, octocoral	Bougainvillidae undet, *Campanularia* sp., *Halecium interpolatum, P. belgicae*	acari, bryozoan, nematode, protozoan
S. liouvillei		gravel	*S. exochus*	ofiuroid
S. naumovi	*Eudendrium* sp.1, *O. erratum, O. stepanjantsae, O. tottoni, S. nana, S. unifurcata, S. lobata, Tubularia* sp.1, *Tubularia* sp.2		*H. interpolatum, P. belgicae, S. plectilis*	
S. paulensis				
S. plectilis	*C. hicksoni, O. stepanjantsae, S. nana, S. glomulosa, S. lobata, S. exochus, S. naumovi*	bryozoan, gravel	*H. interpolatum, P. belgicae*	acari, bryozoan, isopoda, polychaete, pycnogonida
Sy. vanhoeffeni		sponge	*R. antarcticum*	acari
S. weddelli	*O. stepanjantsae, O. tottoni, S. nana, S. unifurcata*	sponge	Bougainvillidae undet, *Eudendrium scotti, H. interpolatum, H. tubatum, P. belgicae, R. antarcticum, Stegella lobata, Sy. glacialis*	acari, bryozoan, diatoms, protozoa, polychaete, pycnogonida, sponge
A. operculata				
H. cf. *antarcticum*	*S. nana*		*P. belgicae*	polychaete, sponge
H. banzare	*B. subrufa*			cirripede, bryozoan
H. exaggeratum	*S. lobata*	sponge spicule	*P. belgicae*	
H. incertus		gravel, stone	Bougainvillidae undet, *Campanularia* sp., *Sy. glacialis, ?Sarsia* sp., *S. lobata*	bryozoan, cirripede, nudibranch
H. interpolatum	*E. scotti, C. hicksoni, H. arboreum, H. pseudodelicatulum, O. stepanjantsae, S. nana, S. polarsterni, S. lobata, S. anae, S. cumberlandicus, S. curvatus, S. exochus, Sy. glacialis, S. naumovi, S. plectilis, S. weddelli, T. longstaffi, Tubularia* sp.1	polychaete tube, sponge	*Campanularia* sp., *E. antarcticum, H. dendritica, L. longitheca, P. belgicae, R. antarcticum, Z. parvula*	nematode, amphipod, protozoan, entoprocta
H. jaederholmi		bryozoan	*P. belgicae, S. curvatus, Sy. glacialis*	bryozoan
H. pseudodelicatulum	*S. nana*	dead octocoral	*H. interpolatum, L. longitheca, S. lobata*	bryozoan, cirripede, polychaete, protozoan
H. pseudoincertus				
H. secundum			*Campanularia* sp., *P. belgicae, R. antarcticum, S. anae, Sy. glacialis*	acari, bivalves, bryozoan, entoprocta, polychaeta, protozoa, pycnogonid

	Substrate		**Epibionts**	
	Hydroids	**Other**	**Hydroids**	**Other**
H. tubatum	*S. nana, S. weddelli*	sponge		
H. arboreum		sponge, stone	*C. hicksoni, H. interpolatum, O. delicata*	bryozoan, nematode, polychaete, protozoa, pycnogonida, sponge
Sertularella sp.				
A. baggins				algae, diatoms
Sc. glacialis				
S. nana		gravel	*B. subrufa,* Bougainvillidae undet*, C. hicksoni, Campanularia* sp.*, E. generale, F.* cf. *bouvetensis, F.* cf. *magnificum, H.* cf. *antarcticum, H. interpolatum, H. pseudodelicatulum, H. tubatum, H. dendritica, L. dumosa, P. belgicae, R. antarcticum, S. lobata, S. curvatus, S. exochus, Sy. glacialis, S. naumovi, S. plectilis, S. weddelli*	bryozoan, cirripede, entoprocta, foraminifera, nematode, octocoral, polychaete, protozoan, pycnogonida, sponge
S. unifurcata		sponge	Bougainvillidae undet, *Hydractinia dendritica, L. dumosa, R. antarcticum, S. lobata, S. naumovi, S. weddelli, Z. parvula*	bryozoan, cirripede, sponge
O. delicata	*H. arboreum*			
O. erratum		gravel, polychaete tube	*Billardia subrufa, Campanularia* sp.*, Eudendrium* sp.1, *Filellum* cf. *magnificum, Sy. glacialis, S. naumovi*	ascidian, bryozoan, cirripedia, foronidea, polychaeta, sponge
O. rigida				sponge
O. stepanjantsae		gravel, sponge, stone	*A. elongatus, B. subrufa, C. hicksoni, Campanularia* sp.*, E. generale, Eudendrium* sp.1*, H. interpolatum, H. dendritica, Hydractinia* sp.*, P. belgicae, R. antarcticum, T. longstaffi, L. longitheca, S. lobata, S. cumberlandicus, S. naumovi, S. plectilis, S. weddelli, Z. hicksoni*	bryozoan, entoprocta, polychaete, protozoa, sponge
O. tottoni			*S. naumovi, S. weddelli*	bryozoan, sponge
B. subrufa	*E. generale, Eudendrium* sp.1*, O. erratum, O. stepanjantsae, S. nana, S. polarsterni, S. lobata*	ascidian, bryozoan, dead octocoral, gravel, octocoral, polychaete tube, sponge, stone	*E. antarcticum, Campanularia* sp.*, F.* cf. *bouvetensis, H. banzare, L. dumosa, L. longitheca, R. antarcticum, S. lobata, P. belgicae, S. anae, S. exochus, Sy. glacialis*	bivalve, bryozoan, protozoan, sponge

Table S5 Previous records of benthic hydroids from the Weddell Shelf, indicating expedition, station, current name of the species, and subsequent reference

Expedition	**Station**	**Recorded as**	**Accepted name**	**Reference**
-	-	*Lafoea wedelli*	*Symplectoscyphus liouvillei*	Blanco (1991)
Norvegia 1927-1928	-	*Billardia subrufa*	*Billardia subrufa*	Broch (1948)
Norvegia 1927-1928	-	*Staurotheca dichotoma*	*Staurotheca dichotoma*	Broch (1948)
ANT XVII-3	119.1	*Sarsia medelae*	*Sarsia medelae*	Gili et al. (2006)
ANT XVII-3	122.2	*Sarsia medelae*	*Sarsia medelae*	Gili et al. (2006)
ANT XVII-3	124	*Sarsia medelae*	*Sarsia medelae*	Gili et al. (2006)
Discovery	Flagon Point	*Campanularia laevis*	*Campanularia hicksoni*	Hickson and Gravely (1907)
Discovery	Flagon Point	*Tubularia ralphi*	*Ectopleura crocea*	Hickson and Gravely (1907)
James Clark Ross 1923-1924	-	*Sertularella articulata*	*Antarctoscyphus elongatus*	Jäderholm (1917)
USARP	001/011	*Oswaldella delicata*	*Oswaldella delicata*	Peña Cantero and Vervoort (2004)
USARP	001/011	*Oswaldella erratum*	*Oswaldella erratum*	Peña Cantero and Vervoort (2004)
USARP	002/002	*Oswaldella billardi*	*Oswaldella billardi*	Peña Cantero and Vervoort (2004)
USARP	002/009	*Oswaldella encarnae*	*Oswaldella encarnae*	Peña Cantero and Vervoort (2004)
ANT VIII-5	16-405	*Schizotricha turqueti*	*Schizotricha turqueti*	Peña Cantero et al. (1996)
ANT VIII-5	16-454	*Schizotricha nana*	*Schizotricha nana*	Peña Cantero et al. (1996)
ANT VIII-5	16-481	*Schizotricha glacialis*	*Schizotricha glacialis*	Peña Cantero et al. (1996)
ANT VIII-5	16-496	*Schizotricha unifurcata*	*Schizotricha unifurcata*	Peña Cantero et al. (1996)
ANT IX-3	123	*Oswaldella tottoni*	*Oswaldella tottoni*	Peña Cantero et al. (1997b)
ANT IX-3	129	*Oswaldella rigida*	*Oswaldella rigida*	Peña Cantero et al. (1997b)
ANT IX-3	160	*Oswaldella obscura*	*Oswaldella obscura*	Peña Cantero et al. (1997b)
ANT IX-3	160	*Oswaldella rigida*	*Oswaldella rigida*	Peña Cantero et al. (1997b)
ANT VIII-5	16-396	*Oswaldella billardi*	*Oswaldella erratum*	Peña Cantero et al. (1997b)
ANT VIII-5	16-399	*Oswaldella billardi*	*Oswaldella erratum*	Peña Cantero et al. (1997b)
ANT VIII-5	16-399	*Oswaldella rigida*	*Oswaldella rigida*	Peña Cantero et al. (1997b)
ANT VIII-5	16-403	*Oswaldella grandis*	*Oswaldella grandis*	Peña Cantero et al. (1997b)
ANT VIII-5	16-405	*Oswaldella garciacarrascosai*	*Oswaldella garciacarrascosai*	Peña Cantero et al. (1997b)
ANT VIII-5	16-434	*Oswaldella obscura*	*Oswaldella obscura*	Peña Cantero et al. (1997b)

Expedition	**Station**	**Recorded as**	**Accepted name**	**Reference**
ANT VIII-5	16-434	*Oswaldella rigida*	*Oswaldella rigida*	Peña Cantero et al. (1997b)
ANT VIII-5	16-454	*Oswaldella stepanjantsae*	*Oswaldella stepanjantsae*	Peña Cantero et al. (1997b)
ANT VIII-5	16-475	*Oswaldella grandis*	*Oswaldella grandis*	Peña Cantero et al. (1997b)
ANT VIII-5	16-475	*Oswaldella obscura*	*Oswaldella obscura*	Peña Cantero et al. (1997b)
ANT VIII-5	16-477	*Oswaldella delicata*	*Oswaldella delicata*	Peña Cantero et al. (1997b)
ANT VIII-5	16-477	*Oswaldella encarnae*	*Oswaldella encarnae*	Peña Cantero et al. (1997b)
ANT VIII-5	16-477	*Oswaldella grandis*	*Oswaldella grandis*	Peña Cantero et al. (1997b)
ANT VIII-5	16-481	*Oswaldella bifurca*	*Oswaldella bifurca*	Peña Cantero et al. (1997b)
ANT VIII-5	16-484	*Oswaldella delicata*	*Oswaldella delicata*	Peña Cantero et al. (1997b)
ANT VIII-5	16-484	*Oswaldella encarnae*	*Oswaldella encarnae*	Peña Cantero et al. (1997b)
ANT VIII-5	16-484	*Oswaldella gracilis*	*Oswaldella gracilis*	Peña Cantero et al. (1997b)
ANT VIII-5	16-486	*Oswaldella garciacarrascosai*	*Oswaldella garciacarrascosai*	Peña Cantero et al. (1997b)
ANT VIII-5	16-496	*Oswaldella obscura*	*Oswaldella obscura*	Peña Cantero et al. (1997b)
ANT VIII-5	16-496	*Oswaldella rigida*	*Oswaldella rigida*	Peña Cantero et al. (1997b)
ANT VIII-5	16-496	*Oswaldella stepanjantsae*	*Oswaldella stepanjantsae*	Peña Cantero et al. (1997b)
ANT I-2	216	*Oswaldella billardi*	*Oswaldella erratum*	Peña Cantero et al. (1997b)
ANT VII-4	274	*Oswaldella rigida*	*Oswaldella rigida*	Peña Cantero et al. (1997b)
ANT II-4	308	*Oswaldella grandis*	*Oswaldella grandis*	Peña Cantero et al. (1997b)
ANT II-4	310	*Oswaldella grandis*	*Oswaldella grandis*	Peña Cantero et al. (1997b)
ANT II-4	450	*Oswaldella bifurca*	*Oswaldella bifurca*	Peña Cantero et al. (1997b)
ANT II-4	460	*Oswaldella grandis*	*Oswaldella grandis*	Peña Cantero et al. (1997b)
ANT II-4	524	*Oswaldella rigida*	*Oswaldella rigida*	Peña Cantero et al. (1997b)
ANT IX-3	123	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT I-2	129	*Staurotheca dichotoma*	*Staurotheca dichotoma*	Peña Cantero et al. (1997c)
ANT I-2	129	*Staurotheca juncea*	*Staurotheca pachyclada*	Peña Cantero et al. (1997c)
ANT IX-3	129	*Staurotheca polarsterni*	*Staurotheca polarsterni*	Peña Cantero et al. (1997c)
ANT I-2	135	*Staurotheca glomulosa*	*Staurotheca glomulosa*	Peña Cantero et al. (1997c)
ANT IX-3	160	*Staurotheca plana*	*Staurotheca plana*	Peña Cantero et al. (1997c)
ANT IX-3	162	*Staurotheca glomulosa*	*Staurotheca glomulosa*	Peña Cantero et al. (1997c)

Expedition	**Station**	**Recorded as**	**Accepted name**	**Reference**
ANT IX-3	162	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT VIII-5	16-396	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT VIII-5	16-396	*Staurotheca nonscripta*	*Staurotheca nonscripta*	Peña Cantero et al. (1997c)
ANT VIII-5	16-396	*Staurotheca juncea*	*Staurotheca pachyclada*	Peña Cantero et al. (1997c)
ANT VIII-5	16-396	*Staurotheca polarsterni*	*Staurotheca polarsterni*	Peña Cantero et al. (1997c)
ANT VIII-5	16-396	*Staurotheca vanhoeffeni*	*Staurotheca vanhoeffeni*	Peña Cantero et al. (1997c)
ANT VIII-5	16-399	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT VIII-5	16-399	*Staurotheca polarsterni*	*Staurotheca polarsterni*	Peña Cantero et al. (1997c)
ANT VIII-5	16-403	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT VIII-5	16-405	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT VIII-5	16-405	*Staurotheca glomulosa*	*Staurotheca glomulosa*	Peña Cantero et al. (1997c)
ANT VIII-5	16-407	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT VIII-5	16-407	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT VIII-5	16-423	*Staurotheca juncea*	*Staurotheca pachyclada*	Peña Cantero et al. (1997c)
ANT VIII-5	16-434	*Staurotheca frigida*	*Staurotheca frigida*	Peña Cantero et al. (1997c)
ANT VIII-5	16-434	*Staurotheca glomulosa*	*Staurotheca glomulosa*	Peña Cantero et al. (1997c)
ANT VIII-5	16-434	*Staurotheca juncea*	*Staurotheca pachyclada*	Peña Cantero et al. (1997c)
ANT VIII-5	16-454	*Staurotheca frigida*	*Staurotheca frigida*	Peña Cantero et al. (1997c)
ANT VIII-5	16-454	*Staurotheca glomulosa*	*Staurotheca glomulosa*	Peña Cantero et al. (1997c)
ANT VIII-5	16-454	*Staurotheca juncea*	*Staurotheca pachyclada*	Peña Cantero et al. (1997c)
ANT VIII-5	16-456	*Staurotheca glomulosa*	*Staurotheca glomulosa*	Peña Cantero et al. (1997c)
ANT VIII-5	16-456	*Staurotheca juncea*	*Staurotheca pachyclada*	Peña Cantero et al. (1997c)
ANT VIII-5	16-459	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT VIII-5	16-459	*Staurotheca glomulosa*	*Staurotheca glomulosa*	Peña Cantero et al. (1997c)
ANT VIII-5	16-468	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT VIII-5	16-470	*Staurotheca polarsterni*	*Staurotheca polarsterni*	Peña Cantero et al. (1997c)
ANT VIII-5	16-475	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT VIII-5	16-477	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT VIII-5	16-481	*Staurotheca nonscripta*	*Staurotheca nonscripta*	Peña Cantero et al. (1997c)

Expedition	**Station**	**Recorded as**	**Accepted name**	**Reference**
ANT VIII-5	16-486	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT VIII-5	16-492	*Staurotheca glomulosa*	*Staurotheca glomulosa*	Peña Cantero et al. (1997c)
ANT IX-3	165	*Staurotheca nonscripta*	*Staurotheca nonscripta*	Peña Cantero et al. (1997c)
ANT IX-3	165	*Staurotheca vanhoeffeni*	*Staurotheca vanhoeffeni*	Peña Cantero et al. (1997c)
ANT IX-3	212	*Staurotheca polarsterni*	*Staurotheca polarsterni*	Peña Cantero et al. (1997c)
ANT VII-4	212	*Staurotheca nonscripta*	*Staurotheca nonscripta*	Peña Cantero et al. (1997c)
ANT I-2	216	*Staurotheca frigida*	*Staurotheca frigida*	Peña Cantero et al. (1997c)
ANT I-2	216	*Staurotheca nonscripta*	*Staurotheca nonscripta*	Peña Cantero et al. (1997c)
ANT I-2	220	*Staurotheca stolonifera*	*Staurotheca stolonifera*	Peña Cantero et al. (1997c)
ANT I-2	220	*Staurotheca vanhoeffeni*	*Staurotheca vanhoeffeni*	Peña Cantero et al. (1997c)
ANT VII-4	261	*Staurotheca dichotoma*	*Staurotheca dichotoma*	Peña Cantero et al. (1997c)
ANT VII-4	269	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT VII-4	270	*Staurotheca glomulosa*	*Staurotheca glomulosa*	Peña Cantero et al. (1997c)
ANT VII-4	272	*Staurotheca nonscripta*	*Staurotheca nonscripta*	Peña Cantero et al. (1997c)
ANT VII-4	274	*Staurotheca vanhoeffeni*	*Staurotheca vanhoeffeni*	Peña Cantero et al. (1997c)
ANT VII-4	281	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT VII-4	281	*Staurotheca polarsterni*	*Staurotheca polarsterni*	Peña Cantero et al. (1997c)
ANT VII-4	284	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT VII-4	284	*Staurotheca polarsterni*	*Staurotheca polarsterni*	Peña Cantero et al. (1997c)
ANT VII-4	289	*Staurotheca plana*	*Staurotheca plana*	Peña Cantero et al. (1997c)
ANT VII-4	289	*Staurotheca polarsterni*	*Staurotheca polarsterni*	Peña Cantero et al. (1997c)
ANT VII-4	289	*Staurotheca glomulosa*	*Staurotheca glomulosa*	Peña Cantero et al. (1997c)
ANT VII-4	290	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT VII-4	290	*Staurotheca nonscripta*	*Staurotheca nonscripta*	Peña Cantero et al. (1997c)
ANT VII-4	290	*Staurotheca polarsterni*	*Staurotheca polarsterni*	Peña Cantero et al. (1997c)
ANT II-4	310	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT II-4	460	*Staurotheca antarctica*	*Staurotheca antarctica*	Peña Cantero et al. (1997c)
ANT V-3	553	*Staurotheca glomulosa*	*Staurotheca glomulosa*	Peña Cantero et al. (1997c)
ANT V-3	553	*Staurotheca polarsterni*	*Staurotheca polarsterni*	Peña Cantero et al. (1997c)

Expedition	**Station**	**Recorded as**	**Accepted name**	**Reference**
ANT IX-3	123	*Antarctoscyphus spiralis*	*Antarctoscyphus spiralis*	Peña Cantero et al. (1999)
ANT IX-3	129	*Antarctoscyphus spiralis*	*Antarctoscyphus spiralis*	Peña Cantero et al. (1999)
ANT VIII-5	16-396	*Antarctoscyphus elongatus*	*Antarctoscyphus elongatus*	Peña Cantero et al. (1999)
ANT VIII-5	16-396	*Antarctoscyphus spiralis*	*Antarctoscyphus spiralis*	Peña Cantero et al. (1999)
ANT VIII-5	16-403	*Antarctoscyphus elongatus*	*Antarctoscyphus elongatus*	Peña Cantero et al. (1999)
ANT VIII-5	16-403	*Antarctoscyphus spiralis*	*Antarctoscyphus spiralis*	Peña Cantero et al. (1999)
ANT VIII-5	16-405	*Antarctoscyphus elongatus*	*Antarctoscyphus elongatus*	Peña Cantero et al. (1999)
ANT VIII-5	16-407	*Antarctoscyphus elongatus*	*Antarctoscyphus elongatus*	Peña Cantero et al. (1999)
ANT VIII-5	16-423	*Antarctoscyphus elongatus*	*Antarctoscyphus elongatus*	Peña Cantero et al. (1999)
ANT VIII-5	16-423	*Antarctoscyphus fragilis*	*Antarctoscyphus fragilis*	Peña Cantero et al. (1999)
ANT VIII-5	16-434	*Antarctoscyphus elongatus*	*Antarctoscyphus elongatus*	Peña Cantero et al. (1999)
ANT VIII-5	16-434	*Antarctoscyphus spiralis*	*Antarctoscyphus spiralis*	Peña Cantero et al. (1999)
ANT VIII-5	16-454	*Antarctoscyphus elongatus*	*Antarctoscyphus elongatus*	Peña Cantero et al. (1999)
ANT VIII-5	16-454	*Antarctoscyphus spiralis*	*Antarctoscyphus spiralis*	Peña Cantero et al. (1999)
ANT VIII-5	16-459	*Antarctoscyphus elongatus*	*Antarctoscyphus elongatus*	Peña Cantero et al. (1999)
ANT VIII-5	16-459	*Antarctoscyphus grandis*	*Antarctoscyphus grandis*	Peña Cantero et al. (1999)
ANT VIII-5	16-477	*Antarctoscyphus elongatus*	*Antarctoscyphus elongatus*	Peña Cantero et al. (1999)
ANT VIII-5	16-477	*Antarctoscyphus spiralis*	*Antarctoscyphus spiralis*	Peña Cantero et al. (1999)
ANT VIII-5	16-481	*Antarctoscyphus elongatus*	*Antarctoscyphus elongatus*	Peña Cantero et al. (1999)
ANT VIII-5	16-481	*Antarctoscyphus spiralis*	*Antarctoscyphus spiralis*	Peña Cantero et al. (1999)
ANT VIII-5	16-486	*Antarctoscyphus grandis*	*Antarctoscyphus grandis*	Peña Cantero et al. (1999)
ANT VIII-5	16-492	*Antarctoscyphus grandis*	*Antarctoscyphus grandis*	Peña Cantero et al. (1999)
ANT VIII-5	16-496	*Antarctoscyphus admirabilis*	*Antarctoscyphus admirabilis*	Peña Cantero et al. (1999)
ANT VIII-5	16-496	*Antarctoscyphus elongatus*	*Antarctoscyphus elongatus*	Peña Cantero et al. (1999)
ANT VIII-5	16-496	*Antarctoscyphus grandis*	*Antarctoscyphus grandis*	Peña Cantero et al. (1999)
ANT VII-4	270	*Antarctoscyphus elongatus*	*Antarctoscyphus elongatus*	Peña Cantero et al. (1999)
ANT VII-4	284	*Antarctoscyphus spiralis*	*Antarctoscyphus spiralis*	Peña Cantero et al. (1999)
ANT IX-3	129	*Symplectoscyphus frigidus*	*Symplectoscyphus frigidus*	Peña Cantero et al. (2002)
ANT IX-3	129	*Symplectoscyphus glacialis*	*Symplectoscyphus glacialis*	Peña Cantero et al. (2002)

Expedition	**Station**	**Recorded as**	**Accepted name**	**Reference**
ANT I-2	135	*Symplectoscyphus glacialis*	*Symplectoscyphus glacialis*	Peña Cantero et al. (2002)
ANT I-2	135	*Symplectoscyphus naumovi*	*Symplectoscyphus naumovi*	Peña Cantero et al. (2002)
ANT IX-3	135	*Symplectoscyphus exochus*	*Symplectoscyphus exochus*	Peña Cantero et al. (2002)
ANT IX-3	135	*Symplectoscyphus naumovi*	*Symplectoscyphus naumovi*	Peña Cantero et al. (2002)
ANT VIII-5	16-399	*Symplectoscyphus naumovi*	*Symplectoscyphus naumovi*	Peña Cantero et al. (2002)
ANT VIII-5	16-399	*Symplectoscyphus vanhoeffeni*	*Symplectoscyphus vanhoeffeni*	Peña Cantero et al. (2002)
ANT VIII-5	16-399	*Symplectoscyphus weddelli*	*Symplectoscyphus weddelli*	Peña Cantero et al. (2002)
ANT VIII-5	16-403	*Symplectoscyphus anae*	*Symplectoscyphus anae*	Peña Cantero et al. (2002)
ANT VIII-5	16-403	*Symplectoscyphus glacialis*	*Symplectoscyphus glacialis*	Peña Cantero et al. (2002)
ANT VIII-5	16-405	*Symplectoscyphus anae*	*Symplectoscyphus anae*	Peña Cantero et al. (2002)
ANT VIII-5	16-405	*Symplectoscyphus exochus*	*Symplectoscyphus exochus*	Peña Cantero et al. (2002)
ANT VIII-5	16-407	*Symplectoscyphus anae*	*Symplectoscyphus anae*	Peña Cantero et al. (2002)
ANT VIII-5	16-407	*Symplectoscyphus exochus*	*Symplectoscyphus exochus*	Peña Cantero et al. (2002)
ANT VIII-5	16-407	*Symplectoscyphus glacialis*	*Symplectoscyphus glacialis*	Peña Cantero et al. (2002)
ANT VIII-5	16-407	*Symplectoscyphus liouvillei*	*Symplectoscyphus liouvillei*	Peña Cantero et al. (2002)
ANT VIII-5	16-407	*Symplectoscyphus naumovi*	*Symplectoscyphus naumovi*	Peña Cantero et al. (2002)
ANT VIII-5	16-407	*Symplectoscyphus vanhoeffeni*	*Symplectoscyphus vanhoeffeni*	Peña Cantero et al. (2002)
ANT VIII-5	16-407	*Symplectoscyphus weddelli*	*Symplectoscyphus weddelli*	Peña Cantero et al. (2002)
ANT VIII-5	16-421	*Symplectoscyphus sofiae*	*Symplectoscyphus sofiae*	Peña Cantero et al. (2002)
ANT VIII-5	16-423	*Symplectoscyphus sofiae*	*Symplectoscyphus sofiae*	Peña Cantero et al. (2002)
ANT VIII-5	16-423	*Symplectoscyphus naumovi*	*Symplectoscyphus naumovi*	Peña Cantero et al. (2002)
ANT VIII-5	16-434	*Symplectoscyphus frigidus*	*Symplectoscyphus frigidus*	Peña Cantero et al. (2002)
ANT VIII-5	16-434	*Symplectoscyphus glacialis*	*Symplectoscyphus glacialis*	Peña Cantero et al. (2002)
ANT VIII-5	16-434	*Symplectoscyphus naumovi*	*Symplectoscyphus naumovi*	Peña Cantero et al. (2002)
ANT VIII-5	16-434	*Symplectoscyphus sofiae*	*Symplectoscyphus sofiae*	Peña Cantero et al. (2002)
ANT VIII-5	16-454	*Symplectoscyphus glacialis*	*Symplectoscyphus glacialis*	Peña Cantero et al. (2002)
ANT VIII-5	16-454	*Symplectoscyphus nesioticus*	*Symplectoscyphus nesioticus*	Peña Cantero et al. (2002)
ANT VIII-5	16-454	*Symplectoscyphus vanhoeffeni*	*Symplectoscyphus vanhoeffeni*	Peña Cantero et al. (2002)
ANT VIII-5	16-456	*Symplectoscyphus anae*	*Symplectoscyphus anae*	Peña Cantero et al. (2002)

Expedition	Station	Recorded as	Accepted name	Reference
ANT VIII-5	16-456	*Symplectoscyphus exochus*	*Symplectoscyphus exochus*	Peña Cantero et al. (2002)
ANT VIII-5	16-459	*Symplectoscyphus exochus*	*Symplectoscyphus exochus*	Peña Cantero et al. (2002)
ANT VIII-5	16-459	*Symplectoscyphus naumovi*	*Symplectoscyphus naumovi*	Peña Cantero et al. (2002)
ANT VIII-5	16-468	*Symplectoscyphus naumovi*	*Symplectoscyphus naumovi*	Peña Cantero et al. (2002)
ANT VIII-5	16-468	*Symplectoscyphus glacialis*	*Symplectoscyphus glacialis*	Peña Cantero et al. (2002)
ANT VIII-5	16-475	*Symplectoscyphus glacialis*	*Symplectoscyphus glacialis*	Peña Cantero et al. (2002)
ANT VIII-5	16-475	*Symplectoscyphus vanhoeffeni*	*Symplectoscyphus vanhoeffeni*	Peña Cantero et al. (2002)
ANT VIII-5	16-475	*Symplectoscyphus weddelli*	*Symplectoscyphus weddelli*	Peña Cantero et al. (2002)
ANT VIII-5	16-477	*Symplectoscyphus anae*	*Symplectoscyphus anae*	Peña Cantero et al. (2002)
ANT VIII-5	16-477	*Symplectoscyphus exochus*	*Symplectoscyphus exochus*	Peña Cantero et al. (2002)
ANT VIII-5	16-481	*Symplectoscyphus anae*	*Symplectoscyphus anae*	Peña Cantero et al. (2002)
ANT VIII-5	16-481	*Symplectoscyphus naumovi*	*Symplectoscyphus naumovi*	Peña Cantero et al. (2002)
ANT VIII-5	16-484	*Symplectoscyphus naumovi*	*Symplectoscyphus naumovi*	Peña Cantero et al. (2002)
ANT VIII-5	16-486	*Symplectoscyphus anae*	*Symplectoscyphus anae*	Peña Cantero et al. (2002)
ANT VIII-5	16-486	*Symplectoscyphus exochus*	*Symplectoscyphus exochus*	Peña Cantero et al. (2002)
ANT VIII-5	16-486	*Symplectoscyphus glacialis*	*Symplectoscyphus glacialis*	Peña Cantero et al. (2002)
ANT VIII-5	16-486	*Symplectoscyphus vanhoeffeni*	*Symplectoscyphus vanhoeffeni*	Peña Cantero et al. (2002)
ANT VIII-5	16-486	*Symplectoscyphus weddelli*	*Symplectoscyphus weddelli*	Peña Cantero et al. (2002)
ANT VIII-5	16-486	*Symplectoscyphus naumovi*	*Symplectoscyphus naumovi*	Peña Cantero et al. (2002)
ANT VIII-5	16-492	*Symplectoscyphus frigidus*	*Symplectoscyphus frigidus*	Peña Cantero et al. (2002)
ANT VIII-5	16-492	*Symplectoscyphus naumovi*	*Symplectoscyphus naumovi*	Peña Cantero et al. (2002)
ANT VIII-5	16-492	*Symplectoscyphus plectilis*	*Symplectoscyphus plectilis*	Peña Cantero et al. (2002)
ANT VIII-5	16-496	*Symplectoscyphus exochus*	*Symplectoscyphus exochus*	Peña Cantero et al. (2002)
ANT VIII-5	16-496	*Symplectoscyphus vanhoeffeni*	*Symplectoscyphus vanhoeffeni*	Peña Cantero et al. (2002)
ANT IX-3	179	*Symplectoscyphus glacialis*	*Symplectoscyphus glacialis*	Peña Cantero et al. (2002)
ANT I-2	213	*Symplectoscyphus glacialis*	*Symplectoscyphus glacialis*	Peña Cantero et al. (2002)
ANT I-2	213	*Symplectoscyphus vanhoeffeni*	*Symplectoscyphus vanhoeffeni*	Peña Cantero et al. (2002)
ANT I-2	216	*Symplectoscyphus glacialis*	*Symplectoscyphus glacialis*	Peña Cantero et al. (2002)
ANT IX-3	220	*Symplectoscyphus weddelli*	*Symplectoscyphus weddelli*	Peña Cantero et al. (2002)

Expedition	**Station**	**Recorded as**	**Accepted name**	**Reference**
ANT I-2	220	*Symplectoscyphus exochus*	*Symplectoscyphus exochus*	Peña Cantero et al. (2002)
ANT VII-4	230	*Symplectoscyphus exochus*	*Symplectoscyphus exochus*	Peña Cantero et al. (2002)
ANT VII-4	261	*Symplectoscyphus curvatus*	*Symplectoscyphus curvatus*	Peña Cantero et al. (2002)
ANT VII-4	270	*Symplectoscyphus exochus*	*Symplectoscyphus exochus*	Peña Cantero et al. (2002)
ANT VII-4	274	*Symplectoscyphus frigidus*	*Symplectoscyphus frigidus*	Peña Cantero et al. (2002)
ANT VII-4	281	*Symplectoscyphus frigidus*	*Symplectoscyphus frigidus*	Peña Cantero et al. (2002)
ANT VII-4	281	*Symplectoscyphus glacialis*	*Symplectoscyphus glacialis*	Peña Cantero et al. (2002)
ANT VII-4	290	*Symplectoscyphus exochus*	*Symplectoscyphus exochus*	Peña Cantero et al. (2002)
ANT VII-4	290	*Symplectoscyphus nesioticus*	*Symplectoscyphus nesioticus*	Peña Cantero et al. (2002)
ANT II-4	310	*Symplectoscyphus glacialis*	*Symplectoscyphus glacialis*	Peña Cantero et al. (2002)
ANT II-4	310	*Symplectoscyphus vanhoeffeni*	*Symplectoscyphus vanhoeffeni*	Peña Cantero et al. (2002)
ANT II-4	341	*Symplectoscyphus glacialis*	*Symplectoscyphus glacialis*	Peña Cantero et al. (2002)
ANT II-4	386	*Symplectoscyphus exochus*	*Symplectoscyphus exochus*	Peña Cantero et al. (2002)
ANT II-4	460	*Symplectoscyphus liouvillei*	*Symplectoscyphus liouvillei*	Peña Cantero et al. (2002)
ANT II-4	460	*Symplectoscyphus naumovi*	*Symplectoscyphus naumovi*	Peña Cantero et al. (2002)
ANT II-4	524	*Symplectoscyphus curvatus*	*Symplectoscyphus curvatus*	Peña Cantero et al. (2002)
ANT V-4	672	*Symplectoscyphus frigidus*	*Symplectoscyphus frigidus*	Peña Cantero et al. (2002)
ANT V-4	672	*Symplectoscyphus glacialis*	*Symplectoscyphus glacialis*	Peña Cantero et al. (2002)
ANT IX-3	123	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT IX-3	129	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT IX-3	129	*Stegella lobata*	*Stegella lobata*	Peña Cantero et al. (2004)
ANT I-2	135	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT I-2	135	*Filellum magnificum*	*Filellum magnificum*	Peña Cantero et al. (2004)
ANT I-2	135	*Lafoea dumosa*	*Lafoea dumosa*	Peña Cantero et al. (2004)
ANT I-2	135	*Opercularella belgicae*	*Phialella belgicae*	Peña Cantero et al. (2004)
ANT I-2	135	*Stegella lobata*	*Stegella lobata*	Peña Cantero et al. (2004)
ANT IX-3	135	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT IX-3	135	*Filellum antarcticum*	*Filellum antarcticum*	Peña Cantero et al. (2004)
ANT I-2	154	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)

Expedition	**Station**	**Recorded as**	**Accepted name**	**Reference**
ANT IX-3	158	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT IX-3	158	*Filellum magnificum*	*Filellum magnificum*	Peña Cantero et al. (2004)
ANT VIII-5	16-?	*Opercularella belgicae*	*Phialella belgicae*	Peña Cantero et al. (2004)
ANT VIII-5	16-396	*Abietinella operculata*	*Abietinella operculata*	Peña Cantero et al. (2004)
ANT VIII-5	16-396	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VIII-5	16-396	*Opercularella belgicae*	*Phialella belgicae*	Peña Cantero et al. (2004)
ANT VIII-5	16-396	*Stegella lobata*	*Stegella lobata*	Peña Cantero et al. (2004)
ANT VIII-5	16-399	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VIII-5	16-399	*Filellum antarcticum*	*Filellum antarcticum*	Peña Cantero et al. (2004)
ANT VIII-5	16-403	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VIII-5	16-403	*Hebella plana*	*Hebella plana*	Peña Cantero et al. (2004)
ANT VIII-5	16-403	*Stegella lobata*	*Stegella lobata*	Peña Cantero et al. (2004)
ANT VIII-5	16-405	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VIII-5	16-405	*Filellum antarcticum*	*Filellum antarcticum*	Peña Cantero et al. (2004)
ANT VIII-5	16-405	*Opercularella belgicae*	*Phialella belgicae*	Peña Cantero et al. (2004)
ANT VIII-5	16-407	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VIII-5	16-407	*Hebella plana*	*Hebella plana*	Peña Cantero et al. (2004)
ANT VIII-5	16-407	*Opercularella belgicae*	*Phialella belgicae*	Peña Cantero et al. (2004)
ANT VIII-5	16-407	*Stegella lobata*	*Stegella lobata*	Peña Cantero et al. (2004)
ANT VIII-5	16-423	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VIII-5	16-423	*Hebella plana*	*Hebella plana*	Peña Cantero et al. (2004)
ANT VIII-5	16-423	*Lafoeina longitheca*	*Lafoeina longitheca*	Peña Cantero et al. (2004)
ANT VIII-5	16-423	*Stegella lobata*	*Stegella lobata*	Peña Cantero et al. (2004)
ANT VIII-5	16-434	*Opercularella belgicae*	*Phialella belgicae*	Peña Cantero et al. (2004)
ANT VIII-5	16-454	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VIII-5	16-454	*Campanularia hicksoni*	*Campanularia hicksoni*	Peña Cantero et al. (2004)
ANT VIII-5	16-454	*Opercularella belgicae*	*Phialella belgicae*	Peña Cantero et al. (2004)
ANT VIII-5	16-454	*Stegella lobata*	*Stegella lobata*	Peña Cantero et al. (2004)
ANT VIII-5	16-456	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)

Expedition	**Station**	**Recorded as**	**Accepted name**	**Reference**
ANT VIII-5	16-456	*Filellum antarcticum*	*Filellum antarcticum*	Peña Cantero et al. (2004)
ANT VIII-5	16-459	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VIII-5	16-459	*Campanularia antartica*	*Campanularia antarctica*	Peña Cantero et al. (2004)
ANT VIII-5	16-459	*Filellum antarcticum*	*Filellum antarcticum*	Peña Cantero et al. (2004)
ANT VIII-5	16-468	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VIII-5	16-468	*Lafoea gaussica*	*Lafoea gaussica*	Peña Cantero et al. (2004)
ANT VIII-5	16-470	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VIII-5	16-475	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VIII-5	16-475	*Hebella plana*	*Hebella plana*	Peña Cantero et al. (2004)
ANT VIII-5	16-475	*Opercularella belgicae*	*Phialella belgicae*	Peña Cantero et al. (2004)
ANT VIII-5	16-475	*Stegella lobata*	*Stegella lobata*	Peña Cantero et al. (2004)
ANT VIII-5	16-481	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VIII-5	16-481	*Filellum magnificum*	*Filellum magnificum*	Peña Cantero et al. (2004)
ANT VIII-5	16-486	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VIII-5	16-486	*Filellum antarcticum*	*Filellum antarcticum*	Peña Cantero et al. (2004)
ANT VIII-5	16-486	*Lafoea gaussica*	*Lafoea gaussica*	Peña Cantero et al. (2004)
ANT VIII-5	16-486	*Stegella lobata*	*Stegella lobata*	Peña Cantero et al. (2004)
ANT VIII-5	16-492	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VIII-5	16-496	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VIII-5	16-496	*Campanularia hicksoni*	*Campanularia hicksoni*	Peña Cantero et al. (2004)
ANT IX-3	165	*Abietinella operculata*	*Abietinella operculata*	Peña Cantero et al. (2004)
ANT IX-3	173	*Abietinella operculata*	*Abietinella operculata*	Peña Cantero et al. (2004)
ANT IX-3	220	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT IX-3	220	*Lafoea dumosa*	*Lafoea dumosa*	Peña Cantero et al. (2004)
ANT VII-4	260	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VII-4	261	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VII-4	274	*Campanularia hicksoni*	*Campanularia hicksoni*	Peña Cantero et al. (2004)
ANT VII-4	281	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT VII-4	284	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)

Expedition	**Station**	**Recorded as**	**Accepted name**	**Reference**
ANT II-4	303	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT II-4	308	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT II-4	310	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT II-4	310	*Filellum antarcticum*	*Filellum antarcticum*	Peña Cantero et al. (2004)
ANT II-4	310	*Stegella lobata*	*Stegella lobata*	Peña Cantero et al. (2004)
ANT II-4	341	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT II-4	341	*Filellum antarcticum*	*Filellum antarcticum*	Peña Cantero et al. (2004)
ANT II-4	341	*Stegella lobata*	*Stegella lobata*	Peña Cantero et al. (2004)
ANT II-4	369	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT II-4	372	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT II-4	372	*Hebella plana*	*Hebella plana*	Peña Cantero et al. (2004)
ANT II-4	386	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT II-4	438	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT II-4	438	*Filellum antarcticum*	*Filellum antarcticum*	Peña Cantero et al. (2004)
ANT II-4	450	*Acryptolaria* sp.	*Acryptolaria frigida*	Peña Cantero et al. (2004)
ANT II-4	450	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT II-4	450	*Lafoea gaussica*	*Lafoea gaussica*	Peña Cantero et al. (2004)
ANT II-4	460	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT II-4	474	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT II-4	474	*Filellum antarcticum*	*Filellum antarcticum*	Peña Cantero et al. (2004)
ANT II-4	490	*Hebella plana*	*Hebella plana*	Peña Cantero et al. (2004)
ANT II-4	502	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT II-4	502	*Filellum magnificum*	*Filellum magnificum*	Peña Cantero et al. (2004)
ANT II-4	502	*Hebella plana*	*Hebella plana*	Peña Cantero et al. (2004)
ANT II-4	502	*Opercularella belgicae*	*Phialella belgicae*	Peña Cantero et al. (2004)
ANT II-4	502	*Stegella lobata*	*Stegella lobata*	Peña Cantero et al. (2004)
ANT II-4	524	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT II-4	524	*Filellum antarcticum*	*Filellum antarcticum*	Peña Cantero et al. (2004)
ANT II-4	524	*Stegella lobata*	*Stegella lobata*	Peña Cantero et al. (2004)

Expedition	**Station**	**Recorded as**	**Accepted name**	**Reference**
ANT V-3	553	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
ANT V-4	672	*Billardia subrufa*	*Billardia subrufa*	Peña Cantero et al. (2004)
Scotia 1902-1904	411	*Halecium robustum*	*Halecium jaederholmi*	Ritchie (1907)
Scotia 1902-1904	411	*Hebella striata*	*Hebella striata*	Ritchie (1907)
ANT VIII-5	16-405	*Monocaulus parvula*	*Zyzzyzus parvula*	Svoboda and Stepanjants (2001)
ANT VIII-5	16-421	*Monocaulus parvula*	*Zyzzyzus parvula*	Svoboda and Stepanjants (2001)
ANT VIII-5	16-454	*Monocaulus microrhiza*	*Corymorpha microrhiza*	Svoboda and Stepanjants (2001)
ANT VIII-5	16-468	*Monocaulus microrhiza*	*Corymorpha microrhiza*	Svoboda and Stepanjants (2001)
ANT VIII-5	16-475	*Monocaulus parvula*	*Zyzzyzus parvula*	Svoboda and Stepanjants (2001)
ANT VIII-5	16-477	*Monocaulus parvula*	*Zyzzyzus parvula*	Svoboda and Stepanjants (2001)
ANT VIII-5	16-484	*Monocaulus microrhiza*	*Corymorpha microrhiza*	Svoboda and Stepanjants (2001)
ANT VIII-5	16-486	*Monocaulus parvula*	*Zyzzyzus parvula*	Svoboda and Stepanjants (2001)
ANT VIII-5	16-490	*Monocaulus microrhiza*	*Corymorpha microrhiza*	Svoboda and Stepanjants (2001)
-	-	*Hydractinia vallini*	*Hydractinia vallini*	Svoboda et al. (1997)
ANT XXII/3	63-2	*Bouillonia denhartogi*	*Bouillonia denhartogi*	Svoboda et al. (2006)
ANT XVII/3	Mooring AWI1233-4	*Bouillonia denhartogi*	*Bouillonia denhartogi*	Svoboda et al. (2006)

ANTARCTIC
BENTHIC HYDROIDS
JOAN J. SOTO ÀNGEL
PhD THESIS

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