

Two sea anemones (Cnidaria: Anthozoa: Actiniaria) from the Southern Ocean with evidence of a deep-sea, polar lineage of burrowing sea anemones

LUCIANA C. GUSMÃO*[✉] and ESTEFANÍA RODRÍGUEZ

Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, 10024, New York, NY, USA

Received 17 July 2020; revised 17 November 2020; accepted for publication 20 November 2020

Hexacorals are important components of macrobenthic communities in the Southern Ocean, dominating Antarctic continental shelves. Most of the 119 sea anemones recorded for the Southern Ocean are endemic (81% and 25% endemic species and genera, respectively, one endemic family) with only two species extending beyond the limits of the Southern Ocean. Over 70% of the 83 genera in the Southern Ocean are monotypic, including half of the generic diversity in superfamily Actinostoloidea, which suggests that Antarctica has been isolated long enough for the evolution of new genera but not for many families to evolve. Here, we describe *Chitinaectis marmara* gen. & sp. nov., a new monotypic actinostoloidean genus from Antarctica diagnosed by its unique bi-layered cuticle on column, hexamerous symmetry, unequal development of younger mesenteries and mesogleal tentacle musculature. We also re-describe and extend the geographic distribution of *Scytophorus striatus*, another endemic Antarctic species. Based on morphological and molecular data, we establish the phylogenetic position of *C. marmara* and discuss the implications of the phylogenetic position of *S. striatus* for the resurrection and circumscription of the family Halcampoididae and the evolution of burrowing sea anemones. Finally, we discuss evidence for an actinostoloidean deep-sea, polar lineage of burrowing sea anemones.

ADDITIONAL KEYWORDS: actinostoloidea – Antarctica – burrowers – chitin – sub-Antarctic.

INTRODUCTION

Hexacorals are important components of macrobenthic communities in the Southern Ocean and can dominate the Antarctic continental shelves (Rodríguez & Fautin, 2014). To date, 119 species of sea anemones (order Actiniaria) have been recorded in the Southern Ocean, which corresponds to around 11% of the order total diversity at the species-level and ~45% at the family-level (Rodríguez *et al.*, 2007, Rodríguez & Fautin, 2014). Actiniaria in the Southern Ocean follows the general biogeographic pattern of other invertebrates in the region: high endemism, circumpolar species and differentiation between East and West Antarctica (Rodríguez *et al.*, 2007). The level of species endemism

among sea anemones falls in the higher range of that recorded for other invertebrates (81% for the Southern Ocean; 53% for the Antarctic Region) with the Antarctic Peninsula (AP) holding the highest number of endemic species (Rodríguez *et al.*, 2007). However, endemism is low at higher taxonomic levels with 25% endemic genera and only one endemic family (Rodríguez & Fautin, 2014; Gusmão *et al.*, 2019).

At the family level, five of the 29 actiniarian families distributed in the Southern Ocean (Actinernidae Stephenson, 1922, Actiniidae Rafinesque, 1815, Actinostolidae Carlgren, 1932, Halcampoididae Appellöf, 1896, Hormathiidae Carlgren, 1932 and Sagartiidae Gosse, 1858) account for over 60% of the generic and species-level diversity, with the family Actinostolidae being the second most genus-rich (Rodríguez *et al.*, 2007). Actinostolidae has a long and complex taxonomic history and is comprised of narrowly defined, monotypic genera (e.g. *Hadalanthus* Carlgren, 1956 and *Hormosoma* Stephenson, 1918),

*Corresponding author. E-mail: Lgusmao@amnh.org
[Version of record, published online 18 February 2021; <http://zoobank.org/> urn:lsid:zoobank.org:pub:D000BAA9-51C4-46FE-AC9B-BB361B601FA2]

as well as large, heterogeneous ones (e.g. *Actinostola* Verrill, 1883 and *Sicyonis* Hertwig, 1882) (Rodríguez *et al.*, 2008). While the original circumscription of Actinostolidae included both deep-sea and polar species (e.g. Carlgren, 1949; Fautin & Barber, 1999), the transferal of anemones from chemosynthetic habitats (clade Chemosynthina *sensu* Rodríguez *et al.*, 2012) from Actinostolidae to Metridioidea Carlgren, 1893 by Rodríguez *et al.* (2008) and Rodríguez & Daly (2010), left only polar and temperate species within Actinostolidae.

Actinostolidae is placed within the superfamily Actinostoloidea Carlgren, 1925, together with the family Exocoelactinidae Carlgren, 1925. Members of both families may be characterized by a particular pattern in the development of mesenteries: some actinostolids exhibit an unequal development of partners in pairs of the youngest cycle or cycles in which the partner nearest the adjacent pair in the next oldest cycle is usually smaller (i.e. *Actinostola* rule), whereas exocoelactinids exhibit unequal development of partners in pairs of the third and higher cycles that are arranged bilaterally with youngest pairs in the middle of secondary exocoels (i.e. *Exocoelactis* rule) (Carlgren, 1949; Yanagi *et al.*, 2015). The unusual mesenterial arrangement of actinostoloideans *sensu* Rodríguez & Daly (2010) was detected previously by Hertwig (1882) after studying deep-sea species from the Challenger expedition. This unusual development of a pair of mesenteries in actinostoloideans does not depend on the type of symmetry, being present in both hexamerous (e.g. *Actinostola*) or octamerous genera (e.g. *Sicyonis*, *Stomphia* Gosse, 1859).

Similar to Actinostolidae, most genera within the former family Halcampoididae (five out of seven genera) are distributed in the Southern Ocean and other polar regions (Rodríguez *et al.*, 2007). Initially, Halcampoididae included seven genera of burrowing actinarians grouped mainly by an elongate column, few tentacles and mesenteries, and the lack of a marginal sphincter muscle (Carlgren, 1949). Rodríguez *et al.* (2012) recently transferred Halcampoididae from the superfamily (tribe) Athenaria of Carlgren (1949) to the superfamily Metridioidea, based on molecular phylogenetic analysis. These authors also modified the membership of the former Halcampoididae to include genera within Halcampidae Andres, 1883 (the latter name has the priority) when synonymizing both families because no mayor morphological differences hold after revision of the familial diagnoses (Rodríguez *et al.*, 2012). Thus, according to the last circumscription of the family (i.e. Halcampidae *sensu* Rodríguez *et al.*, 2012), this family is the fourth most-diverse at the generic and species level (with eight genera and 16 species) in the Southern Ocean.

In an effort to increase our knowledge of Antarctic sea anemone diversity, and to contribute reliable taxonomic information to understand its biogeography, we describe a putative new monotypic actinostoloidean genus (as *Chitinactis marmara* **gen. & sp. nov.**, described below) based on its unique combination of morphological characters: bi-layered cuticle on column, hexamerous symmetry, unequal development of younger mesenteries and mesogleal tentacle musculature. We also re-describe *Scytophorus striatus* Hertwig, 1882, an endemic burrowing species from the Southern Ocean only known from the original description. We use morphological and molecular data to establish their phylogenetic position and discuss implications for the taxonomy of the superfamily Actinostoloidea, the family Actinostolidae and the former burrowing family, Halcampoididae. In addition, we extend the geographic range of *S. striatus* from the Kerguelen Islands to the Burdwood/Namuncurá Bank in sub-Antarctica, based on newly collected material, and discuss the implications for the biogeography of Southern Ocean species. Finally, based on the phylogenetic position of *S. striatus*, we hypothesize a deep-sea, polar origin for burrowing sea anemones in the families Halcampulactidae Gusmão *et al.*, 2019 and Halcampoididae, building on recent discussions on biogeographic patterns and the origin of sea anemone fauna in the Southern Ocean (e.g. Rodríguez *et al.*, 2007; Rodríguez & Fautin, 2014).

MATERIAL AND METHODS

ANATOMY, MICROANATOMY, CNIDAE

The morphological description of the new species (*Chitinactis marmara* – AMNH 4662, 4663, 4775, AMNH_IJC 00331550, 00361336, 00361337, NHMUK) and *Scytophorus striatus* (AMNH 5254, 5268, 5275, AMNH_IJC 00361338) is based on specimens collected in the Southern Ocean (Fig. 1) and deposited in the American Museum of Natural History (AMNH) in New York and the Natural History Museum (NHM) in London. Formalin-fixed specimens were examined whole, in dissection and as serial sections. We made 10-µm thick longitudinal and cross-sectional serial sections from at least two specimens for each species, using standard paraffin techniques and stained with Heidenhain Azan stain (Presnell & Schreiber, 1997). We macerated small pieces of tissue from each region of the body (actinopharynx, column, mesenterial filaments and tentacles) on a slide, and photographed and measured undischarged cnida capsules using differential interference contrast (DIC) microscopy at 1000× magnification. Except for the rarer types, we measured at least 20 capsules from

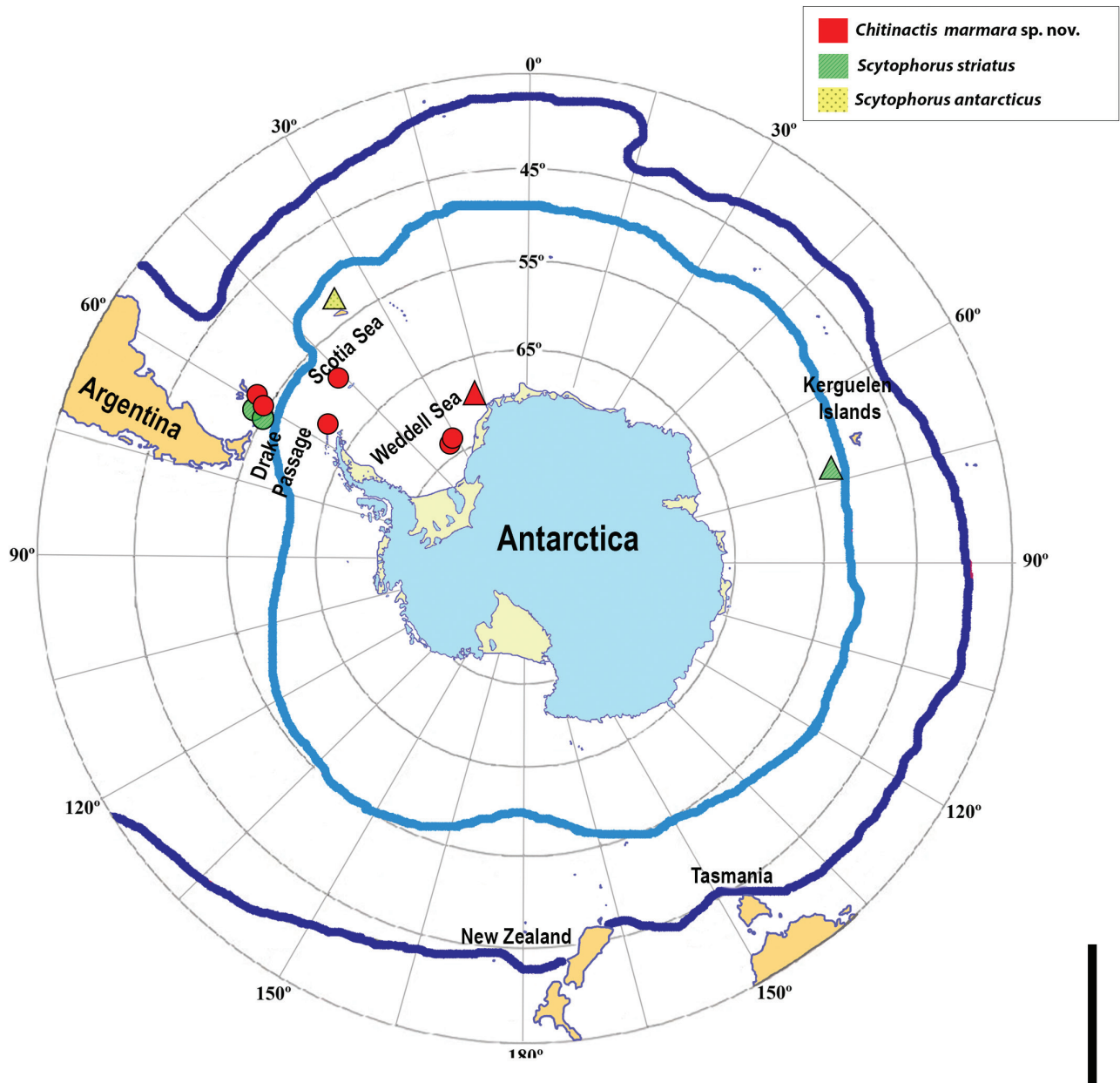


Figure 1. Detail of known localities for *Chitinactis marmara* (solid red shapes; triangle indicates type locality), *Scytophorus striatus* (dashed green shapes) and *Scytophorus antarcticus* (dotted yellow shape) in the Southern Ocean. Triangles mark type localities and circles mark additional localities for each species; lines indicate the Antarctic Polar Front (inner circle; light blue) and the Subtropical Front (outer circle; dark blue) (following Rintoul, 2007). Scale bar, 1600 km.

each tissue to calculate the range for length and width. We confirmed the presence of each type of cnidaria in each tissue in histological slides. Means and standard deviations are given to provide information about variability in capsule size, but these values are not statistically significant (see: Sanamyan & Sanamyan, 2012). We follow the nematocyst terminology described by Gusmão *et al.* (2018) and provide photographs of each type of nematocyst for reliable comparison

across terminologies and taxa (see: Fautin, 1988). We follow the higher level classification for Actiniaria of Rodríguez *et al.* (2014).

MICRO-CT SCANNING AND 3D-MODELLING

We stained one specimen of the new species (AMNH 4775) and one specimen of *Scytophorus striatus* (AMNH 5268) fixed in 8% formalin and preserved in

75% ethanol, using 1% osmium tetroxide following the protocol described by [Gusmão *et al.* \(2018\)](#). Once stained and washed, we transferred specimens to a 50 mL polyethylene tube filled with 100% ethanol, where the specimen was scanned on a phoenix v|tome|x s240 GE (General Electric, Fairfield, CT, USA) at 60 kV and 70 μ A with a molybdenum target at the Microscopy and Imaging Facility (MIF) at AMNH. The exposure time for the detector was 500.155 ms for a final resolution of 8.0998 microns/voxel for the new species and 400.145 and 8.51994 microns/voxel for *S. striatus*. We used the software Phoenix datos|x (General Electric, Wunstorf, Germany) to reconstruct the raw data, and processed and edited the resulting files and images on 3D slicer ([Fedorov *et al.*, 2012](#)). Full micro-CT scan data are deposited in the Morphobase (www.morphosource.org) under the project 'AMNH 4775' for the new species and 'AMNH 5268' for *S. striatus*.

MOLECULAR DATA COLLECTION AND PHYLOGENETIC ANALYSES

We isolated genomic DNA from approximately 25 mg of tissue each from both taxa using the Total DNA from Animal Tissues protocol of the Qiagen DNeasy kit. We amplified whole genomic DNA for three mitochondrial markers (12S, 16S, COIII) and nuclear markers (18S, 28S), using published primers (e.g. [Geller & Walton, 2001](#); [Daly *et al.*, 2008](#); [Lauretta *et al.*, 2014](#)). We cleaned polymerase chain reaction (PCR) products using Thermo Scientific Fermentas clean-up protocol, using Exonuclease I and FastAP thermosensitive alkaline phosphatase per manufacturer's specifications (shrimp alkaline phosphatase replaced by FastAP). We cycle-sequenced a total of 5 μ L of cleaned PCR product, at a concentration of 25 ng of product for every 200 base pairs (bp) of marker length, in an ABI BigDye Terminator v.3.1 (Applied Biosystems) reaction following the manufacturer's protocols using PCR amplification primers. We cleaned cycle sequencing products using Centri-Sept columns (Princeton Separations; following the manufacturer's protocol) containing DNA-grade Sephadex (G-50 fine; GE Healthcare) and sequenced them on an ABI 3770x at the in-house facilities of the AMNH. We assembled and edited forward and reverse sequences in GENEIOUS v.10.0.9 ([Kearse *et al.*, 2012](#)) and blasted the assembled sequences against the nucleotide database of GenBank to confirm amplification of target marker/organism.

The newly generated sequences were combined to the dataset analysed by [Gusmão *et al.* \(2019\)](#), which contains most sea anemone sequences available for phylogenetic studies (see [Supporting Information, File S1](#)). Sequences were aligned separately for each marker using MAFFT v.7.0 online at [http://mafft.](http://mafft.cbrc.jp/alignment/server/)

cbrc.jp/alignment/server/ ([Katoh & Standley, 2013](#); [Katoh *et al.*, 2017](#)) and the following settings: strategy L-INS-I; scoring matrix for nucleotide sequences, 200 PAM/k = 2; gap open penalty, 1.53; offset value, 0.05. We chose the best model of nucleotide substitution for each marker using the Akaike Information Criterion (AIC) on jModelTest2 ([Guindon & Gascuel, 2003](#); [Darrriba *et al.*, 2012](#)) implemented on the CIPRES Portal ([Miller *et al.*, 2010](#)). Maximum likelihood (ML) analyses were performed on RAxML-NG v.0.6.0 ([Kozlov *et al.*, 2018](#)) for each marker separately and as a concatenated dataset of mitochondrial, nuclear and all sequences, using the appropriate model of nucleotide substitution for each marker. We used the Majority Rule Criterion to access clade support and allowed automatic halt (-autoMRE). An additional ML analysis of each separate and concatenated datasets was conducted on PhyML v.3.0 online at <http://www.atgc-montpellier.fr/phyml/> ([Guindon *et al.*, 2010](#)) allowing automatic model selection using the AIC criterion ([Lefort *et al.*, 2017](#)) and 1000 rounds of bootstrap for each marker separately and in combination. Maximum parsimony (MP) analyses were conducted in TNT v.1.1 ([Goloboff *et al.*, 2008](#)), using random and constrained sectorial searches, tree drifting and 100 rounds of tree fusing; trees of minimum length were found at least ten times. Clade support on the obtained strict consensus tree was accessed after 1000 bootstrap rounds for each dataset. Gaps were treated as missing data in all analyses.

RESULTS

MOLECULAR DATA AND PHYLOGENETIC ANALYSES

Scytophorus striatus and the new species are recovered in a clade of species found in the poles or temperate waters (~Actinostoloidea, except for *Exocoelactis* [Carlgren, 1925](#), which is found in the tropical Indo-Pacific) in both ML and MP analyses, but never as sister to each other. Within the actinostoloidean clade, the new species was generally recovered as sister to a clade of actinostolids, except for *Hormosoma scotti* [Stephenson, 1918](#) and *Anthosactis janmayeni* [Danielssen, 1890](#), although its position varied slightly due to differences in the position of clade *Anthosactis* + *Hormosoma* between MP and ML analyses. *Scytophorus striatus* consistently recovered in all separate and concatenated datasets in ML and MP analyses within a clade containing two burrowing anemones: *Halcampulactis solimar* [Gusmão *et al.*, 2019](#) and *Halcampoides purpureus* [Studer, 1879](#). However, the position of this clade is inconsistent between analyses, varying from being sister to Enthemonae in the MP and RAxML analyses (see [Fig. 2](#)), to sister to superfamily Actinostoloidea in the PhyML analysis

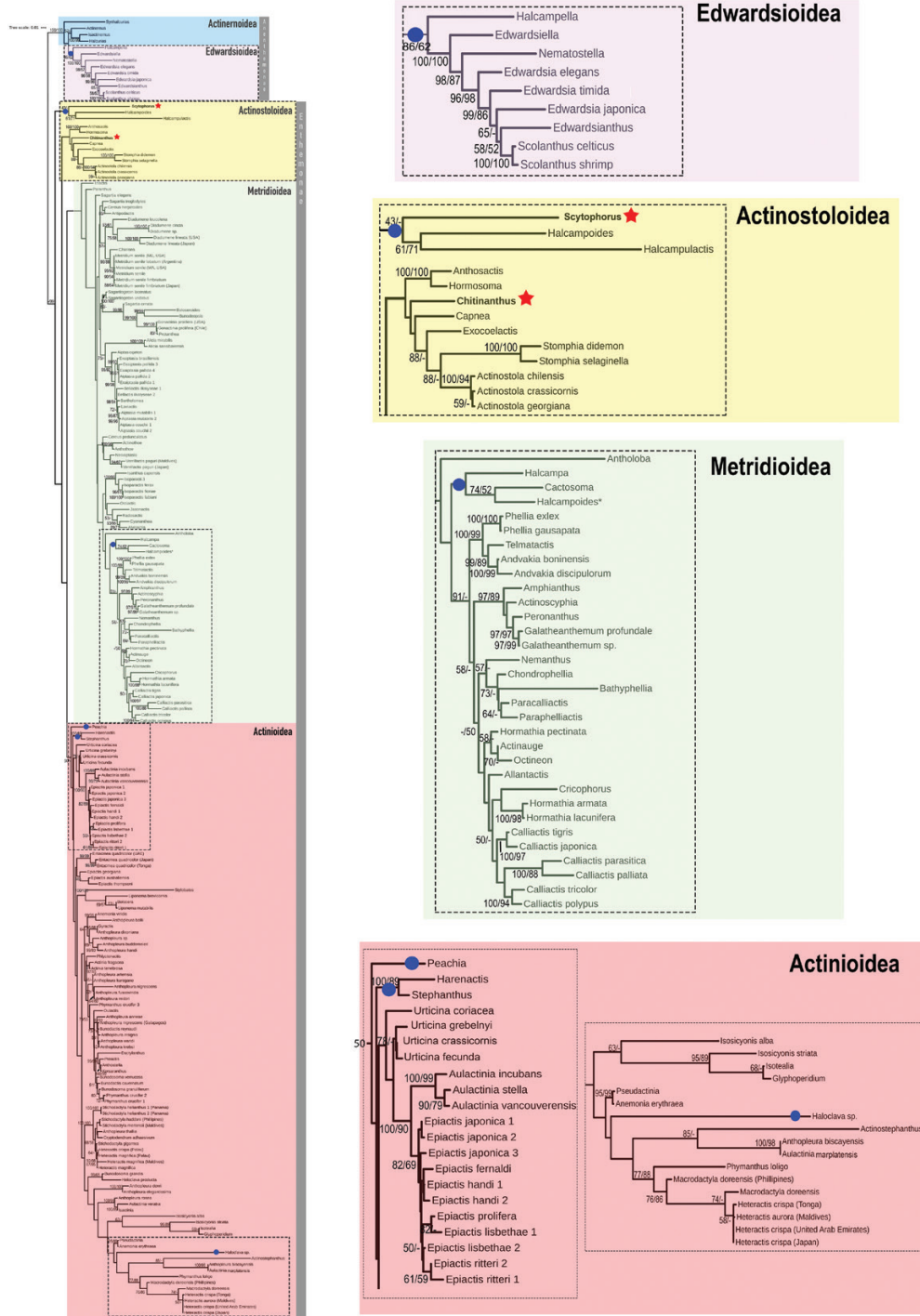


Figure 2. Phylogenetic reconstruction resulting from maximum likelihood analysis using a concatenated dataset of three mitochondrial (12S, 16S, *COIII*) and two nuclear markers (18S, 28S). Coloured boxes indicate actiniarian superfamilies with hypothesized phylogenetic position of *Chitinactis marmara* and *Scytophorus striatus* indicated by red stars; clade of burrowing anemones indicated by blue circle. Bootstrap resampling values indicated above branches (ML/MP); only support values > 50% are shown.

(tree not shown; similar to Fig. 2, except for the position of the clade in question).

Length and marker variability for sequences of the new species and *Scytophorus striatus* fell within those previously reported for Actiniaria (e.g. Daly *et al.*, 2008, 2010; Gusmão & Daly, 2010; Rodríguez *et al.*, 2012, 2014; Laretta *et al.*, 2014; Gusmão *et al.*, 2018). The concatenated dataset had a total of 219 taxa and 8205 sites (2040 mitochondrial sites; 6165 nuclear sites). Maximum likelihood and MP phylogenetic analyses of the concatenated dataset agreed in basic topology (Fig. 2) and concur to the two major suborders (Anthemoneae and Enthemonae) and five superfamilies (Actinernoidea Stephenson, 1922, Actinioidea Rafinesque, 1815, Actinostoloidea, Edwardsioidea Andres, 1881 and Metridioidea), and levels of support comparable to previous broadscale studies of Actiniaria (e.g. Rodríguez *et al.*, 2012, 2014; Laretta *et al.*, 2014; Grajales & Rodríguez, 2016; Gusmão *et al.*, 2019).

TAXONOMIC DESCRIPTION

ORDER ACTINIARIA HERTWIG, 1882

SUBORDER ENTHEMONAE RODRÍGUEZ & DALY, 2014 IN RODRÍGUEZ *ET AL.* (2014)

SUPERFAMILY ACTINOSTOLOIDEA CARLGREN, 1932

Diagnosis (after Gusmão *et al.* (2019) with additions in italics). *Enthemoneae* usually with basilar muscles, mesogleal marginal sphincter and no acontia or acontoids; rarely lacking basilar muscles and marginal sphincter muscle. Aboral end mostly flat and adherent; sometimes with physa. Column usually smooth; rarely with cuticle and rows of tubercles. Mesenteries usually not differentiated into macro- and microcnemes; rarely differentiated into macro- and microcnemes. Mesenteries of same pair often unequally developed. Retractors usually diffuse weak or strong, sometimes circumscribed. Cnidom: gracile spirocysts, basitrichs, holotrichs, *b*-mastigophores and *p*-mastigophores A.

Included families: Actinostolidae, Exocoelactinidae, Halcampoididae and Halcampulactidae.

Remarks: We modified the diagnosis of the superfamily Actinostoloidea to reflect the characters observed in the new species (*Chitinactis marmara*; e.g. rows of tubercles formed by thickenings of mesoglea and strong cuticle on column). In addition, we modified the superfamilial diagnosis to reflect recent changes in the higher level classification of Actiniaria (i.e. Rodríguez *et al.*, 2014) and the nematocyst terminology used in this study (see: Gusmão *et al.*, 2018). These

modifications have been made in all other diagnoses included in this study.

FAMILY ACTINOSTOLIDAE CARLGREN, 1932

Diagnosis (after Rodríguez *et al.* (2008) with modifications in italics). *Enthemoneae* with basilar muscles and mesogleal marginal sphincter; column commonly smooth, rarely tuberculate or with papillae. Tentacles regularly arranged; their aboral sides sometimes with nematocysts batteries, sometimes thickened. Mesenteries not divisible into macro- and microcnemes. Younger mesenteries not bilaterally arranged. Retractor muscles diffuse, rarely circumscribed. No acontia. Cnidom: gracile spirocysts, basitrichs and *b*-mastigophores and *p*-mastigophores A.

Type genus: *Actinostola* Verrill, 1883.

Other valid genera: *Antholoba* Hertwig, 1882 (?); *Anthosactis* Danielssen, 1890; *Antiparactis* Verrill, 1899; *Bathydactylus* Carlgren, 1928; *Chitinactis*; *Cnidanthus* Carlgren, 1927; *Glandulactis* Riemann-Zürneck, 1978; *Hadalanthus*; *Hormosoma*; *Ophiodiscus* Hertwig, 1882; *Paranthus* Andres, 1883 (?); *Parasicyonis* Carlgren, 1921; *Pseudoparactis* Stephenson, 1920; *Pycnanthus* McMurrich, 1893; *Sicyonis*; *Stomphia*; *Synsicyonis* Carlgren, 1921; *Tealidium* Hertwig, 1882.

Remarks: We follow the circumscription given by Rodríguez *et al.* (2008) for Actinostolidae, except for the addition of genus *Glandulactis* to the family and removal of *Cnidanthea* Carlgren, 1959 now included in the family Isanthiidae Carlgren, 1938 (Metridioidea) following Fautin (2016). The question mark after genera *Antholoba* and *Paranthus* reflects the uncertainty in their taxonomic placement due to every molecular phylogenetic analysis to date placing them within the superfamily Metridioidea (e.g. Laretta *et al.*, 2014; Rodríguez *et al.*, 2014; Grajales & Rodríguez, 2016; Gusmão *et al.*, 2018, 2019, 2020). The diagnosis of Actinostolidae was not required to be modified by the inclusion of the new genus *Chitinactis*.

CHITINACTIS GUSMÃO & RODRÍGUEZ

Zoobank registration: urn:lsid:zoobank.org:act:8BEB8002-DA39-40B2-B1C0-00CF77A01F54

Diagnosis: Actinostolidae with a broad base. Column low, firm, slightly rugose, with rows of mesogleal tubercles. Margin distinct. Sphincter mesogleal, strong.

Tentacles without aboral thickenings or batteries of nematocysts; mesogleal longitudinal musculature in tentacles. Considerably more mesenteries proximally than distally; one cycle of perfect mesenteries. Younger cycles of mesenteries with unequal development between members of the pairs. Retractors well developed, diffuse; strong parietobasilar and basilar musculature. Cnidom: gracile spirocysts, basitrichs, *b*-mastigophores and *p*-mastigophores A.

Type species: Chitinactis marmara by original designation.

Etymology: From *chitine* the Latinized form of the Greek χιτών, a tunic, referring to the thick cuticle covering species of this genus, and the Latinized Greek suffix *-actis*, from ακτίνα, a ray. The gender is feminine.

CHITINACTIS MARMARA GUSMÃO & RODRÍGUEZ

(FIGS 3–5; TABLE 1)

Zoobank registration: urn:lsid:zoobank.org:act:BE47D4D3-33D1-47E9-84A6-CE5AF0C96A51

Material: Holotype AMNH_IZC 00331556 (1 specimen), ANT XV/3 Cruise, EASIZ II Program, R/V ‘Polarstern’, Sta. PS48/197, Kapp Norvegia, Antarctica, Southern Ocean, 71°17’S 12°36.30’W, 416 m, 15 February 1998, Agassiz Trawl, collected by P. López-González. Paratypes AMNH 4775 (five specimens), same collection data as holotype. AMNH 4662 (one specimen), ANT XIX/5 Cruise, LAMPOS Program, R/V ‘Polarstern’, Sta. PS61/150, Burdwood/Namuncurá Bank, Scotia Sea, Antarctica, Southern Ocean, 54°30.22’S 56°08.20’W, 286.3–290.3 m, 6 April 2002, Agassiz Trawl, collected by E. Rodríguez. AMNH 4663 (ten specimens), ANT XIX/5 Cruise, LAMPOS Program, R/V ‘Polarstern’, Sta. PS61/153, Burdwood/Namuncurá Bank, Scotia Sea, Antarctica, Southern Ocean, 54°31.22’S 56°08.93’W, 277–296 m, 6 April 2002, Bottom Trawl, collected by E. Rodríguez. AMNH_IZC 00331550 (one specimen), ANT XXIII/8 Cruise, EBA Program, R/V ‘Polarstern’, Sta. PS69/662-1, South Shetland Islands, Antarctica, Southern Ocean, 61°35.91’S 57°17.04’W / 61°35.41’S, 57°20.60’W, 425.4–431.8 m, 30 December 2006, Bottom Trawl, collected by P. López-González. AMNH_IZC 00361336 (one specimen), ANT XXIX/9 Cruise, FOS Program, R/V ‘Polarstern’, Sta. PS82/283-2, Weddell Sea, Antarctica, Southern Ocean, 74°59.61’S 29°22.89’W, 406.7–411 m, 7 February 2014, Agassiz Trawl, collected by R. Zapata. AMNH_IZC 00361337 (one specimen), ANT XXIX/9 Cruise, FOS Program, R/V ‘Polarstern’, Sta. PS82/283-2, Weddell Sea, Antarctica, Southern Ocean, 74°59.46’S 29°22.75’W, 406.7–411 m,

7 February 2014, Agassiz Trawl, collected by R. Zapata. NHMUK (one specimen), JCR15005, event #61, NW of Coronation Island, South Orkney Islands, Scotia Sea, Antarctica, 60°21.3180’S 46°41.0820’W, 516.97 m depth, 9 March 2016, Agassiz trawl, collected by E. Rodríguez.

Additional material examined for comparison: *Stomphia selaginella* (Stephenson, 1918): AMNH 4326 (20 specimens); locality: ANT XV/3 Cruise, EASIZ II Program, R/V ‘Polarstern’, Sta. PS48/220, Southern Ocean, Antarctica, Weddell Sea, Austasen, 70°50.40’S 10°35.40’W, collected on 19 February 1998 by P. López-González (236 m). *Actinostola crassicornis* (Hertwig, 1882): AMNH 4698 (three specimens); locality: ANT XIX/5 Cruise, LAMPOS Program, R/V ‘Polastern’, Sta. 61/153, Drake Passage, Antarctica, Burdwood/Namuncurá Bank, 54°31.22’S 56°08.93’W, collected on 6 April 2002 by E. Rodríguez (277 m). *Actinostola georgiana* Carlgren, 1927: AMNH 4803 (one specimen); locality: ANT XXI/2 Cruise, BENDEX Program, Sta. PS65/019-1, Southern Ocean, Bouvet Island, 54°30.09’S 03°14.13’W, collected on 24 November 2003 by E. Rodríguez (247 m).

Diagnosis: Species with mesogleal marginal sphincter and tentacular longitudinal musculature, younger mesenteries unequally developed, no acontia and well-developed, thick chitinous cuticle on column.

Etymology: The species name is Latinized Greek from μάρμαρο, marble. It is named in honour of Pablo López-González (Universidad de Sevilla, Spain). He was the first to collect this species and we thank him for his contributions to the diversity of Anthozoa in the Southern Ocean and his mentoring of systematists working on this group.

External anatomy (Fig. 3): Some specimens are flat with triangular body, with elevated central column (Fig. 3A, B) and broad, flat pedal disc (Fig. 3B, C), others more elongate (Fig. 3C). Pedal disc broader than column, irregular in shape (Fig. 2B) with mesenterial insertions visible on limbus (Fig. 3C); 9–21 mm in diameter in preserved specimens. Column cylindrical, broader proximally, becoming less so distally due to contraction of scapulus into scapus in most specimens (Fig. 3B, D); in less contracted specimens, column visibly divided into short, smooth scapulus and long scapus (Fig. 3E); column diameter 5–16 mm at mid-column and 7–22 mm length in preserved specimens. Scapus with small tubercles in longitudinal rows throughout scapus (Fig. 3F); column epidermis may be absent in certain regions (Fig. 3F). Thick, golden cuticle on column (Fig. 3A, F); may form a thick ‘crust’ easily detached from animal (Fig. 3G); cuticle completely absent from column in some specimens (Fig. 3C, E). Margin of column tentaculate (Fig. 3C, E). Oral disc

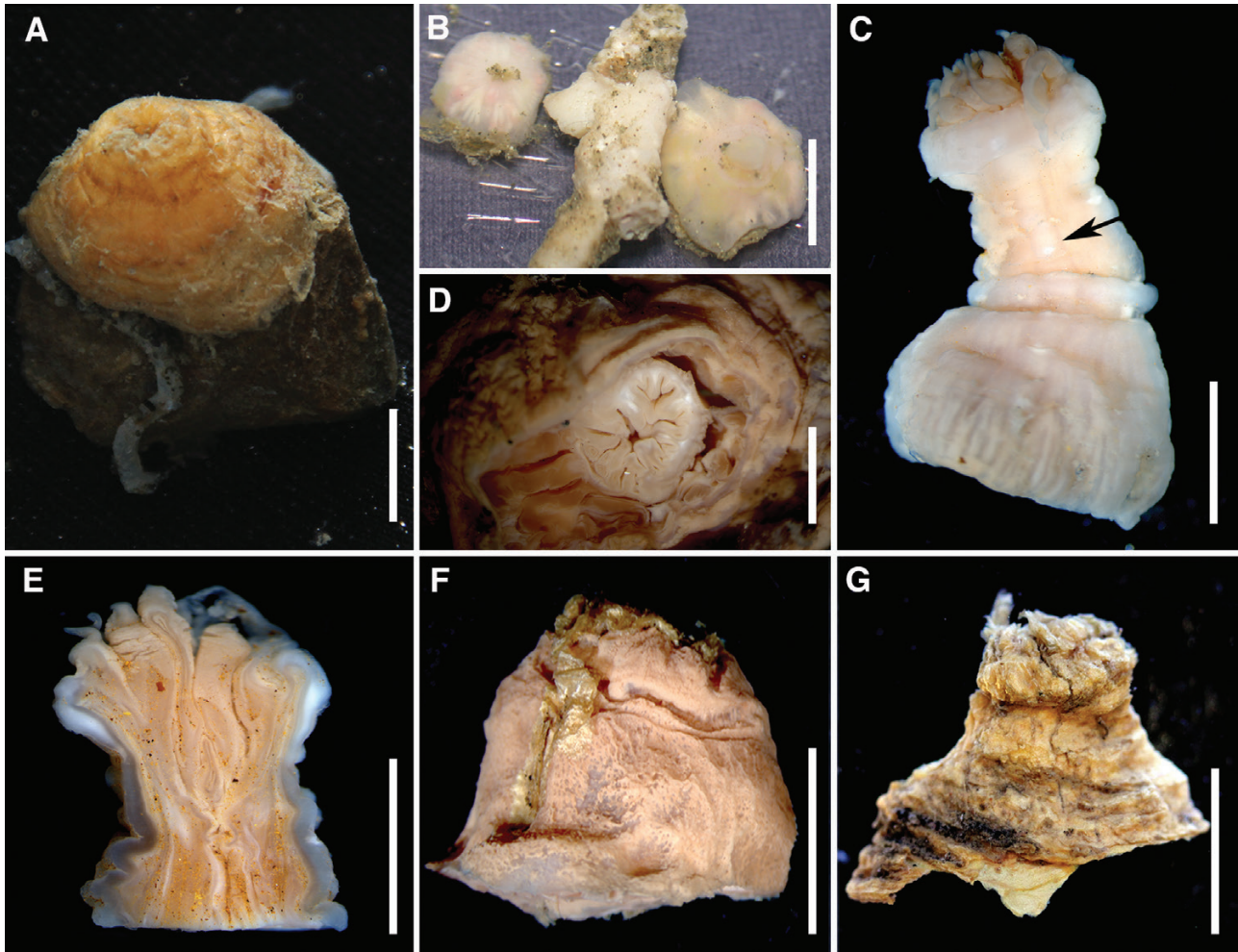


Figure 3. External anatomy of *Chitinactis marmara*. A, lateral view of live specimen; B, two live specimens without cuticle; C, lateral view of preserved specimen showing row of columnar tubercles (indicated by arrow) and mesenterial insertions on limb; D, cross-section through distal column showing scapulus with thick mesoglea; E, longitudinal section through distal column showing; note marginal sphincter musculature (white) on scapulus; F, detail of column with epidermis and cuticle; G, detail of columnar cuticle detached from epidermis. Scale bars, A, 10 mm; B, 20 mm; C, E, 4 mm; D, G, 20 mm; F, 10 mm.

small, circular in contracted specimens; diameter 1–3 mm in preserved specimens. Tentacles about 50, slender (Fig. 3C, E); putatively arranged in four cycles; up to 5 mm in preserved specimens.

Internal anatomy, microanatomy (Fig. 4): Aboral end flat, not physa-like (Fig. 4A). Overall body wall thickness varies along column (Fig. 4A–C): scapus epidermis 85–271 μm , mesoglea 92–398 μm and gastrodermis 40–190 μm (Fig. 4D); scapulus epidermis 101–169 μm , mesoglea 79–248 μm and gastrodermis 91–158 μm (Fig. 4E). Thick, brown, non-stratified cuticle on scapus (Fig. 4B, C, E), absent from scapulus (Fig. 4D); cuticle also on pedal disc (Fig. 4A). Longitudinal circular endodermal musculature of column strong, with

high muscle processes in distal column (Fig. 4F), also observed in dissections (Fig. 4B, arrow). Mesogleal marginal sphincter musculature (Fig. 4G). Longitudinal musculature of tentacles mesogleal (Fig. 4H). Actinopharynx short, strongly longitudinally sulcate (Fig. 4A); siphonoglyphs not differentiated (Fig. 4I).

Two cycles of mesenteries distally at scapulus-level (Fig. 4J): six pairs of perfect mesenteries of first cycle and four pairs of second cycle with a single mesentery of a pair in the dorso- and ventral-lateral exocoels (but seen in scapulus: Fig. 4K). Three cycles of mesenteries at distal column: six pairs of perfect mesenteries of first cycle, two cycles of imperfect mesenteries (6 + 6 + 12: Fig. 4K, L). More mesenteries proximally than distally (6 + 6 + 12 + 24: Fig. 4L, N). Retractors of mesenteries of

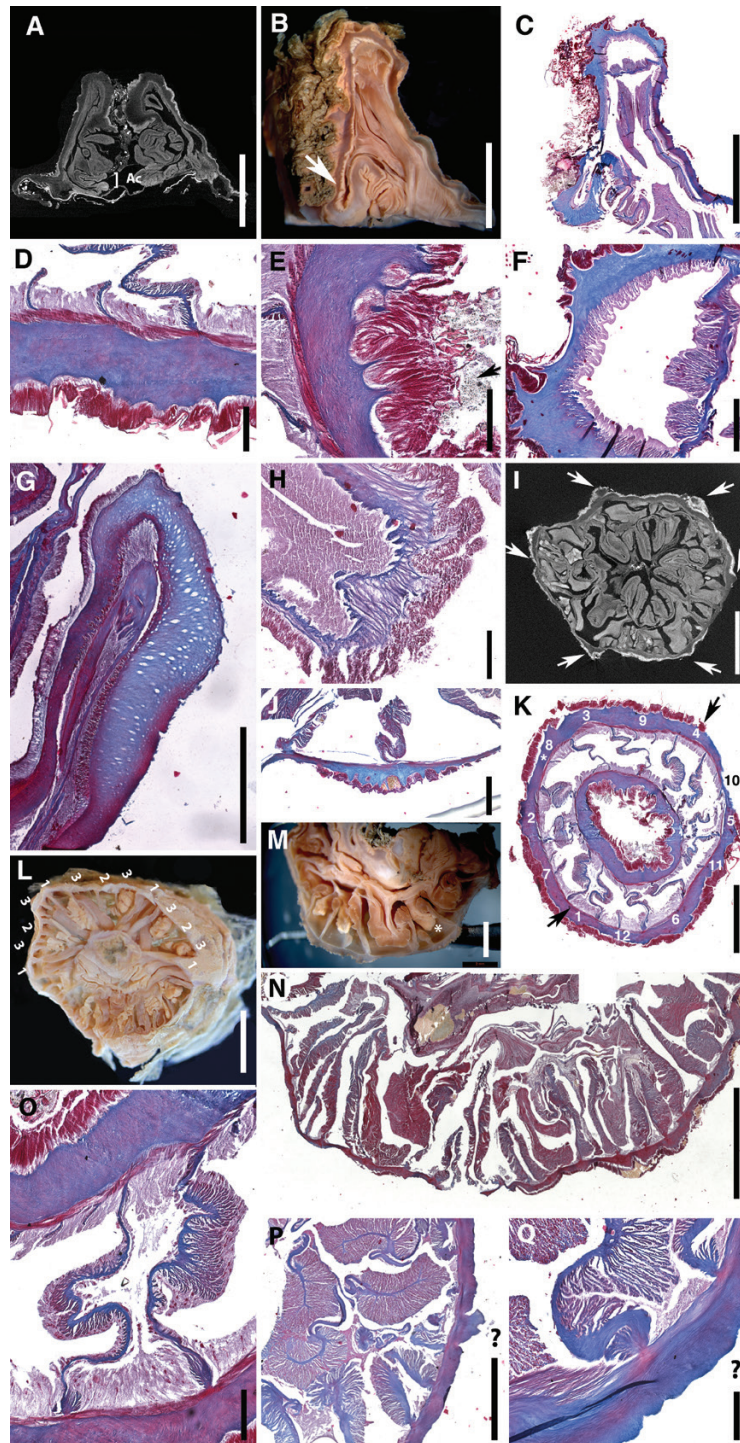


Figure 4. Internal anatomy and microanatomy of *Chitinactis marmara*. A, micro-CT longitudinal scan through whole specimen showing broad, flattened pedal disc, wide oral disc, short actinopharynx and gastrovascular cavity; note cuticle on both pedal disc and column (stained in white); B, longitudinal section through half of distal column showing body layers and strong cuticle; C, longitudinal histological section through half of distal column showing body wall layers; D, detail of histological cross-section through scapulus showing body layers; note thick mesoglea; E, detail of histological cross-section through scapus showing relatively thinner mesoglea and thicker epidermis compared to scapulus; note cuticle attached to epidermis (indicated by arrow); F, histological longitudinal section through column showing strong, longitudinal, circular

first cycle strong, diffuse (Fig. 4K, N, O); well developed, pinnate, with well-developed central mesogleal lamella proximally (Fig. 4P). Retractors of second and third cycles weaker than in first cycle, diffuse, occupying entire mesentery length (Fig. 4K, N). Mesenteries of fourth cycle small, without well-developed musculature (Fig. 4P). Parietobasilar musculature well developed, strong in mesenteries of first to third cycles both distally (Fig. 4O) and proximally (Fig. 4Q); absent in mesenteries of fourth (Fig. 4N). Basilar musculature present (not shown). Gametogenic tissue in third cycle mesenteries (Fig. 4L); specimens collected in December sterile and those in February females. Species inferred gonochoric.

Cnidom: spirocysts, basitrichs, *b*-mastigophores and *p*-mastigophores A. See Figure 5 and Table 1 for size and distribution.

Distribution and natural history: Multiple individuals of *Chitinactis marmara* were collected around the South Shetland Islands in the Antarctic Peninsula, the south-west of the South Orkney Islands and east of Burdwood/Numuncurá Bank in the Scotia Arc, from 277–517 m depth. Specimens of *C. marmara* were also collected from the eastern Weddell Sea (at Kapp Norvegia) between 400 and 416 m depth, some of them collected together with multiple individuals of *Aulactinia sulcata* (Clubb, 1902). We consider *C. marmara* a shelf endemic in Antarctica and sub-Antarctica. The new record of *A. sulcata* extends the circumpolar distribution of the species found in the Bransfield Strait, South Shetland Islands, Elephant Islands and the Drake Passage in the Antarctic Peninsula and McMurdo Sound (Victoria Island) in the Ross Sea (Rodríguez & López-González, 2013), to include the south-eastern Weddell Sea.

Remarks: *Chitinactis* is a monotypic genus easily differentiated from other actinostolids based on

the following combination of characters: mesogleal tubercles and distinct columnar cuticle, mesogleal longitudinal tentacle musculature and unequal development of younger mesenteries. Although the large and common *b*-mastigophores found in *C. marmara* (Fig. 5G) strongly resemble those in the tentacles of some actinostolids (e.g. *Hormosoma*, *Stomphia* and *Actinostola*), they are always only found in the filaments. To date, no specimens having the attributes described for *C. marmara* have been reported in the literature for the Southern Ocean or anywhere else.

FAMILY HALCAMPOIDIDAE APPELLÖF, 1896

Diagnosis (after Carlgren, 1949; additions in bold and modifications in italics). *Enthemonae* with elongate body with proximal end physa-shaped, rarely flat. Column sometimes without regional differentiation, sometimes divisible into physa, scapus and scapulus. No sphincter. Tentacles few up to 40, the inner not shorter than the outer ones. Often with a single siphonoglyph, rarely with two *indistinct* ones. Perfect pairs of mesenteries variable in number up to 20. Retractors of perfect mesenteries strong, diffuse to restricted, more or less reniform. Parietal muscles distinct. *Cnidom*: gracile spirocysts, basitrichs, holotrichs, *b*-mastigophores and *p*-mastigophores A.

Type genus: *Halcampoides* Danielssen, 1890

Included genera: *Acthelmis* Lütken, 1875 (?), *Calamactinia* Carlgren, 1949 (?), *Calamactis* Carlgren, 1951 (?), *Halcampella* Andres, 1883 (?), *Pentactinia* Carlgren, 1900 (?), *Scytophorus* Hertwig, 1882 and *Siphonactinopsis* Carlgren, 1921 (?).

Remarks: Rodríguez *et al.* (2012) synonymized Halcampoididae with Halcampidae based on the

endodermal musculature with high muscle processes; G, histological longitudinal section through distal column showing mesogleal marginal sphincter musculature; H, histological cross-section through tentacle showing mesogleal longitudinal musculature (indicated by arrow); I, micro-CT cross-section scan through oral disc showing wide oral disc with tentacles; note six rows of columnar tubercles (indicated by arrows) and an introverted tentacle (indicated by asterisk); J, histological cross-section through mid-column showing columnar tubercle; K, histological cross-section through inverted scapulus and scapus showing one cycle of six perfect pairs of mesenteries (numbers 1–6; directives indicated by arrows); second cycle of mesenteries with one missing mesentery of a pair (numbers 7–12; missing mesentery indicated by asterisk), but noticed complete pair on opposite scapulus; L, cross-section dissection through mid-scapus showing three cycles of mesenteries on half of the column (indicated by numbers); M, cross-section dissection through distal column showing arrangement of mesenteries; note introverted tentacle (indicated by asterisk); N, histological cross-section through mid-column showing arrangement of mesenteries; note the unequal development of mesenteries of some pairs (indicated by asterisks); O, detail of a pair of directive pair of mesenteries on distal column; P, detail of a pair of small pair of fourth cycle of mesenteries; note the strong, circumscribed retractor of mesenteries; Q, detail of parietobasilar musculature on a pair of mesentery of first cycle. Abbreviations: ac, actinopharynx; e, epidermis; g, gastrodermis; m, mesoglea; od, oral disc; sc, scapus; sp, scapulus. Scale bars, A, N, 2.5 mm; B, C, 4 mm; D, E, H, O, Q, 0.2 mm, F, 0.6 mm; G, J, 0.5 mm; I, 3, 2 mm; K, L, P, 1 mm; M, 3 mm.

position of an unidentified species of *Halcampoides* (type genus of Halcampoididae) as the sister-group to an unidentified species of *Halcampa* Gosse, 1858 (type genus of Halcampidae). Based on the results of our phylogenetic analyses, we consider Halcampidae and Halcampoididae as separate families (Studer, 1879). Thus, we resurrect family Halcampoididae and reclassify it as an actinostoloidean, given its position in our phylogenetic analysis. We include *H. purpureus*

and *S. striatus* Hertwig, 1882 until a complete revision of remaining former halcampaoid genera.

GENUS *SCYTOPHORUS* HERTWIG, 1882

Diagnosis (after Carlgren, 1949; modifications in italics). Halcampoididae with elongate body and flat aboral end. Column indistinctly divisible into scapus and scapulus. Cuticle developed chiefly on scapus, with modified weak tenaculi more or less visible to the naked eye. No sphincter. Tentacles 14, with longitudinal muscles ectodermal. A single weak, ventral siphonoglyph without conchula. Mesenteries 14, six pairs plus one couple; individual mesenteries of couple with retractors faced towards dorsal pairs of directives, wherefore there is seemingly a single pair of directives. All mesenteries perfect, with retractors strong, restricted to kidney-like. Parietal muscles well developed. As a rule, all mesenteries fertile. Ciliate tracts of filaments may be discontinuous. Cnidom: spirocysts, basitrichs, *p-mastigophores* A.

Type species: Scytophorus striatus by monotypy.

Included species: Scytophorus antarcticus (Pfeffer, 1889) and *S. striatus*.

Remarks: We modified the generic diagnosis by removing the mention of a physa-like structure in members of *Scytophorus*. Although Hertwig (1882) described *S. striatus* as lacking a pedal disc and with a round aboral end, all of the *S. striatus* specimens

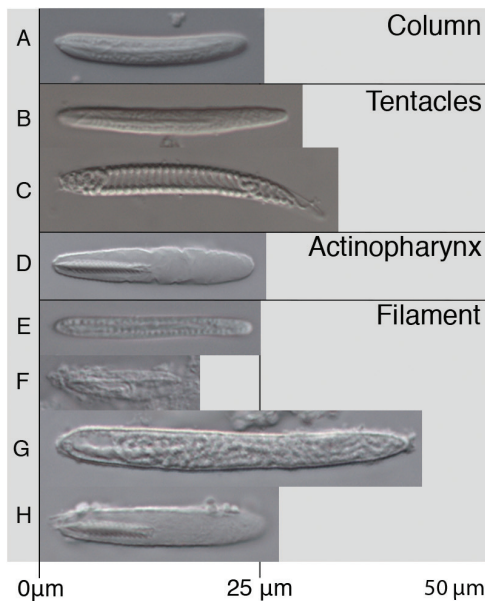


Figure 5. Cnidom of *Chitinactis marmara*. A, B, E, F, basitrichs; C, gracile spirocyst; D, H, *p-mastigophore* A; G, *b-mastigophore*.

Table 1. Size ranges of the cnidae of *Chitinactis marmara*; M, mean; SD, standard deviation; S, proportion of specimens in which each cnidae was found; N, total number of capsules measured; F, frequency; +++, very common; ++, common; +, fairly common; -, rare.

Categories	Range of length and width of capsules (μm)	± SD	S	N	F
COLUMN					
Basitrichs (A)	21.2–28.1 × 2.8–5.0	24.9 ± 1.5 × 3.9 ± 0.4	146	4/4	+++
TENTACLES					
Basitrichs (B)	18.7–35.1 × 2.6–4.7	28.6 ± 2.7 × 3.5 ± 0.4	158	4/4	+++
Spirocysts (C)	17.8–52.7 × 2.2–6.6	34.6 ± 7.5 × 4.1 ± 0.8	254	4/4	+++
PHARYNX					
<i>P-mastigophores</i> A (D)	23.0–36.7 × 3.3–7.7	31.8 ± 2.2 × 6.1 ± 0.6	116	4/4	+++
Basitrichs (E)	34.5 × 3.5		-	1	1/4
FILAMENT					
Basitrichs (F)	15.0–16.1 × 4.0–5.2	15.4 ± 0.5 × 4.7 ± 0.6	4	1/4	-
<i>b-mastigophores</i> (G)	37.3–57.9 × 5.0–8.0	46.0 ± 3.2 × 6.2 ± 0.6	120	4/4	+++
<i>P-mastigophores</i> A (H)	18.7–37.0 × 4.1–7.1	26.1 ± 3.6 × 5.5 ± 0.5	123	4/4	+++

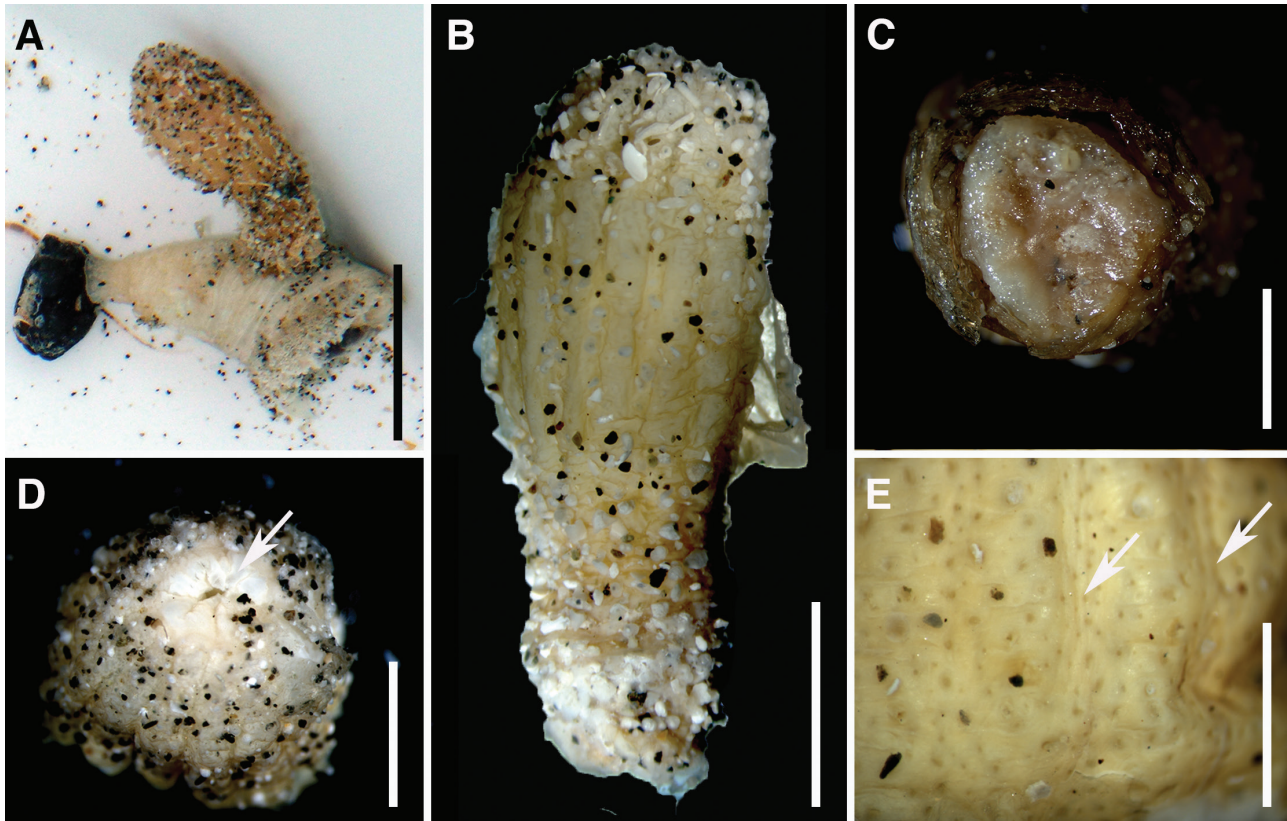


Figure 6. External anatomy of *Scytophorus striatus*. A, lateral view of live specimen attached to scleractinian coral; B, lateral view of preserved specimen showing elongate shape, columnar cuticle and sand grains attached to column; C, detail of flattened pedal disc; D, oral view of preserved specimen showing short scapulus (indicated by arrow); E, detail of column showing small tenaculi with attached sand grains and yellow cuticle; note longitudinal columnar furrows (indicated by arrows). Scale bars: A, E, 2 mm; B, 5 mm; C, D, 4 mm.

examined had a distinct flat aboral end (Figs 6C, 7A, F) as seen attached to solid substrates (Fig. 6A). Although most of the specimens of *S. striatus* observed had their distal column and oral disc contracted, when they are relaxed, the scapulus can be easily distinguished from the rest of the column (see Fig. 6D). We left in the diagnosis the presence of a weak siphonoglyph, but this structure was difficult to observe in dissections (Fig. 7G), histological sections or micro-CT scans (Fig. 7K), as noted by others (e.g. Carlgren, 1921).

SCYTOPHORUS STRIATUS HERTWIG, 1882

(FIGS 6–8; TABLE 2)

Material: AMNH 5268 (nine specimens), Nathaniel B. Palmer R/V, NBP11-03 Expedition, Sta. 14, off Burdwood/Namuncurá Bank, Drake Passage, Antarctica, 54°42.84'S 62°14.99'W, 732 m, 11 May 2011, Hein Dredge, collected by M. R. Brugler. AMNH 5275 (three specimens), 'Nathaniel B. Palmer' R/V,

NBP11-03 Expedition, Deep Site – North Grassy Knoll, Sta. 10, Burdwood/Namuncurá Bank, Drake Passage, Antarctica, 54°43.35'S 62°14.21'W, 720 m, 11 May 2011, Blake Trawl, collected by M. R. Brugler. AMNH 5254 (20 specimens), Nathaniel B. Palmer R/V, NBP11-03 Expedition, Sta. 16, off Burdwood/Namuncurá Bank, Drake Passage, Antarctica, 54°48.52'S 62°07.20'W, 1423 m, 13 May 2011, Hein Dredge, collected by M. R. Brugler. AMNH_IZC 00361338 (three specimens), Nathaniel B. Palmer R/V, NBP11-03 Expedition, Sta. 22, off Burdwood/Namuncurá Bank, Drake Passage, Antarctica, 54°50.50'S 62°07.53'W, 1922 m, 14 May 2011, Hein Dredge, collected by M. R. Brugler.

Additional material examined for comparison: *Scytophorus antarcticus* ZMH C1452 (one specimen: holotype); locality: South Georgia. *Halcampoides purpureus* AMNH 4498 (one specimen); locality: Southern Ocean, Antarctica, Kapp Norvegia, Sta. PS56/105-1, 10°57'S 12°15.05'W, GKG, giant box corer, collected in 2000 by P. López-González

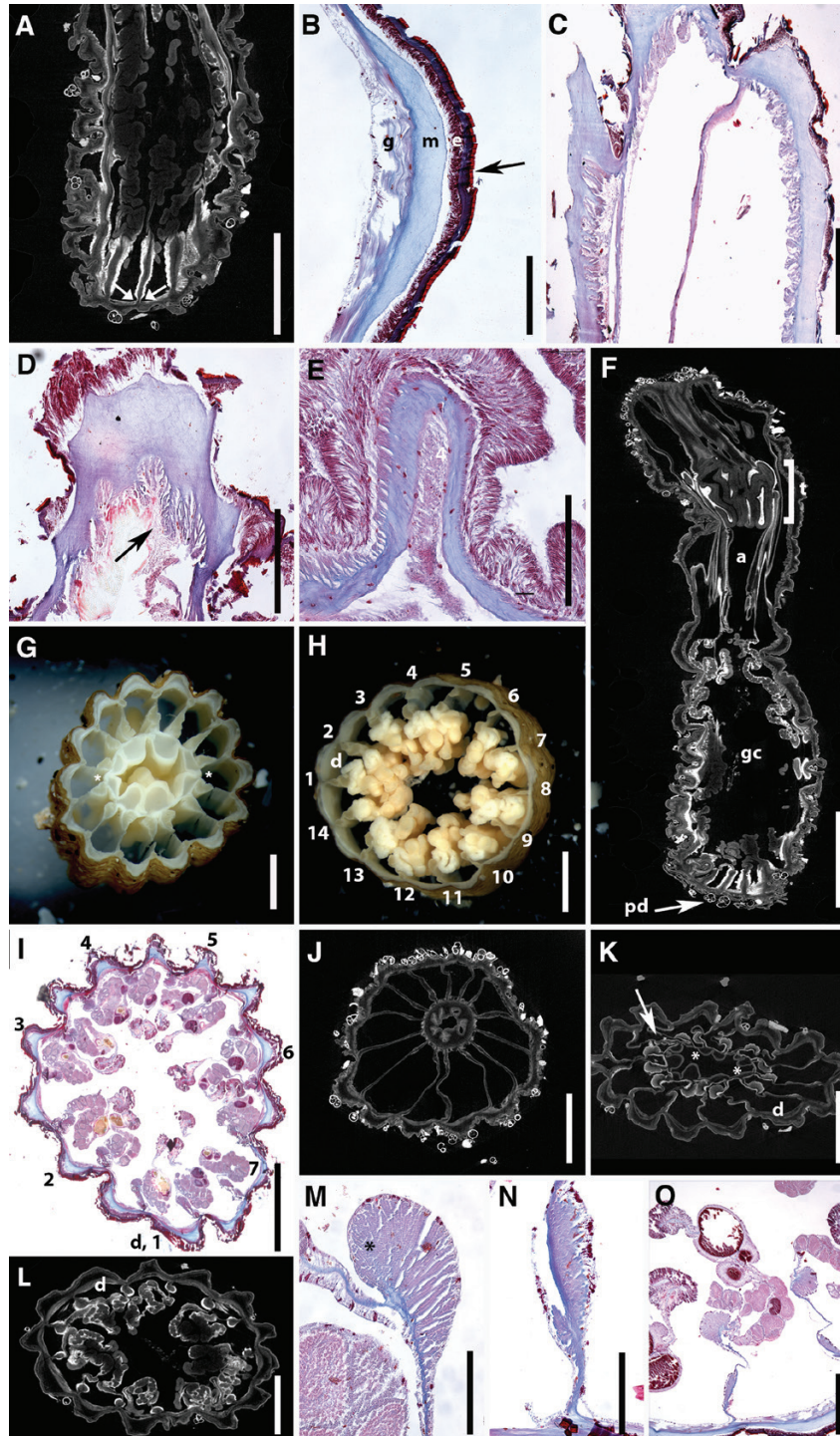


Figure 7. Internal anatomy and microanatomy of *Scytophorus striatus*. A, micro-CT scan of longitudinal section through flattened pedal disc; note absence of basilar musculature (arrows); B, cross-section through mid-scapus showing area between furrows; note body layers and bilayered cuticle (indicated by arrow); C, histological longitudinal section through distal column showing strong, circular endodermal musculature; D, detail of distal scapus showing high muscle processes of strong, circular endodermal musculature (indicated by arrow); E, histological longitudinal section through tentacle showing ectodermal longitudinal musculature; F, micro-CT longitudinal scan through a whole specimen showing flattened pedal disc, actinopharynx, tentacles and gastrovascular cavity; note foreign material attached to epidermis of column and pedal

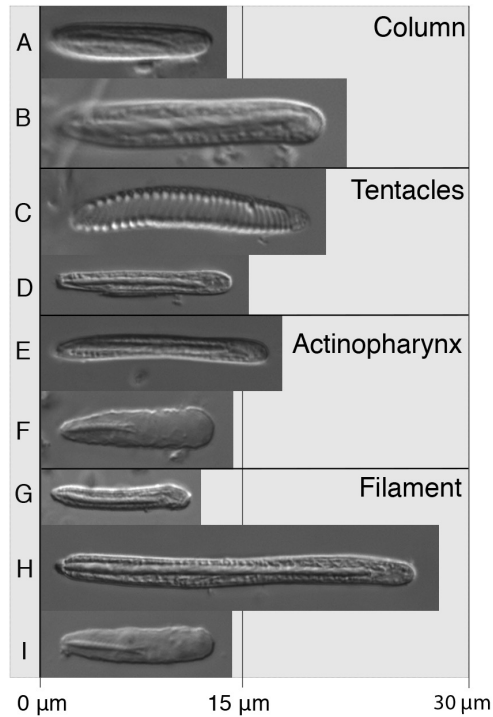


Figure 8. Cnidom of *Scytophorus striatus*. A, B, D, E, G, H, basitrich; C, spirocyst; F, I, *p*-mastigophore A.

(330–331 m). AMNH 4501 (one specimen); locality: Southern Ocean, Antarctica, Bransfield Strait, Sta. PS56/164-1, 63°04.80'S 59°32.80'W, Agassiz Trawl, collected on 28 April 2000 by P. López-González (858–859 m). AMNH 4502 (one specimen); locality: Southern Ocean, Antarctica, West Deception Island, Sta. PS56/183-1, 62°07.15'S 60°22.60'W, Bottom Trawl, collected on 3 May 2000 by P. López-González (200–204 m). *Halcampoides abyssorum* Danielssen, 1890 USNM 53297 (seven specimens); locality: North Pacific Ocean, Bering Sea, Alaska, Punuk Islands, Stranger M/S, collected on 15 July 1937 by W. Williams (27 m).

Diagnosis: Fourteen mesenteries arranged in seven pairs, 14 tentacles, hermaphrodite, strongly attached,

bi-layered cuticle on column with foreign material attached to it, *p*-mastigophores A in actinopharynx.

External anatomy (Fig. 6): Body elongate in preserved specimens (Fig. 6A, B) but with aboral end flattened without a well-defined physa (Fig. 6A–C). Column cylindrical with 14 longitudinal furrows/evaginations (Fig. 6B), divided into scapulus and scapus (Fig. 6D) and tenaculi throughout scapus (Fig. 6E); column with epidermis covered by yellow cuticle distributed on scapus (Fig. 6B, E). Column diameter 5–11 mm distally and 7–9 mm proximally; 18–40 mm length in preserved specimens. Oral disc small, circular, contracted in all specimens (Fig. 6A, B, D); diameter 2–7 mm in preserved specimens. Margin of column tentaculate; tentacles 14, smooth; putatively arranged in a single cycle.

Internal anatomy, microanatomy (Fig. 7): Aboral end flat, not physa-like, but without basilar musculature (Fig. 7A). Overall body wall thickness varies along column: generally thicker on furrows (epidermis 53–119 µm, mesoglea 33–119 µm, gastrodermis 50–122 µm) than rest of column (epidermis 32–84 µm, mesoglea 19–88 µm, gastrodermis 50–94 µm) (Fig. 7B). Bi-layered cuticle on column (19–35 µm) (Fig. 7B). Longitudinal endodermal musculature of column strong (Fig. 7C); higher muscle processes in distal column, but not forming a differentiated marginal sphincter muscle (Fig. 7D). Longitudinal musculature of tentacles ectodermal (Fig. 7E). Actinopharynx approximately one-third of the length of the column, longitudinally sulcate, more heavily folded proximally (Fig. 7F). Two indistinct siphonoglyphs (Fig. 7G, K).

Mesenteries with unusual arrangement: 14 perfect mesenteries arranged in seven pairs, including a single pair of directives (Fig. 7H, I). Macrocemes span entire length of body, from proximal (Fig. 7J) to distal column (Fig. 7L). Retractors of macrocemes small, strong, circumscribed, with clear pennon distally (Fig. 7M). Parietal musculature well developed,

disc; G, micro-CT scanning through distal column showing actinopharynx and two indistinct siphonoglyph (indicated by asterisks); H, cross-section through mid-scapus showing 14 macrocemes (indicated by numbers) arranged in seven pairs; I, histological cross-section through mid-scapus showing arrangement of mesenteries in seven pairs (indicated by numbers); J, micro-CT cross-section scan through scapulus showing 14 mesenteries; K, micro-CT cross-section scan through distal scapus showing actinopharynx and weak siphonoglyphs (indicated by asterisks); note weak parietobasilar musculature of extra mesentery (indicated by arrow); L, micro-CT cross-section scan through proximal column; note all 14 mesenteries with gonads (= macrocemes); M, detail of retractor of macroceme with pennon distally (indicated by asterisk); N, detail of strong parietobasilar musculature of macroceme; O, detail of macroceme with both oocytes and spermatic cysts. Abbreviations: ac, actinopharynx; d, directive pair; ep, epidermis; ga, gastrodermis; gc, gastrovascular cavity; me, mesoglea; pd, pedal disc; t, tentacles. Scale bars: A, E, M, N, 0.2 mm; O, 0.3 mm; B, F, 4 mm; C, D, 1 mm; G–L, 2 mm.

Table 2. Size ranges of the cnidae of *Scytophorus striatus*; M, mean; SD, standard deviation; S, proportion of specimens in which each cnidae was found; N, total number of capsules measured; F, frequency; +++, very common; ++, common; +, fairly common; -, rare.

Categories	Range of length and width of capsules (µm)	± SD	S	N	F
COLUMN					
Basitrichs (A–B)	14.4–34.2 × 3.2–5.6	21.3 ± 5.5 × 4.1 ± 0.5	98	4/4	+++
TENTACLES					
Spirocysts (C)	17.8–41.1 × 2.9–6.1	30.0 ± 4.3 × 4.3 ± 0.7	198	4/4	+++
Basitrichs (D)	24.0–37.6 × 2.5–5.3	29.2 ± 2.1 × 3.5 ± 0.5	114	4/4	+++
PHARYNX					
Basitrichs (E)	22.2–51.1 × 3.1–6.5	30.4 ± 5.2 × 4.0 ± 0.6	93	4/4	+++
<i>P</i> -mastigophores A (F)	14.4–25.9 × 4.6–7.0	20.9 ± 2.0 × 5.6 ± 0.5	105	4/4	+++
FILAMENT					
Basitrichs I (G)	19.0–27.2 × 3.0–4.5	23.0 ± 1.7 × 3.7 ± 0.3	37	4/4	+
Basitrichs II (H)	48.9–86.6 × 4.0–6.1	63.0 ± 6.7 × 5.1 ± 0.4	130	4/4	+++
<i>P</i> -mastigophores A (I)	19.4–28.2 × 4.1–6.2	23.1 ± 2.2 × 5.3 ± 0.4	29	4/4	+

strong (Fig. 7N), equally developed in all mesenteries (Fig. 7I), more developed proximally (Fig. 7L). Basilar musculature absent (Fig. 7A). The four specimens examined hermaphroditic (Fig. 7O): one to three oocytes per macroneme (major axis of oocytes 217–597 µm) and many spermatic cysts (major axis of spermatic cysts 94–311 µm); all specimens collected in May.

Cnidom: spirocysts, basitrichs and *p*-mastigophores A. See Figure 8 and Table 2 for size and distribution.

Distribution and natural history: Over a dozen specimens of *Scytophorus striatus* were collected in the same trawl suggesting they might be locally abundant in the Burdwood Bank (also known as Namuncurá Bank) at 1423 m. Many of these specimens were collected attached to scleractinian corals (Fig. 6A) indicating that at least some of them live burrowed in the sand but attached to solid substrates, which were plentiful in the trawl (e.g. coarse sand and coral gravel). The species was collected in an area in which octocorals and stylasterid hydroids were also trawled. *Scytophorus striatus* was previously known only from its type locality between the Kerguelen Islands and Heard Island and McDonald Islands (52°4'S, 71°22'E) in somewhat shallow waters (274 m). This new record for *S. striatus* extends the distribution of the species from the Indian Ocean region of Antarctica (Kerguelen) to the Atlantic portion of the sub-Antarctic region (Burdwood/Namuncurá Bank), a region that connects continental South America to the northern region of the Antarctic Peninsula. We also extend significantly the bathymetric range of

S. striatus to 720–1922 m depth. *Scytophorus* is one of only six genera found in both Antarctic and sub-Antarctic regions (~7% of Antarctic fauna: Rodríguez *et al.*, 2007).

Remarks: Specimens of *Scytophorus striatus* examined in this study largely agree with the original description in terms of external anatomy and musculature. We document and provide the cnidom and musculature size ranges of *S. striatus* for the first time (see Fig. 8 and Table 2) and show that it differs from the one given for *S. antarcticus* by Carlgren (1927) and our own examination of its holotype (ZMH C1452; see Fig. 9). Both species differ in the size of basitrichs in the column and the actinopharynx, which in the column only overlaps in the lower range of those in *S. striatus*, and the presence of *p*-mastigophores in the actinopharynx in *S. striatus*. Although Carlgren (1927) does not specify the types of nematocysts in *S. antarcticus*, we confirmed their identity (Table 2), including those of the mesenterial filaments not provided by him (i.e. basitrichs, *p*-mastigophores A). One of the most consistent differences between *S. antarcticus* and *S. striatus* is fertility: *S. antarcticus* is gonochoric, whereas *S. striatus* is hermaphrodite. Although hermaphrodite and gonochoric specimens may coexist in a population, hermaphrodites tend to be rare (e.g. Jennison, 1981; Van Praët, 1990; Rodríguez *et al.*, 2013). The fact that all five specimens of *S. striatus* examined in this study were hermaphrodite leads us to believe that it is a specific character of *S. striatus*. Likewise, we confirmed that the holotype of *S. antarcticus* (ZMH C1452) is female, corroborating the reproductive differences between the two species.

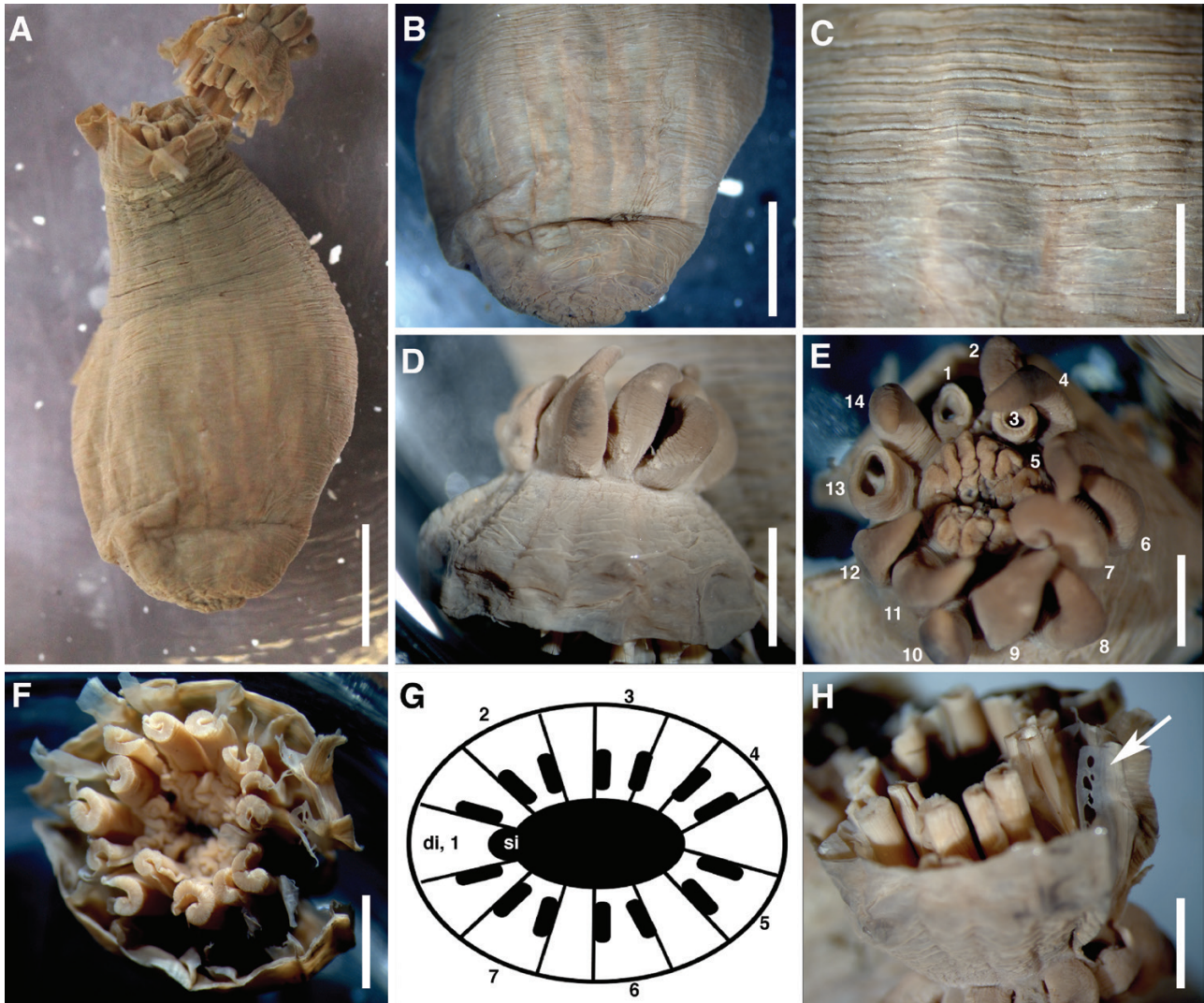


Figure 9. External and internal anatomy of *Scytophorus antarcticus* (Holotype: ZMH C1452). A, lateral view of sectioned specimen; B, detail of round pedal disc; C, detail of smooth column without cuticle; D, distal column with marginal tentacles; E, oral view of specimen showing its 14 tentacles (indicated by numbers); F, cross-section dissection of distal column showing the arrangement and morphology of mesenteries; G, diagram of mesentery arrangement; H, detail of distal column showing multiple marginal stomata in a mesentery (indicated by arrow). Abbreviations: di, directive mesenteries; si, siphonoglyph. Scale bars: A, 10 mm; B, D, 5 mm; C, E, F, H, 2 mm.

DISCUSSION

FAMILIAL AND GENERIC PLACEMENT OF *CHITINACTIS MARMARA*

The placement of *Chitinactis marmara* based on anatomy and microanatomy is corroborated by its phylogenetic position within a clade of actinostolids in both ML and MP analyses (see Fig. 2). Its taxonomic position is also supported by cnidae: *C. marmara* has only gracile spirocysts (lacks robust spirocysts) and *p*-mastigophores A (plus basitrichs and *b*-mastigophores; lacks *p*-mastigophores B) – a feature that characterizes the family Actinostolidae

(Riemann-Zürneck, 1978; Sanamyan & Sanamyan, 2007). Despite the difficulty in distinguishing *p*-mastigophores A from *p*-mastigophores B with light microscopy (Östman, 2000), this character proved useful in identifying former actinostolid species from chemosynthetic environments as metridioideans (Rodríguez & Daly 2010). Likewise, despite holotrichs in the tentacles being inducible in some species (e.g. Fautin, 1988; Edmands & Fautin, 1991), and potentially uninformative as a taxonomic or phylogenetic character, holotrichs in the tentacles of *Chemosynthina* carry phylogenetic signal grouping them and their allies within Metridioidea (Rodríguez *et al.*, 2008).

The types of nematocysts in the tentacles have also been used as a generic character in Actinostolidae (e.g. [Carlgren, 1949](#); [Fautin & Hessler, 1989](#)); the presence of *b*-mastigophores and arrangement of batteries in the tentacles, for example, distinguishes *Anthosactis*, *Hormosoma* and *Tealidium* from other actinostolids (see: [Carlgren, 1949](#); *contra* [López-González et al., 2003](#)). Actinostolid genera are distinguished from each other by a combination of anatomical (development of mesenteries of a single pair, number of cycles of mesenteries, number of perfect cycles of mesenteries, fertility and basal tentacle mesogleal thickenings), microanatomical (nature of tentacle musculature, development of sphincter musculature, sphincter position in mesoglea and development of parietobasilar musculature) and cnidae characters (batteries of *b*-mastigophores in tentacles whether or not they form batteries, *p*-mastigophores A in tentacles). The 17 actinostolid genera (*sensu* [Fautin, 2016](#)) include two major groups: (1) genera with at least some species with mesenteries of a pair following the ‘*Actinostola*-rule’ (i.e. *Actinostola*, *Ophiodiscus*, *Parasicyonis*, *Sicyonis*, *Stomphia* and *Synsicyonis*) and (2) species with mesenteries of a pair equally developed (i.e. *Antholoba*, *Anthosactis*, *Antiparactis*, *Bathydactylus*, *Cnidanthus*, *Hadalanthus*, *Hormosoma*, *Paranthus*, *Pseudoparactis*, *Pycnanthus* and *Tealidium*) ([Carlgren, 1949](#); [Rodríguez et al., 2008](#)). Genera with species following the *Actinostola*-rule generally also have mesogleal longitudinal tentacle musculature (i.e. *Actinostola*, *Ophiodiscus*, *Parasicyonis*, *Sicyonis* and *Synsicyonis*, except for *Stomphia*, which can have mesogleal to ecto-mesogleal musculature) and those with equally developed mesenteries of a single pair tend to have ectodermal tentacle musculature (i.e. *Antholoba*, *Anthosactis*, *Antiparactis*, *Bathydactylus*, *Hadalanthus*, *Paranthus*, *Pseudoparactis* and *Tealidium*, except for *Cnidanthus*, *Hormosoma* and *Pycnanthus*, which have mesogleal tentacle musculature) ([Carlgren, 1949](#)). *Chitinactis marmara*, like other actinostolids, does not follow the *Actinostola* rule distinctly (e.g. *Sicyonis*: [Sanamyan et al., 2015](#)) but exhibits unequal development of mesenteries in some of its younger mesenteries.

The arrangement of mesenteries seen in *Chitinactis marmara* follows the *Actinostola*-rule indistinctly but its tentacles have mesogleal musculature falling within the group including actinostolid genera *Actinostola*, *Ophiodiscus*, *Parasicyonis*, *Sicyonis*, *Stomphia* and *Synsicyonis*. *Chitinactis marmara* is most similar to the genera *Parasicyonis*, *Sicyonis* and *Synsicyonis* but can be unambiguously distinguished from these genera by a novel combination of morphological features: column with conspicuous columnar cuticle (absent from all other actinostolid genera), marginal sphincter distributed in entire mesoglea

(not centred, close to gastrodermis or epidermis and absent from all other actinostolid genera), distinct parietobasilar musculature (found only in *Sicyonis*), no basal mesogleal tentacle thickenings (also absent in *Parasicyonis* and *Stomphia*), no mesenteries of second or third cycles perfect and no *p*-mastigophores A or *b*-mastigophores in tentacles (*b*-mastigophores in filament).

The ability to secrete chitin is shared broadly across Actiniaria, often expressed on the column as a cuticle that can be stratified and mostly adherent to the epidermis ([Stephenson, 1928](#)). Exceptionally, it is secreted by the pedal disc forming carcinoecia in some members of metridioidean Hormathiidae and actinioidean *Stylobates* [Dall, 1903](#). A chitinous cuticle developed to the degree seen in *Chitinactis marmara* ([Fig. 3A, G](#)) is rare among sea anemones and it has never been observed in actinostoloideans. Thus, although the ability to secrete chitin is convergent among groups that secrete it ([Gusmão et al., 2020](#)), it is still an uncommon characteristic that distinguishes *Chitinactis* from all other actinostolid genera. In fact, the cuticle seen in *Chitinactis* is thicker than that seen in the metridioidean *Octineon* Moseley in Fowler, 1894 characterized by producing a somewhat thick layer of cuticle around the scapus and pedal disc ([Carlgren, 1921, 1931, 1942, 1949](#); [Sanamyan et al., 2018](#)). Members of the metridioidean family Galatheanthemidae [Carlgren, 1956](#) also produce a thick columnar cuticle that forms an elongated tube described as chitinous for *Galatheanthemum profundale* [Carlgren, 1956](#) ([Dunn, 1983](#); [Rodríguez & López-González, 2013](#)) but whose precise nature needs confirmation ([Cairns et al., 2007](#)). A shorter tube-like structure and a circular plate-like base are also produced by *G. hadale* ([Carlgren, 1956](#)). Although most species that produce chitin by the column or pedal disc are found in deeper waters, the link between depth and production of chitin is somewhat weak and hard to interpret (see: [Gusmão et al., 2020](#)). That the thick cuticle produced by *C. marmara* is an exception in Actinostolidae, a clade of mostly deep-sea species, confirms the weak correlation between bathymetry and secretion of chitin among sea anemones.

SCYTOPHORUS STRIATUS AND THE TAXONOMY AND EVOLUTION OF BURROWING SEA ANEMONES

Our recovery of *Scytophorus* within Actinostoloidea supports the existence of a clade of burrowing anemones within the superfamily, as suggested by the recent description of *Halcampulactis* by [Gusmão et al. \(2019\)](#). The phylogenetic position of *Scytophorus* within Actinostoloidea [or at least outside of Metridioidea in which it was recently reclassified by [Rodríguez et al. \(2012\)](#)] is supported by cnidae: *S. striatus* and *S. antarcticus* have only

p-mastigophores A (and no *p*-mastigophores B), a combination found among actinostoloideans and actinioideans but not metridioideans. These results indicate that detailed nematocyst information is not only helpful, but fundamental to reclassify burrowing sea anemones, particularly those without marginal sphincter, such as halcampoidids. Our phylogenetic analyses confirm that halcampoidids *Scytophorus* and *Halcampoides*, as well as *Halcampella fasciata* Rodríguez & López-González, 2002 and possibly other genera in the family, do not belong to Metridioidea and need separate, detailed taxonomic revisions to address their monophyly and classification. In particular, the well-supported position of *H. fasciata* within the superfamily Edwardsioidea is unexpected (86% MP; Fig. 2). However, using 1729 loci captured with a targeted-enrichment approach to address anthozoan relationships, Quattrini *et al.* (2020) also recovered *H. fasciata* within the suborder Anenthemonae with high support but within a different superfamily (Actinernoidea). Although the position of *H. fasciata* remains unresolved and requires increased taxonomic sampling of the suborder Anenthemonae, the fact that it is repeatedly recovered within Anenthemonae points to, and supports, the existence of previously unknown burrowing lineages. Despite the polyphyly of burrowing sea anemones (formerly athenarians) (Daly *et al.*, 2002; Rodríguez *et al.*, 2014; Gusmão *et al.*, 2019), the recovery of a clade of burrowing anemones, *Scytophorus* + *Halcampoides* + *Halcampulactis*, from Antarctica is not only interesting from an adaptive point of view, but also from a developmental one, given their unique mesenterial arrangement. *Halcampoides* and *Halcampulactis* are the only genera with species that stop after the development of protomesenteries [= protocnemes *sensu* Carlgren (1949)], whereas *Scytophorus* is the only genus with heptamerous symmetry (i.e. 14 mesenteries arranged in seven pairs in a single cycle; no microcnemes) within Actiniaria. Halcampoididae, the family in which *Scytophorus* has been traditionally classified (Carlgren, 1949), is particularly heterogeneous in regard to symmetry: its type genus, *Halcampoides*, as well as *Calamactis*, *Calamactinia* and *Achtelmis*, are hexamerous, whereas *Pentactinia* is decamerous (Carlgren, 1949). The close relationship recovered in our analyses between octamerous *Halcampulactis*, hexamerous *Halcampoides* and heptamerous *Scytophorus*, suggests that symmetry is fluid and probably not relevant for the taxonomy of actinostoloidean burrowers, as hypothesized by Carlgren (1921). In fact, most sea anemones are flexible as regards their symmetry, even during their ontogeny: from an octamerous, bilaterally symmetrical early *Edwardsia*-stage they transition to a hexamerous, biradially symmetrical *Halcampoides*-stage (Stephenson, 1928) and either

remain hexamerous adults or revert to an octamerous or another pattern of symmetry as adults.

Although the position of this clade of burrowing Antarctic species is somewhat unstable in our analyses, differences in the arrangement of mesenteries have been used to define taxa at different hierarchical levels (e.g. former suborder Endocoelanthaeae Carlgren, 1925, Edwardsiidae and related families) (Yanagi *et al.*, 2015) and carry significant phylogenetic signal (Rodríguez *et al.*, 2014). Therefore, based on our phylogenetic and morphological examination, we putatively classify the Antarctic clade of burrowing species, including *Scytophorus*, within Actinostoloidea, and consider that a broader taxon sampling including close relatives will improve resolution and help to consolidate its position within the superfamily. The revision of other halcampoidid genera, as well as other species currently classified in actinioidean or metridioidean families, will probably reveal additional actinostoloidean burrowers.

BIOGEOGRAPHY OF SEA ANEMONES IN THE SOUTHERN OCEAN

Chitinactis marmara and *Scytophorus striatus* belong to the family Actinostolidae, whose distribution is restricted to the deep-sea of high latitudes and illustrate the unique sea anemone shelf diversity of Antarctica. This distinctiveness results from the long-term isolation and tectonic (e.g. Gondwana break-up), oceanographic [e.g. Antarctic Circumpolar Current (ACC) formation] and climatic history (e.g. gradual and long-term cooling of Antarctica; extinctions of warm-adapted taxa and the radiation of cold-adapted taxa) of Antarctica (Clarke & Crame, 1992, 2010; Gutt *et al.*, 2010; Koubbi *et al.*, 2014). Even the taxa in the abyssal zone of the Southern Ocean show high species richness, probably as a result of its large size and stability (Brandt *et al.*, 2014). Hypotheses related to speciation, adaptive radiations and diversification, selective extinction and dispersal have been raised to explain the distinctiveness of the Antarctic fauna and may contribute alone or combined to different taxa (Krug *et al.*, 2009; Pearse *et al.*, 2009; Saucède *et al.*, 2014).

The description of *Chitinactis* raises the number of endemic actinostoloidean genera in the Southern Ocean to five and the total number of endemic genera to 21. Endemicity at higher taxonomic levels is low, with 25% endemic genera (Rodríguez *et al.*, 2007) and only one endemic family in Actiniaria (Gusmão *et al.*, 2019). Within Cnidaria, a similar pattern is seen among benthic hydroids with high levels of endemism at the species level (80%) and almost non-existent at the generic level in Antarctica (Peña Cantero, 2014). This pattern in Antarctic hydroids is partly due to

the suppression of the free-swimming stage, as most Antarctic hydroids have fixed gonophores (Peña Cantero & García Carrascosa, 1999). Similarly, sea anemones show disproportionate levels of brooding in the poles (Rodríguez *et al.*, 2013), particularly in the Southern Ocean (Larson & Daly, 2015; Larson, 2017). Although the relationship between biogeographic patterns and evolutionary processes among sea anemones is not yet clear, the preponderance of brooding species of sea anemones in high latitudes (Rodríguez *et al.*, 2013), particularly in the Southern Hemisphere (Larson & Daly, 2015), may suggest that *in situ* radiation is further reinforced by the conditions that promote diversity in the Antarctic region (e.g. 'species diversity pump': Pearse *et al.*, 2009). The high endemism at the species-level for Actiniaria in the Southern Ocean and Antarctica falls within the average suggested for many taxa in the region (e.g. bivalves, bryozoans: Griffiths *et al.*, 2009, ascidians: Primo and Vazquez, 2007; pycnogonids: Munilla & Soler-Membrives, 2009) and approximate those in large, isolated regions worldwide (e.g. New Zealand: Griffiths *et al.*, 2009).

Among sea anemones, many genera in the Southern Ocean are monotypic (Rodríguez & López-González, 2013; Rodríguez & Fautin, 2014), including eight actinostoloidean genera (i.e. ~50% of the diversity of the superfamily). Likewise, all endemic demosponge genera are currently found to be monotypic, although endemic *Calcarea* genera and one endemic hexactinellid genus are polytypic (Janussen & Downey, 2014). This characteristic, combined with the fact that all five actiniarian superfamilies have representatives in the Southern Ocean and many genera show bipolar distribution, suggests that the anemone fauna in the Southern Ocean may represent relictual distributions shaped by glacial periods (Rodríguez *et al.*, 2009). Alternatively (or in addition), sea anemones may also have colonized the Southern Ocean several times at different periods or independently from different ocean basins at the same time as seen in other taxa (e.g. echinoids: Eléaume *et al.*, 2014). Polar emergence from the deep sea following the retreat of multiyear sea ice in interglacial periods, with subsequent speciation in the Antarctic shelf, could also explain this pattern (Pearse *et al.*, 2009), particularly because the diversity at the generic level of deep-sea organisms in the Southern Ocean is similar to those in other deep-sea areas of the world (Clarke & Johnston, 2003), including for sea anemones. The population genetics and phylogeographic work necessary to test these hypotheses are still needed.

The distribution of *Chitinactis marmara* and *Scytophorus striatus* suggest that physical forces acting on the Southern Ocean (e.g. West-Wind Drift and ACC)

translocate the larvae of low-dispersal organisms from the Weddell Sea or South America eastwards in the direction of the Scotia Arc and sub-Antarctic islands (Helmuth *et al.*, 1994; Barnes & De Grave, 2001; Nikula *et al.*, 2010, 2013). While the distribution of *C. marmara* indicates the permeability of the Scotia–Weddell confluence, as is the case for other animals (e.g. krill, nemerteans and channichthyid fish: Patarnello *et al.*, 2011; Saucède *et al.*, 2014), the distribution of *S. striatus* suggests an affinity between Southern South America and the Kerguelen Plateau Subregion, which is somewhat uncommon for sea anemones (Rodríguez *et al.*, 2007). The permeability of the Antarctic Polar Front on recent timescales (Griffiths *et al.*, 2009; Janussen & Downey, 2014) reflects specific evolutionary and life histories and dispersal capabilities of organisms (Díaz *et al.*, 2011; Janosik *et al.*, 2011; Saucède *et al.*, 2014) and thus differ between taxa. That *S. striatus* has a broader distribution compared to *S. antarcticus* may be related to their reproduction strategy: *S. striatus* is hermaphrodite, whereas *S. antarcticus* (as far as it is known) is gonochoric, which may influence the type of fertilization and duration of larvae and, thus, species dispersal.

The description of *Chitinactis marmara* and the first redescription of *S. striatus* after more than 100 years since its original description highlights the under-described diversity of sea anemones in the Southern Ocean, even in well-explored areas of Antarctica (i.e. Antarctic Peninsula, Magellanic region and Weddell Sea: Bax & Cairns, 2014). Because levels of endemism are taxa-dependent and cannot be easily generalized, explicit, detailed morphological work is fundamental to properly describe sea anemones that are among the most diverse sessile megafauna in the region (Brandt *et al.*, 2014). Only solid taxonomy can provide the valuable biogeographic information necessary to discern broader biogeographic patterns and evolutionary processes for the actiniarian fauna in the Southern Ocean, all of which is particularly needed to understand marine biodiversity and hotspots, detect environmental changes, monitor biodiversity and model future distributions in the Southern Ocean and elsewhere (De Broyer & Koubbi, 2014; Koubbi *et al.*, 2014).

CONCLUSIONS

In an effort to describe the unique diversity of Antarctic sea anemones and to contribute reliable taxonomic information to understand the biogeography of the region, we combined morphology, molecular data and phylogenetic analyses to describe two Southern Ocean endemics: *Chitinactis marmara* and *Scytophorus*

striatus. These two species belong to the superfamily Actinostoloidea, whose distribution is concentrated in hard-to-access areas, such as the deep-sea of high latitudes, and whose phylogenetic cohesion and position within Actiniaria are still unresolved. Superfamily Actinostoloidea epitomizes the taxonomic challenges involved in the taxonomy of sea anemones, whose morphological variation falls into a spectrum of monotypic genera distinguished by a mosaic of features that is hard to interpret, and species-rich genera, whose members show uniform morphology and are differentiated mainly by geography (Rodríguez *et al.*, 2009). While our study highlights the laborious work that goes into identifying and classifying uniquely challenging actinostoloideans from the Southern Ocean, it also shows the benefits of combining morphology, molecular data and a complete survey of cnidae. Micro-CT scanning and 3D-modelling are particularly useful when examining species whose morphologies are hard to interpret using dissections and histology, and benefit from the three-dimensionality brought by these techniques.

Based on the phylogenetic position of *Scytophorus striatus* in our analyses, we resurrected the family Halcampoididae, which is additionally supported by morphological characters and cnidae. We recovered a new lineage of Antarctic burrowing sea anemones, characterized by an uncommon arrangement of mesenteries, among other features, that we have tentatively placed within the superfamily Actinostoloidea. Thus, we hypothesize a deep-sea, polar origin for burrowing anemones in families Halcampulactidae and Halcampoididae, building on recent discussions of biogeographic patterns and origin of the sea anemone fauna in the Southern Ocean (e.g. Rodríguez *et al.*, 2007; Rodríguez & Fautin, 2014). This study shows that we are still far from revealing the total diversity of sea anemones in the Southern Ocean, which holds high levels of endemism and uniquely challenging species. The laborious work that goes into describing sea anemones, combined with the lack of sampling and molecular markers for population-level studies, continue to represent bottlenecks for proper phylogeographic and biogeographic treatments for the order.

ACKNOWLEDGEMENTS

We give special thanks to Pablo J. López-González (Universidad de Sevilla, Spain), J. M. Gili (Institut Ciències del Mar, CMIMA-CSIC, Spain), Prof. W. Arntz (Alfred Wegener Institute [AWI], Germany), J. Gutt (AWI) and Rainer Knust (AWI) for access to material collected during the R/V *Polarstern* cruises ANT XV/3, ANT XIX/5, ANT XXIII/8, ANT XXIX/9; P. J. López González collected specimens of *Chitinactis marmara*

for the first time. We thank the British Antarctic Survey (BAS), particularly H. Griffiths (BAS), for providing access to E. Rodríguez in the RRS *James Clark Ross JR15005* cruise; we thank R. Waller (University of Maine) for access to the R/V *Nathaniel B. Palmer NBP11-03* cruise and M. R. Brugler (University of South Carolina Beaufort) for collecting specimens of *Halcampoides* and *Scytophorus*. We thank Vanessa van Deusen (San Diego State University) for assistance with the collection of molecular data during her internship at the American Museum of Natural History (AMNH) and Lily Berniker (AMNH) for the accession of material and loans. Loan of specimens from the JR cruise was facilitated by H. Griffiths (BAS); M. Lowe assisted with depositing material at the Natural History Museum (London, UK). Cherie Qu and Sadie Lee Burke from the Science Research Mentoring Program/American Museum of Natural History (SRMP/AMNH) assisted in the lab. Support for the Science Research Mentoring Program (SRMP) is provided by Christopher C. Davis, The Shelby Cullom Davis Charitable Fund; The Pinkerton Foundation; the Bezos Family Foundation; the Doris Duke Charitable Foundation; the Solon E. Summerfield Foundation; Inc.; and the Adolph and Ruth Schnurmacher Foundation. The authors also thank Janine Luke for the support of ER's research programme and LCG. We extend our acknowledgments to the officers, crew and scientists aboard the R/V *Polarstern*, Nathaniel B. Palmer and the RRS *James Clark Ross* during the ANT XV/3, ANT XIX/5, ANT XXIII/8, ANT XXIX/9 and JR15005 cruises of the SCAR Programs EASIZ (Coastal and Shelf Ecology of the Antarctic Sea-Ice Zone), EBA (Evolution Biology Antarctica), FOS (Filchner Outflow System) and SO-AntEco (South Orkneys-State of the Antarctic Ecosystem), respectively. Partial funding for this project came from the Spanish Comisión Interministerial de Ciencia y Tecnología projects: ANT97–1533-E, ANT98–1739-E, ANT99-1608-E, REN2003-04236. Partial funding for the NBP11-03 cruise was provided under the National Science Foundation Office of Polar Program grants OPP #1127582 (to R. Waller and L. Robinson).

REFERENCES

- Andres A. 1881.** Prodrómus neapolitanae actinariae faunae addito generalis actinariae bibliographiae catalogo. *Mittheilungen aus der Zoologischen Station zu Neapel* **2**: 305–371.
- Andres A. 1883.** Le Attinie. *Atti dell'Accademia de Lincei* **14**: 211–673.
- Appellöf A. 1896.** Die Actiniengattungen *Fenja*, *Aegir* u. *Halcampoides*, DAN. *Bergens Museums Aarbog* **1896**: 1–16.

- Barnes DKA, De Grave S. 2001.** Ecological biogeography of southern polar encrusting faunas. *Journal of Biogeography* **28**: 359–365.
- Bax N, Cairns S. 2014.** Stylasteridae (Cnidaria: Hydrozoa). In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B, d'Udekem d'Acoz C, Van de Putte A, Danis B, David B, Grant S, Gutt J, Held C, Hosie G, Heuttmann F, Post A, Ropert-Coudert Y, eds. *Biogeographic atlas of the southern ocean*. Cambridge: Scientific Committee on Antarctic Research, 107–112.
- Brandt A, Van de Putte A, Griffiths H. 2014.** Southern Ocean benthic deep-sea biodiversity and biogeography. In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B, d'Udekem d'Acoz C, Van de Putte A, Danis B, David B, Grant S, Gutt J, Held C, Hosie G, Heuttmann F, Post A, Ropert-Coudert Y, eds. *Biogeographic atlas of the Southern ocean*. Cambridge: Scientific Committee on Antarctic Research, 233–239.
- Cairns SD, Bayer FM, Fautin DG. 2007.** *Galatheanthemum profundale* (Anthozoa: Actiniaria) in the western Atlantic. *Bulletin of Marine Science* **80**: 191–200.
- Carlgren O. 1893.** Studien über Nordische Actinien. *Kongliga Svenska Vetenskaps-akademiens Handlingar* **25**: 1–148.
- Carlgren O. 1900.** Über *Pentactinia californica* n. gen. n. sp. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* **57**: 1165–1172.
- Carlgren O. 1921.** Actiniaria I. *Danish Ingolf-Expedition* **5**: 1–241.
- Carlgren O. 1925.** Zur Kenntnis der Hexacorallen. *Zoologischer Anzeiger* **65**: 87–99.
- Carlgren O. 1927.** Actiniaria and Zoantharia. In: Odhner T, ed. *Further Zoological Results of the Swedish Antarctic Expedition 1901–1903*. Stockholm: P. A. Norstedt & Söner, 1–102.
- Carlgren O. 1928.** Actiniaria der Deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer 'Valdivia' 1898–1899* **22**: 125–266.
- Carlgren O. 1931.** Zur Kenntnis der Actiniaria Abasilaria. *Arkiv für Zoologi* **23**: 1–48.
- Carlgren O. 1932.** Die Ceriantharien, Zoantharien und Actinarien des arktischen Gebietes. In: Römer F, Schaudinn F, Brauer A, Arndt W, eds. *Eine Zusammenstellung der arktischen Tierformen mit besonderer Berücksichtigung des Spitzbergen-Gebietes auf Grund der Ergebnisse der Deutschen Expedition in das Nördliche Eismeer im Jahre 1898*. Jena: Gustav Fischer, 255–266.
- Carlgren O. 1938.** South African Actiniaria and Zoantharia. *Kungliga Svenska Vetenskapsakademiens Handlingar* **17**: 1–148.
- Carlgren O. 1942.** Actiniaria Part II. *Danish Ingolf-Expedition* **5**: 1–92.
- Carlgren O. 1949.** A survey of the Ptychodactiaria, Corallimorpharia and Actiniaria. *Kungliga Svenska Vetenskapsakademiens Handlingar* **1**: 1–121.
- Carlgren O. 1951.** The actinian fauna of the Gulf of California. *Proceedings of the United States National Museum* **101**: 415–449.
- Carlgren O. 1956.** Actiniaria from depths exceeding 6000 meters. *Galathea Reports* **2**: 9–16.
- Carlgren O. 1959.** Corallimorpharia and Actiniaria with description of a new genus and species from Peru. Reports of the Lund University Chile Expedition 1948–49, 38. *Lunds Universitets Arsskrift (NF) Adv* **2** **56**: 1–39.
- Clarke A, Crame JA. 1992.** The Southern Ocean benthic fauna and climate change: a historical perspective. *Philosophical Transactions of the Royal Society B* **338**: 299–309.
- Clarke A, Crame J. 2010.** Evolutionary dynamics at high latitudes: speciation and extinction in polar marine faunas. *Philosophical Transactions of the Royal Society B* **365**: 3655–3666.
- Clarke A, Johnston NM. 2003.** Antarctic marine benthic diversity. *Oceanography and Marine Biology* **41**: 47–114.
- Clubb JA. 1902.** Actiniae. With an account of their peculiar brood chambers. In: *Report on collections of natural history made in the Antarctic Regions during the voyage of the 'Southern Cross'*. London: British Museum (Natural History), 294–309.
- Dall WH. 1903.** A new genus of Trochidae. *Nautilus* **17**: 61–62.
- Daly M, Lipscomb DL, Allard MW. 2002.** A simple test: evaluating explanations for the relative simplicity of the Edwardsiidae (Cnidaria: Anthozoa). *Evolution; international journal of organic evolution* **56**: 502–510.
- Daly M, Chaudhuri A, Gusmão L, Rodríguez E. 2008.** Phylogenetic relationships among sea anemones (Cnidaria: Anthozoa: Actiniaria). *Molecular Phylogenetics and Evolution* **48**: 292–301.
- Daly M, Gusmão LC, Reft AJ, Rodríguez E. 2010.** Phylogenetic signal in mitochondrial and nuclear markers in sea anemones (Cnidaria, Actiniaria). *Integrative and Comparative Biology* **50**: 371–388.
- Danielssen DC. 1890.** *Actinida. Den Norske Nordhavs-Expedition 1876–1878*. Zoologi. Christiania: Grøndahl & Søn.
- Darriba D, Taboada GL, Doallo R, Posada D. 2012.** jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* **9**: 772.
- De Broyer C, Koubbi P. 2014.** The biogeography of the Southern Ocean. In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B, d'Udekem d'Acoz C, Van de Putte A, Danis B, David B, Grant S, Gutt J, Held C, Hosie G, Heuttmann F, Post A, Ropert-Coudert Y, eds. *Biogeographic atlas of the Southern Ocean*. Cambridge: Scientific Committee on Antarctic Research, 2–9.
- Díaz A, Féral JP, David B, Saucède T, Poulin E. 2011.** Evolutionary pathways among shallow and deep-sea echinoids of the genus *Sterechinus* in the Southern Ocean. *Deep-Sea Research II* **58**: 205–211.
- Dunn DG. 1983.** Some Antarctic and sub-Antarctic sea anemones (Coelenterata: Ptychodactiaria and Actiniaria). *Biology of the Antarctic Seas XIV, Antarctic Research Series* **39**: 1–67.
- Edmands S, Fautin DG. 1991.** Redescription of *Aulactinia veratra* n. comb. (= *Cnidopus veratra*) (Coelenterata: Actiniaria) from Australia. *Records of the Western Australian Museum (Perth)* **15**: 59–68.
- Eléaume M, Hemery LG, Roux M, Améziane N. 2014.** Southern Ocean crinoids. In: De Broyer C, Koubbi P,

- Griffiths HJ, Raymond B, d'Udekem d'Acoz C, Van de Putte A, Danis B, David B, Grant S, Gutt J, Held C, Hosie G, Heuttmann F, Post A, Ropert-Coudert Y, eds. *Biogeographic atlas of the Southern Ocean*. Cambridge: Scientific Committee on Antarctic Research, 208–212.
- Fautin DG. 1988.** The importance of nematocysts to actiniarian taxonomy. In: Hessinger DA, Lenhoff HM, eds. *The biology of nematocysts*. New York: Academic Press, 487–500.
- Fautin DG. 2016.** Catalog to families, genera, and species of orders Actiniaria and Corallimorpharia (Cnidaria: Anthozoa). *Zootaxa* **4145**: 1–449.
- Fautin DG, Barber BR. 1999.** *Maractis rimicarivora*, a new genus and species of sea anemone (Cnidaria: Anthozoa: Actiniaria: Actinostolidae) from an Atlantic hydrothermal vent. *Proceedings of the Biological Society of Washington* **112**: 624–631.
- Fautin DG, Hessler RR. 1989.** *Marianactis bythios*, a new genus and species of actinostolid sea anemone (Coelenterata: Actiniaria) from the Mariana vents. *Proceedings of the Biological Society of Washington* **102**: 815–825.
- Fedorov A, Beichel R, Kalpathy-Cramer J, Finet J, Fillion-Robin JC, Pujol S, Bauer C, Jennings D, Fennessy F, Sonka M, Buatti J, Aylward S, Miller JV, Pieper S, Kikinis R. 2012.** 3D Slicer as an image computing platform for the Quantitative Imaging Network. *Magnetic Resonance Imaging* **30**: 1323–1341.
- Geller JB, Walton ED. 2001.** Breaking up and getting together: evolution of symbiosis and cloning by fission in sea anemones (*Genus Anthopleura*). *Evolution; International Journal of Organic Evolution* **55**: 1781–1794.
- Goloboff PA, Farris J, Nixon K. 2008.** TNT, a free program for phylogenetic analysis. *Cladistics* **24**: 774–786.
- Gosse PH. 1858.** Synopsis of the families, genera, and species of the British Actiniae. *Annals and Magazine of Natural History* **1**: 414–419.
- Gosse PH. 1859.** Characters and descriptions of some new British sea-anemones. *Annals and Magazine of Natural History* **3**: 46–50.
- Grajales A, Rodríguez E. 2016.** Elucidating the evolutionary relationships of the Aiptasiidae, a widespread cnidarian-dinoflagellate model system (Cnidaria: Anthozoa: Actiniaria: Metridioidea). *Molecular Phylogenetics and Evolution* **94**: 252–263.
- Griffiths HJ, Barnes DKA, Linse K. 2009.** Towards a generalised biogeography of the Southern Ocean benthos. *Journal of Biogeography* **36**: 162–177.
- Guindon S, Gascuel O. 2003.** A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* **52**: 696–704.
- Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O. 2010.** New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology* **59**: 307–321.
- Gusmão LC, Daly M. 2010.** Evolution of sea anemones (Cnidaria: Actiniaria: Hormathiidae) symbiotic with hermit crabs. *Molecular Phylogenetics and Evolution* **56**: 868–877.
- Gusmão LC, Grajales A, Rodríguez E. 2018.** Sea anemones through X-rays: visualization of two species of *Diadumene* (Cnidaria, Actiniaria) using micro-CT. *American Museum Novitates* **3907**: 1–45.
- Gusmão LC, Berniker K, Van Deusen V, Rodríguez E. 2019.** Halcampulactidae (Actiniaria, Actinostoloidea), a new family of burrowing sea anemones with external brooding from Antarctica. *Polar Biology* **42**: 1271–1286.
- Gusmão LC, Van Deusen V, Daly M, Rodríguez E. 2020.** Origin and evolution of the symbiosis between sea anemones (Cnidaria, Anthozoa, Actiniaria) and hermit crabs, with additional notes on anemone-gastropod associations. *Molecular Phylogenetics and Evolution* **148**: 106805.
- Gutt J, Hosie G, Stoddart M. 2010.** Marine life in the antarctic. In: McIntyre AD, ed. *Life in the World's Oceans: Diversity, Distribution, and Abundance*. Oxford: Blackwell Publishing Ltd., 203–220.
- Helmuth B, Veit RR, Holberton R. 1994.** Long-distance dispersal of a subantarctic brooding bivalve (*Gaimardia trapesina*) by kelp-rafting. *Marine Biology* **120**: 421–426.
- Hertwig R. 1882.** *Die actinien der challenger expedition*. Jena: Gustav Fischer.
- Janosik AM, Mahon AR, Halanych KM. 2011.** Evolutionary history of Southern Ocean *Odontaster* sea star species (Odontasteridae; Asterozoa). *Polar Biology* **34**: 575–586.
- Janussen D, Downey RV. 2014.** Porifera. In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B, d'Udekem d'Acoz C, Van de Putte A, Danis B, David B, Grant S, Gutt J, Held C, Hosie G, Heuttmann F, Post A, Ropert-Coudert Y, eds. *Biogeographic Atlas of the Southern Ocean*. Cambridge: Scientific Committee on Antarctic Research, 94–102.
- Jennison BL. 1981.** Reproduction in three species of sea anemones from Key West, Florida. *Canadian Journal of Zoology* **59**: 1708–1719.
- Katoh K, Standley DM. 2013.** MAFFT multiple sequence alignment software v.7: improvements in performance and usability. *Molecular Biology and Evolution* **30**: 772–780.
- Katoh K, Rozewicki J, Yamada KD. 2017.** MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Brief in Bioinformatics* **20**: 1160–1166.
- Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A. 2012.** Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics (Oxford, England)* **28**: 1647–1649.
- Krug AZ, Jablonski D, Valentine JW. 2009.** Signature of the end-Cretaceous mass extinction in the modern biota. *Science* **323**: 767–771.
- Koubbi P, De Broyer C, Griffiths HJ, Raymond B, d'Udekem d'Acoz C, Van de Putte A, Danis B, David B, Grant S, Gutt J, Held C, Hosie G, Heuttmann F, Post A, Ropert-Coudert Y, Stoddart M, Swadling KM, Wadley V. 2014.** Conclusions: present and future of Southern Ocean biogeography. In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B, d'Udekem d'Acoz C, Van de Putte A, Danis B, David B, Grant S, Gutt J, Held C, Hosie G, Heuttmann F, Post A, Ropert-Coudert Y, eds. *Biogeographic atlas of the*

- Southern Ocean*. Cambridge: Scientific Committee on Antarctic Research, 470–475.
- Kozlov AM, Darriba D, Flouri T, Morel B, Stamatakis A. 2018.** RAxML-NG: a fast scalable, and user-friendly tool for maximum likelihood phylogenetic inference. *Bioinformatics* **35**: 4453–4455.
- Larson P. 2017.** Brooding sea anemones (Cnidaria: Anthozoa: Actiniaria): paragon of diversity in mode, morphology, and maternity. *Invertebrate Zoology* **136**: 92–112.
- Larson P, Daly M. 2015.** ‘Putting names with faces’: a description of *Epiactis handi* sp. nov. helps to solve taxonomic confusion in species of the sea anemone *Epiactis* (Actiniaria, Actiniidae). *Journal of Marine Biological Association of the United Kingdom* **95**: 913–928.
- Lauretta D, Häussermann V, Brugler MR, Rodríguez E. 2014.** *Isoparactis fionae* sp. n. (Cnidaria: Anthozoa: Actiniaria) from southern Patagonia with a discussion of the family Isanthidae. *Organisms Diversity and Evolution* **14**: 31–42.
- Lefort V, Longueville J, Gascuel O. 2017.** SMS: Smart model selection in PhyML. *Molecular Biology and Evolution* **34**: 2421–2424.
- López-González PJ, Rodríguez E, Gili J, Segonzac M. 2003.** New records on sea anemones (Anthozoa: Actiniaria) from hydrothermal vents and cold seeps. *Zoologische Verhandlungen* **345**: 215–243.
- Lütken C. 1875.** A revised catalogue of the Anthozoa and Calycozoa of Greenland. In: Jones TR, ed. *Manual of the natural history, geology, and physics of Greenland and the neighbouring regions*. London: Her Majesty’s Stationery Office, 186–187.
- McMurrich JP. 1893.** Report on the Actiniae collected by the United States Fish Commission Steamer *Albatross* during the winter of 1887–1888. *Proceedings of the United States National Museum* **16**: 119–216.
- Miller MA, Pfeiffer W, Schwartz T. 2010.** Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, 1–8.
- Munilla T, Soler Membrives A. 2009.** Check-list of the pycnogonids from Antarctic and sub-Antarctic waters: zoogeographic implications. *Antarctic Science* **21**: 99–111.
- Nikula R, Fraser CI, Spencer HG, Waters JM. 2010.** Circumpolar dispersal by rafting in two subantarctic kelp-dwelling crustaceans. *Marine Ecology Progress Series* **405**: 221–230.
- Nikula R, Spencer HG, Waters JM. 2013.** Passive rafting is a powerful driver of transoceanic gene flow. *Biology Letters* **9**: 20120821.
- Östman C. 2000.** A guideline to nematocyst nomenclature and classification, and some notes on the systematic value of nematocysts. *Scientia Marina* **64**: 31–46.
- Patarnello T, Verde C, di Prisco G, Bargelloni L, Zane L. 2011.** How will fish that evolved at constant sub-zero temperatures cope with global warming? Notothenioids as a case study. *Bioessays: News and Reviews in Molecular, Cellular and Developmental Biology* **33**: 260–268.
- Pearse JS, Mooi R, Lockhart SJ, Brandt A. 2009.** Brooding and species diversity in the Southern Ocean: selection for brooders or speciation within brooding clades? In: Krupnik I, Lang MA, Miller SE, eds. *Smithsonian at the Poles: Contributions to International Polar Year Science. Proceedings of Smithsonian at the Poles Symposium, Smithsonian Institution, Washington, DC, 3–4 May 2007*. Washington, DC: Smithsonian Institution Scholarly Press, 181–196.
- Peña Cantero AL. 2014.** Benthic hydroids (Cnidaria: Hydrozoa). In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B, d’Udekem d’Acoz C, Van de Putte A, Danis B, David B, Grant S, Gutt J, Held C, Hosie G, Heuttmann F, Post A, Ropert-Coudert Y, eds. *Biogeographic atlas of the Southern Ocean*. Cambridge: Scientific Committee on Antarctic Research, 103–116.
- Peña Cantero AL, García Carrascosa AM. 1999.** Biogeographical distribution of the benthic thecate hydroids collected during the Spanish ‘Antártida 8611’ expedition and comparison between Antarctic and Magellan benthic hydroid faunas. *Scientia Marina* **63**: 209–218.
- Pfeffer G. 1889.** Zur Fauna von Süd-Georgien. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten* **6**: 39–55.
- Presnell JK, Schreibman MP. 1997.** *Humason’s animal tissue techniques*. Baltimore: Johns Hopkins University Press.
- Primo C, Vázquez E. 2007.** Zoogeography of the Antarctic ascidian fauna in relation to the sub-Antarctic and South America. *Antarctic Science* **19**: 321–336.
- Quattrini AM, Rodríguez E, Faircloth BC, Cowman PF, Brugler MR, Farfan GA, Hellberg ME, Kitahara MV, Morrison CL, Paz-García DA, Reimer JD, McFadden CS. 2020.** Palaeoclimate ocean conditions shaped the evolution of corals and their skeletons through deep time. *Nature Ecology & Evolution* **4**: 1531–1538.
- Rafinesque CS. 1815.** *Analyse de la nature ou tableau de l’univers et des corps organisés*. Palermo: Rafinesque.
- Riemann-Zürneck K. 1978.** Actiniaria des Südwestatlantik IV. *Actinostola crassicornis* (Hertwig, 1882) mit einer Diskussion verwandter Arten. *Veröffentlichungen des Institutes für Meeresforschung Bremerhaven* **17**: 65–85.
- Rintoul S. 2007.** Antarctic circumpolar current. In: Riffenburgh B, ed. *Encyclopedia of the Antarctic*. New York: Routledge, 234–239.
- Rodríguez E, Daly M. 2010.** Phylogenetic relationships among deep-sea and chemosynthetic sea anemones: Actinoscyphiidae and Actinostolidae (Actiniaria: Mesomyaria). *PLoS One* **5**: e1095.
- Rodríguez E, Fautin DG. 2014.** Antarctic hexacorals (Cnidaria: Anthozoa: Hexacorallia). In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B, d’Udekem d’Acoz C, Van de Putte A, Danis B, David B, Grant S, Gutt J, Held C, Hosie G, Heuttmann F, Post A, Ropert-Coudert Y, eds. *Biogeographic atlas of the Southern Ocean*. Cambridge: Scientific Committee on Antarctic Research, 113–116.
- Rodríguez E, López-González PJ. 2002.** A new species of *Halcampella* (Actiniaria: Halcampoididae) from the eastern

- Weddell Sea and the Antarctic Peninsula. *Scientia Marina* **66**: 43–52.
- Rodríguez E, López-González PJ. 2013.** New records of Antarctic and sub-Antarctic sea anemones (Cnidaria, Anthozoa, Actiniaria and Corallimorpharia) from the Weddell Sea, Antarctic Peninsula, and Scotia Arc. *Zootaxa* **3624**: 1–100.
- Rodríguez E, López-González PJ, Gili J. 2007.** Biogeography of Antarctic sea anemones (Anthozoa, Actiniaria): what do they tell us about the origin of the Antarctic benthic fauna? *Deep-Sea Research II* **54**: 1876–1904.
- Rodríguez E, Castorani CN, Daly M. 2008.** Morphological phylogeny of the family of Actinostolidae (Anthozoa: Actiniaria) with description of a new genus and species of hydrothermal vent sea anemone redefining the family Actinoscyphidae. *Invertebrate Zoology* **22**: 439–452.
- Rodríguez E, López-González PJ, Daly M. 2009.** New family of sea anemones (Actiniaria, Acontiaria) from deep polar seas. *Polar Biology* **32**: 703–717.
- Rodríguez E, Barbeitos M, Daly M, Gusmão LC, Häussermann V. 2012.** Toward a natural classification: phylogeny of acontiate sea anemones (Cnidaria, Anthozoa, Actiniaria). *Cladistics* **1**: 1–18.
- Rodríguez E, Orejas C, López-González PJ, Gili JM. 2013.** Reproduction in the externally brooding sea anemone *Epiactis georgiana* in the Antarctic Peninsula and the Weddell Sea. *Marine Biology* **160**: 1–14.
- Rodríguez E, Barbeitos MS, Brugler MR, Crowley LM, Grajales A, Gusmão L, Häussermann V, Reft A, Daly M. 2014.** Hidden among sea anemones: first comprehensive phylogenetic reconstruction of the order Actiniaria (Cnidaria: Anthozoa: Hexacorallia) reveals a novel group of hexacorals. *PLoS One* **9**: 1–15.
- Sanamyan NP, Sanamyan KE. 2007.** Deep-water Actiniaria from East Pacific hydrothermal vents and cold seeps. *Invertebrate Zoology* **4**: 83–102.
- Sanamyan N, Sanamyan K. 2012.** *Edwardsia sojabio* sp. n. (Cnidaria: Anthozoa: Actiniaria: Edwardsiidae), a new abyssal sea anemone from the Sea of Japan. *Deep Sea Research II* **86–87**: 225–230.
- Sanamyan NP, Sanamyan KE, Lundsten L. 2015.** Two new deepwater sea anemones (Cnidaria: Anthozoa: Actiniaria) *Sicyonis heliodiscus* sp. n. (Actinostolidae) and *Hormathia pacifica* sp. n. (Hormathiidae) from Pacific. *Invertebrate Zoology* **12**: 131–149.
- Sanamyan NP, Sanamyan KE, McDaniel N, Bocharova ES. 2018.** First record of two genera of sea anemones (Cnidaria, Actiniaria), *Octineon* and *Edwardsiella* from the North Pacific Ocean. *Invertebrate Zoology* **15**: 1–18.
- Saucède T, Pierrat B, Danis B, David B. 2014.** Biogeographic processes in the Southern Ocean. In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B, d'Udekem d'Acoz C, Van de Putte A, Danis B, David B, Grant S, Gutt J, Held C, Hosie G, Heuttmann F, Post A, Ropert-Coudert Y, eds. *Biogeographic atlas of the Southern Ocean*. Cambridge: Scientific Committee on Antarctic Research, 456–463.
- Stephenson TA. 1918.** Coelenterata. Part I. – Actiniaria. *Natural History Reports on British Antarctic ('Terra Nova') Expedition 1910* **5**: 1–68.
- Stephenson TA. 1920.** On the classification of Actiniaria. Part I.—Forms with acontia and forms with a mesogloal sphincter. *Quarterly Journal of Microscopical Science* **64**: 425–574.
- Stephenson TA. 1922.** On the classification of Actiniaria. Part III. Definitions connected with the forms dealt with in Part II. *Quarterly Journal of Microscopical Science* **66**: 247–319.
- Stephenson TA. 1928.** *The British sea anemones, Vol. 1*. London: Ray Society.
- Studer T. 1879.** Übersicht der Anthozoa Alcyonaria, welche während der Reise S.M.S. Gazelle um die Erde gesammelt wurden. *Monatsberichte der Königlich Preussische Akademie des Wissenschaften zu Berlin* **1878**: 632–688.
- Van Praët M. 1990.** Gametogenesis and the reproductive cycle in the deep-sea anemone *Paracalliactis stephensoni* (Cnidaria: Actiniaria). *Journal of the Marine Biological Association of the United Kingdom* **70**: 163–172.
- Verrill AE. 1883.** Reports on the Anthozoa, and on some additional species dredged by the 'Blake' in 1877–1879, and by the U. S. Fish Commission Steamer 'Fish Hawk' in 1880–82. *Bulletin of the Museum of Comparative Zoology (Harvard University)* **11**: 1–72.
- Verrill AE. 1899.** Descriptions of imperfectly known and new Actinians, with critical notes on other species, IV. *American Journal of Science and Arts* **7**: 205–218.
- Yanagi K, Fujii T, Hirose M. 2015.** Redescription of the sea anemone *Exocoelactis actinostoloides* (Cnidaria: Anthozoa: Actiniaria) based on a topotypic specimen collected from Tokyo Bay, Japan. *Species Diversity* **20**: 199–209.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

File S1. Molecular data used in this study.