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Revision of the genus *Actinostella* (Cnidaria: Actiniaria: Actinioidea) from tropical and subtropical western Atlantic and eastern Pacific: redescriptions and synonymies

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ABSTRACT

Sea anemone species of the genus *Actinostella* live in tropical and subtropical shallow waters. They are characterized by having a marginal ruff harboring zooxanthellae that expands during the day and retracts at night, allowing the anemone to catch prey with the tentacles. Currently, 10 or 11 species are considered valid depending on the author; however, most species within the genus were described in the 1800s or in early 1900s and, thus, most descriptions are incomplete by modern standards. In addition, several species of *Actinostella* have reported wide geographical distributions. We evaluate the morphology of newly collected and type material to assess potential synonymies and geographical distributions; we perform phylogenetic analysis using five standard molecular rDNA markers for sea anemones to corroborate our morphological results and to investigate the phylogenetic relationships of *Actinostella*, other actinioideans, and those *Actinostella* species present in the eastern Pacific and western Atlantic

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tropical region. Based on morphological and cnida differences, we find six species of *Actinostella* valid. We redescribe *A. bradleyi*, *A. californica*, *A. digitata*, and *A. flosculifera* and synonymize *A. californica* pro parte (Pacific specimens with four cycles of mesenteries and *p*-mastigophores A in the marginal ruff) with *A. bradleyi* (found in the Panamanian and Mexican Pacific and the Gulf of California). We also find that *A. ornata* does not belong within *Actinostella*. We discuss the membership of *Actinostella*, including species of the genus *Phyllactis*, and synonymize *Phyllactis* with *Actinostella*. We propose that the combination of the presence of *p*-mastigophores A in the marginal ruff and the arrangement and fertility of mesenteries are diagnostic characteristics to differentiate species of *Actinostella* from the American coasts. Finally, our phylogenetic analyses based on rDNA markers differentiated between the western Atlantic and eastern Pacific species but lacked support and resolution to elucidate relationships within species in the eastern Pacific.

INTRODUCTION

Sea anemones are relatively simple soft-body marine invertebrates with few external diagnostic morphological characters to distinguish among taxa; most of these external characters, such as acrorhagi, vesicles, verrucae, tubercles, and marginal ruff are specialized outgrowths or modifications of the column or column margin (Stephenson, 1928). The marginal ruff, in particular, is a very distinct external character present in only a handful of actiniarians; it is an extension of the margin of the column that folds below the tentacles and lies above the substrate in which the anemone has burrowed. On its upper side, the thin-layered ruff exhibits frondlike papillae arranged radially in each exo- and endocoel; on the underside, the marginal ruff might bear verrucae and possibly host zooxanthellae.

Currently, there are two views on the number of genera of sea anemones with a marginal ruff. According to Fautin (2016), there are four genera bearing a marginal ruff (i.e., *Onubactis* López-González et al., 1995; *Oulactis* Milne Edwards and Haime, 1851; *Phyllactis* Milne Edwards and Haime, 1851; and *Actinostella* Duchassaing, 1850). However, Häussermann (2003) considered three genera following Carlgren (1949), who synonymized *Phyllactis* and *Actinostella* (but Carlgren incorrectly used *Phyllactis* as the senior synonym instead of *Actinostella*). Although some authors agreed with this synonymy (e.g., Corrêa, 1964; Schlenz and Belém, 1992; Ocaña and den Hartog, 2002; Häussermann, 2003), others (Gomes and Mayal, 1997; Melo and Amaral, 2005; Fautin, 2016) still consider *Phyllactis* and *Actinostella* different genera.

Among the few genera with a marginal ruff, *Onubactis* is the most recently described genus with a single species; *Oulactis* includes seven species, *Phyllactis* has four species, and *Actinostella* includes 10 species, resulting in a total of 22 species with a marginal ruff (Rodríguez et al., 2024). *Onubactis* and *Oulactis* are easily distinguishable from *Actinostella: Onubactis* has no verrucae nor zooxanthellae in the marginal ruff or column (López-González et al., 1995); *Oulactis* holds (or may hold) acrorhagi on the margin, bears no zooxanthellae, has no distinct fosse and has a diffuse endodermal marginal sphincter muscle (Häussermann, 2003). In contrast, *Phyllactis* closely resembles *Actinostella*, with similarities such as verrucae in the column, the presence of zooxanthellae, fosse, circumscribed endodermal marginal sphincter muscle, same number of mesenteries distally and proximally, and the lack of acrorhagi (Häussermann, 2003). In fact, original descriptions of both genera overlap and are not helpful to distinguish them.

Species of *Actinostella* are common and conspicuous in intertidal to shallow waters in the tropical and subtropical Pacific and Atlantic basins as well as the Red Sea. They are usually found in crevices or burrows in the sand, sometimes attached to rocks, often with debris attached to the column (Corrêa, 1964; Schlenz and Belém, 1992; Ocaña and den Hartog, 2002, Ocaña et al., 2007; Häussermann, 2003; González-Muñoz et al., 2012; Barragán et al., 2019; Durán-Fuentes et al., 2023). Accurate identification of species is critical to draw valid conclusions about the conservation and ecology of marine organisms, especially within the dynamic and climate-sensitive intertidal environment (Mace, 2004). However, most of the species within *Actinostella* were described in the 1800s or early 1900s and, thus, most descriptions are incomplete or ambiguous by contemporary standards in that they lack information about internal anatomy or images of cnidae, etc. Furthermore, all species currently in *Actinostella* were originally described within different genera (i.e., *Asteractis* Verrill, 1869; *Cradactis* McMurrich, 1893; *Lophactis* Verrill, 1869; *Oulactis*, and *Phyllactis*) creating a complex history of synonymies.

Of the 10 valid species of *Actinostella* according to Fautin (2016), three do not belong within the genus: *Actinostella variabilis* (Hargitt, 1911) was synonymized with *Lebrunia coralligens* (Wilson, 1890) by González-Muñoz et al. (2012), and *A. excelsa* (Wassilieff, 1908) and *A. striata* (Wassilieff, 1908) from Japan do not belong to *Actinostella* based on the original descriptions (Ocaña, 1994; Häussermann, 2003). From the seven putatively valid species left, *A. bradleyi* (Verrill, 1869) and *A. ornata* (Verrill, 1869) likewise have incomplete descriptions: only the holotype of each of these two is known from the Pacific coast of Panama and these sole specimens are undissected. The rest of the species in the genus are also not free of issues. For example, *A. flosculifera* (Le Sueur, 1817) has a wide distribution, including both sides of the Atlantic, and the type specimen of *A. radiata* (Duchassaing and Michelotti, 1860) is half-sectioned and only the proximal part can be analyzed.

At present, the genus *Phyllactis* has four valid species: *P. cichoracea* (Milne Edwards in Haeckel, 1876), *P. conquilega* (Duchassaing and Michelotti, 1860), *P. formosa* (Duchassaing, 1850), and *P. praetexta* (Couthouy in Dana, 1846) (Fautin, 2016). These species are distributed in the Caribbean Sea, with the exception of *P. cichoracea*, which is from the Red Sea. However, other authors consider only *P. cichoracea* as a distinct species within this genus, with the other three species currently assigned to *Phyllactis* considered synonymies of *A. flosculifera* (e.g., Schlenz and Belém, 1992; Ocaña and den Hartog, 2002; Häussermann, 2003); these later authors provide an alternative view to that from Fautin (2016), considering only the genus *Actinostella* to be valid, which includes 11 species.

Here, we examine type, museum, and newly collected material of five species attributed to the genus *Actinostella*: *A. bradleyi*, *A. californica* (McMurrich, 1893), *A. digitata* (McMurrich, 1893), *A. flosculifera*, and *A. ornata*. In addition, we reexamine the only available type specimen of any species within the genus *Phyllactis*, *P. conquilega*, to clarify the validity or synonymy of

Phyllactis and *Actinostella*. Finally, we performed molecular phylogenetic analyses using rDNA to corroborate our morphological results and to investigate the phylogenetic relationships of members of *Actinostella* and other actinioideans.

Materials and Methods

Morphological Study: The studied material was newly collected or gathered through loans from several museum collections: American Museum of Natural History (AMNH) in New York, National Museum of Natural History (USNM) in Washington DC, Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN) in Buenos Aires, Museu de Zoologia da Universidade de São Paulo (MZUSP) in São Paulo, Yale Peabody Museum (YPM) in New Haven, CT, and Swedish Museum of Natural History (SMNH) in Stockholm, Sweden. During 2013–2016, 12 specimens of *Actinostella bradleyi* were collected, nine from Baja California Sur (Mexico) and three from the Pacific Ocean off Panama—with one specimen collected in the Azuero Peninsula, Los Santos Province, and two in the Pearl Islands, Gulf of Panama Province. Twenty-two specimens of *A. californica* were collected during 2013–2016, 20 specimens from Baja California Sur (Mexico) and two in the Pearl Islands, Gulf of Panama Province (Panama). A single specimen of *A. digitata* was collected in Chubut (Argentina) in 2010. Sixteen specimens of *A. flosculifera* were collected, 13 in Bocas del Toro (Panama) in 2016 and three in São Paulo (Brazil) in 2017. All newly collected specimens were collected by hand while snorkeling intertidally in Mexico, Panama, and Brazil, or through scuba diving in the subtidal in Mexico, Panama and Argentina (fig. 1). Freshly collected specimens were relaxed with menthol crystals, photographed alive, and subsequently fixed in 10% seawater formalin. Small pieces from the pedal disc of several specimens were fixed in 100% ethanol for molecular studies. Newly collected material for this study was deposited at the AMNH, MACN, MZUSP, and USNM. For locality details, see table 1.

Preserved specimens were examined whole and dissected. Histological sections 5–10 µm thick were made from different parts and were stained with Azocarmine triple stain (Humason, 1967). Small pieces of tissue were smeared on slides and examined using differential interference microscopy (DIC) at 1000× magnification to measure the cnidae. We scanned through the slides and haphazardly measured 20 capsules of each type (when possible) to generate a range: frequencies given are subjective impressions based on all the cnidae seen on the slides. Measurements of body region sizes and cnidae were made from preserved material.

Cnidae terminology follows Gusmão et al. (2018). We emphasize that we use a combination of classifications to better capture the underlying variation in cnidae morphology but do not imply any evolutionary relationship among these types of capsules. Finally, because of the complexity of several of the terminology issues discussed by Gusmão et al. (2018), we underscore that any comparison of nematocysts among taxa going forward should be based on images (drawings or photographs) in order to be considered reliable.

We have followed the taxonomic classification implemented in Rodríguez et al. (2014). Within each genus, taxa are discussed in alphabetical order. The list of synonymies we provide

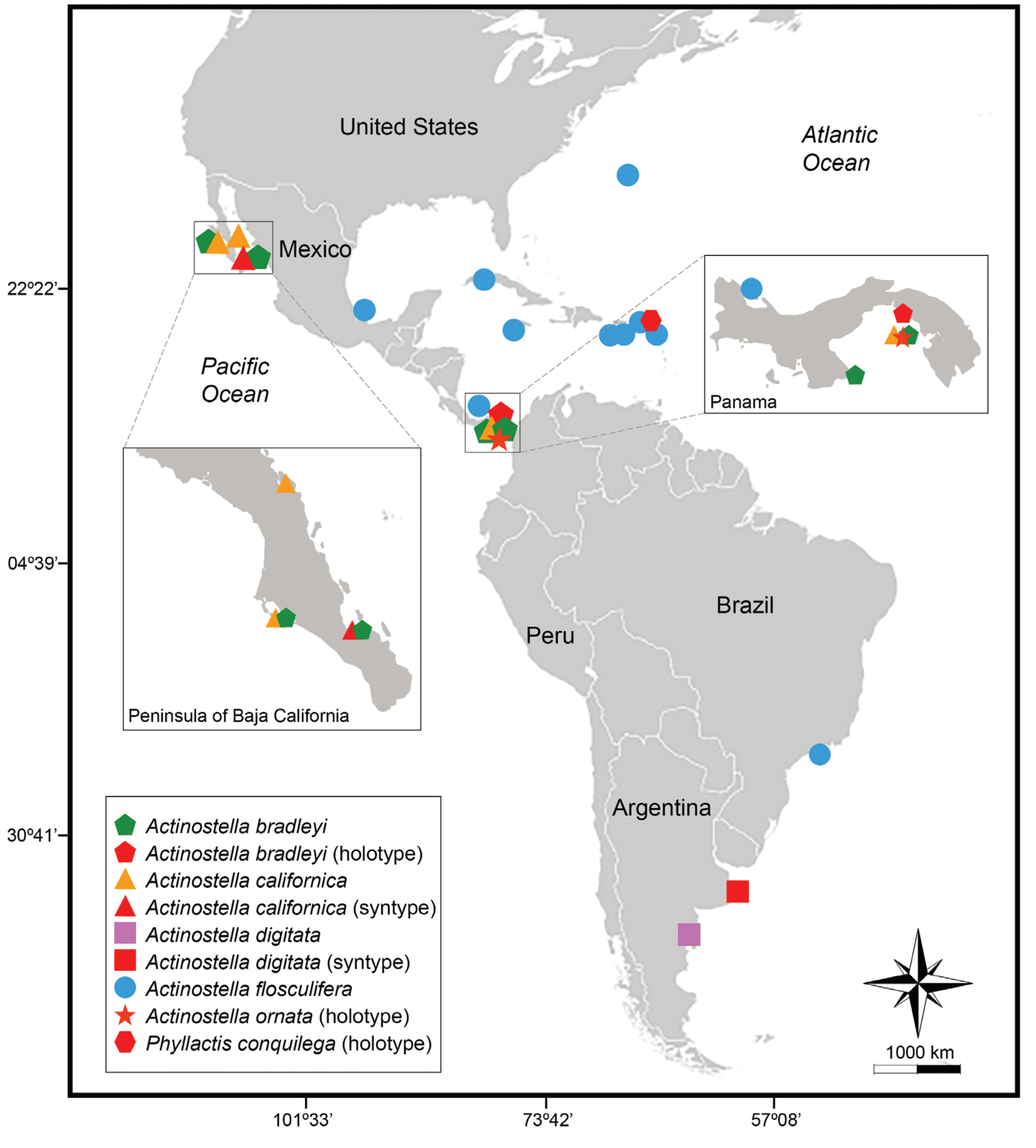


FIG. 1. Geographic distribution of species of *Actinostella*.

for each species is not exhaustive. We provide only references to the first citation of a species by a particular name. We include all references citing specimens under an incorrect species name because it is important to note incorrect species records.

Molecular Methodology: Genomic DNA was isolated from approximately 25 mg of tissue using the Qiagen DNeasy kit or the Qiagen Gentra Puregene Tissue Kit following the manufacture's protocol. Whole genomic DNA was amplified using published primers and the

TABLE 1. Material examined in this study. Catalogue number, locality, coordinates, depth and date of collection are provided. Abbreviations: **AMNH,** American Museum of Natural History; **MACN,** Museo Argentino de Ciencias Naturales Bernardino Rivadavia; **MZUSP,** Museu de Zoologia da Universidade de São Paulo; **SMNH,** Swedish Museum of Natural History; **USNM,** National Museum of Natural History; **YPM,** Yale Peaboy Museum; (*), data transcribed from museum label, but does not correspond with type locality.

Species	Museum and catalogue number	Locality	Longitude	Latitude	Date	Depth (m)	Specimens (no.)
Actinostella bradley (Verrill, 1869)	YPM 1009 (Holotype)	Panama Reef (Gulf of Panama, Panama); Pacific Ocean	–	–	1866	Intertidal	1
	AMNH_IZC 00361355	Conquista Agraria, (Mexico); Pacific Ocean	23°57′18″N	110°52′27″W	Oct 2013	Intertidal	3
	AMNH_IZC 00361356	Magdalena Bay (Mexico); Pacific Ocean	24°39′08″N	112°10′33″W	Nov 2013	Intertidal	1
	AMNH_IZC 00361357	Pichilingue Bay, Gulf of California (Mexico)	24°17′11″N	110°19′57″W	Aug 2013	Intertidal	3
	AMNH_IZC 00361358	Telecote, Gulf of California (Mexico)	24°20′09″N	110°19′28″W	May 2013	Intertidal	2
	USNM 1606849	Porrocas, Pedasi (Los Santos, Panama); Pacific Ocean	7°32′25.92″N	79°59′38.33″W	Oct 2015	3	1
	USNM 1606850	Pearl Islands (Gulf of Panama Province, Panama); Pacific Ocean	8°37′58.50″N	79°02′23.40″W	Oct 2015	10	2
Actinostella californica (McMurrich, 1893)	USNM 17812 (Syntype)	Pichilingue Bay, Gulf of California (Mexico)	24°17′03″N	110°19′58″W	–	–	1
	USNM 1606851	Pearl Islands (Gulf of Panama, Panama); Pacific Ocean	08°37′58.50″N	79°02′23.40″W	Oct 2015	10	2
	AMNH_IZC 00361339	Concepción Bay, Gulf of California (Mexico)	26°38′25″N	111°49′50″W	May 2013	Intertidal	3
	AMNH_IZC 00361340	Concepción Bay, Gulf of California (Mexico)	26°38′25″N	111°49′50″W	Mar 2016	Intertidal	1
	AMNH_IZC 00361341	Magdalena Bay (Mexico); Pacific Ocean	24°39′08″N	112°10′33″W	Nov 2013	Intertidal	1
	AMNH_IZC 00361342	Magdalena Bay (Mexico); Pacific Ocean	24°39′08″N	112°10′33″W	Nov 2013	Intertidal	1

TABLE 1 *continued*

Species	Museum and catalogue number	Locality	Longitude	Latitude	Date	Depth (m)	Specimens (no.)
	AMNH_IZC 00361343	Concepción Bay, Gulf of California (Mexico)	26°38′25″N	111°49′50″W	Mar 2016	Intertidal	1
	AMNH_IZC 00361344	Concepción Bay, Gulf of California (Mexico)	26°38′25″N	111°49′50″W	Mar 2016	Intertidal	1
	AMNH_IZC 00361345	Concepción Bay, Gulf of California (Mexico)	26°38′25″N	111°49′50″W	Mar 2016	Intertidal	1
	AMNH_IZC 00361346	Concepción Bay, Gulf of California (Mexico)	26°38′25″N	111°49′50″W	Mar 2016	Intertidal	1
	AMNH_IZC 00361347	Concepción Bay, Gulf of California (Mexico)	26°38′25″N	111°49′50″W	Mar 2016	Intertidal	1
	AMNH_IZC 00361348	Concepción Bay, Gulf of California (Mexico)	26°38′25″N	111°49′50″W	Mar 2016	Intertidal	1
	AMNH_IZC 00361349	Concepción Bay, Gulf of California (Mexico)	26°38′25″N	111°49′50″W	Mar 2016	Intertidal	1
	AMNH_IZC 00361350	Concepción Bay, Gulf of California (Mexico)	26°38′25″N	111°49′50″W	Mar 2016	Intertidal	1
	AMNH_IZC 00361351	Concepción Bay, Gulf of California (Mexico)	26°38′25″N	111°49′50″W	Mar 2016	Intertidal	1
	AMNH_IZC 00361352	Concepción Bay, Gulf of California (Mexico)	26°38′25″N	111°49′50″W	Mar 2016	Intertidal	1
	AMNH_IZC 00361353	Concepción Bay, Gulf of California (Mexico)	26°38′25″N	111°49′50″W	Mar 2016	Intertidal	1
	AMNH_IZC 00361354	Concepción Bay, Gulf of California (Mexico)	26°38′25″N	111°49′50″W	May 2013	Intertidal	3
Actinostella digitata (McMurrich, 1893)	USNM 17776 (Syntypes)	Off Rio de La Plata (Argentina)	36°47′S	56°23′W	Dec 1888	20	2
	MACN-In 43521	Paraná Beach, Chubut (Argentina)	42°47′S	64°56′W	Feb 2010	5–10	1
Actinostella flosculifera (Le Sueur, 1817)	USNM 1606853	Bocas del Toro (Panama); Atlantic Ocean	09°21′04″N	82°15′25″W	June 2016	Intertidal	1

TABLE 1 *continued*

Species	**Museum and catalogue number**	**Locality**	**Longitude**	**Latitude**	**Date**	**Depth (m)**	**Specimens (no.)**
	USNM 1606854	Bocas del Toro (Panama); Atlantic Ocean	09°21′04″N	82°15′25″W	June 2016	Intertidal	1
	USNM 1606855	Bocas del Toro (Panama); Atlantic Ocean	09°21′04″N	82°15′25″W	June 2016	Intertidal	1
	USNM 1606856	Bocas del Toro (Panama); Atlantic Ocean	09°21′04″N	82°15′25″W	June 2016	Intertidal	1
	USNM 1606857	Bocas del Toro (Panama); Atlantic Ocean	09°21′04″N	82°15′25″W	June 2016	Intertidal	1
	USNM 1606852	Bocas del Toro (Panama); Atlantic Ocean	09°21′04″N	82°15′25″W	June 2016	Intertidal	1
	USNM 1606858	Bocas del Toro (Panama); Atlantic Ocean	09°21′04″N	82°15′25″W	June 2016	Intertidal	2
	USNM 1606859	Bocas del Toro (Panama); Atlantic Ocean	09°21′04″N	82°15′25″W	June 2016	Intertidal	1
	USNM 1606860	Flat rock Beach (Panama); Atlantic Ocean	09°21′48″N	82°14′19.9″W	June 2016	Intertidal	1
	USNM 1606861	Flat rock Beach (Panama); Atlantic Ocean	09°21′48″N	82°14′19.9″W	June 2016	Intertidal	1
	USNM 1606862	Flat rock Beach (Panama); Atlantic Ocean	09°21′48″N	82°14′19.9″W	June 2016	Intertidal	1
	USNM 1606863	Flat rock Beach (Panama); Atlantic Ocean	09°21′48″N	82°14′19.9″W	June 2016	Intertidal	1
	AMNH Cat. Cnidaria 587	Bermuda	–	–	1897	–	3
	AMNH Cat. Cnidaria 694	Culebra (Puerto Rico)	–	–	Nov 1899	–	2
	AMNH Cat. Cnidaria 741	Jamaica	–	–	1899–1901	–	2
	AMNH Cat. Cnidaria 1283	Havana (Cuba)	–	–	June 1918	–	3
	AMNH Cat. Cnidaria 1324	Guanica Harbor (Puerto Rico)	–	–	June 1915	–	1
	AMNH Cat. Cnidaria 1330	Guanica Harbor (Puerto Rico)	–	–	June 1915	–	1
	AMNH Cat. Cnidaria 1352	Montalva Bay (Puerto Rico)	–	–	June 1915	–	1

TABLE 1 *continued*

Species	Museum and catalogue number	Locality	Longitude	Latitude	Date	Depth (m)	Specimens (no.)
	AMNH Cat. Cnidaria 3585	Mary Creek, St. John (Virgin Islands)	–	–	June 1966	–	3
	AMNH Cat. Cnidaria 5308	Vera Cruz (Mexico); Caribbean Sea	19°13′17.22″N	96°07′38.20″W	May 2010	<1	1
	MZUSP 8405	Praia do Cabelo Gordo, São Sebastião, São Paulo (Brazil)	23°49′37.87″S	45°25′19.41″W	Sept 2017	Intertidal	3
Phyllactis conquilega (Duchassaing and Michelotti, 1860) [= *A. flosculifera*]	SMNH 1170 (Holotype)	Saint Thomas (West Indies); Atlantic Ocean	73°27′N (*)	23°00′E (*)	1898	–	1
Actinostella ornata (Verrill, 1869) [=*Telmatactis panamensis* (Verrill, 1869)]	YPM 2105 (Holotype)	Pearl Islands (Gulf of Panama; Panama); Pacific Ocean	–	–	1866	–	1

protocol detailed in Lauretta et al. (2014) for the mitochondrial genes 12S, 16S, and CO3, and the nuclear 18S and 28S. PCR products were cleaned using ExosapIT (Exonuclease I and FastAP thermosensitive alkaline phosphatase per manufacturer's specifications, except that shrimp alkaline phosphatase was replaced with FastAP). Cycle sequencing reactions used a total of 5 µL of cleaned PCR product, at a concentration of 25 ng of product for every 200 base pairs (bp) of marker length. Cycle sequencing products were cleaned using Centri-Sept columns (Princeton Separations; following the manufacturer's protocol) containing DNA-grade Sephadex (G-50 fine; GE Healthcare) and later sequenced using PCR amplification primers on an ABI 3730x at the in-house facilities of the AMNH. Forward and reverse sequences were assembled and edited in Geneious v.11.1.4 (Kearse et al., 2012) and blasted against the nucleotide database of GenBank to confirm that the obtained sequences corresponded to the target sequence/organism and not to their endosymbiotic algae. Sequences have been deposited in GenBank (see table S1 in the online supplement: https://doi.org/10.5531/sd.sp.62).

Newly generated rDNA sequences for each of the five markers were combined and analyzed with sequences from Gusmão and Rodríguez, 2021(see table S1). Sequences for each marker were separately aligned using MAFFT v.7.307 (Katoh and Standley, 2013) using the following settings: Strategy, L-INS-I; Scoring matrix for nucleotide sequences, 200PAM/k = 2;

Gap open penalty, 1.53; Offset value, 0.05. Alignments for each marker were analyzed separately and as a concatenated dataset.

Phylogenetic Inference: For the rDNA dataset (12S, 16S, CO3, 18S, 28S) each gene region, the best model of nucleotide substitution was chosen using Akaike information criterion (AIC) on jModeltest2 (Guindon and Gascuel, 2003; Darriba et al., 2012) implemented on the CIPRES Portal (Miller et al., 2010). Maximum likelihood (ML) analyses were performed using RAxML-NG v0.6.0 (Kozlov et al., 2019) using the appropriate model of nucleotide substitution for each marker. We used the majority rule criterion to access clade support and allowed automatic haul(-autoMRE). An additional ML analysis was conducted on PhyML v.3.0 online (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. All analyses were run with gaps treated as missing data. The actiniarian *Nematostella vectensis* Stephenson, 1935, was used as an outgroup for the analyses. Phylogenetic trees were edited using FigTree v1.4.3 and Adobe Photoshop.

RESULTS

Taxonomic Account

Order Actiniaria Hertwig, 1882

Suborder Enthemonae Rodríguez and Daly, 2014, in Rodríguez et al., 2014

Superfamily Actinioidea Rafinesque, 1815

Family Actiniidae Rafinesque, 1815

Genus *Actinostella* Duchassaing, 1850

Asteractis Verrill, 1869.
Cradactis McMurrich, 1893.
Lophactis Verrill, 1869.
Metridium Dana, 1846.
Oulactis Milne Edwards and Haime, 1851.
Phyllactis Milne Edwards and Haime, 1851.

Diagnosis (after Häussermann, 2003; changes in boldface): Actiniidae with well-developed pedal disc **and basilar muscles**. Oral disc round; column more or less elongate, with verrucae **distally**. Wide marginal ruff or collar between verrucae and column margin, with series of small frondlike papillae **(= vesicles)** containing basitrichs and sometimes ***p*-mastigophores A**. Above vesicles a more or less distinct fosse. Generally 48 tentacles, but **up to 96 in some species**. No acrorhagi. All mesenteries might be perfect, hexamerously and regularly arranged. Same number of mesenteries proximally and distally. Endodermal marginal sphincter muscle strong to very weak, circumscribed. Longitudinal muscles of tentacles ectodermal.

As a rule, two siphonoglyphs. Retractors typically strong, diffuse to restricted. Parietobasilar muscles well developed. Zooxanthellae **present**. Cnidom: spirocysts, basitrichs, basitrichs S, *b*-mastigophores, *p*-mastigophores A and *p*-mastigophores B1.

Type Species: *Actinostella formosa* Duchassaing, 1850.

Species Included: *Actinostella bradleyi; A. correae* Schlenz and Belém, 1992; *A. californica*; *A. digitata; A. flosculifera;* and *A. cichoracea*.

Remarks: We amend the diagnosis to include species having up to 96 tentacles (i.e., *Actinostella bradleyi*) and use more specific terms for the description of structures (e.g., distally); in addition, we combine cnidae terminology that allows us to describe the diversity of mastigophore nematocysts. Based on the redescription of *A. flosculifera* from the east Atlantic by Ocaña (1994), Häussermann (2003) modified the diagnosis of *Actinostella* by Carlgren (1949) to acknowledge the possible presence of holotrichs in the column. However, the presence of holotrichs is not known within any other species of *Actinostella* and because we have noticed other inconsistencies in the description of the material studied by Ocaña (1994) (see observations below in species' descriptions and in Discussion), we prefer to not incorporate features in that material until this species has been reexamined.

Actinostella bradleyi (Verrill, 1869)

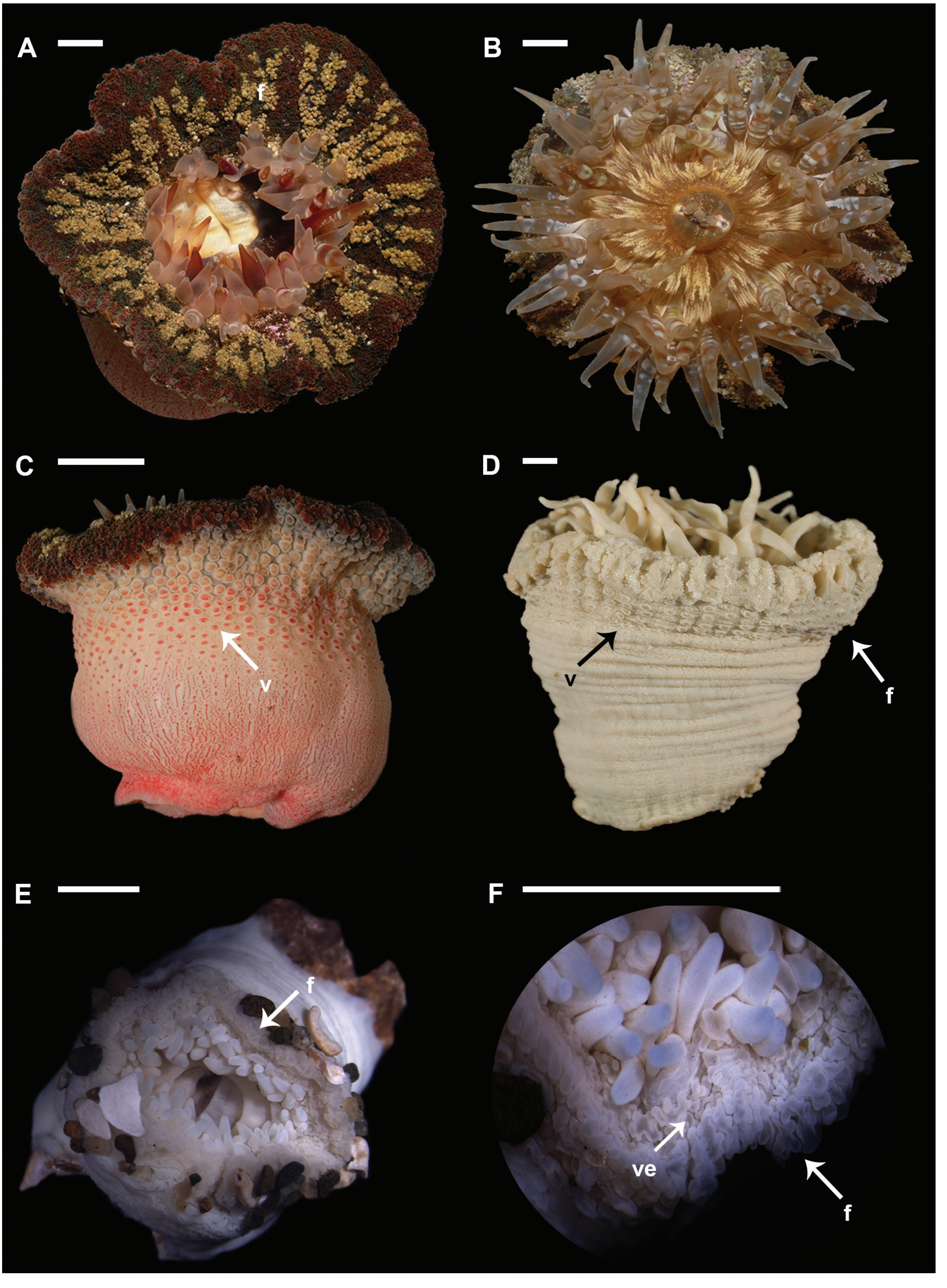
Figures 2–6, tables 1, 2

Asteractis bradleyi Verrill, 1869.
Phyllactis bradleyi (Verrill, 1869): Stephenson, 1922.
Non *Phyllactis bradleyi* (Verrill, 1869): Carlgren, 1951.
Actinostella bradleyi (Verrill, 1869): Häussermann, 2003.
Actinostella californica (McMurrich, 1893): Barragán et al., 2019 pro parte.

Differential Diagnosis: *Actinostella* with up to four cycles of mesenteries and 96 tentacles, all mesenteries, including directives, perfect and fertile. Marginal ruff and column with *p*-mastigophores A and basitrichs.

Examined Material: *Actinostella bradleyi*: AMNH_IZC 00361355, AMNH_IZC 00361356, AMNH_IZC 00361357, AMNH_IZC 00361358, USNM 1606849, USNM 1606850; *Asteractis bradleyi* Verrill, 1869 [= *A. bradleyi*]: YPM 1009 (holotype). *Lophactis ornata* Verrill, 1869 [= *Telmatactis* cf. *panamensis* (Verrill, 1869)]: YPM–2015 (holotype). YPM repository IZAR.001433: Frank Howe Bradley Correspondence; 1866–1867; Correspondence from F.H. Bradley to A.E. Verrill; all sent from his expedition to America Central (letters transcribed by E. Lazo-Wasem).

Description: *External anatomy* (figs. 2, 5): Well-developed pedal disc, to 23 mm diameter. Column elongate, to 55 mm height and 42 mm diameter, with 96 longitudinal rows of verrucae distally in each endo- and exocoel. Marginal ruff with rows of vesicles. Oral disc to 34 mm diameter. Fosse deep. Tentacles, to 96 in five cycles; simple, smooth, all similar length, to 18 mm. Mesenterial insertions visible in pedal disc.


A
f
B
C
v
D
v
f
E
f
F
ve
f

Internal anatomy (figs. 3, 5): Same number of mesenteries distally and proximally. Forty-eight pairs of mesenteries hexamerously arranged in four cycles (6 + 6 + 12 + 24 = 48). All cycles perfect and fertile, including directives (fig. 3B). Two pairs of directives attached to two clearly distinct siphonoglyphs. Gonochoric, developed oocysts 0.06–0.15 mm in diameter (fig. 3F) in specimen collected in May 2013, developed spermatic cysts 0.09–0.23 mm in diameter (fig. 3E) in specimens collected in August, October, and November 2013. Retractor muscles strong, bandlike, and restricted. Parietobasilar muscles well developed (fig. 3G), with long free mesogleal lamella. Basilar muscles well developed, processes short and thin (fig. 3H). Endodermal marginal sphincter muscle circumscribed (fig. 3A, C). Longitudinal muscles of tentacles ectodermal (fig. 3D). Zooxanthellae present in tentacles and marginal ruff.

Color (fig. 2): Variable in live specimens. In specimens from Mexico, pedal disc and column pinkish or opaque orange; verrucae darker than column. Oral disc olive green with beige radial lines. Marginal ruff olive green with radial brown and beige stripes. Tentacles brownish or reddish with brown base and spots with a brown dot along the entire tentacle. Specimens from Panama, same pedal disc, column, and oral disc, but with brownish marginal ruff. Preserved material beige and marginal ruff lighter.

Cnidom (figs. 4, 6): Basitrichs, basitrichs S, *b*-mastigophores, *p*-mastigophores A, *p*-mastigophores B1, and spirocysts. Sizes and distribution in table 2.

Geographic and Bathymetric Distribution and Natural History: *Actinostella bradleyi* can be found in the Pacific Ocean in Mexico and Panama. Although Verrill (1869) did not specify the location of the type locality (i.e., Panama Reef) in the Pacific, we confirm the type locality of *A. bradleyi* in the Pacific side of Panama, off the coast of Panama City based on transcriptions of the original correspondence (archived record IZAR.001433) between Verrill and F.H. Bradley (collector). In Mexico, *A. bradleyi* can be found on the intertidal shore in Pichilingue Bay in the Gulf of California and in Conquista Agraria and Magdalena Bay on the Pacific side. In Panama, this species was collected in the Azuero Peninsula (Los Santos Province) and the Pearl Islands (Gulf of Panama Province) between 3–10 m. The specimens were found burrowed in sand attached to a buried rock or shell, or hidden in rock crevices, with the marginal ruff above the substratum. *Actinostella bradleyi* and *A. californica* live in sympatry, although in Mexico, *A. californica* is more common (and found at shallower depths) than its Pacific congener.

Remarks: *Actinostella bradleyi* differs from the five other species of the genus by the combination of the number of tentacles (up to 96), perfect mesenteries and distribution of fertile cycles of mesenteries (all four cycles), and the presence of *p*-mastigophores A in the marginal ruff and column (figs. 4, 6). Until the specimens analyzed by Ocaña (1994) from the Canary Islands are examined, *A. bradleyi* is the only species within the genus with up to five cycles of tentacles and

FIG. 2. External anatomy of *Actinostella bradleyi* (Verrill, 1869). **A,** Oral view of live semiexpanded specimen showing the marginal ruff; **B,** oral view of live and expanded specimen; **C,** lateral view of live semiexpanded specimen; notice rows of distal verrucae (v); **D,** lateral view of preserved specimen; **E,** detail of oral view of a semiexpanded preserved specimen; **F,** detail of the vesicles (ve) in the marginal ruff (f) of a preserved specimen. Abbreviations: **f,** marginal ruff; **v,** verrucae; **ve,** vesicles. Scale bars: **A–F,** 5 mm.

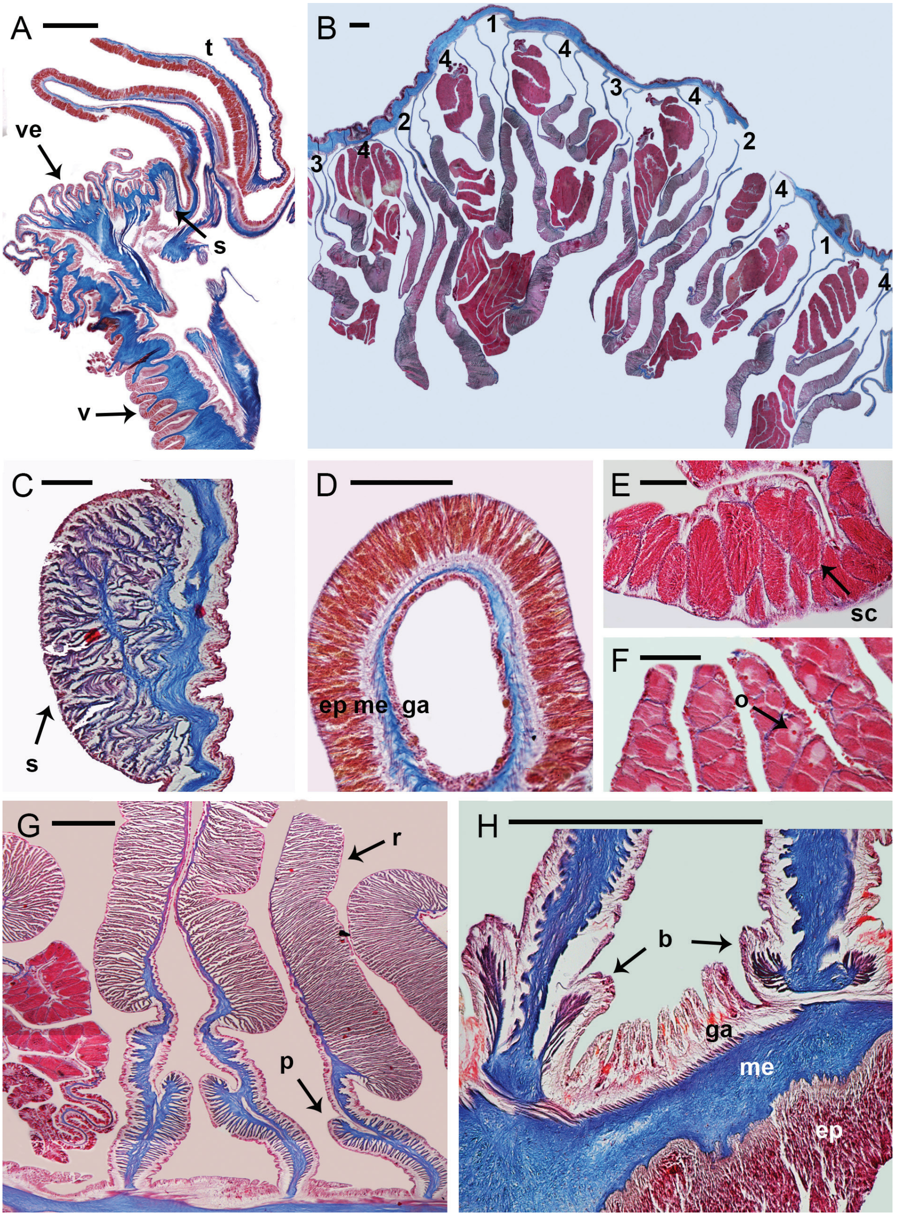


FIG. 3. Internal anatomy of *Actinostella bradleyi* (Verrill, 1869). **A,** longitudinal section of the distal column showing distal verrucae (v), vesicles (ve) in the marginal ruff, marginal sphincter muscle (s), and the fosse; **B,** cross section at the actinopharynx level showing four cycles of mesenteries; numbers between pairs of mesenteries indicate the corresponding cycle; **C,** detail of the endodermal marginal sphincter muscle; **D,** cross section of a tentacle showing the ectodermal longitudinal muscles; **E,** detail of developing spermatic cysts (sc); **F,** detail of developing oocytes (o); **G,** detail of a cross section showing the retractor (r) and parietobasilar (p) muscles; **H,** cross section of proximal end showing the basilar muscles (b). Abbreviations: **b,** basilar muscles; **ep,** epidermis; **ga,** gastrodermis; **me,** mesoglea; **o,** oocytes; **p,** parietobasilar muscle; **r,** retractor muscle; **s,** sphincter; **sc,** spermatic cysts; **t,** tentacle; **v,** verrucae; **ve,** vesicles. Scale bars: **A, B, G, H,** 0.5 mm; **C–F,** 0.1 mm.

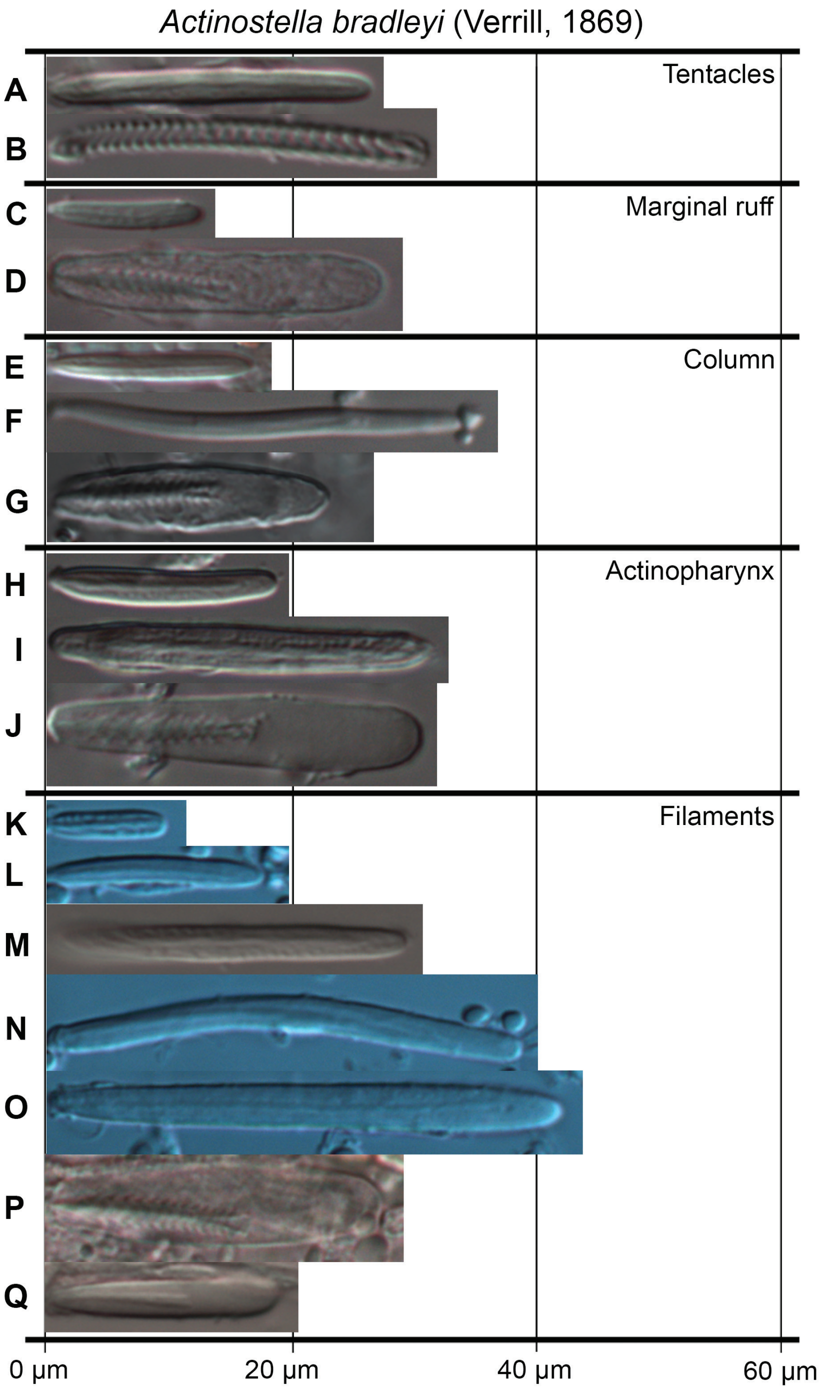


FIG. 4. Cnidae of *Actinostella bradleyi* (Verrill, 1869). **A, C, E, H, I, K, L, M,** basitrichs; **B,** spirocysts; **F, N,** basitrichs S; **D, G, J, P,** *p*-mastigophore A; **O,** *b*-mastigophore; **Q,** *p*-mastigophore B1.

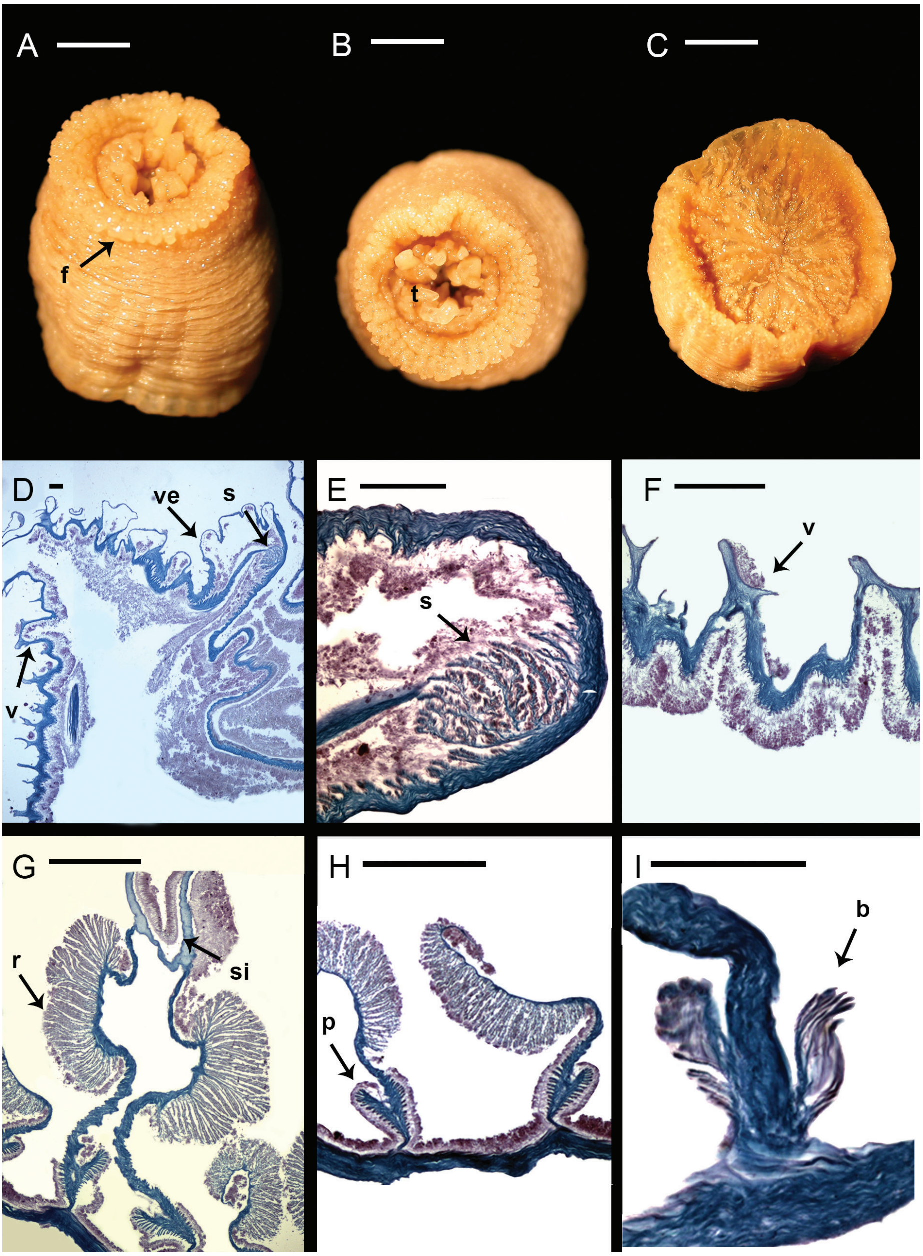


FIG. 5. External and internal anatomy of the holotype of *Asteractis bradleyi* Verrill, 1869 (YPM-1009) (= *Actinostella bradleyi*). **A,** lateral view of holotype, showing the marginal ruff; **B,** oral view of holotype; **C,** detail of the pedal disc of holotype; **D,** longitudinal section of the distal column showing distal verrucae (v), vesicles (ve) in the marginal ruff, marginal sphincter muscle (s), and the fosse; **E,** detail of the endodermal marginal sphincter muscle; **F,** detail of the verrucae in the distal column; **G,** cross section at the actinopharynx level showing the directive mesenteries, retractor muscle (r), and siphonoglyphs (si); **H,** detail of a pair of mesenteries of the third cycle showing the parietobasilar muscle (p); **I,** longitudinal section of proximal end showing basilar muscles (b). Abbreviations: **b,** basilar muscle; **f,** marginal ruff; **p,** parietobasilar muscle; **r,** retractor muscle; **s,** sphincter; **si,** siphonoglyphs; **v,** verrucae; **ve,** vesicle. Scale bars: **A–C,** 5 mm; **D–I,** 0.5 mm.

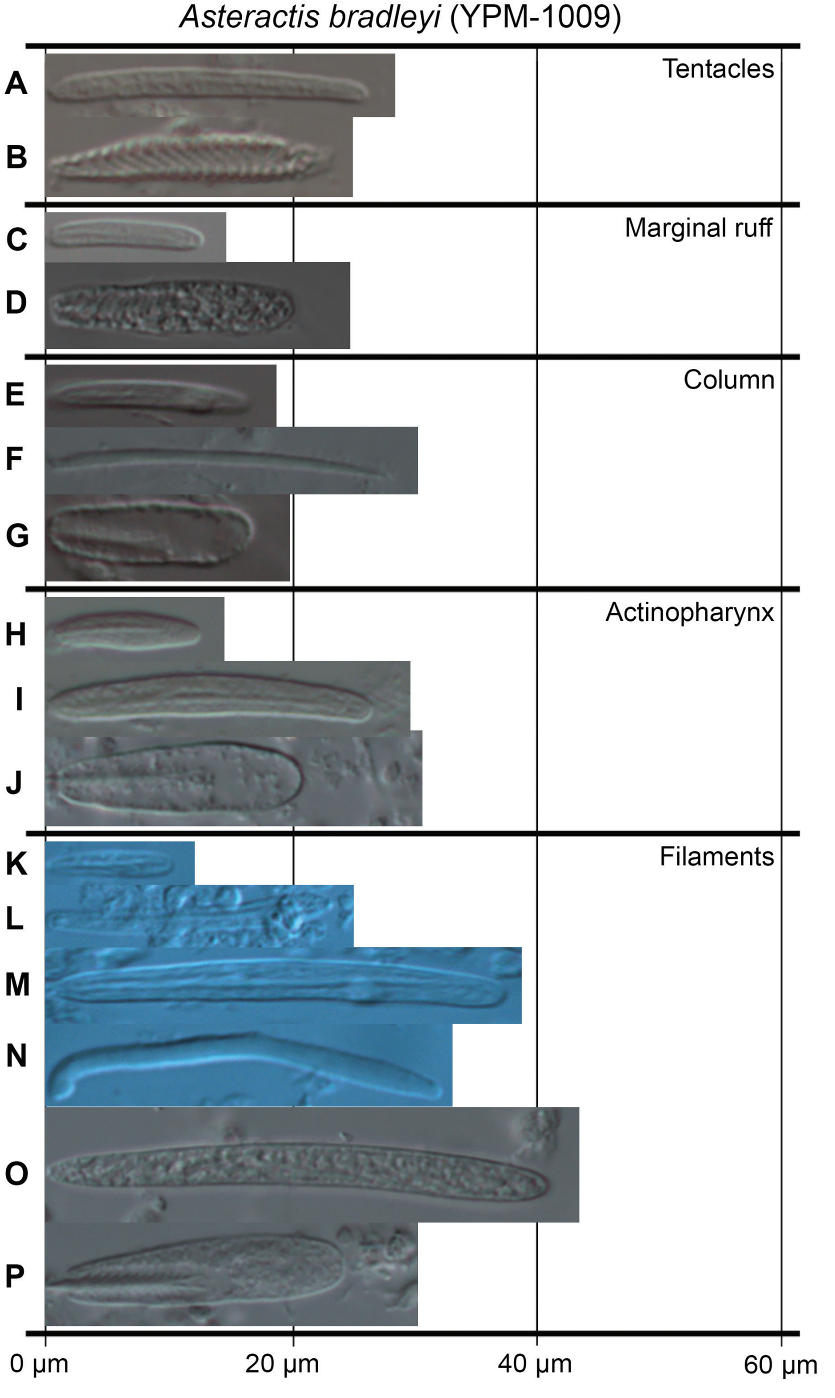


FIG. 6. Cnidae of holotype of *Actinostella bradleyi* (Verrill, 1869) (YPM-1009). **A, C, E, H, I, K, L, M,** basitrichs; **B,** spirocysts; **F, N,** basitrichs S; **D, G, J, P,** *p*-mastigophore A; **O,** *b*-mastigophore.

TABLE 2. Size ranges and distribution of cnidae of *Actinostella bradleyi* (Verrill, 1869). N, Total number of capsules measured; M, Ratio of number of specimens in which each cnidae was found to number of specimens examined; F, Frequency, +++ = very common, ++ = common, + = rather common, --- = sporadic; SD, standard deviation; NF, not found. Sizes in micrometers. Letters in parenthesis correspond to images in figures 4 and 6.

Tissue / Categories	M	N	F	Range of length and width of capsules	Mean ± SD	YPM 1009
TENTACLES						
Basitrichs (A)	6/6	99	+++	11.3–30.1 × 1.8–3.4	21.1±4.4 × 2.4±0.3	23.0–27.0 × 3.0–3.0
Spirocysts (B)	6/6	153	+++	12.3–35.0 × 1.5–3.5	22.4±5.6 × 2.5±0.4	20.0–26.0 × 3.0–4.0
MARGINAL RUFF						
Basitrichs (C)	6/6	167	+++	08.2–14.4 × 1.7–2.8	11.2±1.3 × 2.1±0.2	10.0–13.0 × 1.8–2.4
p-mastigophores A (D)	6/6	72	+	14.9–26.2 × 2.9–6.7	19.9±4.7 × 2.0±0.7	20.4–31.0 × 3.0–4.5
COLUMN						
Basitrichs (E)	6/6	161	+++	09.0–19.4 × 1.6–2.6	15.1±2.0 × 2.2±0.2	10.6–18.0 × 1.6–2.2
Basitrichs S (F)	5/6	47	++	18.4–38.0 × 1.5–2.6	30.4±3.4 × 2.0±0.3	28.5–31.0 × 1.8–1.9
p-mastigophores A (G)	5/6	39	---	16.3–25.0 × 3.9–6.0	20.0±1.7 × 4.8±0.5	15.3–22 × 3.9–6.0
ACTINOPHARYNX						
Basitrichs 1 (H)	6/6	60	+++	07.9–15.7 × 1.5–2.9	12.2±1.8 × 2.2±0.2	12.0 × 3.0
Basitrichs 2 (I)	6/6	77	+++	16.2–31.0 × 2.1–3.8	24.3±3.5 × 2.9±0.4	19.2–28.1 × 2.6–4.0
p-mastigophores A (J)	6/6	65	++	19.6–31.4 × 4.6–6.5	25.3±2.5 × 5.4±0.4	18.2–21.9 × 5.0–6.8
FILAMENTS						
Basitrichs 1 (K)	6/6	70	+	07.4–11.9 × 1.6–2.5	09.7±1.4 × 2.0±0.2	10.0–15.0 × 1.9–2.5
Basitrichs 2 (L)	5/6	52	+++	12.0–17.6 × 1.7–2.9	13.2±1.0 × 2.2±0.2	17.8–25.7 × 2.1–3.0
Basitrichs 3 (M)	5/6	42	---	22.0–33.2 × 2.0–3.1	27.7±.2.1 × 2.4±02	36.2–43.0 × 3.0–3.4
Basitrichs S (N)	6/6	61	+	25.9–43.0 × 1.9–2.9	34.2±4.2 × 2.4±0.3	30.3–36.7 × 2.0–2.6
b-mastigophores (O)	6/6	72	++	29.6–42.4 × 2.4–4.2	35.7±2.6 × 3.5±0.3	35.7–42.8 × 3.2–5.0
p-mastigophores A (P)	6/6	83	++	21.8–29.4 × 3.8–6.9	26.4±1.7 × 5.1±0.6	18.9–24.0 × 4.0–7.3
p-mastigophores B1 (Q)	4/6	60	+	14.9–24.8 × 2.3–3.2	18.4±1.8 × 2.7±0.2	NF

four cycles of mesenteries. Although externally *A. bradleyi* closely resembles the only other species of the genus recorded from the eastern Pacific, *A. californica*, they can be easily distinguished in the field by the number of tentacles (to 96 in *A. bradleyi* and up to 48 in *A. californica*). However, both species live in sympatry and when specimens of *A. bradleyi* are not completely mature, as it is the case of the holotype of the species (YPM 1009), they can be confused with *A. californica*. Attributes of the cnidom can differentiate them. Barragán (2015) redescribed one sterile specimen with three cycles of mesenteries collected in Pichilingue Bay in the Gulf of California (Mexico) and considered it as *A. californica* based mainly on its distribution. Our detailed revision of this material here shows that this specimen is an immature specimen of *A. bradleyi* in which the fourth cycle of mesenteries is not yet developed.

Fautin (2016: 177) cited under the list of synonymies of *Actinostella bradleyi* the following: "*Oulactis californica* McMurrich, 1893 [Ref. 386], p. 196–197, 198, 206 (original description)." This synonymy is incorrect because those specimens correspond to the type material of the species *A. californica*. In addition, Fautin (2016) mentioned as valid names used for *Oulactis californica* McMurrich, 1893, both *A. bradleyi* and *A. californica*. In this study, we show that *O. californica* is a synonym of *A. californica* (McMurrich, 1893) and different from *A. bradleyi* (see remarks under *A. californica*).

Actinostella californica (McMurrich, 1893)

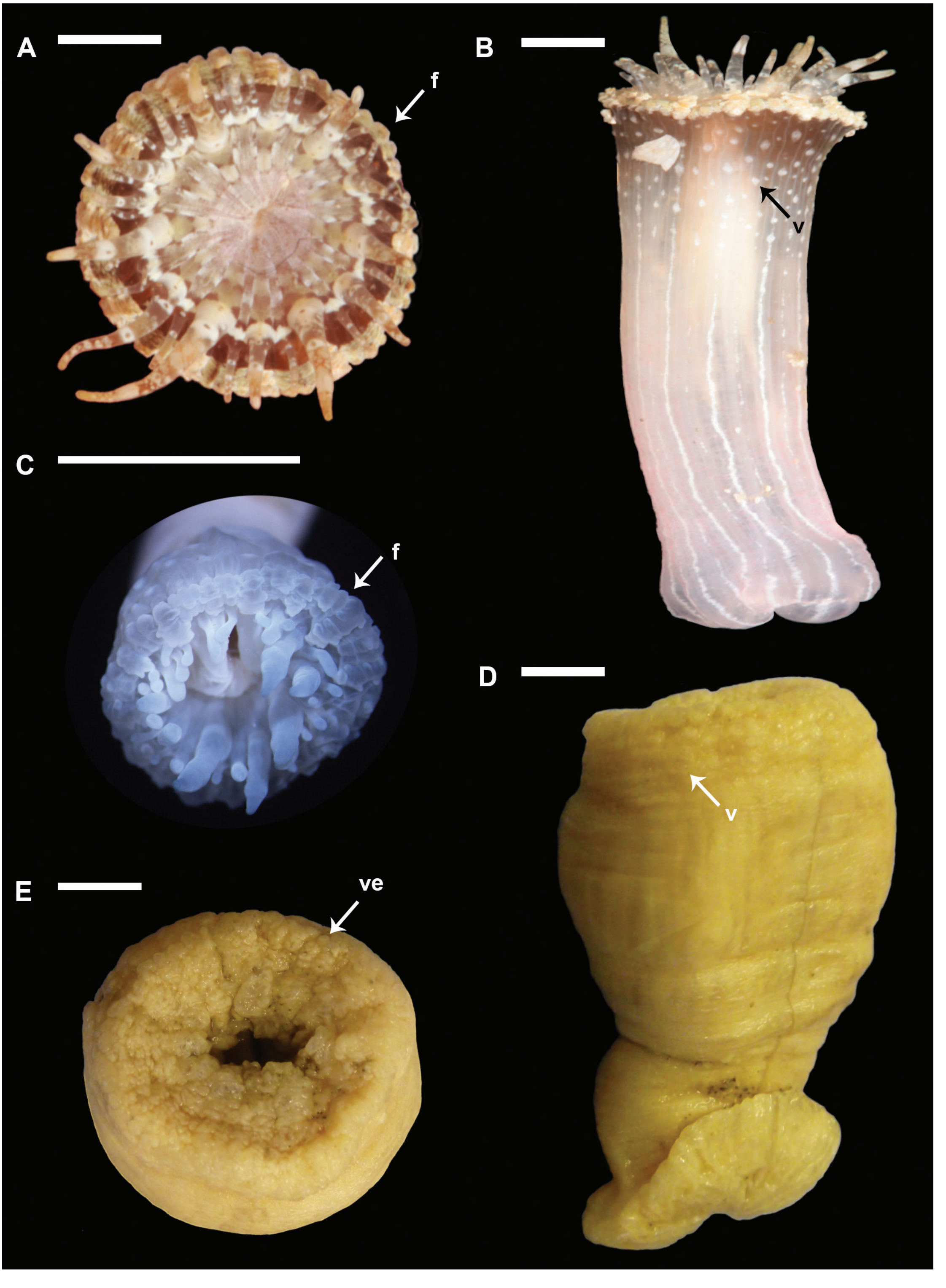
Figures 7–9, tables 1, 3

Oulactis californica McMurrich, 1893.
Non *Asteractis concinnata* (Drayon in Dana, 1846): Pax 1912.
Phyllactis californica (McMurrich, 1893): Stephenson, 1922.
(?)*Phyllactis bradleyi* (Verrill, 1869): Carlgren, 1951.
(?)*Phyllactis concinnata* (Drayon in Dana, 1846): Carlgren, 1951.
Actinostella californica (McMurrich, 1893): Häussermann, 2003.
Actinostella californica (McMurrich, 1893): pro parte Barragán, 2015; Barragán, 2019; Barragán et al., 2019.

Differential Diagnosis: *Actinostella* with three cycles of mesenteries, first and second perfect, third imperfect. All mesenteries fertile including directives. Column and marginal ruff only with basitrichs and no *p*-mastigophores A.

Examined Material: *Actinostella californica*: AMNH_IZC 00361339, AMNH_IZC 00361340, AMNH_IZC 00361341, AMNH_IZC 00361342, AMNH_IZC 00361343, AMNH_IZC 00361344, AMNH_IZC 00361345, AMNH_IZC 00361346, AMNH_IZC 00361347, AMNH_IZC 00361348, AMNH_IZC 00361349, AMNH_IZC 00361350, AMNH_IZC 00361351, AMNH_IZC 00361352, AMNH_IZC 00361353, AMNH_IZC 00361354; USNM 1606851; USNM 17812 (syntype). See table 1 for material details.

Description: *External anatomy* (fig. 7): Well-developed pedal disc, to 25 mm diameter. Column elongate, to 65 mm height and 52 mm diameter, with 48 longitudinal rows of verrucae distally in each endo- and exocoel. Marginal ruff with rows of vesicles. Oral disc, to 38 mm


A
f
B
v
C
f
D
v
E
ve

diameter. Fosse deep. Tentacles, 48, arranged in four cycles; simple, smooth, all of similar length, to 16 mm. Mesenterial insertions visible in pedal disc and column.

Internal anatomy (fig. 8): Same number of mesenteries distally and proximally. Twenty-four pairs of mesenteries hexamerously arranged in three cycles (6 + 6 + 12 = 24). First and second cycles perfect, third imperfect (fig. 8B). All mesenteries fertile including directives (fig. 8B). Two pairs of directives attached to two clearly distinct siphonoglyphs. Gonochoric, developed oocysts 0.08–0.18 mm in diameter (fig. 8E) in specimens collected in May and November 2013, and March 2016. Retractor muscles strong, diffuse to restricted; variability within studied specimens. Parietobasilar muscles well developed, with short free mesogleal lamella in juveniles, longer in adults (fig. 8F). Basilar muscles well developed, processes short and thin (fig. 8G). Endodermal marginal sphincter muscle weakly circumscribed (fig. 8A, C). Longitudinal muscles of tentacles ectodermal (fig. 8D). Zooxanthellae present in tentacles and marginal ruff.

Color (fig. 7): Variable in live specimens. Specimens with pedal disc and column pinkish, beige, or opaque orange; verrucae darker than column. Oral disc olive green with white radial lines. Marginal ruff olive green with lighter stripes and a brown ring closer to the mouth. Mouth light pink. Tentacles translucent greenish, brownish, or reddish, with white bases; white spots with brown dots along entire tentacles. Preserved material beige, oral disc and marginal ruff lighter.

Cnidom (fig. 9); Basitrichs, basitrichs S, *b*-mastigophores, *p*-mastigophores A, *p*-mastigophores B1 and spirocysts. Sizes and distribution in table 3.

Geographic and Bathymetric Distribution and Natural History: *Actinostella californica* can be found in the Pacific Ocean from Mexico to Panama (McMurrich, 1893; Carlgren, 1951). Although Carlgren (1951) cited *A. bradleyi* (= *A. californica* pro parte in this study) in the Pearl Islands (Panama) he did not examine specimens from this locality, but he was referring to Verrill's original description of *A. bradleyi*. Häussermann (2003) and Fautin (2016) considered the citation of *Asteractis concinnata* from Peru by Pax (1912) to correspond to *A. californica*; however, Pax (1912) described his Peruvian specimens having 4–5 cycles of tentacles and without zooxanthellae, and thus we consider those specimens to be *Oulactis concinnata*. In Mexico, *A. californica* can be found in the Pacific side (west of Baja Peninsula) in Magdalena Bay, and in the Gulf of California it can be found in La Paz Bay and Concepcion Bay. In addition, this species was collected in Panama in the Pearl Islands. The specimens were found burrowed in sand, attached to a rock or shell, buried, or hidden in rock crevices with the marginal ruff above the substratum. They are often found in the intertidal to up to 12 meters in La Paz Bay (Gulf of California; see Barragán et al., 2019).

Remarks: *Actinostella californica* is distinguished from congeners by the combination of having three cycles of fertile mesenteries, first and second cycles perfect, and only basitrichs in the marginal ruff and column (table 6). It was initially described by McMurrich (1893) as *Oulactis*

FIG. 7. External anatomy of *Actinostella californica* (McMurrich, 1893). **A,** Oral view of live semiexpanded specimen; **B,** lateral view of live specimen; notice row of distal verrucae (v); **C,** oral view of live semiexpanded specimen showing the marginal ruff (f); **D,** lateral view of preserved syntype USNM 1776; **E,** oral view of preserved syntype USNM 1776 showing the vesicles (ve). Abbreviations: **f,** marginal ruff; **v,** verrucae; ve, vesicles. Images in A and B courtesy of V. Häussermann. Scale bars: **A–D,** 5 mm.

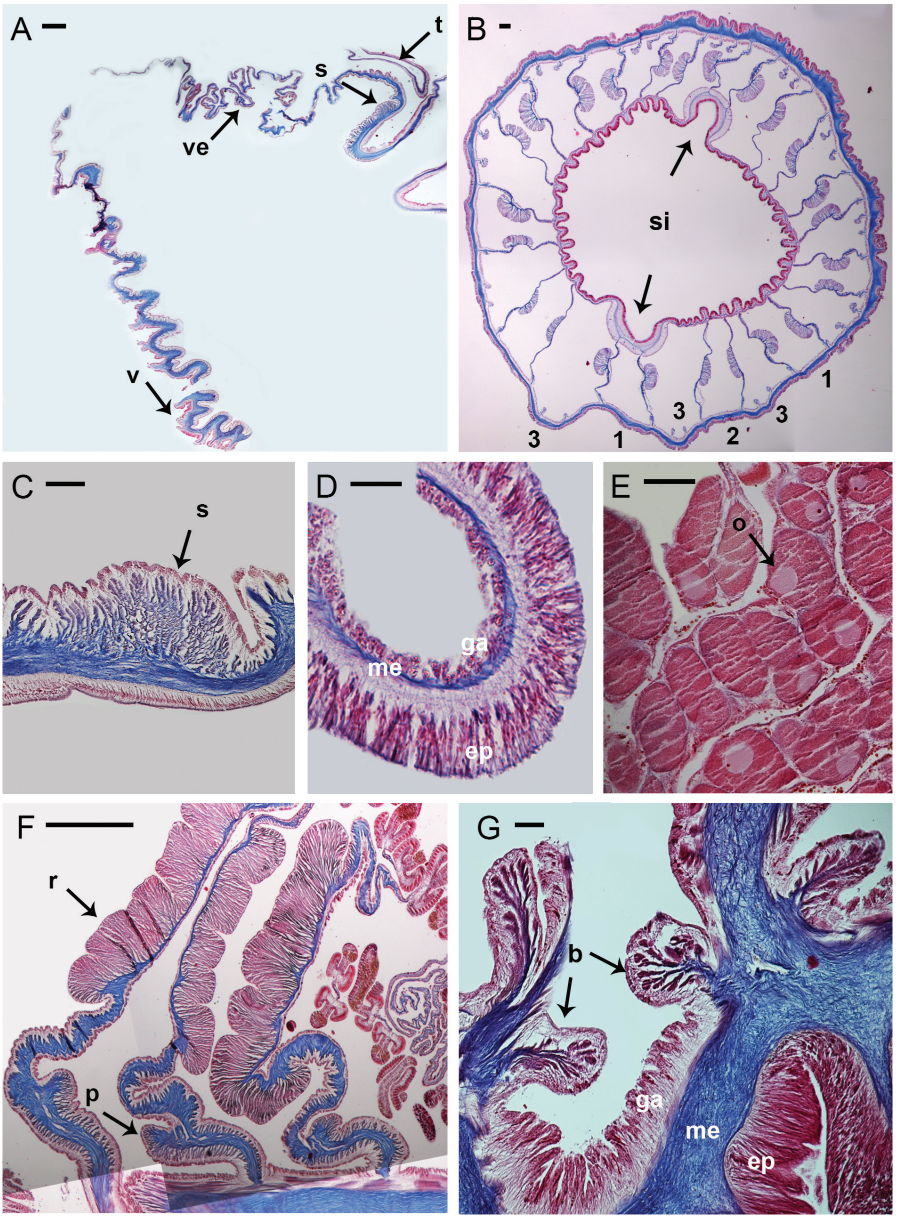


FIG. 8. Internal anatomy of *Actinostella californica* (McMurrich, 1893). **A,** longitudinal section of the distal column showing distal verrucae (v), vesicles (ve) in the marginal ruff, marginal sphincter muscle (s), and the fosse; **B,** cross section at the actinopharynx level showing cycles of mesenteries and siphonoglyphs (si); numbers between pairs of mesenteries indicate the corresponding cycle; **C,** detail of the endodermal marginal sphincter muscle; **D,** cross section of a tentacle showing the ectodermal longitudinal muscles; **E,** detail of developing oocytes (o); **F,** detail of a cross section showing the retractor (r) and parietobasilar (p) muscles; **G,** cross section of proximal end showing the basilar muscles (r). Abbreviations: **b,** basilar muscles; **ep,** epidermis; **ga,** gastrodermis; **me,** mesoglea; **o,** oocytes; **p,** parietobasilar muscle; **r,** retractor muscle; **s,** sphincter; **si,** siphonoglyph; **t,** tentacle; **v,** verrucae; **ve,** vesicles. Scale bars: **A, B, F,** 0.5 mm; **C–E, G,** 0.1 mm.

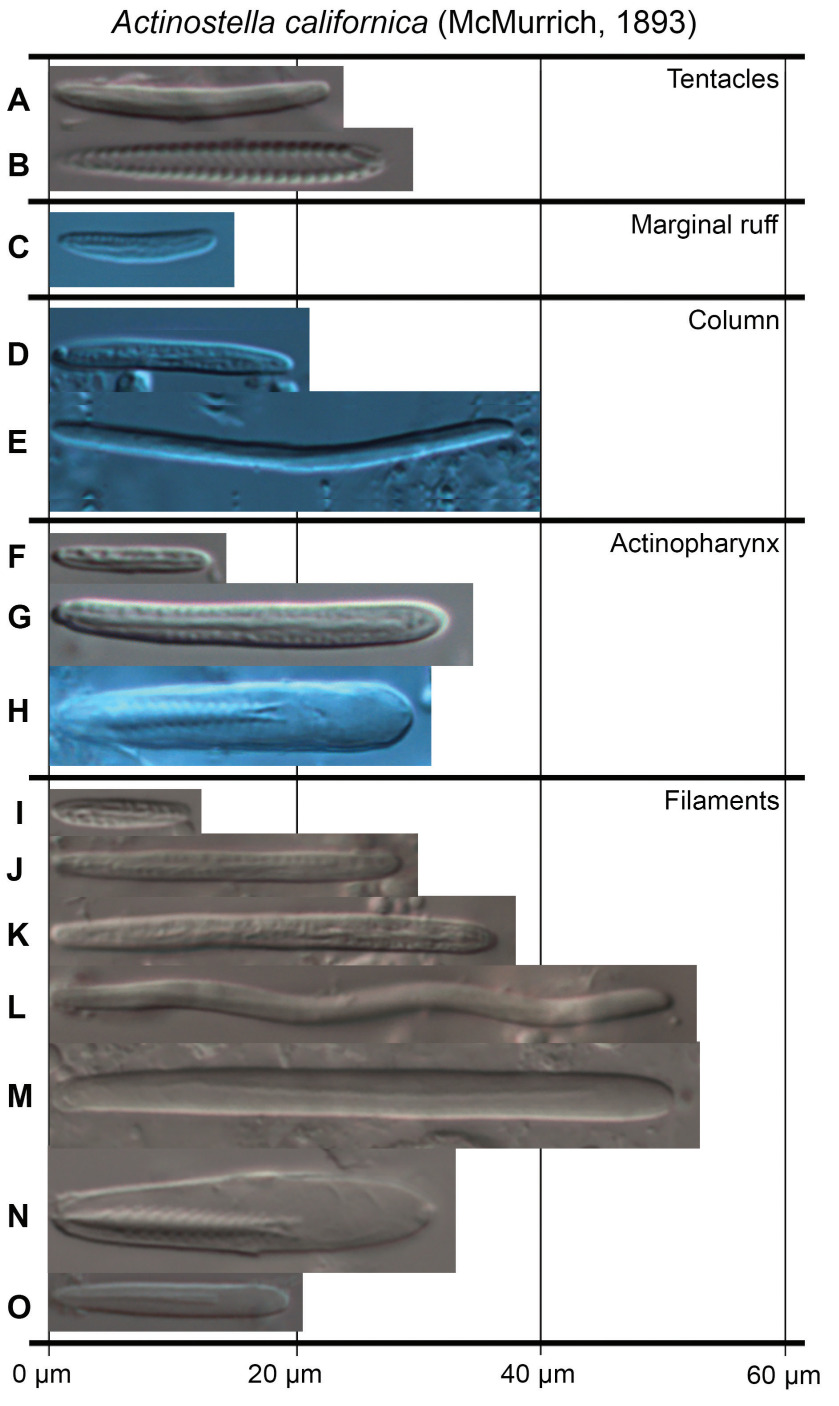


FIG. 9. Cnidae of *Actinostella californica* (McMurrich, 1893). **A, C, D, F, G, I, J, K,** basitrichs; **B,** spirocysts; **E, L,** basitrichs S; **H, N,** *p*-mastigophore A; **M,** *b*-mastigophore; **O**, *p*-mastigophore B1.

TABLE 3. Size ranges and distribution of cnidae of *Actinostella californica* (McMurrich, 1893). Data in parenthesis of *Phyllactis concinnata* (Drayton) from Carlgren (1951). N, Total number of capsules measured; M, Ratio of number of specimens in which each cnidae was found to number of specimens examined; F, Frequency, +++ = very common, ++ = common, + = rather common, --- = sporadic; SD, standard deviation; ND, no data; NF, not found. Sizes in micrometers. Letters in parenthesis after categories correspond to images in figure 9. (*) Category named as basitrichs by Carlgren (1951).

Tissue / Categories	M	N	F	Range of length and width of capsules	Mean ± SD	USNM 17812
TENTACLES						
Basitrichs (A)	3/3	43	+++	15.9–26.8 × 2.2–2.8	21.6±2.5 × 2.5±0.2	(21–33.8 × 2.5–2.8) 24.0–30.0 × 2.0–3.0
Spirocysts (B)	3/3	50	+++	10.1–23.9 × 1.6–3.1	17.0±4.8 × 2.3±0.4	(ND) 18.0–34.0 × 2.0–3.0
MARGINAL RUFF						
Basitrichs (C)	4/4	107	+++	07.8–15.4 × 1.6–2.4	12.3±1.2 × 2.0±0.2	(10–14 × 1.8–2.3) 10.0–14.0 × 1.8–2.3
COLUMN						
Basitrichs 1 (D)	5/5	100	+++	08.0–20.4 × 1.8–2.5	15.1±3.3 × 2.1±0.2	(12.7–18.3 × 2.2–2.5) 09.0–21.4 × 1.7–2.2
Basitrichs S (E)	5/5	47	++	24.0–37.1 × 1.3–2.3	31.9±3.2 × 1.8–0.3	(ND) / NF
ACTINOPHARYNX						
Basitrichs 1 (F)	4/4	39	+++	08.8–16.9 × 1.7–2.8	11.6±2.4 × 2.1±0.2	(ND) 14.0–16.0 × 2.0–2.0
Basitrichs 2 (G)	4/4	69	+++	18.9–32.6 × 1.8–4.0	26.6±2.8 × 3.1±0.4	(19.7–32.4 × 2.8–3.5) 28.0–31.0 × 3.0–3.0
p-mastigophores (H)	4/4	40	++	22.0–29.0 × 4.4–6.8	25.3±1.7 × 5.7±0.7	(21.0–31.8 × 4.0–6.3) 23.0–28.0 × 5.0–6.0
FILAMENTS						
Basitrichs 1 (I)	4/4	57	++	07.6–11.9 × 1.6–2.3	09.9±1.4 × 2.0±0.2	(10.0 × 2.5) / NF
Basitrichs 2 (J)	4/4	36	+++	12.0–19.7 × 1.0–2.6	16.3±5.9 × 2.1±0.3	(ND) 10.0–13.0 × 2.0–2.0
Basitrichs 3 (K)	4/4	38	+	20.0–35.7 × 1.8–3.0	25.2±5.8 × 2.4±0.3	(ND) / NF
Basitrichs S (L)	4/4	40	++	29.6–49.5 × 1.6–2.7	39.1±3.8 × 2.3±0.2	(ND) / NF
b-mastigophores (M)	4/4	51	++	33.7–48.9 × 3.0–4.4	40.9±3.6 × 3.6±0.3	(31.0–49.3 × 3.0–4.2)* 37.0–45.0 × 4.0–5.0
p-mastigophores A (N)	4/4	55	++	21.8–30.6 × 4.2–6.1	25.4±1.5 × 5.3±0.4	(21.31.8 × 4.2–5.6) 23.0–29.0 × 5.0–6.0
p-mastigophores B1 (O)	3/4	39	---	14.7–22.3 × 2.3–3.2	17.2±1.3 × 2.7–0.3	(ND) / NF

californica without any mention of the cnidom (a common practice in those days). Later, Carlgren (1951) redescribed *Phyllactis bradleyi* and *P. concinnata* (Drayton in Dana, 1846; current valid name: *Oulactis concinnata*) based on specimens from the Gulf of California, emphasizing they might need to be revised. Carlgren (1951) mentioned only the number of mesenteries (24) without describing their arrangement for the two specimens of *P. bradleyi* from the Gulf of California. The presence of only three cycles of mesenteries and the brief description of the cnidom suggest the two specimens might be *A. californica*. However, we cannot state confidently that the specimens of *P. bradleyi* from the Gulf of California redescribed by Carlgren (1951) are synonyms of *A. californica* because *p*-mastigophores A are easily overlooked unless surveying thoroughly; thus, we report this citation with a question mark (see synonymy list).

We agree with Haüssermann (2003) that Carlgren's (1951) redescription of seven specimens from the Gulf of California as *Phyllactis concinnata* actually corresponds to specimens of *Actinostella californica*. Like Haüssermann (2003), we think that *Oulactis concinnata* and *A. californica* (both previously described as *Phyllactis*) are clearly different species, with *O. concinnata* having many more tentacles and mesenteries (up to 400 tentacles), often acrorhagi and fighting tentacles (and thus holotrichs) but no zooxanthellae, whereas *A. californica* has only up to 48 tentacles and zooxanthellae, but lacks acrorhagi (see Haüssermann, 2003). The only attribute from Carlgren's (1951) treatment that does not fit *A. californica* is the presence of three perfect cycles of mesenteries: in the type material from McMurrich (1893) and the other 22 specimens we studied, the third cycle of mesenteries is imperfect. We observed in the studied specimens longitudinal lines of tissue (corresponding to the third cycle of mesenteries) attached to the actinopharynx side distally, which might be interpreted as broken perfect mesenteries; it is highly unlikely that this artifact occurred in every single specimen examined, and most feasible that Carlgren's (1951) observation might have been an artifact of observing the mesenteries distally. Consequently, we consider the third cycle in *A. californica* as imperfect. Alternatively, the specimens from the Gulf of California revised by Carlgren (1951) might have been juveniles of *A. bradleyi* with only three cycles of mesenteries developed (similar to the holotype of the species). Although the absence of *p*-mastigophores A in the marginal ruff and column suggests they were specimens of *A. californica*, we still consider this attribution an open question because it is also possible that Carlgren (1951) might have overlooked this cnida: we therefore reflect this in the synonymy list.

Actinostella digitata (McMurrich, 1893)

Figures 10–12, tables 1, 4

Cradactis digitata McMurrich, 1893.
Phyllactis digitata (McMurrich, 1893): Carlgren, 1949.
Actinostella digitata (McMurrich, 1893): Häussermann, 2003.

Differential Diagnosis: *Actinostella* with three cycles of mesenteries, all perfect and fertile, including directives. Marginal ruff with *p*-mastigophores A and basitrichs; column only with basitrichs.

Examined Material: *Actinostella digitata:* MACN-In 43521; *Cradactis digitata*: USNM 17776 (syntypes). See table 1 for material details.

Description: *External anatomy* (fig. 10): Well-developed pedal disc, to 35 mm diameter. Column elongate, to 70 mm height and 30 mm diameter, with 48 longitudinal rows of verrucae distally in each endo- and exocoel. Marginal ruff with rows of vesicles. Oral disc to 17 mm diameter. Fosse deep. Tentacles, 48, arranged in four cycles; simple, smooth, all of similar length, to 12 mm, with terminal pore. Mesenterial insertions not visible in pedal disc or column.

Internal anatomy (fig. 11): Same number of mesenteries distally and proximally. Twenty-four pairs of mesenteries hexamerously arranged in three cycles (6 + 6 +12 = 24). All cycles perfect. All mesenteries fertile including directives. Two pairs of directives attached to two clearly distinct siphonoglyphs (fig. 11B). Gonochoric, developed spermatic cysts to 0.15 mm in diameter (fig. 11E) in specimen collected in February 2010. Retractor muscles strong, band-like, restricted. Parietobasilar muscles well developed, with short, free mesogleal lamella (fig. 11F). Basilar muscles poorly developed, processes short and thin (fig. 11G). Endodermal marginal sphincter muscle strong, circumscribed with thin central lamella of mesoglea (fig. 11A). Longitudinal muscles of tentacles ectodermal (fig. 11D). Zooxanthellae present in tentacles and marginal ruff.

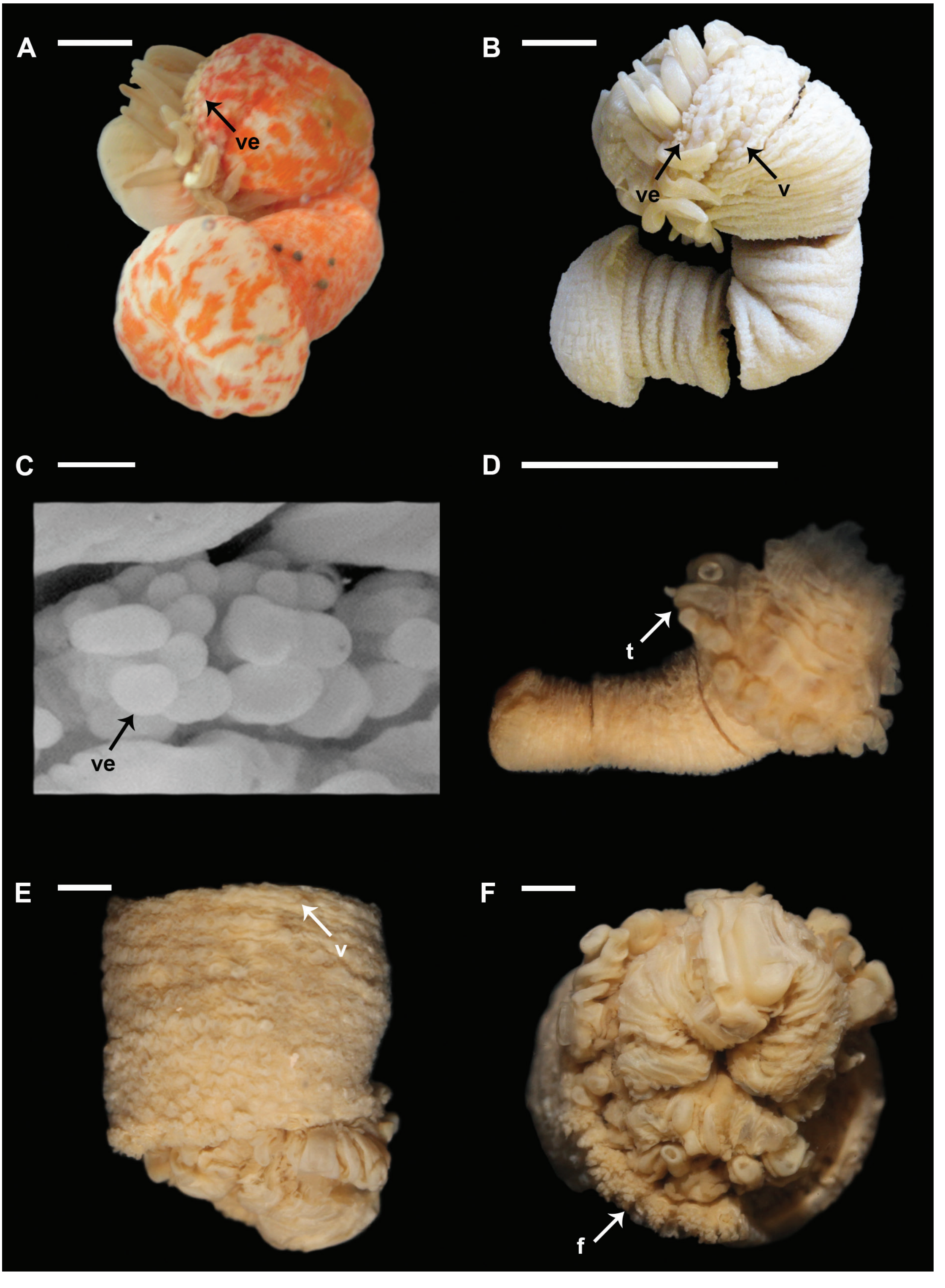
Color (fig. 10): Newly collected specimen from Chubut (Argentina) with beige pedal disc with irregular bright orange spots. Column orange over a beige base color, with verrucae darker orange. Oral disc beige with darker radial lines. Marginal ruff same color as column with beige vesicles. Tentacles translucent brownish, with darker longitudinal lines. Preserved material beige, oral disc and marginal ruff lighter.

Cnidom (fig. 12): Basitrichs, *b*-mastigophores, *p*-mastigophores A, *p*-mastigophores B1, and spirocysts. Sizes and distribution in table 4.

Geographic and Bathymetric Distribution and Natural History: *Actinostella digitata* can be found in the southern Atlantic Ocean off the coast of Argentina (McMurrich, 1893). This is the second record of the species, and it was collected in Paraná Beach, Chubut, southward to the type locality (La Plata River) in Argentina. The single specimen from Paraná Beach was found attached to a rolling stone with only the oral disc above the substratum. Despite working in the area for several years, this was the first and only time the collectors noticed this species. It can be found from 5 to 10 meters (Paraná Beach).

Remarks: *Actinostella digitata* is distinguished by the combination of having three cycles of perfect and fertile mesenteries and only small basitrichs in the column; it shares having *p*-mastigophores A and basitrichs in the marginal ruff with *A. flosculifera* and *A. bradleyi*. It was originally described by McMurrich (1893) as *Cradactis digitata*. We analyzed the type specimens and one newly collected specimen from Paraná Beach (in Chubut, Argentina),

FIG. 10. External anatomy of *Actinostella digitata* (McMurrich, 1893). **A,** lateral view of live semiexpanded specimen; **B,** lateral view of preserved specimen; **C,** detail of vesicles (ve) in the marginal ruff; **D,** lateral view of preserved syntype (USNM 1776); **E,** lateral view of preserved syntype (USNM 1776) showing rows of verrucae (v) in distal column; **F,** oral view of preserved syntype (USNM 1776) showing the marginal ruff (f). Abbreviations: **f,** marginal ruff; **v,** verrucae; **ve,** vesicles. Scale bars: **A, B, D,** 10 mm; **E, F,** 5 mm; **C,** 0.1 mm.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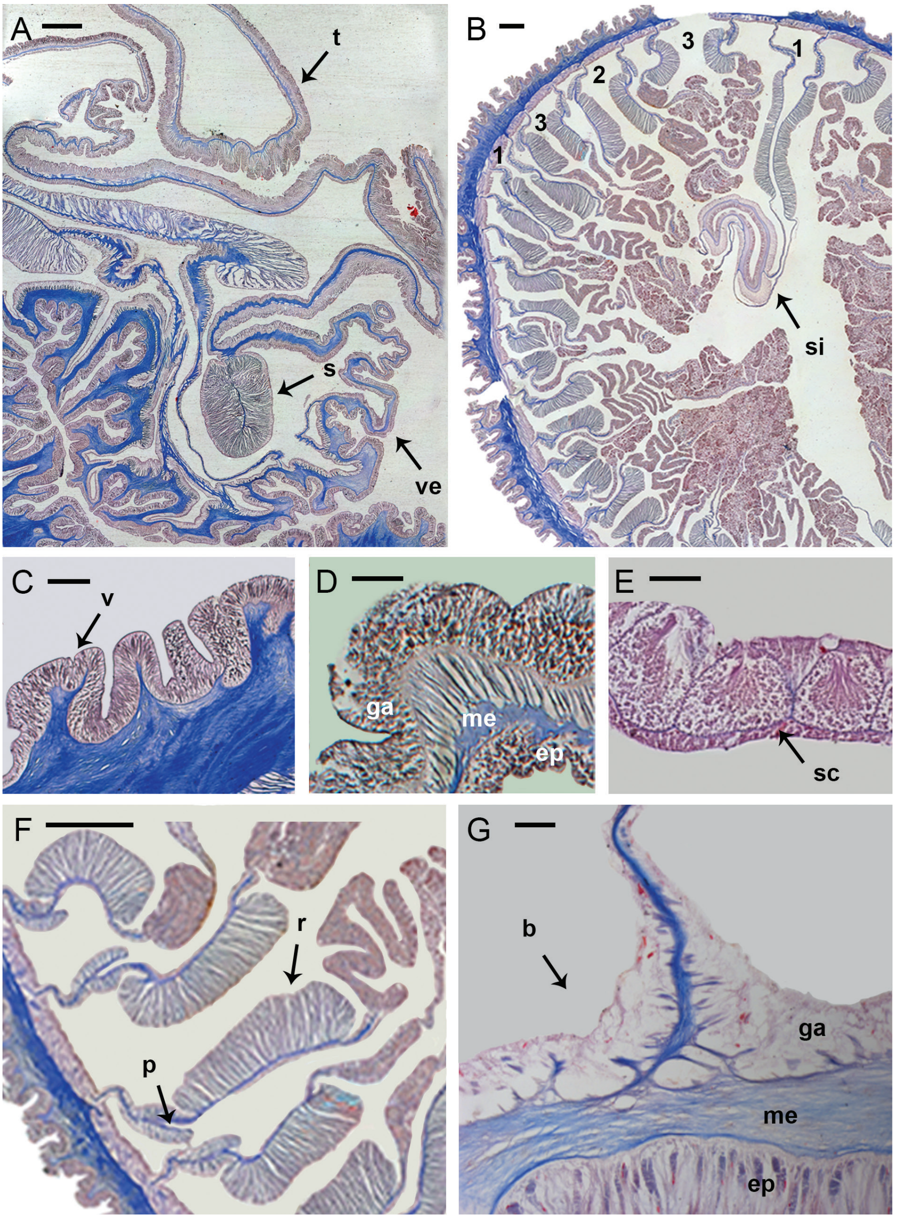


FIG. 11. Internal anatomy of *Actinostella digitata* (McMurrich, 1893). **A,** longitudinal section of the distal column showing distal vesicles (ve) in the marginal ruff, marginal sphincter muscle (s), and the fosse; **B,** cross section proximal to the actinopharynx level showing cycles of mesenteries, and the siphonoglyph (si); numbers between pairs of mesenteries indicate the corresponding cycle; **C,** detail of verrucae (v) in distal column; **D,** cross section of a tentacle showing ectodermal longitudinal muscles; **E,** detail of developing spermatic cysts (sc); **F,** detail of a cross section showing the retractor (r) and parietobasilar (p) muscles; **G,** cross section of proximal end showing weak basilar muscles (b). Abbreviations: **b,** basilar muscles; **ep,** epidermis; **ga,** gastrodermis; **me,** mesoglea; **sc,** spermatic cysts; **p,** parietobasilar muscle; **r,** retractor muscle; **s,** sphincter; **si,** siphonoglyph; **t,** tentacle; **v,** verrucae; **ve,** vesicles. Scale bars: **A, F,** 5mm; **B–E, G,** 1 mm.

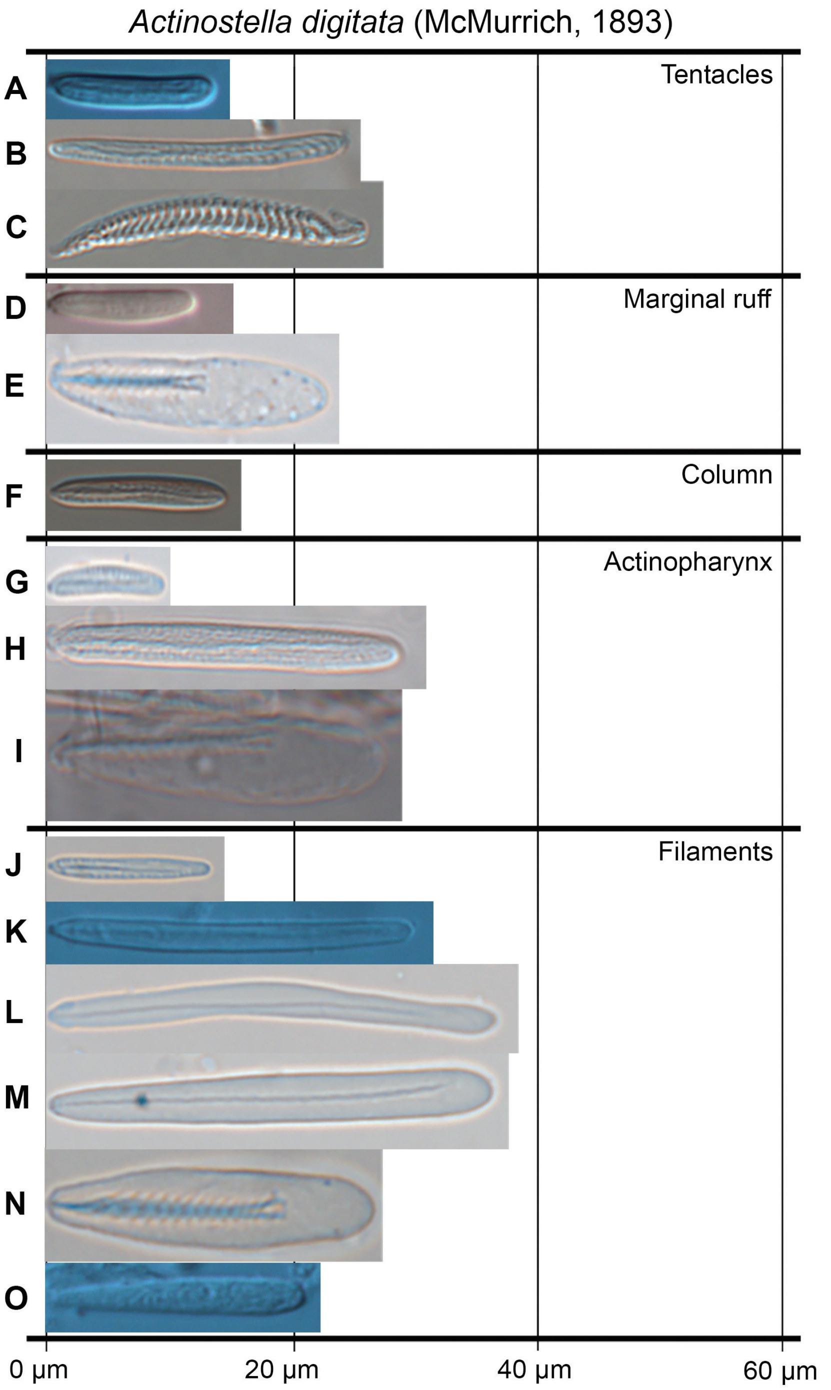


FIG. 12. Cnidae of *Actinostella digitata* (McMurrich, 1893). **A, B, D, F, G, H, J, K,** basitrichs; **C,** spirocysts; **L,** basitrichs S; **E, I, N,** *p*-mastigophore A; **M,** *b*-mastigophore; **O,** *p*-mastigophore B1. Capsules depicted in K and O were found only in type specimens.

TABLE 4. Size ranges and distribution of cnidae of *Actinostella digitata* (McMurrich, 1893). Data in parenthesis from Carlgren (1934). N, Total number of capsules measured; M, Ratio of number of specimens in which each cnidae was found to number of specimens examined; F, Frequency, +++ = very common, ++ = common, + = rather common, --- = sporadic; SD, standard deviation, ND, no data; NF, not found. Sizes in micrometers. Letters in parenthesis correspond to images in figure 12.

Tissue / Categories	M	N	F	Range of length and width of capsules	Mean ± SD	USNM 17776
TENTACLES						
Basitrichs 1 (A)	1/1	7	+	11.5–15.7 × 2.0–2.3	14.4± 1.4 × 2.3 ± 0.3	(ND) 14.0–15.0 × 2.0–3.0
Basitrichs 2 (B)	1/1	40	+++	25.0–29.8 × 2.0–2.7	27.3± 1.1 × 2.3 ± 0.4	(25.0–28.0 × 2.5) 17.0–26.9 × 2.0–4.5
Spirocysts (C)	1/1	42	+++	15.0–30.0 × 1.5–3.5	22.5± 4.5 × 2.6 ± 0.5	(17.0–34.0 × 2.0–3.0) 24.0–29.4 × 2.8–4.0
MARGINAL RUFF						
Basitrichs (D)	1/1	41	+++	11.7–15.0 × 1.7–2.7	12.8± 0.7 × 2.1 ± 0.2	(ND) 11.0–15.0 × 2.0–3.0
p-mastigophores A (E)	1/1	2	---	23.4–24.4 × 5.5–7.9	–	(ND) 15.2–23.1 × 3.0–5.4
COLUMN						
Basitrichs (F)	1/1	39	+++	12.1–18.6 × 1.9–3.5	15.5± 1.3 × 2.6 ± 0.3	(11.0–12.0 × 2.0) 11.0–15.0 × 2.0–3.1
ACTINOPHARYNX						
Basitrichs 1 (G)	1/1	1	---	07.3 × 0.8	–	(ND) 10.1–13.0 × 1.9–2.9
Basitrichs 2 (H)	1/1	38	+++	17.1–33.3 × 2.7–4.3	27.4± 4.1 × 3.5 ± 0.4	(24.0–31.0 × 3.0) 22.2–32.1 × 2.0–3.6
p-mastigophores A (I)	1/1	8	+	21.2–27.0 × 5.1–7.9	25.1± 1.9 × 6.4 ± 0.9	(ND) 28.2–29.0 × 5.9–6.1
FILAMENTS						
Basitrichs 1 (J)	1/1	14	+	15.1–22.2 × 2.2–2.9	18.5± 2.3 × 2.5 ± 0.2	(ND) 11.8–14.5 × 1.9–2.3
Basitrichs 2 (K)	–	–	–	NF	–	(ND) 23.7–29.9 × 2.0–2.6
Basitrichs S (L)	1/1	4	---	36.9–43.9 × 2.4–3.3	41.0± 3.2 × 2.7 ± 0.4	(ND) / 32.2 × 1.9
b-mastigophores (M)	1/1	29	++	33.7–40.6 × 3.9–5.3	38.0± 1.9 × 4.4 ± 0.3	(ND) 34.5–36.7 × 3.7–3.9
p-mastigophores A (N)	1/1	24	++	21.2–28.0 × 4.5–8.3	24.8± 1.7 × 6.3 ± 0.8	(ND) 24.9–29.0 × 4.4–6.3
p-mastigophores B1 (O)	–	–	–	NF	–	(ND) 19.5–19.8 × 2.6–2.8

southward of the type locality in La Plata River (Argentina). In the type specimens, the perfect second cycle was hard to discern because of the state of preservation; Carlgren (1934) had analyzed the same specimens and suggested that the three cycles might be perfect, a characteristic we confirmed in the newly collected specimen, which clearly has the three cycles perfect and fertile, including directives.

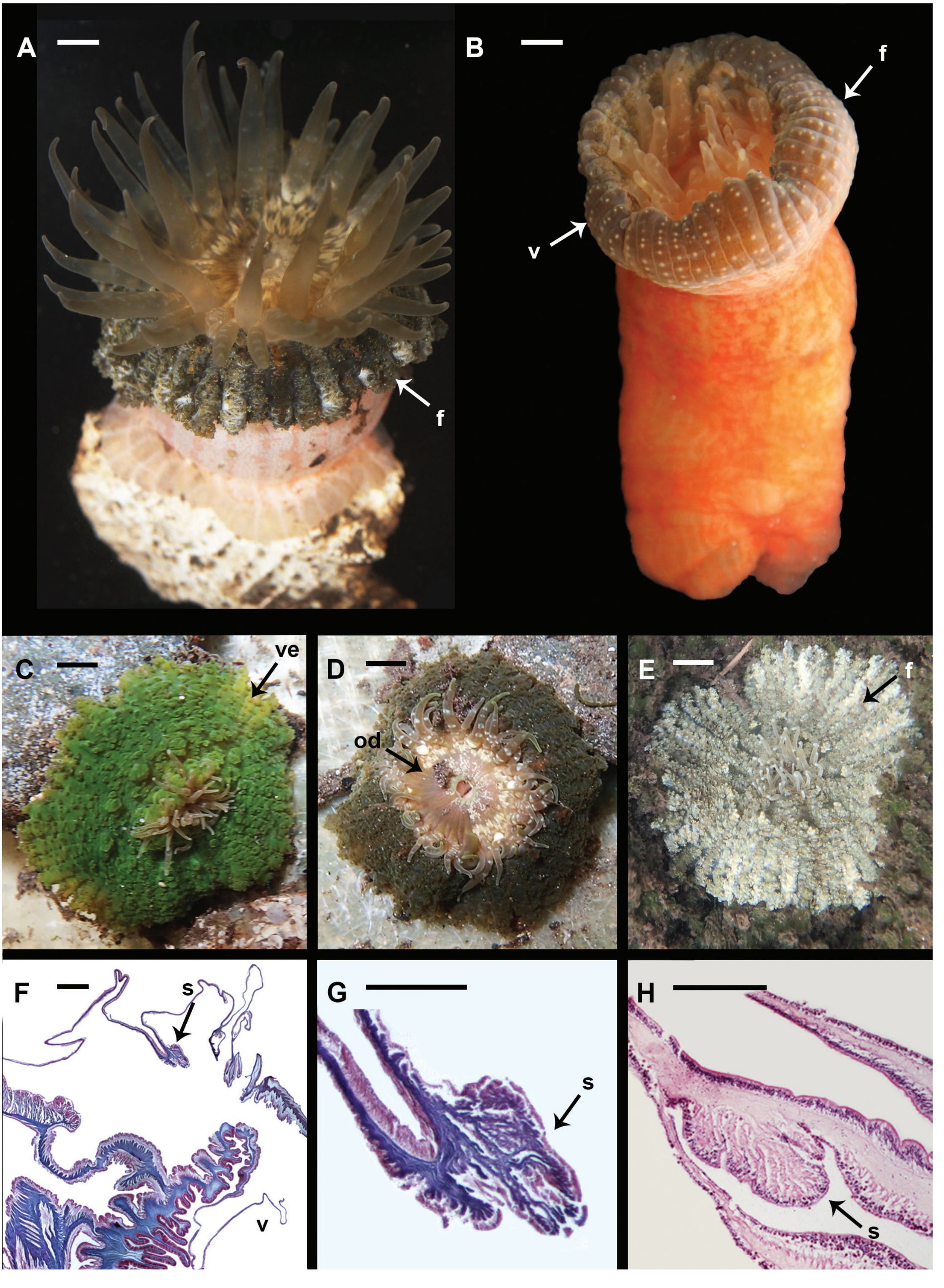
Actinostella flosculifera (Le Sueur, 1817)

Figures 13–14, tables 1, 5

Actinia flosculifera Le Sueur, 1817.
Oulactis flosculifera [no author]: Milne Edwards, 1857.
Oulactis flosculifera (Lesueur): Milne Edwards, 1857.
Oulactis flosculifera (Le Sueur, 1817): Duchassaing and Michelotti, 1860.
Actinostella formosa Duchassaing, 1850.
Asteractis formosa (Duchassaing, 1850): Verrill, 1899.
Oulactis formosa Duchassaing and Michelotti, 1860.
Asteractis flosculifera (Le Sueur, 1817): Verrill, 1899.
Cradactis fasciculata (McMurrich, 1889): Haddon, 1898.
Evactis flosculifera (Le Sueur, 1817): Andres, 1883.
Oulactis fasciculata McMurrich, 1889.
Oulactis foliosa Andres, 1883.
Actinactis [sic] *flosculifera*: Verrill, 1900.
Actinostella flosculifera (Le Sueur, 1817): McMurrich, 1905.
Phyllactis flosculifera (Le Sueur, 1817): Stephenson, 1922.
Oulactis conquilega Duchassaing and Michelotti, 1860.
Actinostella conchilega (Duchassaing and Michelotti, 1860): McMurrich, 1905.
Asteractis conquilega (Duchassaing and Michelotti, 1860): Verrill, 1899.
Phyllactis conchilega (Duchassaing and Michelotti, 1860): Stephenson, 1922.
Phyllactis conquilega (Duchassaing and Michelotti, 1860): Carlgren, 1949.
Phyllactis conquilegia [sic] (Duchassaing and Michelotti, 1860): Voss et al., 1969.
Metridium prætextum Couthouy in Dana, 1846.
Asteractis, n. sp.: Duerden, 1897.
Asteractis expansa Duerden in McMurrich, 1898.
Oulactis radiata Duchassaing and Michelotti, 1860.
Lophactis radiata (Duchassaing and Michelotti, 1860): Andres, 1883.
Actinostella radiata (Duchassaing and Michelotti, 1860): McMurrich, 1905.
Phyllactis radiata (Duchassaing and Michelotti, 1860): Stephenson, 1922.

Differential Diagnosis: *Actinostella* with three cycles of mesenteries, first and second perfect, third imperfect; all fertile, including directives. Marginal ruff and column with *p*-mastigophores A and basitrichs.

Examined Material: *Actinostella flosculifera*: AMNH Cat.Cnidaria 587, AMNH Cat. Cnidaria 694, AMNH Cat.Cnidaria 741, AMNH Cat.Cnidaria 1283, AMNH Cat.Cnidaria 1324,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AMNH Cat.Cnidaria 1330, AMNH Cat.Cnidaria 1352, AMNH Cat.Cnidaria 3585, AMNH Cat.Cnidaria 5308, USNM 1606852, USNM 1606853, USNM 1606854, USNM 1606855, USNM 1606856, USNM 1606857, USNM 1606858, USNM 1606859, USNM 1606860, USNM 1606861, USNM 1606862, USNM 1606863; MZUSP 8405; *Phyllactis conquilega* [= *A. flosculifera*]: SMNH-1170 (holotype). See table 1 for material details.

Description. *External anatomy* (fig. 13): Well-developed pedal disc, to 29 mm diameter. Column, to 65 mm height and 38 mm diameter, with 48 longitudinal rows of verrucae distally in each endo- and exocoel. Marginal ruff with rows of vesicles. Oral disc, to 34 mm diameter. Fosse deep. Tentacles, 48, arranged in four cycles; simple, smooth, all of similar length, to 13 mm. Mesenterial insertions visible in oral disc, column, and pedal disc.

Internal anatomy (fig. 13): Same number of mesenteries distally and proximally. Twenty-four pairs of mesenteries hexamerously arranged in three cycles (6 + 6 + 12 = 24). First and second cycles perfect. All mesenteries fertile, including directives. Two pairs of directives attached to two clearly distinct siphonoglyphs. Gonochoric, developed oocysts 0.18–0.29 mm in diameter in specimens collected in May 2010, June 1966, and November 1899. Retractor muscles restricted and strong. Parietobasilar muscles well developed, with free mesogleal lamella. Basilar muscles well developed, processes short and thin. Endodermal marginal sphincter muscle weakly circumscribed, without central mesogleal lamella (fig. 13F–I). Longitudinal muscles of tentacles ectodermal. Zooxanthellae present in tentacles and marginal ruff.

Color (fig. 13): Variable in live specimens. Specimens from Panama with pedal disc and column pinkish, beige, or opaque orange; verrucae darker than column. Oral disc brownish with white radial lines. Marginal ruff white, green, or brown, with lighter stripes and a brownish ring near the mouth. Mouth light brownish. Tentacles translucent white, brownish, or reddish with lighter spots and dots along the entire aboral side of tentacles. Preserved material beige, oral disc, and marginal ruff lighter.

Cnidom (fig. 14): Basitrichs, basitrichs S, *b*-mastigophores, *p*-mastigophores A, *p*-mastigophores B1, and spirocysts. Sizes and distribution in table 5.

Geographic and Bathymetric Distribution and Natural History: *Actinostella flosculifera* is distributed along the entire Caribbean Sea (from Bermuda to the Lesser Antilles), Gulf of Mexico, Colombia, and the South Atlantic off the coast of Brazil (see Schlenz and Belém, 1992; González-Muñoz et al., 2012, 2013; Durán-Fuentes et al., 2022; 2023). The species has been also reported in the east Atlantic in the Cameroon, Canary Islands, Cape Verde Island, and Senegal (Ocaña and den Hartog, 2002; Ocaña et al., 2015) and the Gulf of Guinea (Wirtz, 2003), but these records need to be checked to confirm species-level identification. Individuals in Bermuda have been described as viviparous (Cairns and den Hartog, 1986).

←

FIG. 13. External and internal anatomy of *Actinostella flosculifera* (Le Sueur, 1817). **A,** lateral view of living relaxed specimen in aquarium, **B,** lateral view of semirelaxed live specimen; notice rows of distal verrucae (v); **C-E,** oral view of specimens in the field, burrowed with only marginal ruff above the substratum; **F,** longitudinal section of the distal column showing the position of the endodermal marginal sphincter muscle (s); **G, H,** detail of variability of the endodermal marginal sphincter muscle in two specimens. Abbreviations: **f,** marginal ruff; **od,** oral disc; **s,** sphincter; v, verrucae; **ve,** vesicle. Image in A courtesy of V. Häussermann. Scale bars: **A, B,** 5 mm; **C, D, E,** 10 mm; **F,** 1 mm; **G, H,** 0.5 mm.

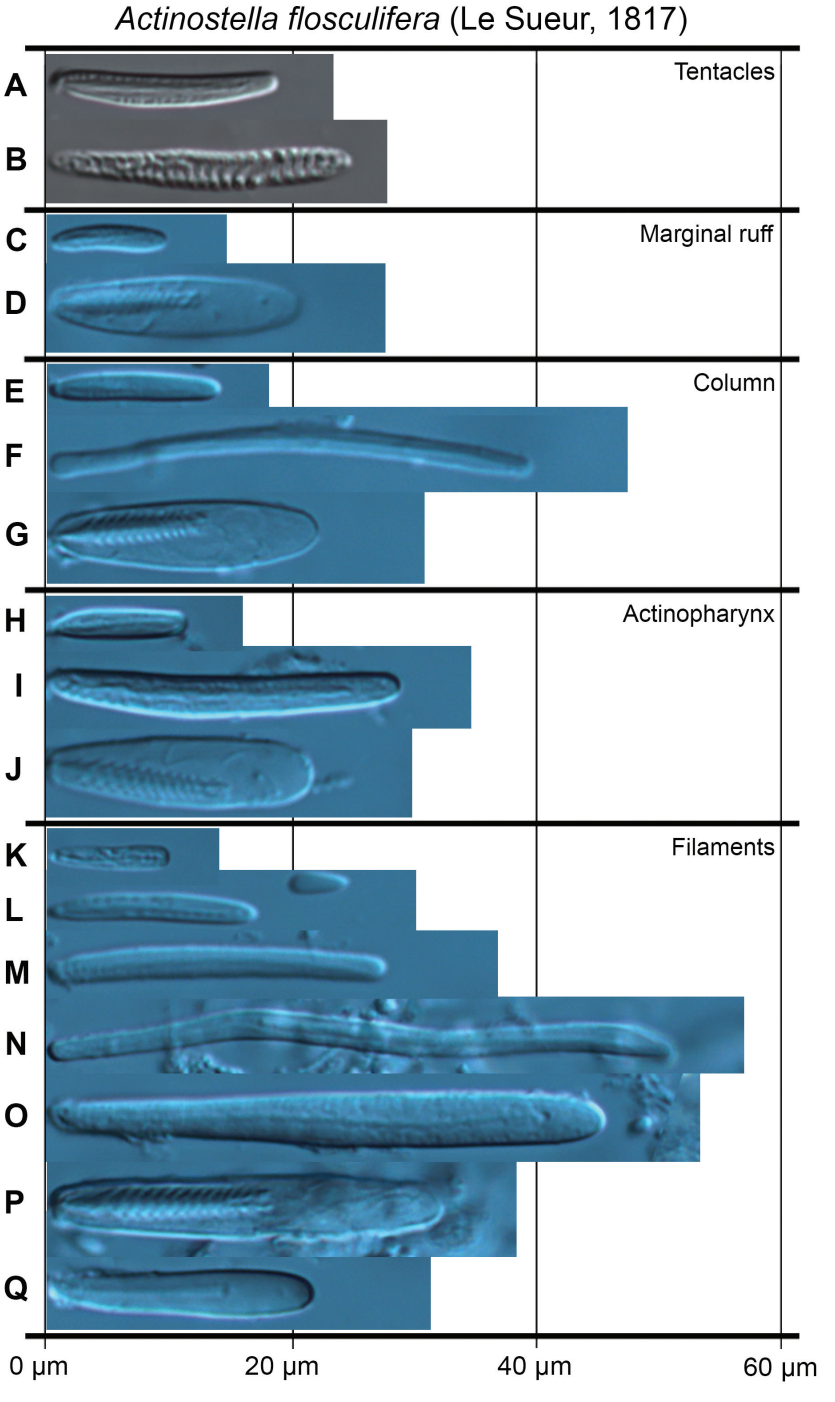


FIG. 14. Cnidae of *Actinostella flosculifera* (Le Sueur, 1817). **A, C, E, H, I, K, L, M,** basitrichs; **B,** spirocysts; **F, N,** basitrichs S; **D, G, J, P,** *p*-mastigophore A; **O,** *b*-mastigophore; **Q,** *p*-mastigophore B1.

REMARKS: *Actinostella flosculifera* is distinguished by the combination of having three cycles of fertile mesenteries in which only the first and second cycles are perfect and *p*-mastigophores A in the marginal ruff and column. All members of *Actinostella* except for *A. bradleyi* are known to have up to three cycles of mesenteries. Nevertheless, Ocaña (1994) described specimens from the Canary Islands (east Atlantic) as *A. flosculifera* with four or five cycles of mesenteries and four cycles of tentacles. Because having more cycles of mesenteries than cycles of tentacles is not a common condition in Actiniaria (Stephenson, 1928), we suspect this might be a mistake and consider it as such until the specimens are reexamined.

Actinostella flosculifera was formerly clearly distinguished within the genus by lacking an endodermal marginal sphincter muscle and bearing only two fertile (first and second) cycles of mesenteries (McMurrich, 1905; González-Muñoz et al., 2012). However, after we reexamined the material (AMNH Cat.Cnidaria 5308) analyzed by González-Muñoz et al. (2012) and examined an additional 19 museum and 13 newly collected specimens from Panama (Atlantic side) (see table 1), an endodermal marginal sphincter muscle and gametogenic tissue in the third cycle were observed in all fertile specimens. Our observations of an endodermal marginal sphincter present in this species agree with those of Corrêa (1964), Schlenz and Belém (1992), and Ocaña (1994).

Corrêa (1964) did not report the presence of *p*-mastigophores A in the marginal ruff or the column of the material of *A. flosculifera* she studied. However, because capsules of *p*-mastigophores A in the ruff and in the column are not very abundant in specimens of *A. flosculifera* (and easy to miss unless looking for them specifically) and because we found this category of capsules in our examination of different specimens across the Caribbean and on those from Brazil (see tables 1, 5), we think Corrêa (1964) just overlooked this category of cnidae. Although this species has been redescribed a few times (e.g., Corrêa, 1964; Ocaña, 1994; González-Muñoz et al., 2012; Durán-Fuentes et al., 2022), the amount of revised material examined here allowed us to clarify the presence of an endodermal marginal sphincter muscle, all mesenteries fertile, *p*-mastigophores A in the marginal ruff and column, and S-shape basitrichs in column.

PHYLOGENETIC ANALYSES

We could amplify sequences only for a single specimen of *Actinostella bradleyi*. All ML analyses of the rDNA dataset recovered a monophyletic *Actinostella* within the superfamily Actinioidea with high support (fig. 15). Members of *Actinostella* were recovered either sister to a clade formed by *Anthopleura biscayensis* (Fisher, 1874) + *Aulactinia marplatensis* (Zamponi, 1977) sister to *Actinostephanus* Kwietniewski, 1897, or as sister to a clade formed by *A. biscayensis* + *Au. marplatensis* and *Actinostephanus* sister to a clade of several species symbiotic with clownfish e.g., *Heteractis crispa* (Hemprich and Ehrenberg in Ehrenberg, 1834), *H. aurora* (Quoy and Gaimard, 1833), etc.

Within the *Actinostella* clade, we consistently recovered two main clades with low support (64% and 59%, respectively): one corresponding to specimens of *A. flosculifera* from the Panamanian Caribbean Sea and the Gulf of Mexico (i.e., from the Atlantic Ocean) and a second clade

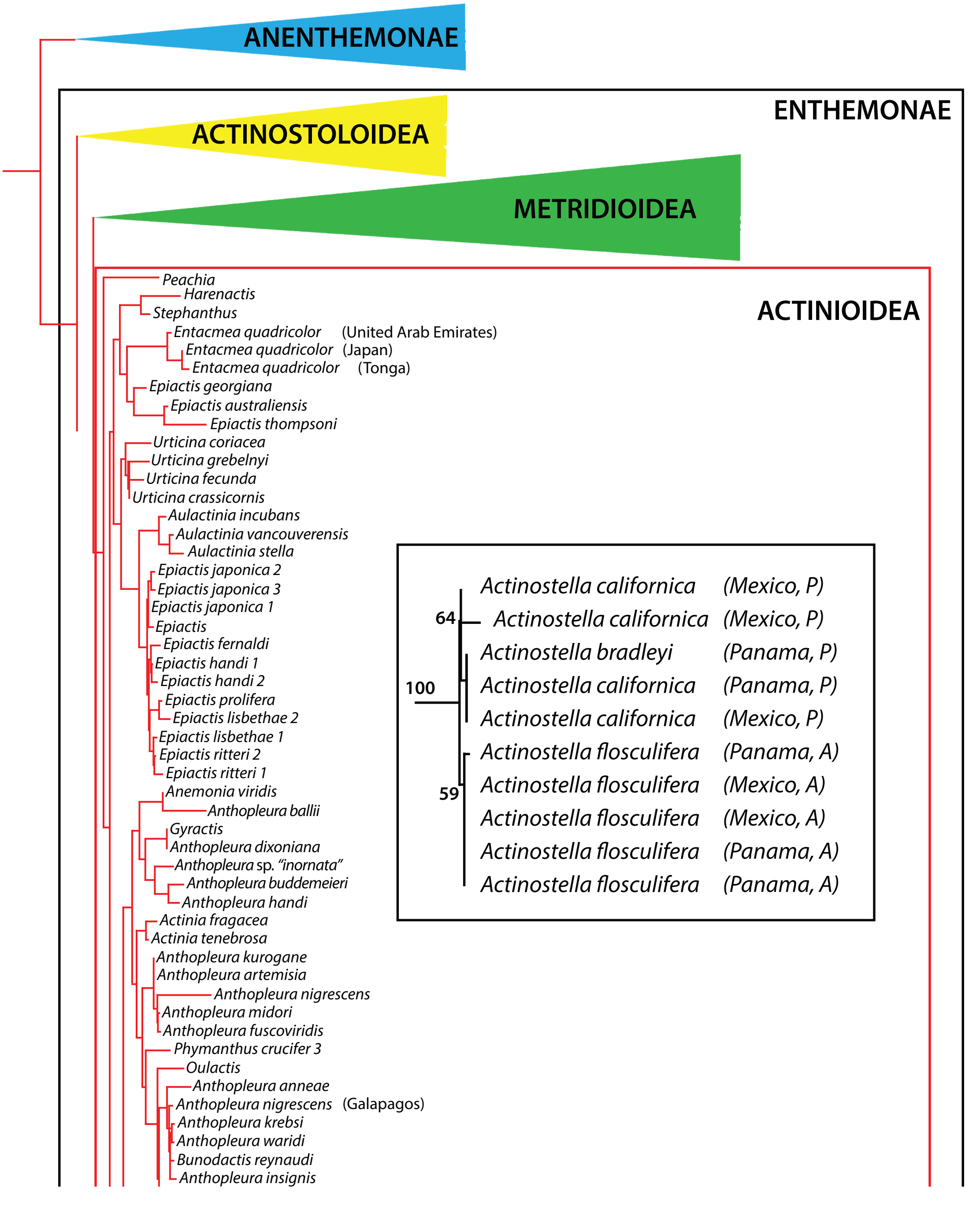
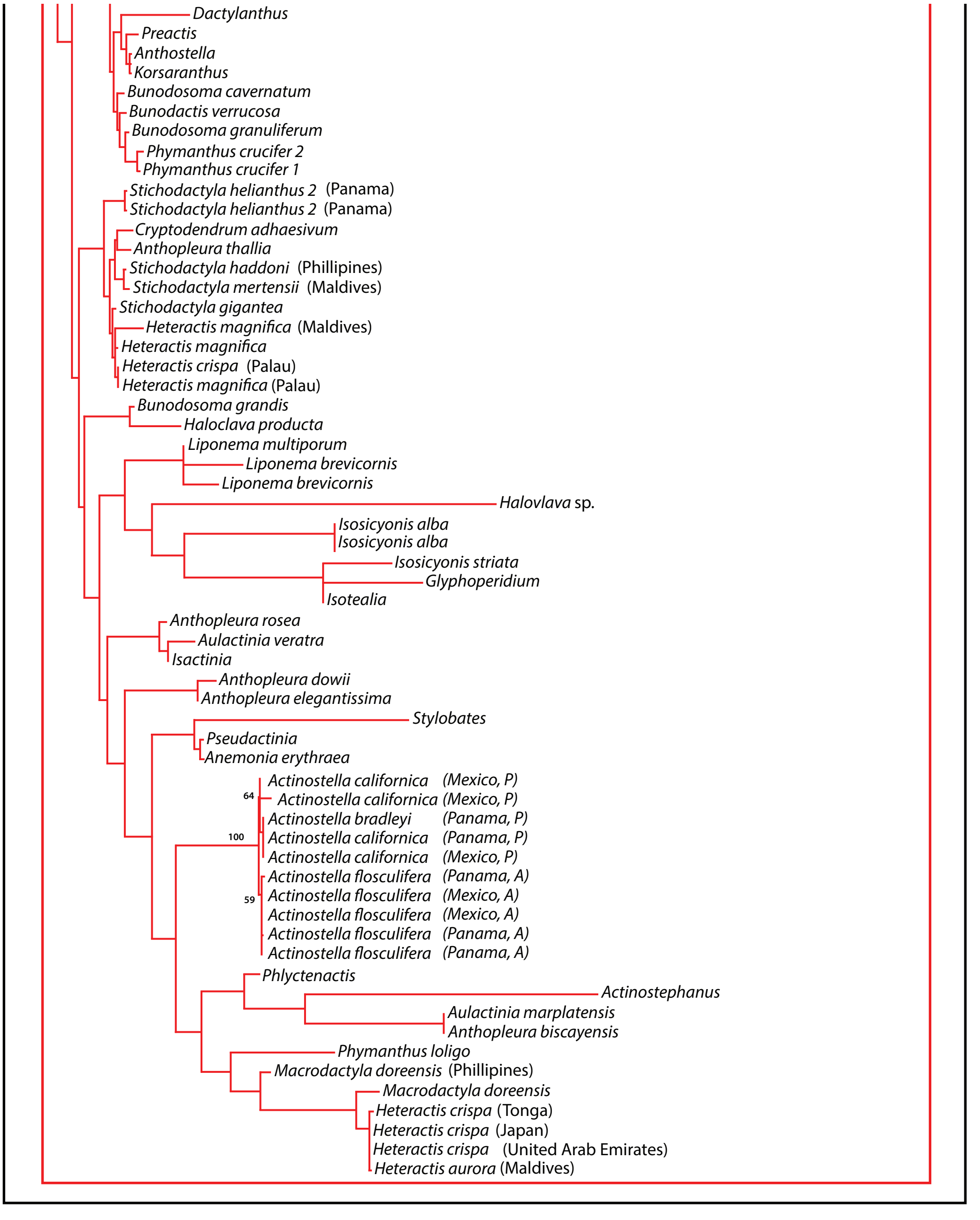


FIG. 15. (*above and on opposite page*) Phylogenetic reconstruction of rDNA dataset using RaxML-NG. Colored triangles depict collapsed suborder Anenthemonae, and superfamilies Actinostoloidea and Metridioidea; dotted line represents suborder Enthemonae. Only bootstrap support for taxa within the genus *Actinostella* showed.


Dactylanthus
Preactis
Anthostella
Korsaranthus
Bunodosoma cavernatum
Bunodactis verrucosa
Bunodosoma granuliferum
Phymanthus crucifer 2
Phymanthus crucifer 1
Stichodactyla helianthus 2 (Panama)
Stichodactyla helianthus 2 (Panama)
Cryptodendrum adhaesivum
Anthopleura thallia
Stichodactyla haddoni (Phillipines)
Stichodactyla mertensii (Maldives)
Stichodactyla gigantea
Heteractis magnifica (Maldives)
Heteractis magnifica
Heteractis crispa (Palau)
Heteractis magnifica (Palau)
Bunodosoma grandis
Haloclava producta
Liponema multiporum
Liponema brevicornis
Liponema brevicornis
Halovlava sp.
Isosicyonis alba
Isosicyonis alba
Isosicyonis striata
Glyphoperidium
Isotealia
Anthopleura rosea
Aulactinia veratra
Isactinia
Anthopleura dowii
Anthopleura elegantissima
Stylobates
Pseudactinia
Anemonia erythraea
Actinostella californica (Mexico, P)
64
Actinostella californica (Mexico, P)
Actinostella bradleyi (Panama, P)
100
Actinostella californica (Panama, P)
Actinostella californica (Mexico, P)
Actinostella flosculifera (Panama, A)
59
Actinostella flosculifera (Mexico, A)
Actinostella flosculifera (Mexico, A)
Actinostella flosculifera (Panama, A)
Actinostella flosculifera (Panama, A)
Phlyctenactis
Actinostephanus
Aulactinia marplatensis
Anthopleura biscayensis
Phymanthus loligo
Macrodactyla doreensis (Phillipines)
Macrodactyla doreensis
Heteractis crispa (Tonga)
Heteractis crispa (Japan)
Heteractis crispa (United Arab Emirates)
Heteractis aurora (Maldives)

with species of *Actinostella* from the Pacific Ocean, namely, *A. californica* + *A. bradleyi*. The single specimen of *A. bradleyi* sequenced (from the Panamanian Pacific) grouped with specimens of *A. californica* from Panama and the Gulf of California but without much support.

DISCUSSION

East Pacific and West Atlantic *Actinostella* Species

The genus *Actinostella* is characterized externally by having a marginal ruff covered by rows of vesicles, a column with rows of verrucae from middle to the distal column, and a more or less distinct fosse; internally, it is characterized by bearing an endodermal and somewhat circumscribed marginal sphincter muscle, and three to four cycles of mesenteries (e.g., Corrêa, 1964; Häussermann, 2003; González-Muñoz et al., 2012). Traditionally, species of *Actinostella* were distinguished by the number of tentacles, cycles, and fertility of mesenteries, slight differences in the ramification of the marginal ruff, presence and/or shape of endodermal marginal sphincter, and geographic distribution. However, not all descriptions mention all these characters (e.g., Verrill, 1869; see table 6); most species within the genus have similar numbers of tentacles and mesenteries, and at least two (*A. bradleyi* and *A. californica*) live in sympatry.

Corrêa (1964), in her exhaustive research on *Actinostella flosculifera* (named *Phyllactis flosculifera* following Carlgren, 1949), analyzed many specimens from the Caribbean Sea, type locality of all species of *Phyllactis* except *P. cichoracea* (which is from the Red Sea) and of several of the species of *Actinostella*. She synonymized all the material studied with *A. flosculifera*, arguing that they inhabited close localities and that the original descriptions did not mention relevant differences to separate them (Corrêa, 1964). Similarly, here we revised several specimens collected from different localities along the Caribbean Sea (e.g., Puerto Rico, Jamaica, Bermuda, Virgin Islands, Cuba, etc.; see table 1) identified as different species (e.g., *Asteractis expansa*, *Phyllactis flosculifera*, etc.) and found no differences in morphology or cnidae among them. We revised the holotype of *P. conquilega* (SMNH-1170, from the Virgin Islands); although only the distal part of the specimen is available, we were able to check the cnidae of the column, tentacles, and marginal ruff. All the specimens examined had the *p*-mastigophores A in marginal ruff and column, three cycles of mesenteries (only the first and second perfect) diagnostic characters of *A. flosculifera*, and therefore we agree with Corrêa (1964) that *P. conquilega*, *P. formosa*, *P. praetexta*, and *A. radiata* should be synonymized with *A. flosculifera*. Thus, we consider *Phyllactis* to have only one valid species, *P. cichoracea*. However, as the type specimen is not available for examination, and the original description of *P. cichoracea* by Milne Edwards in Haeckel (1876) fits within the diagnosis of *Actinostella*, we consider this species valid within *Actinostella* until new material from the type locality (Red Sea) is examined.

Actinostella correae (Schlenz and Belém, 1992) is not revised here, its original description is comprehensive, and this species can be easily distinguished from the others within *Actinostella* because it is a hermaphrodite and only the first cycle of mesenteries (including the directives) is fertile. Although Schlenz and Belém (1992) described the third cycle of mesenteries of *A. correae* as microcnemes, because microcnemes are defined as lacking retractor muscles

TABLE 5. Size ranges and distribution of cnidae of *Actinostella flosculifera* (Le Sueur, 1817). N, Total number of capsules measured; M, Ratio of number of specimens in which each cnidae was found to number of specimens examined; F, Frequency, +++ = very common, ++ = common, + = rather common, --- = sporadic; SD, standard deviation, ND. Sizes in micrometers. Letters in parenthesis correspond to images in figure 14.

Tissue / Categories	M	N	F	Range of length and width of capsules	Mean ± SD
TENTACLES					
Basitrichs (A)	3/3	60	+++	11.7–26.7 × 1.8–2.6	21.0± 2.3 × 3.9 ± 0.2
Spirocysts (B)	3/3	54	+++	12.6–27.8 × 1.4–4.0	21.4± 4.5 × 2.6 ± 0.5
MARGINAL RUFF					
Basitrichs (C)	14/14	97	+++	08.6–15.4 × 1.5–2.3	10.5± 1.4 × 1.9 ± 0.2
p-mastigophores A (D)	12/14	43	+/++	10.3–24.8 × 3.6–6.6	17.8± 2.4 × 4.5 ± 0.5
COLUMN					
Basitrichs (E)	16/16	159	++	07.0–29.9 × 1.5–2.9	13.8± 3.8 × 2.1 ± 0.2
Basitrichs S (F)	15/16	58	++	22.6–43.8 × 1.1–2.5	32.2± 4.1 × 1.7 ± 0.3
p-mastigophores A (G)	16/16	89	+++	15.2–24.7 × 3.5–6.8	20.6± 2.2 × 4.7 ± 0.6
ACTINOPHARYNX					
Basitrichs 1 (H)	3/3	97	+++	08.7–16.1 × 1.6–2.7	12.2± 1.8 × 2.1 ± 0.2
Basitrichs 2 (I)	3/3	98	+++	16.9–31.5 × 2.2–3.9	24.5± 3.6 × 2.8 ± 0.3
p-mastigophores A (J)	3/3	27	+	19.7–28.0 × 4.1–5.5	21.7± 2.1 × 4.9 ± 0.4
FILAMENTS					
Basitrichs 1 (K)	7/7	41	+++	07.2–11.9 × 1.6–2.6	10.7± 0.9 × 2.0 ± 0.2
Basitrichs 2 (L)	7/7	80	+++	12.0–18.5 × 1.9–3.0	13.8± 1.5 × 2.1 ± 0.2
Basitrichs 3 (M)	5/5	22	+++	20.2–27.0 × 1.6–2.6	23.8± 2.1 × 2.2 ± 0.2
Basitrichs S (N)	7/7	21	++	30.0–49.7 × 1.5–2.8	39.1± 5.6 × 2.1 ± 0.3
b–mastigophores (O)	7/7	100	+++	29.9–51.1 × 3.0–4.5	40.5± 5.4 × 3.8 ± 0.4
p-mastigophores A (P)	7/7	90	+++	19.0–30.5 × 4.0–6.0	25.1± 2.0 × 4.7 ± 0.4
p-mastigophores B1 (Q)	7/7	27	---	15.2–24.5 × 2.6–3.7	18.6± 3.1 × 2.1 ± 0.3

TABLE 6. Differential diagnostic characters of *Actinostella* species from American coasts.

	Actinostella bradleyi (Verrill, 1869)	*Actinostella californica* (McMurrich, 1893)	*Actinostella correae* Schlenz and Belém, 1992	*Actinostella digitata* (McMurrich, 1893)	*Actinostella flosculifera* (Le Sueur, 1817)
Tentacles	96	48	24	48	48
Cycles mesenteries	4 cycles	3 cycles	3 cycles	3 cycles	3 cycles
Cycles of perfect mesenteries	All 4 cycles perfect	1st and 2nd cycles perfect	1st and 2nd cycles perfect	all 3 cycles perfect	1st and 2nd cycles perfect
Cycles of imperfect mesenteries	None	3rd cycle imperfect	3rd cycle imperfect	none	3rd cycle imperfect
Fertility	All 4 cycles fertile	3 cycles fertile	1st cycle	3 cycles fertile	3 cycles fertile
Marginal ruff cnidae	*p*-mastigophores A, basitrichs	basitrichs	basitrichs	*p*-mastigophores A, basitrichs	*p*-mastigophores A, basitrichs
Column cnidae	Basitrichs Basitrichs S *p*-mastigophores A	basitrichs basitrichs S	basitrichs	basitrichs	basitrichs basitrichs S *p*-mastigophores A
Distribution	Pacific Ocean	Pacific Ocean	Atlantic Ocean	Atlantic Ocean	Atlantic Ocean

and gametogenic tissue (Carlgren, 1949) and Schlenz and Belém (1992) described the third cycle of *A. correae* as having retractor muscles, we consider those mesenteries imperfect (i.e., not reaching the actinopharynx) mesenteries rather than microcnemes.

After the reexamination and dissection of the only known specimen of *Lophactis ornata* (= *Actinostella ornata*), a species from the Pacific side of Panama (Pearl Islands), we found that it shows diagnostic characteristics of the genus *Telmatactis* Gravier, 1916 (i.e., tentacles with rounded tips, column with periderm but without protuberances, mesogleal marginal sphincter muscle, and *p*-mastigophores B2a; see fig. 16, table 7). Because the only species of *Telmatactis* reported for the tropical eastern Pacific is *T. panamensis* (Verrill, 1869), *L. ornata* is most probably a junior synonym of this species.

Our revision of the type material of *Actinostella bradleyi*, *A. californica*, *A. digitata*, *A. ornata*, *Phyllactis conquilega*, and additional material of *A. flosculifera* (type material of this species is not available) highlights the need to reevaluate the diagnostic characteristics for

FIG. 16. External and internal anatomy and cnidae of *Lophactis ornata* Verrill, 1869 (YPM 2105) (= *Telmatactis* cf. *panamensis*). **A,** lateral view of preserved specimen; **B,** oral view of preserved specimen; notice the capitulum (c); **C,** proximal view of preserved specimen; **D,** longitudinal section of the distal column showing mesogleal marginal sphincter muscle (s); **E,** detail of the muscle fibers within the mesoglea; **F–H,** basitrichs; **I,** *p*-mastigophores B1. Scale bars: **A–D**, 5 mm; **E,** 1 mm.

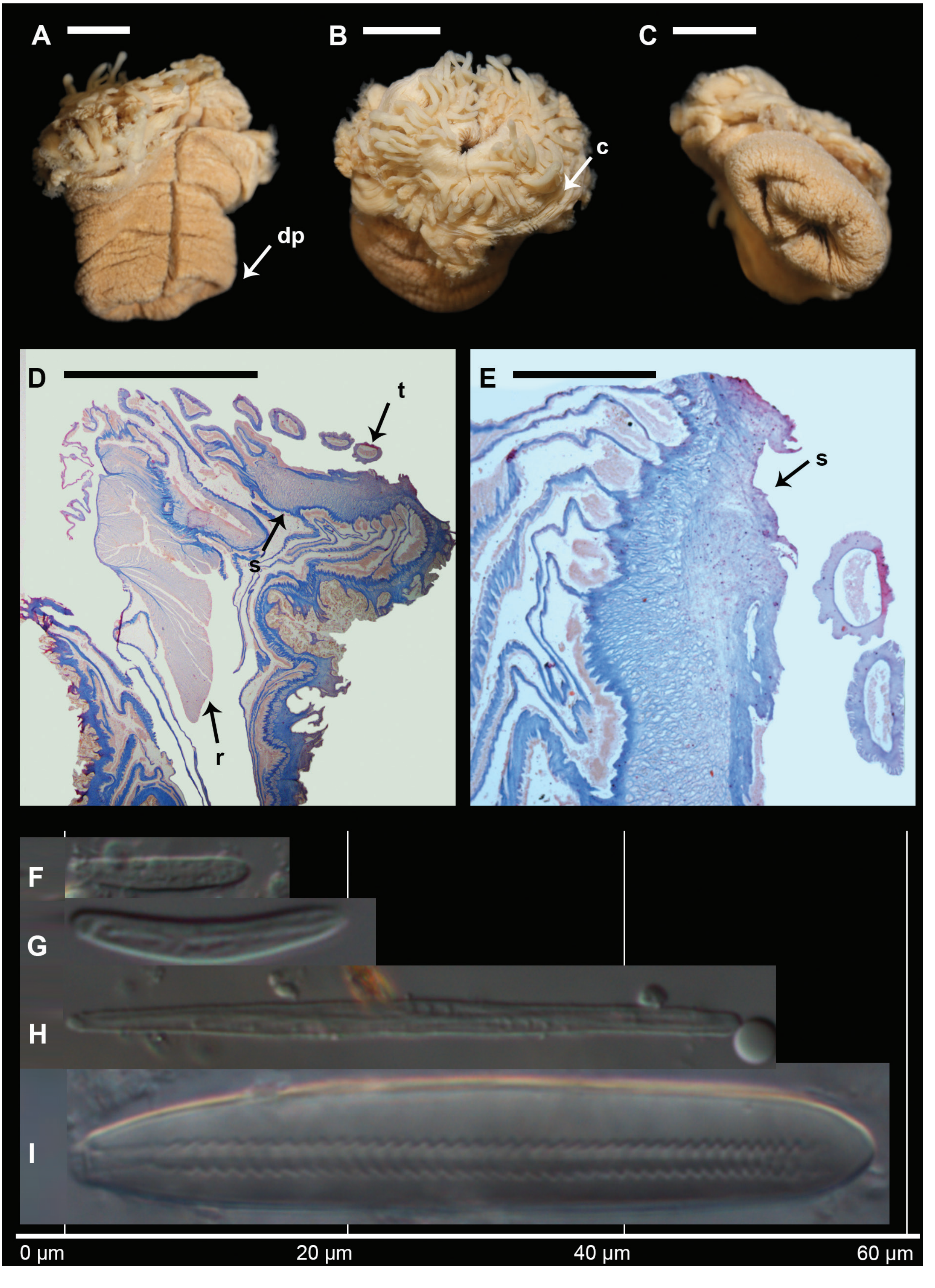

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TABLE 7. Size ranges and distribution of cnidae of *Lophactis ornata* Verrill, 1869 [=*Telmatactis panamensis*]. N, Total number of capsules measured; M, Ratio of number of specimens in which each cnidae was found to number of specimens examined; F, Frequency, +++ = very common, ++ = common, + = rather common, --- = sporadic; ND, no data. Sizes in micrometers. Letters in parenthesis correspond to images in figure 16. Data sources: [1]Fautin et al. (2007); [2]Carlgren (1951).

Tissue / Categories	M	N	F	Range of length and width of capsules	*Telmatactis panamensis*[1]	*Telmatactis panamensis*[2]
TENTACLES						
Basitrichs	–	–	–	NF	(31.1–69.5) × (1.8–3.9)	(33.8–70.5) × (2.5–2.8)
Spirocysts	–	–	–	NF	(17.2–45.7) × (1.8–4.6	ND
p-mastigophores B1	1/1	5	+	15.2–23.1 × 3.0–5.4	(29.6–37.9) × (4.3–7.2	ND
COLUMN						
Basitrichs (F)	1/1	28	++	13.0–25.0 × 2.0–4.0	(13.9–25.9) × (2.6–4.1)	ND
p-mastigophores B1	–	–	–	NF	(17.7–26.1) × (5.0–6.5)	ND
ACTINOPHARYNX						
Basitrichs 1 (G)	1/1	14	+++	14.0–17.0 × 3.0	(13.1–18.9) × (1.6–3.2)	(12.7–18.3) × (1.5–2.0)
Basitrichs 2 (H)	1/1	5	++	21.0–23.0 × 2.0–3.0	(24.1–36.2) × (1.7–4.7)	(22.6–31.0) × (2.8–3.0)
p-mastigophores B1	1/1	1	---	16.0 × 4.0	(26.8–33.1) × (3.8–5.9)	(25.4–32.0) × (4.2–5.5)
p-mastigophores B1	–	–	–	NF	(35.2–62.4) × (6.7–12.7)	ND
FILAMENTS						
Basitrichs 1	–	–	–	NF	(12.1–29.5) × (1.1–3.3)	(12.7–22.0) × (1.5–2.0)
Basitrichs 2 (H)	1/1	8	++	47.0–70.0 × 2.0–3.0	(36.7–53.1) × (2.5–3.7)	(38.0–60.6) × (8.5–11.3)
p-mastigophores B1	–	–	–	NF	(12.6–25.1) × (2.5–6.2)	(11.3–19.7) × (3.5–4.2)
p-mastigophores B1 (I)	1/1	2	---	58.0–62.0 × 8.0–10.0	(57.2–81.9) × (9.4–15.9)	ND
ACONTIA						
Basitrichs	–	–	–	NF	(19.6–31.9) × (1.8–3.8)	(21.0–25.4) × (2.0–2.5)
p-mastigophores B1	–	–	–	NF	(55.8–72.3) × (9.3–14.7)	(42.3–73.3) × (8.5–12.7)

Actinostella. We consider that the traditional characters used to differentiate species of *Actinostella* must be complemented with the distribution of the cnidae. Therefore, (1) the number of cycles, (2) the fertility of the mesenteries, and (3) the distribution of cnidae (in particular those cnidae capsules in the marginal ruff and the column) are the diagnostic characters to distinguish the current species of *Actinostella* (table 6). We do not consider the presence of an endodermal marginal sphincter as diagnostic for species within *Actinostella* because all its species have a more or less circumscribed sphincter muscle; we also found that differences in the ramifications of the marginal ruff are hard to assess (especially in old, preserved material), and thus not useful or reliable to distinguish within species of *Actinostella.*

Phylogenetic Relationships of and within *Actinostella*

Our dataset of standard rDNA markers used for anemones (12S, 16S, CO3, 18S, 28S) recovered a monophyletic *Actinostella* not closely related to other genera with marginal ruff included in our analysis (i.e., *Oulactis*) with high support. Thus, our molecular results suggest that the marginal ruff has evolved independently at least twice (in *Actinostella* and *Oulactis*) based on the present subset of sampled actiniarians.

Similar to the pattern recovered for other members of Actinioidea (see Daly et al., 2017), our dataset split the species of *Actinostella* according to geography (i.e., Atlantic species separated from Pacific species) although with low support (fig. 15). Despite the anatomy of *A. flosculifera* and *A. californica* being very similar (see table 6), our molecular results do not support a finding of these two species as siblings (fig. 15). These results render the use of anatomy to identify and assess phylogenetic relationships of species within this genus unreliable; similarities in anatomy might reflect morphological convergence as it has been found multiple times within Actiniaria (e.g., Rodríguez et al., 2012, 2014; Daly et al., 2017). Because *A. flosculifera* and *A. californica* are distributed on each side of the Panama Isthmus, one potential evolutionary scenario to explain anatomical similarities despite the recovered genetic divergence between the two species (besides morphological convergence) is that the species divergence might have predated the closure of the isthmus; a similar pattern has been suggested and discussed for cerianthids (Stampar et al., 2012). However, the low support recovered, together with the fact that we could get molecular data for only one specimen of *A. bradleyi*, render the phylogenetic relationships within *Actinostella* and the associated hypothesis on their diversification uncertain until more specimens and genomic approaches are used.

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REFERENCES

Andres, A. 1883. Le Attinie. Atti dell'Accademia de Lincei 14: 211–673.

Barragán, Y. 2015. Taxonomía de anémonas de mar (Cnidaria: Anthozoa: Actiniaria) de la Bahía de La Paz, Golfo de California, México. Undergraduate thesis, Departamento de Ciencias Biológicas y fisiológicas, Universidad Peruana Cayetano Heredia, Lima, Peru, 123 pp.

Barragán, Y. 2019. Taxonomía de anémonas de mar (Cnidaria: Anthozoa: Actiniaria) del Pacífico Mexicano y Panameño. Master's thesis, Departamento Académico de Ciencias Marinas y Costeras, Universidad Autónoma de Baja California Sur, La Paz, Mexico, 140 pp.

Barragán, Y., C. Sánchez, Y. Hooker, and E. Rodríguez. 2019. First inventory of sea anemones (Cnidaria: Actiniaria) from La Paz Bay, Southern Gulf of California (Mexico). Zootaxa 4559 (3): 501–549.

Cairns, S., and J.C. den Hartog. 1986. Class Anthozoa. *In* W. Sterrer and C. Schoepfer-Sterrer (editors), Marine fauna and flora of Bermuda: a systematic guide to the identification of marine organisms: 159–194. New York: Wiley-Interscience.

Carlgren, O. 1934. Zur Revision der Actiniarien. Arkiv für Zoologi 26 (A): 1–36.

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 (3282): 415–449.

Corrêa, D.D. 1964. Corallimorpharia e Actiniaria do Atlantico oeste tropical. Ph.D. dissertation, Faculdade de Filosofia e Letras, Universidade de São Paulo, 39 pp.

Daly, et al. 2017. *Anthopleura* and the phylogeny of Actinioidea (Cnidaria: Anthozoa: Actiniaria). Organisms, Diversity, and Evolution 17: 545–564.

Dana, J.D. 1846. Zoophytes. Volume VII of the United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, U.S.N. Philadelphia: Lea and Blanchard, 740pp.

Darriba, D., G.L. Taboada, R. Diallo, and D. Posada. 2012. jModeltest 2: more models, new heuristics and parallel computing. Nature Methods 9: 772.

Duchassaing, P. 1850. Animaux radiaires des Antilles. Paris: Plon Frères.

Duchassaing, P., and G. Michelotti. 1860. Mémoire sur les coralliaires des Antilles. Turin: Imprimerie Royale.

Durán-Fuentes, J., A. Gracia, and R. González-Muñoz. 2022. Sea anemones (Cnidaria, Anthozoa, Actiniaria) in high sedimentation environments influenced by the Magdalena River (Colombian Caribbean). Annals of the Brazilian Academy of Sciences 94 (1): e20190862.

Durán-Fuentes, J. et al. 2023. Ecological notes on *Actinostella flosculifera* (Le Sueur, 1817) (Cnidaria: Actiniaria: Actiniidae) in the southwestern Atlantic, Brazil. Journal of the Marine Biological Association of the United Kingdom 103 (e20): 1–6.

Ehrenberg, C.G. 1834. Beiträge zur physiologischen Kenntniss der Corallenthiere im allgemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin 1: 225–380.

Fautin, D.G. 2016. Catalog to families, genera, and species of orders Actiniaria and Corallimorpharia (Cnidaria: Anthozoa). Zootaxa 4145: 1–449.

Fautin, D.G., C.P. Hickman, M. Daly, and T. Molodtsova. 2007. Shallow-Water Sea Anemones (Cnidaria: Anthozoa: Actiniaria) and Tube Anemones (Cnidaria: Anthozoa: Ceriantharia) of the Galápagos Islands. Pacific Science 61 (4): 549–573.

Fisher, P. 1874. Recherches sur les actinies des côtes océaniques de France. Nouvelles Archives du Muséum d'Histoire Naturelle de Paris 10: 193–244.

Gomes, P.B., and E.M. Mayal. 1997. Levantamento preliminar das anêmonas-do-mar (Cnidaria: Actiniaria) da costa de Pernambuco, Brasil. Biociências 5 (2): 45-52.

González-Muñoz, R., N. Simões, J. Sanchez-Rodriguez, E. Rodríguez, and L. Segura-Puertas. 2012. First inventory of sea anemones (Cnidaria: Actiniaria) of the Mexican Caribbean. Zootaxa 3556: 1–38.

González-Muñoz, R., N. Simões , J.L. Tello-Musi, and E. Rodríguez. 2013. Sea anemones (Cnidaria, Anthozoa, Actiniaria) from coral reefs in the southern Gulf of Mexico. Zookeys 341: 77-106.

Gravier, C. 1916. Sur un type nouveau d'actinie de l'île San Tomé (Golfe de Guinée). Bulletin du Muséum National d'Histoire Naturelle (Paris) 22 (5): 234–236.

Grajales, A., and E. Rodríguez. 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.

Guindon, S., and O. Gascuel. 2003. A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. Systematic Biology 52: 696–704.

Guindon, S., et al. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Systematic Biology 59: 307–321.

Gusmão, L.C, A. Grajales, and E. Rodríguez. 2018. Sea anemones through X-rays: visualization of two species of *Diadumene* (Cnidaria, Actiniaria) using micro-CT. American Museum Novitates 3907: 1–45.

Gusmão, L.C., and E. Rodríguez. 2021. Two sea anemones (Cnidaria: Anthozoa: Actiniaria) from the Southern Ocean with evidence of a deep-sea, polar lineage of burrowing sea anemones. Zoological Journal of the Linnean Society 193: 1392–1415.

Haddon, A.C. 1898. The Actiniaria of Torres Straits. Scientific Transactions of the Royal Dublin Society 6: 393–520.

Haeckel, E. 1876. Arabische Korallen. Berlin: Georg Reimer, 49 pp.

Hargitt, C.W. 1911. *Cradactis variabilis*: an apparently new Tortugan actinian. Papers from the Tortugas Laboratory of the Carnegie Institution of Washington 3: 51–53.

Häussermann, V. 2003. Redescription of *Oulactis concinnata* (Drayton in Dana, 1846) (Cnidaria: Anthozoa: Actiniidae), an actiniid sea anemone from Chile and Perú with special fighting tentacles; with a preliminary revision of the genera with a "frond-like" marginal ruff. Zoologische Verhandelingen 345: 173–207.

Hertwig, R. 1882. Die Actinien der Challenger Expedition. Jena, Germany: Gustav Fischer.

Humason, G.L. 1967. Animal tissue techniques. San Francisco: W.H. Freeman and Company.

Katoh, K., and D.M. Standley. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30: 772–780.

Kearse, M., et al. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28 (12): 1647–1649.

Kozlov, A.M., et al. 2019. RAxMLNG: A fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. Bioinformatics 35: 4453–4455.

Kwietniewski, C.R. 1897. Ein Beitrag zur Anatomie und Systematik der Actiniarien. Jena, Germany: Universitaet Jena, 34 pp.

Lauretta, D., V. Häussermann, M.R. Brugler, and E. Rodríguez. 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., J.M. Longueville, and O. Gascuel. 2017. SMS: Smart Model Selection in PhyML, Molecular Biology and Evolution 34 (9): 2422–2424.

Le Sueur, C.A. 1817. Observations on several species of the genus *Actinia*; illustrated by figures. Journal of the Academy of Sciences of Philadelphia 1: 149–154, 169–189.

López-González, P.A., J.C. den Hartog, and J.C. García-Gómez. 1995. *Onubactis rocioi* gen. et spec. nov., a new species of Actiniidae (Anthozoa: Actiniaria) from the southern Iberian Peninsula. Zoologische Mededelingen 69: 375–383.

Mace, G.M. 2004. The role of taxonomy in species conservation. Philosophical Transactions: Biological Sciences 359 (1444): 711–719.

McMurrich, J. P. 1889. A contribution to the actinology of the Bermudas. Proceedings of the Academy of Natural Sciences of Philadelphia 1889: 102–126.

McMurrich, J.P. 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 (930): 119–216.

McMurrich, J.P. 1898. Report on the Actiniaria collected by the Bahama Expedition of the State University of Iowa, 1893. Bulletin from the Laboratories of Natural History, State University of Iowa 4: 225–249.

McMurrich, J.P. 1905. A revision of the Duchassaing and Michelotti actinian types in the Museum of Natural History, Turin. Bolletino del Musei di Zoologia ed Anatomia Comparata 20 (494): 1–23.

Melo, K., and F. Amaral. 2005. Ampliação da distribuição das anêmonas-do-mar (Cnidaria, Actiniaria) no estado de Pernambuco. Brasil. Tropical Oceanography 33 (1): 19–31.

Milne Edwards, 1857. Histoire naturelle des coralliaires ou polypes proprement dits, vol. 1. Paris: Librairie Encyclopédique de Roret, 326 pp.

Milne Edwards, H., and J. Haime. 1851. *In* Archives du Muséum d'Histoire Naturelle. Monographie des polypiers fossiles des terrains palfozooques, précédér d'un tableau général de la classification des polypes: [vol. 5] 1 –502. Paris: Gide et J. Baudry.

Miller, M.A., W. Pfeiffer, and T. Schwartz. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop (GCE): 1–8.

Ocaña, O. 1994. Anémonas (Actiniaria y Corallimorpharia) de Macaronesia Central: Canarias y Madeira. Estudio Sistemático, Faunístico, Anatómico comparado y Biogeográfico. Ph.D. dissertation, Departamento de Biología Animal (Zoología) Universidad de La Laguna, Spain, 484 pp.

Ocaña, O., and J.C. den Hartog. 2002. A catalogue of Actiniaria and Corallimorpharia from the Canary Islands and Madeira. Archipelago. Life and Marine Sciences 19 (A): 33–54.

Ocaña, O., L. Moro, J. Ortea, J. Espinosa, and M. Caballero. 2007. Guía visual de la biodiversidad marina de Guanahacabibes. I. Anémonas (Anthozoa: Actiniaria, Corallimorpharia, Ceriantharia y Zoanthidea). Avicennia 19: 133–142.

Ocaña, O., et al. 2015. A survey on Anthozoa and its habitat along the Northwest African coast and some islands: new records, descriptions of new taxa and biogeographical, ecological and taxonomical comments. Part I. Revista de la Academia Canaria de Ciencias 27: 9–66.

Pax, F. 1912. Les actinies de la côte du Pérou. Paris: Gauthier-Villars Imprimeur-Libraire.

Quoy, J.R.C., and P. Gaimard. 1833. Voyage de découvertes de l'astrolabe exécuté par ordre du roi, pendant les années 1826-1827-1828-1829, sous le commandement de M.J. Dumont D'Urville. Paris: J. Tastu, 390 pp.

Rafinesque, C.S. 1815. Analyse de la nature ou tableau de l'univers et des corps organisés. Palerme, Italy: C.S. Rafinesque.

Rodríguez, E., M. Barbeitos, M. Daly, L. Gusmão, and V. Häussermann. 2012. Toward a natural classification: phylogeny of acontiate sea anemones (Cnidaria, Anthozoa, Actiniaria). Cladistics 28: 375-392.

Rodríguez, E., et al. 2014. Hidden among sea anemones: the first comprehensive phylogenetic reconstruction of the order Actiniaria (Cnidaria, Anthozoa, Hexacorallia) reveals a novel group of hexacorals. PLoS ONE 9: 1–15.

Rodríguez, E., D. Fautin, and M. Daly. 2024. World list of Actiniaria. *Actinostella* Duchassaing, 1850. Internet resource (https://www.marinespecies.org/actiniaria/aphia.php?p=taxdetails&id=267202), accessed April 2024.

Schlenz, E., and M.J. Belém. 1992. *Phyllactis corrêae* n. sp. (Cnidaria, Actiniaria, Actiniidae) from Atol das Rocas, Brazil, with notes on *Phyllactis flosculifera* (Lesueur, 1817). Boletim de Zoologia (Sao Paulo) 12: 91–117.

Stampar, S.N., M.M. Maronna, M.J.A. Vermeij, F.L.D. Silveira, and A.C. Morandini. 2012. Evolutionary diversification of banded tube-dwelling anemones (Cnidaria; Ceriantharia; Isarachnanthus) in the Atlantic Ocean. PLoS ONE 7 (7): e41091.

Stephenson, T.A. 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, T.A. 1928. The British Sea anemones, vol. I. London: Ray Society, 148 pp.

Stephenson, T.A. 1935. The British Sea anemones, vol. II. London: Ray Society, 426 pp.

Verrill, A.E. 1869. Review of the corals and polyps of the west coast of America. Transactions of the Connecticut Academy of Arts and Sciences 1 (6): 377–558.

Verrill, A.E. 1899. Descriptions of imperfectly known and new actinians, with critical notes on other species. American Journal of Science 7: 41–50, 143–146, 205–218, 375–380.

Verrill, A.E. 1900. Additions to the Anthozoa and Hydrozoa of the Bermudas. Anthozoa. Transactions of the Connecticut Academy of Arts and Sciences 10: 551–572.

Voss, G.L., F.M. Bayer, C.R. Robins, M. Gomon, and E.T. LaRoe. 1969. The marine ecology of the Biscayne National Monument. Unpublished document from the University of Miami, 128 pp.

Wassilieff, A. 1908. Japanische Actinien. Abhandlungen des Mathematischen-Physikalischen Institutes der Kaiserlichen Bayerischen Akademie der Wissenschaften 1 (2): 1–49.

Wilson, H.V. 1890. On a new actinia, *Hoplophoria coralligens*. Studies from the Biological Laboratory of Johns Hopkins University 4: 379–387.

Wirtz, P. 2003. New records of marine invertebrates from São Tomé Island (Gulf of Guinea). Journal of the Marine Biological Association of the United Kingdom 83: 735–736.

Zamponi, M.O. 1977. La anemonofauna de Mar del Plata y localidades vecinas. I. Las anemonas Boloceroidaria y Endomyaria. (Coelentherata: Actiniaria). Neotropica 23: 137–153.

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