



A new vermiform sea anemone (Anthozoa: Actiniaria) from Argentina: *Harenactis argentina* sp. nov.

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Abstract

During 2007, 2008, and 2010, 23 specimens of an undescribed vermiform sea anemone were collected on Punta Pardelas and Fracaso Beach (Península Valdés, Argentina). The specimens have longitudinal rows of cinclides distally, all mesenteries perfect, tentacles hexamerously arranged without acrospheres, column not divisible into regions, no marginal sphincter and no conchula. We describe these specimens as a new species within the genus *Harenactis* (family Haloclavidae). *Harenactis argentina* sp. nov. is the second species of *Harenactis*; it represents the first record of this genus in the southern hemisphere and the first record of a soft bottom-dwelling sea anemone in the Argentine continental zone. Furthermore, we discuss the familial placement and relationships of the genus *Harenactis* and other athenarian sea anemones.

Key words: Athenaria, Anthozoa, benthos, Chubut

Introduction

Athenarian sea anemones are usually found burrowing in soft bottoms. They are characterized by the lack of basilar muscles, elongated body, round aboral end, and strong retractor muscles of the mesenteries (Carlgren 1949). Although Carlgren's (1949) classification was intended to be practical rather than phylogenetic, Carlgren thought that the presence of basilar muscles was important and that athenarian sea anemones were a natural and primitive group (Carlgren 1942). Several authors have argued that the main morphological features unifying athenarians (lack of basilar muscles and elongated column) could be an adaptation to the burrowing way of life and hence a result of convergent evolution (Hand 1966; Riemann-Zürneck 1979; Rodríguez & López-González 2002; Schmidt 1974). Recent molecular work (Daly *et al.* 2008; Rodríguez & Daly 2010) has confirmed that athenarians are a polyphyletic group: some athenarian sea anemones nest within groups having basilar muscles such as Endomyaria (e. g. *Peachia* Gosse, 1855 and *Haloclava* Verrill, 1899; family Haloclavidae Verrill, 1899) and Acontiarina, a group of actiniarians characterized by acontia (e. g. *Andvakia* Danielssen, 1890 and *Halcampoides* Danielssen, 1890, families Andvakiidae Danielssen, 1890 and Halcampoididae Appellöf, 1896, respectively). Thus, we use the term "athenarian" hereafter to refer to actiniarians without basilar muscles but do not imply any close relationship among them.

We describe a new species of *Harenactis* Torrey, 1902 (Haloclavidae) from 23 specimens inhabiting soft bottoms around Península Valdés (Chubut, Argentina). *Harenactis argentina* sp. nov. differs from the only other species of the genus, *H. attenuata* Torrey, 1902, in size, tentacle coloration, fertility of mesenteries, cnidae, and geographical distribution. The finding of specimens of *Harenactis* in Argentinean waters is the first report of this genus for the southwest Atlantic and the first new record worldwide since 1925 (Uchida 1938). Furthermore, the description of *H. argentina* sp. nov. provides an opportunity to address the familial placement and relationships of the genus *Harenactis* and other athenarian sea anemones.

Material and methods

The examined specimens were collected by Daniel Laretta (DL) by SCUBA diving to 10 m at Punta Pardelas (42° 37'S, 64° 15'W) and by hand intertidally at Fracaso beach (42° 25'S, 64° 07'W) and Villarino beach (42° 24'S, 64° 17'W) (Fig 1). Specimens were carefully removed by digging next to them to prevent damage. Photographs were taken in vivo and in situ. The specimens were relaxed using menthol crystals, fixed in 4% seawater formalin, and transferred to 70% alcohol for long-term storage after a few months.

Specimens were examined whole and some were dissected. Histological sections 5 to 10 μ m thick were made from parts of six specimens; they were stained with Azocarmin triple stain (Humason 1967). The distribution of the cnidae in the tissues was analyzed in four specimens, using a light microscope (1000x, magnification oil immersion). Forty non-fired capsules of each cnida type (when possible) were haphazardly chosen, measured, and photographed with Axio Vision 4.4 software. Mean and standard deviation have been provided to give an idea of the distribution of sizes; these are not statistically significant (see Williams 1998, 2000 for minimal requirements for statistical significance in cnida sizes) but provide some qualitative information about variability in capsule size for each type of nematocyst. Cnida nomenclature follows England (1991).

The studied material has been deposited in the American Museum of Natural History (AMNH) in New York, U.S.A.; Museo Argentino de Ciencias Naturales "Bernardino Rivdavia" (MACN) and in the Museo de La Plata (MLP) in Buenos Aires, Argentina. For the purpose of comparison, we have examined the holotype of *Calamactis praelonga* Carlgren, 1951 from the Smithsonian National Museum of Natural History (USMN 49453) in Washington, U.S.A.

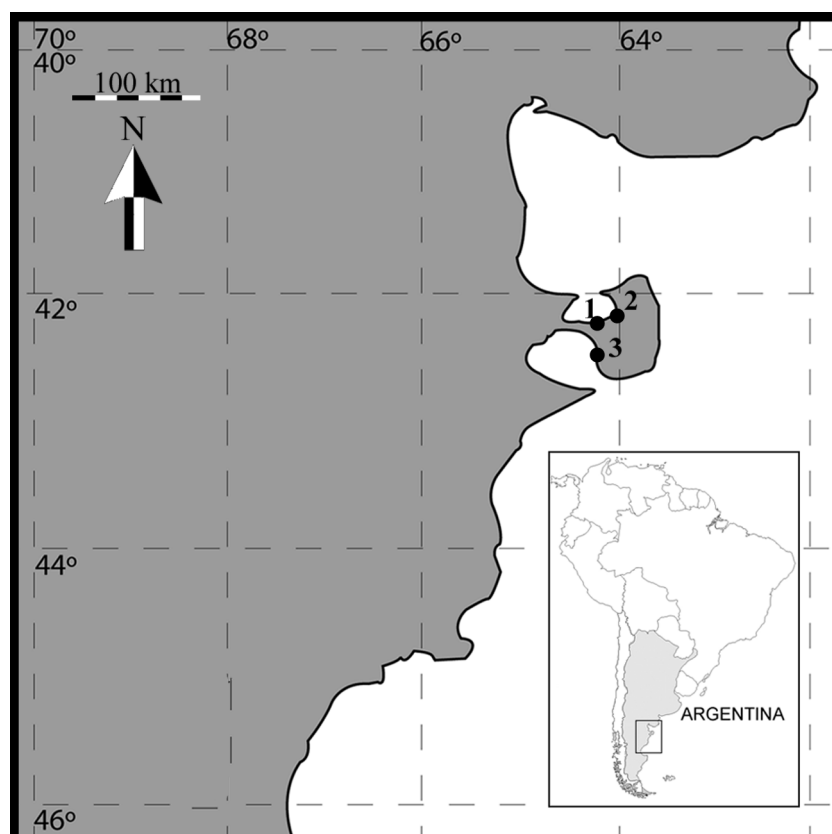


FIGURE 1. Geographic distribution of *Harenactis argentina* sp. nov. 1, Fracaso beach 2, Villarino beach 3, Punta Pardelas.

Results

Family Haloclavidae Verrill, 1899

Genus *Harenactis* Torrey, 1902

Diagnosis (after Carlgren (1949), modifications in bold). Elongate Haloclavidae with a physa-like aboral end which can flatten into a disc. Column smooth with **longitudinal** rows of cinclides **distally**. No **marginal** sphincter. Tentacles 24, the inner shorter than the outer ones (?); their longitudinal muscles ectodermal. A single siphonoglyph, without a conchula. All mesenteries macrocnemes. The fifth and sixth couples **may be** weaker than the eight other mesenteries of the first cycle. **All mesenteries or only those of the first cycle** fertile. Retractors and parietal muscles of the older mesenteries strong, the former reniform. Cnidom: spirocysts, basitrichs, **microbasic b-mastigophores** and microbasic *p*-mastigophores.

Type species. *Harenactis attenuata* Torrey, 1902.

Remarks. The diagnosis from Carlgren (1949) has been modified to accommodate the new species within the genus; this includes the possibility of all mesenteries being fertile, the fifth and sixth couples of mesenteries not always being weaker than the others, and the presence of microbasic *b*-mastigophores. Some changes in the wording have been made (e. g. vertical/longitudinal, upper part/distally) to standardize the language in the diagnosis.

Harenactis argentina sp. nov.

Type material. Holotype: MACN - IN 39376; Punta Pardelas, Chubut, Argentina (42° 37'S, 64° 15'W), April 2008, 5–10 m depth. Paratype: Invertebrate Collection of MLP 8791, one specimen. Collecting data same as those of holotype.

Additional material. AMNH, one specimen. Punta Pardelas, Chubut, Argentina (42° 37'S, 64° 15'W), 5–10 m depth.

Description. External anatomy: Base not adherent, physa-like, variable in shape, round or flat depending on the specimen (Fig. 2a). Diameter to 21 mm (holotype 11 mm). Some specimens with abundant sand and debris attached to aboral end. Mesenterial insertions visible.

Column vermiform (Fig. 2b), to 121 mm in length and 25 mm in diameter in preserved specimens (holotype 121 mm in length and 7–20 mm in diameter), smooth. In preserved specimens, column usually narrows proximally. Inconspicuous cinclides present at least distally (Fig. 2c), forming 24 longitudinal rows (reaching proximal end at least in one specimen). Cinclides not perforated (Fig. 3b), one row in each endo- and exo-coel. Column color whitish in vivo and in preserved specimens.

Tentacles 24 in number, arranged in three cycles; about 50% longer than oral disc diameter in live specimens; inner tentacles more or less equal in length to outer ones (Fig. 2d). No apical pore. In vivo, 12 tentacles of inner cycles typically held erect, 12 of outermost cycle held parallel to substratum; tentacles completely covered in contracted specimens. Tentacles of preserved and living specimens brown. In specimens from Punta Pardelas (larger than those from Fracaso beach), 12 erected, inner tentacles brownish, with two small, whitish, V-shaped marks at adoral side of base; those 12 of outermost cycle white, with V-shaped mark at basal adoral part (to a third of tentacle length) (Fig. 2d).

Oral disc round, same diameter as column. Mouth central, elevated on a cone; lips bright red in live specimens from Punta Pardelas.

Internal anatomy: Twelve pairs of mesenteries hexamerously arranged in two cycles (6 + 6), both perfect and fertile (Fig. 3a). Equal number of mesenteries proximally and distally; mesenteries more developed distally, so second cycle of mesenteries poorly developed and without retractor muscles proximally. Two pairs of directives, one attached to differentiated and well-developed siphonoglyph; second pair of directives attached to more or less distinct fold of actinopharynx that is not histologically differentiated from the rest of actinopharynx (Fig. 3a). Gonochoric, developing oocytes and spermatid cysts (oocytes to 0.39 mm and spermatid cysts to 0.027 mm in diameter) in specimens collected in April. Retractor muscles strongly restricted, reniform (Fig. 3a). Pairs of mesenteries differentially developed: most pairs with one mesentery more developed than its partner, with larger retractor muscles

(condition more evident proximally). Parietobasilar muscles strong, differentiated on all mesenteries, with short broad processes and short free mesogloal pennon (Fig. 3a).

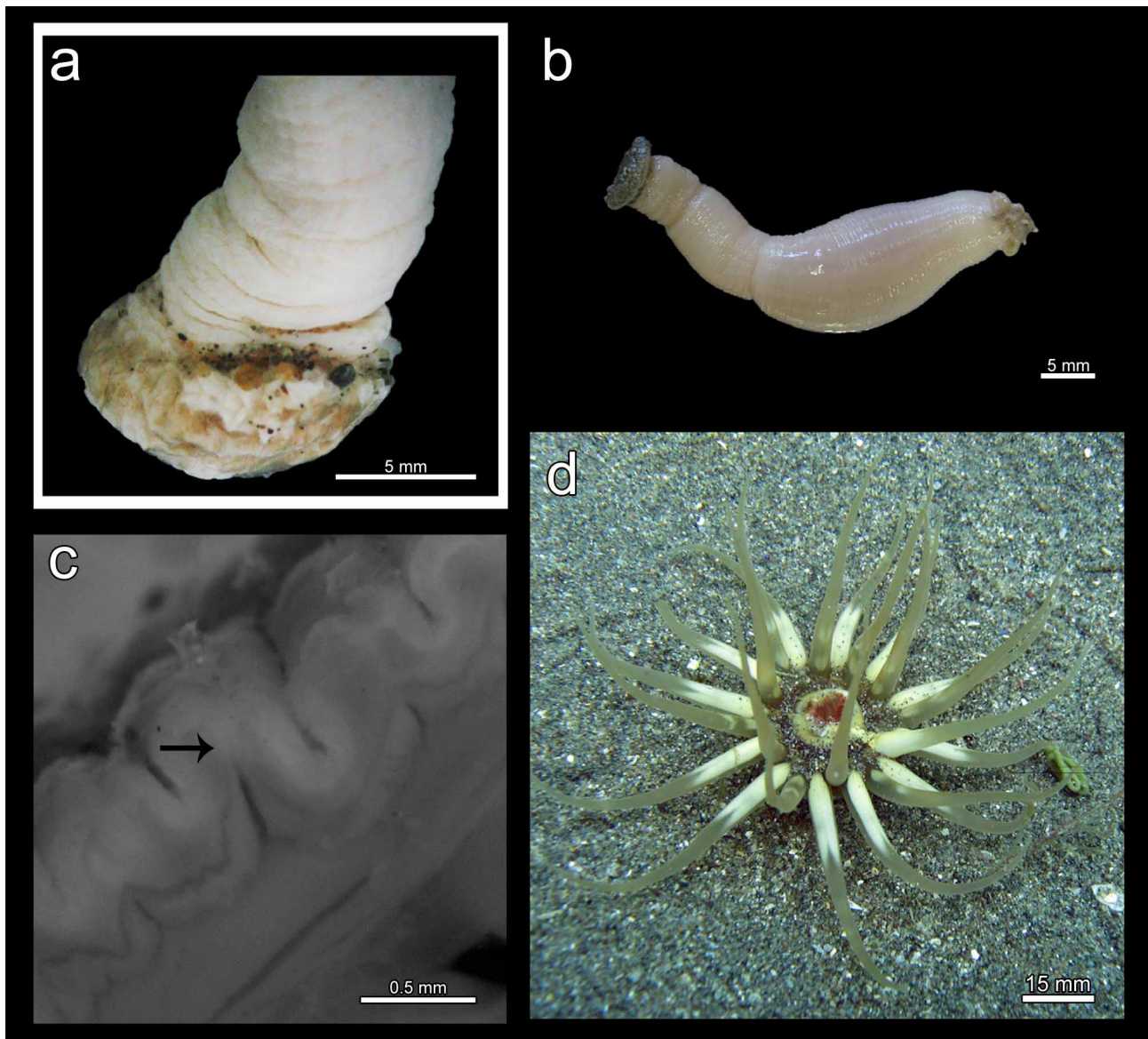


FIGURE 2. External anatomy of *Harenactis argentina* sp. nov. a) Detail of the base. b) View of a whole specimen. c) Longitudinal section of the body wall showing a cinclide (arrow). d) Oral view of a live specimen in situ.

Longitudinal muscles of tentacles and oral disc ectodermal (Figs. 3c, d). Marginal sphincter muscle absent (Fig. 3e). Mesogloea thick, to 0.78 mm; epidermis and gastrodermis 0.15–0.06 mm and 0.13–0.06 mm respectively at actinopharynx level. No basilar muscles (Fig. 3f).

Cnidom and distribution of cnidae: Spirocysts (in tentacles, column, actinopharynx and base), basitrichs (in all tissues), microbasic *p*-mastigophores (in actinopharynx and mesenterial filaments) and microbasic *b*-mastigophores (in mesenterial filaments) (Fig. 4). See table 1 for size and distribution.

Distribution and natural history. *Harenactis argentina* sp. nov. inhabits soft bottoms of the Argentinean coast of Patagonia, on both sides of Península Valdés (Villarino beach, Fracaso beach and Punta Pardelas). On Fracaso beach, *H. argentina* sp. nov. was found on the intertidal zone, to seven specimens per square meter (the subtidal zone was not explored); it was the only sea anemone present at the beach. During low tide it is possible to see the holes this sea anemone leaves in the substratum after it contracts. On Villarino beach, *H. argentina* sp. nov. was found in the intertidal zone but not in the subtidal zone. On Punta Pardelas, it was only found in the subtidal zone, starting at 5 m depth; the specimens were at least 1 m apart, co-existing with *Parabunodactis imperfecta* Zamponi & Acuña, 1992 (see Laretta *et al.* 2009), *Metridium senile lobatum* (Carlgren, 1899) and *Antholoba achatas*

TABLE 1. Sizes ranges and distribution of the cnidae of *Harenactis argentina* sp. nov. Values in parenthesis correspond to Carlgren's (1945) data for *H. attenuata*. Letters in parenthesis after the different categories of cnida indicate the corresponding image in Fig. 4; n: number of capsules measured; N: proportion of specimens with the particular type of capsule; Ab: abundance of each type of capsule: scarce (+), abundant (++) , very abundant (+++).

Tissue / Cnida type	Length (µm)	Mean (µm)	Standard deviation (µm)	Width (µm)	Mean (µm)	Standard deviation (µm)	n	N	Ab
Tentacles									
Spirocysts (a)	16.6–30.2 (to 19.7)	23.4	3.3	1.9–3.6 (3.5)	2.7	0.4	42	4/4	+++
Basitrichs (b)	21.0–25.4 (7.7–9.2/17.6–22.6)	23.6	0.9	2.0–3.5 (2.5/2.8)	2.8	0.3	41	4/4	+++
Column									
Spirocysts (c)	16.9–27.3	23.5	3.3	2.2–3.9	2.9	0.5	13	3/4	+
Basitrichs 1 (d)	16.0–18.4	17.1	0.7	1.9–2.9	2.4	0.3	20	4/4	+
Basitrichs 2 (e)	9.1–10.8 (10.0–16.9)	10.0	1.2	1.3–1.8 (1.5–2.5)	1.6	0.4	2	3/4	+
Actinopharynx									
Spirocysts (f)	18.7–27.3	23.5	2.2	2.4–5.8	4.7	0.9	19	3/4	+
Basitrichs (g)	24.3–33.2 (22.6–28.2)	27.9	1.6	2.8–4.6 (3.5)	3.6	0.4	44	4/4	+
Microbasic <i>p</i> -mastigophores (h)	21.6–27.3 (21.0–22.6)	24.2	1.5	4.1–6.0 (4.0)	5.1	0.5	38	4/4	+
Mesenterial filaments									
Microbasic <i>b</i> -mastigophores (i)	39.9–45.0	41.9	1.6	5.5–6.4	5.9	0.4	8	4/4	+
Basitrichs (j)	8.6–13.1 (18.3)	11.5	2.5	1.3–2.4 (2.8)	1.9	0.6	3	3/4	+
Microbasic <i>p</i> -mastigophores (k)	17.1–26.6 (14.1–19.7/25.4–31.0)	23.2	2.4	2.9–6.7 (4.0/4.2–5.6)	4.6	0.8	52	3/4	++
Pedal disc									
Spirocysts (l)	21.9–23.9	22.9	1.4	2.4–3.2	2.8	0.6	2	2/4	+
Basitrichs (m)	9.9–17.9	14.4	2.5	1.4–2.5	2.0	0.3	42	2/4	+++

(Drayton in Dana, 1846); this record of the two latter species extends their known distribution to the Santa Cruz province (DL pers. obs.).

Etymology. The specific epithet (*argentina*) refers to the country where the species has been found. The specific name *argentina* is used as a noun in opposition.

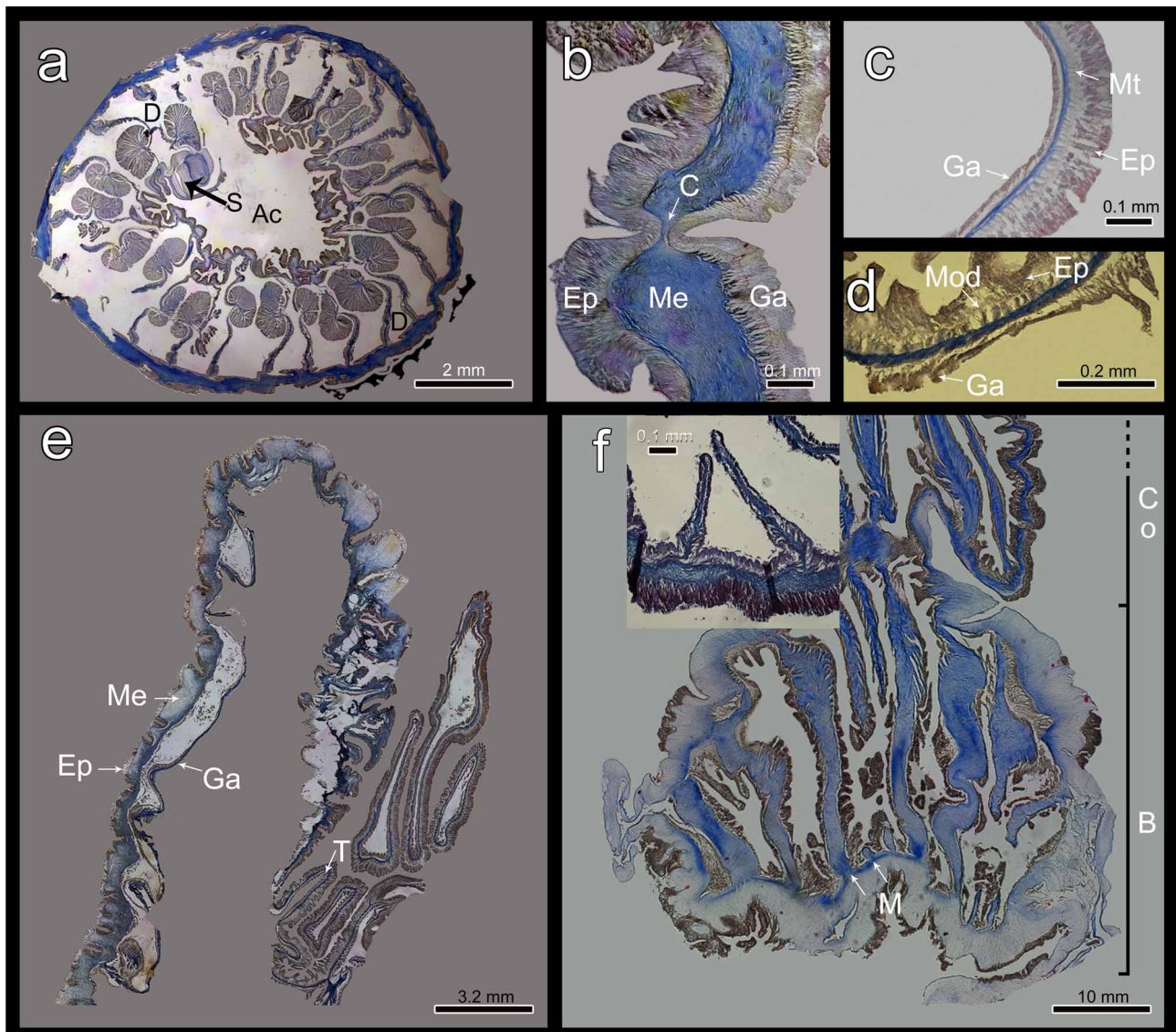


FIGURE 3. Internal anatomy of *Harenactis argentina* sp. nov. a) Cross section at the actinopharynx level showing all mesenteries perfect. b) Detail of a cinclide. c) Cross section of a tentacle showing the ectodermal longitudinal muscles. d) Cross section of the oral disc showing the ectodermal longitudinal muscles. e) Longitudinal section of distal part of the column. f) Longitudinal section of the pedal disc. Abbreviations: Ac, actinopharynx; B, base; C, cinclide; Co, column; D, directives; Ep, epidermis; Ga, gastrodermis; M, mesenteries; Me, mesogloea; Mod, longitudinal muscles of the oral disc; Mt, longitudinal muscles of the tentacle; S, siphonoglyph; T, tentacle.

Discussion

Differential diagnosis from similar species. Only four species of athenarian sea anemones have been reported from Argentina: *Scolanthus intermedius* (McMurrich, 1893) within Edwardsiidae Andres, 1881 (Carlgren 1899, 1927; McMurrich 1893), *Parahalcampa antarctica* Carlgren, 1927 within Halcampidae Andres, 1883 (Carlgren 1927), and *Peachia hastata* Gosse, 1855 and *P. koreni* McMurrich, 1893 within Haloclavidae (Acuña 1996, McMurrich 1893; Zamponi 1982). *Scolanthus intermedius* is reported for Southern Chile (51° 02'S, 74° 08'W, Magellan Strait: Punta Arenas and Gente Grande), Southern Argentina (Tierra del Fuego: Ushuaia, collected

between 11–30 m) and Antarctica (South Georgia and Graham Land) (Carlgren 1899, 1927; McMurrich 1893); however, this species is probably part of a species complex (see Carlgren 1959, Williams 1981). *Parahalcampa antarctica* is reported from Staten Island (Tierra de Fuego) from 36 m (Carlgren 1927). The diagnosis of Edwardsiidae or Halcampidae does not fit the description of our specimens at the family level. Edwardsiidae has only eight perfect mesenteries whereas our specimens have 12 pairs of perfect mesenteries; Halcampidae is characterized by having a single or double mesogloal sphincter, but a marginal sphincter is absent in our specimens.

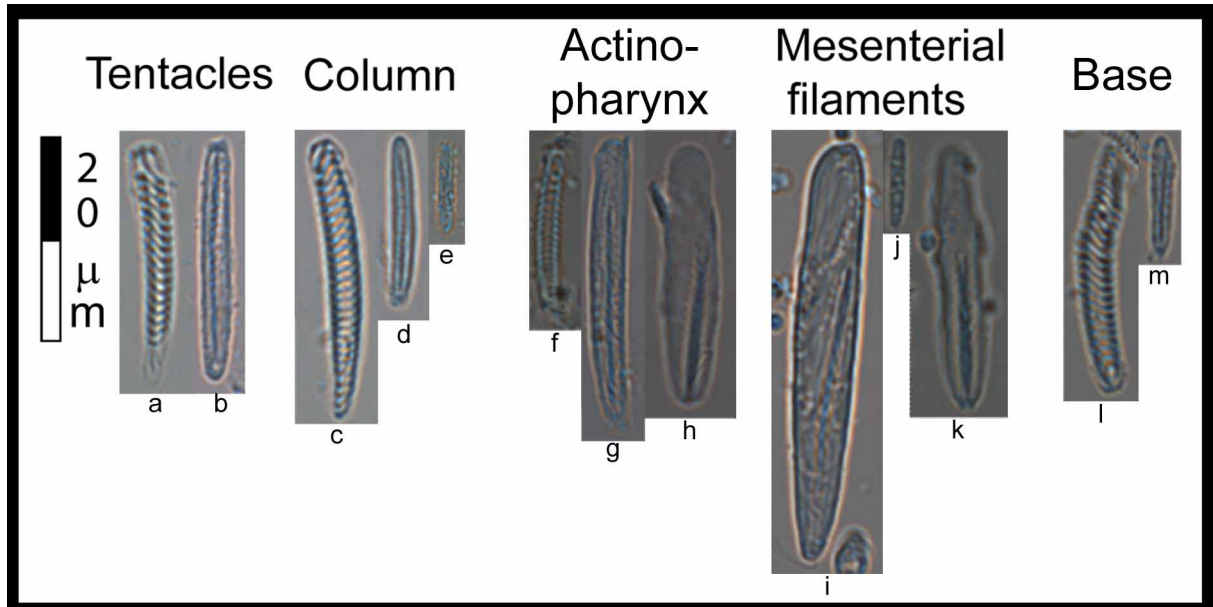


FIGURE 4. Cnidae of *Harenactis argentina* sp. nov. a) Spirocyst. b) Basitrich. c) Spirocyst. d) Basitrich 1. e) Basitrich 2. f) Spirocyst. g) Basitrich. h) Microbasic *p*-mastigophore. i) Microbasic *b*-mastigophore. j) Basitrich. k) Microbasic *p*-mastigophore. l) Spirocyst. m) Basitrich.

The family Haloclavidae currently includes 11 genera (Fautin 2010; Rodríguez & López-González 2003). Genera within Haloclavidae share relatively longer tentacles in the outer cycle and lack of basilar muscles, but are heterogeneous in terms of the column anatomy and the morphology of the sphincter muscle, which is either absent, weak and endodermal, or relatively strong and endodermal (Carlgren 1949; Rodríguez & López-González 2003; Stephenson 1935). *Peachia* includes most of the species known worldwide within Haloclavidae and the two haloclavid species reported for Argentina are attributed to this genus (Acuña 1996; McMurrich 1893; Zamponi 1982). However, *Peachia* is easily differentiated from other haloclavid genera due to a distinct external structure called the conchula; none of our specimens has a conchula.

Familial and generic placement. Because *Harenactis argentina* sp. nov. has few tentacles, at least six pairs of perfect mesenteries, a single well-developed siphonoglyph but lacks basilar muscles, acontia and marginal sphincter muscle, it corresponds to the diagnosis of the families Haloclavidae and Halcampoididae. The differences between these two families are unsatisfactory, because almost all the characters used to separate them overlap (e. g. relative size of the tentacles from inner and outer cycles: inner not shorter than the outer ones in Halcampoididae whereas inner tentacles are shorter or of same length as the outer ones in Haloclavidae; siphonoglyph: a single or no distinct siphonoglyph in Halcampoididae whereas the single siphonoglyph is usually very strong in Haloclavidae—see Carlgren 1949; Rodríguez & López-González 2003). A single, rather well-developed siphonoglyph is most common in haloclavid genera however, a strong siphonoglyph also characterizes the Halcampoididae genus *Calamactis* Carlgren, 1951 (Carlgren 1949). Thus, we have compared all genera included within the two families with our material.

Only the diagnosis of *Calamactis* (Halcampoididae) and *Harenactis* (Haloclavidae) fit the characters observed in our specimens (elongate body with physa-like aboral end; column smooth and not divisible into regions; few tentacles; 12 pairs of perfect mesenteries; a single well-developed siphonoglyph; and no marginal sphincter). Previously, *Harenactis* only included *H. attenuata*, its type species by monotypy. *Harenactis* differs from the other haloclavid genera in having longitudinal rows of cinclides distally, all mesenteries perfect, tentacles hexamerously arranged, a single siphonoglyph without conchula and not separated from actinopharynx, column not divisible into

regions, no sphincter and no acrospheres (Carlgren 1949, Rodríguez & López-González 2003). Neither the diagnosis of *Calamactis* nor the description of its only species *C. praelonga* mention cinclides (Carlgren 1949, 1951); we did not find them in our re-examination of the type material either. However, cinclides are present in *Harenactis*: "...cinclides in twenty-four regular longitudinal rows" (Torrey 1902: 384). Since both *H. attenuata* and our specimens have cinclides in 24 longitudinal rows, we place our specimens in this genus and therefore within Haloclavidae. Although *Halcampoides* (Halcampoididae) and *Anemonactis* Andres, 1881 (Haloclavidae) also have cinclides, our specimens cannot be placed within those genera; *Halcampoides* has only 12 tentacles and six pairs of mesenteries. *Anemonactis* has papillae in the column, 20 tentacles with acrospheres, and ten pairs of perfect and fertile mesenteries.

Cinclides can be hard to see and are easily overlooked, but recent works emphasized the value of this character assessing phylogenetic relationships. For example, the presence of a distal ring of cinclides links species from chemosynthetic environments without acontia with acontiarian sea anemones (Rodríguez *et al.* 2008; Rodríguez & Daly 2010; Sanamyan & Sanamyan 2007). Among Haloclavidae, the presence of longitudinal rows of cinclides on the distal column is unique to *Harenactis*. Furthermore, phylogenetic analyses of molecular data suggest that Haloclavidae is not monophyletic; the type genus, *Haloclava*, clusters with some members of Actiniidae Rafinesque, 1815 (see Berntson *et al.* 1999; Daly *et al.* 2003, 2008). On the other hand, some members of the acontiate family Haliactiidae Carlgren, 1949 are characterized by having distal longitudinal rows of cinclides (e. g. *Pelocoetes* Annandale, 1915; *Phytocoetes* Annandale, 1915; *Phytocoetopsis* Panikkar, 1936 and *Stephensonactis* Panikkar, 1936). Although other characters as microcnemes or presence of two siphonoglyphs differentiate these genera from *Harenactis* (Carlgren 1949), since the familial membership and relationships of athenarians has to be reassessed in many cases (Daly *et al.* 2008; Rodríguez *et al.* 2007), a relationship between *Harenactis* and some members of Haliactiidae may be possible.

Differential diagnosis of *Harenactis* species. *Harenactis argentina* **sp. nov.** differs from *H. attenuata* in external and internal features, cnidae and geographic distribution. In *H. attenuata*, tentacles are pale green with three or four grayish-whitish bands and a longitudinal row of fine milky white dots on each side (Torrey 1902), whereas in *H. argentina* **sp. nov.**, tentacles are brown or brownish, in the specimens from Punta Pardelas, with two small whitish V-shaped marks at the adoral side of the base and those of the outermost cycle with a white, V-shaped basal part. *Harenactis attenuata* is about three times the size of *H. argentina* **sp. nov.** (to 400 mm length and to 121 mm, respectively). In *H. argentina* **sp. nov.**, all mesenteries are fertile, whereas in *H. attenuata*, the second cycle is only occasionally fertile.

Torrey (1902) did not use the cnidom or the distribution of cnidae in the original description of *H. attenuata*; however, in comparing our data with those available from Carlgren (1945) for *H. attenuata*, we found several differences in the cnidae: *Harenactis argentina* **sp. nov.** has an additional type of nematocyst in the mesenterial filaments (microbasic *b*-mastigophores) and the distribution and size ranges of the cnidae differs between these species (see Table 1). The small basitrichs reported in tentacles of *H. attenuata* were not found in *H. argentina* **sp. nov.** We found slightly smaller basitrichs in the filaments of *H. argentina* **sp. nov.** (basitrichs 2, to 13.1 µm in *H. argentina* **sp. nov.** vs 18.3 µm in *H. attenuata*). Only one category of microbasic *p*-mastigophores with a continuous size range was found in the filaments of *H. argentina* **sp. nov.** Carlgren separated the microbasic *p*-mastigophores in the filaments of *H. attenuata* into two different categories (see Carlgren 1945 and Table 1); the size range of the only category of microbasic *p*-mastigophores in the filaments of *H. argentina* **sp. nov.** is slightly more restricted than those of *H. attenuata*. Furthermore, *H. argentina* **sp. nov.** has microbasic *b*-mastigophores in the filaments which are lacking in *H. attenuata*; the size range of these microbasic *b*-mastigophores is large enough not to be overlooked or confused with any other cnidae of either species. In addition, we found spirocysts in the column and the actinopharynx of *H. argentina*; these are not reported from *H. attenuata*. Both species also differ in distribution: *H. argentina* **sp. nov.** is reported only for the southwest Atlantic, in the waters surrounding Península Valdés, whereas *H. attenuata* is reported only for the northern hemisphere, in California (Torrey 1902) and Japan (Uchida 1938). In our opinion, the differences above described taken as a whole justify the specific distinction of *H. argentina* **sp. nov.**

Currently, no athenarian sea anemone could be confused for *Harenactis argentina* **sp. nov.** in Argentina: *H. argentina* **sp. nov.** is the first athenarian sea anemone registered for the continental Argentine intertidal zone. Nevertheless, there is one other actiniarian described from Argentina resembling *H. argentina* **sp. nov.** in external appearance and geographic distribution: *Neoparacondylactis haraldoi* Zamponi, 1974. According to the original

description, *N. haroldoi* is easily differentiated from *H. argentina* **sp. nov.** because it has basilar muscles (although not explicitly stated in the description, the genus was placed in Actiniidae and thus we assume that basilar muscles are present) and an endo-mesogloal palmate circumscript marginal sphincter (Zamponi 1974); other anatomical differences between both species are detailed in Table 2. Although most cnida data are missing and the original description of *N. haroldoi* points towards some irregularities in the mesenterial arrangement (see Zamponi 1974), we could not dissect the only undissected existing specimen of the species (the holotype) because of museum's policies. Thus, based on the original description of *N. haroldoi*, *Harenactis argentina* **sp. nov.** is a different species.

TABLE 2. Comparison between *Harenactis argentina* **sp. nov.** and *Neoparacondylactis haraldoi*.

	<i>Neoparacondylactis haraldoi</i>	<i>Harenactis argentina</i> sp. nov.
Distribution	San Matías Gulf	San José and Nuevo Gulf
Number of tentacles	24	24
Shape of base	Narrow, ampoule-like	Physa-like
Basilar muscles	Present	Absent
Sphincter	Endo-mesogloal, palmate circumscript	None
Retractor muscles	Diffuse on 1 cycle; reniform in the others	Restricted (reniform) on all mesenteries
Mesenterial cycles	6	2
Number of mesenteries	24 + 1 + 4 + 4 + 4 + 4 = 41	24
Perfect mesenteries	1st cycle	All cycles
Fertile mesenteries	3rd and 4th cycle	All cycles
Directives	1 pair	2 pairs
Siphonoglyph	1	1
More mesenteries distally than proximally	Yes	No

Acknowledgements

This work was supported by a PIP 5301, PIP 2788 and UBACyT X171 grants. Support was provided by a CONICET (Argentina) grant to DL. Guido Pastorino is thanked for the specimens collected on Villarino beach. Alejandra Lauretta helped improved the English version of the manuscript. Many thanks to *C. Damborenea* (MLP) and *S. Cairns* (USMN) for the loan of the type material of *Neoparacondylactis haraldoi* and *Calamactis praelonga*.

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