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The gastropod-symbiotic sea anemone genus *Isosicyonis* Carlgren, 1927 (Actiniaria: Actiniidae): a new species from the Weddell Sea (Antarctica) that clarifies the taxonomic position of the genus

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SUMMARY: A second species of the sea anemone genus *Isosicyonis* is described and illustrated from 16 specimens collected in the Weddell Sea (Antarctica) on the *Polarstern* cruises ANT XVII/3, ANT XXI/2 and ANT XXIII/8. *Isosicyonis striata* n. sp. is easily distinguishable externally from the other species of the genus *Isosicyonis alba* by its pattern: white longitudinal stripes on the column, oral disc, and tentacles. It is also distinguished by internal features including the retractor muscles, parietobasilar muscles, marginal sphincter muscles, number of mesenteries, and cnidae. The genus *Isosycionis* is currently only known from the Southern Ocean. Both species of *Isosicyonis* live in association with a gastropod, with a single sea anemone occupying almost the whole shell of its gastropod host. The description of this new species, and our re-examination of *Isosicyonis alba*, resolves the controversial higher taxonomic position of the genus, confirming its placement within the Endomyaria.

Keywords: sea anemone, Actiniaria, Actiniidae, Endomyaria, Mesomyaria, Antarctica.

RESUMEN: EL GÉNERO DE ANÉMONA DE MAR SIMBIONTE CON GASTERÓPODOS *ISOSICYONIS* CARLGREN, 1927 (ACTINIARIA, ACTINIIDAE): UNA NUEVA ESPECIE DEL MAR DE WEDDELL (ANTÁRTIDA) CLARIFICANDO LA POSICIÓN TAXONÓMICA DEL GÉNERO. – La segunda especie del género de anémonas de mar *Isosicyonis* es descrita e ilustrada a partir de 16 ejemplares recolectados durante las campañas oceanográficas *Polarstern* ANT XVII/3, ANT XXI/2 y ANT XXIII/8 en el mar de Weddell (Antártida). *Isosicyonis striata* n. sp. se distingue fácilmente externamente de la otra especie del género, *Isosicyonis alba*, por su patrón cromático con líneas longitudinales blancas en la columna, disco oral y tentáculos. Además, esta nueva especie se diferencia en caracteres internos que incluyen las musculaturas del esfínter marginal, retractora y parietobasilar, el número de mesenterios y cnidae. Actualmente, el género *Isosycionis* sólo se conoce en el océano Sur. Ambas especies de *Isosicyonis* viven en asociación con un gasterópodo, con una sola anémona que ocupa casi toda la concha del hospedador. La descripción de esta nueva especie, así como el reexamen de *Isosicyonis alba* acaba con la controversia sobre la posición taxonómica superior del género, confirmando su emplazamiento en Endomyaria.

Palabras clave: anémona de mar, Actiniaria, Actiniidae, Endomyaria, Mesomyaria, Antártida.

INTRODUCTION

The genus *Isosycionis* Carlgren, 1927 is currently only known from the Southern Ocean. Members of this genus live in association with gastropods of the genus *Harpovoluta*, with a single sea anemone covering almost the entire shell of its gastropod host (Riemann-Zürneck, 1980; Fautin, 1984). Although *Isosicyonis* is currently placed within the Endomyaria (Actiniidae), its higher taxonomic position is equivocal due to the nature of the marginal sphincter (Riemann-Zürneck, 1980; Fautin, 1984). In the type species of the genus, *Isosicyonis alba* (Studer, 1879), the marginal sphincter has been described as intermediate between meso-endodermal and endodermal, and may vary in development (Carlgren, 1927, 1949; Riemann-Zürneck, 1980; Fautin, 1984). The intermediate nature of the sphincter raises the question of whether *Isosycionis* belongs to "Tribus" Endomyaria or Mesomyaria, or whether it represents a transitional form between them. In turn, this uncertainly raises questions about the origin and significance of the marginal sphincter (Carlgren, 1927, 1949; Riemann-Zürneck, 1980). In addition, Riemann-Zürneck (1980) questioned whether *Isosicyonis* belonged in Actiniidae, pointing out that the marginal sphincter muscles and the cnidom of *I. alba* did not correspond to those of the family Actiniidae; however, she did not suggest any alternative placement.

Our description of *Isosicyonis striata* n. sp., a new species of *Isosicyonis* from the Weddell Sea, and our re-description of *I. alba* allow us to address these larger taxonomic questions. We re-describe and illustrate *I. alba* based on newly collected material, and provide a similar treatment of the characters in order to compare the similarities and differences of the two species in the genus. We find that *Isosicyonis* has an endodermal marginal sphincter, and thus belongs to Endomyaria. We concur with Riemann-Zürneck's (1980) observation that the basitrichs of the column are particularly large in *Isosicyonis*. However, we found that the cnidae of *I. striata* n. sp. are generally smaller than those of *I. alba*, thus diminishing the distinctiveness of the cnidom of *Isosicyonis* as compared to other groups within Actiniidae.

MATERIAL AND METHODS

The material we studied was collected on the R/V *Polarstern* cruises ANT XV/3, ANT XVII/3, ANT XIX/3, ANT XIX/5, ANT XXI/2 and ANT XXIII/8 to the Weddell Sea, Antarctic Peninsula, and Scotia Arc, Antarctica, sponsored by the Alfred-Wegener-Institut für Polar- und Meeresforschung in Bremerhaven, from 1998 to 2007 (Table 1). Sea anemones were relaxed on board using menthol crystals and photographed alive. Small pieces of tissue from selected specimens were preserved in absolute ethanol for DNA analysis, and then the animals were fixed in 10% seawater formalin. Fragments of several specimens were dehydrated in butanol (Johansen, 1940), and embedded in paraffin. Histological sections 7-8 μm thick were stained with Ramón y Cajal's Triple Stain (Gabe, 1968).

Squash preparations of cnidae from preserved material were measured at 1000x magnification with Nomarski differential interference contrast optics. The nomenclature for cnidae is from Mariscal (1974) and Östman (2000), with modifications: the nomenclature for basitrichs and microbasic *b*-mastigophores follows Carlgren (1940) and Mariscal (1974). Cnidae capsules were chosen randomly for measurement. The frequencies given are subjective impressions based on squash preparations. The presence of each type of cnidae in each tissue was confirmed in histological sections of the tissues.

The newly collected material has been deposited in the Zoologisches Institut und Zoologisches Museum in Hamburg (ZMH), the National Museum of Natural History, Smithsonian Institution in Washington (USMN), and the collection of the research team "Biodiversidad y Ecología de Invertebrados Marinos" at the University of Seville in Spain (BEIM). For the purpose of comparison, we examined the holotype (which is in three pieces) from the Swedish Natural History Museum (SMNH): *Paractis alba* Studer, 1879. Type-56. "*Gazelle Exp*.; O. Patagonien; 60 fathoms; Det. Studer". Also labelled: "Holotype according to Fautin, 2002".

The lists of citations for the described species are not exhaustive; we provide only those references in which the species is discussed in detail suitable for taxonomic identification.

RESULTS

Order Actiniaria Hertwig, 1882
Suborden Nynantheae Carlgren, 1899
Family Actiniidae Rafinesque, 1815
Genus *Isosicyonis* Carlgren, 1927

Diagnosis: Actiniidae with very wide pedal disc, enclosing shells of gastropods. Column smooth, broad proximally, with well developed fosse. Marginal sphincter muscle meso-endodermal to endodermal, diffuse to restricted. Tentacles up to 80, conical, in two or four cycles, about same number or half as numerous as the mesenteries. Longitudinal

Table 1. – Collection data of the material studied. Abbreviations: 1) Gear: AGT, Agassiz trawl; BT, bottom trawl; D, small trawl; 2) Areas: AUS, Austasen; BB, Burdwood Banc; BFS, Bransfield strait; DP, Drake Passage; EI, Elephant Island; HB, Halley Bay; JV, Joinville Island; KG, King George Island; KN, Kapp Norvegia; N/NK, north Kapp Norvegia; P, Antarctic Peninsula; SO, South Orkney Islands; SS, South Shetland Islands; S/VK, South VestKapp; W/D, West Deception Island.

Cruise	Station	Coordinates	Area	Depth (m)	Date	Gear
ANT XV/3	PS48/095	73°33.50'S 22°15.30'W	S/VK	920-866	05/02/1998	BT
ANT XV/3	PS48/097	73° 35.80'S 22°12.90'W	S/VK	629-659	05/02/1998	BT
ANT XV/3	PS48/100	73°36.40'S 22º07.00'W	S/VK	440-444	05/02/1998	BT
ANT XV/3	PS48/120	73°33.50'S 22°14.80'W	S/VK	928-826	07/02/1998	BT
ANT XV/3	PS48/123	73°35.80'S 22°14.60'W	S/VK	638-670	07/02.1998	BT
ANT XV/3	PS48/150	74°38.00'S 27°00.20'W	HB	710-758	11/02/1998	BT
ANT XV/3	PS48/168	75°26.30'S 26°41.70'W	HB	233-228	12/02/1998	BT
ANT XV/3	PS48/194	71°14.10'S 12°27.70'W	KN	244-246	16/02/1998	AGT
ANT XV/3	PS48/197	71°17.00'S 12°36.30'W	KN	415-416	16/02/1998	AGT
ANT XV/3	PS48/206	71°00.40'S 11°42.60'W	KN	602-594	18/02/1998	AGT
ANT XV/3	PS48/220	70º50.40'S 10º35.40'W	KN	236-272	19/02/1998	BT
ANT XV/3	PS48/222	70º50.60'S 10º35.50'W	KN	234-267	19/02/1998	BT
ANT XV/3	PS48/303	62°16.50'S 58°43.10'W	KG	430-450	14/03/1998	AGT
ANT XV/3	PS48/338	61°33.90'S 58°11.00'W	DP	417-416	19/03/1998	AGT
ANT XVII/3	PS56/085-1	71°11.30'S 12°15.40'W	KN	309-318	02/04/2000	BT
ANT XVII/3	PS56/135-1	70°50.20'S 10°34.70'W	AUS	274-273	10/04/2000	BT
ANT XVII/3	PS56/136-1	70°50.20'S 10°35.40'W	AUS	271-251	10/04/2000	BT
ANT XVII/3	PS56/158-1	63°04.70'S 57°31.60'W	BFS	94-95	26/04/2000	AGT/D
ANT XVII/3	PS56/159-1	62º55.20'S 57º39.20'W	BFS	214-218	26/04/2000	AGT
ANT XVII/3	PS56/165-1	63°00.80'S 59°06.90'W	BFS	621-618	28/04/2000	AGT/D
ANT XVII/3	PS56/166-1	63°02.30'S 59°10.40'W	BFS	666-673	28/04/2000	BT
ANT XVII/3	PS56/173-1	63°01.20'S 61°08.70'W	W/D	352-379	30/04/2000	BT
ANT XVII/3	PS56/177-1	62°49.50'S 60°49.30'W	W/D	202-200	01/05/2000	BT
ANT XVII/3	PS56/178-2	61º58.50'S 60º18.70'W	W/D	804-930	02/05/2000	BT
ANT XVII/3	PS56/183-1	62º06.70'S 60º21.70'W	W/D	200-204	03/05/2000	BT
ANT XVII/3	PS56/184-1	62º00.90'S 60º20.70'W	W/D	338-374	03/05/2000	BT
ANT XIX/3	PS61/045-1	60°59.14'S 55°11.38'W	EI	196-269	29/01/2002	BT
ANT XIX/3	PS61/058-1	60°59.76'S 55°43.16'W	EI	106-113	01/02/2002	BT
ANT XIX/3	PS61/059-1	61º25.42'S 56º08.90'W	EI	298-326	02/02/2002	BT
ANT XIX/3	PS61/065-1	60°52.51'S 55°29.65'W	DP	242-250	03/02/2002	BT
ANT XIX/3	PS61/067-1	60°55.89'S 55°27.63'W	EI	114-181	04/02/2002	BT
ANT XIX/3	PS61/068-1	60°55.14'S 55°39.16'W	EI	164	04/02/2002	BT
ANT XIX/3	PS61/070-1	60°57.76'S 55°54.43'W	DP	202-212	05/02/2002	BT
ANT XIX/3	PS61/071-1	60°59.95'S 55°51.81'W	DP	165-170	05/02/2002	BT
ANT XIX/3	PS61/103-1	61º44.90'S 58º 01.04'W	DP	256-296	13/02/2002	BT
ANT XIX/3	PS61/121-1	61°23.55'S 61°24.20'W	DP	297-363	18/02/2002	BT
ANT XIX/3	PS61/124-1	62°26.28'S 55°44.36'W	P	217-220	21/02/2002	BT
ANT XIX/3	PS61/125-1	62°34.63'S 55°39.96'W	P	157-167	21/02/2002	BT
ANT XIX/5	PS61/150-1	54°30.22'S 56°08.20'W	BB	286-290	06/04/2002	AGT
ANT XIX/5	PS61/231-1	60°59.19'S 46°27.42'W	SO	402-399	22/04/2002	AGT
ANT XIX/5	PS61/253-1	61°23.40'S 55°26.99'W	EI	282-276	25/04/2002	BT
ANT XXI/2	PS65/090-1	70°56.14'S 10°31.70'W	AUS	278-288	09/12/2003	AGT
ANT XXI/2	PS65/166-1	70°56.83'S 10°32.61'W	AUS	338-258	15/12/2003	BT
ANT XXI/2	PS65/173-1	70°56.82'S 10°31.76'W	AUS	296-279	16/12/2003	AGT
ANT XXI/2	PS65/245-1	70°56.74'S 10°42.60'W	AUS	318-337	22/12/2003	BT
ANT XXI/2	PS65/336-1	70°56.59'S 10°31.86'W	AUS	276-281	05/01/2004	AGT
ANT XXIII/8	PS69/622-1	60°56.70'S 55°52.71'W	DP	218-307	23/12/2006	BT
ANT XXIII/8	PS69/623-1	60°58.00'S 55°54.63'W	DP	209-214	23/12/2006	BT
ANT XXIII/8	PS69/624-1	61°0.33'S 55°51.03'W	DP	151-186	23/12/2006	BT
ANT XXIII/8	PS69/626-1	60°58.70'S 55°49.68'W	DP	164-241	24/12/2006	BT
ANT XXIII/8	PS69/628-1	61°00.45'S 55°45.62'W	EI	159-166	24/12/2006	BT
ANT XXIII/8	PS69/631-1	61°01.37'S 55°51.41'W	EI	146-161	25/12/2006	BT
ANT XXIII/8	PS69/632-1	60°59.36'S 55°49.22'W	DP	144-158	25/12/2006	BT
ANT XXIII/8	PS69/633-1	61°0.25'S 55°53.11'W	EI	168-213	25/12/2006	BT
ANT XXIII/8	PS69/634-1	61°0.98'S 55°56.23'W	EI	275-278	25/12/2006	BT
ANT XXIII/8	PS69/637-1	61°05.67'S 56°10.00'W	EI	357-425	26/12/2006	BT
ANT XXIII/8	PS69/640-1	61°12.72'S 55°52.29'W	EI	136-154	26/12/2006	BT
ANT XXIII/8	PS69/641-3	61°06.36'S 55°53.84'W	EI	132-133	26/12/2006	AGT
ANT XXIII/8	PS69/644-1	61°03.19'S 55°54.36'W	EI	150-187	27/12/2006	BT
ANT XXIII/8	PS69/646-1	61°00.79'S 55°58.23'W	EI	277-315	27/12/2006	BT
ANT XXIII/8	PS69/647-1	61°00.35'S 55°58.17'W	EI	282-288	27/12/2006	BT

TABLE 1 (Cont.). – Collection data of the material studied. Abbreviations: 1) Gear: AGT, Agassiz trawl; BT, bottom trawl; D, small trawl; 2) Areas: AUS, Austasen; BB, Burdwood Banc; BFS, Bransfield strait; DP, Drake Passage; EI, Elephant Island; HB, Halley Bay; JV, Joinville Island; KG, King George Island; KN, Kapp Norvegia; N/NK, north Kapp Norvegia; P, Antarctic Peninsula; SO, South Orkney Islands; SS, South Shetland Islands; S/VK, South VestKapp; W/D, West Deception Island.

Cruise	Station	Coordinates	Area	Depth (m)	Date	Gear
ANT XXIII/8	PS69/648-1	61°04.70'S 56°01.30'W	EI	241-265	27/12/2006	BT
ANT XXIII/8	PS69/652-1	61°24.42'S 56°09.49'W	EI	179-305	28/12/2006	BT
ANT XXIII/8	PS69/653-1	61°18.54'S 55°57.92'W	EI	305-343	28/12/2006	BT
ANT XXIII/8	PS69/657-1	61°13.48'S 55°49.41'W	EI	131-133	29/12/2006	BT
ANT XXIII/8	PS69/663-1	61°38.26'S 57°29.85'W	SS	414-432	30/12/2006	BT
ANT XXIII/8	PS69/668-1	61°49.10'S 58°36.69'W	SS	193-205	31/12/2006	BT
ANT XXIII/8	PS69/672-1	62°07.22'S 59°27.99'W	SS	84-95	01/01/2007	BT
ANT XXIII/8	PS69/674-1	62°00.20'S 59°54.14'W	SS	259-286	01/01/2007	BT
ANT XXIII/8	PS69/676-1	62°11.06'S 60°47.49'W	SS	418-472	02/01/2007	BT
ANT XXIII/8	PS69/677-1	62°10.94'S 60°34.93'W	SS	204-209	02/01/2007	BT
ANT XXIII/8	PS69/680-1	62°24.13'S 61°24.06'W	SS	336-341	02/01/2007	BT
ANT XXIII/8	PS69/682-1	62°33.78'S 61°49.03'W	SS	169-175	03/01/2007	BT
ANT XXIII/8	PS69/686-1	62°33.40'S 55°27.87'W	JV	158-167	04/01/2007	BT
ANT XXIII/8	PS69/687-1	62°34.46'S 54°43.91'W	JV	263-271	04/01/2007	BT
ANT XXIII/8	PS69/689-5	62°27.20'S 55°25.93'W	JV	210-211	04/01/2007	D
ANT XXIII/8	PS69/690-1	62°12.88'S 55°17.06'W	JV	354-360	05/01/2007	BT
ANT XXIII/8	PS69/692-1	62°20.73'S 55°37.30'W	JV	276-305	05/01/2007	BT
ANT XXIII/8	PS69/693-1	62°25.71'S 55°38.35'W	JV	236-243	05/01/2007	BT
ANT XXIII/8	PS69/695-1	63°00.58'S 58°41.21'W	JV	268-289	06/01/2007	BT
ANT XXIII/8	PS69/722-6	64°41.35'S 60°31.81'W	P	272-279	21/01/2007	D
ANT XXIII/8	PS69/728-2	63°42.63'S 56°01.63'W	JV	293-298	24/01/2007	AGT

muscles of tentacles and radial muscles of oral disc ectodermal, very strong. One or two siphonoglyphs, well developed if present. One or two pairs of directives. To about 20 pairs of mesenteries perfect, filamented and sterile; an equal or higher number of imperfect mesenteries, fertile but most without filaments. Retractor and parietobasilar muscles weak or well developed. Cnidom: spirocysts, basitrichs, microbasic *b*-mastigophores, microbasic *p*-mastigophores, and atrichs. Type species: *Paractis alba* Studer, 1879.

Nominal species of the genus: *Isosicyonis alba* Studer, 1879; *Isosicyonis striata* n. sp.

Remarks: The diagnosis of the genus is modified from Carlgren (1949) with changes underlined. This was necessary to include *Isosicyonis striata* n. sp.

Isosicyonis alba (Studer, 1879)
(Figs. 1-4, Table 2)

Paractis alba Studer, 1879: 545; Ridley, 1882: 101.
Paractis studerii Andres, 1883: 271.
Isosicyonis alba, Carlgren, 1927: 52; Carlgren, 1949: 42, 57; Riemann-Zürneck, 1980: 19, 24, 32; Fautin, 1984: 9.

Material examined: *Polarstern* ANT XV/3: st. PS48/095 (BEIM: ANT-4243, 1 specimen); st. PS48/097 (BEIM: ANT-4382, 4 specimens; BEIM: ANT-4383, 4 specimens); st. PS48/100 (BEIM: ANT-4278, 1 specimen; BEIM: ANT-4412, 7 specimens; BEIM: ANT-4411, 7 specimens; ZMH: C 11713, 8 specimens); st. PS48/120 (ZMH: C 11715, 3 specimens BEIM: ANT-4453, 1 specimen); st. PS48/123 (ZMH: C 11714, 6 specimens); st. PS48/150 (BEIM: ANT-4233, 4 specimens); st. PS48/168 (BEIM: ANT-4282, 2 specimens); st. PS48/194 (BEIM: ANT-4281, 1 specimen; BEIM: ANT-4283, 2 specimens); st. PS48/197 (BEIM: ANT-4384, 1 specimen); st. PS48/206 (BEIM: ANT-4402, 1 specimen); st. PS48/220 (BEIM: ANT-4233, 1 specimen); st. PS48/222 (BEIM: ANT-4273, 1 specimens); st. PS48/303 (BEIM: ANT-4436, 3 specimens); st. PS48/338 (BEIM: ANT-4228, 2 specimens).
Polarstern ANT XVII/3: st. PS56/135-1 (BEIM: ANT-4577, 1 specimen); st. PS56/136-1 (BEIM: ANT-4567, 1 specimen; BEIM: ANT-4571, 1 specimen); st. PS56/158-1 (BEIM: ANT-4540, 1 specimen); st. PS56/159-1 (BEIM: ANT-4516, 1 specimen); st. PS56/165-1 (BEIM: ANT-4538, 1 specimen); st. PS56/166-1 (BEIM: ANT-4469, 2 specimens); st. PS56/173-1 (BEIM: ANT-4474, 1 specimens; BEIM: ANT-4475, 1 specimens; BEIM: ANT-4515, 1 specimen; BEIM: ANT-4517, 1 specimen); st. PS56/177-1 (BEIM: ANT-4527, 3 specimens; BEIM: ANT-4537, 1 specimen); st. PS56/178-2 (BEIM: ANT-4586, 3 specimens); st. PS56/183-1 (BEIM: ANT-4504, 4 specimens; BEIM: ANT-4591, 10 specimens); st. PS56/184-1 (BEIM: ANT-4480, 2 specimens).
Polarstern ANT XIX/3: st. PS61/045-1 (BEIM: ANT-4053, 1 specimen); st. PS61/58-1 (BEIM: ANT-4070, 2 specimens); st. PS61/59-1 (BEIM: ANT-4084, 1 specimen); st. PS61/65-1 (BEIM: ANT-4059, 2 specimens); st. PS61/67-1 (BEIM: ANT-4072, 3 specimens); st. PS61/68-1 (BEIM: ANT-4168, 14 specimens); st. PS61/70-1 (BEIM: ANT-4142, 1 specimen); st. PS61/071-1 (BEIM: ANT-4068, 2 specimens); st. PS61/103-1 (BEIM: ANT-4058, 6 specimens); st. PS61/121-1 (BEIM: ANT-4021, 1 specimen); st. PS61/124-1 (BEIM: ANT-4082, 2 specimens); st. PS61/125-1 (BEIM: ANT-4185, 1 specimen).
Polarstern ANT XIX/5: st. PS61/150-1 (BEIM: ANT-4746, 1 specimen); st. PS61/231-1 (BEIM: ANT-4655, 3 specimens); st. PS61/253-1 (BEIM: ANT-4656, 1 specimen; BEIM: ANT-4670, 1 specimen).
Polarstern ANT XXIII/8: st. PS69/622-1 (BEIM: ANT-6000, 3 specimens); st. PS69/623-1 (BEIM: ANT-6001, 3 specimens); st. PS69/624-1 (BEIM: ANT-6002, 2 specimens); st. PS69/626-1 (BEIM: ANT-6003, 1 specimen); st. PS69/628-1 (BEIM: ANT-6004, 8 specimens); st. PS69/631-1 (BEIM: ANT-6005, 6 specimens); st. PS69/632-1 (BEIM: ANT-6006, 1 specimen); st. PS69/633-1 (BEIM: ANT-6007, 5 specimens); st. PS69/634-1 (BEIM: ANT-6008, 4 specimens); st. PS69/637-1 (BEIM:

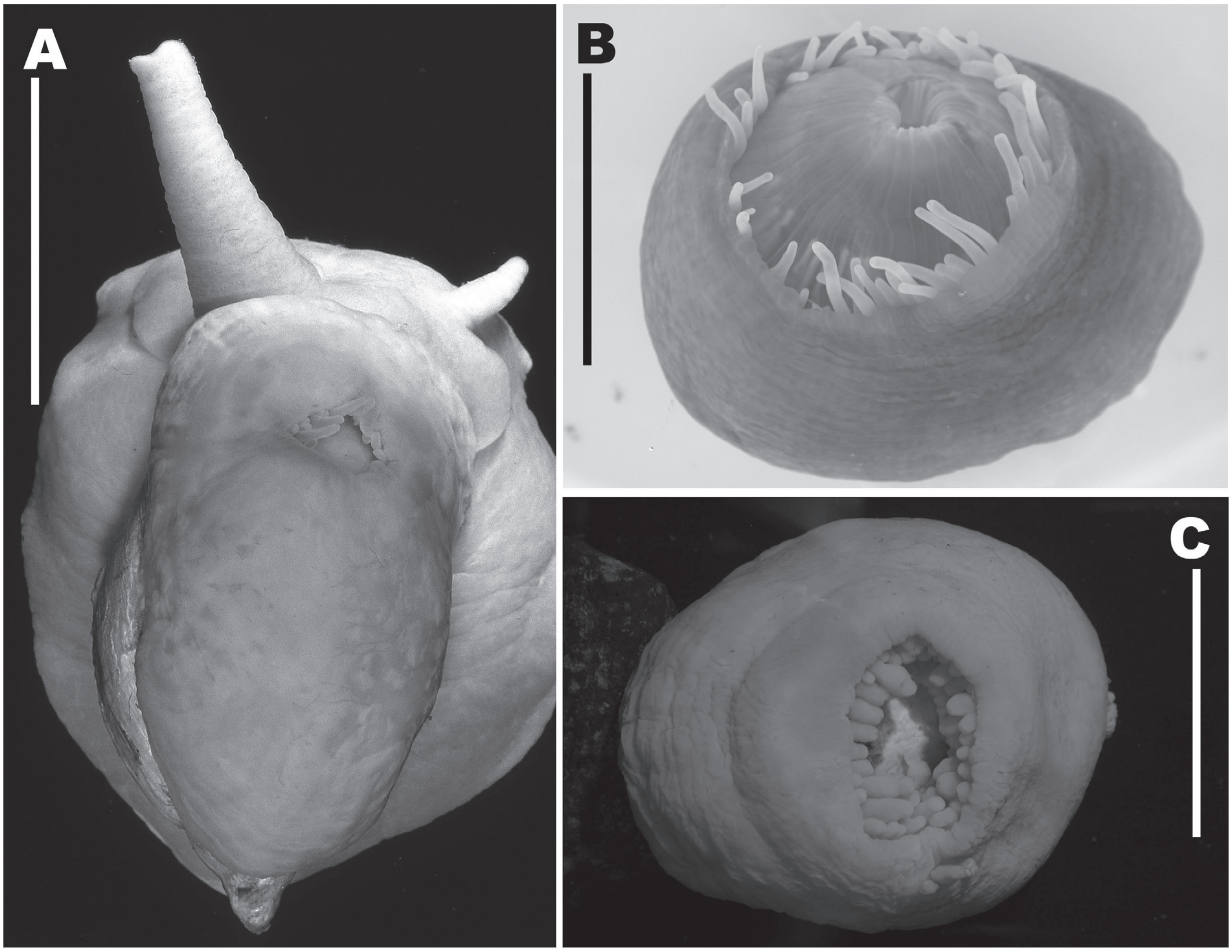

Fig. 1. – *Isosicyonis alba* (Studer, 1879). External anatomy: A) oral view of living contracted specimen [BEIM(ANT-4676)]; B) lateral-oral view of living expanded specimen [BEIM(ANT-4070)]; C) oral view of preserved specimen [BEIM(ANT-4591)]. Scale bars: A, B, C, 20 mm.

ANT-6009, 1 specimen); st. PS69/640-1 (BEIM: ANT-6010, 2 specimens); st. PS69/641-3 (BEIM: ANT-6011, 5 specimens); st. PS69/644-1 (BEIM: ANT-6012, 2 specimens); st. PS69/646-1 (BEIM: ANT-6013, 5 specimens); st. PS69/647-1 (BEIM: ANT-6014, 2 specimens); st. PS69/648-1 (BEIM: ANT-6016, 1 specimen); st. PS69/652-1 (BEIM: ANT-6017, 1 specimen); st. PS69/653-1 (BEIM: ANT-6018, 1 specimen); st. PS69/657-1 (BEIM: ANT-6019, 2 specimens); st. PS69/663-1 (BEIM: ANT-6020, 1 specimen); st. PS69/668-1 (BEIM: ANT-6021, 1 specimen); st. PS69/672-1 (BEIM: ANT-6022, 3 specimens); st. PS69/674-1 (BEIM: ANT-6023, 2 specimens); st. PS69/676-1 (BEIM: ANT-6024, 2 specimens); st. PS69/677-1 (BEIM: ANT-6025, 1 specimen); st. PS69/680-1 (BEIM: ANT-6026, 2 specimens); st. PS69/682-1 (BEIM: ANT-6027, 2 specimens); st. PS69/689-5 (BEIM: ANT-6028, 1 specimen); st. PS69/690-1 (BEIM: ANT-6029, 3 specimens); st. PS69/692-1 (BEIM: ANT-6030, 1 specimen); st. PS69/693-1 (BEIM: ANT-6031, 1 specimen); st. PS69/695-1 (BEIM: ANT-6032, 1 specimen); st. PS69/728-2 (BEIM: ANT-6033, 3 specimens).

External anatomy (Fig. 1). Pedal disc wider than column, major axis to 54 mm diameter, extremely thin, concave, conforms to shape of gastropod shell.

Column flattened in oral-aboral axis, smooth, more or less corrugated in preserved specimens, to 30 mm height. Mesenterial insertions visible in most proximal part of column, near limbus. Fosse not prominent.

Oral disc to 28 mm wide in retracted preserved specimens but tentacles and mouth visible. Mesenterial insertions visible. Internal surface of pedal disc visible through gaping, large, central mouth. Tentacles about 80, restricted to margin, apparently in two cycles; all of similar size, delicate and smooth in living and relaxed specimens, to 15 mm length; in preserved specimens to 7.5 mm length, digiform, transversely sulcated, with perforated tip.

Internal anatomy (Fig. 2): Same number of mesenteries proximally and distally, between 48 and 68 pairs, hexamerously arranged in five cycles: first, second, and part of third cycle (to 18 pairs in examined material) perfect, sterile with mesenterial filament, remaining pairs imperfect, fertile but most

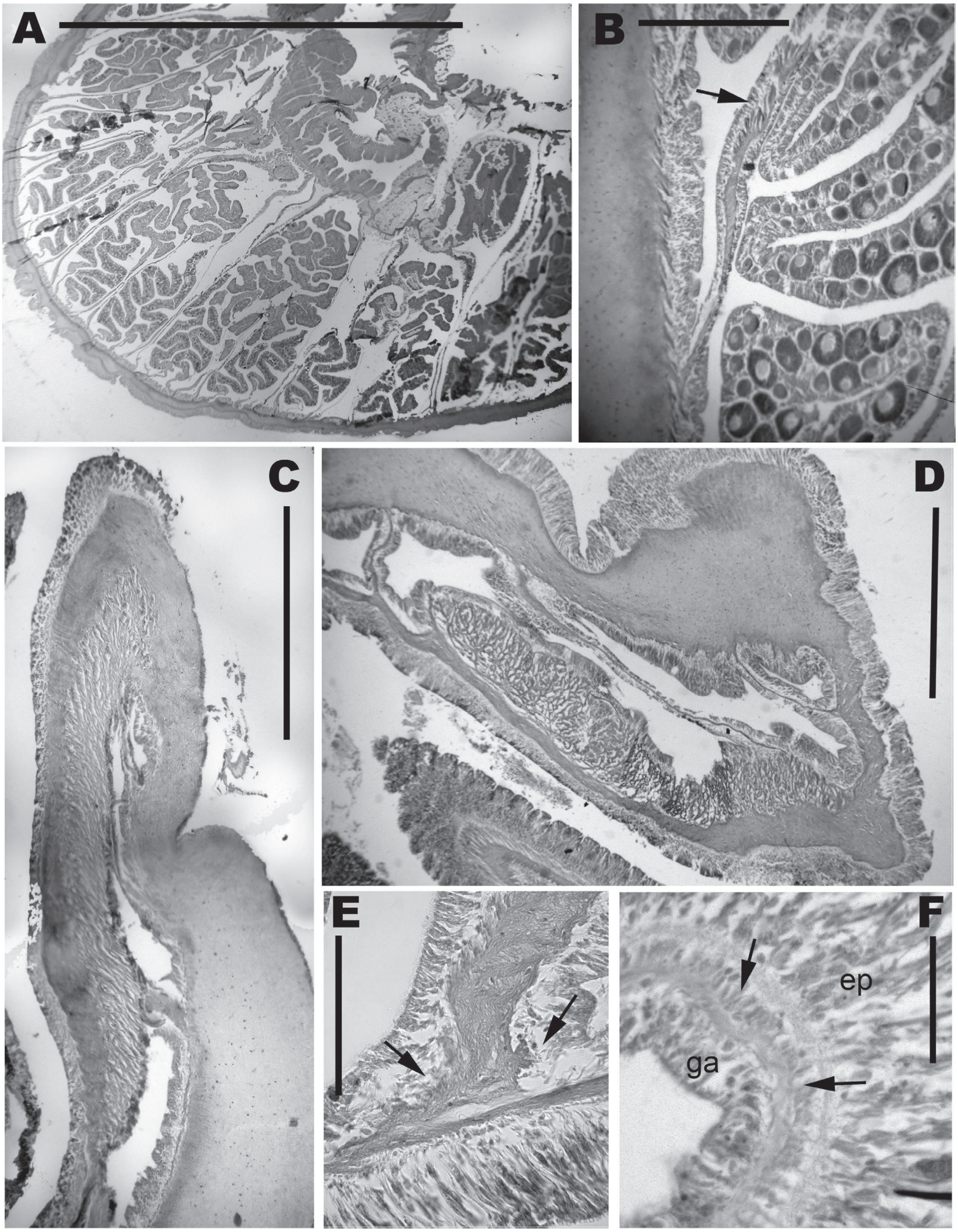

FIG. 2. – *Isosicyonis alba* (Studer, 1879). Internal anatomy: A) cross section at the actinopharynx level [BEIM(ANT-4591)]; B) detail of weak retractor muscles (arrow) and developing oocytes [BEIM(ANT-4591)]; C) longitudinal section of distal margin column showing the meso-endodermal sphincter [BEIM(ANT-4411)]; D) detail of diffuse endodermal sphincter [BEIM(ANT-4591)]; E) detail of basilar muscles [BEIM(ANT-4591)]; F) cross section of the ectodermal longitudinal muscles of the tentacles [BEIM(ANT-4411)]. Scale bars: A, 10 mm; B, 0.5 mm; C, 1 mm; D, 0.4 mm; E, 0.1 mm; F, 0.5 mm. Abbreviations: ep, epidermis; ga, gastrodermis.

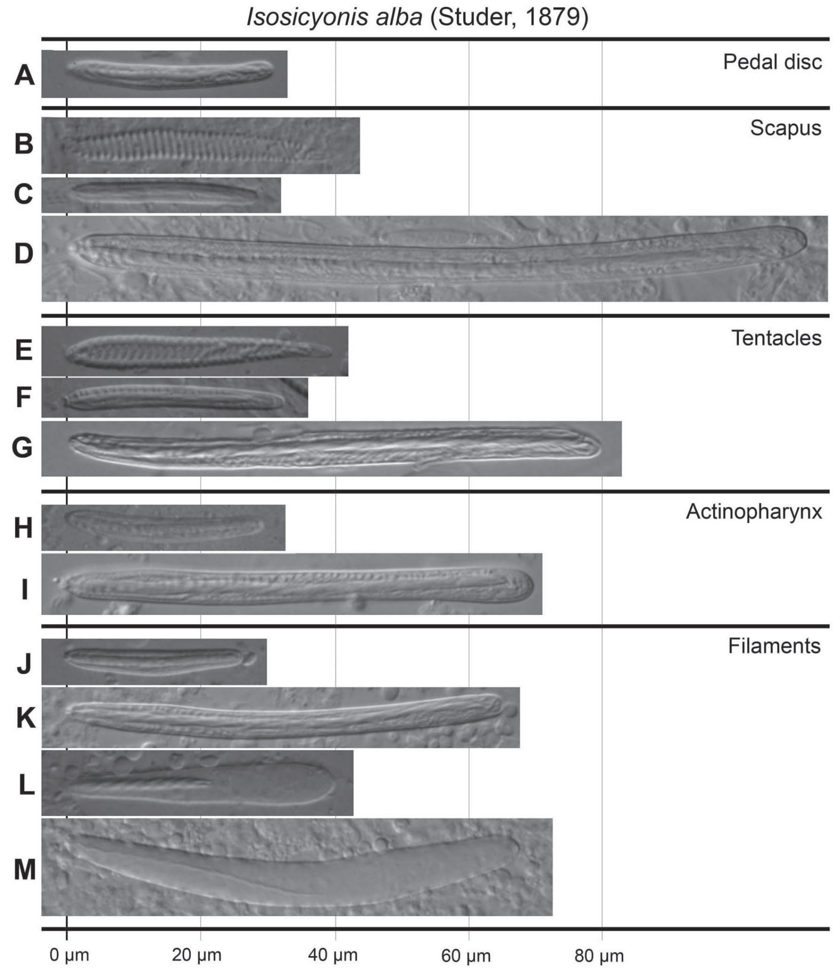

Fig. 3. – *Isosicyonis alba* (Studer, 1879). Cnidae: A) basitrich; B) spirocyst; C) basitrich 1; D) basitrich 2; E) spirocyst; F) basitrich 1; G) basitrich 3; H) basitrich 1; I) basitrich 2; J) basitrich 1; K) basitrich 2; L) microbasic *p*-mastigophore; M) microbasic *b*-mastigophore.

without mesenterial filament; fifth cycle incomplete, members of a pair unequally developed. Two pairs of sterile directives. Siphonoglyphs not differentiated. Gonochoric, developing oocytes and spermatic vesicles (oocytes 0.03-0.18 mm, spermatic vesicles 0.09-0.3 mm in diameter) in specimens collected from February to May. Retractor muscles diffuse, weak. Parietobasilar muscles not differentiated. Basilar muscles well developed.

Marginal sphincter muscles meso-endodermal to endodermal, diffuse (Fig. 2C, D). Longitudinal tentacle muscles and oral disc muscles ectodermal. Body wall thickness decreases from the margin to the limbus: mesogloea 0.17-0.32 mm, epidermis 0.15-0.35 mm, gastrodermis 0.10-0.12 mm at actinopharynx level.

Cnidom (Fig. 3, Table 2): Spirocysts, basitrichs, microbasic *b*-mastigophores, microbasic *p*-mastigophores.

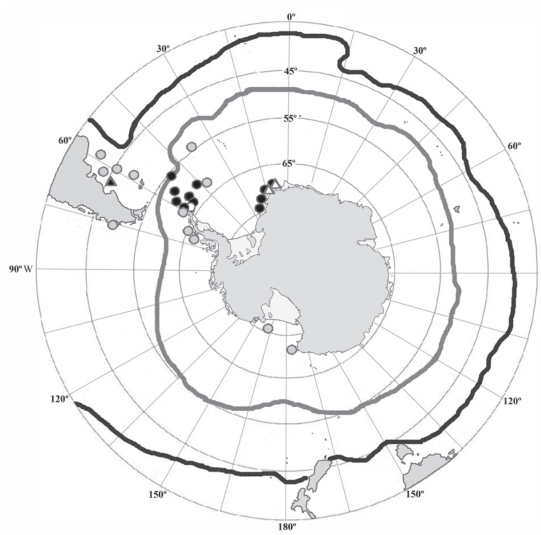

Fig. 4. – Geographic distribution of the species. *Isosicyonis alba* (Studer, 1879): black triangle, type locality; grey circles, previous localities where the species has been reported; black circles, localities from the present study. *Isosicyonis striata* n. sp.: white triangle, type locality; white circle, additional localities. Black line, Subtropical Front; grey line, Polar Front.

TABLE 2. – Size ranges of the cnidae of *Isosicyonis striata* n. sp. (BEIM: ANT-4555, ANT-4929, ANT-4944, ANT-4945) and *I. alba* (Studer, 1879) (BEIM: ANT-4411, ANT-4537, ANT-4591). S: sample, the ratio indicates the number of specimens in which each cnidae was found compared to the number of specimens examined. N: indicates the total number of capsules measured. F: Frequency: +++ = very common, ++ = common, + = rather common, --- = sporadic. Abbreviations: Mc, Microbasic.

Categories	Range of length and width of capsules (μm) of *I. striata* n. sp.	S	N	F	Data *I. alba* (present study)	S	N	F	Data *I. alba* (Fautin, 1984)	S	N	Data *I. alba* (Riemann-Zürneck, 1980)
PEDAL DISC												
Basitrichs	No data				26.0-28.0 x 3.0-4.0	1/2	4	---	No data			22-25 x 3
SCAPUS												
Spirocysts		0/5			32.0-95.0 x 4.0-7.0	3/5	24	+	33.5-67.0 x 2.5-5.0	6/7	26	60 x 5
Basitrichs 1	15.0-$\overline{37.0}$ x 3.0-4.0	5/5	63	+/++	24.0-43.0 x 3.0-4.0	5/5	27	+	21.1-34.7 x 2.3-3.5	6/7	25	
Basitrichs 2	—	0/5			107.0-140.0 x 6.0-11.0	5/5	41	+++	93.0-116.6 x 4.8-6.2	7/7	33	61.5-$\overline{93}$ x 4-5.5
TENTACLES												
Spirocysts	21.0-35.0 x 3.0-6.0	3/3	60	++/+++	21.0-54.0 x 3.0-6.0	3/3	51	+++	21.1-50.8 x 2.5-5.0	7/7	59	47 x 4
Basitrichs 1	15.0-29.0 x 3.0-4.0	3/3	60	++/+++	22.0-37.0 x 3.0-4.0	3/3	9	+	21.1-37.2 x 2.5-3.7	5/7	14	
Basitrichs 2	36.0-47.0 x 3.0-5.0	3/3	60	++/+++	55.0-88.0 x 3.0-6.0	3/3	55	++	49.6-75.6 x 3.1-5.2	7/7	63	64-$\overline{74}$ x 3.5-4
ACTINOPHARYNX												
Basitrichs 1	18.0-28.0 x 3.0-4.0	2/3	8	---	26.0-31.0 x 4.0	3/3	5	---				
Basitrichs 2	32.0-47.0 x 4.0-5.0	3/3	60	++/+++	35.0-82.0 x 4.0-6.0	3/3	63	+++	47.1-$\overline{67.0}$ x 4.3-5.5	7/7	47	37-$\overline{55}$ x 3-4
FILAMENTS												
Basitrichs 1	18.0-30.0 x 3.0-4.0	4/4	60	++	22.0-31.0 x 3.0-4.0	3/3	53	++	21.1-34.7 x 2.7-3.9	6/7	37	17-26 x 2.5-3
Basitrichs 2	—	0/4			56.0-65.0 x 4.0-5.0	2/3	4	---	40.9-59.2 x 3.7-5.2	4/7	19	
Mc. *p*-mastigophores	—	0/4			28.0-48.0 x 4.0-6.0	3/3	43	++	31.0-38.4 x 3.5-5.6(*)	5/7	12	32-$\overline{35}$ x 4.5
Mc. *b*-mastigophores	—	0/4			49.0-83.0 x 6.0-11.0	3/3	45	++	52.1-65.7 x 5.2-7.4	6/7	27	46.6-67 x 6-7.5
Atrichs	33.0-$\overline{44.0}$ x 4.0-6.0	4/4	61	++/+++	—	0/3						

(*) This category is named as microbasic *b*-mastigophores by Fautin (1984).

Colour (Fig. 1). Column, tentacles, and actinopharynx of living specimens whitish-pink to light brownish. Preserved specimens pinkish to yellowish.

Geographic and bathymetric distribution: *Isosicyonis alba* is an Antarctic and sub-Antarctic species, probably circumpolar, from shelf and bathyal depths (Fig. 4). The type locality of *I. alba* is off the coast of Argentina (Studer, 1879). It has also been reported from the Chilean coast, Antarctic Peninsula, South Shetland Islands, South Orkney Islands, and the Ross Sea, between 100 and 800 meters depth (Ridley, 1882; Fautin, 1984; Riemann-Zürneck, 1986; Zamponi *et al*., 1998).

We report it for the first time here in the eastern Weddell Sea, and expand its known bathymetric range to 84-928 m.

Isosicyonis striata n. sp.
(Figs. 4-7, Table 2)

Material examined: *Polarstern* ANT XVII/3: st. PS56/085-1 (BEIM: ANT-4555, 2 specimens; BEIM: ANT-4714, 1 specimen).
Polarstern ANT XXI/2: st. PS65/090-1 (BEIM: ANT-4808, 1 specimen); st. PS65/166-1 (ZMH: C 11712, holotype); st. PS65/173-1 (BEIM: ANT-4944, 1 specimen; BEIM: ANT-4945, 2 specimens); st. PS65/245-1 (BEIM: ANT-6034, 1 specimen); st. PS65/336-1 (BEIM: ANT-4942, 1 specimen).
Polarstern ANT XXIII/8: st. PS69/686-1 (USMN: 1110556, 1 specimen); st. PS69/687-1 (BEIM: ANT-6035, 3 specimens); st. PS69/692-1 (BEIM: ANT-6036, 1 specimen); st. PS69/693-1 (BEIM: ANT-6037, 1 specimen); st. PS69/722-6 (BEIM: ANT-6038, 1 specimen).

External anatomy (Fig. 5): Pedal disc wider than column, major axis to 23 mm in diameter, thin, concave, conforms to shape of gastropod shell.

Column relatively tall in oral-aboral axis, smooth, more or less corrugated in preserved and contracted specimens, to 11 mm height. Mesenterial insertions visible in most proximal part of column, near limbus. Fosse not prominent.

Oral disc to 10 mm diameter in preserved specimens, slightly wider than column in expanded specimens. Mesenterial insertions visible. Large, central mouth. Tentacles to 48, restricted to margin, in two cycles; all of similar size, delicate and smooth in living and relaxed specimens, to 10 mm long; in

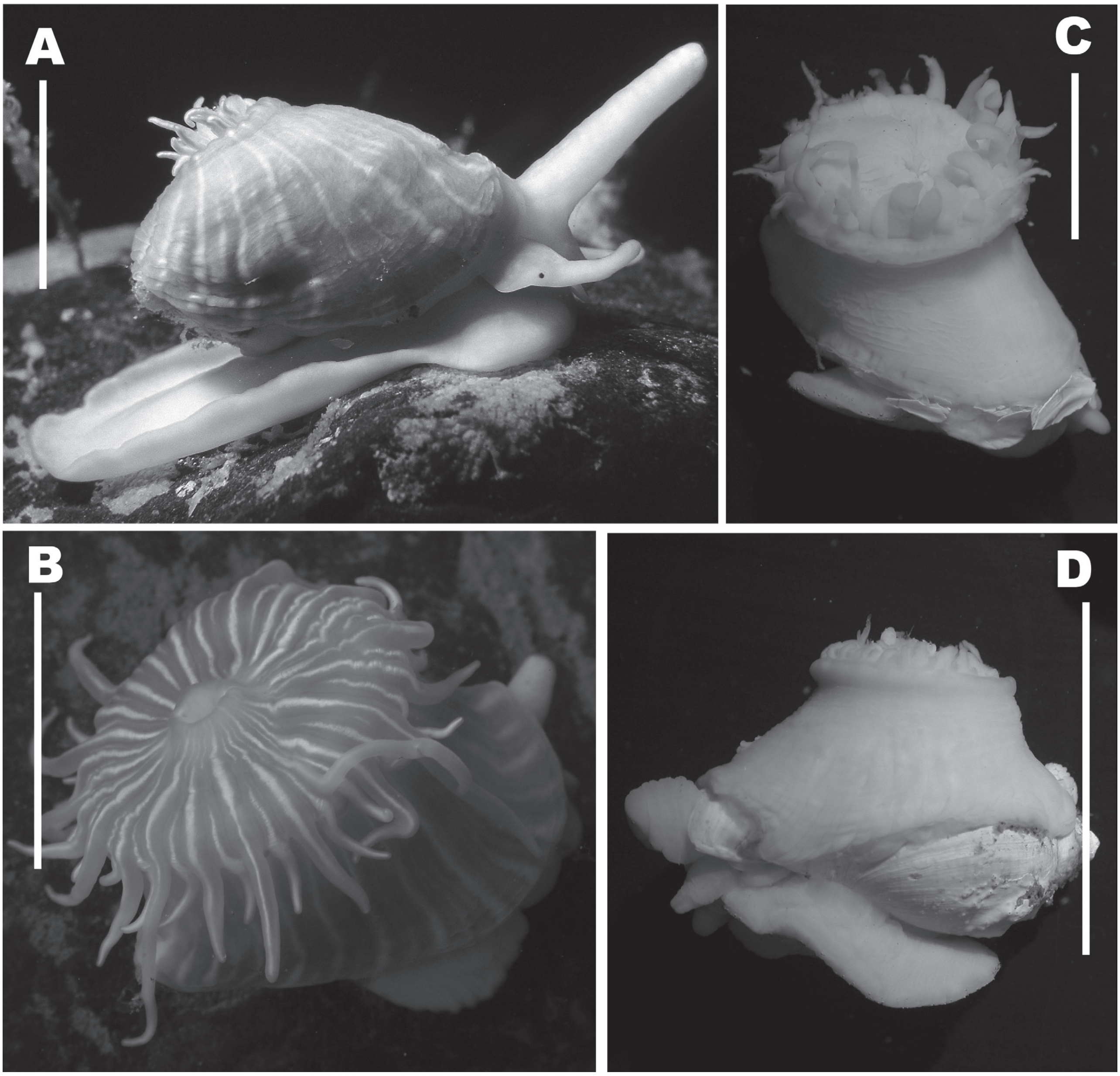

FIG. 5. – *Isosicyonis striata* n. sp. External anatomy: A) lateral view of a semi-expanded living specimen on the host [BEIM(ANT-4555)]; B) lateral-oral view of a living specimen with expanded oral disc showing the pattern [BEIM(ANT-4944)]; C) lateral view of a preserved specimen on its host [BEIM(ANT-4555)]; D) lateral view of a preserved specimen on its host [BEIM(ANT-4555)]. Scale bars: A, B, C, 10 mm; D, 20 mm

preserved specimens to 4 mm length, digiform, and transversely sulcate.

Internal anatomy (Fig. 6): Same number of mesenteries proximally and distally, to 42 pairs in examined specimens, hexamerously arranged in four cycles: first and part of second cycle (to 10 pairs in examined material) perfect, sterile, with mesenterial filaments; rest of second cycle and third cycle imperfect, fertile, usually without mesenterial filaments; forth cycle incomplete, members of a pair unequally developed (Fig. 6C). One pair of sterile directives attached to a single well-differentiated siphonoglyph (Fig. 6A, B). Gonochoric, developing oocytes and spermatic vesicles (oocytes 0.04-0.18 mm, spermatic vesicles 0.06-0.3 mm in diameter) in specimens collected in December and April. Retractor muscles diffuse. Parietobasilar muscles well developed in stronger mesenteries, differentiated as independent lamella. Basilar muscles well developed.

Marginal sphincter muscles endodermal, strong, restricted (Fig. 6E). Longitudinal tentacle muscles

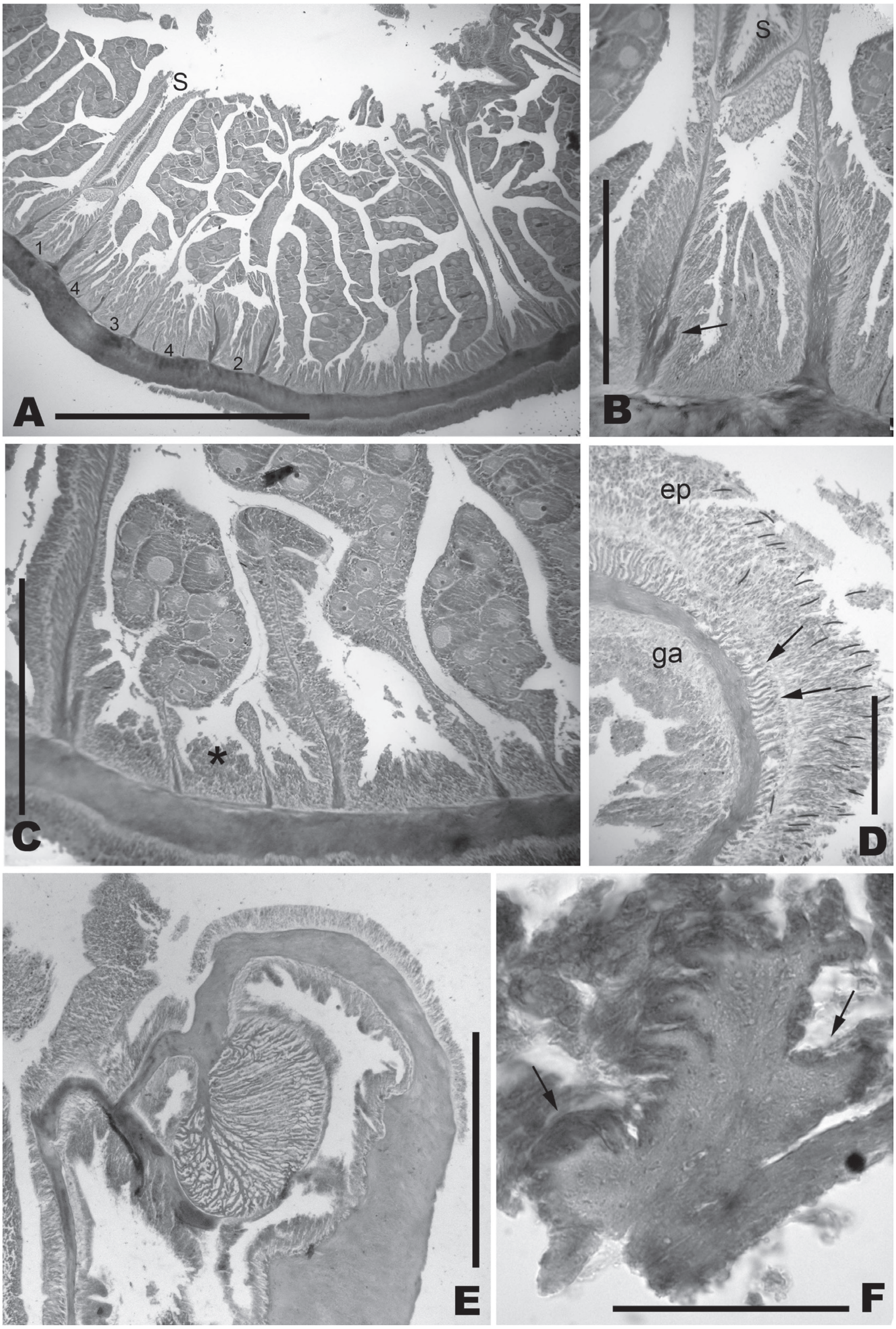

Fig. 6. – *Isosicyonis striata* n. sp. Internal anatomy, [BEIM(ANT-4945)]: A) cross section at the actinopharynx level; B) detail of directive mesenteries attached to the siphonoglyph and parietobasilar muscles (arrow); C) detail of unequally developed mesenteries of a pair (*) and developing oocytes; D) cross section of the ectodermal longitudinal muscles of the tentacles (arrows); E) longitudinal section of distal margin column showing the strong endodermal sphincter [ZMH(C 11712)]; F) cross section of pedal disc showing basilar muscles (arrows). Scale bars: A, 2.5 mm; B, 0.5 mm; C, 0.5 mm; D, 0.2 mm; E, 1 mm; F, 0.5 mm. Abbreviations: ep, epidermis; ga, gastrodermis, S, siphonoglyph; 1, endocoele between pairs of mesenteries of first cycle; 2, endocoele between pairs of mesenteries of second cycle; 3, endocoele between pairs of mesenteries of third cycle; 4, endocoele between pairs of mesenteries of fourth cycle.

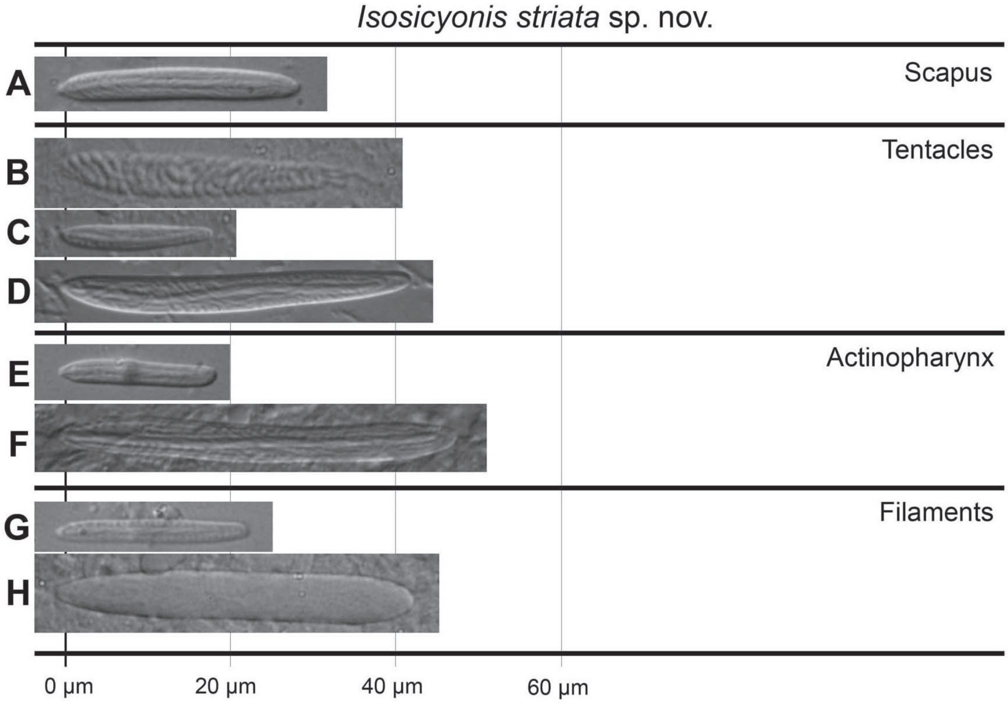

FIG. 7. – *Isosicyonis striata* n. sp. Cnidae: A) basitrich; B) spirocyst; C) basitrich 1; D) basitrich 2; E) basitrich 1; F) basitrich 2; G) basitrich; H) atrich

and oral disc muscles ectodermal. Body wall same thickness from margin to limbus: mesogloea 0.10-0.15 mm, epidermis 0.10-0.20 mm, gastrodermis 0.20-25 mm at actinopharynx level.

Cnidom (Fig. 7, Table 2): Spirocysts, atrichs, basitrichs.

Colour (Fig. 5): Column, tentacles, and actinopharynx of living specimens brown. Column with white-yellowish longitudinal stripes. Oral disc with white radial stripes that extend onto oral side of tentacles. Preserved specimens pinkish or yellowish.

Geographic and bathymetric distribution: *Isosicyonis striata* n. sp. is endemic to the Antarctic continental shelf (Fig. 4), having been collected only in the Weddell Sea at depths from 158 to 338 m.

DISCUSSION

Variability of *Isosicyonis alba*

The material studied agrees with previous descriptions of *Isosicyonis alba* (Studer, 1879; Carlgren, 1927; Riemann-Zürneck, 1980; Fautin, 1984). It corresponds in the distribution, types and categories of the cnidae, and in the chromatic patterns with material identified as *I. alba* by Fautin (1984). We concur with Fautin (1984) regarding the material studied and described by Riemann-Zürneck (1980): the cnidae in the material studied by Riemann-Zürneck (1980) are generally smaller than the cnidae of the Antarctic material, and the Antarctic material includes some categories of cnidae that are absent in Riemann-Zürneck's material (Table 2). The most significant difference between the two previous accounts is the differences in the categories of cnidae in the mesenterial filaments. Riemann-Zürneck (1980) refers to microbasic *p*-mastigophores, whereas Fautin (1984) refers to microbasic *b*-mastigophores. Although it is true that the capsules are difficult to differentiate, we agree with Riemann-Zürneck that they are microbasic *p*-mastigophores (Fig. 3L). We interpret the slight differences in size of cnidae to population-level differences. Riemann-Zürneck (1980) studied specimens from sub-Antarctic waters off the Argentinean coast, whereas Fautin (1984) studied material from Antarctic waters.

All of the specimens of *Isosicyonis alba* we studied have two pairs of directive mesenteries. We saw no differentiated siphonoglyphs associated with the directives. The siphonoglyphs were also not clear to Carlgren (1927), who observed only one pair of directives. Riemann-Zürneck (1980) and Fautin

(1984) described *I. alba* with two pairs of directives and two siphonoglyphs. The anatomy of this species is difficult to interpret and it is possible that there are two weak siphonoglyphs.

We found *Isosicyonis alba* associated with the gastropod identified as *Harpovoluta charcoti* (Lamy, 1910) (K. Linse pers. com.). One polyp takes up the whole gastropod shell, leaving the parietal and palatal edges of the shell free. Nevertheless, previous descriptions of *I. alba* identified the gastropod as *Provocator corderoi* Carcelles, 1947 (Riemann-Zürneck, 1980) or as *Provocator* sp. (Fautin, 1984). The specimens studied by Riemann-Zürneck (1980) are from the sub-Antarctic region, off the Argentinean coast; similarly, *P. corderoi* is distributed in sub-Antarctic waters, along the Argentinean coast to the Falkland Islands.

Isosicyonis striata n. sp.

Isosicyonis striata n. sp. is different from its congener *I. alba* in its chromatic pattern, cnidae, internal anatomy, and some details of its general morphology. Among our specimens of *Isosicyonis*, we could distinguish three chromatic patterns: column yellowish-pinkish; column and oral disc brownish, with tentacles slightly lighter; column and tentacles brownish with yellow-whitish longitudinal stripes (the stripes are radial in the oral disc). We consider the first two patterns as variants of *I. alba* and the third one diagnostic of *I. striata* n. sp.

The distribution and categories of cnidae in *Isosicyonis striata* n. sp. differ from those of *I. alba*. The characteristically large basitrichs and spirocysts in the scapus of *I. alba* are absent in *I. striata* n. sp. The basitrichs from the tentacles and filaments are smaller in *I. striata* n. sp. than in *I. alba*, with size ranges that do not overlap in the case of tentacle basitrichs. The larger category of basitrichs, and the microbasic *p*- and *b*-mastigophores of the filaments of *I. alba* are absent in *I. striata* n. sp. Furthermore, we found a category of nematocyst in the filaments of *I. striata* n. sp. that does not overlap in size with the microbasic *b*-mastigophores of the filaments of *I. alba*. These nematocysts are absent in *I. alba*. There is no evidence of distinguishable shaft or spines therefore we identified these as atrichs; however, most atrichs are found to be holotrichs (Cutress, 1955; Westfall, 1965). We will refer to these cnidae as atrichs in *I. striata* n. sp. pending further study. Spirocysts, basitrichs, and microbasic *p*-mastigophores are the most common cnidae in actiniarians (Carlgren, 1949; Fautin, 1988). Holotrichs are common in acrorhagi and catch tentacles of actiniids, and also in the tentacles of actinostolids from chemosynthetic habitats (see Fautin and Hessler, 1989; López-González *et al*., 2003, 2005; Daly and Gusmão, 2007; Sanamyan and Sanamyan, 2007). Although they are not typically found in the filaments of actiniarians, this is not the first time they have been reported from these structures (e.g., Sanamyan and Sanamyan, 2007). Moreover, holotrichs might be inducible, so systematic weight should not be attached to their presence/absence (Fautin, 1988; Edmands and Fautin, 1991). Thus, we considered the presence (and the relatively high abundance in all examined specimens) of these nematocysts in the filaments of *I. striata* n. sp. very remarkable, but not sufficient justification to place it in a different genus to *I. alba*. In our opinion, both species share enough similarities in general morphology, internal anatomy, and ecological habits (see below) to belong to the same genus.

Isosicyonis alba and *I. striata* n. sp. also differ in their retractor and parietobasilar musculature. In *I. alba*, these muscles are very small, almost invisible, whereas in *I. striata* n. sp., they are distinctly developed. The parietobasilar muscle of *I. striata* n. sp. is differentiated as an independent lamella in the stronger mesenteries (Fig. 6A, B, C). Furthermore, the marginal endodermal sphincter is stronger and more restricted in *I. striata* n. sp. than in *I. alba*.

We could only observe clearly one pair of directive mesenteries attached to a single well-differentiated siphonoglyph in *Isosicyonis striata* n. sp. There are fewer cycles of mesenteries in *I. striata* n. sp. than in *I. alba*. However, this could be due to the size of the animal, as all the specimens collected of *I. striata* n. sp. are smaller than the those of *I. alba*. The shape of the column is of debatable value as a taxonomic feature because of its variability according to the degree of contraction (Shick, 1991); nevertheless, in *I. striata* n. sp., the column is remarkably longer than in *I. alba*.

The geographic and bathymetric distributions of both species overlap: *Isosicyonis alba* has been found mainly off the Argentinean coast, the Scotia arc, the Antarctic Peninsula and the Ross Sea, whereas the known distribution of *I. striata* n. sp. is restricted to Antarctic waters of the Weddell Sea. However, there is general concern about the real limits of the geographic and bathymetric distribution of newly or recently described species, especially of those from areas such as the Southern Ocean where sampling effort has been heterogeneous. In Antarctica, we have always found *I. striata* n. sp. and *I. alba* associated with the gastropod identified as *Harpovoluta charcoti* (K. Linse pers. com.). Specimens of *I. alba* from the Argentinean coast are associated with gastropods identified as *Provocator corderoi,* a species not present in Antarctica.

Taxonomic position of the genus *Isosicyonis*

In his speculative treatment of the origin, development, and evolutionary meaning of the mesogleal and endodermal sphincter, Carlgren (1927) placed *Isosicyonis alba* within Mesomyaria. However, in 1949 he revised his opinion, placing it instead in Endomyaria. Carlgren (1949) described the sphincter as mesogloeal in small specimens and endodermal in large ones. However, Riemann-Zürneck (1980) described the reverse, considering the sphincter mesogloeal in large specimens and endodermal in small ones; she hypothesized that the apparently endodermal nature of the sphincter relates to the shape the anemone adopts when adapting to the gastropod's shell. Based on this interpretation, and on the cnidom of *I. alba*, Riemann-Zürneck (1980) argued for removing *Isosicyonis* from Actiniidae, but did not propose any alternative placement for the genus. Fautin (1984) concurred with Riemann-Zürneck (1980) regarding the nature of the sphincter of *I. alba*. However, the sphincter muscles of her larger specimens of *I. alba* do not have such an endodermal appearance as those described by Riemann-Zürneck (1980), and she therefore argued for further study of the sphincter before assigning *Isosicyonis* to a new higher taxon (Fautin, 1984).

Only the smaller specimens of *Isosicyonis alba* examined in the present study show a meso-endodermal to endodermal morphology of the sphincter (Fig. 2C). Large specimens show an endodermal but diffuse sphincter (Fig. 2D). The endodermal nature of the sphincter does not seem to be due to the effects of the anemones adapting their shape to the gastropod's shell. It seems more probable to us that it is more difficult to observe and interpret this small muscle in histological sections of small individuals. Furthermore, the endodermal nature of the sphincter of *I. striata* n. sp. is clear. Molecular evidence supports the placement of *Isosicyonis* within Actiniidae (unpublished data).

One remarkable characteristic of the cnidom of the two species of *Isosicyonis* is the large basitrichs of the tentacles and column (especially in the column of *I. alba*). Despite the comments by Riemann-Zürneck (1980), large basitrichs are common in other taxa currently placed in Actiniidae, including the genera *Bolocera* and *Phymactis* among others (see Fautin, 1984; Häussermann, 2004). Nevertheless, the family Actiniidae is one of the largest families of Actiniaria (Carlgren, 1949), and its monophyly is far from certain (Daly *et al*., 2003); thus, it is probably necessary to subdivide this family. More studies on the phylogeny of Actiniaria and on the significance of the cnidom are necessary to address this question.

Another feature of the genus *Isosicyonis* is the symbiotic association of its species with gastropods. Currently, sea anemone species known to live in symbiosis with gastropods or associated with their shells belong to four families: Hormathiidae, Sagartiidae, Sagartiomorphidae (the three families included in Acontiaria), and Actiniidae (Endomyaria) (Carlgren, 1949; Daly *et al*., 2004). The relationship between *Isosicyonis* and the other actiniid symbiotic genus, *Stylobates* Dall, 1903, and the relationship of these to the acontiarian symbiotic genera, remains to be investigated further.

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