

A new species of sea anemone from Chile, *Anemonia alicemartinae* n. sp. (Cnidaria: Anthozoa). An invader or an indicator for environmental change in shallow water?

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Abstract

The new species, *Anemonia alicemartinae* (Actiniidae), is described from rocky shores of north and central Chile. Its members' abundance, occurrence in exposed positions, and bright red colour make it one of the most eye-catching species of northern Chile. The description is based on 74 specimens collected between 1975 and 2001, and on live observations of several hundred animals in their habitats and in aquaria. The natural microhabitats are positions exposed to currents but protected from surge surf, ranging from tide pools down to depths of 16 m. In 1998, the southern distribution limit was 37° S, the southernmost extent of the southerly Chile Coastal Countercurrent. The species is similar to *Anemonia natalensis* and *Pseudactinia varia* from South Africa. The most distinctive features of *A. alicemartinae* n. sp. are its bipartite acrorhagi on the margin, uniform red colour, and marks from frequent longitudinal fission. Bud-like structures were observed in two specimens. Evidence of frequent fission and the absence of fertile males in the sample indicate a predominance of asexual reproduction in the population. The fact that such a conspicuous species was not reported in previous surveys of Chilean sea anemones suggests that it has been increasing in abundance and/or expanding its range during the last 50 years. Reasons for this may be human impact on benthic communities or recent introduction of this species into the area.

Key words: Actiniaria, *Anemonia alicemartinae*, Chile, benthos, biogeography, longitudinal fission

See also Electronic Supplement at <http://www.senckenberg.uni-frankfurt.de/odes/01–05.htm>

Resumen

Se describe la nueva especie, *Anemonia alicemartinae* (Actiniidae), del litoral rocoso del norte y centro de Chile. Su abundancia, posición expuesta, y color rojo intenso la hace una de las especies más vistosas de la zona inter-marea y de aguas poco profundas del norte de Chile. La descripción se basa en 74 animales recolectados entre 1975 y 2001, y en observaciones de cientos de animales en sus habitats o en acuario. Esta especie ocupa microhabitats expuestos a corrientes pero protegidos del oleaje, en la zona inter-marea hasta profundidades de 16 m. En 1998, el límite sur de esta especie fue 37° S, la extensión más austral de la contracorriente costal de Chile, la cual se dirige hacia el sur. Esta especie es similar a *Anemonia natalensis* y *Pseudactinia varia* de Sudafrica. Las características más distintivas de *A. alicemartinae* n. sp. son sus acrorragios bipartidos en el margen, su color rojo uniforme, y marcas de fisión longitudinal frecuente. Estructuras semejantes a brotes fueron observados en dos animales. Evidencia de fisión longitudinal frecuente y la ausencia de machos fértiles en la muestra indican una predominancia de reproducción asexual en la población. El hecho de que una especie tan llamativa no haya sido notada en estudios anteriores de actinias chilenas, indica que esta especie ha estado aumentando en abundancia, extendiendo su distribución durante los últimos 50 años, o ambos. Una posible explicación incluye alteraciones en las comunidades bénticas a causa de la influencia humana. Otra posibilidad es que la especie haya sido introducida recientemente en el área.

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Introduction

The fauna and flora of the photic zone off the coast of northern Chile and southern Perú are remarkable for their high biomass and high turn-over rates. Primary production and plankton concentrations reach exceptionally high values, especially in summer, when the surface water is characterized by high light levels and by high nutrient concentrations due to upwelling (Codispoti et al. 1982). Although seasonally fluctuating bands of macroalgae and kelp are present in the northern Chilean coastal regions (Guiler 1959a), filter-feeders (e.g. barnacles and mussels), macroherbivores (e.g. chitons and limpets), and predators (e.g. sea stars, gastropods, and sea anemones) dominate the intertidal benthic communities (Guiler 1959a, Carter 1965). The adjacent shallow-water benthic communities are likely to show a similar structure. Sea anemones are a conspicuous component of the macrozoobenthos of rocky shores of northern Chile, represented by at least 15–20 species (Carter 1965; Sebens & Paine 1979; Försterra 1998, unpublished; Häussermann 1998, unpublished).

In this article we describe a new species of sea anemone, *Anemonia alicemartinae*, from the intertidal and infra-littoral of north and central Chile (see Electr. Suppl. 2001-05, Pt 4: figs 9, 10). Despite the noticeable size, bright red colour, and high abundance of its members at this time, this species was not mentioned in surveys of Chilean sea anemones until 1979, when it was referred to as *Actinia* sp. (Sebens & Paine 1979). This study is based upon the results of our sampling between 1994 and 2001, and upon the examination of specimens collected by K. P. Sebens and R. T. Paine in 1975.

Additional information on this study is available from the Organisms Diversity and Evolution Electronic Supplement 5 (2001), on the internet at <http://www.senckenberg.uni-frankfurt.de/odes/>. The four parts of Electr. Suppl. 2001-05 offer comprehensive site and sample data for the present study (in Part 1) and that of Sebens and Paine (Pt 2), detailed information about the examined material (Pt 3), colour versions of the printed text figures (Pt 4: figs 1–8), and additional colour pictures (Pt 4: figs 9–15).

Material and methods

From 1997 to 2001 we collected 26 specimens of *Anemonia alicemartinae* n. sp. (Electr. Suppl. 2001-05, Pt 3; Fig. 1). Between 1994 and 2001 we also observed several hundred specimens in the intertidal zone and down to depths of 16 m in north and central Chile between Arica (18°31'S, 70°24'W) and Concepción (36°34'S, 72°58'W) (Fig. 1; Electr. Suppl. 2001-05, Pt 1, Pt 4: figs 9, 10). Some animals previously collected in the Bahía de Coquimbo were taken from the aquarium of the Uni-

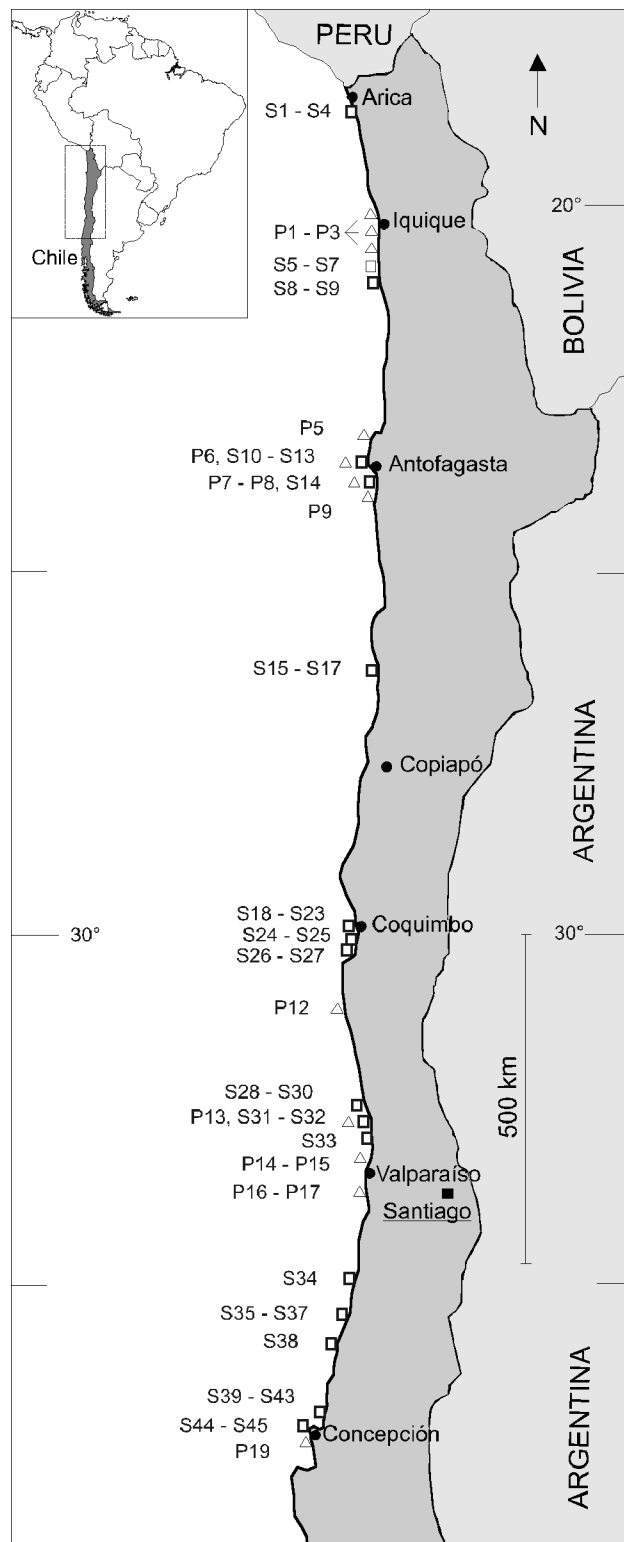


Fig. 1. Sites studied by VH and GF (S1–S45) and K. P. Sebens and R. T. Paine (P1–P19) in north and central Chile. See Electr. Suppl. 2001–05, Pts 1 and 2, for precise localities and short descriptions of stations.

versidad Católica del Norte in Coquimbo (in the following called Aq. Co.). In 1975, K. P. Sebens and R. T. Paine collected 48 specimens (Fig. 1; Electr. Suppl. 2001-05, Pt 2). Geographic data were taken from Turistel (1995).

In vivo photographs were taken both in situ and in the aquarium, where animals were observed for several days. Specimens to be analyzed were relaxed in O₂-enriched 7% MgCl₂ for 10–15 min and fixed in 15% seawater formalin or preserved in 96% alcohol. Specimens were kept in formalin for at least 4 months before being transferred to 70% alcohol. Cnidae from 2 living and 9 preserved specimens were examined with a light microscope (1000×, oil immersion, phase or interference contrast), drawn or photographed. Cnidae from 1 living and 5 preserved specimens were measured. The discharge of fresh cnidae was provoked with distilled water or 4% vinegar solution. Nematocyst terminology follows that of England (1991). Two complete specimens and parts of 12 specimens were embedded in paraffin, sectioned at 8 or 9 µm, respectively, and stained with azocarmine triple stain or hematoxylin and eosin (Humason 1967).

The following material of *Anemonia natalensis* Carlgren, 1938 was examined: 6 syntypes ex coll. Swedish Museum of Natural History (NRS 89 × 6) from Durban, South Africa; 17 specimens deposited at Zoologische Staatssammlung München, Germany (1 paraffin-embedded, 11 in 10% formalin: ZSM 234; 5 in 96% alcohol: ZSM 235), from Umdloti Beach, KwaZulu-Natal, South Africa (29°40'S; 31°08'E).

Results

Anemonia alicemartinae n. sp.

Material examined (for more details see Electr. Suppl. 2001-05, Pt 3)

Type locality: Chile, Coquimbo, intertidal zone of La Herradura (Fig. 1; site S19).

Holotype: female, 3.1.1998, leg. V. Häussermann & G. Försterra; deposited at Zoologische Staatssammlung München, Germany (ZSM 224, ZSM 224/1). One quarter of animal on 9 microscope slides of transverse sections and sphincter. In preserved state pedal disc diameter 20 mm, column height 13 mm, oral disc diameter 30 mm, tentacle length up to 17 mm.

Paratypes (fixed in 10–15% formalin, unless mentioned): 20 specimens deposited at ZSM, Munich, Germany: ZSM 225 (3 specimens): S19, intertidal; ZSM 226: S2, 3.5 m depth, as series of histological sections; ZSM 227 (2 specimens): S2, 3.5 m depth; ZSM 228 (preserved in 96% alcohol): S43, intertidal; ZSM 229: S43, intertidal; ZSM 230 – ZSM 232 (3 specimens): Aq. Co., including histological sections; ZSM 233 (5 specimens): Aq. Co.; ZSM 20012947 (2 specimens): S43, intertidal; ZSM 20012948 (2 specimens preserved in 96% alcohol): S43, intertidal. 48 specimens deposited at Na-

tionaal Natuurhistorisch Museum, Leiden, Netherlands (leg. K. P. Sebens & R. T. Paine, 1975): RMNH Coel. 24378/10: P8, intertidal; RMNH Coel. 24379/24: P8, subtidal, including histological sections of 4 female animals and of one with a bud-like structure; RMNH Coel. 24380/11: P2, intertidal. RMNH Coel. 24381/3: P1, intertidal. 1 female specimen deposited at Natural History Museum, University of Kansas, USA (KUMNH, Division of Invertebrate Zoology, catalog nr 001529), including histological sections: Aq. Co. 1 specimen deposited at Museo de la Universidad de Concepción, Chile (UCCC-25632): S19, intertidal, including histological sections. 1 specimen deposited at Swedish Museum of Natural History, Stockholm (SMNH-5227): S19, intertidal. 1 specimen deposited at Zoological Museum, University of Hamburg, Germany (C 11664): S19, intertidal. 1 specimen deposited at U. S. National Museum of Natural History, Washington (USNM 100647): Aq. Co.

Sampling sites (Fig. 1; for details see Electr. Suppl. 2001-05, Pts 1, 2): P1: 20°16' S, 70°08' W, Iquique lab, intertidal; P2: 20°25' S, 70°11' W, Pozo Toyo, intertidal; P8: 23°42' S, 70°27' W, S. Antofagasta, subtidal; S2: 18°31' S, 70°24' W, La Capilla, intertidal; S19: 29°53' S, 71°22' W, Playa La Herradura, Coquimbo, intertidal; S43: 36°34' S, 72°58' W, Cocholgüe, intertidal. Aq. Co.: 29°53' S, 71°22' W, middle of Bahía La Herradura, Coquimbo.

Morphology

General. Entire animal solid bright red; tentacles slightly paler than column. Preserved animals brownish to brownish-grey or whitish. Most animals of medium size (55 of 74 preserved specimens with pedal disc diameter between 13 and 18 mm). All specimens examined show one or two scars or other signs of fission. These appear as regions without acrorhagi and with smaller tentacles (Fig. 2; Electr. Suppl. 2001-05, Pt 4: figs 1, 11), as remaining openings (mainly in proximal part of column or on pedal disc) with protruding mesenterial filaments, or as irregularities such as the mouth position being peripheral on the oral disc. Large scars may cover up to 1/6 of column. Length and arrangement of tentacles and mesenteries irregular in all examined animals due to fission.

Column. Smooth; low, never higher than broad (Fig. 3; Electr. Suppl. 2001-05, Pt 4: fig. 2); in life usually 5–20 mm high (maximum 25 mm) and 10–25 mm diameter (max. 35 mm); preserved 5–15 mm high (max. 22 mm) and 10–20 mm diameter (max. 28 mm). Margin (Fig. 4; Electr. Suppl. 2001-05, Pt 4: fig. 3) with 5–70 weak to well-developed simple or bipartite acrorhagi which are composed of two parts with a common stem

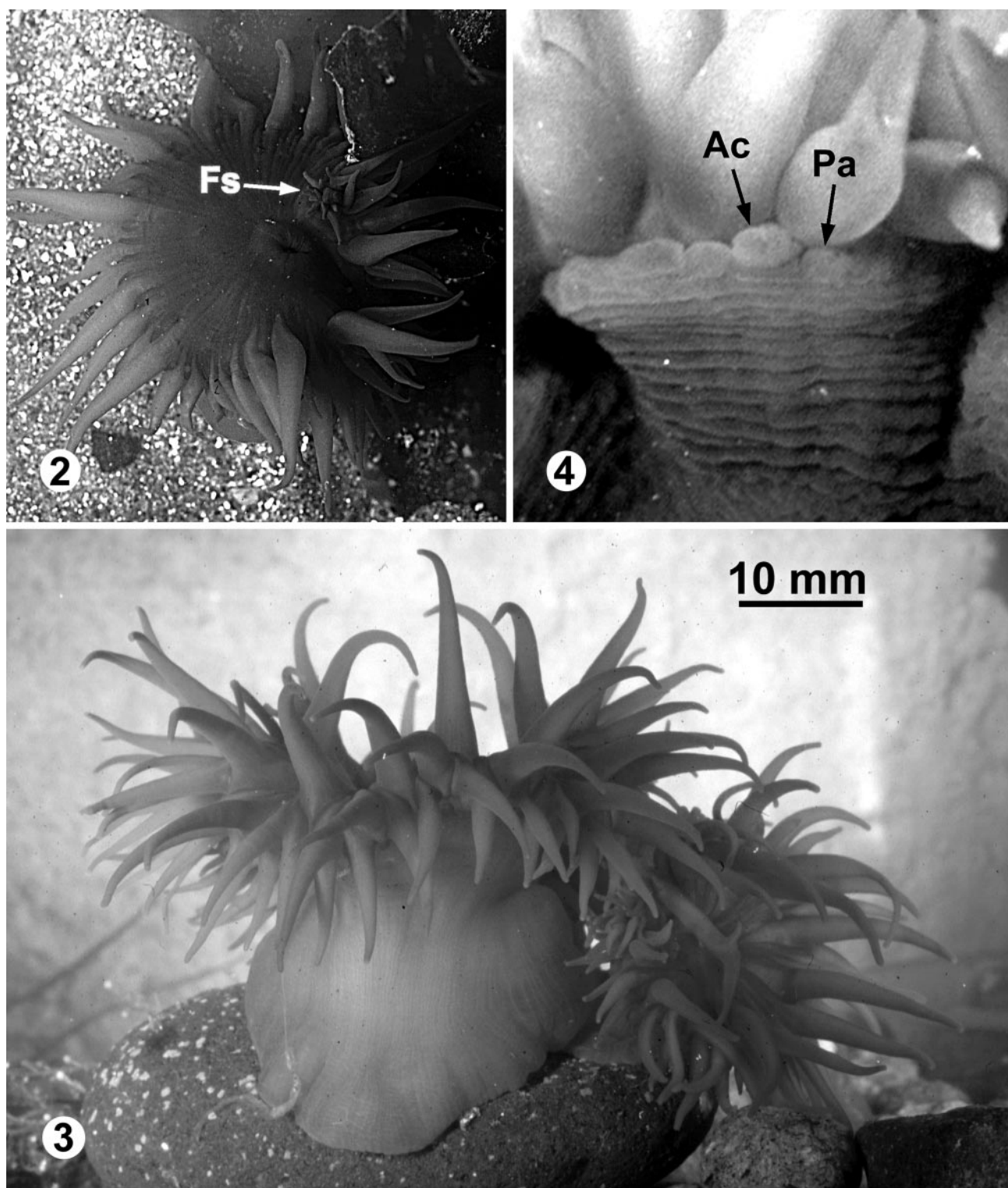


Fig. 2. Oral disc of *A. alicemartinae* with fission scar (Fs). See also colour plates in Electr. Suppl. 2001–05, Pt 4.

Fig. 3. Lateral view of *A. alicemartinae*.

Fig. 4. Margin of *A. alicemartinae* with pseudoacrorhagi (Pa) and small acrorhagi (Ac).

(exclusively containing batteries of holotrichs); acrorhagi alternate with pseudoacrorhagi (exclusively containing basitrichs) (Electr. Suppl. 2001-05, Pt 4: fig. 12); largest acrorhagi corresponding to endocoels of first and second cycle, endocoels of the youngest cycles with weakly developed corresponding pseudoacrorhagi; more pseudoacrorhagi than acrorhagi; transition forms between pseudoacrorhagi and acrorhagi (Fig. 5) present in many animals, contain basitrichs and holotrichs; every acrorhagus with whitish area on its oral apical side bearing holotrichs, the size of the whitish area proportional to the size of the acrorhagus. Fosse distinct. Two specimens with bud-like structures. Larger one on column with 53 tentacles, mouth opening, fosse, sphincter, mesenteries; oral disc preserved 9 mm diameter, column 4 mm high (Fig. 6; Electr. Suppl. 2001-05, Pt 4: fig. 4). Smaller one at margin with 10 very small tentacles.

Oral disc and tentacles (Fig. 2; Electr. Suppl. 2001-05, Pt 4: fig. 1). Oral disc circular to slightly oval; in life slightly transparent; without tentacles 15–30 mm diameter (maximum 45 mm), preserved 13–25 mm (maximum 30 mm). Insertions of mesenteries in life visible as red lines; mouth central, circular, slightly prominent; after fission in some animals at edge of the oral disc and/or oval. In many preserved specimens pharynx protruded, covering as much as half diameter of oral disc. Tentacles non-retractile, only at margin, number 45 to about 220; relatively long, conical, with broad base, few with short branch. Length highly variable; longest equal to diameter of oral disc; shortest near fission sites; in life 1–35 mm; preserved 1–25 mm.

Pedal disc. Wider than column, round to oval, limbus slightly lobed; in life slightly transparent; 15–30 mm di-

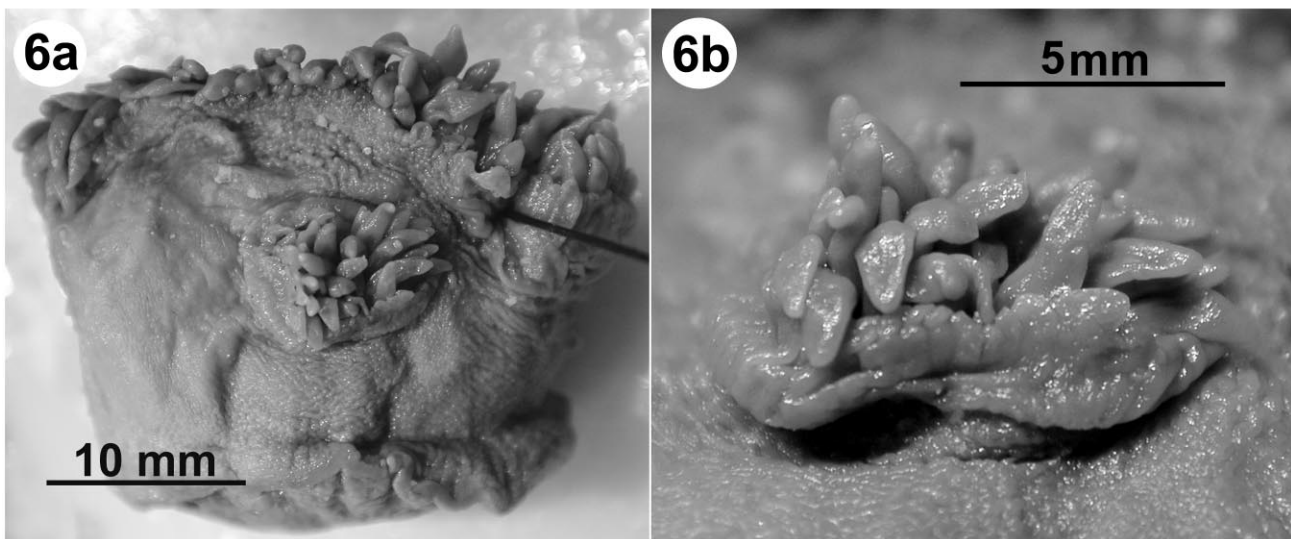
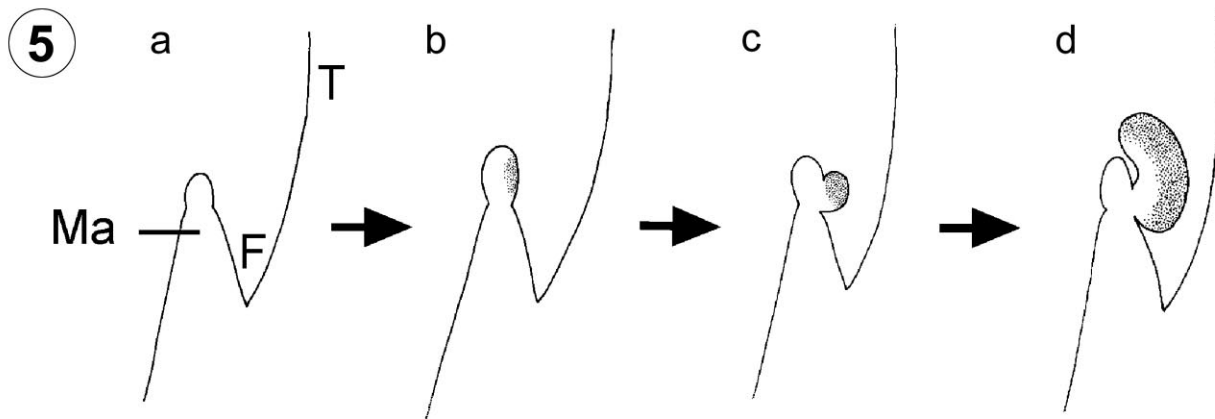


Fig. 5. Developmental stages of acrorhagi (schematic longitudinal section): a) pseudoacrorhagus. b-d) acrorhagi with holotrichs (spotted regions). F: fosse; Ma: margin; T: tentacle.

Fig. 6. Bud-like structure of *A. alicemartinae*: a) view on oral disc b) lateral view.

ameter (maximum 40 mm), preserved 11–25 mm (maximum 34 mm). Of 74 preserved specimens 10 with diameter of pedal disc smaller than 13 mm, 57 specimens with diameter of 13–18 mm, and 7 specimens with diameter larger than 18 mm. Insertions of mesenteries visible in life as red lines.

Internal anatomy

Fourteen individuals examined had 25 to 131 pairs of mesenteries each, 7 to 26 pairs perfect, no directives. Mesenteries irregularly arranged; members of a pair may differ in size; some animals with unpaired mesenteries. 8 (11%) of 74 examined specimens fertile: all female. Four of the eight females collected in October 1975 in Antofagasta (P8, subtidal), one collected in January 1998 in Coquimbo (S19, intertidal), and three taken from the Aquarium in Coquimbo in January 1998 (Fig. 1, Electr. Suppl. 2001-05, Pts 1, 2). All female animals of large size (pedal disc diameter larger than 17 mm after preservation); with reproductive tissue on 8 of 50, 7 of 64, 3 of 66, 13 of 70, 3 of 77, 11 of 77, 17 of 85, and 6 of 110 pairs of mesenteries; no recognizable pattern to fertile mesenteries, in 7 animals all reproductive tissue on one side of body. All cycles of mesenteries except youngest ones may be fertile; most fertile mesenteries of medium size.

Actinopharynx about 2/3 column length, with deep longitudinal furrows 1 to 7 of which are much broader than others.

Cnidom

Comprises spirocysts, basitrichs, microbasic amastigophors A, holotrichs (Fig. 7).

Table 1 provides data on cnidae size, as ranges respectively pooled from 5 preserved and one live specimen with pedal disc diameters from 10 to 20 mm.

Approx. 20% of the examined specimens of *A. alicemartinae* have scattered holotrichs in the column, approx. 50 % have nematocysts in the mesenterial filaments ($12.6\text{--}16.2\text{ }\mu\text{m} \times 2.7\text{--}3.6\text{ }\mu\text{m}$) that fit Schmidt's (1969) definition of p-rhabdoids B. The basitrichs found in the pseudoacrorhagi correspond to those in the column. The size ranges of fresh cnidae fell within those from preserved animals.

Histology

Musculature. Sphincter endodermal, diffuse, weak, strongly branched (Fig. 8; Electr. Suppl. 2001-05, Pt 4: fig. 5). Mesenterial retractors diffuse, broad (Fig. 9; Electr. Suppl. 2001-05, Pt 4: fig. 6). Basilar muscles strong (Electr. Suppl. 2001-05, Pt 4: fig. 13). Parieto-basilar muscles with short free pennon in distal part (Fig. 9; Electr. Suppl. 2001-05, Pt 4: fig. 6), with long free pennon on the older mesenteries in proximal part.

Epithelia. Palisade-like ectoderm, in distal part of column richly supplied with gland cells. Mesogloea with non-homogenous structure in the column, with acidophilic inclusions in trilobed filaments; thick on

Table 1. Types (capital letters, see Fig. 7), sizes and distribution of cnidae of *Anemonia alicemartinae* n. sp., in each tissue in order of abundance: v = very common, c = common, f = few, s = sporadic. Column titles "m_i" and "m_w": means, "d_i" and "d_w": standard deviations, "t": number of turns on proximal part of tube, "#": number of capsules measured, "p": proportion of animals examined with respective type of cnida present. Exceptional sizes in parentheses.

Tissue/Cnidae type, abundance	Capsule length (μm)	m _i	d _i	Capsule width (μm)	m _w	d _w	t	#	p
TENTACLES									
large basitrichs v (A)	(20.0) 21.6–34.7	28.98	3.54	2.1–3.6	2.83	0.34	6–7	95	6/6
spirocysts c (B)	10.8–41.6	24.31	7.16	1.6–4.1	2.63	0.56		108	6/6
small basitrichs f (C)	13.1–18.9 (21.3)	16.10	2.01	1.7–2.8	2.30	0.34	4–5	76	6/6
ACRORHAGI									
holotrichs v (D)	34.2–42.5	38.18	2.02	4.5–6.5	5.96	0.59		46	6/6
PSEUDOACRORHAGI									
large basitrichs c (E)	19.8–32.4	25.67	2.81	2.25–3.44 (4.09)	2.94	0.41	5–6	48	6/6
small basitrichs s (F)	9.9–13.0	11.40	1.30	1.8–2.0	1.9	0.12	?	4	1/6
COLUMN									
large basitrichs c (E)	20.8–31.2	24.67	1.94	2.2–3.3 (3.8)	2.85	0.37	5–6	95	6/6
small basitrichs s (F)	6.3–12.9 (16.6)	11.13	3.44	1.0–2.1	1.60	0.43	?	15	3/6
ACTINOPHARYNX									
large basitrichs v (G)	24.8–31.5 (34.2)	27.95	2.10	2.7–3.8 (4.4)	3.23	0.39	4–5	69	6/6
small basitrichs c (H)	14.2–22.5	19.01	1.91	2.2–3.1	2.64	0.24	3–4	41	6/6
microbasic amastigophors A f (I)	(14.4) 19.0–23.4	20.14	1.60	3.6–5.9 (6.3)	4.94	0.73	?	30	5/6
MESENTERIAL FILAMENTS									
microbasic amastigophors A c (L)	(15.5) 17.1–24.4	20.39	1.82	3.6–6.3	4.73	0.64	6–7	58	6/6
large basitrichs f (J)	20.7–29.7	24.37	2.10	3.2–5.5	3.91	0.51	?	56	6/6
small basitrichs f (K)	12.2–19.8	15.58	2.16	1.7–2.8	2.27	0.36	4–5	53	6/6

older mesenteries and at base of tentacles, in apical part of tentacles reduced to a thin band. Very weak siphonoglyphs with weakly developed “reticulated pads” (Riemann-Zürneck & Griffiths 1999); tissue of

siphonoglyphs not differentiated but with slightly thicker endoderm and longer cilia than adjacent tissue (Fig. 10; Electr. Suppl. 2001-05, Pt 4: fig. 7). No zooxanthellae.

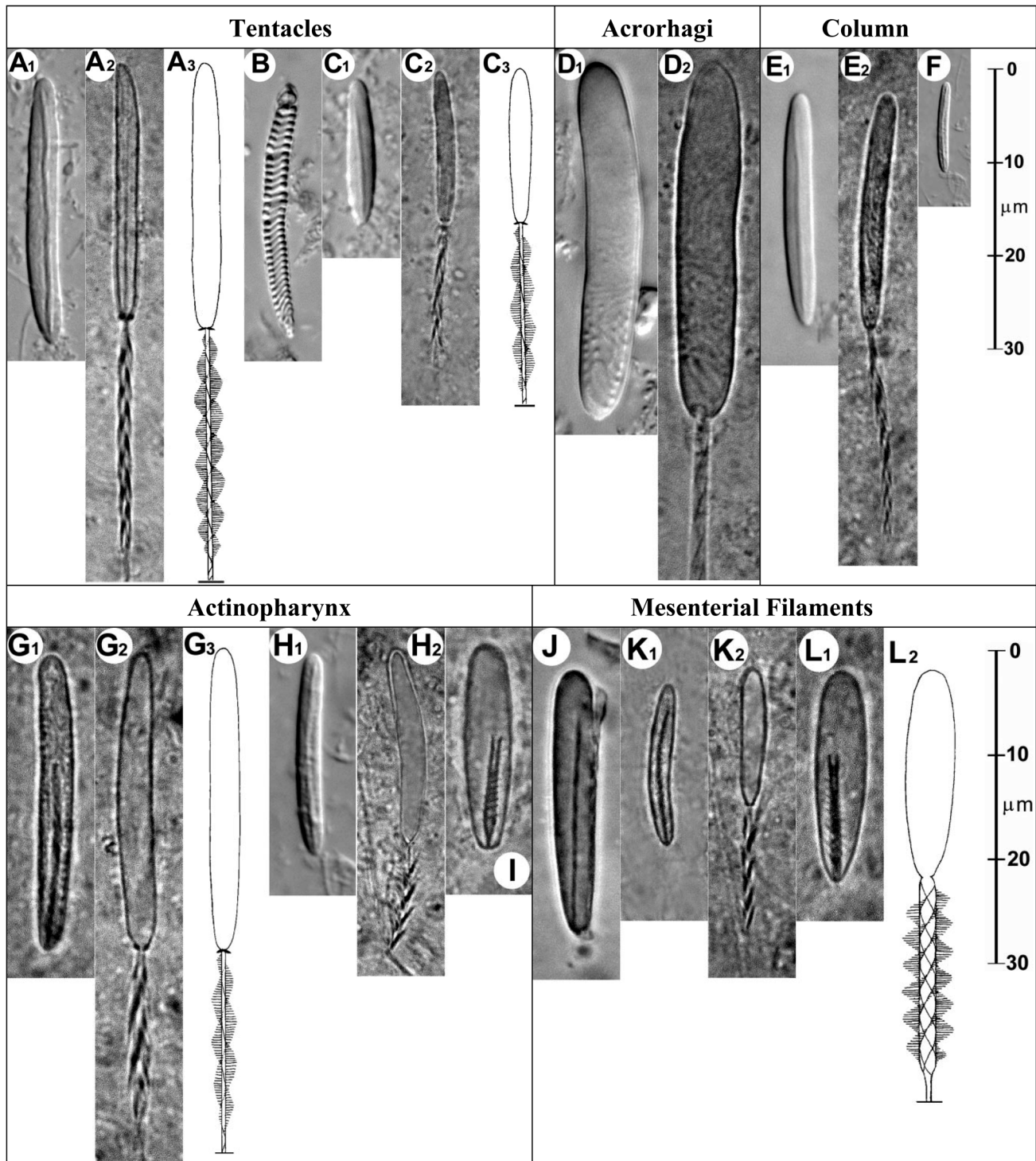


Fig. 7. Cnidae of *A. alicemartinae*. Letters A-L correspond to cnidae types listed in Table 1.

Etymology

Anemonia alicemartinae n. sp. is named after Mrs. Alice Martin, as a dedication to his wife by Mr. Manuel Martin within the BIOPAT program to support biodiversity research (<http://www.gtz.de/biopat/>).

Differential diagnosis

Diagnostic characters are listed in Table 2.

Distribution

Anemonia alicemartinae was one of the most abundant sea anemones observed in the intertidal zone and the upper infra-littoral down to depths of 16 m in north Chile, from Arica to Antofagasta (S1–S14; Fig. 1). Further south its density decreases, as that of *Anthothoe*

chilensis (Lesson, 1830), which is less abundant in the north, increases. Between Tongoy (S26, S27; Fig. 1) and Cocholgue (S43; Fig. 1), *A. alicemartinae* was found only intertidally. It was not found between Cocholgue and Punta Arenas (Strait of Magellan).

Habitat and associated species

Anemonia alicemartinae occurs in the intertidal and down to depths of 16 m, generally attached to bare rock. In tide pools where waves prevent water stagnation, animals of this species occur almost up to the mean high tide level where they frequently form groups of 5–10 specimens. They occur in places without direct surge that are exposed to currents. Commonly, *A. alicemartinae* is associated with the sea anemones *Phymactis clematis* (Drayton in Dana, 1846) and *Phymanthea pluvia* (Drayton in Dana, 1846), which extend to sites with

Table 2. Diagnostic characters of *Anemonia alicemartinae* n. sp. in comparison to the similar species *Anemonia natalensis* and *Pseudactinia varia*.

Characters	<i>Anemonia alicemartinae</i> n. sp.	<i>Anemonia natalensis</i> Carlgren, 1938	<i>Pseudactinia varia</i> Carlgren, 1938
Colour	column, oral disc, tentacles, and pedal disc red	column brick or dark purplish red or dark brown, tentacles may be greenish and have lilac tips; paler markings on oral disc (C. L. Griffiths, University of Cape Town, in litt. 2000)	column and tentacles rose red to red brown; tentacles with white band at the base, some with violet tips; oral disc grey; marginal spherules and vesicles may be red
Maximal expanded size	pedal disc diameter 40 mm, oral disc diameter 45 mm, height 25 mm; most animals smaller	pedal disc diameter 13 mm, oral disc diameter 18×25 mm, column height 9 mm	oral disc diameter 80×70 mm, but most animals smaller
Number of tentacles	45–220	85–115	72– >300
Location of acrorhagi (generic character)	on margin	on margin	in fosse
Vesicles on column (generic character)	none	none	1 (–2) rows on distal region
Sphincter muscle	diffuse: strongly branched	diffuse: few branches	diffuse: strongly branched
Number of complete mesenteries	7–26	23–28	up to 36 (or more?)
Fertile mesenteries	all except the weakest	all stronger	1 st cycle always sterile
Parietobasilar muscles	weak, proximally distinct	weak (J. C. den Hartog, Museum of Natural History, Leiden, in litt. 2000)	distinct in younger mesenteries
Longitudinal fission	very common	possible, incorrectly called "budding" by Lambert & Lambert (1978)	animals sometimes asymmetric, but no asexual reproduction observed
Basitrichs of column	two sizes	one size	two sizes
Microbasic amastigophors A of pharynx	present	present	none
Habitat	intertidal zone, infra-littoral to 16 m (Chile)	intertidal zone (South Africa)	intertidal zone, infra-littoral to 102 m (South Africa)

direct wave impact. Outside of tide pools, *A. alicemartinae* lives below the mean low tide level. Tides at Antofagasta are 0.8 m on average and 1.6 m at spring tide, and show little variation in the study region (Guiler 1959a). Single specimens were found emerged at low tide, some exposed to direct insolation when the sea was calm.

Most animals were found at depths of 1–6 m, where they are typically associated with the sea anemones *Anthothoe chilensis* and *Phymanthea pluvia*. *Anemonia alicemartinae* and *P. pluvia* mainly occupy more exposed positions than *A. chilensis* (Fig. 11; Electr. Suppl. 2001-05, Pt 4: fig. 8). Individuals of *A. alicemartinae* are most

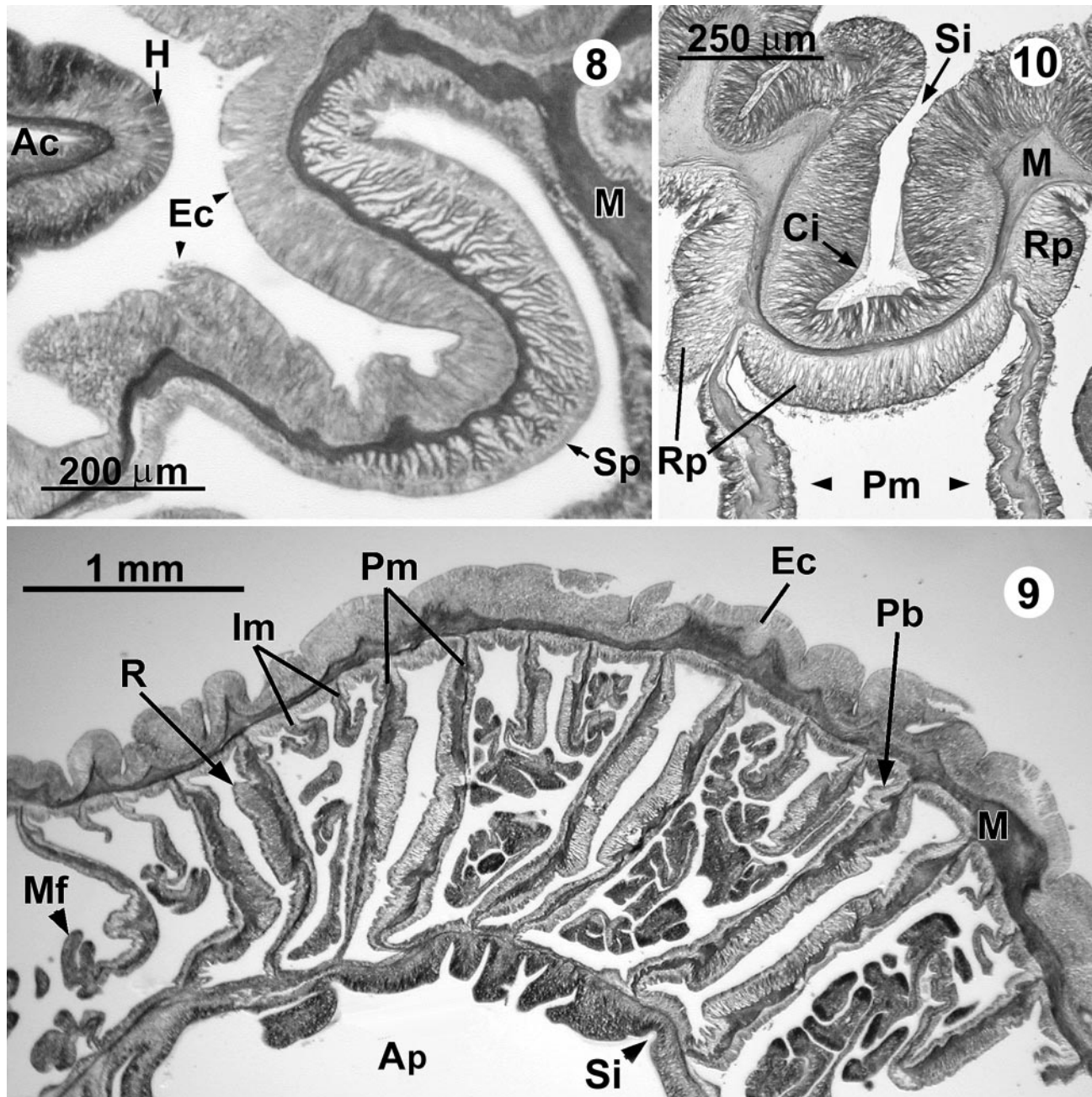


Fig. 8. Endodermal sphincter (Sp) of *A. alicemartinae* (azocarmine triple staining). Ac: acrorhagus; Ec: ectoderm; H: holotrichs; M: mesogloea.
Fig. 9. Transverse section of *A. alicemartinae* (azocarmine triple staining). Ap: lumen of actinopharynx; Ec: ectoderm; Im: pair of imperfect mesenteries; M: mesogloea; Mf: trilobed mesenterial filament; Pb: parietobasilar muscle; Pm: pair of perfect mesenteries; R: retractor; Si: siphonoglyph.

Fig. 10. Siphonoglyph (Si) with "reticulated pads" (Rp) of *A. alicemartinae* (eosin-hematoxylin staining). Ci: ciliae; M: mesogloea; Pm: pair of perfect mesenteries.

abundant in the absence of other epifaunal organisms, especially on rocks cleared by the sea urchin *Tetrapygus niger* (Molina, 1782) (Fig. 11; Electr. Suppl. 2001-05, Pt 4: fig. 8). The clusters can be dense with the animals touching each other. *A. alicemartinae* was not found at sites with high sedimentation.

Between Arica (S2: Fig. 1) and Tongoy (S27: Fig. 1), *A. alicemartinae* was regularly found between the rhizoids of the macroalgae *Lessonia trabeculata* Villouta & Santelices, 1986 (Electr. Suppl. 2001-05, Pt 4: fig. 14). Where high population densities of *A. alicemartinae* occur, the animals can also be found on the rhizoids or even phylloids of macroalgae, on small stones, on shells, or even on garbage such as bottle caps. One specimen was found on the center of the carapace of the crab *Cancer polyodon* Poëppig, 1836. Some animals were seen unattached, drifting in the current or rolling on the substratum.

Water temperature in the habitat during sampling ranged from 13 to 23 °C, and salinity from 33 to 36‰.

Biology and field notes

Anemonia alicemartinae was never observed to contract much and seems unable to retract completely. When emersed, the animals become covered with a layer of mucus, and the inner tentacles bend toward the center of the oral disc and cover it. The outer tentacles stick together, forming a rim that keeps water on the oral disc (Electr. Suppl. 2001-05, Pt 4: fig. 15).

The adhesion of the pedal disc to the substrate is not very strong. Specimens of *A. alicemartinae* can be removed easily and reattach within minutes in the sampling jar or aquarium. Once attached again, they do not change position.

Specimens of *A. alicemartinae* that are transferred to formalin without previous relaxation react with an extreme expansion of the oral disc and actinopharynx.

Twenty-one of the 64 examined animals (excluding 10 from the aquarium) had foreign material in the gastrocoel that can be interpreted as food. These food particles included parts of and whole Mytilidae (Bivalvia)



Fig. 11. *A. alicemartinae* (darker animals) in a typical habitat together with the sea anemone *Anethothoe chilensis* (white animals) and the sea urchin *Tetrapygus niger*.

2–7 mm long (in 7 animals), parts of other bivalvia (in 1 animal), parts of porcellanid crabs (in 7 animals), a shrimp 2 mm long (in 1 animal), parts and whole sea urchins (in 4 animals), gastropod shells 3–6 mm long (in 5 animals), pieces of macroalgae 1–5 mm long (in 6 animals), a sea anemone (an unidentified species with verrucae on the column) 5 mm diameter (in 1 animal), a tube of a polychaete worm 5 mm long (in 1 animal), and a 6 mm long stone which was covered with small polychaete tubes (in 1 animal). Three animals had undefinable, soft particles in their gastrocoel. Many animals contained small stones and sand particles. The complete sea urchin found in one specimen had almost the same diameter (without spines) as the column of the sea anemone and almost filled its lumen, pressing the mesenteries against the inner wall of the column and the pharynx against the oral disc.

In the aquarium of the Universidad Católica del Norte in Coquimbo, the porcellanid crab *Allopetrolisthes spinifrons* (Milne Edwards, 1837) was observed clinging to the column of one specimen of *A. alicemartinae*. It is likely that the crab was brought into the aquarium together with the anemone as the relation of the crab with its host has been suggested to be obligatory (Baeza & Stotz 1995). This crustacean was reported by Baeza & Stotz (1995) to be a commensal on the sea anemones *Phymactis clematis* and *Phymanthea pluvia*, and on the sea star *Heliaster helianthus* (Lamarck, 1816). We also observed this crab on the sea anemone *Antholoba achates* (Drayton in Dana, 1846) and *Isoulactis chilensis* Carlgren, 1959. This relationship might not be purely commensalistic, because at Chañaral (S15: Fig. 1) a specimen of *A. spinifrons* was observed pulling out the pharynx of its host, *Phymanthea pluvia*.

Discussion

Taxonomy

Carlgren (1928) pointed out that, when superficially examined, members of the genus *Pseudactinia* Carlgren can be confused with those of *Actinia* Browne or *Anemonia* Risso, and vice versa.

The main distinction between *Actinia* and *Anemonia* is considered to be the position of the acrorhagi (Carlgren 1949). The large acrorhagi of *Anemonia alicemartinae* n. sp. are composed of two parts with a common stem, and arise from the margin. Marginal projections form a continuum with pseudoacrorhagi (exclusively containing basitrichs) at one extreme, and composite acrorhagi (exclusively containing holotrichs in batteries) at the other. Therefore we suggest that a pseudoacrorhagus may develop into an acrorhagus by branching off an outgrowth on its oral face which bears the holotrichs

(Fig. 5). When the oral branch is large, it may give the impression of originating from inside the fosse (Fig. 5). This may be the reason why *A. alicemartinae* was recorded as *Actinia* sp. by Sebens & Paine (1979).

Although the generic descriptions of *Pseudactinia* (Carlgren 1928, 1938, 1949) clearly exclude *Anemonia alicemartinae*, the species description of *Pseudactinia varia* Carlgren, 1938 and Carlgren's (1928) description of one specimen of *Pseudactinia flagellifera* (Hertwig, 1882), which he synonymized with *P. varia* in 1938, indicate many similarities between *P. varia* and *A. alicemartinae*. One or two rows of vesicles in the upper part of the column and the sterility of the first cycle of mesenteries in *P. varia* seem to be the most important characters to distinguish the two species (Table 2). This could not be verified as type specimens of *P. varia* do not exist.

Cnidae

Concerning the cnidae we follow the nomenclature of England (1991), because it allows fine differentiation of nematocysts and facilitates integration of characters of fired cnidae. A comparison of nematocyst nomenclatures of several authors is given by England (1991).

The size ranges of cnidae in Table 1 are results pooled from several specimens of different sizes. Consequently, ranges of the two size types of basitrichs appear not far apart within some tissues. Within each individual, however, the size ranges are clearly distinct. Size ranges of nematocysts were not used as a diagnostic feature because statistical data such as standard deviations and means are missing for the species with which *A. alicemartinae* was compared. Since type material of *Pseudactinia varia* is missing, further data on cnidae cannot be obtained for this species. Without statistics nematocyst comparisons are of minor usefulness (Williams 1996).

Endomyarian actiniids are considered not to have "p-rhabdoids B" (Schmidt 1974). The "p-rhabdoid B"-like nematocysts that were found in the mesenterial filaments of some preserved specimens of *Anemonia alicemartinae* could not be examined in fired state. It cannot be excluded that these capsules are developmental stages of another type of cnidae, or pollution.

Reproduction and dispersion

Frequent longitudinal fission is perhaps one of the most typical characters of *Anemonia alicemartinae* as all observed specimens showed scars and/or irregularities. Early states of fission observed in 6 specimens (of all sizes) indicate that fission starts with a split of the pedal disc and proceeds distally.

Three of the 8 fertile specimens were from a sample of 10 from the aquarium of the Universidad Católica del Norte where they had been kept for an unknown period

of time, and therefore should not be used for further conclusions about fertility. Most of the examined individuals that were collected in the field were infertile (92%) and the 5 fertile ones were female (8%). This may indicate either that the population of *A. alicemartinae* reproduces exclusively asexually, like most populations of *Haliplanella luciae* (Verrill, 1898) (Shick & Lamb 1977, Dunn 1982), or that sexual reproduction is seasonal with retarded development of male reproductive tissues. The fertile specimens were collected between October and January. All fertile animals had at least some well-developed eggs, and some specimens had eggs of various developmental stages. Sampling year-round could reveal patterns in the occurrence of reproductive tissues, and molecular studies could help test whether *A. alicemartinae* forms a clonal population.

The growth of bud-like structures on the columns of 2 specimens is very likely the result of regeneration after injury (Stephenson 1929, Hand & Uhlinger 1995). The liberation of such a new individual by fission would simulate budding quite precisely, "... but to date no sea anemone is known to bud new individuals from its column" (Hand & Uhlinger 1995).

Many specimens of *A. alicemartinae* were observed passively rolling on the substrate or drifting in the current. This and the ability of this sea anemone to detach and to reattach very quickly indicate that the entire animal may function as a dispersal unit, as in *Haliplanella luciae* (Minasian & Mariscal 1979, Riemann-Zürneck 1998).

Zoogeography

The highest population density of *A. alicemartinae* occurred at Arica, the northernmost locality examined (Fig. 1). We presume this species extends farther north, possibly to the Golfo de Guayaquil, as the region between northern Perú (2–6° S) and central Chile (30–37° S) is considered a zoogeographical unit (the Peruvian Province) characterized by warm-temperate waters of high salinity (Brattström & Johanssen 1983).

Anemonia alicemartinae was not noted in taxonomic surveys of Chilean sea anemones between 1851 and 1949 (Carlgren 1899, McMurrich 1904, Carlgren 1959). It was also not mentioned as a component of the intertidal and infra-littoral communities of Chile by Guiler (1959a, b), nor was it found in a 1963/1964 inventory of sea anemones in the intertidal zone in Montemar (Fig. 1: P15), central Chile (Carter 1965). In 1975/1976, *A. alicemartinae*, referred to as *Actinia* sp., was found both intertidally and subtidally in Iquique (P1, P2; see Fig. 1 and Electr. Suppl. 2001-05, Pt 2) and Antofagasta (P7, P8), north Chile, but not in El Teniente (P12) or southward (Sebens & Paine 1979). Since 1980 and possibly earlier, it has been common in Coquimbo (Fig. 1) (W. Stotz, Universidad Católica del Norte, Coquimbo, Chile,

in litt. 2000). Despite intense examination, we did not find *A. alicemartinae* in 1994/1995 around Concepción, where we first found it in 1998/1999 in the intertidal zone (Fig. 1: S43). The population observed at S43 increased from 7 specimens in 1998 (1 specimen extracted) and 7 specimens in 2000 (2 specimens extracted) to 21 specimens in 2001 (4 specimens extracted).

Because this species can hardly be overlooked, the causes for its late appearance in the literature and the pattern of occurrence are best explored through the following hypotheses:

1) *Anemonia alicemartinae* n. sp. is an invader and has not been recorded in its country of origin. Having reached north Chile, it started to increase in abundance between 1949 and 1975, and spread southward.

2) *A. alicemartinae* is endemic to the west coast of South America, but its southern limit originally lay north of Chile. Ecological changes have allowed this species to spread south, reaching Concepción between 1995 and 1997.

3) The geographical distribution of *A. alicemartinae* has not changed substantially, but originally it was less abundant and/or inhabited less conspicuous places such as infra-littoral rocky habitats, which could not be sampled with the techniques used by former investigators. Recent ecological changes have led to increased abundance and the colonization of intertidal habitats.

Hypothesis 1 is consistent with the increase in transfer of marine species due to human activities. Shipping is the largest single vector for inter-oceanic dispersal of marine invertebrates (Carlton 1985, Ruiz et al. 1997). The sea anemone *Haliplanella luciae* can be carried over long distances attached to ship hulls (Gollasch & Riemann-Zürneck 1996). The release and reattachment abilities of *A. alicemartinae* probably make it easy for this species to use ships as carriers. This hypothesis is also consistent with the sudden occurrence of the species.

The hydrological situation along the Chilean coast is consistent with a southward spread of *A. alicemartinae*, postulated by hypotheses 1 and 2. Although the flow of the sea off Chile is dominated by the equatorward cold Humboldt Current, some areas at the shore are strongly influenced by countercurrents and upwelling. In north and central Chile, the southward Chile Coastal Countercurrent carries warm (16–20 °C) surface water, which is rich in salt (>35‰) and O₂ (>5 ml/l), along the shore. The maximum depth of this surface current (30 m) includes the habitats of *A. alicemartinae*, and the southernmost extension of the Chile Coastal Countercurrent (37°S in summer) (Brattström & Johanssen 1983) coincides precisely with the southern limit of this sea anemone.

Hypotheses 2 and 3 postulate ecological changes. Increased predation by humans (Castilla & Durán 1985, Defeo & Castilla 1998) is altering competition in Chilean benthic communities (Castilla 1976, Castilla & Bahamondes 1979, Santelices et al. 1980, Castilla 1981,

Castilla & Durán 1985) and often leads to decreased prey abundance and mean prey size (Bustamante & Castilla 1990, Davis 1995). As a consequence, species that are not harvested, like sea anemones, may benefit from decreased abundance of space and food competitors, and predators.

The population of *Anemonia alicemartinae* probably benefits from the increased abundance of the black sea urchin *Tetrapygyus niger* which, in some parts of northern Chile, has quadrupled between 1982 and 1988 (W. Stotz, Universidad Católica del Norte, Coquimbo, Chile, in litt. 2000). Rock surfaces cleared by this echinoid are common habitats of *A. alicemartinae* (Fig. 11; Electr. Suppl. 2001-05, Pt 4: fig. 8).

A poleward shift of *A. alicemartinae* due to an increase of mean shoreline ocean temperatures, as observed for benthic invertebrates at comparable coastlines (Barry et al. 1995), can be excluded. A comparison of temperature data along the northern Chilean coast revealed rather a slight decrease of sea surface temperatures between 1982 and 1995 (Brandt & Knudsen 1997).

None of the species descriptions from surveys of Peruvian sea anemones (Lesson 1830, Dana 1846, Milne Edwards 1857, Verrill 1869, Pax 1912) fits *Anemonia alicemartinae*, which makes hypothesis 2 appear very unlikely.

The available data do not allow conclusive testing of the three hypotheses posed above. All three postulate an increase in abundance of *Anemonia alicemartinae* in Chile. The determination of the northern limit of *A. alicemartinae* could give a further hint as to a possible starting point on the west coast of South America. Molecular studies could help uncover a possible founder effect which would be consistent with hypothesis 1. Exclusion experiments could be a helpful approach to test whether the abundance of *A. alicemartinae* is influenced by human activities.

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