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A new species of sea anemone (*Saccactis coliumensis* n. sp.) living under hypoxic conditions on the central Chilean shelf

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ABSTRACT: The new species *Saccactis coliumensis* is described with an emendation of genus *Saccactis* Lager, 1911 (family Actiniidae). The taxonomic relations of the genus are discussed giving additional information on *Isoulactis chilensis* Carlgren, 1959 and *Isocradactis magna* sensu Carlgren, 1924. The terms "verrucae", "vesicles" and "acrorhagi" are discussed and taxonomically valuated. The anemone *S. coliumensis* lives in eutrophicated sediments on the central Chilean shelf that is at least temporarily under the impact of deoxygenated waters from the Peru-Chile-Subsurface-Current. The most conspicuous features of the new species (the ruff of delicate, gill-like vesicles beneath the tentacles and its thick pedal disc ectoderm with small, fragile spirocysts and cilia-like structures) may be considered adaptive in this peculiar habitat.

INTRODUCTION

Off the coast of north and central Chile, a peculiar sublittoral benthic system is known (Gallardo, 1963, 1976, 1977, 1985), associated with the deoxygenated waters of the Peru-Chile-Subsurface-Countercurrent impinging onto the shelf and slope of the region. Although usually poor in macrofauna, this benthic community shows a certain abundance of small macrofauna dominated by Polychaeta, and meiofauna. The most conspicuous component of the system is, however, a complex community of Prokaryota, dominated by filamentous sulphur bacteria of the genus *Thioploca* (Maier & Gallardo, 1984).

The layer of water influencing the peculiar character of the benthos is normally found between 50 to about 400 m depth but there is some variation both latitudinally and bathymetrically, with the strongest impact on the shelf of Central Chile in spring and summer. Besides being very poor in oxygen content (less than 1 ml O_2/l), this layer is high in salinity and carries a high load of organic matter.

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In recent years, a number of medium sized sea anemones have been collected from the fringe of that benthic community off the Bay of Coliumo (40 to 55 m depth), which stand out morphologically with their ruff of delicate gill-like vesicles. These anemones are assigned to the genus *Saccactis* Lager, 1911, the type material of which had been collected from Australia. No further material has been described since the establishment of the genus.

DESCRIPTION

Genus *Saccactis* Lager, 1911, p.219 (Emended diagnosis)

Actiniidae with well developed pedal disc. Column divisible in a thin-walled marginal region (carrying small blisters and delicate fronds- or gill-like structures that form a ruff) and the column proper with typical actiniid verrucae in its uppermost part. Acrorhagi may be present or not, when present they are usually concealed between "ruff" and outer tentacles. Endodermal sphincter diffuse and rather tiny above thin-walled marginal region. Tentacles and mesenteries hexamerously arranged, two strong siphonoglyphs with thickened and reticulated endoderm. Two pairs of directives. Retractor muscles of mesenteries diffuse but relatively strong. Cnidom similar to genus *Anthopleura* but without heterotrichs in column ectoderm. Spirocysts are present not only in tentacles, oral disc and acrorhagi, but also in fairly high density in the ectoderm of the pedal disc.

Type species of the genus: *Saccactis mcmurrichi* Lager, 1911, p.220.

Saccactis coliumensis n.sp.

Material. Seven specimens were collected with a 0.1 m^2 Smith-McIntyre grab between November 24th, 1984 and April 3rd, 1985 off the Bay of Coliumo, Chile (36° 30′ S, 73°W) on a line perpendicular to the coast at depths between 40 and 55 m (Table 1). Some additional specimens were collected in May, 1989. Holotype: Specimen from Station 84–08; deposited in the Zoological Museum of the University of Hamburg. Three specimens were sectioned after paraffin embedding and stained with Azokarmin triple staining.

Saccactis coliumensis seems to be absent from other depths. Some of the anemones were found to be attached to worm tubes or other debris. However, it seems that *S.*

Table 1. Material of *Saccactis coliumensis*

Station	Depth (m)	No.	Height (cm)	Diameter (cm)	Weight (g)	Acrorhagi
84–01M1	40	1	3.5	3.0	6.0	no
84–07M2	55	1	0.8	0.5	0.1	no
84–08M2	45	1	2.5	3.5	4.5	yes (tiny)
84–12M1	40	3	1.6–2.0	1.8–2.5	2.3–2.7	yes
84–16M2	40	1	1.2	1.5	1.0	yes

coliumensis lives buried in the soft sediment with only the ruff and the tentacular crown visible. In aquaria they can spread their pedal disc on the glass.

Colour. Living specimens seem to show little colour variation. The column is of a rusty brown, with lighter shades toward the limbus. Verrucae on upper column cream with white centre or plain white. Vesicles of marginal ruff dark olive-green with white tips. Tentacles olive, transparent, sometimes with a rusty tinge at the tips. The endoderm of tentacles, ruff and in particular the oral disc contains dark brownish granules (see chapter "Associated fauna and ecological implications"). No zooxanthellae present. Preserved animals are greyish pink, endoderm of oral disc and inner tentacles olive, ruff vesicles with dark endoderm and white tips.

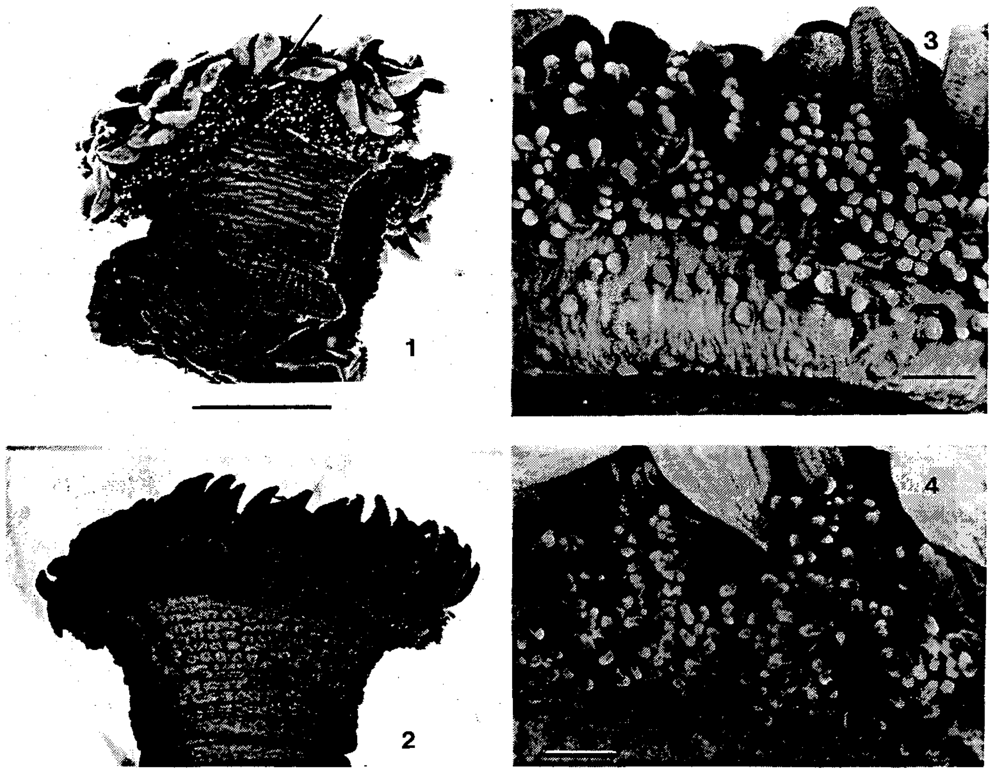
Habit. Body shape and size see Figures 1 and 2. Small to medium sized species, whose tentacular crown remains opened in preserved animals. Usually higher than broad with a number of deep horizontal constrictions in the lower part of the column and a general corrugation of both column and pedal disc which tends to run in a more vertical direction near the limbus. The pedal disc exhibits a quite regular pattern with concentric and radial furrows (Fig. 1). Whole body giving the impression of a robust though very flexible muscular animal.

Upper part of the column with typical actiniid verrucae which in preserved specimens are so closely set as to conceal their arrangement in (48) vertical rows (Fig. 2). In some specimens, verrucae are only evident on histological sections. Verrucae seem to be non-adhesive, as none of the collected animals had anything stuck to their column. Disc never retracted, usually wider than column. 96 tentacles closely packed on outer half of wide disc, all of about the same length, pointed, with longitudinal furrows. Mouth with prominent lips, wide and usually open.

The most peculiar feature of *Saccactis coliumensis* is the thinwalled region of its upper column with the ruff of delicate dendritic vesicles encompassing the tentacular crown and an area of blister-like protuberances beneath the ruff (Figs 3 and 4). Vesicles are bundled on (24?) bigger fronds from which they branch off in a dendritic manner. Tips of vesicles weakly knobbed. Acrorhagi present in 5 out of 7 specimens, usually concealed in the fosse, and varying in size (Fig. 1), easily recognizable with Bengal rose staining.

General structure. Mesenteries arranged hexamerously in 4 cycles: 6 + 6 + 12 + 24 = 48 pairs, only the first cycle perfect. Strongest mesenteries meet in the centre of the pedal disc. 96 tentacles. Actinopharynx delicate with 2 deep siphonoglyphs with thickened and reticulated endoderm. All but the last cycle of mesenteries with gonads and filaments, gonads poorly developed, the 3 sectioned animals are males, thus, sexes are probably separate.

Histology. (a) Cnidom (Table 2 and Fig. 5). The cnidom of *Saccactis coliumensis* contains several characteristic elements: (1) Small, fragile spirocysts in the high ectoderm of the pedal disc. These spirocysts are difficult to isolate on smears, but are most obvious on histological sections (Fig. 6). (2) Acrorhagi are armed with two different holotrichs. (3) Actinopharynx with only one strong basitrich, without p-mastigophores. (4) Column ectoderm with only one small basitrich, no holo- or heterotrichs. Other features of the cnidom may occur also in related genera like *Anthopleura, Oulactis, Isoulactis, Isocradactis* and *Phyllactis* (see Discussion). Size relation: In a small animal (84–16), the holotrichs 1 of the acrorhagi are 49–55 × 6–6.5 μm. In the tiny animal (84–07), the b-mastigophores of the mesenteric filaments are only 26–31 × 3.5–4.5 μm.



Figs 1–4. *Saccactis coliumensis.* n.sp. Fig. 1. Habit of specimen 84–12M1 with corrugated column and pedal disc; note acrorhagi (arrow) between ruff of marginal vesicles (Bengal rose staining). Fig. 2. Upper half of specimen 84-01M1 showing belt of verrucae below marginal ruff of vesicles (scale bar for 1 and 2: 1 cm). Fig. 3. Specimen 84-08M2: delicate marginal region with blister-like and dendritic vesicles (scale bar 1 mm). Fig. 4. Specimen 84-01M1: magnified detail of Fig. 2 showing dendritic marginal vesicles (scale bar 1 mm)

(b) Musculature. Circular musculature of the body wall strong, absent in delicate marginal region. Longitudinal musculature of the tentacles ectodermal (Fig. 7, with faint double line encircling muscular sheet = nerve plexus?). Retractors of the mesenteries diffuse, strong, parietobasilar musculature weak. Endodermal marginal sphincter tiny (Fig. 8), between marginal fronds and bases of tentacles.

(c) Histological characters of epithelia. On longitudinal sections the strong and flexible body wall exhibits a characteristic, perhaps specific structure with all layers (ectoderm, mesoglea, circular musculature and endoderm) strongly developed (Fig. 8). The 200 µm thick ectoderm is richly supplied with gland cells and is not easy to remove (contrary to most other anemones). Pedal disc ectoderm thick with small spirocysts and edged with a brush of strong cilia-like structures (Fig. 6). The ectoderm of the tentacles shows a similarly looking bristly surface.

The upper, delicate region of the column wall differs grossly as there is no muscula-

Table 2. Nematocysts of *Saccactis coliumensis* n.sp. (numbers refer to Fig. 5)

Station	Body region	Nematocysts	Dimensions (μm)
84–01	Column	1 basitrichs	13–19 × 2–2.5
84–12	Pedal disc	2 basitrichs	17–20 × 2–2.5
		3 spirocysts	17–20 × 2–2.5
84–01/08	Marginal vesicles	4 basitrichs	14.5–19 × 2–2.5
84–12	Acrorhagi	5 holotrichs 1	50–64 × 5–6.5
		6 holotrichs 2	32–43.5 × 3.5–4
		7 spirocysts	23–25 × 1.5–2.5
84–01	Tentacles	8 spirocysts	max.size 33 × 3–3.5
–08		9 basitrichs	23–29 × 2–2.5
84–01	Actinopharynx	10 basitrichs	26–33 × 3
84–01	Filaments	11 basitrichs	14.5–17.5 × 1.5–2.5
–08		12 p-mastigoph.	17.5–20 × 3.5–4.5
–12		13 ?p-mast.(opaque)	20–25 × 3–4.5
		14 b-mastigoph.	35–46 × 4.5–6.5 (rarely up to 55 μm)

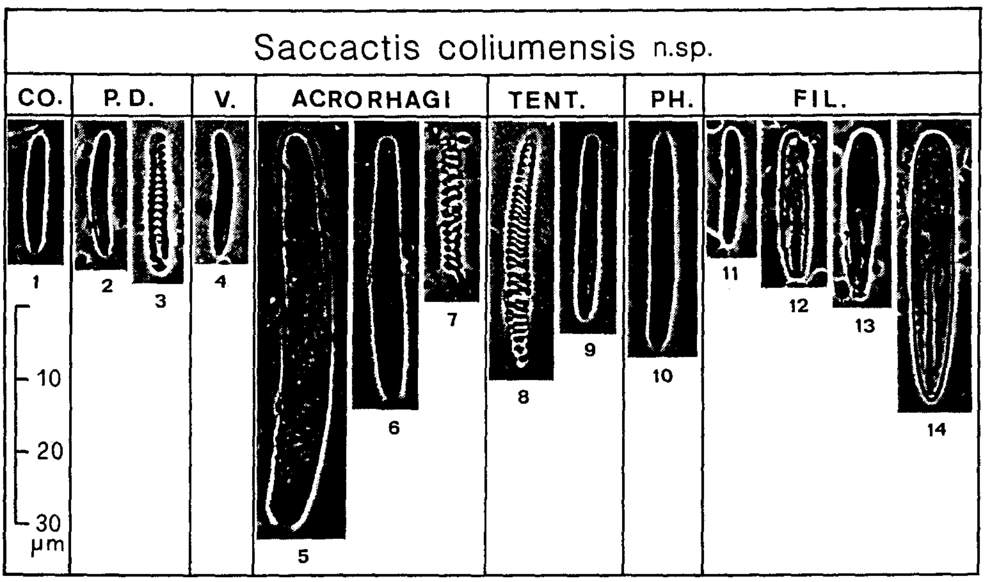
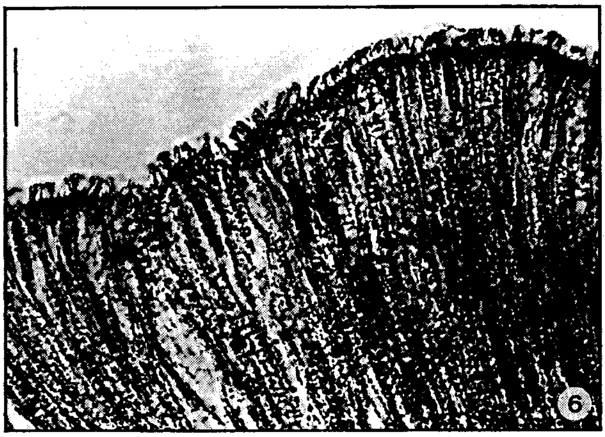


Fig. 5. Nematocysts of *Saccactis coliumensis* n.sp. (see Table 2 for explanation)

ture and all layers are very thin. Tips of vesicles with thickened ectoderm containing small basitrichs and a central weak spot where the mesoglea is absent. Acrorhagi with a 200 μm thick basophilic matrix of unknown nature between mesoglea and the layer of holotrichs.



Figs 6–7. *Saccactis coliumensis* n.sp. Fig. 6. Pedal disc ectoderm with spirocysts and cilia-like structures (scale bar 20 μm). Fig 7. Cross-section of tentacle showing mesogleal processes that support the ectodermal musculature and overlying faint double line (nerve plexus?) (scale bar 100 μm)

TAXONOMIC DISCUSSION

All three *Saccactis* species described by Lager in 1911 from Australia (*S. mcmurrichi, S. australis* and *S. musculosa*) are deposited in the Zoological Museum of the University of Hamburg (No. C 5317, C 5320, C 5321, C 5330). In 1911, the material was already in a rather poor condition (Lager 1911; see also Carlgren 1950, p.133) and is now almost disintegrated. The only specimen of *S. mcmurrichi* that allows some comparison is the animal designated by Lager as „Varietät" (No. C 5320). This animal together with Lager's comprehensive description led us to the decision that this genus is not synonymous with *Oulactis* as stated by Carlgren (see below). The formation of a delicate ruff composed of tiny, dendritic vesicles makes this new species a member of the genus *Saccactis*, Lager. The cnidom and the unique equipment of the pedal disc ectoderm with spirocysts and strong cilia-like structures distinguishes *Saccactis coliumensis* n.sp. from the type species *S. mcmurrichi. S. australis* and *S. musculosa* are considered here as species inquirendae.

Carlgren (1949, p.52; 1950, p.133; 1954, p. 572) suspected that Lager's genus *Saccactis is* a synonym of genus *Oulactis* Milne-Edwards & Haime, 1851, more so as they both are Australian genera agreeing in the number of septae and tentacles and in the presence of acrorhagi. However, *Oulactis* is provided with a multitude of small, adhesive verrucae at the margin, whereas in *Saccactis* the upper portion of the column is a very delicate region, differing greatly in general histology from the verrucae-region below, with delicate, gill-like vesicles that never seem to have adhesive properties. What we know of the nematocyst equipment of *Oulactis*, with holo- or heterotrichs in the column ectoderm (Carlgren 1945, 1950, 1954), rather points towards a closer relationship to genus *Anthopleura* (compare Hand, 1955, and England, 1987).

There are three other genera whose relation with *Saccactis* will be discussed in the following as they may be confused with *S. coliumensis* either because they are known

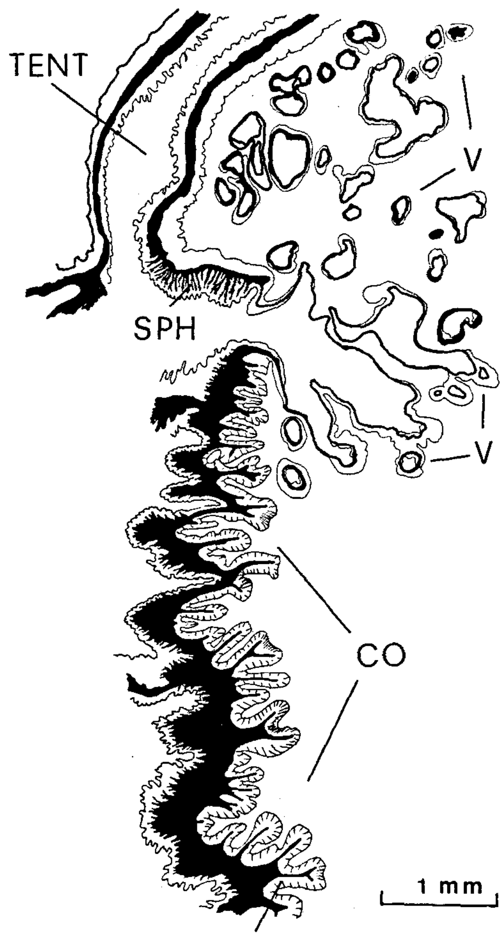


Fig. 8. *Saccactis coliumensis* n.sp. Longitudinal section of upper column (specimen 84-01M1). CO = column with mesoglea solid black, SPH = endodermal sphincter, TENT = tentacle, V = vesicles of delicate marginal region (ruff)

from the Chilean coast *(Phyllactis, Isoulactis)* and/or because their diagnostic characters are but poorly known *(Isoulactis, Isocradactis)*. For clarification, pictures of the habit and cnidom of the latter genera are given (Figs 9–12).

The first genus, *Phyllactis* Milne-Edwards & Haime, with species on both sides of tropical South America, looks quite similar. However, it lacks acrorhagi, the number of tentacles is only 48, and the known nematocyst profile of the *Phyllactis* species (Carlgren 1945, 1951; Corrêa, 1964) does not support this assumption, either.

The monotypic genus *Isoulactis* Carlgren, 1959 with *I. chilensis* had been described from Chilean rockpools. According to Sebens & Paine (1978), Carter's data for *"Phyllactis concinnata"* refer also to *Isoulactis chilensis*. The holotype of that species was obtained from the Naturhistoriska Riksmuseet in Stockholm (Nr. 1422). This animal is of relatively large size, "almost the whole column of which is provided with longitudinal rows of

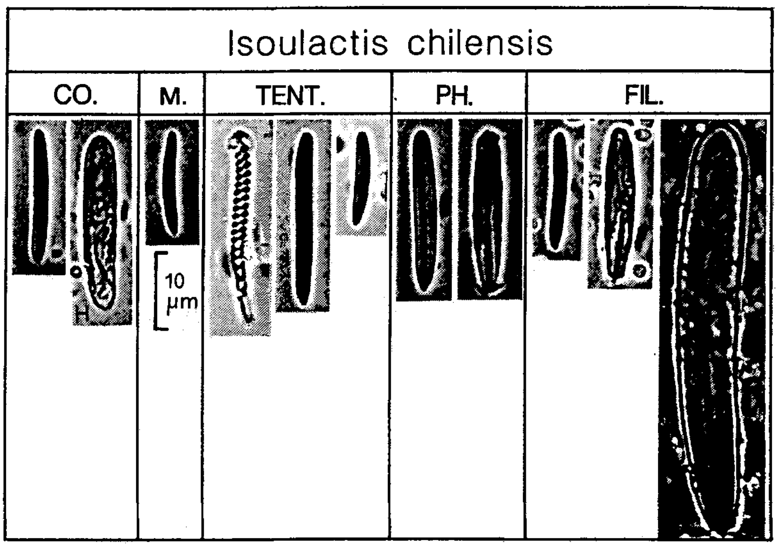
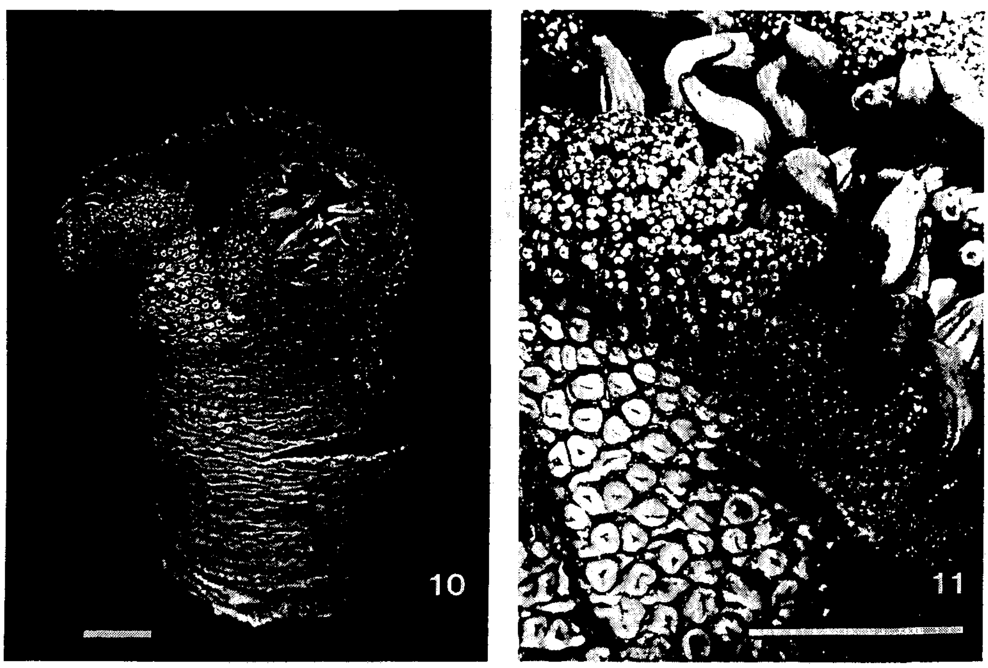


Fig. 9. Nematocysts of *Isoulactis chilensis* Carlgren, 1959, Holotype (Naturhistoriska Riksmuseet, Stockholm, Nr. 1422). CO = column, FIL = filaments, H = holotrich, M = margin, PH = actinopharynx, TENT = tentacle



Figs 10–11. *Isocradactis magna* sensu Carlgren, 1924. Fig. 10. Habit showing verrucose column (scale bar 1 cm). Fig. 11. Magnification of margin with transition from bigger to smaller, more numerous verrucae (scale bar 1 cm)

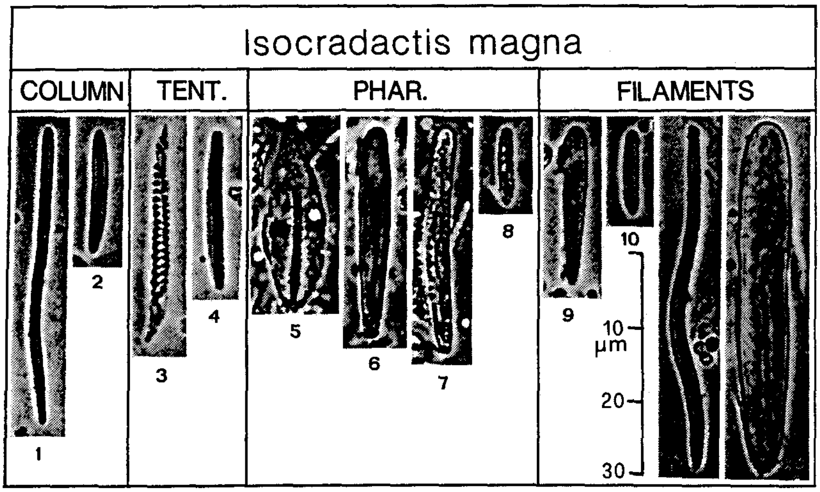


Fig. 12. Nematocysts of *Isocradactis magna* sensu Carlgren, 1924 (see Table 3 for explanation)

strong verrucae, simple but in the uppermost part compound and set on lobes" (Carlgren, 1959). Histological sections of the marginal region confirmed this description as even the uppermost very small protuberances that arise from frond-like structures are verrucae according to the definition given below. There is no upper delicate region of the body wall, the verrucae are adherent with shell fragments firmly fixed to them and the species lacks acrorhagi. It is questionable whether the number of tentacles is as high as Carlgren stated (280–290), as the tentacular disc is thrown in lobes and strongly compressed, 6 hexamerous cycles (about 192 tentacles) being perhaps more realistic. Carlgren has given a good account of the cnidom of *Isoulactis chilensis*. In addition, we have found a small basitrich in the tentacles and the maximal dimensions of the rather rare, delicate, inconspicuous tentacle spirocysts are 28 × 2.5 μm (Fig. 9).

Finally, another monotypic genus, *Isocradactis* (Stuckey), with *I. magna* from New Zealand has been mentioned already by Carlgren (1959) in connection with *Isoulactis chilensis*. Carlgren described *Isocradactis magna* in 1924, 1947 (cnidom) and 1954, using only a single specimen, which was kindly lent to us by the Zoological Museum of the University of Copenhagen. As Carlgren (1954) stated, it is not at all sure whether this animal is Stuckey's species; thus, we can only refer to it as *Isocradactis magna* sensu Carlgren, 1924. In order to facilitate future comparison, we give pictures of the habit, upper column and cnidom of that specimen (Figs 10–12) together with the distribution and size of the nematocysts (Table 3). The size, number and shape of tentacles and the verrucose structure of the column is similar to *Isoulactis chilensis*; however, *Isocradactis magna* is much less contracted, and there are no foreign particles stuck to the column, thus giving a clearer view of the proportions of the whole animal. The cnidom, however, differs from that of *Isoulactis*, the only similarities being the fragile, rather inconspicuous spirocysts of the tentacles and the big b-mastigophores in the filaments. The most peculiar nematocyst which has not been described before in *Isocradactis magna*, is the rod-like basitrich that occurs in the column ectoderm near the limbus and in the filaments

Table 3. Nematocysts of *Isocradactis magna* (numbers refer to Fig. 12)

Body region		Nematocysts	Dimensions (μm) Own observation	Carlgren (1947)
Column	1	rod-like basitr.	33–44 × 1.5–2	–
	2	basitrichs	15.5–18 × 2	14.1–15.5 × 1.5
Tentacles	3	spirocysts	25–30 × 2–2.5	–
	4	basitrichs	20–24.5 × 2–2.5	20–21 × 2.2–2.8
Actinopharynx	5	p-mastigophores	26 × 6–8	24.4–26.8 × 6–7
	6	p-mastig. (opaque)	29 × 4–4.5	–
	7	basitrichs 1	26–32 × 3–3.5	27.5–32 × 3–3.5
	8	basitrichs 2	9.5–13.5 × 1.5–2	–
Filaments	9	p-mastig. (opaque)	22–26 × 3.5	22.6–27 × 5.6–7 18.3–24 × 3–3.5
	10	basitrichs	9–12 × 2	–
	11	rod-like basitr.	35–48 × 1.5–2	–
	12	b-mastigoph.	46–55 × 6–7	45–56.4 × 6–8.5

(photographs 1 and 11 in Fig. 12). Hand (1955) and den Hartog (1987) have both reported on this sort of cnidae in the filaments of other actiniid species and in the column of one species. *Isocradactis magna* is the first actiniid anemone with these strange basitrichs in both tissues.

DISCUSSION OF THE TERMS "VERRUCAE", "VESICLES" AND "ACRORHAGI"

The classification of most genera of the family Actiniidae depends on the definition and taxonomic evaluation of the different wart-, blister- and frond-like structures that may occur in the upper part of their column. Occasionally, several different protuberances are present, rendering differentiation and classification even more difficult. On the other hand, there are species whose marginal or columnar evaginations may be quite discrete, or their presence may even vary between specimens of the same species.

This confusing situation is not improved by the terms and definitions used for the different structures as these again may vary between authors and languages used. Quite recently, den Hartog (1987) and England (1987) have both given a summary of the relevant literature with their opinions of the terms "verrucae" and "vesicles" (den Hartog), respectively "spherules" and "acrorhagi" (England).

Of all actiniid protuberances the "verrucae" are certainly best defined, irrespective of whether they are adhesive or not, with apparently no variation between taxa. They are hollow evaginations of the whole body wall with all three body layers showing some modification within the verruca: central part of ectoderm with supporting cells and gland cells but probably always devoid of nematocysts (den Hartog, 1987). Also, the mesoglea is thinner towards the centre of the verruca, and the endodermal circular muscle sheet is very weak or absent. Verrucae are usually arranged in a defined number of longitudinal rows, and often are a different colour in living anemones. They are capable of strongly attaching foreign particles, although there are species as well as specimens that never seem to attach anything to their verrucae. As den Hartog demonstrates (1987, his Figs 1, 2), both the shape and the adhesive properties of the verrucae may vary with environmental conditions.

Den Hartog preferred to restrict the term "vesicle" to the evaginations of the column-wall of the Boloceroidaria. However, this term appears to be best suited, as a more universal and less defined term, to accommodate all marginal or columnar structures other than verrucae and acrorhagi in the way it is used by Stephenson (1928).

Contrary to England (1987), the terms "acrorhagus" and "pseudoacrorhagus" should be retained, because "acrorhagi" are well established in the literature on aggression in sea anemones (Francis, 1988). The following definition is favoured: Acrorhagi are blunt, hollow structures that are developed in connection with the top of the column (margin) beneath the outer cycle of tentacles (on the parapet or in the fosse). They are armed with special nematocysts and are concerned with aggression.

The presence of acrorhagi is generally considered a generic character. However, as Hand (1955, p.48) pointed out, they "are sometimes very difficult to observe. They are commonly absent from young individuals, are frequently difficult to observe on living animals . . ., and upon preservation become very brittle and are easily destroyed." Moreover, the description of the above new species implies that this character may even vary between specimens of the same species; thus, the taxonomic significance of the acrorhagi obviously has to be reconsidered independently for each taxon.

ASSOCIATED FAUNA AND ECOLOGICAL IMPLICATIONS

Saccactis coliumensis lives in naturally eutrophicated coastal muds. The area is one of very high primary production resulting from strong seasonal upwelling events, typical of eastern boundary current systems. Besides another anemone of the family Edwardsiidae (*Edwardsia* aff. *intermedia*), the accompanying fauna during the sampling period was found strongly dominated by polychaetes, in particular by the following species: *Cossura chilensis*, *Mediomastus branchiferus* and *Paraprionospio pinnata*. Also the ampeliscid amphipod *Ampelisca araucana* appears quantitatively important.

Both the character of the sediment and the associated fauna suggest that this habitat is at least temporarily under the impact of the low oxygen regime of the Peru-Chile-Subsurface-Current. Sea anemones in general can withstand low oxygen levels or anoxia for some time, the record being held by the Texas Gulf anemone *Bunodosoma cavernata* surviving 6 weeks of total anoxia (Mangum, 1980), whereas the Baltic Sea variety of *Metridium senile* is known to survive at least 3 weeks (Wahl, 1984), and the infaunal anemone, *Haloclava producta*, recovered after 11 days of anoxia (Sassaman & Mangum, 1972). Thus, sea anemones can be considered facultative anaerobic invertebrates, exhibiting remarkable adaptations to life in microenvironments where oxygen availability fluctuates frequently (Ellington, 1982). As may be expected, anemones are regularly associated with hydrothermal vents (Doumenc & Van-Praët, 1988; Hessler & Smithey, 1983), where they usually occur at the fringe of hydrothermal activity and seem to benefit from this borderline habitat with its higher amount of dissolved and particulate organic matter.

As far as *Saccactis coliumensis* is concerned, it seems likely that this species is well adapted to living under drastically changing conditions on the Chilean shelf, taking advantage of the annual variation of the oceanographical regime, with oxygenated environment during wintertime and low oxygen content with high organic load during summer (Gallardo, 1976, 1985). Although there are no observations or experiments on how the anemone responds to the varying oxygen level in the ambient water, the "gill"-like appearance and structure of the ruff and its underlying delicate columnar region strongly suggest some exchange function. Both the delicacy and the enormous increase in surface favours the uptake and transition of oxygen (Sassaman & Mangum, 1972; Shick et al., 1979) and may ensure that the anemone quickly recovers after a certain time span of oxygen deficiency. In this context, the nature of the dark brownish granules in the endoderm of oral disc, tentacles and vesicles would be of special interest, as living in hypoxic and sulphide rich environments is often associated with black precipitates (Giere et al., 1988; Sassaman & Mangum, 1972).

As pointed out by Giere et al. (1988), mucus can have a favourable function in these extreme environments at least in oligochaetes. There is no respective information on the mucus of sea anemones except the assumption that it protects against oil pollution (Wicksten, 1984). However, the fact that *Saccactis coliumensis*, unlike other members of the family, is equipped with spirocysts in the ectoderm of its pedal disc, may mean something in this context. Spirocysts are known to produce a web of fine microfibrillae during discharge (Mariscal, 1984) with adhesive and presumably other properties. Also, the cilia-like structures on the pedal disc and other ectodermal surfaces of *Saccactis coliumensis* should be considered.

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