

New records on sea anemones (Anthozoa: Actiniaria) from hydrothermal vents and cold seeps

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During several cruises carried out by the Ifremer (Institut français de recherche pour l'exploitation de la mer) with the submersible "Nautile" at different hydrothermal sites and cold seeps, an important collection of anthozoans - mainly actiniarians - was sampled. Additional material was collected by an American cruise with the submersible "Alvin". The goal of the present contribution is to describe part of this actiniarian fauna inhabiting three chemoautotrophic sites, one of them in the Mid-Atlantic Rise and the other two in the Eastern Pacific. A new genus and species of actinostolids is proposed after the study of specimens collected at hydrothermal vents in the Guaymas Basin (East Pacific Rise, Gulf of California, 27°00'N-111°24'W, 2020 m). Furthermore, some specimens collected in cold seeps along the MAT (Middle America Trench, off Mexico, 18°21'-20°01'N 104°21'-106°17'W, 3354-3795 m) are reported as *Hadalanthus* aff. *knudseni*. This material is discussed and compared with the existing type material of *H. knudseni* Carlgren, 1956, and *Tealidium jungerseni* Carlgren, 1921. In addition, some specimens of *Maractis rimicarivora* Fautin & Barber, 1999, were collected at hydrothermal vents of the Mid Atlantic Ridge Snake Pit (23°22.9'N-44°55.8'W, 3490 m) site. This species is collected for the first time after its original description at Trans-Atlantic Geotraverse (TAG, 26°08'N 44°49.6'W, 3650 m). Some ecological remarks are given from in situ and video observations.

Introduction

Hydrothermal vents and cold seeps are characterized by low diversity - but high-biomass - communities. Tube worms (polychaetes and vestimentifera), large bivalves, gastropods, different types of crustaceans (copepods, amphipods, shrimps, brachyurans), and fishes are representative faunistic elements of hydrothermal vent and cold seep sites. Little is known about hydrothermal and cold seep sea anemones (see review by Van Dover, 2000 for vents and Sibuet & Olu, 1998 for seeps), although they have sometimes been observed to be abundant enough to play an important role in the deep sea environments and in the hydrothermal vent food web (see Doumenc & Van Praët, 1988; Gage & Tyler, 1991; Van Dover, 2000, for additional references). They

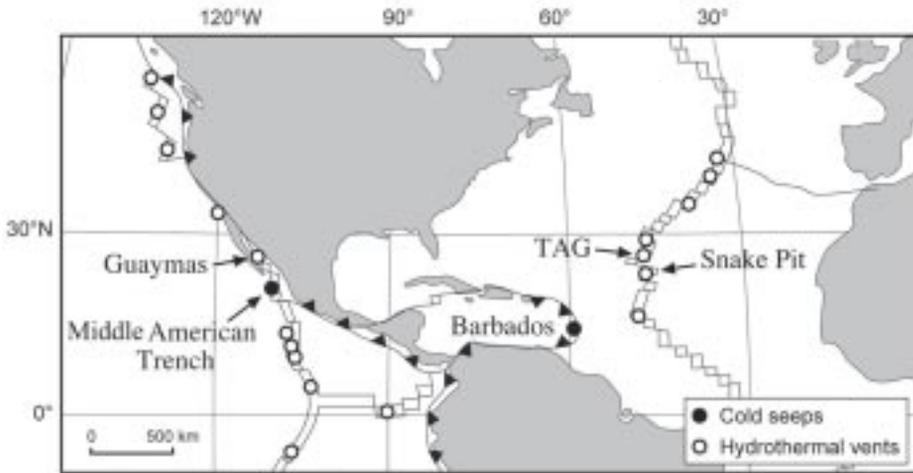


Fig. 1. Locator map indicating the hydrothermal vents or cold seep where the species described in this paper are present.

were often reported at seeps, attached on bivalve shells or on other substrates (e.g. Juniper & Sibuet, 1987; Barry et al., 1996; Olu et al., 1997). In spite of the presence of locally dense beds, an endo- or episyntrophic relationship with chemoautotrophic bacteria has not been empirically determined. Sea anemones are presumed to be suspension feeders capturing a wide range of prey including large prey items (e.g. Shick, 1991; Van Dover et al., 1997; Fautin & Barber, 1999; Van Dover, 2000).

Nothing is known about speciation, evolution or biogeographic processes in sea anemones inhabiting these chemoautotrophic environments. A high level of endemism is expected and may corroborate the idea of reduced gene flow between locations. The evaluation of the potentially restricted gene flow is particularly important with respect to speciation. The Indo-Pacific shows a complex tectonic history in comparison with the Mid-Atlantic Ridge, including four of the six biogeographic provinces (Van Dover, 2000; Van Dover et al., 2001, 2002). In this scenario, most of the sea anemone species reported from hydrothermal vents are currently known from Indo-Pacific sites, while only two species are known inhabiting Atlantic hydrothermal vents.

Seven species of sea anemones have been documented from hydrothermal vents. Five species are members of the family Actinostolidae and two species were Hormathiidae, they all belong to the two richest families of deep-sea actinarians (Desbruyères & Segonzac, 1997; Fautin & Barber, 1999). The Atlantic actinostolids associated with hydrothermal vents only include two species, namely, *Parasicyonis ingolfi* Carlgren, 1942 and *Maractis rimicarivora* Fautin & Barber, 1999 (see Segonzac, 1992; Fautin & Barber, 1999). *P. ingolfi* was collected at Snake Pit (23°22.94'N-44°56.09'W, 3480 m), while *M. rimicarivora* was found at a northern location, Trans-Atlantic Geotraverse (TAG, 26°08'N 44°49.6'W, 3650 m). From the Pacific, three other actinostolid species have been reported (one of them identified only at generic level): *Actinostola* sp., *Cyananthea hydrothermala* Doumenc & Van-Praët, 1988, and *Marianactis bythios* Fautin & Hessler, 1989 (see Doumenc & Van-Praët, 1988, Fautin & Hessler, 1989). The

two former species were collected at 12°48'-49'N-103°56' (2630-2635 m), while *M. bythios* was found at Mariana back-arc basin 18°10.9'-12.6'N 144°42.4'-43.2'E (3660 m). The hormathid species reported from hydrothermal vents, one of them only identified at generic level, were collected at 12°48'-49'N-103°56' (2630-2635 m) in the Eastern Pacific Rise (EPR): *Chondrophellia coronata* (Verrill, 1883) and *Phelliactis* sp. (see Doumenc & Van-Praët, 1988).

Three species of sea anemones have been reported from cold seep sites, the Hormathidae *Monactis vestita* (Gravier, 1918), from deep Barbados prism mud volcanoes, 4980 m (Olu et al., 1997) and two Actinostolidae from the Monterey Bay seeps, both only identified at generic level, *Stomphia* sp. and *Paractinostola* sp., 1000 m (Barry et al., 1996).

In this paper, we describe a new genus and species of actinostolid from hydrothermal vents at Guaymas Basin collected during the GUAYNAUT cruise (Eastern Pacific, Nov-Dec 1991). Furthermore, we describe as *Hadalanthus* aff. *knudseni* some specimens attributable to the monotypic genus *Hadalanthus* Carlgren, 1956, collected from cold seeps at Middle America Trench off Mexico (18°-19°N; Mercier de Lépinay, 1997) during the NAUTIMATE cruise (Eastern Pacific Rise, Jan-Feb 1994). Finally, we give descriptions of the four specimens of *Maractis rimicarivoora* collected from the hydrothermal vents at Snake Pit during the recent American cruise DIVERSExpedition (Mid-Atlantic Ridge, Jul 2001).

Material and Methods

This paper is based in part on the material collected in three chemoautotrophic environments, two of them were hydrothermal sites [Guaymas Basin, 2020 m (Eastern Pacific Rise, EPR) and Snake Pit, 3500 m (Mid-Atlantic Ridge, MAR)] and the last one a cold seep system, 3354-3795 m (Middle American Trench) (fig. 1).

The GUAYNAUT cruise was supported by the Ifremer, Brest, and the Universidad Autónoma de México (UNAM), and was conducted by A-M. Alayse, (Ifremer, Centre de Brest), on board the R/V "Nadir" and the R/V "El Puma", the former equipped with the submersible "Nautile", from 8 November to 7 December 1991. The main goal of this cruise was the study of the ecology of the Guaymas Basin hydrothermal vent system, mainly from the point of view of its bacterial communities and the chemistry of the fluids and the sediments (Marchand et al., 1994; Guézennec et al., 1996), but also the distribution of the mega- and meiofauna.

The NAUTIMATE cruise was supported by the Université UPMC, Paris, Ifremer, UNAM (México) and Texas A&M University, and was conducted by B. Mercier de Lépinay (Université de Nice-Sophia-Antipolis) and F. Michaud (Laboratoire de Géodynamique sous-marine, Villefranche-sur-mer), on board the R/V "Nadir" equipped with the submersible "Nautile", from 16 January to 9 February 1994. The main goal of this cruise was the study of some geodynamic aspects of the neogene subsidence along the Middle America Trench off Mexico (18°-19°N). In addition some biological observations and samples were collected from this cold seep.

The American cruise DIVERSExpedition was conducted by C. Van Dover (College of William & Mary, Williamsburg, USA), with the participation of American, Portuguese and French institutions (e.g. College of William & Mary, WHOI, Universidade dos Açores and Ifremer), on board the R/V "Atlantis" equipped with the sub-



mersible "Alvin", from 26 June to 29 July 2001. The main goal of this cruise was to prospect and compare the invertebrate composition and biomass associated with beds of the bivalves *Bathymodiolus* spp. at different hydrothermal sites in MAR (Logatchev, Snake Pit, Lucky Strike, Broken Spur).

The sea anemones collected in the before mentioned cruises were fixed in 10% seawater formalin, and then preserved in 70% ethanol. Fragments from selected specimens were dehydrated in buthanol (Johansen, 1940), and embedded in paraffin. Histological sections 7-8 μm thick were stained with Ramón y Cajal's Triple Stain (Gabe, 1968).

Cnidae measurements were taken from preserved material in squash preparations at 1000x magnification with Nomarski differential interference contrast optics. Frequencies given are subjective impressions based on squash preparations.

For purposes of comparison, the following type material was examined:

- *Tealidium jungerseni* Carlgren, 1921. 1 syntype (SMNH-type-5568), Ingolf-Expedition, stn 11, Danmark Strait, 64°34'N-31°12'W, 1300 fms, 21 May 1895; 2 specimens (ZMUC), Ingolf Expedition, stn 11, Danmark Strait, 64°34'N-31°12'W, 1300 fms, 21 May 1895; 1 specimen (ZMUC), Ingolf Expedition, stn 38, Davis Strait, 59°12'N-51°05'W, 1870 fms, 30 Jul 1895.
- *Hadalanthus knudseni* Carlgren, 1956. 2 paratypes (ZMUC), Galathea Expedition, stn 658, 35°51'S-178°31'W, SW Pacific, 6660-6720 m. Remarks: From these fragmented specimens only a few cnidae measurements were obtained. Tenaculi are present as described in the original description by Carlgren (1956).

The material studied in this article is deposited in the Muséum national d'Histoire naturelle in Paris (MNHN), the Zoological Museum in Copenhagen (ZMUC), the Swedish Museum of Natural History in Stockholm (SMNH), and in the Zoology Section of the Faculty of Biology at the University of Seville in Spain (SZ).

Results

Family Actinostolidae Carlgren, 1932

Paranthosactis gen. nov.

Diagnosis.— Actinostolidae with well developed pedal disc. Column smooth (dome-shaped to cylindrical in preserved material), not divisible into scapus and scapulus.

- ◀ Fig. 2. Photographs taken in situ at the different chemoautotrophic environments prospected. A) specimens of *Paranthosactis denhartogi* gen. nov. spec. nov. with the vestimentiferan *Riftia pachyptila* (one living specimen and two dead ones) on active hydrothermal edifice at the Guaymas Basin at 2020 m depth. Copyright: "Photograph Ifremer/Guaynaut-1991"; B) detail of *Paranthosactis denhartogi* gen. nov. spec. nov. close to some living specimens of *Riftia pachyptila*. Copyright: "Photograph Ifremer/Guaynaut-1991"; C) specimens of *Hadalanthus* aff. *knudseni* Carlgren, 1956 (brownish tentacles) on dead and living bivalve shells of *Calyptogena* sp., and the galatheid crab *Munidopsis subsquamosa* at cold seeps, 3795 m depth, in the Middle American Trench. Copyright: "Photograph Ifremer/Nautimate-1994"; D) oral view of some specimens of *H. aff. knudseni* living next to cold seeps. Copyright: "Photograph Ifremer/Nautimate-1994"; E) general view of Snake Pit-Elan hydrothermal site at Mid-Atlantic Ridge, 3500 m depth, showing some actinarians, the mytilid *Bathymodiolus putoserpentis*, the ophiurid *Ophioctenella acies* and the fish *Pachycara thermophilum*. Copyright: "WHOI/DIVERSExpedition-2001"; F) Detail of the sea anemone *Maractis rini-carivora* Fautin & Barber, 1999 at Snake Pit-Elan, 3500 m. Copyright: "WHOI/DIVERSExpedition-2001".

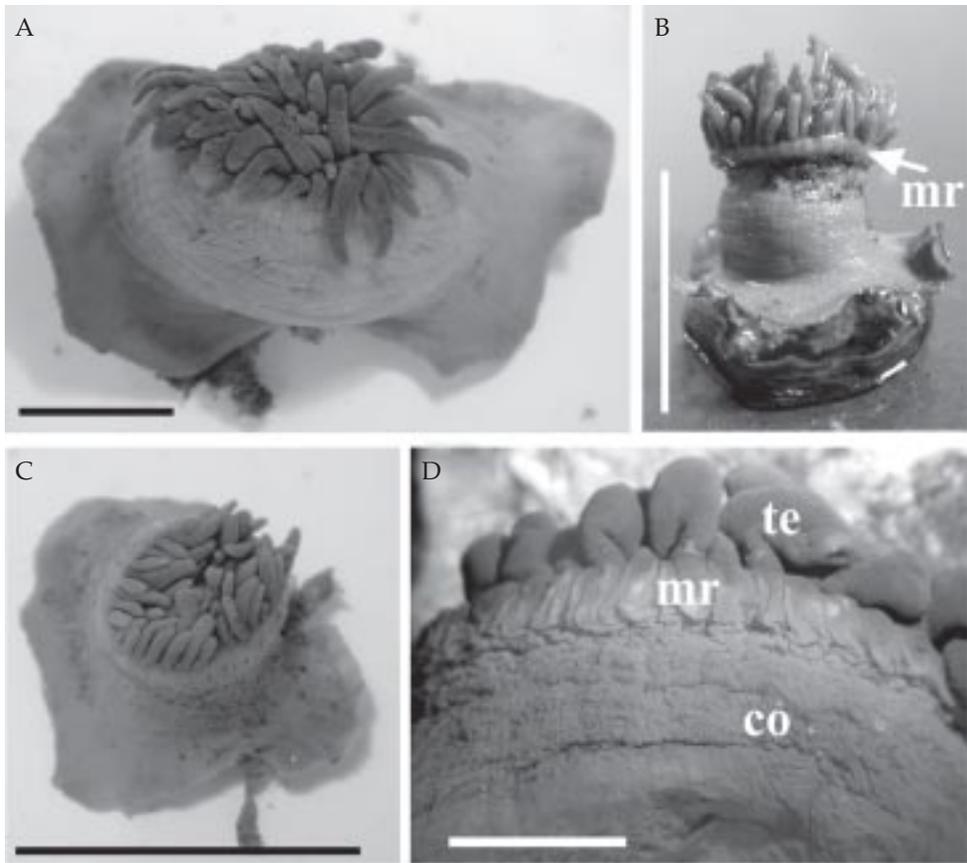


Fig. 3. *Paranthosactis denhartogi* gen. et spec. nov. Preserved specimens. A) holotype, MNHN; B) SZ (ANT-2138); C) SZ (ANT-2138); D) MNHN, detail of the distal part of the column and tentacles. Abbreviations: co, column; mr, marginal ring; te, tentacles. Scale bars: A-C, 10 mm; D, 4 mm.

Sphincter distinctly marked on the surface of the column as a prominent circumferential marginal ring; moderately strong, mesogloal. Tentacles of uniform thickness along entire length (not completely hidden in preserved retracted material). Inner tentacles longer than outer; not numerous (about 70). Longitudinal tentacle and oral disc circular musculature ectodermal; that of tentacles equally well developed on all sides. Mesenteries not arrayed according to *Actinostola* rule; first cycle of mesenteries perfect; all stronger ones fertile, including the directives. Two well developed siphonoglyphs and two pairs of directives. Retractor muscles diffuse; parietobasilar muscles not differentiated; basilar musculature differentiated. Mesogloea relatively thin. Same number of mesenteries distally and proximally. Cnidom: spirocysts, basitrichs, microbasic b-mastigophors(?), microbasic p-mastigophors.

Type species.— *Paranthosactis denhartogi* spec. nov.

Etymology and gender.— The generic name refers to the morphological similitude of the new taxon to the genus *Anthosactis* Danielssen, 1890. The gender is feminine.

Table 1. Size ranges of the cnidae of *Paranthosactis denhartogi* gen. et spec. nov. X: average. SD: standard deviation. Samples: the ratio indicates the number of polyps in which each cnidae was found out and the number of polyps of each species examined. N: indicates the total number of capsules measured. F: Frequency: +++ = very common, ++ = common, + = rather common, --- = sporadic. Abbreviation: Mc, Microbasic.

Categories	Range of length and width of capsules in μm	X \pm SD	Sample	N	F
Pedal disc					
Basitrichs (B,C)	(17.2-20.2) \times 3.0	18.6 \pm 1.2 \times 3.0 \pm 0.0*	1/1	17	+ / ++
Column					
Basitrichs (B,C)	(15.1-21.2) \times (3.0-4.0)	18.3 \pm 1.4 \times 3.6 \pm 0.5	4/4	67	++
Tentacles apex					
Spirocysts (A)	(17.2-56.6) \times (3.0-9.1)	31.2 \pm 8.0 \times 5.0 \pm 0.2	6/6	80	+++
Basitrichs (B,C)	(19.2-30.3) \times (2.0-4.0)	25.4 \pm 2.9 \times 3.2 \pm 0.4	6/6	77	++ / +++
Mc. <i>b</i> -mastigophores(?) 1 (D)	(24.2-27.3) \times 4.0	25.6 \pm 1.5 \times 4.0 \pm 0.0*	2/6	3	---
Mc. <i>p</i> -mastigophores 1 (F)	(16.2-19.2) \times (4.0-5.0)	18.2 \pm 1.1 \times 4.5 \pm 0.5*	5/6	7	---
Tentacles base					
Spirocysts (A)	(11.1-50.5) \times (4.0-9.1)	27.3 \pm 7.5 \times 5.3 \pm 1.3	6/6	80	++ / +++
Basitrichs (B,C)	(17.2-25.2) \times (2.0-4.0)	21.1 \pm 1.65 \times 3.0 \pm 0.3	6/6	47	++ / +++
Actinopharynx					
Basitrichs (B,C)	(15.1-33.3) \times (2.0-4.0)	26.8 \pm 3.8 \times 3.1 \pm 0.4	4/4	46	+ / ++
Mc. <i>p</i> -mastigophores 2 (G)	(30.3-43.4) \times (4.0-6.1)	34.7 \pm 2.3 \times 4.6 \pm 0.5	4/4	80	++ / +++
Mc. <i>p</i> -mastigophores 3 (H)	(31.3-42.4) \times (4.0-6.1)	38.2 \pm 3.4 \times 5.2 \pm 0.6*	3/4	21	+
Mc. <i>b</i> -mastigophores(?) 2 (E)	(39.4-45.4) \times (4.0-5.0)	42.4 \pm 3.03 \times 4.7 \pm 0.6*	1/4	3	---
Filaments					
Basitrichs (B,C)	(12.1-21.2) \times (2.0-4.0)	15.5 \pm 2.0 \times 2.8 \pm 0.5*	4/4	31	--- / +
Mc. <i>p</i> -mastigophores 2 (G)	(24.2-40.4) \times (4.0-6.1)	34.7 \pm 2.7 \times 4.7 \pm 0.6	4/4	70	++ / +++
Mc. <i>p</i> -mastigophores 3 (H)	37.4 \times (5.0-6.1)	37.4 \pm 0.0 \times 5.6 \pm 0.7*	1/4	2	+

* Average based on less than 40 measured capsules. The measurement of at least 40 capsules is usually considered enough to have significance.

Paranthosactis denhartogi spec. nov.
(figs 2A-B, 3-7, table 1)

Material.— MNHN, holotype, one specimen, GUAYNAUT cruise, Gulf of California, Guaymas Basin, PL 16, 27°00.94'N-111°24.66'W, 2025 m depth, 28.xi.1991; MNHN, paratypes, 2 specimens, with the same sampling data as the holotype; MNHN, 2 specimens, GUAYNAUT cruise, Gulf of California, Guaymas Basin, PL 07, 27°00.45'N-111°24.53'W, 2020 m depth, 16.xi.1991; SZ (ANT-2137), 2 specimens, GUAYNAUT cruise, Gulf of California, Guaymas Basin, PL 07, 27°00.45'N-111°24.53'W, 2020 m depth, 16.xi.1991; SZ (ANT-2138), 2 specimens, GUAYNAUT cruise, Gulf of California, Guaymas Basin, PL 16, 27°00.94'N-111°24.66'W, 2025 m depth, 28.xi.1991.

Description.— External anatomy (fig. 3): Column smooth, much broader proximally than distally; to 16 mm diameter and 15 mm height in preserved and partially retracted specimens. Pedal disc well developed and enlarged, to 35 mm at maximum axis; some specimens with foreign sulphide particles adhered to it. Column smooth, with a marginal prominent ring corresponding to the muscular sphincter (fig. 3B, D).

Oral disc not observed in preserved material. Tentacles about 70 in number, outer tentacles shorter than inner ones, up to 8 mm and not completely withdrawn in pre-

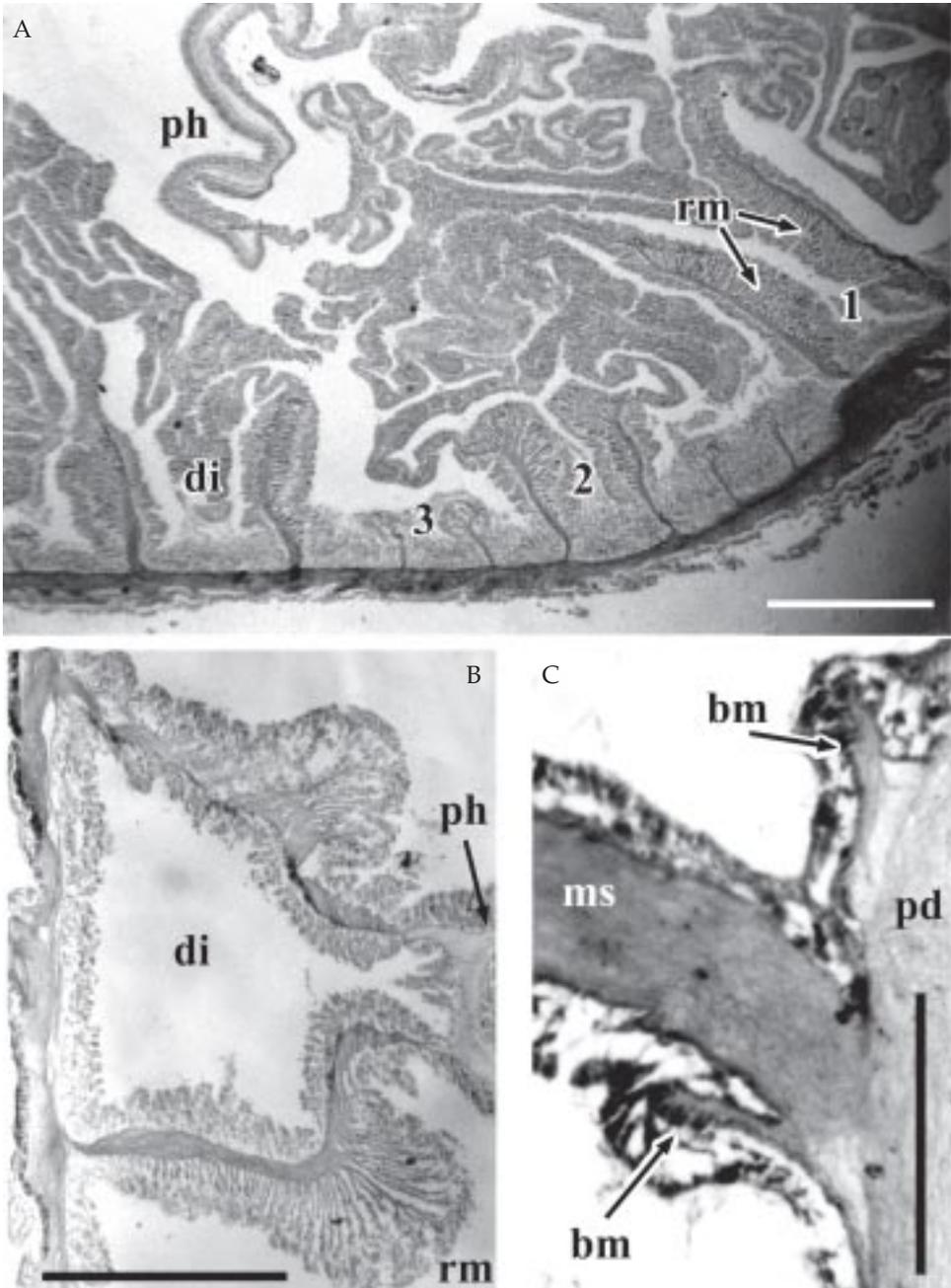


Fig. 4. *Paranthosactis denhartogi* gen. et spec. nov. (SZ (ANT-2138)) A) cross section at stomodaeum level; B) directives; C) basilar musculature. Abbreviations: 1, pair of mesenteries of the first cycle; 2, pair of mesenteries of the second cycle; 3, pair of mesenteries of the third cycle; bm, basilar muscle; di, directives; ms, mesentery; pd, pedal disc; ph, pharynx; rm, retractor muscle. Scale bars: A, 0.6 mm; B, 0.45 mm; C, 0.1 mm.

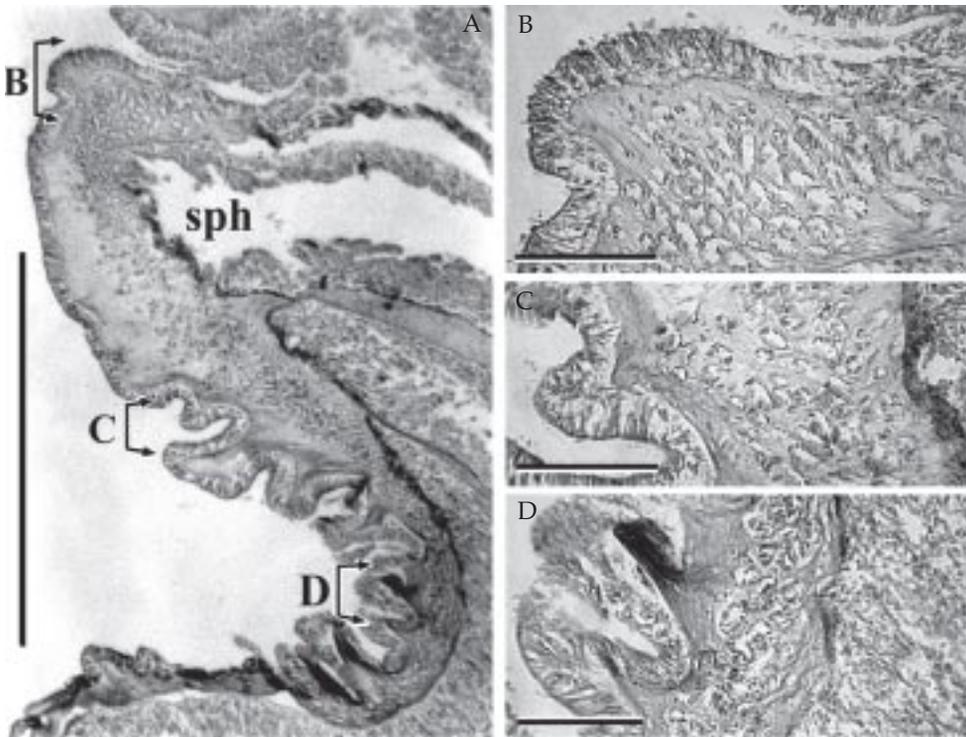


Fig. 5. *Paranthosactis denhartogi* gen. et spec. nov. (SZ (ANT-2138)) A) longitudinal section at margin showing mesogloal sphincter, details showed in the figures B, C, and D are indicated; B-D) details from A. Abbreviation: sph, sphincter. Scale bars: A, 0.5 mm; B-D, 0.06 mm.

served specimens. Not thickened at base, with longitudinal and transverse furrows due to contraction.

Internal anatomy (figs 4, 5, 6): Equal number of mesenteries distally and proximally. Mesenteries hexamerously arranged in four cycles, only the first cycle perfect. Three oldest cycles fertile, including directives. Fourth cycle incomplete, poorly developed and sterile. Two pairs of directives, connected with well-developed siphonoglyphs, mesogloea and gastrodermis of the siphonoglyphs slightly wider than the mesogloea and the gastrodermis of the actinopharynx. Retractor musculature diffuse at stomodaeum level (fig. 4A-B). Parietobasilar musculature not developed. Basilar musculature distinct but poorly developed (fig. 4C). Gametogenic tissue well developed in specimens collected in November; gonochoric; developing oocytes (to 0.13 mm in diameter on histological sections). Sphincter muscle mesogloal, moderately strong, and relatively short (fig. 5). Oral disc and tentacles with ectodermal longitudinal musculature (fig. 6). Musculature of tentacles with similar development aboral and oral. Column wall of similar thickness entire length. Epidermis 0.02-0.08 mm thick; mesogloea 0.05-0.08 mm thick, and gastrodermis 0.10-0.15 mm thick.

Cnidom: Spirocysts, basitrichs, microbasic *b*-mastigophores(?), and microbasic *p*-mastigophores. No batteries of microbasic *b*-mastigophores (or supposed microbasic

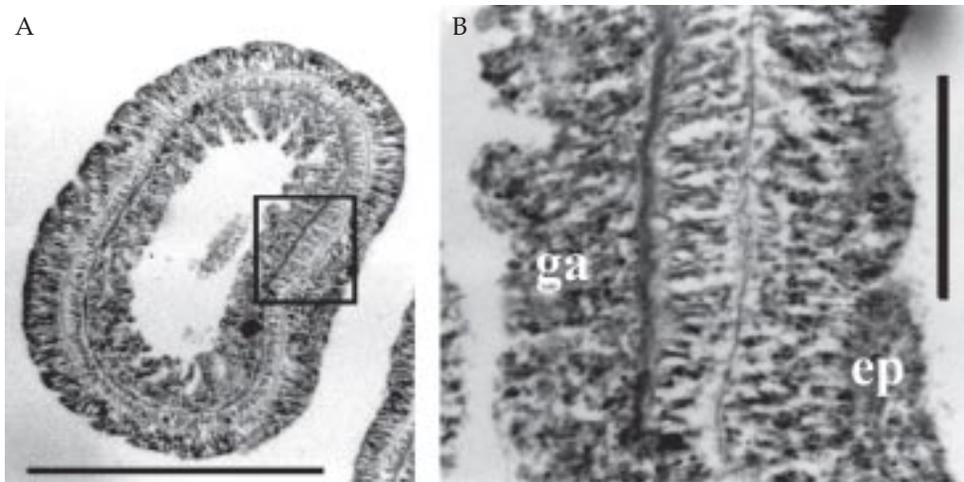


Fig. 6. *Paranthosactis denhartogi* gen. et spec. nov. (SZ (ANT-2138)) A) cross section of a tentacle; B) detail of A showing ectodermal musculature. Abbreviations: ep, epidermis; ga, gastrodermis. Scale bars: A, 0.5 mm; B, 0.1 mm.

p-amastigophores) have been observed. A survey of the cnidae is presented in table 1 and figure 7.

A sporadic cnida has been observed in the tentacles and actinopharynx of five of the six examined specimens. The nature of this cnida is extremely difficult to identify, there is not any "V" shaped end in the poorly defined but thick shaft (fig. 7D-E). This cnida is here reported as microbasic *b*-mastigophore(?). In the tentacles, this cnida has been only observed at the apex, being absent at its bases.

Colour.— Preserved material of a brownish colour, the tentacles darker. Some specimens orange in colour due to the presence of sulphide particles. According to the photographs and video tapes taken in situ (fig. 2A-B), living animals show a brown crown of tentacles, while the column is dirty white.

Etymology.— The specific name *denhartogi* is chosen in honour to Koos den Hartog (1942-2000), colleague and naturalist who was an authority on the taxonomy of soft hexacorallians, and curator of coelenterates at the Rijksmuseum van Natuurlijke Historie (RMNH), Leiden.

Distribution and habitat.— At present, *Paranthosactis denhartogi* is known only at Guaymas Basin, Gulf of California at 2020-2025 m depth. The Guaymas Basin area is a hydrothermally active site located in the center of the Gulf of California (2000 m depth), covered by a deep layer (300-500 m) of pelagic sediment. This organic-rich sediment contains petroleum-like hydrocarbons. It is crossed by hot hydrothermal fluids (320°C) rich in sulphides, which form vertical and horizontal chimneys. Diffusing sulphide-rich fluids occur around these chimneys. These conditions allow the development of very abundant microbial communities which sustain an assemblage community (fig. 2A-B) composed of chemosynthetic species known from other hydrothermal vents: tube-worms *Paralvinella* spp., *Riftia pachyptila*, vesicomid bivalve *Calyptogena magnifica*, and other species from abyssal environment: decapod shrimp *Lebbeus washingtonianus*, lithod *Neolithodes diomedea* and *Munidopsis alvisca*, and fish *Pachycara gymminium* to

quote only the megafauna (Desbruyères & Segonzac, 1997). The anemone *P. denhartogi* lives among *Riftia* on sediment where 10 cm deep a temperature of 98°C was recorded. The temperature of the fluids is ca 10°C, while that of ambient seawater is 2.8°C. Some oil traces with strong odour were present with the collected anemones. Very few is known about the trophic behaviour of hydrothermal sea anemones (Doumenc & Van Praët, 1988). Although they can catch some medium-sized prey like shrimps (Van Dover et al., 1997), such prey is quite rare in the Guaymas area. Sea anemones can take up dissolved inorganic carbon from the diffusing fluids and support symbionts based on the documented C and N stable isotopic composition. They are filter feedings species that may well nourish by ingesting free-living bacteria (Escobar et al., 1996).

Taxonomic remarks.— According to Carlgren's monograph (1949), Fautin & Hessler's key (1989), and Fautin & Barber (1999), the present material shares the following set of characters with the actinostolid genera *Anthosactis*, *Tealidium* Hertwig, 1882, *Marianactis* Fautin & Hessler, 1989, *Maractis* Fautin & Barber, 1999, and *Hadalanthus* Carlgren, 1956: 1) mesenteries not arrayed according to the *Actinostola* rule, 2) fertility of all stronger mesenteries, 3) longitudinal muscles of tentacles ectodermal, and 4) six pairs of perfect mesenteries.

In general, the presence of cnidae batteries or any special nematocysts, like microbasic *b*-mastigophores or microbasic *p*-amastigophores, has been used in recent years as a generic character (this last terminology according to Östman, 2000). However, the constancy of this feature is not always clear. Indeed, Fautin & Hessler (1989) used this feature as a character in their key to some actinostolid genera [modification of the sections "B" to "BBBB" of Carlgren's key (1949: 71)]. This key updated the recognized actinostolid genera in that section since Carlgren's monograph, and *Tealidium* and *Anthosactis* are separated by the presence of microbasic *b*-mastigophores in tentacles (forming batteries or not). Carlgren (1921: 190-198) described the "well-developed stinging batteries" on the exterior side at the base (or all along the aboral surface) of the outer tentacles in describing some *Anthosactis* and *Tealidium* species. Carlgren (1949) included this type of cnida in the diagnosis of *Anthosactis* but was not completely sure in the case of *Tealidium*. Subsequent authors (White et al., 1999) reported and illustrated these microbasic *b*-mastigophores in *Anthosactis* (as holotrichs for Riemann-Zürneck, 1997: 489), although they were not always so representative and abundant as previously described (White et al., 1999 for *A. nomados*: 43 measured capsules in 7 of 12 examined specimens, present at the tips of tentacles but not at the bases). With respect to the microbasic *p*-amastigophores, this is a category that could be corroborated only in exploded capsules, but is indistinguishable using unexploded ones. Thus, although of possible evolutionary significance, the identification of this cnida category is difficult to use as a practical routine with preserved material because of the irregular artificial discharge under laboratory conditions of preserved cnidae. Fautin & Hessler (1989) also cast some doubts about the true placement of the nematocyst batteries reported at the tentacle bases, they stated that the basal position could be just a distal placement on the column. These authors (in the key) separated the genera *Marianactis* and *Hadalanthus* by the presence/absence of microbasic *p*-amastigophores, the character of the column's nature being used at a second order. Taking into account the above, we conclude that the structure of the column - smooth (in *Marianactis*) or differentiated in scapus (covered by tenaculi) and scapulus (in *Hadalanthus*, see also below) - is more useful for identification keys.

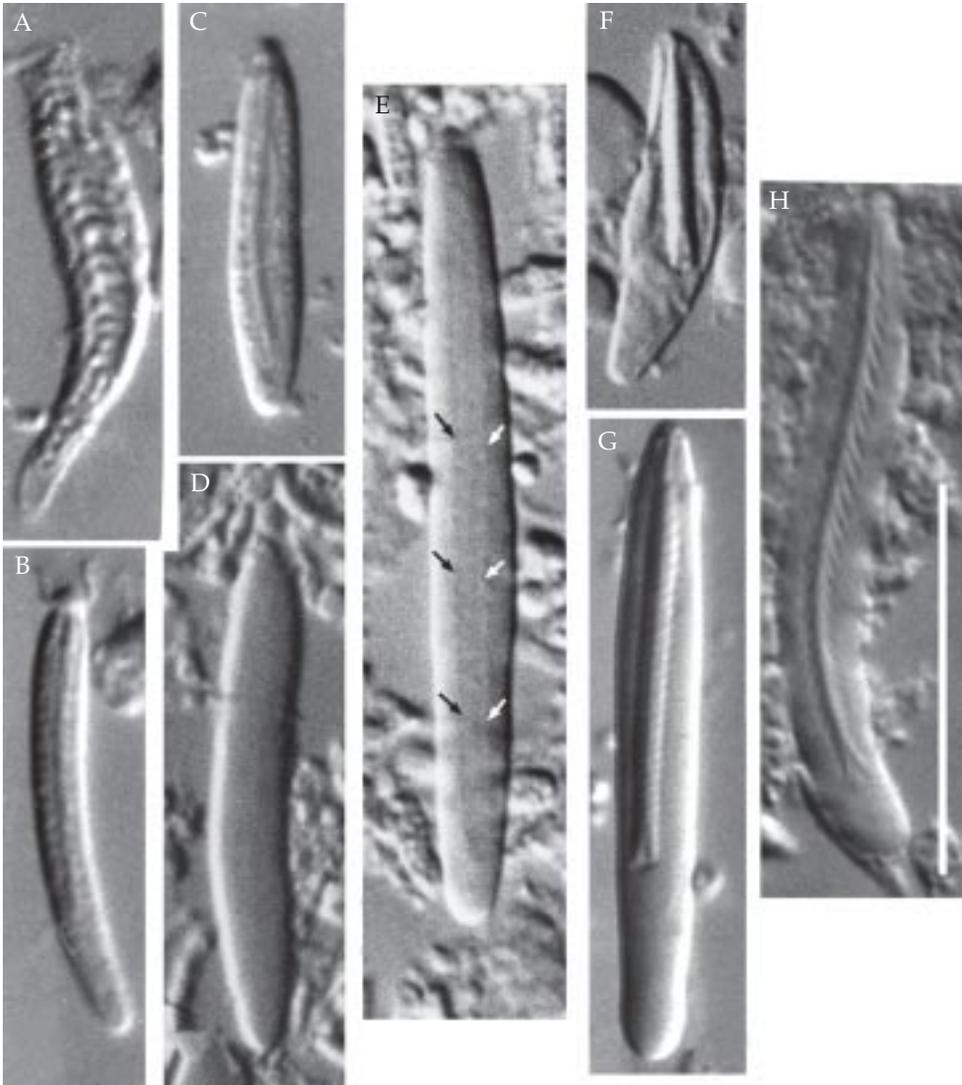


Fig. 7. *Paranthosactis denhartogi* gen. et spec. nov. Cnidae. A) spirocyst; B) basitrich; C) basitrich; D) microbasic *b*-mastigophore(?) 1; E) microbasic *b*-mastigophore(?) 2, the limits of the shaft are arrowed; F) microbasic *p*-mastigophore 1; G) microbasic *p*-mastigophore 2; H) microbasic *p*-mastigophore 3. See text and table 1 for explanation. Scale bar: 20 μ m.

Following the re-description of the type species of the genus *Anthosactis*, *A. janmayeni* Danielssen, 1890, (Riemann-Zürneck, 1997), and the re-definition of the diagnosis of *Anthosactis* given by White et al. (1999), the present material is here allocated to a new generic unit different from *Anthosactis*. The new genus differs in the similar development of the longitudinal musculature of tentacles on the aboral and oral sides (strongest on the oral side in *Anthosactis*), and by the absence of parietobasilar muscles

Table 2. Tabular key comparing the diagnostic characters of the group of actinostolid genera above discussed. **Column:** **S**, smooth; **M**, with mesogloal papillae; **T**, with tenaculi; **D**, divisible into scapus and scapulus; **N**, not divisible into scapus and scapulus; **Tn**, thin; **Tc**, thick. **Parietobasilar muscles:** **D**, differentiated as a separate lamella; **N**, not differentiated as a separate lamella; **Longitudinal tentacles muscles:** **O**, stronger developed on the oral sides than on the aboral sides; **S**, similar developed on oral and aboral sides. **Sphincter:** **R**, marked as a circumferencial marginal ring; **N**, no marked as a circumferencial marginal ring; **nd**, no data. **Tentacular cnidae:** **Sp**, Spirocysts; **Bs**, Basitrichs, **m-bm**, Microbasic *b*-mastigophores; **m-pam**, Microbasic *p*-amastigophores; **m-pm**, Microbasic *p*-mastigophores.

Column	Parietobasilar muscles	Longitudinal tentacles muscles	Sphincter	Tentacular	Genus
S, N, Tc	D	S	N	Sp, Bs, m-pam	<i>Marianactis</i> Fautin and Hessler, 1989
S, N, Tn ⁽¹⁾	N ⁽⁵⁾	S	N	Sp, Bs, H	<i>Maractis</i> Fautin and Barber, 1999
S, N, Tn	N	S	R	Sp, Bs, m-bm?, m-pm	<i>Paranthosactis</i> gen. nov.
S, N, Tn	N ⁽²⁾	O	R/N ⁽³⁾	Sp, Bs, m-bm	<i>Anthosactis</i> Danielssen, 1890
M, N, Tn	nd	O	R ⁽⁴⁾ /N	Sp, Bs, m-bm	<i>Tealidium</i> Hertwig, 1882
T, D, Tn	N	S	N	Sp, Bs, m-pm	<i>Hadalanthus</i> Carlgren, 1956

⁽¹⁾ Described as relatively thin (Fautin & Barber, 1999).

⁽²⁾ Distinctly marked but without forming a separate lamella (Hertwig, 1882:194).

⁽³⁾ Only the type species of the genus -*A. janmayeni* Danielssen, 1890- has the peculiar sphincter that forms a solid ridge around the margin (Riemann-Zürneck, 1997: 491).

⁽⁴⁾ Sphincter very strong, in certain states of contraction issuing as a strong circular fold in the uppermost part of the column (Hertwig, 1882: 196).

⁽⁵⁾ Only clearly differentiable in the stronger cycles (Fautin & Barber, 1999: 626).

(distinctly marked but without forming a separate lamella in *Anthosactis*). In addition, *Paranthosactis* lacks stinging batteries of microbasic *b*-mastigophores at the base of the aboral side of the outer tentacles, or along its whole aboral side. Finally, microbasic-*p* mastigophores are present in the tentacles of *Paranthosactis* and absent in *Anthosactis*.

Paranthosactis is clearly distinguishable from *Tealidium* by the absence of mesogloal papillae on the column; these structures are distinctly observable in the type material of *T. jungerseini* examined for comparative purposes in the present study. Furthermore, in *Tealidium* (as in *Anthosactis*) the longitudinal musculature of tentacles is stronger on the oral side than on the aboral side, unlike *Paranthosactis* (above commented).

Marianactis differs from *Paranthosactis* due to its developed parietobasilar musculature (not differentiated in *Paranthosactis*), the thick mesogloal layer in the column (remarkably thinner in *Paranthosactis*, compare fig. 2 in Fautin & Hessler, 1989, and fig. 4A-B in this paper) and the sphincter not marked as a circumferencial marginal ring.

Maractis differs from *Paranthosactis* due to its differentiable parietobasilar muscles on the stronger cycles, the sphincter not marked as a circumferencial ring, and the absence of mastigophore nematocysts in the tentacles.

Hadalanthus can be easily differentiated from *Paranthosactis* by its column divided into scapus covered by distinct tenaculi (completely absent in *Paranthosactis*) and scapulus.



Fig. 8. *Hadalanthus* aff. *knudseni* Carlgren, 1956. Preserved specimens. A) SZ (ANT-2139); B) MNHN, pedal disc; C) MNHN; D) SZ (ANT-2140). Scale bars: A, B, D, 15 mm; C, 30 mm.

In table 2, we present a tabular key comparing the groups of actinostolid genera above discussed.

Genus *Hadalanthus* Carlgren, 1956

Diagnosis (modified from Carlgren, 1956, modification in bold).— Actinostolidae with well developed pedal disc. Column more or less cylindrical, divisible into scapus and scapulus. Scapus with numerous papillae forming weak tenaculi, scapulus ridged. Sphincter strong or very strong, mesogloea. Tentacles rather long, **up to about 140**, their longitudinal muscles ectodermal as also the radial muscles of oral disc. Six pairs of mesenteries perfect. Dioecious. At least the two first cycles of mesenteries fertile. Two well developed siphonoglyphs and two pairs of directives. Retractors strong, diffuse,

below the actinopharynx curved to the exocoels in the nondirectives, towards the endocoels in the directives. Parietobasilar muscles weak. Same number of mesenteries distally and proximally. Cnidom: spirocyst, basitrichs, microbasic *p*-mastigophors.

Hadalanthus aff. *knudseni* Calgren, 1956
(figs 2C, D, 8-13, table 3)

Material.— MNHN, one specimen, NAUTIMATE cruise, NM09, Eastern Pacific, 18°21'N-104°21'W, 3443 m depth, 27.i.1994; MNHN, 2 specimens, with the same sampling data as the holotype; SZ (ANT-2139) 2 specimens, NAUTIMATE cruise, NM09, Eastern Pacific, 18°21'N-104°21'W, 3443 m depth, 27.i.1994; MNHN, one specimen, NAUTIMATE cruise NM01, Eastern Pacific, 18°20.42'N-104°21.73'W, 3354 m depth, 19.i.1994; MNHN, one specimen, NAUTIMATE cruise, NM01-04, Eastern Pacific, 18°20.42'N-104°21.73'W, 3354 m depth, 19.i.1994; SZ (ANT-2140), one specimen, NAUTIMATE cruise, NM 01-04, Eastern Pacific 18°20.42'N-104°21.73'W, 3354 m depth, 19.i.1994; MNHN, 2 specimens, NAUTIMATE cruise, NM16 site A, Eastern Pacific, 20°01.79'N 106°17.33'W, 3795 m depth, 4.ii.1994.

Description.— External anatomy (figs 8-9): All specimens completely retracted, dome-shaped, to 46 mm diameter and 18 mm height in preserved state (figs 8A, C, D). Pedal disc well developed and enlarged, delicate (often damaged in examined material), and translucent so mesenterial insertions visible (fig. 8B). Column divisible into scapus and scapulus. Scapus with numerous tenaculi flattened distally (fig. 9A), but pointed to rounded proximally (fig. 9B-C), not regularly arranged, with thin cuticle, and no foreign particles adhered to them. Scapulus apparently smooth, but ridged by contraction.

Oral disc not observed in preserved and retracted specimens. Tentacles completely hidden in retracted state. Tentacles smooth, rounded distally, up to 140 in number, inner longer than outer ones, not thickened at base.

Internal anatomy (figs 10, 11, 12): Mesenteries thin, hexamerously arranged in four cycles, only first cycle perfect. All stronger mesenteries, except last cycle, fertile (fig. 10). The same number of mesenteries distally and proximally. Two pairs of fertile directives, connected with strong and well-developed siphonoglyphs. Mesogloea and gastrodermis of the siphonoglyphs slightly wider than the mesogloea and the gastrodermis of the actinopharynx. Retractor musculature diffuse with several short mesogloea branches forming pennons at actinopharynx level (fig. 10). Parietobasilar muscle not distinctly developed. Basilar musculature weak but distinctly developed. Gametogenic tissue well developed in specimens collected in January; gonochoric; developing spermatic vesicles to 0.30 mm in diameter on histological sections. Sphincter muscle mesogloea, strong, closer to the ectoderm (fig. 11A, B). Oral disc and tentacles (fig. 11C) with ectodermal longitudinal musculature. Column wall of similar thickness along entire length. Tenaculi on mesogloea papillae, with thin, 0.01-0.02 mm, clearly stratified cuticle (figs 11D, 12). Epidermis 0.07-0.35 mm thick; mesogloea 0.45-0.80 mm thick, and gastrodermis 0.20-0.50 mm thick.

Cnidom: Spirocysts, basitrichs, holotrichs(?) and microbasic *p*-mastigophores. A survey of the cnidae is presented in table 3 and figure 13. The presence of holotrichs has not been included in the diagnosis of the genus (see above) as the true nature of this cnida is not resolved.

Colour: Preserved material of a flesh to yellowish colour, with dark brownish tenaculi. According to the photographs and video tapes taken in situ (fig. 2C-D), living

Table 3. Size ranges of the cnidae of *Hadalanthus* aff. *knudseni* Carlgren, 1956. X: average. SD: standard deviation. Samples: the ratio indicates the number of polyps in which each cnidae was found out and the number of polyps of each species examined. N: indicates the total number of capsules measured. F: Frequency: +++ = very common, ++ = common, + = rather common, --- = sporadic. Abbreviation: Mc, Microbasic.

Categories	Range of length and width of capsules in μm	X \pm SD	Sample N	F
Pedal disc				
Basitrichs (C)	(20.2-25.2) \times (2.0-3.0)	23.1 \pm 1.4 \times 2.8 \pm 0.4*	2/2	26 ---/++
Scapus				
Basitrichs (C)	(18.2-24.2) \times (2.0-3.0)	21.2 \pm 1.3 \times 2.5 \pm 0.5	3/3	60 +++
Mc. <i>p</i> -mastigophores (D)	(20.2-29.3) \times (3.0-6.1)	26.1 \pm 1.6 \times 4.6 \pm 0.7	3/3	55 ++
Scapulus				
Basitrichs (C)	(21.2-27.3) \times (3.0-4.0)	23.7 \pm 1.2 \times 3.2 \pm 0.4	3/3	60 ++/+++
Mc. <i>p</i> -mastigophores (D)	(24.2-35.3) \times (4.0-6.1)	28.3 \pm 2.0 \times 5.1 \pm 0.7	3/3	60 +++
Tentacles				
Spirocysts (A)	(18.2-50.5) \times (5.0-11.1)	30.1 \pm 7.2 \times 7.2 \pm 1.6	5/5	75 ++/+++
Spirocysts (B)	(18.2-36.4) \times (4.0-10.1)	26.3 \pm 4.4 \times 5.1 \pm 1.2*	3/5	33 +/-++
Basitrichs (C)	(14.1-35.3) \times (2.0-4.0)	21.9 \pm 4.6 \times 2.8 \pm 0.5	5/5	100 ++
Mc. <i>p</i> -mastigophores (D)	(20.2-34.3) \times (4.0-7.1)	24.9 \pm 4.9 \times 5.0 \pm 0.9	5/5	85 +/-++
Holotrachs ? (E)	(23.2-33.3) \times (6.1-8.1)	29.9 \pm 3.3 \times 6.8 \pm 0.7*	4/5	8 ---
Actinopharynx				
Basitrichs (B,C)	(14.1-26.3) \times (2.0-4.0)	20.3 \pm 3.8 \times 2.7 \pm 0.5	3/3	44 ++
Mc. <i>p</i> -mastigophores (D)	(22.2-38.4) \times (4.0-7.1)	31.5 \pm 3.8 \times 5.3 \pm 0.9	3/3	43 ++/+++
Filaments				
Basitrichs (B,C)	(16.2-25.2) \times (2.0-3.0)	18.9 \pm 2.2 \times 2.8 \pm 0.4	3/3	43 +/-++
Mc. <i>p</i> -mastigophores (D)	(23.2-36.4) \times (4.0-6.1)	30.1 \pm 3.5 \times 4.8 \pm 0.5	3/3	48 +/-++

* Average based on less than 40 measured capsules. The measurement of at least 40 capsules is usually considered enough to have significance.

animals show a brownish crown of tentacles, while the column is dirty white.

Distribution and habitat.— At present, *Hadalanthus* aff. *knudseni* is known from the Eastern Pacific in the Middle American Trench off Manzanillo (Mexico), between 3354 and 3795 m. This area is the seat of cold seeps coming from the tectonic plate Rivera subduction, on the level of a fault system whose principal one is prolonged to the north into the basin of Guaymas. Colonies of bivalves vesicomid *Calyptogena* sp. live on the sediment, often covered by a bacterial mat, at the exit of cold fluids charged of reduced compounds (CH₄ and SH₂). The sea anemones are fixed on these bivalves (fig. 2C-D), alive, or more frequently on the shells, which constitutes the only hard substrate of these sedimentary areas. The accompanying fauna of these communities is very little diversified. It consists of a rare galathea crab *Munidopsis subsquamosa* (fide E. Macpherson), of zoarcid fish, and serpulid polychaetes *Neovermilia* sp. (fide H. Zibrowius).

Taxonomic remarks.— According to Carlgren's diagnosis (1956) and Fautin & Hessler's key (1989), the present material can be included in the deep-sea genus *Hadalanthus* Carlgren, 1956 by the following set of features: 1) fertility of all stronger mesenteries, 2) ectodermal nature of longitudinal tentacles muscles, 3) six pairs of perfect mesenteries, 4) absence of microbasic *b*-mastigophores in tentacles, 5) presence of microbasic *p*-mastigophores in tentacles, 6) presence of a column divided into scapus

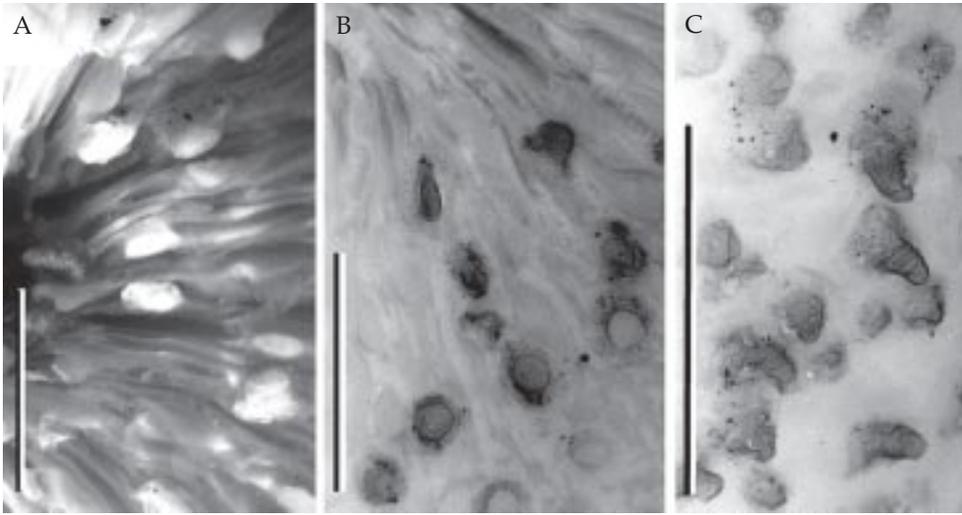


Fig. 9. *Hadalanthus* aff. *knudseni* Carlgren, 1956. Tenaculi on scapus. Note the variability in shape, flattened distally (A) [MNHN, to rounded or pointed at mid-column level (B and C) [MNHN]. Scale bars: A, 3 mm; B, 4 mm; C, 3.5 mm.

and scapulus, and 7) presence of distinct tenaculi on low mesogloal papillae.

Carlgren (1956: 13) pointed out the similar appearance of the column of *Hadalanthus* and *Daontesia* Carlgren, 1942, taking into account the absence of acontiae in the former genus. Among the actinostolid genera, the presence of mesogloal papillae (eroded tenaculi?) in the genus *Tealidium* could be considered a common feature with *Hadalanthus* (see Hertwig, 1882, Carlgren, 1921, 1949). However, sensu Carlgren (1949: 77) and Fautin & Hessler (1989: 817), the absence of batteries of nematocysts in tentacles is a distinctive character between both genera. In the examined type material of *Tealidium jungerseni*, there is no trace of cuticle or tenaculi, although the mesogloal papillae are clearly visible on the column. However, in the examined type material of *Hadalanthus knudseni*, the tenaculi - visible at low magnification - are formed by a yellowish cuticle on small mesogloal papillae.

Despite the examination of the type material of *Hadalanthus knudseni*, it is difficult to decide whether the material collected during the NAUTIMATE cruise should be described as a new species or included under the name of the single species named in the genus *Hadalanthus*. The current state of the type material of *H. knudseni* does not allow to obtain more information about the structure of the distal tenaculi (in fact most of them are eroded), additional measurements of undischarged cnidae in order to obtain a positive or negative significance based on statistic analyses (most of them are exploded as indicated in the table 4), and other anatomical structures commonly used to solve specific questions. Thus, although our NAUTIMATE specimens show darker tenaculi (yellowish in the type material), flattened tenaculi distally (can not be observed in the type material due to the poor state of conservation) and some slight differences in the cnidae (these can not be compared by the scarce data obtained from the tissues of the type material, see tables 3 and 4), we identify the NAUTIMATE

Table 4. Size ranges of the cnidae of *Hadalaranthus knudseni* Carlgren, 1956 (Syntypes ZMUC). X: average. SD: standard deviation. Samples: the ratio indicates the number of polyps in which each cnidae was found out and the number of polyps of each species examined. N: indicates the total number of capsules measured. F: Frequency, +++ = very common, ++ = common, + = rather common, — = sporadic. Abbreviation: Mc, Microbasic

Categories	Range of length and width of capsules in μm	X \pm SD	Sample	N	F	Data from Carlgren, 1956
Pedal disc						
Basitrichs	(26.6-30.3) \times 3.0	29.0 \pm 1.9 \times 3.0 \pm 0.0*	1/1	4	+	no data
Scapus (1)						
Basitrichs	(19.2-30.3) \times 3.0	24.4 \pm 2.5 \times 3.1 \pm 0.3	2/2	55	++	(24-32) \times (2.8-3.5)
Tentacles						
Spirocysts						
Basitrichs 1	(27.3-51.5) \times (6.1-7.1)	40.0 \pm 0.5 \times 5.6 \pm 0.8*	2/2	11	++	50 \times 5.6
Basitrichs 2	(34.3-42.4) \times 3.0	38.9 \pm 3.0 \times 3.0 \pm 0.0*	1/2	6	+	(38-43) \times (2.8-3.5)
Basitrichs 3	not found					(48-53.6) \times 5
Mc. p-mastigophores(2)						
	(14.1-24.2) \times (2.0-3.0)	19.0 \pm 2.3 \times 3.0 \pm 0.3*	2/2	22	++	no data
	(29.3-35.3) \times (4.0-5.0)	33.1 \pm 2.6 \times 4.8 \pm 0.4*	2/2	9	+ / ++	(39.0-50.8) \times 5
Actinopharynx						
Basitrichs						
	(20.2-30.3) \times (3.0-4.0)	24.6 \pm 2.8 \times 3.1 \pm 0.3*	1/1	20	++	no data
Mc. p-mastigophores(3)						
	(41.4-51.5) \times (5.0-6)	45.3 \pm 3.7 \times 5.2 \pm 0.4*	1/1	8	++	no data
Filaments						
Basitrichs						
	(16.2-26.3) \times (3.0-4.0)	21.0 \pm 2.4 \times 3.1 \pm 0.2	2/2	83	++	(19.7-24) \times 3
Mc. p-mastigophores(4)						
	(35.3-50.5) \times (4.0-5.0)	41.4 \pm 4.6 \times 4.8 \pm 0.4*	2/2	15	+++	(23-48) \times 4.5

* Average based on less than 40 measured capsules. The measurement of at least 40 capsules is usually considered enough to have significance.

(1) 4 exploded capsules (25.2-29.3) \times 5.0 have been also found.

(2) 8 exploded capsules (30.3-40.4) \times (4.0-5.0) have been also found.

(3) numerous exploded capsules (42.4-50.5 \times 4.0-5.0) have been also found; 5 exploded capsules (42.4-46.5) \times (5.0-6.1) have been also found.

(4) numerous exploded capsules (42.4-50.5 \times 4.0-5.0) have been found; 52 exploded capsules (23.2)(31.3-48.5) \times (4.0-6.1) have been also found.

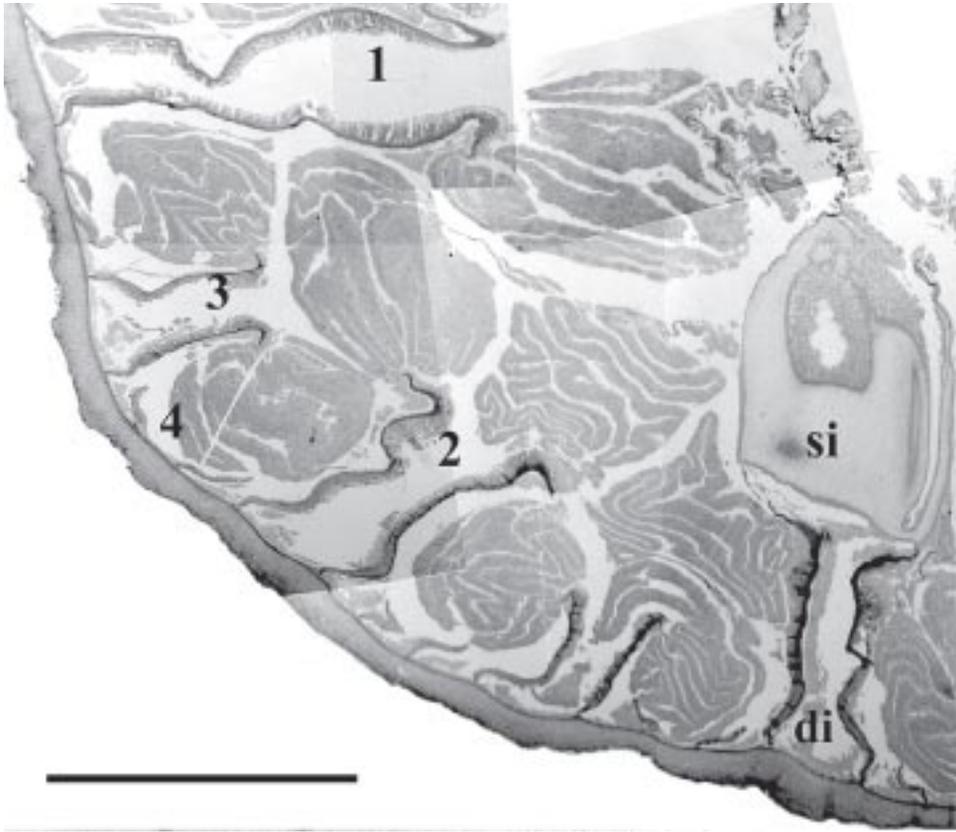


Fig. 10. *Hadalanthus* aff. *knudseni* Carlgren, 1956. (SZ (ANT-2139)). Cross section at stomodaeum level. Abbreviations: 1, pair of mesenteries of the first cycle; 2, pair of mesenteries of the second cycle; 3, pair of mesenteries of the third cycle; 4, pair of mesenteries of the fourth cycle; di, directives; si, siphonoglyph; Scale bar: 5 mm.

specimens as *H. aff. knudseni* because of the similitude in the other comparable characters. The available differentiating characters could be product of the large size of the NAUTIMATE specimens (e.g. about 140 tentacles in the larger individual, but about 70 in an individual of similar size as the type material of *H. knudseni*).

Genus *Maractis* Fautin & Barber, 1999
Maractis rimicarivora Fautin & Barber, 1999
 (figs 2E, F, 14-16, table 5)

Maractis rimicarivora Fautin & Barber, 1999: 625, figs. 1-4.

Material.— MNHN, 2 specimens, DIVERSExpedition cruise, Snake Pit-Elan (Mid-Atlantic Ridge), dive 3674, 23°22.90'N-44°55.80'W, 3490 m depth, 16.vii.2001; SZ (ANT-2141), 2 specimens, DIVERSExpedition cruise, Snake Pit-Elan (Mid-Atlantic Ridge), dive 3674, 23°22.90'N-44°55.80'W, 3490 m depth, 16.vii.2001.

Table 5. Size ranges of the cnidae of *Maractis rimitarivora*. X: average. SD: standard deviation. Samples: the ratio indicates the number of polyyps in which each cnidae was found out and the number of polyyps of each species examined. N: indicates the total number of capsules measured. F: Frequency: +++ = very common, ++ = common, + = rather common, --- = sporadic. Abbreviation: Mc, Microbasic.

Categories	Range of length and width of capsules in µm	X±SD	Sample	N	F	Fautin & Barber (1999)	
						Range of length and width of capsules in µm	Sample N
Present study							
Snake Pit, 3500 m							
Pedal disc							
Basitrichs (B)	(22.2-30.3) × (3.0-4.0)	24.4±2.2 × 3.1±0.3	4/4	58	+/++	-----	
Column							
Basitrichs (B)	(19.2-29.3) × (3.0-4.0)	23.7±1.9 × 3.1±0.3	4/4	80	++/+++	(19.5-31.5) × (1.9-3.9)	5/5 71
Mc. <i>p</i> -mastigophores 1 (D)	(25.2-30.3) × (4.0-5.0)	27.4±1.9 × 4.3±0.5*	2/4	19	---/++	(21.3-31.9) × (3.4-6.2)	4/5 54
Tentacles							
Spirocysts (A)	(27.3-81.8) × (4.0-7.1)	47.9±12.9 × 5.1±1.0	4/4	80	+++	(30.0-78.5) × (2.8-7.3)	5/5 91
Basitrichs (B)	(19.2-45.4) × (3.0-4.0)	35.4±5.2 × 3.5±0.5	4/4	67	++	(31.0-48.4) × (2.5-3.8)	5/5 50
						(17.2-25.5) × (1.6-2.9)	5/5 54
						(19.2-43.4) × (1.9-3.8)	5/5 74
						(30.4-53.9) × (4.5-6.4)	5/5 39
Holotrichs (G)							
	(35.3-48.5) × (5.0-8.1)	42.4±3.9 × 6.0±0.7*	3/4	22	---/+		
Actinopharynx							
Basitrichs (B,C)	(16.2-36.4) × (3.0-4.0)	23.8±6.9 × 3.1±0.2*	2/4	17	---/+	(23.4-34.9) × (2.3-3.2)	3/4 9
Mc. <i>p</i> -mastigophores 1 (D, E)	(29.3-41.4) × (3.0-5.0)	35.4±3.1 × 4.5±0.6	4/4	100	++/+++	(28.6-42.1) × (4.1-5.2)	3/4 31
Mc. <i>p</i> -mastigophores 2 (F) ⁽¹⁾	(30.3-39.4) × (4.0-6.1)	34.1±2.7 × 4.4±0.6*	2/4	15	+		
Filaments							
Basitrichs (C)	(14.1-21.2) × (2.0-3.0)	17.3±1.7 × 2.9±0.3*	4/4	38	---/++	(16.1-34.1) × (1.8-4.5)	5/5 61
Mc. <i>p</i> -mastigophores 1 (D, E)	(28.3-39.4) × (4.0-5.0)	34.6±2.6 × 4.7±0.5	4/4	100	++/+++	(26.9-38.9) × (3.3-5.7)	5/5 61
Mc. <i>p</i> -mastigophores 2 (F) ⁽¹⁾	(30.3-37.4) × (4.0-6.1)	34.9±2.1 × 5.1±0.4*	2/4	15	---/+		

* Average based on less than 40 measured capsules. The measurement of at least 40 capsules is usually considered enough to have significance.

⁽¹⁾ Although this category could be included with the precedent cnida by the overlapping size range, low frequency and low constancy in the sampled specimens, we have preferred to maintain it separated from the other microbasic *p*-mastigophore (D,E) by the short V-shaped end and relative length of the shaft. Examination of exploded capsules could give additional information about the structure of the spines rows and solve definitively if they should be considered as the same category or maintained them separated.

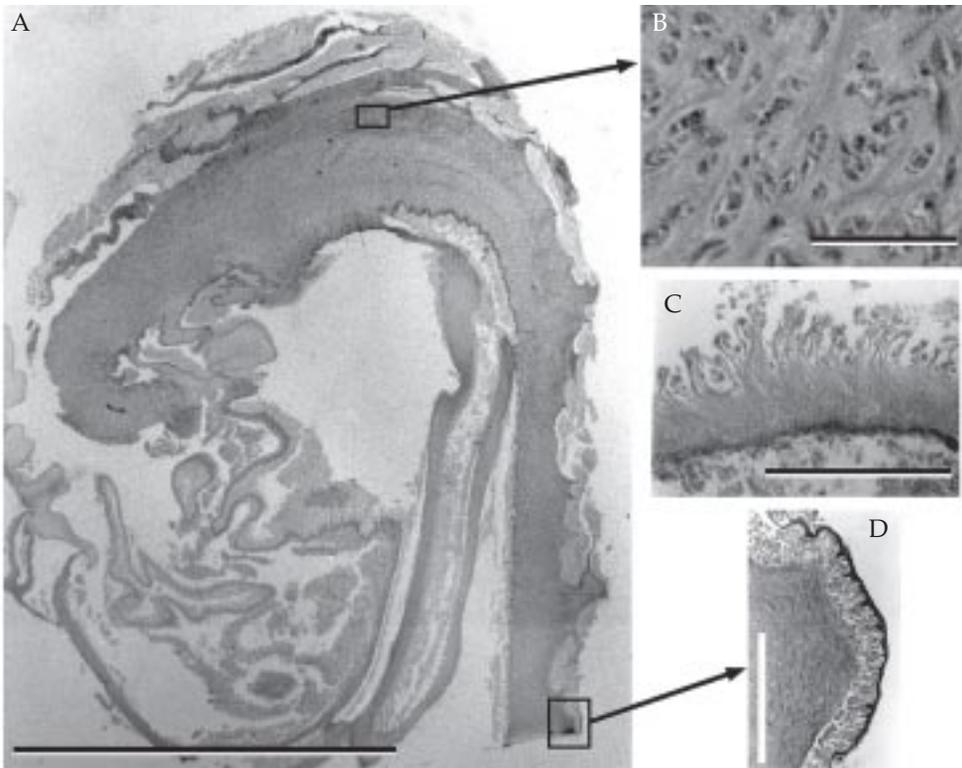


Fig. 11. *Hadalanthus* aff. *knudseni* Carlgren, 1956. (SZ (ANT-2139)). A) longitudinal section at margin showing mesogloal sphincter; details showed in figures B and C are indicated; B) detail of mesogloal sphincter; C) cross section of a tentacle, showing ectodermal musculature; D) tenaculi. A, 5 mm; B, 0.15 mm; C, 0.2 mm; D, 0.25 mm.

Description.— External anatomy (fig. 14): Column with rough texture, much broader proximally than distally; to 28 mm diameter and 20 mm height in preserved specimens. Column with transversal furrows due to the contraction of the animals, some sulphide particles adhered to them. Pedal disc well developed and enlarged, to 41 mm along maximum axis, in some specimens with foreign sulphide particles adhered to it.

Oral disc not observed in preserved material. Tentacles about 100, outer tentacles shorter than inner ones, up to 16 mm long, and not completely withdrawn in preserved specimens (fig. 14). No thickening at base, with longitudinal and transverse furrows due to the contraction.

Internal anatomy (fig. 15): Equal number of mesenteries distally and proximally. Mesenteries hexamerously arranged in four cycles, only the first cycle perfect. All stronger mesenteries fertile. Two pairs of fertile directives, connected with strong and well-developed siphonoglyphs. Mesogloea and gastrodermis of the siphonoglyphs slightly wider than the mesogloea and the gastrodermis of the actinopharynx. Retractor musculature diffuse at stomodaeum level (fig. 15A). Parietobasilar musculature only clearly differentiable in the stronger cycles. Basilar musculature poorly developed.

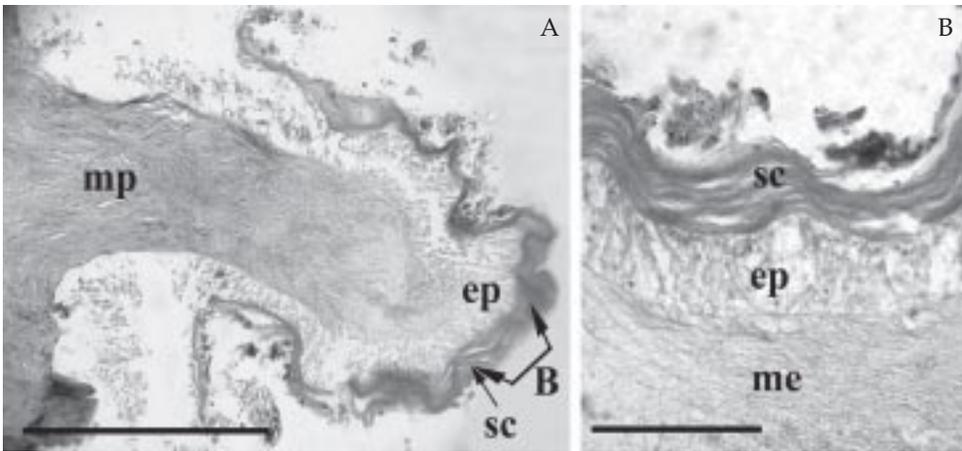


Fig. 12. *Hadalanthus* aff. *knudseni* Carlgren, 1956. (SZ (ANT-2139)). A) tenaculi and its mesogloal papilla, longitudinal section. Distal portion showed in B is indicated; B) detail of A. Abbreviations: ep, epidermis; me, mesogloea; mp, mesogloal papilla; sc, stratified cuticle. Scale bars: A, 0.25 mm; B, 0.05 mm.

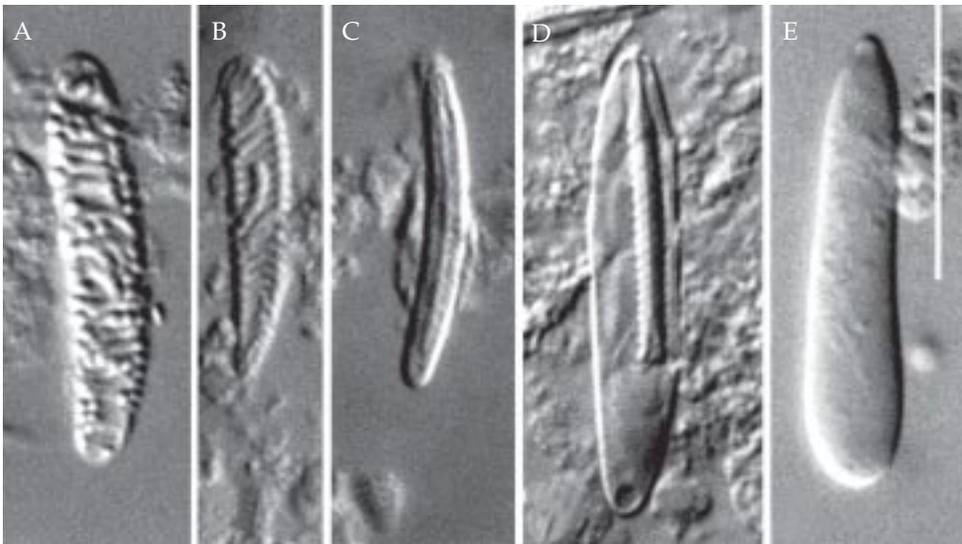


Fig. 13. *Hadalanthus* aff. *knudseni* Carlgren, 1956. Cnidae. A) spirocyst A; B) spirocyst B; C) basitrich D) microbasic *p*-mastigophore E) holotrich(?). See text and table 3 for explanation. Scale bar: 20 μ m

Gametogenic tissue well developed in specimens collected in July; gonochoric; developing spermatic vesicles (to 0.25 mm in diameter in preserved specimens). Sphincter muscle mesogloal, strong, relatively short, occupying all mesogloea with the muscle bundles reticulated (fig. 15B). Oral disc and tentacles with ectodermal longitudinal musculature (fig. 15C-D). Column wall of similar thickness along entire length. Epidermis 0.04-0.12 mm thick; mesogloea 0.06-0.19 mm thick, and gastrodermis 0.02-0.12 mm thick.

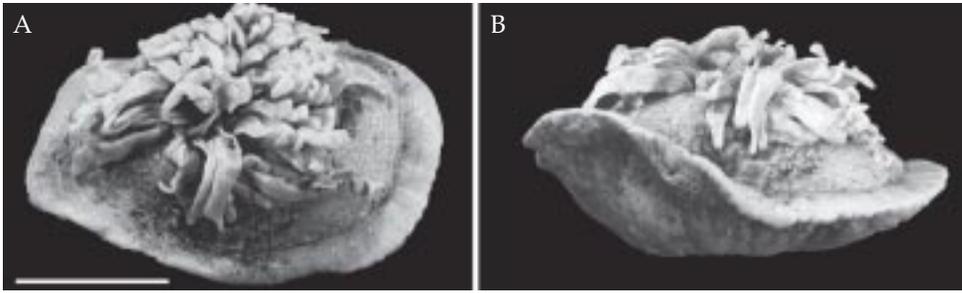


Fig. 14. *Maractis rimicarivora* Fautin & Barber, 1989. Preserved specimen (SZ (ANT-2141)). A) Oral view; B) lateral view. Scale bar A-B: 15 mm.

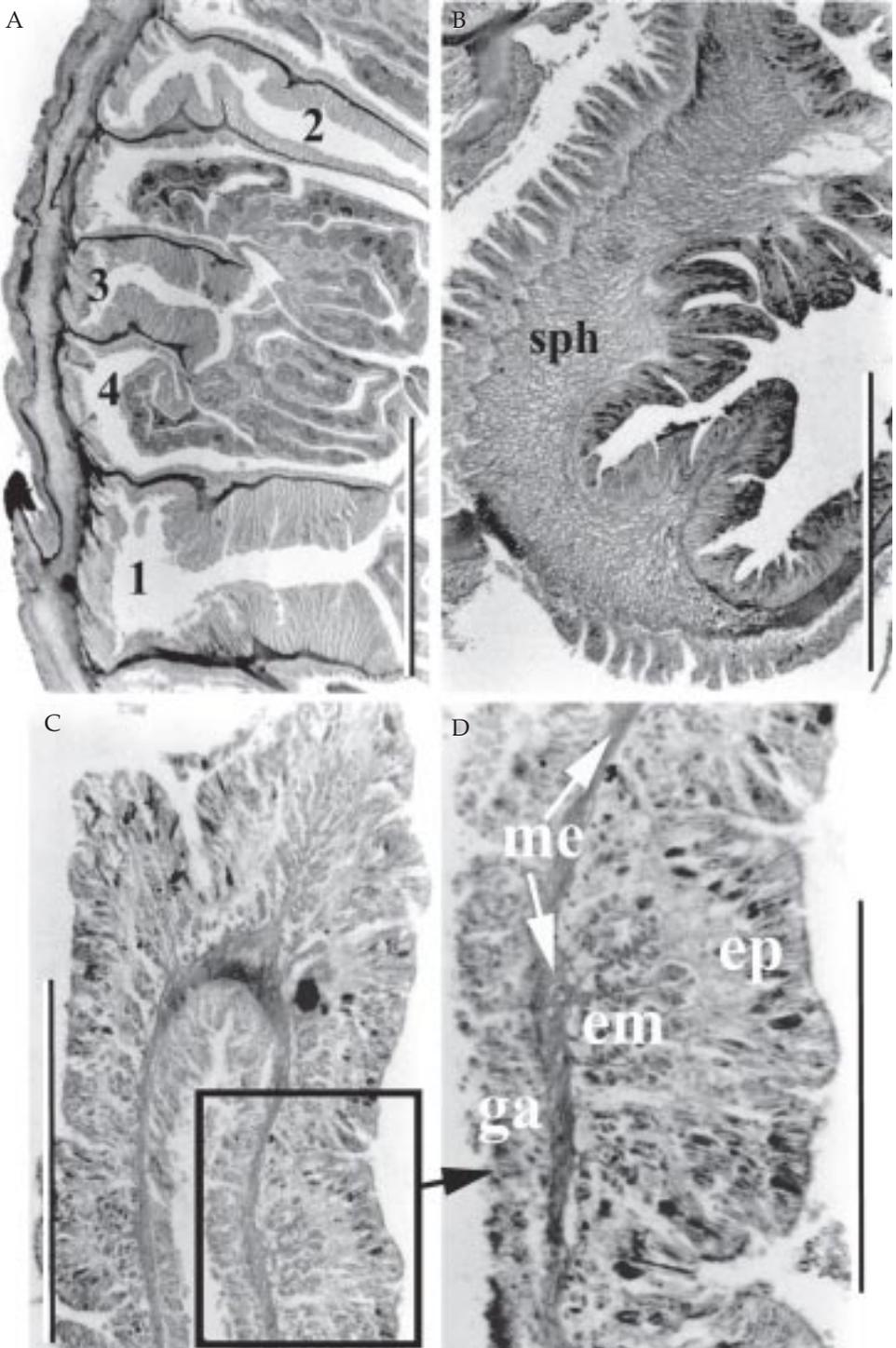
Cnidom: Spirocysts, basitrichs, holotrichs and microbasic *p*-mastigophores. A survey of the cnidae is presented in table 5 and figure 16.

Colour: Preserved material of a yellowish to whitish colour. According to the photographs and video tapes taken in situ (fig. 2E-F) living animals are whitish in colour.

Distribution and habitat.— At present *Maractis rimicarivora* is known to live in two hydrothermal sites at the Mid-Atlantic Ridge, TAG, 3650 m (Fautin & Barber, 1999), and Snake Pit-Elan, 3490 m (Segonzac, 1992, and present account). On these two sites, the sea anemones are fixed on sulphide rocks. They are increasingly dense as one approaches to the active area (until several tens of ind/m²), which makes the presence of this group a good indicator of presence of active sites. Some specimens are observed at the base of the black smokers where the temperature of fluids is ca 10°C. On the Elan site, accompanying fauna is composed by the tube-worm polychaetes Chaetopteridae, gastropods *Phymorhynchus*, shrimps *Rimicaris exoculata* and *Chorocaris chacei*, bivalves *Bathymodiolus puteoserpentis* and zoarcid fish *Pachycara thermophilum*. Shrimps *R. exoculata* can constitute prey for sea anemones living close to the black smokers (Van Dover et al., 1997), but not for the majority of the population that lives at distances the shrimps do not reach.

Taxonomic remarks.— The material here described and collected at Snake Pit area agrees well in general aspects with the original description of *Maractis rimicarivora* (see Fautin & Barber, 1999). Only a relatively shorter, stronger and reticulate mesogloal sphincter and the presence - in some specimens - of a sporadic nematocyst (fig. 16F) are the apparently differentiating features between TAG and Snake Pit material.

Fautin & Barber (1999: 630) pointed out the presence of a small sea anemone in TAG with a muscular sphincter similar to that observed in the present study; that specimen was initially considered as a possible different species to *M. rimicarivora* and *P. ingolfi*. In the examined material of *M. rimicarivora* from Snake Pit we have also observed sphincters of different sizes depending on the specimens [some examples of ratio pedal disc diameter measured on the preserved specimens (in mm) / length of sphincter measured on histological sections (in mm) are: 41/6.5, 30.4/ 3.5, and 21.5/3]. In general, the TAG material of *M. rimicarivora* studied by Fautin & Barber (1999) reached larger sizes than that available for this study from Snake Pit. Thus, in this case, the relative length of the muscular sphincter could depend on the size of the specimen, and its utility as differentiating character should be taken with caution.



With respect to the cnidae types, sizes and distribution, TAG and Snake Pit material agree in all anatomical parts except for the presence (in Snake Pit specimens) of a rather common/sporadic cnida present in the actinopharynx and mesenterial filaments. Moreover, this cnida (apparently a microbasic *p*-mastigophore in which the shaft has a very short V-shaped end) has only been observed in two of the four examined specimens.

In our opinion the slight morphological differences between the material examined here from Snake Pit and the original description based on specimens from TAG (Fautin & Barber, 1999) does not justify a separation at specific level.

Concluding remarks

With the present records included, eight sea anemone species have been reported from hydrothermal vents, two species in the Atlantic [*Parasicyonis ingolfi* (Snake Pit) and *Maractis rimicarivora* (TAG and Snake Pit-Elan)], and six species have been found associated with Pacific hydrothermal sites - two of them identified only at generic level - [*Actinostola* sp., *Chondrophellia coronata*, *Phelliactis* sp., *Cyananthea hydrothermala* (all four species at 12°48'N-103°56'W, 2630-2635 m), *Marianactis bythios* (Mariana back-arc Basin), and *Paranthosactis denhartogi* (Guaymas Basin)]. Considering the recent collections, four sea anemone species are now known from cold seeps - two of them identified only at generic level - [*Monactis vestita* (Barbados prism), *Stomphia* sp. (Monterey Bay), *Paractinostola* sp. (Monterey Bay), and *Hadalanthus* aff. *knudseni* (MAT)].

Doumenc & van Praët (1988) reported the studied material collected during the French Biocyatherm cruise from EPR, 11°N, 2000 m depth. However, the original files of that cruise place the sampled sites in EPR, 12°48'-49'N-103°56', 2630-2635 m depth. Taken into account the possible mistake, we have used in the present paper the original sampling data (Desbruyères et al., 1982).

According to the opinion of Doumenc & van Praët (1988), not all reported sea anemones could be strictly considered related to hydrothermal sites. This is also applicable to cold seeps. Those species present in the periphery of the vents (such as *Actinostola* sp., *Chondrophellia* sp., and *Phelliactis* sp.) are well known representatives of non-vent deep sea fauna (e.g. Doumenc, 1975). However, other actinarians locally form dense beds, sometimes placed directly on the chimneys or on oxidized sulphide areas surrounding black smokers (such as *Cyananthea hydrothermala*, *Marianactis bythios*, and *Maractis rimicarivora*).

The knowledge of sea anemones in hydrothermal sites and cold seeps is recent, Grassle (1986) reported that sea anemones are common in the vicinity of hydrothermal vents but none has been described yet. During the last 15 years, 12 species have been described (four of them at generic level) from chemoautotrophic environments (7 species from hydrothermal vents and 5 species from cold seeps). Even with the enormous efforts of the deep sea cruises, the number of known species is low in spite of

◀ Fig. 15. *Maractis rimicarivora* Fautin & Barber, 1989. A) cross section at stomodaeum level; B) longitudinal section of the marginal sphincter; C) cross section of a tentacle; D) detail of the ectodermal longitudinal musculature of a tentacle. Abbreviations: 1, pair of mesenteries of the first cycle; 2, pair of mesenteries of the second cycle; 3, pair of mesenteries of the third cycle; 4, pair of mesenteries of the fourth cycle; em, ectodermal longitudinal musculature; ep, epidermis; ga, gastrodermis; me, mesogloea; sph, sphincter. Scale bars: A, 0.5 mm; B, 2 mm; C, 0.4 mm; D, 0.2 mm.

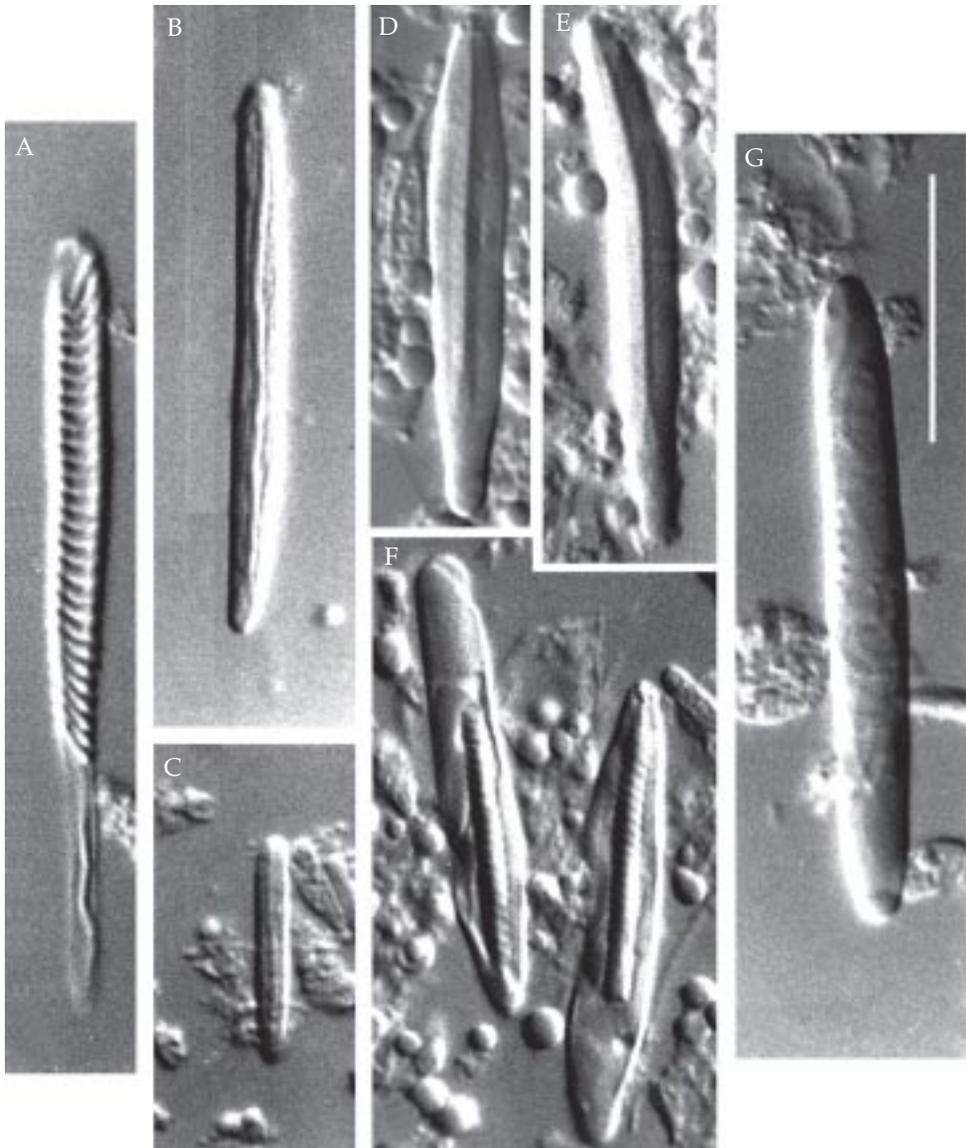


Fig. 16. *Maractis rimicariavora* Fautin & Barber, 1989. Cnidae. A) spirocyst; B) basitrich; C) basitrich; D) microbasic *p*-mastigophore 1; E) microbasic *p*-mastigophore 1; F) microbasic *p*-mastigophore 2; G) holotrich. See text and table 5 for explanation. Scale bar: 20 μ m.

the abundance of anemones observed in some sites. With the scarce available data very little could be speculated about the origin and ecology of this deep-sea group. Taking in account the above mentioned species, 75% could be considered endemic in hydrothermal vents and cold seeps. In other deep sea habitats, such as the seamounts, the fauna is equally dominated by widespread cosmopolitan species (Rogers, 1994)

and endemic ones. The seamounts appear to provide step habitats for trans-oceanic deep-sea species. The dispersal of these species probably occurs by active swimming and passively by planktonic larvae (Wilson & Kaufmann, 1987). Deep sea anemones have reduced potential of dispersal abilities because of their reproductive mechanisms (Fautin, 2002). Because of this reproductive strategy and the time required to arrive at other chemoautotrophic communities, their endemism may be higher than that of other sessile organisms, but more studies are required to test this observation.

A major effort should be made to understand speciation and gene flux processes in sea anemones from these ephemeral ecosystems, sometimes considered as biogeographic islands. The existence of cryptic species (morphologically identical but genetically distinct) has been already documented for some vent invertebrate groups (Vrijenhoek et al., 1994, 1997), and our knowledge of the possible role as biogeographic filters of some tectonic fracture (such as that present in MAR) is still very imprecise (Van Dover, 1995, 2000). Hydrothermal vents and cold seeps share similar assemblages of animals which are at least partially depending on autotrophic production associated with seafloor emission of dissolved reducing substances. The fauna of cold seep and hydrothermal vent probably have a common origin and evolutionary history (Gage & Tyler, 1991, for additional references). Our knowledge of the diversity and phylogenetic relationships of the sea anemones from these particular environments is still very poor. Future efforts should be made to combine both morphological and genetic tools in order to understand all these open questions.

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