

CARIBBEAN SHALLOW WATER CORALLIMORPHARIA

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With 8 tables, 20 text figures and 14 plates

CONTENTS

Abstract	3
Introduction	4
Historical notes	4
Material and methods	6
Terminology	7
Classification and identification of corallimorpharian nematocysts	7
Systematic part	9
Corallimorphidae Hertwig, 1882	10
<i>Corynactis</i> Allman, 1846	11
<i>C. parvula</i> Duchassaing & Michelotti, 1860	12
<i>Pseudocorynactis</i> gen. nov.	19
<i>P. caribbeorum</i> spec. nov.	19
Ricordeidae Watzl, 1922	26
<i>Ricordea</i> Duchassaing & Michelotti, 1860	26
<i>R. florida</i> Duchassaing & Michelotti, 1860	27
Discosomatidae Duchassaing & Michelotti, 1864	34
<i>Discosoma</i> Rüppell & Leuckart, 1828	37
<i>D. sanctithomae</i> (Duchassaing & Michelotti, 1860)	40
<i>D. carlgreni</i> (Watzl, 1922)	57
<i>D. neglecta</i> (Duchassaing & Michelotti, 1860)	61
General discussion of the cnidom of the Corallimorpharia	63
Preliminary notes concerning the cnidom of Scleractinia; distribution of penicilli E in the scleractinian and corallimorpharian body	66
The systematic position of the Corallimorpharia	70
Zoogeographical considerations	73
Acknowledgements	78
References	79

ABSTRACT

The present paper comprises a review of the Caribbean shallow water Corallimorpharia. Six species, belonging to four genera and three families are treated, including *Pseudocorynactis caribbeorum* gen. nov. spec. nov., a species with tentacular acrospheres containing the largest spirocysts ever described.

Several genera and species have been synonymised.

The monotypic family Ricordeidae Watzl, 1922, has been re-established to accommodate *Ricordea* Duchassaing & Michelotti, 1860. In *Ricordea florida* a correlation was noticed between depth of occurrence and the rate of asexual reproduction; shallow water specimens of this species as a rule exhibit clonal growth, specimens from deeper water invariably are solitary.

All genera of Discosomatidae (= Actinodiscidae sensu Carlgren, 1949), save one, have been lumped together in a single genus, *Discosoma* Rüppell & Leuckart, 1828. Speculations about food uptake in Discosomatidae are put forward.

The structure of corallimorpharian and scleractinian nematocysts is quite similar.

Actinarian and zoantharian penicilli (p-rhabdoids) A and corallimorpharian, scleractinian and antipatharian penicilli D, both sensu Schmidt (1969, 1972, 1972a and 1974), do not essentially differ in structure; they are to be regarded as sub-types of a single basic type. Three more or less distinct varieties of corallimorpharian penicilli D can be distinguished.

Schmidt's scleractinian and corallimorpharian holotrichs I (cf. Schmidt, 1972; 1974) in fact represent an additional type of penicilli, here defined as penicilli E. The distribution of penicilli E in the scleractinian polyp tends to be considerably more restricted than in the corallimorpharian polyp.

The systematic status of the Corallimorpharia is discussed. The group does not fundamentally differ from the Scleractinia and should be classified among the latter as a separate sub-order.

The distributional patterns of *Discosoma* sensu lato, *Ricordea* and *Corynactis* are discussed. *Discosoma* and *Ricordea* have a discontinuous distribution in tropical waters. *Corynactis* has a world-wide, continuous distribution in tropical and temperate waters. Long distance transport seems a possible way of dispersal in *Corynactis*, not in *Discosoma* and *Ricordea*.

INTRODUCTION

The Corallimorpharia form a small, little known group of Hexacorallia, comprising about 30 known species. The most significant surveys of the group are given by Stephenson (1922: 300-306) and Carlgren (1949: 11-16). Other information occurs scattered in the literature.

During a stay of over two years in Curaçao, while working at the Caribbean Marine Biological Institute (Carmabi), I had the opportunity to bring together a fairly large collection of Caribbean shallow water Corallimorpharia, which served as the basis of the present study. So far a general survey of Caribbean shallow water Corallimorpharia has not been available. The present study, apart from being an attempt to such a survey, also gives information about the Corallimorpharia in general.

HISTORICAL NOTES

The systematic position and status of the Corallimorpharia has long been (and, in a restricted sense, actually still is) a point of dispute. Many of the older authors included them in the Actiniaria. Like Actiniaria they lack any trace of a calcareous skeleton, and in conformity with certain Actiniaria their tentacles (except in the Sideractidae, including two species only) are arranged

in radial rows. Andres (1883: 480) united all these forms with radially arranged tentacles in a family Stichodactylinae (based on *Stichodactyla* Brandt)¹); this tentacular arrangement hence became known as stichodactylinae. The Stichodactylinae were attributed higher systematic rank (order, sub-order, tribe) by later authors (e.g. Haddon & Schackleton, 1893: 117; Haddon, 1898: 465; Duerden, 1900: 135-137; Carlgren, 1900: 77; 1900a: 277; Gravier, 1918: 2). A number of other authors (Krempf, 1904; Stephenson, 1921: 510-516; 1922: 300-306; Migot, 1922: 271-272; Weill, 1934: 614-617), however, soon became aware of the heterogeneous character of the group. They noticed a striking resemblance with the stony corals (Madreporaria = Scleractinia) of those species nowadays included in the Corallimorpharia, and they concluded that the species concerned actually represent madreporarian corals without a skeleton. Krempf therefore (1904: 819), proposed a subdivision of these corals into Sclerocorallia and Asclerocorallia.

Duerden (1898; 1900), who also noticed the similarity of Corallimorpharia and Scleractinia, none the less maintained the corallimorpharians in the Stichodactylinae and even classified them in two different, new, sub-orders (Heterodactylinae and Homodactylinae), both including Actiniaria also (Duerden, 1900: 137).

It may here be mentioned that already Gosse (1860: 292-293) and Jourdan (1880: 31-32) supposed a close relationship between the corallimorpharian *Corynactis viridis* Allman, 1846, and Scleractinia. Gosse explicitly mentioned the similarity of this species with the solitary coral *Caryophyllia smithii* Stokes & Broderip, 1828, and even stated: "I have often more than half suspected that the former is the immature condition of the latter. Both are found in the same localities...". Moseley (1877: 301) suggested a similar relationship with regard to *Corallimorphus* Moseley and solitary deep-sea

¹) The monotypic genus *Stichodactyla* Brandt, 1835 (:16) (based on *Stichodactyla mertensii* Brandt), the type-genus of the family Stichodactylinae Andres, 1883 (with proper suffix: Stichodactylidae), was included by Andres as a genus incertae sedis in the sub-family Discosomidae Duchassaing & Michelotti, 1864 (with proper suffix Discosomatinae), based on *Discosoma* Rüppell & Leuckart, 1828. Apart from the fact that the latter family-group name is older, and hence should have priority, this is not in accordance with Art. 37 of the International Code of Zoological Nomenclature, which dictates that the sub-family containing the type-genus bears the same name as the family, except for the suffix.

Stichodactyla mertensii, moreover, although a nomen dubium, very probably is not a corallimorpharian but an actinian (possibly a stoichactid); the original description strongly suggests the presence of verrucae (never present in Corallimorpharia and other Anthozoa) in the upper part of the column (Brandt, 1835: 16, "Corpus cylindricum, maximum, viride, parte superiore punctis ex albido rubellis notatum").

corals like *Stephanophyllia* Michelin, 1841; he suspected *Corallimorphus* to represent forms from which the corals were developed.

Carlgren (1900: 31-32, 77-81; 1900a: 277-279), initially failed to notice the similarity of Corallimorpharia and Scleractinia, probably because at that time he was not yet familiar with the latter group. In later papers (1924: 180; 1936: 16-17; 1940: 57-59), he step by step accepted a closer kinship of both groups. In 1940 (: 59) he recognized the Corallimorpharia as a separate order, and actually proposed the name Corallimorpharia. Carlgren never came so far as to include the Corallimorpharia in the Scleractinia. His arguments for this will be discussed later (cf. p. 71). Carlgren's views were accepted by Wells & Hill (1956: F 232-233)²). Since Carlgren, the systematic position of the Corallimorpharia has exclusively been discussed by Schmidt (1972: 1974). In accordance with several of the older authors, Schmidt concluded that Corallimorpharia and Scleractinia are fundamentally alike and that both groups should be united in a taxon of higher rank (Madreporaria).

MATERIAL AND METHODS

Material for the present study was collected in Curaçao, Bonaire, Saba, St. Eustatius, St. Martin, Puerto Rico and Bermuda, with the aid of snorkel- and SCUBA equipment. The entire collection thus obtained, also including material from other localities, presented by various persons, was preserved in 5 to 10% formalin in sea-water, and is now deposited in the Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands (RMNH; numbers in the text refer to the Coelenterata collection). Additional material, partly preserved in alcohol was borrowed from: The National Museum of Natural History (Smithsonian Institution), Washington, D.C. (USNM); Yale Peabody Museum, New Haven, Connecticut (YPM); the Zoological Museum, Lund, Sweden (ZML); Naturhistoriska Riksmuseet, Stockholm (NRS); the Marine Laboratory of the University of Miami (UMML), "Pillsbury" (P) and "Gerda" (G) stations; the British Museum (Natural History), London (BM(NH)) and from the Natur-museum und Forschungsinstitut "Senckenberg", Frankfurt am Main, Germany (SMF).

The general morphology and anatomy of the material was studied by means of a Wild M-5 dissecting microscope. Microscopical sections (of specimens embedded in paraffin wax), stained with Mallory triple stain, were prepared on small scale for the study of anatomical and histological details. Nematocysts were studied and photographed in squash preparations

²) Wells & Hill incorrectly attribute the name Corallimorpharia to Stephenson, 1937.

of living and preserved tissue with the aid of phase- and interference-contrast, using a magnification varying between 500 and 1000 \times .

Several collectors are indicated in the text by abbreviations: C. Arneson (C.A.), P. Creutzberg Jr. (P.C.), J. C. den Hartog (J.C.H.), R. M. den Hartog-van Ter Tholen (R.M.H.), K. Larson (K.L.), R. J. Larson (R.J.L.), J. C. Post (J.C.P.), K. Sandved (K.S.), A. E. Verrill & party (A.E.V.), H. de Windt (H.W.) and K. de Windt (K.W.).

TERMINOLOGY

The terminology used with regard to morphology and anatomy of Corallimorpharia conforms to a large extent to actiniarian terminology (see Stephenson, 1928; Carlgren, 1949: 7-10).

Although I am essentially in agreement with Schmidt (1972, 1974) as to the delimitation of the different types of corallimorpharian nematocysts, I prefer a different terminology. Instead of Schmidt's b- and p-rhabdoids (= b- and p-mastigophores sensu Carlgren (1940: 4)) Stephenson's completely synonymous terms spirulae and penicilli are here used (Stephenson, 1928: 62-63). The term holotrich has been replaced by homotrich. I disagree with Schmidt about the status of his holotrichs I, which in my opinion are a special type of penicilli, as discussed on pp. 65-66.

CLASSIFICATION AND IDENTIFICATION OF CORALLIMORPHARIAN NEMATOCYSTS

All anthozoan nematocysts, including those of Corallimorpharia, are generally considered stomocnidae (Weill, 1934: 37, 45-48), defined as cnidae of which the tube is open at its terminus³). Unlike several types of actiniarian nematocysts, but in conformity with the situation in all other Hexacorallia, corallimorpharian nematocysts are invariably devoid of so-called apical flaps (Westfall, 1965).

On the basis of light microscopical investigations, corallimorpharian nematocysts may be classified as follows (cf. pls. 1-6):

I. Atrichonemata. — Nematocysts with a tube devoid of armature.

A. Spirocysts. — Thin-walled, elongate, often slightly curved and bilaterally symmetrical nematocysts with a long tube, which in undischarged state is coiled in numerous densely, and as a rule regularly, arranged spirals. After discharge the tube is surrounded by swelling substance, which gradually dissolves. Instead of discharging properly, spirocysts often rupture in a rather characteristic manner in squash preparations, the apical part of the capsule and the inverted tube becoming detached from the rest of the capsule.

Whereas all other anthozoan nematocysts are basophilic or more or less neutral, spirocysts are strongly acidophilic.

B. Atrichs *sensu stricto*. — These nematocysts are not known to occur in Corallimorpharia. Among Anthozoa, they have exclusively been reported from Ceriantharia ³⁾ and Actiniaria.

II. Trichonemata. — Nematocysts with a tube provided with armature in the form of spines.

A. Homotrichs (= Holotrichs II *sensu* Schmidt). — Spines all along the tube about equally long (isotrichous) or gradually diminishing towards the tip (anisotrichous). Tube accordingly about isodiametrical (isorhizic) or tapering (anisorhizic), very long, its many irregular coils often completely filling the undischarged capsule.

B. Heterotrichs. — Spines showing a sudden change in development, so that a coarsely spined basal shaft, and a minutely spined (in Actiniaria and Zoantharia often unarmed) terminal tube can be distinguished.

a. Spirulae (b-rhabdoids *sensu* Schmidt). — Tube isodiametrical or with a slightly dilated shaft. Shaft in undischarged state without V-shaped notch, rather slender, usually not exceeding half of the length of the capsule.

b. Penicilli (p-rhabdoids *sensu* Schmidt). — Tube with a short to extremely long, isodiametrical, distinctly dilated shaft. Shaft in undischarged state thick, provided with a V-shaped notch.

i. Penicilli D ⁴⁾. — Shaft short, in undischarged state reaching about 1/6 to 3/4 of the length of the capsule. V-shaped notch very distinct. Terminal tube long.

³⁾ Mariscal, Conklin & Bigger (1977) stated that the tube of ceriantharian atrichs has no terminal orifice. In addition, on the basis of electron microscopical studies, they found that the undischarged tube of these atrichs is pleated in a way fundamentally different from the way of pleating in other anthozoan cnidae. To classify this type of nematocyst, the authors introduced a new main category of cnida, viz., the ptychocyst. It remains to be checked whether the structure of genuine actiniarian atrichs (i.e., atrichs *sensu* Schmidt (1969: 289-290 fig. 1, f-g; 1972: 429; 1972a: fig. 3d, e); not atrichs *sensu* Weill (1934: 50-51) and Cutress (1955: 135-136)), the tube of which has proved to be provided with minute spines all along its length) is fundamentally alike or not. Pending such a study I prefer to maintain the well-established name atrich.

⁴⁾ The classification of this category of cnidae as penicilli D, co-ordinate in status with actiniarian penicilli A (also occurring in Zoantharia), B and C, as advocated by Schmidt, is disputable. Penicilli D (restricted in distribution to Corallimorpharia, Scleractinia and Antipatharia) are very similar to penicilli A, both in shape and structure. The only difference between the two categories lies in the condition of the terminal tube, which is long and minutely spined in penicilli D, short and devoid of spines in penicilli A. In my view therefore, penicilli A and D represent sub-categories only of a single basic type, which has an equal status as actiniarian penicilli B and C.

2. Penicilli E (Holotrachs I sensu Schmidt). — Shaft very long, arranged in several to many coils in the undischarged capsule. V-shaped notch indistinct. Terminal tube vestigial (visible only under optimal conditions, both regarding optics and quality of squash preparations).

For further information about the cnidom, I refer to the discussion on p. 65.

SYSTEMATIC PART

CORALLIMORPHARIA Carlgren, 1940

Styrodactylinae pro parte, Andres, 1883 : 480 (272) (cf. p. 5).

Asclerocorallia Krempf, 1904 : 819 (cf. p. 5).

Corallimorphiae Carlgren, 1936 : 16.

Corallimorpharia Carlgren, 1940 : 59.

Diagnosis. — Sedentary shallow water and deep-sea forms. Deep-sea forms solitary. Shallow water forms nearly always gregarious or sub-colonial as a result of asexual reproduction by longitudinal fission or pedal laceration. Zooxanthellae present or absent.

Body lubricous by excreted mucus; consistency soft to very rigid, dependent on the degree of development of the mesogloea. Base in shallow water forms irregular in outline and immovably fixed to the substrate, in deep-sea forms often unattached. Column smooth and devoid of specialised organs, occasionally separable into scapus and scapulus. The oral disc usually can be withdrawn, at least to some extent. Tentacles retractile or not so, with or without acrospheres; usually (in shallow water forms always) more than one tentacle communicating with each endocoel; exocoelic tentacles probably always single. Stomodaeum short, with deep folds and ridges, the latter continuous with the filaments of the perfect mesenteries; siphonoglyphs absent or indistinct. Mesenteries as a rule numerous and often irregularly arranged; directives present or absent. Mesenterial filaments consisting of a simple cord of cnido-glandular tract only. Musculature, including the retractors of the mesenteries, as a rule weakly developed; Sphincter diffuse, occasionally absent; basilar muscles absent; ectodermal musculature present or absent. Cnidom basically similar to that of the Scleractinia, made up of: spirocysts (except in Discosomatidae), homotrachs (not always), spirulae, penicilli D and penicilli E.

Four families: Sideractidae Danielssen (1890: 14), Corallimorphidae Hertwig, Ricordeidae Watzl and Discosomatidae Duchassaing & Michelotti. Of these, the Sideractidae only are not represented in Caribbean shallow water.

Key to the families recorded from Caribbean shallow water:

- 1a. Polyps not disc-shaped. Zooxanthellae invariably absent. Tentacles retractile, provided with distinct, brightly coloured, globular acrospheres Corallimorphidae, p. 10.
- b. Polyps flat, disc-shaped. Zooxanthellae invariably present. Tentacles very short, non-retractile, often compound or wart-like, and invariably without acrospheres 2
- 2a. Tentacles simple, with rounded or clavate to capitate tips, well provided with spirocysts Ricordeidae, p. 26.
- b. Tentacles generally vesicle-like and compound (often distinctly dendritic) or reduced to wart-like discal protuberances, occasionally completely reduced. Spirocysts absent. Margin with fine finger-shaped tentacles or drawn out into small or large lobes, rarely smooth Discosomatidae, p. 34.

CORALLIMORPHIDAE Hertwig, 1882

Corallimorphidae Hertwig, 1882: 21.

Corynactidae Andres, 1883: 480 (272) (subjective junior synonym).

Protostichodactylinae Carlgren 1900: 39 (Not based on any existing genus and hence not available, cf. Art. 10 (e) International Code of Zoological Nomenclature).

Diagnosis. — Deep-sea and shallow water forms, invariably without zooxanthellae. Body rather firm to extremely rigid and cartilaginous. The column may be divided into scapus and scapulus, but this differentiation is not always distinct. Tentacles simple, provided with well developed acrospheres. At least the older endocoels communicating with 2 or more radially arranged tentacles. Directives as a rule present. Ectodermal musculature present or absent. Sphincter present or absent. Cnidom: As in the order. Large spirocysts and long penicilli D with a short shaft are always present in the tentacles.

Three genera: *Corallimorphus* Moseley (1877: 21-23 (18-20)), *Corynactis* Allman and *Pseudocorynactis* n.g. *Corallimorphus* is a deep-sea genus. *Corynactis* and *Pseudocorynactis* are shallow water genera, both represented in the Caribbean.

Key to the genera recorded from Caribbean shallow water:

- 1a. Polyps nearly always gregarious, due to frequent asexual reproduction. Base rarely exceeding 1 cm in diameter. Endocoelic tentacles purely ectacmaceous. Both, perfect and imperfect mesenteries present. Mesenteries without distinct parietal ridges *Corynactis* p. 11.

- b. Polyps solitary. Base up to 4 cm in diameter. Endocoelic tentacles principally ectacmaceous, but the penultimate tentacle exceeding the outermost one in size. All mesenteries perfect and characterized by conspicuous, circumscribed, parietal ridges (cf. fig. 3)
 *Pseudocorynactis* p. 19.

Corynactis Allman, 1846

Corynactis Allman, 1846: 417 (type *Corynactis viridis* Allman, 1846: 417-419, by monotypy).
Draytonia Duchassaing & Michelotti, 1864: 124 (30) (type *D. myrcia* Duchassaing & Michelotti, 1864: 124 (30) by monotypy).

Diagnosis. — Small, gregarious forms. Body variable in shape, when fully expanded often wide, trumpet-shaped, mammiform when retracted. Base rarely exceeding 1 cm in diameter. The oral disc can easily be withdrawn and enclosed by the columnar wall. Tentacles well developed, ectacmaceous, motile and retractile; acrospheres extremely well developed. Endocoelic tentacles arranged in radial rows of 2-7 tentacles each. The single exocoelic tentacles distinctly longer than the outer endocoelic ones. Siphonoglyphs and directive mesenteries may be present or absent in different specimens of the same species. Mesenteries never provided with circumscribed, mesogloal, parietal ridges. At least some of the mesenteries imperfect. Sphincter invariably present, distinct. Cnidom as in the family.

Corynactis is a temperate to tropical genus (cf. fig. 20) of predominantly subtidal shallow water forms, which has not been recorded from depths exceeding ca. 200 meters. Carlgren (1949: 13-14) listed 15 species, but the status of several of these is doubtful. As a result of the present study two of the three known Caribbean species have disappeared into the synonymy (*Corynactis myrcia* and *C. bahamensis*; the latter species even appeared to belong to a different genus, viz., *Ricordea*). The only Caribbean species is *Corynactis parvula* Duchassaing & Michelotti, 1860.

Nomenclature. — *Corynactis* Allman is one of the most characteristic and best established genera of Anthozoa. Its synonymy with the junior name *Draytonia* Duchassaing & Michelotti is discussed on pp. 17-18.

Verrill (1869: 39-40) incorrectly claimed *Melactis* Milne Edwards (cited by him as Edwards & Haime) 1857 (: 260) to be a junior synonym. *Melactis* was based on two species, *Actinia vas* Quoy & Gaimard, 1834 (: 147-148, pl. 12 fig. 6) and *A. globulosa* Quoy & Gaimard, 1834 (143-144, pl. 9 fig. 4a, b). The tentacles of these two species, unlike *Corynactis*, are not arranged in radial rows, and the tips of their tentacles, though more or less globular,

are definitely not provided with pronounced acrospheres, so characteristic of all Corallimorphidae. Both species are certainly Actiniaria. *Actinia vas* in my opinion is a species of *Telmatactis* Gravier, 1918. At present I have no definite suggestion as to the identity of *Actinia globulosa*. As *Actinia vas* is the type (by monotypy) of *Metactis* Milne Edwards & Haime, 1851 (: 8), *Melactis* Milne Edwards almost certainly is a misspelling of *Metactis* Milne Edwards & Haime, to be regarded as a senior synonym of *Telmatactis* Gravier. In case *Melactis* is to be considered a valid genus, I select for it as type *Actinia vas* Quoy & Gaimard, 1834; *Melactis* then automatically becomes an objective junior synonym of *Metactis*. *Ectacmaea* Ehrenberg was erected as a sub-genus to include *Actinia candida* O. F. Müller, 1766 (: 231, a nomen dubium, but definitely no corallimorpharian; see also the more extensive description of the species by Abildgard, 1789: 58, pl. 115 figs. 1-6) and *A. globulifera* Ehrenberg, 1834 (: 39), a species of *Corynactis*. As Ehrenberg (or anyone else) did not designate a type-species, the name *Ectacmaea* Ehrenberg, 1834 is a nomenclatorial threat to *Corynactis* Allman, 1846. Therefore, to maintain the well established name *Corynactis*, I here select *Actinia candida* as the type of *Ectacmaea*.

***Corynactis parvula* Duchassaing & Michelotti, 1860**

(table 1; figs. 1, 2; pls. 1, 7)

Type-material: Probably no longer extant (not present in the Duchassaing & Michelotti collection in the Zoological Museum of Turin, Italy).

Corynactis parvula Duchassaing & Michelotti, 1860: 40-41 (316-317) (details on morphology and colour; St. Thomas; no type-designation) pl. 4 fig. 10 (expanded disc); 1864: 30 (123) (name only); Andres, 1883: 484-485 (repetition of the description by Duchassaing & Michelotti); Duerden, 1898: 637 (name only); Carlgren, 1949: 13 (name only).

Draytonia myrcia Duchassaing & Michelotti, 1864: 30 (124) (details on morphology and colour; St. Thomas; no type designation) pl. 2 fig. 8 (oro-lateral view of closed polyp).

Corynactis myrcia - Andres, 1883: 484-485 (repetition of the description of Duchassaing & Michelotti); Duerden, 1898a: 102 (Jamaica); 1898b: 449-450 (details on morphology and colour; Drunkenman Cay and Kingston Harbour, Jamaica); 1898 (scattered details on morphology, anatomy, histology and nematocysts); 1900: 181-187 (extensive description of morphology, colour, anatomy, histology and nematocysts); 1900: 181-187 (extensive description of morphology, colour, anatomy and histology of Jamaican specimens) pl. 10 fig. 10 (retracted and expanded polyp, connected by basal coenosarc), pl. 12 fig. 7 (plan of tentacular arrangement), pl. 13 figs. 3-5 (histological details), pl. 15 fig. 3 (transverse section through a mesentery); Carlgren, 1949: 13 (name only).

Material examined:

Bermuda. — RMNH 13578 (John Smiths Bay, 26.VI.1979, 1 specimen; leg. W. E. Sterrer).

Bonaire. — South-west coast, 2 miles north of Kralendijk, between coral rubble beach

and *Acropora*-fringe, under loose coral blocks and boulders in clear shallow water and tidal pools (pl. 7 fig. 5): RMNH 11475 (9.IV.1973; leg. J.C.H.), 11476 (15.IV.1973; leg. J.C.H.), 11478 (11.IV.1973; leg. J.C.H.).

Curacao. — RMNH 11480 (South-coast, Playa Chikitu, in deep tidal pool on south-east side of bay, under overhanging edge, 21.VII.1973, 1 specimen; leg. J.C.H.), 11477 (South-coast, Playa Hundu, under eroded blade of *Acropora palmata*, depth 1.5 m., 9.VIII.1973; leg. J.C.H.), 11474 (Oostpunt, entrance of Lagoen Blancu, intertidally in holes among coral debris cemented together by encrusting calcareous algae, 4.VIII.1973; leg. J.C.H.).

Morphology (pl. 7). — Base irregular in outline, spreading, often with long thin-walled expansions, which may connect different polyps; diameter ca. 5-8 mm, the expansions not taken into account.

Column smooth, circular in outline, except for the spreading basal part; in expanded state often longer than the diameter of the base, in contraction rather flat, often more or less mammiform. Column-wall in expanded polyps thin and transparent, mesenteries showing through; in contracted or in preserved specimens often with longitudinal ridges (indicating the insertions of the mesenteries) and furrows.

Oral disc circular or slightly elliptical in outline, transparent; diameter up to 8 mm. Hypostome often slightly conical and mouth often slightly open, showing stomodaeal ridges.

Tentacles well developed, with very distinct, globular acrospheres. Number of radii and radial rows of tentacles variable (due to asexual reproduction), varying from 28 to 36 in six well developed specimens. Exocoelic tentacles in fully expanded state exceeding the diameter of the disc. Endocoelic radii with 3 to 5 tentacles, the inner tentacles hardly stalked and visible as very small globular buds only, the outer ones reaching about half the length of the exocoelic tentacles. The total number of tentacles will probably never exceed 100. In three well developed specimens the number was 74, 77 and 86 respectively; usually it is less. The tentacles of the first two specimens were arranged according to the following schemes: 1 - 4 - 1 - 4 - 1 - 5 - 1 - 3 - 1 - 4 - 1 - 3 - 1 - 5 - 1 - 4 - 1 - 4 - 1 - 3 - 1 - 4 - 1 - 4 - 1 - 3 - 1 - 5 - 1 - 4 = 74, and 1 - 5 - 1 - 4 - 1 - 5 - 1 - 3 - 1 - 4 - 1 - 5 - 1 - 4 - 1 - 4 - 1 - 4 - 1 - 5 - 1 - 3 - 1 - 4 - 1 - 3 - 1 - 5 - 1 - 4 = 77.

Colour and pattern. — Column almost colourless, or faint to bright orange or orange-brown. Duerden (1900: 182) described the column of specimens from Jamaica as brown below and almost colourless or crimson above. Tentacle-stems as a rule colourless, sometimes faintly yellowish (Duerden, l.c.) or greenish. Acrospheres orange, orange-red or rose. On the aboral side of the insertions of the tentacles, both on the disc and along the margin, a green spot may be present or absent. Along the margin these spots are not

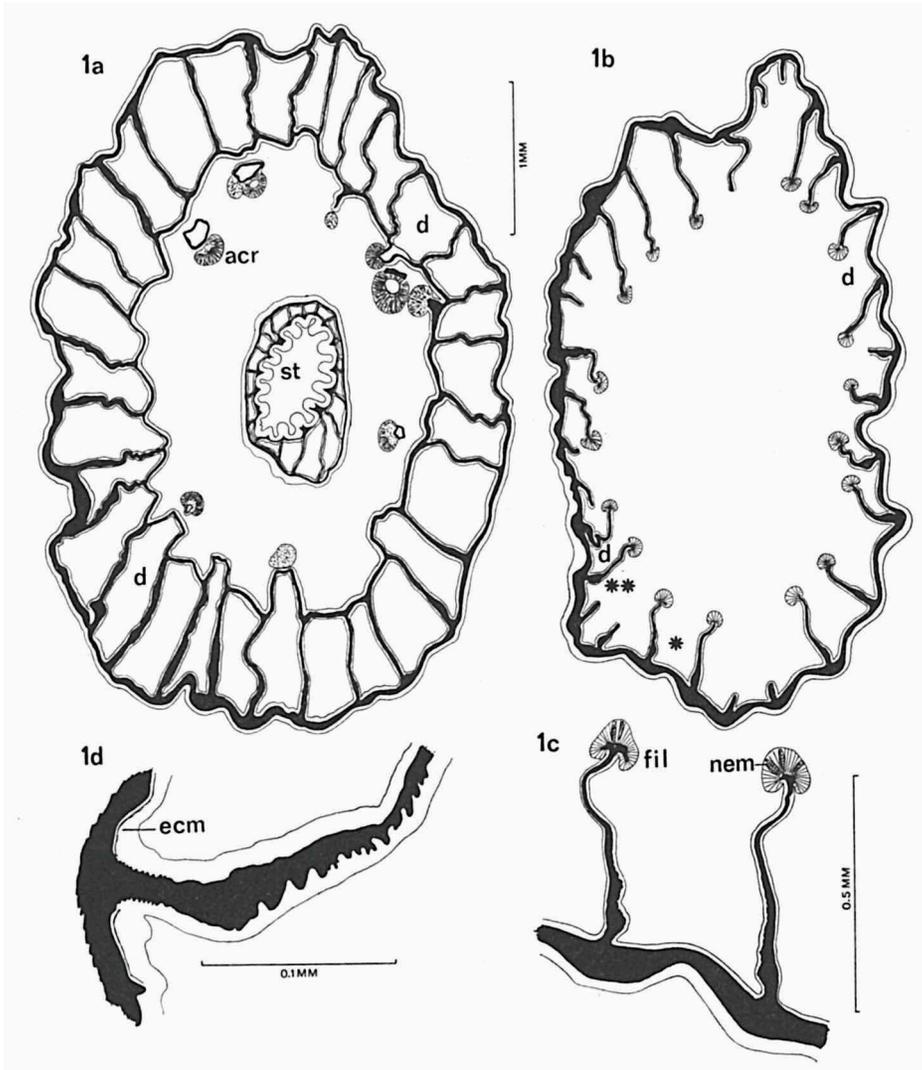


Fig. 1. *Corynactis parvula*. Anatomical details (RMNH 11477). Mesogloea black. 1a, Cross-section through the uppermost part of the column. 1b, Cross-section through the lower part of the column. 1c, Enlarged detail of 1b (*). 1d, Enlarged detail of 1b (**).

Explanation of the symbols: acr = Acrospheres of the tentacles; d = Directive mesenteries; ecm = Endodermal circular muscle; fil = Filaments; nem = Nematocysts (penicilli E); st = Stomodaeum.

rarely united in a bright green marginal ring. Faintly brown radii may run from the mouth to the margin. Duerden's Jamaican specimens had brown discs with white radiating lines and emerald green spots around the mouth.

Anatomy (fig. 1). — Number of mesenteries aborally and adorally equal, ca. 14-20 pairs in well developed specimens. In the only specimen sectioned (RMNH 11477), 15 pairs were present, $9\frac{1}{2}$ of these perfect, including two pairs of directives. Below the level of the stomodaeum 8 relatively well developed pairs alternate with 7 less developed younger pairs, partly without filaments. Gonads were not developed in any of the mesenteries. At a short distance from the columnar wall, on the retractor side, the mesenterial mesogloea is distinctly thickened and plaited (by no means, however, producing such distinct parietal ridges as in *Pseudocorynactis caribbeorum*; cf. fig. 3).

Stomodaeum devoid of siphonoglyphs.

Sphincter diffuse. Retractors of the mesenteries weak and hardly differentiated. Parietabasilar muscles very weak.

So far, the anatomy of this species had only been studied by Duerden. According to this author half of the number of mesenteries was perfect. He also claimed the presence of a tetramerous arrangement of the mesenteries, which I cannot confirm on the basis of the present study.

Cnidom (table 1, pl. 1). — In addition to the survey of the cnidom presented in table 1, of a specimen from Bonaire, details were checked in several other specimens from Bonaire and Curaçao. Except for a variable range in the diameter of the tentacular penicilli E (II.d), no obvious variations were noticed.

Biological notes. — During the present study *Corynactis parvula* was collected intertidally and subtidally in very shallow water, sheltered under stones, pieces of dead coral etc. Duchassaing & Michelotti and Duerden obtained their specimens also from shallow water. There is, however, no reason to assume that the species does not occur somewhat deeper.

The species frequently reproduces asexually by means of pedal laceration. This process apparently does not normally give rise to the formation of large clones of hundreds or thousands of specimens, as is not unusual in, e.g., the Lusitanian-Mediterranean *Corynactis viridis*. *Corynactis parvula* so far has only been found in small clusters or in groups of a few individuals.

Occurrence and distribution (fig. 2). — Although *Corynactis parvula* probably is not truly common, it may often have been overlooked because it

TABLE I

Corynactis parvula and *C. spp.* 1 and 2. Survey of the cnidom. A = *Corynactis parvula*, RMNH 11475, Bonaire; B = *Corynactis spec.* 1, USNM 52348, Hatteras Island, North Carolina; C = *Corynactis spec.* 2, RMNH 12868, Cabo Frio Island, Brazil.

Organ	Species	Average and range of length and width of nematocyst capsules in microns	Number of capsules measured	Abundance
<u>Nematocyst type</u>				
<u>I. Column</u>				
a. Spirocysts	A	ca. 25 - 50 x 2.5 - 4.5	--	uncommon
	B	23.8(19 - 26.3) x 4.1(3.7 - 4.5)	10	rather common
	C	no intact capsules observed	--	sporadic
b. Spirulae	A,1	9 (8.6 - 9.9) x 3.1(2.6 - 3.3)	10	rather common
	2	17.1(15.2 - 20.5) x 5.4(4.6 - 6.6)	20	rather common
	B	16.2(13.9 - 19.8) x 4 (3.3 - 4.6)	20	common
c. Penicilli D	C	15.3(13 - 18.6) x 3.5(3.1 - 3.7)	20	rather common
	A	15.9(12.5 - 17.8) x 5.4(4.6 - 6.6)	20	rather common
	B	19.9(16 - 24.8) x 6.9(5.5 - 8)	8	sporadic
d. Penicilli E	C	19 (16.1 - 22.3) x 6.3(5.6 - 7.4)	20	rather common
	A	43.6(39.6 - 47.5) x 18.1(15.8 - 19.8)	20	rather common
	B	39.9(30.4 - 46.9) x 11.9(8.9 - 15.8)	20	rather common
C	37.6(34.1 - 43.4) x 12.2(10.5 - 13.6)	20	rather common	
<u>II. Tentacles</u>				
a. Spirocysts	A	59.5(36.3 - 95.7) x 3.2(2 - 4.3)	20	very common
	B	ca. 25 - 75 x 2 - 4.5	--	very common
	C	ca. 20 - 50 x 2 - 4	--	very common
b. Spirulae	A	38.2(26.4 - 46.2) x 4 (3.3 - 4.6)	20	rather common
	B	37.3(33 - 42.9) x 5 (4 - 6.6)	20	uncommon
	C	35.1(24.8 - 45.3) x 4 (3.1 - 5)	10	uncommon
c. Penicilli D	A	68.6(58.1 - 75.9) x 5.3(5 - 6)	20	common
	B,1	30.8(25 - 36.3) x 5.6(4.6 - 7.3)	20	rather common
	2	54.1(48.8 - 66) x 6.5(6 - 7.3)	20	rather common
d. Penicilli E	C,1	28.4(19.8 - 37.2) x 5.9(4.3 - 7.4)	35	rather common
	2	46.5(42.2 - 52.7) x 6 (5 - 6.8)	10	uncommon?
	A	60.5(56.1 - 67.3) x 24 (21.1 - 30.4)	20	uncommon
B	70.8(66 - 79.2) x 23.2(19.8 - 27.7)	20	uncommon	
C	58.7(48.4 - 68.2) x 20.2(17.4 - 21.7)	20	rather common	
<u>III. Stomodaeum</u>				
a. Spirulae	A	33.2(30.4 - 36.3) x 5.6(5.3 - 6.6)	20	rather common
	B	29.3(24.4 - 33) x 4.1(4 - 4.6)	20	rather common
	C	26 (21.7 - 29.8) x 3.8(3.1 - 4.3)	10	uncommon
b. Penicilli E	A	54.9(48.8 - 63.4) x 22.7(19.8 - 25)	15	uncommon
	B	48 (39.6 - 59.4) x 15.7(13.2 - 19.8)	20	rather common
	C	47.2(37.2 - 55.8) x 18.3(14.9 - 21.1)	10	uncommon
<u>IV. Filaments</u>				
a. Spirocysts	A	ca. 25 - 50 x 2 - 3.5	--	rare
	B	ca. 20 - 40 x 3 - 4.5	--	rare
	C	ca. 30 x 3	--	uncommon
b. Spirulae	A	9.2(8.6 - 9.9) x 3 (2.6 - 3.3)	10	uncommon
	B	10.3(9.5 - 11.7) x 3.1(2.6 - 3.3)	10	sporadic
	C	10.5(9.9 - 11.2) x 3.4(3.1 - 3.7)	5	sporadic
c. Penicilli D	A,1	17.5(15.2 - 21.1) x 5.5(4.3 - 7.3)	20	rather common
	2	42.8(39.4 - 46.7) x 12.1(11 - 13.2)	20	rather common
	B,1	20.5(18.5 - 22.4) x 6.2(5.3 - 7.3)	20	rather common
d. Penicilli E	2	37.6(29.7 - 43.8) x 10.5(8.6 - 11.7)	20	common
	C,1	22.1(18.6 - 24.8) x 6.2(5.6 - 6.8)	20	common
	2	38.3(29.8 - 43.4) x 9.8(8.1 - 11.8)	20	rather common
d. Penicilli E	A	47.1(36.5 - 58.4) x 22.2(16.3 - 27.7)	40	rather common
	B,1	42.7(36.3 - 52.6) x 13.6(10.4 - 16.5)	20	common
	2	68 (54 - 80.3) x 29.2(20.4 - 36.3)	20	rather common
C	68.1(46.5 - 86.8) x 27.3(16.1 - 34.1)	30	rather common	

is an inconspicuous species; small and in expanded state rather transparent, occurring in small numbers and tending to occupy dark, sheltered places.

The species has been collected in St. Thomas (type-locality), Jamaica, Bonaire and Curaçao. Dr. W. E. Sterrer recently found it on several occasions in Bermuda (in litt. 22.VIII.1979). According to Dr. C. E. Cutress (in litt., 23.I.1973), the species also occurs in Puerto Rico. Mr. R. W. Seaton (in litt., 2.V.1978) collected it in two localities in Florida, viz.: Pompano Beach (depth 15-20 ft., on small boulders along reef) and Grassy Key, near town of Marathon (in shaded culvert under road; depth 1-1.5 ft., on loose pebbles, marl bottom).

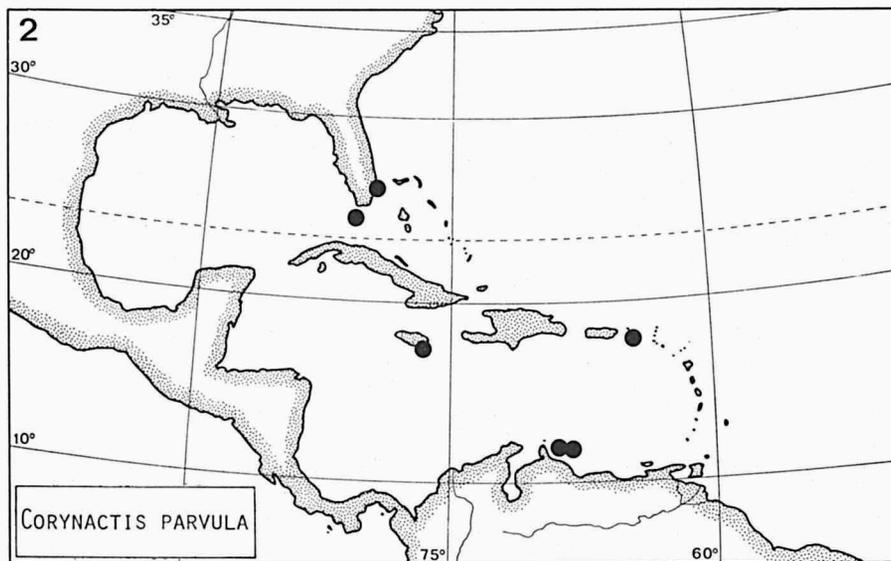


Fig. 2. *Corynactis parvula*. Map showing the known geographical distribution of the species. The occurrence of the species in Bermuda is not indicated as it was reported to me when the line block of the figure had already been prepared by the printer.

Systematics, nomenclature and miscellaneous notes. — With respect to the identity of the species here under discussion, only two Caribbean species come into consideration, viz., *Corynactis parvula* Duchassaing & Michelotti, 1860 and *Draytonia myrcia* Duchassaing & Michelotti, 1864. Although these two species, according to Duchassaing & Michelotti, differ exclusively in the absence or presence of “glandulae chromatophorae virides” along the margin and on the oral disc, the authors considered this difference so fundamental, that a new genus, *Draytonia*, was erected for the second species. Andres (1883: 485) synonymised the two genera. In my opinion the “glandulae chromatophorae virides” of *Draytonia* represent nothing but green spots,

the presence of which as mentioned on p. 13 proved to be a variable specific character in the species here discussed. Consequently, I consider *Draytonia myrcia* a junior synonym of *Corynactis parvula*.

Two samples of *Corynactis* from the Western Atlantic (North Carolina and Brazil) were studied in addition to the material of *C. parvula*. Although a specific identification of these samples appeared impossible, and although, strictly spoken, not collected in the Caribbean, these samples are here recorded for the sake of completeness and also as they are of importance for our knowledge of the distribution of the genus *Corynactis*.

Corynactis spec. 1 (table 1)

Material examined. — North Carolina: 14 miles east of north tip of Hatteras Island, depth 16 to 18 fms, 28.II.1962; leg. M. Cerame Vivas: USNM 52384.

The material consists of a clone of ca. 20 specimens on a polychaete tube and was identified as *Corynactis parvula* by Dr. C. E. Cutress in 1962. The specimens are preserved in alcohol. They represent usual *Corynactis* polyps, but their condition does not allow a relevant morphological or anatomical description; there are no colour notes either.

Two specimens were sectioned transversely. One of these had 24 pairs of mesenteries, including two pairs of asymmetrically arranged directives (separated by 7 and 15 normal pairs). The other specimen had 25 pairs of mesenteries, including one pair of directives only. Both specimens were fertile but the distribution of the gonads could not be determined. It appeared also impossible to determine the ratio of perfect and imperfect mesenteries.

A study of the nematocysts (cf. table 1) revealed that the cnidom of the specimens differs from the cnidom of *Corynactis parvula* by the presence of two size-classes of penicilli D in the tentacles (the usual condition in several other species, e.g., in *Corynactis viridis* Allman, 1846, *C. annulata* (Verrill, 1866) and *C. californica* Carlgren, 1936). The specimens concerned therefore, almost certainly belong to another species.

It is remarkable that *Corynactis delewarei* Widersten, 1976 (: 858-860), described from about the same region (39°56' N., 69°45' W., depth 201 m) was also collected on a polychaete tube. Widersten's account of the cnidom, however, is quite different from what I found in the North Carolina material.

Corynactis spec. 2 (table 1)

Material examined. — Brazil: South-side of Cabo Frio Island, cold upwelling water, depth 10 to 20 m, 30.VIII.1977, 10 specimens; leg. C. Haggs: RMNH 12868.

The specimens probably represent a clone. Some of them are very small. They are preserved in alcohol. One well developed specimen was transversely sectioned. It had 29 pairs of mesenteries: 14 perfect (p; including two pairs of directives), 13 imperfect (i) and two pairs of uncertain status (i?), alternating in an irregular manner (p, p, p, i, i, p, i, p, i, p, i, p, i?, p, i?, p, i, p, i, i, p, i, p, i, p, i, p, i, p, i, i), presumably in correlation with asexual reproduction. All mesenteries were fertile, with the exception of a few of the youngest, but the directives included. In the lower part of the column three more or less distinct size-classes of mesenteries could be observed. The mesenterial mesogloea is distinctly thickened on the retractor-side. Longitudinal sections (of a second specimen) showed the presence of a distinct, diffuse sphincter.

Probably owing to the state of preservation of the specimens, many cnidae were opaque, concealing the internal structures, so that identification of the different types

appeared difficult. In addition to the types and size-classes listed in table 1, the tentacles appeared to contain sparse numbers of a category of nematocysts (average and range in microns: $36.8 (34.1-41.5) \times 6.6 (5.6-8.7)$), which I have hesitatingly identified as homotrichs.

According to Miss Haggis (in litt., 15.VII.77), the species shows great colour variation, tending to occur in patches of one colour (undoubtedly clones). A colour photograph of the species, which I received from Miss Haggis, shows two orange specimens with white tipped tentacles and with white marks on the oral disc (in one specimen in the form of white patches, in the other specimen as a conspicuous central field of irregular outline, interrupted by a single orange sector roofing about 1/6 of the total number of mesenteries).

***Pseudocorynactis* gen. nov.**

Diagnosis. — Fairly large, solitary forms. Body variable in shape, when fully expanded often wide trumpet-shaped, mammiform when retracted. Column differentiated into scapus and scapulus. Base up to 4 cm in diameter. The oral disc and the tentacles can easily be withdrawn into the column. Tentacles well developed, ectacmaceous, motile and retractile; acrospheres extremely well developed. Endocoelic tentacles arranged in radial rows of 3-5 tentacles each; in each row the penultimate tentacle exceeds the outermost one in length. The single exocoelic tentacles are the longest of all. Siphonoglyphs absent, two pairs of directives present. All mesenteries perfect and fertile, provided with very distinct, circumscribed, mesogloal parietal ridges. Sphincter distinct. Cnidom as in the family.

Type by monotypy: *Pseudocorynactis caribbeorum* spec. nov.

***Pseudocorynactis caribbeorum* spec. nov.** (table 2, figs. 3, 4, pls. 2, 3, 8, 9 fig. 1, 12, 13 fig. 10)

"Undescribed corallimorpharian" Roessler, 1977: fig. 138 (coloured photograph of largest specimen of RMNH 11483; Curaçao); Colin, 1978: 199 (size, colour, 10 to 30 m deep, expanded at night; Puerto Rico), 200 (coloured photograph of a specimen).

Material examined:

Off Colombia. — UMML, P 420 (09°30'7" N, 78°26'0" W, 50 m deep, scallop dredge, 1 specimen).

Curaçao. — South-coast, area between the entrance of Piscadera Bay and Blauw Bay, depth ca. 6-15 m: RMNH 11479 (IV.1971, 1 specimen; leg. J.C.P.), 11481 (holotype) and 11482 (1 specimen) (both: 30.XI.1972; leg. P.C. & H.W.), 11483 (1972, 3 specimens; leg. P.C. & H.W.), 11485 (23.V.1973, 4 specimens; leg. P.C. & H.W.). From other localities in Curaçao came: RMNH 11484 (Porto Marie Bay, depth 6 m, 1 specimen; leg. B. de Boer), 11486 (Playa Abao, on side of large, dead coral head, depth 4 m, 3.VI.1972, 1 specimen; leg. J.C.H.), 12817 (Slangen Bay, between 2 species of coral, depth 22.5 m, 7.VIII.1973, 1 specimen; leg. R.M.H. & P.C.).

Saba. — RMNH 11487 (Giles Quarter, Tom's Ghaut, depth 10 m, 4.X.1972, 1 specimen; leg. P.C.).

Off Venezuela. — UMML, P 734 (11°01'0" N, 65°36'3" W, depth 33-37 fms, 10' otter trawl, 22.VII.1968, 11 specimens), USNM sine num. (Oregon sta. 4459, 10°50' N, 66°58' W, depth 53 fms, 6' tumbler dredge, bottom temperature 22.8° C, X.1963, 1 specimen).

Morphology (pls. 8, 9 fig. 1, 12, 13 fig. 10). — Base irregular in outline, adapting to the substrate, often spreading; with or without short, rounded basal expansions. Diameter up to 4 cm, generally less.

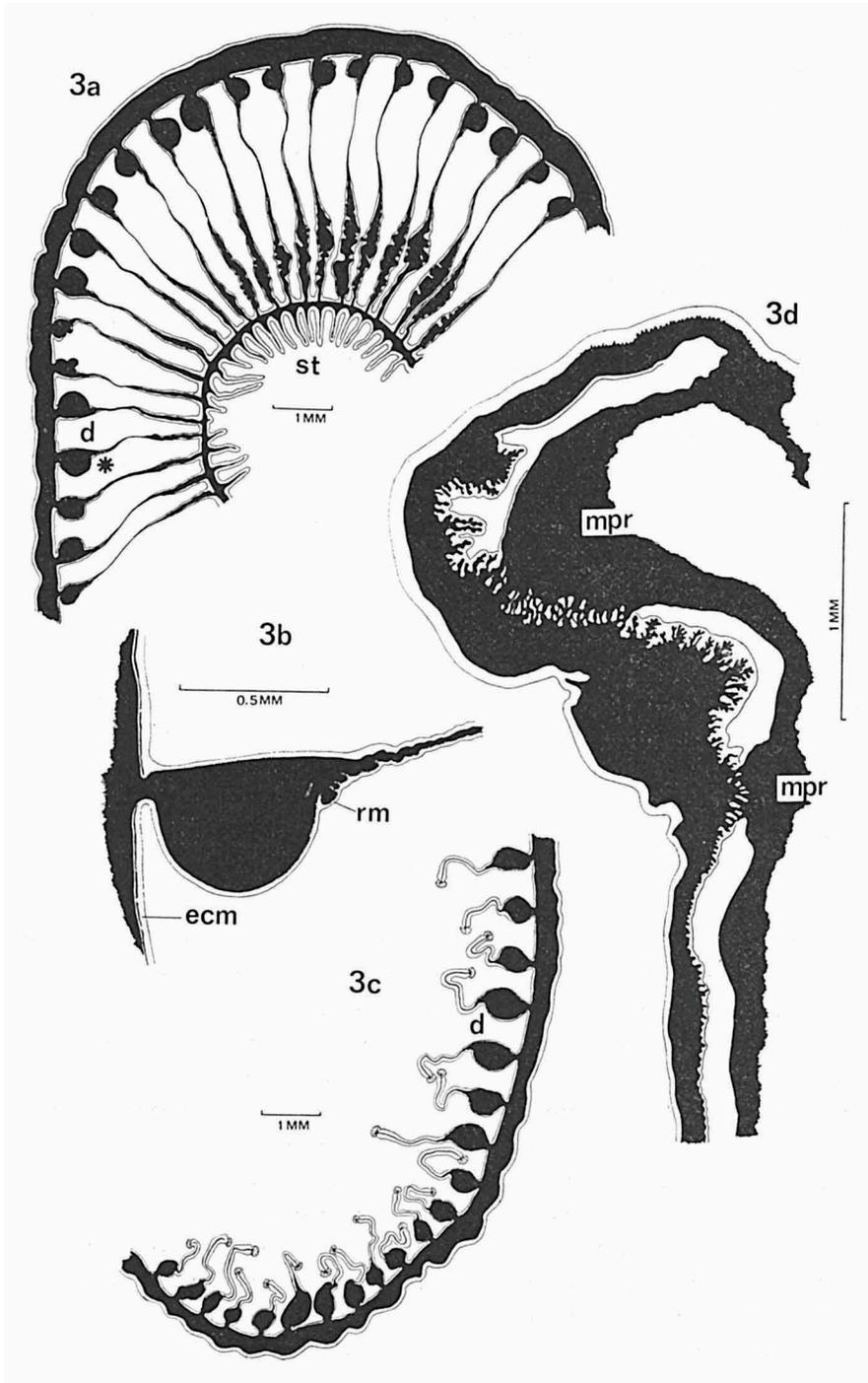
Column smooth, distinctly differentiated into two regions, a large scapus and a narrow marginal scapulus. Scapus thickwalled, rigid and more or less cartilagenous, as a rule with a pattern formed by fine longitudinal ridges and grooves crossed by circular ridges (This feature cannot always be clearly observed, but it can be checked by touch). In contracted or semi-contracted polyps the longitudinal ridges as a rule are knobby and more prominent, especially in the upper part of the scapus. They cease abruptly at the borderline of scapus and scapulus. The scapulus, besides, often makes a distinct angle with the erect wall of the scapus and is frequently marked by a different colouration. In fully contracted specimens the scapulus often takes the shape of a mammiform elevation on top of the scapus, surrounded by a shallow fossa (cf. pl. 13 fig. 10). In the lower part of the scapus, the mesenterial insertions are often visible on the outside, especially in preserved specimens (which have lost their colours).

Oral disc circular in outline, up to 4 cm in diameter, semi-transparent, in living specimens often with a distinct, conical hypostome. Number of exo- and endocoelic radii ca. 25 to 30 each.

Tentacles well developed, with very distinct, globular acrospheres. Exocoelic radii with a single, large, marginal tentacle, which in full extension exceeds the diameter of the disc. Endocoelic radii with 3 to 5 basically ectacmaceous tentacles. In each row, however, the penultimate tentacle exceeds the ultimate tentacle in length, being almost as long as the exocoelic tentacles. Total number of tentacles in well developed specimens about 125 to 200.

Fig. 3. *Pseudocorynactis caribbeorum*. Anatomical details of the holotype (RMNH 11481). Mesogloea black. 3a, Cross-section through the upper part of the column. Note the conspicuous mesogloea parietal ridges. Note also the increase in thickness of the mesenterial mesogloea towards the stomodaeum; the exaggerated condition present in the mesenteries in the right hand sector of the figure are caused by the fact that this section just touched the oral disc of the specimen. 3b, Enlarged detail of one of the directive mesenteries (3a, *). 3c, Cross-section through the lower part of the body. 3d, Longitudinal section through the upper part of the column showing the distinct, diffuse sphincter. Note that the mesogloea parietal ridge (mpr) has also been traversed.

Explanation of the symbols: d = Directive mesenteries; ecm = Endodermal circular muscle; mpr = Mesogloea parietal ridge; rm = Retractor muscle; st = Stomodaeum.



Pattern and colour. — Although the column occasionally is uniform in colour, there is usually a difference in colour (or colour intensity) between scapus and scapulus. The scapus may be of a pale to vivid orange, lilac, or different shades of brown (orange-brown, yellowish brown, purplish brown), with or without opaque, whitish, greenish or blackish streaks or specks. The scapulus often is less intensely coloured than the scapus and may be marked by 6 dark, longitudinal bands (cf. pl. 12 fig. 1), which become faint and disappear in the upper part of the scapus. Occasionally the scapulus is opaque white. The oral disc is semi-transparent, as a rule with opaque patches or streaks of cream, white, or faint green. Peristome often opaque white. Tentacles colourless with vivid orange-red acrospheres.

Anatomy (fig. 3). — Number of mesenteries aborally and adorally equal; 23, 25 and 25 pairs, all perfect and including 2 pairs of directives, were counted in three dissected specimens. At the level of the stomodaeum all mesenteries are about equally well developed (cf. fig. 3a). In the lower part of the body relatively well developed and less developed mesenteries generally alternate (cf. fig. 3c); a distinct arrangement in cycles (either tetra- or hexamerous) could not be detected. In four dissected specimens all mesenteries were fertile; in a fifth specimen (the holotype) developing gonads were present in 8 adjacent mesentery-pairs. Distinct, circumscribed parietal ridges are developed on the retractor-side of all mesenteries (cf. fig. 3a, b, c).

Stomodaeum devoid of siphonoglyphs.

Sphincter diffuse, but rather well developed (cf. fig. 3d). Retractors very weak. Parietobasilar muscles very weak. Ectodermal musculature of the oral disc distinct.

Cnidom (table 2; pls. 2, 3). — In addition to the detailed study of the cnidom of RMNH 11486, presented in table 2, the cnidoms of several other specimens were studied partly or in detail. The tentacular homotrichs (II.b) appeared rather variable in distribution, size and abundance. They were extremely common and very large (up to 120×8 microns) in a specimen kept under aquarium conditions for more than a year (RMNH 11479). In some specimens they were not found at all, but it should be noted that never more than ten samples of tissue of the tentacular acrospheres of a single specimen were examined. It was further noticed that the filamental penicilli E (IV.d) of some specimens (e.g. the holotype and the largest specimen of RMNH 11483) were considerably larger than in RMNH 11486, often reaching dimensions of about $80-90 \times 35-40$ microns. Finally it may here be mentioned that certain small nematocysts present in the filaments (IV.b),

TABLE 2

Pseudocorynactis caribbeorum. Survey of the cnidom of a specimen from Curaçao (RMNH 11486).

Organ	Average and range of length and width of nematocyst capsules in microns		Number of capsules measured	Abundance
Nematocyst type				
<u>I. Column</u>				
a. Spirocysts	ca. 20 - 40	x 3 - 4.5	--	rare
b. Spirulae, 1	10.6(9.9 - 11.2)	x 3.3	10	uncommon
2	18.2(16.5 - 21.1)	x 6.6(5.6 - 7.3)	20	uncommon
c. Penicilli D	21.8(17.2 - 28.2)	x 6.4(5 - 7.9)	20	rather common
d. Penicilli E	28.8(24.4 - 34.3)	x 10.7(9.2 - 11.9)	20	common
<u>II. Tentacles</u>				
a. Spirocysts	196 (89.1 - 247.5)	x 4.2(2.3 - 6.6)	20	very common
b. Homotrichs	87.5(56.6 - 98.7)	x 6.1(4 - 6.6)	10	rather common
c. Spirulae	33.9(29.7 - 38.3)	x 4 (3.6 - 4)	10	rather common
d. Penicilli D	112.6(92.4 - 124.1)	x 5.8(5.3 - 5.9)	20	common
e. Penicilli E	153.9(138.6 - 168.3)	x 17 (16.5 - 18.5)	20	rather common
<u>III. Stomodaeum</u>				
a. Homotrichs	27.6(22.4 - 29.7)	x 4.5(4 - 5.3)	20	common
b. Penicilli E	62.9(58.1 - 68)	x 20.6(17.2 - 23.8)	20	common
<u>IV. Filaments</u>				
a. Spirocysts	ca. 30 - 120	x 3 - 7.5	--	rather common
b. Spirulae	14.1(12.5 - 15.8)	x 4.1(4 - 4.3)	20	uncommon
c. Penicilli D	18.6(15.2 - 19.8)	x 5.9(5.3 - 6.6)	20	common
d. Penicilli E	69.1(64.7 - 72.6)	x 28.8(26.4 - 31)	20	common

although strongly reminding of penicilli D, were provisionally identified as spirulae, as I was unable to discern a V-shaped notch at the end of the undischarged shaft of these cnidae.

Biological notes. — *Pseudocorynactis caribbeorum* apparently is chiefly a reef species. On the south coast of Curaçao, between 4 and 22.5 m depth, the species appeared to be fairly common. It thrives on bare rock, or more or less hidden among coral colonies. It is a solitary, nocturnally active species, which, except in submarine caves, has never been observed in expanded state during the day or in the early evening. Most specimens were collected in shadowy and dark places, but at least one specimen (RMNH 11486) was detected in a location where it received direct solar radiation. "Pillsbury" and "Oregon" specimens from deeper water (up to 53 fms) were collected on marl bottoms.

The very sticky tentacles enable the species to get hold of large prey, but this was not observed under natural conditions. Specimens in the aquarium easily held and engulfed large pieces of fish, oyster and living crabs of moderate size. Under experimental conditions, when being approached by an

object, the tentacles were observed to make apparent "catch movements". The approaching object was invariably seized by a quick, sweeping movement of one or several of the tentacles. This behaviour shows that the species is able to register and to locate the presence of possible prey before the tentacles are actually touched. Catching prey therefore, is to be regarded an active process in *Pseudocorynactis caribbeorum* (and it seems likely that this is also true for the representatives of the closely allied genus *Corynactis*). The fact that this behaviour was not only observed when food was administered, but also when specimens were approached by a clean dissecting-needle (i.e. excluding possible chemical stimuli), seems to indicate that the ability to locate objects is at least partly correlated with the presence of extremely sensitive tactile organs.

The species is characterised by a great power of regeneration. Badly damaged specimens, even specimens of which the pedal disc had been ripped off, easily recovered within a few weeks or months under aquarium conditions. In spite of this regenerative power, and although basal expansions and anatomical irregularities occur commonly, the species apparently does not normally reproduce asexually, as is indicated by the fact that it is always found solitary. No sign of spontaneous asexual reproduction, moreover, was noticed during two years of regular observation of several aquarium specimens (a.o. RMNH 11479). There is one dubious case, concerning a small, regenerated piece of tissue, provided with few tentacles, which was noticed close to a well developed specimen of the same colour, a week after this specimen (RMNH 11485) was collected. This may have been a case of spontaneous asexual reproduction, initially overlooked, but I consider it more likely that this piece of tissue was ripped off during collecting and had regenerated since.

Systematics, nomenclature and miscellaneous notes. — The species conforms to a large extent to the description of *Corynactis*, but differs from all the representatives of that genus by its unusually large size and its solitary habit, apparently correlated with the absence of asexual reproduction. The arrangement of its tentacles also differs from the condition present in *Corynactis*; in *Pseudocorynactis caribbeorum* the penultimate tentacle of each endocoelic row exceeds the outermost one in length, while in *Corynactis* the endocoelic tentacles are purely ectacmaceous (Mr. P. G. R. Tranter, Laboratory of the M.B.A., Plymouth, kindly checked and confirmed the presence of this condition in living specimens of *Corynactis viridis* Allman, the type of the genus). As to the anatomy, the conspicuous, mesogloea parietal ridges of the mesenteries of *Pseudocorynactis* call for notice. These ridges are

invariably absent in *Corynactis*, although a parietally slightly thickened mesogloea may be present in the mesenteries of some species (e.g. *C. parvula*). Another feature likely to be of generic importance is presented by the condition of the mesenteries. In *Pseudocorynactis caribbeorum* all mesenteries are perfect and able to develop gonads. In those species of *Corynactis*, which so far have been investigated in this respect, at least part of the mesenteries is imperfect. Whether the cnidom of *Pseudocorynactis caribbeorum* (notably with regard to the size of certain types of nematocysts) differs generically from that of *Corynactis* cannot yet be properly judged.

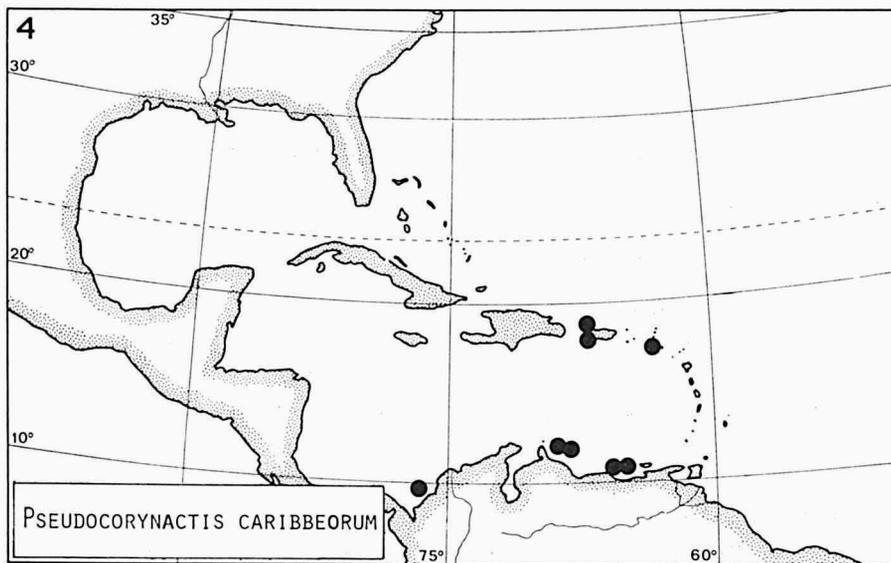


Fig. 4. *Pseudocorynactis caribbeorum*. Map showing the known geographical distribution of the species.

Occurrence and distribution (fig. 4). — Although here presented as a species new to science, *Pseudocorynactis caribbeorum* is fairly common in the southern and eastern Caribbean. Its obscurity must be due to the fact that it only expands at night. Apart from the localities cited on pp. 19-20, the species was also found on the south-west coast of Bonaire (reef in front of Trans World Radio station, common in 1973; J. C. Post, personal communication) and around Puerto Rico (caves at Arecibo, C. E. Cutress & C. Arneson, personal communication, IX, 1973; "several other places, and it is quite common around La Parquera", C. Arneson, in litt., 13.IX.1976).

RICORDEIDAE Watzl, 1922

Ricordeidae Watzl, 1922: 6, 78.

Diagnosis. — Body rather firm and flat. Tentacles simple and short, with rounded, clavate or capitate tips, never with distinctly differentiated acrospheres. Up to 20 tentacles may occur in each endocoelic row. The oral disc and the tentacles cannot be withdrawn. Superimposed on the radial arrangement of the tentacles, there is an indistinct differentiation into discal and marginal tentacles. Directive mesenteries present or absent. Sphincter absent. Cnidom as in the order; spirocysts rather sparse.

Ricordeidae are tropical shallow water forms, invariably associated with zooxanthellae. The single genus *Ricordea* Duchassaing & Michelotti, is represented in the Caribbean by the type species, *R. florida* Duchassaing & Michelotti.

Ricordea Duchassaing & Michelotti, 1860

Ricordea Duchassaing & Michelotti, 1860: 317 (42).

Diagnosis as in the family.

Systematics, nomenclature and miscellaneous notes. — 1. The genus *Ricordea* is not monotypic, as suggested by Carlgren (1949: 14). A study of the corallimorpharian literature convinced me that there is, apart from *Ricordea florida*, at least one other species, viz., *R. yuma*, described and figured by Carlgren himself (Carlgren, 1900: 83-84, pl. 2 figs. 14, 15) from Zansibar, but incorrectly classified as a *Discosoma*.

Another species mentioned in the literature, which possibly represents a *Ricordea* is *Discostoma* (= *Discosoma*) *fungiforme* Verrill (1869: 36-37, pl. 1 fig. 7) from the Bonin Islands. Although Verrill did mention the resemblance of this species to *Ricordea florida*, he nevertheless, for obscure reasons, included it in *Discostoma*. It was actually referred to *Ricordea* by Haddon (1898: 481), together with two other species: *Phialactis neglecta* Fowler (1888: 148-151; pl. 15 figs. 10-16; type of the monotypic genus *Phialactis* Fowler, 1888) from Tahiti and *Homactis rupicola* Verrill (1869: 37-38; type of the monotypic genus *Homactis* Verrill, 1869) from Honkong. The latter two species, however, certainly do not belong in *Ricordea*. An examination of the type-series of *Phialactis neglecta* (present in BM(NH)) convinced me that this species is a discosomatid. Dr. D. F. Dunn (California Academy of Sciences, San Francisco; in litt., 5.IV.1979), after examining the type (present in YPM), informed me that *Homactis rupicola* represents a species belonging in the actiniarian genus *Stoichactis* Haddon, 1898 (: 472).

Apart from the indications in the literature, mentioned above, that *Ricordea* apparently is also represented in the Indian Ocean (by at least one — presumably other — species), I have seen and examined actual samples of a *Ricordea* species from Singapore (private collection of Major K. W. England, deposited in BM(NH)).

2. *Ricordea* takes in several respects an intermediate position between Corallimorphidae and Discosomatidae. The cnidom resembles that of Corallimorphidae, although spirocysts (absent in Discosomatidae) are comparatively small and less numerous. The tentacles of *Ricordea* are simple as in Corallimorphidae, but very short, not motile and devoid of acrospheres as in Discosomatidae; their number in each radial endocoelic row also is in better agreement with the condition present in Discosomatidae, as is the tendency towards a differentiation into discal and marginal tentacles. Lastly, species of *Ricordea* are adapted to a way of life in symbiosis with zooxanthellae like Discosomatidae; they have a similar flat, spreading body and are unable to withdraw oral disc and tentacles.

Carlgren (1949: 14) included *Ricordea* in the Corallimorphidae, but accommodation of the genus in a family of its own, as proposed by Watzl, is in my view more in agreement with the characteristics of the genus.

3. McMurrich (1889: 46-47) considered *Ricordea* and *Heteranthus* Klunzinger, 1877, to be synonymous and although he was aware that in that case *Heteranthus* was a junior synonym of *Ricordea*, he disregarded the latter name: "... since the characters which were assigned to it by its authors are, if anything, specific and not generic". This of course was not a relevant reason to suppress *Ricordea* and McMurrich himself corrected this error (1896: 188).

Apart from this nomenclatorial side step, and judging from the original description and figure of *Heteranthus verruculatus* Klunzinger (1877: 83; type by monotypy of *Heteranthus* Klunzinger), it is very clear that *Heteranthus* is not even a genus of Corallimorpharia, as can be deduced from the fact that adherent warts ("klebenden Saugwarzen") are present on the column. I fully agree with Carlgren (1949: 74-75), who (1900: 92) investigated the holotype, that *Heteranthus verruculatus* should be accommodated in the actiniarian family Phymanthidae.

Ricordea florida Duchassaing & Michelotti, 1860 (table 3; figs. 5, 6; pl. 4, 9 figs. 2, 10)

Ricordea florida Duchassaing & Michelotti, 1860: 317-318 (41-42) (short description, partly incorporated in generic description, colour; St. Thomas; no holotype designation) pl. 4 fig. 11 (habitus); Duchassaing & Michelotti, 1864: 122 (28) (colour variation);

Andres, 1883: 572 (repetition of data by Duchassaing & Michelotti); McMurrich, 1896: 188 (*Ricordea* is synonymous with, and has priority over *Heteranthus* Klunzinger, 1877); Haddon, 1898: 481 (name); Duerden, 1898: 637 (common in Jamaica); Duerden, 1898b: 452 (morphology, variation in colour; asexual reproduction; Port Antonio, Jamaica); Duerden, 1900: 156-161 (extensive description of morphology, anatomy, histology, colour; Port Royal Cays and at Laughlands, St. Ann, Jamaica), pl. 10 fig. 7 (habitus), pl. 11 fig. 5 (tentacular arrangement), pl. 11 fig. 6, pl. 12 figs. 1, 2, pl. 13 fig. 1 (anatomical and histological details); Carlgren, 1900: 79, 81 (name); McMurrich, 1905: 11 (a Duchassaing & Michelotti-specimen of *Ricordea florida* present in the Zoological Museum of Turin); Pax, 1910: 219-222 (morphology, anatomy, histology; Kingston, Jamaica), pl. 15 fig. 20 (habitus); Watzl, 1922: 8-9 (data on nematocysts, similarity with those of *Corynactis bahamensis*); Carlgren, 1947: 95-96 (cnidom; discussion on systematic position; *Ricordea florida* sensu Weill, 1934 is very probably no *Ricordea*); Carlgren, 1949: 14 (name only); Zeiller, 1974: 28 (colour photograph of a representative clone; the picture at the right, below, is certainly not *Ricordea*, but a specimen of *Discosoma sanctithomae* with aberrantly reduced tentacles; the picture at the right is a solitary specimen in poor condition); Sebens, 1976 (longitudinal fission, aggression towards other Anthozoa; Galeta Island, Panama Canal Zone).

?*Heteranthus floridus* — McMurrich, 1889: 47-50 (morphology, anatomy, colour; New Providence, Bahamas) pl. 1 fig. 10 (habitus), pl. 4 figs. 4, 5 (histological details).

Corynactis bahamensis Watzl, 1922: 3-7 (morphology, anatomy, cnidom; symbiotic with zooxanthellae; Mastic Point, Andros, Bahamas), pl. 1 fig. 1 (habitus).

[Not *Ricordea florida* sensu Verrill, 1900: 556 (Bermuda); Weill, 1934: 605-606 (Bermuda) (see under *Discosoma carlgreni*, p. 59)].

Material examined (unless stated otherwise, the samples relate to the sub-colonial growth form):

Bahamas. — ZML type nr. 178 (Andros, Mastic Point, VII. 1908, 1 specimen; leg. N. Rosén; holotype of *Corynactis bahamensis* Watzl, 1922).

Bonaire. — RMNH 11499 (South-west coast, ca. 2 miles north of Kralendijk, in front of *Acropora palmata*-fringe, depth ca. 3.5 m, 9.IV.1973; leg. J.C.H.).

British Honduras (Belize). — Carrie Bow Cay: USNM sine num. (South of Carrie Bow, depth 5 to 6 m, 31.III.1977; leg. R.J.L.), 56582 (5.V.1974; leg. K.S.); 56576 (5.V.1974; leg. K.S.), 56602 (23.V.1974, leg. K.S.), 56903 (Outer fore reef slope, depth 60 ft., on dead *Acropora cervicornis* and *Agaricia agaricites*, solitary specimens, 23.III.1978; leg. R.J.L. & K.L.), 56904 (depth 45 ft., on *Agaricia agaricites*, solitary specimen; leg. R.J.L. & K.L.), 56905 (South-west of Carrie Bow, on patch reefs, depth 15-20 ft., solitary specimen, 1.IV.1978; leg. R.J.L.), 56922 (outer ridge of fore reef slope, depth 50 ft., on *Acropora cervicornis* branches, specimens more or less gregarious ("like a thicket"), but on the average well separated, 23.III.1978; leg. R.J.L.).

Cayman Islands. — BMNH. 1951.4.7.85 (Georgetown, ½ fm., 26.IV.1958; Oxford University Exped.).

Curaçao. — RMNH 11495 (South-coast, between Piscadera Bay and Blauw Bay, depth 120 ft., solitary specimen, 9.VII.1973; leg. P.C.), 11496 (idem, depth 150 ft., solitary specimen, 26.IV.1973; leg. R.M.H.), 11500 (idem, shallow water, VII or VIII. 1972; leg. P. Colin), 11494 (South-coast, between Hilton hotel and water plant, depth 160 ft., solitary specimen, 23.VII.1973; leg. K.W. & B. de Boer), 12003 (South-coast, Playa Chikutu, depth ca. 10 m, 8.V.1971; leg. J.C.P.), 12005 (South-coast, Playa Chikutu, depth 3-6 m, on rock and coral, 21.VII.1973; leg. R.M.H. & K.W.), 11491 (South-coast, Jan Thiel, depth 120 ft., solitary specimen, 8.VII.1973; leg. R.M.H.), 11492 (idem, depth 100 ft., on dead coral, solitary specimen, 8.VII.1973; leg. R.M.H.), 12001 (idem, depth ca. 100 ft., 27.V.1973; leg. R.M.H.), 12004 (idem, depth 80 ft., solitary

specimen, IV.1971; leg. J.C.P.), 11493 (North-coast, Boca Canoa, in tidal pools, 22.V.1971; leg. J.C.H.), 12002 (idem, 5.VIII.1972; leg. J.C.H.).

Jamaica. — USNM 19043 (Port Royal Cays, Inst. of Jamaica, acc. no. 34800); BMNH 1976.9.7.1 (Port Royal Cays, 1860; leg. J. E. Duerden).

Panama Canal Zone. — RMNH 11488 (Galeta Island, depth 15 ft., on dead coral, 5.VIII.1973; leg. K. B. Meyer).

Puerto Rico. — USNM 51082 (Parquera, Majimo reef, shallow water, on coral, I.1959; leg. J. Rivera Lopez), 53266 (Parquera, Cayo Henrique, depth 1.5 m, on dead coral, 18.VIII.1964; leg. C. E. Cutress).

Saba. — RMNH 11490 (Cove Bay, depth 1-6 m, among coral, X.1972; leg. J.C.H.).

St. Eustatius. — RMNH 11498 (Gallows Bay, depth ca. 1-3 m, 30.IX.1972; leg. J.C.H.), 11497 (ca. 800 m south of Gallows Bay, depth 3 m, on rocks, 1.X.1972; leg. J.C.H.).

St. Martin. — RMNH 11489 (Anse de Péres, sandy beach with rock boulders, depth 1 m, X.1972; leg. J.C.H.).

Tobago. — USNM sine num. (Man-o-War Bay, intertidal, 21.V.1977; leg. R.J.L. & K.L.; acc. no. 327397).

Virgin Islands. — USNM 52014 (St. John, depth 65 ft., 5.I.1961; leg. J. Randall).

Morphology (pl. 9 fig. 2, pl. 10). — Base irregular and very variable in outline, varying from more or less circular in solitary specimens, to elongate and sinuous in semi-colonial specimens.

Column smooth, short and spreading over the substrate; in expanded state firm and semi-transparent, mesenterial insertions externally visible.

Oral disc more or less circular in solitary specimens, elongate and sinuous in relation with semi-colonial growth. In large solitary specimens it may reach a diameter of 8 cm, in semi-colonial polyps it may measure up to ca. $10 \times 2-3$ cm, but polyps usually are considerably smaller. The number of oral openings per polyp varies in relation to semi-colonial growth. In more or less radially symmetrical specimens the number is usually 1 or 2. In elongate, sinuous specimens up to 7 mouths were counted. Hypostome(s) slightly raised to long conical. Mouth(s) circular to elliptical. The oral disc is densely covered with hundreds of short, non-retractile, slightly to distinctly capitate tentacles. These are in principle arranged in numerous endocoelic rows, alternating with single exocoelic tentacles. This arrangement of the tentacles is not always easy to detect because of their large number and the presence of irregularities resulting from asexual reproduction. The number of endocoelic rows varies in radially symmetrical specimens from ca. 40 to 100. In semi-colonial specimens the number may be even larger. The number of tentacles in each row is quite variable. The principal rows normally bear 10 to 12, in large solitary specimens up to 18, relatively well developed tentacles. The radii corresponding with the youngest endocoels only bear 2 or 3 tentacles, situated in the peripheral region. Apart from the arrangement of the tentacles in radial rows, distinction can be made between discal and marginal tentacles. This, however, is often difficult to establish

in preserved condition. The marginal tentacles are represented by the most peripherally inserted, endocoelic tentacles and by the exocoelic tentacles, which are distinctly larger and inserted slightly more inwards. In living, expanded specimens, the marginal tentacles usually are more elongate and slender than the discal tentacles. The tips of the marginal tentacles in addition often tend to be rounded to clavate or conical rather than capitate, as in the usual condition of the discal tentacles.

Pattern and colour. — Column usually chocolate to purplish brown, especially in the upper part; paler towards the base. Periphery of the oral disc often bright blue; central part dull bluish, purplish or brownish, often with a bright green hypostome. The stems of the tentacles usually have the same colour-shades as the disc. The tips of the marginal tentacles are often bright green, contrasting with those of the discal tentacles, which usually are dull green in various shades, greyish or rust-coloured to nice orange brown. However, some of the discal radial rows occasionally are also brighter coloured than the rest.

Anatomy (fig. 5). — Due to the flat, spreading character of the species I did not succeed in making proper transverse sections and I cannot add anything to what is already known. There are numerous pairs of mesenteries, both perfect and imperfect, often irregularly arranged in relation with asexual reproduction. Directives apparently are present or absent (Duerden, 1900: 160; Pax, 1910: 222; McMurrich, 1889: 49).

Longitudinal sections were made of two specimens; one solitary deep water specimen (RMNH 12005) and one semi-colonial shallow water specimen (RMNH 11490). In agreement with the data in the literature, a sphincter appeared to be absent in both specimens, though a distinct, endodermal circular muscle layer appeared to be present (fig. 5).

Cnidom (table 3; pl. 4). — A survey of the nematocysts of a shallow water semi-colonial specimen and of a solitary specimen from deeper water is presented in table 4. Details were checked in various other specimens.

In spite of the morphological similarity of the marginal and discal tentacles (the marginals just tend to be slightly longer), their cnidom shows one obvious difference. Large penicilli D, with a short shaft, which occur rather common to common in the marginal tentacles (II.d2), are rare or absent in the discal tentacles, here being partly or entirely replaced by another, more voluminous size-class of penicilli D, with a long shaft (II.d3). Not a single capsule of the latter type was found in the marginal tentacles.

TABLE 3

Ricordea florida. Survey of the cnidom. A = RMNH 12003, Curaçao, clonal specimen from shallow water. B = RMNH 12004, Curaçao, solitary specimen from deeper water.

Organ	Specimen	Average and range of length and width of nematocyst capsules in microns	Number of capsules measured	Abundance
<u>Nematocyst type</u>				
<u>I. Column</u>				
a. Spirocysts	A	ca. 13 - 40 x 2.6 - 4.5	--	rather common
	B	not measured	--	uncommon
b. Spirulae	A	21.1(17.2 - 25.1) x 6.7(5.3 - 7.9)	20	rather common
	B	18.1(13.9 - 21.8) x 5.8(4 - 6.9)	20	rather common
c. Penicilli D	A	20.3(17.8 - 23.1) x 7.2(6.6 - 7.9)	20	rather common
	B	17.9(13.9 - 20.5) x 5.8(4.6 - 7.3)	20	rather common
d. Penicilli E	A	50.4(47.5 - 55.4) x 18.8(16.5 - 19.8)	20	uncommon
	B	47.9(38.3 - 55.4) x 17.4(14.5 - 19.8)	20	uncommon
<u>II. Marginal tentacles</u>				
a. Spirocysts	A	ca. 25 - 60 x 2 - 4	--	common
	B	not measured	--	common
b. Homotrachs	A	60.5(40.3 - 72.6) x 5.5(4.3 - 6.6)	20	uncommon
	B	54.2(36.3 - 69.3) x 6.5(5.3 - 7.9)	40	common
c. Spirulae	A	24.7(19.8 - 36.3) x 3.6(3 - 4.3)	10	rather common
	B	20.7(16.5 - 23.8) x 3.6(3.3 - 4)	20	rather common
d. Penicilli D	A,1	20.3(17.8 - 23.1) x 7.2(6.6 - 7.9)	20	rather common
	2	80.6(73.9 - 87.1) x 6.7(5.9 - 7.3)	20	common
	B,1	18.9(15.2 - 23.4) x 6.2(4.6 - 7.9)	25	uncommon
	2	79.3(69.3 - 82.5) x 6.6(5.9 - 7.9)	20	common
e. Penicilli E	A	72.1(63.4 - 89.1) x 12.3(11.2 - 13.9)	20	common
	B	73 (60.7 - 85.8) x 12.5(10.6 - 13.9)	20	common
<u>III. Discal tentacles: Nematocysts as in the marginal tentacles; one size-class of penicilli D in addition</u>				
d. Penicilli D	A,3	77.4(72.6 - 84.5) x 10.2(9.2 - 11.2)	20	uncommon
	B,3	80.3(75 - 84) x 11 (9.8 - 12)	20	uncommon
<u>IV. Stomodaeum</u>				
a. Homotrachs	A	30.8(27.7 - 36.3) x 4.8(4.3 - 5.3)	20	rather common
	B	26.3(21.1 - 30.4) x 4.6(3.6 - 5.3)	20	rather common
b. Penicilli E	A	55.5(49.5 - 62.7) x 16.2(13.2 - 19.1)	20	rather common
	B	51.5(43.6 - 63.4) x 16.3(13.9 - 18.5)	20	rather common
<u>V. Filaments</u>				
a. Spirocysts	A	16.4(15.2 - 21.1) x 3.5(3.3 - 4)	20	common
	B	15.3(12.5 - 18.5) x 3.4(3 - 4)	20	common
b. Penicilli D	A,1	22.7(16.5 - 29.7) x 6.1(5.3 - 7.3)	20	common
	2	46.6(39.6 - 54.1) x 9 (7.9 - 9.9)	20	common
	B,1	22.4(15.8 - 33) x 4.7(4 - 6.6)	20	common
	2	55 (50.2 - 68.6) x 11.6(10.6 - 12.5)	20	common
c. Penicilli E	A	60 (44.9 - 64.7) x 22.3(15.8 - 25.1)	20	rather common
	B	52.9(34.3 - 59.4) x 18.8(11.9 - 23.1)	20	rather common

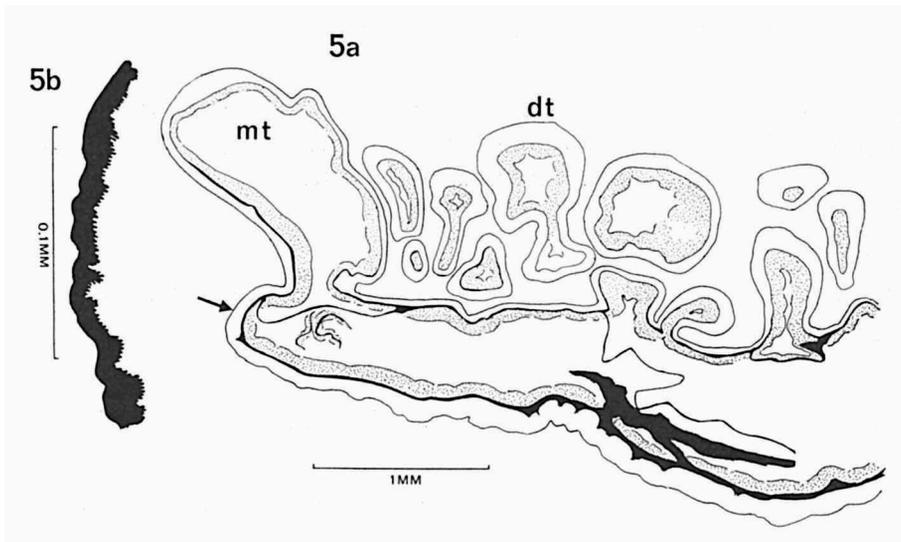


Fig. 5. *Ricordea florida*. Anatomical details (RMNH 11490). Mesogloea black. 5a, Longitudinal section through the marginal region; note the absence of a sphincter. 5b, Enlarged detail of the mesogloea in the region of the best developed part of the endodermal circular muscle layer (5a, see arrow).

Explanation of the symbols: dt = Discal tentacles; mt = Marginal tentacle.

The homotrachs of the marginal tentacles (II.b) vary considerably in size and abundance, in different tentacles of the same specimen as well as in different specimens. In the discal tentacles they are often completely absent, but here too they are occasionally common. These homotrachs and the tentacular spirulae (II.c) seem to merge into each other. Apparent transitional stages, with a short, slightly thickened portion at the base of the tube, were frequently observed. In the larger, more typical homotrachs, the tube is uniform in diameter and in undischarged state fills up the capsule in dense tangles.

The data in table 4 suggest that the tentacular spirulae (II.c) are rather slender. In other specimens, however, they were thicker and more like those occurring in the column (I.b).

Biological notes. — *Ricordea florida* occurs on coral reefs, growing on dead hermatypic corals and on rocky bottoms, at depths varying from ca. $\frac{1}{2}$ to at least 54 metres. In two localities, in Curaçao and Tobago, the species was collected in tidal pools; the specimens from Curaçao even were exposed during low tide.

Ricordea florida is invariably associated with zooxanthellae. A commen-

salic shrimp, *Periclimenes spec.*, has occasionally been noticed on the oral disc of specimens in Curaçao, but was unfortunately not collected. Colin (1978: 339) published a picture of the species from Jamaica, with (presumably) the same shrimp. Stock (1975) described two new copepods found associated with the species, viz., *Asteropontius longipalpus* and *Paramolgus antillianus*.

The material examined during the present study seems to indicate that *Ricordea florida* tends to a solitary habit with increasing depth (cf. pl. 10 fig. 2). In shallow water the species is almost invariably sub-colonial. This phenomenon is related to the frequent rate of asexual reproduction, proceeding — as is usual in Corallimorpharia — by means of basal expansions, which develop into new individuals. Longitudinal fission is probably also involved, although I have never observed the actual process. Clones of *Ricordea florida* are as a rule composed of closely arranged polyps of variable outline, which fit into each other as pieces of a jigsaw puzzle (cf. pl. 10 fig. 1); they may cover considerable patches of substrate, occasionally forming carpets of a square meter or more. A number of the polyps generally remains connected by a basal coenenchyme. Different clones frequently meet or mix up on the spot, but as a rule they are easily distinguished by obvious or subtle colour differences.

At depths of about 10 to 15 meters, the sub-colonial growth apparently comes to an end. Specimens collected at these depths were either solitary or more or less gregarious, though mutually well separated. This suggests a slower rate of asexual reproduction. Specimens from deeper water were invariably solitary, provided with a single oral opening and occasionally reaching considerable dimensions. This suggests a very slow rate, if not total absence of asexual reproduction. In a few of these solitary specimens (all from Curaçao: RMNH 11491, 11495, 11496) I noticed the presence of several larvae (about 1.5 to 3 mm long), each of which occupied the lumen of a tentacle. This indicates that *Ricordea florida*, at least occasionally, is viviparous. To what extent vivipary is correlated with depth and with a solitary habit needs to be studied further. The correlation between depth and the rate of asexual reproduction, as established here, also needs confirmation and further investigation, preferably by field studies.

Systematics, nomenclature and miscellaneous notes. — 1. *Corynactis bahamensis* Watzl, 1922, was described from a single, preserved specimen of ca. 1 cm in diameter, with about 200 to 300 tentacles. Watzl stated that the specimen was well provided with zooxanthellae. This would be a unique phenomenon within the genus *Corynactis*, which made me doubt the correctness of Watzl's identification. A subsequent re-examination of the holotype

revealed that it is a small specimen of *Ricordea florida*. The specimen actually does not resemble a *Corynactis* at all.

2. It is difficult to confuse *Ricordea florida* with any other Caribbean species. Large solitary specimens superficially resemble small specimens of the actinian *Stoichactis anemone* (Ellis), from which it may at once be distinguished by the totally different cnidom, by the absence of a detachable base, the structure of the filaments etc.

Distribution (fig. 6). — *Ricordea florida* is a common Caribbean species, not reported from the Gulf of Mexico and so far also not from Brazilian reefs. Records from Bermuda have proved to be based on misidentifications. The Florida records indicated on the map are from Mr. R. W. Seaton (in litt., 2.V.1978).

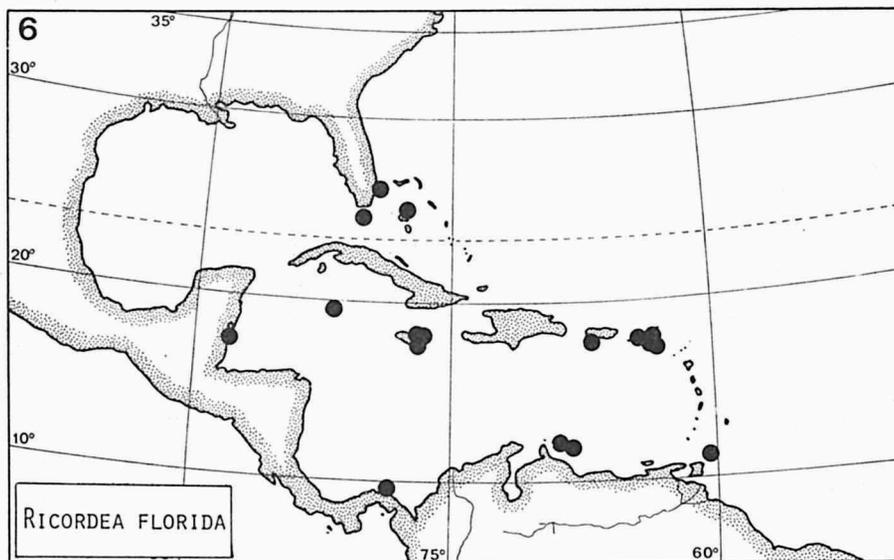


Fig. 6. *Ricordea florida*. Map showing the known geographical distribution of the species.

DISCOSOMATIDAE Duchassaing & Michelotti, 1864

Discosomae Duchassaing & Michelotti, 1864 : 121 (27).

Discostominae Verrill, 1869 : 35.

Rhodactidae Andres, 1883 : 498 (290).

Phialactidae Fowler, 1888 : 149.

Actinodiscidae Carlgren, 1949 : 14.

Diagnosis. — Body soft to very rigid, wide calyciform to flat saucer-shaped. Oral disc generally more or less circular to elliptical in outline;

of tentacles may be present, discal and marginal. Discal tentacles radially arranged, varying in shape from inconspicuous protuberances to well developed, branched outgrowths. Marginal tentacles often reduced; when present, they are tiny, acute or fingershaped appendages, often provided with small acrospheres. Mesenteries numerous, many pairs perfect. Mesogloea usually thick to very thick. Sphincter very weak to possibly absent. Ectodermal musculature absent. Cnidom: as in the order; spirocysts are completely absent and the tentacles are not provided with long penicilli D with a short shaft. Nematocyst batteries, mainly containing homotrichs, may develop along the margin, or, if marginal tentacles are present, on top of these in the form of small acrospheres.

Discosomatidae are tropical shallow water forms, invariably associated with zooxanthellae. Several genera have been described (cf. Carlgren, 1949: 14-16). The delimitation of these genera, however, is rather vague. Pending a thorough revision of the whole family, all species are here included in a single genus, *Discosoma* Rüppell & Leuckart, 1828.

Discussion. — 1. The family Discosomatidae is based on *Discosoma* Rüppell & Leuckart, 1828 (: 3) (type species: *Discosoma nummiforme* Rüppell & Leuckart, 1828 (: 3-4)). Duchassaing & Michelotti (1864) introduced the family name Discosomae. Verrill (1869: 35; 1869: 461), accepting Ehrenbergs incorrect change of the genus name *Discosoma* into *Discostoma* (cf. p. 37) proposed a sub-family Discostominae of the (actinarian) family Thalassianthidae. He explicitly stated this sub-family to be different from the Discosomae of Duchassaing & Michelotti. From the viewpoint of nomenclature, however, these taxa are objective synonyms, as they are both based on *Discosoma* Rüppell & Leuckart, 1828. Discosomae Duchassaing & Michelotti, 1864, therefore has priority over Discostominae Verrill, 1869, and adding the proper suffix, the correct family name thus is Discosomatidae Duchassaing & Michelotti, 1864.

Carlgren, who in practically all his papers used the valid names *Discosoma* and Discosomatidae (though incorrectly spelled Discosomidae), unfortunately abandoned these names in his monumental "Survey of the Ptychodactaria, Corallimorpharia and Actinaria" (1949). In that paper he followed Blainville (1830: 287; 1834: 320) in replacing the name *Discosoma* by the junior name *Actinodiscus* (cf. p. 37). Accordingly he adopted the name Actinodiscidae for Discosomatidae, adding another junior synonym.

Phialactidae Fowler and Rhodactidae Andres also are subjective junior synonyms because of the subjective synonymy of *Rhodactis*, *Phialactis* and *Discosoma*, discussed on pp. 37, 39.

Stichodactylidae Andres, although originally intended to include all Discosomatidae, is not only junior to the name Discosomatidae, but moreover is not a synonym, as it was actually based on a genus of *Actiniaria* (cf. p. 5: note 1).

2. A striking feature of all Discosomatidae is the complete absence of spirocysts. The distribution of these cnidae is so universal among Hexacorallia, that their presence is considered an important diagnostic character of the group; they are absent in all other Anthozoa. Only one other taxon of Hexacorallia, viz., the burrowing actiniarian genus *Anemonactis* Andres, 1880, is known to be practically devoid of spirocysts.

The occurrence of spirocysts in Hexacorallia roughly speaking is restricted to the tentacles, where they are usually present in enormous numbers; in addition they may be sparsely present in other organs. Spirocysts are generally assumed to play an important role in catching and holding prey; the sticky, adhesive character of hexacorallian tentacles is usually attributed to their presence.

Not only are spirocysts absent in the tentacles of Discosomatidae, other ectodermal cnidae too are very scarce and the tentacles themselves actually are of a quite unusual character, being non-retractile, non-motile, and practically devoid of musculature. They are either reduced to insignificant, wart-like protuberances or developed into vesicle-like structures with or without appendages. It is difficult to assume that these tentacles are functional catching devices, and bearing in mind that Discosomatidae are invariably associated with extremely numerous zooxanthellae, it seems more likely that this group of Corallimorpharia is primarily, if not entirely, dependant on these associates (and therefore on light) for nutrition. In this context it may be mentioned that the flat, saucer shaped body of Discosomatidae and their ability to vary the shape of the oral disc from concave to convex and vice versa, can be explained as a structural adaptation to receive an optimal amount of solar radiation. Apart from the nutritional benefits resulting from the association with zooxanthellae, there may of course be some intake of organic particles by ciliary currents on the oral disc, or by extra-coelenteric feeding by means of extruded mesenterial filaments, as is also not uncommon among hermatypic corals (Lang, 1971).

Considering the above-mentioned data, the feeding biology of Discosomatidae appears to be worthy of an experimental approach.

Discosoma Rüppell & Leuckart, 1828

- Discosoma* Rüppell & Leuckart, 1828: 3 (type *Discosoma nummiforme* Rüppell & Leuckart, 1828: 3-4).
Actinodiscus Blainville, 1830: 320 (type *Discosoma nummiforme* Rüppell & Leuckart, 1828: 3-4).
Discostoma Ehrenberg, 1834: 32 (type *Discosoma nummiforme* Rüppell & Leuckart, 1828: 3-4).
Rhodactis Milne Edwards & Haime, 1851: 12 (type *Metridium rhodostomum* Ehrenberg, 1834: 39).
Actinotryx Duchassaing & Michelotti, 1860: 321 (45) (type *Actinotryx sanctithomae* Duchassaing & Michelotti, 1860: 321 (45)).
Orinia Duchassaing & Michelotti, 1860: 328 (52) (type *Orinia torpida* Duchassaing & Michelotti, 1860: 328-329 (52-53)).
Phialactis Fowler, 1888: 148 (type *Phialactis neglecta* Fowler, 1888: 148-151).
Platysoanthus Saville Kent, 1893: 155 (type *Platysoanthus mussoides* Saville Kent, 1893: 155).
Paradisocosoma Carlgren, 1900: 80 (type *Isaura neglecta* Duchassaing & Michelotti, 1860: 327 (51)).
? *Metarhodactis* Carlgren, 1943: 18 (type *Metarhodactis boninensis* Carlgren, 1943: 18-19).

Diagnosis as in the family; no long penicilli D with a short shaft present in the filaments.

Carlgren (1949: 15-16) listed 18 species of *Discosoma* (sensu lato); several of these, however, are definitely synonymous. Three species are known to occur in the Caribbean: *Discosoma sanctithomae*, *D. carlgreni* and *D. neglecta*. For the identification of these species, see table 4.

Systematics and nomenclature. — In practically all the publications consulted for the present study (including the nomenclatorial works of Agassiz (1842-1846: 2) and Hesse, Schulze, Kükenthal & Heider (1928: 1034), the name *Discosoma* is attributed to Leuckart. Only Sherborn (1928: 4441) and Neave (1939: 123) correctly (i.e., in accordance with Art. 50 of the International Code of Zoological Nomenclature) attribute the genus to Rüppell & Leuckart, 1828. Nothing in the original publication of Rüppell & Leuckart indicates clearly that Leuckart alone has been responsible for the description.

Blainville (1830: 287; 1834: 320) replaced the name *Discosoma* by *Actinodiscus*, which thus simply is an objective junior synonym.

Ehrenberg (1834: 32) stated *Discosoma* to be a junior homonym of *Discosomus* Oken (1816: 310; a genus of lizards) and proposed to change the name into *Discostoma*. *Discosomus* Oken, however, is not a homonym in the sense of the International Code of Zoological Nomenclature (Art. 58d). Besides, the name has been published in a work rejected for nomenclatorial purposes (I.C.Z.N., 1956 Opinion 417) and was later placed on the Official

TABLE 4
Survey of the main differences between the Caribbean species of *Discosoma*.

species characters	<i>Discosoma sanctithomae</i> (Duchassaing & Michelotti, 1860)	<i>Discosoma carlgreni</i> (Watzl, 1922)	<i>Discosoma neglecta</i> (Duchassaing & Michelotti, 1860)
1. Growth habit	Often occurring in large clones.	Generally occurring in clusters of a few specimens.	Generally solitary or occurring in clusters of a few specimens.
2. Diameter of the oral disc	Up to ca. 6 cm.	Up to ca. 5 cm.	Up to ca. 8 cm.
3. Consistency of the body	Generally rather soft.	Rather rigid.	Rather to very rigid.
4. Condition of the marginal region	Margin generally with well developed marginal tentacles, often bearing small but distinct, globular acrospheres. A distinct, naked zone between margin and discal tentacles is nearly always present.	Margin generally with many short, square to trifid lobes, occasionally with short marginal tentacles. A naked marginal zone is invariably absent.	Margin with distinct, large lobes. Marginal tentacles and a naked marginal zone are invariably absent.
5. Discal tentacles; condition and number	Nearly always well developed and generally compound, bearing distinct appendages. Number up to about 300, often considerably less.	As a rule compound but rather small, occasionally reduced to wart-like protuberances. Number up to a 1000 or more.	In principle compound, but often very small and visible only as fine corrugations, arranged in many radial rows. Number extremely large.
6. Colour of specimens	Column and oral disc generally soft yellowish- to pale purplish brown or green. Tentacles generally greenish, less commonly whitish, delicate blue or fine iridescent. Stomodaeal ridges white.	Body very variable in colour. Common colours on the (usually) variegated oral disc are: shades of green and brown, rubiginous, dark purple etc. Tentacles as a rule of the same colour as the disc, but some may be brightly coloured (white, yellow, green, pearl grey) and usually large. Stomodaeal ridges often greenish or yellowish.	Column greenish and/or brownish with scattered dark brown spots. Oral disc variegated with green, brown, white and cream; occasionally also with blue and faint purple. Tentacles of the same colour shades as occur on the oral disc. Stomodaeal ridges white.
7. Nematocysts; average and range (in microns) of:			
a. columnar penicilli D	30.8(22.5 - 40.5) x 8.3(6 - 10.5)	17.1(13.5 - 26.6) x 6.1(5.3 - 8)	14.5(11.2 - 19.5) x 5.8(4.7 - 6.8)
b. largest size-class of filamental penicilli D	37.7(30 - 46.5) x 8.4(6.8 - 10.5)	29.7(25.5 - 36) x 8	28.6(25.8 - 35.3) x 8 (6.8 - 9.5)

Index of Rejected and Invalid Generic names in Zoology (I.C.Z.N., 1963 Opinion 651: name number 1617).

The synonymy of *Rhodactis* and *Actinotryx* has been discussed already by McMurrich (1889: 42) and Carlgren (1943: 12-13, 16). The only significant difference between these genera is the (supposed)⁵⁾ absence, respectively presence of a naked zone separating the marginal and discal tentacles. McMurrich as well as Carlgren considered this difference specific rather than generic, and Carlgren pointed to the existence of species characterized by a more or less intermediate condition (viz., *Rhodactis bryoides* Haddon & Shackleton, 1893; *R. indosinensis* Carlgren, 1943). On the basis of my study of Caribbean Discosomatidae, separately discussed on pp. 53, 54, I have reached the same conclusion: *Actinotryx sanctithomae* (type of *Actinotryx*; nearly always with a distinct, naked marginal zone) and *Rhodactis carlgreni* Watzl (without a naked marginal zone) are not generically different. I also fail to see why *Paradiscosoma* (type *P. neglecta*) should be maintained as a separate genus. *Orinia*, another Caribbean genus, in my opinion was based on an aberrant specimen of *Actinotryx sanctithomae* (cf. p. 57).

Phialactis neglecta Fowler, 1888 (: 148-151, pl. 15 figs. 10-16), type of the monotypic genus *Phialactis* from Tahiti, also fits well in with the forms discussed above (the syntypes of this species, present in BM(NH), were examined). The same holds for *Platyzoanthus mussoides* Saville Kent, 1893 (: 155, fig.), from the Great Barrier Reef, actually a dubious species, of which a figure only was published and of which no type exists.

The type-genus of the Discosomatidae, *Discosoma* Rüppell & Leuckart, 1828, in my opinion is not essentially different from the genera so far discussed. I have examined the type-species, *Discosoma nummiforme* (material from the Red Sea: RMNH 12813, 12814, 12815; SMF. 33, i.e., the type-series). The cnidom of this species is fundamentally similar, as is the principally dendritic character of the discal tentacles. The marginal tentacles, moreover, are able to develop similar nematocyst batteries as in *Actinotryx sanctithomae*, provided with numerous homotrichs. However, unlike the type-species of the other genera so far discussed, the oral disc of *Discosoma nummiforme* bears distinctly thickened mesogloea ridges, which are par-

⁵⁾ It is even questionable whether this difference is really extant. The type of *Metridium rhodostomum* Ehrenberg, 1834 (:39), type-species of *Rhodactis*, has become lost (cf. Klunzinger, 1877: 88; pl. 8 fig. 3), so that we have only the descriptions of Ehrenberg and Klunzinger, and the figure published by the latter, to rely upon. The descriptions do not explicitly mention the absence of a naked zone and the, seemingly rather schematic, figure also does not entirely convince me that a naked marginal zone is absent indeed in *Rhodactis rhodostomum*. To verify this a morphological study of topotypical material is necessary.

ticularly conspicuous in the periphery. After some hesitation I have concluded that this probably does not concern a generic character; in the first place because I have noticed that, in each of the Caribbean species of Discosomatidae, the thickness of the mesogloea of the oral disc varies a great deal (although, as mentioned already, never forming pronounced ridges); secondly, because Carlgren (1943), who noticed comparable ridges in *Rhodactis inochata* Carlgren, 1943, *R. indosinensis* Carlgren, 1943 and *Metarhodactis boninensis* Carlgren, 1943 (type of the monotypic genus *Metarhodactis* Carlgren), did not attribute generic significance to this character. ⁶⁾

In conclusion, it is here advocated that, due to the lack of relevant structural differences, all genera of Discosomatidae are best lumped together and included in a single genus, *Discosoma* Rüppell & Leuckart, 1828. An exception may be made for *Metarhodactis*; the mesenterial filaments of *M. boninensis*, according to Carlgren (1943: 18; 1949: 16) contain numerous palissadelike arranged penicilli D with a short shaft (cf. p. 64; variety 1), which are completely absent in all other Discosomatidae. Carlgren's observations, however, need verification.

The conception of the genus *Discosoma* as presented here, has nomenclatorial implications for one species, *D. neglecta* (Fowler, 1888), which becomes a junior homonym of *D. neglecta* (Duchassaing & Michelotti, 1860). I therefore propose the name *Discosoma fowleri* **nom. nov.** as a substitute name for *Phialactis neglecta* Fowler.

Discosoma sanctithomae (Duchassaing & Michelotti, 1860) (tables 4, 5, 6, figs. 7, 8, 16, pls. 5, 6, 11, 13 figs. 1, 2)

Type-material: Apparently lost; not present in the Duchassaing & Michelotti collection in the Zoological Museum of Turin, Italy.

Actinotryx sanctithomae Duchassaing & Michelotti, 1860: 321 (45) (short description, partly incorporated in the genus-description, colour; St. Thomas, on stony corals; no type designation), pl. 7 fig. 2 (habitus); Duchassaing & Michelotti, 1864: 135 (41) (name only); Andres, 1883: 509, 510 (repetition of data of Duchassaing & Michelotti; discussion); Duerden, 1900: 148-154 (extensive description of morphology, anatomy, histology and colour; Port Royal Cays, Maiden Cay and Port Antonio, Jamaica), pl. 10 figs. 3-6 (habitus and detail of tentacle and tentacular arrangement), pl. 11 figs. 3-4, pl. 12 fig. 3 (anatomical and histological details); Verrill, 1900: 555 (pro parte;

⁶⁾ If a future world-wide revision of the Discosomatidae might after all prove this character to be of generic importance, the genus *Discosoma* sensu stricto will have to be re-established. At the present moment, however, considering the current conceptions of *Discosoma* and the other genera discussed above (here synonymised; oldest name: *Rhodactis* Milne Edwards & Haime, 1851), which are based on irrelevant, often very variable characters (cf. Carlgren 1949: 14-16) it would be quite meaningless and even confusing to maintain *Discosoma* and *Rhodactis* as separate genera.

- Bermuda), pl. 48 fig. 5 (habitus); Verrill, 1907: 276-280 (pro parte; diagnosis, colour; asexual reproduction by fission and fragmentation of basal expansions); Carlgren, 1900: 79, 81 (name only); Stephenson, 1922: 306 (name only); Watzl, 1922: 11-13 (diagnosis, cnidom, differences with *Rhodactis carlgreni* n. sp.); Weill, 1934: 600-604 (morphology, cnidom; *Actinotryx macropapillata* Weill, 1929, is a synonym) figs. 401-408 (habitus, details of morphology, nematocysts).
- Rhodactis sanctithomae* — McMurrich, 1889: 42-46 (morphology, anatomy, histology, colour; larviparous; New Providence, Bahamas), pl. 1 fig. 9 (habitus); pl. 4 figs. 2, 3 (anatomical details); Duerden, 1898 (scattered information); Duerden, 1898a: 102 (name only); Duerden, 1898b: 451-452 (morphology, colour); Carlgren, 1949: 16 (name only); Corrêa, 1964: 29-32 (morphology, anatomy, cnidom; Piscadera Bay, Curaçao) figs. 10, 11 (lateral and oral view), Riemann-Zürneck, 1972: 74 (cnidom; Santa Marta, Colombia).
- Actinotryx macropapillata* Weill, 1929: 891-892 (location and size of discal tentacles; Bermuda).
- Orimia torpida* Duchassaing & Michelotti, 1860: 328-329 (52-53) (short description, colour; St. Thomas; on stony coral; no type designation), pl. 7 fig. 12 (habitus); Duchassaing & Michelotti, 1864: 134 (40) emphasis on exactness of pl. 7 fig. 12 in afore-cited publication; Andres, 1883: 572 (repetition of data of Duchassaing & Michelotti); Carlgren, 1900: 79-80 (a single type present in the Zoological Museum of Turin); McMurrich, 1905: 12 (notes on morphology of distal tentacles); Stephenson, 1921: 511, 544 (name); Stephenson, 1922: 304 (urn-shaped tubular tentacles are probably collapsed vesicle-like tentacles); Carlgren, 1934: 2-5 (morphology, anatomy; urn-shaped tentacles are regenerated artefacts), fig. 1 (part of oral disc), figs. 2, 3 (anatomical details of tentacles, body wall and sphincter); Carlgren, 1949: 15 (name).

Material examined:

- Antigua. — USNM sine num. (Freeman's Bay, English Harbour, Smithsonian Bredin Expedition Sta. 194, 12.IV.1959, 12 specimens).
- Barbados. — RMNH 12016 (St. James, in front of Bellairs Research Institute on outer bank, depth 10 to 15 m, 1973, several specimens; leg. F. Sander).
- Bermuda. — RMNH 12014 (Hamilton, east side of Coney Island, depth 2 m, 1.X.1973, 5 specimens; leg. J.C.H.); YPM 8436 (1898, 4 specimens; leg. A.E.V.), 9820 (1898, 7 specimens; leg. A.E.V.).
- Bonaire. — Observations in situ, IV.1972.
- British Honduras (Belize). — Carrie Bow Cay: USNM 56548 (IV.1974; leg. K.S.), sine num. (Sand trough on outer fore reef, depth 50 to 60 ft., 25.III.1978, 1 specimen with vesicular discal tentacles lacking appendages; leg. R.J.L.), sine num. (Fore reef slope, depth 70 to 80 ft., 27.III.1978, 1 specimen with vesicular discal tentacles; leg. R.J.L.).
- Colombia. — Santa Marta, Punta de Betin. Observations in situ, III.1972.
- Curaçao, South coast. — RMNH 11468 (Piscadera Bay, among *Madracis spec.*, depth 5 m, 20.VIII.1972, 2 specimens; leg. P.C.), 11469 (Jan Thiel; among *Madracis spec.*, depth 5 m, 19.VIII.1973, 1 specimen; leg. R.M.H.), 12013 (Jan Thiel, depth 3 to 5 m, 8.VII.1973, 1 specimen; leg. R.M.H.), 12025 (Reef between Piscadera Bay and Blauw Bay, on rock, shadow, depth 16 m, 14.VI.1977, 3 specimens; leg. R. P. M. Bak), 12026 (Jan Thiel, depth 6 to 8 m, on dead coral, 8.VII.1973, 1 specimen with vesicular discal tentacles lacking appendages; leg. R.M.H.), USNM 51641 (Piscadera Bay, depth 1.5 m, 30.XII.1961-2.I.1962; leg. J. Randall).
- Florida. — RMNH 12816 (Hawk's Channel, off Marathon, depth 25 to 30 ft., VIII.1976, 1 specimen with vesicular discal tentacles lacking appendages; leg. R. W. Seaton).
- Jamaica. — USNM 19042 (Port Royal Cay, 3 specimens), 51641 (Port Royal Cay, on reef flat, 1.XII.1959, 10 specimens).

Panama Canal Zone. — RMNH 12011 (Galeta Island, coral rubble, 5.VIII.1973, few specimens; leg. D. L. Meyer).

Puerto Rico. — RMNH 12027 (Parquera, coral rubble flat in shallow water with growth of *Thalassia*, coral and *Millepora* surrounding mangrove bushes, depth 1 m, 11.IX.1973, 10 specimens; leg. C.A. & J.C.H.); USNM 51047 (Parquera, Lajas, on coral, depth 1 m, 13.XI.1957, 2 specimens; leg. J. Rivera Lopez), 53260 (Parquera, Cayo Enrique, on dead coral, depth 1 m, 18.VIII.1964, 22 specimens; leg. C. E. Cutress), YPM 7655 (Off Parquera, Head of Drunken Horse, depth 1 m, 29.VII.1962, 4 specimens; leg. Elba Más).

Saba. — RMNH 11470 (Cove Bay, on *Porites spec.*, depth 1 to 6 m, 3.X.1972, several specimens; leg. J.C.H.).

Saba Bank. — RMNH 12023 (17°27' N. 63°21' W., sand, stones and algae, depth 22 m, CICAR 34/35 sta. 142, 14.VI.1972, 1 specimen).

St. Eustatius. — RMNH 12022 (Gallows Bay, 30.IX.1972, 1 specimen; leg. J.C.H.).

St. Martin. — RMNH 12012 (Bay of Marigot, coral reef with sand and turtle grass, depth 0 to 15 m, CICAR 34/35 sta., 122, 11.VI.1972, several specimens on tunicates); 12015 (Great Bay, Point Blanc, depth 0 to 5 m, between *Caulerpa*, 27.IX.1972, several specimens, including a clone with very reduced tentacles; leg. J.C.H.).

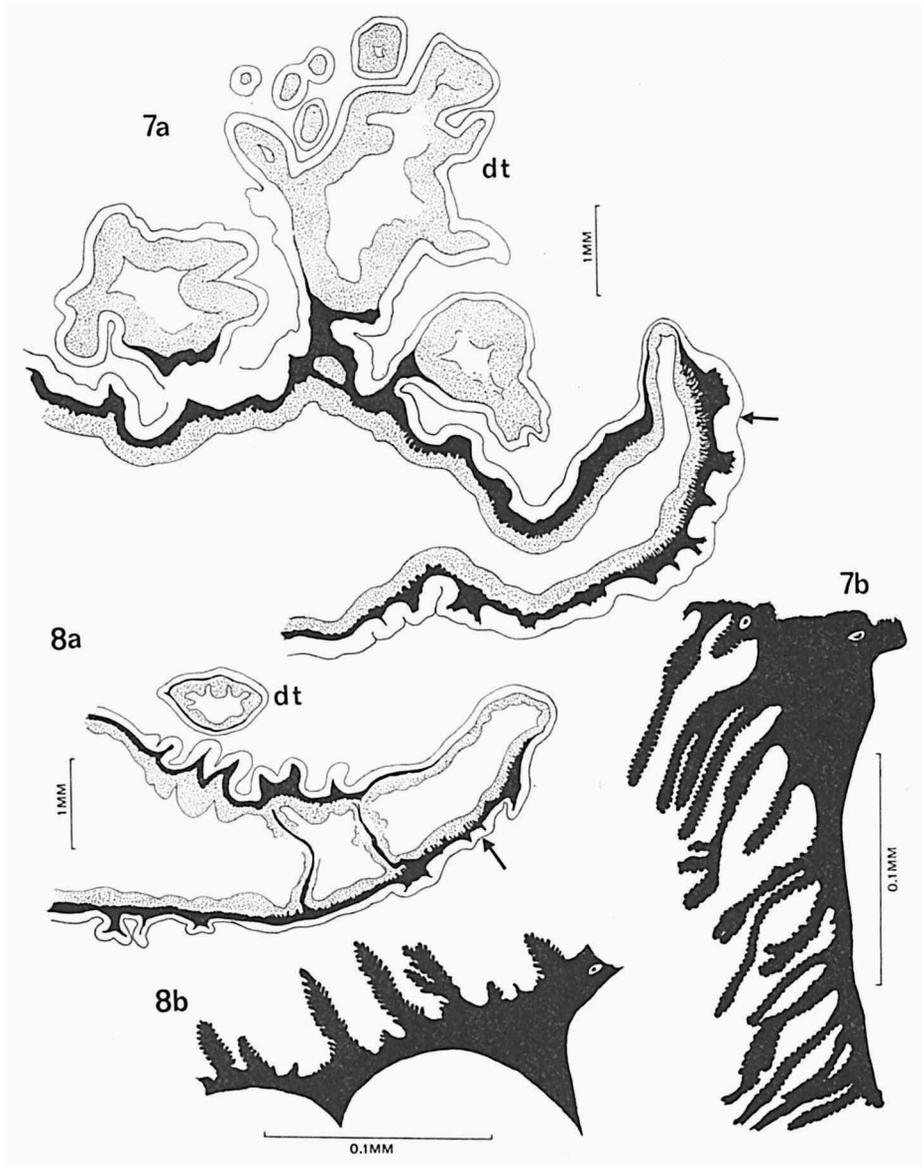
Morphology (pls. 11, 13, fig. 1, 2). — Body (also when preserved in formalin) smooth and extremely lubricous. Consistency as a rule soft, rarely rigid (RMNH 12015).

Base irregular in outline, spreading, and able to secrete a chitinous membrane; diameter up to ca. 4.5 cm, basal expansions not taken into account.

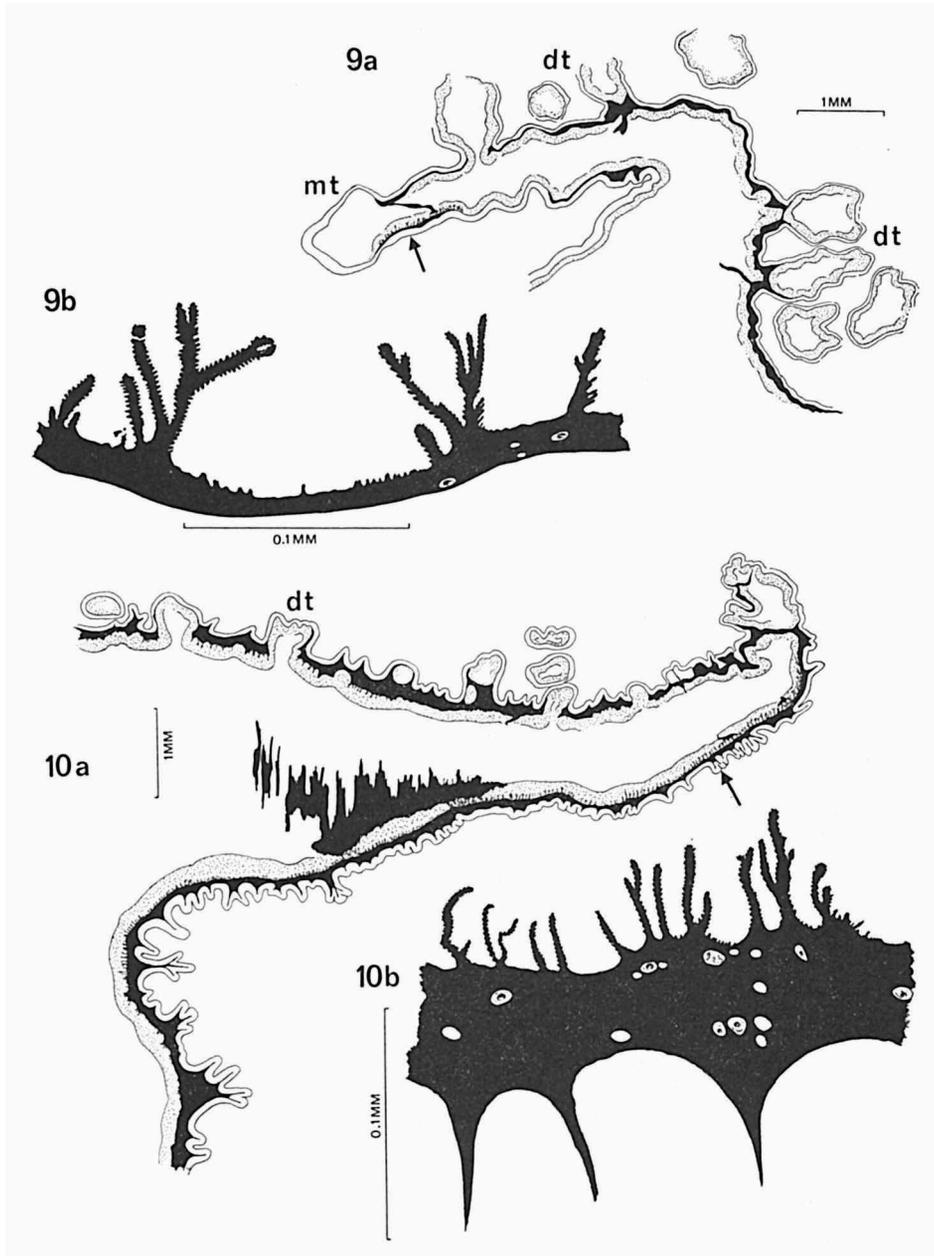
Column in fully expanded state wide calyciformous, with the marginal region often folded downwards and overhanging the base. The column frequently shows a more or less distinct constriction about halfway between the base and the margin. Mesenterial insertions are often visible from the outside.

Oral disc circular to elliptical in outline, up to about 6 cm in diameter, and exceeding the base. Three more or less distinct zones can be distinguished: 1. a narrow, delicate, naked, peripheral zone; 2. a subsequent zone, densely covered with discal tentacles, and 3. a central area, including the often distinctly raised hypostome, with relatively few, reduced tentacles.

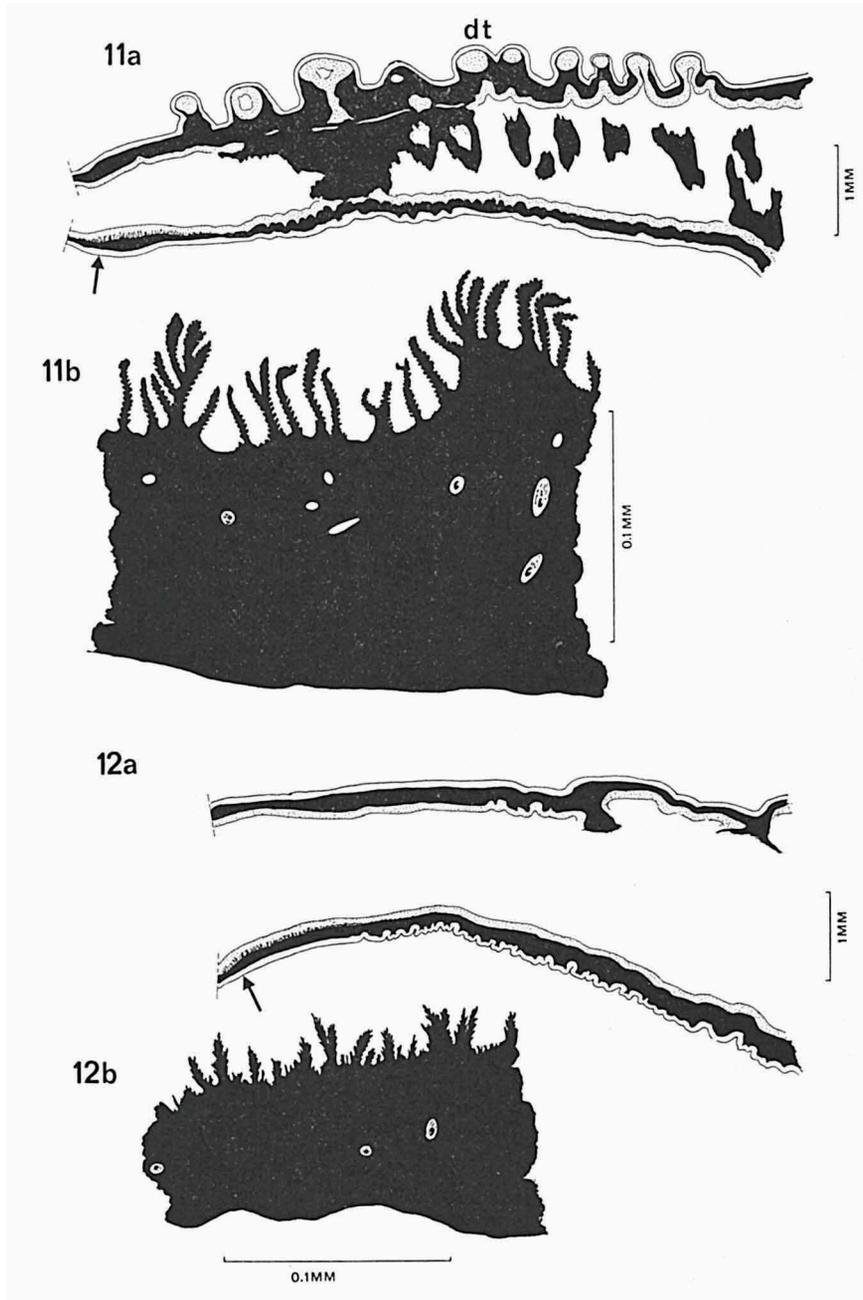
The naked, peripheral zone is usually bordered by a large number of small, finger-shaped or acute marginal tentacles, often provided with distinct, soft acrospheres. These tentacles correspond to the endo- and exocoels and, in conformity with these, are arranged in cycles of different order. Relatively large tentacles as a rule correspond with the older endocoels, smaller tentacles with the younger endocoels and with the exocoels, but irregularities occur frequently. The acrospheres of part of the marginal tentacles are often swollen to such an extent that no proper distinction can be made between tentacular stem and acrosphere. Occasionally a number of adjacent tentacles have completely lost their individual character and have become confluent into a distinctly swollen rim (e.g. RMNH 11468, 11469; cf. pl. 13 fig. 1).



Figs. 7-8. *Discosoma sanctithomae*. Anatomical variation; longitudinal sections through the marginal region of two specimens (7a, 8a) (both RMNH 12015, St. Martin), with enlarged details of their sphincters (see arrows) (7b, 8b). Mesogloea black.
 Explanation of the symbols : dt = Discal tentacles.

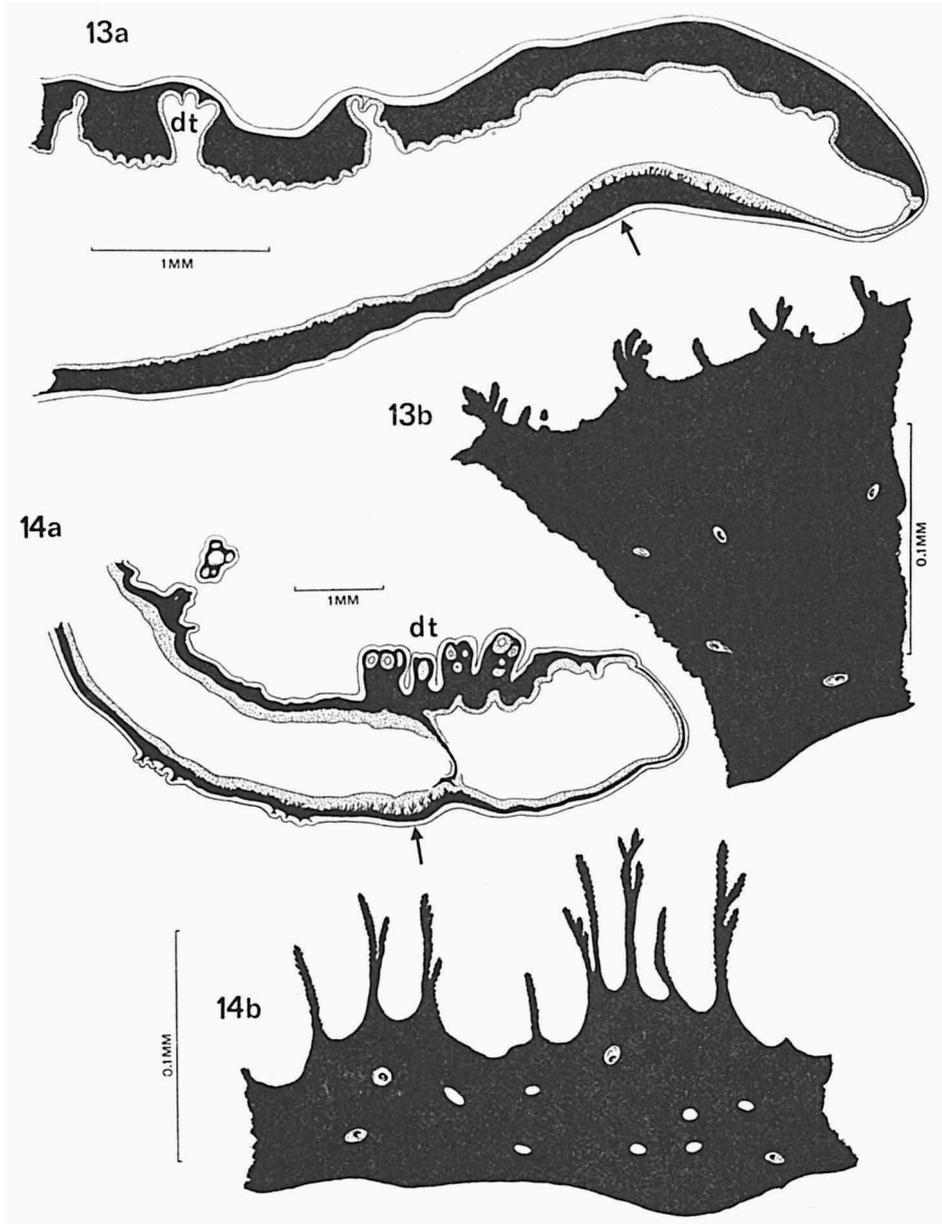


Figs. 9-12. *Discosoma carlgreni*. Anatomical variation; longitudinal sections through the marginal region of four specimens (9a-12a) from different localities, with enlarged details of their sphincters (see arrows) (9b-12b). Mesogloea black. 9, RMNH 11473



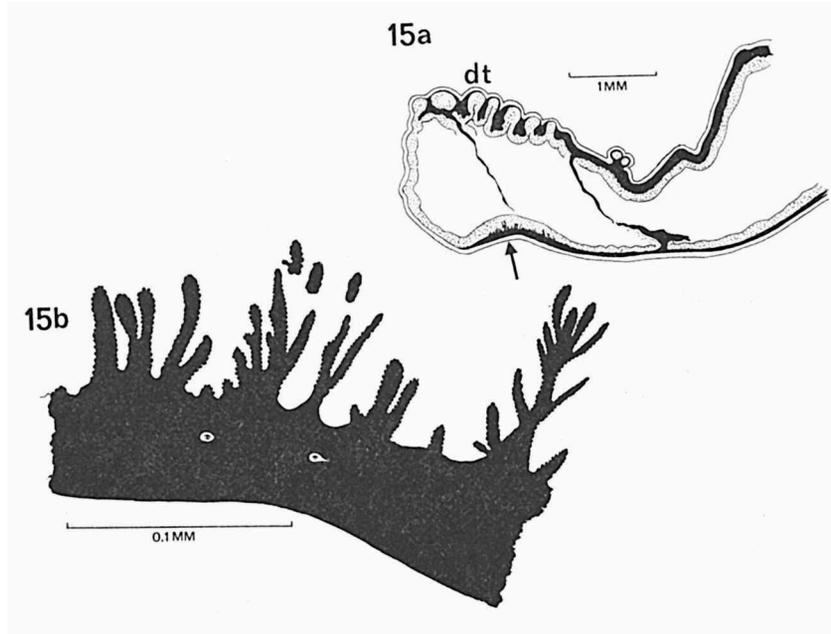
(Bermuda); 10, USNM sn. (Bermuda); 11, ZML, Type nr. 182 (Andros, Bahamas; type specimen); 12, USNM 53273 (Puerto Rico). Mesogloea black.

Explanation of the symbols: dt = Discal tentacles; mt = Marginal tentacle.



Figs. 13-15. *Discosoma neglecta*. Anatomical variation; longitudinal sections through the marginal region of three specimens (13a-15a) from different localities, with enlarged details of their sphincters (see arrows) (13b-15b). Mesogloea black. 13, RMNH 12006 (Curaçao); 14, USNM 51674 (St. John, Virgin Islands); 15, USNM 12505 (Jamaica).

Explanation of the symbols: dt = Discal tentacles.



In three aberrant specimens from St. Martin (RMNH 12015) the discal tentacles are present as reduced, rigid protuberances (cf. pl. 13 fig. 2), but they normally are vesicular and provided with 5 to 20 acute, finger-shaped or filiform appendages. Occasionally such appendages are virtually absent (cf. *Orinia torpida*, pp. 51, 52). The arrangement of the discal tentacles is in radial rows, although this is not always obvious. The tentacle rows corresponding with the older endocoels as a rule bear 3 to 7 tentacles, other endocoels only 0 to 2, whereas the exocoels apparently are devoid of discal tentacles. The total number of discal tentacles in well developed specimens does not exceed 300; often, the number is considerably less, especially in small specimens.

Pattern and colour. — Colour of the column light yellowish- to purplish brown, often greenish towards the margin and pale towards the base, the basal expansions included. The oral disc and the discal tentacles are usually uniformly brownish or greenish, but the latter may also be whitish, bluish or beautifully iridescent. Stomodaeal ridges inside the mouth are white.

Anatomy (figs. 7-15). — The anatomy of *Discosoma sanctithomae* and of the other two Caribbean species of *Discosoma* will here be discussed simultaneously. Due to the flat shape of the specimens I had little success in making proper transverse sections so that I have no more than an impression of the

mesenterial arrangement. In all three species the number of mesentery-pairs varies between 100 and 150; about 1/4 of that number being perfect, about 1/4 being rather well developed though imperfect, and the rest being much smaller and imperfect. These three categories may regularly alternate, but irregularities occur very commonly in relation to asexual reproduction. Directives are present (at least one or two pairs) or absent.

The mesogloea of each species invariably contains scattered "inclusive" cells. The mesogloea of at least *Discosoma carlgreni* and *D. neglecta* varies greatly in thickness in different specimens.

Longitudinal sections to study the sphincter were made of two specimens of *Discosoma sanctithomae*, of four specimens of *D. carlgreni* and of three specimens of *D. neglecta*. In all three species the sphincter is diffuse and very weak, situated close to the margin. The mesogloal muscle processes supporting the muscular tissue always are more or less dendritic. The state of development of these processes appears to be so variable that no diagnostic value at the specific level can be attributed to it (cf. figs. 7-15).

Cnidom (table 5, 6; pls. 5, 6). — The results of the study of the cnidom of the three Caribbean species of *Discosoma*, like their anatomy, are here discussed simultaneously.

It appeared difficult to get an exact impression of the nematocysts occurring in the marginal tentacles (or marginal lobes) and in the discal tentacles. Several of the smaller cnidae apparently are rare, irregularly distributed, and besides (especially in preserved material) easily overlooked. It is difficult to decide, therefore, whether such capsules are really absent, when not observed. On the other hand, the accidental presence of a number of such capsules in a squash preparation may give the incorrect impression, that they form a significant component of the cnidom.

Small penicilli D (II.c), although easily overlooked, were found in the marginal tentacles (respectively lobes) of the majority of specimens of all three species. A second, larger size-class of penicilli D (II.c2) was noticed in most specimens of *Discosoma sanctithomae*, though in two specimens of this species (RMNH 12012, 12014) the presence of one size-class only could be ascertained, approximately intermediate in size (ca. 24×8 microns). Penicilli D (II.c2) proved to be practically absent in the marginal lobes of *Discosoma carlgreni* and *D. neglecta*; a single or a very few of these nematocysts were noticed in some specimens.

Small elliptical penicilli E (I.c) occur in the column of all three species; in addition, these cnidae were found in sparse numbers in the (ectoderm of the) discal tentacles of *Discosoma neglecta*.

TABLE 5

Discosoma sanctithomae, *D. carlgreni* and *D. neglecta*. Survey of the cnidom. A = *Discosoma sanctithomae*, Curaçao (Unfortunately, this specimen was not preserved after being studied); B = *Discosoma carlgreni*, RMNH 11473, Bermuda; C = *Discosoma neglecta*, RMNH 12007, Curaçao.

Organ	Species	Average and range of length and width of nematocyst capsules in microns		Number of capsules measured	Abundance
<u>Nematocyst type</u>					
<u>I. Column</u>					
a. Spirulae	A	17.1(13.9 - 19.8)	x 6.3(5.9 - 6.6)	20	rather common
	B	16.4(13.2 - 18.5)	x 6 (4.6 - 7.3)	10	rare
	C	14.4(12.5 - 16.5)	x 5.3(5 - 5.9)	20	uncommon
b. Penicilli D	A	30.6(23.8 - 35.6)	x 6.9(5.3 - 8.6)	20	rather common
	B	17.1(14.5 - 19.8)	x 5.7(5.3 - 6.6)	10	rare
	C	12.6(10.6 - 15.2)	x 4.1(3.6 - 5.3)	20	uncommon
c. Penicilli E	A	27.9(26.3 - 30.7)	x 9.3(8.8 - 10.2)	8	sporadic
	B	19.9(13.2 - 23.1)	x 6 (5 - 6.6)	10	rare
	C	17.7(15.2 - 19.8)	x 5 (4 - 5.9)	20	uncommon
<u>II. Marginal tentacles/lobes</u>					
a. Homotrachs	A	45.6(21.1 - 66)	x 6.7(4 - 7.9)	20	very common
	B	33.3(23.1 - 52.8)	x 7.2(4.6 - 9.2)	20	variable
	C	33.3(26.4 - 40.9)	x 7.4(6.3 - 8.6)	20	variable
b. Spirulae	A	Not observed			
	B	16 (13.9 - 17.8)	x 6.3(5.9 - 6.6)	20	uncommon
	C	14.6(12.5 - 16.5)	x 5.8(5 - 6.6)	10	uncommon
c. Penicilli D	A,1	16.4(15.2 - 17.2)	x ca. 5	10	rare
	2	30 (27.7 - 34.3)	x 6.9(5.9 - 8.6)	20	uncommon
	B	14.6(13.2 - 19.1)	x 5 (4 - 6.6)	10	uncommon
d. Penicilli E	C	14 (11.9 - 15.8)	x 4.8(4 - 5.9)	10	uncommon
	A,1	34.3(31.7 - 37.6)	x 12.6(10.6 - 14.5)	20	uncommon
	2	75 (59.4 - 87.1)	x 29.4(23.1 - 37)	20	rather common
B,1	1	37.1(34.3 - 41)	x 15.6(14.5 - 17.2)	10	rather common
	2	65.1(58.1 - 79.2)	x 32 (26.4 - 37)	10	rather common
	C,1	39.6(36.3 - 42.2)	x 14.5(12.5 - 15.8)	20	common
	2	90.2(55.4 - 128.7)	x 42.4(27.7 - 56.1)	20	rather common
	<u>III. Discal tentacles</u>				
a. Spirulae	A	Not observed			
	B	15 (14.6 - 17.5)	x 5.5(5.1 - 5.8)	7	sporadic
	C	12.9(11.2 - 14.5)	x 5.1(4.6 - 5.9)	20	uncommon
b. Penicilli D	A,1	16.2(14.6 - 17.5)	x 4.5(4.4 - 5.1)	10	sporadic
	2	28.8(26.4 - 31.7)	x 7.6(6.6 - 9.2)	10	uncommon
	B,1	ca. 15	x 5	3	sporadic
	2	27.4(24.8 - 33.6)	x 8.8(7.3 - 10.2)	5	sporadic
	C,1	12.4(10.6 - 15.8)	x 3.6(3 - 4.6)	20	uncommon
c. Penicilli E	2	25.7(23.8 - 28.4)	x 6.9(5.3 - 7.9)	10	rare
	A,1	35.1(31.7 - 37)	x 14.3(13.2 - 15.8)	20	common
	2	78.7(72.6 - 89.1)	x 34.4(28.4 - 38.3)	10	rather common
	B,1	38.4(36.3 - 39.6)	x 14.8(13.2 - 17.2)	20	common
	2	69.5(62 - 85.8)	x 34 (26.4 - 42.2)	20	rather common
C,1	1	37.8(35.6 - 40.9)	x 13.3(11.9 - 16.5)	20	uncommon
	2	65.3(60.7 - 75.9)	x 28.8(26.4 - 31)	10	rare
	3	16.5(14.5 - 17.8)	x 4.3(4 - 5.3)	20	uncommon
<u>IV. Stomodaeum</u>					
a. Penicilli E	A	64.1(59.4 - 72.6)	x 19.8(18.5 - 23.1)	20	common
	B	60.5(51.5 - 64.7)	x 20.6(17.2 - 23.1)	20	rather common
	C	57 (51.5 - 62.7)	x 17.9(15.8 - 20.5)	20	rather common

continuing table 5

V. Filaments

a. Penicilli D	A,1	16.4 (14.5 - 19.1)	x	3.7 (3.3 - 5)	20	rather common
	2	36.3 (33 - 39.6)	x	7.1 (6.6 - 8.9)	20	common
	B,1	16.9 (14.5 - 19.8)	x	4 (3.3 - 4.3)	10	rare
		28.2 (25.1 - 33)	x	7.7 (6.6 - 9.2)	20	rather common
	C,1	15.8 (13.2 - 17.2)	x	3.5 (3.3 - 4)	20	rather common
		28 (25.1 - 31)	x	7.3 (6.6 - 8.3)	20	rather common
b. Penicilli E	A,1	38.3 (36.5 - 40.9)	x	14.3 (12.4 - 16.1)	20	rare
		170.9 (156.8 - 214.5)	x	62.8 (52.8 - 74.3)	20	common
	B,1	39.3 (35 - 42.3)	x	13.8 (13.1 - 14.6)	20	rare
		157.8 (145.2 - 178.2)	x	60 (56.1 - 67.3)	20	common
	C,1	36.6 (34.3 - 38.9)	x	11.9 (11.2 - 13.2)	20	rare
		193.1 (161.7 - 206.3)	x	63 (59.4 - 66)	20	common

Spirulae of the type characteristic of the column (I.a) were also found scattered over the discal tentacles of *Discosoma carlgreni* and *D. neglecta* (III.a), but not in those of *D. sanctithomae*. In the latter species I occasionally noticed the presence of another, smaller type of spirulae.

Apart from the minor, from a practical point of view unimportant, differences mentioned above, the table suggests diagnostic differences between the three species in the size of certain common and/or conspicuous cnidae, notably: the columnar penicilli D (I.b), the homotrachs (II.a) of the marginal tentacles (or lobes) and the filamental penicilli D (V.a2) and penicilli E (V.b2).

The homotrachs of the marginal tentacles (lobes) not only vary considerably in size, but also in abundance. They are probably homologous with spirulae of the columnar type (I.a). Apparent intermediates between the two types, with a shaft of variable length, are frequently to be observed. The smaller these capsules are, the more they resemble spirulae; the larger they are, the more they conform to the definition of homotrachs. This variable development of the cnidoblast, as well as the highly variable abundance and size of the homotrachs, may well be ecologically determined and linked with inter- and/or intra-specific aggressive behaviour in spatial competition (den Hartog, 1977a). Hence, the differences in abundance and size between the homotrachs of *Discosoma sanctithomae* and the two other species, as presented in the table, in my view are individual variations without diagnostic value.

An impression of the variation in size of the other above-mentioned types of nematocysts in the three species here discussed, can be derived from table 6. From this table it appears that the columnar and filamental penicilli D (I.b; V.a2) of *Discosoma sanctithomae* are distinctly larger than in *D. carlgreni* and *D. neglecta*.

The size of filamental penicilli E (V.b2) of the three species shows about the same overall average and range, and hence is of no diagnostic value.

In conclusion it can be stated that the cnidom of the three species is of very little diagnostic value on the species level.

McMurrich (1889: 44) as well as Duerden (1900: 151) made mention of the total absence of nematocysts in the ectoderm of *Discosoma sanctithomae*. Small ectodermal nematocysts, however, occur in all species of *Discosoma*, though always sparingly. All columnar and tentacular nematocysts listed in table 4 and 5 are ectodermal, with the exception of the large penicilli E of the marginal and discal tentacles (II.d1, 2; III.c1, 2), which are endodermal.

Systematics, nomenclature and miscellaneous notes. — 1. *Orinia torpida* was described from St. Thomas by Duchassaing & Michelotti (1860: 328-329). Its most peculiar feature was presented by the shape of the discal tentacles, which were described as tubular openings ("orifices tubuleux"). In the Duchassaing & Michelotti collection present in the Zoological Museum of Turin, Carlgren (1900: 80) found a single specimen fitting the description of *Orinia torpida*, and labelled as such. As nothing in the original description proves or indicates that the species was based on more than one specimen, this specimen should be regarded as the holotype. Carlgren recognized the specimen as a discosomatid and noticed its affinity with *Discosoma sanctithomae* (presence of distinct discal and marginal tentacles, separated by a distinct, naked zone). McMurrich (1905: 12) re-examined the specimen and noticed that not all the discal tentacles had a terminal orifice. Stephenson (1922: 304) thereupon suggested that the urn-shaped tentacles probably just were collapsed vesicular tentacles. This was subsequently denied by Carlgren (1934: 2-5), who, on the basis of a study of microscopical sections, noticed that the margin of the urns was covered with epithelium. He concluded the urns to be artefacts, regenerated remains of tentacles, of which the upper part had been torn of or bitten of by some animal, probably a fish. Although being convinced of the freak nature of these tentacles, Carlgren nevertheless stated that *Orinia* differs from the closely allied genera *Discosoma* and *Rhodactis* (synonymised in the present paper) by the shape and the arrangement of these tentacles. I do not agree with this conclusion. Although I have seen only a small fragment of the type-specimen of *Orinia torpida* (NRS typ. nr. 71), I am convinced that this specimen represented nothing but an aberrant specimen of *Discosoma sanctithomae*. The type-specimen itself has probably become lost; it is no longer present in the Duchassaing & Michelotti collection in the Museum in Turin.

The presence of aberrant tentacles in "*Orina*" is not unique. This phe-

nomenon was also observed in various degrees in several specimens of *Discosoma sanctithomae* during the present study. In particular specimens with vesicular tentacles, without or practically without appendages, are not uncommon. I have seen such specimens from: Florida (RMNH 12816), Belize (USNM sine num., 2 lots) and Curaçao (RMNH 12026). At the time of my stay in Curaçao, they were rather common in Jan Thiel Bay, where I repeatedly observed them in situ. Zeiller (1974: 28) gives a beautiful colour photograph of such a specimen from Florida, understandably identified as *Orinia torpida*.

TABLE 6

Discosoma sanctithomae, *D. carlgreni* and *D. neglecta*. Variation in size (in microns) of columnar penicilli D (I.b), filamental penicilli D (V. a2) and filamental penicilli E (V. b2) in specimens from various localities. 10 Capsules of each kind of nematocyst were measured of each specimen. * = Atypical specimen (cf. "Material examined" and the discussion on pp. 51-53).

Species		Columnar penicilli D (I.b)		
Museum number	size	Geographic origin	Average and range of length and width	
<i>Discosoma sanctithomae</i>				
RMNH Coel. 12014	small	Bermuda	27.8 (24 - 30.8) x 9.2 (7.5 - 10.5)	
11468	large	Curacao	34.8 (24 - 39) x 8.2 (6 - 9.8)	
12026*	medium	Curacao	35.4 (31.5 - 40.5) x 8.9 (7.5 - 10.5)	
12011	medium	Panama	29 (24 - 33) x 8.2 (7.5 - 9.8)	
12022	medium	St. Eustatius	25.7 (22.5 - 30) x 7.4 (6 - 8.3)	
12012	large	St. Martin	31.5 (28.5 - 34.5) x 8.2 (7.5 - 9.8)	
12015*	medium	St. Martin	31.4 (25.5 - 35.3) x 7.7 (6 - 9.8)	
Overall average and range:			30.8 (22.5 - 40.5) x 8.3 (6 - 10.5)	
<i>Discosoma carlgreni</i>				
RMNH Coel. 11473	medium	Bermuda	20.6 (18 - 26.3) x 7 (6 - 7.5)	
ZML Type nr 182	small	Bahamas (Andros)	14.7 (13.5 - 16.5) x 5.6 (5.3 - 6)	
RMNH Coel. 12010	small	Puerto Rico	16.7 (15 - 18) x 6 (5.3 - 8)	
USNM 53273*	large	Puerto Rico	16.4 (14.3 - 18) x 5.6 (5.3 - 6.2)	
Overall average and range:			17.1 (13.5 - 26.6) x 6.1 (5.3 - 8)	
<i>Discosoma neglecta</i>				
ZML s.n.	small	Bahamas (Andros)	13.6 (12.4 - 16.5) x 5.7 (4.7 - 6.2)	
RMNH Coel. 12006	medium	Curacao	16.7 (14.3 - 19.5) x 6.2 (5.3 - 6.8)	
12007	medium	Curacao	15.2 (13.5 - 17.3) x 5.9 (5.3 - 6)	
USNM 57505	small	Jamaica	13 x 5 (only one capsule measured)	
RMNH Coel. 12009	small	Saba	12.5 (11.2 - 13.6) x 5.5 (5 - 6.2)	
Overall average and range:			14.5 (11.2 - 19.5) x 5.8 (4.7 - 6.5)	

The regular presence of aberrant discal tentacles in *Discosoma sanctithomae* might be correlated with interactions with other (reef) organisms, in conformity with the marginal tentacles (cf. den Hartog, 1977a). Unlike the latter, however, aberrant discal tentacles do not show alterations in the composition of the cnidom.

The synonymy of *Actinotryx sanctithomae* and *Orinia torpida*, both originally described in the same paper by Duchassaing & Michelotti (1860), implies that one of these names formally has to be chosen as the valid name. It needs no explication that the well known *Actinotryx sanctithomae* is maintained as such.

2. For a discussion of *Actinotryx macropapillata* Weill, 1929, I refer to p. 60.

3. The three Caribbean species of Discosomatidae, *Discosoma (Actinotryx) sanctithomae*, *D. (Rhodactis) carlgreni* and *D. (Paradiscosoma) neglecta*, differ so distinctly in a number of features, that their specific status can hardly be doubted. The three species do, however, illustrate that the difference between the genera *Actinotryx*, *Rhodactis* and *Paradiscosoma* is not very obvious. A number of supposed generic characters (the presence

Filamental penicilli D (V.a2)	Filamental penicilli E (V.b2)
Average and range of length and width	Average and range of length and width
33.6 (30 - 37.5) x 7.8 (7.5 - 9)	182.9 (166.5 - 205.5) x 70 (64.5 - 78)
39.2 (36 - 43.5) x 7.8 (7.5 - 8.3)	197.4 (166.5 - 187.5) x 68.3 (63 - 72)
40.4 (36 - 46.5) x 8.9 (7.5 - 9.8)	217.7 (202.5 - 232.5) x 79.4 (73.5 - 82.5)
40.4 (33 - 45) x 9.1 (7.5 - 10.5)	185.7 (171 - 201) x 67.4 (57 - 72)
33.2 (31.5 - 36) x 7.8 (7.5 - 8.3)	175 (159 - 190.5) x 61.1 (54 - 75)
38.4 (34.5 - 40.5) x 8.3 (6.8 - 9.8)	184.1 (171 - 195) x 66.2 (63 - 69)
38.4 (33 - 46.5) x 8.8 (7.5 - 10.5)	175.8 (168 - 192) x 61 (55.5 - 66)
37.7 (30 - 46.5) x 8.4 (6.8 - 10.5)	188.4 (159 - 232.5) x 67.6 (54 - 82.5)
31.6 (28.5 - 34.5) x 8.3 (7.5 - 9)	192.9 (169.5 - 220.5) x 65.6 (57 - 70.5)
27 (25.8 - 28.4) x 8 (7.2 - 8.8)	159.1 (138.6 - 173.3) x 68 (63 - 72.5)
28.8 (25.5 - 34.5) x 7.9 (6.8 - 9.8)	167.4 (150 - 187.5) x 56.3 (51 - 61.5)
31.3 (28.5 - 36) x 7.7 (7.5 - 8.3)	183 (156 - 204) x 63.6 (58.5 - 67.5)
29.7 (25.5 - 36) x 8 (6.8 - 9.8)	175.6 (138.6 - 220.5) x 63.4 (51 - 72.5)
29.9 (28.5 - 34.5) x 8.1 (7.5 - 8.3)	165.8 (157.5 - 180) x 67.7 (60 - 76.5)
29.5 (27 - 35.3) x 7.7 (7.5 - 8.3)	206.1 (195 - 225) x 79.7 (70.5 - 87)
28.7 (27 - 30) x 7.7 (6.8 - 8.3)	181.3 (159 - 195) x 75.3 (67.5 - 87)
27.5 (25.8 - 30.2) x 8.3 (7.6 - 9.5)	166.6 (151.2 - 179.6) x 63.9 (59.9 - 66.2)
27.6 (25.8 - 28.4) x 8 (6.9 - 9.5)	177.7 (167 - 189) x 75.2 (66.2 - 78.8)
28.6 (25.8 - 35.3) x 8 (6.8 - 9.5)	179.5 (151.2 - 225) x 72.4 (59.9 - 87)

or absence of marginal tentacles or lobes, the presence or absence of a naked marginal zone and the complexity and development of the discal tentacles) appear to be rather variable as shown by the present study.

Actinotryx sanctithomae and *Paradiscosoma neglecta* as a rule are so entirely different in appearance that at first sight it would not occur to anybody to classify them in the same genus. *Rhodactis carlgreni*, however, shows characters intermediate between the two species just mentioned, as is already indicated in the literature by the fact that Watzl stated the species to be more allied to *Actinotryx sanctithomae* than to any other West-Indian "actinian", while Carlgren (1947: 95) transferred it to *Paradiscosoma*.

The body of *Rhodactis carlgreni* is usually rigid, approaching the condition found in *Paradiscosoma neglecta*, while the tentacles are often distinctly branched and reminescent of those of *Actinotryx sanctithomae* (cf. pl. 13 figs. 1, 3), although they may also be reduced to wart-like protuberances or be almost absent (cf. pl. 13 fig. 9). Distinct marginal tentacles, although less pronounced than in *Actinotryx sanctithomae* are occasionally present (cf. pl. 13 fig. 3), but most specimens examined were provided with short marginal lobes (cf. pl. 13 figs. 4, 6-8), a condition resembling that found in *Paradiscosoma neglecta* (cf. pl. 14). Occasionally the margin is almost smooth (cf. pl. 13 figs. 5, 9).

The body of *Actinotryx sanctithomae* usually is of soft texture, and as a rule bears well developed, branched discal tentacles and distinct marginal tentacles (cf. pl. 11, pl. 13 fig. 1). A clone of specimens from St. Martin (RMNH 12015), however, had reduced marginal tentacles, rudimentary, wart-like discal tentacles (cf. pl. 13 fig. 2), and a rather thick mesogloea giving the body a fairly firm consistency, as is more characteristic of the two other species here under discussion.

The general anatomy of the three taxa, although never studied in detail, is at least superficially similar. Their sphincters show a high degree of variability and are of no diagnostic value (cf. p. 48 and figs. 7-15)⁷). Their cnidoms also are practically similar (cf. pp. 48-51 and tables 5, 6).

On the basis of these data I conclude that it is not tenable to maintain the three taxa in different genera. Their fundamental similarity would rather indicate conspecificity and it did occur to me that *Discosoma carlgreni* might be a hybrid of *D. sanctithomae* and *D. neglecta*. The latter two species roughly

⁷ In this context I may refer to a figure by Carlgren (1943: fig. 3), showing a cross-section of the sphincters of *Discosoma dawydoffi* Carlgren, *D. inochata* (Carlgren) and *D. indosinensis* (Carlgren). Bearing in mind the results of the present study, the diagnostic value of the differences between these three sphincters seems doubtful. A similar variation as shown in Carlgren's figure, might just as well occur within each of the three species.

occur all over the Caribbean, while *Discosoma carlgreni* has exclusively been reported from the north-eastern Caribbean (cf. figs. 16, 17, 18). This situation presents the picture of two taxa, which, in the greater part of their area of distribution, behave like separate species, and which interbreed in a limited area only. No actual proof of interbreeding, however, is available, and the fact that *Discosoma sanctithomae* and *D. carlgreni* both occur in isolated Bermuda, in the absence of *D. neglecta*, is definitely not in favour of a hybrid nature of *D. carlgreni*.

A purely phenotypical explanation of the three forms is also not acceptable. It is true, *Discosoma carlgreni* is morphologically an intermediate between *D. sanctithomae* and *D. neglecta*, but not to such an extent that the three forms virtually merge into each other. The difference in their geographical distribution, moreover, contradicts this possibility. Other evidence against the phenotypical nature of the three forms is provided by the fact that *Discosoma sanctithomae* and *D. carlgreni* have been collected side by side in exactly the same habitat, viz., a bed of coral rubble in very shallow water at Parquera, Puerto Rico.

In conclusion, on the basis of the available data, it seems justified to maintain the three forms as separate species.

Comparative growth experiments in the laboratory and/or in the field are necessary to determine to what extent the condition of various characters (e.g., the development of the mesogloea and of discal and marginal tentacles) is ecologically determined. As Discosomatidae are invariably associated with zooxanthellae, experiments under variable light conditions are in particular of importance. Discosomatidae probably offer favourable possibilities for such experiments. All species reproduce asexually and therefore usually occur in clones. Hence experiments in principle can always be performed with genetically identical stocks, so that differences observed in such experiments without restriction can be attributed to environmental conditions.

Apart from abiotic factors it seems obvious that biotic factors also affect morphology. The development of e.g. the marginal tentacles of *Discosoma sanctithomae* and *D. carlgreni* apparently is affected by the presence of other coelenterates in the immediate vicinity and correlated with inter- and intra-specific spatial competition (cf. pl. 11; den Hartog, 1977a: 464-465).

Finally, the possibility should be investigated, whether polyploidy is involved in the variability of Discosomatidae, and whether the difficulties in generic and specific delimitation can be credited to this phenomenon.

Biological notes. — *Discosoma sanctithomae* is a typical reef species occurring in shallow water on and around coral reefs, under variable light

conditions (in bright, direct sunlight or in shadowy niches, but never in truly light-protected places). The specimens examined during the present study were all collected between 1 and 22 meter depth.

The species frequently reproduces asexually, often by basal expansions which develop into new individuals, but, as I observed convincingly in Santa Marta (Colombia), also by longitudinal fission, which unlike in Actiniaria, may result in the origin of more than two individuals. Asexual reproduction in this species may give rise to huge clones, covering several m² of substratum (dead coral, rock). McMurrich (1889: 46), Duerden (1900: 154-155) and Verrill (1907: 279; apparently quoting the former authors) reported the species to be viviparous, but this was not confirmed during the present study.

Discosoma sanctithomae is invariably associated with zooxanthellae. The matter of spatial competition with other coelenterates has already been touched upon (cf. pp. 50, 55).

Distribution and occurrence (fig. 16). — A common Caribbean species occurring on and around coral reefs. The species also occurs in the Bahamas and Bermuda, but has not been reported from the Gulf of Mexico and from Brazil.

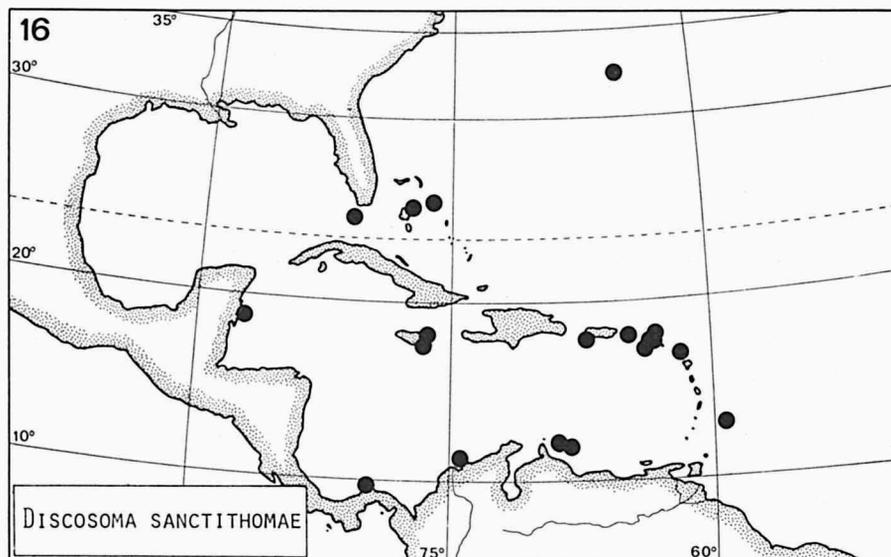


Fig. 16. *Discosoma sanctithomae*. Map showing the known geographical distribution of the species.

Discosoma carlgreni (Watzl, 1922) (tables 4, 5, 6, figs. 9-12, 17, pl. 13 figs. 3-9)

Actinotryx sanctithomae — Verrill, 1900: 555 (pro parte; shape, colour; Bermuda), fig. 5? (habitus); Verrill, 1907: 276-279 (pro parte; morphology, colour; vivipary and asexual reproduction by fission and basal expansions), fig. 121 (photograph of specimen), fig. 122? (habitus drawing), fig. 123a, b (diagram of arrangement of discal and marginal tentacles); Weill, 1929: 891 (name).

Rhodactis sanctithomae — den Hartog, 1977a: 464 (pro parte, viz., RMNH 11473).

Ricordea florida — Verrill, 1900: 556 (habits and colours very much like *Actinotryx sanctithomae* sensu Verrill, 1900: 555); Weill, 1934: 605-606 (morphology not in agreement with description by Verrill, 1907; cnidom; Bermuda) figs. 409-413 (habitus and various morphological details; nematocysts).

Rhodactis carlgreni Watzl, 1922: 13-17, 80-81 (morphology, anatomy, histology; cnidom; Mastic point, Andros, Bahamas, VII.1908, 3 specimens, coll. N. Rosén; no holotype designated — type-series in Z.M.L.).

Paradiscosoma carlgreni — Carlgren, 1947: 95 (morphological details, cnidom; not a *Rhodactis*); Carlgren, 1949: 15 (name only); Corrêa, 1964: 24, 28 (name in discussion concerning the genus *Paradiscosoma*).

?*Heteranthus floridus* — McMurrich, 1889: 47-50 (morphology, anatomy, colour; New Providence, Bahamas), pl. 1 fig. 10 (habitus), pl. 4 fig. 4-5 (histological details).

Material examined:

Bahamas. — ZML typ.nr. 182 (Andros, Mastic Point, VII.1908, 2 specimens = type-series; leg. N. Rosén).

Bermuda. — RMNH 11473 (Hamilton, east side of Coney Island, among brown and green algae, depth 1.5 m, I.X.1973, 2 clones of several specimens; leg. J.C.H.), USNM sine num. (6 specimens; leg. C. L. Bristol, New York University), YPM 8435 (Long Bird Island, 1898, 6 specimens; leg. A.E.V.), 8437 (IV.1898, 5 specimens; leg. A.E.V.), 8914 (1898, ca. 15 specimens; leg. A.E.V.), 8915 (1898?, ca. 10 specimens; leg. A.E.V.).

Puerto Rico. — RMNH 12010 (Parquera, coral rubble flat in shallow water with growth of *Thalassia*, coral and *Millepora* surrounding mangrove bushes, depth 1 m, 11.IX.1973, 6 small specimens; leg. C.A. & J.C.H.), USNM 53273 (Parquera, Cayo Enrique, on dead coral head, depth 1 m, 18.VIII.1964, 5 specimens without tentacles; leg. C. E. Cutress).

Morphology (pl. 13, figs. 3-9). — Body smaller than in the former species, rather rigid, due to the well developed mesogloea.

Base up to 3 cm in diameter in large specimens.

Column wide calyciform in expansion, often spreading over the substrate.

Oral disc generally circular in outline, far exceeding the base, up to 5 cm in diameter. A well marked, naked peripheral zone is absent. The margin may be smooth (cf. pl. 13 figs. 5, 9) but it is generally drawn out into small, blunt, more or less square to trifid expansions (cf. pl. 13 figs. 4, 6, 7).

Marginal tentacles are as a rule wanting, but occasionally they are present (cf. pl. 13 fig. 3), complete with acrospheres, which, like in the former species, in places may be fused into a swollen rim.

The discal tentacles usually are small and numerous. Their total number may attain a thousand or more in large specimens. They may be vesicle-like and bear appendages as in *D. sanctithomae* (cf. pl. 13 figs. 1, 3) or be reduced (especially in small specimens) to form more or less compound or simple wart-like protuberances. Occasionally they may be reduced to such an extent as to be practically absent (cf. pl. 13 fig. 9). A few tentacles may be unusually well developed and brightly coloured. As many as 20 discal tentacles may occur in the principal rows of a well developed specimen. When tentacles are present, these invariably decrease in size, and become wart-like, towards the margin.

Pattern and colour. — Verrill's description of the colour of *Discosoma sanctithomae* (1907: 278-279), which obviously mainly refers to *D. carlgreni* (cf. p. 59), indicates that the colour of this species is often variegated and very variable. Part of the specimens which I collected in Bermuda were completely dark brown-red with small greenish dots. Other specimens had a variegated dark brown-red and green oral disc with few of the tentacles greenish or whitish and with a cream-coloured marginal region. A colour slide which I received from Dr. W. Sterrer (Bermuda Biological Station for Research) shows a well developed greenish specimen from Bermuda, with greenish, bluish and white discal tentacles. The stomodaeal ridges, visible inside the mouth of this specimen are yellowish. Verrill (1907: 279) mentioned that the inside of the mouth of this species is often light green, sometimes greenish brown. In the other two Caribbean species of *Discosoma* (*D. sanctithomae* and *D. neglecta*) the stomodaeum is invariably white.

The specimens of *Discosoma carlgreni* collected in Puerto Rico had variegated oral discs; rust-coloured with green and white and with a few white radial strands, extending from the mouth to the margin. The discal tentacles were greenish-blue and to a lesser degree, whitish.

Anatomy and cnidom (table 5, 6, figs. 9-12). — Cf. pp. 47-51.

Biological notes. — All specimens reported in the literature and also the specimens examined by me, were obtained in very shallow water. In Bermuda, east of Coney island, I collected two small clones of the species together with a clone of *Discosoma sanctithomae* in the same habitat, viz., on rock among short brown and green algae. One of these clones, composed of small specimens with wart-like discal tentacles and a more or less smooth margin, was found under an overhanging rock. The other clone thrived under somewhat brighter light conditions; its individuals were larger, with better developed discal tentacles, and with slightly developed marginal tentacles. The clone of

Discosoma sanctithomae, just mentioned, grew in the immediate vicinity, on top of a piece of rock, i.e., in brighter light conditions. In Puerto Rico, around La Parquera, I also found the two species together in a coral rubble flat, this time under exactly the same (bright) light conditions.

Discosoma carlgreni undoubtedly reproduces asexually by laceration of basal expansions, but I have no impression about the frequency of this process. My own observations on the species have reference to small clones only. These observations, however, are too incidental to conclude that under favourable conditions laceration may not occur as prolifically as in *Discosoma sanctithomae*. The only author who hitherto observed the species in its natural environment, is Verrill (1907: 277-279). He unfortunately confused the species with *Discosoma sanctithomae* (see below) so that it is impossible to make out with certainty whether his statements that: "... It often grows in large groups or colonies ..." and: "... this actinian can produce young, both by direct fission and by fragmentation of the edges of the lobulate basal disc" refer to both species or to *Discosoma sanctithomae* only. Considering, however, that Verrill's material now present in YPM mainly concerns *Discosoma carlgreni*, it can be assumed that his description mainly refers to that species.

Systematics, nomenclature and miscellaneous notes. — Verrill (1900; 1907) reported only one species of *Discosoma* from Bermuda, viz., *D. sanctithomae*. The range of colours, however, mentioned by him is more in agreement with *Discosoma carlgreni*, as is the maximum number of (dendritic) discal tentacles in a single radial row. A drawing, published twice (Verrill, 1900: pl. 68 fig. 5; 1907 fig. 122), shows a specimen more or less intermediate between both species, viz., with radial tentacle-rows composed of many tentacles each (as in *Discosoma carlgreni*) and the presence of a naked marginal zone, bordered by a neat cycle of short marginal tentacles (as in *Discosoma sanctithomae*). Another figure (Verrill, 1907: 121 - habitus photograph) undoubtedly concerns *Discosoma carlgreni*, as has already been suggested by Watzl (1922: 17). Added to these data the fact that *Discosoma sanctithomae* and *D. carlgreni* both are represented in Verrill's Bermuda collections (deposited in YPM), it is obvious that Verrill did not recognize them as separate species.

Verrill's *Ricordea florida* (Verrill, 1900: 556) from Bermuda almost certainly concerns juvenile specimens of *Discosoma carlgreni*, with reduced, wart-like tentacles. As regards this identification, Verrill refers to McMurrich (1889: 47-50, pl. 1 fig. 10) and states: "It is possible, that it is not the true *florida* of Duchassaing & Michelotti, but it appears the species

described under this name by McMurrich". Verrill's statement is intelligible as McMurrich' description and habitus figure are not very characteristic of *Ricordea florida*; some details seem to point at *Ricordea* but others to *Discosoma carlgreni*.

Weill (1929; 1934) obtained two species of *Discosoma* from Bermuda, undoubtedly *D. sanctithomae* and *D. carlgreni*. Basing himself on Verrill's description (1907: 276-279) he incorrectly identified *Discosoma carlgreni* as *D. sanctithomae*, while proposing a new name for the genuine *D. sanctithomae*, viz., *Actinotryx macropapillata* (1929: 891). In 1934 (: 601) he corrected the latter error, having consulted Duchassaing & Michelotti's original description of *Discosoma sanctithomae* and Duerden's elaborate report on that species (Duerden, 1900: 148-154). Unfortunately he again misidentified *Discosoma carlgreni*, this time as *Ricordea florida*. The correctness of this identification was already seriously doubted by Carlgren (1947: 96).

Distribution (fig. 17). — *Discosoma carlgreni* so far has only been found in the north-eastern part of the Caribbean. The Florida record presented in the map was reported to me by Mr. R. W. Seaton (Florida Atlantic University, Boca Raton) and concerns specimens found at Knight's Key (on rock, amongst *Halimeda*, sponges and *Thalassia*, depth 1 to 2 ft.).

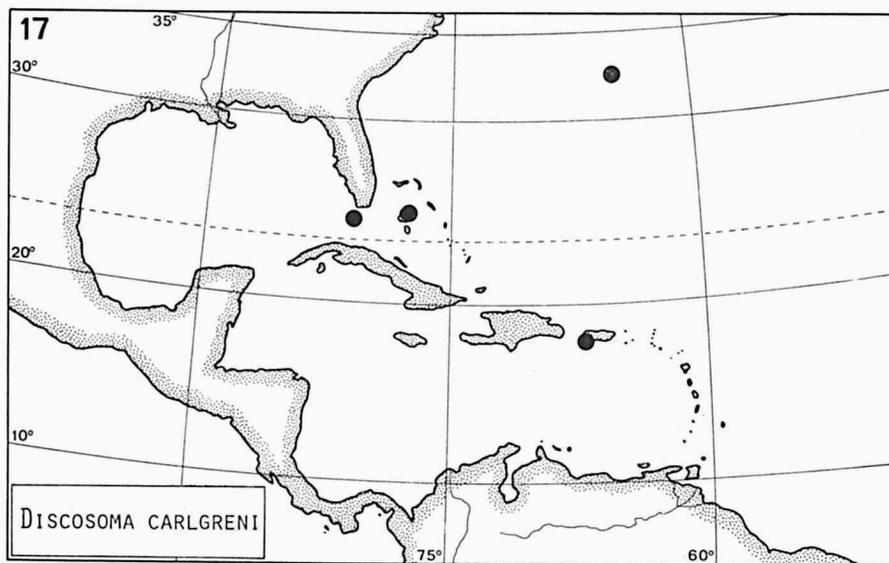


Fig. 17. *Discosoma carlgreni*. Map showing the known geographical distribution of the species.

Discosoma neglecta (Duchassaing & Michelotti, 1860) (tables 4, 5, 6, figs. 13-15, 18, pl. 14)

Isaura neglecta Duchassaing & Michelotti, 1860: 327 (51) (morphology, colour; Antilles; no type designation), pl. 8 fig. 10 (habitus); Duchassaing & Michelotti 1864: 134 (40) (name only).

Zoanthus incultus Andres, 1883: 543 (335) (data of Duchassaing & Michelotti; classified among "Zoanthi dubii").

Paradiscosoma neglecta — Carlgren, 1900: 80 (St. Thomas, specimen in Museum of Copenhagen); Pax, 1910: 214-218 (morphology, anatomy, histology, cnidom; Port au Prince, Haiti; St. Thomas; Jamaica) fig. A¹, B¹ (cross-sections through sphincter and oral disc), pl. 12 fig. 12 (habitus photograph of 3 specimens from St. Thomas), pl. 19 fig. 30 (cross-section through stomodaeum); Stephenson, 1922: 305 (name only); Watzl, 1922: 17-20, 80-81 (morphology, anatomy, histology, cnidom; Andros, Bahamas); Carlgren, 1945: 21 (cnidom); Carlgren, 1947: 93-94 (detailed study of tentacles), fig. 1 (detail of tentacle), fig. 2 (cross-section of body, showing sphincter); Carlgren, 1949: 15 (name only); Corrêa, 1964: 25-29 (morphology, anatomy, cnidom, colour; Curaçao).

Material examined:

Bahamas. — ZML sine num. (Andros, Mastic Point, II.1908, 5 specimens; leg. N. Rosén).

Curaçao, South coast. — Between Piscadera Bay and Blauw Bay: RMNH 12006 (depth ca. 15 m, clone of 5 specimens, 18.VII.1973; leg. R.M.H. & K.W.), 12007 (depth 5 to 10 m, clone of 6 specimens, 25.VIII.1972; leg. P.C.), 12008 (1 specimen, XI.1971; leg. J.C.P.); several photographs and colour slides from specimens in situ, made by R.M.H.

Jamaica. — UMML, P 1223 (17°47' N. 77°41' W., depth 26 to 29 m, 6.VI.1970, 9 specimens), USNM 52505 (Port Royal, Biddlecomb shoal, depth 20 m, 3.XII.1961, 1 specimen; leg. D. M. Goodbody).

Panama Canal Zone. — Colour slides made by Dr. K. Sebens (Museum of Comparative Zoology, Cambridge, Massachusetts).

Saba Bank. — RMNH 12009 (17°20' N. 63° 15' W, coral reef, depth 20 m, CICAR 34/35 sta. 67, 16.V.1972, 1 specimen).

Virgin Islands. — USNM 51674 (St. John, Cabritte Horn Point, depth 22.5 m, 24.III.1960, 1 specimen; leg. Chess & White).

Morphology (pl. 14). — Body often reaching fairly large dimensions; consistency as a rule very rigid, due to the heavily developed mesogloea.

Base probably not exceeding 5 cm in diameter.

Column long to widely calyciform in expansion, often spreading over the substrate.

Oral disc usually wide and concave, generally not exceeding 8 cm in diameter. Margin in fully developed specimens drawn out into a variable number of distinct lobes, often rather large and of variable shape. Relatively large marginal lobes often alternate with smaller lobes. The tips of the lobes usually are more or less trifid (cf. pl. 14 fig. 3b), and besides thinner and more inflatable than the rest of the body. The outline of juvenile specimens

of about 1-2.5 cm in diameter is almost circular, slightly angular, or marked by distinct, short lobes.

Marginal tentacles are invariably absent. The discal tentacles are arranged in numerous radial rows (up to about 200 in large specimens). The tentacles of the principal rows, corresponding with the older endocoels, generally are represented by little developed protuberances of subglobular or irregular shape, provided with secondary, warty outgrowths; in exceptional cases some tentacles may reach a size and complexity comparable with the condition commonly present in *Discosoma sanctithomae* and *D. carlgreni*. In the younger endocoels (and exocoels?) the discal tentacles are externally visible as fine corrugations only. Anatomically these tentacles represent branched or simple endodermal invaginations in the thick mesogloea of the oral disc, which hardly or not at all reach the surface (cf. fig. 13a).

Pattern and colour (based on specimens from Curaçao). — Column usually chocolate brown, the lower part often pale, the upper part dark, with or without green streaks and patches, or completely greenish. Dark brown spots, loosely arranged in longitudinal rows, are invariably present, especially in the upper half. The oral disc is variegated with white, cream and different shades of green and brown, occasionally also with faint purple or blue; in addition a number of continuous or discontinuous, white to yellow radial stripes is often present. The stomodaeal ridges inside the mouth are white.

Anatomy and Cnidom (figs. 13-15, table 5, 6). — Cf. pp. 47-51.

Biological notes. — Another typical reef species, obtained from shallow water between 5 and 29 meters depth. Judging from underwater photographs and from information by divers, the species seems to occur in more shadowy places than *Discosoma sanctithomae* and *D. carlgreni*.

Discosoma neglecta is usually found solitary or in clusters of a few specimens together (van der Vlugt, 1976: 310; information by diverse and personal observations). These clusters undoubtedly are the result of asexual reproduction by pedal laceration, which apparently proceeds less prolifically than in *D. sanctithomae*. Longitudinal fission has not been observed in this species, neither is there any indication of its occurrence.

Distribution and occurrence (fig. 18). — *Discosoma neglecta* is widely distributed in the Caribbean area, but evidently is considerably less common than *D. sanctithomae*. The species is not (yet?) known from Bermuda and from Brazil.

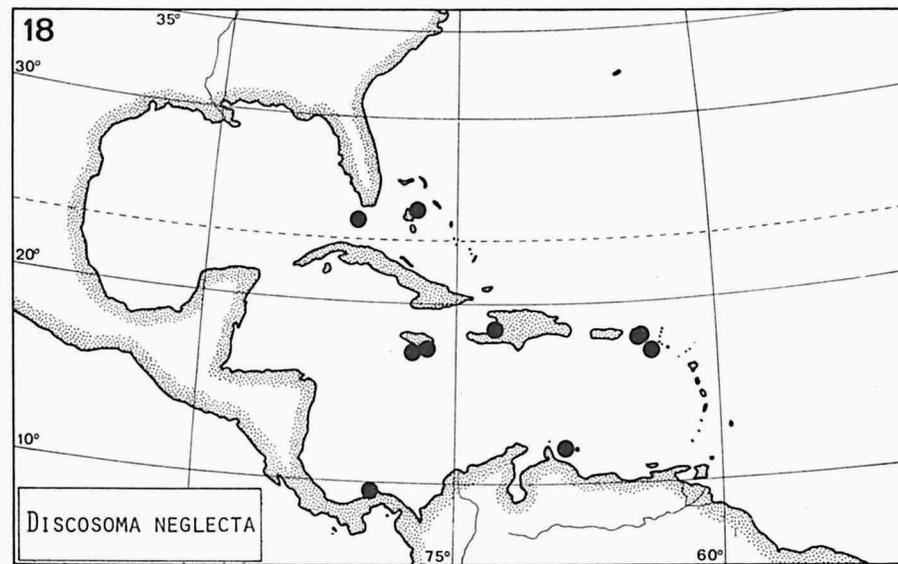


Fig. 18. *Discosoma neglecta*. Map showing the known geographical distribution of the species.

GENERAL DISCUSSION OF THE CNIDOM OF THE CORALLIMORPHARIA

Information necessary to identify the different types of corallimorpharian nematocysts has already been presented on pp. 7-9. In comparison with Actinaria the cnidom of Corallimorpharia shows little variation. There are only 5 distinct types of nematocysts (spirocysts, homotrachs, spirulae, penicilli D and penicilli E), which here will be further discussed:

Spirocysts. — These cnidae are totally absent in the Discosomatidae. In other Corallimorpharia they occur abundantly in the tentacles and sparsely or in small quantities in column and filaments. Corallimorpharian spirocysts may vary considerably in size, both within a single organ of a given species, as in different species. In the filaments of *Ricordea florida* they are small, ca. 15×3 microns. The spirocysts occurring in the acrospheres of the tentacles of *Pseudocorynactis caribbeorum*, on the other hand, may reach a length of over 300 microns, being the longest cnidae known to occur in Anthozoa (cf. pl. 2, IIa).

Homotrachs. — These nematocysts are particularly present in the marginal tentacles or lobes of Discosomatidae (cf. pl. 5 fig. 1), which probably are functional in inter- and/or intraspecific spatial competition. They were also observed in variable numbers in the tentacles of *Ricordea* and *Corynactis*,

and, besides, in the stomodaeum of *Ricordea* and *Pseudocorynactis caribbeorum*.

It is sometimes very difficult to distinguish between corallimorpharian homotrichs and certain corallimorpharian spirulae, especially in undischarged state. This is due to the fact that the tube of the homotrichs is often anisotrichous, with a slightly dilated basal portion, while the spirulae involved have a short to very short shaft only. Transitional stages between both types of cnidae, moreover, are of common occurrence (in conformity with observations in Scleractinia (den Hartog, 1977a: 465, 467 table 2) and Actiniaria (den Hartog, in preparation)). It is not unlikely therefore, that they have occasionally been mixed up in this paper.

The existence of intermediates between corallimorpharian homotrichs and spirulae indicates that these nematocysts are homologous. This view is supported by the fact that the two types may replace each other in corresponding tissues of related species (e.g., in the stomodaeum of *Corynactis parvula* and *Pseudocorynactis caribbeorum*; cf. pl. 1 (III.a), pl. 3 (III.a).

Spirulae. — Corallimorpharian spirulae occur throughout the polyp. They can be subdivided into two different types:

1. A relatively large type with a short, in undischarged state rather thin, shaft, and a long, irregularly coiled, little refractive terminal tube.

This is the type discussed above, homologous and easily confused with homotrichs. These spirulae occur invariably in the tentacles and in the column; they may also be present in the stomodaeum. In the tentacles they are always elongate. In the column they are as a rule rather thick, ovoid in shape, and usually provided with a slightly curved shaft.

2. A very small type of spirulae, with a relatively long and heavily developed, refractive shaft and a distinct, in undischarged state neatly coiled, terminal tube.

These spirulae resemble small penicilli D, but I have not been able to establish the presence of a V-shaped notch at the end of the undischarged shaft. They occur in the filaments and in the columnar ectoderm of at least the Corallimorphidae, and they may also be present in the stomodaeum. They are easily overlooked in squash preparations, and therefore probably much more common than suggested in table 1 and 2.

Penicilli D. — The penicilli D of Corallimorpharia occur in all organs, except the stomodaeum. Three more or less distinct varieties, each with a rather specific distribution in the corallimorpharian polyp, may be distinguished:

1. A long, narrow, bilaterally symmetrical, often slightly curved variety, with a short, heavily developed shaft, ca. 1/3-1/6 of the capsule-length. This

variety is completely absent in the Discosomatidae. The statement of Carlgren (1943: 18-19) therefore, that these nematocysts occur palissade-like in the mesenterial filaments of *Metarhodactis boninensis* Carlgren, needs to be verified. In all other known Corallimorpharia (and Scleractinia) they occur exclusively in the tentacles.

2. A generally short, rather thick, bilaterally symmetrical variety, with a shaft ca. $1/2-2/3$ of the capsule-length. This variety is characteristic of the ectoderm of column and oral disc.

3. A radially symmetrical, ovate to rather elongate variety, variable in size, with a shaft of ca. $1/2-2/3$ the capsule-length. This variety is characteristic of the filaments, and is often present in two distinct size-classes.

Although the three varieties listed above represent conspicuous morphological tendencies, the differences between them are neither structural (as occurs in actinarian penicilli B, which can be divided into various distinct subtypes), nor absolute. It is sometimes difficult or impossible to assign certain penicilli to one of these varieties. The distributional pattern of the three varieties in the corallimorpharian polyp, as outlined above, is also not absolute, although generally valid.

Penicilli E. — These nematocysts occur throughout the corallimorpharian body in various size-classes. As a rule they are radially symmetrical (elliptical to lanceolate) to slightly bilaterally symmetrical (slightly flattened on one side to more or less bean-shaped). Penicilli E may be rather small (e.g., in the column of *Discosoma neglecta*: $15-20 \times 4-6$ microns), but they usually are relatively large. Those penicilli E occurring in the filaments of Discosomatidae actually are the most voluminous anthozoan nematocysts known to exist, generally reaching a size of $150-200 \times 50-70$ microns (cf. pl. 6 (V.b2), in exceptional cases up to 250×80 microns.

Cutress (1955: 134; fig. 8e) was the first to recognize the nematocysts here discussed as penicilli. His observations, however, were disregarded by Schmidt (1972: 435; 1974) who preferred to regard them as holotrichs, though as a separate category, viz. holotrichs I. He stated that only the very end of the tube of these nematocysts was (slightly) tapering and devoid of spines, a condition little characteristic of penicilli. I disagree with Schmidt. The large examples of these nematocysts occurring in the filaments of Discosomatidae, due to their size, offer the most favourable possibility to be studied in detail. I have regularly observed the distal end of the tube of these nematocysts in squash preparations and in my opinion this end is abruptly narrowed into a vestigial (presumably naked) thread (cf. pl. 6 figs. 2, 3), comparable to the rudimentary tube of the majority of actinarian penicilli B and C. It is definitely not slightly tapering as stated by Schmidt. In un-

discharged state, moreover, there is a shallow, terminal V-shaped notch, comparable to that present in ceriantharian penicilli and actiniarian penicilli C. The cnidae here discussed consequently answer the definition of penicilli and fitting them in Schmidt's system, which in my view presents the most acceptable typology of anthozoan nematocyst categories, I refer to them as penicilli E (cf. den Hartog, 1977a: 465).

It may here be noticed that the terminal tube of the penicilli E, even in the largest examples, can only occasionally be observed. The general appearance of these cnidae, however, with their long, thick, coarsely armed shaft, is sufficiently characteristic for instant recognition. The terminal tube is not only very small, but also very little refractive, so that — in squash preparations — it is often hidden from view by other objects, in undischarged (by coils of the shaft) as well as in discharged condition. Penicilli E, moreover, usually do not discharge fully in squash preparations, so that the terminal tube in the majority of cases remains unevaginated.

A remark must be made with regard to those penicilli E, occurring in the ectoderm of the column. Schmidt (1972: 435; 1974: fig. 14 nr. 37) incorrectly included these cnidae into his otherwise correctly defined holotrachs II (= homotrachs). The nematocysts involved, however, in contradiction to Schmidt's definition, do not differ in shape, nor in the character of the tube (shaft) and spines, from other penicilli E (Schmidt's holotrachs I) (cf.: pl. 3 (I.d, IV.d), pl. 4 (I.d, II.e, III.b, IV.c)).

Schmidt (1974, fig. 14 nr. 37) noticed the presence of a naked portion at the base of the tube of the columnar penicilli E of *Rhodactis* spec. (material from the Red Sea). This condition can only be properly checked in discharged nematocysts. During my stay in Curaçao, when working with living material, I unfortunately was not alert to the possible existence of such a naked portion, so that I can neither confirm, nor deny its presence in the columnar penicilli E of the three Caribbean species of Discosomatidae. I am positive, however, that the tube of the corresponding penicilli E of *Pseudocorynactis caribbeorum* and *Corynactis viridis* is not characterized by such a naked basal portion. It seems likely that this portion is comparable and homologous with the "folded portion" characterizing the shaft of various sub-categories of all other known principal types of penicilli.

PRELIMINARY NOTES CONCERNING THE CNIDOM OF SCLERACTINIA; DISTRIBUTION OF PENICILLI E IN THE SCLERACTINIAN AND CORALLIMORPHARIAN BODY

In anticipation of an intended large scale study of the types of scleractinian cnidae and their distribution, so as to test, and where possible to improve,

the present classification of Scleractinia, I have examined the cnidoms of 33 species of corals (for the majority on the basis of preserved material), belonging to all 5 sub-orders distinguished by Vaughan & Wells (1943) and Wells (1956).

This examination confirmed the striking structural similarity of scleractinian and corallimorpharian nematocysts, noticed by all those authors, who to some extent have studied the subject (e.g., Duerden, Stephenson, Weill, Carlgren, Schmidt).

In Scleractinia, like in Corallimorpharia, certain differences in size and shape of the various types of nematocysts strongly suggest to be of taxonomic importance at higher taxonomic levels. To judge whether, and to what extent, such differences are also of practical importance at the specific level requires the study of many more species.

The distribution of the various types of nematocysts within the scleractinian body appeared to be very uniform. An obvious exception, however, is formed by the penicilli E (cf. table 7). In 23 species, i.e. in 70% of the species examined, the occurrence of Penicilli E appeared to be restricted to the mesenterial filaments. In 10 species (i.e. 30%) their presence was also noticed in other tissues. In 6 out of these 10 species (i.e. 18% of the total: 1 species of Fungiina; 3 species of Caryophylliina; 2 species of Dendrophylliina) they were found in the tentacles only. In the remaining 4 species (2 species of Faviina, Oculinidae; 1 species of Caryophylliina; 1 species of Dendrophylliina) they were also found in the coenosarc. Particularly the difference between the two species of Oculinidae (*Madrepora oculata* and *Galaxea fascicularis*) and the other representatives of the Faviina calls for notice, but the difference between *Euphyllia glabrescens* and *Eusmilia fastigiata* (Caryophylliina, Caryophylliidae), both accommodated in a single sub-family (Eusmiliinae), is also quite remarkable.

Contrary to their restricted distribution in most Scleractinia, penicilli E are invariably present in all principal organs of Corallimorpharia. It may be remarked, however, that one cannot without restriction compare the condition present in the corallimorpharian family Discosomatidae with the one present in the other Corallimorpharia and Scleractinia. In the latter two groups the presence of tentacular penicilli E is restricted to the ectoderm, in Discosomatidae predominantly or entirely to the endoderm. A high degree of reduction, not only of tentacular ectodermal penicilli E, but of all types of tentacular ectodermal cnidae (both in size and number), is a general feature of the Discosomatidae.

Like corallimorpharian penicilli E, scleractinian penicilli E are usually rather voluminous, but I have never seen any that approached the size they

TABLE 7

Distribution of penicilli E in the principal organs of various species of Scleractinia belonging to all five sub-orders distinguished by Vaughan & Wells (1943) and Wells (1956).

Explanation of the symbols: — = Absent; + = Present.

Higher taxa and Species	Geographic origin (Museum or station number)	Edge zone/ Coenosarc	Tent- acles	Filam- ents
Suborder Astrocoeniina				
Family Pocilloporidae				
1. <i>Madracis spec.</i>	Puerto Rico (With RMNH Coel. 11469)	-	-	+
Family Acroporidae				
2. <i>Acropora cervicornis</i> (Lamarck, 1816)	St. Eustatius (RMNH Coel. 12426)	-	-	+
Suborder Fungiina				
Superfamily Agaricicae				
Family Agariciidae				
3. <i>Agaricia spec.</i>	St. Eustatius (Luymes Saba-bank exp. 1972, stat. 121)	-	-	+
Family Siderastreidae				
4. <i>Siderastrea radians</i> (Pallas, 1766)	Bermuda (With RMNH Coel. 11473)	-	-	+
Superfamily Fungiicae				
Family Fungiidae				
5. <i>Fungia actiniiformis</i> (Quoy & Gaimard, 1833)	Tawitawi, Sulu Archipel (RMNH Coel. 10480)	-	-	+
6. <i>F. vaughani</i> Boschma, 1923	Honolulu (RMNH Coel. 8285)	-	-	+
Superfamily Poriticae				
Family Poritidae				
7. <i>Porites spec.</i>	Puerto Rico (With RMNH Coel. 11470)	-	-	+
Suborder Faviina				
Superfamily Faviicae				
Family Faviidae				
8. <i>Favia fragum</i> (Esper, 1795)	St. Eustatius (RMNH Coel. 12425)	-	-	+
9. <i>Diploria clivosa</i> (Ellis & Solander, 1786)	St. Eustatius (RMNH Coel. 12423)	-	-	+
10. <i>Manicina areolata</i> (Linnaeus, 1758)	Puerto Rico (RMNH Coel. 12417)	-	-	+
11. <i>Montastrea cavernosa</i> (Linnaeus, 1767)	Bermuda; St. Eustatius (RMNH Coel. 11471; 12422)	-	-	+
Family Oculinidae				
12. <i>Madrepora oculata</i> Linnaeus, 1758	Norway, Trondheimfjord (RMNH Coel. 2771)	+	+	+
13. <i>Galaxea fascicularis</i> (Linnaeus, 1767)	Java Sea (RMNH Coel. 10487)	+	+	+
Family Meandrinidae				
14. <i>Meandrina meandrites</i> (Linnaeus, 1758)	St. Eustatius (RMNH Coel. 12424)	-	-	+
Family Mussidae				
15. <i>Scolymia lacera</i> (Pallas, 1766)	Curaçao (Not preserved)	-	-	+

Higher taxa and Species	Geographic origin (Museum or station number)	Edge zone/ Coenosarc	Tent- acles	Filam- ents
16. <i>S. cubensis</i> (Milne-Edwards & Haime 1849)	Curaçao (Not preserved)	-	-	+
17. <i>Isophyllastrea rigida</i> (Dana, 1846)	St. Eustatius (RMNH Coel. 12419)	-	-	+
18. <i>Mycetophyllia spec.</i>	St. Eustatius (RMNH Coel. 12421)	-	-	+
Suborder Caryophylliina				
Superfamily Caryophylliicae				
Family Caryophylliidae				
19. <i>Caryophyllia smithii</i> Stokes & Broderip, 1828	Madeira; Sweden (RMNH Coel. 12411; 2775)	-	-	+
20. <i>C. inornata</i> (Duncan, 1878)	Madeira (RMNH Coel. 12418)	-	+	+
21. <i>Polycyathus muelleræ</i> (Abel, 1959)	Madeira (RMNH Coel. 12412)	-	+	+
22. <i>Stephanocyathus moseleyanus</i> (Sclater, 1886)	West of Morocco, 1000m (RMNH Coel. 12414)	-	-	+
23. <i>Odontocyathus spec.</i>	Kei-Islands (Danish exp. Kei-Islands, 1922, stat. 41)	-	-	+
24. <i>Lophelia pertusa</i> (Linnaeus, 1758)	Norway, Trondheimfjord (RMNH Coel. 2768)	-	+	+
25. <i>Euphyllia glabrescens</i> (Chamisso & Eysenhardt, 1821)	North Sumatra, Pulu Wéh (RMNH Coel. 10477)	+	+	+
26. <i>Eusmilia fastigiata</i> (Pallas, 1766)	St. Eustatius (RMNH Coel. 12420)	-	-	+
Superfamily Flabellicae				
Family Flabellidae				
27. <i>Flabellum alabastrum</i> Moseley, 1873	Rockall Trough, 1880m (RMNH Coel. 12416)	-	-	+
28. <i>F. chunii</i> Marenzeller, 1904	West of Morocco, 500m (RMNH Coel. 12415)	-	-	+
Suborder Dendrophylliina				
Family Dendrophylliidae				
29. <i>Dendrophyllia cornigera</i> (Lamarck, 1816)	Spain, Ria de Arosa (RMNH Coel. 2247)	-	+	+
30. <i>Balanophyllia regia</i> (Gosse, 1860)	Madeira (RMNH Coel. 12413)	-	+	+
31. <i>Tubastrea tenuilamellosa</i> (Milne-Edwards & Haime, 1848)	Bonaire (With RMNH Coel. 11422)	-	-	+
32. <i>Astroides calycularis</i> (Pallas, 1766)	Italy, Gulf of Salerno (RMNH Coel. 10503)	+	+	+

(In this survey the stomodaeum is not taken into account. Owing to the condition of the available specimens and added to this the small size of the stomodaeum itself, it appeared impossible in many species to obtain reliable, uncontaminated samples of this organ. However, in accordance with the state of affairs in Corallimorpharia, it seems likely that penicilli E are invariably present in the stomodaeum of Scleractinia).

In addition to the 32 species listed in the table, one other species was investigated, viz., the peculiar deep-sea coral *Leptopenus spec.* (Fungiina, Fungiicae, Micrabaciidae) (South Atlantic, 22°05'7" S 10°19'8" E, depth 3806 m, Jean Charcot cruise Walda Pr 51 IC408, 22.VI.1971). In this species penicilli E were found to be present in the mesenterial filaments and in the acrospheres of the tentacles, but not in the columnar ectoderm.

reach in the filaments of the corallimorpharian family Discosomatidae. Their extremely small size in *Acropora cervicornis* (ca. 7-10 × 4-6 microns) is noticeable.

Apart from the general information concerning the cnidom of Scleractinia presented above, two striking observations are here added:

1. Very characteristic, voluminous spirulae with a heavy shaft, but with a terminal tube, which could hardly be discerned in the well preserved, undischarged capsules, were present in the tentacles and the edge-zone of *Stephanocyathus moseleyanus* (Sclater, 1886) and *Odontocyathus* spec. These species, usually placed in the Caryophylliidae, possibly therefore should be included in a separate family. To which extent this view conflicts or conforms with current conceptions needs to be checked by coral specialists.

2. In the coenosarc of *Dendrophyllia cornigera* (Lamarck, 1816) I observed large and conspicuous penicilli D (size 50-60 × 12-15 microns), with a distinct folded portion at the base of the tube and a slightly yellowish brown capsular wall (influence of preservative?), reminding of the penicilli of Cerantharia, but with the characteristic, deep V-shaped notch of usual penicilli D. Penicilli D with a (distinct) folded portion thus far were reported from five or six species of Scleractinia only, viz.: *Fungia actiniformis* (Fungiina, Fungiidae; cf. Schmidt, 1974, fig. 15 no. 38), *Goniopora* spec. (Fungiina, Poritidae; cf. Abe, 1938: 509-510, fig. 30), *G. pectinata* (cf. Wafar, 1974: 120-121), *Favia pallida*, *F. valenciennesi* and *Favites abducens* (all Faviina, Faviidae; cf. Wafar, 1974: 120-121).

The occurrence of these penicilli D in *Fungia actiniformis*, a species also examined during the present study, could not be confirmed. As I investigated specimens identified by Boschma (who was a coral taxonomist, specialized in Fungiidae), it seems possible that Schmidt's observations actually refer to another species of *Fungia*.

The penicilli here discussed, so far have not been reported from Corallimorpharia.

THE SYSTEMATIC POSITION OF THE CORALLIMORPHARIA

It is now obvious and generally accepted that Corallimorpharia and Scleractinia are more closely related to each other than to any other taxon of Anthozoa. This relationship is most strikingly illustrated by the similarity of the nematocysts of the two groups, but it is also clear from similar morphological and anatomical characters (e.g., by the regular presence of acrospheres on the tips of the tentacles and by the structure of the mesenterial filaments).

Most authors consider Corallimorpharia and Scleractinia to be of equal systematic rank (e.g., Krempf, 1904 — Sclerocorallia versus Asclerocorallia; Carlgren, 1940: 56-59; 1943: 3; 1949: 6, 11-16; Wells & Hill, 1956: F233; Schmidt, 1972; 1974 — Corallimorpharia and Scleractinia united in a taxon of higher systematic rank, viz., Madreporia). Stephenson (1921: 510-516), on the other hand, suggested to classify the Corallimorpharia among the Madreporaria (sensu Scleractinia). He admitted, however, that he had not the slightest idea where exactly to accommodate the different families (Stephenson, 1922: 300).

Carlgren (1940, 1943, 1949) regarded Corallimorpharia and Scleractinia as separate orders, a conception accepted by Wells & Hill (1956: F233) in R. C. Moore's well known "Treatise on Invertebrate Paleontology". Apart from the absence or presence of a skeleton, Carlgren (1940: 51, 58; 1943: 3) listed a number of supposedly fundamental differences between the two groups, with regard to: 1. the tentacular arrangement, 2. the composition of the cnidom, and 3. the structure of the mesogloea. This is an incorrect generalisation of the facts, as will be discussed below.

ad 1: The tentacular arrangement of most Corallimorpharia is stichodactyline (cf. note 1, p. 5). In the corallimorpharian family Sideractidae (cf. Carlgren, 1949: 12), however, only one tentacle corresponds to each endo- and exocoel, in accordance with the condition regarded to be characteristic of Scleractinia. The difference in the tentacular arrangement of Corallimorpharia and Scleractinia, therefore, is not absolute and, although definitely of significance, can hardly be regarded fundamental at the ordinal level. In this context it may be noted that, in the classification of Actiniaria, the stichodactyline condition of the tentacles is regarded as a character at the family level only (to distinguish such closely related families as Actiniidae, Phymanthidae and Stoichactidae).

ad 2: Apart from the nematocyst types shared with the Scleractinia, the cnidom of Corallimorpharia, according to Carlgren, includes atrichs. Schmidt (1972: 435) has confirmed this difference, but pointed to the fact that the cnidae involved have a tube bearing minute spines. These cnidae therefore, actually are homotrichs (Schmidt's holotrichs pro parte). Although apparently more common in Corallimorpharia (but certainly not present in all species or in all specimens of a given species), these homotrichs have since been reported to occur in large quantities in the so-called sweeper tentacles of the scleractinian coral *Montastrea cavernosa* Linnaeus, 1767 (den Hartog, 1977a: 465-467), and during the present study their presence was noticed in the tentacles of *Fungia actiniformis* (Quoy and Gaimard, 1834) and another unidentified discoid coral (Danish exp. Kei Islands, 1922, sta. 41).

So, this difference between Corallimorpharia and Scleractinia is not absolute either and besides, as discussed on p. 64, the homotrichs actually are ill-defined, as they seem to merge into certain spirulae. Moreover, even if the cnidoms of Scleractinia and Corallimorpharia would differ in the invariable presence or absence of a particular type of cnida, this would not necessarily imply the ordinal status of the two taxa. Among Hexacorallia such differences commonly occur at infra-ordinal levels, e.g. in Actinaria (Schmidt, 1969; 1972a, 1974) and Ceriantharia (den Hartog, 1977). As the matter of fact, the absence of spirocysts in the corallimorpharian family Discosomatidae may also be referred to as an example.

ad 3: According to Carlgren, the structure of the mesogloea in Corallimorpharia differs from the condition present in Scleractinia by the regular presence of "inclusive" cells. This, however, is only true with regard to the Discosomatidae and the Ricordeidae. Duerden (1898: 647) and Matthai (1923: 111) mentioned that the mesogloea of *Corynactis* (Corallimorphidae) exactly recalls that of Scleractinia in being very clear, structureless and practically devoid of "inclusive" cells. According to Matthai (1923: 111) the main difference between the mesogloea of *Corynactis* and of scleractinian polyps is the unusual thickness of the former. A thick to very thick and rigid mesogloea actually characterizes the majority, if not all, Corallimorpharia, while Scleractinia generally are considered to have a thin mesogloea (e.g. Van Praët, 1977: 294-296). However, this difference too does not seem very fundamental, especially as certain deep sea corals, like e.g., *Leptopenus* Moseley, 1881 and *Stephanocyathus* Seguenza, 1864 (classified in different sub-orders), most certainly do have an extremely well developed and rigid mesogloea, comparable to that of the Corallimorpharia.

Recapitulating, the differences between Corallimorpharia and Scleractinia discussed above are not absolute and hence of insufficient importance to justify the recognition of the Corallimorpharia as a separate order. On the other hand, it cannot be denied that the condition of the characters involved definitely shows a distinctly different trend in the two groups.

An additional difference exists with regard to the distribution of penicilli E, as discussed on p. 67; these nematocysts usually have a restricted distribution in the scleractinian polyp and a more general distribution in the tissues of Corallimorpharia.

A résumé of the various differences between Corallimorpharia and Scleractinia is presented in table 8. It appears that the Corallimorpharia not only lack a skeleton, but in addition are invariably characterized by two or more of the other characters listed in this table. The Scleractinia on the other

hand, apart from being characterized by a skeleton, are never stichodactyline (unless the bifurcate condition of the endocoelic tentacles present in the hermatypic coral genus *Siderastrea* Blainville, 1830, is to be regarded as such). This stresses the homogeneity of the two groups. The Corallimorpharia, therefore, in contrast to Stephenson's suggestion, are not likely to be a heterogeneous mixture of Scleractinia, which evolved independently by reduction of the skeleton. For the same reason it is unlikely that the skeleton forming corals have evolved polyphyletically in various corallimorpharian lineages.

TABLE 8

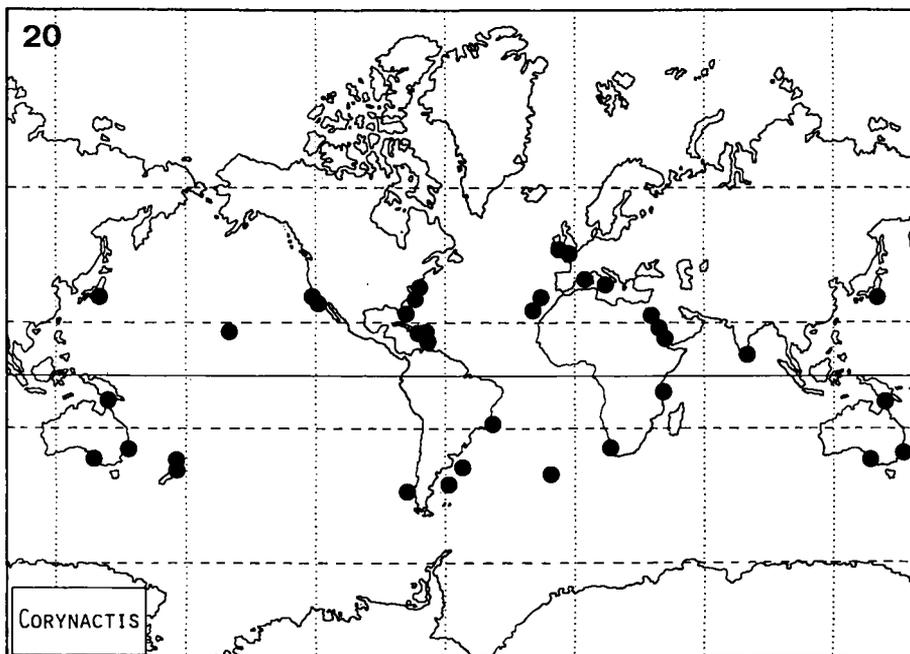
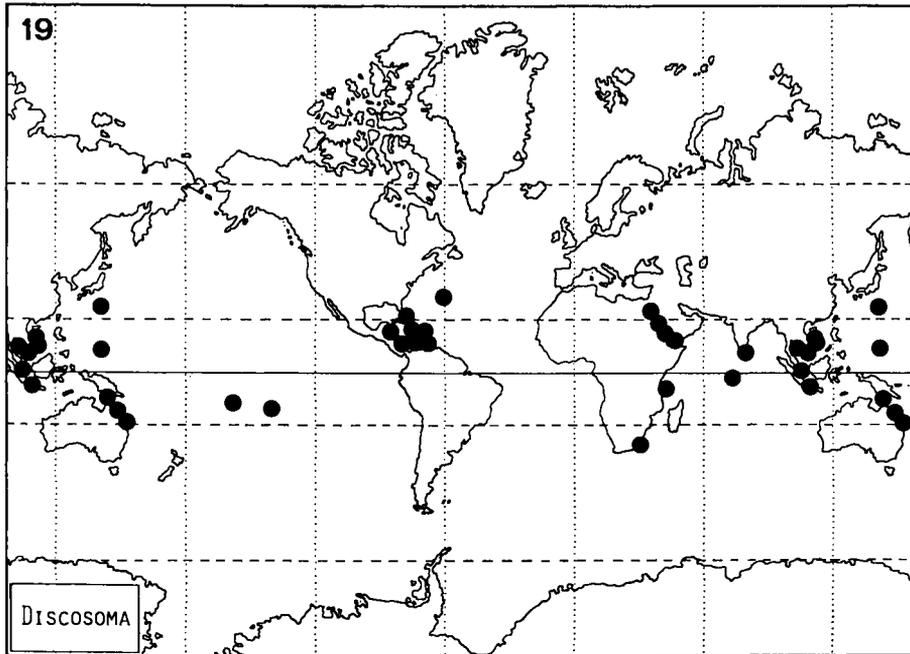
Survey of the (mainly gradual) differences between Corallimorpharia and Scleractinia sensu stricto.

Characters \ Taxa	CORALLIMORPHARIA	SCLERACTINIA S.S.
1. Skeleton	Absent	Present
2. Condition of the mesogloea	Often thick and firm	Generally thin
3. Tentacular arrangement	Nearly always stichodactyline	Never stichodactyline
4. Homotrichs in the tentacles (or marginal lobes)	Often present	At least occasionally present
5. Distribution of penicilli E	Non-restricted; invariably present in all principal organs	Restricted; often absent in the tentacles and generally in the column

In conclusion, the Corallimorpharia, in my view, should be included in the Scleractinia as a sub-order, in addition to the five sub-orders currently distinguished (Wells, 1956). Considering the differences among the Corallimorpharia themselves, one might even consider to classify the Discosomatidae as a separate sub-order. The remaining Corallimorpharia (comprising Sideractidae, Corallimorphidae and Ricordeidae) in several respects show a greater overall similarity with many skeleton forming corals, than with this small, highly specialised taxon.

ZOOGEOGRAPHICAL CONSIDERATIONS

The members of the genus *Discosoma* live in symbiosis with zooxanthellae and thus occur in shallow water only. The distribution of the genus (sensu



lato) is presented in fig. 19. This figure shows that the genus occurs exclusively in tropical waters and that its area of distribution is distinctly discontinuous; restricted to the Indo-West Pacific and the Caribbean. The genus has not been recorded from the eastern Atlantic (including the Mediterranean), the Pacific coast of the Americas and from Brazilian reefs (Riemann-Zürneck, 1972: 74 mistakenly mentions that *Discosoma sanctithomae* is reported from Brazil by Corrêa, 1964). It is true, these areas belong to the zoologically least known of the world. The chance, however, that the genus is really absent in these areas is considerable, as its representatives, apart from occurring in shallow water only, are so conspicuous, that they probably would have been among the first anemones to be reported or collected, if they had occurred there.

The current geographical and hydrographical conditions on the earth are generally thought to have become roughly established in the late Tertiary (Ekman, 1967: 63-80; Briggs, 1974). Thus, if before that time the genus *Discosoma* had not occurred in the present-day Caribbean or in adjacent waters, the only possible explanation for its recent presence in that region would be by colonisation of Indo-West Pacific specimens transported by means of currents around Cape Good Hope. As *Discosoma* is a genus of sessile forms, always immovably attached to solid substrates (rock, coral, sponges), possible transport by sea currents could only take place in larval condition. Considering, however, 1. the (presumably) very short pelagic stage of the larvae, 2. the distance to be traversed and 3. the stenothermal character of the species involved, this seems very unlikely. Besides, in case of such a way of dispersal, one might wonder why the genus has not settled in tropical West Africa and in Brazil, both situated less far away from the Indo-West Pacific region than the Caribbean. I therefore have no better explanation for the origin of the three Caribbean species of *Discosoma* than the assumption that they are either relicts or descendants of a world-wide, more or less continuous, tropical shallow water Tethys fauna, the genus *Discosoma* having vanished from the present-day Mediterranean, the coast

Fig. 19. *Discosoma* sensu lato. Map showing the known geographical distribution of the genus (Main sources: Carlgren (1949: 14-16) and the literature cited by him; the private collection of Major K. W. England, deposited in BM(NH); material present in RMNH).

Fig. 20. *Corynactis*. Map showing the known distribution of the genus. (Main sources: Carlgren (1949: 13-14), Cutress (1977: 130), Widersten (1976: 858); material present in RMNH). Distributional records from Bermuda (cf. pp. 12, 17) and from the Azores (*Corynactis viridis*, IX-X.1979; leg. J.C.H. & M.S.S. Lavaleye) have not been indicated in the map. These records came to my attention when the line block of the figure had already been prepared by the printer.

of West Africa and the west coast of Central America under the influence of changing geographical, hydrographical and climatic conditions.

The same reasoning as for *Discosoma* can be applied to *Ricordea*, until now considered to be a monotypic, endemic Caribbean genus, but as mentioned before (pp. 26, 27) certainly also present in the Indo-West Pacific.

The new genus *Pseudocorynactis* for the present moment has to be regarded as an endemic Caribbean genus.

The known distribution of the genus *Corynactis* is presented in fig. 20. Taking into account that *Corynactis* is a genus of small forms, often difficult to collect and easily overlooked when not particularly searched for, this map seems to demonstrate that the genus has a world-wide distribution in the temperate and tropical waters, without striking discontinuities.

At the present moment it is hardly possible to speculate seriously on the question how this distributional pattern developed, as the affinities of the various (supposed) species are not yet clarified. Specimens collected in remote areas have often been described rather uncritically as new species. Morphology and anatomy are very uniform throughout the genus, as has already been pointed out by Carlgren (1927: 4; 1941: 2). Carlgren considered differences in colour and in cnidom to provide the only useful criteria for specific delimitation. Colour, however, may be extremely variable within a single species, as is demonstrated in e.g. *Corynactis haddoni* Farquhar (cf. 1898: 532-533), *C. australis* Haddon & Duerden (cf. 1896: 151) and in the well-known European *C. viridis* (cf. Gosse, 1860: 290, pl. 9). Differences in the cnidoms of the various species, moreover, as far as present, are slight. In the acrospheres of the tentacles of some species occur two size-classes of penicilli D (e.g. in *Corynactis viridis*, *C. californica*, *C. annulata*), in others only one (e.g., *Corynactis parvula*). Carlgren's claim that specific differences exist in the size of various nematocyst-types is most probably correct. The majority of authors, however, Carlgren included, so far have only presented rough size-ranges in their papers, without a mean and not even based on a fixed number of cnidae. Such size-ranges do not allow a reliable comparison, and hence are in practice of very restricted diagnostic value only.

With this state of affairs concerning the classification of *Corynactis*, it is, in my view impossible to say whether the genus comprises a number of temperate and tropical species, or whether it also includes widely spread eurythermal temperate to tropical species. However, even when excluding the latter possibility, and assuming that a tropical warm water belt has always existed in the marine environment, some temperate species may have crossed the tropics by equatorial submergence, if we take into account that several

species have been found at depths up to 100 meters and occasionally even up to 200 meters (Widersten, 1976: 858). In this context the eastern Atlantic *Corynactis viridis* may be discussed. The known area of distribution of this species ranges from the English Channel eastward to the Azores and southward to the Canary Islands. In the Canaries the mean annual surface temperature of the water roughly ranges from 17 to 23° C, and comparing these temperatures with those at a depth of 100 meters in tropical West Africa (maximally 19° C in a small region just around the equator: Ekman, 1967: 56), this species must be regarded potentially capable to cross the tropics, provided that sufficient solid substrates are available. The tropical waters of the Central American West coast also do not necessarily have to be an insuperable barrier for moderately eurythermal, temperate species.

In the temperate regions, long-distance transport is likely to be a distributional factor of importance. Several temperate forms have been found intertidally or subtidally on the rhizoids and stalks of large Phaeophyceae (kelp - Laminariales). Farquhar (1898: 534; New Zealand) mentioned *Lessonia*, Carlgren (1941: 1; Inaccessible Archipelago) *Laminaria*, and I know from personal experience that *Corynactis viridis* may occur on the rhizoids of Laminariales along the Channel coasts of England and France. When detached, as may happen in stormy weather or by the activities of man, these algae remain floating and are often transported over considerable distances before being washed ashore. I have once established an actual case of dispersal in this way, viz., 4 specimens of *Corynactis viridis* settled on the disc-shaped rhizoid of *Himanthalis elongata*, washed ashore at Den Helder, the Netherlands, some 500-800 km north of the nearest place of occurrence of the species (den Hartog, 1960: 47-49), and it seems quite possible that the species which occurs in the Inaccessible Archipelago, has reached these islands in a similar way, either from South Africa or from South America. Carlgren (1941: 4) considered this species a variety of the South African *Corynactis annulata*, but his data do not equivocally support this view. In my opinion Carlgren's data rather indicate that *Corynactis annulata* is more similar to the South American species *C. carnea* Studer, 1878 and *C. chilensis* Carlgren, 1941, than to the form found in the Inaccessible Archipelago. The latter form, unlike the other three, seems to have only one size-class of penicilli D (Carlgren's microbasic p-matigophores) in the acrospheres of the tentacles (Carlgren, 1941: 3).

The most accurate and complete description of a species of *Corynactis* is the description by Hand (1954: 349-355) of *C. californica* Carlgren, 1936, from the California coast. This description fits the Lusitanian-Mediterranean *Corynactis viridis* in detail (specimens from Plymouth examined), perhaps

with the exception of the colour. The similarity of these two species (if to be regarded as such) is striking as their areas of distribution are at present separated by the American continent and by the Atlantic, and as at least one other, distinctly different species occurs in the intervening area, viz., the Caribbean *C. parvula*. The explanation of this distributional pattern is a difficult matter, which readily leads to superficial, general speculations about a possible continuous, east-west distribution in the late Tertiary Tethys sea of a practically similar "mother" species. To explain this distributional pattern as a relict of a once continuous post-Tertiary distribution area around the tip of South America is even less acceptable, unless future systematic studies will reveal that most or all the temperate forms so far described, are not actually separable.

In conclusion, a world-wide revision of the genus *Corynactis* is urgently needed, not only from the viewpoint of pure classification, but also to obtain a better understanding of the evolution and (the history of) the present distribution of the genus.

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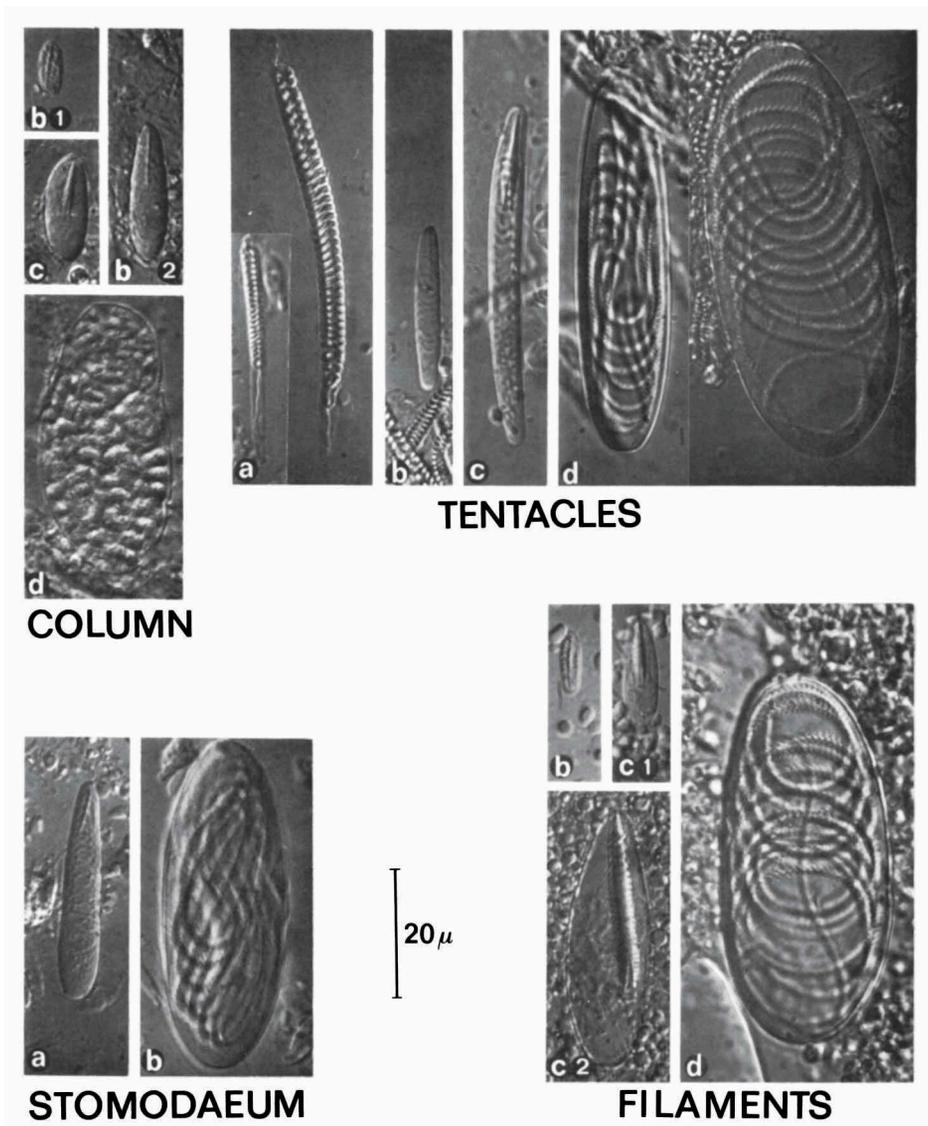
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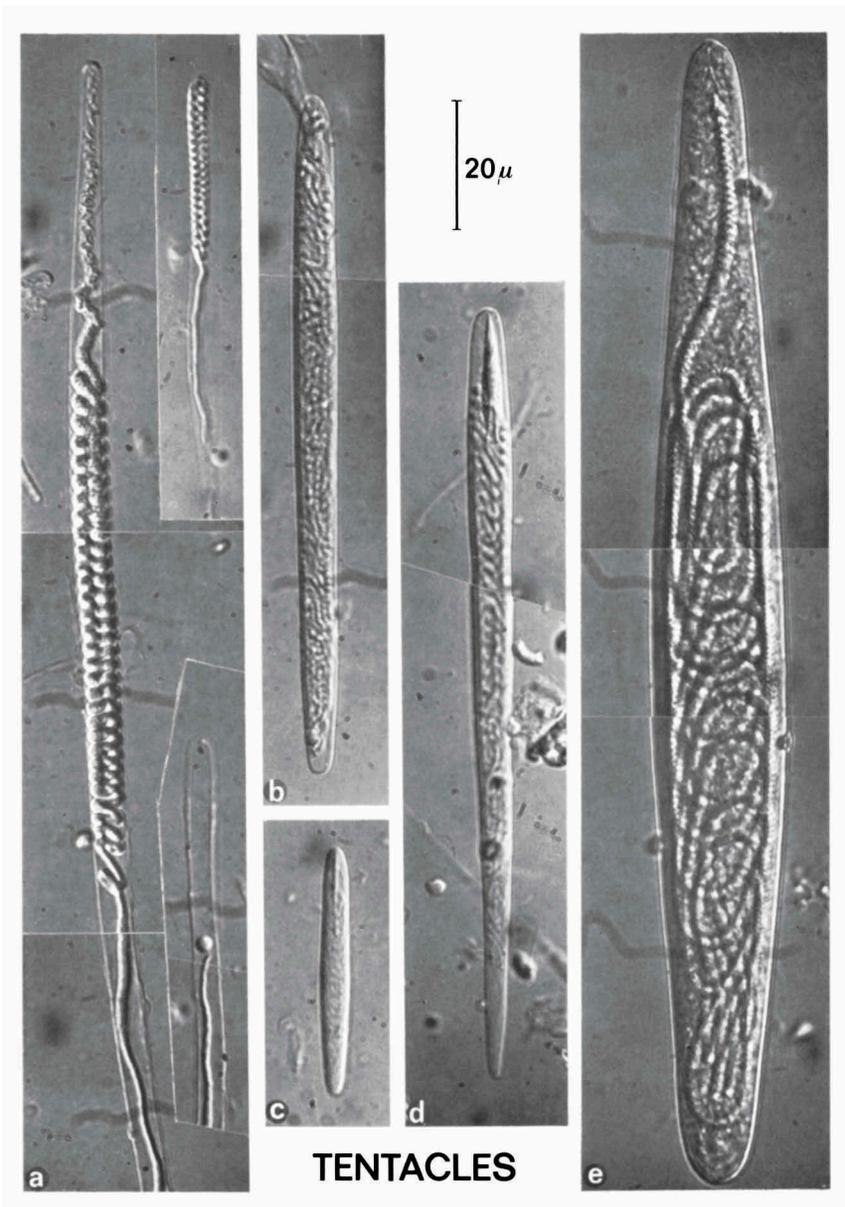
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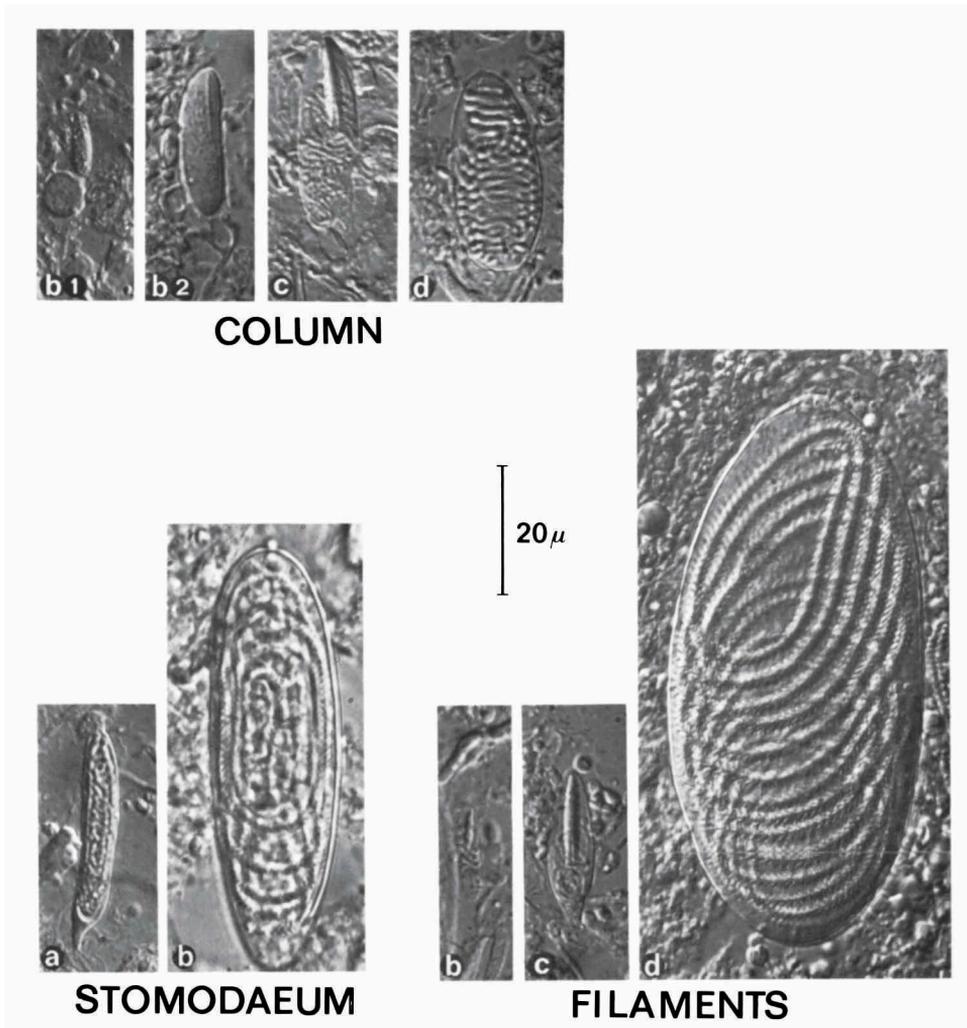
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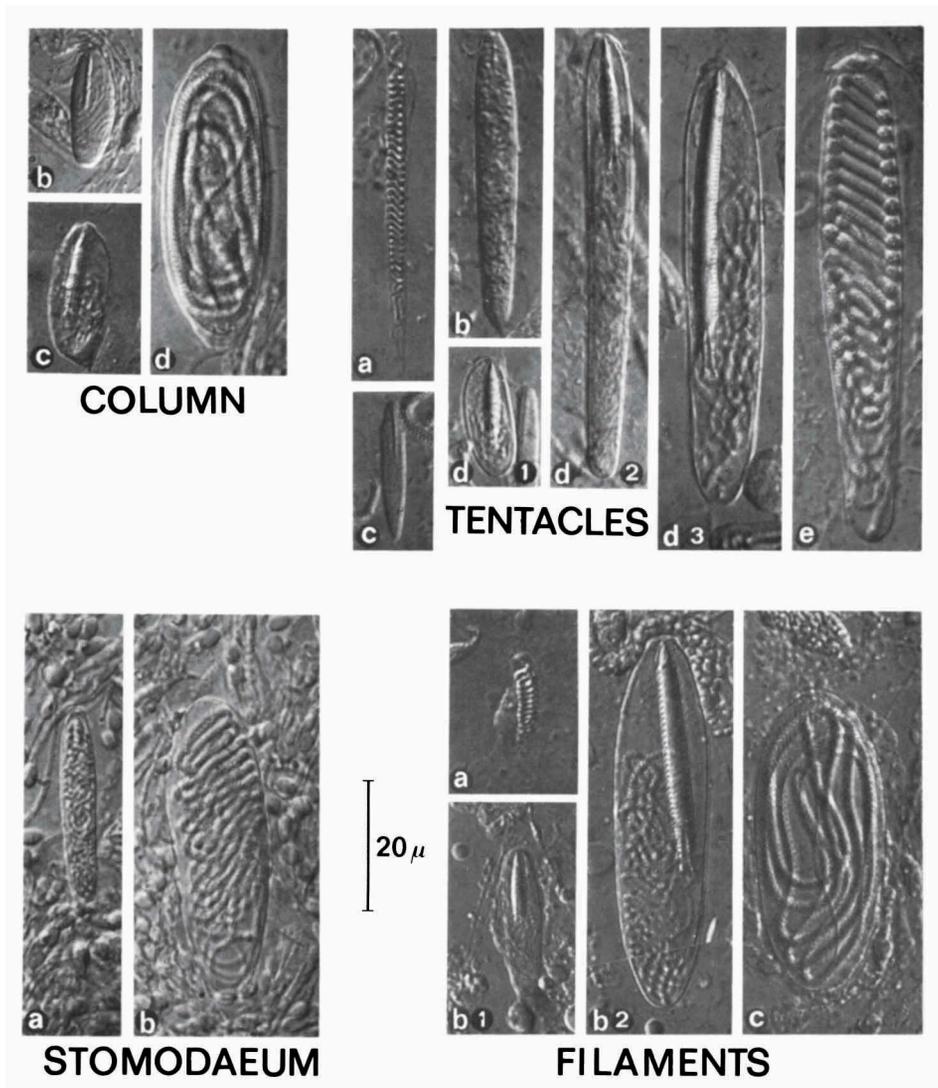


Corynactis parvula. Pictorial survey of the cnidom. The letters in the plate correspond to those used in table 1 (p. 16). I. Column: b1. spirula; b2. spirula; c. penicillus D; d. penicillus E. II. Tentacles: a: spirocysts (about indicating the size range); b. spirula; c. penicillus D; d. penicilli E (about indicating the size range). III. Stomodaeum: a. spirula; b. penicillus E. IV. Filaments: b. spirula; c1. penicillus D; c2. penicillus D; d. penicillus E.

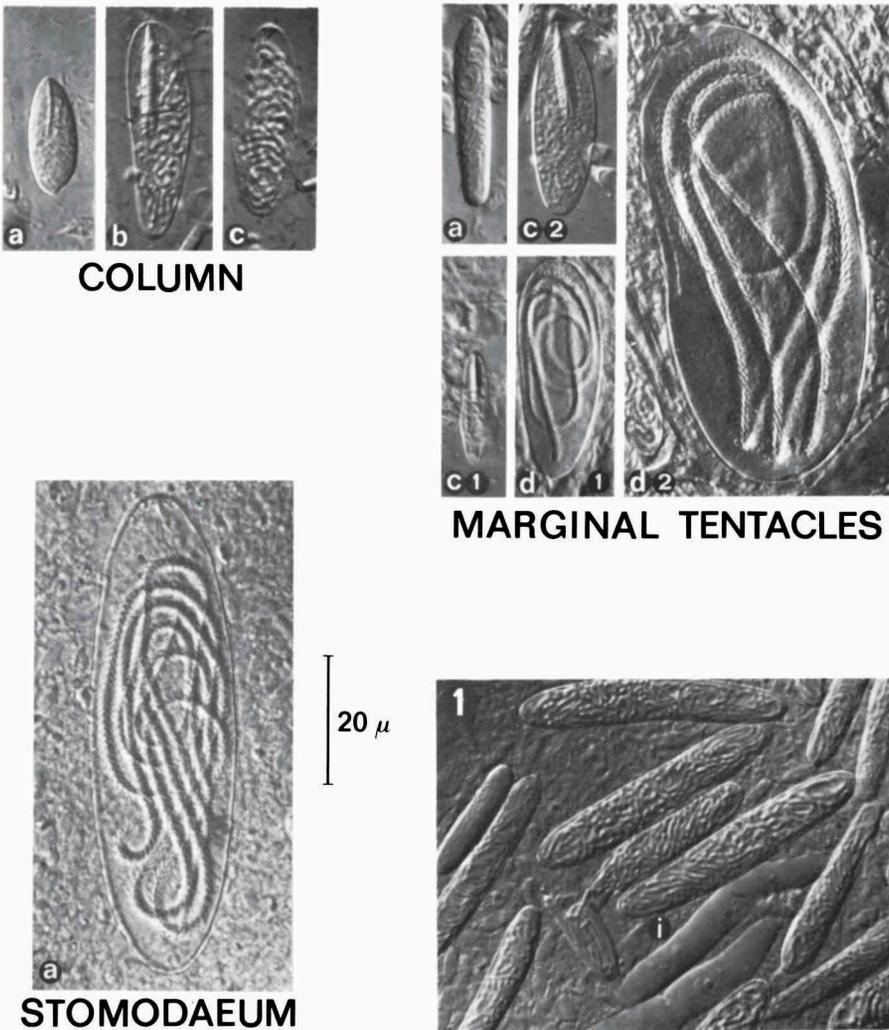




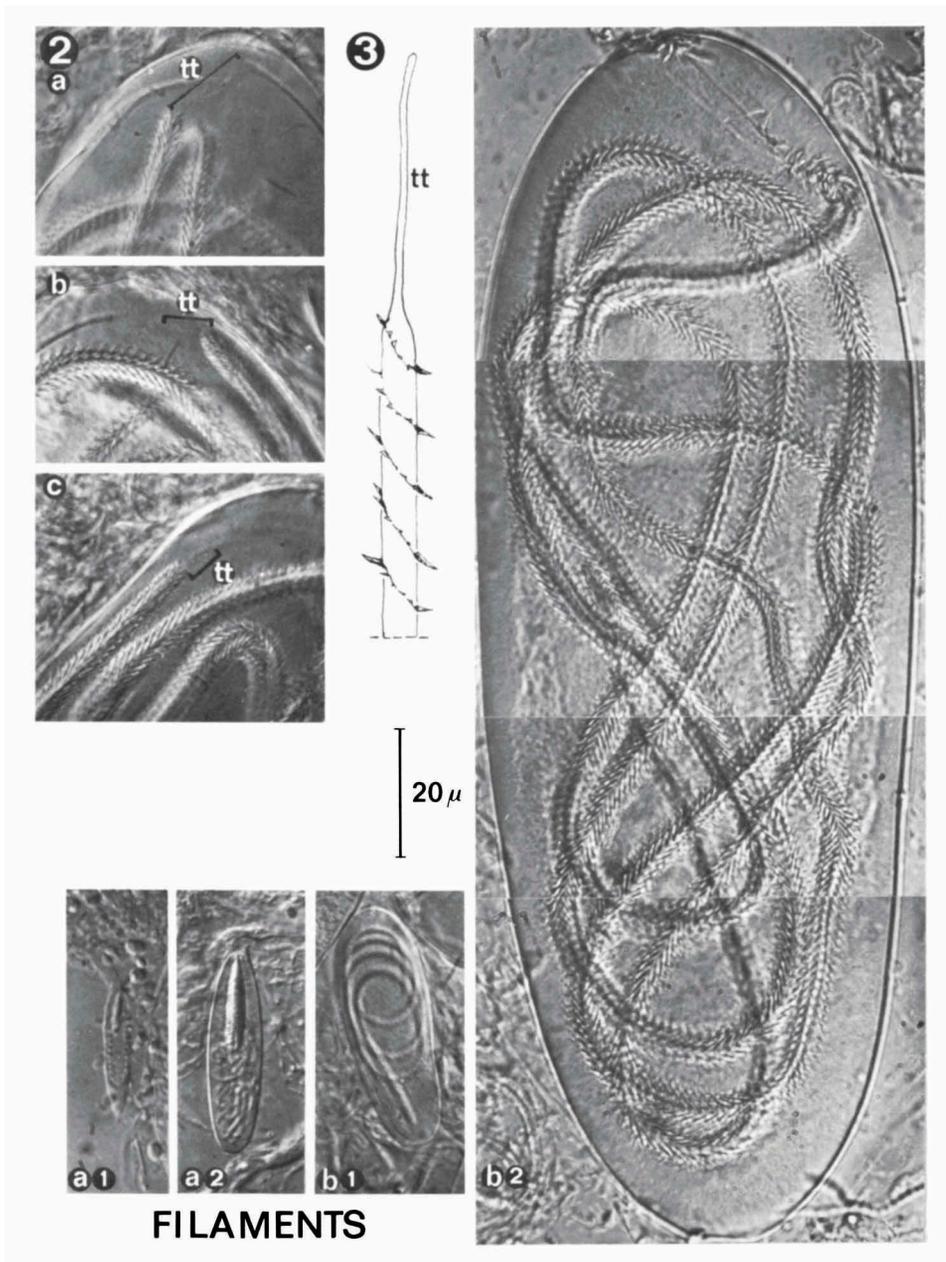
Plates 2-3. *Pseudocorynactis caribbeorum*. Pictorial survey of the cnidom. The letters in the plates correspond to those used in table 2 (p. 23). I. Column: b1. spirula; b2. spirula; c. penicillus D; d. penicillus E. II. Tentacles: a. spirocysts (about indicating the size range); b. homotrich; c. spirula; d. penicillus D; e. penicillus E. III. Stomodaeum: a. homotrich; b. penicillus E. IV. Filaments: b. spirula; c. penicillus D; d. penicillus E.

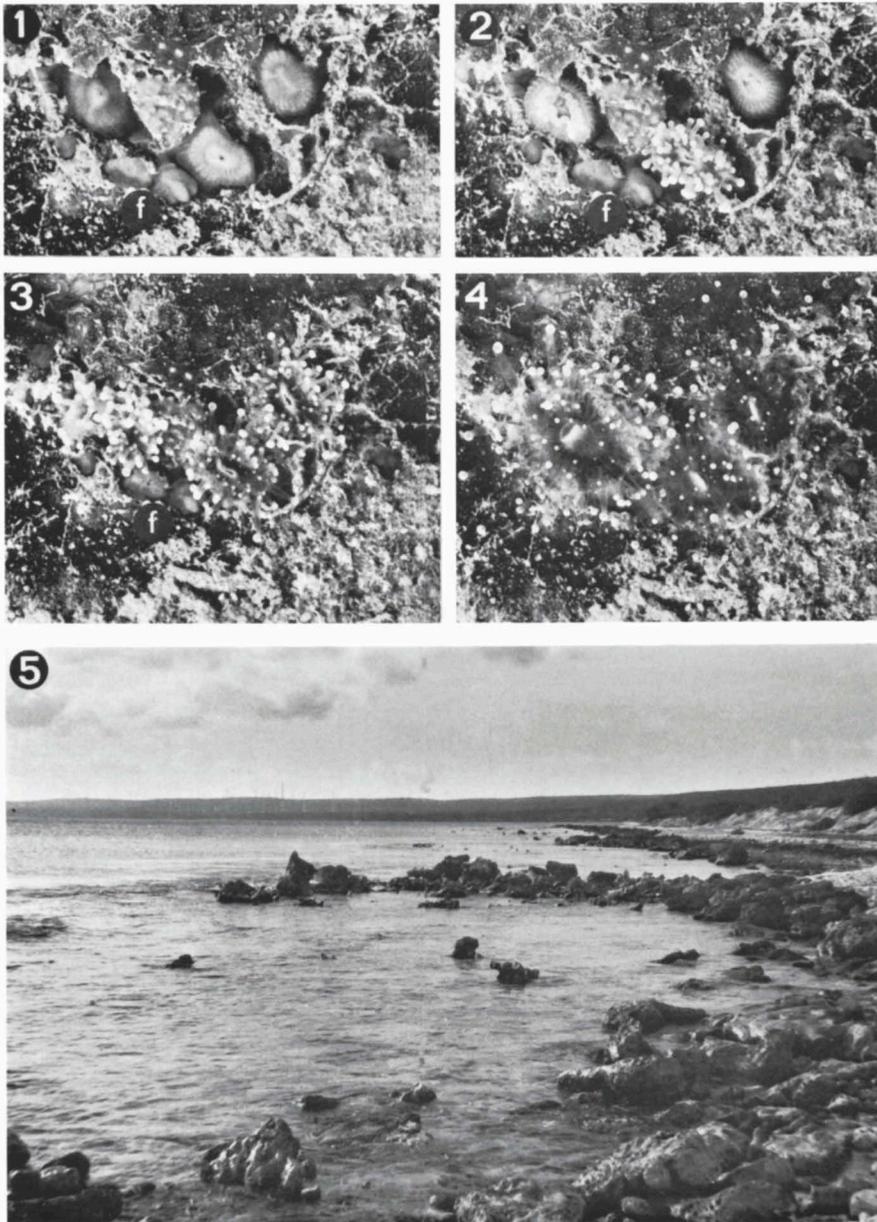


Ricordea florida. Pictorial survey of the cnidom. The letters in the plate correspond to those used in table 3 (p. 31). I. Column: b. spirula; c. penicillus D; d. penicillus E. II-III. Marginal and discal tentacles: a. spirocyst; b. homotrich; c. spirula; d1. penicillus D; d2. penicillus D; d3. penicillus D; e. penicillus E. IV. Stomodaeum: a. homotrich; b. penicillus E. V. Filaments: a. spirocyst; b1. penicillus D; b2. penicillus D; c. penicillus E.

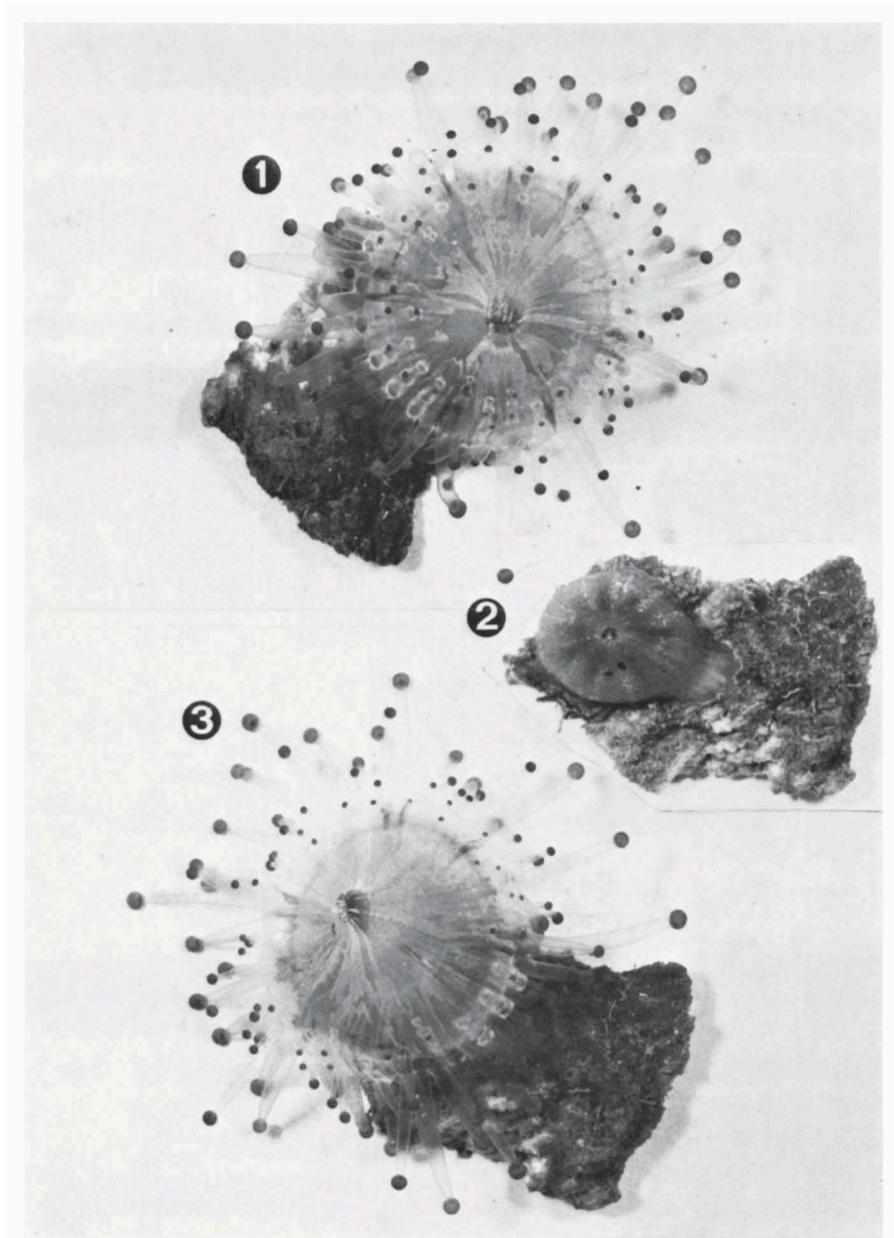


Plates 5-6. *Discosoma sanctithomae*. Pictorial survey of the cnidom. The letters in the plates correspond to those used in table 5 (p. 49). I. Column: a. spirula; b. penicillus D; c. penicillus E. II. Marginal tentacles: a. homotrich; c1. penicillus D; c2. penicillus D; d1. penicillus E; d2. penicillus E. IV. Stomodaeum: a. penicillus E. V. Filaments: a1. penicillus D?; a2. penicillus D; b1. penicillus E; b2. penicillus E. Fig. 1. Detail of a squash preparation of the acrospheres of the marginal tentacles showing homotrichs. i = immature ontogenetic stages. Fig. 2a, b, c. Details of the tip of the shaft of large undischarged penicilli E from the filaments (V. b2), showing the vestigial terminal tube (tt). Fig. 3. Detail (drawn at the same scale) of the everted terminal tube (tt) of a discharged filamental penicillus E (V. b2).





Corynactis parvula. Figs. 1-4. Specimens from Curaçao (RMNH 11477) in various states of expansion; aquarium photo. Note the irregularly shaped fragments (f.), which are produced by pedal laceration and which will develop into new individuals; \times 1.2. Fig. 5. View of the locality in Bonaire (cf. pp. 12, 13), where several samples of the species were collected.



Pseudocorynactis caribbeorum. Habitus of the holotype (RMNH 11481); aquarium photos. Fig. 1. Oral view of the expanded specimen; $\times 1.25$. Fig. 2. The specimen in contracted state; $\times 1.1$. Fig. 3. Slightly oro-lateral view of the expanded specimen. Note the protruding hypostome; $\times 1.25$.

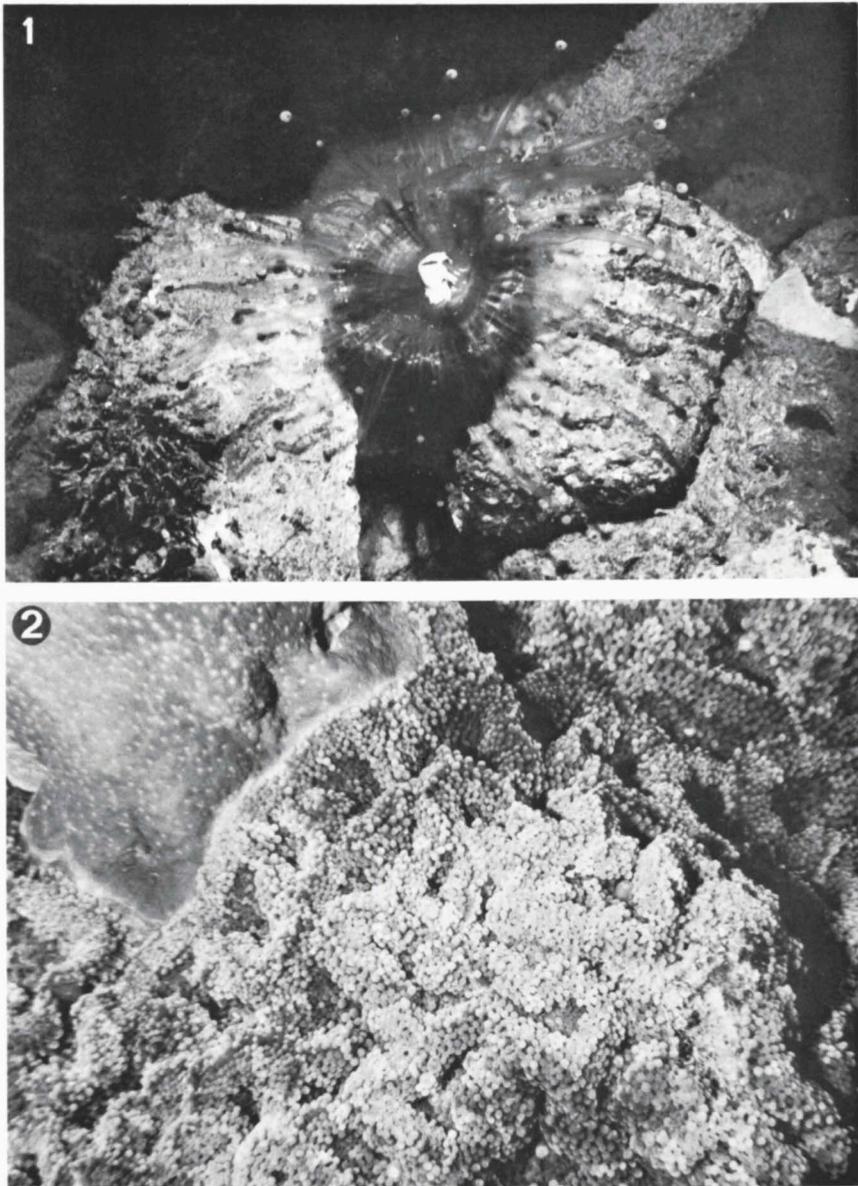
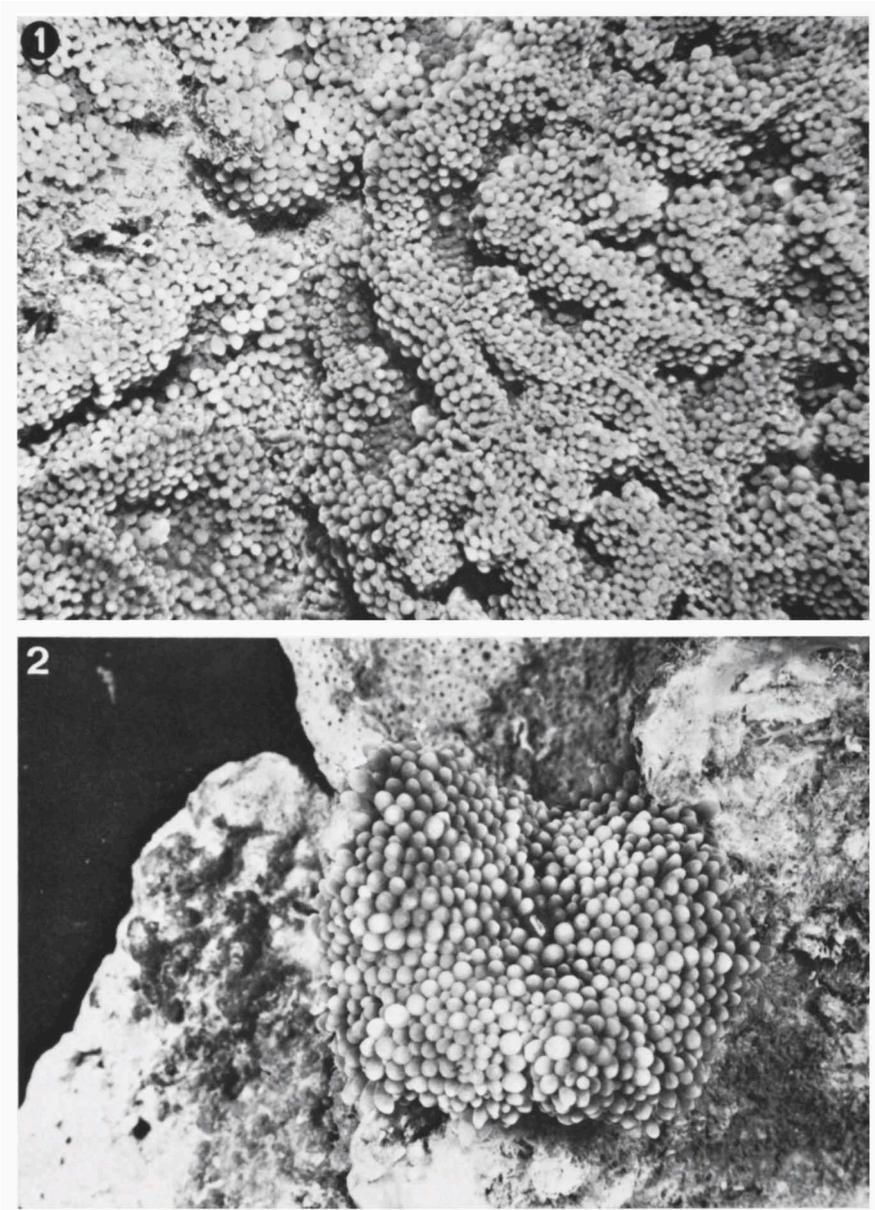
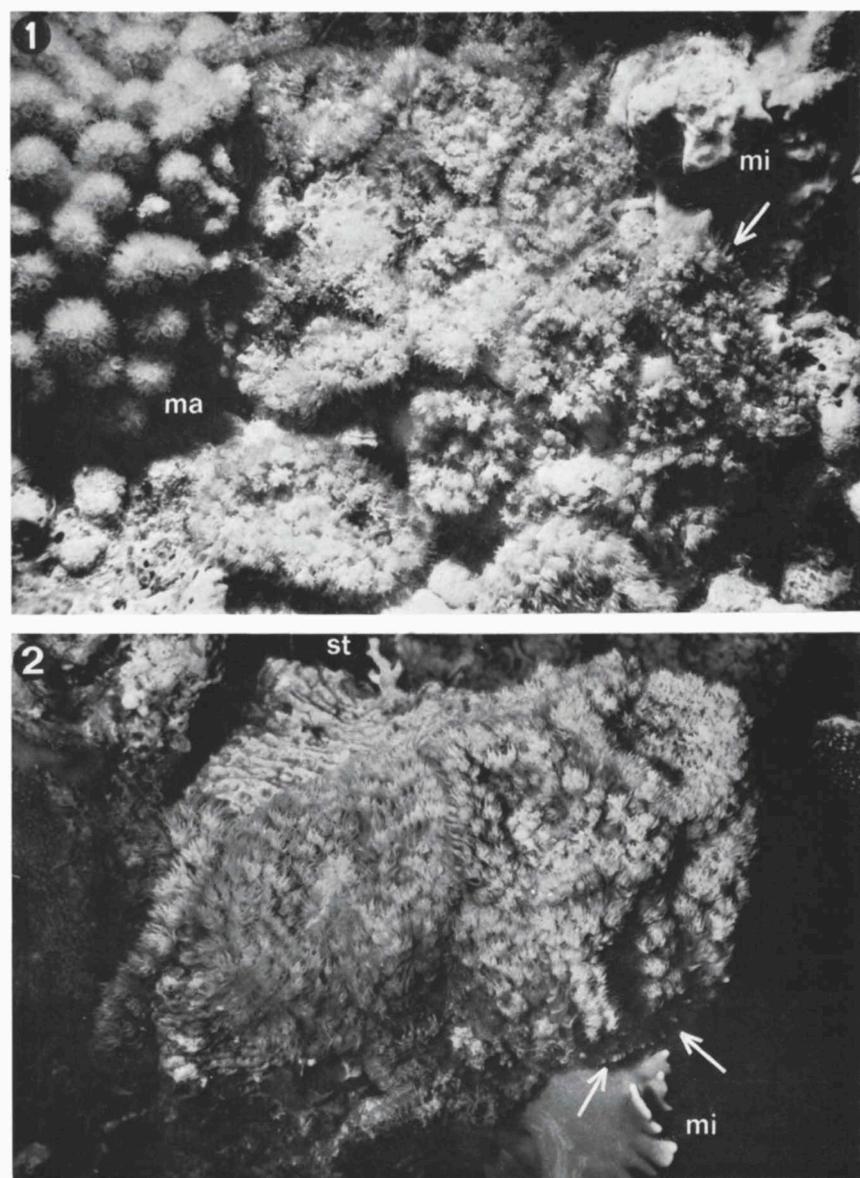


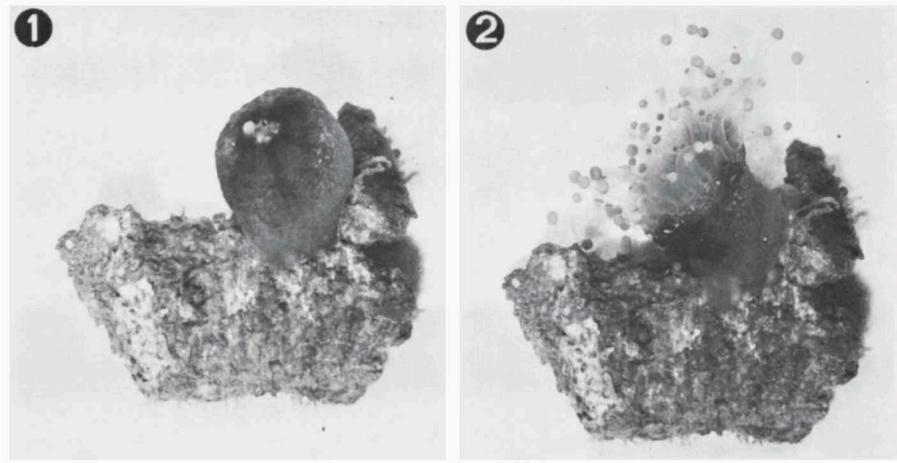
Fig. 1. *Pseudocorynactis caribbeorum*. Expanded specimen (RMNH 11485); aquarium photo; ca. \times 1. Fig. 2. *Ricordea florida*. View of a clone of the semi-colonial shallow water form in situ; 21.VII.1973, Playa Chikitu, Curaçao; photo by R. M. den Hartog-van Ter Tholen; ca. \times 0,8.



Ricordea florida. Fig. 1. Close-up of the semi-colonial shallow water form in situ; 21.VII.1973, Playa Chikitu, Curaçao; photo by R. M. den Hartog-van Ter Tholen; ca. \times 1.2. Fig. 2. Close-up of a solitary specimen from deeper water in Curaçao (RMNH 12001); aquarium photo; \times 0.9.

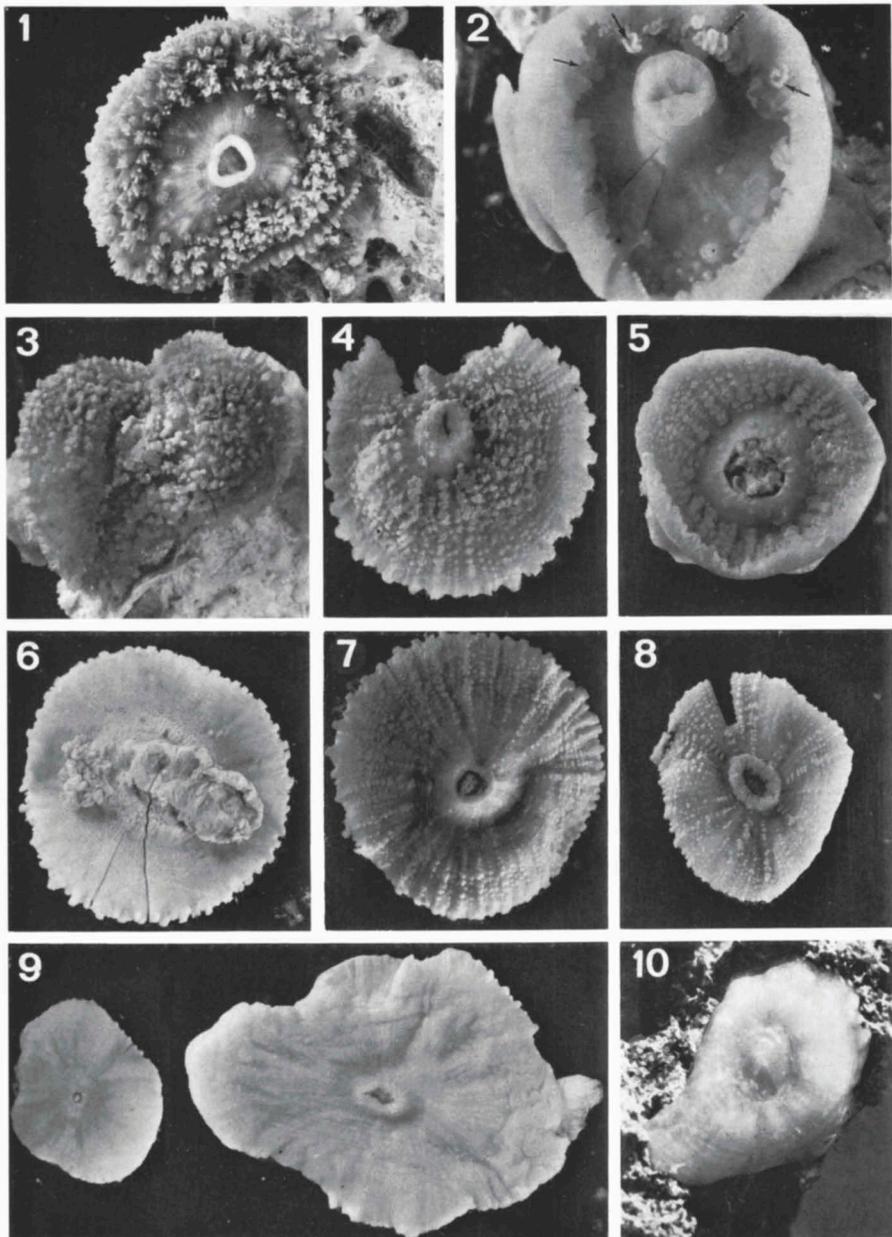


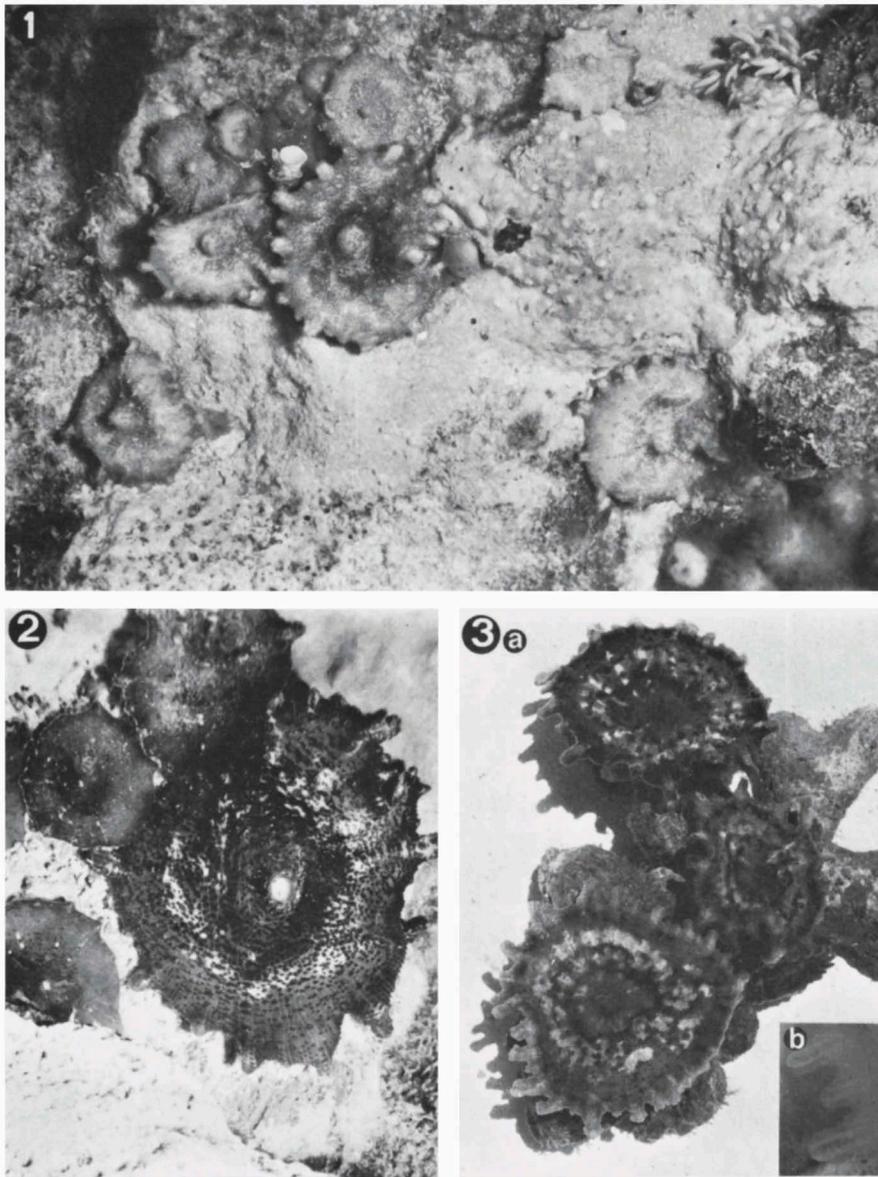
Figs. 1-2. *Discosoma sanctithomae*. Two clones from shallow water in Curaçao (Piscadera Bay); photos by R. M. den Hartog-van Ter Tholen. Note the swollen tips of the marginal tentacles (indicated by arrows) of specimens facing other coelenterates. ma = *Madracis* spec., mi = *Millepora* spec., st = *Stylaster roseus* (Pallas); both photos ca. $\times 0.7$.



Figs. 1-2. *Pseudocorynactis caribbeorum*. Oro-lateral view of a specimen from Curaçao (RMNH 11482) in semi-contracted and in semi-expanded state. Note the pattern of 6 dark bands in the upper part of the column, which fade away aborally; \times 0.9.

Plate 13. Figs. 1-2. *Discosoma sanctithomae*, Fig. 1. A specimen from Curaçao (RMNH 11469). Note the swollen marginal tentacles; \times 0.85. Fig. 2. A specimen from St. Martin (RMNH 12015) with extremely reduced tentacles; arrows indicate extruded mesenterial filaments; \times 1.9. Figs. 3-9. *Discosoma carlgreni*. 3, A specimen from Bermuda (RMNH 11473) with marginal tentacles (partly swollen) and well-developed compound discal tentacles; \times 1.35. 4, A specimen from Bermuda (USNM sine num) without marginal tentacles, but with short marginal lobes and well-developed discal tentacles; \times 1. 5, A specimen from Bermuda (YPM 8437) with a partially smooth margin; \times 1. 6-7, A specimen from Bermuda (YPM 8435) from below and from above, with short but distinct marginal lobes and rather reduced discal tentacles; \times 0.8. 8, Syntype, from Andros, Bahamas. Note the poorly developed marginal lobes and discal tentacles; \times 1.2. 9, Two specimens from Parquera, Puerto Rico (USNM 53273), with a rather smooth margin and completely reduced discal tentacles; \times 1. Fig. 10, *Pseudocorynactis caribbeorum*. Contracted specimen from Curaçao, showing the typical mammiform habitus. The groove indicates the boundary between scapus and scapulus; aquarium photo; \times 1.2.





Discosoma neglecta. Figs. 1-2. View of two clones in situ; Piscadera Bay, Curaçao; photos R. M. den Hartog-van Ter Tholen; ca. $\times 0.7$ and $\times 1$. Fig. 3a. Specimens from Piscadera Bay, Curaçao (RMNH 12007). The dark dots in the centre of the central area of the oral disc are distinctly compound discal tentacles; aquarium photo; $\times 0.66$. Fig. 3b. Detail of inflated marginal lobes. Note the position of the mesenteries.