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DESCRIPTIONS OF TWO NEW CERIANTHARIA FROM THE CARIBBEAN REGION, *PACHYCERIANTHUS CURACAOENSIS* N.SP. AND *ARACHNANTHUS NOCTURNUS* N.SP., WITH A DISCUSSION OF THE CNIDOM AND OF THE CLASSIFICATION OF THE CERIANTHARIA

by
J. C. DEN HARTOG
Rijksmuseum van Natuurlijke Historie, Leiden

with 5 text-figures and 6 plates

CONTENTS

ABSTRACT

Two new Ceriantharia, *Pachycerianthus curacaoensis* and *Arachnanthus nocturnus*, both from the Caribbean region, are described. It is recommended to avoid the terms proto- and metamesenteries in taxonomic descriptions. The cnidom of the Ceriantharia is discussed; a subdivision of the spirulae (=b-rhabdoids) and penicilli (=p-rhabdoids) differing from that of Schmidt (1972) is given. The anoplotelic character of the terminal tube of the penicilli (Schmidt, 1972) is doubted on the basis of light microscopical investigations.

Mainly on the basis of the study of *Botruanthus benedeni* (Torrey & Kleeberger, 1909) (Botrucnidiferidae), the 2 newly described species (respectively belonging to the Cerianthidae and the Arachnactidae), and of the data available in the existing literature, it is concluded that the Ceriantharia may be subdivided into 2 suborders, for which the names Spirularia and Penicillaria are proposed. The Spirularia include the Cerianthidae and the Botrucnidiferidae. The Penicillaria include the Arachnactidae only. Diagnoses of the newly proposed suborders are given in addition.

INTRODUCTION

The Ceriantharia are generally considered to be a small order of Anthozoa. Only a few dozen species based on adult bottom dwelling forms, belonging to 3 families and 8 genera, have been described. Their obscurity is at least partly due to their buried way of life and their often nocturnal habits. The discovery of many more species is to be expected, as may be deduced from the fact that about twice as many larval forms as adults are known. Leloup (1964: 254, 268, 280) enumerated 31 genera based on larvae, and at least one new genus has been described since (Leloup, 1968: 6).

Reports on Ceriantharia from the Caribbean region in particular are very scanty. Verrill (1901: 47, pl. 9 fig. 16) incompletely described a species from Bermuda, *Cerianthus natans*, which has never been collected since. Duerden (1902: 329-330) reported a species from Puerto Rico, which he could not identify, since the single specimen was badly damaged, the lower part of the column being torn off. He explicitly stated, however, that it was not *Cerianthus americanus* Verrill, 1864 (:32-33). The latter species was described and repeatedly reported since from the U. S. east coast (a.o. McMurrich, 1887: 63; 1890; Parker, 1900: 756; Field, 1949: 19); later it was designated by Carlgren (1912a: 41) as the type of the monotypic genus *Ceriantheopsis*. Cary (1906: 51) reported *Cerianthus americanus* from the Louisiana Gulf Coast (Chandeleur Islands) but as he gave no descriptive data, his record is not fully reliable. Pax (1910: 168) reported the species from Bird Key (Tortugas), but as he failed to study the anatomy of the single specimen at his disposal, due to its poor condition, his identification has also to be regarded with the greatest reserve. In 1924 (:118) Pax reported *Ceriantheopsis* spec. from Curaçao, but again he did not give any substantial proof that it really concerned a *Ceriantheopsis*.

A re-examination of the material from Curaçao studied by Pax (ZMA s.n., 4 lots) showed that it actually belongs to *Arachnanthus nocturnus* n. sp., described in the present paper.

The only fairly reliable record of a Caribbean cerianthid dates from Carlgren & Hedgpeth (1952: 169-170) and concerns 2 specimens of *Ceriantheomorphe brasiliensis* Carlgren 1931, (:2-6) from the northwestern Gulf of Mexico. Carlgren & Hedgpeth stated that morphology and anatomy agreed with the type of *Ceriantheomorphe brasiliensis*, but considered the possibility that the specimens from the Gulf of Mexico might represent a different species, as no data of the nematocysts of the type were available. They apparently neglected to compare the nematocyst data of their specimens with those given by Carlgren himself (1940: 12) of a topotypical specimen from São Paulo. These data agree rather well and therefore the identification is probably correct.

The present paper deals with the descriptions of 2 hitherto undescribed Caribbean species, *Pachycerianthus curacaoensis* and *Arachnanthus nocturnus*. Furthermore the cnidom and the classification of the Ceriantharia are discussed.

TERMINOLOGY

The terminology used in the study of the Ceriantharia is rather complicated, and actually not yet well established, which is at least partly due to the fact that various authors have applied different names to similar or almost similar concepts. A useful survey of the terminology is given by Arai (1965: 210-216). In the descriptions given here, I have tried to avoid the use of certain terms, notably with regard to the filamental differentiations; the existing terminologies being confusing rather than elucidating. Besides I have avoided the use of the terms proto- and metamesenteries, while a new term, pseudo-cycle, is introduced with regard to the tentacular arrangement (see remarks 1 and 2 at the end of this chapter). For the rest I have mainly followed Carlgren (1912a), whose paper undoubtedly is the most important survey of the general structure and classification of the Ceriantharia.

Concerning the nematocysts, the classification used in the present paper differs slightly from that of Schmidt (1969; 1972: 427-433). Besides, I have replaced the term holotrich by homotrich and instead of the terms b- and p-rhabdoids used by Schmidt, I prefer to use the terms spirulae and penicilli, introduced by Stephenson (1928: 62-63), which cover exactly the same concepts (Den Hartog; in press). I like to add here two remarks.

Remark 1 concerns the terms proto- and metamesenteries and their use in the taxonomy of the Ceriantharia. Since McMurrich's (1910) and Carlgren's (1912a) studies it has become common practise to distinguish between proto- and metamesenteries in descriptions of Ceriantharia. The metamesenteries are those mesenteries which regularly develop, couple after couple, in the so-called multiplication chamber. The protomesenteries, the first few couples to develop, originate in a different sequence. Opinions differ whether the first 3 couples (Carlgren, 1912a: 50, 54-59) or the first 4 couples (McMurrich, 1910: 5-9) have to be considered as protomesenteries, and a statisfactory solution of this problem is still wanting. The differing opinions of McMurrich and Carlgren led to unnecessary complications. Following Carlgren's conception, the arrangement of the so-called metamesenterial quartets can be given as mbMB; according to McMurrich it would be BmbM. Apart from practical difficulties involved in the use of the terms proto- and metamesenteries, I fail to see why these terms are at all necessary in taxonomic descriptions, even though they may be relevant in ontogenetic studies. Actually it is peculiar that these terms have entered Ceriantharian taxonomy and are still in use there (e.g. Arai, 1971), while they are not used with regard to other Anthozoan groups, although the distinction between proto- and metamesenteries has been made in Anthozoa in general.

Remark 2 concerns the introduction of the term pseudo-cycle. The principal mesenterial arrangement in the predominantly — although never perfectly — radially symmetrical Hexacorallia is in pairs, which originate in subsequent cycles of different order, each cycle being normally built up of members of about the same age and stage of development. The mesenterial cycles correspond to tentacular cycles, which are also of about the same age and development. A more or less distinct arrangement of the tentacles in cycles of different order is as a rule also obvious in the Ceriantharia. Unlike the other orders of Hexacorallia, however, the Ceriantharia principally have bilateral symmetry; the mesenteries are not arranged in pairs but exclusively in couples, which one after the other develop in the single multiplication chamber. Consequently they can impossibly be grouped in cycles; the tentacular cycles of the Ceriantharia therefore can not be ascribed the same significance as in the other Hexacorallia. For this reason I prefer the use of the term pseudocycle. For an explanation of the terms pair and couple I refer to Stephenson (1928: 45-47).

MATERIAL AND METHODS

Most material used for the description of the 2 new species was selectively collected on the south coast of Curaçao (Netherlands Antilles) with the aid of snorkle- and SCUBA-diving gear. The material was preserved in about 8-10% formalin in sea-water, when possible after being relaxed in menthol, to which the animals appeared to be very sensitive. Most material has been deposited in the Rijksmuseum van Natuurlijke Historie at Leiden (RMNH). Paratypes of both species have been donated to the U. S. National Museum of Natural History in Washington (USNM).

For a better understanding of the cnidom and the classification of the Ceriantharia, several other species (identified as well as unidentified) present in U. S. National Museum of Natural History (USNM) and Rijksmuseum van Natuurlijke Historie (RMNH), were also studied.

In conformity with common practice the descriptions of the general anatomy are based on longitudinally dissected specimens. For this purpose specimens were relaxed in menthol, cut longitudinally, laid open, fastened with pins to a paraffin-wax plate and either studied alive and preserved afterwards, or first preserved and then studied. Preparation in the manner described above is to be recommended for general anatomical purposes. Due to the hardening properties of the preservative with regard to the mesogloea, the specimens thus always remain in a favourable condition for a study of the general anatomy. Besides, this method ensures quick penetration of the preservative (fixative) in the internal organs. If previously preserved specimens are longitudinally cut and pinned down, the same hardening properties, notably after a long time of preservation, will generally make proper dissection difficult or even impossible and may increase the risk of damage to the specimens involved.

The nematocysts were studied by means of squash-preparations of living tissue in sea-water. These preparations were examined with a phase-contrast microscope, using a magnification of 1000 × (Oil-immersion 100 ×, ocular 10 ×). Additional preparations of preserved tissue were studied with an interference-contrast microscope. Measurements were made with an ocular micrometer 5 mm/100.

Although the study of nematocysts preferably should be performed on living tissue, this is not always possible, notably when working with museum specimens. If specimens have to be preserved for a later study of the nematocysts, fairly concentrated formalin in sea-water (ca. 6-10%) is an acceptable preservative, particularly as it keeps the ecto- and endodermal tissues soft and easy to squash, this unlike alcohol and bouin, which tend to toughen these tissues.

Pachycerianthus curacaoensis n. sp. (figs. 1, 2; pl. 2 fig. 2, pl. 4 figs. 2-4, pl. 5)

Material examined.

CURAÇAO. — Southcoast, between Piscadera Bay and Blauw Bay, on a flat sandy-mud bottom ca. 65 to 75 meter deep, leg. P. Creutzberg Jr. and H. de Windt: RMNH coel. 11357 (17 May 1972; damaged specimen and tube); RMNH coel. 11358 (8 February 1973; 1 juvenile, length 6 mm, and 2 longitudinally dissected adult specimens with commensal phoronids); RMNH coel. 11359 (holotype; 17 May 1972; in longitudinally dissected tube with commensal phoronids); RMNH coel. 11360 (15 March 1973; 2 damaged specimens and 1 complete, longitudinally dissected specimen, with tubes; pl. 4 fig. 2-4); RMNH coel. 11361 (22 February 1973; 4 damaged specimens with tubes); USNM 54236 (17 May 1972; corresponding with RMNH coel. 11357, 1 specimen plus tube and commensal phoronids); USNM 54237 (15 March 1973; corresponding with RMNH coel. 11360, 1 longitudinally dissected specimen). Colour slides of part of this material are present in RMNH.

Description. — Tube (pl. 2 fig. 2, pl. 4 figs. 2, 4): Thickwalled, soft, tough and very flexible, consisting of numerous thin, closely packed sheets of discharged nematocysts (atrichs), not incrusted with sand or other foreign material. Diameter up to about 35 mm, length up to ca. 250-300 mm. Inner surface smooth; outer surface with loose rags of torn nematocyst sheets. A small quantity of sand and gravel adheres to the blind end of the tube.

Body: Smooth, very variable in length, depending on the state of contraction or expansion. Large specimens in expanded state reach a length of ca. 130 mm (the holotype) and a diameter of about 15 mm, distally slightly wider.

Oral disc and tentacles: Both marginal and labial tentacles slender in life, filiform when preserved; marginal tentacles more or less distinctly arranged in 3 pseudo-cycles, ca. 25 to 35 mm long in preserved material (much longer in life), the number varying between 74 and 105 (in 5 well developed specimens examined). Labial tentacles more or less arranged in 5 pseudo-cycles, ca. 10-12 mm long, the number varying from 76 to 118. A conspicuous naked area of about 5-9 mm is situated between the marginal and the labial tentacles.

Colour and pattern: Body yellowish brown or faint purplish brown, distally often darker. A faint orange lining may be present at the mesenterial insertions. Naked area on the oral disc between marginal and labial tentacles dark purple to dark purplish brown, but the radii may show differences in colour intensity. Mesenterial insertions on the oral disc darker than the radii. Marginal tentacles purple, yellowish brown or whitish with a purple tip, devoid of any pattern or with a single longitudinal row of about 8 to 12 fine white spots on the oral face (pl. 2 fig. 2). Labial tentacles white, with a greyish to brownish base.

Anatomy (fig. 1). — Stomodaeum: Short, not exceeding 10 mm in length in the largest specimen examined, extending over about 1/8 to 1/12 of the total length of the body, provided with fine, longitudinal ridges, which become more conspicuous and thicker towards the free edge of the stomodaeum and which are continuous with the mesenterial filaments. Sulcus smooth, connected with the first 2 mesenterial couples (i.e. the directives and an additional couple), aborally with a short, about 2 mm long hyposulcus and distinct hemisulci.

Mesenteries: Arranged in distinct quartets, each quartet (Q) consisting of 2 long fertile macromesenteries (m,M) and 2 short sterile micromesenteries (b,B); arranged BmbM. Superimposed on this arrangement there is a gradual decrease in length of the mesenteries of all four categories towards the multiplication chamber. Irregularities, however, occur frequently. In the specimen of fig. 1 (RMNH coel. 11358) Q_3 was aberrantly small (notably with regard to couple m_3 and couple M_3). In a second specimen this condition was found in Q_2. In a third specimen Q_2 was small, while Q_7 was unusually well developed.

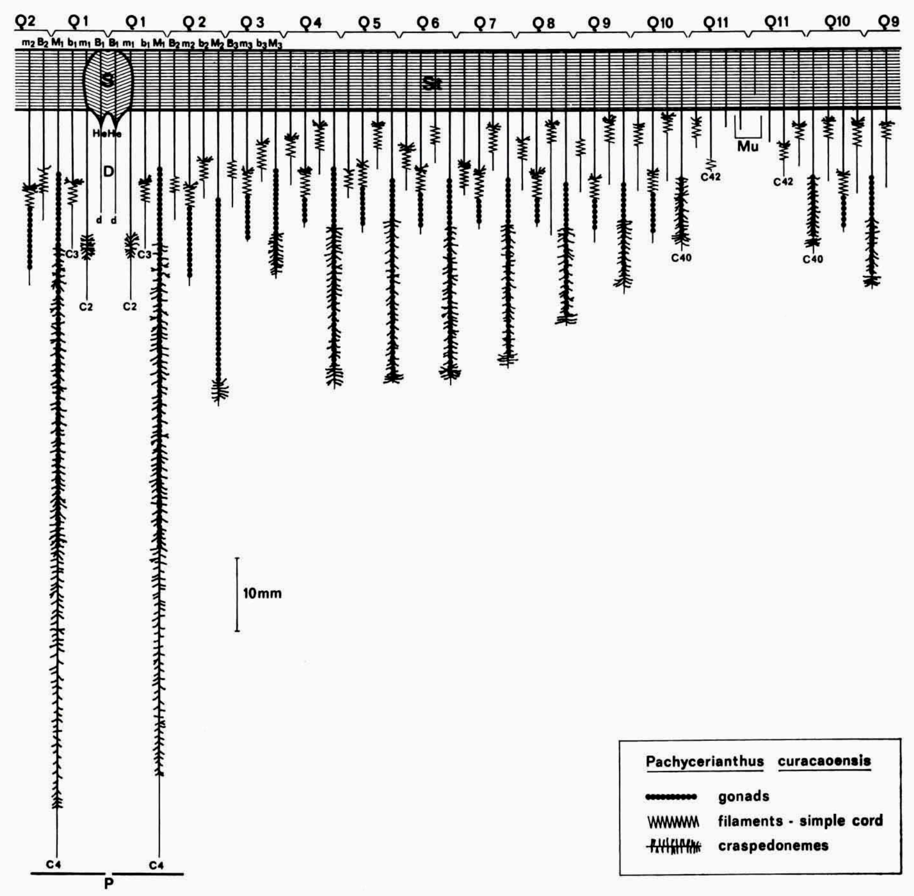

Fig. 1. *Pachycerianthus curacaoensis* n. sp. Schematic representation of the arrangement of the mesenteries in a well developed, longitudinally dissected specimen (RMNH coel. 11358). The indicated scale is exclusively relevant with regard to the length. Explanation of the symbols: $b_{1, 2, 3, \text{etc.}}$ = brachycnemes or micromesenteries (relatively short); $B_{1, 2, 3, \text{etc.}}$ = brachycnemes or micromesenteries (relatively long); $C_{2, 3 \text{ etc.}}$ = mesenteries belonging to couple 2, 3 etc.; d = directive mesenteries = mesenterial couple 1 = mesenterial couple B_1; D = directive chamber; He = hemisulci; $m_{1, 2, 3, \text{etc.}}$ = macrocnemes or mesenteries (relatively short); $M_{1, 2, 3, \text{etc.}}$ = macrocnemes or macromesenteries (relatively long); Mu = multiplication chamber; P = terminal porus; $Q_{1, 2, 3, \text{etc.}}$ = mesenterial quartet 1, 2, 3 etc.; S = sulcus; St = stomodaeum.

The b- and B-mesenteries bear adorally a double cord of filament which usually merges aborally through a few craspedonemes into a short but distinct, much coiled, simple cord, connected with the broadened, thin and flabby portion of the mesentery. In the m-mesenteries a similar situation is to be observed, with the exception that a tract of gonads is present aborally of the short simple cord. In the M-mesenteries the double cord of the filament merges aborally into a long tract of craspedonemes, which are usually concentrated in a distinct bunch at the end of the mesenteries; the development of the gonads of these mesenteries usually begins within the reach of the double filamental tract, to continue aborally all along the mesentery.

Q_1 deviates from the general picture. Couple B_1 (directive mesenteries) is devoid of filaments. Couple m_1 is sterile, provided with a relatively well developed bunch of craspedonemes, and lacks the much coiled simple cord. Couple b_1 conforms to the usual condition found in the other b-mesenteries. Couple M_1 finally also principally conforms to the situation of the other M-mesenteries. However, the members of this couple are unusually long, extending aborally up to the terminal porus (so-called continuous mesenteries or telocnemes), they are not provided with a distinct terminal bunch of craspedonemes, and their gonads do not extend all along the mesentery. For a good impression of the proportions of the various mesenteries and of the distribution of gonads, filaments, etc., see fig. 1.

Cnidom (fig. 2; pl. 5): Spirocysts, atrichs, homotrichs and spirulae are present. Penicilli are absent.

The following specified survey of the cnidom was taken from a well developed specimen from the type-locality (RMNH coel. 11361). The data relating to the nematocyst types indicate respectively: average size and range (between brackets) in microns, number of capsules measured, and abundance.

I. Column (upper part):

a. Atrichs	:	57.2 (49.5-66) × 22.3 (17.8-26.4)	20	very numerous
b. Atrichs	:	32.1 (31.7-33) × 9.9 (8.6-11.9)	10	rather common
c. Homotrichs	:	56.8 (53.4-60.7) × 18.1 (15.2-21.1)	20	rather common
d. Spirulae 2	:	38 (35.6-43.6) × 7.5 (6.6-9.2)	20	rather common
e. Spirulae	:	35.8 (33-38.9) × 5.6 (5-5.9)	20	common
f. Spirulae 2	:	20.3 (17.2-25.1) × 4.1 (4-4.6)	20	rather common

II. Marginal tentacles (tips):

a. Spirocysts	:	31.3 (19.8-39.6) × 4.3 (2-5.9)	20	numerous
b. Spirulae 2	:	36.5 (33-38.9) × 9.1 (7.3-10.6)	20	numerous
c. Spirulae	:	27.9 (24.4-29.7) × 4.5 (4-4.6)	20	common
d. Spirulae 1	:	25.7 (19.8-29.7) × 4.4 (3.3-5.3)	20	numerous

III. Labial tentacles (tips):

a. Spirocysts	:	32.4 (26.4-39.6) × 4.7 (3.6-7.3)	20	very numerous
b. Atrichs	:	30 (27.1-33) × 5.5 (5.3-5.9)	20	common
c. Spirulae 2	:	34.4 (29.7-37.6) × 5.8 (5.3-7.3)	20	common
d. Spirulae	:	23.1 (21.1-24.4) × 3.2 (2.6-3.3)	20	common
e. Spirulae 1	:	20.3 (17.8-24.4) × 2.9 (2.6-3.3)	20	common

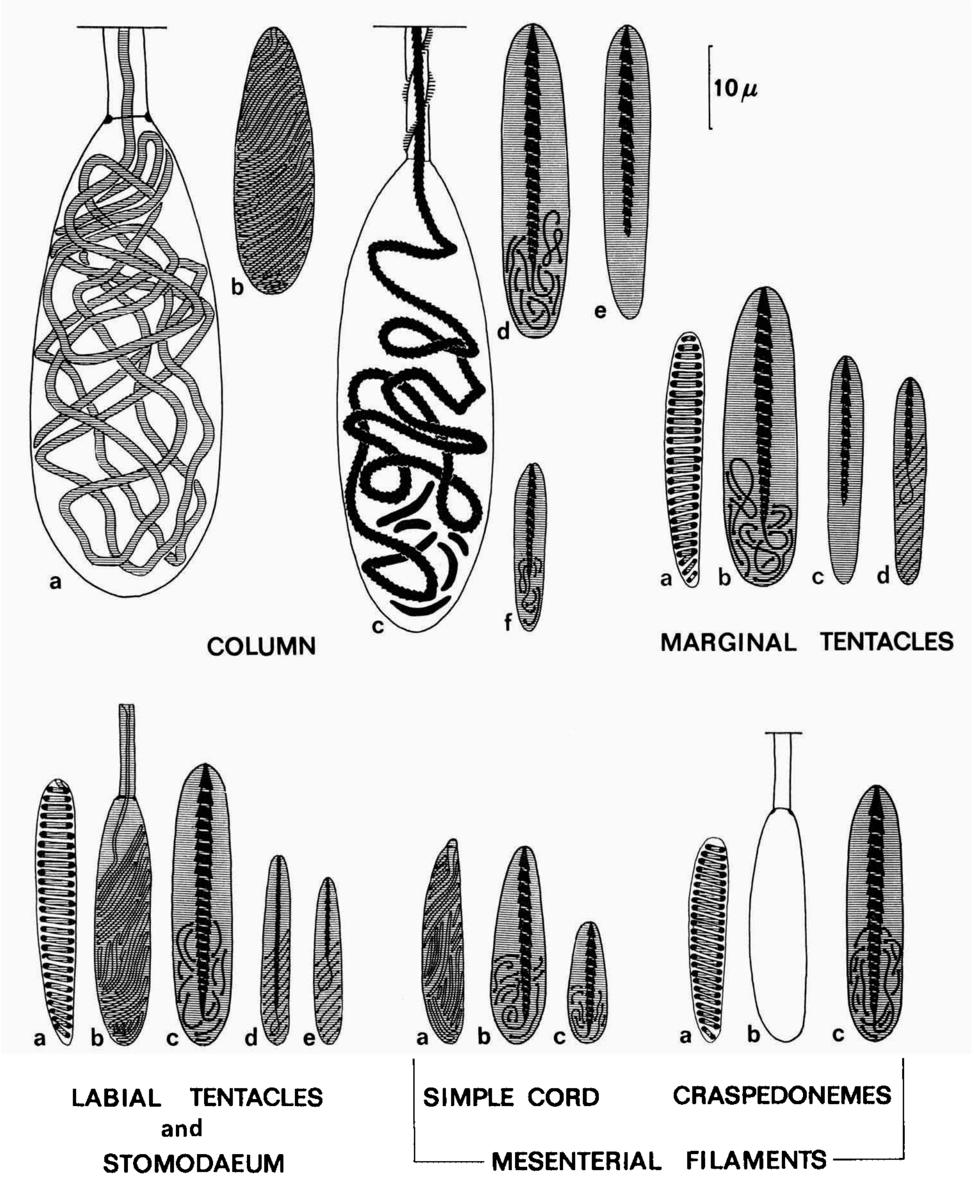

Fig. 2. *Pachycerianthus curacaoensis* n. sp. Pictorial survey of the cnidom. The letters in the figure correspond to those used in the text. Column (I) : a, atrich (in progressed state of discharge) ; b, atrich ; c, homotrich (in progressed state of discharge) ; d, spirula 2 ; e, spirula (immature stage of f?) ; f, spirula 2. spirula 2. Marginal tentacles (II) : a, spirocyst ; b, spirula 2 ; c, spirula (immature stage of d?) ; d, spirula 1. Labial tentacles (III) and Stomodaeum (IV) : a, spirocyst ; b, atrich (at the beginning of discharge) ; c, spirula 2 (shaft in discharged state ca. 1.25-1.5 × the length of the capsule) ; d, spirula (shaft in discharged state ca. 1.75 × the length of the capsule) ; e, spirula 1. Mesenterial filaments—simple cord of the b- and B-mesenteries (V) : a, atrich ; b, spirula 2 ; c, spirula 2. Mesenterial filaments—Craspedonemes of the M-mesenteries (telocnemes-C4) in the lower part of the body (VI) : a, spirocyst ; b, atrich (completely discharged) ; c, spirula 2.

IV. Stomodaeum:

a. Spirocysts	: not measured		uncommon
b. Atrichs	: 30.8 (29-34.3) × 6.3 (5.3-7.3)	20	common
c. Spirulae 2	: 34.3 (27.1-41.6) × 6.3 (5.3-7.3)	20	common
d. Spirulae	: 24 (21-26.4) × 3.8 (3-3.4)	20	rather common
e. Spirulae 1	: 22.6 (20.5-27.1) × 3.4 (3.3-3.6)	20	rather common

V. Mesenterial filaments - Simple cord of the b- and B-mesenteries:

a. Atrichs	: 24.3 (22.4-26.4) × 4.9 (4.6-5.3)	20	uncommon
b. Spirulae 2	: 23.8 (21.8-25.7) × 6.3 (5.9-7.3)	20	numerous
c. Spirulae 2	: 15.3 (13.9-17.2) × 4.8 (4-5.3)	20	rather common

VI. Mesenterial filaments - Craspedonemes of the M1-mesenteries (telocnemes-C4) in the lower part of the body.

a. Spirocysts	: 25 (21.1-29) × 3.4 (3.3-4)	20	common
b. Atrichs	: 28.8 (23.1-33.7) × 5.6 (5.3-6.6)	20	uncommon
c. Spirulae 2	: 32.4 (29-40.3) × 5.7 (5.3-6.9)	20	common

In addition an almost complete survey of the cnidom of one other well developed specimen was obtained (USNM 54236). The nematocysts of this specimen were on the average somewhat smaller than those listed above. This was particularly conspicuous with regard to the atrichs and the homotrichs in the column (atrichs: 39.4 (29.7-44.9) × 13.6 (8.6-16.5); homotrichs: 42.5 (35.6-48.1) × 11.1 (9.2-14.5); 20 capsules of each type measured).

Details were checked in several other specimens. It was not easy to get a correct impression of the cnidom of this species. Some of the less common, but characteristic categories were not found in all squash preparations examined of a particular organ. Spirocysts are apparently totally absent in the column and also in the simple cord of the filaments. It was possible to distinguish between several classes of spirulae on the basis of the length of the shaft. In the simple cord of the mesenterial filaments of the b- and B-mesenteries spirulae of a distinct ovoid shape (Vb, c) were found. Certain spirulae of the column (Ie) (pl. 5 figs. 1, 3) and of the marginal tentacles (IIc) are in undischarged state characterised by a rather loosely arranged shaft, while it is also extremely difficult to discern a terminal tube. These characters indicate as a rule immaturity of capsules. Taking into consideration that the capsular content of the immature capsule undergoes a process of contraction before maturity is reached and also that the capsule reduces in size during this process, it may be assumed that Ie is the juvenile stage of If and that IIc will ultimately develop into IId, but there is no definite proof for this.

For the time being I have provisionally kept these ill-defined groups of capsules separately.

The cnidom of the stomodaeum and that of the labial tentacles were found to differ only with regard to the ratio in number of the various categories of nematocysts. Types and size classes were identical.

Small atrichs were found in all organs except in the tips of the marginal tentacles; in the lower part of these tentacles they appeared to be present in modest numbers.

Biological notes. — Habits and way of life: According to the collectors (Mr. P. Creutzberg Jr. and Mr. H. de Windt) the tubes were buried in the bottom, in a J-shaped curve, not fixed to stones or other foreign material, and as a consequence they were easy to collect. The population density at the type-locality was estimated by the collectors to be about 2 specimens per m^2. The species was found to be expanded during the daytime, but this fact is not likely to be of relevant significance as the species was collected at a depth of about 65 to 75 meters.

Commensalism: Phoronids were found on the inside of the tube of several specimens, located under the most superficial nematocyst sheets. It seems doubtful whether the calcareous worms found on some of the tubes (pl. 4 fig. 2) have to be considered as commensals.

Arachnanthus nocturnus n. sp. (figs. 3-5; pl. 1, pl. 2 fig. 1, pl. 3, pl. 4 fig. 1, pl. 6)

Material examined.

BONAIRE. — Little Bonaire, eastside, opposite Kralendijk, on sandy bottom under a stone among *Acropora cervicornis* (Lamarck), depth ca. 1 meter: RMNH coel. 11372 (16 April 1973, leg. J. C. den Hartog; 1 juvenile without tube).

CURAÇAO. — Southcoast, Piscadera Bay, in front of Caribbean Marine Biological Institute, between the entrance of the "inner" Bay and Hilton Hotel, on sandy bottom with gravel, shells and dead coral boulders, depth ca. 1-5 meters: RMNH coel. 11362 (holotype; 21 February 1973, leg. P. Creutzberg Jr. and J. C. den Hartog; adult fertile 22 cm long specimen devoid of marginal tentacles, rest of the longitudinally dissected specimen in good condition, arrangement of the mesenteries clear, well developed acontioids present at the aboral end of M_2-M_6); RMNH coel. 11363 (21 February 1973, leg. P. Creutzberg Jr. and J. C. den Hartog; upper part of specimen and a number of tubes, including the tube of the holotype); RMNH coel. 11364 (28 November 1972, leg. P. Creutzberg Jr. and H. de Windt; a large specimen (pl. 3 fig. 1), 29 cm long, tube lost); RMNH coel. 11365 (27 March 1972, leg. J. C. den Hartog; oral part of specimen and part of tube); RMNH coel. 11366 (13 September 1972, leg. J. C. den Hartog; oral part of specimen and part of tube); RMNH coel. 11367 (21 February 1973, under stones, leg. J. C. den Hartog; 2 juveniles without tubes); RMNH coel. 11371 (January 1972, under stone, leg. J. C. den Hartog; 1 badly damaged juvenile without tube); USNM 54239 (28 November 1972, see RMNH coel. 11364, longitudinally dissected specimen, 17,5 cm long, with tube); USNM 54240 (21 February 1973, see RMNH coel. 11363, oral part of specimen).

Southcoast, between Piscadera Bay and Blauw Bay, sandy bottom in shallow water: RMNH coel. 11375 (9 December 1972, leg. P. Creutzberg Jr.; 1 fertile specimen (fig. 3), 11.5 cm long).

Southcoast, Playa Hundu, on sandy bottom under stones among dead stems of *Acro-*

pora palmata (Lamarck), ca. 1 meter depth: RMNH coel. 11368 (12 March 1972, leg. J. C. den Hartog; 3 juveniles without tubes).

Southcoast, Caracas Bay, under stones along the shore: ZMA s.n. (3 May 1920; leg. C. J. van der Horst; 7 juveniles, 1 with tube); ZMA s.n. (18 May 1920 leg. C. J. van der Horst; 4 juveniles, without tubes).

Southcoast, Spaanse Haven: ZMA s.n. (6 May 1920, leg. C. J. van der Horst; 1 juvenile and part of tube); ZMA s.n. (20 May 1920, leg. C. J. van der Horst, 2 juveniles with tubes; original label lost).

Northcoast, Boca Playa Canoa, eastside, in deep hole in the rocks under stone in sand: RMNH coel. 11370 (21 February 1972, leg. J. C. den Hartog; 2 juveniles without tubes).

JAMAICA. — Rackham's Cay, Port Royal: USNM 54238 (6 September 1960, don. I. Goodbody; 1 juvenile without tube).

PUERTO RICO. — Southcoast, Parquera, Henrique reef, in *Thalassia*-field ca. 1 meter depth: RMNH coel. 11369 (11 September 1973, leg. C. Arneson and J. C. den Hartog; 1 juvenile without tube).

Colour slides of specimens in situ at the type-locality are present in RMNH.

Description. — Tube (pl. 3 fig. 1): More or less felty to soft cardboard-like in texture, fragile; consisting of several sheets of discharged nematocysts (mainly atrichs), encrusted with sand and fine shell- and coral-gravel. In places the sheets of nematocysts are completely separated by a thin layer of this material. The oral part of the tube, surrounding the open end, is flexible and not, or at least in a much lesser degree, encrusted with foreign material. Diameter of the tube up to ca. 65 mm, length up to ca. 650 mm; inner surface smooth and shiny; outer surface with much adherent sand and gravel.

Body: Firm, smooth, with fine longitudinal grooves, very variable in length, depending on the state of contraction or expansion. Large specimens in expanded state reach a length of about 300 mm and a diameter of ca. 35 mm, distally slightly wider.

Oral disc and tentacles: Both marginal and labial tentacles rather firm in life as well as in preserved condition. Marginal tentacles up to 54 in number, arranged in 2 pseudo-cycles, about 1 to 4 cm long in preserved specimens, but able to extend greatly in life (pl. 1). Labial tentacles much shorter than the marginal ones, and their number apparently always 2 less; they are arranged in 3 pseudo-cycles in addition to which there are 2 isolated tentacles,

Fig. 3. *Arachnanthus nocturnus* n. sp. Schematic representation of the arrangement of the mesenteries in a rather small, longitudinally dissected specimen (RMNH coel. 11375). The indicated scale is exclusively relevant with regard to the length of the specimen. Explanation of the symbols: Ac = acontioids; $B_{1,\,2,\,3,\,\mathrm{etc.}}$ = brachycnemes or micromesenteries; $c_{2,\,3,\,\mathrm{etc.}}$ = mesenteries belonging to couple 2, 3 etc.; d = directive mesenteries = mesenterial couple 1 = mesenterial couple B_1; D = directive chamber; $Du_{1,2,3\ \mathrm{etc.}}$ = mesenterial duplet 1, 2, 3 etc.; Hy = hyposulcus; $M_{1,\,2,\,3,\,\mathrm{etc.}}$ = macrocnemes or macromesenteries; Mu = multiplication chamber; P = terminal porus; S = sulcus; St = stomodaeum.

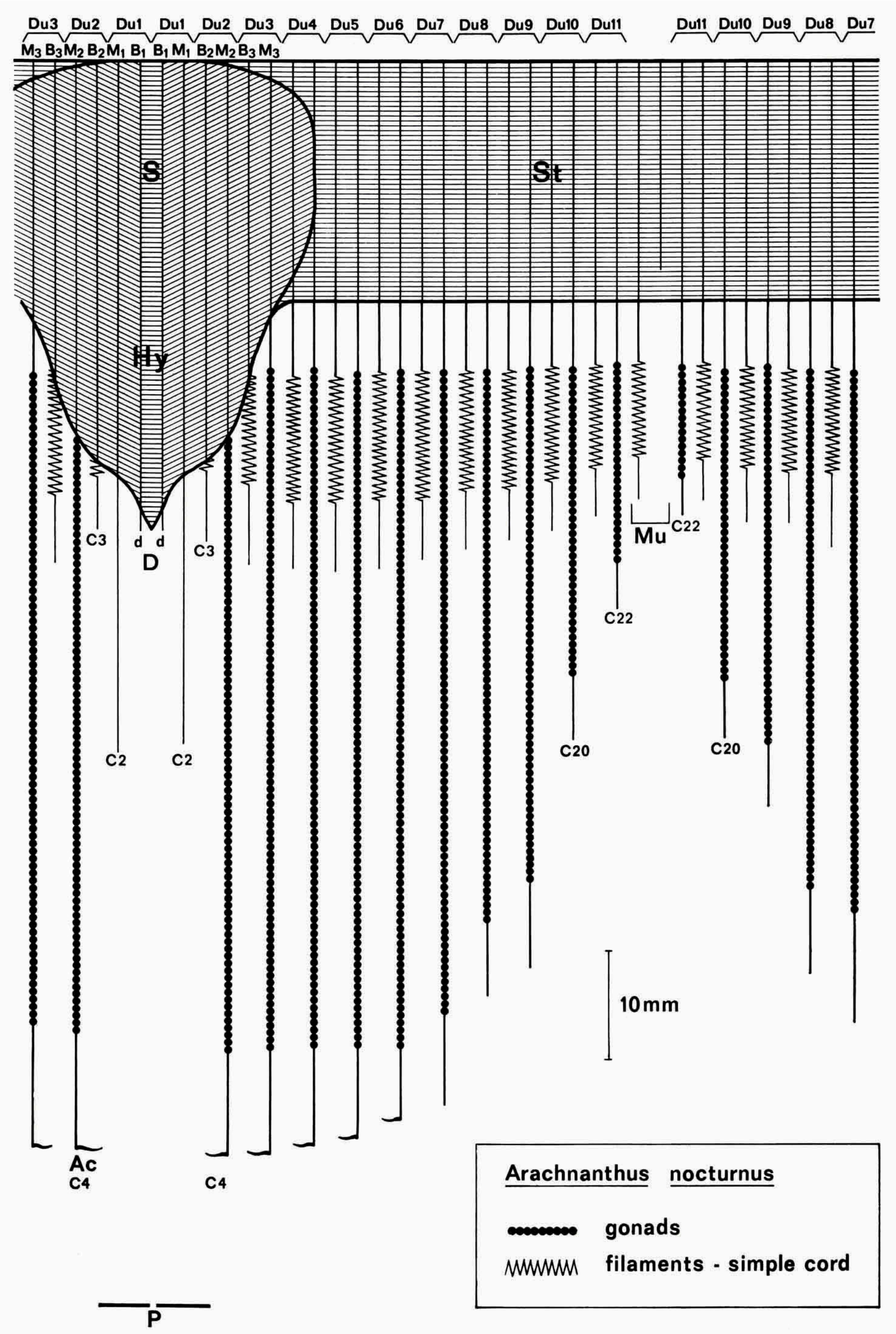

Fig. 3. Explanation see previous page.

placed more inwards and situated on either side of the directive chamber, clearly indicating the symmetry-axis of the body.

Colour and pattern: Body uniformly yellowish brown or with a few dark brown, more or less longitudinally directed streaks; pale near the insertions of the tentacles. Occasionally this region is marked by a pale brown ring, below which there is an almost white ring, about half as wide. Faint emerald green streaks occur between the insertions of the marginal tentacles. The oral disc is generally not markedly coloured; in one specimen a distinct pattern of alternating dark purplish brown radii (corresponding with the labial tentacles), and creamy semi-translucent radii (corresponding with the marginal tentacles), was observed. The marginal tentacles have as a rule a yellowish brown oral face (proximally often more intensely coloured) with pale transverse bars, and a uniformly brownish to almost colourless underside. The labial tentacles are uniformly brownish without crossbars, the oral face darker than the aboral face.

Anatomy (fig. 3). — Stomodaeum: Rather long, about 1/5 to 1/6 of the total length of the body (based on 3 well stretched specimens, in which the lengths of the stomodaeum and the body were respectively: 23 and 115 mm (RMNH coel. 11375), 45 and 290 mm (RMNH coel. 11364) and 30 and 175 mm (USNM 54239)), provided with distinct, longitudinal ridges, which are continuous with the mesenterial filaments. Sulcus broad, connected with about 1/3 of the total number of mesenteries (i.e., about 8 to 10 couples), aborally merging into a long and broad hyposulcus, almost as long as the stomodaeum itself. Although less distinct than in the rest of the stomodaeum, the sulcus is also provided with longitudinal ridges, except for a rather conspicuous smooth tract in connection with the directive chamber (the siphonoglyph proper). Hyposulcus connected with the directives only, but covering about 5 or 6 couples of neighbouring mesenteries; it is bordered by a distinct rim of filamental differentiation and terminates in an acute tip. Hemisulci are absent.

Mesenteries: Arranged in duplets (Du) of alternating short sterile micromesenteries (B) and long fertile macromesenteries (M), i.e., there is no differentiation into M- and m- and B- and b-mesenteries. Superimposed on this arrangement there is a gradual decrease in size towards the multiplication chamber, insignificant in the B-mesenteries, very distinct in the M-mesenteries. The B-mesenteries do not, or only slightly, extend below the hyposulcus; they adorally bear a double cord of filament, which below the level of the stomodaeum merges into a much coiled, simple cord. The M-mesenteries bear over almost their entire length a double filamental cord, adorally distinct and thick, aborally gradually becoming very thin. The older

M-mesenteries, to start with couple M_2, extend over the greater part (at least 9/10) of the body and terminate at a short distance of the terminal porus in a simple, short, about 5 to 10 mm long acontioid. Ten of such mesenteries were found in a 115 mm long specimen with 47 mesenteries (RMNH coel. 11375; fig. 3) and in the holotype (RMNH coel. 11362), and 14 in a specimen of 290 mm length and with 54 mesenteries (RMNH coel. 11364). Acontioids are already present in small specimens of a few cm in length.

Du_1 deviates from the general picture. Couple B_1 (directive mesenteries) is sterile, very short and unlike the other B-mesenteries devoid of any trace of filament. Couple M_1 is provided with a thin double cord of filament in conformity with the other M-mesenteries, but unlike these it is relatively short, rather poorly developed and sterile.

Cnidom (figs. 4, 5; pl. 6): Spirocysts, atrichs, spirulae and penicilli are present. Homotrichs are absent.

The following specified survey of the cnidom was taken from a large specimen from the type-locality (RMNH coel. 11364). The data relating to the nematocyst types indicate respectively: average size and range (between brackets) in microns, number of capsules measured, and abundance.

I. Column (upper part):

a. Spirocysts	:	30.4 (29.7-31.7) × 3.9 (3.6-4)	10	uncommon
b. Atrichs	:	88.8 (64.7-95.7) × 17.8 (8.6-21.8)	20	very numerous
c. Atrichs	:	28.5 (23.8-35.6) × 7.9 (6.6-10.6)	20	common
d. Spirulae 1	:	not measured; see marginal tentacles (IIc)		sporadic
e. Spirulae 1	:	not measured; see marginal tentacles (IId)		sporadic
f. Penicilli 2	:	71.4 (67.3-73.9) × 8 (7.3-9.9)	20	rather common
g. Penicilli 1	:	28.9 (23.8-31) × 7.4 (5.3-7.9)	20	common
h. Penicilli 1	:	17.8 (16.5-19.1) × 4.2 (4-4.6)	10	sporadic

II. Marginal tentacles (tips):

a. Spirocysts	:	57.1 (46.9-68.7) × 6 (3.3-11.2)	20	very numerous
b. Atrichs	:	58.8 (46.2-64) × 9.5 (9.2-15.2)	10	uncommon
c. Spirulae 1	:	51.8 (49.5-54.1) × ca. 2.6	10	uncommon
d. Spirulae 1	:	38.9 (34.3-49.5) × 4.5 (4-4.6)	10	rather common
e. Penicilli 2	:	113.9 (105.6-125.4) × 32.6 (28.4-36.3)	15	uncommon
f. Penicilli 2	:	64.5 (59.4-72.6) × 7.6 (6.6-9.9)	20	rather common
g. Penicilli 1	:	18.6 (17.1-21.8) × 4.5 (3.6-5.3)	10	uncommon

III. Labial tentacles (tips):

a. Spirocysts	:	46.5 (29.7-59.4) × 6.4 (3.3-9.2)	20	numerous
b. Atrichs	:	58.8 (46.2-64) × 9.5 (7.9-11.2)	10	rather common
c. Spirulae 1	:	38.4 (36.3-43.6) × 5.6 (5-6.6)	20	rather common
d. Penicilli 2	:	81.5 (68-92.4) × 18.9 (14.5-23.8)	10	uncommon
e. Penicilli 1	:	19.5 (13.2-25.7) × 4.3 (3.6-4.6)	5	sporadic

IV. Stomodaeum:

a. Spirocysts	:	40.3 (26.4-54.8) × 4.9 (3.3-7.3)	10 uncommon
b. Atrichs	:	62.8 (44.9-81.2) × 9.3 (5.9-11.9)	20 common
c. Spirulae 1	:	44.6 (40.9-46.2) × 6.6 (6.3-7.3)	10 uncommon
d. Penicilli 2	:	69.4 (46.2-84.5) × 15 (8.6-19.8)	20 common
e. Penicilli 1	:	16.8 (15.6-19.6) × 4 (3.6-4.3)	5 sporadic

V. Mesenterial filaments - Simple cord of the B-mesenteries:

a. Penicilli 1	:	20.6 (17.8-23.1) × 7.3 (6.6-8.6)	20 numerous
b. Penicilli 1	:	19.1 (17.2-20.5) × 7.6 (6.6-9.6)	20 numerous

VI. Mesenterial filaments - Double cord of the M-mesenteries:

a. Spirocysts	:	32 (26.4-36.3) × 4.4 (3.3-4.6)	20 rather common
b. Atrichs	:	63.6 (56.1-69.3) × 9.5 (8.6-11.2)	20 common
c. Spirulae 1	:	40.5 (38.3-42.9) × 5.3	10 uncommon
d. Penicilli 2	:	84.6 (79.2-102.3) × 15.6 (13.2-18.5)	10 uncommon
e. Penicilli 1	:	25.7 (23.8-27.7) × 5.3 (4.6-5.9)	20 common

VII. Acontioids:

a. Spirocysts	:	25.1 (20.5-33) × 3.9 (3.3-4.6)	10 rather common
b. Penicilli 2	:	102 (72.6-112.2) × 20.7 (13.2-26.4)	20 very numerous
c. Penicilli 1	:	22.7 (15.2-27.7) × 4.8 (4.3-6.6)	10 uncommon
d. Penicilli 1	:	21.3 (19.8-23.8) × 7.3 (6.6-8.6)	10 uncommon

In addition, several other specimens were checked or partly investigated, including juveniles of only a few cm in length. Apart from differences in the size of nematocysts correlated with overall length of the body, no significant differences were noticed.

The dominating types of capsules are spirocysts, atrichs and penicilli in various size-classes. The large penicilli 2 of the column (If) seem to concern a heterogeneous group. In part of these capsules the shaft is of the usual, heavily built type (If_1), while in other capsules the shaft is rather short and thin and the terminal tube often difficult to discern (If_2) (fig. 4; pl. 6 fig. 2).

Spirulae as a rule were found to be uncommon, except in the tips of the labial and marginal tentacles. A very slender type of spirulae, which consequently is easily overlooked and apparently is also quite rare, was found to

Fig. 4. *Arachnanthus nocturnus* n. sp. Pictorial survey of the cnidom (A). The letters in the figure correspond to those used in the text. Column (I): a, spirocyst; b, atrich; c, atrich; d, spirula 1; e, spirula 1; f1, 2, penicilli 2; g, penicillus 1; h, penicillus 1. Marginal tentacles (II): a1, 2, spirocysts (about indicating the range in size); b, atrich (at the beginning of discharge); c, spirula 1; d, spirula 1; e, penicillus 2 (shaft in discharged state about 18-20 × the length of the capsule; ratio folded portion: shaft s.s. = ca. 4-5 : 1); f, penicillus 2 (shaft in discharged state about 2 × the length of the capsule); g, penicillus 1 (shaft in discharged state about 1.2 × the length of the capsule).

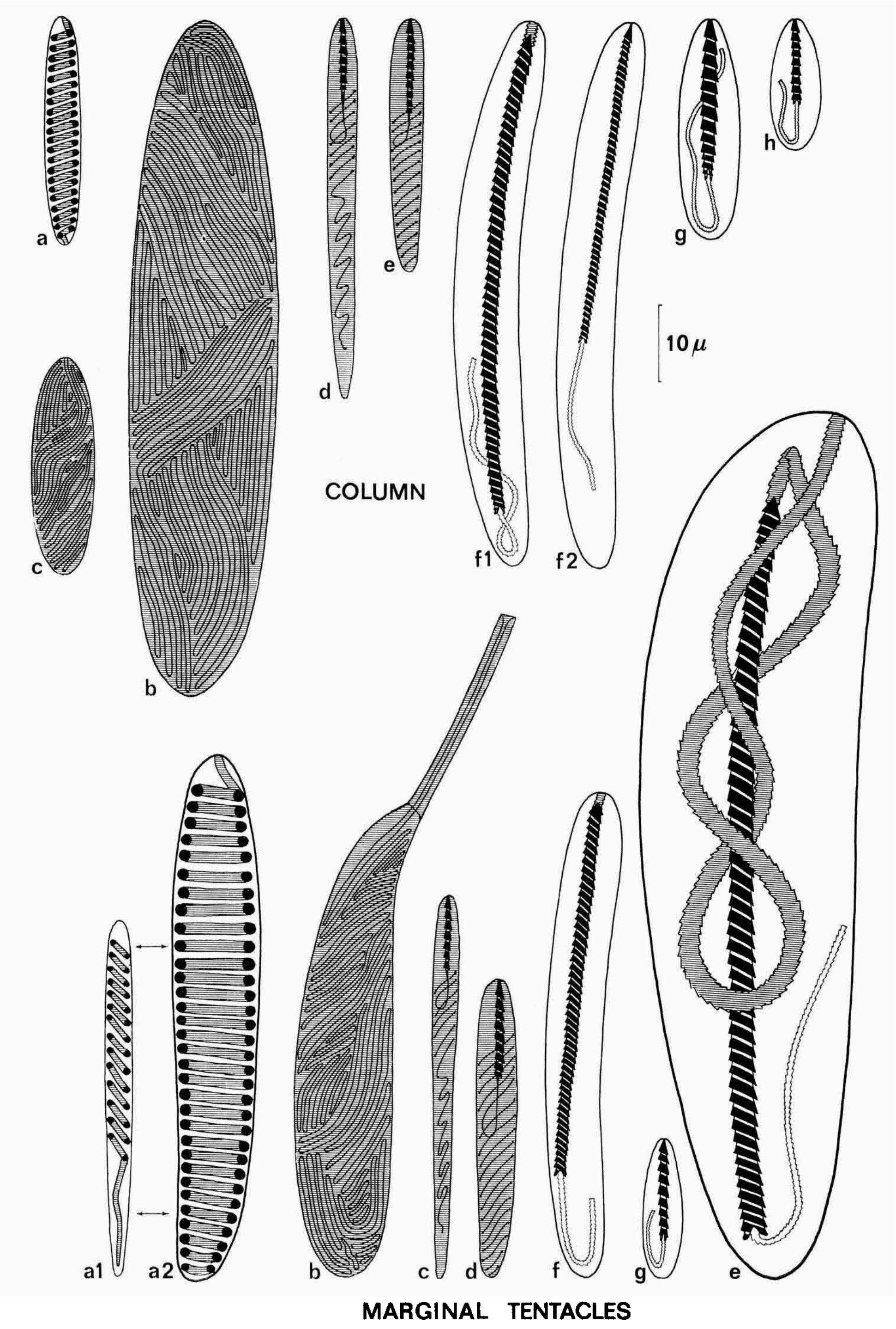

Fig. 4. Explanation see previous page.

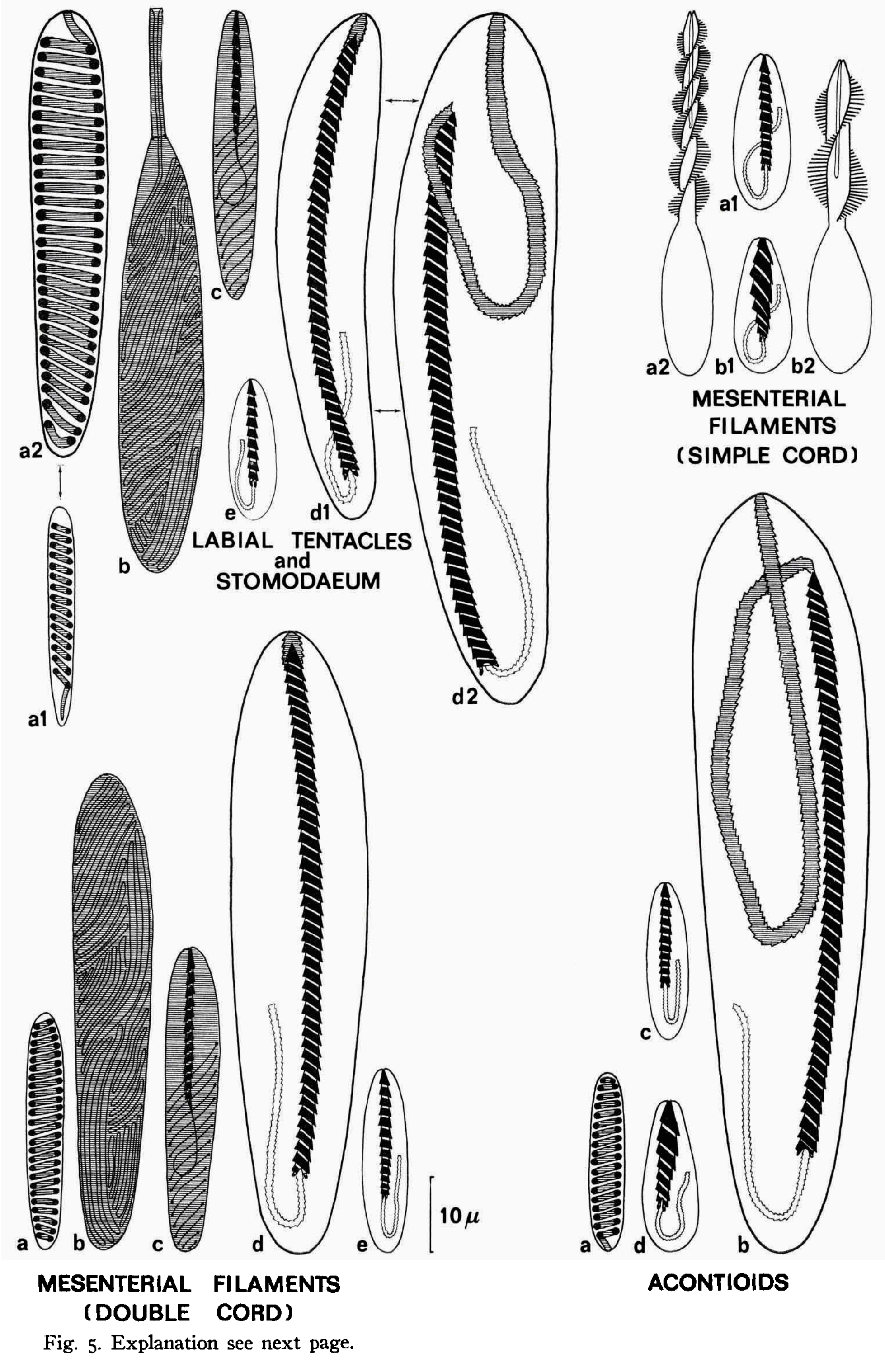

Fig. 5. Explanation see next page.

be characteristic of the marginal tentacles (IIc) and (in even smaller numbers) of the upper part of the column (Id).

In conformity with the former species, *Pachycerianthus curacaoensis* n. sp., the cnidom of the labial tentacles and the stomodaeum was found to be essentially similar, the ratio in number of the various categories of nematocysts being the only point of difference.

Biological notes. — Habitat and way of life: *Arachnanthus nocturnus* is a nocturnal species, which is only very seldom seen to expand its tentacles by day. It seems to be a true shallow water species. In the evening and during the night the species can be observed to emerge out of its tube for often more than 10 cm, the marginal tentacles greatly expanded (pl. 1) and moving about. When mechanically disturbed (turbulence in the water or actual touching) the animals quickly withdraw into their tubes. The flash of the strobe caused the tentacles to curl spirally (pl. 1, pl. 2 fig. 1) and a repetition of flashes also resulted in the ultimate withdrawal of the anemones into their tubes.

In the few fully developed, adult specimens that were dug out completely, including their tube, the tube appeared to penetrate the bottom for a distance of about 15 to 25 cm and then curved strongly, to run more or less parallel to the bottom surface, at places fixed to buried stones, etc.; as a result the tubes were invariably damaged during collecting. Generally not more than 3 to 7 cm of the tube protrudes above the sand, including the thin, terminal part, which due to its flexible texture usually collapses when the animal withdraws, concealing the opening. Moreover, the part protruding above the sand is often covered with adhering sand, growth of algae, etc., so that the tubes are easily overlooked when the anemones are not expanded.

On one occasion a rather well developed specimen was found out of its tube during the day, just lying on the bottom (RMNH coel. 11375). Small

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Fig. 5. *Arachnanthus nocturnus* n. sp. Pictorial survey of the cnidom (B). The letters correspond to those used in the text. Labial tentacles (III) and stomodaeum (IV): a1, 2, spirocysts (about indicating the range in size); b, atrich (at the beginning of discharge); c, spirula 1 (shaft in discharged state ca. 1 × the length of the capsule); d1, 2, penicilli 2 (about indicating the range in size and showing the variation in the length of the folded portion in relation to the size of the capsules); e, penicillus 1. Mesenterial filaments — simple cord of the B-mesenteries (V): a1, 2, penicilli 1 (undischarged and discharged); b1, 2, penicilli 1 (undischarged and discharged). Mesenterial filaments— Double cord of the M-mesenteries (VI): a, spirocysts; b, atrich; c, spirula 1 (shaft in discharged state ca. 1.25 × the length of the capsule); d, penicillus 2; e, penicillus 1. Acontioids (VII): a, spirocyst; b, penicillus 2; c, penicillus 1 (shaft in discharged state ca. 1.5 × the length of the capsule); d, penicillus 1 (shaft in undischarged state ca. equal to or slightly exceeding the length of the capsule).

specimens with about 12 to 24 tentacles and about 4 to 8 cm long are not rarely found, devoid of a tube, under stones (see material examined; pl. 3 fig. 3).

Commensalism: No commensals were found inside the tube. Polychaetes, Sipunculoids etc., may settle on the outside, but this is almost certainly a matter of available substrate rather than true commensalism. On few occasions a little fish (probably *Apogon* spec.) was seen hiding under and among the tentacles of expanded specimens during the night.

DISCUSSION ON THE CNIDOM OF THE CERIANTHARIA

The nematocysts of the Ceriantharia have recently been discussed by Schmidt (1972: 431-433; 1974: 539-541). On the whole the results of the present study confirm his observations; only little can be added and few objections can be made.

Schmidt has correctly stressed that the cnidom of the Ceriantharia, apart from spirocysts, atrichs and homotrichs, is made up of spirulae and penicilli (Schmidt's b- and p-rhabdoids), though in the majority of species known at present the penicilli are lacking. Carlgren (1940: 49) stated that the rhabdoids of the Ceriantharia exclusively belong to the b-category (i.e. spirulae); paradoxally in the very publication in which he actually proposed to separate both categories (in the Actiniaria). However, it should be noted that Carlgren's opinion was mainly, if not entirely, based on the study of preserved material, and that the difference between the spirulae and the penicilli of the Ceriantharia is less obvious than in any other order of Hexacorallia (Schmidt, 1972: 448-449). Nevertheless, proper examination will always reveal constant characteristic differences; intermediate types are not known to exist.

The penicilli of the Ceriantharia are invariably characterised by a shallow V-shaped notch on the end of the undischarged shaft (figs. 4, 5; pl. 6 fig. 7) and by a very short terminal tube, which after discharge of the capsule remains attached to the tip of the shaft, but does not evaginate (pl. 6 fig. 9). The length of the armature on the shaft does not exceed the diameter of the discharged shaft (pl. 6 figs. 4, 8-10).

Two more or less distinct subtypes may be distinguished among the penicilli:

1. A relatively small capsule of radially symmetrical, often distinctly ovoid, shape. Shaft straight without a folded portion ("Faltstück"—Schmidt, 1969: 294), in undischarged state reaching about 1/2 to 2/3 of the length of the capsule; in discharged state ca. 1 to 1.5 times as long as the capsule. Coils of armature relatively few in number (figs. 4-5; pl. 6 figs. 3-5). This

subtype is characteristic for the simple cord of the filaments, but it also occurs in small quantities in other tissues.

2. A relatively large, distinctly bilaterally symmetrical, slightly curved to distinctly banana-shaped capsule. Shaft with a folded portion of extremely variable length (figs. 4, 5; pl. 6 fig. 6), rarely absent (pl. 6 fig. 2); shaft s.s. in undischarged state as a rule slightly curved and generally reaching about 3/4 to 5/6 of the length of the capsule; in discharged state about 3 to 4 times as long as the capsule. Coils of armature abundant. This subtype is characteristic of all tissues, except the simple cord of the filaments.

The subdivision of the penicilli given here differs from that presented by Schmidt (1972: 433). Schmidt also distinguished between a sub-category without a folded portion (I), and another subcategory with a distinct folded portion (II). However, his subdivision is exclusively based on this difference, and on nothing else. As a consequence Schmidt's penicilli I form a heterogeneous group, including part of the penicilli 2 as defined here and the penicilli 1 (the latter is not clear from Schmidt's description and the accompanying figure 5a, but may be derived from the explanation of his fig. 3b, c).

For practical purposes Schmidt's subdivision into penicilli without and those with a distinct, folded portion may be maintained with regard to the penicilli 2 (2I, without a folded portion; 2II, with a folded portion), but it should be stressed that this difference is actually insignificant and arbitrary. Unlike the situation generally found in the penicilli of the Actiniaria, the presence or absence of a folded portion in the penicilli 2 of the Ceriantharia is not correlated with any obvious additional characters and represents a structure of very variable length (more or less correlated with capsule-size), even within a single organ (see fig. 5: labial tentacles and stomodaeum $d_{1, 2}$).

Schmidt (1972: 432) stated the terminal tube of the penicilli of the Ceriantharia to be anoplotelic (i.e. devoid of armature), as in the Actiniaria. This statement needs confirmation by electron microscope. Light-microscopical investigations strongly suggest the presence of armature (see pl. 6 fig. 7). It is true, that the 3-armed, folded structure (Westfall, 1965: 380) of the undischarged tube of the spirocysts (particularly in large capsules) and of the folded portion of the penicilli 2 of the Ceriantharia (pl. fig. 6) also may give the impression of armature, although these structures are actually completely anoplotelic (pl. 6 figs. 8, 10). However, it should be noted that in these cases it concerns a reticulate structure, (pl. 6 fig. 6), while the terminal tube of the penicilli of the Ceriantharia is characterised by a herringbone structure, as is the armed shaft s.s. (pl. 6 fig. 7).

The spirulae of the Ceriantharia are provided with a shaft of variable length and diameter. A folded portion is rarely present. A well developed hoplotelic (i.e. armed) terminal tube is invariably present. The length of the armature of the shaft does not, or hardly exceed the diameter of the shaft. Although certainly not as obvious as in the penicilli, one might provisionally distinguish 2 more or less distinct subtypes among the spirulae, viz.:

1. A category with a short, slightly refractive, often thin shaft, less than half the capsular length, and with a thin terminal tube, often difficult to observe.

2. A category with a thick, long, strongly refractive shaft and a thick terminal tube which is mainly or entirely contained in the blind end of the capsule. This type may be provided with a distinct hoplotelic folded portion, a condition so far exclusively known from *Pachycerianthus multiplicatus* Carlgren. Thus, in conformity with the penicilli 2, distinction can be made between spirulae 2I (without a folded portion) and spirulae 2II (with a folded portion) (cf. Schmidt, 1972: 431-432).

Unlike the two more definite subtypes to be distinguished within the penicilli, the subtypes of the spirulae are not restricted in their occurrence to certain parts of the body; both categories may occur in the same organ (fig. 2). On the other hand it must be noted that subtype 2 is entirely absent in the Arachnacthidae. In this respect it is striking that the spirulae 2 of *Pachycerianthus curacaoensis* n. sp. and the penicilli 1 and 2 of *Arachnanthus nocturnus* n. sp. not only more or less replace each other in the various organs of both species, but also show certain similarities in size and form. This is quite distinctly seen in the simple cord of the filaments. Here the dominating penicilli 1 of *Arachnanthus nocturnus* and the dominating spirulae 2 of *Pachycerianthus curacaoensis* both display the same radially symmetrical shape, and both may be separated into two more or less distinct size-classes. This parallel between the penicilli of the Arachnacthidae and the spirulae 2 of the Cerianthidae was also noticed by Schmidt (1972: 448) and I fully agree with his conclusion that this parallel is — in terms of phylogeny — strongly in favour of a common origin of both spirulae and penicilli. Schmidt's statement that the origin of the folded portion in both spirulae 2 and penicilli 2 concerns a case of convergence seems a bit rash. It is based on the fact that spirulae 2 with a distinct folded portion are present in the marginal tentacles of *Pachycerianthus multiplicatus*, while a distinct, folded portion is absent in the corresponding penicilli 2 of the marginal tentacles of *Cerianthoides* spec., a species still to be described by Schmidt. The situation observed in *Arachnanthus nocturnus* n. sp., however, is unlike that in *Cerianthoides* spec., completely comparable with that in *Pachycerianthus multiplica-*

tus, i.e., also with respect to the development of the folded portion. Therefore it is not at all unlikely that the folded portion of both spirulae and penicilli of the Ceriantharia is a symplesiomorphous (shared ancestral) character.

The homotrichs of the Ceriantharia are of a very uniform type. In my experience they occur exclusively and invariably in the column of the Cerianthidae (fig 2; pl. 5 fig. 2) and the Botrucnidiferae (8 species checked: *Cerianthus membranaceus* (Spallanzani), *C. lloydi* Gosse, *Pachycerianthus multiplicatus* Carlgren, *P. curacaoensis* n. sp., *Botruanthus benedeni* (Torrey & Kleeberger) and 3 unidentified species). Schmidt (1972: 429) also reported them exclusively from the column. The homotrichs mentioned by Carlgren (1940: 9-14, fig. I 4; 1973: 180, fig. 4d) to occur in the labial tentacles and the stomodaeum of a number of species are undoubtedly spirocysts (the tube of which — as mentioned already — may suggest the presence of armature), as far as they do not concern contaminations.

The atrichs of the Ceriantharia are also of a very uniform kind and occur in all, or practically all parts of the body, being extremely numerous and fairly large in the ectoderm of the column-wall (figs. 2, 4-5; pl. 5 fig. 1, pl. 6 fig. 1). Atrichs are the main constituents of the dwelling tubes of the Ceriantharia. When a cerianthid is removed from its tube, the initial formation of a new tube may instantly be observed in the form of a fresh, thin, opaque, milky white layer around the column, consisting of a fine network of newly discharged tubes of atrichs (pl. 3 fig. 2, pl. 4 figs. 1, 4). The ultimate dwelling tube consists of many of these layers, with or without encrustations of sand and/or other foreign material.

The spirocysts of the Ceriantharia may occur in practically all parts of the body. Their size may be very variable, even within a single organ (see figs. 4, 5).

The Classification of the Ceriantharia

The first attempt to classify the Ceriantharia has been made by Van Beneden (1897), who on the basis of a study of larval forms distinguished between Acontifères (1897: 42 — with acontia) and Botrucnidifères (1897: 113 — with botrucnidae).

McMurrich (1910), studying adults as well as larvae, proposed a subdivision of Van Beneden's Acontifères, based on the position of the oldest couple of so-called continuous mesenteries (i.e. mesenteries which reach or almost reach the aboral end of the Ceriantharian body). He came to the following classification (1910: 23-24):

Order Ceriantharia
Sub-order Acontiferae
  Family Cerianthidae (couple 2 continuous)
  Family Arachnactidae (couple 4 continuous)
Sub-order Botrucnidiferae

The position of the oldest couple of continuous mesenteries appeared so fundamental to McMurrich, that he arranged two genera, exclusively composed of adults without acontia, viz. *Cerianthus* Delle Chiaje and *Pachycerianthus* Roule, among the Acontiferae, apparently assuming that the acontia had disappeared during ontogenesis. This opinion has never been confirmed by facts [1]) and was not accepted by Carlgren (1912a: 38-39), who, also disregarding McMurrich's subdivision of the Ceriantharia into two sub-orders, proposed a new classification of adult Ceriantharia into 3 families, and 6 genera (Carlgren, 1912a: 40-48), to which he added 2 more genera in 1924 (:186) and 1931 (:1). This classification has generally been accepted, and is still in use; at the family-level also in the taxonomy of larvae (e.g., Leloup, 1964; 1968).

Apart from the description of a number of new species no changes or additions above the species-level have occurred since. A survey of Carlgren's classification is given below:

Order Ceriantharia (including 3 families):

1. Cerianthidae (no acontioids; no cnidoragae)
   genera: a. *Cerianthus* Delle Chiaje, 1830: pl. 82 (see McMurrich, 1910: 26, footnote)
   b. *Pachycerianthus* Roule, 1904: 708-709.
   c. *Ceriantheopsis* Carlgren, 1912a: 41.
   d. *Ceriantheomorphe* Carlgren, 1931: 1.
2. Arachnanthidae (acontioids present; no cnidoragae).
   genera: a. *Arachnanthus* Carlgren, 1912a: 41.
   b. *Isarachnanthus* Carlgren, 1924: 186-187.

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[1]) Actually the statements of McMurrich (1910) about the acontia of the Acontiferae are rather conflicting. On page 13 he stated in agreement with Van Beneden:... "In the Acontiferae will be found certain variations in the mesenteries which bear the acontia, and in correlation with these apparently certain other peculiarities of structure. Unfortunately the acontia are in some cases a little late in making their appearance, and some of the larvae obtained do not possess them, but in several cases one or more of the other peculiarities are evident and from these it may be predicted upon what mesenteries the acontia will appear." On page 22 he stated: "The distribution of the acontia has already been described, and concerning their structure I have nothing to add to what has been given by Van Beneden (1898). I have not been able to find them in the adult animals examined".

In agreement with his second statement (but not with the facts) he inserted in the diagnosis of the Acontiferae (:24): "Ceriantheae in which the second or fourth protocnemes or in some cases both these mesenteries, are provided with acontia at least during the early stages of development".

3. Botrucnidiferidae (no acontioids; cnidoragae — as a rule united to form botrucnidae — invariably present)
   genera: a. *Botrucnidifer* Carlgren, 1912a: 42.
   b. *Botruanthus* McMurrich, 1910: 11.

A remark must be made with regard to the family name Arachnanthidae Carlgren (1924: 372). This name was introduced to replace the name Acontiferidae Carlgren (1912a: 41). The correct name for this family, however, is Arachnactidae McMurrich (1910: 23). The family name Arachnactidae was based on *Arachnactis* M. Sars, 1846. This genus — exclusively composed of larval forms — was correctly included by Carlgren in his Arachnanthidae. Arachnanthidae therefore is a junior synonym of Arachnactidae. Other names employed for this family: Cnidonemiæ Van Beneden (1923: 154), Acontiferidae and Acontioidiferidae (see e.g. Leloup, 1964: 268), are also junior synonyms and besides these names do not suffice Art. 10(e) of the International Code of Zoological Nomenclature, as they are not based on any existing genus. As a consequence these names are not available.

The recent separation of the Cerianthidae and the Arachnactidae (Schmidt, 1972: 433; 1974: 539-540) on the basis of the cnidom (presence of absence of penicilli), confirmed by the present study of *Pachycerianthus curacaoensis* n. sp. and *Arachnanthus nocturnus* n. sp., strongly supports the taxonomic validity of both groups. Apart from a fundamentally different cnidom and the presence or absence of acontia (= acontioids), both families show additional differences in a number of anatomical features (see the diagnoses at the end of this chapter), notably with regard to the arrangement of the mesenteries, as is discussed below (see also figs. 1, 3).

Since Faurot (1891: 67-68) discovered and described the distinct arrangement of the mesenteries of *Cerianthus membranaceus* (Spallanzani) in quartets of 2 macromesenteries (M and m), and 2 micromesenteries or brachycnemes (B and b) the idea has generally become established that this arrangement is characteristic of all Ceriantharia. It became common practice to quote this arrangement with the above mentioned symbols (M,m and B,b). As noted in the description of *Arachnanthus nocturnus* n. sp., I did not find the quartet-arrangement in this species, but instead observed a distinct arrangement in duplets. I therefore checked descriptions of all known species of adult Arachnactidae, viz. *Arachnanthus oligopodus* Cerfontaine (1891: 32-38, also Cerfontaine, 1909: 653-700, pl. 24 fig. 16; Carlgren, 1912b: 378-380, fig. 5), *A. sarsi* Carlgren (1912a: 27-30, fig. 5), *A. bockii* Carlgren (1924: 193-194, fig. 16), *A. australiae* Carlgren (1937: 177-180, fig. 1), *Isarachnanthus panamensis* Carlgren (1924: 190-193, figs. 14, 15), and *I. bandanensis* Carlgren (1924: 187-190, fig. 11). Fortunately the arrangement of the mesenteries of all these species has been figured, and from the figures as well as from the descriptions it is clear that all these forms, like *Arachnanthus nocturnus,* are characterised by an arrangement of the mesenteries in duplets, not in quartets. In all cases Carlgren's remarks are of the following tenor: "I have not found any decided grouping in quartets" (*A. sarsi*—1912: 28); "No difference between the oldest M and m" (*A. bockii*—1924: 193), etc.

Apparently preoccupied by the supposition that the arrangement of the mesenteries of all Ceriantharia had to be in quartets, his diagnoses of *Arachnanthus* (1912: 41) as wel as of *Isarachnanthus* (1924: 186-187) equivocally read: "... Arrangement of the metamesenteries in each quartet MBmb more or less distinct.", although particularly his figures are completely in disagreement with this statement.

Only two adult Ceriantharia belonging to the Botrucnidiferidae, viz., *Botrucnidifer norvegicus* Carlgren and *Botruanthus benedeni* (Torrey & Kleeberger), are known. No accurate information on the nematocysts of the Botrucnidiferidae is available in the literature. Nevertheless the survey of the nematocysts of *Botrucnidifer norvegicus* given by Carlgren (1940: 14 fig. 1, 9-11) beyond any doubt indicates a close resemblance with the cnidom of the Cerianthidae (homotrichs present; spirulae 2 present; penicilli absent). Carlgren's survey of the cnidom of *Botruanthus benedeni* (1951: 434) is less reliable, as it is not supported by figures. Fortunately I had the opportunity to investigate the cnidom of this species myself (USNM 49400, 49403, 49411; these are the specimens also studied by Carlgren). The cnidom appeared to be in complete agreement with that of the Cerianthidae.

With regard to the larvae of the Botrucnidiferidae I have checked drawings of nematocysts given by Van Beneden (1898: pls. 10-15 — *Calpanthula* Van Beneden, *Hensenanthula* Van Beneden) and Leloup (1964: pls. 14, 16, 21 — *Angianthula* Leloup, *Cerianthula* Van Beneden, *Hensenanthula* Van Beneden, *Atractanthula* Leloup). All figures, although sometimes very poor, represent spirulae. If penicilli had been present, these would certainly have been figured by the authors as they are more conspicuous; they have actually been figured in the case of several larval Arachnactidae).

Apart from the cnidom, the Cerianthidae and the Botrucnidiferidae also agree in other respects. The original descriptions of *Botrucnidifer norvegicus* and *Botruanthus benedeni* and the accompanying figures indicate an arrangement of the mesenteries in distinct quartets as in the Cerianthidae. The quartet-arrangement in specimens of *Botruanthus benedeni* which I have studied appeared to be even more striking than suggested by Torrey & Kleeberger (1909) in their original description and does not only concern the length of the mesenteries, but also the location and the development of the filamental differentiations, to some extent comparable to the situation found in *Pachycerianthus curacaoensis* n. sp. (see fig. 1). Besides, the mesenteries of both the Cerianthidae and the Botrucnidiferidae may bear craspedonemes and invariably have no acontioids. Actually, the only conspicuous difference between the two groups is the absence or presence of cnidoragae (usually united to form botrucnidae). This difference, however, cannot be considered fundamental. Though very conspicuous structures, the cnidoragae are merely specialised filamental differentiations. In *Botruanthus benedeni* they originate secondarily from the craspedonemes, which themselves are specialised filamental tracts. Considering the fact that craspedonemes have not even been used in the present generic classification, I fail to see why the cnidoragae should be considered a character at the family level. Their presence does in no way affect the general plan of organisation of the Botrucnidiferidae versus the Cerianthidae, and as a consequence it is hardly tenable to maintain the Botrucnidiferidae as a separate family. Considering the relative large number of larval Botrucnidiferidae known at present compared to the number of known adults (in the Atlantic about 20 against only 1), it seems likely that the possession of cnidoragae and botrucnidae is essentially a larval character, disappearing when maturity is reached. The (rare) condition found in *Botrucnidifer* and *Botruanthus* might then be considered neotenic.

A systematic revision of the Ceriantharia is badly needed. A more natural classification, also at the generic level, can undoubtedly be achieved on the basis of an accurate survey of the cnidom of the group and by an additional re-evaluation of a number of morphological and anatomical characters.

Since an alternative is not available at the present moment, Carlgren's classification into 3 families and 8 genera may provisionally be retained. On the basis of the present study and of data in the literature, it can be concluded that all Ceriantharia hitherto described are to be classed into 2 fundamentally different main groups: a suborder for which I propose to name Spirularia, which includes all taxa at the present moment placed in the Cerianthidae and Botrucnidiferidae, and a second suborder, the Penicillaria, including the Arachnactidae only. Diagnoses of the 2 suborders are given below.

A. Suborder Spirularia.

Ceriantharia devoid of penicilli; spirulae being the only type of heteronemae. Homotrichs (probably always) present in the column. Mesenteries arranged in more or less distinct quartets. Stomodaeum with a short, often inconspicuous hyposulcus and with more or less distinct hemisulci. Acontioids absent. Craspedonemes often present. Cnidoragae present or absent, as a rule united to form botrucnidae.

B. Suborder Penicillaria.

Ceriantharia with penicilli and in a lesser degree also with spirulae. Homotrichs absent. Mesenteries arranged in duplets. Stomodaeum with a long hyposulcus (ca. 0.5-1 time the length of the stomodaeum proper), bordered by a rim of filamental differentiation (ciliary tract). Craspedonemes and cnidoragae always absent. Acontioids invariably present.

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REFERENCES

ARAI, M. N., 1965. A new species of Pachycerianthus with a discussion of the genus and an appended glossary. — Pacif. Sci., 19: 205-218, fig. 1.

——, 1971. Pachycerianthus (Ceriantharia) from British Columbia and Washington. — J. Fish. Res. Bd. Canada, 28: 1677-1680, figs. 1-2.

BENEDEN, E. VAN, 1897. Les Anthozoaires de la "Plankton-expedition". — Ergebn. Planktonexped., 2 K(e): 1-222, text-figs. 1-59, 1-16.

——, 1923. Travaux posthumes sur les Cérianthaires. Arch. Biol. Volume hors Série: 1-242, pls. 1-21. (not seen).

CARLGREN, O., 1912a. Ceriantharia. — Dan. Ingolf-Exped., 5(3): 1-xviii, 1-76, pls. 1-5.

——, 1912b. Uber Ceriantharien des Mittelmeers. — Mitt. zool. Sta. Neapel, 20: 356-394, figs. 1-6, pl. 15-17.

——, 1924. Ceriantharia. Papers from Dr. Th. Mortensen's Pacific Expedition 1914-16, XVI. — Vidensk. Medd. dansk. naturh. Foren. Kbh., 75: 169-195, figs. 1-16.

——, 1931. On some Ceriantharia. — Ark. Zool., 23A(2): 1-10, figs. 1-7.

——, 1937. Ceriantharia and Zoantharia. — Scient. Rep. Gr. Barrier Reef Exped., 5(5): 177-207, figs. 1-34, pl. 1.

——, 1940. A contribution to the knowledge of the structure and distribution of the cnidae in the Anthozoa. — Act. Univ. Lund., (n. ser.) 36(3): 1-62, figs. 1-16.

——, 1951. The Actinian fauna of the Gulf of California. — Proc. U. S. nat. Mus., 101: 415-449, figs. 78-84, pl. 14.

CARLGREN, O. & J. W. HEDGPETH, 1952: Actiniaria, Zoantharia and Ceriantharia from shallow water in the northwestern Gulf of Mexico. — Publ. Inst. Mar. Sci. Univ. Texas, 2(2): 141-172, figs. 1-9, pls. 1-4.

CARY, L. R., 1906. A contribution to the fauna of the coast of Louisiana. — Bull. Gulf biol. Sta., 6:50-59.

CEREFONTAINE, P., 1891. Sur un nouveau Cérianthe du Golfe de Naples, Cerianthus oligopodus n. sp. — Bull. Acad. Belg. Cl. Sci., (3) 21 (4): 32-38.

——, 1909. Contribution à l'étude des "Cerianthides". Nouvelles recherches sur le Cerianthus oligopodus. — Arch. Biol., Paris, 24: 653-700, pls. 23-25.

DUERDEN, J. E., 1902. Report on the actinians of Porto Rico. — Bull. U. S. Fish Comm., 20(2): 321-374, figs. 1-4, pls. 1-12.

FAUROT, L., 1891. Sur le Cerianthus membranaceus (Gmelin). — Mém. Soc. zool. France, 4: 66-74, 1 fig.

FIELD, L. R., 1949. Sea anemones and corals of Beaufort, North Carolina. — Bull. Duke Univ. Mar. Sta., 5: 1-39, pls. 1-10.

LELOUP, E., 1964. Larves des Cérianthaires. — "Discovery" Rep., 33: 251-307, pls. 8-21.

——, 1968. Larves des Cérianthaires du Golfe de Guinée. — Bull. Inst. Sci. nat. Belg., 44 (7): 1-22, pls. 1, 2.

MCMURRICH, J. P., 1887. Notes on the fauna of Beaufort, North Carolina. I. Notes on Actiniae obtained from Beaufort, N. C. — Stud. biol. Univ. Johns Hopkins, 4: 55-63.

——, 1890. Contributions on the morphology of the Actinozoa, I. The structure of Cerianthus americanus. — J. Morph. 4: 131-152, pls. 6-7.

——, 1910. The Actiniaria of the Siboga Expedition, I. Ceriantharia. — Siboga Exped., 15a: 1-78, figs. 1-13, pl. 1.

PARKER, G. H., 1900. Synopsis of North-American Invertebrates XIII. The Actiniaria. — Amer. Nat., 34 (405): 747-758, fig. 1-22.

PAX, F., 1910. Studien an Westindischen Aktinien. Zool. Jb., suppl. 11(2): 157-330, 46 figs., pls. 11-19.

——, 1924. Actiniarien, Zoantharien und Cerianthарien von Curaçao. — Bijdr. Dierk., 23 (7): 93-122, figs. 1-22, pl. 9.

ROULE, L., 1904. Note préliminaire sur quelques formes nouvelles de Cerianthaires. — C. R. Ass. franç. Av. Sci., 32 (2): 791-793.

SCHMIDT, H., 1969. Die Nesselkapseln der Aktinien und ihre differentialdiagnostische Bedeutung. — Helgoländ. wiss. Meeresunters., 19: 284-317, figs. 1-11.

——, 1972. Die Nesselkapseln der Anthozoen und ihre Bedeutung für die phylogenetische Systematik. — Helgoländ. wiss. Meeresunters., 23: 422-458, fig. 1-10.

——, 1974. On evolution in the Anthozoa. — Proc. Sec. Int. Coral Reef Symp., 1: 533-560, figs. 1-16.

STEPHENSON, T. A., 1928. The British sea-anemones, 1. — Ray Soc. Publ., 113: 1-148, figs. 1-39, pls. 1-14.

TORREY, H. B. & F. L. KLEEBERGER, 1909. Three species of Cerianthus from southern California. — Univ. Calif. Publ. Zool., 6: 115-125, figs. 1-4.

VERRILL, A. E., 1864. Revision of the polypi of the eastern coast of the United States. — Mem. Boston Soc. nat. Hist., 1: 1-45, pl. 1.

——, 1901. Additions to the fauna of the Bermudas from the Yale Expedition of 1901. — Trans. Connecticut Acad. Arts Sci., 2: 15-62, pls. 1-9.

WESTFALL J. A., 1965. Nematocysts of the sea anemone Metridium. — Amer. Zool., 5: 377-393, pls. 1-8.

EXPLANATION OF THE PLATES

Plate 1

Arachnanthus nocturnus n.sp. Side view of an expanded specimen in situ; Curaçao, Piscadera Bay (type locality), 23 August 1973 at 10 h. p.m.; photo: R. M. den Hartog—van Ter Tholen; × 0.5.

Plate 2

Fig. 1. *Arachnanthus nocturnus* n.sp. Oro-lateral view of a specimen in situ; note the typically curled tentacles as a reaction to the flash of the underwater strobe; Curaçao, Piscadera Bay (type locality), 23 August 1973 at 10 h. p.m.; photo: R. M. den Hartog—van Ter Tholen; × 0.5.

Fig. 2. *Pachycerianthus curacaoensis* n.sp. Semi-expanded specimen from the type locality in its tube; aquarium photo; × 0.9.

Plate 3

Arachnanthus nocturnus n.sp. Fig. 1, dug out tube, showing the inner and the outer aspect, and the living, contracted occupant (RMNH coel. 11364), which lost nearly all its marginal tentacles during collecting; × 0.3; bl. = blind end of the tube. Fig. 2, squash-preparation, showing tubes of discharged and discharging atrichs of the column, demonstrating the microscopic structure of the dwelling tubes of Ceriantharia in general; × 400. Fig. 3, habitus of a juvenile, live specimen from the type locality; specimens of about this size and smaller were almost exclusively found without tube; × 0.8.

Plate 4

Fig. 1. *Arachnanthus nocturnus* n.sp. Habitus of a medium sized specimen from the type-locality, devoid of its tube; note the constriction in the lower part of the body, which is caused by the fact that the body, being in the process of elongation, moves through a freshly formed, apparently tough, partly pushed up sheet of discharged atrichs(sh), the initial formation of a new tube; × 0.66.

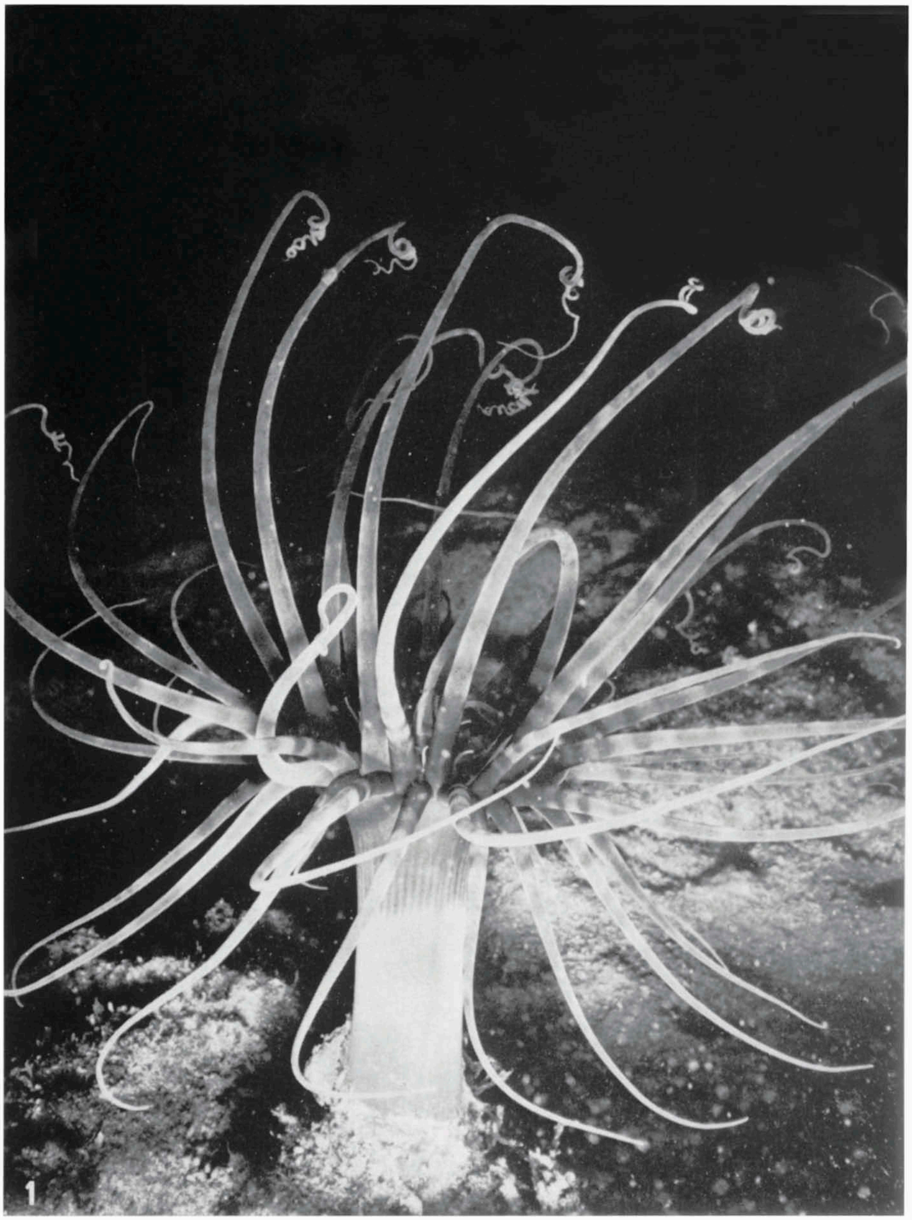
Figs. 2-4. *Pachycerianthus curacaoensis* n.sp. Fig. 2, closed tube (RMNH coel. 11360); note the calcareous worms (c.w.); bl. = blind end of the tube; × 0,4. Fig. 3, the same tube longitudinally dissected, with the (damaged) occupant withdrawn into the blind end (bl.); note the diameter of the tube-wall in the upper and in the lower part of the tube; × 0.4. Fig. 4, the same specimen of fig. 3 out of its tube and slightly magnified; sh. = sheet of freshly discharged atrichs; × 0.6.

Plate 5

Pachycerianthus curacaoensis n.sp. Various nematocysts; The letters in the plate correspond to the text and to text-fig. 2. Figs. 1-3, nematocysts of the column (I). Fig. 1, atrichs(a) in different stages of discharge and spirula(e); × 400. Fig. 2, homotrich(c) in state of discharge; × 400. Fig. 3, spirulae 2(d), discharged and undischarged, and spirula(e); × 400. Figs. 4-5, nematocysts of the labial tentacles (III). Fig. 4, spirulae (d); × 1100. Fig. 5, spirocysts(a), atrichs(b), spirula 2(c) and spirulae 1(e); × 960. Figs. 6-7, nematocysts of the simple cord of the mesenterial filaments of the b- and B-mesenteries (V); spirulae 2(b), discharged and undischarged; × 400.

Plate 6

Arachnanthus nocturnus n.sp. Various nematocysts. The letters in the plate, as far as not explained below, correspond to those used in the text and in text-figs. 4-5. Figs. 1-2, nematocysts of the column (I). Fig. 1, atrich(a), fully discharged; × 400. Fig. 2, penicillus 2(f2); × 400 Fig. 3, nematocysts of the marginal tentacles (II); spirocysts(a), spirulae 1(d), penicillus 1(g); × 400. Figs. 4-10, nematocysts of the Acontioids (VII). Fig. 4, penicilli 1(c) penicilli 1(d), discharged and undischarged; × 400. Fig. 5, penicilli 1(c); × 400. Fig. 6, penicilli 2(b); × 400. Fig. 7, penicillus 2(b), blind end of undischarged capsule, showing the characteristic V-shaped notch at the end of the shaft, and the apparently armed terminal tube, which shows the same herring-bone structure as the shaft; × 940. Fig. 8, penicillus 2(b), upper part of the discharged shaft, showing the armed shaft s.s. and part of the anoplotelic folded portion; ratio of the length of the shaft s.s. and the folded portion ca. 1 : 3; × 400. Fig. 9, penicillus 2(b), tip of the discharged shaft, showing the short uneverted terminal tube; × 500. Fig. 10, penicillus 2(b), transitional region between the naked folded portion and the shaft s.s., which clearly shows the arrangement of the armature in 3 helicoidal strands, an arrangement considered to be characteristic of all armature-bearing nematocysts; × 500. Explanation of symbols with regard to figs. 6-10: f = folded portion; s = shaft sensu stricto, i.e. the armed part of the shaft; tt = terminal tube; v = v-shaped notch.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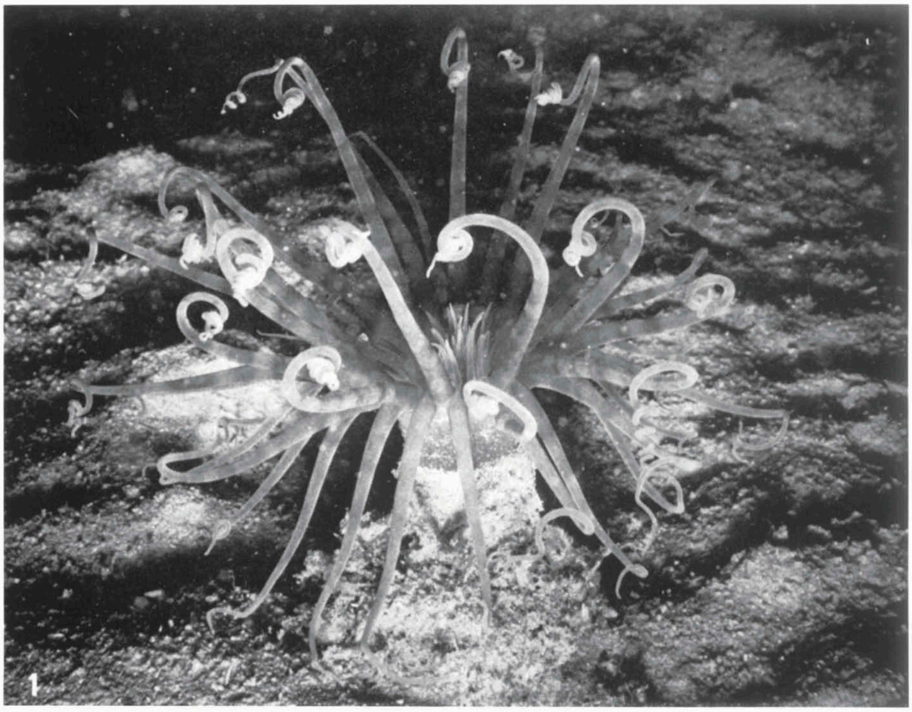

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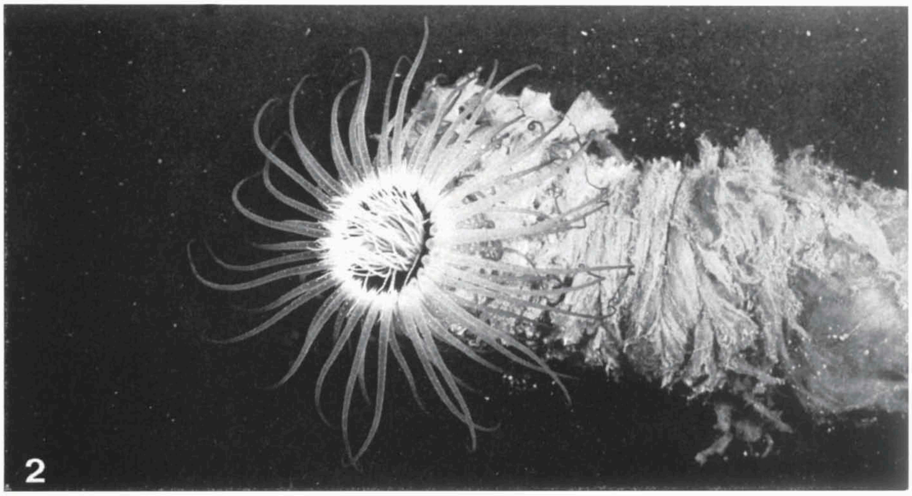

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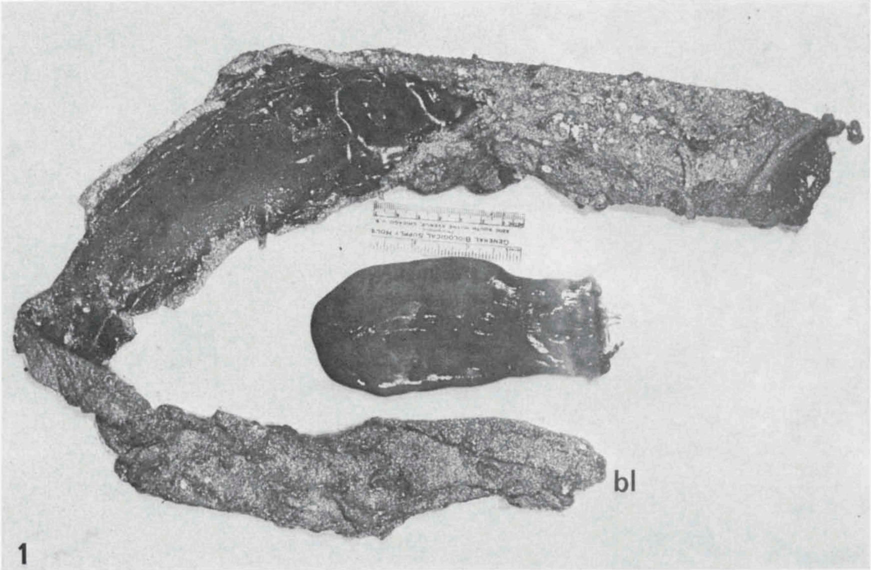

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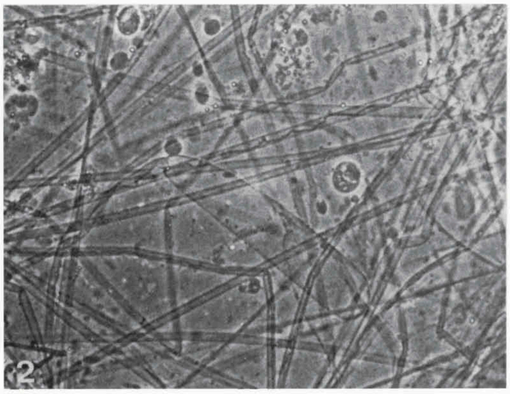

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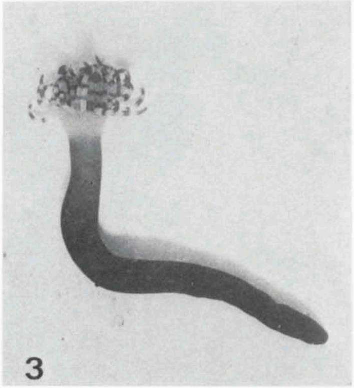

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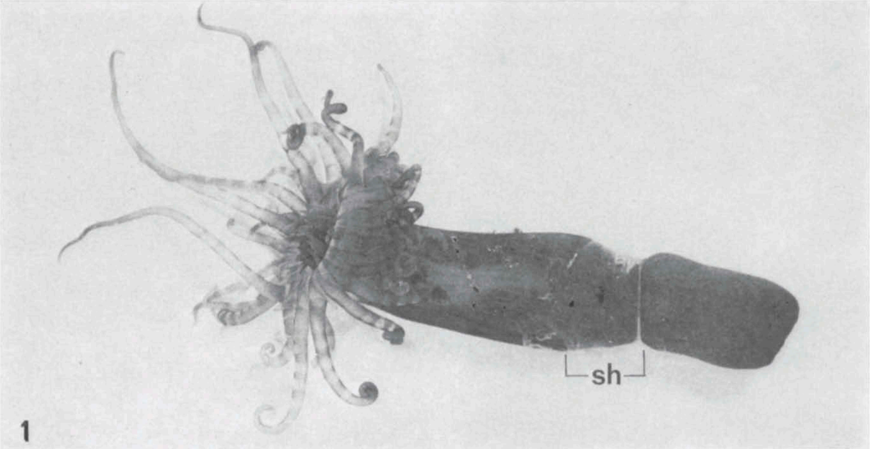

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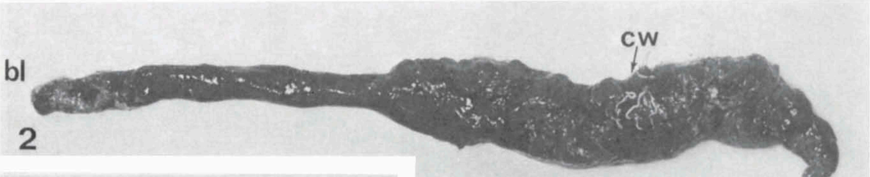

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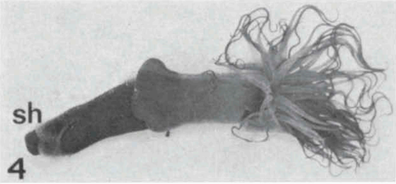

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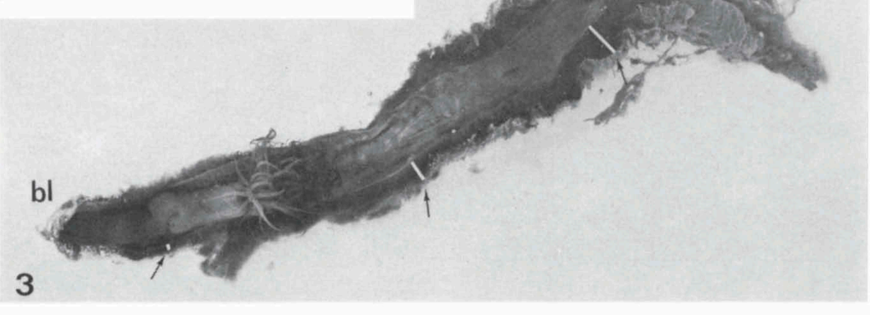

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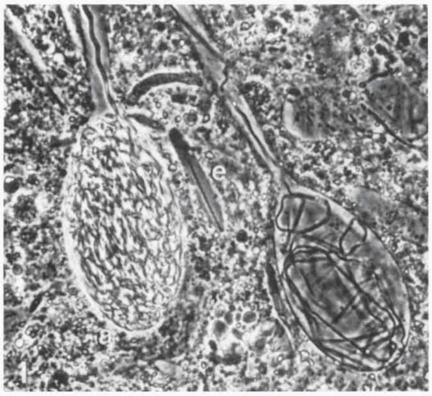
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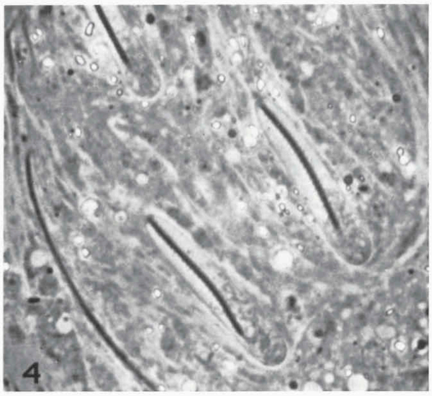
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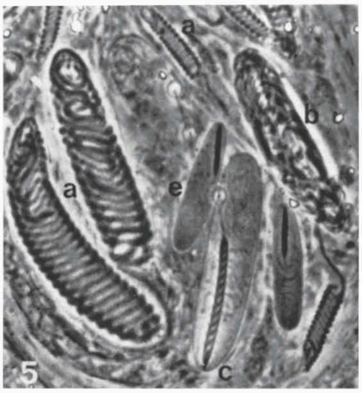
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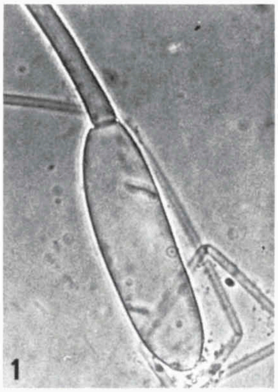
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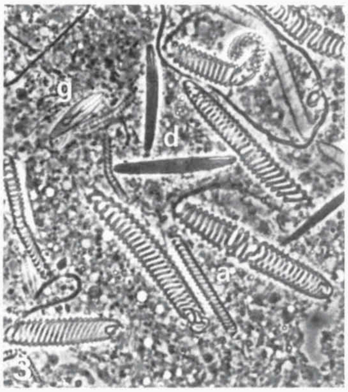
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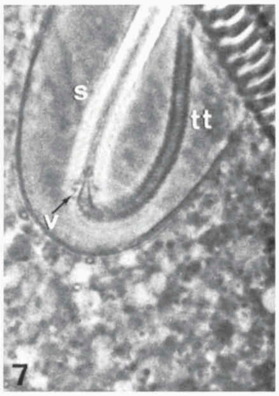
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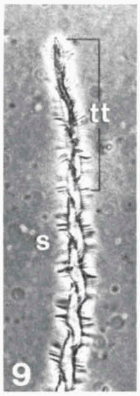
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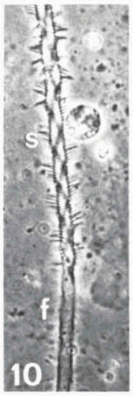
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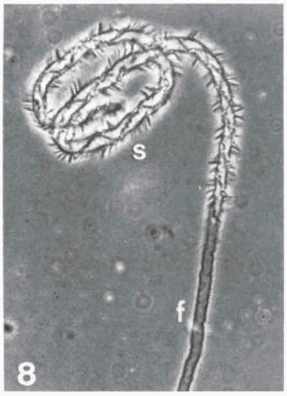
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