Corallimorpharia collected during the CANCAP expeditions (1976-1986) in the south-eastern part of the North Atlantic*

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Key words: Corallimorpharia; Corallimorphidae; *Corallimorphus*; *Corynactis*; *Pseudocorynactis*; *Sideractis*; *Nectactis*; nematocysts; ontogeny; distribution; feeding; CANCAP-project; south-eastern North Atlantic; Macaronesia.

Species of Corallimorpharia collected during the CANCAP expeditions in the south-eastern part of the North Atlantic are described and discussed, altogether five species belonging to three genera of Corallimorphidae: the shallow water forms *Corynactis viridis* Allman, 1846, *Pseudocorynactis caribbeorum* den Hartog, 1980, and *P. caboverdensis* spec. nov., and the deep-sea forms *Corallimorphus* cf. *atlanticus* Carlgren, 1934, and *C. ingens* Gravier, 1918.

The taxonomic status of the representatives of the genus *Corynactis* Allman, 1846, is discussed. All temperate to subtropical species described so far belong to a group of closely related allopatric taxa forming the *Corynactis viridis*-complex, possibly representing a single species only. The colours of *Corynactis viridis* sensu stricto (i.e. the species occurring in the Mediterranean and the south-eastern North Atlantic) are quite variable throughout its distributional range, but not necessarily so in any given area within this range. In the Canary Islands orange to orange-brown forms predominate, suggesting a considerable degree of genetic isolation of at least this population.

Noticeable sympatric variation is shown to occur in the cnidom of *Corynactis viridis*, notably with respect to the presence of penicilli D in the column. This variation ranges from the condition in which there are two distinct, about equally common size classes, to the condition in which the largest size-class is totally absent. These extremes are connected by a gradual range of intermediates in which the large category varies in frequency. The small size-class is invariably present in significant numbers, as a rule rather to very common.

Pseudocorynactis caribbeorum, so far exclusively known from the Caribbean, is recorded for the first time from the eastern Atlantic Canary Islands. A second species, *P. caboverdensis* spec. nov., tentatively included in this genus, is reported from the Cape Verde Islands.

An atypical variety of penicilli D, present in some species of the genus *Corallimorphus* Moseley, 1877, reminescent of, and previously confused with penicilli E (= "classical holotrichs") is described and depicted for *C. atlanticus*. The discovery of this variety challenges the conception that the tube of the "classical holotrichs" should be regarded as a shaft, stamping them as penicilli (= p-mastigophores or p-rhabdoids) as advocated by Cutress (1955) and den Hartog (1980).

The ontogenetic development of the tentacular arrangement of *Corallimorphus ingens* is discussed, and speculations are presented on the feeding habits of *Corallimorphus* spp. and *Nectactis singularis* Gravier, 1918.

Sideractis glacialis Danielssen, 1890, previously recorded from subarctic and arctic latitudes in the eastern Atlantic, is here reported for the first time from the Mediterranean. It was also not previously known that this species is capable of asexual reproduction by pedal laceration and that its tentacular acrospheres are characterized by the presence of atrichs sensu stricto, a nematocyst type so far only reported from a limited number of species of Actiniaria.

Sideractis glacialis and *Nectactis singularis* representing the only two species contained in the family Sideractidae Danielssen, 1890, are transferred to the Corallimorphidae R. Hertwig, 1882, implicitly degrading Sideractidae to a subjective junior synonym of Corallimorphidae.

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Contents

Introduction

The present study deals with the Corallimorpharia collected during the CANCAP expeditions of the Rijksmuseum van Natuurlijke Historie in the south-eastern part of the North Atlantic, 1976-1986. For general information about these expeditions, see den Hartog (1984) and van der Land (1987); the publication by van der Land provides detailed lists of stations, including those of supplementary land based collecting trips to the Azores (AZO stations) (see also den Hartog & Lavaleye, 1981) and Senegal.

The Corallimorpharia form a relatively small, taxonomically neglected group of skeletonless Anthozoa most closely related to the scleractinian corals or possibly even to be considered as such, and comprising no more than some 40 to 50 species. The taxonomy of the group is not well established and there is as yet no concensus about the number of genera and families. In the most liberal view there are four families, two of which, Discosomatidae Duchassaing & Michelotti, 1864, and Ricordeidae Watzl, 1922, are composed of zooxanthellate forms occurring exclusively in tropical shallow waters of the Indo-West-Pacific and the western Atlantic. The two other families, Corallimorphidae R. Hertwig, 1882 (three genera: *Corallimorphus* Moseley ,1877; *Corynactis* Allman, 1846; *Pseudocorynactis* den Hartog, 1980), and Sideractidae Danielssen, 1890 (two genera and species: *Sideractis glacialis* Danielssen, 1890, and *Nectactis singularis* Gravier, 1918), are non-zooxanthellate. They are represented in both shallow coastal waters and the deep sea, and all five genera currently recognized in these families occur in the eastern Atlantic. Although the CANCAP expeditions only yielded Corallimorphidae, the two species of Sideractidae are also briefly treated for the sake of completeness. Sampling in shallow coastal waters yielded numerous samples of *Corynactis* and two samples of *Pseudocorynactis*. Additional samples of these genera were collected in the Canary Islands by the junior authors. Only three CANCAP deep-sea stations yielded specimens of *Corallimorphus*, altogether four specimens. This may seem little, but it is not less than obtained by most other expeditions, including those of e.g. the Challenger and the Valdivia. Species of *Corallimorphus* evidently are generally uncommon, as is also confirmed by their poor representation in museum collections.

Material and methods

The classification and terminology of nematocysts used is essentially after Schmidt (1969, 1972, 1974), as adapted by den Hartog (1980: 7-9). The surveys of the cnidom of the species (tables 1-2, 4-6, 8-10) present means and ranges of length and (maximal) width of nematocyst capsules, or ranges only where means are obviously irrelevant due to scarcity of cnidae or to the wideness of the range, as usually holds for spirocysts. Frequencies given are subjective impressions based on squash preparations, but they do at least give some idea of the absolute and relative abundance of the various types, varieties, and size-classes. All nematocysts are figured on the same scale.

The following codes are used in the tables: +++ = very common, ++ = common, + = rather common, - = uncommon, - - = rare, - - - = sporadic; +/++ = rather common to common; -/+ = uncommon to rather common, etc.; ? = data insufficient to even suggest numbers because of the condition of the tissue concerned; inc. = inconspicuous; cont? = contamination?

Systematic part

Corallimorphidae R. Hertwig, 1882

Corynactis Allman, 1846

Corynactis viridis Allman, 1846

(figs. 1-25, tabs. 1-2)

Corynactis viridis Allman, 1846: 417-419, pl. 11; Gosse, 1860: 289-294, pl. 9 figs.1-5 (description, colour varieties, field notes, = C. *Allmani*, distribution in British Isles); Andres, 1883: 482-484 [274-276] [1884: 266-268], pl. 10 figs. 1-3 (description and summary of known data, synonymy); Weill, 1934: 597-599, figs. 399-400 (cnidom); Ates, 1987: 314-316, col. phots (distribution; aquarium care); Muntz, et al., 1972 (ecology); Manuel, 1981/1988: 206-207, figs. 5C, 76, pl. 2B (description, distribution); Pérez & Moreno, 1991: 91 (col. phot. of orange morph; Canary Islands); van Schie, 1991 (zonation of colour varieties); Beansch & Debelius, 1992: 438-439 (col. phots.; aquarium care; NE Atlantic to southern Spain).

Corynactis Allmani Thompson, in Johnston, 1847: 474-475, fig. 85.

Corynactis allmani Cocks, 1851: 4, pl. 1 fig. 6.

Corynactis mediterranea M. Sars, 1857: 22-28, pl. 1 figs. 1-4.

Material (all samples presumably represent individuals of single clones unless stated otherwise):

Ireland.— RMNH Coel. 17776 (SW coast, County Cork, near Skibberdeen, Lough Ine Rapids, intertidal; 10.viii.1978; don. R.W.M. van Soest; specimens possibly representing more than one clone).

English Channel.— RMNH Coel. 17743 (England, Plymouth, breakwater; viii.1969, coll. J.C. den Hartog) [one additional sample from Plymouth was collected and studied in August 1969, but not preserved (see table 2)]; RMNH Coel. 11426 (France, Brittany, Roscoff, N of Ile de Batz, 80 m; 28.vii.1976; coll. J.C. den Hartog); RMNH Coel. 17775 (idem, Ile de Callot, in small caves; 18.viii.1954; don. R.W.M. van Soest);

Portugal.— RMNH Coel. 18620 (Algarve, Sagres, dark zone in sea cave, 3-4 m, in dead colony of the scleractinian coral *Pourtaleosmilia anthophyllites* (Ellis & Solander, 1786), 11.ix.1986, coll. H. Zibrowius).

Mediterranean.— RMNH Coel. 17744 (France, Cap Beár, between Banyuls and Port Vendres, snorkeling; ix.1987; coll. R.M.L. Ates); RMNH Coel. 17774 (idem, Banyuls, Cap l'Abeille, intertidal; 7.iv.1967; don. R.W.M. van Soest); RMNH Coel 17977 (Spain, Costa Brava, just S of French-Spanish frontier at Port-Bou, Punta Clapé, ca. 30-40 m offshore, 1 m; 21.vii.1990; coll. J.C. den Hartog); RMNH Coel. 17991 (Greece, N Aegean Sea, Northern Sporades, Alonissos Island, 63 m, community with *Corallium rubrum* (Linnaeus, 1758), 1989 or 1990, don. D. Vafidis).

Azores.— RMNH Coel. 17751 (São Miguel, Ilhéu da Vila Franca, 37°42'N 25°27'W, 15 m, 31.v.1981, Sta. CANCAP 5.D05); RMNH Coel. 17750 (Ilhéus Formigas, 37°16'N 24°47'W, tidal pools and fissures with strong currents, 27.v.1981, Sta. CANCAP 5.K01); RMNH Coel. 17752 (Ilhéus Formigas, bank in open sea, to 15 m, 27.v.1981, Sta. CANCAP 5.D02, 3 clones); RMNH Coel. 18613 (Santa Maria, Baia de São Lourenço, 37°00'N 25°03'W, rocky flat with tidal pools surrounded by sand, 16.ix. 1979, Sta. AZO 07); RMNH Coel. 17753 (Faial, Horta, sea front inside harbour, 38°32'N 28°38'W, sandy bottom with rocks and stones, up to 6 m, 10/11.x.1979, Sta AZO 32, 5 clones).

Madeira Archipelago.— RMNH Coel. 17942 (Porto Santo, E coast of Baixo, 33°00N 16°23'W, rocky coast, 5-20m, 9.vi.1980, Sta. CANCAP 4.D16); RMNH Coel. 18622 (Madeira, S coast, Caniço de Baixo, in front of Hotel Roca Mar, 2 m, on smooth rock; ix.1992; coll. P. Wirtz).

Selvagens Islands.— RMNH Coel. 17745 (Selvagen Grande, S coast, Enseada das Cagarras, 30°08'N 15°52'W, 5-20 m, 21.x.1978, Sta. CANCAP 3.D06).

Canary Islands.— RMNH Coel. 13969 (Fuerteventura, S coast near Punta del Morro Jable, 28°04'N 14°21'W, rocky and sandy bottom, 10-15 m, 30.viii.1977, Sta CANCAP 2.D05 2 clones); RMNH Coel. 17747 (Lanzarote, sheltered bay on S. coast W of Punta Papagayo, 28°50'N 13°47'W, snorkeling in shallow water, 19.v.1980, Sta. CANCAP 4.D01, 5 clones); RMNH Coel. 17748 (Gran Canaria, NW coast, Puerto de las Nieves, 28°06'N 15°42'W, submerged rock barrier, 0-8 m, 7.v.1980, Sta. CANCAP 4.K11); RMNH Coel. 17749 (Tenerife, Roques de Fasnia, Cabo de Nasa Perdido, 348(?) m, from fish trap, 11.xi.1985; coll. A. Brito); RMNH Coel.18618 (idem, Poris de Abona, 5 m, ceiling of excavation in rocky wall, 9.vi.1990, 2 specimens, reddish, histological sections only); RMNH Coel. 18612 (La Palma, S coast, Punta Malpique, 28°27'N 17°51'W, exposed rocky coast, up to 20 m, 28.v.1980, Sta. CANCAP 4.D09).

U.S.A.— [?] USNM 52384 (North Carolina, 14 miles E of northern tip of Hatteras Island, 16-18 fms, 28.ii.1962, coll. M. Cerame Vivas).

Brazil.— [?] RMNH Coel. 12868 (Rio de Janeiro, Cabo Frio Island, S side, 10-20 m, dominant at some sites, in cold upwelling water; 30.viii.1977, coll. C. Haggs).

In addition to the material listed above, the species was recorded (but not collected) at the following stations and localities:

Canary Islands.— Gran Canaria: Las Palmas, Sta. CANCAP 2.K19, Sta. CANCAP 2.K20, Sta. CANCAP 4.K01; Arinaga, Sta. CANCAP 4.K06; Puerto de San Nicolas, Sta. CANCAP 2.K09; Playa de la Laja, Sta. CANCAP 2.K21; Puerto de las Nieves, Sta. 2.K23.— Hierro: Puerto de Naos, Punta de la Restinga, Sta. CANCAP 2.K14b; Punta de la Orchilla, Sta. CANCAP 2.K16.

Azores.— Pico: Lagens, Sta. CANCAP 5.K06.— Flores: Santa Cruz, harbour, Sta. AZO 39a.

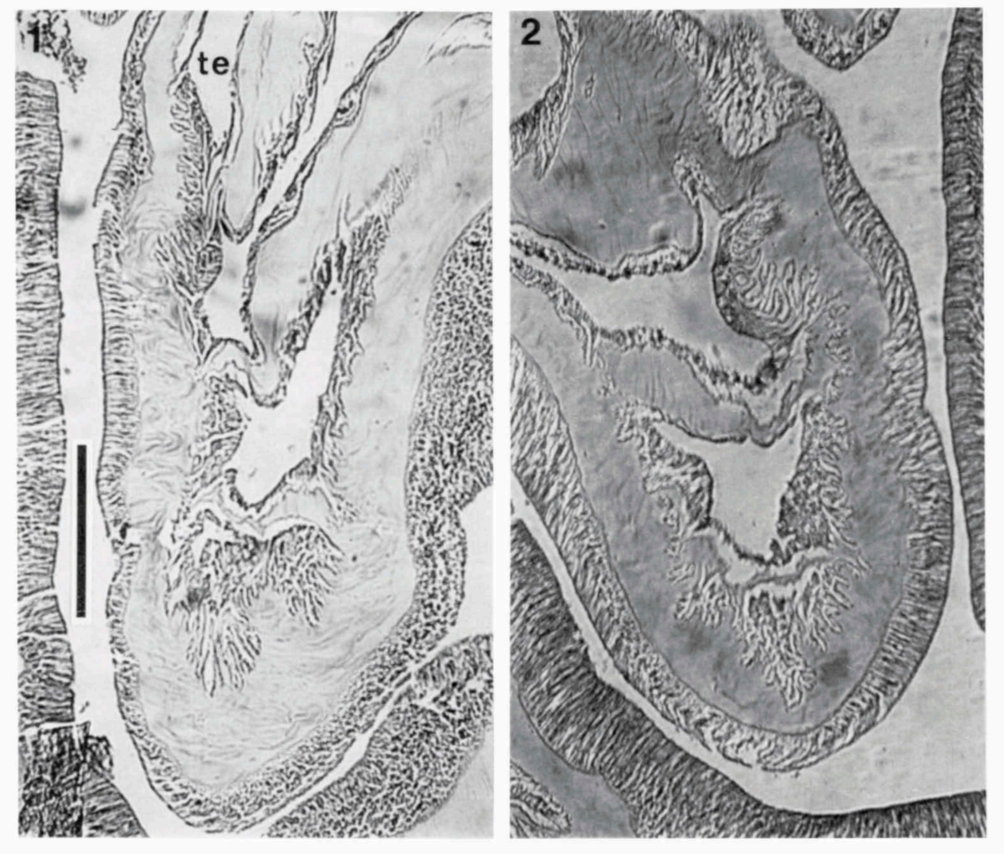
Madeira.— Recorded by Mr J. de Castro, Funchal (personal communication,1976) and photographed by him at Ponta de São Laurenço (see fig. 25), plus various recent records records by Drs. P. Wirtz and A. Svoboda (1992).

Description: Morphology.— Base about 5 to 8 mm in diameter, rarely exceeding 10 mm, often irregular in outline due to habitual asexual reproduction; separate polyps frequently connected by basal expansions.

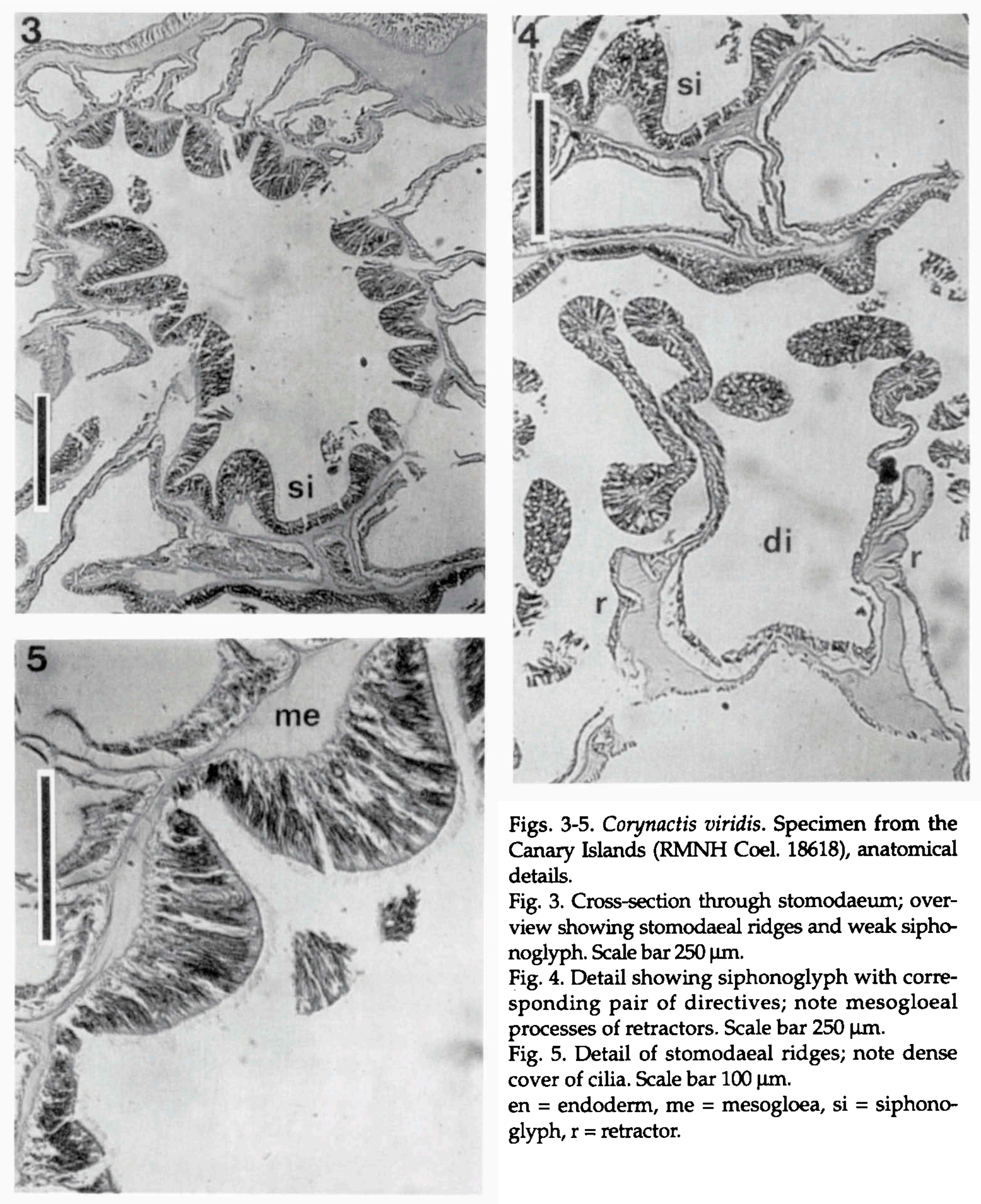
Column not divided into regions or only vaguely so, in some preserved specimens the ectoderm of the marginal region being longitudinally corrugate, whereas the rest of the column tends to be smooth or transversely corrugate, suggesting a differentiation into scapus and scapulus (but this was not confirmed anatomically and histologically). In expanded polyps the column varies in shape from short cylindrical to elongate and more or less trumpet-shaped. Contracted polyps are subglobular to mammiform.

Oral disc equalling to slightly exceeding the diameter of the base.

Tentacles ectacmaceous, in well-developed polyps arranged in about 25-30 endocoelic radial rows of 2 to 4 (5) tentacles each, alternating with single, large, exocoelic marginal tentacles. The total number of tentacles varies between about 100 and 120. [According to Manuel (1981/1988: 206), with reference to British material, the number of tentacles in the endocoelic rows may amount to a maximum of 8. This suggests that the number of tentacles may (in exceptional cases?) amount to about 200 or even more. This condition, however, was not observed in any of the samples here examined].



Figs 1-2. *Corynactis viridis*. Specimen from the Canary Islands (RMNH Coel. 18618), cross-sections of diffuse endodermal sphincter. Note relative thin ectoderm of the area corresponding with the sphincter (the marginal region) as compared to the rest of the column notably in fig. 2, below to the left ; te = tentacle base. Scale bar 250 µm.



Figs. 3-5. *Corynactis viridis*. Specimen from the Canary Islands (RMNH Coel. 18618), anatomical details.

Fig. 3. Cross-section through stomodaeum; overview showing stomodaeal ridges and weak siphonoglyph. Scale bar 250 µm.

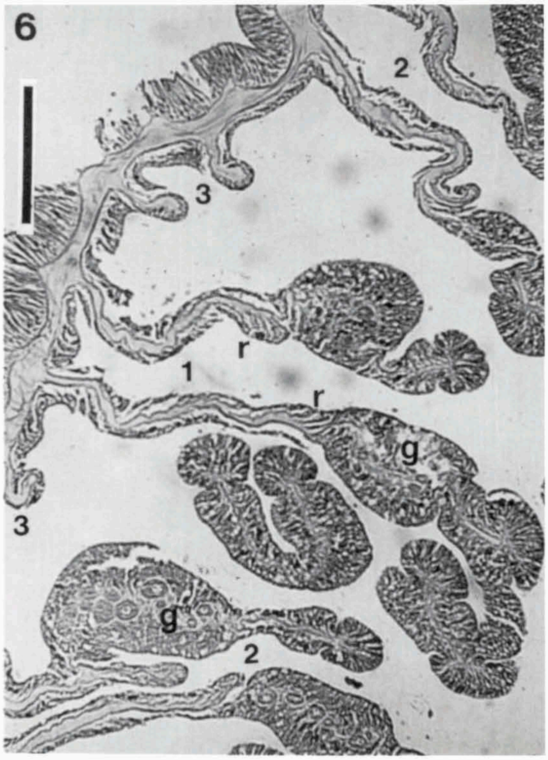
Fig. 4. Detail showing siphonoglyph with corresponding pair of directives; note mesogloeal processes of retractors. Scale bar 250 µm.

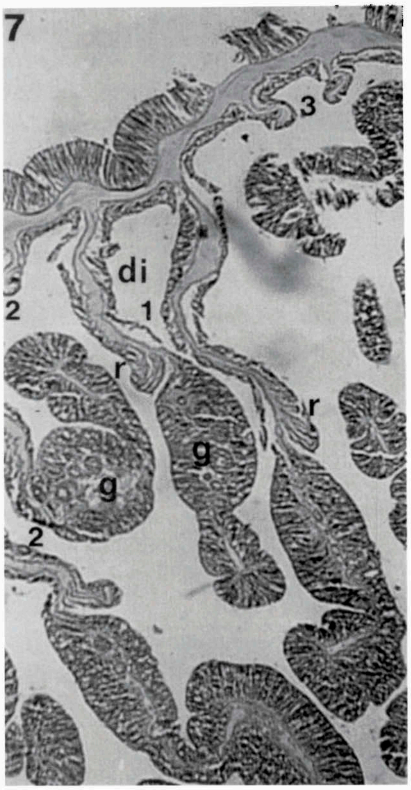
Fig. 5. Detail of stomodaeal ridges; note dense cover of cilia. Scale bar 100 µm.

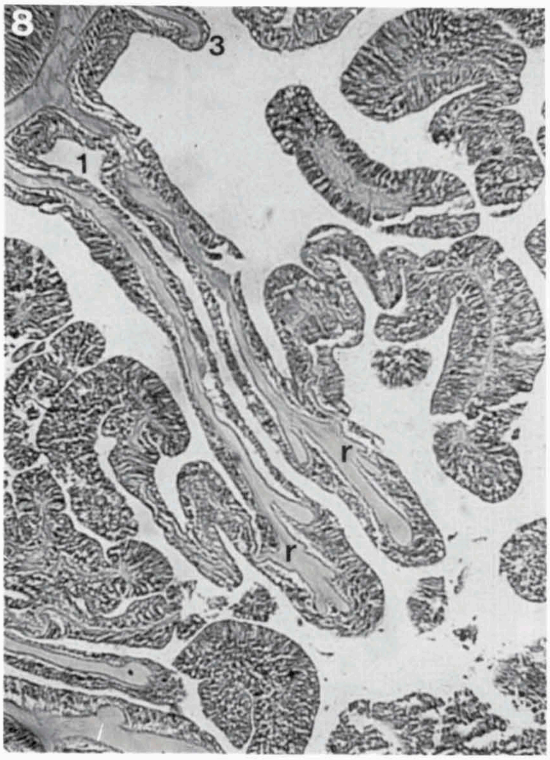
en = endoderm, me = mesogloea, si = siphonoglyph, r = retractor.

Anatomy (figs. 1-13).— Sphincter distinct, diffuse with simple to slightly branched muscle processes (figs. 1, 2).

In average specimens about 25 to 32 mesentery pairs, often with the mesogloea somewhat thickened parietally, arranged in three more or less distinct, though irregular cycles: 1. a cycle of large, perfect and fertile mesenteries with well-developed filaments, 2. a cycle of short to very short, imperfect and sterile mesenteries without filaments, and 3. a cycle of mesenteries intermediate in size, generally fertile and with filaments, but occasionally without. Histological sections below the level of the sto-







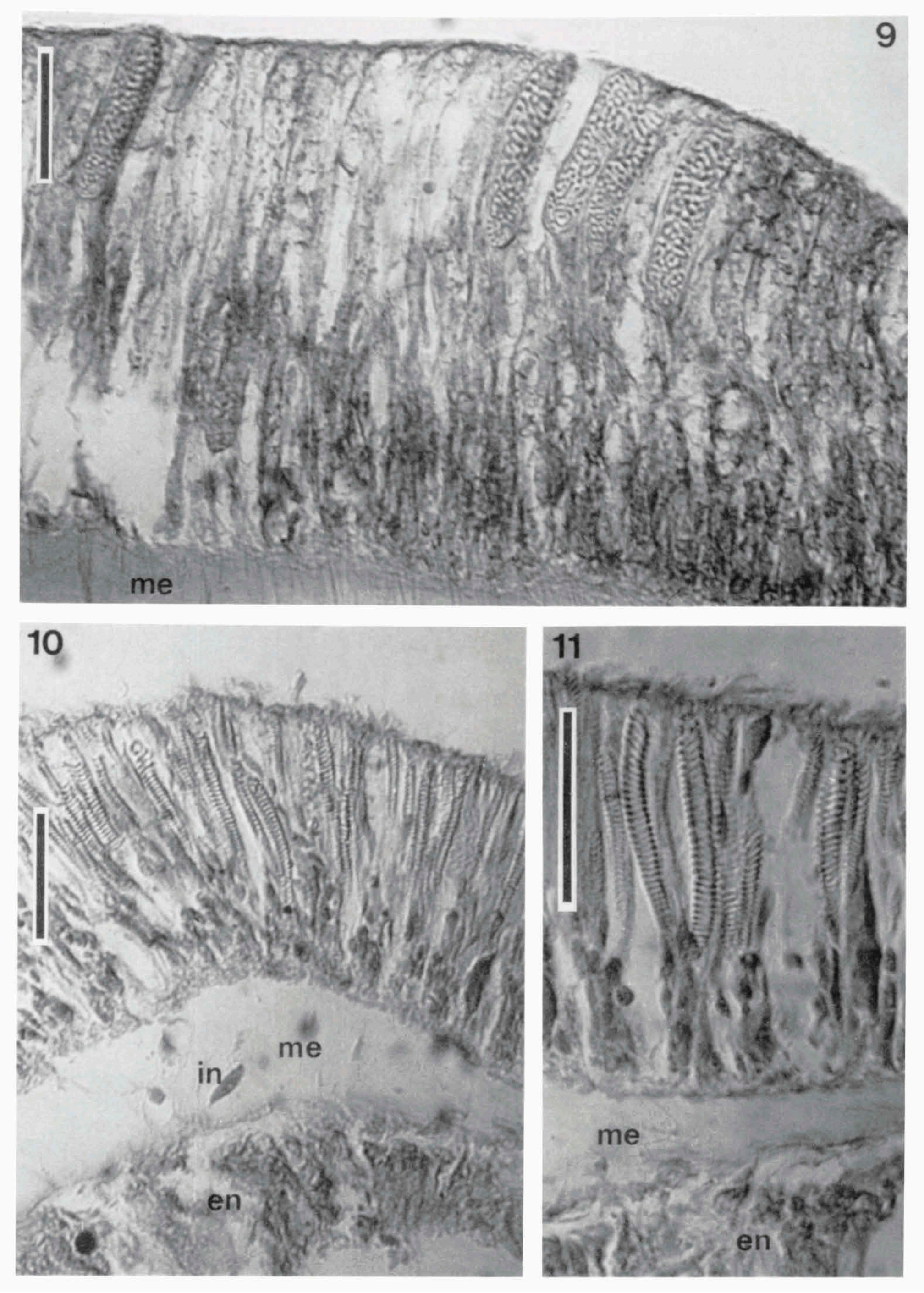
Figs. 6-8. *Corynactis viridis*. Specimen from the Canary Islands (RMNH Coel. 18618), anatomical details. All figures at same scale; scale bar = 250 µm.

Fig. 6. Non-directive primary mesentery pair, flanked by two tertiary and two secondary pairs; note retractors and developing gonads with egg cells.

Fig. 7. Directive and secondary mesentery pair, both about equally developed and with developing gonads (note egg cells), and pair of tertiaries (without gonads and filaments).

Fig. 8. Well-developed primary mesentery pair; note large mesogloeal processes of retractors.

1 = primary tentacles; 2 = secondary tentacles; 3 = tertiary tentacles; di = directives; g = gonad; r = retractor.



Figs. 9-11. *Corynactis viridis*. Specimen from the Canary Islands (RMNH Coel. 18618), cross-sections of column-wall and tentacular acrospheres. Fig. 9. Columnar ectoderm, largely consisting of glandular cells with scattered penicilli E. Fig. 10. Acrosphere showing ectoderm with numerous spirocysts, mesogloea (me) with single inclusive cell (in) and endoderm (en). Fig. 11. Enlarged detail of fig. 10 (cf. fig. 37, *Pseudocorynactis caribbeorum*). All scale bars 25 µm.

Figs. 12-13. *Corynactis viridis*. Specimen from the Canary Islands (RMNH Coel. 18618), anatomical details. Fig. 12. Longitudinal section through a tentacle; ac = acrosphere, co = column, sp = marginal sphincter, st = stalk. Fig. 13. Cross-section through tentacle stalks; note more or less uniform thickness of mesogloea as compared to *Pseudocorynactis caribbeorum* (cf. fig. 36). Scale bars 250 µm.

modaeum showed the presence of only one pair of directives in a specimen from the Azores (RMNH Coel. 17753), and two irregularly placed pairs in a specimen from the Canary Islands (RMNH Coel. 18618). Relative to the frequent occurrence of asexual reproduction the number of directive pairs presumably varies considerably.

Stomodaeum distinctly ciliated, with well-developed longitudinal endodermal ridges supported by a slightly thickened mesogloea (figs. 3, 5); number of these ridges considerably less than number of mesenteries connected with the stomodaeal wall. No obvious siphonoglyphs were recognized in several specimens that were dissected under low magnification, but histological sections through the stomodaeal region of the above-mentioned specimen from the Canary Islands showed a single, faintly indicated siphonoglyph connected with one of the directive pairs (figs. 3-4).

Older mesentery cycles with distinct, diffuse to restricted retractor muscles, supported in the oldest cycle by strong mesogloeal processes (figs. 6-8). Youngest mesentery cycle without significant retractors. Parietobasilar muscles weak and inconspicuous. Mesogloea well-developed, up to ca 130 µm thick in column, base and stomodaeum; its structure is fibrillar, the central matrix as a rule relatively dense with few lacunae containing one or a few cells.

No differentiation of the column into scapus and scapulus, although the ectoderm of the narrow marginal region corresponding with the sphincter tends to be relatively thin (figs. 1-2). Ectoderm of column and base ca. 80-130 µm thick, largely consisting of glandular mucus cells with scattered nematocysts (fig. 9), in the base with some additional thickly granulate glandular cells. Ectodermal musculature weakly developed. Ectoderm of the tentacular acrospheres ca. 50-80 µm high, with large numbers of epithelial muscle cells; cnidae predominantly one size-class of spirocysts, densely arranged in a single surface layer (figs. 10, 11; cf. *Pseudocorynactis caribbeorum*, fig. 37) with scattered spirulae, penicilli D and penicilli E. Ectoderm of the tentacle stalks considerably thinner, ca. 20-45 µm, with abundant glandular mucus cells and clusters of smaller, relatively broad spirocysts. The mesogloea of the tentacle stalks forms a layer of more or less uniform thickness (fig. 13), quite different from the condition in *Pseudocorynactis* (fig. 36).

Colouration (figs. 16-25).— The colours of *Corynactis viridis* are extremely variable and often brilliant, the vernacular English name "Jewel anemone" being well-chosen. The varieties may at first sight seem infinite, but on closer examination the basic colours prove limited; the column may be whitish, yellowish, green, orange, brownish, flesh-coloured, pink or lilac, to deep purple, with the margin often marked by a bright green line. The same colours, though as a rule less intense (and more transparent in expanded specimens), may be found in the tentacle stalks; the acrospheres on the other hand are always opaque: sparkling white, creamy, orange, pink to deep red or even dark purplish brown. Unlike the column the acrospheres are apparently never green or yellow.

Over the major part of the distributional range, whether in south-west England, the Azores, or in the Mediterranean, a host of colour varieties may be found together in any locality where the species occurs. By contrast the population of the Canary and Selvagens Islands appears to be less variable, being dominated by orange to orange-brown or reddish-brown forms, often marked by white to grey splashes on the oral disc and not rarely with white acrospheres or entirely white tentacles (personal observations). During the CANCAP expeditions only two clones of different colour (one with green polyps and purplish-red acrospheres, the other orange-brown with pink tentacles) were collected in the Canary Islands (Lanzarote, near Punta Papagayo, Sta. 4D01). Pérez Sánchez & Moreno Batet (1991: 91), in a book on marine invertebrates of the Canary Islands, mention that the colour is very variable, but it is not entirely clear whether this is meant as a general statement or one with reference only to the Canary Islands; the coloured photograph with the text shows the usual orange-brown variety. The limited variability in colour of the Canary Islands population would seem to indicate a considerably restricted genetic exchange with other populations. Orange to orange-brown forms also seem to predominate in the Adriatic (Dr A. Svoboda, Bochum, Germany, personal communication).

The *Corynactis* population of Cabo Frio Island, Brazil, which I am unable to distinguish from *C. viridis*, but which, for reasons of allopatry and geographical distance, is tentatively and with hesitation regarded as *C. viridis* (see p. 21, "Distribution"), has also been reported to display great colour variation (den Hartog, 1980: 19).

Whether the colours of *Corynactis* are entirely genetically determined is questionable, but, as illustrated by the fact that many colour varieties may occur side by side in the same locality, this is undoubtedly true to a great extent. On the other hand it is possibly no coincidence that clones growing among algae may have a greenish to brownish hue more or less matching with their surroundings (cf. figs. 16-17). And the fact that in the Canary islands orange to brownish colours are especially common in shallow water among the coastal *Cystoseira*-fringe and just below it, might also not be without significance. Certain pigments of algae might be incorporated in the polyp body by the uptake of free molecules liberated in the surrounding water by decay and/or indirectly by the intake of herbivorous phyto-pigment accumulating prey such as small amphipods and isopods, and thus accentuate certain colours. It may further be mentioned that individuals of orange to orange-brown clones occurring among more faintly coloured yellow or orange sponges may appear somewhat paler than clonemates that are not in contact with these sponges. In this connection the clone of whitish specimens shown in fig. 23, growing among whitish sponges and bryozoans, also calls for notice, although it must be added that this particular clone was located in a cave, and that light conditions, too, presumably have an effect on pigmentation. In this same connection it is also interesting to note that Van Schie (1991), in an unpublished student's essay, found indications that the colour varieties of *Corynactis viridis* are not evenly distributed in relation to depth. To confirm or disprove the above indications and speculations on the presence of a phenotypical component in the colours of *Corynactis viridis*, further study is necessary.

Cnidom (tab. 1, fig. 14a-b).— Nematocysts of *Corynactis viridis*, notably the large penicilli E (= classical holotrichs), and their similarity to those of the cup coral *Caryophyllia smithii* Stokes & Broderip, 1828, already drew the attention of the nineteenth century scientists Gosse (1860: xxxii-xxxiii, pl. 11 fig. 9) and Möbius (1866: 8, pl. 1 figs. 9-12), and in more recent years were the subject of extensive studies on the mechanism of nematocyst discharge (e.g. Picken, 1953; Robson, 1953; 1973; Skear & Picken, 1965). In spite of this, no inventory of the cnidom of the species meeting modern taxonomic standards is available in the literature. Weill (1934: 597-599), indeed, did present a survey of the types, but failed to indicate their distribution in the body.

A detailed survey of the cnidoms of four clones from widely separated localities is here presented in table 1 and fig 14. Apart from a general similarity the table reveals considerable variation between these four clones. First of all, the nematocysts of the clone from Ile de Batz, Brittany, France (A), seem comparatively large, notably the penicilli E of the column (1d) and the penicilli D of column ($1c_2$) and filaments ($5b_2$).

In addition the four clones vary with regard to the spirulae present in column and tentacles. In the clones from Brittany and Lanzarote there are two more or less distinct size-classes: 1. a narrow translucent form with a straight, distinct shaft and well delimited terminal tube ($1b_1$, $2b_1$), and 2. a more expanded, rather opaque form in which the shaft seems more flexible and merging more gradually into the terminal tube ($1b_2$, $2b_2$). This latter category either represents a juvenile stage of the former, or a transitional stage between spirulae and homotrichs. A transition of spirulae into homotrichs was previously demonstrated for the sweeper tentacles of the scleractinian coral *Montastrea cavernosa* (Linnaeus, 1767) (den Hartog, 1977: 465, 477). This phenomenon must be considered phenotypic and the presence of these two more or less different categories/size-classes of spirulae in some clones of *Corynactis* is therefore without taxonomic significance.

Table 1. *Corynactis viridis*. Survey of the cnidom of 4 clones from widely separate localities of the distributional range. A = clone from Ile de Batz, Brittany, France (RMNH Coel. 11426; B = clone from São Miguel, Azores (RMNH Coel. 17751); C = clone from the Mediterranean coast of France (RMNH Coel. 17744A); D = clone from Lanzarote, Canary Islands (RMNH Coel. 17747C).
For the significance of the symbols with respect to "Frequency", see page 5: "Material and methods".

Organ	Clone	Nematocyst type	Mean and range (in parentheses) of length and width of nematocyst capsules in µm	N	Frequency
1. Column	A	a. Spirocysts	ca. 20-36 x 2.5-4.5	—	+
	B		25.6(22.3-28.5) x 4.6(4.0-5.3)	20	-
	C		ca. 22.5 - 27 x 2.9 - 3.6	—	?
	D		ca. 21.5-27 x 4.5	—	+
	A	b. Spirulae $_1$	16.7(15.6-18.7) x 3.8(3.6-4.5)	20	++
		$_2$	25.5(22.3-28.5) x 6.3(5.3-7.1)	10	-
	B	$_1$	16.4(15.1-19.6) x 4.1(3.6-4.5)	20	+
	C	$_1$	20.5(18.7-24.9) x 6.2(5.3-7.1)	25	+
	D	$_1$	16.0(13.4-17.8) x 3.7(3.3-4.0)	20	+
		$_2$	20.5(16.0-24.9) x 5.2(4.5-6.2)	20	+
	A	c. Penicilli D $_1$	23.2(16.0-31.2) x 6.3(5.3-8.0)	30	+
		$_2$	46.9(40.0-54.3) x 9.7(8.9-11.1)	25	+
	B	$_1$	21.8(19.6-30.3) x 6.7(5.8-8.0)	50	+
	C	$_1$	20.5(18.7-24.9) x 6.2(5.3-7.1)	25	+
		$_2$	32.7(30.3-35.6) x 10.9(10.7-11.6)	4	- - -
	D	$_1$	19.8(15.2-24.9) x 5.9(5.1-6.7)	40	+
		$_2$	29.5(26.7-36.5) x 7.6(6.2-9.8)	10	- - -
	A	d. Penicilli E	50.6(39.2-57.0) x 13.8(9.4-16.9)	20	+
	B		38.7(32.0-49.0) x 13.9(9.8-16.5)	25	+
	C		40.1(33.8-48.9) x 13.4(11.6-16.0)	30	+
	D		38.9(36.5-44.5) x 10.3(8.9-11.6)	20	+
2. Acrospheres of tentacles	A	a. Spirocysts	ca. 25-70 x 2-5	—	+++
	B		ca. 33-71 x 3.3-6.2	—	+++
	C		ca. 22-55 x 2-5.5	—	++
	D		ca. 22-80 x 2.3-5.3	—	+++
	A	b. Spirulae $_1$	36.6(31.2-40.9) x 4.5(4.2-5.3)	20	+
		$_2$	44.5(33.8-56.1) x 8.0(6.0-8.9)	20	-
	B	$_1$	39.0(35.6-42.7) x 4.1(3.6-4.5)	20	+
		$_2$	ca. 45-50 x 7.6	—	- - -
	C	$_1$	35.5(31.2-41.8 x 3.6(3.3-4.5)	15	-
		$_2$	43.9(40.1-53.4) x 5.7(4.5-6.7)	25	+
	D	$_1$	36.8(33.8-40.1) x 3.8(3.6-4.0)	18	-
		$_2$	45.2(40.1-49.8) x 5.4(5.3-5.6)	6	- - -
	A	c. Penicilli D $_1$	31.8(27.6-37.4) x 6.0(5.3-6.7)	20	+
		$_2$	64.2(50.8-71.2) x 6.1(5.3-6.5)	20	+
	B	$_1$	33.3(29.4-39.2) x 5.8(5.3-6.7)	20	+
		$_2$	58.7(49.0-68.5) x 5.8(5.3-6.2)	20	-
	C	$_1$	27.6(24.0-30.3) x 5.5(4.9-6.2)	30	+
		$_2$	50.2(41.8-64.1) x 5.4(4.9-6.2)	30	++

	D	1	31.1(27.6-35.6) x 5.1(4.9-5.8)	27	+
		2	50.3(44.5-62.3) x 5.3(4.9-5.8)	22	+
	A	d. Penicilli E	77.0(69.4-89.9) x 24.3(21.4-26.7)	20	-
	B		70.5(61.4-87.2) x 23.2(21.4-25.8)	20	+
	C		59.5(53.4-66.7) x 21.7(17.8-24.9)	30	+
	D		73.8(65.9-84.6) x 19.6(16.9-21.4)	17	-
3. Tentacle stalks	A	a. Spirocysts	ca. 27-39 x 2.0-5.0	—	+++
	B		ca. 25?-32 x 2.25-4.5	—	+++
	C		ca.25?-34 x 2.0-4.5	—	+++
	D		ca.25?-32 x 2. -4.5	—	+++
4. Stomodaeum	A	a. Spirulae	28.3(24.9-32.0) x 4.5(4.2-4.9)	20	++
	B		26.6(24.9-27.6) x 4.3(4.0-4.5)	20	+
	C		25.3(22.3-29.4) x 4.0(3.6-4.5)	10	+
	D		26.0(23.1-27.6) x 4.1(4.0-4.5)	25	+
	A	b. Penicilli E	44.0(40.9-49.8) x 15.0(13.4-17.8)	20	+
	B		45.8(35.6-57.0) x 16.2(12.5-20.5)	30	-
	C		36.5(31.2-40.9) x 13.8(12.5-15.2)	10	+
	D		43.8(34.7-53.4) x 12.9(9.8-16.9)	20	+
5. Filaments	A	a. Spirulae	10.4(8.9-11.6) x 2.8(2.7-3.6)	15	-?
	B		ca. 10-12 x 2.5-3.3	—	?
	C		9.8(8.0-11.6) x 2.9(2.7-3.3)	10	- - -
	D		11.4(9.8-14.2) x 3.3(2.4-4.0)	7	- - -
	A	b. Penicilli D 1	24.7(21.4-31.2) x 6.5(5.3-7.6)	30	+
		2	45.2(39.2-52.5) x 10.8(9.3-12.0)	30	+
	B	1	21.2(18.7-24.0) x 5.9(5.3-6.7)	22	+
		2	36.6(31.2-45.4) x 9.6(7.6-12.0)	39	++
	C	1	21.1(17.8-24.9) x 6.1(5.3-7.1)	30	+
		2	37.8(31.2-40.9) x 9.9(8.9-10.7)	30	+
	D	1	21.7(20.5-24.0) x 5.7(4.9-6.7)	30	++
		2	35.6(30.3-39.2) x 8.9(7.6-11.1)	30	+
	A	c. Penicilli E 1	49.4(40.1-58.7) x 17.6(14.2-20.5)	20	-
		2	82.0(71.2-97.9) x 36.7(31.2-43.6)	25	++
	B	1	45.2(35.6-57.8) x 16.5(12.5-24.0)	30	+
		2	73.7(65.9-89.0) x 34.5(30.3-39.2)	20	+
	C	1	39.7(32.0-47.2) x 15.7(13.4-17.8)	20	++
		2	72.0(65.8-76.5) x 33.9(31.2-39.2)	25	++
	D	1	40.6(37.4-41.8) x 13.9(12.5-15.1)	3	- - -
		2	77.4(64.1-85.4) x 29.9(24.0-35.6)	20	-

A more striking variation is shown by the penicilli D of the columnar ectoderm ($1c_{1,\,2}$) of the four clones. In the clone from Brittany (A) there are two distinct size classes, about equally common, whereas only one small size-class was found in the clone from the Azores (B). In the clones from the Mediterranean and the Canary Islands (C, D) the smaller size-class strongly predominates; examples of the large size-class were only found sporadically in these clones and after prolonged search. Because of this unexpected outcome the majority of the available *Corynactis* samples was checked on this character for a possible geographically correlated, clinal variation (tab. 2).

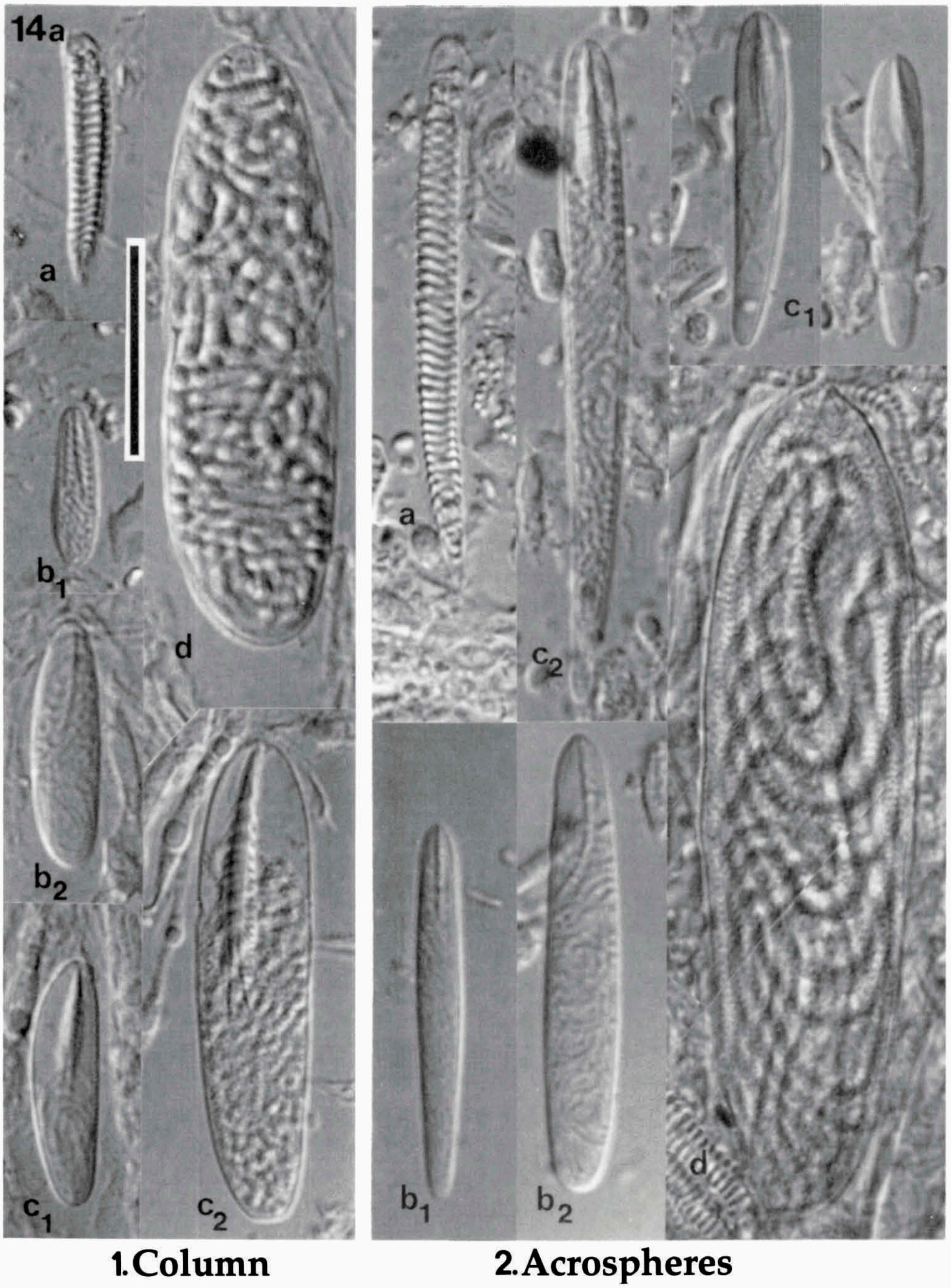
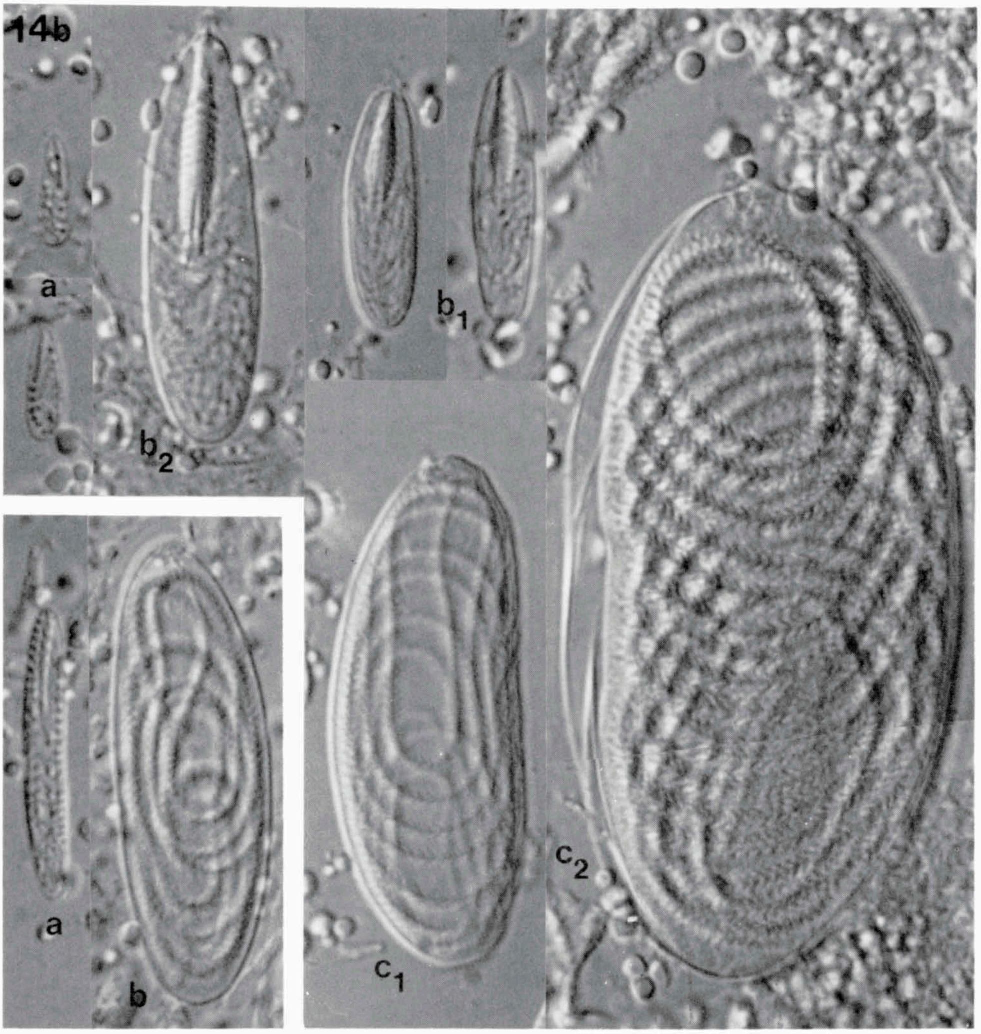


Fig. 14a-b. *Corynactis viridis*. Pictorial survey of the cnidom, mainly based on clone from Brittany, France (RMNH Coel 11426). Numerals and characters correspond to those used in table 1. Scale bar 20 µm.
1. Column: a. Spirocyst; $b_{1,2}$. Spirulae; $c_{1,2}$. Penicilli D; d. Penicillus E. **2. Acrospheres**: a. Spirocyst; $b_{1,2}$. Spirulae; $c_{1,2}$. Penicilli D; d. Penicillus E. **3. Tentacle Stalks**: cnidae not figured. **4. Stomodaeum**: a. Spirula ; b. Penicillus E. **5. Filaments**: a. Spirulae; $b_{1,2}$. Penicilli D; $c_{1,2}$. Penicilli E.

The data presented in table 2 do not convincingly show that such a correlation exists, and more data are necessary for a statistically sound interpretation. However, these data certainly afford some discussion. First of all it is shown that all clones share the presence of the small size-class of penicilli D ($1c_1$), invariably rather common, and that striking variations in frequency and size occur exclusively with regard to the large size-class ($1c_2$), even if the division into two size-classes is somewhat arbitrary in some cases. In the Mediterranean clones the small size-class strongly predominates, whereas the large penicilli D were found to vary in abundance from (apparently) absent to uncommon. In the material from the Canary Islands and the single sample from the Selvagens the large category was found to vary from absent to rather common, up to equalling the small size-class in abundance. The same variation was found in material from the Azores. In the clones from Ireland and the English Channel the two size-classes are about equally common and it is noticeable



4.Stomodaeum 5.Filaments

that the dimensions of the large size-class in these clones by far exceed those in all other clones examined (both as regards mean and maximum), with the exception of the easternmost Mediterranean sample from Greece in which they are about equally large, but, in contrast, very scarce (penicilli D were altogether not common in the column of these specimens; frequencies, however, may have been biased by the poor condition of the specimens).

Table 2. *Corynactis viridis*. Number of size classes (1 or 2), size, and relative abundance of columnar Penicilli D in clones from throughout the known distributional area.
As to the number of size-classes: [1] indicates that one size-class strongly predominates, the second being rare to practically absent; [2] indicates that the two size classes are merging, yet being represented by two distinct size peaks.
For the significance of the symbols with respect to "Frequency", see page 5: "Material and methods".

Geographic origin/ RMNH number/ co-ordinates	Number of size-classes	Mean and range (in parentheses) of length and width of penicilli D in µm	N	Frequency
		Southwestern Ireland		
Skibberdeen/17776/ 51°30'N 9°20'W	2	22.9(19.6-31.2) x 6.1(5.3-7.2) 43.9(36.9-48.6) x 8.8(7.2-10.8)	50 20	+ +
		English Channel		
Plymouth/17743/ 50°20'N 4°10'W	2	21.5(19.6-25.8) x 6.3(4.9-7.1) 43.3(39.2-47.2) x 9.6(7.6-11.6)	23 20	+ +
Idem/not preserved	2	24.9(19.0-31.5) x 7.4(5.5-9.0) 44.6(35.0-55.0) x 10.8(9.5-12.5)	17 15	+ +
Roscoff, Ile de Batz/11426/ 48°40'N 4°W	2	23.2(16.0-31.2) x 6.3(5.3-8.0) 46.9(40.0-54.3) x 9.7(8.9-11.1)	30 25	+ +
Idem, Ile de Callot/17775	2	23.2(19.8-30.6) x 6.0(5.4-6.5) 41.4(36.9-46.8) x 8.6(7.2-9.0)	20 20	+ +
		Mediterranean		
France, Banyuls, Cap Béar/17744A/ 42°30'N 3°08'E	[1]	20.5(18.7-24.9) x 6.2(5.3-7.1) 32.7(30.3-35.6) x 10.9(10.7-11.6)	25 4	+ ---
Idem, 17744B	[1]	21.6(17.8-26.7) x 6.1(4.9-7.1) 32.9 x 8.0; 35.6 x 8.9	50 2	+ ---
France, Banyuls, Cap l'Abeille/17774	1	21.3(18.7-26.7) x 5.7(4.9-6.7)	30	+
Spain, Costa Brava/Punta Clapé/17977A/ 42°25'N 3°10'E	2	19.8(16.9 - 24.9) x 5.7(4.5 - 7.1) 38.3(33.8 - 44.5) x 8.7(7.1 - 9.8)	30 30	+ -

Idem, 17977B	[2]	24.1(17.8 - 32.0) x 6.0(4.5 - 7.1) [maxima at ca. 23 and ca. 28; ratio of smaller and larger capsules ca. 2 : 1]	60	+
Greece, Alonissos Island/ 17991/ca. 39°30'N 23°15'E	[1]	21.1(16.9-26.7) x 5.9(4.5-8.0)	25	- /+?
		42.9(38.4-47.2) x 9.4(8.0-11.6)	10	- - -?
		Azores		
São Miguel/17751/ 38°N 26°W	1	21.8(19.6-30.3) x 6.7(5.8-8.0)	50	+
Ilhéus Formigas/ 17752A/37°N 26°W	[1]	22.7(19.1-26.7) x 6.1(5.3-7.1)	33	+
		31.0(29.4-32.0) x 8.1(6.2-9.8)	7	- - -
Idem, 17752B	[1]	19.6(16.9-24.0) x 5.8(4.5-6.2)	30	+
		38.5(37.8-40.9) x 8.2(8.0-8.9)	4	- - -
Faial/17753A/ 38°N 29°W	2	21.5(17.8-24.9) x 6.2(5.3-8.0)	20	+
		35.6(31.2-40.9) x 8.3(6.7-9.8)	23	+
Idem, 17753B	2	20.6(16.9-27.6) x 6.2(5.3-7.6)	20	+
		35.3(32.0-40.1) x 8.7(7.1-9.8)	20	+
Idem, 17753C	1	23.3(19.6-27.6) x 6.5(5.3-8.9)	60	+
Idem, 17753D	[1]	22.2(19.6-25.8) x 5.9(5.3-6.2)	20	+
		33.2(32.0-33.8) x 8.2(8.0-8.9)	4	- - -
		Madeira Archipelago		
Porto Santo/17942/ 33°N 16°W	1	22.2(18.9-28.8) x 5.8(5.0-6.8)	40	++
Madeira/18622/ 32°38'N 16°49'W	[1]	20.9(18.7-24.0) x 5.8(4.9-6.5)	40	+/++
		one observed: 36.5 x 8.9	1	- - -
		Selvagens Islands		
Selvagem Grande/17745/ 30°N 16°W	1	19.7(16.9-24.9) x 6.3(5.3-7.1)	40	+
		Canary Islands		
Lanzarote/17747A/ 29°30'N 14°W	2	19.6(16.9-24.0) x 6.0(5.3-8.0)	27	+
		35.6(32.0-37.4) x 9.0(8.0-10.6)	13	-
Idem, 17747B	1	19.7(16.0-26.7) x 6.2(5.3-8.0)	45	++
Idem, 17747C	[1]	19.8(15.2-24.9) x 5.9(5.1-6.7)	40	+
		29.5(26.7-36.5) x 7.6(6.2-9.8)	10	- -
Idem, 17747D	[1]	20.5(17.8-24.9) x 6.2(5.3-7.1)	27	+
		36.1(32.9-38.3) x 9.6(8.5-10.2)	11	- -

Idem, 17747E	2	19.5(17.8-22.3) x 6.0(5.3-7.1)	25	+
		37.3(33.8-43.6) x 10.1(8.9-11.6)	27	+
Fuertaventura/17746/ 29°N 14°W	2	21.7(18.7-26.7) x 6.1(5.3-7.1)	28	+
		30.2(26.7-35.6) x 8.0(7.1-8.9)	22	+
Gran Canaria/17748/ 29°N 15°30'W	[1]	20.1(17.8-24.0) x 6.1(5.3-6.7)	20	+
		35.2(30.3-37.4) x 8.5(8.0-8.9)	10	- -
Tenerife/17749/ 29°N 16°30'W	1	22.5(16.9-24.9) x 6.4(5.3-7.1)	10	?
		Brazil		
Cabo Frio Island/12868/ 23°S 42°W	1	19.0(16.1-22.3) x 6.3(5.6-7.4)	20	+

Biological and ecological notes.— Asexual reproduction by longitudinal fission, not necessarily in two parts (den Hartog, 1962: 14, observation of specimen that split in four parts), occurs commonly, giving rise to clones of the same colour and pattern 1).

In the Canary Islands the species is generally found sublittorally in more or less exposed localities, on bare rock, among sponges or epizoic on bivalves, tunicates, etc. In moderately exposed localities its vertical distribution generally ranges subtidally from 0 to 6 m depth, in and especially just below the *Cystoceira*-fringe, where it may form dense carpets. In more exposed localities the species ranges deeper down, being common between 0 and 15 m (again with maximal numbers just below the *Cystoceira*-fringe), but is not normally found below 20 m depth.

Occasionally small fishes such as species of Blenniidae and Tripterygiidae (suborder Blennoidea) that occur in the same habitat as *Corynactis viridis*, may be seen in touch with the potentially dangerous tentacles, without the slightest indication of harm (see fig. 24). Palmer (1990: 160) presents a colour photograph taken on a St. Kilda cliffside (Britain) of a juvenile of *Taurulus bubalis* (Euphrasen, 1786) (Cottidae) resting among a clone of (predominantly closed) *Corynactis* polyps. The same phenomenon has been observed in species of the tropical corallimorpharian genus *Discosoma* Rüppell & Leuckart, 1828 (observations J.C. den Hartog).

The parasitic copepod *Mesoglicola delagei* Quidor, 1906, which may occur in the mesogloea of the species, or in galls, and which has been reported from the Atlantic and the Mediterranean coasts of France (Humes, 1982: 103; Gotto, 1993: 218), was not encountered during the present study.

To our knowledge there is hardly any information in the literature on predators of *Corynactis viridis*. In the Azores the gastropod *Philippia* spec. (Architectonicidae) was occasionally found associated with the species (observations J.C. den Hartog) and suspected to feed on it, but this was not checked by a study of the gut contents. Edmunds et al. (1974: 945) ascertained in experiments that the nudibranch *Aeolidia*

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1) This way of asexual reproduction in *Corynactis* is possibly better referred to as longitudinal laceration, because it does not represent the same rather neat splitting in two about equally sized halves as is usual in species of Actiniaria.

papillosa (Linnaeus, 1761) does accept *C. viridis* as food, but only reluctantly so, and van Schie (1991: 36), in an unpublished student's essay, incidentally noted that the species is preyed upon by "some species of sea-urchin", basing herself on unpublished information by J.R. Turner.

Distribution (fig. 15).— All around Ireland and on the south and west coasts of Britain, up to extreme northern Scotland (Manuel, 1981: 207), but evidently absent from as far to the north as the Farøer (den Hartog: fieldtrip 1985) and also not known from south western Norway where temperature conditions throughout the year are only slightly different from those in northernmost Scotland (cf. Gorshkov, 1978: maps 142-143). The known distribution along the continental coast of Europe extends from northern France, southward along the coasts of Spain (Ramil, 1985: 159; Ramil & Pulpeiro, 1990: 25) and Portugal (Nobre, 1931: 59; 1937: 27; RMNH Coel. 18620) into the Mediterranean, penetrating eastward into the Adriatic (Dr A. Svoboda; personal communication) and the northern Aegean Sea, where it was found in relatively cool water in depths between ca. 60 and 100 m (Dr D. Favidis, personal communication; see "Material"). There is one record from the Netherlands bearing on adventitious material found attached to drifting seaweeds washed up on the beach (den Hartog, 1960; 1980: 77). The present study shows the species to be also widely distributed in the Macaronesian islands (Madeira Archipel, Azores, Canary- and Selvagens Islands), but it is presumably absent from the Cape Verdes (CANCAP expeditions 1982, 1986) and the Cape Verde Peninsula, Senegal (den Hartog: field trips 1982, 1983). Whether the allopatric but morphologically similar population of Cabo Frio Island, Brazil (see p. 6; also den Hartog, 1980: 16 table 1, 18-19), represents *Corynactis viridis* sensu stricto is quite possible, but this needs further study. In spite of the geographical situation of Cabo Frio Island, at the edge of the tropics (ca. 42°W 23°S), shallow water temperatures there are unexpectedly low; the average monthly summer maximum in shallow water (25 m: ca 22°C) hardly or not exceeding that in the Canary Islands (ca. 21-22°C), though the average monthly winter minimum is higher (ca. 22°C versus 18-19°C) (cf. Gorshkov, 1978: maps 142-143); cold upwelling water, however, might further lower the temperature locally [Cabo Frio (Portuguese) = Cape Cold]. The specimens from off Cape Hatteras on the U.S. east coast (see p. 6), previously briefly described by den Hartog (1980: 18) as *Corynactis* spec. 1, may also be referable to *Corynactis viridis*. If the Brazilian specimens really are *Corynactis viridis*, it would seem probable that *C. carnea* Studer, 1878, described from off the coast of Argentina (Carlgren, 1927: 2-4) is also conspecific; this matter is discussed in more detail in the next section ("Validity of the species of *Corynactis*").

Validity of the species of *Corynactis*.— Carlgren (1949: 13-14), in his still authorative though in many respects outdated "Survey of the Ptychodactiaria, Corallimorpharia and Actiniaria", listed no less 15 species of *Corynactis* (table 3). However, in previous publications he repeatedly entertained doubts as to the separation of at least some of the species listed. With reference to *Corynactis carnea* Studer, he stated (Carlgren, 1927: 4): "It is very difficult to erect good characters separating the known *Corynactis*-species. In anatomic respect they agree very well. The diagnosis of *C. carnea* is therefore tentative". Later, in connection with his original description of *C. californica*, he wrote (Carlgren, 1936: 18): "It is very difficult to give good diagnoses of the species of *Corynactis*, as they agree very much in their structure. The species [i.e. *C. californica*] cannot be identical with the West Indian *C. bahamensis* and *C. myrcia* ...... , and probably not with *C. carnea*,

Table 3. Species of *Corynactis* listed by Carlgren, 1949, and species described since, with their distribution and synonymies.

C. viridis Allman, 1846	Type species; temperate and subtropical eastern Atlantic and western Mediterranean; ?Cabo Frio, Brazil; ?eastern North America.
C. parvula Duchassaing & Michelotti, 1860	Eastern Caribbean and Bermuda.
C. myrcia (Duchassaing & Michelotti, 1864)	Idem; subjective junior synonym of *C. parvula* (see den Hartog, 1980: 17-18).
C. bahamensis Watzl, 1922	Andros, Bahamas; misidentification; subjective junior synonym of *Ricordea florida* Duchassaing & Michelotti, 1860 (see den Hartog, 1980: 33).
C. carnea Studer, 1878	Atlantic coast of Argentina.
C. chilensis Carlgren, 1941	Central and southern Chile.
C. californica Carlgren, 1936	California, USA, to British Columbia, Canada; ca. 32 - 50°N; Japan.
C. annulata (Verrill, 1866)	South-Africa and Inaccessible Archipelago.
C. australis Haddon & Duerden, 1896	New South Wales and Tasmania
C. haddoni Farquhar, 1898	New Zealand; subjective junior synonym of *C. australis*.
C. mollis Farquhar, 1898	New Zealand, North Island, Wellington; subjective junior synonym of *C. australis*.
C. gracilis Farquhar, 1898	New Zealand, Wellington; subjective junior synonym of *C. australis*.
C. albida Stuckey, 1909	New Zealand; subjective junior synonym of *C. australis*.
C. globulifera Ehrenberg, 1834	Red Sea; western Indian Ocean; a species of *Pseudocorynactis*.
C. hoplites Haddon & Shackleton, 1893	Torres Straits, Indian Ocean; ?Gulf of Manaar, India.
C. delawarei Widersten, 1976	Edge of continental shelf off New Jersey, USA.
C. sanmatiensis (Zamponi, 1976)	Described as *Sphincteractis sammatiensis* gen. et spec. nov., Sideractidae; off Argentina, ca. 40°54' 41°42'S 64°01'-67°07'W; undoubtedly a junior synonym of *C. carnea*.

which is unknown on the west coast of Central America and has not been taken north of Guaytecas Islands [southern Chile] on the west coast of South America". In 1938 (: 14) he lacked conviction about the specific identity of the South African *Corynactis annulata* (Verrill, 1866) by stating: "The species is closely related to *Corynactis carnea*, but is probably not identical with that species, among other reasons because the colour is different. If the two are identical the name *annulata* has priority". Finally, in the framework of a study of specimens of *Corynactis* from the Inaccessible Archipelago in the southern part of the South Atlantic, he again discussed the issue of *C. annulata* and *C. carnea*. (Carlgren, 1941: 2-4). On the basis of [alleged] differences in cnidom and colour he then not only concluded that they represent different species, but also that the Atlantic (East Patagonian) and Pacific (Chilean) populations of *C. carnea*, until then considered conspecific, were specifically different, and hence proposed a new name, *C. chilensis*, for the latter. Considering the variation in the cnidom of *Corynactis viridis* as established during the present study, and the variation in colour of the genus *Corynactis* in general, Carlgren's criteria to separate these three southern species should be looked upon with reserve, and a revision of these three species and of the genus in general therefore remains a necessity.

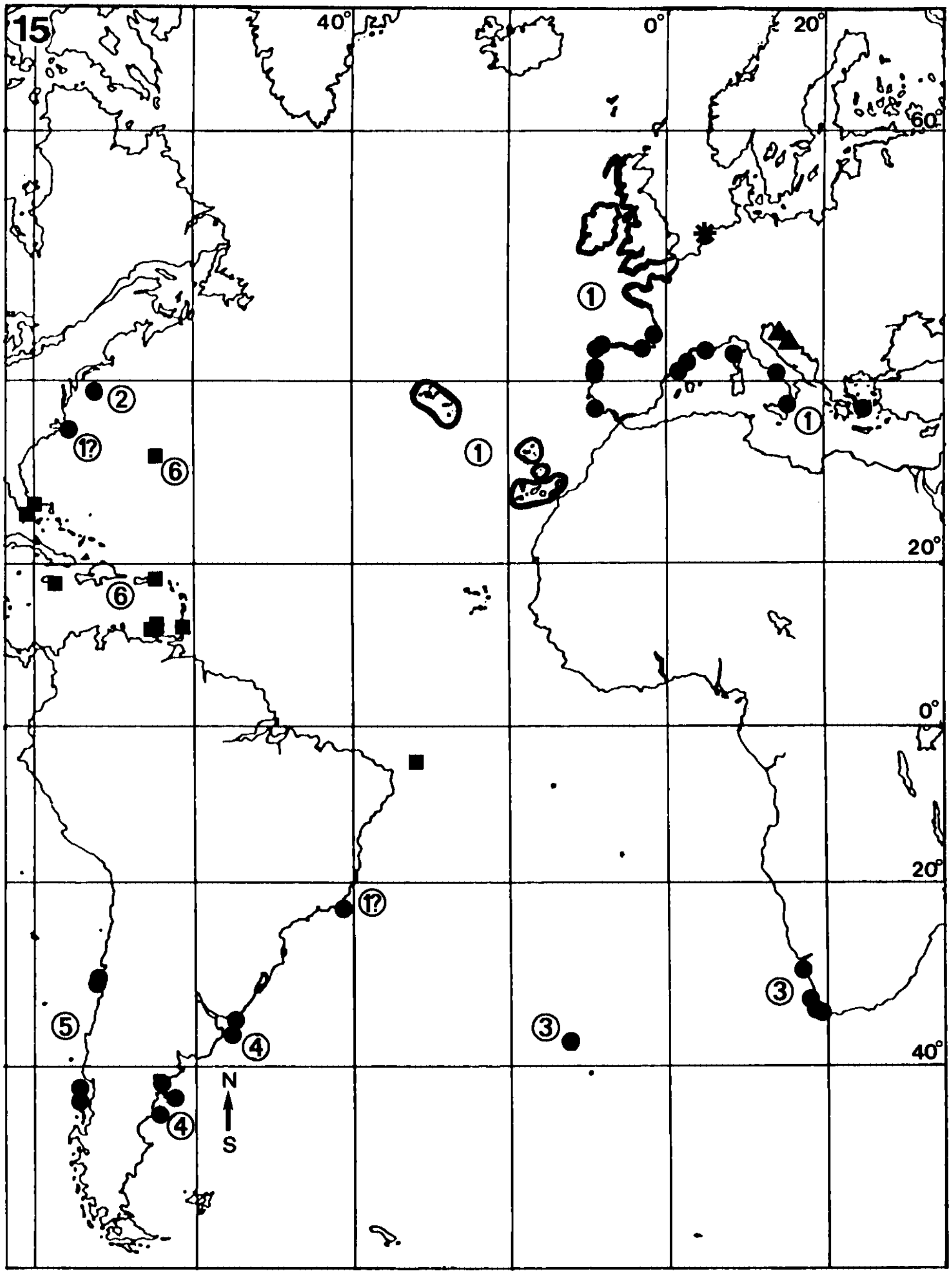

Fig. 15. Distribution of the *Corynactis viridis*-complex (dots and heavy contours) in the Atlantic and western South America; for the sake of completeness the distribution of the tropical *C. parvula* Duchassaing & Michelotti, 1860, is also indicated (squares).

1. *Corynactis viridis* Allman, 1846 (* = adventitious record; Δ = Adriatic Sea [no specified locality records available], A. Svoboda, personal communication; 2. *C. delawarei* Widersten, 1976; 3. *C. annulata* (Verrill, 1866); 4. *C. carnea* Studer, 1878; 5. *C. chilensis* Carlgren, 1941; 6. *C. parvula* Duchassaing & Michelotti, 1860. Sources: Ates, 1987: 315; Carlgren, 1927: 3; 1938: 13; 1941: 1; 1949: 13-14; 1959: 10; Gili, 1982: 125; den Hartog, 1980: 12-13, 14-19; den Hartog et al., present paper; Manuel, 1981/1988: 207; McMurrich, 1893: 147, 208; Nobre, 1931: 59; 1937: 27; Pires et al., 1992: 12; Ramil 1985: 159; Ramil Blanco & Pulpeiro, 1990: 25; Riemann-Zürneck, 1979: 234; Sars 1857: 22; Steiner, 1983: 57; Studer, 1878: 542; Verrill, 1870: 74; Zamponi, 1976: 131.


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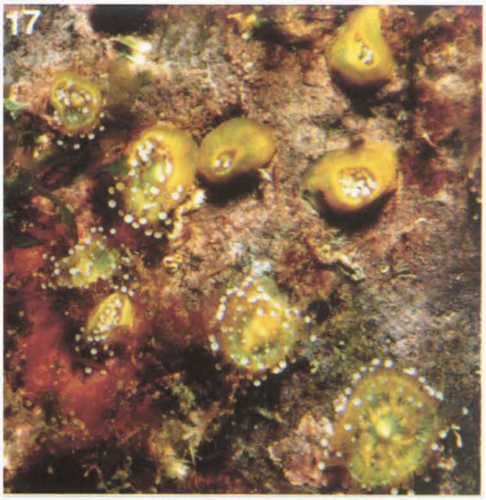
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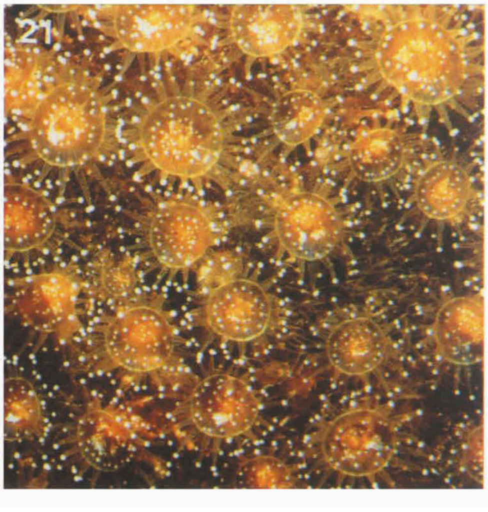
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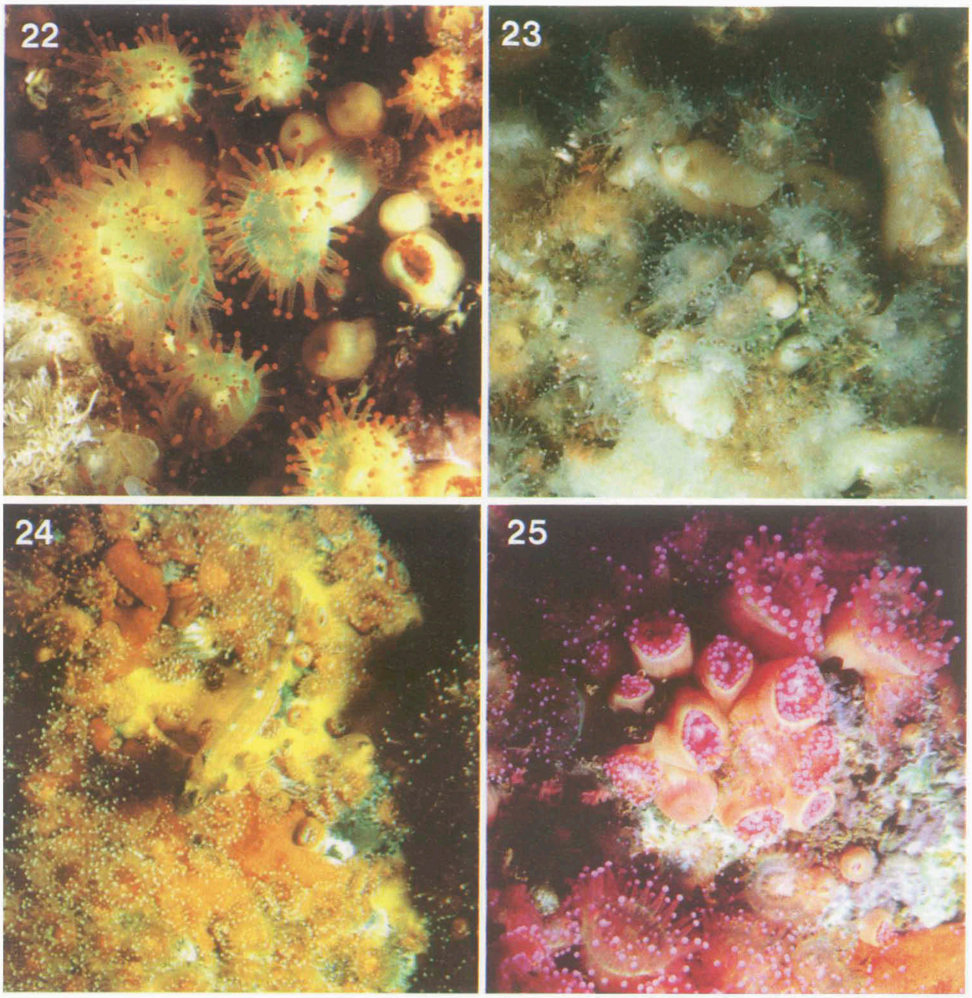


Figs. 16-25. *Corynactis viridis*. Variation in colour. Figs 16-23. Clones from the Azores, Faial (vicinity of Horta) and Pico, 0-7 m, xi. 1990-vi.1991 (photos P. Wirtz); note greenish to brownish hue of column in figs. 16-17, and whitish clone among white sponge in fig. 23 (taken at a depth of 5 m in diffuse light at the entrance of a cave). Fig. 24. Additional clone(s) from the Azores, Ilhéus Formigas, Sta. CANCAP 5.D02; note small fish, *Tripterygion* spec., apparently unharmed by the potentially dangerous polyps (photo CANCAP archive); fig. 25. Clone from Madeira, Ponta de São Laurenço, 1976 (photo J. de Castro). Magnifications mostly ca. × 1 to × 2.

Why Carlgren maintained the four New Zealand species in his list of 1949 is difficult to understand and possibly just a slip, for in 1924 (: 181) he considered them synonymous (selecting *C. haddoni* Farquhar, 1898, as the valid name) and in a later paper (Carlgren, 1950: 131-132) he evidently still held that opinion and moreover implicitly synonymized them with *Corynactis australis* Haddon & Duerden, 1896. Although the types of the New Zealand species described by Farquhar (1898: 532-535) and Stuckey (1909: 390) were never re-examined there is little ground to maintain them as separate species; the differences presented in the descriptions are little convincing and the exclusive occurrence in New Zealand of no fewer than four sympatric species of the

C. viridis-complex, against none in the rest of the area of distribution, would seem most unlikely. Parry (1951: 87) likewise stated that *Corynactis australis* and the four species described from New Zealand probably are one and the same species, and one year later (1952: 139) lumped all species listed by Carlgren "since, without further evidence, there appear to be no differences between them other than colour", thus formally synonymizing all these species with *C. viridis* Allman, 1846. However, in spite of this he kept using the junior name *C. haddoni*. Parry's view seems very close to the truth if we exclude *C. parvula* (definitely a separate and valid species; see den Hartog, 1980: 17-18), the poorly known *C. hoplites* Haddon & Shackleton, 1893, and *C. globulifera* Ehrenberg, 1834 (which almost certainly belongs in the genus *Pseudocorynactis*; den Hartog, in preparation). The remaining species, allopatric and distributed discontinuously over the temperate regions of the world, may well represent a single species (or at the most a superspecies), *Corynactis viridis* Allman, 1846, possibly composed of a number of morphologically rather less than more distinct subspecies (or semispecies). There could be overall differences in size from one "species" or population to another, and the gamut of colours might also vary considerably (and probably does so), but such differences give little practical holdfast for identification and are presumably blurred to a large extent by the frequent occurrence of asexual reproduction. On the other hand already Haddon (1898: 468) drew attention to the fact that polyps of such geographically widely separated "species" as *C. viridis*, *C. carnea* and *C. australis* may be similar in sharing the presence of a subtle character like a green ring around the oral disc (cf. figs.16-25). In *C. viridis*, this ring may also be orange to reddish, a condition that has also been reported from the South African *C. annulata* (cf. Verrill, 1870: 74; Carlgren, 1938: 13), which for that matter may also have a greenish ring (cf. Branch & Branch, 1988: col.fig. 15), as in the other species just mentioned.

In conclusion, a definitive decision about the taxonomic status of the majority of "species" of *Corynactis* can only be based on a thorough comparative study (general anatomy, histology and cnidom, and possibly more sophisticated techniques) of its members. Existing descriptions are not sufficiently detailed to allow for a meaningful comparison, maybe with the exception of those of *C. viridis* and *C. californica* (cf. Hand, 1955: 349-355). Possibly except for overall colour range and different frequencies of the various colour varieties (which, however, may even vary strikingly from one locality to another, as shown for *C. viridis*; see above), the descriptions of these two last-named "species" show them to be very similar indeed. A possible difference between them concerns behaviour. Chadwick (1987; 1991) ascertained that *C. californica* successfully competes for space with other Anthozoa by interspecific aggression through extrusion of filaments. This behaviour has not been reported from *C. viridis*, but studies focused on the occurrence of such behaviour in that species have not been performed so far, neither in other species. However, often being the predominant species in sites where it occurs, *C. viridis*, too, evidently is a successful competitor (possibly in the same way), and the same may apply to other "species" of *Corynactis*.

2. Distribution of the genus *Corynactis*.— Den Hartog (1980: 74 fig. 20) stated that species of *Corynactis* range world-wide in temperate to tropical shallow waters. As discussed above, the majority of these species form part of the temperate to subtropical *C. viridis*-complex; even the presence of the Brazilian population of Cabo Frio, although in a strict geographical sense occurring in the tropics, is clearly related to the presence of unexpectedly cold water at this latitude.

The distribution of the *Corynactis viridis*-complex (if not a single species), notably in the southern hemisphere (southern South America, South Africa, south-eastern Australia and New Zealand), suggests that this complex is either very old (possibly of Gondwana origin), or that *Corynactis* larvae are long-lived and easily dispersed via the West Wind Drift, the South Atlantic Gyre, etc., but unfortunately nothing is known about this.

The number of tropical species is probably very limited. A current study (den Hartog, in preparation) reveals that *C. globulifera*, described and reported from a few localities in the tropical Indo-Pacific and the Red Sea, almost certainly is a species of *Pseudocorynactis*. The same holds for *Corynactis* spec. recorded from Hawaii by Cutress (1977: 130, fig. 1), and possibly for *Corynactis* spec. mentioned from the Gulf of Manaar, India, by Ramunni Menon (1927: 37), but the latter species is more likely to be referable to *Corynactis hoplites*. In conclusion, the only tropical species of *Corynactis* to be maintained are the Caribbean *C. parvula* and the Indo-West-Pacific *C. hoplites*.

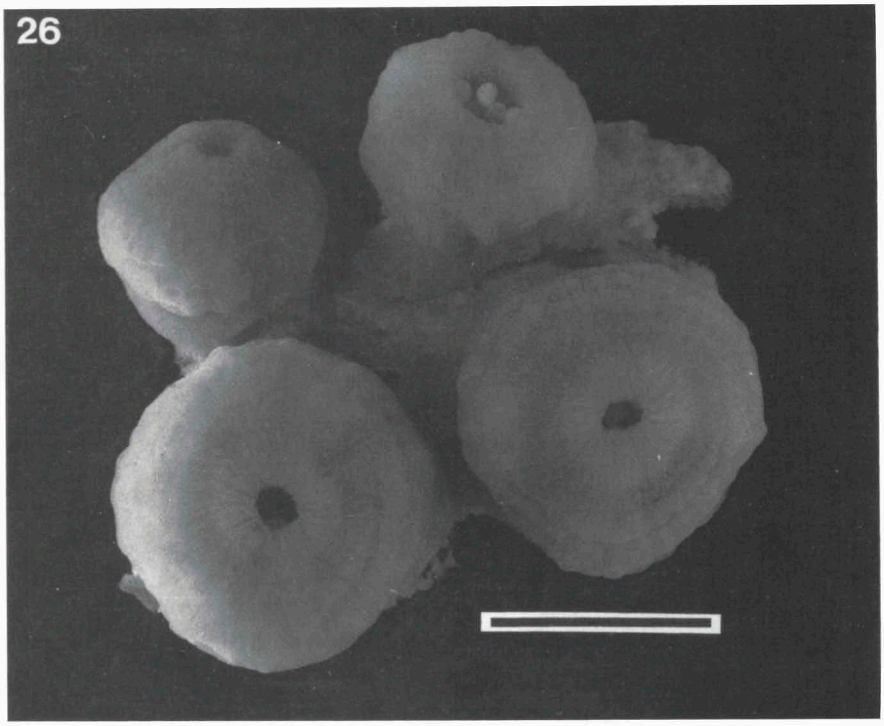


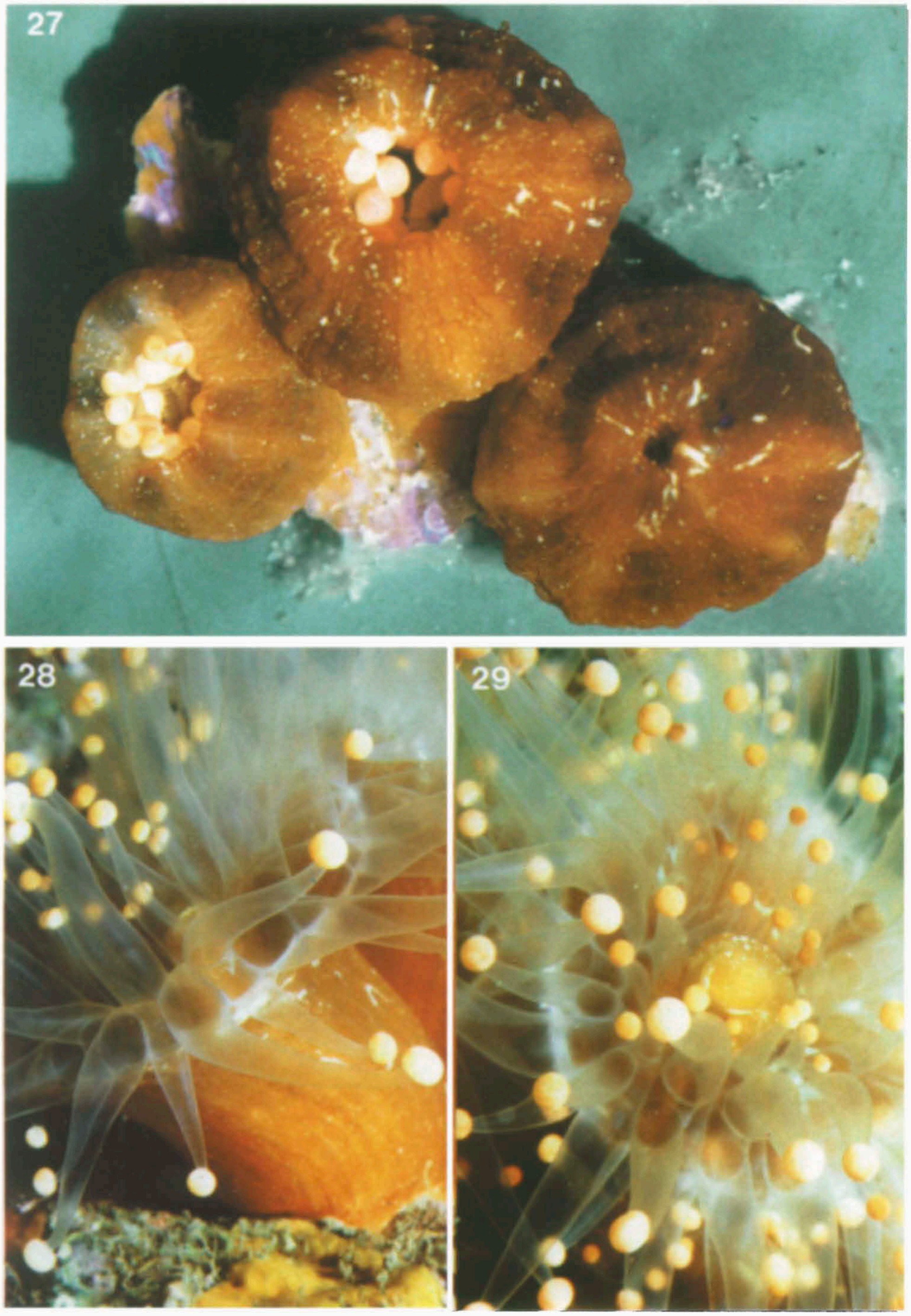
Fig. 26. *Pseudocorynactis caribbeorum*. Preserved clone from La Palma, Canary Islands (RMNH Coel. 17757), consisting of four basally connected individuals. Scale bar 2 cm.

Pseudocorynactis den Hartog, 1980

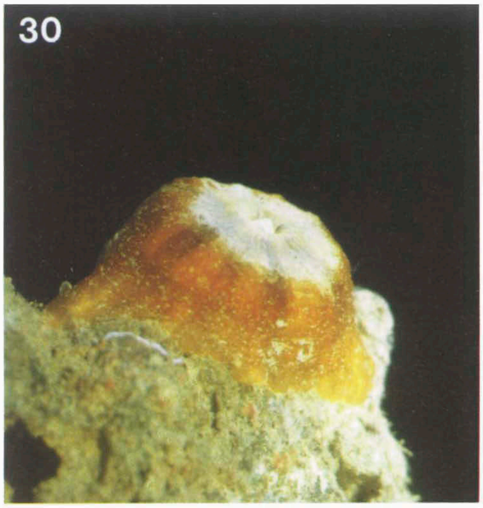
Pseudocorynactis caribbeorum den Hartog, 1980

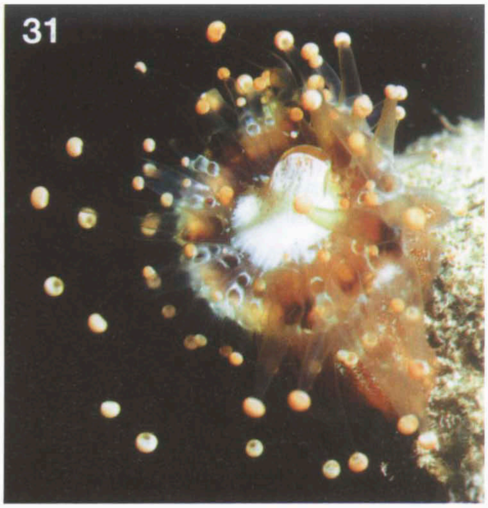
(figs. 26-31, 34-38, tab. 4)

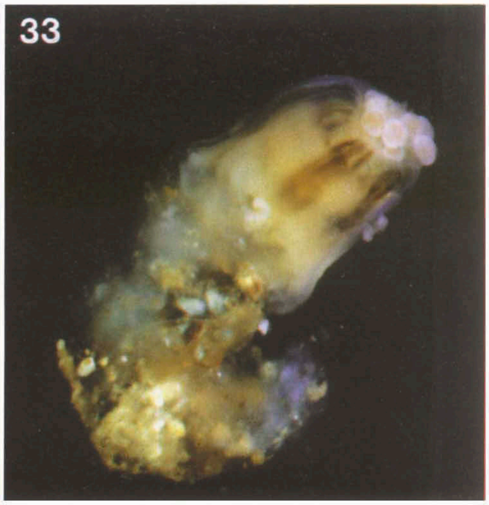
Pseudocorynactis caribbeorum den Hartog, 1980: 19-25, figs. 3, 4, pls. 2, 3, 8, 9 fig. 1, 12, 13 fig. 10 (morphology, anatomy, cnidom; Caribbean); Perrine, 1985: 214-218, phots.; Sefton & Webster, 1986: 50-



Figs. 27-29. *Pseudocorynactis caribbeorum*. Habitus and colour of clone from La Palma (RMNH Coel. 17757). Fig. 27. Three connected specimens in vitro (photo M.S.S. Lavaleye); ca. × 2. Figs. 28-29. Oral and lateral view of an individual of the same clone in situ; note large size of the exocoelic and penultimate endocoelic tentacles (photos R. Rozendaal); ca. × 1.5.







Figs. 30-31. *Pseudocorynactis caribbeorum*. Caribbean specimen from Curaçao, contracted and expanded (photo fig. 31 by C. Roessler); ca. × 1.
Fig. 32-33. *Pseudocorynactis caboverdensis* spec. nov. Live holotype (RMNH Coel. 16760) photographed in vitro; actual size ca. 4 x 3 mm.

51, col. phot.; Steene, 1990: 117 col. phot., 316 (Grand Cayman); Humann, 1992: 107, col. phot.; Beansch & Debelius, 1992: 440-441, col. phot.

Not *Pseudocorynactis* spec.; Pires et al., 1992: 12 (Fernando de Noronha, Brazil) [=*Corynactis parvula* Duchassaing & Michelotti, 1860; specimen examined].

Unidentified; Colin, 1978: 199, 200 col. phot.; Naglschmid, 1978: 36, 37 col. phot.

Material.— RMNH Coel. 17757 (CANCAP sta. 4.D14, Canary Islands, La Palma, W coast, Tijarafa 28°42'N 17°58'W, 9 m, shadowy rock-wall, 5.vii.1980, coll. M.S.S. Lavaleye, clone of 4 connected individuals); RMNH Coel. 17758 (Canary Islands, Tenerife, Los Abrigos, Calheta de Agua Dulce, 8 m, on rocky wall at entrance of cave, 22.xi.1980, coll. A. Brito, 1 specimen); RMNH Coel. 17759 (Canary Islands, Tenerife, Tabaiba, 108 m, between dead calcareous algae in community of the stony coral *Dendrophyllia ramea* (Linnaeus, 1758), 23.i.1982, coll. A. Brito, 1 specimen); RMNH Coel. 18619 (Canary

Islands, La Palma, Tazacorte, 25 m, vertical rock-wall, *Asparagopsis taxiformis*-community, 10.x.1989, 1 specimen [histological sections only]).

Additional individuals were observed in the Canary Islands but not collected.— **Tenerife:** Las Galletas, 6 m, on rocky wall among calcareous algae at entrance of small cave, 10.viii.1981, A. Brito, 1 individual; Las Américas, tidal pool, 1.iv.1983, A. Brito, 1 individual; Aqua Dulce, depth 10 m, at the end of cave, 5 unconnected specimens, regularly observed from 1980 on, A. Brito & O. Ocaña; **La Palma:** Tazacorte, 25 m, vertical wall with red alga *Asparagopsis armata*, 6.viii.1990, O. Ocaña, 2 connected specimens of unequal size; **El Hierro:** Punta de la Restinga, 5 m, in small cave, 26.vi.1990, O. Ocaña; 10 gregarious specimens, part of them basally connected, of two different colour varieties, presumably representing 2 clones.

Description (for Caribbean specimens see den Hartog, 1980: 19ff): Morphology.— Base irregular in outline, often somewhat spreading. Column firm, more or less distinctly differentiated into scapus and scapulus; diameter in preserved specimens up to ca. 30 mm.

Anatomy.— Sphincter diffuse and well developed, principally endodermal, but embedded in the strongly developed mesogloea where it traverses the insertions of the thick parietal ridges (fig. 34).

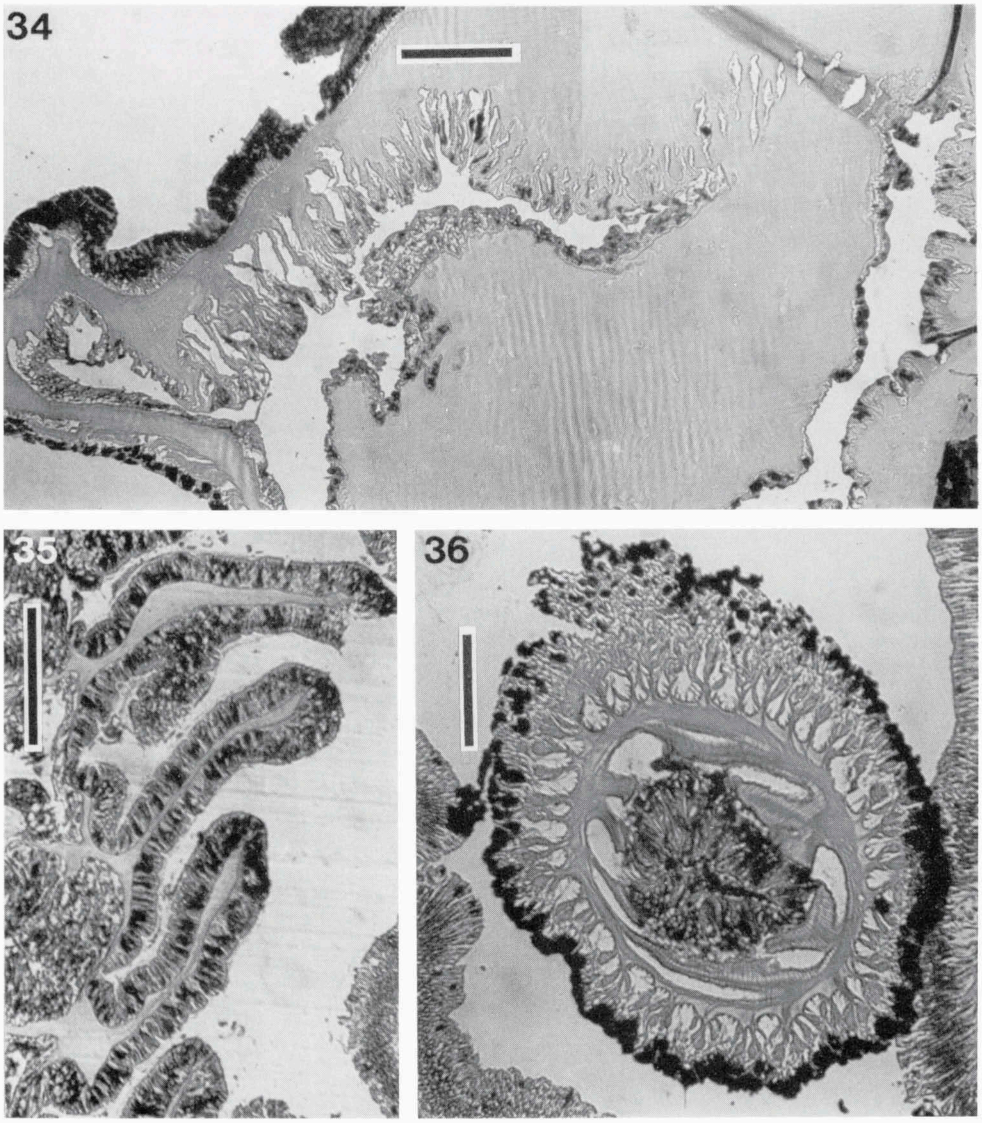
Number of mesenteries 34 (17 pairs) in a specimen of the clone from La Palma (RMNH Coel. 17757), 43 (21 pairs plus one unpaired) in a specimen from Tenerife (RMNH Coel. 17758) and 38 (19 pairs) in another specimen from La Palma (RMNH Coel 18619). Retractors distinct and diffuse, often showing a tendency to be double. Parietobasilar muscles insignificant. Stomodaeum with distinct, narrow, projecting mesogloeal lamellae, equalling the mesenteries in number and situated in direct line with them, and, unlike in *Corynactis viridis*, covered by a densely ciliated endodermal layer of rather uniform thickness (ca. 50-100 µm) (fig. 35; cf. fig. 5). There are two faintly indicated, though not histologically differentiated, siphonoglyphs (each enclosed by two mesogloeal lamellae that are relatively short) corresponding to the directive mesentery pairs [this condition is also present in Caribbean specimens, but was previously overlooked].

Ectoderm of the column about 40-100 µm high, that of the tentacular acrospheres strongly developed, up to ca. 300 µm high (cf. fig. 37 and figs. 10-11, *Corynactis viridis*); cnidae predominantly spirocysts of two widely unequal size-classes (table 4), both very common, so that an arrangement in two distinct, overlapping layers is visible in histological sections; the large size-class forms a layer matching the ectoderm itself in thickness, whereas the small size-class only occupies the peripheral quarter to third part of the ectoderm (fig. 37).

Tentacle stalks with strongly developed ectodermal muscle sheet supported by numerous, most characteristic, brush-like mesogloeal processes (cf. fig. 36 and fig. 13, *Corynactis viridis*); endodermal face of mesogloea of the tentacle stalks finely striated and with conspicuous tranversely arranged, band-like swellings (due to muscular contraction?).

Colouration (figs. 27-31).— The specimens collected in La Palma and Tenerife shared the same brown to orange-brown colour of the column with scattered whitish splashes, especially on the scapulus and the oral disc. The tentacle stalks were fully transparent; the globular acrospheres opaque, yellow-orange to pinkish orange. More brightly coloured individuals were observed in Hierro (observations O. Ocaña). Filaments of members of the clone from La Palma were lilac (fig. 27).

Cnidom (tab. 4; den Hartog 1980: tab. 2, pls. 2-3).— A survey of the cnidoms of the three samples from the Canary Islands, presented in table 4, shows a high degree of



Figs. 34-36. *Pseudocorynactis caribbeorum*. Specimen from La Palma, Canary Islands (RMNH Coel. 18619), anatomical/histological details. Fig. 34. Cross-section of diffuse sphincter. Fig. 35. Stomodaeal pleats; note thin mesogloeal lamellae and endoderm of uniform thicknes (cf. fig. 5, *Corynactis viridis*). Fig. 36. Transverse section of tentacle stalk showing strongly developed ectodermal longitudinal musculature supported by conspicuous, brush-like, mesogloeal processes (cf. fig. 13, *Corynactis viridis*). Scale bar in all three figs. 250 µm.

uniformity. The differences in size of the cnidae of the small specimen from Tenerife (RMNH Coel. 17759) and the other two specimens evidently correlate with body size, a general phenomenon in Anthozoa. On that account it is noticeable that the sizes of the the cnidae of even this small specimen amply exceed those of a considerably larger Caribbean specimen (RMNH Coel. 11486) (cf. den Hartog, 1980: 23 table 2). In addition to the acrospheres, the tentacle stalks were examined; unlike in *Corynactis viridis* and *Pseudocorynactis caboverdensis* spec. nov., these proved practically devoid of cnidae [in all, two small penicilli D, three small spirulae, and not a single spirocyst were found in two squash preparations of each of the three RMNH specimens].

Table 4. *Pseudocorynactis caribbeorum*. Survey of the cnidom of 3 samples from the Canary Islands. A = small specimen from Tenerife (RMNH Coel. 17759); B = specimen from Tenerife (RMNH Coel.17758), C = clone from La Palma (RMNH Coel. 17757). For a pictorial survey, see den Hartog, 1980: pls. 2-3. For the significance of the symbols with respect to "Frequency" see page 5: "Material and methods".

Organ	Specimen/ Clone	Nematocyst type	Mean and range (in parentheses) of length and width nematocyst capsules in µm	N	Frequency
1. Column	A	a. Spirulae $_1$	9.1(8.0 - 9.8) x 3.7(3.3 - 4.0)	7	+[inc.]
	A	$_2$	21.6(18.7 - 24.0) x 6.3(5.8 - 7.1)	15	+
	B	$_1$	11.9(8.9 - 14.2) x 3.7(3.3 - 4.0)	20	-
	B	$_2$	25.2(21.4 - 30.3) x 6.1(5.3 - 6.4)	20	-
	C	$_1$	only one measured, 12 x 3.6		-?
	C	$_2$	24.8(23.1 - 26.7) x 6.4(5.8 - 7.6)	10	-
	A	b. Penicilli D	20.5(16.9 - 24.9) x 7.5(6.7 - 8.0)	11	+
	B		23.5(20.0 - 29.4) x 6.8(5.3 - 7.1)	20	-
	C		24.7(20.5 - 30.3) x 6.1(4.9 - 7.1)	10	-
	A	c. Penicilli E	34.0(30.3 - 37.4) x 11.2(8.9 - 13.4)	11	+
	B		37.6(31.2 - 42.7) x 10.7(8.9 - 11.6)	30	-
	C		37.2(32.0 40.1) x 11.5(9.8 - 12.5)	30	+
2. Acrospheres of tentacles	A	a. Spirocysts	ca. 50 - 275 x 2.7 - 7.1	--	+++
	B		ca. 75 - 275 x 2.7 - 7.6	--	+++
	C		ca. 80 - 222.5 x 3.6 - 6.7	--	+++
	A	b. Homotrichs	92.4(67.6 - 105.0) x 5.7(4.9 - 6.2)	17	+
	B		one 111 x 6.7; several collapsed	--	-?
	C		ca. 93.5 - 102.4 x 5.8 - 6.2	4	-
	A	c. Spirulae	39.0(35.6 - 43.6) x 4.7(4.5 - 4.9)	20	+
	B		39.4(34.7 - 44.5) x 5.3(4.9 - 6.2)	10	--
	C		44.6(40.1 - 53.4) x 5.1(4.5 - 5.8)	25	+
	A	d. Penicilli D	122.0(113 - 133.5) x 6.2(5.8 - 6.7)	14	+
	B		131.8(111.3 - 138.0) x 6.2(5.8 - 6.7)	20	+
	C		129.3(117.5 - 142.4) 6.6(6.2 - 7.1)	20	+
	A	e. Penicilli E	166.4(155.8 - 182.5) x 16.5(15.1 - 182.5)	6	--
	B		176.9(155.8 - 191.4) x 18.1(14.2 - 20.5)	20	+
	C		174.5(146.9 - 191.4) x 19.2(17.8 - 22.3)	20	+
3. Tentacle stalks			In all three specimens practically devoid of cnidae		
4. Stomodaeum	A	a. Homotrichs	31.5(29.4 - 35.6) x 4.9(4.5 - 5.5)	10	+?
	B		34.8(29.4 - 40.1) x 5.2(4.5 - 6.2)	17	+
	C		39.1(34.7 - 42.7) x 5.4(4.5 - 6.2)	20	++
	A	b. Penicilli D	66.5(58.7 - 71.2) x 21.1(18.7 - 24.0)	10	+?
	B		75.2(66.8 - 87.2) x 22.2(17.8 - 24.0)	20	+
	C		75.7(72.1 - 80.1) x 288.8(27.6 - 30.3)	10	- /+

5. Filaments	A	a. Spirulae	only one observed, 11.6 x 4.2	1	- - -
	B		not observed	--	—
	C		14.2(12.5 - 15.1) x 3.9(3.6 - 4.5)	10	-?
	A	b. Penicilli D	20.2(18.7 - 22.3) x 6.8(6.2 - 7.1)	10	-
	B		22.7(18.7 - 26.7) x 6.3(5.8 - 6.7)	35	+
	C		25.4(22.3 - 26.7) x 6.6(6.2 - 7.1)	20	+
	A	c. Penicilli E	75.8(62.3 - 89.0) x 29.1(21.4 - 35.6)	45	+
	B		83.3(65.0 - 93.5) x 31.0(21.4 - 40.0)	40	+
	C		86.5(82.8 - 90.8) x 39.2(33.8 - 42.7)	20	+
			[in addition two smaller capsules: 76.5 x 30.3 and 83.7 x 26.7]		

Biological notes.— Den Hartog (1980: 23), with reference to aquarium specimens, stated that "the very sticky tentacles enable the species to get hold of large prey", such as "large pieces of fish, oyster and living crabs of moderate size". Predation on large prey under natural condition seems confirmed by Perrine (1985), who published suggestive photos showing a specimen in situ engulfing a cardinal fish (*Apogon* spec.), though without stating explicitly whether the fish was actively caught or offered to the anemone [unfortunately this could not be verified; a letter to Mr Perrine, dated 27.xi.1992, with a request for additional information, returned undeliverable].

In the original description of the species (den Hartog, 1980: 24) it was suggested that the species does not normally reproduce asexually, in spite of a "great power of regeneration". The statement of Perrine (l.c.: 218) with reference to Caribbean specimens that the species is found "growing alone or in pairs", and even more so the observations in the Canary Islands of uniformly coloured groups of basally connected individuals, necessitates reconsideration of this idea.

Distribution.— So far the species was exclusively known from the Caribbean. The present new records from the Canary Islands prove it to have an amphi-Atlantic distribution, and a recent study (den Hartog, in preparation) provides evidence that this same species, or an almost similar form, also occurs in the Indo-West-Pacific.

A recent record by Pires et al. (1992) of a specimen of *Pseudocorynactis* spec. from Fernando de Noronha, Brazil, turned out to bear upon *Corynactis parvula* Duchassaing & Michelotti, 1860, as was ascertained by a re-examination of the external morphology and cnidom of the specimen concerned.

Discussion.— Considering overall morphology, anatomy and cnidom, there is no doubt that the Canary Islands and Caribbean populations are conspecific. However, there may be slight differences of a gradual nature. The colouration of Caribbean specimens is rather variable, whereas Canary Islands specimens seems more uniform in colour, although noticeable variation was observed in animals from Hierro. Also, the sparse data so far available suggest a more pronounced tendendy to cloning in the population of the Canary Islands, and added to this it seems the nematocysts of Caribbean specimens tend to be somewhat smaller. It therefore seems possible that the two populations deserve subspecific status, but pending a study of more material, we have refrained from a premature decision in this matter.

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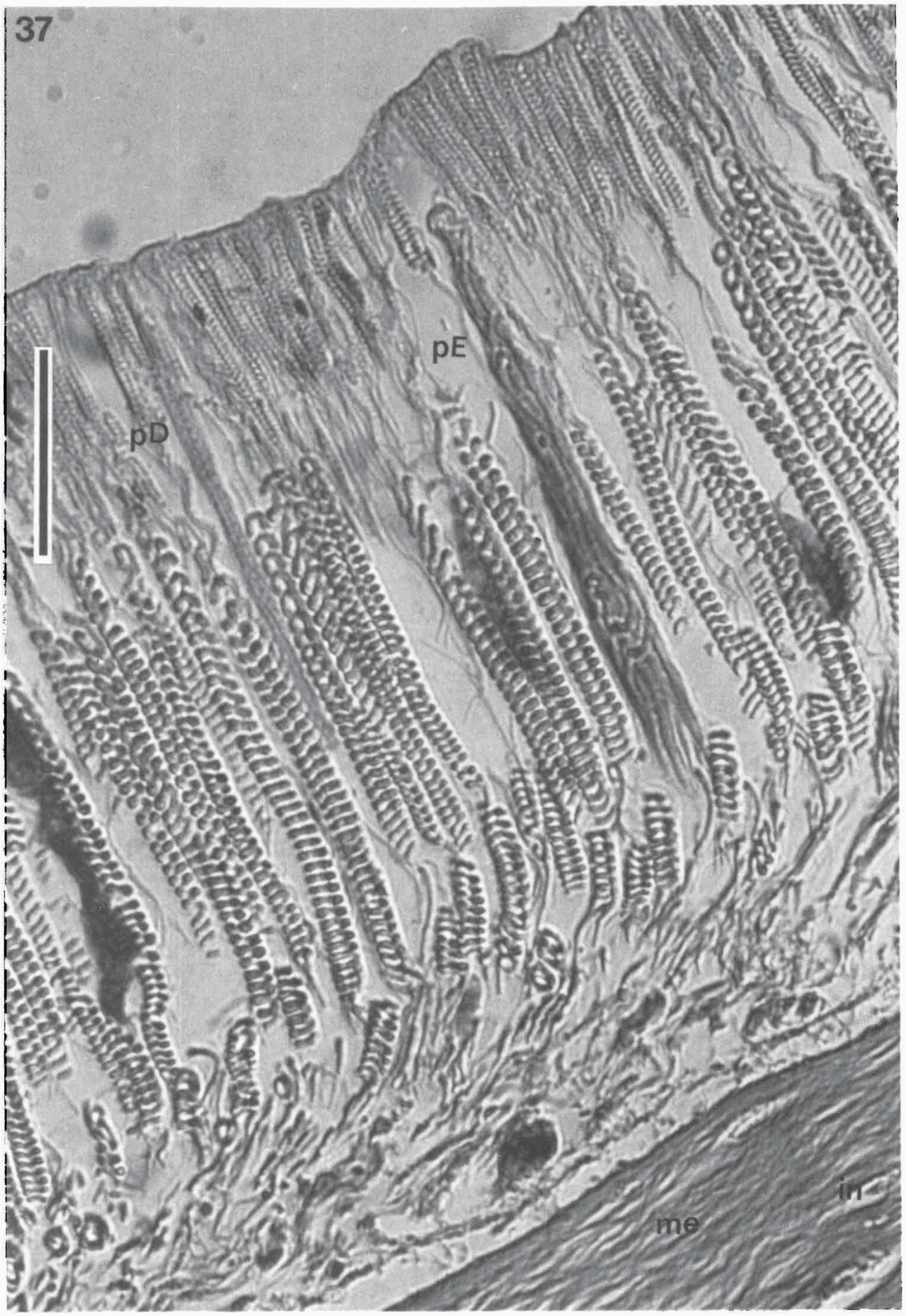

Fig. 37. *Pseudocorynactis caribbeorum*. Specimen from Canary Islands (RMNH Coel. 18619), cross-section through tentacular acrosphere; note numerous spirocysts arranged in two layers. Although the photo may suggest that the layer of small spirocysts lies on top of the layer of large spirocysts, this is an illusion: the tips of both categories reach unto the ectodermal surface. This illusion is mainly due to the fact that the proximal portion of the large spirocysts tapers, whereas the tube in this part is not coiled (cf. den Hartog, 1980: pl. 2a), and therefore less refractile and less conspicuous than the densely coiled central portion. The small spirocysts largely occupy the spaces between the tapering ends of the large spirocysts. Symbols: pD = penicillius D; pE = penicillus E; in = undifferentiated inclusive cells; me = mesogloea. Scale bar 40 µm.

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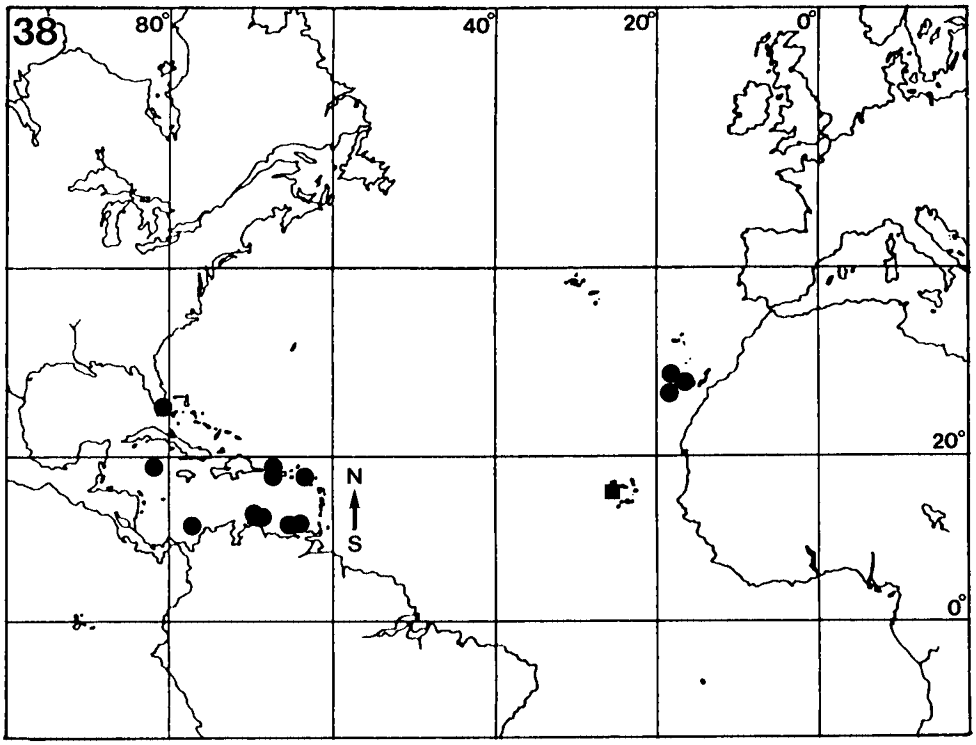


Fig. 38. Known distribution of *Pseudocorynactis caribbeorum* (dots) and *P. caboverdensis* spec. nov. (square). Sources: den Hartog, 1980: 19-20, 25; den Hartog et al., present study; Steene, 1990: 316.

Pseudocorynactis caboverdensis spec. nov.
(figs. 32-33, 38-41, tab. 5)

Material.— RMNH Coel. 17760 (CANCAP Sta. 7.169, Cape Verde Islands, SW of São Vicente, Baia da Ribeirinha, 16°48'N 25°08'W, 165 m, clinkers with many epizoa, rectangular dredge, 7.ix.1986, 1 specimen, the holotype).

Morphology (figs. 32-33).— The specimen is semi-contracted and very small, ca. 4 mm long and 3 mm in cross-section; the lower part of the column and the base are damaged. The body wall is smooth and, in conformity with *Pseudocorynactis caribbeorum*, rather rigid. The tentacles are withdrawn, part of the globular acrospheres remaining visible.

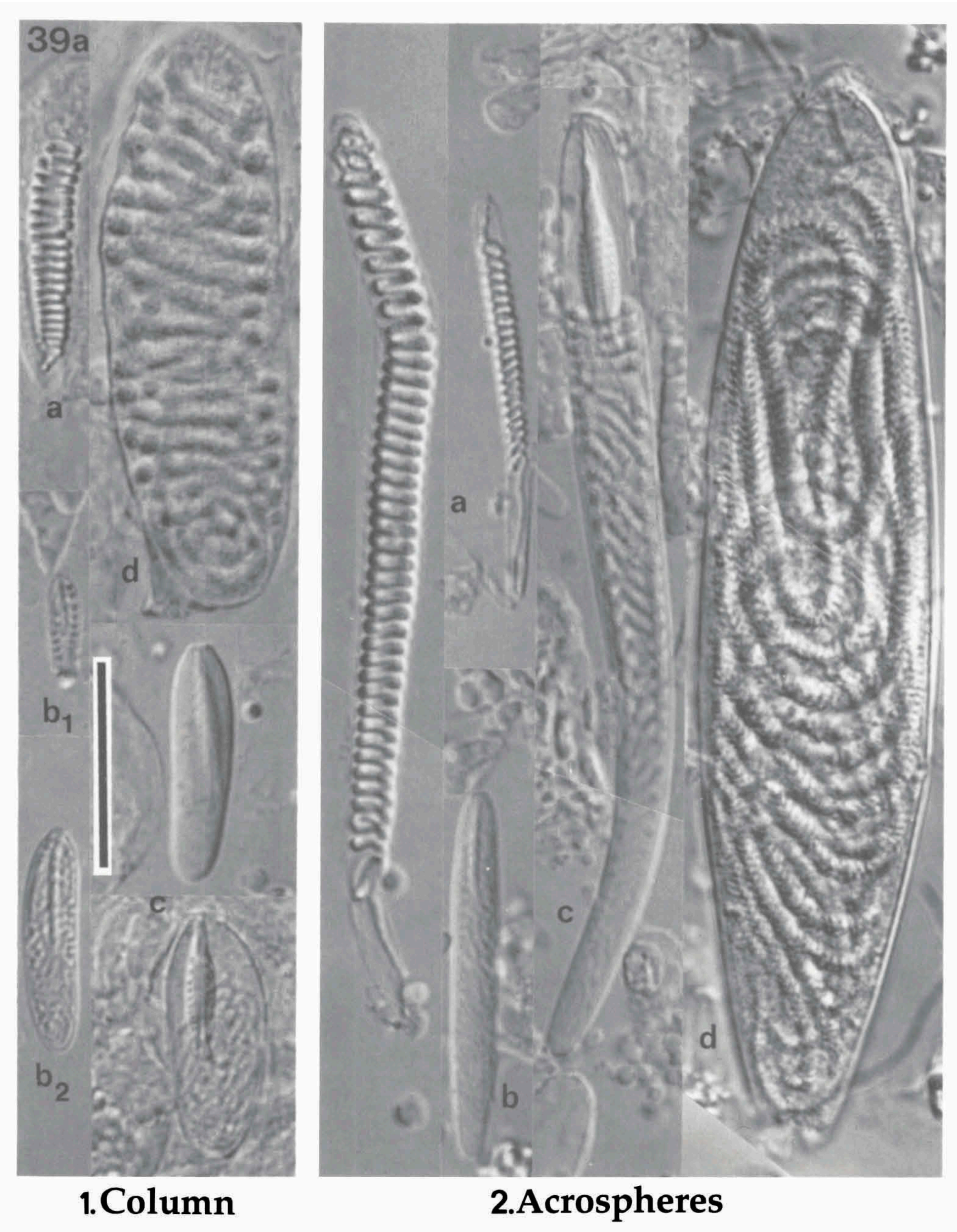
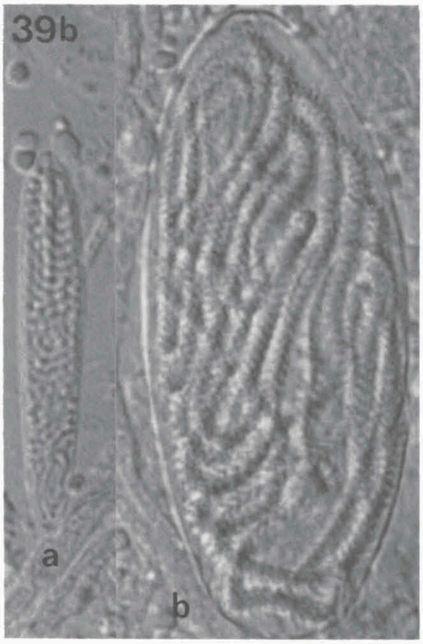
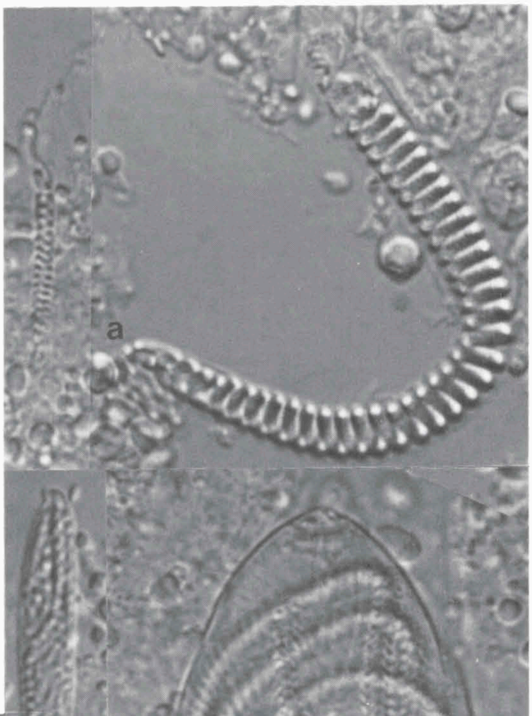
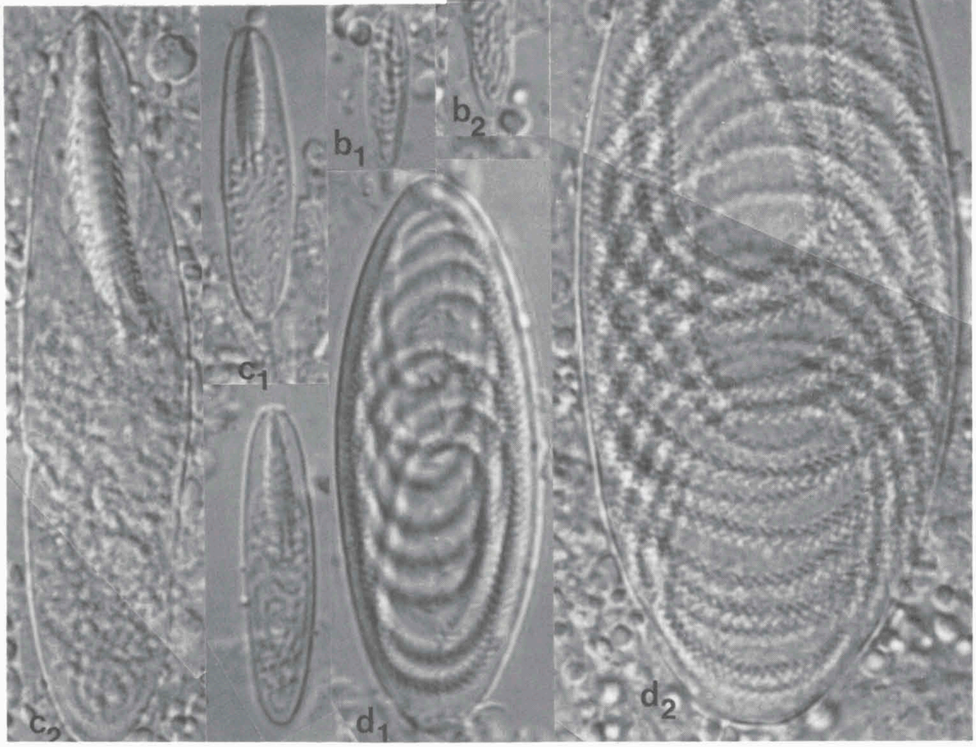


Fig. 39a-b. *Pseudocorynactis caboverdensis* spec. nov. Pictorial survey of the cnidom of the holotype (RMNH Coel. 17760). Numerals and characters correspond to those used in table 5. Scale bar 20 µm.
1. Column: a. Spirocyst; $b_{1, 2}$. Spriulae; c. penicilli D; d. Penicillus E. **2. Acrospheres**: a. Spirocysts; b. Spirula; c. Penicillus D; d. penicillus E. **3. Tentacle stalks**: see figs. 40-41. **4. Stomodaeum**: a. Spirula; b. Penicillus E. **5. Filaments**: a. Spirocysts; $b_{1, 2}$. Spirulae; $c_{1, 2}$. Penicilli D; $d_{1, 2}$. Penicilli E.

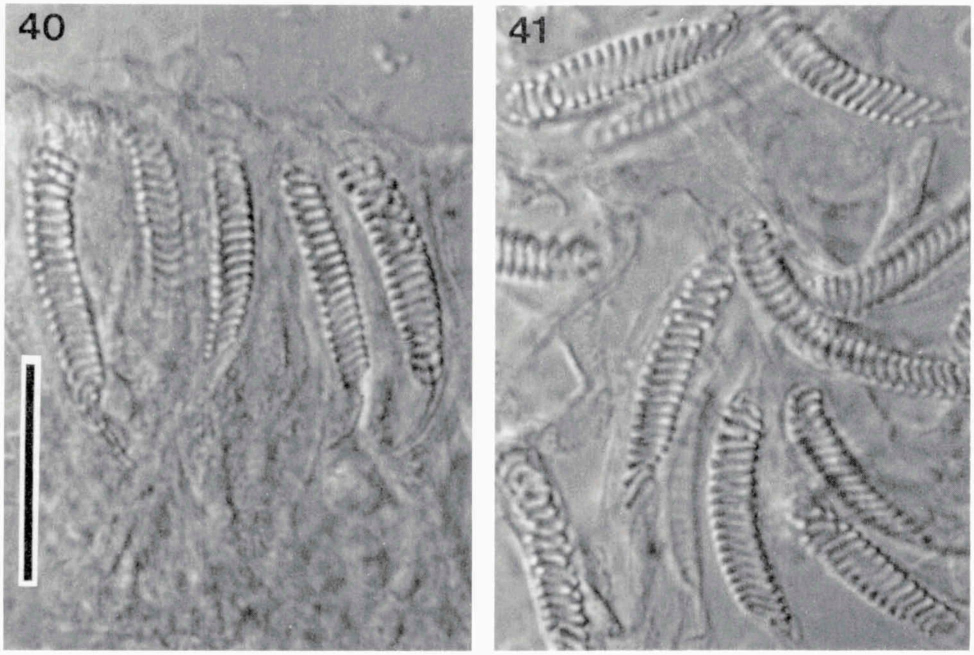


4. Stomodaeum





5. Filaments



Figs. 40-41. *Pseudocorynacytis caboverdensis* spec. nov. Squash preparations of tentacle stalks showing spirocysts and their arrangement in the ectoderm (fig. 40; gently squashed). Scale bar 20 µm.

Colouration (figs. 32, 33).- - The column is semi-opaque with 6 conspicuous dark brown longitudinal bands (as may also be present in *P. caribbeorum*; fig. 30; cf. also den Hartog, 1980: 22, pl. 12 fig. 1), alternating in the marginal region with inconspicuous, pale green markings. The acrospheres of the tentacles are opaque pinkish.

Anatomy.— Not studied, as only one specimen of minute size is available.

Cnidom (tab. 5, figs. 39-41).— Apart from similarities with the cnidom of *Pseudocorynactis caribbeorum* (table 4; see also den Hartog, 1980: 23 table 2, and pls. 2, 3), there are also considerable differences, which cannot simply be correlated with body size. In spite of its minute size, the specimen of *Pseudocorynactis caboverdensis* differs from *P. caribbeorum* by the following characters: 1. the penicilli E in the columnar ectoderm (1d) are much larger; 2. its acrospheral penicilli E (2d) are smaller and of a different shape, their ratio of length and width being about 4-5 : 1 versus 9-10 : 1 in *P. caribbeorum*; 3. the ectoderm of its tentacle stalks contains numerous, relatively short and broad spirocysts (3a), absent in *P. caribbeorum*, 4. in the filaments were found significant numbers of spirocysts (5a) (which, however, may represent contaminations of the acrospheres), spirulae of the stomodaeal type ($5b_2$), and a very conspicuous if sporadical category of large penicilli D ($5c_2$), all absent in *P. caribbeorum*, 5. there are two more or less distinct size-classes of penicilli E ($5d_{1,2}$) with a total range exceeding that of the single size-class present *P. caribbeorum*; and 6. there is no general proportionate correlation between body size and nematocyst size, some nematocysts being smaller, some being larger than in mature, much larger specimens of *P. caribbeorum*.

In several respects *Pseudocorynactis caboverdensis* seems closer to species of the genus *Corynactis* (cf. table 2 and fig. 14a-b) notably to *C. parvula* (although definitely not identical with that species; cf. den Hartog, 1980: tab. 1, pl. 1), viz.: 1. by shape of the spirocysts in the acrospheres (2a) with a roundish apical end (cf. fig. 14.2a); in *Pseudocorynactis caribbeorum* the apical end is narrow and tapered (den Hartog, 1980: pl. 2a), 2. by the presence of spirocysts (3a) in the tentacle stalks (figs. 40-41), 3. by the size of the columnar Penicilli E (1d); and 4. by the presence in the filaments of two distinct size-classes of both penicilli D and penicilli E (5d$_{1,2}$, 5c$_{1,2}$).

Table 5. *Pseudocorynactis caboverdensis* spec. nov. Survey of the cnidom of the holotype (RMNH Coel. 17760).
For the significance of the symbols with respect to "Frequency", see page 5: "Material and methods".

Organ	Nematocyst type	Mean and range (in parentheses) of length and width of nematocyst capsules in µm	N	Frequency
1. Column	a. Spirocyst	ca. 30-50 × 4.0-5.5	--	- - -
	b. Spirulae $_1$	10.8(9.8 -12.5) × 3.2(2.7 - 3.6)	10	?[inc.]
	$_2$	21.0(16.9 - 24.9) × 5.1(4.2 - 6.2)	25	+
	c. Penicilli D	23.1 × 5.8, 23.1 × 8.9	2	- - -
	d. Penicilli E	56.5(53.4 - 61.4) × 18.5(16.9 - 20.5)	10	- -
2. Acrospheres of tentacles	a. Spirocysts	ca. 50-125 × 2.7-6.7	--	+++
	b. Spirulae	42.5(36.5 49.0) × 4.8(4.5 - 5.3)	20	+
	c. Penicilli D	79.5(65.0 - 96.1) 6.8(6.2 - 6.8)	20	+
	d. Penicilli E	107.1(83.7 - 118.8) × 26.5(22.5 - 30.6)	10	- -
3. Tentacle stalks	a. Spirocysts	ca. 30 - 45 × 4.0 - 5.5	--	+++
	b. Spirulae	ca. 30-40 × 5.0-6.2	--	- - [cont?]
4. Stomodaeum	a. Spirulae	33.5(31.2 - 40.1) × 5.7(5.3 - 6.7)	20	++
	b. Penicilli E	55.6(49.0 - 62.3) × 23.3(19.6 - 24.9)	10	-
5. Filaments	a. Spirocysts	ca. 30 × 2.5 - 93.5 × 5.3	--	+
	b. Spirulae $_1$	12.8(10.7 - 16.0) × 3.4(3.1 - 3.8)	10	?[inc.]
	$_2$	35.3(31.2 - 40.1) × 5.8(4.9 - 6.7)	20	+
	c. Penicilli D $_1$	25.8(24.0 - 29.4) × 6.0(5.3 - 6.5)	20	+
	$_2$	70.3(67.6 - 73.0) × 16.0(15.6 - 16.5)	4	- - -
	d. Penicilli E $_1$	51.7(45.4 - 61.4) × 22.0(18.7 - 25.8)	20	-
	$_2$	85.9(71.2 - 106.8) × 35.2(30.3 - 42.3)	20	-

Discussion.— The single specimen is sterile and obviously a juvenile. On the basis of its general morphology and cnidom it is here tentatively accommodated in *Pseudocorynactis*, even though in some respects it seems closer to *Corynactis* and anatomical information is wanting. Due to differences in the cnidom (see above) the specimen cannot be included in *P. caribbeorum*. To what extent these differences with *P. caribbeorum* might be attributed to larval characters of the really small specimen, is impossible to decide in the absence of any knowledge about corallimorpharian larvae, but on the basis of the evidence at hand, it seems legitimate to regard the present specimen as a separate species, *P. caboverdensis*, although this view may need revision when more material from the Cape Verde Islands becomes available.

Etymology.— The specific name refers to the Cape Verde Islands.

Distribution (fig. 38).— Sofar the species is exclusively known from the type locality in Cape Verdes.

Corallimorphus R. Hertwig, 1882

Corallimorphus cf. **atlanticus** Carlgren, 1934

(figs. 42-46, tab. 6)

Corallimorphus atlanticus Carlgren, 1934: 7, pl. 1 fig. 5 (short description, almost exclusively concerning external morphology; 45°26'N 9°20'W, 4700 m; 1 specimen); Carlgren 1949: 13 (name); Dunn, 1984: 8 (probably conspecific with *C. stephensoni* Carlgren, 1928, and possibly also with *C. rigidus* Moseley, 1877).

?*Corallimorphus rigidus*; Stephenson, 1920: 179-186, figs. 1-2, pls. 19-20 (description).

?*Corallimorphus stephensoni* Carlgren, 1928: 128 (new species based on the Atlantic specimens described and identified by Stephenson, 1920, as *C. rigidus* Moseley, 1877).

Material.— RMNH Coel. 17756 (CANCAP sta 5.004, Azores, NE of São Miguel, 38°06'N 24°49'W, depth 2400-3100 m, deep sea clay with much pumice; 5 m beam-trawl, 24.v.1981, 1 specimen without substrate).

Material examined for comparison.— Bergens Museum 39195 (holotype of *Corallimorphus atlanticus*, Michael Sars Expedition 1910, Sta. 10, 45°26'N 9°20'W, 4700 m, trawl, 19-20.iv.1910); NMI 70.1920 (smallest of two syntypes of *C. stephensoni*, SR 336, 51°19'N 12°20'W, 673-720 fm, trawl, 12.v.1906)

Description: Morphology (fig. 42).— Body rigid and rather firm, and, except for the base, almost deprived of ectoderm; mesogloea thick and semi-translucent. Symmetry regularly pentamerous.

Base relatively thin-walled, more or less circular in outline, ca. 35 × 33 mm, slightly convex with incurved limbus.

Column smooth, without grooves and ridges, slightly oblique with a maximal height of 13 mm and a minimal height of 10 mm. Mesenterial insertions showing through and externally well visible along the entire length of the column; they are about equally spaced, except near the margin.

Oral disc 40 × 36 mm (i.e. about equalling the base if the incurved limbus is taken into account), slightly elevated towards the mouth (10 × 6.5 mm wide) and separated from the column by a fringe of 40 very short, stout, rigid marginal tentacles (some reduced and/or damaged, representing no more than marginal crenations), arranged in three cycles: 10 + 10 + 20 = 40. Tentacles of the primary cycle up to 5 mm long, including the acrosphere (deprived of ectoderm, however); tentacles of the secondary cycle up to ca. 3.5-4 mm and of the tertiary cycle ca. 2.5-3 mm. Length of tentacles about equalling to slightly exceeding the diameter of their base (= the distance between the members of the corresponding mesentery pairs).

Discal tentacles almost vestigial, represented only by insignificant knobs, sunk in shallow pits in the peripheral region of the oral disc, and basically arranged in two cycles of 10 tentacles each: an inner cycle corresponding with the primary marginal cycle, inserted at some 5-7 mm from the margin (= ca. 0.3-0.4 × radius length), and an even less significant outer cycle (corresponding with the secondary marginal cycle) inserted at some 3 mm from the margin (= ca. 0.15-0.2 × radius length). There is one small irregularity, viz., one tentacle of the outer discal cycle is missing, whereas a

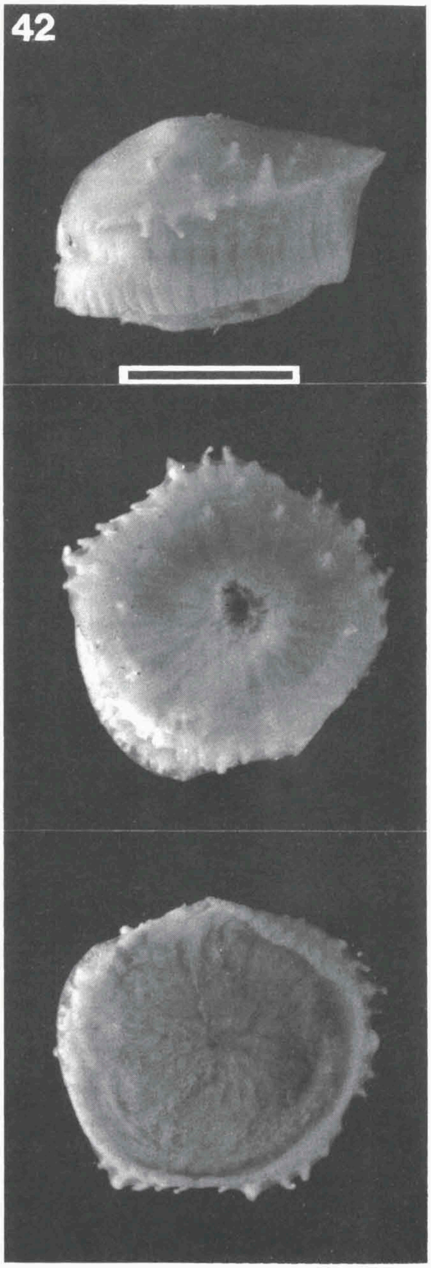


Fig. 42. *Corallimorphus* cf. *atlanticus*. CANCAP specimen (RMNH Coel. 17756) in lateral, oral, and basal view. Scale bar 20 mm.

subsequent tentacle of the inner cycle has doubled (a minute additional one being present). The arrangement of the tentacles and the general plan of the body seem pentamerous, or possibly decamerous; this distinction cannot properly be made.

Anatomy.— The internal structures of the specimen are badly preserved, and especially towards the centre of the body cavity tissues have become completely macerated; hence it is impossible to verify whether all mesenteries are perfect, but at least they all seem to bear well-developed male gonads, partly with ripe or almost ripe spermatozoa (figs. 43-44) which fill the entire body cavity. Filaments and stomodaeal ridges are indistinguishable, and the same holds for the structure of the mesenteries, except for the part inserting onto the body wall. This part shows a thin mesogloea of uniform thickness without any thickened ridges and without any conspicuous musculature. The mesogloea of the body wall is firm, ca. 0.75-1.25 mm thick, that of the base much thinner.

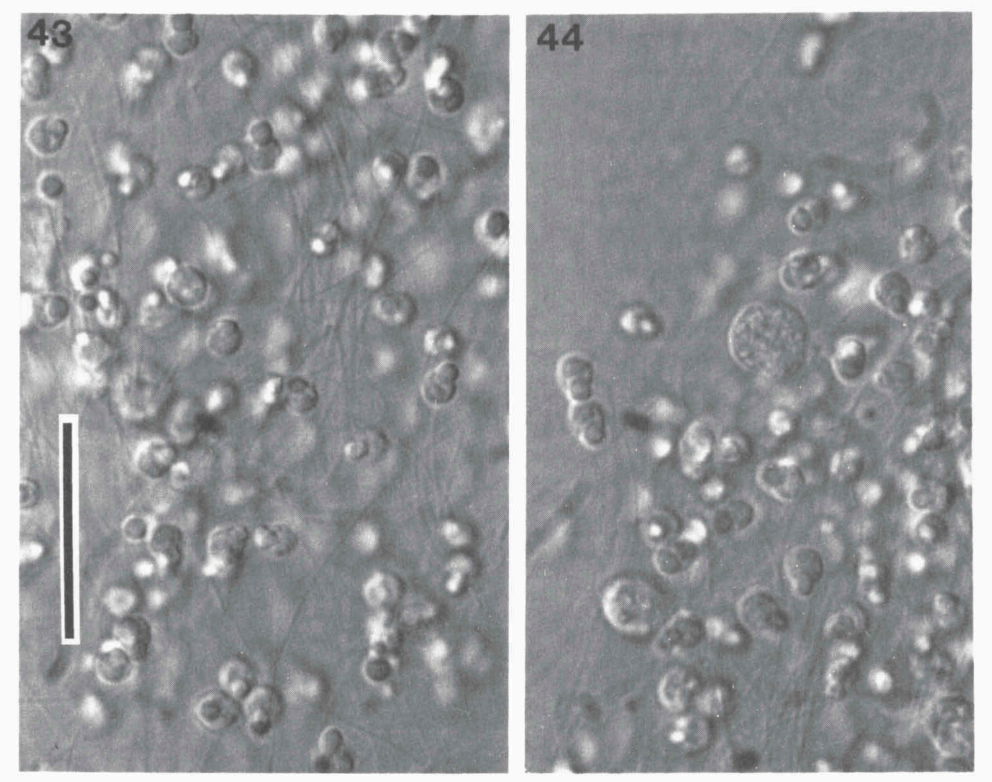
Cnidom (tab. 6, fig. 45a-b).— As mentioned above, the CANCAP specimen is largely deprived of ectoderm. Some ectodermal tissue, however, could be obtained from the pedal disc, the lower part of the column, and from radial grooves and depressions in the oral disc. Tentacle stems and acrospheres lack any trace of ectoderm, but some macerated tentacular ectoderm (identifiable by the presence of spirocysts), mainly deriving from the stems (as is obvious from the the size of the spirocysts), was obtained from pits surrounding the base of the inner discal tentacles. A study of this tissue also revealed the presence of a few stray acrospheral nematocysts. Stomodaeal tissue, though macerated, could easily be extracted from the distended mouth of the anemone. Smears of macerated tissue taken from the coelenteron revealed the composition of the cnidom of the filaments. Altogether the survey of the cnidom of the CANCAP specimen presented in table 6 and fig. 45 may be regarded representative, for obvious reasons except with respect to the tentacular acrospheres. One of the categories not found in the sloughed tentacular tissue were the large, conspicuous, oblong to lanceolate

Table 6. *Corallimorphus atlanticus*. Survey of the cnidom of the CANCAP specimen (A) (RMNH Coel. 17756) and of the holotype (B) (Bergens Museum 39195).
For the significance of the symbols with respect to "Frequency", see page 5: "Material and methods".

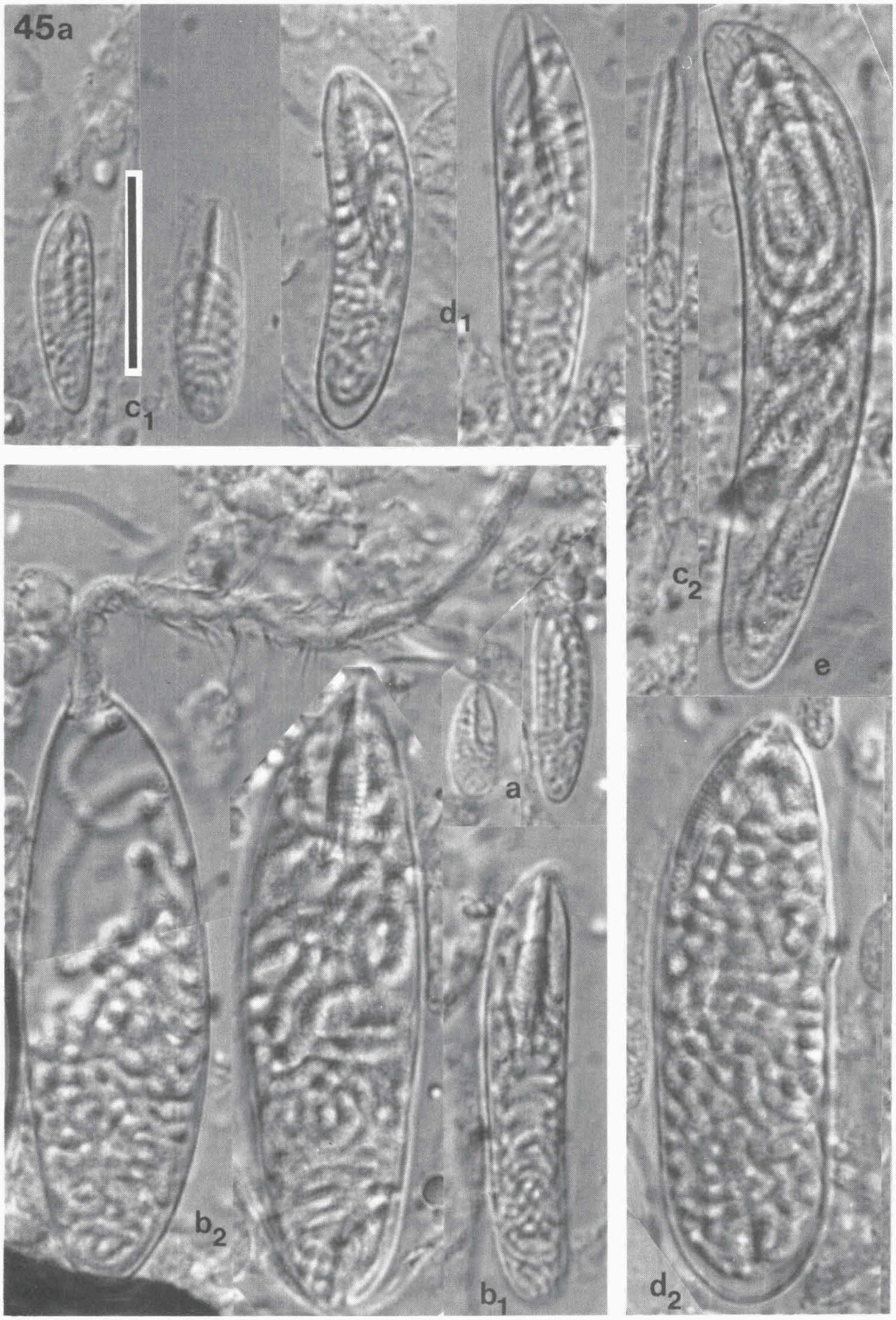
Organ	Specimen	Nematocyst type	Mean and range (in parentheses) of length and width of nematocyst capsules in µm	N	Frequency
1. Pedal disc	A	a. Spirulae	14.6(9.8 - 19.6) x 5.1(4.5 - 6.2)	18	?[inc.]
	B		13.7(11.3 - 17.1) x 4.3(4.1 - 5.0)	10	-
	A	b. Penicilli D$_1$	37.9(30.3 - 46.3) x 9.0(7.6 - 10.2)	20	+
		$_2$	60.3(49.0 - 69.4) x 19.7(15.1 - 21.4)	20	+
	B	$_1$	36.7(28.8 - 45.0) x 9.1(7.2 - 10.8)	45	+
		$_2$	66.2(54.0 - 76.5) x 19.1(15.3 - 21.6)	23	+
2. Column	A	a. Spirulae	ca. 19 x 5.3 - 5.8	2	?
	B		ca. 12 - 17 x 4.0 - 5.5	2	?
	A	b. Penicilli D$_1$	35.2(28.5 - 40.9) x 8.1(7.1 - 8.9)	15	+
		$_2$	ca. 53 - 67 x 17 - 20	---	-?
	B	$_1$	34.9(30.6 - 40.5) x 8.5(7.2 - 9.9)	25	+
		$_2$	not observed	---	---
3. Oral disc	A	a. Spirulae	not observed	---	---
	B		23.0(17.1 -26.1) x 5.9(5.0 - 7.2)	27	+
	A	b. Penicilli D$_1$	38.7(30.3 - 44.5) x 8.7(7.6 - 9.8)	16	+
		$_2$	62.0(53.4 - 70.3) x 17.8(15.1 - 21.4)	20	+
	B	$_1$	30.9(26.1 - 34.2) x 8.1(7.2 - 9.0)	38	+
			[in addition 1 capsule 43.6 x 16.0]		
		$_2$	not observed	---	---
4. Tentacular tissue (mostly from stalks)	A	a. Spirocysts	41.8(35.6 - 49.0) x 5.2(4.0 - 5.8)	55	+
	B		not measured	---	?
	A	b. ?Homotrichs	76.5 x 10.2	1	?
	B		not observed	---	--
	A	c. Spirulae $_1$	21.9(16.9 - 26.7) x 5.7(4.5 - 6.7)	65	+
		$_2$	57.0(53.4 - 62.3) x 3.6(3.6 - 3.8)	4	?
	B	$_1$	22.0(18.7 - 26.7) x 5.6(4.5 - 6.7)	10	- -
		$_2$	one observed, 63 x 4.1	1	?
	A	d. Penicilli D$_1$	38.8(30.3 - 47.2) x 9.0(6.7 - 10.7)	50	- /+
		$_2$	59.7(49.8 - 69.4) x 18.7(16.0 - 21.8)	45	-
		$_3$	one 133.5 x 7.1; several collapsed	---	?
	B	$_1$	28.5(23.1 - 34.7) x 7.6(7.1 - 8.5)	16	-
		$_2$	not observed	---	---
		$_3$	not observed	---	---
	A	e. Penicilli E	64.4(56.1 - 71.2) x 15.1(12.5 - 16.9)	16	[cont?]
	B		not observed	---	---
5. Stomodaeum	A	a. Homotrichs	68.7(53.4 - 76.5) x 12.6(10.7 - 15.1)	30	++
	B		68.8(63.0 - 76.5) x 11.5(10.4 - 13.5)	28	+
	A	b. Spirulae	ca. 18 - 20 x 3.6 - 4.5	3	- - -
			[in addition 1 capsule 38.3 x 6.7]		
	B		only one observed, 18.7 x 4.5	1	- - -

6. Filaments	A	a. Spirulae	20.3(17.8 - 24.0) x 5.6(4.5 - 6.2)	20	+
	B		22.3(18.9 - 27.0) x 5.1(4.5 - 5.9)	22	+?
	A	b. Penicilli D	74.8(57.8 - 82.8) x 9.2(8.0 - 10.7)	30	+
	B		69.8(54.0 - 82.8) x 8.6(7.7 - 9.9)	28	+
	A	c. Penicilli E	98.0(78.0 - 109.5) x 22.1(18.7 - 25.8)	40	+
	B		102.6(95.4 - 109.8) x 20.5(15.3 - 24.3)	23	+
			[in addition 1 capsule 44 x 10.4]		

penicilli E, characteristic of the acrospheres of all known species of *Corallimorphus*. Instead, the presence of another, unusual variety calls for notice. This variety (4e) is much smaller, bilaterally rather than radially symmetrical, and more or less curved. These nematocysts, which, except for their shape, don't seem to differ from the more usual penicilli E ("holotrichs"), have never been reported from Corallimorpharia. Therefore some doubt remains, especially as their tentacular origin was inferred rather than ascertained, and although there is no obvious evidence to suspect them to be contaminations derived from alien coelenterates, this possibility cannot be excluded. They were not found in other parts of the body. Their presence in the tentacles of the holotype of *Corallimorphus atlanticus* (almost entirely deprived of ectoderm and with damaged and severed acrospheres) and the syntype of *C. stephensoni* (desiccated) could not be confirmed either, but this may well have been due to the condition of these specimens, and forms no conclusive proof of their virtual absence.



Figs. 43-44. *Corallimorphus* cf. *atlanticus*. CANCAP specimen (RMNH Coel. 17756), squash preparation of male gonads showing well-developed, round-headed spermatozoa. Scale bar 20 µm.



1. Pedal Disc

4. Tentacles

Fig. 45a-b. *Corallimorphus* cf. *atlanticus*. CANCAP specimen (RMNH Coel. 17756), pictorial survey of the cnidom [incomplete]. Numerals and characters correspond with those used in table 6. Scale bar 20 µm. **1. Pedal disc**: a. Spirulae; $b_{1, 2}$. Penicilli D. **2/3 Column and Oral disc**: cnidae not figured, similar to those of pedal disc. **4. Tentacles**: $c_{1, 2}$. Spirulae; $d_{1, 2}$. Penicilli D; e. Penicillus E. **5. Stomodaeum**: a. Homotrichs. **6. Filaments**: b. Penicilli D; c. Penicillus E.

A striking feature of the cnidom shared by both specimens is the presence of an unusual, elliptical to oblong variety of penicilli D (ratio of length and maximal diameter ca. 3-3.5 : 1) in the ectoderm of the base ($1b_2$; rather common); in the CANCAP specimen these nematocysts were also found in the column ($2b_2$; not rare) and the oral disc ($3b_2$; rather common) and in the sloughed tentacular tissue ($4d_2$). The usual varieties of penicilli D as a rule are considerably more slender, although varying a good deal in shape and length among themselves. In these varieties the undischarged tube does not normally entirely fill the capsule, so that the apical part remains empty, the dart-like basal shaft of variable length (cf. e.g. figs. 39a.2c, 39b.$5c_{1,2}$, 45b.6b) as a rule being clearly visible. By contrast, the relatively voluminous as yet unreported atypical variety is in undischarged condition crammed with a thick terminal tube laid down in numerous criss-cross-arranged coils that tend to conceal the presence of a distinct basal shaft, ca. 0.25-0.3 × the capsule length, with the usual conspicuous V-shaped notch (cf. especially fig. 45a.$4d_2$). A few of these nematocysts were observed in partly discharged condition, showing the everted shaft to attain about 0.6-0.75 × the capsule length (cf. fig.45a.$1b_2$ left). In point of fact several authors observed and figured these capsules at one time or another, but failed to recognize the shaft (e.g. Stephenson, 1920: 183, pl. 20 fig. 3; Carlgren, 1928: 129, 131, fig. 1) and consequently misidentified them as "holotrichs" (= penicilli E). And indeed, except for the often more or less concealed shaft, the similarity with the columnar penicilli E of many other Corallimorpharia is striking (cf. e.g. *Corynactis viridis*, fig. 14a.1d).

Discussion.— Once having ascertained the occurrence of these atypical penicilli D in *Corallimorphus atlanticus* their presence was verified and confirmed in several other specimens of *Corallimorphus* (presumably including more than one species) from Antarctica and the Indo-Pacific.

Apart from being in many respects morphologically similar to penicilli E, the atypical penicilli D present in the ectoderm of some species of *Corallimorphus* substitute the ectodermal penicilli E of most other Corallimorpharia (including all known species of *Corynactis*, *Pseudocorynactis*, and Discosomatidae), which suggests that these two nematocyst types are homologous. However, their substitutive character and homology is of a secondary nature, for whereas the atypical penicilli D of *Corallimorphus* as a rule are only present in the pedal disc, the corresponding penicilli E of other Corallimorpharia are restricted to the column. The more or less intermediate condition found in the CANCAP specimen of *Corallimorphus atlanticus* (in which atypical penicilli D were, in addition to the base, found in the column and the oral disc), although so far representing an isolated case, supports this idea. The existence of this intermediate condition further suggests that the ocurrence of either capsule type throughout the ectoderm is a plesiomorphy and that restricted occurrence in either the base or the column is a derived condition, as would also seem to hold for the total absence of either type in the ectoderm (with the exception of the tentacular acrospheres) as in part of the species of *Corallimorphus*, *Sideractis glacialis*, and *Nectactis singularis*. As to morphology, whether the type with a distinct shaft (i.e. penicillus D, and more particular the newly discovered atypical variety) represents the plesiomorphic condition, or the type without shaft (i.e. penicillus E = classical holotrich) is a question that is less easy to answer.

Homology of penicilli E and the newly discovered atypical penicilli D, if accepted as such, conflicts with the idea previously advocated by Cutress (1955: 133 fig. 8e, 134) and den Hartog (1980: 9, 65, pl. 6 figs. 2-3) that the long heavily armed tube of classical corallimorpharian holotrichs represents the shaft rather than the tube. Cutress, therefore, preferred to refer to these capsules as macrobasic mastigophores, and den Hartog included them in the system of Schmidt as penicilli E (the term still employed in the present paper). However, accepting homology of these two capsule types, the presence of an additional, distinctly differentiated basal shaft in the atypical penicilli D of *Corallimorphus* would contradict the shaft-concept sensu Cutress and den Hartog; in other words, the tube of the classical holotrichs is in that case indeed a tube and not, as claimed, a shaft with its terminal tube completely reduced or almost so.

Coincidentally, and not without significance for the present discussion, a few penicilli E of the filaments (6c) were observed in discharged condition, allowing for a close examination of the tube. This revealed that the basal portion of the tube of these cnidae is totally devoid of armature over a distance about twice the capsule length. As not a trace of sloughed armature was found to surround this portion, there is no reason to suspect an artefact, and moreover, a similar naked portion was previously reported from the columnar penicilli E of *Discosoma* spec. (Discosomatidae) by Schmidt (1974: 541, fig. 14.34; as *Rhodactis*). The distalmost tapered part is also naked, and ends in an abruptly narrowing orifice without a vestigial terminal tube, unlike the condition reported for the corresponding cnidae of *Discosoma sanctithomae* (Duchassaing & Michelotti, 1860) (cf. den Hartog, 1980: 65). Previous observations on these cnidae by Cutress (l.c.) and especially den Hartog (l.c.: pl. 2 figs. 2-3) therefore seem in need of confirmation; the interpretations and conclusions drawn at that time may have been too rash and based on too few observations; hence, also in view of the above discussion on their being homologous with the atypical penicilli D, the idea to classify these nematocysts as penicilli (= p-rhabdoids = p-mastigophores) is possibly better abandoned. However, for practical reasons, and to avoid further complication, the term penicilli E is retained in the present paper, but this matter will be dealt with further in a later study (den Hartog, in preparation). Quite recently Pires & Pitombo (1992: 241) also challenged the status of these nematocysts as penicilli.

Identification.— In spite of its regular, pentamerous/decamerous symmetry (which we consider aberrant; see footnote 2, page 60), and pending further study of the genus *Corallimorphus* (den Hartog, in preparation), the CANCAP specimen is here tentatively identified as *C. atlanticus* Carlgren. The original description of this species, based on a single specimen, is not sufficiently detailed to allow a full-proof identification, and even a comparison with the holotype proved not fully conclusive. The two specimens show a considerable degree of overall similarity, but there are also differences. They share the presence of large atypical penicilli D in the ectoderm of the pedal disc, but in the CANCAP specimen these penicilli D are also present in the ectoderm of the column and the oral disc and in sloughed ectodermal tentacular tissue. The specimens agree more or less in the number and the small size of the tentacles, as well as in the ratio of discals and marginals, but those of the CANCAP specimen are, unlike in the holotype, truly vestigial, and the column and oral disc, smooth in the CANCAP specimen, are characterized in the holotype by numerous cord-like ridges and deep furrows. It was this condition that made Carlgren, though hesitatingly, describe it as a new species, in spite of observing a close affinity with *Corallimorphus rigidus* Moseley, 1877 (described on the basis of a single specimen from the Banda Sea, Indonesia), but the fact that this last-named species had not at that time been reported from the Atlantic (and still not reliably so) settled the matter for him. In our view the furrowed condition is unlikely to be of importance, and presumably represents individual variation. This does not, however, necessarily implicate that *C. atlanticus* is a junior synonym of *C. rigidus*. In point of fact, *C. rigidus* is a nomen dubium; the original description is not sufficiently detailed and diagnostic to allow recognition (it lacks e.g. any data on the cnidom), and the holotype (BMNH 1889: 11.25.1) is a completely dissociated specimen in which the presence of atypical penicilli D as found in *C. atlanticus* could not be ascertained. Although this may have been due to the condition of the specimen, it nevertheless remains doubtful whether the two species are identical. The matter is further complicated by the fact that the labels of some of the Challenger specimens of *Corallimorphus* in the BMNH were evidently transposed, and will be dealt with further in a later study.

Another species reported from the North Atlantic is *Corallimorphus stephensoni* Carlgren, 1928(:128), based on two specimens taken off south-west Ireland. These specimens were previously described and discussed by Stephenson (1920), who identified them as *Corallimorphus rigidus*, but Carlgren considered them different and (without redescribing them) proposed the new species. Fautin (1984: 8) supposed all North Atlantic species of *Corallimorphus* (viz. *C. atlanticus*, *C. stephensoni* and *C. ingens* Gravier, 1918) to be probably conspecific, but for lack of data refrained from synonymizing them. She may be right as to the identity of *Corallimorphus atlanticus* and *C. stephensoni*, but *C. ingens* definitely is a different species (see p. 51 ff.). Stephenson's description of *Corallimorphus stephensoni* (as *C. rigidus*) was based on one rather large (diameter of oral disc 7 x 6.1 cm) and one smaller specimen (diameter of oral disc 3.8 cm). At first glance Stephenson's specimens (1920: fig. 1, pl. 19) seem to differ from *C. atlanticus* by the relatively large size and less regular arrangement of the tentacles, reminescent of the condition present in *C. ingens*, but without the basal swellings of the tentacles. Also in this case no substantial data on the cnidom are presented in the description, the only nematocyst type figured (and mentioned to derive from the column; Stephenson, 1920: 183, pl. 20 fig. 3) is suggestive of a penicillus E, but this type not being known from the column of any species of *Corallimorphus* it would seem more likely that Stephenson actually observed and figured an atypical penicillus D, having overlooked the shaft. To verify this, one of the syntypes (NMI.70.1920; the smallest specimen) was re-examined. Unfortunately this specimen, having dried out on some occasion in the past, has become hard and shrunk (the oral disc now measures only 19 x 22 mm), and proved almost useless for study. However, a squash preparation of some tiny pieces of tissue from its base, softened in glycerine, conclusively revealed the presence of a few examples of the same atypical penicilli D found in the base of the *C. atlanticus*, confirming that *C. stephensoni* and *C. ingens* are not identical, thus supporting, or rather not contradicting, the view that *C. stephensoni* and *C. atlanticus* may be the same species. Unfortunately the present whereabouts of the large specimen are unknown; it is either lost or possibly hidden somewhere in the collections of the University of Aberystwyth, where Stephenson was demonstrator in zoology when he published his *Corallimorphus* paper. It seems preferable to postpone a definitive decision as to the taxonomic status of *C. stephensoni* until the large syntype is either traced to be studied, or can reasonably be considered lost.

Biological notes: speculations on food intake.— Stephenson (1920: 185) already raised the issue of food intake and the mode of life of species of *Corallimorphus* relative to the rigid, presumably immobile character of the body. As to the tentacles, it is obvious that the rigid and extremely reduced tentacles of e.g. the CANCAP specimen of C. *atlanticus* (see fig. 42) can impossibly represent active catching devices as e.g. in species of *Corynactis* and *Pseudocorynactis*. The range of action of this specimen therefore must have been restricted to the actual surface of the oral disc, which seems quite limited relative to the size and substance of the body. Nevertheless the specimen looked healthy and far from starved, its body cavity being crammed with well-developed gonads. Although the tentacles in species of *Corallimorphus* commonly are short, they are generally longer than in the above mentioned example and sometimes of moderate length; the marginals in preserved specimens may occasionally reach a length of about half the diameter of the oral disc, but even so, considering their weak musculature and rigid character, there is little reason to suspect them to be motile and contractile to a significant degree.

A comparatively passive way of life and feeding strategy, even in terms of Anthozoa, as suggested by the rigid structure of the body, the underdeveloped musculature, and the often small size of the tentacles, would seem to implicate that species of *Corallimorphus* can only thrive under rather special conditions, in locations or areas with a relatively high food supply and relatively undisturbed bottoms with limited sedimentation rates. This would also explain why they are apparently relatively rare, only a few dozen samples being known to science, from widely scattered localities world-wide.

It is possible that species of *Corallimorphus* feed on detritus and fragments of desintegrating organisms that sink to the bottom. However, the composition of the cnidom, including an abundance of spirocysts, suggests that these anemones can easily hold substantial prey that may accidentally come in touch with them. In this connection it is interesting to note that the filaments of the holotype of *Corallimorphus atlanticus* were "contaminated" with considerable numbers of alien nematocysts, mostly hydrozoan or scyphozoan euryteles [tentative identification; dimensions: 16.0(13.4 - 17.8) x 11.0(9.8 - 12.9) (N=24)], but also with a few more or less globular and ovate holotrichs [dimensions ca. 10.7 x 10.7 - 16.9 x 16.0, and ca 8 x 5.8, respectively], and that the same phenomenon [mostly concerning hydrozoan (including siphonophoran) and scyphozoan nematocysts] was noticed in several other specimens of *Corallimorphus* (den Hartog, unpublished). Consequently, the presence of such alien nematocysts in the filaments cannot simply be done with by assuming them to be contaminations. True contaminations with alien nematocysts, resulting from e.g. contacts of different species in the catch of a trawl, as a rule affect the exterior surface of column, oral disc and especially tentacles. It is therefore concluded that the presence of alien nematocysts inside the body cavity (of otherwise clean specimens) or in the (digestive) filaments themselves, can only be the result of feeding activities. It may here be noted in passing that this phenomenon is not otherwise restricted to species of *Corallimorphus*; it is also common in various groups of sea anemones, both deep-sea and shallow water forms (den Hartog, unpublished).

Mobile, bentho-pelagic Coelenterata, such as Lepto- and Scyphomedusae, have been reported from even hadal depths (e.g. Wolff, 1971: 130; Lemche et al., 1972: 273-275, pl. 7), and notably due to their mobility, such organisms would seem to stand an increased chance to meet with a tentacle crown and be relatively vulnerable to predation by sea anemones, although these will, of course, also accept incidental other

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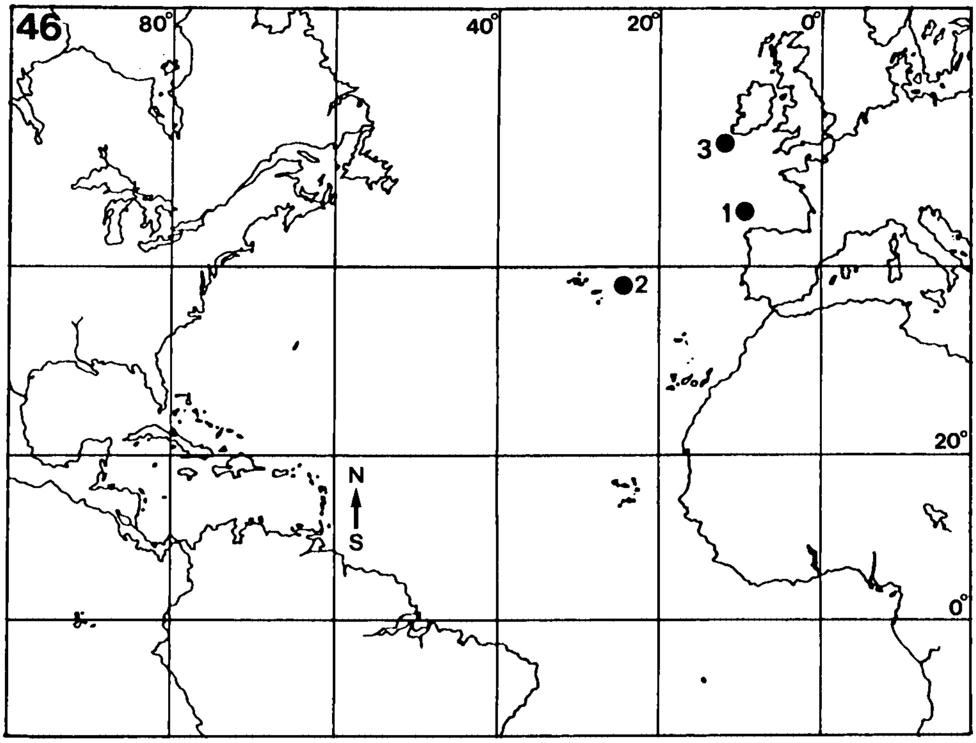


Fig. 46. *Corallimorphus atlanticus* and *C. stephensoni*. Known distribution. 1. holotype (Bergens Museum 39195), 4700 m; 2. CANCAP specimen (RMNH Coel. 17756), 2400-3100 m; 3. type locality of *C. stephensoni* (NMI 70.1920), 1211-1296 m.

prey. Once in touch with the powerful nematocysts batteries of corallimorpharian (or actiniarian) tentacles, these soft, jelly-like, weak swimmers would not stand a chance to escape.

Actiniaria that feed on large prey generally embrace their victim with the tentacles and/or enfold it by muscular contraction of the oral disc, subsequently transporting it by muscular and ciliary action to the distended mouth to be engulfed. For reasons mentioned above, this often fairly rapid process is not likely to happen in the rigid bodied species of *Corallimorphus*. To what extent these species are capable of (slowly) expanding and contracting the body and the tentacles (if developed to any degree) is difficult to judge, but they are definitely incapable of withdrawing or folding the oral disc (as is obvious from preserved specimens). Possibly, the powerful nematocyst batteries of the tentacular acrospheres mainly act as paralizing and holding devices, subsequently allowing for slow distension of the mouth and the stomodaeum so as to engulf the prey. It also seems possible that energy intake may be effectuated by extracoelenteric digestion, via extrusion of the stomodaeum and filaments, in conformity with scleractinian corals and Discosomatidae (cf. e.g. Lang, 1971; Muscatine, 1973: 84-85; Hamner & Dunn, 1980; Chadwick, 1987; 1991).

Distribution (fig. 46).— As mentioned above, *Corallimorphus atlanticus* is exclusively known by its holotype and by the CANCAP specimen here described. Both specimens were hauled from abyssal depths in the south-eastern North Atlantic.

Corallimorphus ingens Gravier, 1918
(figs. 47-55, tabs. 7-8)

Corallimorphus ingens Gravier, 1918: 23-24; 1922: 84-87, pl. 6 fig. 70-71, pl. 13 fig. 133 (description + habitus photos; Azores, Bay of Biscay); Stephenson, 1922: 302 (name only); Carlgren, 1934: 4-6, pl. 1, fig. 9 (cnidom, tentacular arrangements, colour; SW of Azores); Carlgren, 1949 (= *C. rigidus*?): 13; Fautin, 1984: 8 ("a poorly known taxon ....").

Corallimorphus ["Bojador specimens"]; Carlgren & Stephenson, 1929: 6-7 (off Cape Bojador, Morocco).

Not *Corallimorphus rigidus*; Stephenson, 1920: 179-186, figs. 1-2, pls. 19-20.

Not *Corallimorphus stephensoni* Carlgren, 1928: 128 [see *Corallimorphus* cf. *atlanticus*, page 40]; Carlgren, 1949: 13 (= *C. rigidus* sensu Stephenson, 1920).

Material examined.— RMNH Coel. 17754 (Sta. CANCAP 4.054, 18.v.1980, Canary Islands, S of Lanzarote, 28°45'N 13°19'W, 1134-1315 m, 3.5 m Agassiz trawl, fine yellow clay, 2 specimens; RMNH Coel. 17755, Sta. CANCAP 4.055, idem, 28°45'N 13°20'W, 1209-1338 m, idem, 1 specimen).

Material examined for comparison.— Bergens Museum 39190 (Michael Sars Exp. 1910, Sta. 53, 34°59'N 33°1'W, 2615m, 5 specimens; depth and co-ordinates stated on the label agree with those given by Carlgren (1934: 5) and Chumley [1930?: 7], but Helland Hansen [1930: 26*, 39*] gives 35°7'N 32°30'W, 2865m; originally there were 8 specimens (cf. Carlgren & Stephenson, 1929: 6), but 1 specimen was later added by Carlgren (l.c.) so that 4 specimens have apparently been mislaid; see also the discussion on p. 63-64); MOM 130009 (Sta. 575, 13.vii.1895, 38°27'N 26°30'W, 1165 m, tentacle fragments [probably this species; cf. the following MOM numbers from the same region]), MOM 130014 (Sta. 624, 38°59'-56'30'N 28°18'05"-19'45"W, 4.viii.1895, 2102 m, grey mud and fine sand, 4 fragments [2 specimens]), MOM 130016 (Sta. 663, 37°28'30"N 25°31'45"W, 27.vi.1896, 1732 m, grey mud and black sand, 2 specimens), MOM 130017 (Sta. 683, 38°20'N 28°04'45"W, 7.vii.1896, 1550 m, trawl, sandy mud, several fragments [3 specimens + 1 fragment]), MOM 130079 (Sta. 1583, 47°36'N 7°38'W, 15.ix.1903, 1490 m, muddy sand, 1 desiccated and shrunk specimen).

Description: Morphology (based on CANCAP specimens; figs. 47-49).— Body low, rigid and firm, semi-trans-lucent.

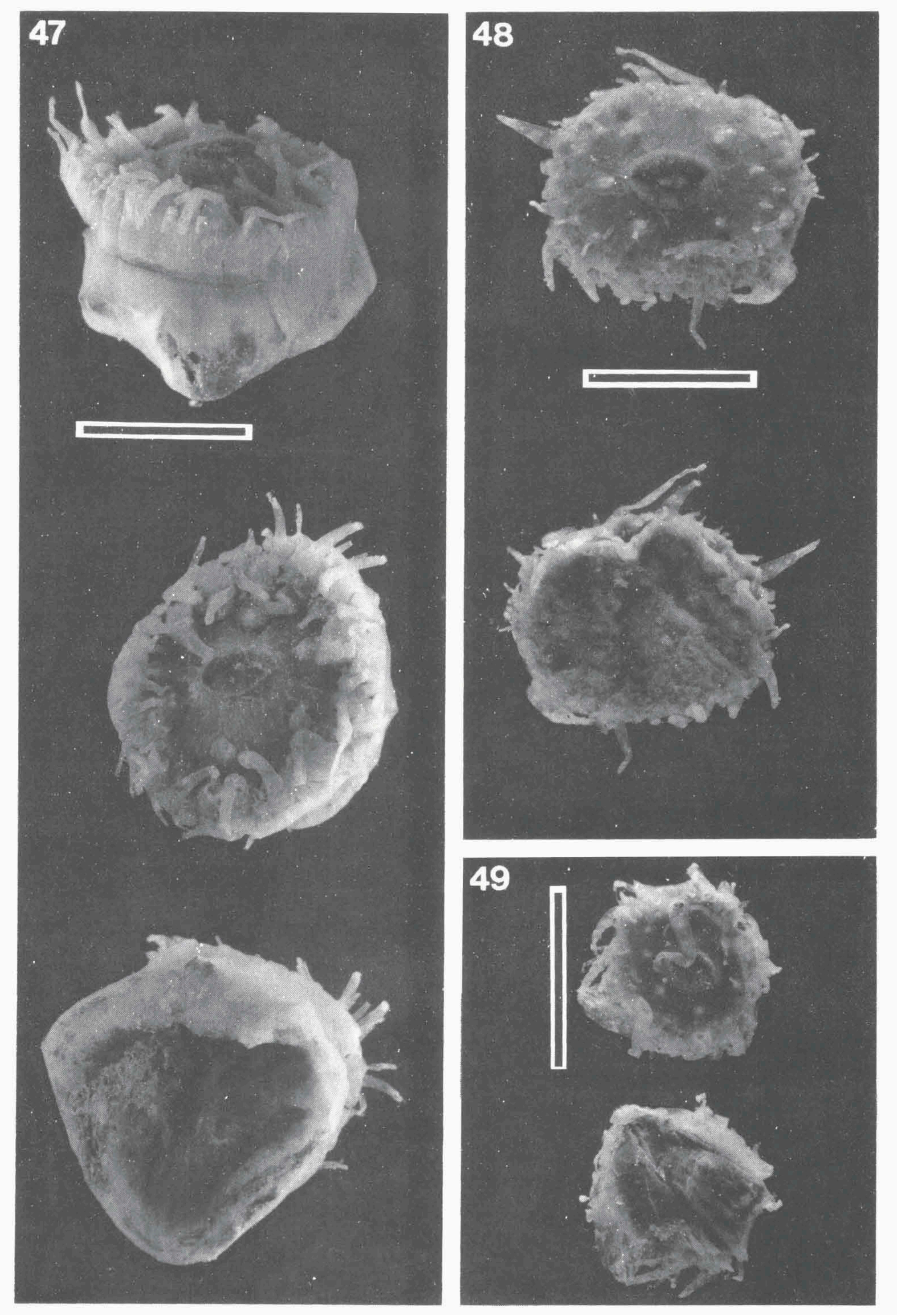
Base relatively thin and membranaceous, concave, attached to, and enveloping solid fragments of cinder (RMNH Coel 17754) and a fragment of a skeleton of a solitary stony coral, *Stephanocyathus* spec. (RMNH Coel 17755), and hence somewhat irregular in outline; maximal diameter varying from 22 to 35 mm.

Column low and spreading, ca. 6-12 mm high measured perpendicularly from the centre of the base to the surface of the oral disc, without conspicuous grooves, and largely without ectoderm. The spreading base and lower part of the largest specimen (RMNH Coel 17754/1) envelop a fragment of cinder, causing the anemone to look more voluminous than it really is and to be somewhat obliquely shaped, the distance from its limbus to the margin ranging from 15 to 22 mm, whereas the central part does not exceed a height of 12 mm.

The oral discs of the three specimens are somewhat convex to slightly raised in the centre and measure 16 × 18 mm, 24 × 30 mm and 32 × 38 mm. They are largely deprived of ectoderm; traces of this body layer are to be found mainly in the periphery in more or less distinct radial furrows and especially in furrows surrounding the firm, thickly swollen bases of the discal tentacles.

Tentacles well-developed, also largely deprived of ectoderm. The discals sprout from conspicuous, solid, bulging to semi-globular mesogloeal thickenings; acrospheres small due to loss of ectoderm. Length of primary marginals up to almost equalling the radius of the disc, but those of subsequent cycles gradually smaller.

Arrangement of the older tentacles hexamerous, but younger cycles of both dis-



Figs 47-49. *Corallimorphus ingens*. Habitus of CANCAP specimens; different views. Fig. 47. RMNH Coel. 17754/1, largest specimen. Fig. 48. RMNH Coel. 17754/2, smallest specimen. Fig. 49 RMNH Coel. 17755. All scale bars 20 mm.

cals and marginals deviating from this plan. The discal tentacles are entacmaceous, arranged in three more or less distinct cycles inserted at different distances from mouth and margin. With the exception of the primary cycle, the distinction of separate marginal cycles tends to be less clear because in one cycle there may be considerable differences in development; members of what basically is a cycle of lower order may be equally large or exceeding those of a previous cycle and vice versa, as will be further elucidated below.

In the smallest specimen (RMNH Coel. 17755) there are 24 discal and 55 marginal tentacles. The discals are arranged in three rather clear hexamerous cycles: 6 + 6 + 12 = 24. Comparing the marginals with the discals it is obvious that a primary marginal cycle of six relatively large tentacles corresponds with the 6 primary discals. A secondary cycle of somewhat smaller marginals likewise corresponds to the secondary discals, but the 12 marginal tertiaries are not equally developed; in four of the six primary (exocoelic) discal sectors one of each of the two tertiaries is relatively well-developed and about equally large as the secondaries, thus affecting the initial hexamerous arrangement, also of subsequent younger cycles, which show the same tendency of unequal development, some of the quaternaries being more or less equal in size to the smaller tertiaries, etc. This phenomenon of unequal development, with two hexamerous sectors and four sectors with a deviating, though equal symmetry, and especially the fact that the younger cycles, to start from the smaller (retarded) tertiaries, tend to merge, hinders the exact recognition of cycles of different order, so that presentation of a tentacle formula would in this case be a most arbitrary matter.

Of the other two specimens (RMNH Coel. 17754/1, 2) the largest (1) is less regular. It has 22 discal and 66 marginal tentacles. The discals are arranged in three irregular cycles 5 + 7 + 10 = 22. One of the primaries has just not developed as is obvious from the presence of six distinct primary marginals, one of which corresponds to an unoccupied primary endocoelic locus; and in one of the primary exocoelic sectors there are two secondaries (i.e. one supranumeral) alternating with three tertiaries (i.e. one short). The tertiary cycle is incomplete; where one would expect 14 tertiaries (due to the presence of the one supranumeral secondary), only 10 are present. Also in this specimen the arrangement of the marginal tentacles does not match that of the discals, except with respect to the primary cycle.

In the second, smaller specimen (RMNH Coel. 17754/2), the development of the discal tentacles is relatively more advanced, a partial additional cycle of minute quaternary tentacles being present. The total number of tentacles of this specimen amounts to 29 discals arranged according to the scheme 6 + 6 + 7 + 10 = 29, and 64 marginals, of which the precise arrangement is difficult to determine for the same reasons mentioned above for the other specimens. The arrangement of the discals, initially hexamerous, deviates from this hexamerous scheme to start with the development of the third cycle. However, the fact that there are only seven tertiaries and 10 quaternaries suggests that part of the latter do in fact represent retarded tertiaries and that the basic arrangement should actually read 6 + 6 + 12 + 5 = 29, or rather, as elucidated in the discussion, 6 + (6 + 6) + 11 = 29. In conformity with the other specimens the hexamerous scheme of the marginal tentacles alters from the tertiaries onwards; half of these are about equally large to only slightly smaller than the secondaries, whereas growth in the other half has apparently been retarded. Again, this allometry also affects the arrangement of the fourth and fifth cycle: to both sides of the larger tertiary tentacles

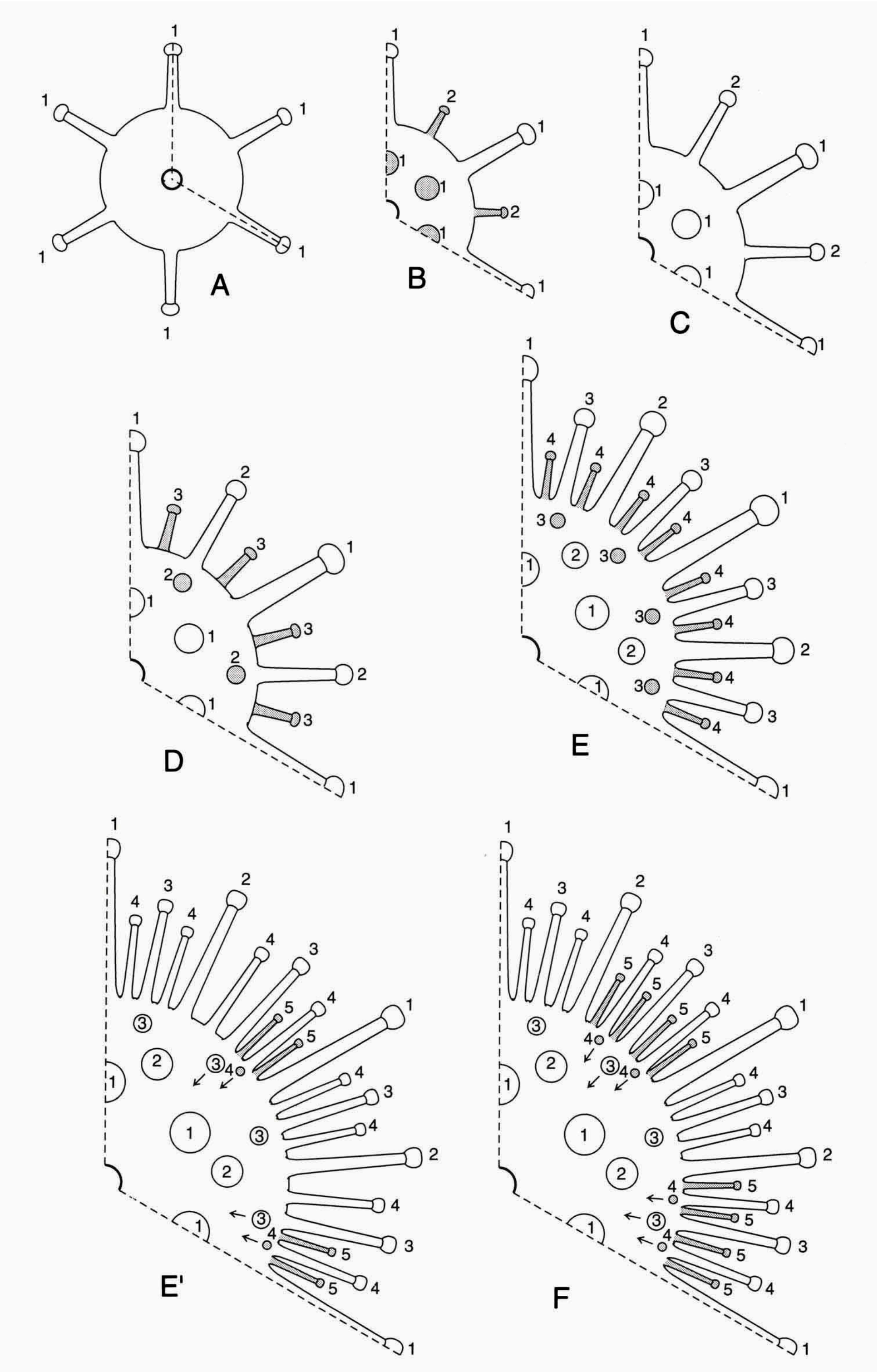

A
B
C
D
E
E'
F

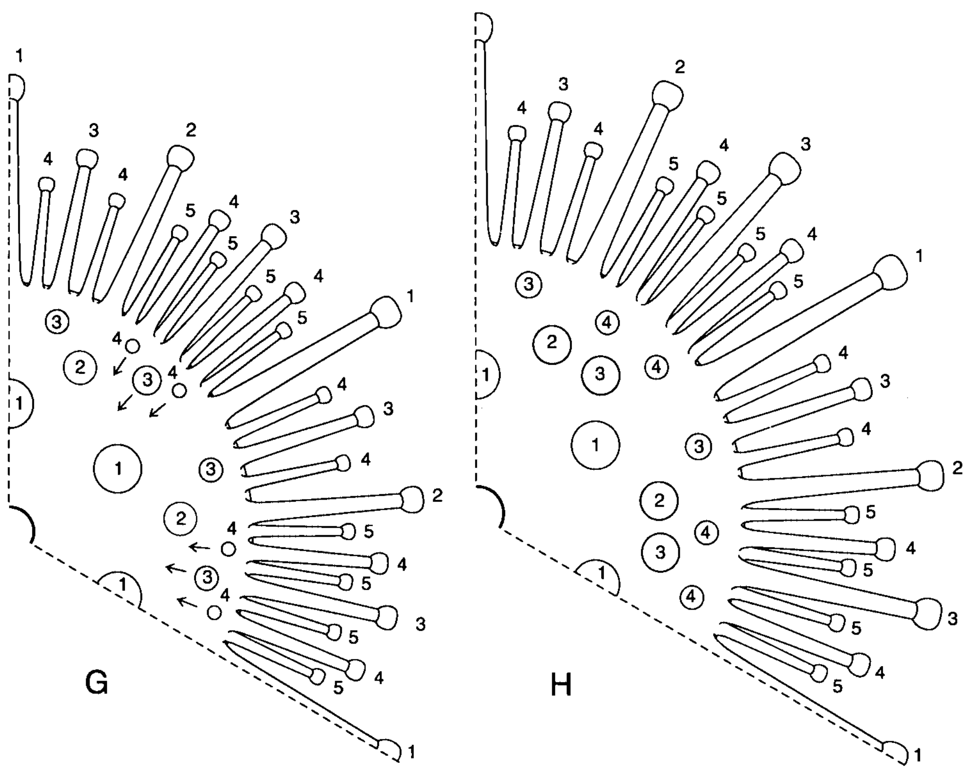
Fig. 50. *Corallimorphus ingens*. Prototypical development of tentacular arrangement as inferred from a study of the three rather small CANCAP specimens and the well-developed Michael Sars specimens. Sequence of development of tentacles indicated by arabic numerals. New tentacles arising in subsequent stages of development shaded. Arrows indicate a (relative) centripetal shift of certain tentacles.
A-E. Regularly hexamerous development up to the stage with four marginal and three discal tentacle cycles.
F-H. Further development deviates from the hexamerous principle. In each primary discal sector (i.e. each sector enclosed by two primary marginal tentacles) one of the two secondary sectors (i.e. those sectors bordered on one side by a primary tentacle and on the other by a secondary tentacle) shows retardation/inhibition of growth, whereas in the other one marginal pentameries emerge on both sides of the two quaternaries (F), or, in some sectors, only alongside the one quaternary tentacle adjacent to the primary tentacle (E'). This allometric growth of alternating secondary body sectors not only has numerical implications for the marginal tentacles, but also affects the tertiary discal tentacles, causing a relative centripetal shift of the ones located in the growing sectors (arrows). In the prototypical case this allometric development ultimately results in stage H. For a total view of this stage, see fig. 51.

The tentacular arrangement of the smallest CANCAP specimen (RMNH Coel. 17755) is basically in accordance with stage E as for the discals; the development of its marginals varies per primary body sector from stage E to E'.

In the largest CANCAP specimen (RMNH Coel. 17754/1) the arrangement of the marginals is basically in accordance with stage F (in two primary body sectors with stage E and E', respectively); the arrangement of the discal tentacles, in spite of several tentacle loci being empty, is basically in accordance with stage E.

The third CANCAP specimen (RMNH Coel 17754/2) is the most regular one, and is almost entirely in accordance with stages E' and F (in one primary sector with stage E).

The Michael Sars specimens are, apart from the occasional presence of secondary discal singletons, triplets or quartets instead of duplets, in accordance with stage H (see also fig. 51). Note that singletons can be explained by retardation of growth in stage E or E', or by the initial hexamerous development in a given sextant proceeding beyond stage E. An elucidation of the formation of triplets and quartets is presented in figs. 52-53).



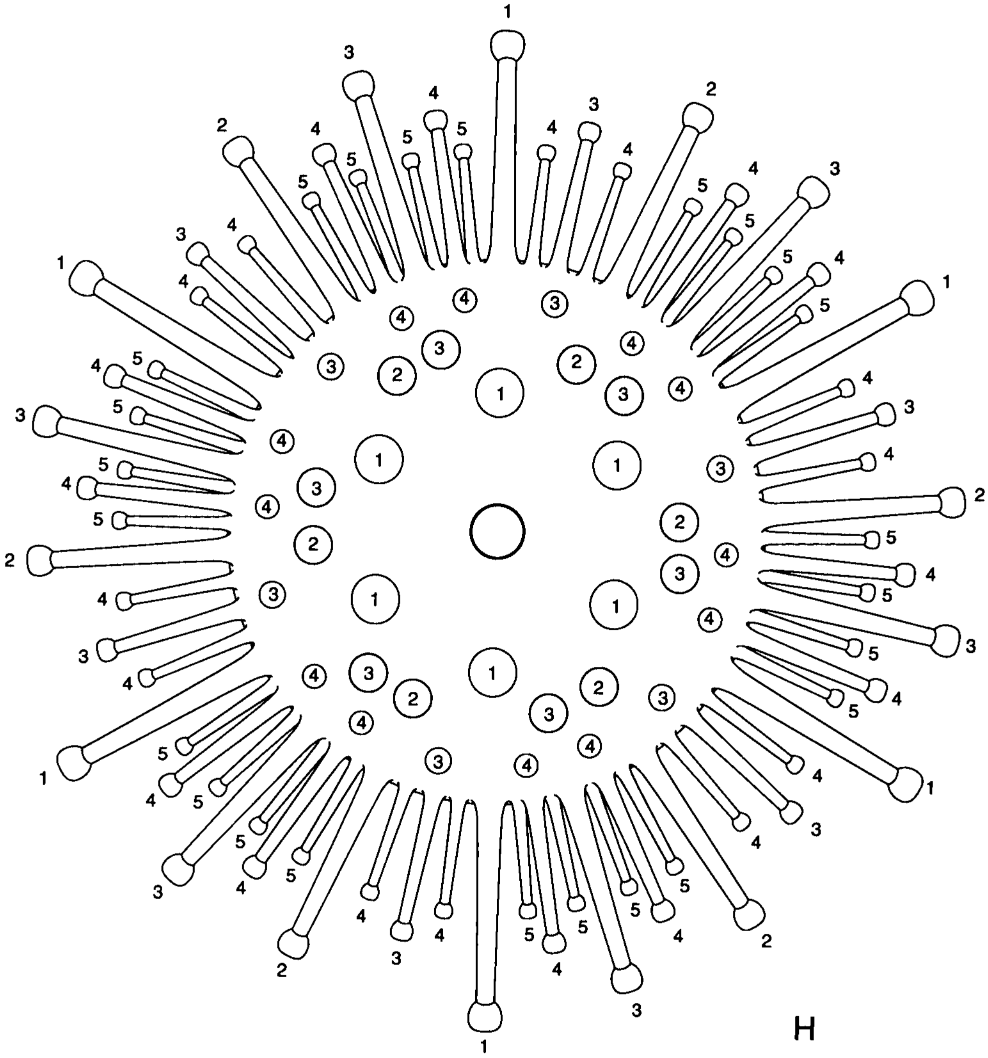


Fig. 51. *Corallimorphus ingens*. Prototypical, secondarily acquired, non-hexamerous, yet regular tentacular arrangement of a fully developed individual with four marginal and three discal cycles according to the schemes: 6 + 12 + 18 + 36 = 72 and 6 + 12 + 18 = 36 (ratio of marginals and discals exactly 2 : 1); note the characteristic secondary discal cycle of pseudo-pairs. Sequence of development indicated by arabic numerals.

there are quaternary tentacles, about equally large as the smaller (retarded) tertiaries, and flanked by two pentameries, whereas the smaller tertiaries are flanked only by two stunted quaternaries, about equal in size to the pentameries. The result is a secondarily acquired arrangement of the marginal tentacles in four cycles of different size (more or less) according to the scheme: 6 + 11 + 17 + 30 = 64.

The ratio of discal and marginal tentacles of the three specimens is 2.21, 3.0 and 2.29, respectively.

Discussion (figs. 50-53).— The three CANCAP specimens are small and obvious-

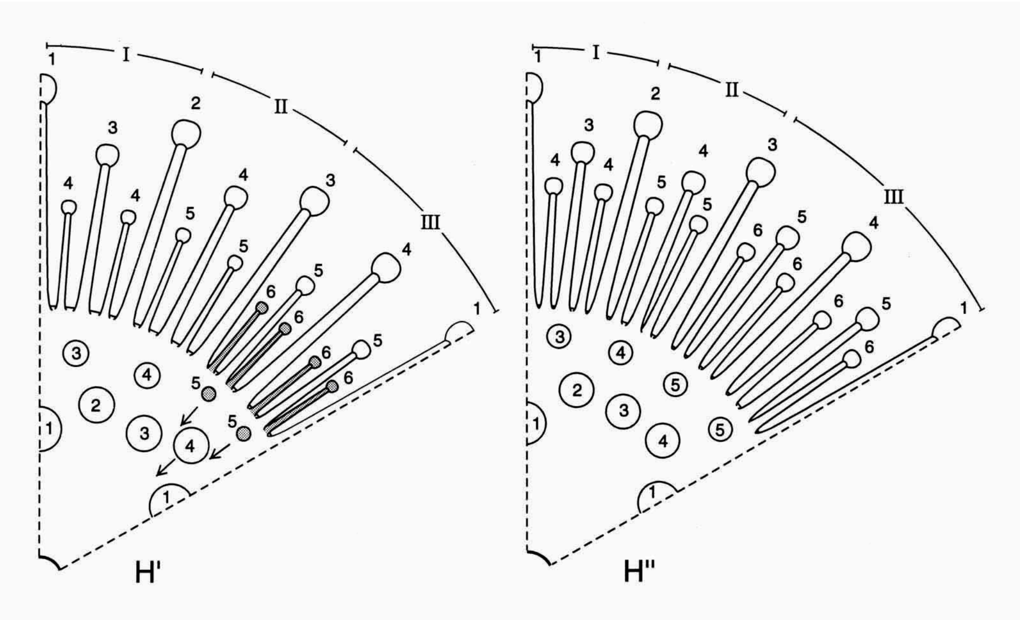


Fig. 52. *Corallimorphus ingens*. Scheme showing hypothetical development of a triplet of secondary discal tentacles via stages H (cf. fig. 50) - H' - H". As new marginal tentacles in a growth-sector first of all tend to emerge close to the single primary tentacle (subsector III) (cf. fig. 50 stages E' and F), this is the most likely possibility, but considering the common occurrence of anomalies, the same condition might also be acquired via e.g. a similar development in subsectors I or II. Sequence of development of tentacles indicated by arabic numerals; arrows indicate a (relative) centripetal shift of certain tentacles.

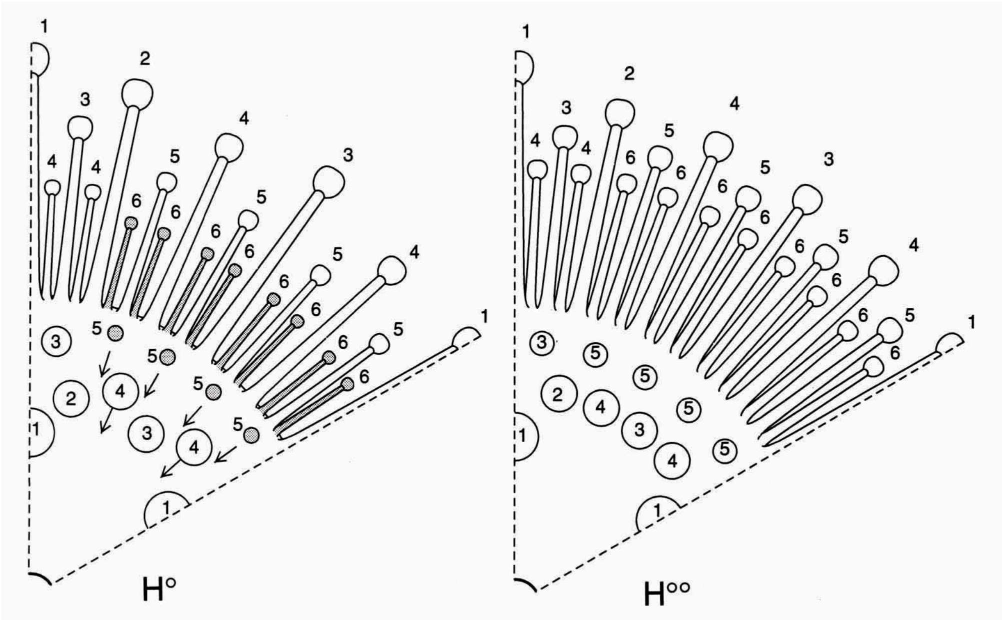
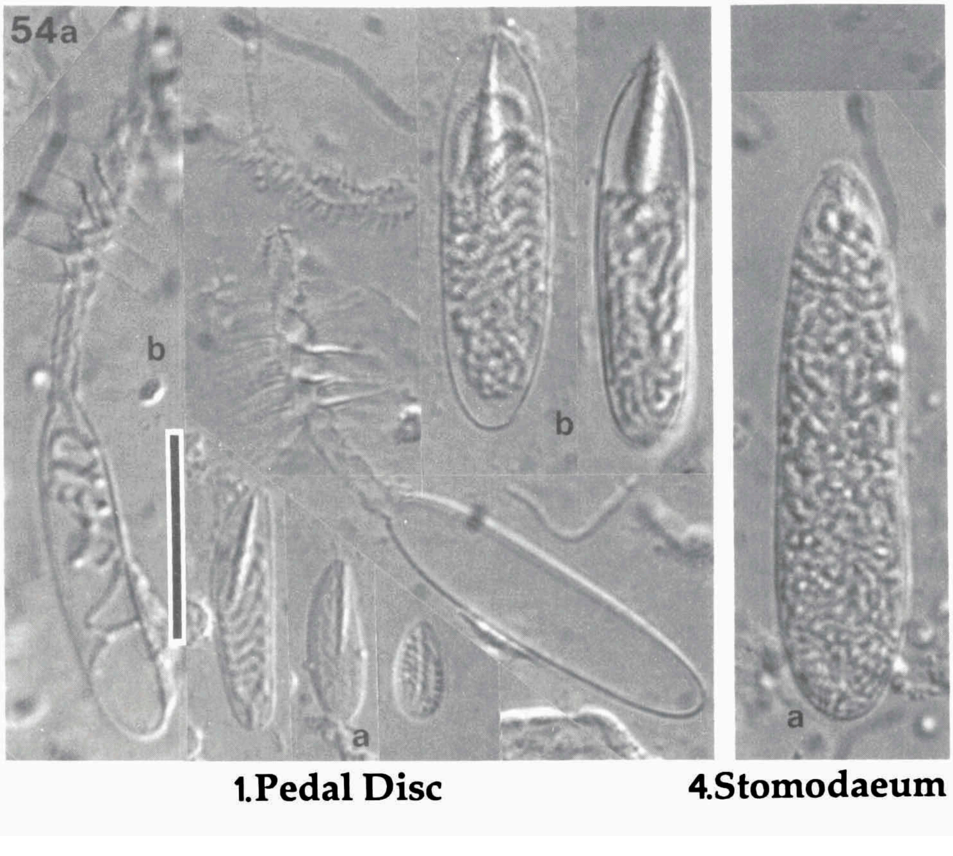


Fig. 53. *Corallimorphus ingens*. Possible development of a quartet of secondary discal tentacles H (see figs. 50-51) - H°- H°°. Sequence of development of tentacles indicated by arabic numerals. Arrows indicate a (relative) centripetal shift of certain tentacles.

ly not fully developed, the numerical development of the tentacles of the second largest specimen (RMNH Coel. 17754/2) being slightly more advanced than in the two others. The specimens show that in this development stage the initial, basically hexamerous arrangement of at least the marginal tentacles, according to the scheme 6 + 6 + 12 + x = 24 + x, merges into a secondarily acquired non-hexamerous, though principally regular arrangement according to the scheme 6 + (6 + 6) + 18 + y = 36 + y (in which x ≤ 24 and y ≤ 36).

In the five larger Michael Sars specimens (Bergens Museum 39190) studied for comparison, and varying in discal diameter from ca. 60 to 100 mm, the arrangement of the marginal tentacles is basically in accordance with that of the CANCAP specimens, but the regularly hexamerous arrangement of the first two discal cycles also is no longer apparent. In these specimens the hexamerous primary cycle neatly alternates with a secondary cycle in principle consisting of "pairs" (duplets) of about equally sized tentacles instead of the usual singletons. All except one of the specimens show irregularities in that one or two of these "pairs" are substituted by a singleton, a triplet or even a quartet. A third cycle alternates in the regular fashion with the primary and secondary tentacles, irrespective of irregularities in these previous cycles and consequently not affecting the ratio of marginals and discals (provided that this third cycle is itself complete and without irregularities) (cf. table 7). This secondarily acquired non-hexamerous symmetry in tentacular arrangement matches that of the marginal tentacles (and supports the assumption that the CANCAP speci-



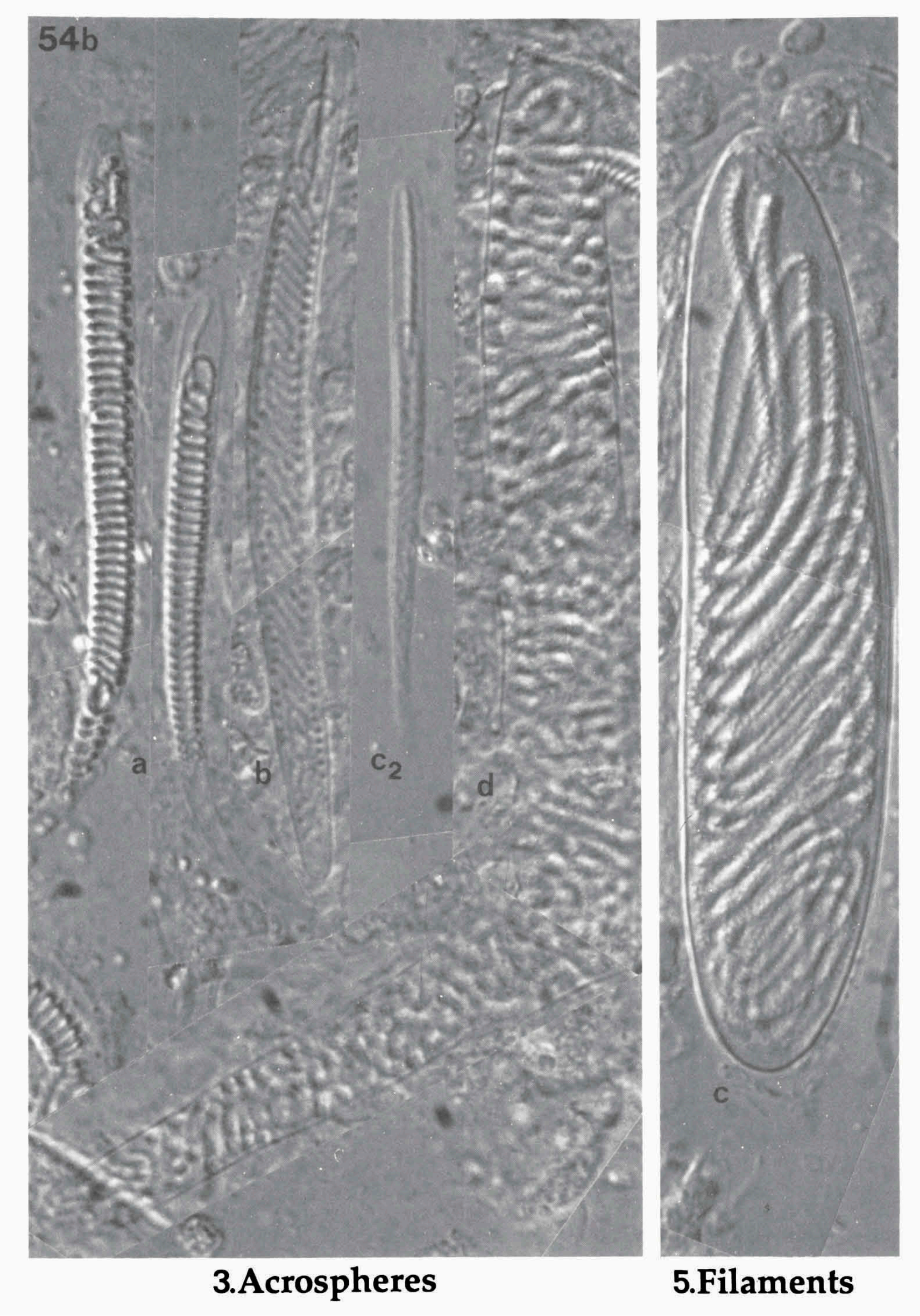


Fig. 54a-b. *Corallimorphus ingens*. Pictorial survey of the cnidom (incomplete). Numerals and characters correspond with those used in table 8. Scale bar 20 µm.

1. Pedal disc: a. Spirulae; b. Penicilli D. **2. Column**: cnidae not figured. **3. Acrospheres**: a. Spirocysts; b. Homotrich?; c_2. Spirula; d. Penicillus E. **4. Stomodaeum**: a. Homotrich. **5. Filaments**: c. Penicillus E.

mens are not fully developed). Starting from the tentacular arrangement of the two least developed CANCAP specimens, the condition of the Michael Sars specimens may have been acquired by allometric growth of the tertiary and secondary tentacles and of their corresponding body sectors, causing these tentacles to shift with respect to each other (via the condition more or less represented by the best developed CANCAP specimen) so as to form duplets or "pairs" (really pseudo-pairs) (figs. 50-51). Deviations from this condition, such as the presence of substitutive singletons, triplets or quartets (cf. table 7; figs. 52-53), might be due to numerical aberrations of the tertiary cycle (and at least partly to earlier ontogenetic anomalies in the primary and secondary cycles) such as the "simple" inhibition or supranumeral development of one or more body sectors and tentacles[2].

Table 7. *Corallimorphus ingens*. Tentacular arrangement of the five Michael Sars specimens (Bergens Museum 39190); * = one regular tentacle plus a doublet of tentacles arising from a single basal thickening and therefore also counted as one; ** = one small additional tentacle arbitrarily included in this cycle, but actually situated solitarily between this and the outer cycle.

Dimensions (in mm)			Schematic arrangement and number of discal tentacles	Number of marginal tentacles	Ratio of marginal and discal tentacles
Oral disc	Base	Height			
1. 59 × 52	25 × 25	13	6 + (2 - 4 - 2 - 2 - 4 - 2) + 22 = 44	88	2.0
2. 77 × 61	39 × 27	15	6 + (3 - 1 - 2 - 2 - 4 - 2*) + 20 = 40	80	2.0
3. 79 × 71	36 × 29	14	6 + (2 - 2 - 2 - 2 - 2 - 2) + 17= 35	64	1.8
4. 86 × 80	35 × 35	16	6 + (2 - 2 - 2 - 1 - 3** - 2) + 18 = 36	72	2.0
5. 98 × 84	46 × 24	19-23	6 + (2 - 4 - 2 - 2 - 3 - 2) + 21 = 42	84	2.0

In spite of the common occurrence of anomalies in *Corallimorphus ingens*, it seems plausible to regard the predominantly paired arrangement of the secondary discal tentacles as the normal condition. Accepting this, the prototypical tentacular arrangement of fully developed specimens of the species is 6 + 12 + 18 + 36 = 72 for the marginals, and 6 + 12 + 18 = 36 for the discals (although part of an additional cycle of both marginals and discals may be expected in extremely large specimens), with a ratio of marginals and discals of exactly 2 : 1 (fig. 51). It is interesting to note that this ideal ratio is present in four out of the five Michael Sars specimens , while only slightly deviating in the fifth (table 7; cf. also Carlgren, 1934: 5).

Colour.— In life the CANCAP specimens were bluish-grey and semi-translucent, with traces of purplish brown ectoderm on the oral disc, notably of the largest individual (RMNH Coel. 17754/1). Stomodaeal ridges as well as the mesenterial filaments were also purplish-brown.

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[2] Being relatively little differentiated organisms capable of considerable regeneration, irregularities and disorders in growth, both resulting from developmental anomalies and mechanical causes, are rather common in Coelenterata, though seemingly more common in some groups than in others. In members of the genus *Corallimorphus* they appear particularly common, varying from the "simple" absence, doubling, bifurcation or supernumeral presence of one or more tentacles, all without affecting the basic symmetry of the body, to the suppression or supranumeral presence of certain body sectors, affecting this symmetry, as e.g. in the pentamerous CANCAP specimen of *C. atlanticus*. This phenomenon is also common in certain Actiniaria; see den Hartog, 1987: 539-541, fig. 8; *Bunodosoma biscayensis*).

Anatomy.— Not studied due to the condition of the specimens.

Cnidom (table 8, fig. 54a-b).— Since the specimens studied are to a large extent deprived of ectoderm, the survey of their cnidom necessarily shows some gaps, but, as far as present, types and size-classes agree rather well, with the exception of the penicilli D of the column (2c), which vary considerably in dimensions, apparently uncorrelated with body size, since the largest capsules were, apart from the large MOM specimen, found in the smallest CANCAP specimen. Due to the incompleteness of the nematocyst data a full comparison of the cnidom with that of other species is impossible, the more so as previous descriptions of *Corallimorphus* spp., if at all including information on cnidae, almost without exception suffer to an even more serious degree from the same shortcoming. However, the results here obtained are nonetheless quite sufficient to distinguish between the present species and *C. atlanticus*. First of all the conspicuous atypical penicilli D present in the base of *C. atlanticus* (and in the CANCAP specimen also in column, oral disc and tentacles) are definitely absent in *C. ingens*. In addition the penicilli D of the filaments of *C. atlanticus* (table 6 and fig. 45b.6b) are about 1.5 times longer than in *C. ingens* (table 8: 5b).

Identification.— There is no doubt about the identity of the CANCAP specimens. Although relatively small, they fully conform to Gravier's description(s) of *Corallimorphus ingens* (Gravier, 1918; 1922). The original description by itself is inadequate, and Carlgren & Stephenson (1929: 6), having overlooked the extensive and rather detailed supplementary description of 1922, therefore initially questioned the status of the species. More recently Fautin (1984: 8) for the same reason still named it "a poorly known species". In point of fact Gravier's definitive description (1922: 84-87,

Table 8. *Corallimorphus ingens*. Survey of the cnidom of the three CANCAP specimens, and additional data on the type series. A = RMNH Coel 17754/2 (oral disc 24 x 30 mm; cf. fig. 48); B = RMNH Coel. 17754/1 (oral disc 32 x 38 mm; cf. fig. 47); C = RMNH Coel. 17755 (oral disc 16 x 18 mm; cf. fig. 49); D = Specimens of type series: MOM 130017 (data on tentacular acrospheres), MOM 683 (spirocysts of tentacular acrospheres) and MOM 130016 (oral disc 60 x 54 mm; rest of data).
For the significance of the symbols with respect to "Frequency", see page 5: "Material and methods".

Organ	Specimen	Nematocyst type	Mean and range (in parentheses) of length and width of nematocyst capsules in µm	N	Frequency
1. Pedal disc	A	a. Spirulae	14.9(8.9 - 23.1) x 4.5(4.0 - 5.3)	17	-?
	B		15.1(12.5 - 16.0) x 4.3(4.0 - 4.5)	10	-
	C		11.4(9.8 - 14.2) x 4.2(3.8 - 4.9)	20	+
			18.7(16.0 - 22.3) x 5.1(4.9 - 5.3)	5	---
	D		20.8(18.7 - 22.3) x 5.9(5.8 - 6.3)	3	---
	A	b. Penicilli D	31.5(26.7 - 35.6) x 8.1(6.7 - 8.9) [1 capsule 18.7 x 6.3]	20	+
	B		33.6(30.3 - 37.4) x 8.0(7.6 - 8.9) [1 capsule 25 x 6.2]	20	+
	C		33.4(24.0 - 40.1) x 8.0(5.8 - 8.9)	25	+
	D		37.9(28.5 - 46.3) x 8.3(7.1 - 9.8)	30	++
2. Column	A	a. Spirocysts	not observed	--	—
	B		ca. 30 - 32 x 4.5 - 5.5	--	?
	C		ca. 45 x 4- 5	5	---?
	D		34 x 4.5 and 41 x 5.3	2	---

	A	b. Spirulae	[14.3 x 4.9, 17.8 x 4.2]	2	- - -
	B		not observed	--	--
	C		[20.5 x 4.5, 21.4 x 5]	2	- - -
	D		not observed	--	--
	A	c. Penicilli D	23.3(20.5 - 27.6) x 7.2(6.2 - 8.5)	20	- /+
	B		23.1(21.4 - 24.9) x 6.4(5.8 - 6.7)	10	?
	C		30.8(23.1 - 40.9) x 7.4(5.8 - 8.9)	40	+
	D		33.2(23.1 - 40.9) x 7.9(6.2 - 8.9)	20	+
3. Acrospheres of tentacles	A	a. Spirocysts	ca. 37 - 59 x 3.3 - 4.5	—	?
	B		ca. 50 - 65 x 5 - 5.5	—	?
	C		ca.35 - 90 x 3.1 - 5.3	—	+
	D		ca. 50 - 90 x 3.6 - 6.2	--	?
	A	b. Homotrishs	not observed	—	—
	B		not observed	—	—
	C		79.7(66.7 - 85.4) x 6.2(5.3 - 6.7)	10	?
	D		58 x 8 and 52 x 7.2	2	?
	A	c. Spirulae 1	22.2(19.6 - 24.9) x 4.8(4.5 - 5.3)	10	- -
		2	63.4(48.9 - 71.2) x 3.7(3.6 - 4.5)	15	+
	B	1	not observed	—	—
		2	ca. 50 - 67 x 3.6	—	?
	C	1	ca. 20 - 24 x 4.5 - 5	3	?
		2	62.4(54.3 - 73.0) x 3.7(3.6 - 4.5)	20	+
	D	1	23.1(21.4 -24.9) x 5.5(4.9 - 5.8)	4	?
		2	74.0(55.2 - 80.1) x 3.8(3.3 - 4.5)	10	?
	A	d. Penicilli D	not observed	—	?
	B		ca. 22.5 x 5.8 - 6.7	2	?
	C		34.4(21.4 - 41.8) x 8.6(6.7 - 10.7)	20	+
	D		69.4 x 8.0	1	?
	A	e. Penicilli E	not observed	--	--
	B		not observed	--	--
	C		170 x 14	1	--
	D		few collapsed capsules, ca. 180 x 14 - 18	—	?
4. Stomodaeum	A	a. Homotrichs	59.9(51.6 - 67.6) x 11.9(10.7 - 13.4)	20	++
	B		55.7(49.0 - 61.4) x 12.4(9.8 - 14.2)	30	++
	C		51.6(42.7 - 57.9) x 10.5(8.9 - 12.1)	20	++
	D		60.7(51.6 - 66.8) x 9.8(8.9 - 10.7)	20	++
5. Filaments	A	a. Spirulae	18.5(16.0 - 19.6) x 4.4(4.0 - 4.9)	5	- -
	B		17.2(15.1 - 18.7) x 5.4(4.9 - 6.2)	25	+
	C		20.1(16.9 - 22.3) x 4.9(4.5 - 5.3)	6	
	D		18.7 x4.5	1	?
	A	b. Penicilli D	51.4(44.5 - 61.4) x 8.9(7.6 - 9.8)	25	- -
	B		49.8(42.7 - 56.9) x 9.9(8.0 - 11.6)	25	+
	C		49.8(46.3 - 55.2) x 9.4(8.0 - 10.7)	20	+
	D		52.5(44.5 - 58.7) x 8.8(7.6 - 9.8)	24	+
	A	c. Penicilli E	89.4(82.8 - 96.1) x 19.9)(16.0 - 22.3)	20	+
	B		83.3(76.5 - 89.0) x 22.6(17.8 - 25.4)	30	+
	C		87.3(80.1 - 97.9) x 21.0(18.7 - 23.1) [inaddition 1 capsule 49 x 14.4]	20	+
	D		92.2(84.6 - 97.9) x 18.2(16.0 - 21.4)	20	+

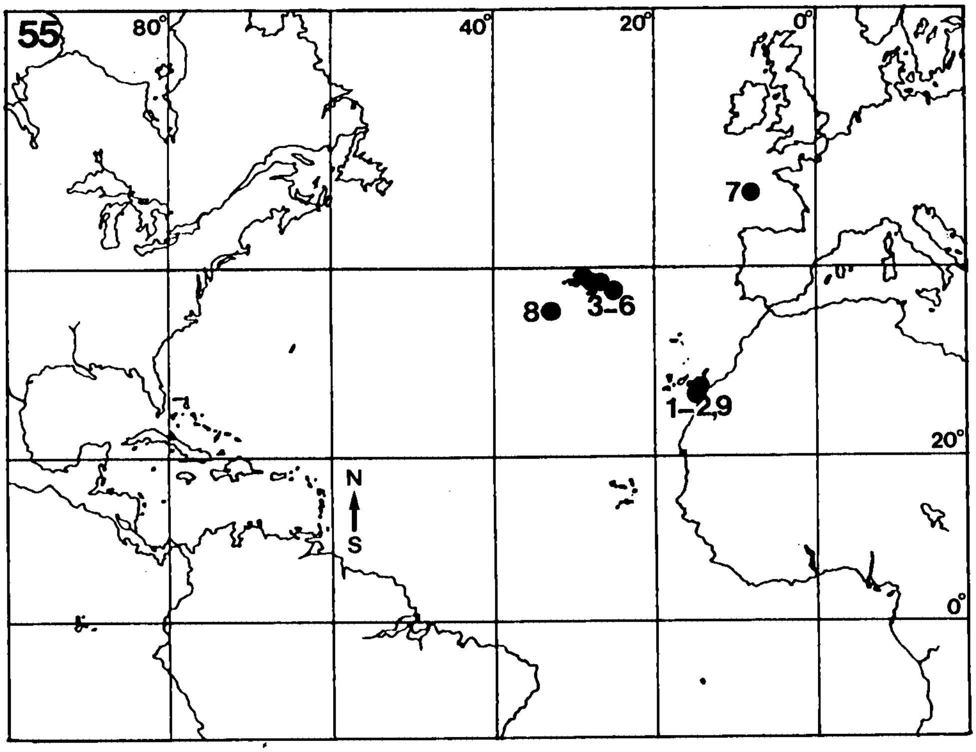

Fig. 55. *Corallimorphus ingens*. Known distribution. 1-2. RMNH Coel. 17754-17755 (CANCAP specimens), 1134-1338 m; 3. MOM 130014, 2102 m; 4. MOM 130017, 1550 m; 5. MOM 130009, 1165 m; 6. MOM 130016, 1732 m; 7. MOM 130079, 1490 m; 8. Bergens Museum nr. 39190, 2615 m; 9. Michael Sars "Bojador specimens" 2603 m (as to 8 and 9 see discussion on pp. 62-63).

pl. 1 figs. 70, 71) of the type series is quite acceptable.

Habitat and depth range.— All specimens known so far were collected on muddy-sandy to clayey deep-sea bottoms, either unattached or attached to solid fragments of substrate such as cinders, coral skeletons, mollusc shells or worm tubes. The known depth range varies between 1134 (present material) and 2615 m, roughly corresponding to water temperatures of ca. 9 to 3°C (cf. Gorshkov, 1978: map 153).

Distribution (fig. 55).— The species is exclusively known from the south-eastern part of the North Atlantic: Azores, Bay of Biscay (Gravier: 1918: 23; 1922: 84) and off Lanzarote (CANCAP material). Carlgren & Stephenson (1929: 6) reported on eight specimens collected during the Norwegian Michael Sars expedition of 1910 in the vicinity of Cape Bojador [situated at 26°06'N 14°33'W], by chance close to the area where the CANCAP specimens were collected, with the remark "habitat somewhat uncertain, possibly west of the Canary Islands". Carlgren (1934: 5) mentioned one more Michael Sars specimen labelled Sta. 53 (34°59'N 33°1'W; 2615 m; see, however, "Material") situated to the south-west of the Azores, and for some reason, not likely to be recovered any more, considered it probable that the other eight specimens also originated from this station, but this remains questionable as the original label information initially only caused doubts between two localities, either "Bojador" [E of the Canary Islands] or W of the Canary Islands". Therefore, it seems just as likely that the single Michael Sars specimen labelled sta. 53 just adds another record and locality, and that the original assumption that the other eight specimens came from the vicinity of Bojador is correct. The CANCAP specimens having also been collected in the vicinity of Cape Bojador anything but contradict this view. Coincidentally the number of the deep-sea station situated most closely to this cape happens to be Sta. 35 (27°27'N 14°52'W, 2603m, fawn coloured, coherent, fine granular *Globigerina* ooze; cf. Chumley [1930?]: 5; Helland-Hansen [1930?]: 24*), i.e. the reverse of Sta. 53, and this may have caused the confusion (note that the depth of the two stations is also practically similar).

Other Corallimorpharia reported from the eastern North Atlantic

Two other species of Corallimorpharia, both representing monospecific genera generally accommodated in a separate family Sideractidae, Danielssen, 1890, have been reported from the north-eastern Atlantic, viz. *Sideractis glacialis* Danielssen, 1890, and *Nectactis singularis* Gravier, 1918. These species were studied to some extent and are included for the sake of completeness. The family Sideractidae is here considered a subjective junior synonym of Corallimorphidae, R. Hertwig, 1882, as discussed on p. 70.

Corallimorphidae R. Hertwig, 1882

Sideractis Danielssen, 1890

Sideractis glacialis Danielssen, 1890
(figs. 56-58, tab. 9)

Sideractis glacialis Danielssen, 1890: 14-16, pl. 1 fig. 1, pl. 7 figs. 10, 12 (description, habitus figure, colour, Norske Nordhavs Exp. Sta. 237, 70°41'N 10°10'W, near Jan Mayen, 3.viii.1877, 481 m, 0.3°C, brown clay and stones, 1 specimen, type of new genus and new family; Sideractidae); Carlgren, 1921: 6-11, figs. 1-5, pl. 1 figs. 17-19 (description of external morphology, anatomy and cnidom; Sunde, mouth Hardanger fiord; Gonactiniidae); Carlgren, 1940: 19-20; figs. 4.12-4.16 (cnidom, Trondheim fiord; Sideractidae); Carlgren, 1942: 72 (distribution map); Carlgren, 1945: 145, fig. 72 (description, habitus fig.; Trondheim fiord); Carlgren, 1949: 12, pl. 4 fig. 2 (name; distribution); Riemann-Zürneck, 1979: 232 (specimens Tromsø Museum, from Økssund [presumably Vest-fjord, 68°02'N 15.16'E], Norway, 220-520 m); Jensen & Frederiksen, 1992: 64 (on dead *Lophelia pertusa* (Linnaeus, 1758); Faroe shelf).

Material.— ZML. s.n. Kat.1 (Gunnerus Sta., 21.vi.1939, Röberg [presumably Röberget, Trondheim fiord, 63°30'N 10°E], 280-300 m, 1 specimen with lacerated regenerating fragment on sponge, "farve: hvit" [= colour: white], Carl Dons); ZMC s.n. (SE of Faroe Islands, 60°33.32'N 06°32.14'W, BIOFAR Sta 90, 22.vii.1987, "skalskrab", 252 m, on *Lophelia pertusa*, 2 specimens); RMNH Coel. 17930 (same data; 2 specimens); RMNH Coel. 18623 (Mediterranean, France, SE coast, Banyuls, 42°04.8'N 3°25'E, Recherches Lacaze-Duthiers, 24.x.1987, 340 m, with samples of the scleractinian *Madrepora oculata* Linnaeus, 1758).

Descriptive notes [mainly based on Carlgren (1921; 1940; 1949) and the present material; Danielssen's original description and figure are highly inaccurate and confusing]: Morphology (fig. 56).— A small species; base spreading and irregular in out-

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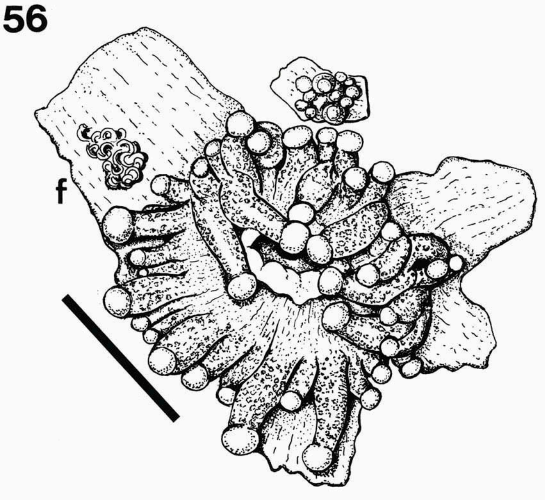

Fig. 56. *Sideractis glacialis*. Habitus of specimen from Trondheim fiord (ZML s.n.). Note the irregular outline of base and the fragment with developing tentacles; f = protruding filaments. Scale bar 5 mm.

line, up to ca 15 mm across in preserved specimens (in life up to ca. 20 mm according to Danielssen), usually smaller. Column low, non-contractile or hardly so, as a rule amply exceeded by the diameter of the base. Tentacles also non-retractile or hardly so, well developed and rather thick with distinct hemispherical acrospheres and with the stems corrugate by the presence of batteries of cnidae (exclusively or almost exclusively spirocysts). Number of tentacles according to Carlgren up to 38 with at least the first three cycles hexamerously arranged; in the "Gunnerus" specimen here studied (ZML s.n.) there were 48 tentacles hexamerously arranged in 4 complete cycles.

[In Danielssen's original description the very characteristic hemispherical/capitate tentacle tips are not properly described and depicted:"...conically acuminated, and appear to have an aperture on their outermost extremity (pl. 1 fig. 1, pl. 7 fig. 12).", and he also erroneously suggested the arrangement of the tentacles to be octamerous and the stomodaeum to be provided with two siphonogyphs].

Anatomy: Musculature weak; sphincter absent. Six pairs (always?) of perfect and fertile mesenteries provided with filaments and an additional number of smaller sterile mesenteries without filaments (always?). Stomodaeum with ca. 12(?), shallow longitudinal grooves, possibly representing the insertions of the primary mesenteries, but without siphonoglyphs.

Cnidom (tab. 9, fig. 57).— The cnidom of the species was previously studied by Carlgren (1921: 1940: 19-20). For the present study only one specimen (ZML. s.n.) was examined more or less in detail. Of the small and rather poorly preserved specimen from the Mediterranean (RMNH Coel. 18623) only the tentacular acrospheres were examined. The results are presented in table 9. The data of Carlgren and those obtained from the ZML specimen, both from the Trondheim fiord, are well in agreement, except for the fact that Carlgren apparently overlooked the large atrichs in the acrospheres (3b) (fig. 57). A few of these atrichs were also found in the Mediterranean specimen. Similar atrichs, though generally uncommon and easily overlooked are present in various Actiniaria, notably in the column of species of Actiniidae and Sagartiidae. They were not previously reported from species of Corallimorpharia or any other order of Anthozoa. The tentacular nematocysts of the Mediterranean specimen are relatively small, possibly in correlation with the small overall size of the specimen.

Table 9. *Sideractis glacialis*. Survey of the cnidom of a specimen from the Trondheim fiord, Norway (ZML s.n.) (A), as compared to the data presented by Carlgren (1940: 19-20) of a specimen from the same locality (B). In addition information is added on the tentacular acrospheres of the Mediterranean specimen (RMNH Coel. 18623) (C).
For the significance of the symbols with respect to "Frequency", see page 5: "Material and methods".

Organ	Specimen	Nematocyst type	Mean and range (in parentheses) of length and width of nematocyst capsules in µm	N	Frequency
1. Base	A	a. Penicilli D	32.3(29.4 - 35.6) x 7.3(6.7 - 8.0)	10	-?
	B		no data	—	—
2. Column	A	a. Spirocysts	few of tentacle stalk type, not measured	—	—
	B		present, no data on size	—	—
	A	b. Spirulae	14.4(13.4 - 16.0) x 4.8(4.0 - 5.8)	6	--
	B		12.5 - 17 x 4.5 - 5.5	—	-
	A	c. Penicilli D	32.4(28.5 - 37.4) x 7.2(6.2 - 8.0)	15	+
	B		31 - 37 x 7 - 8.5	—	+
3. Acrospheres of tentacles	A	a. Spirocysts	ca. 27 - 80 x 2.2 - 5.3	—	++
	B		present, no data on size	—	++
	C		ca. 20 - 50 x 2.4 - 4.0	—	++
	A	b. Atrichs	mostly collapsed, ca. 90 - 120 x 18 - 22.5	—	-/--
	B		not observed	—	—
	C		collapsed, up to ca. 90 x 18	3	?
	A	c. Spirulae	18.2(14.2 - 22.3) x 4.7(4.5 - 4.9)	11	-
	B		15.5 - 23 x 4.5	—	+
	C		14 - 15 x 3.8 - 5	3	---
	A	d. Penicilli D	92.1(80.1 - 105.0) x 6.2(5.8 - 6.7)	18	++
	B		96 - 103 x 7; 77-79 x 5.5	—	+
	C		59.8(48.1 - 80.1) x 5.3(4.5 - 6.2)	15	++
	A	e. Penicilli E	138.1(89.0 - 160.2) x 24.6(16.9 - 31.2)	23	+
	B		94 - 168 x 16.5 - 26	—	+
	C		81.6(46.3 - 119.2) x 19.7(8.9 - 32.9)	25	+
4. Tentacle stalks	A	a. Spirocysts	ca. 45 - 50 x 4.5 - 5.5	—	++
	B		present, no data on size	—	+++
	A	b. Spirulae	only one observed: 18.7 x 5.3	1	---
	B		15.5 - 17 x 4.2 - 5	—	-/--
	A	c. Penicill D	not observed	—	—
	B		48 - 55 x 5.6	—	?
5. Stomodaeum	A	a. Spirulae	28.7(26.7 - 32.0) x 4.8(4.5 - 5.3)	5	?[inc.]
	B		29.5 - 34 x 4.5	—	?
	A	b. Penicilli E	44.5(35.6 - 49.0) x 13.8(11.6 - 16.0)	20	+
	B		43 - 48 x ca 12	—	++
6. Filaments	A	a. Spirulae	only two observed: 15.1 x 4.5 and 20.5 x 4.0	2	---
	B		not observed	—	—
	A	b. Penicilli D	26.0(22.3 - 28.5) x 5.6(5.3 - 6.2)	14	-/+
	B		25.5 - 29.5 x 5.6 - 7	—	++
	A	c. Penicilli E	75.8(65.9 - 81.9) x 25.3(23.1 - 28..5)	20	+
	B		74.5 - 91 x 14.5 - 22 (25)	—	++

Fig. 57. *Sideractis glacialis*. Atrich from tentacular acrospheres (3b) of a specimen from the Trondheim fiord (ZML s.n Kat.1). Scale bar 20 µm.

Biological notes.— The species is usually found on banks of *Lophelia prolifera* (Linnaeus, 1758) and/or *Madrepora oculata* Linnaeus, 1758. The Faroe specimens formed part of a community which also includes *Botrucnidifer norvegicus* Carlgren, 1912 (Ceriantharia: Botrucnidiferae), *Gonactinia prolifera* (M. Sars, 1835) and *Protanthea simplex* Carlgren, 1891 (both Actiniaria: Gonactiniidae), *Kadosactis abyssicola* (Danielssen & Korén, 1877) (Actiniaria: Sagartiidae), and *Epizoanthus* cf. *macintoshi* Haddon & Shackleton, 1891 (Zoantharia). Just like *Sideractis glacialis*, none of these associated species had ever been reported from the Mediterranean, and it therefore is worth mentioning that the sample containing the specimen from Banyuls (RMNH Coel. 18623) also contained three specimens of *Prothanthea simplex* (RMNH Coel. 18665).

Evidence of asexual reproduction, so far not reported from this species, was observed in the specimen from the Trondheim fiord (ZML s.n.) (fig. 56). The base of this specimen is spreading and very irregular in outline, and close to it, orientated parallel to the limbus, a small additional specimen is present, representing no more than a squarish piece of tissue with some developing tentacles, beyond doubt the result of pedal laceration. In conformity with what was previously mentioned in relation to specimens of *Corallimorphus* spp., the filaments of the ZML specimen of *Sideractis glacialis* here examined contained significant numbers of siphonophoran nematocysts, especially homotrichous anisorhizes and to a lesser degree rhopalonemes, desmonemes, large b-mastigophores, and holotrichs (cf. den Hartog, 1980a: pls. 2-3 types 1, 3, 5, 6, 10; van Nierop & den Hartog 1984: figs. 2, 4, 5, 7, 11).

Colour.— Almost transparent, body and tentacles very faintly greenish with a white annulus at the tentacle tips; the oral disc slightly pale red (Danielssen: 16, pl. 1 fig.1). The label of the ZML specimen reads "hvit" (= white).

Distribution (fig. 58).— Until recently the species was exclusively known from northern latitudes: from Jan Mayen and the Trondheim-, Vest-, and Hardanger fiords in Norway. Additional specimens (see "Material") were recently obtained from the Faroe Islands and from the western Mediterranean. The type specimen from Jan Mayen was found on a stone (Danielssen, 1890: pl. 1 fig. 1), but the species is usually found associated with *Lophelia prolifera* and *Madrepora* (= *Amphelia*) *oculata* banks. Due to its inconspicuous colour and its small size the species may often have been overlooked. The present record from the Mediterranean reveals that it is more widely distributed than was generally assumed, and it seems possibly therefore that its distributional range coincides to a large extent with that of *Lophelia* and *Madrepora* banks. For the distribution of these banks, in and beyond the north-eastern Atlantic, see Zibrowius (1980: 37-38, 127-128).

The known vertical distribution ranges from ca. 220-500 m.

Nectactis Gravier, 1918
Nectactis singularis Gravier, 1918
(fig. 58, tab. 10)

Nectactis singularis Gravier, 1918: 18-20, figs. 5-7 (description; provisionally referred to the Minyadidae but similarity with *Corallimorphus* diagnosed); 1922: 76-80, pl. 6 figs. 64-65, pl. 12 figs. 122-126 (further description, discussion on floating way of life); Stephenson, 1922: 306 (a species of Corallimorphidae rather than Minyadidae); Carlgren, 1934: 1-2 (re-appraisal of characters, cnidom in accordance with "Corallimorphiden", not a species of Minyadidae but Sideractidae); Carlgren, 1949: 12 (name; Sideractidae); Riemann-Zürneck, 1979: 229-234, 239, 242, figs. 1-3 (redescription, good habitus photos, photos and sizes of nematocyst types, distribution; Sideractidae).

Material.— Type series of Gravier: MOM 130023 (S.A. Le Prince de Monaco, Sta. 753, 39°50-54'N 17°57'-18°06'W, 18.ix.1896, chalut, 4360 m, vase blanche à globigérines; 11 [originally 14] specimens); MOM 130135 (S.A. Le Prince de Monaco, Sta. 749, 38°54-55'N 21°06'45"-18'45"W, 16-17.ix.1896, chalut, 5005 m, vase blanche à globigérines; 5 specimens).

Diagnostic characters (partly based on Riemann-Zürneck, 1979).— A rather small disc-shaped, circular to somewhat oval species up to 28 mm in diameter (the largest specimen of the type series measuring 24 x 17 mm). Tentacles short, up to about 60 according to Gravier and approximately 60 irrespective of the size of the polyps according to Riemann-Zürneck (1979: 230), provided with distinct acrospheres and arranged in two alternating cycles: a cycle of up ca. 30 relatively large endocoelic tentacles up to 4-5 mm long, alternating with an equally numerous cycle of much smaller exocoelic tentacles. Number of tentacles corresponding with the number of mesenteries. Mesenteries all perfect and in the larger specimens fertile; normally approximately 15 larger pairs alternating with 15 smaller pairs. Musculature completely reduced or almost so. Stomodaeum strongly folded and pleated (i.e. with strongly increased surface). Base reduced, externally visible as a pore, enclosing a small concavity with foreign material and a brownish substance which is probably an excretion product of the base (also present in the Michael Sars specimens of *Corallimorphus ingens*).

Cnidom (tab. 10).— The nematocyst data obtained from the type material here examined (rather soft and macerated and largely devoid of ectoderm), although incomplete and fragmentary, are more or less in accordance with the data given by Riemann-Zürneck (1979: 232 tab. 1, fig. 2), except for the ranges of the tentacular penicilli D (3c) and E (3d), which are considerably narrower than the ranges given by her, and without overlap.

Biological notes.— It is generally agreed that the body shape of *Nectactis singularis* indicates a non-sessile way of life. On that account Gravier (1918: 19; 1922: 79) even tentatively placed it in the pelagic actinian family Myniadidae, but his statements are dualistic and contradictory. He mentioned that the basal concavity, in con-

Table 10. *Nectactis singularis*. Fragmentary survey of the cnidom based on specimens of the type series (MOM 130023 and MOM 130135) compared with data given by Riemann Zürneck (1979) (R). Due to the condition of the material studied only few nematocysts were found, so that it is impossible to present information on frequencies.

Organ	Specimen	Nematocyst type	Mean and range (in parentheses) of length and width of nematocyst capsules in µm	N
1. Basal concavity/ Pedal disc	MOM	a. Spirulae	15.7(13.4 - 17.8) × 5.3(4.9 - 6.2)	6
	R		12 - 16.5 × 5.5 - 6	—
	MOM	b. Penicilli D	27.3(22.3 - 31.2) × 7.3(6.7 - 8.5)	10
	R		23 - 35 × 8.5 - 11.5	—
2. Column	MOM	a. Spirulae	16.5(15.1 - 17.8) × 5.0(4.9 - 5.3)	4
	R		no data	—
3. Acrospheres of tentacles	MOM	a. Spirocysts	ca. 32 - >45 × 4.2 - 5.3	—
	R		no data	—
	MOM	b. Spirulae	17.8(15.1 - 22.3) × 5.0(4.5 - 5.3)	3
	R		no data	—
	MOM	c. Penicilli D_1	33.8 × 8.9	1
		$_2$	90.5(80.1 - 102.4) × 6.5(6.2 - 7.1)	3
	R	$_1$	apparently not observed	—
	R	$_2$	106 - 148 × 6 - 7	—
	MOM	d. Penicilli E	80.7(75.7 - 84.6) × 23.2 (17.8 - 28.5)	10
	R		87 - 183 × 23 - 29	—
4. Stomodaeum	MOM	a. Spirulae	not examined	—
	R		50 - 58 × 5.5 - 8	—
	MOM	b. Penicilli D	not examined	—
	R		68 - 83 × 20 - 30	—
5. Filaments	MOM	a. Spirulae	14.7(13.4 - 16.0) × 4.9 (4.5 - 5.3)	2
	R		19 × 4.5	—
	MOM	b. Penicilli D	28.5 × 6.2	1
	R		29 - 38 × 7 - 8	—
	MOM	c. Penicilli E	not observed	—
	R		70 - 85 × 23 - 30	—

trast to the situation in other species of Minyadidae, does not enclose a (self-produced) "float", but only elements from the surrounding environment, notably Foraminifera ("la cavité [pédieuse] est alors remplie d'éléments empruntés au milieu ambiant, notammant des Foraminifères") (Gravier, 1922: 77). It is obvious that this accumulation of Foraminifera, even if tests of pelagic forms are concerned (but this is not explicitly stated), cannot reasonably have taken place in the pelagic environment, but only after the organisms had died and sunk to the bottom. Similar accumulations of foreign material, including Foraminifera, are also found on, or enveloped in, the base of specimens of *Corallimorphus* spp. that have not succeeded to settle on solid substratum. Therefore, *Nectactis singularis* definitely is a benthic species, but, apparently being non-sessile, it may be subject to any local changes in turbulence and deep-sea bottom currents (as has actually been observed in certain deep-sea Actiniaria; Dunn & Bakus, 1977: 82-83, Riemann-Zürneck, 1979: 241-242) and be (slowly) passively transported along the bottom to be redeposited in locations with more stagnant water (the state of expansion of anemones would seem to be a factor of some importance: the more expanded they are, the more their specific gravity will approach that of the surrounding water, and the easier one would expect them to be conveyed). As this same mechanism would simultaneously generate drift and to some extent accumulation of equally transportable objects, including potential food items in the form of bentho-planktonic prey organisms and/or their desintegrating fragments, the non-sessile way of life of *Nectactis singularis* may be speculated to be a feeding-strategy-related adaptation.

Riemann-Zürneck (1979: 232) did not find a trace of histogicaly discernable musculature in the species, neither in the body, nor in the small-sized tentacles, which, in accordance with the idea put forward in relation to species of *Corallimorphus*, suggests that the tentacles in *Nectactis singularis* cannot be active catching devices. The shortness of the tentacles would also seem prohibitive to transport prey to the mouth. Both Gravier (1918: 18; 1922: 78) and Riemann-Zürneck (l.c.) noted the presence in this species of an unusually large, longitudinally ridged and tranversally pleated stomodaeum, i.e. with a significantly increased endodermal surface, characterized by Riemann-Zürneck (l.c) as ".....,with numerous enclosures and vacuoles, which indicates a nutritional significance....". It therefore seems quite possible that the small tentacles only function as holding devices, as previously suggested for *Corallimorphus* spp. (see p. 50), and that prey is enveloped, engulved and digested by protrusion of the large stomodaeum and the filaments. In this connection it is interesting to note that in several specimens of the type series a cluster of filaments was protruding through the mouth (Gravier, 1922: pl. 6 figs. 64a, b).

Distribution (fig. 58).— Iberian deep sea basin east of the Azores and Bay of Biscay, between 4100 and 5000 m.

Discussion.—*Sideractis glacialis* and *Nectactis singularis* were previously included in a separate family Sideractidae Danielssen, 1890 (cf. Carlgren, 1949: 12; Dunn, 1982: 700), because both species share the absence of discal tentacles, a character unique among Corallimorpharia but in our view not in itself necessarily indicating closer kinship. In point of fact *Nectactis singularis* much more resembles species of *Corallimorphus* (cf. also Riemann Zürneck, 1979: 229-234, figs. 1-2, table 1), and, when comparing these two genera, the absence of discal tentacles in *Nectactis singularis* can be shown to be a difference of degree rather than a fundamental one. All members of the genus *Corallimorphus*, in accordance with *Nectactis*, share the total absence of discal tentacles in connection with the exocoels. The condition of the endocoels is different; in part of the species of *Corallimorphus* each endocoel, in addition to its marginal tentacle, communicates with a single discal tentacle (therefore, provided ontogenetic irregularities, the ratio of marginal and discals in specimens of this group is 2 : 1). In another group the discal tentacles are not only absent from the exocoels, but also from the youngest endocoels (causing the ratio of marginals and discals to be 4 : 1). The subsequent condition, in which the older endocoels are also without discal tentacles, as actually present in *Nectactis singularis*, cannot therefore be regarded so fundamentally different as to justify the inclusion of this species in another family, the more so as the general morphology (including a wide, dish-shaped oral disc) and the cnidom of the two genera are essen-

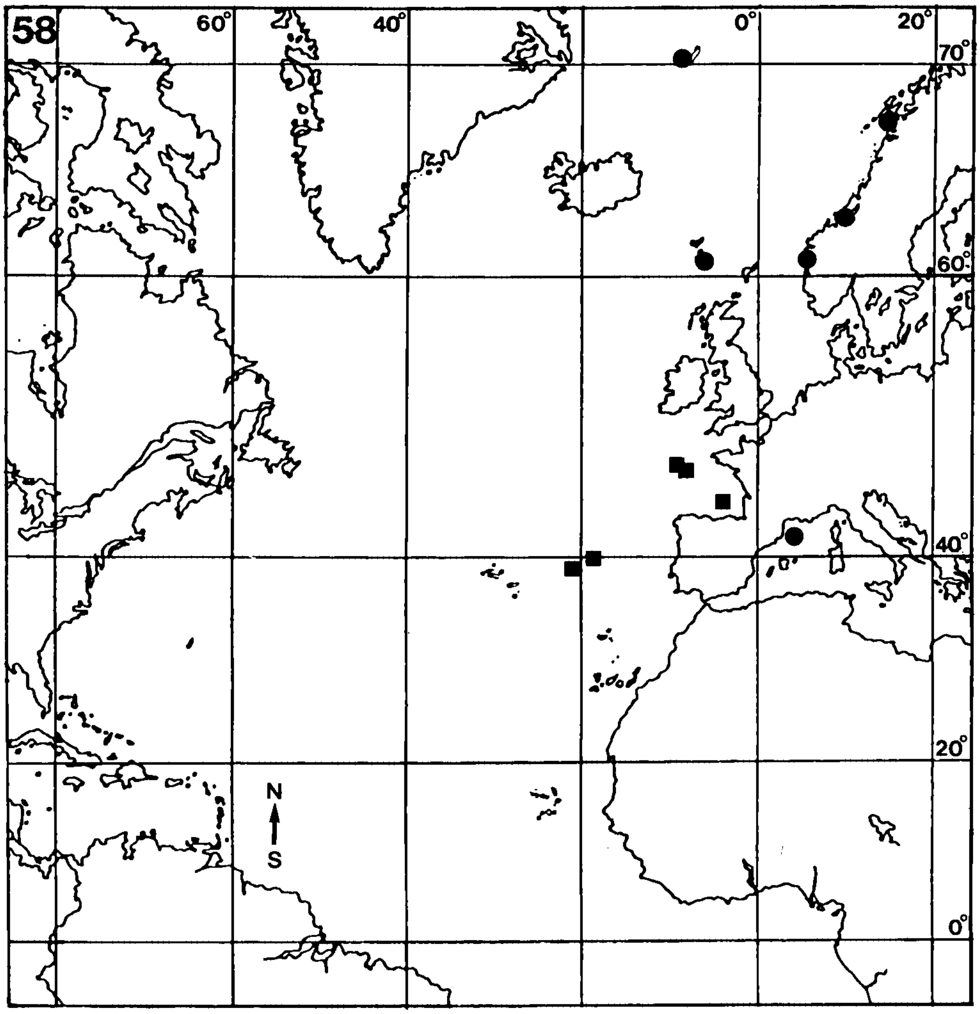

Fig. 58. Known distribution of *Sideractis glacialis* (dots) and *Nectactis singularis* (squares). Sources: Gravier, 1922: 76, 94; Riemann-Zürneck, 1979: 229, 233 fig. 1; den Hartog et al., present paper.

tially similar. Gravier (1918: 19; 1922: 79-80), although including *Nectactis singularis* in the actinian family Minyadidae, already noticed its similarity with Corallimorphidae, and so did Stephenson (1922: 306), who, on the basis of Gravier's original description, did in fact reach the same conclusion. He stated: "It is very difficult to even suggest a position for this form in classification. Gravier suggests Minyadidae, but it would not do for that family as understood here. If there were disc-tentacles one might suggest Corallimorphidae, and possibly that would be best even without them -- but more details are needed".

The systematic position of *Sideractis glacialis* is less evident, but this species too shows similarities with species of Corallimorphidae. In accordance with members of the genus *Corallimorphus* and with *Nectactis singularis* its general musculature is weak and there is no sphincter, and, as mentioned above, the absence of discal tentacles is shared with *Nectactis singularis.* More in accordance with the genera *Corynactis* and *Pseudocorynactis* are the general shape of the body, the spreading base, always attached to solid substrate, and the occurrence of asexual reproduction. The tentacles are well-developed, even relatively large, and the stalks well-provided with spirocyst batteries as in members of the *Corynactis viridis*-complex.

In conclusion, although *Sideractis glacialis* is a distinctive species, its similarities with the other species and genera of Corallimorphidae make it hard to accept accomodation in a family of its own. On the basis of the data available inclusion in the Corallimorphidae seems more realistic. If a division into families were to be considered, it would rather seem more logical to retain the family *Corallimorphus* for the genera *Corallimorphus* and *Nectactis,* and to re-establish the family Corynactidae Andres, 1883, to include the genera *Corynactis, Pseudocorynactis* and *Sideractis.*

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