THE CHEILOSTOMATA (BRYOZOA) OF THE DEEP SEA

P. J. HAYWARD

(Department of Zoology, University College of Swansea, W. Glamorgan, U. K.)

ABSTRACT

Forty-seven species of Bryozoa have been identified in benthic samples from 32 of the deep sea collecting stations of the Galathea Expedition. The depths of the stations ranged from 425 m to 8300 m, with a majority being deeper than 1000 m. The distribution of the stations, with the majority located in the western Indian Ocean and the western Pacific Ocean, and the range of depths sampled are of particular interest, representing geographical regions and bathymetric zones which have been rarely studied by bryozoan specialists. Seventeen new species are described; the geographical and bathymetric distribution patterns of the species identified are discussed. A summary of the known species of deep-sea Cheilostomata concludes with a discussion of the observed patterns of vertical distribution of the most frequently recorded species.

CONTENTS

INTRODUCTION

Recent investigations have shown that the bryozoan fauna of the deep sea is still poorly known and that even in the most intensively studied areas of the oceans, the eastern North Atlantic for example, the bryozoan component of the benthos includes a high proportion of undescribed species. For many parts of the world the only source of information remains the report of the Challenger Expedition (Busk 1884) supplemented by a very few later publications, such as the reports of the Siboga Expedition (Harmer 1915, 1926, 1934, 1957), dealing with more limited geographical areas. This paucity was highlighted by Schopf (1969) in a wide-ranging survey of the literature of deep water bryozoan faunas. In a comprehensive table Schopf listed 48 published sources which contained data on the occurrence and distribution of the Bryozoa between depths of 200 and 6000 metres. While such major surveys as those of the Challenger and Siboga expeditions (each with 54 stations yielding bryozoan material) made significant contributions to the present body of data, it is noteworthy that more than half of the sources listed by Schopf each represent seven or fewer collecting stations. Of the combined total of 703 stations summarized, 55% were located in the North Atlantic, and 75% were within the depth range of 200 to 1000 metres. Thus the greatest depths and the greatest geographical extent of the oceans remained understudied.

Since the publication of Schopf's review there has been a dramatic upsurge of interest in the bryozoan fauna of the deep sea. The decade from 1970 has seen the publication of a number of reports based on the results of several intensive benthic sampling programmes in the Northeast Atlantic (e.gs. d'Hondt 1970, 1973a, 1973b, 1975; Hayward 1978, 1979; Hayward & Ryland 1978), each of which has reinforced the view that the deep-sea Bryozoa offer considerable potential for further research. Despite the fact that these papers describe material from relatively well known areas of the Atlantic significant proportions of new species have been reported, and much new information on bathymetric and geographical distributions has been accumulated. However, the bryozoan faunas of the deep waters of the South Atlantic, Indian and Pacific Oceans have received practically no attention within the present century. A recent exception is the report on the South African Museum's "Meiring Naude" cruises (Hayward & Cook 1979) which described a substantial fauna of 48 species, 23 of which were new to science, from 18 stations between depths of 376 m and 1300 m.

The collections of the Galathea Expedition (1950-1952) included samples of bryozoan material from 32 stations, with depths ranging from 425 m to 8300 m. Only seven of these stations were located in depths of less than 1000 m; 12 were deeper than 4000 m and 13 were distributed between 1000 and 4000 m. Fifteen of these sampling stations were situated in the western Indian Ocean, between Cape Town and Kenya; one was located between the Seychelles and Ceylon, and three more within the Malayan Archipelago. One station was situated off South Australia, three in the Tasman Sea and a total of seven in the region of the Kermadec Trench. The two final samples were obtained from the eastern Pacific, between Acapulco and Panama. Thus, although widely dispersed, these 32 stations coincide with some of the most neglected areas of the deep sea and encompass a range of depths which to date has been represented in only a minority of collections. The "Galathea" collections therefore contribute significantly to the study of the deep-sea Bryozoa.

Forty-seven species of Bryozoa are described in the following report. Of these, seventeen are considered to be new to science, six have been assigned to genus only and two are presented as apparently unrecorded varieties of otherwise well documented and widespread deep-sea species. A preponderance of the species described are Anascan Cheilostomata; the Ascophoran Cheilostomata comprises 12 species, and a single species of Ctenostomata was found in a sample from one of the shallower stations. In Table 1 (p. 51) the occurrence, and number of recognizable colonies, of each species is detailed; the majority are described and figured in the following systematic section. Locality, geographical co-ordinates and depth are given for every specimen examined, but Bruun (1957) should be consulted for complete station data.

The discussion of these results has been extended to include a summary of known species of deep-sea Cheilostomata; this is taken to include all species recorded from depths in excess of 1000 m, constituting the cheilostome benthos of what are generally defined as the bathyal and abyssal zones of the ocean. The summary includes a review of available data on the bathymetric distribution patterns of these species, incorporating the results of the "Galathea" collections. It is hoped that this exercise will assist in characterizing more precisely the nature of the deep-sea bryozoan benthos in terms of taxonomic diversity and bathymetric distribution patterns.

Type material has been deposited in the Zoological Museum, University of Copenhagen, Denmark.

SYSTEMATIC ACCOUNTS

ORDER CHEILOSTOMATA

Family MEMBRANIPORIDAE Busk, 1854

Genus *Nelliella* Mawatari, 1974

Colony erect, branching dichotomously, formed from short, quadrangular internodes linked by chitinous joints. Zooids in four longitudinal series, each constituting one facet of the branch. Gymnocyst reduced or vestigial; cryptocyst typically well developed proximally, delimiting an elliptical opesia. Avicularia vicarious, present or absent. Ovicells absent.

Nelliella nelliformis (Harmer)

Fig. 1A

Acanthodesia nelliformis Harmer, 1926: 218, pl. 13, figs 20-22.
Nelliella nelliformis, Mawatari 1974: 37.

Material:
St. 490. Bali Sea (5°25'S, 117°03'E), 545-570 m.

Description: Colony erect, branching dichotomously, secured by tubular rhizoids; composed of four-sided, angular internodes, up to 5.5 mm long, linked by distinct chitinous joints, a single longitudinal series of zooids forming each of the four facets of the branch. Zooids rectangular, with distal ends slightly rounded, 0.5-0.65 mm long by 0.2 mm broad. Frontal wall entirely membranous, underlain for about half its length by a smooth, distally-sloping cryptocyst. Lateral walls forming a distinct mural rim above the crytocyst. Opesia elliptical. A polymorphic zooid, containing a feeding polypide but with an enlarged and modified operculum, may occur not infrequently; the distal wall is raised and arched, supporting an enlarged semi-elliptical mandible, heavily chitinized and strengthened by thickened sclerites. These polymorphs represent primitive avicularia.

N. nelliformis was described by Harmer (1926) from a single locality in the Malay Archipelago. It does not appear to have been reported since. The genus *Nelliella* was introduced by Mawatari (1974) for four Indo-West-Pacific species formerly assigned to *Acanthodesia,* with *A. nelliformis* Harmer as type species. Superficially similar species of *Acanthodesia* (= *Membranipora*), such as *A. limosa* (Waters), do not develop the chitinous joints characteristic of *Nelliella.*

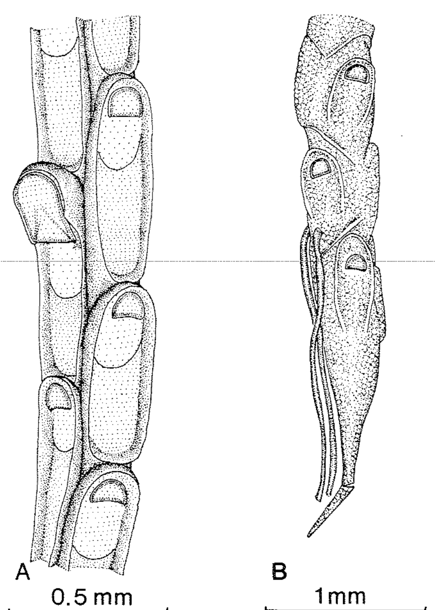


Fig. 1. *Nelliella nelliformis* (Harmer). A, part of an internode, including an avicularium; B, *Cellaria* sp., the ancestrula and first zooids.

Family CELLARIIDAE Hincks, 1880

Genus *Cellaria* Ellis & Solander, 1786

Colony erect, branching dichotomously, with conspicuous chitinous joints linking rigid cylindrical internodes. Zooids lozenge-shaped or hexagonal, arranged in alternating whorls around the axis of the internode. Cryptocyst extensive, opesia scarcely larger than operculum; no gymnocyst. Ovicells immersed, with an irregular opening distal to the border of the zooid. Avicularia vicarious.

Cellaria sp.

Fig. 1B

Material:
St. 182. Cape Town-Durban (33°28'S, 38°32'E), 5110-5340 m.

Description: Three ancestrulate juvenile colonies of an unrecognized species of *Cellaria* were present in the sample from St. 182, the largest was 7.5 mm long. Each consisted of a single, slender internode, flattened in section and comprising an ancestrula and two longitudinal series of zooids. Hayward & Cook (1979) described two anomalous species of *Cellaria* from the eastern coasts of South Africa; the present specimens are reminiscent of *C. paradoxa* but display an astogenetic pattern quite different from that species. It was found (Hayward & Cook 1979: 71) that the characteristic morphological features of *C. paradoxa* developed gradually through a long astogenetic sequence; as the present specimens comprise very few astogenetic generations it is unlikely that they represent the definitive form of the species. Consequently, it would be premature to assign a specific name to these specimens.

Genus *Syringotrema* Harmer, 1926

Colony erect, branching, cylindrical, unjointed; attached by chitinized rhizoids. Zooids lozenge-shaped, with extensive, convex cryptocyst, produced as a flared rim around a subterminal opesia. Avicularia vicarious. Ovicells prominent, globular.

Syringotrema auriculatum Harmer
Fig. 2A

Syringotrema auriculatum Harmer, 1926: 346, pl. 21, figs 22-26.

Material:
St. 490. Bali Sea (5°25'S, 117°03'E), 545-570 m.

Description: Zooids in four alternating longitudinal series, 0.8-0.9 mm long by 0.5 mm wide. Zooid boundaries marked by a raised rim around a convex, granular cryptocyst; opesia practically coincident with orifice, transversely oval, encompassed by a second rim, prominent proximally and laterally, grading distally into the zooid boundary. Ovicell prominent, convex, with a granular surface. Avicularia situated at the axil of each dichotomy; with semicircular mandibles.

Two fragments of this curious species, the largest 1.8 cm long, were recovered from St. 490, little distant from its single previously known locality. Both fragments included zooids with embryos.

Family SCRUPOCELLARIIDAE Levinsen, 1909

Genus *Notoplites* Harmer, 1923

Colony erect, branched, attached by bundles of rhizoids. Branches unilaminar, biserial, each with a distinct basal joint; disposition of zooids and joints at a bifurcation characteristic, referable to Type 15 of Harmer (1923). Zooids elongate, with an extensive opesia; gymnocyst well developed, cryptocyst

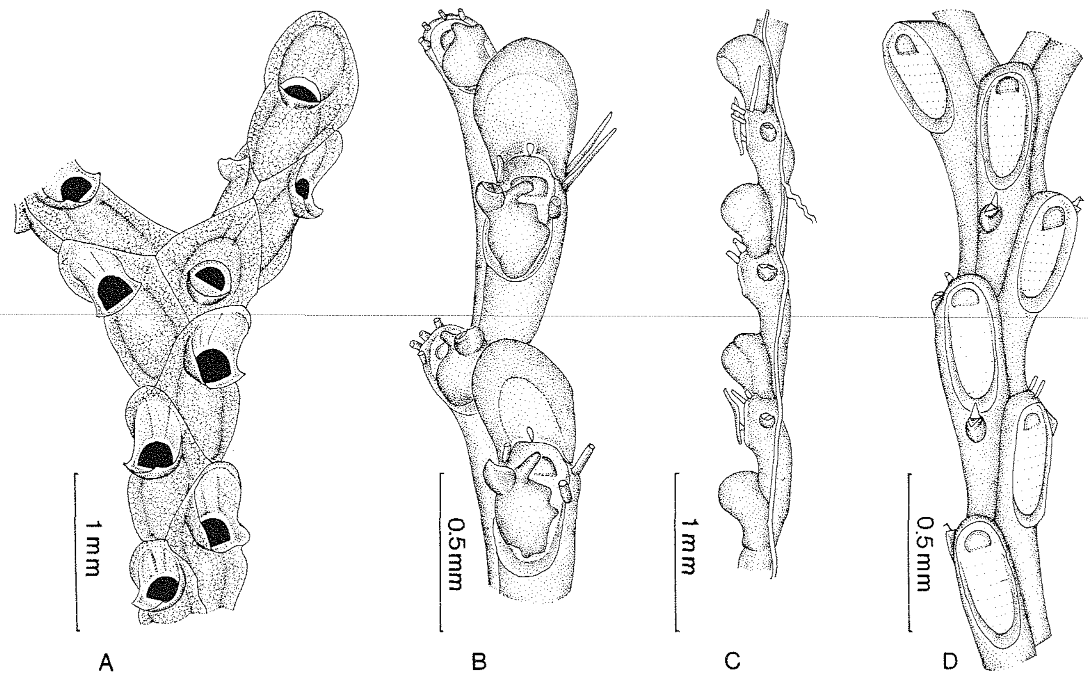


Fig. 2. A, *Syringotrema auriculatum* Harmer, a branch dichotomy, including an avicularium and an ovicellate zooid. B-C, *Notoplites armigera* n. sp. B, part of an internode, note the distal digitiform process of the scutum and the position of the avicularium; C, part of an internode in side view to show lateral avicularia and rhizoids. D, *Notoplites* sp., the specimen from St. 196.

typically a narrow rim. Oral spines present; one usually curved over the opesia, flattened and frequently branching, termed a scutum. Sessile avicularia present, on lateral and frontal surfaces. Ovicells typically longer than wide with a single frontal fenestra.

Notoplites armigera n. sp.

Fig. 2B-C

Holotype:
St. 665. Kermadec Trench (36°38'S, 178°21'E), 2470 m.

Description: Zooids slender, 0.9-1.0 mm long, 0.25-0.3 mm wide; opesiae oval, not overlapping but strictly alternating along the branch, cryptocyst forming a narrow, gently flared rim. Five distal oral spines present, the most proximal on the external border being the largest. Scutum arising from the inner border of the zooid from a point about halfway along its edge, obscuring the proximal two-thirds of the frontal membrane; of characteristic shape, an oval proximal lobe, often with a scalloped lower edge, and a flattened, digitiform distal lobe. Latero-basal avicularia present on most zooids, rostrum acute to the long axis of the zooid and directed proximo-laterally, mandible triangular. Frontal avicularia of sporadic occurrence, similar to latero-basal type but smaller, situated on the scutum close to its point of origin. Ovicell longer than broad, somewhat asymmetrical, with a small, drop-shaped frontal fenestra close to its orifice.

Two large colonies of *N. armigera* were present in the sample, measuring 4.2 cm and 5.1 cm. Species of *Notoplites* are characteristic of the deep water bryozoan benthos in many parts of the world's seas and several new species have been described in recent years (e. g. Hayward & Ryland 1978, Hayward & Cook 1979).

Notoplites armigera may be distinguished from all presently known species by the frontal avicularium, which is intimately associated with the scutum.

Notoplites sp.

Fig. 2D

Material:
St. 196. Off Durban (29°55'S, 31°20'E), 430 m.

Description: Fragments of an unrecognized species of *Notoplites* were present in this sample. Zooids were 0.7 mm long by 0.2 mm wide, with elongate oval opesiae just overlapping along the branch. Minute lateral avicularia were present, and marginally larger frontal avicularia. One or two external distal oral spines were present on some zooids, but a scutum was not evident.

The material was so badly damaged that an adequate description could not be prepared, but must await the collection of further specimens.

Genus *Amastigia* Busk, 1852

Colony erect, branching, unjointed, secured by bundles of rhizoids. Branches unilaminar, typically pluriserial with the central rows of zooids partly or wholly excluded from the basal surface of the branch. Zooids with oval opesiae, rimmed by a narrow cryptocyst; distal oral spines present, one of which may develop as a scutum. Lateral and frontal avicularia occur; basal heterozooids may be developed as avicularia, vibracula or setiform avicularia, not completely obscuring the basal surface of the colony.

Amastigia cf. *nuda* Busk

Fig. 3A-B

Amastigia nuda Busk, 1852: 40, pl. 36, figs 4,5; Hastings 1943: 321, figs 1B, 3D, E.

Material:
St. 665. Kermadec Trench (36°38'S, 178°21'E), 2470 m.

Description: Zooids in three alternating longitudinal series, the basal walls of the middle series partly excluded from the basal surface of the colony (Fig. 3B); slender, tapered proximally, elongate oval opesiae comprising almost half frontal surface. Cryptocyst a narrow, flared rim; gymnocyst smooth, bearing medially a small avicularium, rostrum acute to frontal plane, directed proximally, mandible semielliptical. Three spines on each distal corner of the zooid, one or two of which may be grossly enlarged, up to 0.5 mm long in present material. An oval scutum, frequently damaged or lost, obscures the proximal two-thirds of the opesia. A single latero-basal avicularium present on each marginal zooid, at the outer distal corner; mandible semielliptical, acute to long axis of branch, directed proximally. Basal heterozooids developed as

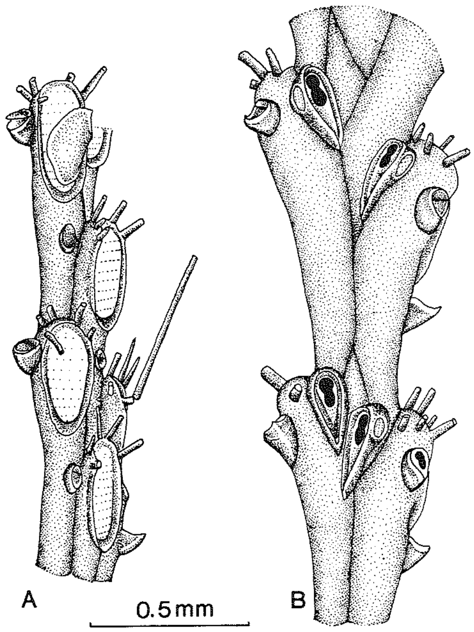


Fig. 3. *Amastigia* cf. *nuda*. A, part of an internode in oblique lateral view; B, basal view to show avicularia, and partial exclusion of middle series of zooids.

elongate avicularia with slender, triangular mandibles; situated at the proximal end of each marginal zooid, directed medio-proximally. A tubular rhizoid arises from the cystid of each basal avicularium, traversing the outer edge of the basal surface of the colony. Ovicells not present.

The arrangement of the zooid rows, such that the median row is partly but not wholly excluded from the basal surface, the form of the basal heterozooid and the development of the oral spines, in this specimen, are all characteristic of the South Atlantic-Subantarctic species, *Amastigia nuda* Busk. However, the "Galathea" material was fragmentary, comprising a portion of a colony just 1.6 cm in length. The frontal surfaces of the specimen were damaged and thus some doubt must be allowed in identifying it with *A. nuda*.

Measurements	n	$\bar{x}$	Sd
Length of zooid, mm	10	0.75	± 0.03
Width of zooid, mm	10	0.18	± 0.01

Genus *Menipea* Lamouroux, 1812

Colony erect, branching, jointed or unjointed, attached by bundles of rhizoids. Branches unilaminar, biserial to pluriserial; bifurcations of Types 17 or 18 (Harmer 1923). Zooids with oval opesiae, typically with well developed cryptocyst. Distal oral spines present, scutum absent. Frontal and marginal avicularia present or absent, basal heterozooids typically absent.

Menipea ignota n. sp.

Fig. 4A-C

Holotype:
St. 665. Kermadec Trench (36°38'S, 178°21'E), 2470 m.

Description: Colony cup-shaped, formed of short bifurcating branches up to 6 mm long radiating from a tangle of rhizoids; branches biserial and unilaminar, frontal surfaces facing outwards. Zooids rather quadrate, the frontal planes of the two series forming an acute angle. Opesiae overlapping; oval, longer than wide, comprising about half total zooid length. Cryptocyst well developed, granular, forming a flared rim around the opesia. Distal end of zooid truncate, with a short cylindrical spine at each angle. Ovicell elliptical, longer than wide, imperforate; recumbent on succeeding zooid and tilted basally, closed by zooidal operculum. No avicularia.

The rhizoids develop on the basal surface of the colony as a series of interconnected kenozooids, some of which may bear small opesiae. They are lightly calcified, often very large, and appear to play an important role in colony construction. The axial kenozooids (Fig. 4C) seem to be a constant feature. The rhizoids fuse basally with those of other branches of the colony, imparting a certain rigidity to the whole.

The pattern of zooids at a bifurcation is not easily observed because of the profusion of basal kenozooids. The branches are unjointed and the bifurcation seems to approximate to Type 17 (Harmer 1923), with zooids C and D mostly proximal to the axil.

The pattern of zooids at bifurcations, the lack of basal, frontal and marginal avicularia, and the well developed cryptocyst govern the inclusion of this species in *Menipea* Lamouroux. Several species of *Menipea* are characteristically unjointed, but the fact that these are almost all pluriserial, and have a

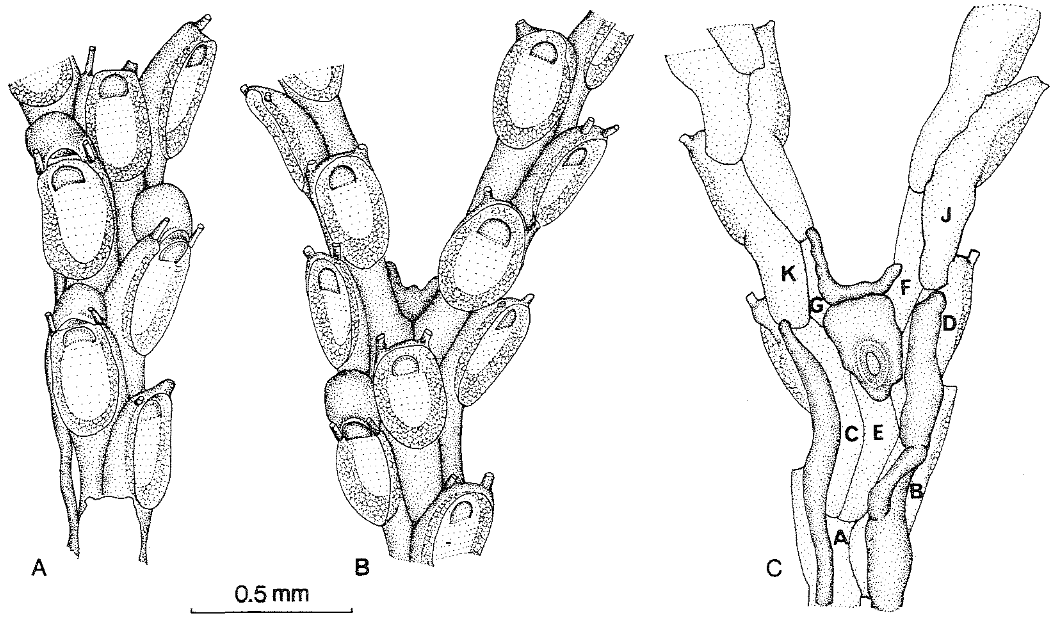


Fig. 4. *Menipea ignota* n. sp. A, part of a branch, including ovicellate zooids; B, frontal view of a dichotomy; C, basal view of a dichotomy; notation of zooids after Harmer (1923).

variety of avicularia, is sufficient to distinguish them from the present species.

Measurements	n	$\bar{x}$	Sd
Length of opesia, mm	10	0.41	0.02
Width of opesia, mm	10	0.24	0.01

Family EUOPLOZOIDAE Harmer, 1926

Genus *Euoplozoum* Harmer, 1923

Colony erect, branching, jointed, attached by bundles of rhizoids. Branches incurled, biserial and unilaminar. Zooids expanded distally, the frontal surfaces largely membranous. Avicularia present, of two types, often gigantic. Ovicell grossly enlarged, borne on a modified zooid.

Euoplozoum cirratum (Busk)

Pl. 5A-B

Cellularia cirrata Busk, 1884: 17, pl. 2, figs 4-4b.
Euoplozoum cirratum, Harmer 1926: 391, pl. 30, figs 1-4.

Material:
St. 281. Seychelles-Ceylon (3°38'N, 78°15'E), 3310 m.

Description: Zooids in two alternating, longitudinal series; elongate, each composed of a tubular proximal portion and an expanded distal portion, the frontal surface of the latter entirely membranous. Distal end of each zooid produced medially into a short, blunt spike. A sessile avicularium present on the outer distal angle of each zooid, of variable size, often gigantic; rostrum perpendicular to long axis of branch, hooked, bearing a trinagular mandible. Pedunculate avicularia sporadically developed throughout colony, attached to inner lateral walls of zooids, variable in size, rostrum sharply hooked, mandible triangular. Gonozooid very conspicuous, grossly expanded distally to form a broad, deep structure supporting a gigantic globular ovicell; distal portion of gonozooid, including ovicell, 1.3 mm long with maximum width of 0.9 mm.

Measurements	n	$\bar{x}$	Sd
Length of zooid, mm	10	1.35	± 0.08
Width of zooid, mm	10	0.36	± 0.06

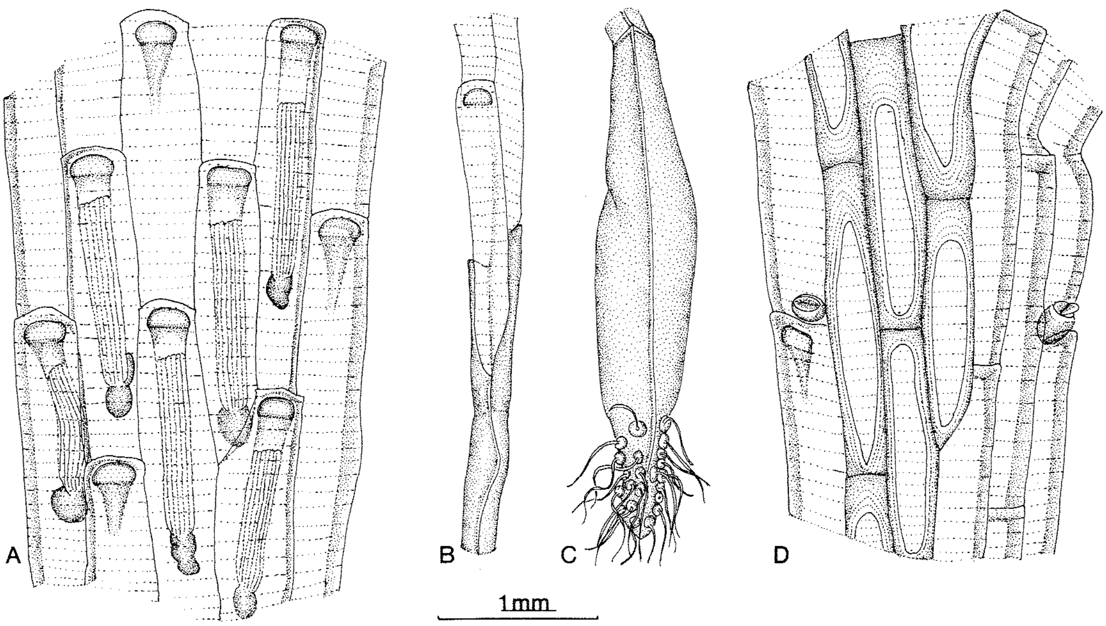


Fig. 5. *Farciminellum hexagonum* (Busk). A, frontal surface of a branch (St. 574); B, proximal region of a colony, to show first zooids (St. 182); C, the ancestrula (St. 182); D, basal surface of a branch; central kenozooids with cryptocystal calcification (St. 574).

Family FARCIMINARIIDAE Busk, 1884

Genus *Farciminellum* Harmer, 1926

Colony erect, slender, flexible, secured by numerous rhizoids; bilaminar, branching dichotomously at irregular intervals, unjointed. Branches differentiated into two distinct surfaces, a frontal surface of autozooids and a basal surface largely composed of kenozooids. Zooids in three to eight longitudinal series. Spines, avicularia and ovicells present or absent.

Farciminellum hexagonum (Busk)

Fig. 5A-D, Pl. 5C

Farciminaria hexagona Busk, 1884: 51, pl. 14, fig. 10; pl. 31, figs 3-3b.

Farciminellum hexagonum, Harmer 1926: 405, pl. 18, figs 8-10.

Material:

St. 182. Cape Town-Durban (33°28'S, 38°32'E), 5110-5340 m.

St. 194. Off Durban (34°09'S, 30°45'E), 4360 m.

St. 453. Makassar Strait (3°56'S, 118°26'E), 2000 m.

St. 574. Tasman Sea (39°45'S, 159°39'E), 4670 m.

St. 601. Tasman Sea (45°51'S, 164°32'E), 4400 m.

St. 663. Kermadec Trench (36°31'S, 178°38'W), 4410 m.

St. 664. Kermadec Trench (36°34'S, 178°57'W) 4540 m.

Description: Zooids elongate, rectangular, 1.4–2.5 mm long by 0.3-0.5 mm wide; frontal surface composed of four to eight longitudinal series of autozooids, basal surface with a single series of autozooids on each margin, the central rows being of kenozooids only. Autozooids with entirely membranous frontal walls, kenozooids developing a granular cryptocyst. Sessile avicularia present sporadically, situated at the inner proximal angle of marginal zooids only, on both surfaces of the colony; mandibles semicircular. Ovicells absent, embryos brooded in enlarged autozooids on the frontal surface of the colony.

Juvenile specimens from St. 182 show the early astogenetic stages of the colony. Each colony arises from a membranous sac, presumably turgid when alive, with a lightly calcified longitudinal rod on one surface. Proximally, the sac bears numerous short curling rhizoids, each developed from a small blister-like structure and perhaps representing a single kenozooid. The distal limit of the sac is marked by a calcified transverse septum. The longitudinal rod extends beyond the septum through the slender proximal part of the colony; here it is continuous with the conjoined basal walls of the first zooids of the colony, which are in two or three alternating longitudinal series. The smallest colonies consist of four longitudinal zooid rows, imparting a rectangular section to the branch, but the rows divide regularly towards the distal tips of the colony and the branch broadens rapidly.

Farciminellum hexagonum has been reported from the Marion Islands, the eastern Indian Ocean and the Malay Archipelago.

Genus *Columnella* Levinsen, 1914

Colony erect, branching dichotomously, slender and lightly calcified; formed from four longitudinal series of zooids, each constituting one facet of a square sectioned branch. Zooids elongate, typically with a small gymnocyst, cryptocyst absent. Avicularia adventitious, developed on the proximal frontal wall. Spines absent. Ovicell hyperstomial, large and globular.

Columnella magna (Busk)

Fig. 6A-B

Farciminaria magna Busk, 1884: 49, pl. 5, fig. 1.
Columnella magna, Hayward & Cook 1979: 67, fig. 9A.

Material:
St. 182. Cape Town-Durban (33°28'S, 38°32'E), 5110-5340 m.
St. 192. Off Durban (32°00'S, 32°41'E), 3430 m.
St. 193. Off Durban (32°34'S, 31°52'E), 3680 m.
St. 194. Off Durban (34°09'S, 30°45'E), 4360 m.
St. 200. Off Natal (29°39'S, 37°01'E), 5110 m.
St. 233. Madagascar-Mombasa (7°24'S, 48°24'E), 4730 m.
St. 234. Madagascar-Mombasa (5°25'S, 47°09'E), 4800 m.
St. 238. Off Kenya (3°23'S, 44°04'E), 3980 m.
St. 668. Kermadec Trench (36°23'S, 177°41'E), 2640 m.

Description: Zooids elongate, quadrangular, 1.4-1.7 mm long by about 0.45 mm broad; vertical walls thin, opaque, visible through the membranous frontal wall, thickened at their free edges in older zooids to form a calcified rim around the frontal membrane. Operculum subterminal with a brown, peripheral chitinous sclerite. A single, small avicularium may be present at the proximal end of the frontal surface of the zooid, globular or egg-shaped with a semicircular mandible orientated perpendicularly to the frontal plane. Ovicell prominent, globose, broader than long, recumbent upon the succeeding zooid, closed by the

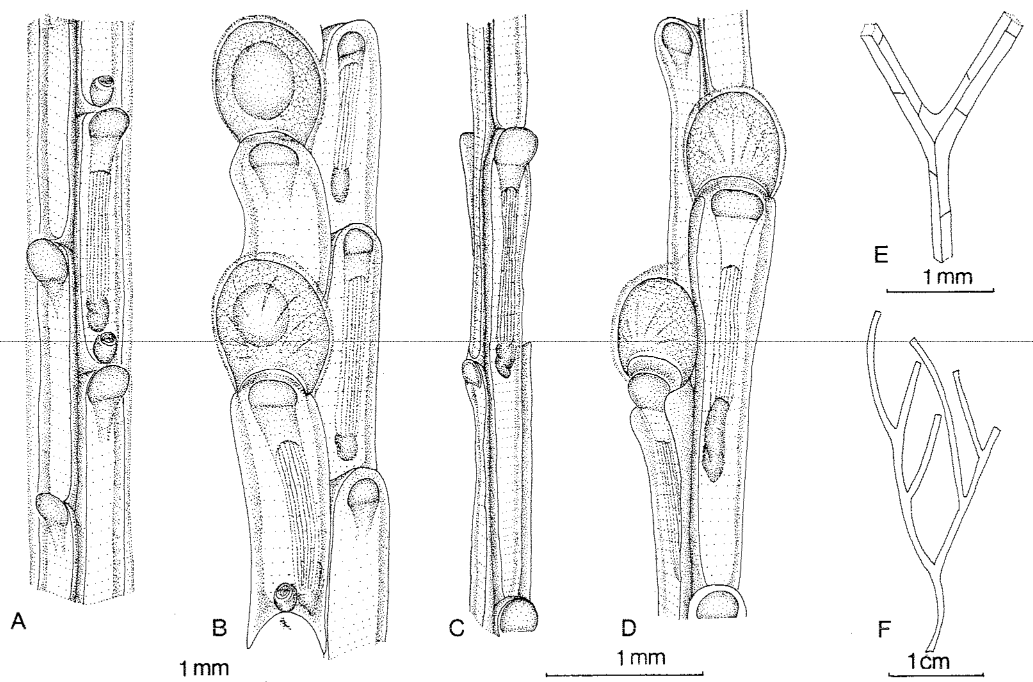


Fig. 6. A-B, *Columnella magna* (Busk). A, portion of a branch, including two zooids with adventitious avicularia; B, ovicellate zooids. C-F, *Columnella delicatissima* (Busk). C, portion of a branch (St. 233); D, ovicellate zooids (St. 238); E, diagram to show pattern of zooids at a bifurcation (St. 238); F, outline drawing to show colony form (St. 233).

operculum of the brooding zooid; ectooecium membranous, entooecium thinly calcified, white and opaque, with a finely granular surface marked by faint radiating striations or creases.

Columnella magna is the largest of the species of this genus recorded here. Much of the material was fragmentary, but the largest fragments were up to 12.3 cm long. Bifurcations were spaced between 1.8 and 2.6 cm apart, and the distalmost rami were up to 5.5 cm long. This species has been reported from the North and South Atlantic, and from the western Indian Ocean (Hayward & Cook 1979); the record from "Galathea" St. 668 marks a significant extension of its known geographical range.

Columnella delicatissima (Busk)
Fig. 6C-F

Farciminaria delicatissima Busk, 1884: 51, pl. 31, fig. 5.

Material:
St. 233. Madagascar-Mombassa (7°24'S, 48°24'E), 4730 m.
St. 238. Off Kenya (3°23'S, 44°04'E), 3960 m.
St. 241. Off Kenya (4°00'S; 41°27'E), 1510 m.

Description: Zooids very elongate, 2.0-2.9 mm long by about 0.4 mm broad; proximal ends truncate, distal ends gently rounded, vertical walls lightly calcified, frontal surface entirely membranous. Orifice subterminal, operculum distinct, with a brown, chitinous peripheral sclerite. Avicularia absent. Ovicell prominent, globose, scarcely longer than wide, entooecium with fine surface granulations and a few radiating striations.

The very elongate zooids, and the absence of avicularia, serve to distinguish this species from all other species of *Columnella*. Colonies tend to be relatively small, not exceeding 4.5 cm in the present material, and the distance between bifurcations is also short, ranging from 0.6 cm in the basal parts of the colony to 3.0 cm towards the distal end.

C. delicatissima was described by Busk (1884) from six widespread localities in the North Atlantic, between 3383 m and 4389 m.

Columnella graminea n. sp.
Fig. 7A-C

Holotype:
St. 182. Cape Town-Durban (33°28'S, 38°32'E), 5110-5340 m.

Other Material:
St. 200. Off Natal (29°39'S, 37°01'E), 5110 m.
St. 233. Madagascar-Mombasa (7°24'S, 48°24'E), 4730 m.
St. 241. Off Kenya (4°00'S, 41°27'E), 1520 m.
St. 281. Seychelles-Ceylon (3°38'N, 78°15'E), 3310 m.

Description: Zooids rectangular, distal ends distinctly rounded and rather prominent, 1.2-1.4 mm long by about 0.3 mm broad. Frontal surface with a small triangular area of calcification in each proximal corner; orifice subterminal, operculum with a conspicuous brown peripheral sclerite. No avicularia. Ovicells globose, prominent, longer than wide; entooecium with a finely tessellated surface.

Columnella graminea is distinctly smaller than all other species of the genus. The colony is typically short and bushy; few of the hundred or more specimens obtained exceeded 4 cm in height, and the distance between bifurcations was mostly less than 1 cm. The small size of the zooids, the absence of avicularia, and the narrow, elongate ovicells further serve to distinguish this species from other described species of *Columnella*. Numerous specimens were obtained, the sample from St. 182 comprised more than 100 colonies; embryos were present in the specimens from Sts 182, 200 & 233.

Columnella accincta n. sp.
Fig. 7D-F

Holotype:
St. 194. Off Durban (34°09'S, 30°45'E), 4360 m.

Description: Zooids rectangular, rounded distally, 1.5-1.8 mm long by about 0.4 mm broad. Vertical walls well calcified and distinct, forming a thin rim around the frontal membrane, flared distally in fertile zooids. Frontal surface with a small triangular area of calcification in each proximal corner; orifice subterminal, operculum with a thickened peripheral sclerite. A relatively large sessile avicularium at the proximal end of the frontal surface, occupying at least half of the total zooid width; mandible semicircular, perpendicular to frontal plane. Ovicell globose, prominent, slightly longer than wide, with a rim around the orifice; entooecium with a coarsely tuberculate surface.

C. accincta is most similar to *C. magna*, in particular the zooids are of comparable dimensions in both species. However, the colony of *C. accincta* is

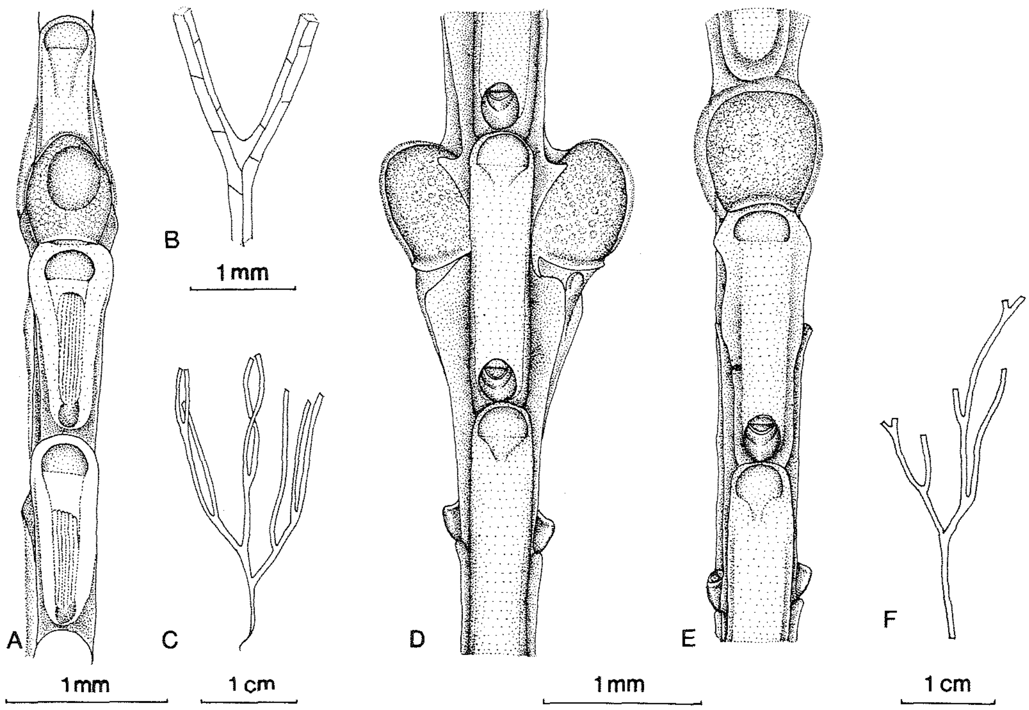


Fig. 7 A-C, *Columnella graminea* n. sp. A, portion of a branch, including an ovicellate zooid (St. 182); B, diagram to show pattern of zooids at a bifurcation (St. 193); C, outline drawing to show colony form (St. 182). D-F, *Columnella accincta* n. sp. D, portion of a branch, including two ovicellate zooids; E, an ovicellate zooid in frontal view; F, outline drawing to show colony form.

relatively small, none of the specimens obtained was greater than 4.4 cm long; the distance between bifurcations is also smaller than that observed in *C. magna,* ranging from 0.5 cm at the base of the colony to 2 cm at the distal end. The avicularium of *C. accincta,* together with the coarsely tuberculate ovicell, readily distinguishes it from other species of *Columnella.*

Family BICELLARIELLIDAE Levinsen, 1909

Genus *Cornucopina* Levinsen, 1909

Colony erect, branching dichotomously, unjointed; secured by bundles of rhizoids. Zooids in two longitudinal series, club-shaped, the slender proximal portions forming the main axis of the branch, the oval distal portion projecting at right angles to the axis, in alternating series. Disto-basal portion of zooid produced as a slender, tubular process, typically bearing few or many long spines along one edge. Avicularia pedunculate. Ovicell prominent, globose.

d'Hondt (1975) produced a key to the species of *Cornucopina,* together with notes on the geographical and bathymetrical distributions of the 17 species known.

Cornucopina collatata **n. sp.**
Fig. 8A-B

Holotype:
St. 281. Seychelles-Ceylon (3°38'N, 78°15'E), 3310 m.

Description: Opesia of zooid 0.6 mm long, distinctly rounded proximally and not extending onto the axis of the colony. Distal process very long, up to 1.5 mm; bearing five or six long spines, usually three or four in a group towards the tip and one or two spaced along its length. Additionally, up to three spines may be present along the dorsal surface of the zooid. Avicularium small, attached to the lower lateral wall of the zooid adjacent to the orifice. Ovicell typical of genus, prominent, elongate, with a frontal lip and fine longitudinal striations.

C. collatata is distinguished principally by the length of the spine-bearing distal process, by the proximally rounded opesia, and by the position of the avicularium, which in other species with similar, long, distal processes is situated close to the colony axis.

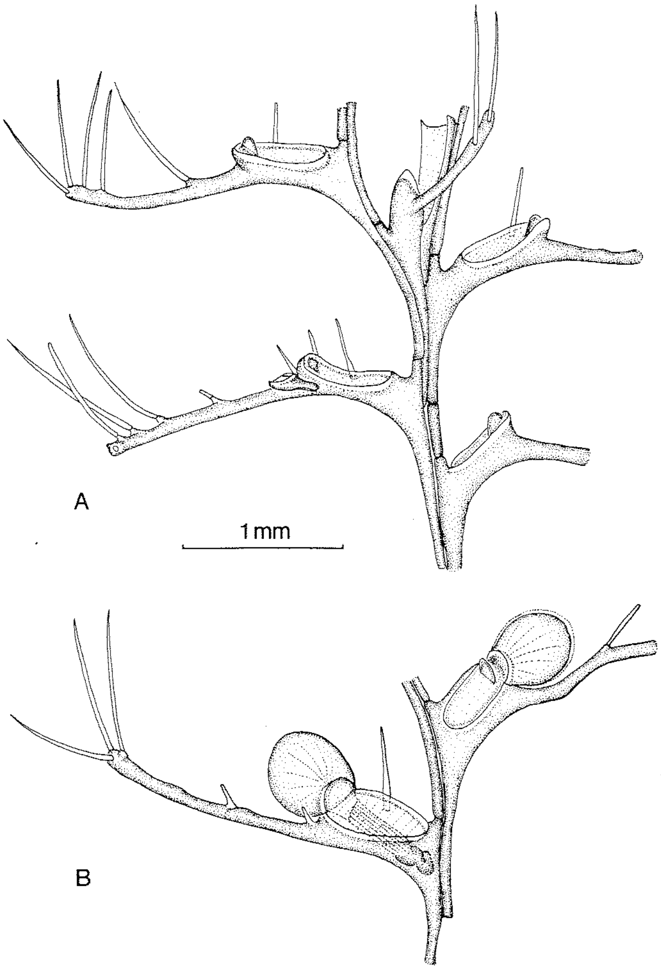


Fig. 8. *Cornucopina collatata* n. sp. A, portion of a colony at a bifurcation, note avicularium on the lowest, left hand zooid; B, two ovicellate zooids.

Cornucopina novissima n. sp.

Fig. 9A-B

Holotype:
St. 186. Cape Town-Durban (32°33'S, 32°01'E), 3620 m.

Other Material:
St. 194. Off Durban (34°09'S, 30°45'E), 4360 m.

Description: Opesia of zooid 0.7-0.85 mm long, angular proximally and extending onto the axis of the colony. Distal process longer than opesia, up to 1.1 mm, with four or five (rarely six) very long spines equally spaced along its distal half; a single, very short, spine present dorsally, close to the axis of the colony. Avicularium very small, situated on the lower lateral wall of the zooid close to the axis. Ovicell typical of genus.

The shape of the opesia and the position of the avicularium in this species correspond most nearly to *C. angulata* (Kluge). However, the latter species has a very short distal process bearing equally spaced spines along its whole length. These three characters, together, are sufficient to distinguish *C. novissima* from other species of *Cornucopina.*

Cornucopina nupera n. sp.

Fig. 10A-B

Holotype:
St. 182. Cape Town-Durban (33°28'S, 38°32'E), 5110-5340 m.

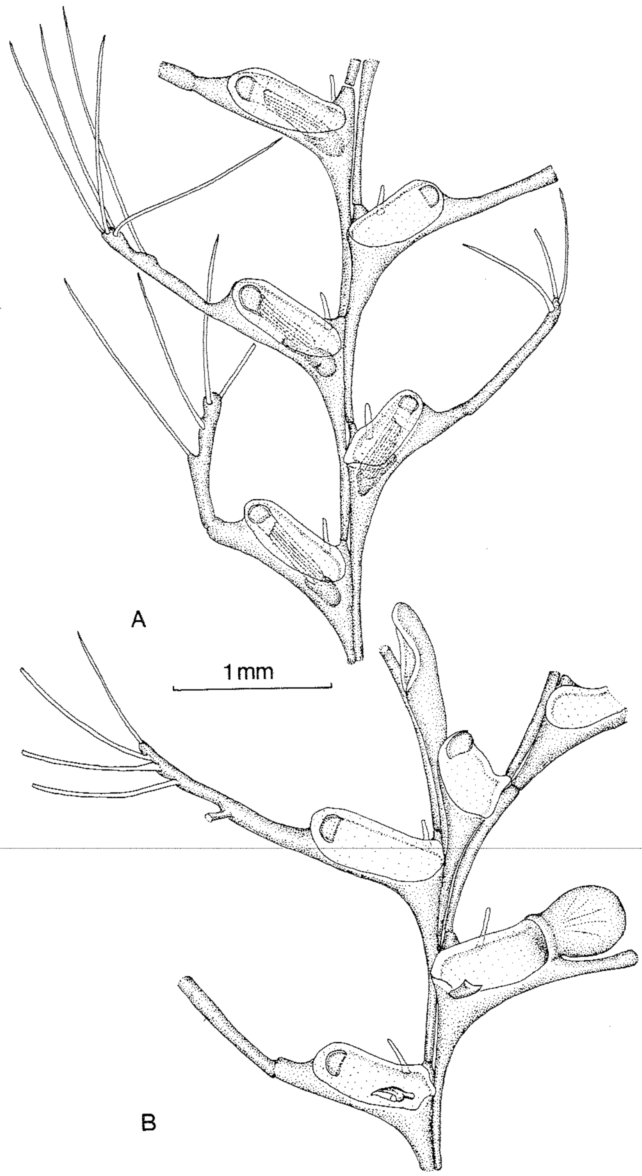


Fig. 9. *Cornucopina novissima* n. sp. A, portion of a branch; B, part of a colony at a bifurcation, including an ovicellate zooid; the avicularium of the lowest zooid is detached, lying on the frontal membrane.

Description: Opesia of zooid 0.75-0.85 mm long, angular proximally and extending onto the axis of the colony. Distal process about the same length as the opesia with four to eight spines, two or three closely grouped at the distal end and the rest spaced along its length. A single short spine present on the dorsal side of the zooid, close to the axis. Avicularium relatively large, situated on the dorsal side of the zooid, almost at the axis. Ovicell typical of genus.

The avicularium of this species, its position and size, is very similar to that of *C. rotundata* (Kluge). The latter species, however, is characterized by a relatively short, rounded opesia and a distal process proportionately longer than that of *C. nupera.*

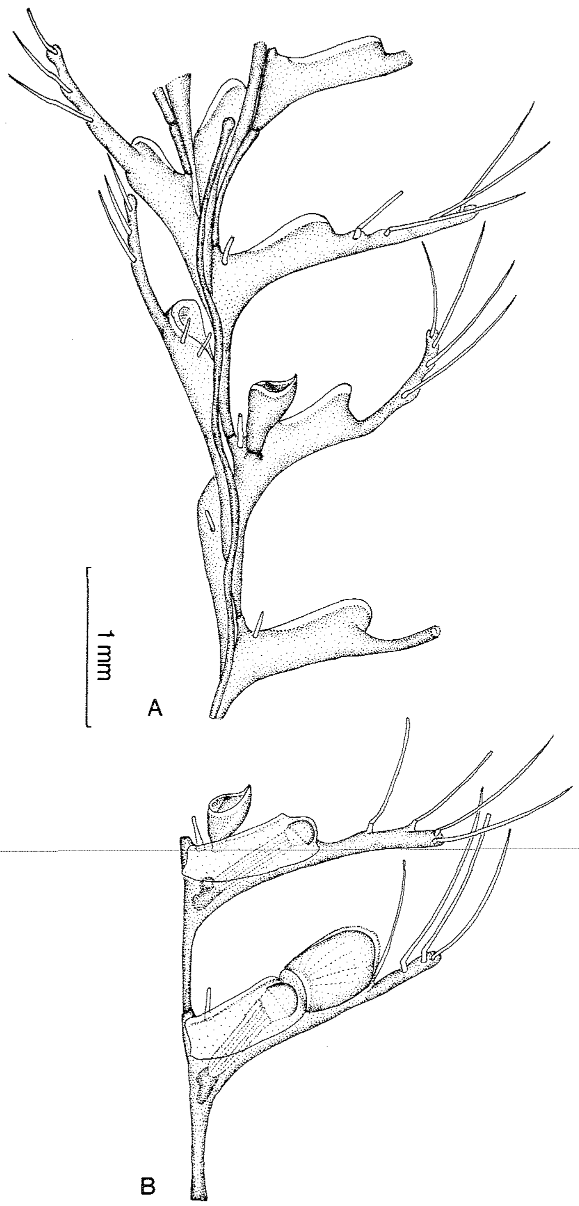


Fig. 10. *Cornucopina nupera* n. sp. A, portion of a colony at a bifurcation, viewed basally to show attachment of avicularium; B, part of a branch including an ovicellate zooid.

Genus *Camptoplites* Harmer, 1923

Colony erect, branching dichotomously, unjointed; secured by a bundle of rhizoids. Zooids in two or more longitudinal series; broadened distally, tapered proximally, with a well developed gymnocyst. Spines present or absent. Avicularia pedunculate, on long flexible stalks, usually occurring in several distinct forms in each species.

Camptoplites bicornis (Busk) var. 1
Fig. 11A-D

Material:
St. 654. Kermadec Trench (32°10'S, 175°54'W), 5850-5900 m.

Description: Zooids in two overlapping longitudinal series, distal ends truncated, with rounded corners, and projecting from the long axis of the branch; 1.6-1.8 mm long. Frontal membrane occupying about one-third of the total zooid length. Avicularia of two sizes, corresponding to the large and small long-headed types of Hastings (1943), attached by flexible stalks to the frontal surface of the zooids, immediately proximal to the frontal membrane; rostrum of the smaller type practically straight, that of the larger gently downcurved, with a bluntly rounded tip. Ovicell dorsally situated, helmet-shaped, occupying the entire width of the brooding zooid, up to 0.6 mm long; entooecium thinly calcified, with distinct longitudinal striations.

Up to three avicularia may occur on each zooid; when more than one is present they may be of different types, but this is not an invariable rule and three of the small type were observed attached to a single zooid. Secondary branches (Hastings 1943) occur in this species. These develop when a single zooid buds from the dorsal surface of a zooid of the main branch, just before or after a bifurcation, or from one of the zooids at a bifurcation, and initiates an additional branch independent of the usual dichotomous arrangement.

Numerous fragments of this species, probably representing a single large colony, were obtained from St. 654. Many of the ovicells contained embryos. The different varieties of *Camptoplites bicornis* (Busk), described and figured by Hastings (1943), are characterized by the size and incidence of the stalked avicularia. Although clearly belonging to the *C. bicornis* group, the present material differs from the typical *C. bicornis* in having truncate distal ends to the zooids, and from the four varieties described by Hastings (1943) in lacking the round-headed type of avicularia. A further distinction lies in the large long-headed avicularium, which in all known varieties of *C. bicornis* has a markedly curved and sharply pointed rostrum.

Measurements	n	$\bar{x}$	Sd
Length of large avicularia, mm	10	0.69	± 0.01
Length of small avicularia, mm	10	0.30	± 0.02

Camptoplites bicornis (Busk) var. 2

Fig. 11E-H

Material:

St. 665. Kermadec Trench (36°38'S, 178°21'E), 2470 m.

Description: Zooids in two overlapping longitudinal series, distal ends truncate with acute corners, occasionally produced as short spines, projecting from the long axis of the branch; 1.2-1.4 mm long. Frontal membrane occupying about two-thirds of total zooid length. Avicularia of three kinds, corresponding to the large and small long-headed, and the short round-headed types of Hastings (1943). Rostrum of large long-headed avicularium sharply hooked, that of small long-headed type almost straight; both types show a thick digitiform process projecting from the palate when the mandible is open. Round-headed avicularia with very short hooked rostrum. Ovicells not observed. Secondary branches present (Hastings 1943).

The specimens obtained from St. 665 differed clearly from those collected at St. 654, assigned to *C. bicornis* var. 1, in having smaller zooids, with acute distal corners, and in the size and type of avicularia present. However, as in the case of the latter, these specimens could not be assigned with confidence to any of the varieties of *C. bicornis* described by Hastings (1943).

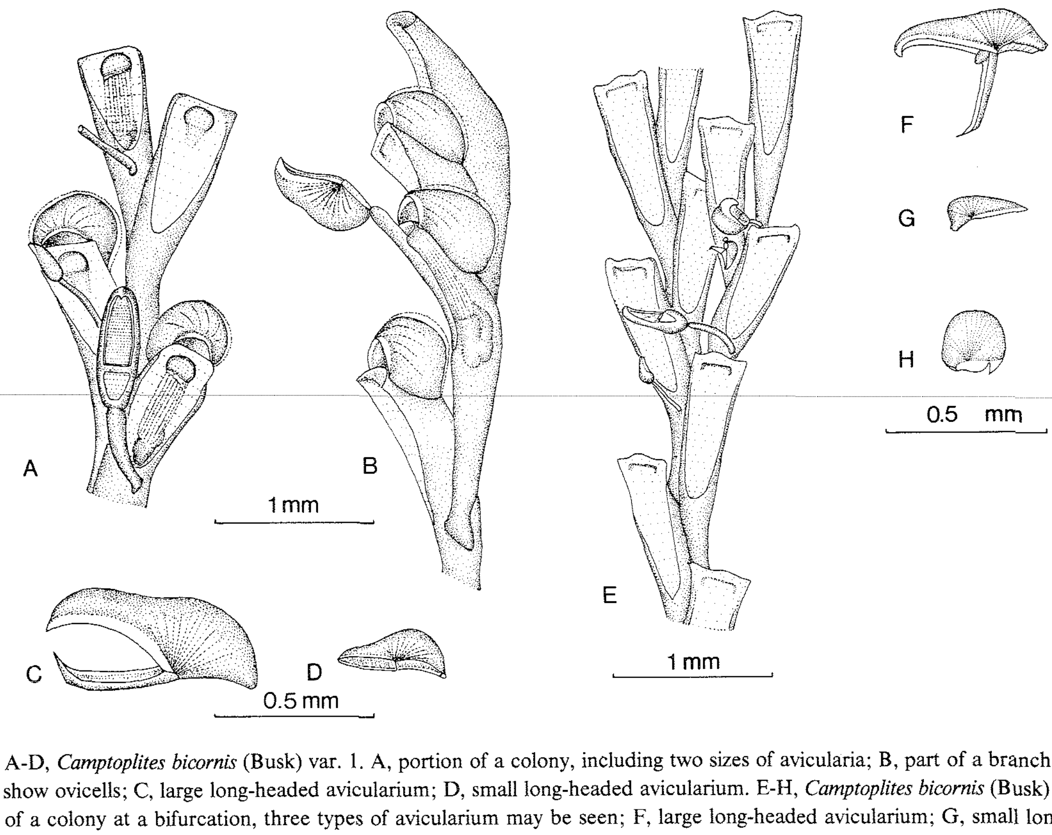


Fig. 11. A-D, *Camptoplites bicornis* (Busk) var. 1. A, portion of a colony, including two sizes of avicularia; B, part of a branch in lateral view to show ovicells; C, large long-headed avicularium; D, small long-headed avicularium. E-H, *Camptoplites bicornis* (Busk) var. 2. E, portion of a colony at a bifurcation, three types of avicularium may be seen; F, large long-headed avicularium; G, small long-headed avicularium; H, round-headed avicularium.

Measurements	n	$\bar{x}$	Sd
Length of large long-headed avicularium, mm	10	0.43	± 0.01
Length of small long-headed avicularium, mm	10	0.21	± 0.01

Camptoplites lunatus Harmer
Fig. 12A-B

Camptoplites lunatus Harmer, 1926: 452, pl. 34, figs 5-8.

Material:
St. 281. Seychelles-Ceylon (3°38'N, 78°15'E), 3310 m.

Description: Zooids in two longitudinal series, strictly alternating to give the impression of a monoserial branch; very elongate, 1.8-2.0 mm long, comprising a slender, tubular proximal half, expanding to form a triangular or oval distal half bearing the frontal membrane. Distal end of zooid truncate, with acute or bluntly rounded corners, the outer bearing a jointed tubular spine of variable length. A short spine (rarely two) also present dorsally at the distal end of the zooid; may be replaced by a tubular cross - connection linking different branches of the colony. Avicularium attached immediately proximal to the frontal membrane, relatively small with a semicircular profile; rostrum downcurved with a finely hooked tip. Ovicell hyperstomial, very distinctive; up to 0.7 mm long by 0.4 mm broad, with a well marked frontal lip, entooecium with longitudinal striations.

Described by Harmer (1926) from Timor, *C. lunatus* was later reported from the Crozet Islands by Hastings (1943). A single colony was recovered from "Galathea" St. 281, the zooids were somewhat larger than those of the type specimen (which ranged between 1.3 and 1.5 mm) but in other respects it was identical to that of Harmer. The "Challenger" specimen discussed by Hastings (1943) has zooids with an identical size range to those of the present material.

Measurements	n	$\bar{x}$	Sd
Length of avicularium mm	12	0.19	± 0.009

Camptoplites sp. 1
Fig. 12C-F

Material:
St. 716. Acapulco-Panama (9°23'N, 89°32'W), 3570 m.

Description: Zooids in two overlapping longitudinal series, 1.5-1.9 mm long, distal one-third projecting from long axis of colony. Distal end of zooid truncate, with acute corners frequently produced as short spines, narrowed proximally; frontal membrane occupying about two-thirds of total zooid length. Avicularia of two types, large and small long-headed (Hastings 1943), both with a hooked rostrum. Ovicells not present.

Dead fragmentary material of this species was obtained from St. 716. Although clearly allied to the *C. bicornis* (Busk) group, its identity remains in doubt as the specimens were too poorly preserved to allow a complete description.

Camptoplites sp. 2
Fig. 12G-H

Material:
St. 188. Off Durban (29°55'S, 31°13'E), 440 m.

Description: The specimen comprised the basal rootlets and first zooids of an unrecognized, biserial, species of *Camptoplites*. The zooids, which were from 1.2 to 1.4 mm long, appeared damaged and nothing can be said of their morphology. Two sizes of small round-headed avicularia were present, both with a curved and sharply pointed rostrum.

Genus *Kinetoskias* Daniellsen, 1868

Colony erect, comprising an elongate kenozooidal peduncle supporting a cup-shaped crown of slender, unilaminar branches. Zooids typically in two longitudinal series, lightly calcified, with an entirely membranous frontal surface. Avicularia pedunculate, attached to the outer lateral walls of the zooids. Ovicells present.

Most of the known species of this typically abyssal genus are described by Harmer (1926) and Kluge (1962, 1975). Their single most unusual feature is the presence of a bundle of muscles in each zooid, originating from the proximal wall and inserting on the frontal membrane, which on contraction cause

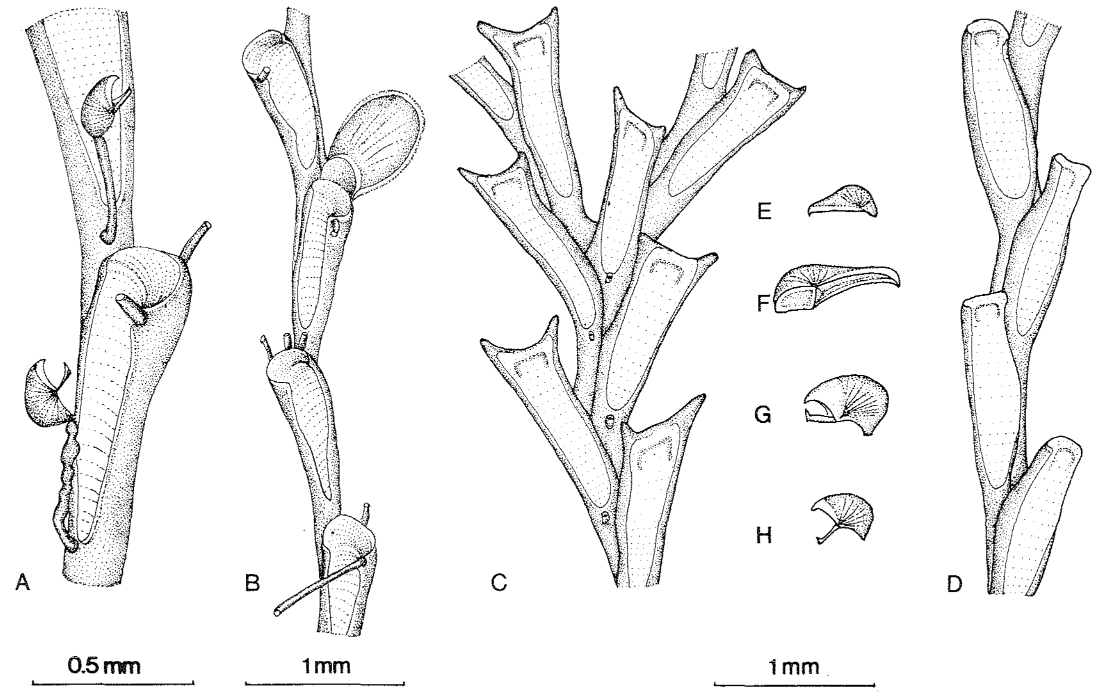


Fig. 12. A-B, *Camptoplites lunatus* Harmer. A, parts of two zooids, with avicularia; B, portion of a branch, including an ovicellate zooid. C-F, *Camptoplites* sp. 1. C, portion of a colony at a bifurcation, the zooids with well developed distal processes; D, part of a branch from the proximal region of the colony; E, small long-headed avicularium; F, large long-headed avicularium. G-H, *Camptoplites* sp. 2. G, large round-headed avicularium; H, small round-headed avicularium.

the branches of the colony to curl inwards. These muscles were termed "flexor zooecii" by Harmer (1926).

Kinetoskias cyathus (Wyville Thomson)

Fig. 13A

Naresia cyathus Wyville Thomson, 1873: 142.
Kinetoskias cyathus, Busk, 1884: 44, pl. 8, fig. 1.

Material:
St. 182. Cape Town-Durban (33°28'S, 38°32'E), 5110-5340 m.
St. 194. Off Durban (34°09'S, 30°45'E), 4360 m.

Description: Zooids broadly linguiform, somewhat sinuate, 0.75-0.85 mm long by 0.35 mm broad; distal ends rounded, external angles produced as short spines. Avicularium attached to outer lateral wall, on proximal half of zooid; wall slightly recessed above point of attachment. Ovicells not present.

This species was described from two localities, in the North and South Atlantic.

Kinetoskias pocillum Busk

Fig. 13B

Kinetoskias pocillum Busk, 1881: 7, pl. 1, figs 2,5; Hastings 1943: 433.

Material:
St. 188. Off Durban (29°55'S, 31°13'E), 440 m.

Description: Zooids linguiform, rounded distally, slightly asymmetrical but without an external distal spine; 0.9-1.0 mm long by 0.35 mm wide. Avicularium situated on the outer lateral wall of the zooid, about halfway along its length. Ovicell globular, attached to the inner distal border of the zooid, entooecium distinctly striated; embryos present.

K. pocillum was described by Busk (1881) from two widely separated localities: at 3953 m off Valparaiso, and at 59-732 m off Brazil.

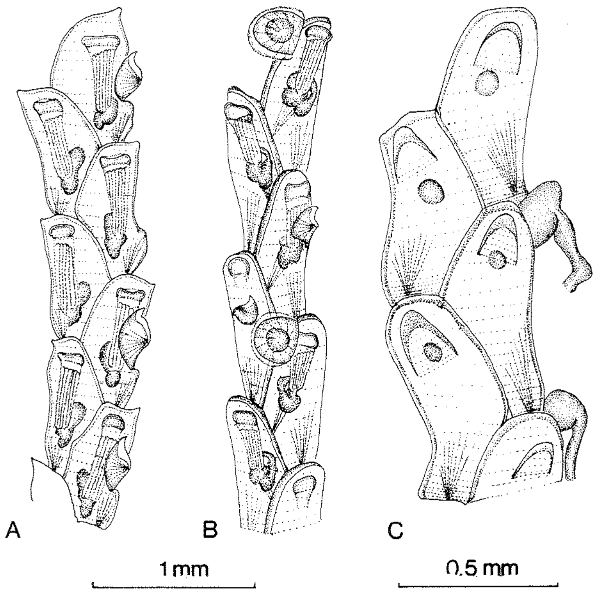


Fig. 13. A, *Kinetoskias cyathus* (W. Thomson). B, *Kinetoskias pocillum* Busk. C, *Kinetoskias* sp.

***Kinetoskias* sp.**
Fig. 13C

Material:
St. 716. Acapulco-Panama (9°23'N, 89°32'W), 3570 m.

Description: The material comprised several fragments of an erect, biserial, unilaminar anascan. It was dead and poorly preserved, but distinct "flexor zooecii" muscles and cylindrical kenozooids attached to the distal ends of some zooids show this to be a species of *Kinetoskias*. The small size of the zooids (0.55×0.3 mm) and a very elongate operculum distinguish it from other known species, but its condition prevents an adequate description; consequently it is merely assigned to the genus.

Genus *Bugulella* Verrill, 1879

Colony erect, delicate, branching dichotomously composed of a single linear series of zooids. Bifurcations characteristic (Fig. 14A). Zooids elongate, with a narrow cryptocyst, and thin marginal spines. Two rosette plates present in each lateral wall. Ovicell prominent, with scattered pores. Avicularia pedunculate.

***Bugulella australis* Hayward & Cook**
Fig. 14A-B

Erymophora sp. Hastings 1943: 469, fig. 56.
Bugulella australis Hayward & Cook 1979: 64, fig. 6A-B.

Material:
St. 626. Tasman Sea (42°10'S, 170°10'E), 610 m.

Description: Colony forming diffuse tangled clumps. Zooids slender, club-shaped, a tubular proximal portion broadening to an oval distal portion bearing the opesia; 0.78-1.06 mm long. A narrow cryptocyst present, surrounded by eight to ten thin spines, the distal pair erect, the rest incurved over the opesia. Ovicell hyperstomial, globular, with a finely tessellated surface and a few small, indistinct pores. Avicularia pedunculate, attached to the disto-basal

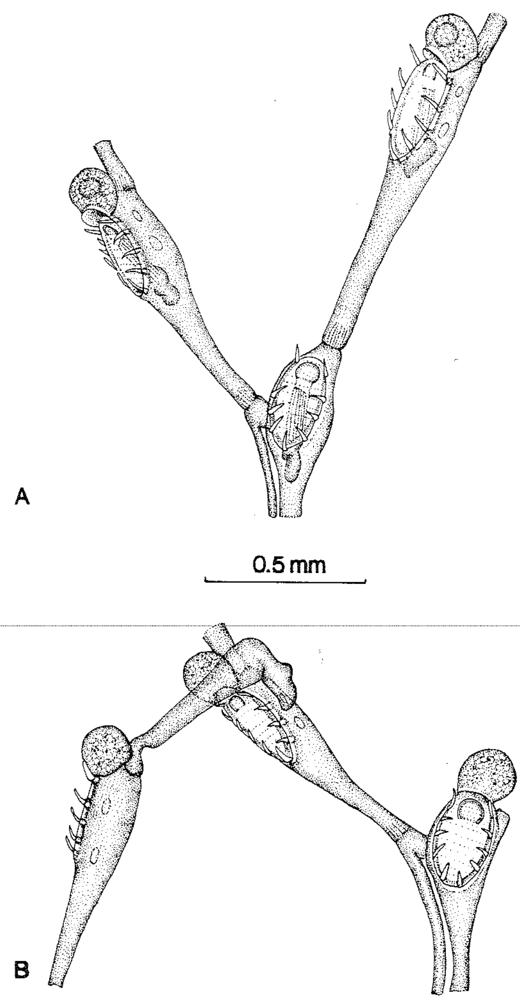


Fig. 14. *Bugulella australis* Hayward & Cook. A, part of a colony at a bifurcation; B, portions of two colonies, linked by at kenozooid.

wall of the zooid, with a short, hooked rostrum and triangular mandible; generally infrequent and absent from many zooids.

Formerly known only by fragmentary material from an unknown locality (Hastings 1943), this species was subsequently reported by Hayward & Cook (1979) from four localities off the eastern coasts of South Africa, between 376 m and 750 m, mostly attached to sponges or other bryozoans. The "Galathea" material comprised a large sample, of perhaps several dozen colonies, with no indication of substratum or method of attachment to the substratum. However, an indication of how such a mass may stabilize itself was shown by two specimens (Fig. 14B), apparently representing distinct colonies. The terminal bud of one branch had produced a tubular kenozooid which was attached to the distal lateral rosette plate of a zooid in the middle of a branch of the second colony. Many of the ovicelled zooids were brooding embryos.

Family BUGULIDAE Gray, 1848

Genus *Bugula* Oken, 1815

Colony erect, branching, attached by tubular rhizoids developed from its proximal regions. Zooids in two or more longitudinal series, with an extensive frontal membrane and a variably developed gymnocyst. Distal oral spines present or absent. Avicularia pedunculate, present or absent. Ovicell hyperstomial, globular, imperforate; rarely, it may be reduced to a small caplike structure.

Zooids at bifurcations disposed according to several distinct patterns (Harmer 1923).

Bugula protensa n. sp.

Fig. 15A-C

Holotype:
St. 726. Gulf of Panama (5°49'N, 78°52'W), 3270-3670 m.

Other Material:
St. 716. Acapulco-Panama (9°23'N, 89°32'W), 3570 m.

Description: Colony slender, straggling, up to 7 cm long, bifurcating regularly. Zooids very elongate, biserially arranged, but spaced such that the distal half of each zooid adjoins the tubular proximal half of its successor on the opposite side; opesiae thus alternating along the branch, giving the impression of a uniserial colony. Bifurcations apparently of Type 3 (Harmer 1923): the connecting process of zooid E does not link directly with zooid F but seems to overlie it (Fig. 15C). Anchoring rhizoids developed from basal surfaces of zooids, closely applied to surface of colony. Zooids very elongate, tubular prox-

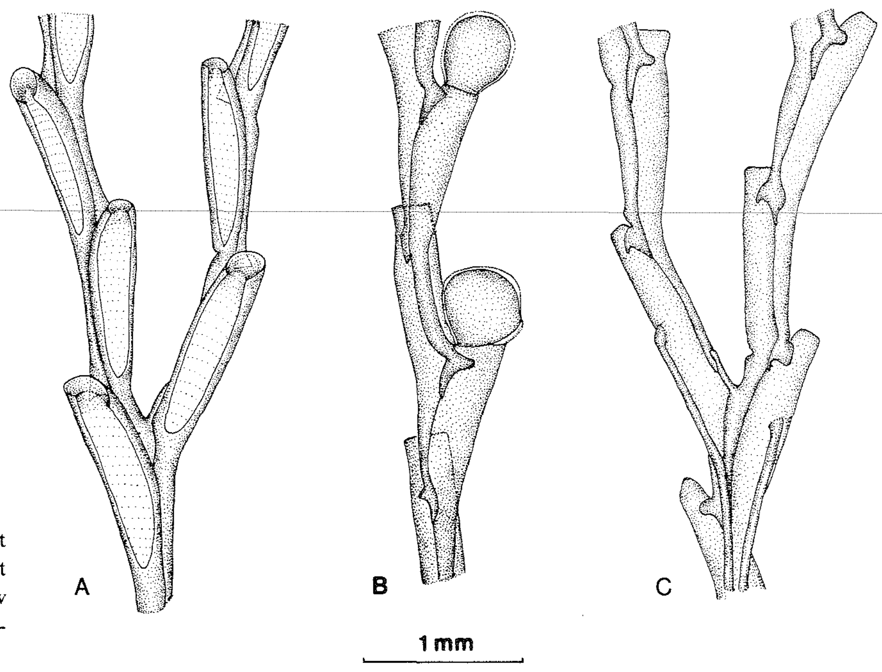


Fig. 15. *Bugula protensa* n. sp. A, part of a colony at a bifurcation; B, part of a branch in lateral view to show ovicells; C, basal view of a bifurcation.

imally, expanding to a rectangular distal portion, total length 1.9-2.2 mm. Distal end truncate, without spines or projecting corners; opesia occupying whole of frontal surface of distal half of zooid. No avicularia. Ovicell hyperstomial, globular, attached to disto-basal wall of zooid and tilted basally, entooecium thinly calcified.

Two other species of *Bugula* are known with strictly biserial branches and excessively elongate zooids. *B. longicauda* (Harmer), recorded from Japan and the Malay archipelago, is distinguished from the present species by its inconspicuous vestigial ovicells and the presence of a single spine on the outer distal angle of each zooid. *B. longissima* (Busk) differs from *B. protensa* in that the arrangement of zooids at a bifurcation (Hastings 1943, fig. 39C) conforms to Type 4 of Harmer (1923), and in having marked radial striations on the entooecium of the ovicell.

Measurements	n	$\bar{x}$	Sd
Length, distal half of zooid, mm	10	1.1	± 0.08
Length, proximal half of zooid, mm	10	0.95	± 0.10
Width, distal half of zooid, mm	10	0.29	± 0.04

***Bugula decipiens* n. sp.**

Fig. 16A-C

Holotype:
St. 200. Off Natal (29°39'S, 37°01'E), 5110 m.

Other Material:
St. 574. Tasman Sea (39°45'S, 159°39'E), 4670 m.

Description: Colony slender, straggling, up to 3.8 cm high in material studied. Branches biserial, but strictly alternating opesiae give a monoserial appearance. Bifurcation distinctive, apparently modified from Type 3 of Harmer (1923). Zooids very elongate, a tubular proximal portion broadening to a rectangular distal portion; truncate terminally, distal corners acute but not produced as spines. Avicularia sparsely developed, attached to the proximal portion of the zooid, immediately distal to its predecessor; with a slender, sharply hooked rostrum supporting a very narrow triangular mandible. Ovicells not found.

The peculiar arrangement of the zooids at a branch bifurcation is the most distinctive feature of B. decipiens (Fig. 16) and serves to distinguish it at once from *B. protensa* (above) and the two species most nearly resembling the latter.

Measurements:	n	$\bar{x}$	Sd
Length, distal end of zooid, mm	10	1.19	± 0.08
Length, proximal end of zooid, mm	10	0.63	± 0.06
Width, distal end of zooid, mm	10	0.31	±0.04

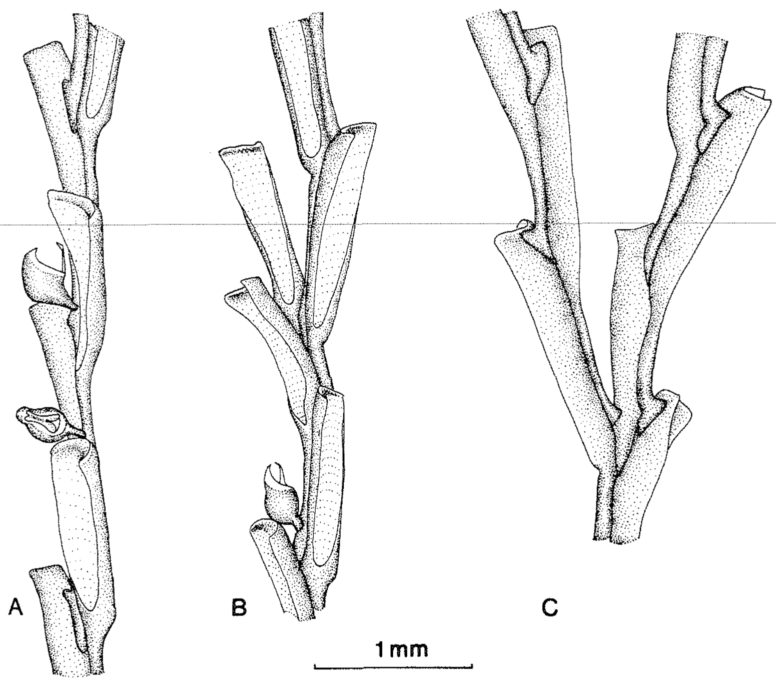


Fig. 16. *Bugula decipiens* n. sp. A, portion of a branch; B, part of a dichotomy; C, basal view of a bifurcation.

Bugula **sp.**

Fig. 17A-C

Material:

St. 649. Kermadec Trench (35°16'S, 178°40'W), 8210-8300 m.

Description: Branches biserial, gently curved about a longitudinal axis, perhaps indicating spiral growth. Zooids slender; opesiae occupying about two-thirds of each frontal surface, just overlapping; a single short spine on the inner distal angle, two on the outer. Avicularium rather short, less than the width of the opesiae, with the pointed rostrum gently downcurved; attached to the outer lateral wall of the zooid, about one-third of its length from the distal end. Ovicells small, spherical, situated squarely on the distal ends of the zooids; entooecium thinly calcified, smooth.

A single tuft of this species was recovered from St. 649; it represented part of a living colony, many of the zooids bore ovicells and a majority of these contained embryos. Considering that this was the deepest record for any bryozoan species collected by the "Galathea", the most extraordinary feature of this specimen is its relatively commonplace appearance, with no suggestion of the morphological features usually associated with abyssal cellularines. Indeed, it is little different from numerous shallow-water coastal species of *Bugula*. However, the specimen was incomplete and fragmentary, a complete astogenetic sequence was absent, and consequently it is left unnamed, until such time as further material becomes available.

Measurements	n	$\bar{x}$	Sd
Length of zooid, mm	10	0.74	± 0.05
Width of zooid, mm	10	0.17	± 0.01

Genus *Himantozoum* Harmer, 1923

Colony erect and branching, anchored by a bundle of long, tubular rhizoids budded from the lateral surfaces of the lowermost zooids. Branches flat, or convex frontally, unilaminar; zooids biserial or multiserial. Frontal surface of zooid largely membranous, with an inconspicuous gymnocyst; distal spines, or lateral processes of the vertical walls, variously developed, marginal zooids typically asymmetrical. Ovicell reduced or absent. Avicularia pedunculate, claviform, attached medially at the proximal end of the frontal surface of the zooids.

d'Hondt (1977) has shown that the morphological characters of some species of *Himantozoum* seem to intergrade with those of the species of *Dendrobeania* Levinsen, and considers that the former might be regarded as a subgenus of the latter.

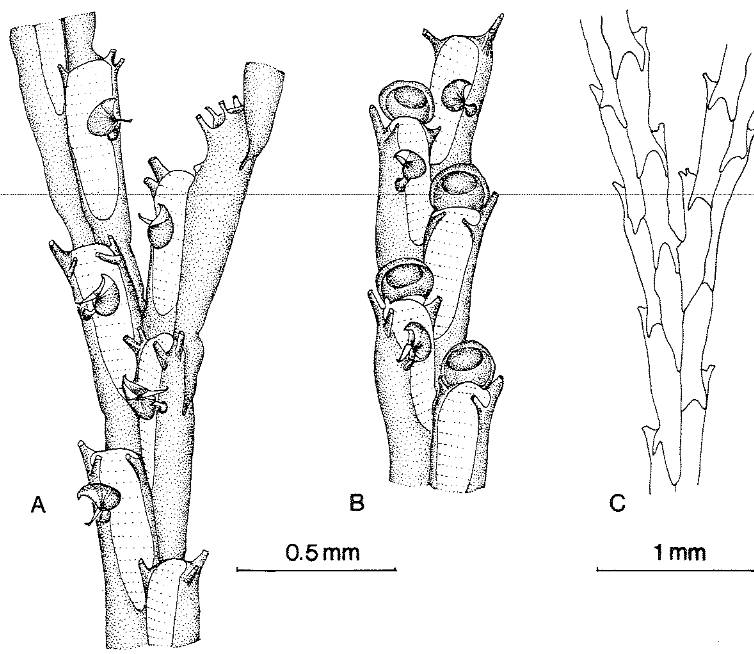


Fig. 17. *Bugula* sp. A, part of the specimen at a dichotomy; B, ovicellate zooids; C, diagrammatic basal view of a bifurcation.

***Himantozoum leontodon* (Busk)**
Fig. 18A-B

Bugula leontodon Busk, 1884: 39, pl. 10, fig. 3.
Himantozoum leontodon, Harmer 1926: 453.

Material:
St. 192. Off Durban (32°00'S, 32°41'E), 3430 m.
St. 193. Off Durban (32°34'S, 31°52'E), 3680 m.
St. 194. Off Durban (34°09'S, 30°45'E), 4360 m.
St. 241. Off Kenya (4°00'S, 41°27'E), 1520 m.

Description: Zooids in three to five alternating longitudinal series; elongate, rectangular, rounded distally, 0.9-1.00 mm long by 0.2-0.3 mm broad. Lateral walls of zooid prominent, raised, typically produced into a pair of hollow spinous processes adjacent to the orifice, symmetrically developed in zooids of the central or inner rows, asymmetrical in zooids of the marginal series. Additionally, flat triangular flanges, or short spines, may be developed elsewhere on the lateral walls, curving over the frontal membrane to a greater or lesser extent. Avicularium broadly club-shaped, recumbent on the frontal surface of the zooid; mandible short, triangular, borne on the distal end of the club, perpendicular to the frontal plane of the zooid.

Ancestrula fusiform, 1.6 mm long, forked proximally and continuous with a pair of long, tubular rhizoids. Lateral walls without processes, but with a pair of prominent curved spines distally.

The proximal rhizoids of the ancestrula are septate, suggesting that each comprises a series of kenozooids. The ancestrula buds a single zooid from its basal surface, similar in appearance to the ancestrula but smaller. The second zooid is budded from the basal surface of the first and the first stages of a colony thus comprise a single linear series of zooids. At a variable level (the second zooid from the ancestrula in one example), a lateral bud forms proximal to the basal bud and develops into a zooid interposed between the zooid developed from the basal bud and the originating zooid. The colony continues for several astogenetic generations as two longitudinal series of zooids, both asymmetrically developed, and a central series of symmetrical zooids may not be initiated until beyond the second or third dichotomy.

This species was formerly known only from a single locality in the North Atlantic ("Challenger" St. 3, south of the Canary Is., 2790 m) and the present records constitute a considerable extension of its geographical range. However, several other North Atlantic deep water bryozoan species have been found to occur in the western Indian Ocean (Hayward & Cook, 1979).

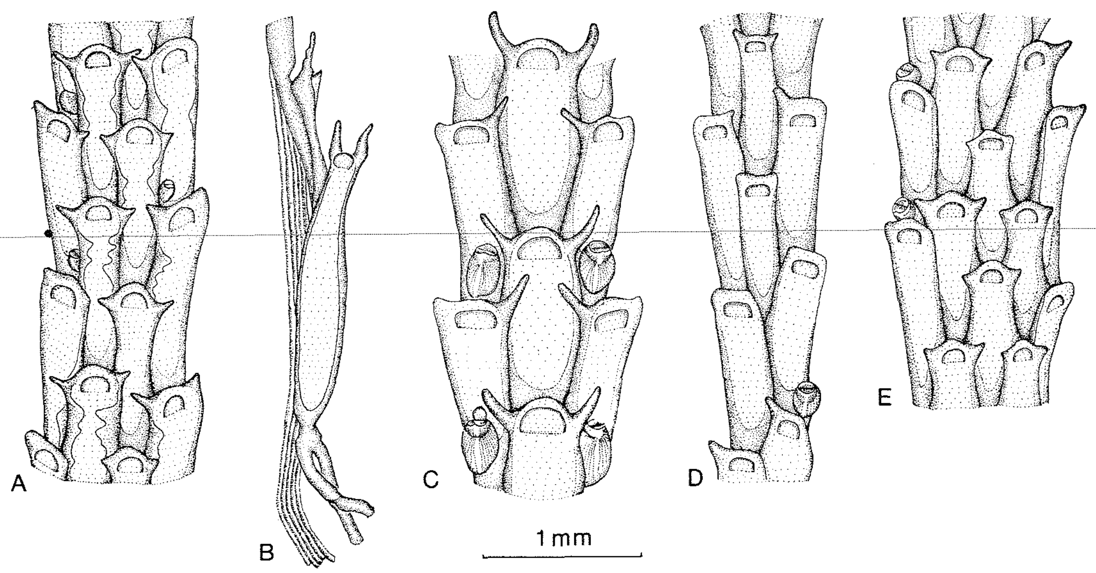


Fig. 18. A-B, *Himantozoum leontodon* (Busk). A, portion of a branch; B, the ancestrula. C-E, *Himantozoum taurinum* Harmer. C, St. 182: zooids from the distal end of a branch; D, St. 182: zooids from the proximal region of the colony; E, St. 665: zooids from the distal end of a branch.

Himantozoum taurinum **Harmer**
Fig. 18C-E

Himantozoum taurinum Harmer, 1926: 454, pl. 18, figs 4, 6, 7, 15.

Material:
St. 182. Cape Town-Durban (33°28'S, 38°32'E), 5110-5340 m.
St. 665. Kermadec Trench (36°38'S, 178°21'E), 2470 m.

Description: Zooids in two to five longitudinal series, elongate, rectangular or hexagonal, 0.9-1.1 mm long by 0.25-0.5 mm broad; broadest zooids in the central row of the more distal parts of the colony. Lateral walls of zooids raised and prominent but without processes; central zooids with long, curved distal spines, occasionally forked, marginal zooids with single curved spines on the inner distal angle, the outer angle acute but not forming a spine. Avicularium globular, up to 0.3 mm long and almost as wide as the zooid bearing it, mandible semi-elliptical, perpendicular to frontal plane; sporadic in occurrence, present on most marginal zooids, absent from many central zooids.

The basal regions of the colony are very different in appearance from the distal regions. They are generally biserial or triserial and consist of slender zooids, usually with rounded distal ends, spines are not developed until much later in the astogenetic sequence. The ancestrula is identical to that of *H. leontodon* and of approximately the same size.

H. taurinum was described by Harmer (1926) from two localities in the East Indies, south of Celebes (at 1158 m) and south of East Timor (at 883 m). The material collected by the "Galathea" is from two widely separated stations, but the range of variation of the specimens from St. 182 seems to encompass those from St. 665 (Fig. 18D & E).

Himantozoum sinuosum **(Busk)**
Fig. 19A-B

Bugula sinuosa Busk, 1884: 39, pl. 10, fig. 2.
Himantozoum sinuosum, Harmer 1926: 453.

Material:
St. 182. Cape Town-Durban (33°28'S, 38°32'E), 5110-5340 m.
St. 234. Madagascar-Mombasa (5°25'S, 47°09'E), 4820 m.
St. 241. Off Kenya (4°00'S, 41°27'E), 1520 m.
St. 281. Seychelles-Ceylon (3°38'N, 78°15'E). 3310 m.

Description: Zooids in two to five longitudinal series; proximal parts of colony biserial, becoming triserial, and broadening to five series at the distal tips. At bifurcations branches may again become biserial, although rapidly developing a third series. Zooids 1.3-1.5 mm long by 0.4-0.5 mm broad, tapered proximally; median zooids rounded distally, with acute corners adjacent to the orifice, marginal zooids asymmetrical with outer distal angle acute, inner smoothly rounded. Avicularium large, oval, up to 0.4 mm long with a pronounced, hooked rostrum, mandible triangular. A small, vestigial ovicell was present in colonies from St. 234.

H. sinuosum was recorded by Busk (1884) from a single locality off the Marion Is., although further "Challenger" material from Kerguelen is now known (Brit. Mus. Nat. Hist. reg. no. 1934. 11.12.24). In the light of the distribution revealed by the "Galathea" collections these early records may be regarded as indicating the southern limits of the species' geographical range.

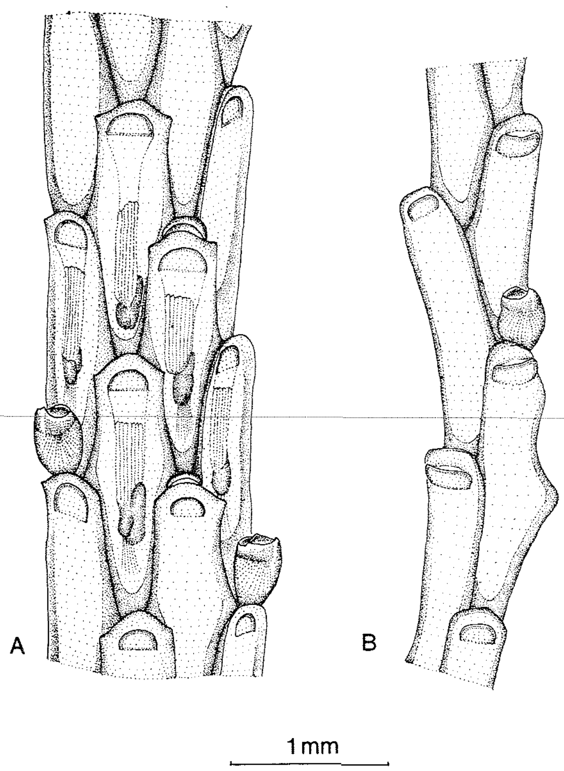


Fig. 19. *Himantozoum sinuosum* (Busk). A, zooids from the distal region of the colony, with vestigial ovicells; B, zooids from the proximal region of the colony.

Himantozoum macilentum n. sp.
Fig. 20A-D

Holotype:
St. 281. Seychelles-Ceylon (3°38'N, 78°15'E), 3310 m.

Description: Colony biserial, the frontal surfaces of the two series of zooids subtending an angle of about 100°, imparting a quadrate appearance to the branch section. Zooids elongate and slender, 1.8-2.1 mm long by 0.3-0.45 mm broad, tapered proximally; distal ends symmetrically rounded or with scarcely acute external angles. No spines. Avicularium oval, 0.25 mm long, occupying the entire width of the proximal extremity of the zooid, mandible triangular. A small, vestigial ovicell present, developed as a shallow, crescentic cap on the distal border of fertile zooids. Ancestrula 2.2 mm long, distal end rounded above acute distal angles; forked proximally and continuous with two long rhizoids. Zooid rows do not increase at bifurcations, thus there is no axial zooid.

Two other species of *Himantozoum* are known to display a biserial arrangement of zooids. *H. margaritifera* (Busk), described from two "Challenger" stations in the Southwest Atlantic, is perhaps most similar to the present species but differs in the smaller size of its zooids, which also show a constant, symmetrically-developed, pair of distal spines. *H. emaciatum* Harmer, reported only from New Guinea, develops a third series of zooids before each bifurcation, and is also distinguished by smaller and more elongate avicularia. The material of *H. macilentum* comprised seven fragmented colonies.

Himantozoum clavulum n. sp.
Fig. 21A

Holotype:
St. 663. Kermadec Trench (36°31'S, 178°38'W), 4410 m.

Description: Zooids in four to six longitudinal series, gently tapered both proximally and distally, with a somewhat linguiform outline; 1.3-1.4 mm long by 0.3-0.4 mm broad, distal ends rounded, acute distal angles developed on most zooids adjacent to orifice. Marginal zooids rather quadrate in outline, only barely asymmetrical, inner distal angle frequently more pronounced than outer. Avicularium large and conspicuous, up to 0.35 mm long, narrowed proximally to give a distinctly club-shaped appearance; rostrum sharply hooked, supporting a triangular mandible. Ovicell not found.

Of the broad fronded species of *Himantozoum, H. sinuosum* (Busk) most nearly resembles the present species, although the zooids of the latter tend to be broader than those of *H. clavulum*. However, *Himantozoum clavulum* is distinguished from all other species of the genus by its prominent, clavate avicularia.

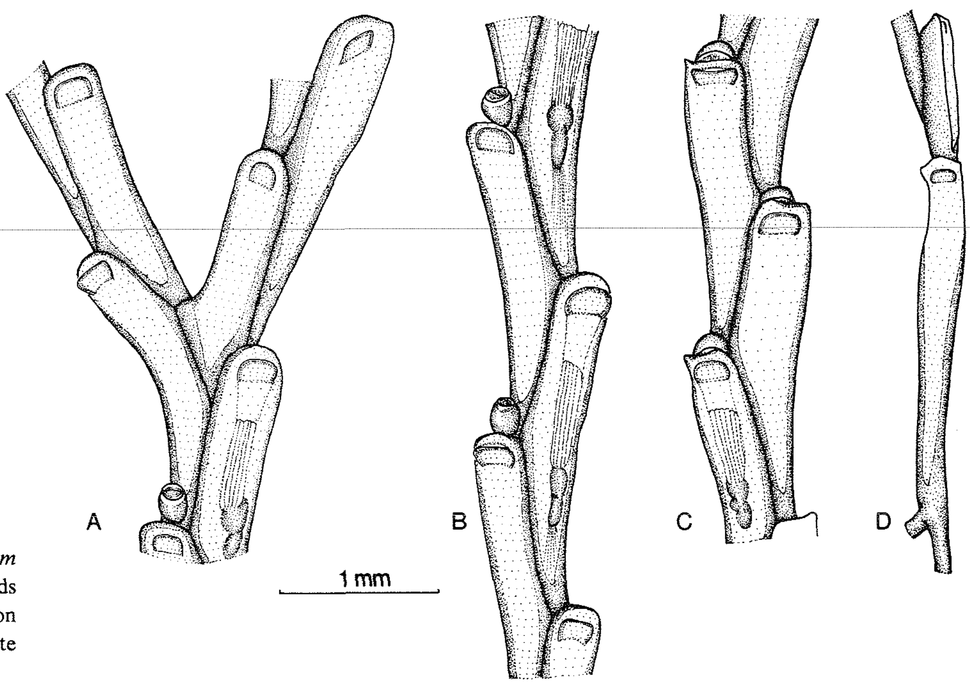


Fig. 20. *Himantozoum macilentum* n. sp. A, zooids at a bifurcation; B, portion of a branch; C, ovicellate zooids; D, the ancestrula.

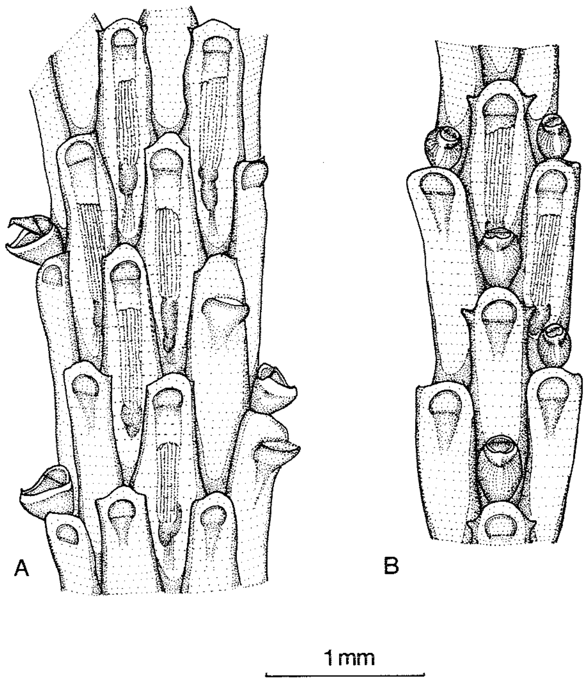


Fig. 21. A, *Himantozoum clavulum* n. sp. B, *Himantozoum inflatum* n. sp.

Himantozoum inflatum n. sp.
Fig. 21B

Holotype:
St. 217. Mozambique Channel (14°20'S, 45°09'E), 3530 m.

Other Material:
St. 281. Seychelles-Ceylon (3°38'N, 78°15'E), 3310 m.

Description: Branches composed of three longitudinal series of zooids, broadening to five before each bifurcation. Zooids elongate, more or less rectangular 1.1-1.4 mm long by 0.2-0.4 mm broad; distal ends smoothly rounded, marginal zooids with scarcely acute external distal angles, median zooids with a pair of short spines lateral to the orifice, occasionally absent. Avicularia prominent, swollen, with semicircular mandibles; up to 0.2 mm long on marginal zooids, as broad as the frontal surface of the zooid at the point of attachment. On median zooids the avicularia are larger, up to 0.35 mm long, and at their broadest circumference exceeding the width of the proximal end of the zooid. Ovicell not found.

The triserial branch arrangement and the comparatively small size of the zooids seem to be important features of *H. inflatum* which distinguish it readily from most other species of the genus. However, its single most characteristic feature is the swollen and distinctive avicularium.

Family ADEONELLIDAE Gregory, 1893

Genus *Adeonella* Busk, 1884

Colony erect, unjointed, bilaminar, branching or reticulate; secured by an encrusting base. Frontal wall of zooid with scattered pores and a central spiramen. Primary orifice obscured by a deep peristome. Adventitious and vicarious avicularia present. Ovicells absent, embryos brooded in modified gonozooids.

Adeonella cracens Hayward & Cook
Fig. 22A

Adeonella cracens Hayward & Cook, 1979: 85, fig. 10 I-L

Material:
St. 196. Off Durban (29°55'S, 31°20'E), 430 m.

Description: Colony composed of slender branches, broadening distally, reaching a width of 5 mm in the present material. Zooids elongate, oval to hexagonal, 0.9-1.2 mm long by about 0.35 mm broad, flat or slightly convex. Frontal wall finely granular, closely punctured by numerous small pores. Primary orifice transversely elliptical, obscured early in ontogeny by a deep, thickened peristome with a semicircular secondary orifice. Spiramen elongate-oval, situated immediately proximal to the secondary orifice. Adventitious avicularia single or paired, situated lateral to the spiramen and directed distally or disto-medially, mandibles triangular. Vicarious avicularia present in a single series along each edge of the branch, mandibles directed distally; similar to adventitious types but a little larger.

This species has only recently been described by Hayward & Cook (1979) who reported it from three stations off the eastern coasts of South Africa, between 400 and 880 m. The "Galathea" specimens, from the same general area, consisted of three fragments, all from living colonies.

Adeonella falcicula n. sp.

Fig. 22B-E

Adeonella sp. Hayward & Cook 1979: 86, fig. 12E.

Holotype:
St. 196. Off Durban (29°55'S, 31°20'E), 430 m.

Other Material:
St. 202. Off Natal (25°20'S, 35°17'E), 630 m.

Description: Colony formed of long slender branches, bifurcating infrequently; cylindrical at first, later becoming oval in section, broadening distally and gently curved to give a sabrelike shape. Up to 4.5 cm long in the present material with a maximum width of 3 mm. Zooids in whorls of four to eight in the proximal parts of the colony, and up to sixteen in the broader distal regions. Zooids elongate, oval or quadrate, 0.9-1.2 mm long by about 0.3 mm broad; frontal walls convex, finely granular, closely punctured by numerous small pores. Primary orifice orbicular, hidden by a thickened peristome with a semicircular secondary orifice. Spiramen oval, situated immediately proximal to the secondary orifice. Adventitious avicularia typically paired, adjacent to the spiramen and directed distally or disto-medially, frequently a second pair is developed on the distal rim of the peristome, orientated medially or proximo-medially; mandibles acute triangular. Marginal vicarious avicularia apparently absent, although the distal adventitious avicularia of marginal zooids may appear to be vicarious.

In those specimens in which the proximal regions of the colony were preserved, the base was found to comprise an amorphous sheet of calcification wrapped around the hydrocaulus of a large hydroid. Secondary calcification thickens the frontal walls of older zooids and the basal part of the colony is almost entirely smooth.

Fragments of this species were first recorded by Hayward & Cook (1979) from three localities off the eastern coasts of South Africa, but were considered to be inadequate for a complete description. The more abundant and better preserved "Galathea" specimens are clearly identical to these, the position of the avicularia relative to the spiramen and the absence of marginal vicarious avicularia are features common to both series of samples. It is now obvious that the earlier material represented only the basal portions of dead colonies and that the "Galathea" specimens present a complete astogenetic sequence.

Measurements	n	$\bar{x}$	Sd
Zooid length, mm	20	0.96	± 0.09
Zooid width, mm	20	0.32	± 0.04

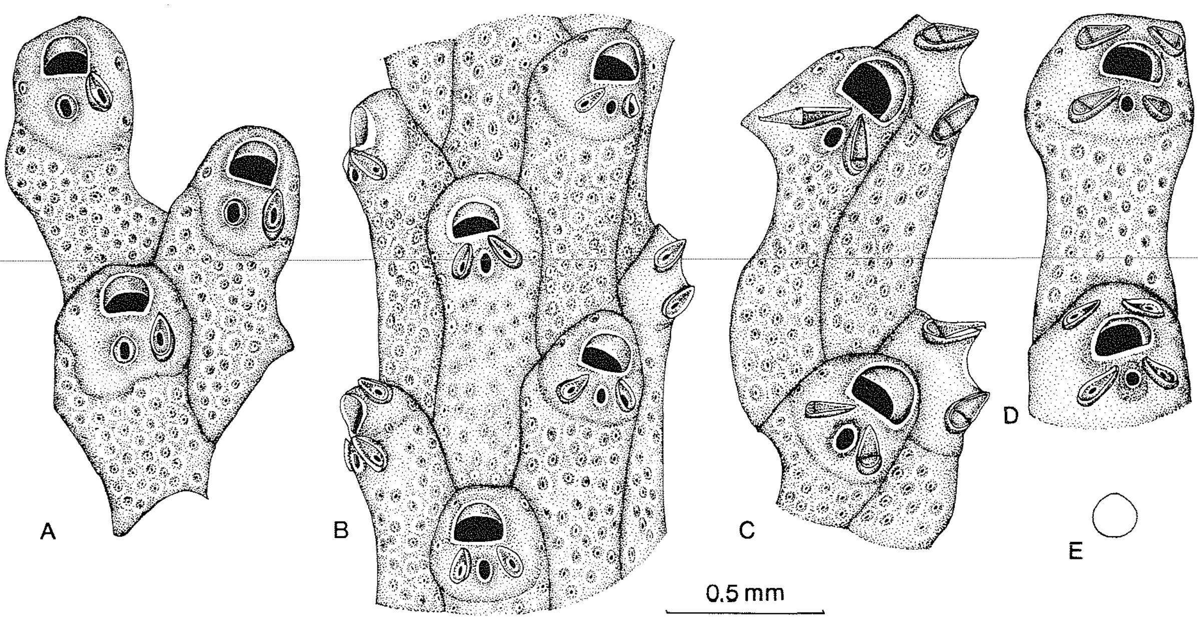


Fig. 22. A, *Adeonella cracens* Hayward & Cook. B-E, *Adeonella falcicula* n. sp. B, portion of a branch; C, the branch edge (on right), showing zooids with prominent peristomial avicularia; D, zooids with two pairs of avicularia; E, outline diagram of primary orifice.

Adeonella cultrata n. sp.

Fig. 23 A-D

Holotype:
St. 202. Off Natal (25°20'S, 35°17'E), 630 m.

Description: Colony attached by an encrusting base to hydroid stems, cylindrical at first, broadening rapidly to form a flat, irregularly curved blade, up to 4 cm long in the present material with a maximum width of 4 mm. Zooids in alternating longitudinal series which divide frequently, diverging towards the colony margin; elongate, oval or irregular in outline, 0.6-1.0 mm long by 0.28 to 0.4 mm broad. Frontal wall finely granular, with numerous small pores. Primary orifice transversely elliptical; peristome well developed, with an oval or semicircular secondary orifice. Spiramen large, oval, situated immediately proximal to the peristome. Adventitious avicularia typically single, very rarely paired, arising proximolateral to the spiramen and directed distally or distomedially, mandible acute triangular. Vicarious avicularia in a single series along each edge of the colony, similar to adventitious type but with a larger cystid, mandible directed distally or proximally.

The shape of the primary orifice, the position of the spiramen relative to the peristome and the position, size and orientation of the adventitious avicularia seem to be the most important features for distinguishing the different species of *Adeonella*. Additionally, it seems that colony form may prove to be a useful character. *A. cultrata* is distinguished from those species described by Hayward & Cook (1979) by the shape of the orifice, the orientation of the avicularia and the relatively distal position of its spiramen. *A. falcicula* (above) seems at present to be the only other species characterized by slender, sabrelike colonies.

Measurements	n	$\bar{x}$	Sd
Zooid length, mm	20	0.81	± 0.14
Zooid width, mm	20	0.35	± 0.03

Family BIFAXARIIDAE Busk, 1884

Genus *Bifaxaria* Busk, 1884

Colony erect, branching, with a characteristic candelabriform shape, anchored by chitinous rhizoids; branches cylindrical, curved proximally, straight distally, each attached by a tubular chitinous joint to the frontal wall of a single zooid at the proximal end of the preceding branch. Zooids in two alternating longitudinal series, in contact basally. Small adventitious avicularia present; ovicell prominent, hyperstomial.

Bifaxaria submucronata Busk

Fig. 24 A

Bifaxaria submucronata Busk, 1884: 80, pl. 13, fig. 1; Hayward & Cook 1979: 86, fig. 11c.

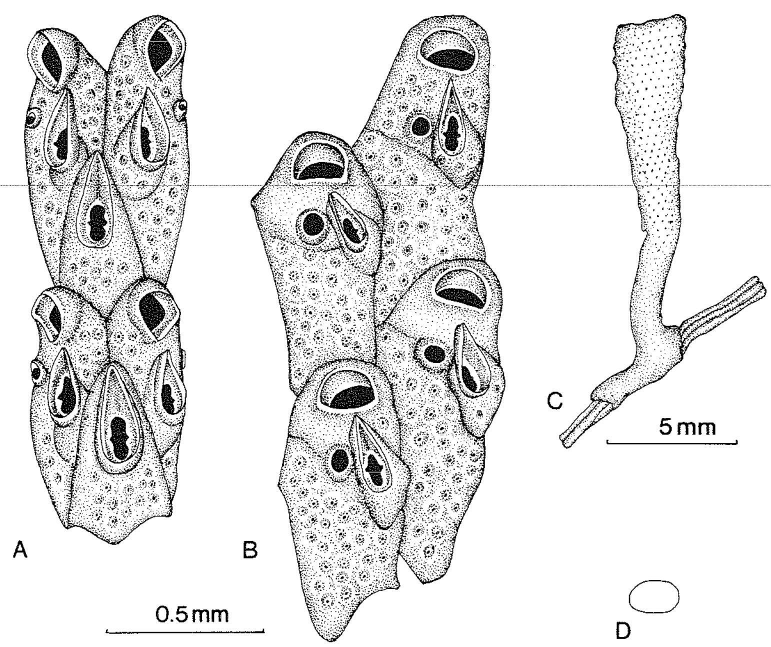


Fig. 23. *Adeonella cultrata* n. sp. A, the branch edge in plane view, showing vicarious avicularia; B, zooids from the centre of the colony; C, sketch of colony habit, attached to hydroid hydrocaulus; D, outline diagram of primary orifice.

Material:

St. 186. Cape Town-Durban (32°33'S, 32°01'E), 3620 m.

St. 192. Off Durban (32°00'S, 32°41'E), 3430-3530 m.

St. 198. Off Durban (30°32'S, 34°27'E), 2690 m.

Description: Zooids vase-shaped, tapered proximally; primary orifice terminal, obscured by a prominent projecting lip. Frontal wall smooth, with a single series of distinct, marginal pores, and a variable number of pores in longitudinal frontal series; overlain by a thick epitheca. Small paired avicularia present on the rim of the orifice in the angles of the lip, mandibles rounded, directed disto-laterally. Ovicell very elongate, smooth surfaced, imperforate.

Genus *Sclerodomus* Levinsen, 1909

Colony erect, branching, unjointed; anchored by chitinous rhizoids. Zooids in two alternating longitudinal series, in contact basally; orifice terminal, obscured by a pronounced lip. Adventitious avicularia present, usually adjacent to orifice, also distributed elsewhere on the zooid frontal wall. Ovicell prominent, inflated.

Sclerodomus corrugatus (Busk)

Fig. 24 B-C

Bifaxaria corrugata Busk, 1884; 80, pl. 13, fig. 3.

Sclerodomus corrugatus, Harmer 1957; 867, pl. 57, figs 10, 16, 23; pl. 58, figs 4, 11.

Material:

St. 192. Off Durban (32°00'S, 32°41'E), 3430-3530 m.

St. 663. Kermadec Trench (36°31'S, 178°38'W), 4410 m.

Description: Zooids vase-shaped, 1.1-1.4 mm long, with a thin but distinct epitheca, separated laterally by well marked sutures forming a zigzag pattern along the branch. Distal end of zooid broadened, with a prominent proximal lip to the orifice. Calcification finely granular, with elongate corrugations in older zooids; small marginal pores present, with others scattered over the frontal surface. A longitudinal median ridge extends from the lip of the zooid to the proximal end of the zooid. Avicularia paired, lateral-oral, within the angles of the peristome or just outside; mandibles semi-elliptical, directed disto-laterally. Ovicell grossly inflated, pear-shaped, practically obscuring the succeeding zooid, with a longitudinal median keel and a short lip

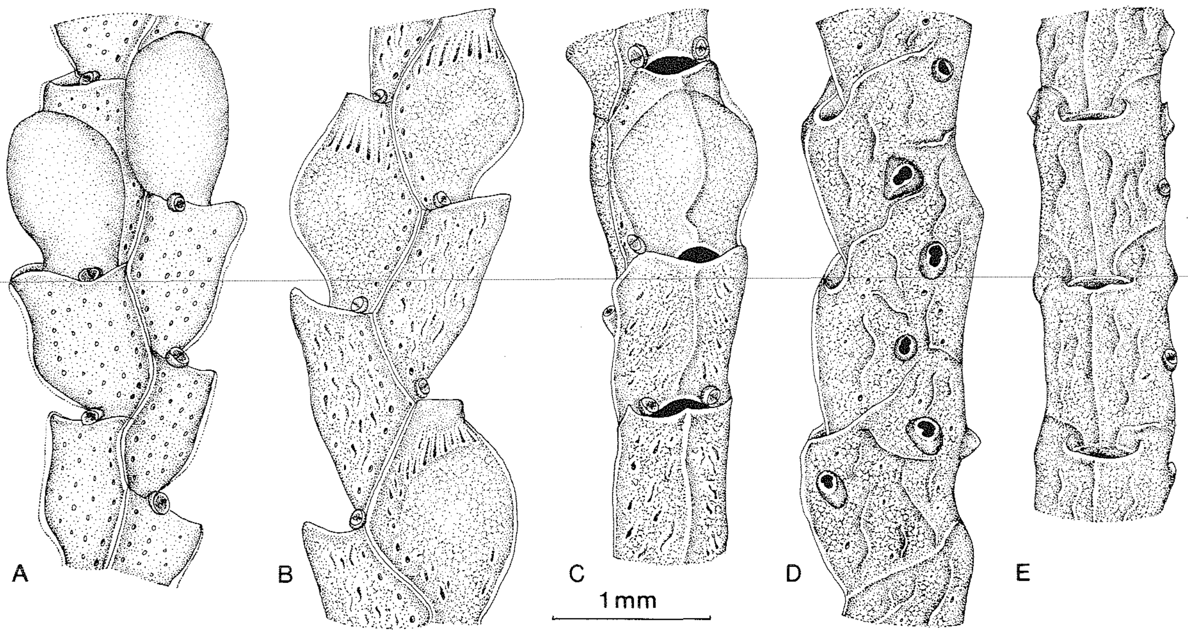


Fig. 24. A, *Bifaxaria submucronata* Busk. B-C, *Sclerodomus corrugatus* (Busk). B, part of a branch in lateral view, including three ovicells (St. 663); C, part of a branch in frontal view (St. 192). D-E, *Sclerodomus inornatus* n. sp. D, part of a branch in lateral view; E, part of a branch in frontal view.

above the orifice; scattered pores present, occasionally developed as more distinct fluting or corrugations marginally. Additional avicularia often present, of variable size, angled to the surface of the zooid and variously orientated.

Sclerodomus rugatus Harmer

Sclerodomus rugatus Harmer, 1957: 870, pl. 57, fig. 24; pl. 58, figs 2, 6, 8.

Material:
St. 661. Kermadec Trench (36°07'S, 178°32'W), 5230-5340 m.

Description: A single fragment, 7 mm long, was collected, comprising the forked proximal portion of an old, thickened colony. Identification can only be tentative, but the prominent lower lip to the orifice, the very rugose calcification and the presence of numerous, small, adventitious avicularia, including a pair within the angles of the peristome, are all characteristic of *S. rugatus* Harmer.

Sclerodomus inornatus n. sp.

Fig. 24 D-E

Holotype:
St. 192. Off Durban (32°00'S, 32°41'E), 3430 m.

Description: Colony cylindrical, lateral branches curving sharply and then continuing parallel to main stem. Zooids 0.9-1.0 mm long by 0.7-0.8 mm broad. Primary orifice transversely elliptical, hidden by the proximal lip. Calcification finely tuberculate, with small, inconspicuous marginal pores; a faint longitudinal median keel extends from the lip of the orifice to the proximal end of the zooid, lateral sutures between zooids visible but not conspicuous. Avicularia present on sides of branch; small and rounded, with semi-elliptical mandibles. Oral avicularia absent. Ovicell not developed in present material.

Sclerodomus is a little-known abyssal genus with few described species. There has been no comprehensive account of this genus since that of Harmer (1957). *S. inornatus* is distinguished from other species of *Sclerodomus* by the absence of lateral oral avicularia and the prominent, but not flared, lip to the orifice.

Family TESSARADOMIDAE Jullien, 1903

Genus *Tessaradoma* Norman, 1869

Colony erect, unjointed, cylindrical, branching dichotomously; attached by an encrusting base. Frontal wall of zooids with distinct marginal pores; orifice obscured by a tubular peristome. Ascus opening via a spiramen medially situated on the frontal wall. Adventitious avicularia present. Ovicell present but generally hidden by the peristome.

Tessaradoma circella Hayward & Cook

Fig. 25 A-D

Tessaradoma circella Hayward & Cook, 1979: 91, fig. 13 E-H.

Material:
St. 188. Off Durban (29°55'S, 31°13'E), 440 m.
St. 202. Off Natal (25°20'S, 35°17'E), 630 m.

Description: Colony attached to erect substrata by a ring-shaped base. Zooids in alternating, back-to-back pairs, elongate, oval, 0.7-0.9 mm long by about 0.3 mm wide. Frontal wall smooth, convex, with small marginal pores; spiramen cylindrical, prominent, medially situated proximal to the peristome in the apparent centre of the zooid. Peristome very deep, comprising almost half zooid length, secondary orifice transversely oval. Ovicell imperforate, immersed and indistinct, seen only at the growing edge or in broken zooids, opening into the peristome. Avicularia small, with semicircular mandibles, developed along the margins of the proximal half of the zooid, variable in number.

Ancestrula oval, tatiform, 0.4 mm long. Opesia occupying whole of frontal surface, overarched by a series of branched marginal spines which fuse along the midline of the zooid. First zooid budded at distal end of ancestrula, rising almost vertically from the substratum, orifice facing in an opposite direction to that of the ancestrula (Fig. 25 C). Second zooid budded from dorsal (basal) surface of first, with orifice orientated in the same direction as that of the ancestrula.

The beginnings of the basal attachment are seen as two slender expansions from the lateral walls of the first zooid budded from the ancestrula (Fig. 25 C). It is not certain whether these constitute part of that zooid, or are actually kenozooids. As the ring thickens calcification extends laterally from these

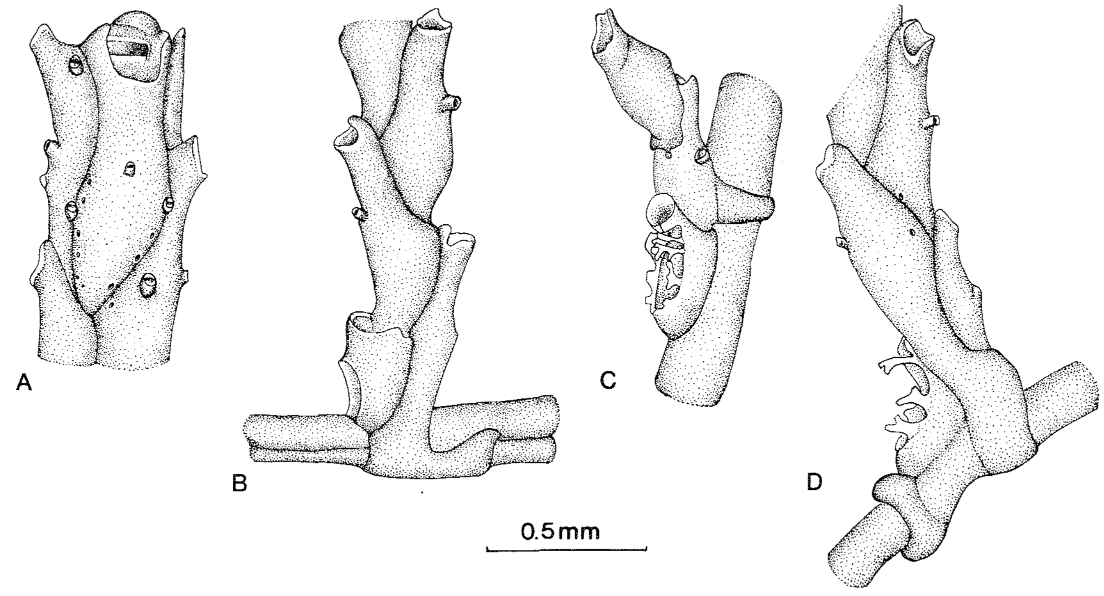


Fig. 25. *Tessaradoma circella* Hayward & Cook. A, the tip of a branch showing an ovicelled zooid; B, the base of a young colony, showing development of the attachment ring; the concavity on the left indicates the position of the lost ancestrula; C, the ancestrula, with the first two zooids budded from it and the beginnings of the attachment ring; D, a more advanced colony, with the ancestrula still intact.

processes, beneath and enclosing the ancestrula, which may thus become completely enveloped. In other specimens it is clear that the ancestrula subsequently breaks away.

T. circella was described by Hayward & Cook (1979) from four localities off the eastern coast of South Africa, between 376 and 720 m. Fourteen further specimens were recovered from the two "Galathea" stations, from the same area of the Indian Ocean. All of the colonies were attached by the characteristic basal ring to hydroid stems and included five juvenile, ancestrulate specimens; the largest "Galathea" specimen was 4.4 mm long.

Tessaradoma brevissima n. sp.

Fig. 26 A-C

Holotype:
St. 626. Tasman Sea (42°10'S, 170°10'E), 610 m.

Description: Colony rising from an encrusting base, branching irregularly, up to 8 mm high in the present material, with an equivalent spread. Zooids in four alternating longitudinal series, elongate, oval, 0,6-0.76 mm long by 0.24-0.26 mm wide. Frontal wall smooth, convex, with inconspicuous marginal pores. Primary orifice orbicular, enclosed by a deep, slightly flared peristome, with a distinct pseudosinus flanked by a pair of minute adventitious avicularia with short rounded mandibles; with further growth the pseudosinus closes to form a complete tube, constituting the spiramen. Small adventitious avicularia, scarcely larger than those on the peristome, developed along the margins of the zooids; mandibles acute to frontal plane, directed medially or proximo-medially; at least two avicularia present on each zooid but six or more may occur. Ovicell spherical, smooth, opening into peristome. The lower regions of the colony thicken considerably and zooid boundaries become increasingly indistinct, but the characteristic secondary orifice remains distinct.

The form of the colony and the arrangement of zooids, the structure of the frontal wall and the disposition of adventitious avicularia are all diagnostic of *Tessaradoma.* However, the most characteristic feature is the spiramen which, in almost all species of the genus is medially situated on the frontal wall. *T. brevissima* most nearly resembles the recently described *T. bispiramina* Hayward & Cook in that the spiramen is incorporated within the peristome. In the latter species, however, the spiramen is twinned and the peristome is without the paired avicularia typical of the present species. All of the specimens collected were attached to spicules of a glass sponge.

Family VITTATICELLIDAE Harmer, 1957

Genus *Vittaticella* Maplestone, 1901

Colony erect, branching and jointed, attached by chitinous rhizoids. Internodes of three kinds, linked by distinctive tubular joints: single zooids; doubled zooids forming branch bifurcations, and ovicelled female zooids forming branch terminations. Paired coelomic cavities (scapular chambers) present laterally: typically small suprascapular chambers distally, followed by larger scapular chambers, and elongate proximal infrascapulars. Paired lateral avicularia present. Primary orifice semicircular, above a reduced costate frontal shield.

Vittaticella incomperta n. sp.

Fig. 26D-E

Holotype:
St. 182. Cape Town-Durban (33°28'S, 38°32'E), 5110-5340 m.

Description: Zooids elongate, slender; daughter zooid of a doubleton not, or only just, shorter than the mother zooid. Orifice with a straight proximal border above a semicircular frontal area formed from the fusion of several short, thick costae, three or four of which bear large frontal lacunae. Suprascapular chamber small, entirely distal to orifice, semielliptical in shape; scapular elongate, extending from above the distal border of the orifice laterally to a level well below its proximal border; infrascapular very long and wide, traversing almost the whole remaining length of the zooid and extending onto its frontal surface. A single drop-shaped chamber occurs medially between the zooids of a doubleton. Exceptionally, the distal part of the scapular chamber may be occupied by a minute avicularium with a semicircular mandible; of infrequent occurrence in the present material, and usually developed only on one side of a zooid. Gonozooids not present.

Few species of *Vittaticella* are known from the western Indian Ocean, but *V. incomperta* is readily distinguished from them, and from those of the more abundant Indo-Malayan and Australasian faunas, by its minute lateral avicularia and its very elongate infrascapular chambers. Further, the doubled zooids which form the bifurcations of the colony are very distinctive in this species, the zooids of the doubleton being little different from those of the linear series.

Measurements	n	$\bar{x}$	Sd
Length of zooid, mm	10	1.06	± 0.04
Width of zooid, mm	10	0.36	± 0.00

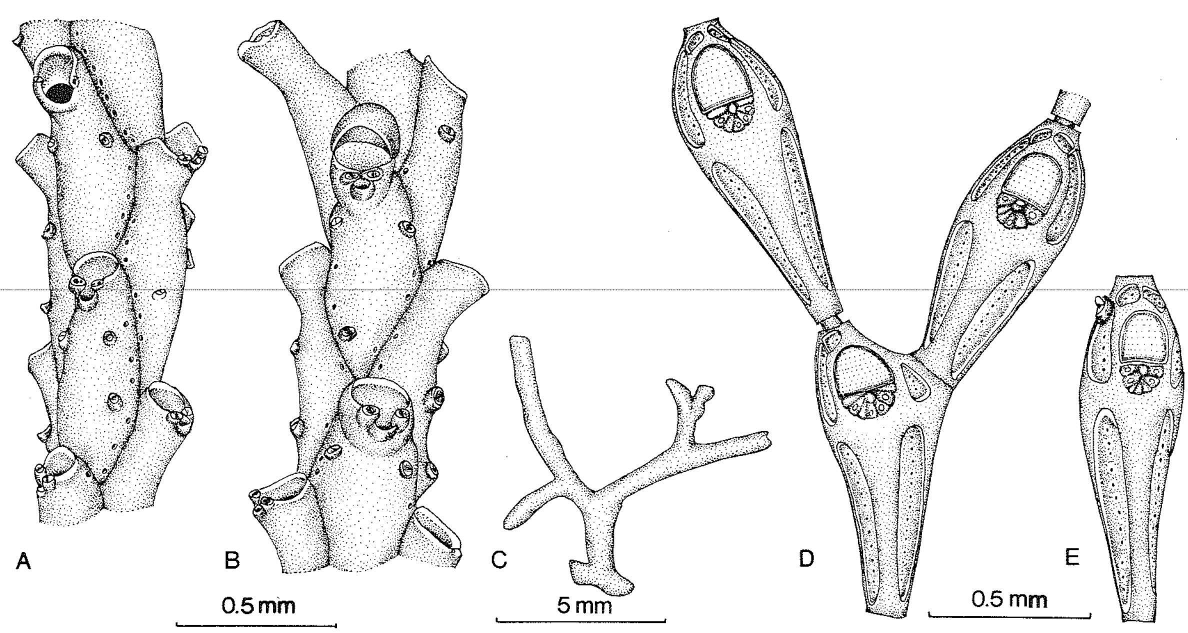


Fig. 26. A-C, *Tessaradoma brevissima* n. sp. A, zooids from the tip of a colony; B, part of a branch, including an ovicellate zooid; C, sketch to show colony habit. D-E, *Vittaticella incomperta* n. sp. D, the zooids at a bifurcation: a doubleton, and one singleton; E, zooid in oblique lateral view, note the minute avicularium.

Table 1. Species of Bryozoa collected by the Galathea Expedition. Numbers of colonies are given for each species recorded. Samples too large to be counted are indicated thus: ∝

Species								1000 m			2500 m		3000 m								4000 m							5000 m				6000 m
	196	188	490	202	626	557	436	241	453	665	668	198	726	281	192	217	716	186	193	238	194	601	663	664	574	233	234	200	182	661	654	649
Nelliella nelliformis	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cellaria sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–
Syringotrema auriculatum	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Notoplites armigera n. sp.	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Notoplites sp.	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amastigia cf. *nuda*	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Menipea ignota n. sp.	–	–	–	–	–	–	–	–	–	17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Euoplozoum cirratum	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Farciminellum hexagonum	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	6	4	1	1	6	–	–	–	36	–	–	–
Columnella magna	–	–	–	–	–	–	–	–	–	–	2	–	–	–	1	–	–	–	1	1	1	–	–	–	–	1	1	2	8	–	–	–
Columnella delicatissima	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–	6	–	–	–	–	–	–
Columnella graminea n. sp.	–	–	–	–	–	–	–	3	–	–	–	–	–	52	–	–	–	–	–	–	–	–	–	–	–	16	–	3	∝	–	–	–
Columnella accincta n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–	–	–	–	–	–	–
Cornucopina collatata n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cornucopina novissima n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	2	–	–	–	–	–	–	–	–	–	–	–
Cornucopina rupera n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	–	–	–
Camptoplites bicornis var. 1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Camptoplites bicornis var. 2	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Camptoplites lunatus	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Camptoplites sp. 1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Camptoplites sp. 2	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Kinetoskias pocillum	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Kinetoskias cyathus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–
Kinetoskias sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bugulella australis	–	–	–	–	∝	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bugula protensa n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bugula decipiens n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–
Bugula sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Himantozoum leontodon	–	–	–	–	–	–	–	3	–	–	–	–	–	–	18	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–
Himantozoum taurinum	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–
Himantozoum sinuosum	–	–	–	–	–	–	–	3	–	–	–	–	–	9	–	–	–	–	–	–	–	–	–	–	–	–	10	–	1	–	–	–
Himantozoum macilentum n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Himantozoum clavulum n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Himantozoum inflatum n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Adeonella cracens	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Adeonella falcicula n. sp.	1	–	–	22	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Adeonella cultrata n. sp.	–	–	–	13	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bifaxaria submucronata	–	–	–	–	–	–	–	–	–	–	–	1	–	–	15	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sclerodomus corrugatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Sclerodomus rugatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Sclerodomus inornatus n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Tessaradoma circella	–	11	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Tessaradoma brevissima n. sp.	–	–	–	–	9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Vittaticella incomperta n. sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–
Costaticella carotica	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sphaeropora fossa	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bockiella angusta	–	–	–	–	–	–	∝	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
No. species/station	4	3	2	3	2	1	1	4	1	5	1	1	1	7	5	1	3	2	2	2	6	1	3	1	2	3	2	3	9	1	1	1
No. bryozoan colonies/station	4	13	3	38	9*	2	*	13	2	27	2	1	1	84	36	4	4	6	2	7	17	4	3	1	7	23	11	6	63*	1	1	1

Genus *Costaticella* Maplestone, 1899

Colony erect, branching and jointed; secured by chitinous rhizoids. Internodes of three kinds, linked by distinctive tubular joints: single zooids, doubled zooids forming branch bifurcations, and ovicelled female zooids forming branch terminations. Lateral chambers well developed, paired lateral avicularia present. Primary orifice semicircular; frontal wall with a costate shield proximal to the orifice, bordered by a series of large pores, or infracostal windows.

Costaticella carotica Hayward & Cook

Costaticella carotica Hayward & Cook, 1979: 101, fig. 16.

Material:

St. 196. Off Durban (29°55'S, 31°20'E), 430 m.

The present material was collected from the same geographical area, and within the same bathymetric range, as that described by Hayward & Cook (1979).

Family ORBITULIPORIDAE Canu & Bassler, 1923

Genus *Sphaeropora* Haswell, 1881

Colony orbicular, flattened at the poles, with an antapical kenozooid complex marking the position of an anchoring rhizoid. Primary orifice of zooid semicircular. Suboral adventitious avicularia present; larger vicarious avicularia with spatulate mandibles sporadically developed.

Sphaeropora fossa Haswell, 1881

Sphaeropora fossa Haswell, 1881: 42, pl. 3, figs 5, 6; Waters 1919: 89, pl. 6, figs 1-3; text-fig. 1a; Cook 1979: 276.

Material:

St. 557. Great Australian Bight (37°13'S, 138°42'E), 680 m.

Two dead colonies of this species were collected. It has been described previously from southern and eastern coasts of Australia (Queensland to South Australia), and from Tertiary deposits of Victoria and Southwest Australia.

ORDER CTENOSTOMATA

Family FLUSTRELLIDRIDAE Bassler, 1953

Genus *Bockiella* Silén, 1942

Colony erect, cylindrical, branching; attached by sheets or chains of autozooids. Orifice of autozooid prominent, labiate or puckered. Large kenozooids present, frontally budded, wedged in between and surrounding autozooids.

Bockiella angusta Silén

Bockiella angusta Silén, 1942: 20, text-figs 15-17; Cook 1964: 296.

Material:

St. 436. East of Cebu, the Philippines (10°12'N, 124°14'E), 710 m.

The sample comprised numerous colonies attached to the hydrocaulus of a large hydroid. Described originally from Japan, this species was shown to extend throughout the Malay Archipelago (Cook 1964).

GENERAL REVIEW OF THE "GALATHEA" COLLECTIONS

The most important feature of the "Galathea" collections of deep-sea Bryozoa is that they were obtained largely from understudied areas of the oceans, with the largest group of stations being located in the western Indian Ocean and the second largest in the western Pacific. Furthermore, they all sampled benthic populations from beyond the edges of the continental shelves and the collection as a whole is thus truly representative of deep-water faunas. Many early systematic accounts, particularly those based on the collections of oceanographical expeditions included material from a wide range of depths with the highest proportion derived from shelf or coastal samples. Insufficient emphasis was placed on vertical distributions, or faunal assemblages, and it is often difficult to extract data on the deep-sea species from these accounts.

As a whole, the "Galathea" collections are typical of deep-water faunas. The predominance of Anasans over Ascophorans is usual in most bryozoan assemblages from depths beyond 1000 m. Similarly, the range of genera is characteristic, with a large proportion of the species, 18 in total, comprising just four genera, *Camptoplites, Columnella, Cornucopina* and *Himantozoum.* The 12 species of Ascophora fall neatly into two groups, the four species of Bifaxariidae (*Bifaxaria* and *Sclerodomus*) representing truly abyssal forms and the rest constituting part of an increasingly distinct fauna of the outer continental shelf and slope. All of the latter occurred in the pre-

Table 2. Geographical distribution of the species

Species	South and East Africa	Seychelles-Ceylon	East Indies	South Australia	Tasman Sea	Kermadec Trench	Acapulco-Panama	Previously Recorded Distribution
	Geographical Regions							
Nelliella nelliformis	–	–	X	–	–	–	–	East Indies
Cellaria sp.	X	–	–	–	–	–	–	
Syringotrema auriculatum	–	–	X	–	–	–	–	East Indies
Notoplites armigera	–	–	–	–	–	X	–	
Notoplites sp.	X	–	–	–	–	–	–	
Amastigia cf. *nuda*	–	–	–	–	–	X	–	S. Atlantic, Kerguelen
Menipea ignota	–	–	–	–	–	X	–	
Euoplozoum cirratum	–	X	–	–	–	–	–	Indian Ocean, East Indies
Farciminellum hexagonum	X	–	X	–	X	X	–	Marion Is., E. Indian Ocean, East Indies
Columnella magna	X	–	–	–	–	X	–	Atlantic, W. Indian Ocean
Columnella delicatissima	X	–	–	–	–	–	–	N. Atlantic
Columnella graminea	X	X	–	–	–	–	–	
Columnella accincta	X	–	–	–	–	–	–	
Cornucopina collatata	–	X	–	–	–	–	–	
Cornucopina novissima	X	–	–	–	–	–	–	
Cornucopina nupera	X	–	–	–	–	–	–	
Camptoplites bicornis var. 1	–	–	–	–	–	X	–	
Camptoplites bicornis var. 2	–	–	–	–	–	X	–	
Camptoplites lunatus	–	X	–	–	–	–	–	East Indies
Camptoplites sp. 1	–	–	–	–	–	–	X	
Camptoplites sp. 2	X	–	–	–	–	–	–	
Kinetoskias pocillum	X	–	–	–	–	–	–	Brazil, Chile
Kinetoskias cyathus	X	–	–	–	–	–	–	N./S. Atlantic
Kinetoskias sp.	–	–	–	–	–	–	X	
Bugulella australis	–	–	–	–	X	–	–	South Africa
Bugula protensa	–	–	–	–	–	–	X	
Bugula decipiens	X	–	–	–	X	–	–	
Bugula sp.	–	–	–	–	–	X	–	
Himantozoum leontodon	X	–	–	–	–	–	–	N./Equatorial Atlantic
Himantozoum taurinum	X	–	–	–	–	X	–	East Indies
Himantozoum sinuosum	X	X	–	–	–	–	–	S. Ocean, E. Indian Ocean
Himantozoum macilentum	–	X	–	–	–	–	–	
Himantozoum clavulum	–	–	–	–	–	X	–	
Himantozoum inflatum	X	X	–	–	–	–	–	
Adeonella cracens	X	–	–	–	–	–	–	South Africa
Adeonella falcicula	X	–	–	–	–	–	–	South Africa
Adeonella cultrata	X	–	–	–	–	–	–	
Bifaxaria submucronata	X	–	–	–	–	–	–	S. Atlantic, Indian Ocean, East Indies
Sclerodomus corrugatus	X	–	–	–	–	X	–	S. Atlantic, East Indies
Sclerodomus rugatus	–	–	–	–	–	X	–	East Indies
Sclerodomus inornatus	X	–	–	–	–	–	–	
Tessaradoma circella	X	–	–	–	–	–	–	South Africa
Tessaradoma brevissima	–	–	–	–	X	–	–	
Vittaticella incomperta	X	–	–	–	–	–	–	
Costaticella carotica	X	–	–	–	–	–	–	South Africa
Sphaeropora fossa	–	–	–	X	–	–	–	South Australia
Number of species	26	7	3	1	4	12	3	
Number of stations	15	1	3	1	3	7	2	

sent collections at depths of less than 1000 m, probably reflecting their actual distribution. While species of *Tessaradoma* are known to extend far deeper than this, the *Adeonella* species may be inferred not to. Hayward & Cook (1979) described two new species of *Adeonella* from the same general area of Southeast Africa as the "Galathea" specimens, and from the same range of depths; it seems that a distinct fauna of Adeonellidae exists in the deep water of the continental slope in this region of the Indian Ocean. Of the formerly described species, most are here reported from depths well within their known vertical ranges but some establish new records. *Himantozoum taurinum,* for example, was reported by Harmer (1926) from 883 m and 1158 m, while the "Galathea" specimens were from 2470 m and 5110 m. Similarly, new lower limits are established for *H. leontodon* (from 2790 m to 4360 m), *Euoplozoum cirratum* (from 2081 m to 3310 m) and *Farciminellum hexagonum* (from 2798 m to 5110 m). The increased lower limit for *Nelliella nelliformis,* from 289 m to 545 m, is probably not significant, while the depth from which the supposed specimen of the shallow water *Amastigia nuda* was obtained, 2470 m, is probably further ground for doubting its identity. The specimen of *Camptoplites bicornis* var. 1 establishes a new limit, at 5850 m, for the *bicornis* group.

The geographical distributions of the species collected are shown in Table 2, in which the 32 stations have been grouped into seven geographical regions. Previously recorded distributions are indicated for the formerly known species. The largest number of species was recorded for the western Indian Ocean (South and East Africa), but this without doubt reflects simply the greater concentration of sampling stations in this region. In fact, the relationship between the number of stations and the number of species is remarkably similar for all areas, with the exception of the region between the Seychelles and Ceylon where a single station produced a total of seven species. Seven species were recorded in more than one region, viz. *Farciminellum hexagonum, Columnella magna, C. graminea, Bugula decipiens, Himantozoum taurinum, H. inflatum* and *Sclerodomus corrugatus;* excepting *C. graminea* and *H. inflatum* the records are sufficiently widely spaced to indicate very extensive geographical ranges. Collections which include an unusually high proportion of new species are not generally of much help in considering patterns of geographical distribution. The "Galathea" collections are again valuable in this respect, comprising as they do a majority of known species. For several of these the present records are not very distant from the type locality, for example *Nelliella nelliformis, Syringotrema auriculatum, Adeonella cracens, Tessaradoma circella, Costaticella carotica* and the single ctenostome *Bockiella angusta* (Table 1). For others, however, significant extensions of the known geographical range are established. *Columnella magna,* formerly known from the North and South Atlantic, was recently reported from eastern South Africa by Hayward & Cook (1979), and its occurrence at "Galathea" St. 668, in the Kermadec Trench, is far to the east of the known range, Similarly, *C. delicatissima* and *Himantozoum leontodon,* here recorded from the western Indian Ocean, were formerly known only from the North Atlantic and North/Equatorial Atlantic respectively. The occurrence of *Camptoplites lunatus* from the central Indian Ocean is not so remote from its type locality, off Timor, and is within the same broad zoogeographical zone, as are the records of *Himantozoum taurinum,* known from the Celebes and Timor, and here recorded from the central Indian Ocean and the Kermadec Trench. The two records of *Sclerodomus corrugatus,* although remote from each other, are by no means more widely spaced than its formerly known localities, Brazil and the Malay Archipelago.

Distributional patterns of deep-sea bryozoans are evidently very diverse, with examples of both very extensive and very limited geographical ranges. However, no firm conclusions may be derived from this, simply because many of the supposed ranges are without doubt artefacts of sampling, emphasizing the lack of data for large areas of the oceans, and may also be influenced by taxonomic uncertainty. The "Galathea" material, like the various collections studied and published upon in recent years (e. g. d'Hondt 1975, Hayward 1978, Hayward & Cook 1979) makes a useful contribution in terms of additional, precise data but no effective analysis of biogeographical patterns for any of the species recorded here may be achieved until much more information has been accumulated.

The problems encountered in attempting to analyse geographical distribution patterns of deep-sea Bryozoa have been discussed briefly above. It is probable that no significant advances will be made in this field of interest for some time, dependent as it is upon large quantities of reliable and precise data. However, useful information may be derived from early studies and, as emphasized in the introduction, considerable research has been published in the last decade. It is thus possible to begin to develop concepts of bathymetric distribution patterns, of taxonomic diversity and of morphological adaptations of deep-water bryozoans, and from these to derive inferences on the ecology of the various species. In the past most comment has been directed towards the Cheilostomata and both Silén (1951) and Schopf (1969) noted that few or no Cyclostomata or Ctenostomata had been recorded from beyond the edges of the continental shelves. It is now known, largely through the researches of d'Hondt that a very specialized, highly distinctive and remarkably diverse deep-sea ctenostome fauna occurs below 1500 m in the North Atlantic. Most of the species have curious morphologies and apparently form only small colonies; they are found only by careful collection and sorting of bottom samples, and demand special attention in fixation and preservation. The lack of early records of deep-sea Ctenostomata probably reflects an inefficiency of techniques for collection and preservation, and possibly also the unfamiliarity of their often bizarre form. However, the calcified Cyclostomata might be expected to be more easily collected, and quite recognizable, and their apparent absence from the deep-sea benthos may in fact be quite real. Most previous records of deep-sea Bryozoa therefore refer to the Cheilostomata. d'Hondt's work has been largely concentrated in a limited geographical area. It seems certain that equally diverse ctenostome faunas will be found to exist in other areas of the deep oceans and it would be premature to attempt a synthesis based on a relatively small quantity of very recent data. As a consequence, the data presented here, and the discussion accompanying it, refer only to the Cheilostomata.

Tables 3 and 4 list respectively the species of Anascan and Ascophoran Cheilostomata recorded from depths greater than 1000 m, from all of the oceans. Maximum and minimum recorded depths are given for each species, together with the appropriate sources, and species known from single records only are indicated. The data have been drawn from all sources presently available to the author, including recent publications up to the end of 1979. Although comprehensive, it is not exhaustive, several of the small papers listed by Schopf (1969) have not been consulted, and a very few papers published prior to the Challenger Report (Busk 1884) have not been available. However, it is not expected that any significant bias is thereby introduced; Schopf's list included papers covering all depths in excess of 200 m and it is unlikely that more than one or two species remain to be extracted from the pre-1884 literature. Several other, deliberate, exceptions should also be noted. Records attributed to genus only have been excluded, as these do not materially assist in the present exercise. Similarly, decisions have been taken regarding the usefulness of certain records. The specimen of *Flustra foliacea* (L.) recorded from 1150 m in the North Atlantic (Hayward 1979) was dead, transported material, and its inclusion here would be spurious. A few other examples may be found in the literature of common shallow water species reported on single occasions from great depths (e.g. *Bugula neritina* (L.) reported by Calvet (1907) from 4060 m in the North Atlantic), and these have also been omitted. The taxonomic identity of such specimens may be in doubt, in most cases cannot be checked, and they do not therefore add usefully to the present survey.

The exclusion of two other small groups of Cheilostomata deserves further explanation. Studies in the North Atlantic have shown that there exists a very small fauna of eurybathyal species whose vertical distribution extends from the shallow waters of the continental shelf, at as little as 50 m or 100 m, into depths of 3000 m or more. Examples in the North Atlantic region are *Bicellarina alderi* (Busk), *Chartella barleei* (Busk), *Pyripora catenularia* (Fleming), *Setosella vulnerata* (Busk) and *Tessaradoma boreale* (Busk), and others will without doubt be shown eventually to occur in all the oceans. The inclusion of these species in any analysis is ultimately desirable, but in view of the overwhelming numbers of shallow water records for all of them, not only does a comprehensive survey become time-consuming and difficult but the deepest records come to assume a very small proportion of the total. The second group is of cold stenothermal species which show a latitudinal submergence as they approach the equator, and ex-

Table 3. Anascan Cheilostomata recorded from depths in excess of 1000 m, arranged in order of decreasing depth. Species marked with an asterisk (*) are at present known from single records only.

Greatest recorded depth	Species	Least recorded depth
5850 m, Kermadec Trench (Galathea)	* _Camptoplites bicornis_ (Busk) var. 1	
5150 m, N. Atlantic, Hayward (unpublished)	_Euginoma vermiformis_ Jullien	200 m, N. Atlantic, Harmelin 1977
5150 m, N. Atlantic, Hayward (unpublished)	_Columnella magna_ (Busk)	680 m, Natal, Hayward & Cook, 1979
5127 m, N. Atlantic, Hayward (unpublished)	_Cornucopina rotundata_ (Kluge)	1900 m, N. Atlantic, Hayward 1978b
5110 m, Natal (Galathea)	_Bugula decipiens_ n. sp.	4670 m, Tasman Sea (Galathea)
5110 m, Natal (Galathea)	_Columnella graminea_ n. sp.	1520 m, Kenya (Galathea)
5110 m, Natal (Galathea)	* _Cornucopina nupera_ n. sp.	
5110 m, Natal (Galathea)	_Farciminellum hexagonum_ (Busk)	256 m, Kerguelen, Busk 1884
5110 m, Natal (Galathea)	_Himantozoum sinuosum_ (Busk)	146 m, Kerguelen, Busk 1884
5110 m, Cape Town (Galathea)	_Himantozoum taurinum_ Harmer	883 m, Malay Archipelago, Harmer 1926
5110 m, Natal (Galathea)	_Kinetoskias cyathus_ (W. Thomson)	2890 m, N. Atlantic, Busk 1884
5032 m, N. Atlantic, Busk 1884	_Columnella delicatissima_ (Busk)	1385 m, N. Atlantic, Calvet 1931
4849 m, S. Atlantic, Busk 1884	_Notoplites crateriformis_ (Busk)	3477 m, S. Atlantic, Busk 1884
4829 m, N. Atlantic, Hayward (unpublished)	_Camptoplites lutaudae_ d'Hondt	4125 m, N. Atlantic, Hayward 1978b
4829 m, N. Atlantic, Hayward (unpublished)	_Camptoplites reticulatus_ var. _unicornis_ (Busk)	3385 m, N. Atlantic, Busk 1884
4620 m, N. Atlantic, d'Hondt 1975	_Notoplites marsupiatus_ (Jullien)	525 m, N. Atlantic, d'Hondt 1975
4620 m, N. Atlantic, d'Hondt 1975	_Scrupocellaria evocata_ Jullien	860 m, N. Atlantic, Hayward 1979
4540 m, N. Atlantic, Silén 1951	_Himantozoum mirabile_ (Busk)	3360 m, N. Atlantic, d'Hondt 1975
4410 m, Kermadec Trench (Galathea)	* _Himantozoum clavulum_ n. sp.	
4360 m, Durban (Galathea)	* _Columnella accincta_ sp.	
4360 m, Durban (Galathea)	_Cornucopina novissima_ n. sp.	3620 m, Durban (Galathea)
4360 m, Durban (Galathea)	_Himantozoum leontodon_ (Busk)	1520 m, Kenya (Galathea)
4270 m, N. Atlantic, d'Hondt 1975	_Camptoplites reticulatus_ (Busk)	430 m, N. Atlantic, d'Hondt 1975
4270 m, N. Atlantic, d'Hondt 1975	* _Columnella voigti_ d'Hondt	
4249 m, N. Atlantic, Hayward (unpublished)	_Notoplites damicornis_ Hayward & Ryland	511 m, N. Atlantic, Hay. & Ryland, 1978
4209 m, N. Pacific, Busk 1884	* _Columnella pacifica_ (Busk)	
4026 m, S. Atlantic, Busk 1884	_Cornucopina navicularis_ (Busk)	640 m, S. Atlantic, Busk 1884
4026 m, S. Atlantic, Busk 1884	_Himantozoum margaritifera_ (Busk)	3477 m, S. Atlantic, Busk 1884
3952 m, S. Pacific, Busk 1884	* _Amastigia pateriformis_ (Busk)	
3952 m, S. Pacific, Busk 1884	_Kenella biseriata_ (Busk)	1509 m, Celebes, Busk 1884
3952 m, S. Pacific, Busk 1884	_Kinetoskias pocillum_ Busk	440 m, Durban (Galathea)
3700 m, N. Atlantic, Calvet 1907	_Heliodoma implicata_ Calvet	200 m, N. Atlantic, Harmelin 1977
3700 m, N. Atlantic, Calvet 1907	_Setosella folini_ Jullien	200 m, N. Atlantic, Harmelin 1977
3614 m, Kerguelen, Busk 1884	_Cornucopina infundibulata_ (Busk)	2928 m, Kerguelen, Busk 1884
3598 m, Kerguelen, Busk 1884	_Salicornaria magnifica_ Busk	640 m, S. Atlantic, Busk 1884
3570 m, E. Pacific (Galathea)	_Bugula protensa_ n. sp.	3270 m, E. Pacific (Galathea)
3550 m, S. Pacific, Busk 1884	_Petalostegus bicornis_ (Busk)	469 m, Malay Arch. Harmer 1957
3530 m, N. Atlantic, Calvet 1907	_Cellaria biseriata_ Maplestone	1732 m, N. Atlantic, Calvet 1931
3530 m, Mozambique (Galathea)	_Himantozoum inflatum_ n. sp.	3310 m, Indian Ocean (Galathea)
3397 m, S. Ocean, Kluge 1914	_Himantozoum sinuosum_ var. _variabilis_ (Kluge)	1668 m, Indian Ocean, Hasenbank 1931
3477 m, S. Atlantic, Busk 1884	_Columnella cribraria_ (Busk)	3360 m, N. Atlantic, d'Hondt 1975
3360 m, N. Atlantic, d'Hondt 1975	* _Dendrobeania antarctica_ var. _rylandi_ d'Hondt	
3310 m, Indian Ocean (Galathea)	_Camptoplites lunatus_ Harmer	2050 m, Malay Arch. Harmer 1926
3310 m, Indian Ocean (Galathea)	* _Cornucopina collatata_ n. sp.	
3310 m, Indian Ocean (Galathea)	_Euoplozoum cirratum_ (Busk)	1158 m, Malay Arch., Harmer 1926
3310 m, Indian Ocean (Galathea)	* _Himantozoum macilentum_ n. sp.	
3138 m, N. Atlantic, Levinsen 1914	* _Columnella borealis_ (Levinsen)	
3111 m, N. Atlantic, Busk 1884	* _Canda simplex_ Busk	
3110 m, N. Atlantic, d'Hondt 1973b	* _Dendrobeania murmanica_ var. _rylandi_ d'Hondt	
3065 m, N. Atlantic, Busk 1884	_Columnella gracilis_ (Busk)	640 m, S. Atlantic, Busk 1884
3065 m, N. Atlantic, Busk 1884	* _Nelliella simplex_ (Busk)	

Greatest recorded depth	Species	Least recorded depth
2928 m, Crozet Is., Harmer 1926	*Cornucopina conica* Harmer	924 m, Malay Arch., Harmer 1926
2928 m, Kerguelen, Busk 1884	* *Foveolaria orbicularis* Busk	
2910 m, S. Ocean, Kluge 1914	* *Flustra linearis* Kluge	
2800 m, Antarctic, Waters 1904	*Amastigia abyssicola* (Kluge)	2450 m, Antarctic, Kluge 1914
2798 m, Malay Arch., Harmer 1926	*Columnella carinata* (Harmer)	462 m, Malay Arch., Harmer 1926
2798 m, Malay Arch., Harmer 1926	*Crepis decussata* Harmer	90 m, Malay Arch., Harmer 1926
2798 m, Malay Arch., Harmer 1926	*Kinetoskias elongata* Harmer	798 m, Malay Arch., Harmer 1926
2798 m, Malay Arch., Harmer 1926	*Nelliella arctata* (Harmer)	1089 m, Malay Arch., Harmer 1926
2653 m, S. Pacific, Busk 1884	*Salicornaria malvinensis* Busk	9 m, Falkland Is., Busk 1884
2470 m, Kermadec Trench (Galathea)	* *Camptoplites bicornis* (Busk) var. 2	
2470 m, Kermadec Trench (Galathea)	* *Menipea ignota* n. sp.	
2470 m, Kermadec Trench (Galathea)	* *Notoplites armigera* n. sp.	
2450 m, Antarctica, Kluge 1914	* *Camptoplites abyssicolus* (Kluge)	
2450 m, Antarctica, Kluge 1914	* *Cornucopina angulata* (Kluge)	
2450 m, Antarctica, Kluge 1914	* *Notoplites perditus* (Kluge)	
2424 m, S. Pacific, Busk 1884	*Amastigia benemunita* (Busk)	9 m, Falkland Is., Busk 1884
2424 m, S. Pacific, Busk 1884	*Tricellaria aculeata* (Busk)	9 m, Falkland Is., Busk 1884
2320 m, N. Atlantic, Calvet 1907	*Caberea ligata* Jullien	896 m, N. Atlantic, Calvet 1907
2320 m, N. Atlantic, Calvet 1907	*Setosellina roulei* Calvet	376 m, S. Africa, Hayward & Cook 1979
2161 m, Gulf of Mexico, Lagaaij 1963	*Euginoma cavalieri* Lagaaij	366 m, Gulf of Mexico, Lagaaij 1963
2100 m, N. Atlantic, d'Hondt 1975	*Scrupocellaria incurvata* Waters	155 m, N. Atlantic, d'Hondt 1975
2100 m, N. Atlantic, d'Hondt 1975	*Setosellina goezi* (Silén)	15 m, Gulf of Mexico, Lagaaij 1963
2081 m, Malay Arch., Harmer 1926	*Cornucopina moluccensis* (Busk)	281 m, Malay Arch., Harmer 1926
2081 m Malay Arch., Harmer 1926	* *Tricellaria aquilina* Harmer	
2050 m, Malay Arch., Harmer 1926	*Notoplites scutatus* Harmer	82 m, Malay Arch., Harmer 1926
2018 m, N. Atlantic, Jullien 1883	*Crepis longipes* Jullien	10 m, Singapore, Harmer 1926
2018 m, N. Atlantic, Jullien 1883	*Jubella enucleata* Jullien	360 m, N. Atlantic, d'Hondt 1975
2018 m, N. Atlantic, Jullien 1883	*Scrupocellaria jullieni* Hayward	610 m, N. Atlantic, Hayward 1978b
1958 m, N. Atlantic, Busk 1884	* *Scrupocellaria macandrei* Busk	
1940 m, N. Atlantic, d'Hondt 1973b	* *Columnella borealis,* var. *spatulata* d'Hondt	
1940 m, N. Atlantic, d'Hondt 1973b	* *Dendrobeania murmanica* var. *cookae* d'Hondt	
1668 m, Somalia, Hasenbank 1931	*Eupaxia quadrata* (Busk)	51 m, Kerguelen, Busk 1884
1668 m, Somalia, Hasenbank 1931	* *Menipea undulata* Hasenbank	
1650 m, N. Atlantic, Harmelin 1975	*Callopora bathyalis* Harmelin	650 m, N. Atlantic, Harmelin 1975
1647 m, N. Atlantic, Busk 1884	*Carbasea pedunculata* Busk	823 m, N. Atlantic, Busk 1884
1647 m, N. Atlantic, Busk 1884	* *Notoplites biloba* (Busk)	
1595 m, Malay Archipelago, Harmer 1926	*Aspidostoma cylindricum* Harmer	270 m, Malay Arch., Harmer 1926
1595 m, Malay Archipelago, Harmer 1926	*Cornucopina bella* (Busk)	1224 m, Malay Arch., Harmer 1926
1557 m, N. Atlantic, Jullien & Calvet 1903	*Farciminellum alice* (Jullien)	712 m, N. Atlantic, d'Hondt 1975
1550 m, N. Atlantic, Hayward 1978b	*Bugulella elegans* Hayward	200 m, N. Atlantic, Harmelin 1977
1550 m, N. Atlantic, Hayward 1978b	* *Nellia clavula* Hayward	
1509 m, Celebes Sea, Busk 1884	* *Brettia australis* Busk	
1509 m, Celebes Sea, Busk 1884	*Carbasea dissimilis* Busk	60 m, Off Port Philip, Busk 1884
1420 m, N. Atlantic, d'Hondt 1977	* *Bugulella gracilis* var. *mawatarii* (d'Hondt)	
1400 m, N. Atlantic, Hayward 1978b	*Nordgaardia pusilla* (Nordgaard)	610 m, N. Atlantic, Hayward 1978b
1267 m, N. Atlantic, Jullien & Calvet 1903	*Membranipora serrulata* (Busk)	150 m, N. Atlantic, Jullien & Calvet 1903
1249 m, Gulf of Mexico, Canu & Bassler 1928	*Columnella brasiliensis* (Busk)	58 m, Brazil, Busk 1884
1200 m, N. Atlantic, d'Hondt 1975	* *Kinetoskias sileni* d'Hondt	
1165 m, Malay Arch., Harmer 1926	* *Cellaria tecta* Harmer	
1165 m, Malay Arch., Harmer 1926	* *Cornucopina geniculata* Harmer	
1158 m, Malay Arch., Harmer 1926	* *Atelestozoum obliquum* Harmer	
1158 m, Malay Arch., Harmer 1926	*Bugula longicauda* Harmer	36 m, Malay Arch., Harmer 1926
1158 m, Malay Arch., Harmer 1926	* *Calyptozoum campanulatum* Harmer	
1158 m, Malay Arch., Harmer 1926	* *Calyptozoum operculatum* Harmer	
1158 m, Malay Arch., Harmer 1926	* *Cellaria praelonga* Harmer	

Greatest recorded depth	Species	Least recorded depth
1158 m, Malay Arch., Harmer 1926	* *Notoplites obliquidens* Harmer	
1158 m, Malay Arch., Harmer 1926	* *Notoplites rostratus* Harmer	
1158 m, Malay Arch., Harmer 1926	*Syringotrema auriculatum* Harmer	289 m, Malay Arch., Harmer 1926
1094 m, N. Atlantic, Jullien 1883	*Aetea lineata* Jullien	392 m, N. Atlantic, Jullien 1833
1000 m, N. Atlantic, Jullien 1883	* *Membranipora tenuis* Jullien	

Table 4. Ascophoran Cheilostomata recorded from depths in excess of 1000 m, arranged in order of decreasing depth. Species marked with an asterisk (*) are at present known from single records only.

Greatest recorded depth	Species	Least recorded depth
5718 m, N. Pacific, Busk 1884	* *Bifaxaria abyssicola* Busk	
5718 m, N. Pacific, Busk 1884	*Cribrilina monoceros* Busk	22 m, Falkland Is., Busk 1884
5230 m, Kermadec Trench (Galathea)	*Sclerodomus rugatus* Harmer	450 m, Malay Arch., Harmer 1957
5110 m, Cape Town (Galathea)	* *Vittaticella incomperta* n. sp.	
4758 m, W. of Tasmania, Busk 1884	* *Cellepora solida* Busk	
4410 m, Kermadec Trench (Galathea)	*Sclerodomus corrugatus* (Busk)	640 m, S. Atlantic, Busk 1884
4270 m, N. Atlantic, d'Hondt 1975	*Sclerodomus reticulatus* (Busk)	3360 m, N. Atlantic, d'Hondt 1975
3700 m, N. Atlantic, Calvet 1907	*Cleidochasma strangulatum* (Calvet)	200 m, N. Atlantic, Harmelin 1977
3700 m, N. Atlantic, Calvet 1907	*Fedora edwardsi* Jullien	500 m, N. Atlantic, Hayward 1978b
3620 m, Natal (Galathea)	*Bifaxaria submucronata* Busk	640 m, S. Atlantic, Busk 1884
3598 m, Kerguelen, Busk 1884	*Onchopora sinclairii* Busk	65 m, Kerguelen, Busk 1884
3430 m, Natal (Galathea)	* *Sclerodomus inornatus* n. sp.	
3307 m, N. Atlantic, Jullien 1883	*Gemellipora eburnea* Smitt	200 m, N. Atlantic, Harmelin 1977
3112 m, Malay Arch., Harmer 1957	*Agalmatozoum decussis* (Canu & Bassler)	455 m, Philippines, Canu & Bassler 1929
3065 m, N. Atlantic, Busk 1884	* *Sclerodomus minutus* (Busk)	
2798 m, Malay Arch., Harmer 1957	*Urceolipora sinuata* Harmer	82 m, Malay Arch., Harmer 1957
2796 m, Malay Arch., Harmer 1957	*Bifaxaria longicaulis* Harmer	1158 m, Malay Arch., Harmer 1957
2653 m, Fiji, Busk 1884	* *Retepora margaritacea* Busk	
2940 m, N. Atlantic, d'Hondt 1975	*Ichthyaria aviculata* Calvet	190 m, N. Atlantic, d'Hondt 1975
2320 m, N. Atlantic, Calvet 1907	* *Retepora ramulosa* Calvet	
2320 m, N. Atlantic, Calvet 1907	*Spiroporina alternata* (Calvet)	1200 m, N. Atlantic, d'Hondt 1975
2161 m, Philippines, Canu & Bassler 1929	*Trochosodon radiatus* (Canu & Bassler)	315 m, Philippines, Canu & Bassler 1929
2081 m, Malay Arch., Harmer 1957	* *Bifaxaria gemella* Harmer	
2081 m, Malay Arch., Harmer 1957	*Trochosodon linearis* Canu & Bassler	635 m, Philippines, Canu & Bassler 1929
2018 m, N. Atlantic, Jullien 1883	*Ascosia pandora* Jullien	200 m, N. Atlantic, Harmelin 1977
2018 m, N. Atlantic, Jullien 1883	*Cribrilaria alcicornis* (Jullien)	201 m, N. Atlantic, Hayward & Ryland 1978
2018 m, N. Atlantic, Jullien 1883	* *Microporella inseparata* Jullien	
2018 m, N. Atlantic, Jullien 1883	*Palmicellaria inermis* Jullien	460 m, N. Atlantic, d'Hondt 1974
2018 m, N. Atlantic, Jullien 1883	*Sertella arborea* (Jullien)	463 m, N. Atlantic, Hayward 1979
2018 m, N. Atlantic, Calvet 1907	*Sertella jullieni* (Calvet)	717 m, N. Atlantic, Calvet 1907
2018 m, N. Atlantic, Jullien 1883	*Smittoidea perrieri* (Jullien)	330 m, N. Atlantic, Hayward 1978b
2018 m, N. Atlantic, Jullien 1883	* *Smittia spectrum* Jullien	
1901 m, Malay Arch., Harmer 1957	* *Siphonicytara cylindracea* Harmer	
1810 m, N. Atlantic, d'Hondt 1975	* *Bifaxaria lagaaiji* d'Hondt	
1810 m, N. Atlantic, d'Hondt 1975	* *Bifaxaria redieri* d'Hondt	
1700 m, N. Atlantic, d'Hondt 1978	*Tegminula venusta* Jullien	392 m, N. Atlantic, Jullien 1883
1633 m, Malay Arch., Harmer 1957	* *Sclerodomus giganteus* Harmer	
1595 m, Malay Arch., Harmer 1957	*Bifaxaria bilabiata* Harmer	1158 m, Malay Arch., Harmer 1957
1595 m, Malay Arch., Harmer 1957	*Vittaticella perlucens* Harmer	567 m, Malay Arch., Harmer 1957
1525 m, N. Atlantic, Jullien 1883	*Hippoporina polygonia* (Jullien)	200 m, N. Atlantic, Harmelin 1977
1509 m, Malay Arch., Busk 1884	* *Sclerodomus papillatus* (Busk)	
1509 m, Malay Arch., Busk 1884	* *Siphonicytara serrulata* (Busk)	

Greatest recorded depth	Species	Least recorded depth
1385 m, N. Atlantic, Calvet 1931	*Malleatia rara* Jullien	135 m, N. Atlantic, d'Hondt 1975
1324 m, Gulf of Mexico, Canu & Bassler 1928	* *Semihaswellia sinuosa* Canu & Bassler	
1300 m, N. Atlantic, Jullien & Calvet 1903	*Onchopora grimaldii* Jullien	1022 m, N. Atlantic, Calvet 1931
1300 m, Malay Arch., Harmer 1957	*Spiroporina brevitubulata* Harmer	204 m, Malay Arch., Harmer 1957
1267 m, N. Atlantic, Jullien & Calvet 1903	* *Lepralia botulus* Jullien	
1267 m, N. Atlantic, Jullien & Calvet 1903	* *Lepralia dautzenbergi* Jullien	
1267 m, N. Atlantic, Jullien & Calvet 1903	* *Lepralia tuberculata* Jullien	
1267 m, N. Atlantic, Jullien & Calvet 1903	*Myriozoum subgracile* d'Orbigny	150 m, N. Atlantic, Jullien & Calvet 1903
1260 m, N. Atlantic, d'Hondt 1975	*Hippothoa amaena* Jullien	110 m, N. Atlantic, d'Hondt 1975
1251 m, Galapagos Is., Canu & Bassler 1930	* *Diplonotos costulatum* Canu & Bassler	
1251 m, Galapagos Is., Canu & Bassler 1930	*Diplonotos striatum* Canu & Bassler	73 m, Galapagos Is., Canu & Bassler 1930
1251 m, Galapagos Is., Canu & Bassler 1930	* *Semihaswellia sulcosa* Canu & Bassler	
1250 m, N. Atlantic, Calvet 1931	* *Jaculina dichotoma* Calvet	
1250 m, N. Atlantic, Calvet 1931	*Osthimosia parvula* Jullien	845 m, N. Atlantic, Calvet 1931
1250 m, N. Atlantic, Calvet 1931	*Smittina azorensis* (Jullien)	190 m, N. Atlantic, d'Hondt 1975
1250 m, N. Atlantic, Calvet 1931	*Tessaradoma flustroides* (Calvet)	780 m, N. Atlantic, d'Hondt 1975
1249 m, Gulf of Mexico, Canu & Bassler 1928	* *Sertella marsupiata* (Smitt)	
1165 m, Malay Arch., Harmer 1957	* *Gigantopora profunda* Harmer	
1165 m, Malay Arch., Harmer 1957	* *Hippopodina pectoralis* Harmer	
1165 m, Malay Arch., Harmer 1957	* *Lepralia biturrita* Harmer	
1165 m, Malay Arch., Harmer 1957	*Sclerodomus tenuis* Harmer	1158 m, Malay Arch., Harmer 1957
1158 m, Malay Arch., Harmer 1957	* *Sclerodomus pauciporosus* Harmer	
1098 m, S. Atlantic, Busk 1884	* *Sclerodomus denticulatus* (Busk)	
1089 m, Malay Arch., Harmer 1957	* *Spiroporina venusta* Harmer	
1069 m, N. Atlantic, d'Hondt 1975	*Myriapora bugei* d'Hondt	470 m, N. Atlantic, d'Hondt 1975
1068 m, N. Atlantic, Jullien 1883	* *Mucronella longicollis* Jullien	
1068 m, N. Atlantic, Jullien 1883	*Schizomavella fischeri* (Jullien)	1000 m, N. Atlantic, d'Hondt 1973
1068 m, N. Atlantic, Jullien 1883	*Schizomavella neptuni* (Jullien)	250 m, N. Atlantic, Hayward & Ryland 1978
1068 m, N. Atlantic, Jullien 1883	* *Smittia vaciva* Jullien	
1068 m, N. Atlantic, Jullien 1883	* *Temachia opulenta* Jullien	
1060 m, Malay Arch., Harmer 1957	* *Conescharellina distalis* Harmer	
1001 m, Hawaii, Canu & Bassler 1927	* *Schizoporella flexilis* Canu and Bassler	
1000 m, N. Atlantic, Jullien 1883	* *Smittia miniacea* Jullien	

tend into depths of up to 1000 m or 1500 m. Some examples of these were reported by Hayward & Ryland (1978), including *Copidozoum exiguum (Barroso)*, *Escharoides bidenkapi* (Kluge) and *Turbicellepora smitti* (Kluge). A practical justification for excluding these species is that their presence in faunal lists or analyses often serves to obscure the characteristic deep-sea fauna and unnecessarily complicates any consideration of vertical zonation.

Finally, certain anomalous records cannot be subjected to any precise rule in deciding whether they should be included in such a summary as this. A good example is "Challenger" St. 320, depth 1098 m (Busk 1884); only two of the 18 species listed by Busk have been incorporated in the present list as likely to be deep-water species, the rest, having been recorded from numerous shallow water stations, are excluded. Records such as these are probably indicative of localized environmental conditions allowing the survival of species elsewhere restricted to shallow waters. However, three species which have been ascribed vertical ranges from very shallow to very deep water (viz. *Setosellina goezi* 15-2100 m, *Amastigia benemunita* 9-2424 m, *Tricellaria aculeata* 9-2424 m) are included in the Tables because there was insufficient evidence to decide whether they might be assigned to one of the excluded groups and no grounds to believe that they were taxonomically confused. These three species are not, however, considered in further analysis (Figs 27-29).

The revision of generic and specific names of the listed species has only been effected in those in-

Table 5. Taxonomic diversity of Anascan Cheilostomata recorded from depths greater than 1000 m.

Family	Genus	Number of Species	
Aeteidae	*Aetea*	1	
Alysidiidae	*Petalostegus*	1	
Aspidostomatidae	*Aspidostoma*	1	
Bicellariellidae	*Bugulella*	2	26
	Calyptozoum	2	
	Camptoplites	7	
	Cornucopina	11	
	Kinetoskias	4	
Bugulidae	*Bugula*	3	15
	Dendrobeania	3	
	Himantozoum	9	
Calloporidae	*Foveolaria*	1	
Cellariidae	*Atelestozoum*	1	9
	Cellaria	3	
	Euginoma	2	
	Salicornaria	2	
	Syringotrema	1	
Cothurnicellidae	*Crepis*	2	
Epistomiidae	*Nordgaardia*	1	
Euoplozoidae	*Euoplozoum*	1	
Farciminariidae	*Columnella*	12	15
	Farciminellum	2	
	Nellia	1	
Flustridae	*Carbasea*	2	4
	Flustra	1	
	Kenella	1	
Membraniporidae	*Callopora*	1	5
	Membranipora	2	
	Nelliella	2	
Scrupariidae	*Brettia*	1	24
Scrupocellariidae	*Amastigia*	3	
	Caberea	1	
	Canda	1	
	Eupaxia	1	
	Jubella	1	
	Menipea	2	
	Notoplites	9	
	Scrupocellaria	4	
	Tricellaria	2	
Setosellidae	*Setosella*	1	
Setosellinidae	*Heliodoma*	1	3
	Setosellina	2	
Number of Families:	17		
Number of Genera:	42		
Number of Species:	111		

stances where good published evidence was available. In most cases, therefore, the name used here is the same as that used in the original source.

Looking at Tables 3 and 4, the most obvious point to be noted is the larger number of Anascans compared to Ascophorans, 111 of the former to 75 of the latter. The preponderance of Anascans in deep-water bryozoan faunas has been noted above and is ap-

Table 6. Taxonomic diversity of Ascophoran Cheilostomata recorded from depths greater than 1000 m.

Family	Genus	Number of Species	
Bifaxariidae	*Bifaxaria*	7	17
	Sclerodomus	10	
Celleporidae	*Cellepora*	1	3
	Osthimosia	1	
	Tegminula	1	
Cleidochasmatidae	*Cleidochasma*	1	
Conescharellinidae	*Agalmatozoum*	1	4
	Conescharellina	1	
	Trochosodon	2	
Cribrilinidae	*Cribrilina*	2	
Escharellidae	*Mucronella*	1	
Euthyrisellidae	*Urceolipora*	1	
Gigantoporidae	*Gigantopora*	1	
Hippopodinidae	*Hippopodina*	1	
Hippoporinidae	*Hippoporina*	1	
Hippothoidae	*Hippothoa*	1	
Mamilloporidae	*Ascosia*	1	2
	Fedora	1	
Microporellidae	*Microporella*	1	
Myriaporidae	*Myriapora*	1	2
	Myriozoum	1	
Onchoporidae	*Ichthyaria*	1	3
	Onchopora	2	
Pasytheidae	*Gemellipora*	1	
Phylactellidae	*Temachia*	1	
Schizoporellidae	*Schizomavella*	2	3
	Schizoporella	1	
Sertellidae	*Diplonotos*	2	8
	Malleatia	1	
	Retepora	2	
	Sertella	3	
Siphonicytaridae	*Siphonicytara*	2	
Smittinidae	*Jaculina*	1	7
	Palmicellaria	1	
	Smittia	3	
	Smittina	1	
	Smittoidea	1	
Tessaradomidae	*Semihaswellia*	2	6
	Spiroporina	3	
	Tessaradoma	1	
Vittaticellidae	*Vittaticella*	2	
Incertae sedis	*Lepralia*	4	
Number of Families:	23		
Number of Genera:	42		
Number of Species:	75		

parent in most reports on deep-sea collections. However, the difference is smaller than might be expected and perhaps correlated with the higher proportion of Ascophorans represented by single records only, 36 species (48%) compared to 41 species (37%) of Anascans. The percentage of ascophoran species reported in from two to five samples (Fig. 28) is lower than that for Anascans, 33% (25 species) instead of 38% (43 species), but the figures for species reported more than five times are similar for both groups, 18% (14 species) for Ascophorans and 20% (23 species) for Anascans (Fig. 27). In both Tables a high proportion of the species known from single records only may be attributed to the work of very few authors (e.g. Harmer 1926, 1957; Jullien & Calvet 1903; Kluge 1914); although suggesting that some of these species may have limited geographical distributions, it also reflects a low intensity of sampling over large areas of the oceans. As noted by Schopf (1969), many of these single records may be assembled in groups each representing a single station (e.g. Harmer 1926: "Siboga" Sts 122: 1165 m, 211: 1158 m), and perhaps indicating limited areas of high species diversity.

It seems reasonable to conclude, therefore, that the Anascan Cheilostomata are better represented in deep-sea faunas than the Ascophora, and the cause is perhaps to be sought in the morphological adaptations necessary for life in the deep sea. In Tables 5 and 6 the data are ordered to display the range of species of both cheilostome groups, and perhaps add some support for the above view. Taxonomic diversity, in terms of numbers of families and genera, is distinctly greater in the Ascophora (notwithstanding the uncertain status of some of the taxa), whereas a majority of the Anasca (72%) may be assembled into four families, Bugulidae, Bicellariellidae, Farciminariidae and Scrupocellariidae, together encompassing 20 (46%) of the genera recorded. A significant proportion of these genera are either limited to depths in excess of 1000 m or have their vertical distribution largely centred below this depth. Of the Ascophora only one family (Bifaxariidae), comprising two genera and 17 species, has primarily a deep water distribution; most of the other 40 genera are widely distributed in shelf waters, each with a few representatives either ranging into, or limited to, greater depths. Thus, it would appear that certain features of the Anasca preadapt them to the deep-sea environment to the extent that they are able to maximize their opportunities in colonization, radiating to produce a broad range of species. Conversely, deep-water Ascophorans, for the most part, represent individual species from a wide systematic spectrum. Some of these may possibly be relict species for which the deep sea is no more than a refuge.

The most characteristic morphological adaptations of deep-sea bryozoans are those which enable them to live in environments deficient in hard substrata. The relationship between species diversity and abundance and the availability of hard substrata has been demonstrated for coastal bryozoan populations by several authors (notably, Eggleston 1972). Beyond the edges of the continental shelves bryozoan species diversity decreases with depth, reflecting, at least initially, a decrease in the amount of hard substrata available for settlement and growth. Cook (1981) has shown that much of the bryozoan benthos of the deep sea has characteristics in common with soft sediment, or "sand fauna", assemblages of certain coastal waters (Cook 1966). These assemblages, in the deep sea, are characterized by species with a highly modified colonial morphology which may be classified into six groups, constituting two major faunal types. The primary fauna of unconsolidated sediments is able to colonize the bottom directly and includes five distinct colony morphotypes (Table 7), while the secondary fauna, in deep water, comprises a single morphotype typically attached to members of the primary fauna. A majority of the "Galathea"

Table 7. Colony morphotypes in deep-sea Bryozoa. From Cook (1981).

Group 1. Setoselliniform:	very small colonies (typically 1-8 mm diameter) encrusting the smallest substrata, usually with setiform avicularian mandibles fulfilling a supportive and/or cleaning function.
Group 2. Cellariiform:	erect, jointed, branched colonies; supported on fine grained or unconsolidated sediments by anchoring rootlets.
Group 3. Vinculariiform:	erect, rigid, branching colonies; supported by small encrusting sheets of zooids or zooid polymorphs.
Group 4. Cellulariiform/ Cellariiform:	erect, flexible, branching colonies anchored by rootlets; typically elongate, delicate and thinly calcified.
Group 5. Pedunculate:	complex colonies with a tripartite structure; an elongate, kenozooidal peduncle supporting a branched or spherical crown of autozooids, and anchored by rootlets; calcified or uncalcified.
Group 6. Conescharelliniform:	very small colonies (1-8 mm diameter), typically globular or conical, stabilized by basal rootlets.

species (Table 2, *Notoplites* to *Himantozoum*) may be classified in Groups 4 and 5. *Nelliella, Cellaria* and *Syringotrema* belong to Group 2, together with *Bifaxaria* and *Sclerodomus, Vittaticella* and *Costaticella,* while *Adeonella* and *Tessaradoma* are secondary fauna, Group 3 species. *Sphaeropora* is the only representative of Group 6. The "Galathea" collections are thus highly typical of deep-sea bryozoans in comprising a majority of species in which kenozooidal rhizoids (or rootlets) are of paramount importance in anchoring the colony. With such species, the need for hard substratum is limited to the smallest particles, sufficient to provide a settlement surface for the ancestrula, which rapidly produces a stabilizing derrick of rhizoids. Judging by the morphology of the inflated ancestrula of *Farciminellum* (Fig. 5C), and the curious elongated ancestrulae of *Himantozoum* (Figs 18B, 20D), even this basic requirement may be dispensed with. Many families of erect Anascans, common in shallow waters, would seem to be preadapted to life on unconsolidated deep-sea sediments, whereas potential primary colonizers of soft sediments among the Ascophora are few. Most erect Ascophorans are secured to their substratum by encrusting sheets of zooids and only those in which the potential exists for producing uncalcified kenozooidal rhizoids seem to achieve any prominence in deep-water faunas. These are primarily cryptocystidean species (such as *Bifaxaria*) in which the outer epitheca of the body wall, and its coelomic cavity, offer possibilities for the development of tubular extensions.

The species assembled in Group 1 (setoselliniform morphotype) are without doubt descended from encrusting species which have simply reduced the need for substratum to a minimum. The majority of these are Anasca, although Hayward & Cook (1979) described a similarly adapted cribrimorph, *Inversiscaphos setifer,* from the continental slope of eastern South Africa. Group 6 species, effectively free-living, minute colonies stabilized by basally developed rooting kenozooids, are almost entirely highly specialized Ascophorans. Substantial faunas of Group 1 and Group 6 species have recently been described from several parts of the world (e.g. Harmelin 1977, Cook & Lagaaij 1976), but whereas the first include a number of species with extensive bathymetric ranges (such as *Heliodoma implicata* Calvet and *Setosellina roulei* Calvet), the second seem to be largely limited to the first 1000 m and include a substantial proportion of shallow water, soft sediment species.

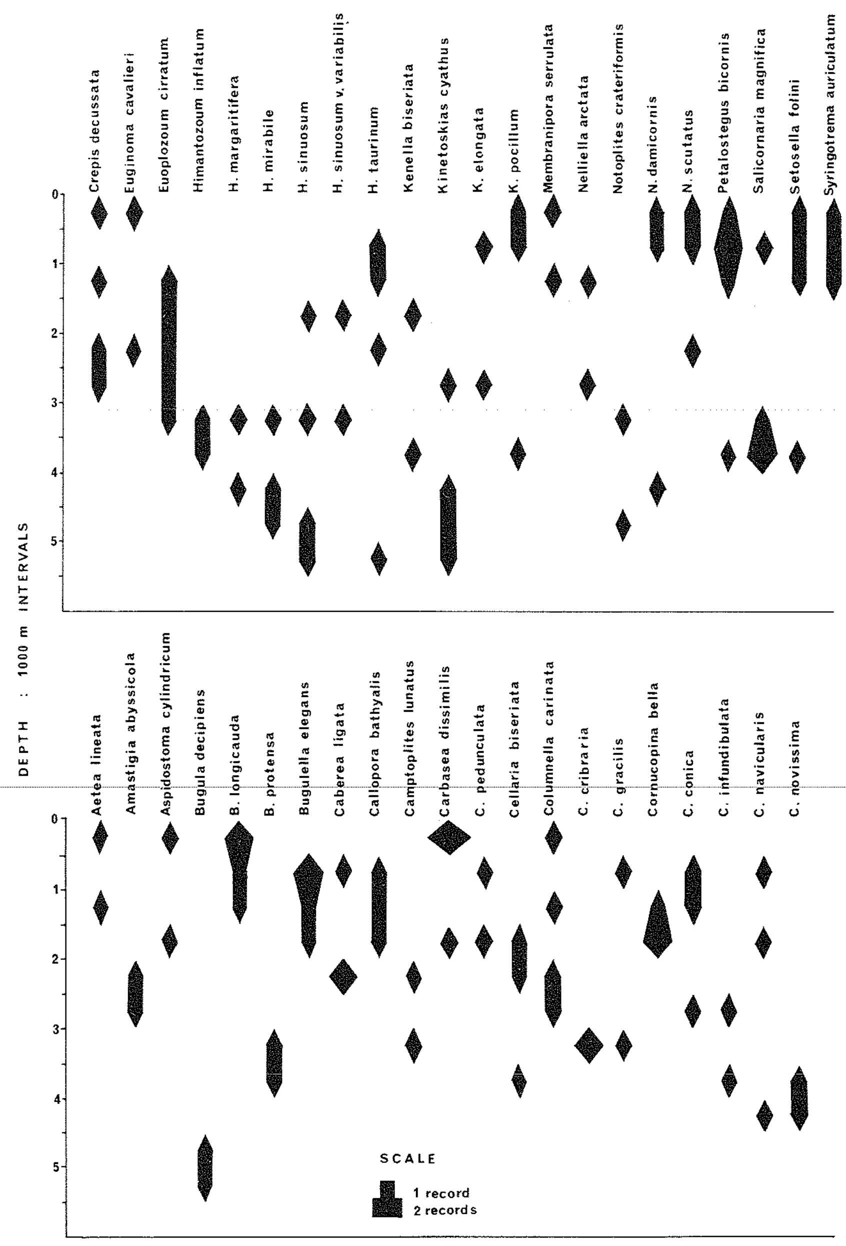
In general, the "Galathea" collections support the classification proposed by Cook (1981) while suggesting that in the greatest depths the proportion of one or two morphotypes (Groups 4 & 5) achieves dominant levels, and that Groups 1 and 6 assume negligible proportions or are absent altogether. However, it should be emphasized that, like the delicate Ctenostomata recorded by d'Hondt (1976) from great depths in the North Atlantic, the minute conescharellniform colonies of Group 6 species are completely unrepresented in the "Galathea" collections (with the exception of the two specimens of *Sphaeropora*), and that specimens of both are recovered only by careful examination of fine bottom sediments. Consequently their absence may be more apparent than real; the deep-sea Ctenostomata will doubtless prove to have a wider geographical distribution, and the widespread conescharelliniform species may yet be shown to range into greater depths.

BATHYMETRIC DISTRIBUTION PATTERNS

The problem of definition has still to be resolved in discussing bathymetric ranges of "deep-sea" bryozoans. Earlier systematic accounts simply noted vertical ranges for each species, rarely commenting upon taxonomic or faunal differences between samples collected from various depths. Hastings (1943) regarded abyssal bryozoans to be those species whose distributions were largely limited to depths greater than 2000 m, but included species distributed between 1000 m and 2000 m in her tabulations, remarking that although not strictly abyssal they would, nevertheless, be more usefully considered as part of the abyssal fauna. Silén (1951) adopted an upper limit of 3000 m for abyssal faunas, whereas Schopf (1969) reviewed all literature related to material from depths of 200 m and below, on the reasonable grounds that the edges of the continental shelves constitute the most marked discontinuities in vertical distribution patterns. This ambiguity probably reflects nothing more than a lack of concensus among oceanographers in defining boundaries for vertical zones in the benthic environment (see, for example, Hedgpeth 1957). Such boundaries have most usually been defined by physical parameters and do not easily equate with apparent patterns of vertical zonation inferred from biological data. Research over the past two decades on a number of animal phyla has suggested that depth related rates of faunal change, and hence zonation, are more complex than any of the schemes tabulated by Hedgpeth (1957).

In this, as in numerous other fields of enquiry, bryozoan research is hopelessly outdated, still hampered by a shortage of reliable quantitative data. Furthermore, discussion of bathymetric distributions still tends to consider simply total vertical ranges for the various species rather than, for example, frequency of occurrence in relation to depth. The latter approach is necessary if a satisfactory characterization of the deep-sea Bryozoa is to be achieved. The upper limit of 1000 m used to select the species to be included in this review was deliberately chosen, partly to reduce the data to manageable levels, but also in order to exclude the deeper records of essentially continental shelf species and thereby to isolate the deep water elements of the bryozoan benthos. As will be apparent from the following discussion, this results in the exclusion of a number of species whose distribution is probably limited to the upper continental slope. However, as it is difficult in practice to

Fig. 27. The vertical distribution of Anascan Cheilostomata: species with 2-5 occurrences. See text for explanation.



differentiate between these and the stenothermal species referred to earlier, without extensive data on geographical distribution, this bias must be tolerated for the present.

From the species listed in Tables 3 and 4 (pp. 56-59) those reported in the literature on more than one occasion, or originally described from more than one sampling station, have been extracted and divided into two groups: those with from 2-5 occurrences, and those with more than 5 occurrences. The frequency of occurrence at 500 m depth intervals is plotted for both groups in Figs 27-29, for both Anasca and Ascophora. In Figs 27 and 28 the occurrence is plotted as numbers of records. An immediate impression is gained of a broader bathymetric range for the Anasca as a whole, with approximately half of the total of 42 species having distributions largely centred below 2000 m, and almost half having vertical ranges extending over 2000 m or more. For seven species a continuous distribution is established over 1500 m. Of the Ascophora, 21 of the 25 species are limited to depths above 2000 m, continuous distributions of 1500 m or more are apparent for only 3 species and the majority have total vertical ranges of less than 2000 m. However, an important feature to be noted in Figs 27 and 28 is the high proportion of discontinuous distributions, probably largely attributable to a lack of data but perhaps compounded in some cases by taxonomic uncertainty (e.g. *Salicornaria magnifica,* Fig. 27; *Cribrilina monoceros,* Fig. 28). Thus, little indication of zonation patterns may be derived from this data.

The data for species with more than five occurrences are plotted in Fig. 29 as percentage occurrence at each depth interval. The number of records is given for each species and includes some unpublished material from the North Atlantic. The patterns revealed are of considerable interest. Again, an apparent difference is revealed between the distributions of anascan and ascophoran species, with the former showing a broader overall depth distribution, a significant proportion of species largely restricted to depths greater than 2000 m, and with more extended vertical ranges, on average, for individual species. A majority of ascophoran species are restricted to, or largely centred upon, depths of less than 1500 m and only 5 species have continuous

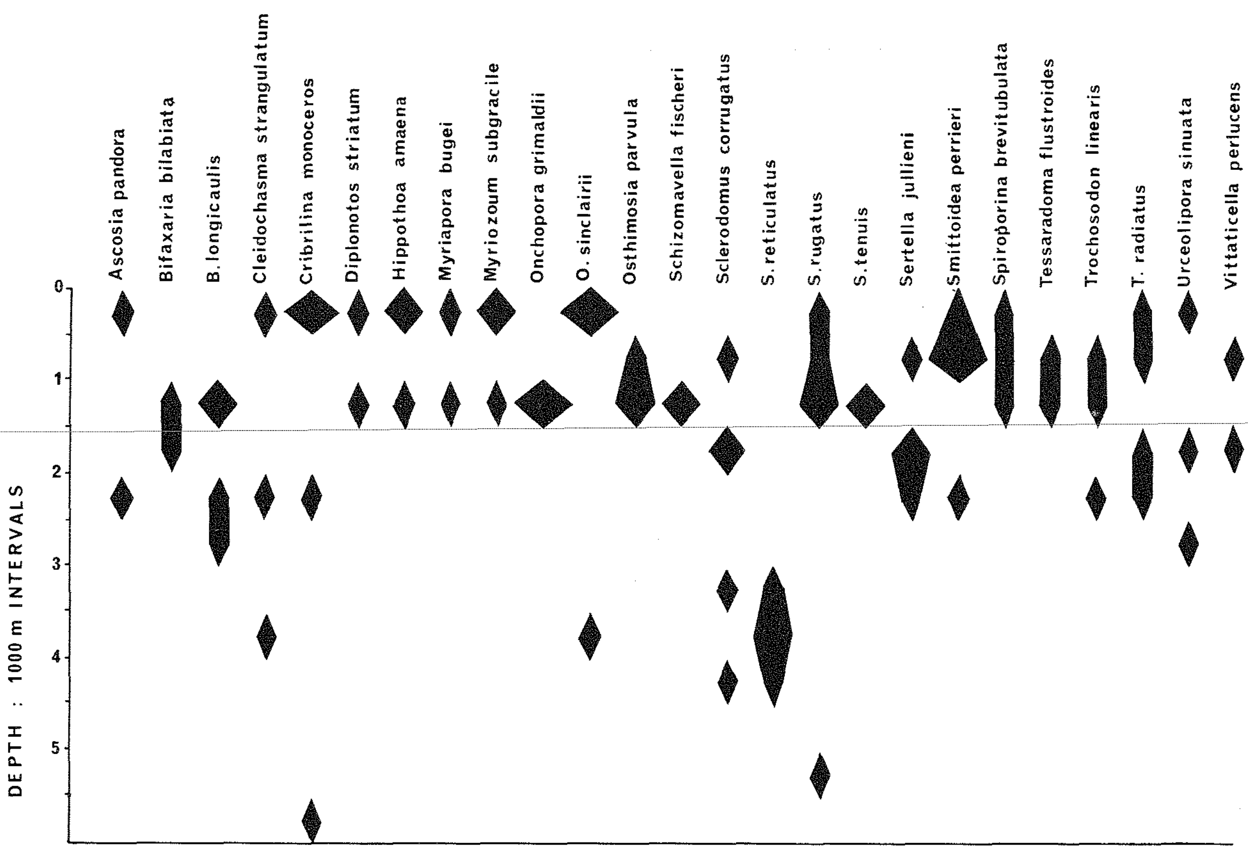


Fig. 28. The vertical distribution of Ascophoran Cheilostomata: species with 2-5 occurrences. See text for explanation. Scale as in Fig. 27.

vertical ranges of 2000 m or more. Disjunct distributions are fewer in both groups, and the discontinuities that exist are generally of a smaller scale than those shown in Figs 27 and 28. Taxonomic uncertainty is probably not a factor in these cases as the 23 anascan and 14 ascophoran species represented in Fig. 29 are all well known and distinctive species. Latitudinal variation may perhaps be of importance; for example, the lowest concentration of *Euginoma vermiformis* (5000-5500 m) represents a number of samples recently collected by the "Campagne Biovema" of the Centre Oceanographique de Bretagne, Brest, from the Gambia abyssal plain, whereas all the other records are from north of the Azores. Among the Anasca greater vertical ranges are seen in the species with the broadest geographical distributions, viz. *Camptoplites reticulatus, Columnella magna, Cornucopina rotundata,* and *Farciminellum hexagonum.*

Several distinct patterns of distribution are evident in Fig. 29, and the variety is greatest among the Anasca. The species of *Camptoplites, Columnella* and *Cornucopina* seem to be limited to depths below 2000 m; *Camptoplites reticulatus* and *Columnella magna* have pockets of distribution above this but, as discussed above, also have wide geographical ranges. Five of these species have their main centres of distribution below 4000 m and perhaps may be regarded

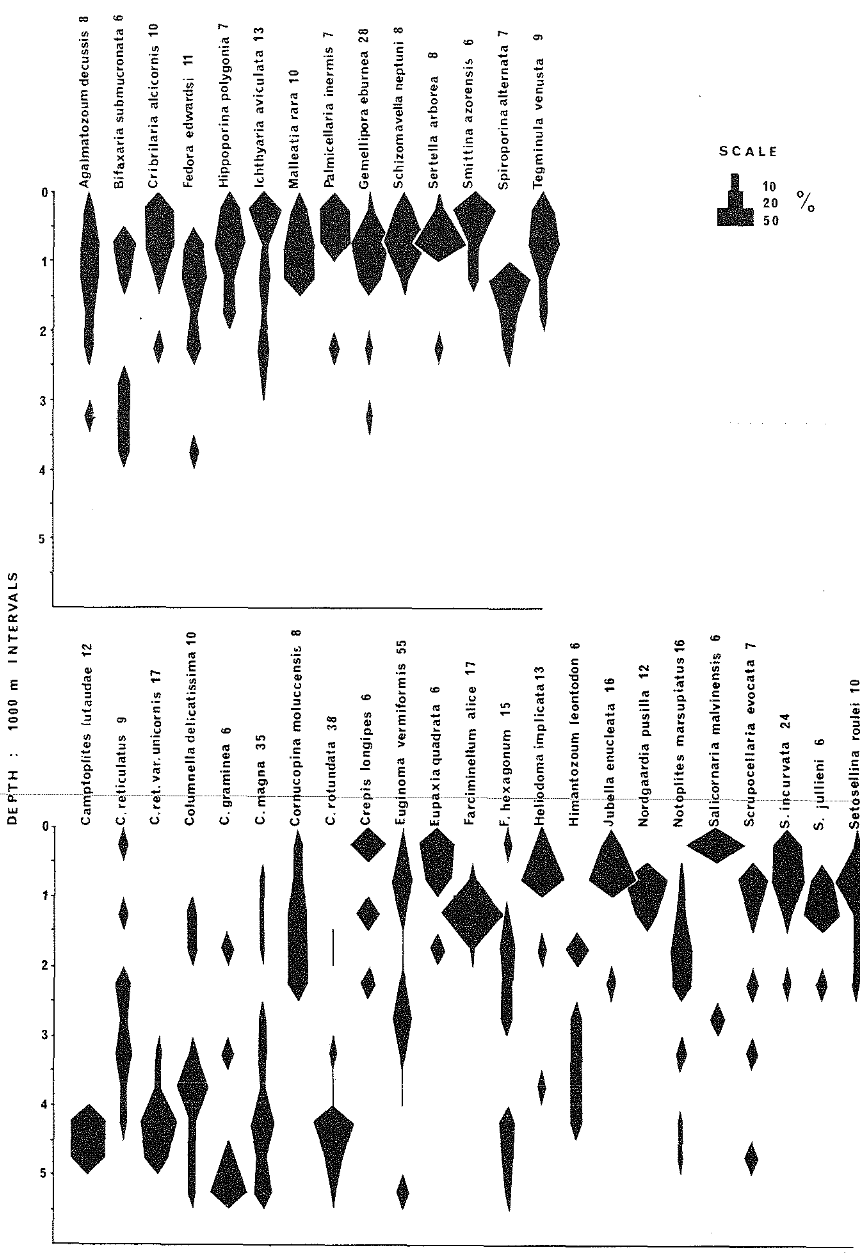


Fig. 29. The vertical distribution of deep-sea Cheilostomata: the frequency of occurrence of the most widely reported species, plotted at 500 m depth intervals. See text for further explanation.

as primarily abyssal species in the classical sense of the term. *Cornucopina moluccensis,* however, is widely distributed in the first 2500 m, with a preponderance of records between 1500 m and 2500 m. An interesting distinction is implied between the distribution patterns of *Camptoplites reticulatus* and its variety *unicornis,* with the main concentration of the latter located below that of the former. Apart from *C. reticulatus* only two species, *Euginoma vermiformis* and *Farciminellum hexagonum,* have distributions extending from the first depth interval (0-500 m) to beyond 4000 m, although two others range from the second depth interval (500 m-1000 m) to beyond 4500 m. The greatest fall-off in distributions is seen to be at 2500 m, where the ranges of 6 species terminate, but a second apparent boundary appears to be at 1500 m, where the ranges of another 5 species terminate. A further indication that the shallower component, from 0-2000 m, comprises several distinctly zoned elements may be derived from the fact that 2 species (*Eupaxia quadrata, Salicornaria malvinensis*) are most frequent in the first depth interval, 5 are most frequent in the second depth interval (*Heliodoma implicata, Jubella enucleata, Nordgaardia pusilla, Scrupocellaria evocata, Setosellina roulei*), and 2 in the third interval (*Farciminellum alice, Scrupocellaria jullieni*).

The variation in distribution patterns among species occurring largely in the first 1500 m is seen also in the Ascophora. Of the 7 species limited to or most commonly distributed within the first 1500 m, the centre of distribution varies for each species between the first three depth intervals. Only 1 species (*Spiroporina alternata*) is apparently limited to depths greater than 1000 m, and only 3 species have continuous distributions which extend below 2000 m. Interestingly, those species with disjunct distributions, and the most extended distributions, are, with the exception of *Bifaxaria submucronata,* those with the most limited geographical ranges.

Recent surveys of the bryozoan fauna of the continental slope of western Europe have suggested that patterns of vertical distribution vary from species to species, and that rates of faunal change seem to be enhanced between depths of 1500 m and 2000 m (Hayward 1978, 1979). The present survey appears to add further weight to this suggestion, although it should be emphasized that a preponderance of the species plotted in Fig. 29 are largely North Atlantic in distribution, and that evidence from other areas of the deep oceans is still needed. Bathymetric distribution patterns are better known for other animal groups of the deep sea. Rex (1977) analysed depth distribution data for 142 species of gastropods, from 25 samples collected along the Gay Head-Bermuda transect between 69 m and 4970 m. Sharp, continual faunal change was shown to occur with increasing depth. Rex was able to indicate narrow boundary zones, between significantly distinct faunal elements, at the shelf edge, at a mid-slope level of about 1100 m to 1400 m, between the lower slope and the abyssal rise, at below 2000 m, and between the abyssal rise and the abyssal plain, below 4000 m. Similar published results were discussed for other groups of benthic organisms. Rex (1977) considered that zonation rates may be influenced, among other factors, by trophic interrelationships, and it is not to be expected that vertical zonation patterns of the filter-feeding Bryozoa may be compared directly with those of epifaunal gastropods. Nevertheless, despite the provisional nature of the survey presented here it is clear that bathymetric distribution patterns of deep-sea Bryozoa are depth zoned, and that the greatest changes occur in the first 2000 m. Testing of any inferences to be drawn from the data assembled here would be most usefully achieved through the analysis of quantitative samples, from a range of depths, with the same order of sampling frequency as those studied by Rex (1977).

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PLATE 5

Figs A-B. *Euoplozoum cirratum* (Busk). A, portion of a colony, including an ovicellate zooid; B, detail of a branch to show avicularium.

Fig. C. *Farciminellum hexagonum* (Busk), frontal surface of a branch with enlarged brooding zooids.