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BRYOZOANS FROM THE PLIOCENE BOWDEN SHELL BED OF JAMAICA

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Nineteen species of bryozoans are illustrated from the Bowden shell bed, including all of the commoner species. Recorded for the first time from the Bowden shell bed are ?*Plagioecia dispar* Canu & Bassler, 1928, *Mecynoecia proboscideoides* (Smitt, 1872), *Schizoporella errata* (Waters, 1879), *Petraliella* cf. *bisinuata* (Smitt, 1873) and *Schedocleidochasma porcellanum* (Busk, 1860). Most of the Bowden bryozoans are widespread in the Caribbean and Gulf of Mexico in the Neogene and at the present day. They represent a tropical shelf fauna, apparently transported without appreciable abrasion into a deeper water setting in sediment gravity flows.

Key words — Bowden shell bed, systematics, Cyclostomata, Cheilostomata, SEM, ecology.

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INTRODUCTION

Canu & Bassler (1919) were the first to describe bryozoans from the Bowden Formation (Bowden Marl or Bowden shell bed) of Jamaica. They described 17 species, 9 of which were new. Subsequently, many of these species were redescribed by Canu & Bassler (1923), reproducing many of the photographs they used in their earlier paper, and the diversity of the fauna was increased to 32 species. Only one paper specifically concerning Bowden bryozoans has been published subsequently, in which Lagaaij (1959) described a further six species. Canu & Bassler's (1923) two Bowden species of ctenostome bryozoans represented by borings, *Terebripora sinefilum* and *T. elongata*, were included in Pohowsky's (1978) monograph of ctenostome borings, the former being retained in *Terebripora* and the latter being placed in synonymy with *Orbignyopora archiaci* (Fischer). Except for Pohowsky (1978), all of the papers describing Bowden bryozoans predate scanning electron microscopy (SEM). The availability of SEM has had a major impact on bryozoan systematics, especially in permitting easier and more accurate illustration of morphological details.

The present paper is not intended to be a monographic revision of the Bowden bryozoan species: such an undertaking would require not only restudy of all of the types, but also extensive comparison with related taxa of diverse geographical and stratigraphical provenance. Instead, we aim to provide a short synopsis concentrating on the most common species, the majority of which are here illustrated for the first time using SEM. Consequently, full species descriptions and synonymies are not given. However, the most important characteristics for distinguishing between the commoner Bowden species are outlined, their taxonomic nomenclature and classification are updated, and some ecological comments are given.

The Bowden Formation is part of the Lower Coastal Group and outcrops in a small area of southeastern Jamaica, around Bowden on the eastern side of Port Morant Bay. Over 600 species of invertebrates have been recorded from the lowermost unit, the so-called 'Bowden shell bed', making it the most famous fossiliferous hori-

zon in Jamaica. The shell bed comprises a series of coarse-grained and conglomeratic layers and lenses within marlstones. Trace fossil and some other evidence suggests that the Bowden Formation is a deep-water deposit, with the fossils in the shell bed being allochthonous and deposited from a sediment gravity flow (Pickerill *et al.*, 1996). The age of the Bowden shell bed is late Pliocene.

METHODS AND MATERIALS

Specimens were studied using an ISI ABT-55 scanning electron microscope equipped with an environmental chamber. The micrographs reproduced in this paper are backscattered electron images of uncoated specimens.

Specimens used in the present study are in the collections of The Natural History Museum, London (BMNH) and the Florida Museum of Natural History, University of Florida, Gainesville (UF).

SYSTEMATIC PALAEONTOLOGY

Order Cyclostomatida Busk, 1852
Suborder Articulina Busk, 1859
Family Crisiidae Johnston, 1847
Genus *Crisia* Lamouroux, 1812

Remarks — Colonies of *Crisia* are jointed and erect ('cellariiform'), with internodes comprising biserially-arranged autozooids separated by elastic articulations. Fossil colonies are invariably disarticulated. Gonozooids are bulbous structures usually situated at a fixed position in the internode.

Crisia sp.

cf. 1838 *Crisia elongata* Milne-Edwards, p. 203, pl. 7, fig. 2.
1959 *Crisia elongata* Milne-Edwards — Lagaaij, p. 484, text-fig. 4.
cf. 1986 *Crisia elongata* Milne-Edwards — Winston, p. 30, figs 71-73.

Material — BMNH D41249.
Remarks — Only one internode of *Crisia* is known from the Bowden shell bed. This has already been well figured by Lagaaij (1959, text-fig. 4) as *Crisia elongata* Milne-Edwards, 1838, a species originally described from the Recent of the Red Sea. SEM examination of the Bowden specimen revealed subcircular pseudopores, whereas a specimen from Panama figured by Winston (1986, figs 71-73) as *C. elongata* has slit-like pseudopores. Cook (1985, p. 202) regarded the *C. elongata* of Maturo (1957, p. 31) from North Carolina as likely to be *C. denticulata* (Lamarck). Maturo's figure (1957, fig. 21) shows subcircular pseudopores like those of the Bowden shell bed specimen. However, it is impossible to be sure of the exact identity of the Bowden *Crisia*, which is therefore not assigned to a species.
Ecology — Species of *Crisia* have a wide bathymetric distribution; for example, Hayward & Ryland (1985) recorded *C. denticulata* from the lower shore, whereas other species of the genus described by Harmelin (1990) range down to almost 1,000 m.

Genus *Crisulipora* Robertson, 1910

Remarks — *Crisulipora* resembles *Crisia*, but the articulated internodes have between 2 and 5 transverse rows of autozooids, and the gonozooid is a more complex structure penetrated by autozooidal apertures.

Crisulipora sp.
Fig. 7

cf. 1910 *Crisulipora occidentalis* Robertson, p. 254, pl. 21, figs 22-24.
cf. 1937 *Crisulipora occidentalis* Robertson — Marcus, p. 21, pl. 3, fig. 5.
1959 *Crisulipora occidentalis* Robertson — Lagaaij, p. 484, text-fig. 5.
cf. 1995 *Crisulipora occidentalis* Robertson — Soule *et al.*, p. 309, pl. 119, figs A-D.

Material — BMNH D41290-41317.
Remarks — None of the Bowden specimens possess gonozooids and therefore it is difficult to be certain of their identity. Recent *Crisulipora occidentalis* was originally described from the Pacific coast of North America, but subsequently recorded from Brazil and Japan. Soule *et al.* (1995) suggested that *C. occidentalis* was either transported into the Atlantic as a fouling organism, or that more than one species exists. Clearly, fouling can be excluded in the case of the Bowden fossil material. Study of material from various localities is required to resolve the systematics of *Crisulipora*, and we prefer not to assign the Bowden specimens to a species until this is done. However, the narrow internodes of the Bowden material prompt a tentative comparison with the Japanese species *Crisulipora ijimai* which was described, but not figured, by Okada (1917).
Ecology — *Crisulipora occidentalis* can be found from low tide to 86 m (Soule *et al.*, 1995).

Suborder Tubuliporina Milne-Edwards, 1838
Family Diastoporidae Gregory, 1899

Genus *Plagioecia* Canu, 1918

Remarks — *Plagioecia* is a multiserial, sheet-like, typically encrusting tubuliporine in which the gonozooid is transversely elongate and pierced by autozooidal apertures.

?Plagioecia dispar Canu & Bassler, 1928
Fig. 1

cf. 1928 *Plagioecia dispar* Canu & Bassler, p. 159, pl. 31, fig. 10.
cf. 1982 *Plagioecia dispar* Canu & Bassler — Winston, p. 155, fig. 94.

Material — BMNH D41289.
Remarks — The single Bowden specimen is detached from its substratum and is infertile. Therefore, its identification as *Plagioecia* can only be tentative. Neither *P. dispar* nor any similar species have previously been recorded from Bowden; *P. dispar* was originally described from the Recent of the Straits of Florida, but Winston (1982) noted its presence as far north as Cape Hatteras.
Ecology — Winston's (1982) material of *P. dispar* came from 60-90 m depth, and Canu & Bassler's (1928) from 102 m.

Family Mecynoeciidae Canu, 1918
Genus *Mecynoecia* Canu, 1918

Remarks — *Mecynoecia* has erect, narrow branches ('vinculariiform') and simple bulbous gonozooids.

Mecynoecia proboscideoides (Smitt, 1872)
Figs 8, 9

1872 *Entalophora deflexa* (Couch) — Smitt, p. 11, pl. 5, figs 28-30.
1872 *Entalophora proboscideoides* Smitt, p. 11, pl. 4, figs 26, 27.
1928 *Mecynoecia deflexa* Smitt — Canu & Bassler, p. 160, pl. 31, fig. 1.
1928 *Entalophora proboscideoides* Smitt — Canu & Bassler, p. 160, pl. 34, fig. 11.

Material — UF 75951-52.
Remarks — Smitt (1872) described two similar species from the Recent of Florida; *Entalophora proboscideoides* and *E. deflexa*. The former was described as a new species, but the latter is evidently a re-attribution of *Tubulipora deflexa* Couch, 1842, a European species now assigned to *Entalophoroecia* (see Hayward & Ryland, 1985, p. 113), which differs from the Floridan species in having a more complex gonozooid. Both of Smitt's putative species have autozooids of about the same size, but his *E. deflexa* has slightly broader branches. However, branch width is notoriously variable in vinculariiform cyclostomes (cf. Flor, 1972) and the two species described by Smitt are provisionally regarded as synonyms.
Ecology — Recorded from 26-110 m depth in Florida and Panama.

Order Cheilostomatida Busk, 1852
Suborder Malacostegina Levinsen, 1902
Family Membraniporidae Busk, 1852
Genus *Biflustra* d'Orbigny, 1852

Remarks — Zooids of *Biflustra* have slightly to moderately developed cryptocysts, and the gymnocyst is absent or present only as tubercles. In well-preserved zooids, cryptocystal denticles may be developed. Ovicells and avicularia are lacking. The ancestrula (rarely seen in fossils) is twinned, as in *Membranipora*, but, unlike the aragonitic *Membranipora*, the skeleton of *Biflustra* is calcitic (Taylor & Monks, 1997). Colony form is variable both within the genus and within species of *Biflustra*. Some colonies are entirely encrusting, whereas others develop erect growth commonly in the form of tubular branches ('cavariiform' or 'hemescharan') or bifoliate fronds.

Biflustra monilifera (Canu & Bassler, 1919)
Figs 2-4

? 1873 *Biflustra savartii* Audouin — Smitt, p. 20, pl. 4, figs 92-95.
1919 *Acanthodesia savartii* forma *monilifera* Canu & Bassler, p. 79, pl. 2, figs 2, 3.
1919 *Acanthodesia savartii* forma *texturata* Reuss — Canu & Bassler, p. 79, pl. 5, figs 1-5.
1923 *Acanthodesia savarti* forma *monilifera* Canu & Bassler — Canu & Bassler, p. 32, pl. 2, figs 2, 3.
1923 *Acanthodesia savarti* forma *texturata* Canu & Bassler — Canu & Bassler, p. 32, pl. 5, figs 1-5; pl. 46, figs 8, 9.

Material — UF 75953-4, BMNH D34301-5, D41113 (sample).
Remarks — The systematics of *Biflustra* require revision and our assignment of this species to *B. monilifera* is provisional. The Bowden species, which has tubular branches, differs from *B. savartii*, described originally from the Recent of Egypt, in having a narrower proximal cryptocyst (see Taylor & Foster, 1994). *Biflustra arborescens* Canu & Bassler, 1928 is another similar species, but this form, from North Africa and the Bay of Biscay, has bilamellar colonies (Alvarez, 1990). Our material shows gymnocystal tubercles which are not mentioned or figured by Smitt (1873) in his description of supposed *B. savartii* from the Recent of Florida. The identity of *Biflustra texturata* (Reuss, 1848) is unclear, although it is

thought unlikely that this species from the Miocene of the Paratethys is conspecific with the Bowden specimens. Canu & Bassler (1919) had only a single specimen of *B. monilifera*, from the Miocene 'Bowden horizon' of Santo Dominigo (Dominican Republic), but the tubular colony-form and existence of gymnocystal tubercles suggests that this may be the most appropriate name for the abundant material of *Biflustra* found in the Bowden shell bed of Jamaica.

Ecology — Tubular colonies of *Biflustra* grow around algae or hydroids (see, for example, Cook, 1968, p. 123), but are not closely adpressed to these organisms and do not make an impression (substrate bioimmuration) of them on the colony underside. Smitt's (1873) tubular colonies of '*B. savartii*' from Florida were dredged at a depth of 53 m.

Suborder Neocheilostomatina d'Hondt, 1985
Family Calloporidae Norman, 1903
Genus *Antropora* Norman, 1903

Remarks — *Antropora* has encrusting colonies, sometimes multilamellar, with autozooids having well-developed cryptocysts, small endozooecial ovicells, and usually interzooecial avicularia (see Osburn, 1950; Cook, 1985).

Antropora parvicapitatum (Canu & Bassler, 1923)
Figs 5, 6

1923 *Membrendoecium parvicapitatum* Canu & Bassler, p. 36, pl. 12, figs 1, 2.

Material — UF 75955, BMNH D34282.

Remarks — Although the type specimen of this species comes from the Miocene of Florida, Canu & Bassler's (1923) original description mentions material from the Bowden shell bed, and the BMNH collections contain a Bowden specimen identified and donated by R.S. Bassler. The species has a pustulose cryptocyst and a variable proximal gymnocyst which may include a single median tubercle. Several zooids show partial closure plates incorporating the operculum. These resemble similar structures described by Lagaaij (1963, p. 165) from '*Membranipora tenuissima*'. Small polymorphic zooids are found between the autozooids and appear to be kenozooids rather than avicularia. The ovicell is very small. Generic placement is uncertain; *Membrendoecium* has been regarded as a junior synonym of *Antropora* (Bassler, 1953, p. G160), but the apparent absence of avicularia in the Bowden species calls into question its assignment to *Antropora*.

Family Quadricellariidae Gordon, 1984
Genus *Nellia* Busk, 1852

Remarks — *Nellia* is characterised by erect articulated colonies ('cellariiform') with quadriserial internodes which invariably become separated on fossilisation. Autozooids have a shelf-like proximal cryptocyst and a narrow gymnocyst with a pair of small avicularia near the proximolateral corners of the gymnocyst. Ovicells are very inconspicuous.

Nellia tenella (Lamarck, 1816)
Fig. 16

1816 *Cellaria tenella* Lamarck, p. 135.
1852 *Nellia oculata* Busk, p. 18, pl. 64, fig. 6; pl. 65 (*bis*), fig. 4.
1919 *Nellia oculata* Busk — Canu & Bassler, p. 82, pl. 2, figs 5-7.
1923 *Nellia oculata* Busk — Canu & Bassler p. 55, pl. 2, figs 5-7.
1959 *Nellia oculata* Busk — Lagaaij, p. 482, text-fig. 1.
1966 *Nellia tenella* (Lamarck) — Cheetham, p. 48, text-fig. 28.
1969 *Nellia oculata* Busk — Lagaaij, p. 167, fig. 2.
1984 *Nellia tenella* (Lamarck) — Winston & Cheetham, p. 257, figs 1, 2.

Material — BMNH D41127-D41206.

Remarks — *Nellia oculata* is regarded as a junior synonym of *N. tenella* (Cheetham, 1966). This species has been labelled as a living fossil, ranging from the Maastrichtian to the Recent (Winston & Cheetham, 1984). At the present day *N. tenella* is widely distributed throughout the tropics and subtropics (Lagaaij, 1959).

Ecology — Rucker (1967) found this species to be abundant on the outer shelf of Venezuela-British Guiana, mainly in calcareous sand facies. Although the species can be found in shallow water (less than 4 m), it may occur at depths of up to 1,000 m, and Winston & Cheetham (1984) noted that palaeoecological interpretation must take into account the possibility of allochthonous deposition.

Family Cupuladriidae Lagaaij, 1952
Genus *Cupuladria* Canu & Bassler, 1919

Remarks — *Cupuladria* is a free-living, so-called lunulite or 'lunulitiform' bryozoan. The colony has the shape of a Chinese hat, with the zooids opening on the upper convex surface. Distal to each autozooid is an avicularium (or vibraculum). The underside of the colony is divided into a series of roughly rectangular sectors with pores.

Cupuladria biporosa Canu & Bassler, 1923
Figs 10-13

1919 *Cupuladria canariensis* Busk — Canu & Bassler, p. 78 (? *partim*).
1923 *Cupuladria biporosa* Canu & Bassler, p. 29, pl. 47,

figs 1, 2.

1965b *Cupuladria biporosa* Canu & Bassler — Cook, p. 203, pl. 1, figs 2A, B, 3A, B, 4A, B, 5, 6A, B; text-fig. 1g-j.

1994 *Cupuladria biporosa* Canu & Bassler — Cook & Chimonides, p. 260, figs 6, 8, 9, 11, 12, 14.

Material — UF 75956-8, BMNH D34293-6, D41117 (sample).

Remarks — *Cupuladria biporosa* has been confused in the past with *C. canariensis*, but the morphology of the vicarious avicularium is different: those of *C. biporosa* have more extensive proximal gymnocysts (see Cook & Chimonides, 1994, figs 7, 8). Originally described from the 'Bowden' of the Dominican Republic, the holotype of *C. biporosa* was refigured by Cook & Chimonides (1994, fig. 9). Cook (1965b, pl. 1, figs 5, 6) figured material of this species from the Bowden shell bed of Jamaica. The name *biporosa* is somewhat inappropriate because, as shown by Cadée (1981, table 2), there are usually more than two pores per basal sector.

Ecology — This Miocene to Recent species ranges from 13-150 m depth at the present day. On the Venezuela-British Guiana shelf it is very abundant throughout the calcareous sand facies of the outer shelf (Rucker, 1967), while in the Ilha Grande region of Brazil it prefers sandy bottoms deeper than 40 m (Tommasi *et al.*, 1972).

Genus *Discoporella* d'Orbigny, 1852

Remarks — *Discoporella* resembles the related *Cupuladria*, but the zooids have a more extensive frontal shield, including a well-developed vestibular arch, and vicarious avicularia are absent (Cook & Chimonides, 1994).

Discoporella umbellata (Defrance, 1823)
Fig. 14

1823 *Lunulites umbellata* Defrance, p. 361, pl. 47, figs 1, 1a, 1b.

1919 *Cupularia umbellata* (Defrance) — Canu & Bassler, p. 85, pl. 1, figs 5-7; pl. 2, figs 17-21.

1923 *Cupularia umbellata* (Defrance) — Canu & Bassler, p. 80, pl. 2, figs 15-19.

1965a *Discoporella umbellata* (Defrance) — Cook, p. 177, pl. 1, fig. 7; pl. 3, figs 1, 3, 5, 6; text-fig. 4.

1985 *Discoporella umbellata* (Defrance) — Cook, p. 93, pls 4C, 5A, 5B.

Material — BMNH D34286-9, D41118 (sample), BZ 3504.

Remarks — *D. umbellata* as presently understood is widely distributed geographically and long-ranging. Cook (1985) regarded it as a species complex.

Ecology — Rucker (1967) noted that *D. umbellata* is abundant in the calcareous sand facies along the outer shelf of Venezuela-British Guiana. Tommasi *et al.* (1972) found it at depths of 11-150 m in the Ilha Grande region of Brazil, where it is particularly common in very fine sand.

Family Candidae d'Orbigny, 1851
Genus *Canda* Lamouroux, 1816

Remarks — *Canda* has thinly-calcified, erect colonies with zooids arranged in two series facing obliquely outwards from a median keel and having well-developed cryptocysts (Gordon, 1984).

Canda caraibica Levinsen, 1909

1909 *Canda caraibica* Levinsen, p. 142.

1959 *Canda caraibica* Levinsen — Lagaaij, p. 483, text-fig. 3a, b.

Material — BMNH D41207.

Remarks — Only one small fragment of this species is known from the Bowden shell bed. This specimen has been adequately illustrated by Lagaaij (1959).

Ecology — Lagaaij (1959) referred to this as a shallow-water form, citing two occurrences from 22 m depth, while Osburn (1914) recorded specimens from 17 m in Florida.

Family Steginoporellidae Hincks, 1884
Genus *Steginoporella* Smitt, 1873

Remarks — *Steginoporella* is characterised by having two types of autozooids, A- and B-zooids. The B-zooids have enlarged mandibles which are reflected in the larger size of the opesium and sometimes in a shelf-like rostrum. The cryptocyst is well developed and has a median process. There is no gymnocyst and ovicells are lacking.

Steginoporella parvicella Canu & Bassler, 1919
Fig. 15

1919 *Steganoporella parvicella* Canu & Bassler, p. 89, pl. 6, figs 6-9.

1923 *Steganoporella parvicella* Canu & Bassler — Canu & Bassler, p. 62, pl. 6, figs 6-9.

1979a *Steginoporella parvicella* Canu & Bassler — Pouyet & David, p. 789, text-fig. 3.

Material — UF 75959, BMNH D34292, D41124 (sample).

Remarks — The only species of *Steginoporella* from the Bowden shell bed has unilamellar colonies and relatively small zooids (Pouyet & David, 1979a).

Ecology — *Steginoporella parvicella* is extinct, but the related *S. magnilabris* (Busk) occurs commonly from low water to 27 m in Florida (Osburn, 1914), and can be found down to almost 70 m. With one exception, *Steginoporella*

is tropical or subtropical (Pouyet & David, 1979b).

Family Thalamoporellidae Levinsen, 1909
Genus *Thalamoporella* Hincks, 1887

Remarks — Caliper-compass or bow-shaped calcareous spicules are present within the coelomic cavity of zooids in *Thalamoporella*, but are not often found in fossils. Autozooids have extensive cryptocysts pierced by opesiules. Ovicells are bilobate, and avicularia tend to be large and acuminate or spatulate.

Thalamoporella biperforata Canu & Bassler, 1919
Figs 18-20

1919 *Thalamoporella biperforata* Canu & Bassler, p. 88, pl. 6, figs 10-15.
1923 *Thalamoporella biperforata* Canu & Bassler — Canu & Bassler, p. 62, pl. 6, figs 10-15.
1992 *Thalamoporella biperforata* Canu & Bassler — Soule *et al.*, p. 42, figs 57-59.

Material — UF 75960-1, BMNH D34297, D41126 (sample).
Remarks — The erect, bifoliate colonies of *T. biperforata* are sometimes preserved with the two layers separated. Avicularia are long and have two large opesiules. Soule *et al.* (1992) were able to find compass-shaped spicules only. Ovicells were not seen in our material and Soule *et al.* (1992) noted only the beginnings of an ovicell in one specimen.

Thalamoporella chubbi Lagaaij, 1959
Figs 17, 21

1959 *Thalamoporella chubbi* Lagaaij, p. 483, text-fig. 2a-c.
1992 *Thalamoporella chubbi* Lagaaij — Soule *et al.*, p. 69, figs 99, 100.

Material — UF 75962, BMNH D41208 (holotype), D41209-47 (paratypes).
Remarks — *Thalamoporella chubbi* differs from *T. biperforata* in having larger zooids, tubular, 'cavariiform' colonies (like those of *Biflustra monilifera*), and avicularia without opesiules. Unlike *T. biperforata*, ovicells are very common in *T. chubbi*. The species is known only from the Bowden shell bed of Jamaica.

Suborder Ascophorina Levinsen, 1909
Infraorder Umbonulomorpha Gordon, 1989
Family Adeonidae Busk, 1884
Genus *Adeonellopsis* MacGillivray, 1886

Remarks — *Adeonellopsis* is an encrusting or more often erect, bifoliate genus characterised by marginal areolae, suboral avicularia, and often vicarious and small adventitious avicularia (see Lidgard, 1996).

Adeonellopsis deformis (Canu & Bassler, 1919)
Figs 22, 23

1919 *Bracebridgia deformis* Canu & Bassler, p. 97, pl. 3, figs 11-16.
1923 *Bracebridgia deformis* Canu & Bassler — Canu & Bassler, p. 160, pl. 8, figs 11-16.
in pr. *Adeonellopsis deformis* (Canu & Bassler) — Cheetham *et al.*

Material — UF 75963-4, BMNH D34290-1, D41115 (10 specimens).
Remarks — As with many other species of *Adeonellopsis* there is considerable frontal thickening which obscures the primary orifice and adventitious avicularia in older branches. Colonies comprise narrow bifoliate branches ('adeoniform').

Family Lepraliellidae Vigneaux, 1949
Genus *Celleporaria* Lamouroux, 1821

Remarks — *Celleporaria* typically has massive colonies formed by frontal budding. Autozooidal orifices are usually non-sinuate (but see below) and ovicells are imperforate (Gordon, 1984).

Celleporaria? hemispherica (Canu & Bassler, 1923)
Figs 24-26

1923 *Holoporella hemispherica* Canu & Bassler, p. 176, pl. 3, figs 9, 10.

Material — UF 75965-6, BMNH D34283-5.
Remarks — This species has small hemispherical colonies formed by piles of frontally budded zooids. Generic attribution of such celleporiform colonies is often difficult in fossil material because the diagnostic ovicells are rarely preserved, as in the Bowden species. Although Gordon (1984, p. 115) described *Celleporaria* as having a non-sinuate orifice, a sinus (or notch) does exist in some species which are traditionally assigned to this genus. Notably *C. brunnea* (Hincks), as figured by Winston (1986, fig. 20), has a shallow but distinct sinus and an overall orifice shape which is very similar to the Bowden species. Consequently, we assign the Bowden species questionably to *Celleporaria* (*Holoporella* is generally regarded as a junior synonym of *Celleporaria*; see Harmer, 1957, p. 664).

Celleporaria? hemispherica lacks the abundant spatulate, interzooecial avicularia found in *C. brunnea* (see, for example, Soule *et al.*, 1995, pl. 101, fig. A).

Family Cheiloporinidae Bassler, 1953
Genus *Hippaliosina* Canu, 1918

Remarks — This encrusting genus has autozooids with granular frontal walls and marginal areolae, an elongate orifice and lateral avicularia.

? Hippaliosina baccata (Canu & Bassler, 1920)
Fig. 27

1920 *Hippodiplosia baccata* Canu & Bassler, p. 397, pl. 87, figs 5, 6.
1923 *Hippodiplosia baccata* Canu & Bassler — Canu & Bassler, p. 131, pl. 3, fig. 1.

Material — BMNH D34298-300, D41120.
Remarks — The Bowden material of ? *H. baccata* consists of unilamellar encrusting colonies with autozooids having a conspicuous granular ornament on the frontal wall. Adventitious avicularia are located singly to one side of the autozooidal orifice. The orifice is not well preserved in the scanned material, but its probable shape can be inferred by comparison with the related species *H. rostrigera* (Smitt) as depicted by Winston (1982, fig. 65). ? *Hippaliosina baccata* differs from this latter species in having more rounded avicularia.

This species was originally described from the Lower Miocene of Mississippi and later identified from the Bowden shell bed of Jamaica. The Mississippi material figured by Canu & Bassler (1920) appears to be more thickly calcified around the orifice, and the Bowden material may perhaps represent a different species.

Family Metrarabdotosidae Vigneaux, 1949
Genus *Metrarabdotos* Canu, 1914

Remarks — In most species of *Metrarabdotos*, colonies are bifoliate ('adeoniform' or 'eschariform'), although a few are encrusting. The elongate autozooids have large marginal areolae and there are polymorphic gonozooids with costulate ovicells.

Metrarabdotos lacrymosum Canu & Bassler, 1919
Figs 28, 29

1919 *Metrarabdotos lacrymosum* Canu & Bassler, p. 96, pl. 3, figs 1-10.
1923 *Metrarabdotos lacrymosum* Canu & Bassler — Canu & Bassler, p. 164, pl. 8, figs 1-10.
1968 *Metrarabdotos (Biavicularium) lacrymosum* Canu & Bassler — Cheetham, p. 87, pl. 9, fig. 5; pl. 12, fig. 1.
1986 *Metrarabdotos lacrymosum* Canu & Bassler — Cheetham, figs 6C, F, 7C.

Material — UF 75967-8, BMNH D34309-12, D41123 (3 pieces).

Remarks — This species was thoroughly redescribed by Cheetham (1968) based on material from Bowden and has since been depicted using SEM (Cheetham, 1986). *Metrarabdotos lacrymosum* ranges from the late Miocene (NN 11) to the late Pliocene (NN 16) (Cheetham, 1986).

Infraorder Lepraliomorpha Gordon, 1989
Family Schizoporellidae Jullien, 1883
Genus *Schizoporella* Hincks, 1877

Remarks — *Schizoporella* is a common and diverse genus with encrusting, often multilamellar colonies. The autozooids have evenly perforated frontal walls, an orifice with a distinct proximal sinus, and single or paired adventitious avicularia lateral to the orifice.

Schizoporella errata (Waters, 1879)
Fig. 32

1879 *Lepralia errata*, stadium *Hemeschara* Waters, p. 39, pl. 10, fig. 5.
1979 *Schizoporella errata* (Waters) — Hayward & Ryland, p. 170, fig. 68.

Material — UF 75969.
Remarks — Using the key given by Hayward & Ryland (1979, p. 167), the Bowden *Schizoporella* is apparently *S. errata* (Waters). This is a widespread warm temperate-subtropical species at the present day. Some of the modern material described by Winston (1984) as *S. ?serialis* (Heller, 1867) from Belize may be the same species.

Family Petraliellidae Harmer, 1957
Genus *Petraliella* Canu & Bassler, 1927

Remarks — *Petraliella* typically has large autozooids with evenly perforate frontal walls and a large orifice indented by two or more small sinuses. The basal surface is smooth except for pores that give rise to rootlets in living colonies (Harmer, 1957).

Petraliella cf. **bisinuata** (Smitt, 1873)
Fig. 33

cf. 1873 *Escharella bisinuata* Smitt, p. 59, pl. 12, fig. 229.
? 1967 *Hippopetraliella marginata* (Canu & Bassler) — Rucker, p. 826, fig. 14h.

Material — UF 75970.
Remarks — The Bowden material differs from Recent *P. bisinuata* (Smitt) in having a proportionally larger orifice (cf. Canu & Bassler, 1928, pl. 16, fig.1), and more closely resembles Rucker's (1967) figure of *Hippopetraliella marginata* (Canu & Bassler). However, Canu & Bassler (1928)

described the orifice of this latter species as having a straight proximal border (the serrations in Canu & Bassler's figures are due to retouching; A.H. Cheetham, pers. comm., December 1996), whereas the Bowden material, when well preserved, shows two small sinuses.
Ecology — The petraliellids from the Gulf of Mexico recorded by Canu & Bassler (1928) have a depth range of 14-55 m. According to Harmer (1957, p. 693) petraliellid colonies '...often loosely encrust Sponges, to which their rootlets are attached. Tubular Hemescharan colonies, as found in *Hippopetraliella magna*, may commence as an encrustation and be prolonged as hollow tubes beyond the attached portion'.

Family Mamilloporidae Canu & Bassler, 1927
Genus *Mamillopora* Smitt, 1873

Remarks — Like *Cupuladria*, the 'lunulitiform' colonies of *Mamillopora* resemble a Chinese hat in shape, with the autozooids opening on the upper convex surface. The large orifice has paired condyles, and is surrounded by a strongly pustulose cryptocystal frontal wall which may support adventitious avicularia. The mamillate underside of the colony contains large chambers which in living colonies represent the points of origin of rootlets for anchoring the colony into the sediment.

Mamillopora tuberosa (Canu & Bassler, 1919)
Figs 30, 31, 34, 35, 37

? 1873 *Mamillopora cupula* Smitt, p. 33, pl. 7, figs 146, 147a-c.
1919 *Stichoporina tuberosa* Canu & Bassler, p. 98, pl. 1, figs 20-23; pl. 6, figs 16-19; pl. 7, figs 1-8.
1923 *Mamillopora tuberosa* (Canu & Bassler) — Canu & Bassler, p. 192, pl. 6, figs 16-19; pl. 7, figs 1-8.
1928 *Mamillopora tuberosa* (Canu & Bassler) — Canu & Bassler, p. 152.

Material — UF 75971-2, BMNH D34306-7, D41122 (sample).
Remarks — Among the specimens used by Canu & Bassler (1919) in their original description of this species were examples from the Bowden shell bed of Jamaica (pl. 7, figs 1-8). It is notable that these Bowden specimens are the only figured specimens retained in *M. tuberosa* by Canu & Bassler (1928); the Costa Rican material they transferred to *M. cavernulosa* Canu & Bassler, 1928, and the Dominican material to *M. cupula*. Cook & Chimonides (1994) found it impossible to decide whether *M. tuberosa* and *M. cavernulosa* are junior synonyms of *M. cupula*, and we have provisionally retained *M. tuberosa* here.
Ecology — The depth range of *M. cupula* was given by Canu & Bassler (1928) as 48-110 m and Rucker (1967) noted that the species is abundant and widely distributed in the calcareous sand facies of the outer Venezuela-British Guiana shelf.

Family Phidoloporidae Gabb & Horn, 1862
Genus *Schedocleidochasma* Soule *et al.*, 1991

Remarks — Colonies of *Schedocleidochasma* are encrusting with autozooids having mamillate frontal walls and a few marginal pores. The orifice is keyhole shaped. Avicularia are short and acute, and ovicells globose and imperforate (Soule *et al.*, 1991).

Schedocleidochasma porcellanum (Busk, 1860)
Fig. 36

1860 *Lepralia porcellana* Busk, p. 283, pl. 31, fig. 3.
1873 *Lepralia cleidostoma* Smitt, p. 62, pl. 11, figs 217-219.
1928 *Hippoporina cleidostoma* (Smitt) — Canu & Bassler, p. 104, pl. 9, fig. 7; pl. 32, fig. 5; text-fig. 18.
1964 *Cleidochasma porcellanum* (Busk) — Cook, p. 11, pl. 1, fig. 4; pl. 2, figs 1, 2; text-figs 4A-E.
1982 *Cleidochasma porcellanum* (Busk) — Winston, p. 147, fig. 80.
1991 *Schedocleidochasma porcellanum* (Busk) — Soule *et al.*, p. 481.

Material — UF 75973.
Remarks — The Bowden fossil retains the porcellanous appearance from which this extant species takes its name.
Ecology — This species has a circumtropical distribution in the Atlantic at the present day. Depth ranges from 9-220m (Shier, 1964; Cook, 1964).

DISCUSSION

The Bowden bryozoan fauna now stands at 43 species (Table 1), of which 19 are considered herein and 17 are figured. In the UF samples, the following species were found to be particularly common: *Biflustra monilifera*, *Cupuladria biporosa*, *Thalamoporella biperforata*, *T. chubbi*, *Adeonellopsis deformis* and *Metrarabdotos lacrymosum*. Three of these have erect bifoliate colonies (*T. biperforata*, *A. deformis*, *M. lacrymosum*), two erect tubular colonies (*B. monilifera*, *T. chubbi*), and one a free-living lunulitiform colony (*C. biporosa*). Encrusting colonies, which often reach high diversities, may be underrepresented in the samples available to us because they included very few shell substrates. Cheilostomes are strongly dominant, comprising 37 (86%) of the species; only four cyclostome species have been recognised. Some species (e.g., *Biflustra monilifera*, *Thalamoporella chubbi*, *Petraliella* cf. *bisinnata*) probably grew loosely around soft-bodied animals or plants.

The Bowden bryozoans clearly represent a shelf as-

semblage. Indeed, Lagaaij (*in* Rácz, 1971) noted that living representatives of the Bowden bryozoan species ranged in depth from 0 to 130 m, and inferred that a depth of deposition of between 44 and 64 metres was most probable for the Bowden shell bed. The surface preservation of the Bowden bryozoans is generally excellent, with little sign of wear, although the erect and many of the free-living colonies are fragmented. It is evident that the bodies of fresh, undecayed animals can be transported for appreciable distances without appreciable abrasion, or disarticulation in the case of animals with multielement skeletons (Allison, 1986). Therefore, lack of surface wear in fossils is not a good indicator of *in situ* deposition. Paradoxically, the unabraded condition of the Bowden bryozoans may imply quite the opposite because autochthonous bryozoan deposits tend to contain an admixture of colonies in various states of abrasion depending on how much time they spent on the sea-bed before becoming finally buried. A suitable model to explain the origin of the Bowden bryozoan fauna may be one of turbidity currents sweeping the shelf, picking up free-living colonies and the distal branches of erect colonies, and transporting and burying them in a deeper water environment.

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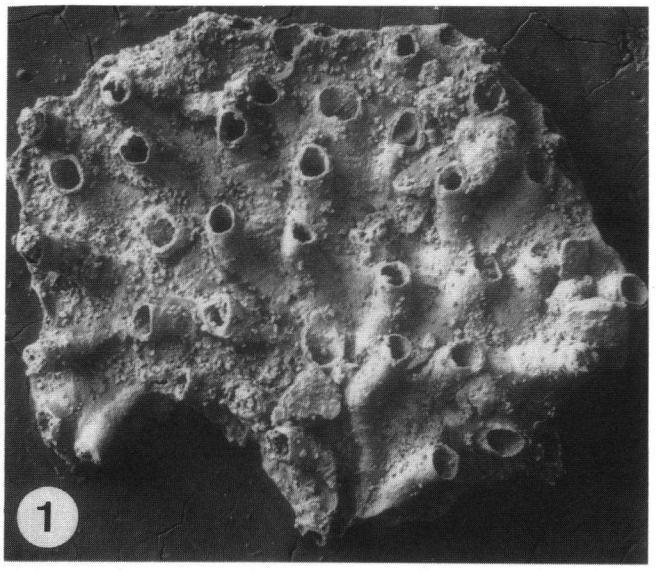
First Bowden reference	Original name	This paper
Canu & Bassler, 1919	*Acanthodesia savartii* forma *texturata* Reuss, 1848	*Biflustra monilifera* (Canu & Bassler, 1919)
Canu & Bassler, 1919	*Adeona heckeli* Reuss, 1848	----------
Canu & Bassler, 1923	*Aimulosia brevis* Canu & Bassler, 1923	----------
Canu & Bassler, 1919	*Bracebridgia deformis* Canu & Bassler, 1919	*Adeonellopsis deformis* (Canu & Bassler, 1919)
Canu & Bassler, 1923	*Callopora dumerilii* Audouin, 1826	----------
Canu & Bassler, 1919	*Callopora tenella* Hincks, 1880	----------
Lagaaij, 1959	*Canda caraibica* Levinsen, 1909	*Canda caraibica* Levinsen, 1909
Canu & Bassler, 1923	*Conopeum lacroixii* Busk, 1872	----------
Canu & Bassler, 1919	*Conopeum ovale* Canu & Bassler, 1919	----------
Lagaaij, 1959	*Crisia elongata* Milne-Edwards, 1838	*Crisia* sp.
Lagaaij, 1959	*Crisulipora occidentalis* Robertson, 1910	*Crisulipora* sp.
Canu & Bassler, 1919	*Cupuladria canariensis* Busk, 1859	*Cupuladria biporosa* Canu & Bassler, 1923
Canu & Bassler, 1919	*Cupularia umbellata* (Defrance, 1823)	*Discoporella umbellata* (Defrance, 1823)
Canu & Bassler, 1923	*Cycloperiella rubra* Canu & Bassler, 1923	----------
Canu & Bassler, 1919	*Gemellipora punctata* Canu & Bassler, 1919	----------
Canu & Bassler, 1919	*Hemiseptella grandicella* Canu & Bassler, 1919	----------
Canu & Bassler, 1923	*Hippodiplosia baccata* Canu & Bassler, 1920	?*Hippaliosina baccata* (Canu & Bassler, 1920)
Canu & Bassler, 1919	*Holoporella albirostris* Smitt, 1873	----------
Canu & Bassler, 1923	*Holoporella hemispherica* Canu & Bassler, 1923	*Celleporaria? hemispherica* (Canu & Bassler, 1923)
Canu & Bassler, 1923	*Mastigophora granulosa* Canu & Bassler, 1923	----------
This paper		*Mecynoecia proboscideoides* (Smitt, 1872)
Canu & Bassler, 1923	*Membranipora osburni* Canu & Bassler, 1923	----------
Canu & Bassler, 1923	*Membrendoecium parvicapitatum* Canu & Bassler, 1923	*Antropora parvicapitatum* (Canu & Bassler, 1923)
Canu & Bassler, 1919	*Metrarabdotos lacrymosum* Canu & Bassler, 1919	*Metrarabdotos lacrymosum* Canu & Bassler, 1919
Lagaaij, 1959	*Nellia oculata* Busk, 1852	*Nellia tenella* (Lamarck, 1816)

This paper		*?Plagioecia dispar* Canu & Bassler, 1928
This paper		*Petraliella* cf. *bisinuata* (Smitt, 1873)
Canu & Bassler, 1923	*Rhamphostomella granulosa* Canu & Bassler, 1923	----------
Canu & Bassler, 1919	*Rhamphostomella laticella* Canu & Bassler, 1919	----------
Canu & Bassler, 1923	*Rhyncozoon verruculatum* (Smitt, 1873)	----------
This paper		*Schedocleidochasma porcellanum* (Busk, 1860)
Canu & Bassler, 1919	*Schizopodrella unicornis* Johnston, 1847	possibly *Schizoporella errata* (Waters, 1879)
This paper		*Schizoporella errata* (Waters, 1879)
Canu & Bassler, 1923	*Smittina ophidiana* Waters, 1878	----------
Canu & Bassler, 1919	*Steganoporella* [sic] *parvicella* Canu & Bassler, 1919	*Steginoporella parvicella* Canu & Bassler, 1919
Canu & Bassler, 1923	*Stephanosella biaperta* Michelin, 1841	----------
Canu & Bassler, 1919	*Stichoporina tuberosa* Canu & Bassler, 1919	*Mamillopora tuberosa* (Canu & Bassler, 1919)
Canu & Bassler, 1923	*Stylopoma minuta* Canu & Bassler, 1923	----------
Canu & Bassler, 1919	*Stylopoma spongites* Pallas, 1766	----------
Canu & Bassler, 1923	*Terebripora elongata* Canu & Bassler, 1923	----------
Canu & Bassler, 1923	*Terebripora sinefilum* Canu & Bassler, 1923	----------
Canu & Bassler, 1919	*Thalamoporella biperforata* Canu & Bassler, 1919	*Thalamoporella biperforata* Canu & Bassler, 1919
Lagaaij, 1959	*Thalamoporella chubbi* Lagaaij, 1959	*Thalamoporella chubbi* Lagaaij, 1959

Table 1. Bryozoan species recorded from the Bowden shell bed.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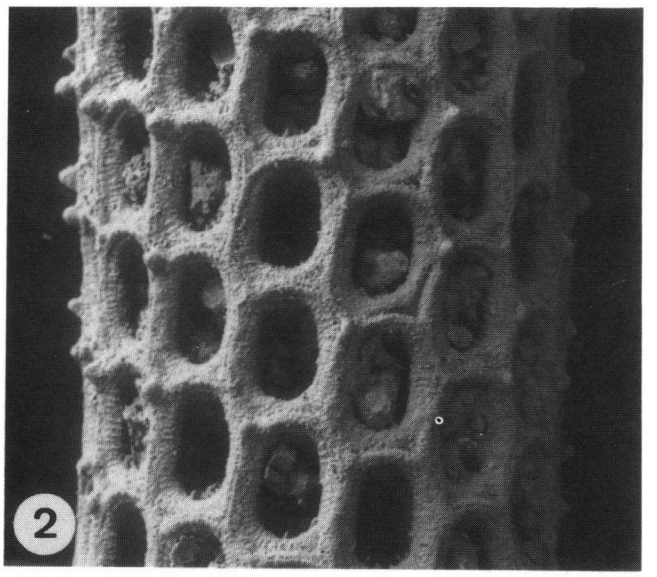
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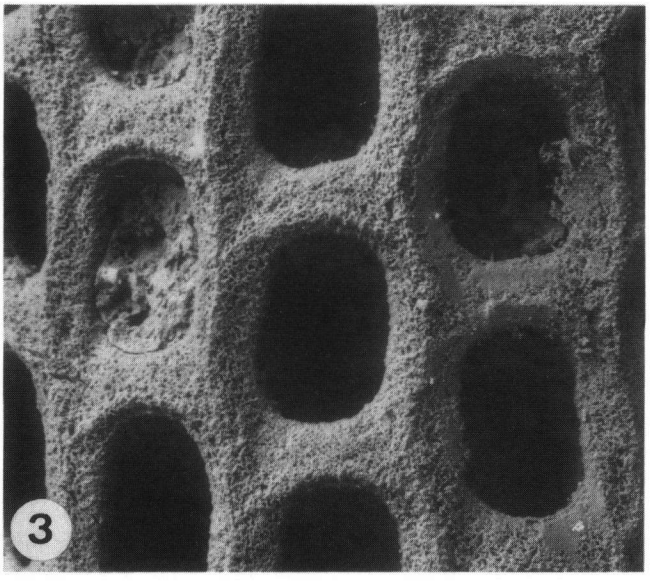
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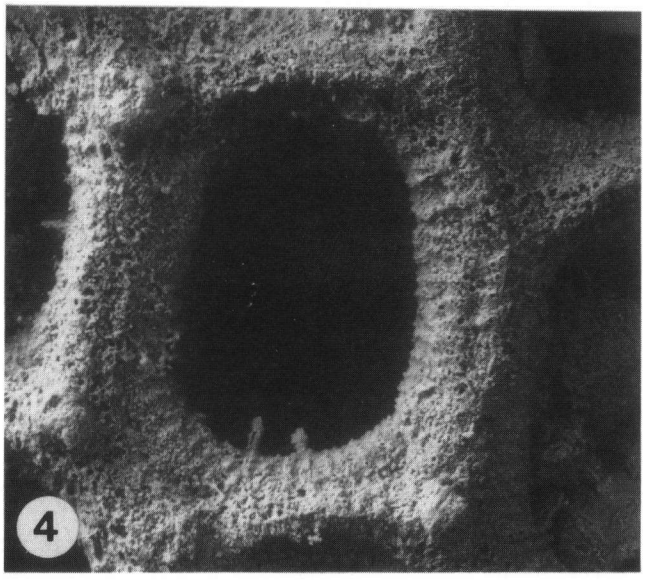
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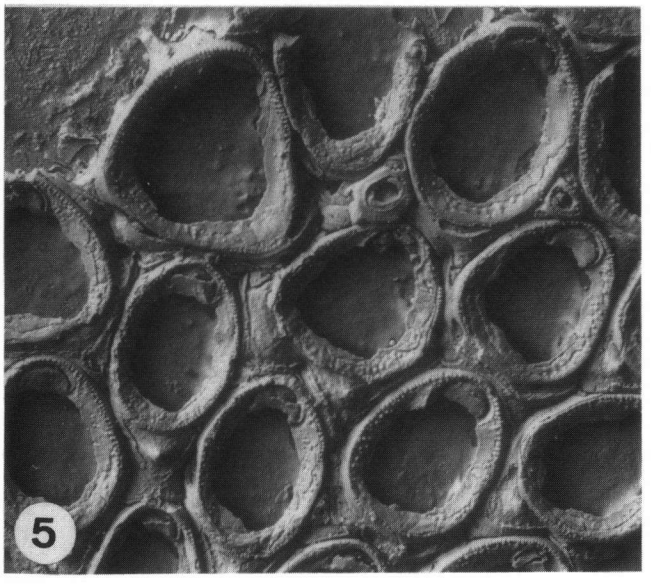
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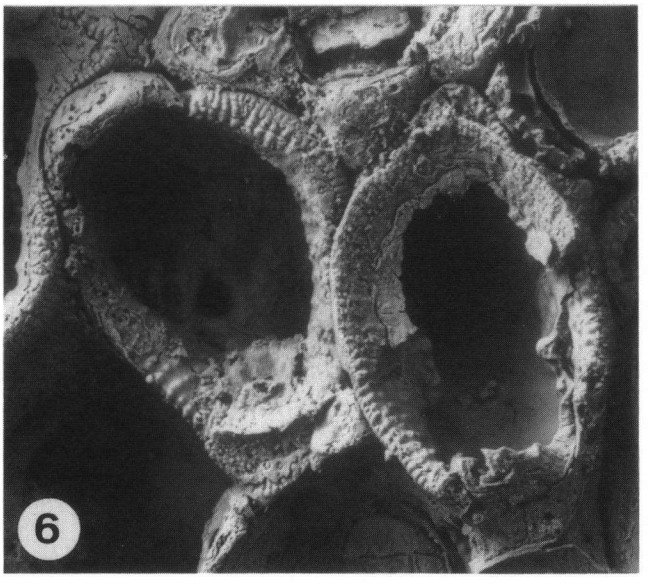
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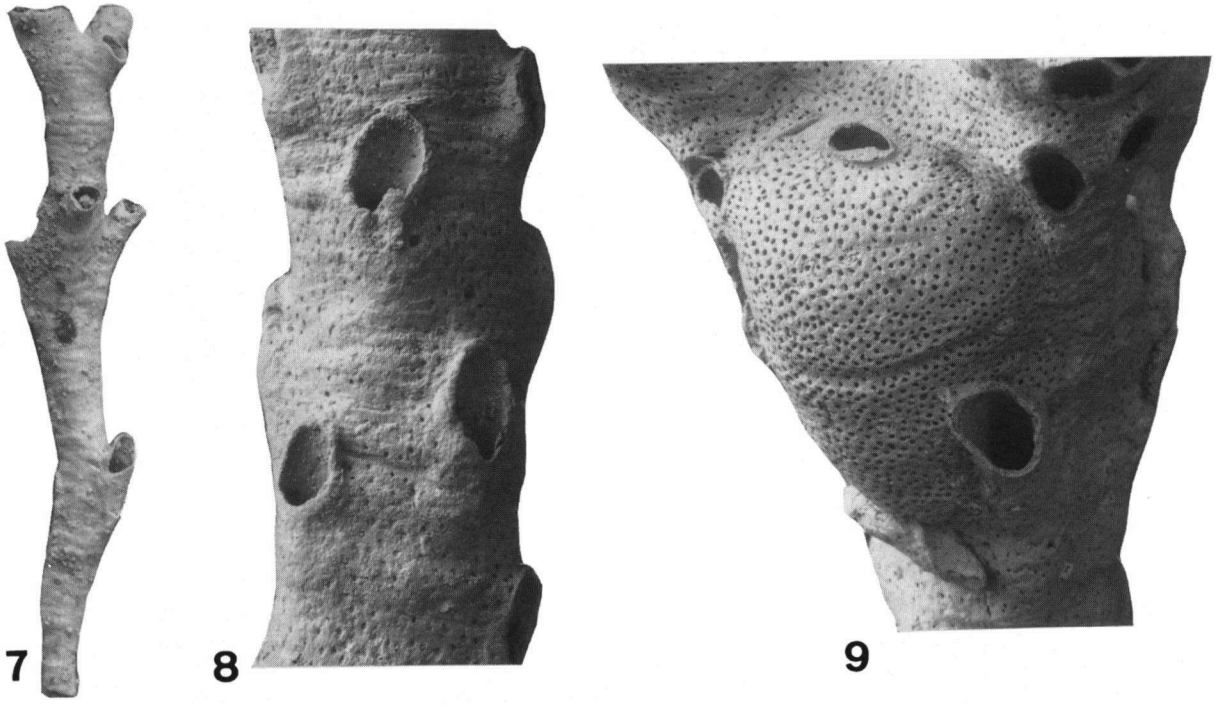
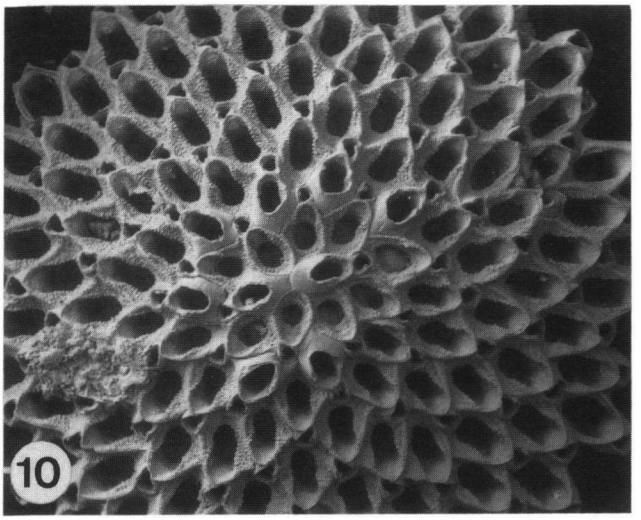
Figs 1-6. Bryozoans from the Pliocene Bowden shell bed, southeast Jamaica; **1** - ? *Plagioecia dispar* Canu & Bassler, BMNH D41289, infertile colony, x 53; **2-4** - *Biflustra monilifera* (Canu & Bassler), UF 75953, part of a tubular branch, x 45 (**2**), UF 75954, group of slightly abraded zooids, x 80 (**3**), UF 75953, well-preserved zooid with cryptocystal denticles, x 160 (**4**); **5, 6** - *Antropora parvicapitatum* (Canu & Bassler), UF 75955, variably-shaped infertile autozooids, some with partial closure plates incorporating the operculum, and small kenozooids, x 90 (**5**), BMNH D34282, autozooid with small ovicell (top left) and infertile autozooid, x 150 (**6**).



Figs 7-9. Bryozoans from the Pliocene Bowden shell bed, southeast Jamaica; **7** - *Crisulipora* sp., BMNH D41290, internode drawn by Lagaaij (1959, text-fig. 5), x 38; **8, 9** - *Mecynoecia proboscideoides* (Smitt), UF 75951, autozooids, x 80 (**8**), UF 75952, gonozooid, x 75 (**9**).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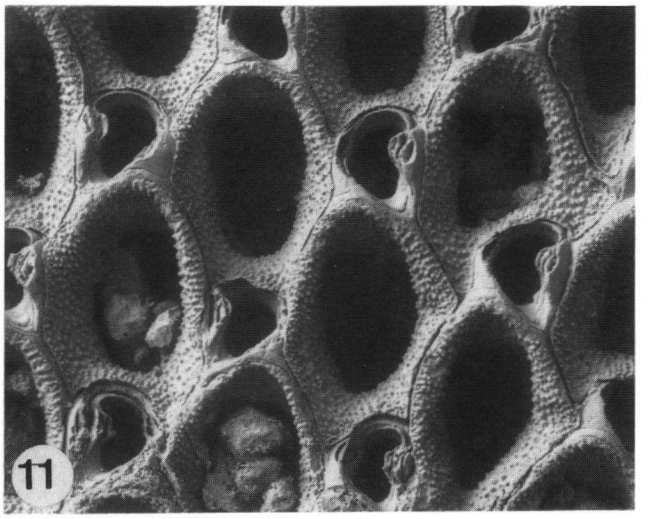
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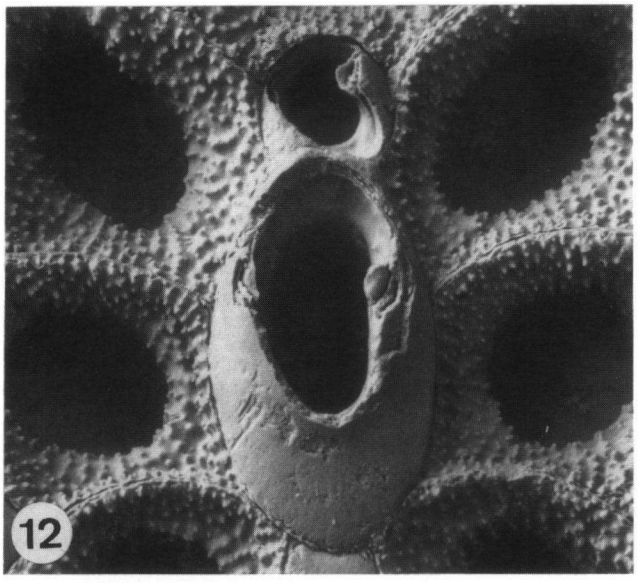
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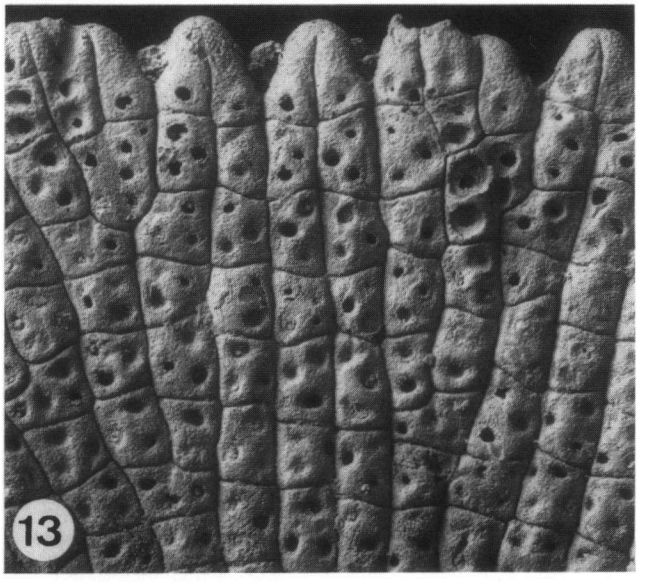
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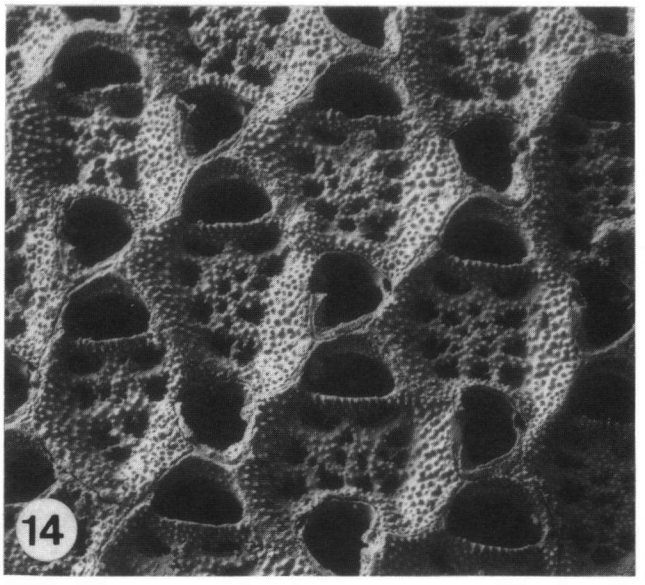
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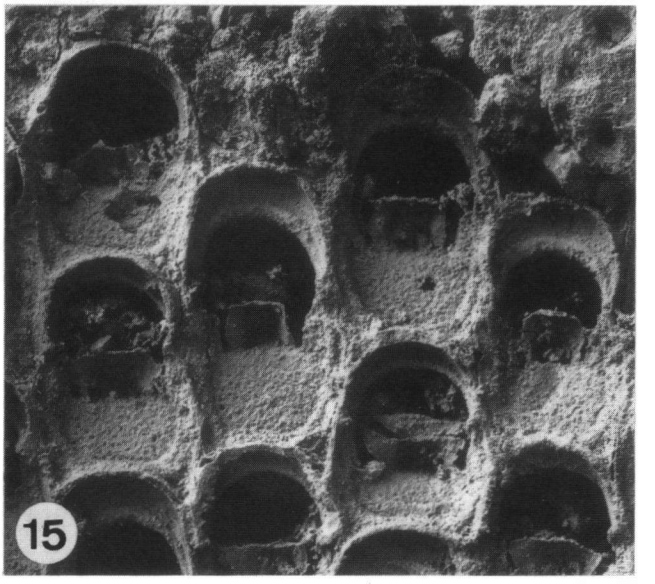
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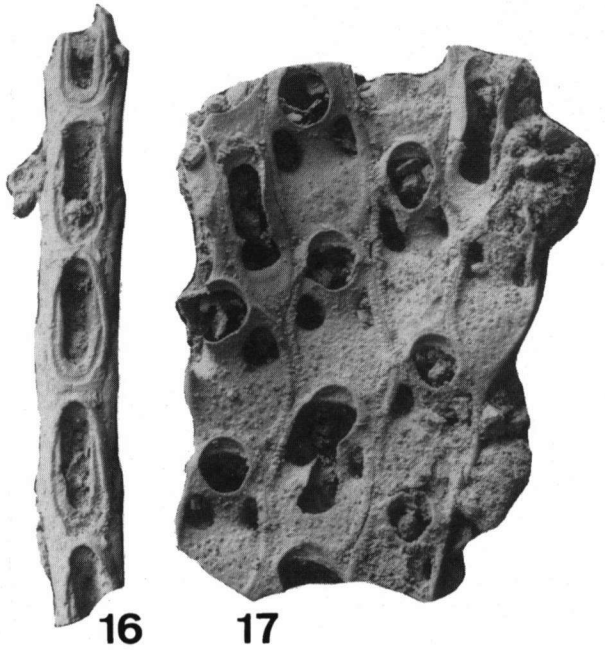
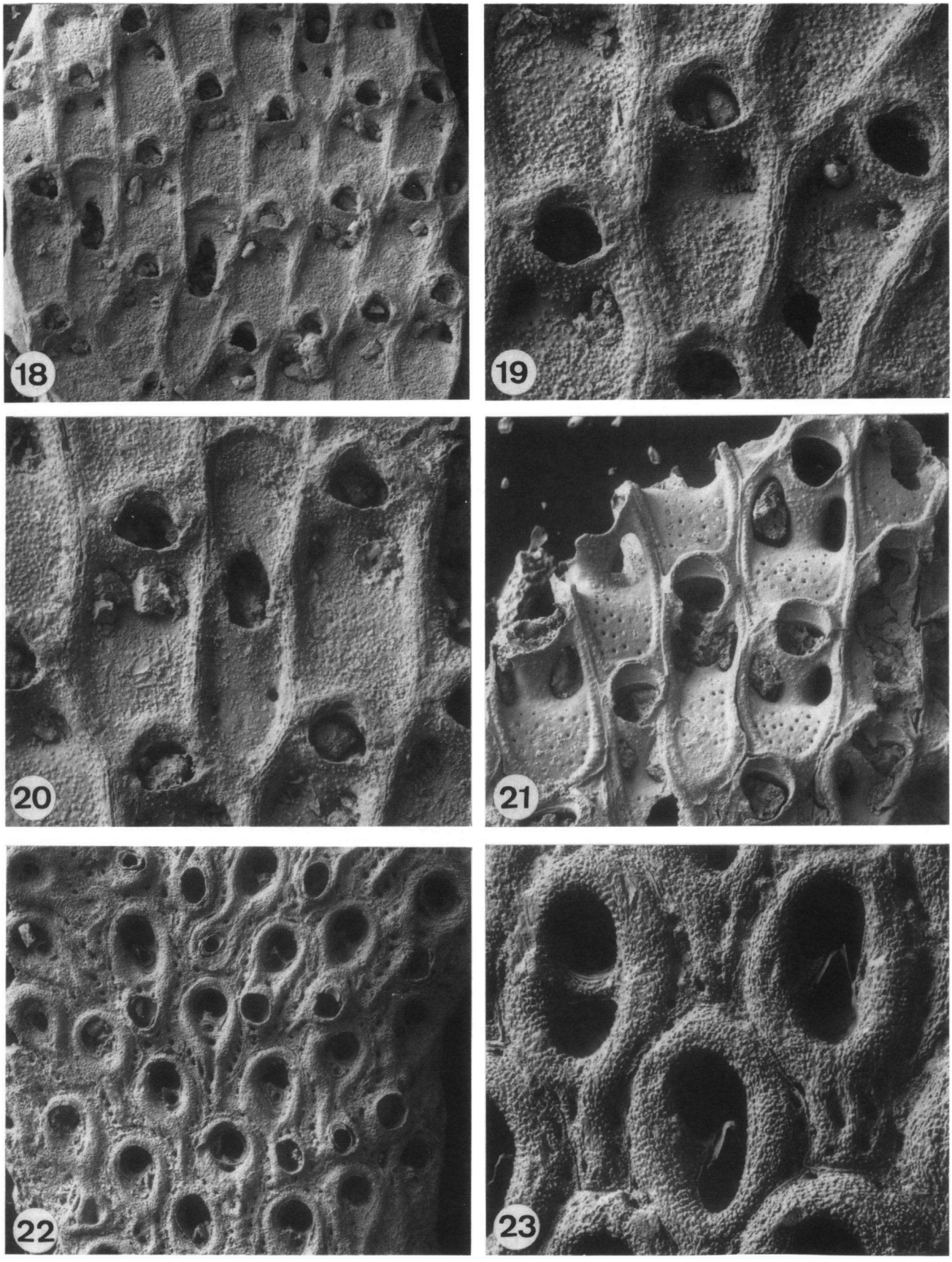
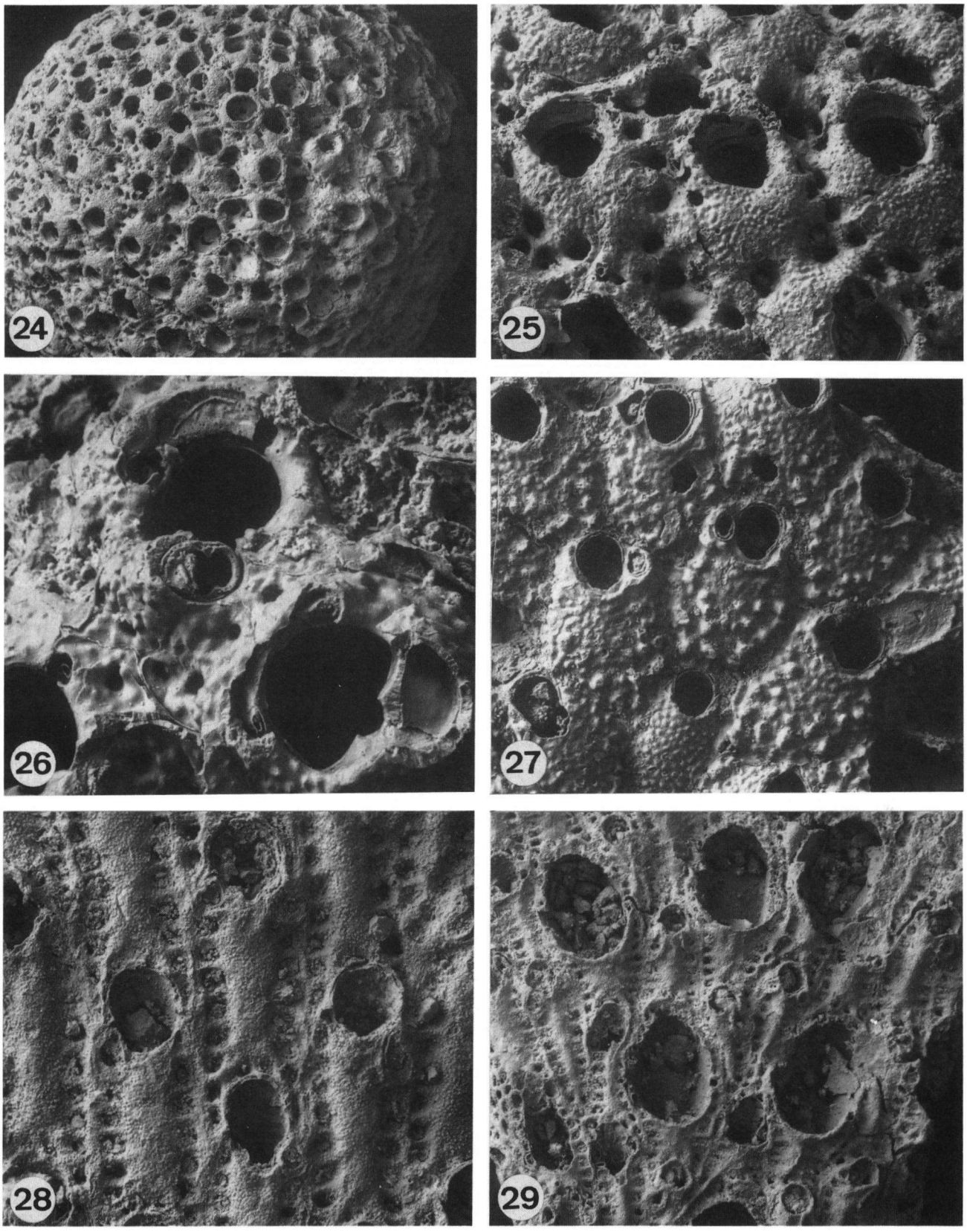
Figs 10-15. Bryozoans from the Pliocene Bowden shell bed, southeast Jamaica; **10-13** - *Cupuladria biporosa* Canu & Bassler, UF 75958, upper surface of lunulitiform colony, x 27 (**10**), UF 75956, group of autozooids with distal interzooidal avicularia, x 70 (**11**), UF 75958, large vicarious avicularium with distal interzooidal avicularium, x 170 (**12**), UF 75957, underside of colony showing sectors with pores, x 30 (**13**); **14** - *Discoporella umbellata* (Defrance), BMNH BZ 3504, group of autozooids with cribrate frontal shields and distal avicularia, x 75; **15** - *Steginoporella parvicella* Canu & Bassler, UF 75959, group of A- and B-zooids, the latter with longer opesia, x 42.



Figs 16, 17. Bryozoans from the Pliocene Bowden shell bed, southeast Jamaica; **16** - *Nellia tenella* (Lamarck), BMNH D41133, internode, x 40; **17** - *Thalamoporella chubbi* Lagaaij, BMNH D41208, holotype specimen drawn by Lagaaij (1959, text-fig. 2A) showing autozooids and two spatulate avicularia, x 38.

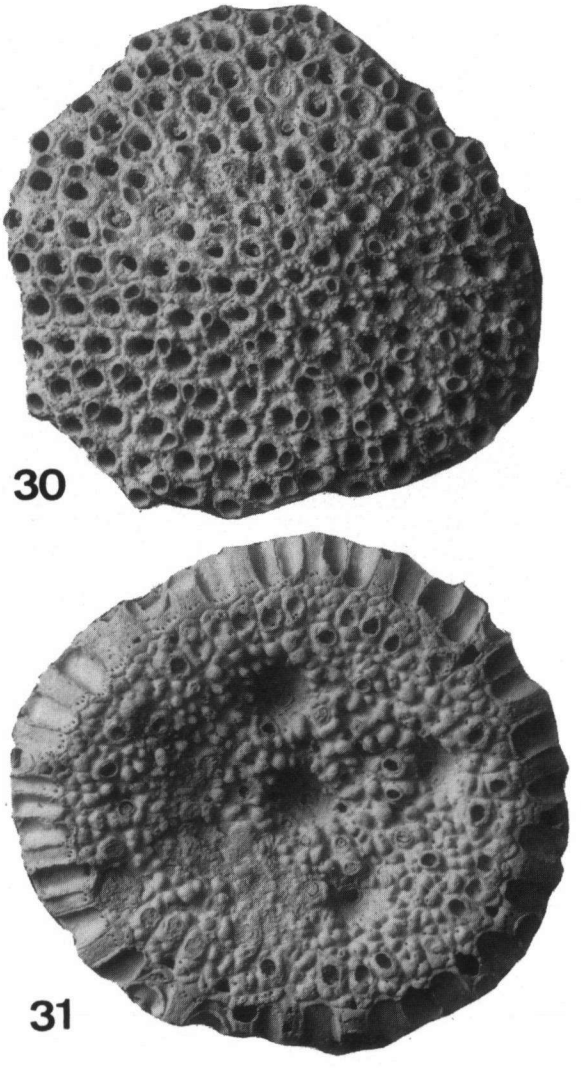


Figs 18-23. Bryozoans from the Pliocene Bowden shell bed, southeast Jamaica; **18-20** - *Thalamoporella biperforata* Canu & Bassler, UF 75960, group of autozooids and two avicularia, x 35 (**18**), UF 75961, autozooids, x 95 (**19**), UF 75961, avicularium, x 85 (**20**); **21** - *Thalamoporella chubbi* Lagaaij, UF 75962, autozooids, x 58; **22, 23** - *Adeonellopsis deformis* (Canu & Bassler), UF 75963, surface of bifoliate branch, x 50 (**22**), UF 75964, autozooids with depressed suboral avicularia, x 140 (**23**).

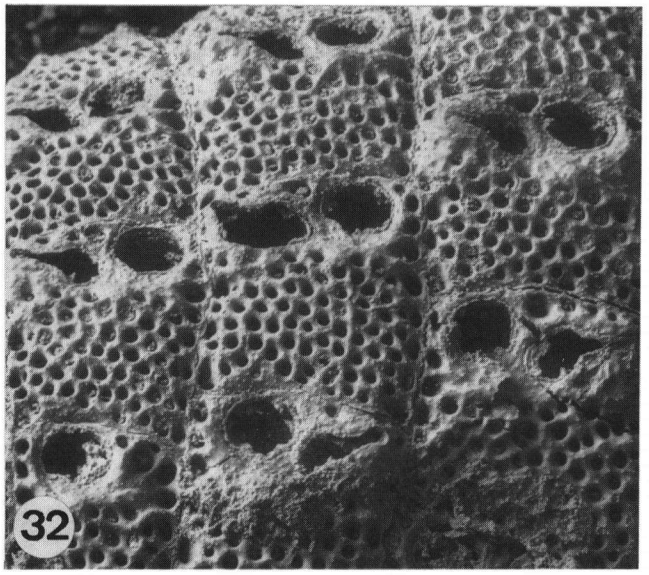


Figs 24-29. Bryozoans from the Pliocene Bowden shell bed, southeast Jamaica; **24-26** - *Celleporaria? hemispherica* (Canu & Bassler), UF 75965, top of a hemispherical colony, x 5 (**24**), UF 75965, autozooids, x 75 (**25**), UF 75966, suboral avicularia and primary orifice with sinus (lower right), x 160 (**26**); **27** - *?Hippaliosina baccata* (Canu & Bassler), BMNH D 34298, group of autozooids with small avicularia, x 80; **28, 29** - *Metrarabdotos lacrymosum* Canu & Bassler, UF 75968, autozooids, x 81 (**28**), UF 75967, gonozooids with abraded ovicells leaving large holes, x 35 (**29**).

Figs 30, 31. Bryozoans from the Pliocene Bowden shell bed, southeast Jamaica; *Mamillopora tuberosa* (Canu & Bassler), UF 75972, upper surface of a colony, x 19 (**30**), UF 75971, colony underside with four prominent rootlet chambers, x 12 (**31**).



Figs 32-37. Bryozoans from the Pliocene Bowden shell bed, southeast Jamaica; **32** - *Schizoporella errata* (Waters), UF 75969, autozooids with adventitious avicularia lateral to the orifice, x 75; **33** - *Petraliella* cf. *bisinnata*, UF 75970, autozooids and sparse adventitious avicularia (top) and ovicell vestiges on the three proximal zooids, x 35; **34, 35, 37** - *Mamillopora tuberosa* (Canu & Bassler), UF 75972, early autozooids, x 105 (**34**), later autozooids with avicularia, x 75 (**35**), autozooid orifice and avicularium, x 230 (**37**); **36** - *Schedocleidochasma porcellanum* (Busk), UF 75973, autozooids, avicularia and two abraded ovicells, x 115.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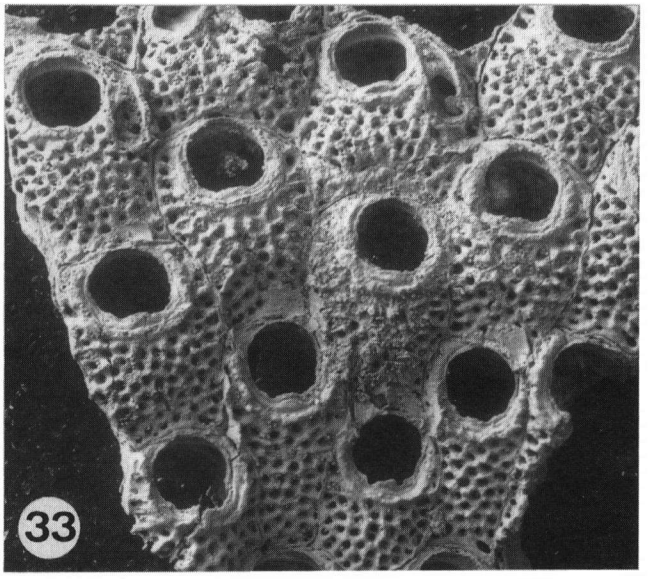
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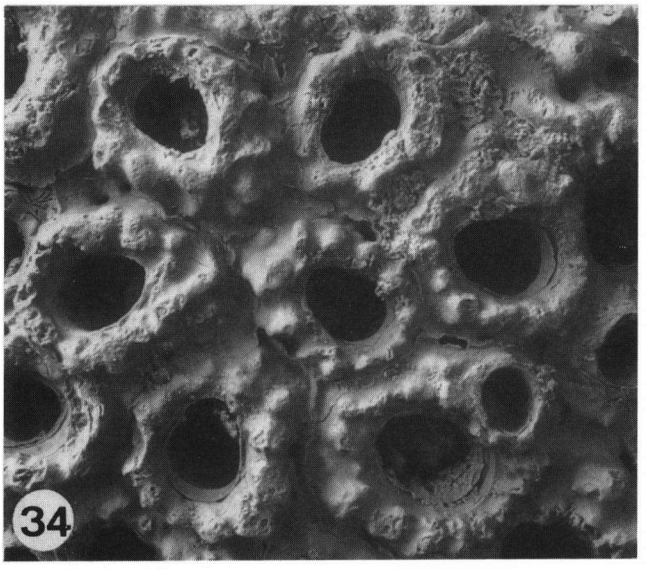
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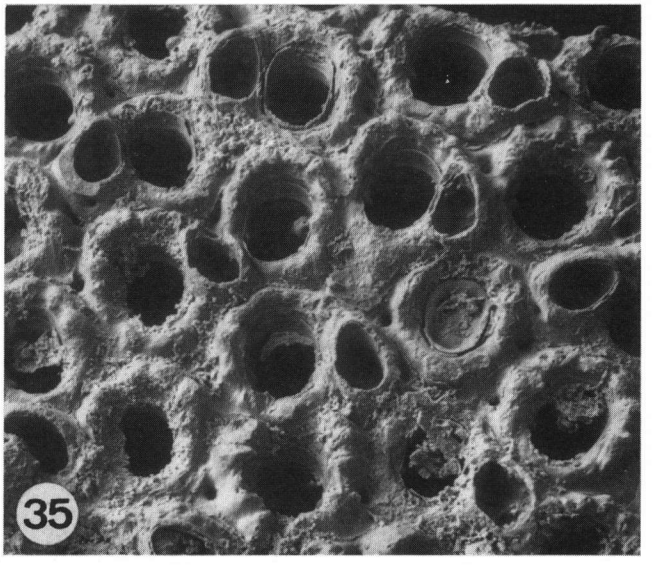
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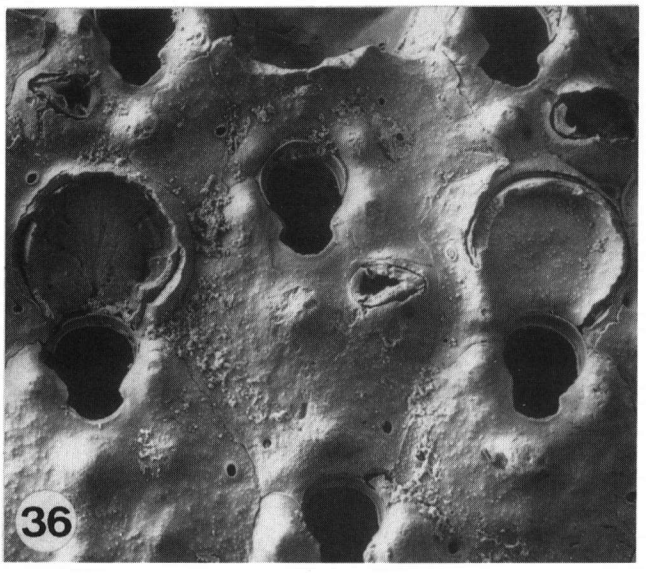
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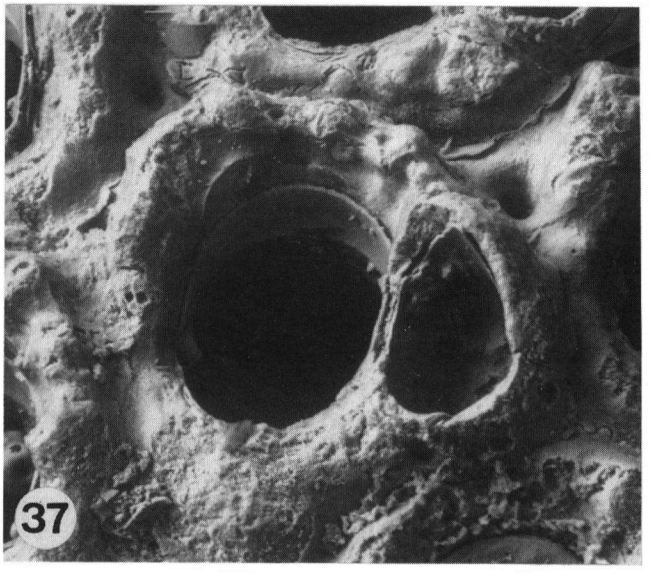
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