

THE POTENTIAL OF MINUTE BRYOZOAN COLONIES IN THE ANALYSIS OF DEEP SEA SEDIMENTS.

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Résumé

Les corrélations entre la forme des colonies (morphotypes) et leur environnement sont bien établies pour les récifs peu profonds de Bryozoaires, particulièrement pour les colonies spécialement adaptées aux milieux marins sableux et vaseux. Des déductions paléocéologiques peuvent être obtenues par l'étude des restes squelettiques dans les sédiments. Les morphotypes d'eaux profondes et de fonds vaseux sont également spécialisés et se répartissent en six groupes, dont quatre ont des systèmes d'ancrage enracinés. Le groupe qui comprend les colonies les plus petites, très calcifiées, a été le mieux préservé dans les sédiments à travers les âges, de l'Eocène à la période récente. Malgré l'abondance des colonies de ce morphotype qui se présentent surtout en groupements monomorphiques ou même monospécifiques de grandes profondeurs, il existe des problèmes concernant la répartition du transport et la répartition bathymétrique des spécimens. La découverte des colonies exige un examen détaillé des sédiments et leur détermination est compliquée par leur faible taille et leur ressemblance frappante avec les colonies de Foraminifères qui les accompagnent. Mais, ce que l'on connaît déjà de la distribution et de la systématique de ces colonies, permet de fournir une contribution utile à l'analyse des sédiments bathaux.

Introduction

General surveys of sedentary faunas have sometimes neglected the contribution of marine bryozoa, although colonies are present in most environments and are often abundant over large areas, particularly in shelf waters from the sublittoral to 500 metres depth.

Most bryozoan larvae require a fairly firm substratum for settlement, metamorphosis and further development of colonies. Substrata may, however, vary from rock, stones, dead or living molluscan shell and echinoderm test, to hydroids, gorgonians, ascidian tests and algal fronds and stipes. Some species show a strong preference, or a hierarchy of preferences, for distinct substrata; others show different colony growth forms (morphotypes) on different substrata (Ryland, 1962; Cook, 1968). After death, skeletons of colonies with calcified body walls accumulate in bottom sediments. Fragments of colonies, particularly those with an erect form of growth, may also be expected to be transported and then deposited, depending upon local conditions. Whole colonies, parts of colonies, single member zooids or even parts of zooids may be identified to species level from these skeletons (Lagaaij, 1968b, 1973).

Specialized morphotypes are associated with sea bottoms of sand, mud or ooze, and may form a significant component of both Recent and fossil fine-grained sediments. The bryozoan nature of some of these morphotypes may not be easily recognized and this paper reviews current information about them, particularly those with minute colony size. Problems in assessing their potential usefulness in ecological and palaeoecological studies are also discussed.

Correlation between environment and morphotype

The form of colony growth, which may be directly observed, or may be reconstructed from fragments, is genetically controlled, but reflects environmental influences to varying degrees. These multivariate influences include depth, temperature, salinity, turbulence and rate of sedimentation, together with substratum type and availability (Lagaaij and Gautier, 1965; Cheetham, 1967, 1972; Labracherie, 1972a, 1972b, 1973b). Distinct groups of morphotypes may be correlated with the overall ecological conditions of the original habitat. For example, encrusting, or erect, flexible colonies often typify sea bottoms of «hard» substrata, high turbulence and low sedimentation. Erect, rigid colonies are often characteristic of areas of lower turbulence and restricted substrata.

Direct observation of shallow shelf living faunas has increased considerably during recent years (Eggleston, 1972; Harmelin, 1973, 1975; Ryland, 1974). Application of known correlations has made detailed analyses of the palaeoecological conditions of fossil assemblages possible (Cheetham, 1963, 1971; Labracherie and Prud'homme, 1966; Labracherie, 1973a; Annoscia and Fierro, 1973; Wass and Yoo, 1975). Although direct observations of living deep water species is not possible, so much new information has been published recently that it is now feasible to describe a parallel set of correlations which may be applied to deep sea assemblages.

"Sand fauna" morphotypes

Sea bottoms consisting of mud and sand are usually unsuitable for successful, direct colonization by Bryozoa. This may be the result of high turbidity and sedimentation rate, more than total lack of available substrata (Lagaaij and Gautier, 1965:45). Areas of mud and sand may, however, be colonized by specially adapted forms. These may be interstitial (e.g. *Monobryozoon* see Franzen, 1960, and *Aethozoon* see Hayward, 1978c); erect, nodal and rooted into sediments (e.g. *Cellaria*, the cellariiform morphotype of Lagaaij and Gautier, 1965); erect, bilaminar and rooted (e.g. *Flabellopora*, the "orbituliporiform" morphotype of Cook and Lagaaij, 1976); or free-living on the surface of the sediments (e.g. *Cupnladria*, the "lunulitiform" morphotype of Lagaaij, 1953; Marcus and Marcus, 1962; Cook, 1963; Tommasi *et al.*, 1972 and "selenariiform" colonies of Harmer, 1957).

In sandy areas where the sedimentation rate is not excessive, "secondary" species, which grow on other animals and plants raised

above the sea bottom, are often abundant. In waters of shallow to moderate depth (10 to 300 metres), the cellariiform, orbituliporiform and lunulitiform morphotypes are often very common (up to several thousand colonies per square metre) and form a significant constituent of the sediment after death. Together with other specialized forms and accompanied by secondary species, these colonies form a "sand fauna" (Cook, 1966, 1968, 1979).

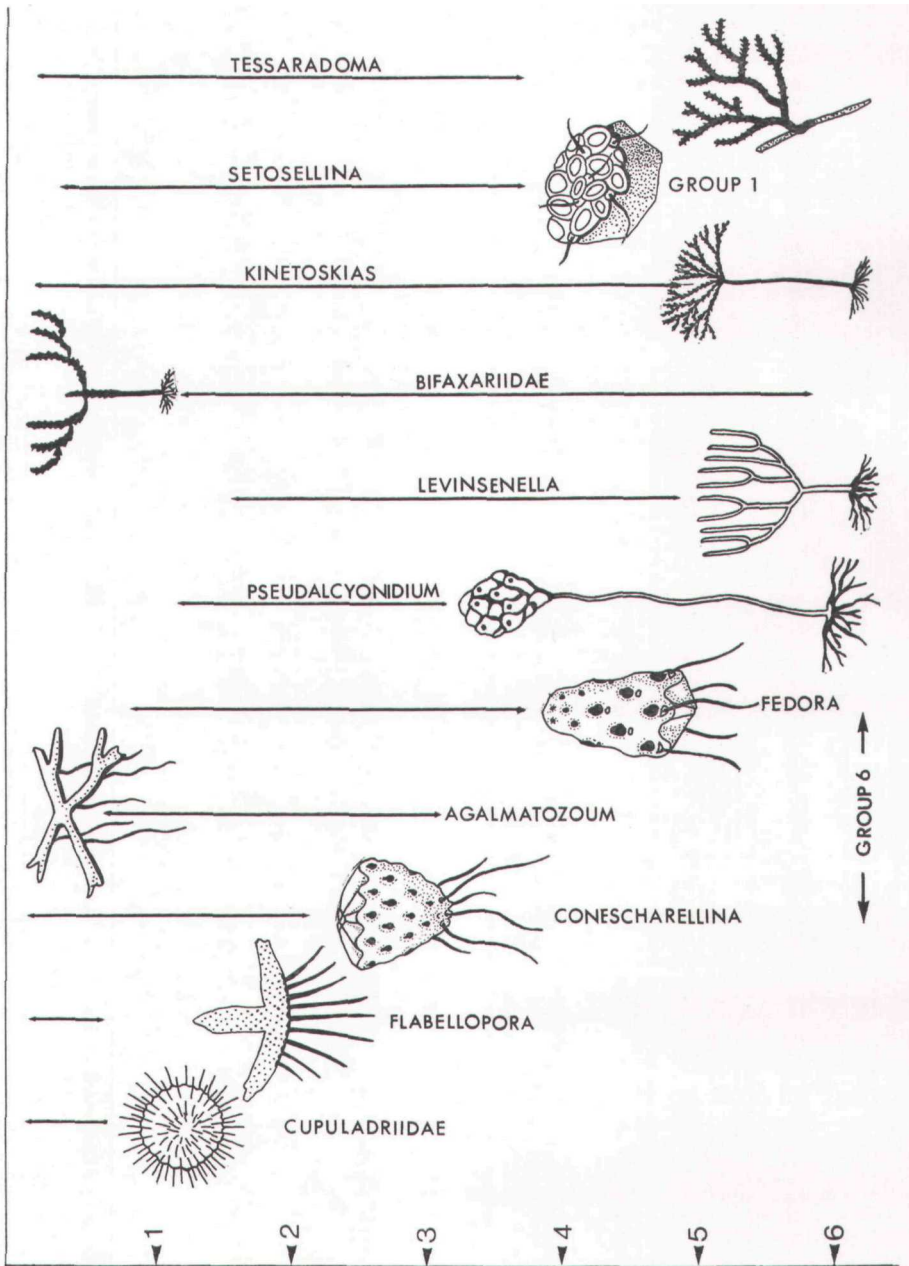
Cellariiform colonies are composed of cylindrical internodes of zooids which usually have calcified body walls, alternating with nodes of zooids which are always uncalcified and flexible. Nodal zooids are often kenozooids (non-feeding zooids consisting principally of cuticular body wall), and colonies are anchored into the sediments by kenozooidal rootlets which emanate in various ways from zooid internodes and which continue to grow in length and number during the life of the colony. Orbituliporiform colonies are erect and bilaminar, and are discoid, lanceolate or trilobate. They possess rooting systems which are progressively extended during colony growth, but which are restricted in position to the primary (periancestrular) regions. Direct observation of living orbituliporiform colonies of *Lanceopora* have been made (Mr. N. Coleman, *pers. comm.* 1976) and they are supported above the sea bottom and anchored into the sediments by a wide, turgid, extrazooidal root. Lunulitiform colonies are conical or discoid. They often develop from metamorphosis of larvae which are highly selective and settle only on a single sand grain or foraminiferan test, but some species are known which apparently require no substratum whatsoever (Hakansson, 1975). The greater part of colony growth is free of any substratum and many colonies (usually those belonging to the Cheilostomata Anasca) are completely free-living, supported on the surface of the sediments by long, bristle-like setae of specialized, avicularian heterozooids. These setae clean deposits from the uppermost, convex colony surface (Cook, 1963), and may even be the means of locomotion in some species (Cook and Chimonides, 1978). In contrast, most Ascophora with lunulitiform colonies are now known to possess rootlets emanating from the basal, concave colony surface and therefore have a different mode of life (Cook and Chimonides, 1981).

Knowledge of the environment of living species with these morphotypes has enabled parallel inferences to be made for fossil assemblages with a high degree of confidence (Lagaaij, 1963b; Lagaaij and Gautier, 1965; Cheetham, 1966). The lunulitiform morphotype is found in abundance in deposits from the late Cretaceous and is easily recognizable even when fragmented. These colonies are useful palaeoecological and stratigraphical indicators (Lagaaij, 1953, 1963b), and Hakansson (1975) has suggested methods and applications of population analysis of such assemblages.

Deep sea Bryozoa

Many deep sea bottoms in excess of 500 metres have features in common with shallower "sand fauna" areas, including instability and small grain-size of sediments, relative lack of larger substrata, and a

constant, but much lower, rate of sedimentation. Although these environments, too, have been regarded as unsuitable for colonization



TEXT-FIG. 1

Bathymetrical range of some genera and families illustrating morphotypes associated with fine grained substrata.

Depth scale at 1000 metre intervals. Sketches of colonies not to scale. Group 1 example *Setosellina*; Group 2 example *Bifaxariidae*; Group 3 example *Tessaradoma*; Group 4 example *Levinsenella*; Group 5 examples *Kinetoskias* and *Pseudalcyonidium*; Group 6 examples *Conescharella*, *Fedora* and *Agalmatozoum*; Lunulitiform example *Cupuladriidae*; Orbituliporiform example *Flabellopora*.

by Bryozoa, the results of recent investigations of the South African and European shelf and slope have revealed an unsuspected abundance and diversity of species, many of which are "rare", or even new to science (Hayward and Ryland, 1978; Hayward, 1979; Hayward and Cook, 1979). Bryozoa have been reported from very deep sea bottoms from all oceans, including the Arctic and Antarctic (Silén, 1951; Schopf, 1969). More than 90 species occur from depths exceeding 2000 metres, the deepest record to date being from 8300 metres (d'Hondt, 1975a:587). The number of species, but not the number of colonies found, decreases with increasing depth, but some deep records show a fairly high diversity. Calvet (1957:358, 362) reported 19 species from 2018 metres and 8 species from 3700 metres; Harmer (1915, 1926, 1934, 1957) reported 19 species from 1157 metres and d'Hondt (1975a) reported 10 species from 4270 metres. Anascan lunulitiform colonies have not been reliably reported as living from great depths, their place being taken by the setoselliniform morphotype (see below). Rooted, Ascophoran lunulitiform species have been collected alive from more than 500 metres. They include *Ascosia pandora* from 2018 metres off North West Spain (Calvet, 1907; Harmelin, 1977), *Anoteropora inarmata* from 732 metres off Zanzibar and 720-810 metres off Durban (Cook, 1966; Hayward and Cook, 1979) and *Mucropetraliella cotyla* from 660 metres off New Zealand (Cook and Chimonides, 1981).

Like the shallow „sand fauna" species, colonies from fine-grained, deep sea bottoms have distinctive morphotypes which fall into the following six groups (see also Text-Fig. 1).

Group 1. Minute (diameter 1 to 8mm), encrusting a single sand grain, etc., with setiform avicularian mandibles. "Setoselliniform" morphotype (e.g. *Setosellina* and *Heliodoma* see Hayward and Cook, 1979).

Group 2. Erect (10 to 30mm high), jointed, rooted. "Cellariiform" morphotype (e.g. *Gemellipora* see Lagaaij and Cook, 1973, *Bifaxaria* see Hastings, 1966).

Group 3. Erect (10 to 40mm high), rigid, arising from a small, encrusting base, part of a secondary fauna. "Vinculariiform" morphotype (e.g. *Tessaradoma* see Cheetham, 1972; Lagaaij and Cook, 1973).

Group 4. Erect (50 to 180mm high), thinly calcified, flexible, rooted. "Cellulariiform" morphotype (e.g. *Levinsenella*, *Farciminellum* and *Himantozoum* see Harmer, 1926).

Group 5. Erect (10 to 110mm high), thinly calcified or uncalcified, rooted, with an elongated, kenozooidal or extrazooidal stalk or peduncle and a head of feeding zooids, (e.g. *Kinetoskias* see Kluge, 1962, *Pseudalcyonidium* see d'Hondt, 1975b).

Group 6. Minute (diameter 1 to 8mm), globular, conical or stellate, rooted. "Conescharelliniform" morphotype (e.g. *Conescharellina*, *Batopora*, *Trochosodon*, *Fedora* and *Lacrimula* see Cook and Lagaaij, 1976 and *Agalmatozoum* see Harmer, 1957).

The potential dangers in defining colony morphotype too rigidly were discussed by Cook (1968) and by Cook and Lagaaij (1976).

Colonies may have different morphotypes at different growth stages; for example, *Heliodoma* is distinctly setoselliniform early in astogeny, but becomes almost lunulitiform as the colony develops (see Plate B,2). Very young colonies of *Agalmatozoum* are conescharelliniform (see Plate A,6), but older stages may resemble an unjointed variant of the cellariiform morphotype, which is also found in the deep water genus *Euginoma* (Hayward, 1978a).

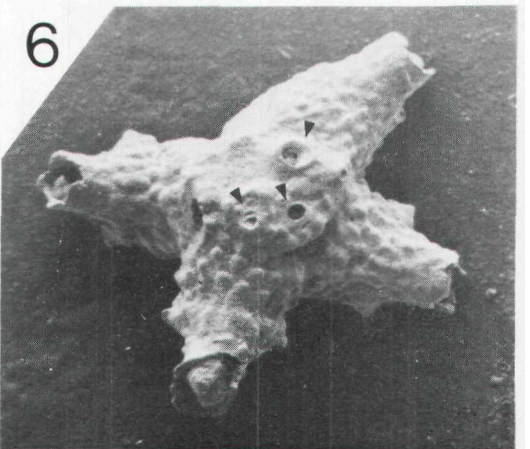
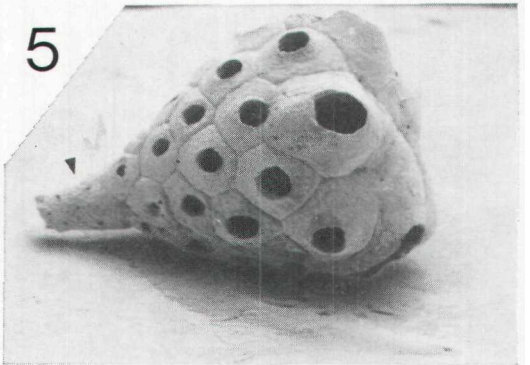
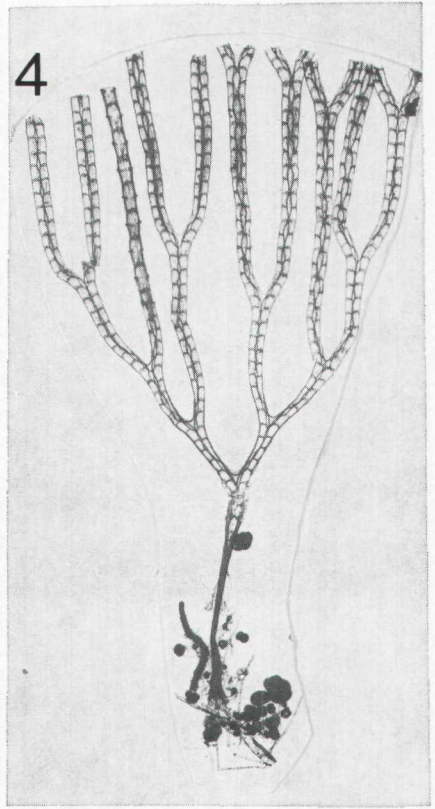
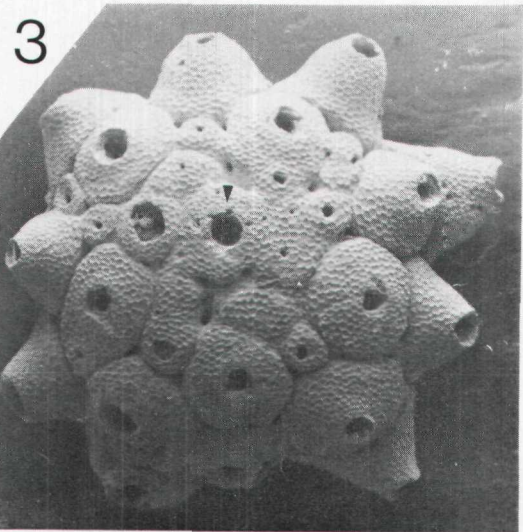
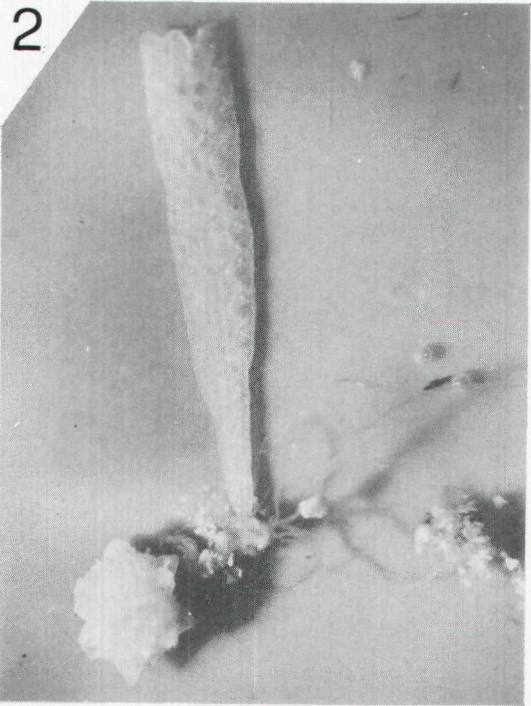
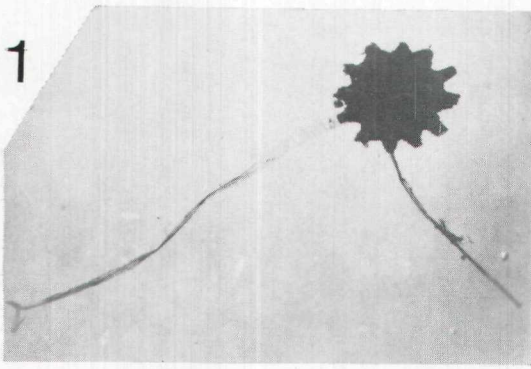
Although there is great diversity in colony structure, four of the six groups possess anchoring rootlets which, in Recent species, have provided evidence for their inferred mode of life. Many colonies from a wide bathymetrical and geographical range have been collected with rooting systems intact and which are attached to, or intricately involved with masses of sand grains and Foraminifera (Busk, 1884; Harmer, 1926, 1957; Hastings, 1943; Silén, 1947). Colonies of more than 30 species, belonging to groups 2, 4 and 5 are present in the British Museum Collections, all showing extensive rooting systems and the associated fine grained substratum. Astogenetic series have been observed in some genera and show that primary growth includes the development of a rootlet as part of the ancestrular complex derived from metamorphosis of the larva. Direct observations of the conescharelliniform *Sphaeropora* (Dr. P. Arnold, *pers. comm.*, 1979) and examination of numerous preserved colonies show that they are supported by a wide, turgid, extrazoidal rootlet similar to that of *Lanceopora* (see above). The minute ancestrular rootlet grows considerably before budding of the primary autozooids takes place. Similar growth series have been described in *Selenariopsis*, *Parastichopora* and *Conescharellina* (Cook, 1979; Cook and Chimonides, 1981).

Origins of rootlets are diverse but are recognizable from special structures preserved in the calcified skeleton (Plate A, 3, 5, 6 and B, 3, 5, 6). Even if cuticular rootlets are absent, rooting systems may therefore be inferred for Recent and fossil colonies. Although the mode of life may be inferred to be similar to that of analogous morphotypes from shallow water which have been observed alive (Silén, 1950), little is known of food and feeding methods, or larval life of

PLATE A

"Sand fauna" morphotypes

1. *Trochosodon optatus* Harmer. Siboga Stn 318, 88 metres. BMNH 1964. 3.2.12. Adapical view with two rootlets in silhouette. Colony diameter 1.4mm. Group 6. X 12.
 2. Left *Sphaeropora fossa* Ha swell. New South Wales, 366 metres. Colony diameter 1.6mm. Group 6. Right *Melicerita* sp. As above. Colony height 5.4mm. Orbituliporiform. X 12.
 3. *Batopora murrayi* Cook. Zanzibar, 805 metres. BMNH 1965.8.24.6. Adapical view showing rootlet pore (arrowed). Colony diameter 2.6mm. Group 6. X 28.
 4. *Levinsenella carinata* Harmer. Siboga Stn 211, 1158 metres. BMNH 1928. 3.6.224. Lateral view showing rootlets. Colony height 27mm. Group 4. X 3.4.
 5. *Lacrimula pyriformis* Cook. Zanzibar, 302 metres. BMNH 1965.8.24.12. Lateral view, with rootlet pore (arrowed). Colony length 2.2mm. Group 6. X 26.5.
 6. *Agalmatozoum* sp. Cape York, Australia, 279 metres. Adapical view of young colony with rootlet pores (arrowed). Colony diameter 1.1mm. Group 6. X 51.
- 3,5 and 6 taken using Scanning Electron Microscope.



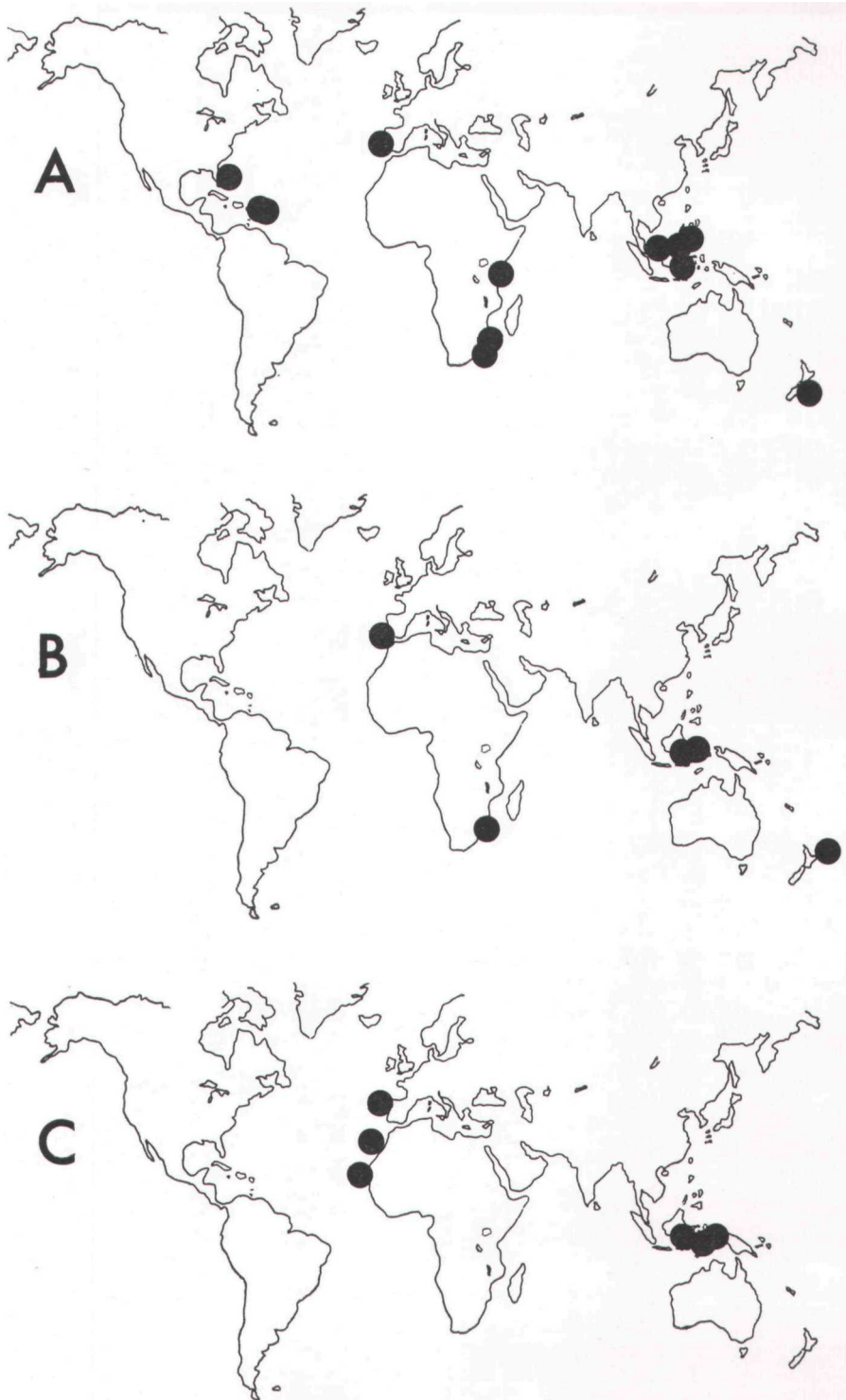
deep water species (Schopf, 1969). A much richer mobile fauna exists on the sea bottom at 2000 to 7000 metres than previously suspected (Isaacs and Schwartzlose, 1975). It seems certain that a food supply, sufficient to maintain a similar abundance and diversity of sedentary forms, including filter feeders like Bryozoa, is also present.

Systematically, most of the delicate, arborescent species from more than 3000 metres belong to the Cheilostomata Anasca (Silén, 1951; d'Hondt, 1975a), and have zooids with much of the body wall thinly calcified except for a frontal membranous area. Genera of the more highly calcified Ascophora include most of the species in Groups 2 and 3. Recent studies have shown that several species of Ctenostomata, which have uncalcified body walls, are also found from depths exceeding 3000 metres (d'Hondt, 1975a, 1975b, 1978; Hayward, 1978b, 1978c). D'Hondt (1975a) also noted that species of Cyclostomata, which have rarely been reported from more than 1000 metres, were also present at much greater depths.

Colonies are not usually very large, most of the erect forms reaching a height of 20 to 30mm. Some may reach 110mm (*Kinetoskias beringi* see Kluge, 1962), 120mm (*Farciminellum alicae* see Jullien and Calvet, 1903), and 180mm (*Levinsenella magna* see Silén, 1951). Very few genera are restricted to depths of more than 1000 metres (see Text-Fig. 1), and some species have an enormous bathymetrical range, although most occurrences are from below 2000 metres. Silén (1951) suggested that re-examination of specimens from their entire range might show that there are specific or subspecific differences within nominal species which are correlated with depth. Geographically, too, deep water species have wide distributions (Hayward, 1978b; Hayward and Cook, 1979). Generally, distribution is not directly temperature dependent, although it may be related to temperature in some unknown way (Lagaaij and Cook, 1973). D'Hondt (1975a) suggested that both distribution and diversity were related to the type of sea bottom more than any other factor.

Setoselliniform (group 1) and Conescharelliniform (group 6) Morphotypes

The very small colonies in Groups 1 and 6 are found in fine grained sediments, often from deep water. Setoselliniform colonies from less than 500 metres were noted by Lagaaij (1963:173) to exhibit «an out-spoken preference for a carbonate sand bottom». Colonies of *Heliodoma* from South Africa from 550-880 metres (see Table 1) originate on sand grains with an average diameter of less than 1mm, so that much of the growth is free living (Plate B, 2). Conescharelliniform colonies belong to several families, nearly all of them Cheilostomata Ascophora. Rootlets have been seen in specimens from depths of 32 to 2029 meters and their former presence may be inferred from skeletal evidence in all colonies. Lagaaij (1963a) discussed the possible mode of life of *Fedora* and related forms, and Cook and Lagaaij (1976) analysed the various types of budding pattern found among conescharelliniform genera. Generally, rootlets emanate from



TEXT-FIG. 2

Geographical and bathymetrical distribution of Groups 1 and 6, and of lunulitiform morphotypes.
 A. from 500 to 1000 metres; B. from 1000 to 2000 metres; C. from more than 2000 metres. See also Table 1.

TABLE 1

Geographical and bathymetrical distribution of Groups 1 and 6, and lunulitiform morphotypes (L) from more than 500 metres depth. Records are plotted in Text-Fig. 2, except those marked*. Specimens in the British Museum = BMNH.

Depth	Locality		Species present	Reference	Group
500	27°03'N	79°40'W	<i>Fedora ovum</i>	BMNH	6
535	6°41'N	120°44'E	<i>Agalmatozoum decussis</i>	Harmer 1957	6
550	27°59'30"S	30°40'48"E	<i>Batopora nola</i>	Hayward and Cook 1979	6
			<i>B. murrayi</i>		6
			<i>Conescharellina africana</i>		6
			<i>Heliodoma implicata</i>		1
			<i>Lacrimula pyriformis</i>		6
			<i>Notocoryne cervicornis</i>		6
			<i>Setosellina roulei</i>		1
600	18°30'N	63°00'W	<i>Fedorella minima</i>	Silén 1947	6
*612	5°30'N	120°07'E	<i>Conescharellina radiata</i>	Canu and Bassler 1929	6
625	4°06'50"N	118°47'20"E	<i>Trochosodon linearis</i>	Canu and Bassler 1929	6
			<i>T. quincuncialis</i>		6
655	0°32'S	119°38'08"E	<i>Agalmatozoum decussis</i>	Harmer 1957	6
660	45°46'S	171°05'E	<i>Mucropetraliella cotyla</i>	Cook and Chimonides 1981	L
677	6°40'N	109°34'30"E	<i>Lacrimula</i> sp.	Cook and Lagaaij 1976	6
680	28°31'42"S	32°34'E	<i>Heliodoma implicata</i>	Hayward and Cook 1979	1
			<i>Setosellina roulei</i>		1
*688	27°00'48"S	33°03'06"E	<i>Conescharellina africana</i>	Hayward and Cook 1979	6
			<i>Heliodoma implicata</i>		1
			<i>Setosellina roulei</i>		1
720	19°00'N	65°00'W	<i>Fedora nodosa</i>	Lagaaij 1963a	6
*720	26°51'06"S	33°12'30"E	<i>Anoteropora inarmata</i>	Hayward and Cook 1979	L
*732	5°21'24"S	39°23'E	<i>Anoteropora inarmata</i>	Cook 1966	L
*750	28°06'12"S	32°43'30"E	<i>Batopora murrayi</i>	Hayward and Cook 1979	6
*800	27°09'36"S	32°58'12"E	<i>Anoteropora inarmata</i>	Hayward and Cook 1979	L
			<i>Batopora lagaaiji</i>		6
			<i>B. murrayi</i>		6
			<i>Heliodoma implicata</i>		1
805	5°36'12"S	39°28'24"E	<i>Batopora murrayi</i>	Cook 1966	6
*810	27°09'36"S	32°58'12"E	<i>B. murrayi</i>	Hayward and Cook 1979	6
			<i>Heliodoma implicata</i>		1
*820	27°10'16"S	32°50'56"E	<i>H. implicata</i>	Hayward and Cook 1979	1
825	38°07'N	9°18'W	<i>Fedora edwardsi</i>	Silén 1947	6
*880	28°41'40"S	32°34'30"E	<i>Batopora nola</i>	Hayward and Cook	6
			<i>Conescharellina africana</i>		6
			<i>Heliodoma implicata</i>		1
			<i>Notocoryne cervicornis</i>		6
*904	10°12'N	125°04'10"E	<i>Vibracellina viator</i>	Canu and Bassler 1929	1
*970	13°21'N	122°18'E	<i>Conescharellina brevicornis</i>	Canu and Bassler 1929	6
1060	7°28'05"S	115°28'E	<i>Conescharellina distalis</i>	Harmer 1957	6
1158	5°40'07"S	125°45'05"E	<i>Agalmatozoum decussis</i>	Harmer 1957	6
1185	38°10'N	9°25'W	<i>Fedora edwardsi</i>	Silén 1947	6
1260	37°34'S	179°22'E	<i>Agalmatozoum</i> sp.	BMNH	6
1300	28°41'S	32°36'48"E	<i>Setosellina roulei</i>	Hayward and Cook 1979	1
*1301	0°34'06"N	119°08'05"E	<i>Agalmatozoum decussis</i>	Harmer 1957	6
			<i>Trochosodon linearis</i>		6
*1900	38°17'N	9°20'W	<i>Setosellina roulei</i>	Calvet 1907	6
*1944	5°26'S	121°18'E	<i>Agalmatozoum decussis</i>	Harmer 1957	6
			<i>Trochosodon radiatus</i>		6
2018	43°00'40"N	9°36'26"W	<i>Ascospia pandora</i>	Calvet 1907	L
			<i>Fedora edwardsi</i>		6
2029	4°22'01"S	118°16'09"E	<i>Agalmatozoum decussis</i>	Harmer 1957	6
2081	4°50'05"S	127°59'E	<i>Trochosodon linearis</i>	Harmer 1957	6
*2150	1°19'S	118°43'E	<i>Conescharellina radiata</i>	Canu and Bassler 1929	6
			<i>C. transversa</i>		6
2330	19°19'N	20°02'W	<i>Fedora edwardsi</i>	Calvet 1907	6
			<i>Setosellina roulei</i>		1
*2798	6°24'S	124°39'E	<i>Agalmatozoum decussis</i>	Harmer 1957	6
3700	29°00'N	16°12'W	<i>Fedora edwardsi</i>	Calvet 1907	6
			<i>Heliodoma implicata</i>		1

specialized structures which are budded in distinct patterns, and orientation of colonies in life is inferred from the position of the rootlets. In many cases, rootlets are periancestrular (adapical) and new zooid buds are proliferated from the opposite pole (antapical), so that zooids face laterally or slightly downward towards the substratum.

Breeding, inferred from the presence of brood chambers (ovicells), commences very early in astogeny, and many colonies less than 1mm in diameter and including a maximum of 12 zooids have one or two brood chambers (see Plate B, 3 and C, 4). Conescharelliniform colonies rarely exceed 8mm in height or diameter, or include more than 100 autozooids.

Group 6 colonies have not been found from high latitudes (see Text-Fig. 2) and, in this respect, resemble the erect deep water genus *Gemellipora* (Lagaaij and Cook, 1973:494). Like the other, typically deep water groups, Group 1 and Group 6 colonies have a wide bathymetrical range. Some may be found in shallow water and few have been reported from depths exceeding 2 000 metres (see Table 1). In view of the large bathymetrical range of other deep sea bryozoans, and the recent increase in the number of species discovered, it seems probable that the distribution of Groups 1 and 6 may also extend to far deeper water. Once the deepest levels of occurrence of the various morphotypes is defined, their usefulness in ecological studies of sediments will be greatly increased. Group 6 colonies seem to have particular potential and the reasons for, and some of the problems arising in assessing this potential, are discussed below.

Preservation

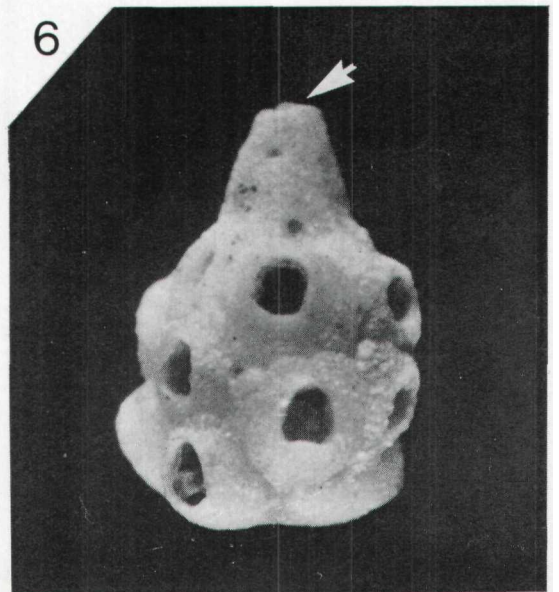
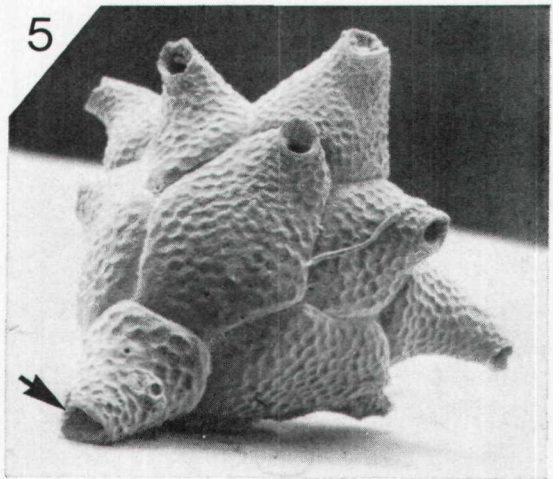
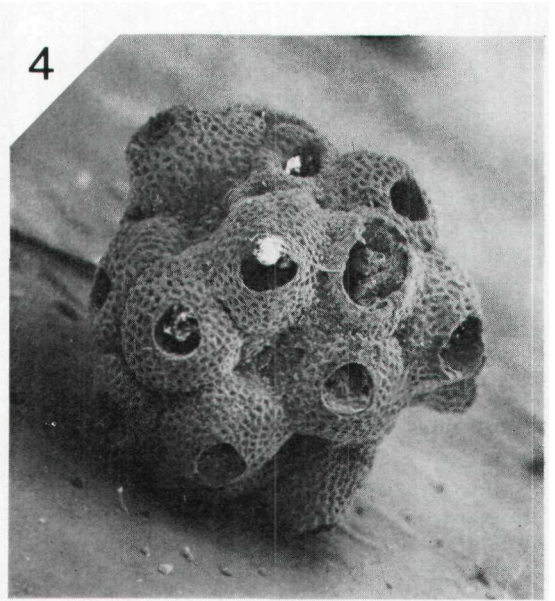
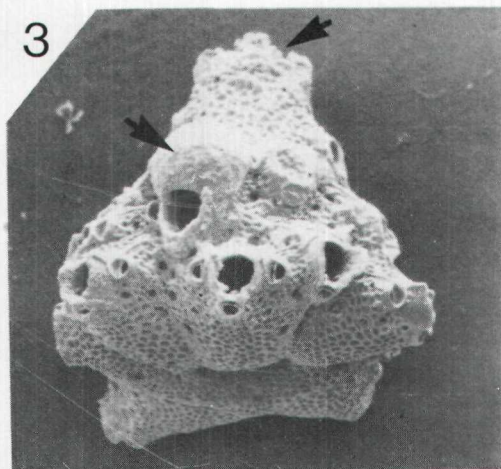
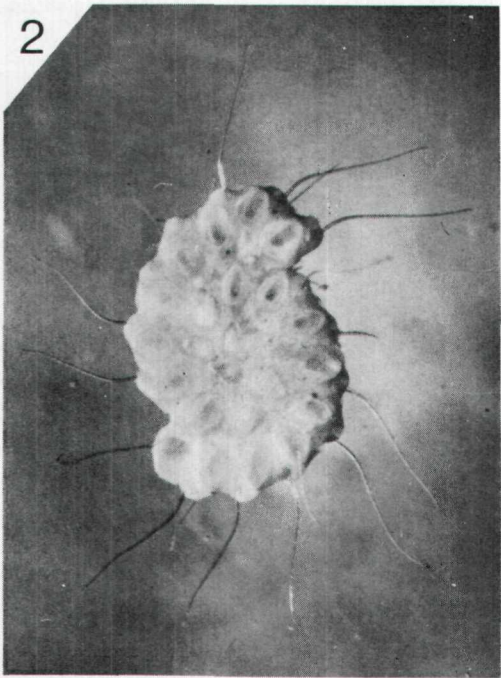
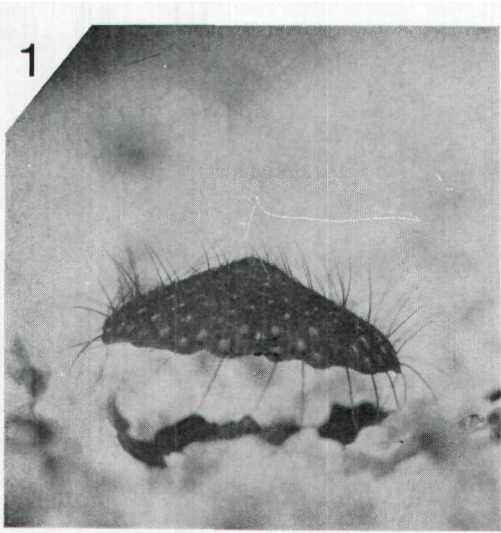
The cuticular body walls of ctenostome Bryozoa would not normally be preserved in bottom deposits after death and the thin calcification of many of the delicate anascan species (Groups 4 and 5) make it unlikely that they would often be preserved in either Recent or fossil deposits, although this is not impossible (see below). Fragments and internodes of the heavily calcified ascophoran species

PLATE B

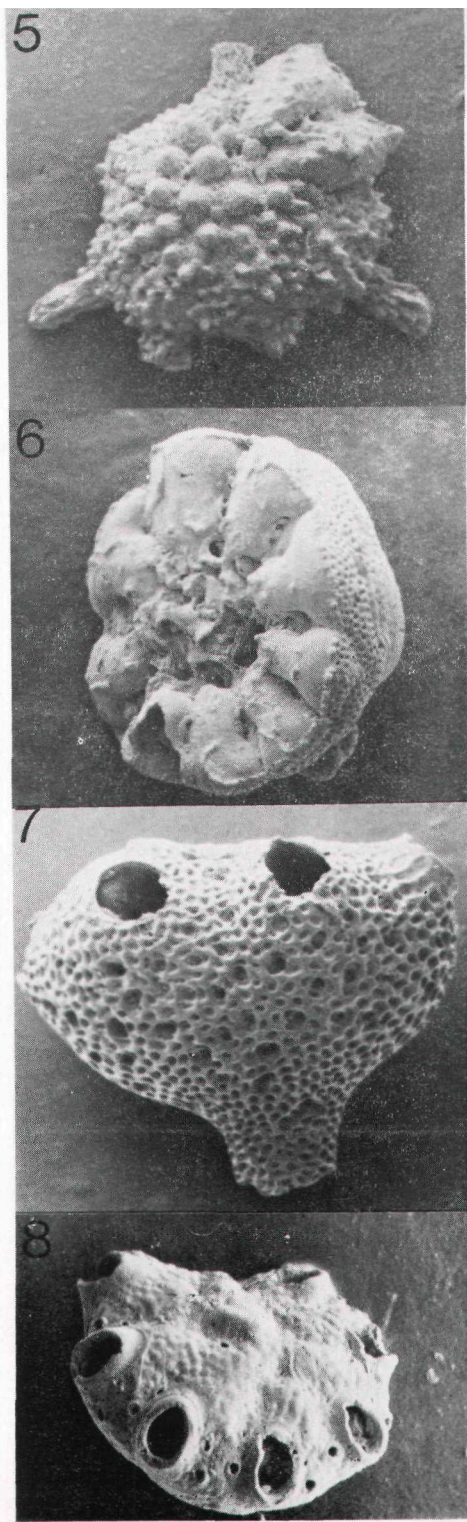
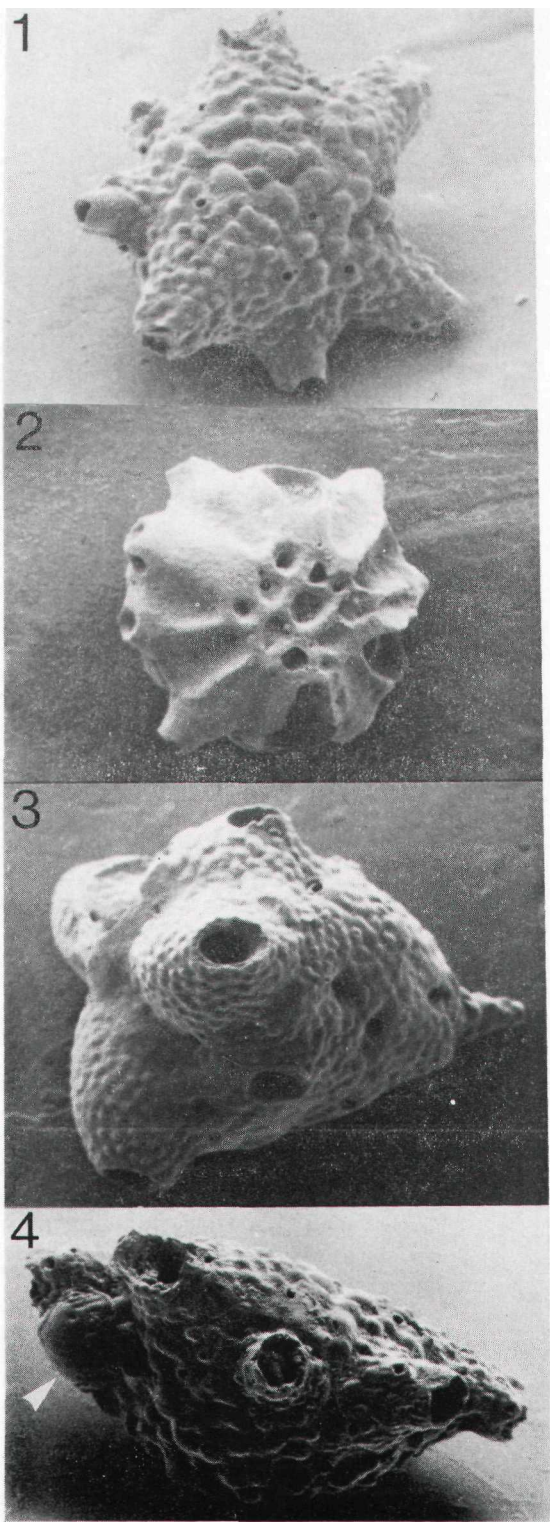
Recent and fossil "sand fauna" colonies

1. *Selenaria maculata* Busk. Recent, Townsville, Australia, 2.5 metres. Lateral view of colony supported by setiform mandibles. Colony diameter 12mm. X 4.
2. *Heliodoma implicate* Calvet. South Africa, 384 metres. Upper surface. Colony diameter (excluding mandibles) 2mm. X 21.
3. *Conescharellina africana* Cook. South Africa, 384 metres. Young colony with brood chamber (arrowed) and adapical rootlet tube (arrowed). Colony diameter 1mm. X 60.
4. *Batopora clithridiata* (Gregory). Eocene, London Clay. BMNH D1357C. Antapical budding surfaces at top right. Colony diameter 1.12mm. X 50.
5. *Batopora nola* Hayward and Cook. Recent, South Africa, 384 metres. Rootlet tube arrowed. Colony diameter 1.10mm. X 48.
6. *Lacrimula borealis* Cook and Lagaaij. Oligocene, North Sea. BMNH D52568. Colony diameter 0.91mm. X 44.

3,4 and 5 taken using Scanning Electron Microscope.



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(Groups 2 and 3) have been found in Eocene to Recent sediments (Cheetham, 1972; Lagaaij and Cook, 1973), as have Group 1 species (Cheetham, 1966; Lagaaij, 1963a). The relatively thick walled Group 6 colonies are both robust and small enough to be preserved entire. They too have been found, sometimes in large numbers, in early Eocene to Recent deposits (Cook and Lagaaij, 1976).

Thus, although they may represent only part of an original fauna of bryozoans, colonies with the conescharelliniform morphotype are among the most likely to be present in an unfragmented condition in an extensive range of fossil and Recent sediments.

Transport

One problem inherent in all analyses of assemblages is that of deciding which criteria are available for assessing if any, and how many of the species included are autochthonous forms.

Even delicate bryozoan fragments have been transported over long horizontal distances and deposited at great depths. For example, Lagaaij (1973) described several shallow water, late Pleistocene species which had been transported down a submarine canyon from the Nigerian-Cameroon shelf as far as 900 kilometres off the coast and deposited in sediments at 4 700 metres. In an earlier study, Lagaaij (1968a) also showed that given sufficient information about the bryozoan fauna, the transporting current could be inferred. Evidence of slumping and displacement from similarly well preserved but fragmentary shallow water assemblages was given by Wass and Yoo (1975).

After death, and disintegration of cuticular structures, the internodes of erect, jointed colonies would be susceptible to transport. Minute Group 6 colonies would be equally susceptible, but in very deep water would almost certainly be preserved *in situ*. In a sediment assemblage, consisting of a wide range of morphotypes originally associated with differing ecological conditions, it would be difficult to assess whether or not any conescharelliniform colonies were

PLATE C

Bryozoa (Figs 1-4) and Foraminifera (Figs 5-8)

1. *Trochosodon* sp. Cape York, Australia, 279 metres. Colony diameter 0.80mm. X 72.5.
 2. *Conescharellina* sp. Indonesia, (il metres. Colony diameter 0.69mm. X 60.
 3. *Lacrimula* sp. China Sea, 677 metres. Colony length 0.94mm. X 89.
 4. *Trochosodon* sp. As above, lateral view, showing brood chamber (arrowed). X 90.
 5. *Calcarina* cf. *hispida* Brady. Cape York, Australia, 279 metres. Diameter 0.83mm. X 73.
 6. *Cymbaloporeta poeyi* (d'Orbigny). Cape York, Australia, 279 metres. Diameter 1.00mm. X 48.
 7. Foraminifera? China Sea, 430 metres. Diameter 0.70mm. X 87.
 8. Foraminifera? Cape York, Australia, 279 metres. Diameter 0.80mm. X 64.
- Scanning Electron Micrographs.

autochthonous, unless their state of preservation was noticeably different from that of the other forms present.

In Recent assemblages, all colonies with rooting systems intact may confidently be assumed not to have been transported. To a slightly lesser extent, the same may be inferred for assemblages consisting of several growth stages and sizes, because they may be assumed to represent a sample of an actual population, not a sorted assemblage.

Bathymetrical range and diversity

Fossil and Recent "sand fauna" assemblages, known or inferred to be from shallow shelf waters, show a high diversity of morphotypes. This is a direct result of the availability of substrata for the settlement of secondary species, as well as the number of specially adapted species. As depth increases, the number of adapted species increases in proportion to that of typically shallow water forms. Diversity then declines with increased depth until only bimorphic or even monomorphic assemblages occur (Cook and Lagaij, 1976:344).

Recent assemblages from fine grained sediments from the Indo-Pacific described by Harmer (1915, 1926, 1934, 1957) and by Canu

TABLE 2

Relationship of morphotype diversity (in number of species) with depth and substratum in Indo-Pacific bryozoans. Data from Harmer (1915, 1926, 1934, 1957) and Canu and Bassler (1929), from Siboga and Albatross Stations where Group 6 colonies were found.

0 = orbituloporiform, L = Lunulitiform, Er = Erect shallow water forms, En = Encrusting shallow water forms.

Station	Depth in metres	Sea bottom	6	1	2-5	0	L	Er	En
Siboga 162	18	sand, shell	1	1	0	0	0	25	12
Siboga 164	32	sand, shell	1	1	0	0	0	27	28
Albatross D5134	45	fine sand	2	1	0	0	1	0	0
Siboga 320	82	mud	1	0	0	0	3	10	0
Siboga 319	82	mud	1	0	1	1	3	7	0
Siboga 318	88	mud	2	0	0	3	4	10	1
Albatross D5213	144	mud, sand, shells	3	1	0	1	0	0	0
Albatross D5135	297	fine sand	1	1	0	0	0	1	2
Albatross D5237	452	mud	3	0	0	0	0	0	0
Siboga 102	535	sand	1	0	0	0	0	0	0
Albatross D5586	626	mud	2	0	0	0	0	0	0
Siboga 87	655	mud	1	0	0	0	0	0	0
Siboga 83	1060	mud	1	0	0	0	0	0	0
Siboga 211	1158	mud	1	0	16	0	0	0	0
Siboga 88	1301	mud	2	0	0	0	0	0	0
Siboga 210a	1944	mud	2	0	0	0	0	0	0
Siboga 76	2029	mud	1	0	0	0	0	0	0
Siboga 227	2081	mud	1	0	7	0	0	0	0
Albatross D5670	2150	mud	2	0	0	0	0	0	0
Siboga 221	2798	mud	1	0	5	0	0	0	0

and Bassler (1929) illustrate a similar sequence (Table 2). Both encrusting and erect, shallow water species are present with Group 6 and lunulitiform morphotypes at depths of less than 100 metres, especially where shell fragments and sand form the available substratum. Group 1 and Group 6 colonies are found with orbituliporiform morphotypes down to depths of 300 metres. Orbituliporiform colonies of *Flabellopora*, *Zeuglopora* and *Lanceopora* (Harmer, 1957) are strongly associated with Group 6 colonies in other Recent faunas, as is *Orbitulipora* in fossil assemblages (Cook and Lagaij, 1976).

At much greater depths, monomorphic, Group 6 assemblages occur, or are accompanied by the typically deep sea Groups 2 to 5. Monomorphic Group 6 assemblages given in Table 2 range from 452 to 2 150 metres; thus it is not possible on present evidence to infer with confidence the original depth of fossil assemblages of this kind. Where other correlative evidence is available (from Foraminifera, etc.), monomorphic fossil assemblages of Group 6 colonies have been considered to have lived in deep water (Cook and Lagaij, 1976:344). Further problems remain, however, because depth estimates derived from study of several animal groups may be conflicting. For example, analyses of sediments from the Rockall Bank included quantitative micropalaeontology, Ostracoda (Benson, 1972) and Bryozoa (Cheetham and Hakansson, 1972). Differing conclusions were reached as to the original depths of the deposits (Laughton *et al*, 1972). In the Paleocene to Eocene sediments, Bryozoa and Ostracoda gave similar results which differed from those from other methods. In the Oligocene sediments, the depth estimate from Bryozoa differed distinctly from all other analyses. The overall history of episodes of subsidence were, however, fairly consistent from all analyses. Obviously, the correlation of species and, for the Bryozoa of colony morphotype, with depth, is related to the nature of the sea bottom and to other, as yet unknown factors.

Collecting bias and abundance

Schopf (1969) discussed records of deep sea Bryozoa and noted the paucity of reports from mid-oceanic localities. At present, records of Groups 1 and 6 morphotypes show a similar bias (Table 1 and Text-Fig. 2) because deep oceanic sediments are only beginning to be collected and analysed. Methods of collection may also introduce bias; Menzies and George (1967:714) remarked: «the dominant number in a fauna is frequently merely a function of the type of collecting gear utilized». Given the usual methods of grab or dredge sampling, the larger, more delicate bryozoan colonies are liable to damage, whereas the minute Groups 1 and 6 colonies, even if they are relatively unaffected, may remain undetected or may even be washed out in the sediment. It is also possible for colonies to be collected accidentally. Harmelin (1977) reported species which were collected by a deep plankton haul, which grazed the surface of a sea-mount. Examination of the sediment revealed colonies of several "rare" species, such as *Ascusia pandora* and *Heliodoma implicata*.

Unfortunately, although fine grained fossil sediments are rou-

finely examined, most similar Recent samples have not received the same attention. Harmer (1957:730), discussing the specimens of *Conescharellina* from the "Siboga" Stations, noted: «I have little doubt that if the bottom deposits had been specifically searched, the number would have been much larger. Many of those found were accidental inclusions». The total number of Group 6 colonies from 142 "Siboga" Stations was less than 50. Examination of bottom sediments in recent years has produced some strikingly different results. One sample (8cu.cm) of a living "sand fauna" from Victoria, Australia, from 366 metres, included more than 140 colonies belonging to 32 species. Over 100 of these were either of the rooted, lunuliti-form or of the conescharelliniform type (Cook, 1979). Each of two samples from Indonesia (50 cu.cm) contained approximately 200 group 6 colonies, none larger than 2mm in diameter. Samples of the bottom deposits from Zanzibar, in which the genus *Lacrimula* was originally found (Cook, 1966; Cook and Lagaaij, 1976) show an abundance of Groups 1 and 6 colonies (2 600 in 100cu.cm). These comprise 70 to 90 percent of the bryozoans present, which themselves contribute 12 to 15 percent of the animal remains in the sample. Numerous Group 1 and Group 6 morphotypes have been found in bottom sediments from South Africa ranging from 376 to 1 300 metres depth. As many as 185 Group 1 and 81 Group 6 colonies have been found in one (100cu.cm.) sample (Hayward and Cook, 1979).

Until many more sediments have been examined, particularly those from deep water, these examples can illustrate only that these minute colony morphotypes may be far more abundant than previously reported.

Recognition

D'Hondt (1975a:590), discussing recent finds of deep sea Bryozoa remarked: «leur aspect n'est pas toujours celui d'un Bryozoaire "classique" et seul un examen minutieux par un trieur averti permet leur récolte». Recognition of Group 6 colonies presents similar problems and, in addition, their small size requires detailed examination of **washed** and graded sediments. Colonies are almost always associated with Foraminifera, which may be more numerous, but are often of the same size range. Apart from these difficulties, Bryozoa and Foraminifera may resemble one another to a remarkable degree.

Accordi (1951) discussed the similarity in appearance of the foraminiferan *Dictyoconus aegyptiensis* Chapman and associated colonies of the bryozoan *Conescharellina perfecta* Accordi from the Eocene of Northern Italy (see Cook and Lagaaij, 1976:358). Some further examples of similarity are illustrated on Plate C. These species were not from very deep water (range 61 to 677 metres), but they indicate the possible confusion which could occur, especially when specimens are sorted using a low-power microscope, when the fine details of structure and sculpturing are not visible as they are using a scanning electron microscope.

The similarity between *Troctwsodon* sp. (Bryozoa) and *Calcarina* cf. *hispida* Brady (Foraminifera), which were from the same sample,

is probably the closest, and stems from their shape and surface rugosities. The similarity between *Conescharellina* sp. (Bryozoa) and *Cymbaloporetta poeyi* (d'Orbigny) (Foraminifera) is due to their camerate structure, which is, however, radial in the bryozoan and spiral in the foraminiferan. The remaining bryozoan examples, *Lacrimula* sp. and *Trochosodon* sp. are compared with two foraminiferans (?) which apparently have "orifices" of the same size and relative position.

Conclusions

It could be argued that the problems inherent in collecting, recognizing and interpreting the occurrence of minute bryozoan colonies might outweigh any information that they could contribute to the assessment of the ecology of sediments, particularly those from deep water. In view of the rapid increase in described faunas of bryozoans, this is a negative approach.

Bryozoa make a significant (sometimes a dominant) contribution to the sessile fauna of many marine environments. Where knowledge of ecological parameters of living faunas is available, analysis of analogous colony morphotypes has already proved useful in inferring palaeoecological conditions of fossil assemblages. Bryozoa are particularly sensitive to changes in rates of sedimentation and populations reflect such changes in time and space (Cheetham, 1963, 1972; Lagaaij and Gautier, 1965; Cheetham and Hakansson, 1972; Wass and Yoo, 1975). The morphotypes associated with "sand faunas" are distinctive and their diversity is correlated with depth. The proportion of bryozoan colonies to other animal remains is high, they are identifiable when fragmented and are often abundant in sediments. Increased knowledge of the systematics, mode of life and bathymetrical range of deep sea morphotype in time and space can only be gained from continued collection and examination of bottom sediments, and the recognition of these colonies as Bryozoa. At present, it seems probable that only the skeletons of the minute Group 1 and Group 6 morphotypes **would** be preserved entire, for long periods of time, in very deep deposits. Some criteria already exist for assessing whether or not they would be autochthonous. Exact estimates of original depth are not at present possible, but the known associations, wide distribution and extensive fossil record of these minute colonies suggest that they could contribute significantly to syntheses of evidence in ecological and palaeoecological studies.

Acknowledgments

When this paper was originally prepared in 1975, much of the data was the result of work over several years with the late Dr. R. Lagaaij. The rapid increase in studies on deep sea bryozoans has necessitated complete revision. Collections in the British Museum (Natural History) were examined by permission of Drs R. C. Kempe, C.G. Adams and B.R. Rosen. Dr. P. Arnold (James Cook University, Queensland) and Mr. N. Coleman (Australasian Marine Photographic Index) gave valuable, direct observations on living colonies. I am also grateful to Prof. J. Gray (Oregon University) and Dr. E. Hakansson (Geological Institute, Copenhagen University), for technical criticism, and to Mr. P.J. Chimonides, British Museum (Natural History) for all his help, particularly with Scanning Electron microscopy and other photography.

Summary

Correlations between colony form (morphotype) and environment are well established for shallow shelf Bryozoa, particularly for colonies specially adapted to sandy or muddy conditions. Palaeoecological inferences may be made from study of fossil assemblages of skeletal remains in sediments. Morphotypes from deep-water, muddy sea bottoms are also specialized, and fall into six groups, four of which have anchoring rooting systems. One group has minute, highly calcified colonies, which are the most likely to be preserved, entire, in Eocene to Recent deposits. Although colonies with this morphotype are often abundant, and tend to occur in monomorphic or even monospecific assemblages at great depths, problems exist in assessing both transport and absolute bathymetrical range. Discovery of colonies requires detailed examination of sediments, and recognition is complicated by their small size and by their striking resemblance to some accompanying Foraminifera. Once more is known of the distribution and systematics of these colonies, they have potential to make a useful contribution to analysis of deep sediments.

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