FURTHER OBSERVATIONS
ON WATER CURRENT PATTERNS
IN LIVING BRYOZOA

by

Patricia L. Cook and **P.J.** Chimonides
British Museum (Natural History)

Résumé

La présence de cheminées exhalantes actives est fréquemment observée chez *Smittoides reticulata, Parasmittina trispinosa* et *Membranipora membranacea.* Chez *M. membranacea,* les groupes de cheminées sont formés par de grands zoïdes alternant avec de petits. La morphologie des zoïdes « cellules en tour », qui se développent plus tardivement au cours de la vie embryonnaire est très semblable ; on présume qu'ils dérivent des groupes de cheminées « actives » et qu'ils fonctionnent comme des cheminées « passives ».

Introduction

Colony-wide patterns of water current flow in bryozoans were first observed by Banta *et al.* (1974), who noted that groups of zooids with elongated tentacles formed regularly spaced excurrent outlets ('chimneys'), in colonies of an anascan cheilostome, *Membranipora* sp. Cook (1977) made observations on colonies of some cyclostome, ctenostome, and both anascan and ascophoran cheilostome species. These observations extended the inferences made by Banta *et al.* (1974), namely, that in some cases, skeletal morphology might reflect the presence, or former presence, of different methods of water current control. Some of these inferences have been further discussed by Taylor (1975, 1979a,b) and by McKinney (1977), for fossil species.

Essentially, water current patterns providing colony-wide, unrestricted flow are inherent in the budding pattern and consequent arrangement of all the zooids in many erect bryozoan species. In encrusting expanses, where very large numbers of closely spaced tentacle crowns produce inwardly directed feeding currents simultaneously, colony-wide, unrestricted water flow is ensured by the presence of regularly spaced excurrent outlets, formed by groups of zooids with polymorphic, ciliated tentacle crowns. These are 'active' chimneys. In other colonies, often those with irregular, semi-erect growth, or with groups of raised (often frontally budded), zooids, 'passive' chimneys are formed. These consist of regularly spaced

groups of zooids which do not feed and may have polymorphic, non-ciliated tentacle crowns and no functional gut (see Cook, 1977). Other passive chimneys are formed by kenozooids, which have no orifices or tentacle crowns (see Cook, 1979). Zooid groups forming passive chimneys often have additional sexual and/or structural functions (see p. 401).

It was not known if active chimney zooids were developed primarily, as part of the patterning of zooids during astogeny, or arose later, as a result of cyclic degenerations and regenerations of the tentacle crowns of the member zooids themselves. Furthermore, it was not known if these chimney zooids differed from other, surrounding autozooids in the morphology of structures other than those of the tentacle crowns.

The observations described below suggest that, in *Membranipora membranacea* at least, both astogenetic and ontogenetic changes are involved in various forms of chimney zooid production, and that the presence of chimneys may be inferred from differences in skeletal, in addition to lophophore (tentacle crown and tentacle sheath) morphology.

Material and methods

Colonies were collected from 10-24 meters depth and from the sublittoral region off Millport, Isle of Cumbrae, in May 1979. The majority encrusted algae *(Laminaria* and *Fucus),* but some encrusted rock, shell and glass. Colonies were observed and photographed in an open sea-water aquarium system at Millport and in a closed system at the British Museum (Natural History) (see Cook and Chimonides, 1978), at 10°C.

Some preserved specimens in the British Museum (Natural History) Collections are referred to by their registration numbers e.g. BMNH 1963.3.26.28. Length of zooids, width of zooids and length of tentacles arc referred to as Lz, lz, and Lt respectively (see also Table 1).

OBSERVATIONS

1. Species examined

All the active chimneys observed were similar to those described by Banta *et al.* (1974) and Cook (1977). In the ascophoran species *Parasmittina trispinosa* (Johnston) and *Smittoidea reticulata (MacGillivray),* (see Hayward and Ryland, 1979) encrusted on rock, shell and glass, colonies ranged from 20-50mm in diameter and comprised 1000-2000 member zooids. The chimneys differed very little in occurrence, nature and dimensions from those of the other ascophoran species already described by Cook (1977). The greatest number of observations was made on the anascan, *Membranipora membranacea* (Linnaeus), which encrusted *Laminaria* and *Fucus.*

The uncalcified frontal body wall of the zooids and their large size, makes study of the tentacles, tentacle sheaths, muscles and viscera much easier in this species than in the ascophoran forms, which have a calcified frontal shield. In addition, the large expanses of unrestricted growth in *M. membranacea* makes colony-wide changes and functions very obvious. Comparisons within and among colonies, and with other species, particularly the anascan *Electra pilosa* (Linnaeus), which was living under the same environmental conditions, has allowed some conclusions as to the relationships of colony budding and colony function (see p. 400).

2. Nature of chimneys

In the colonies of *M. membranacea* observed the lophophores had 17-20 (usually 18 or 19) tentacles, which in most zooids were all of the same length (see Table 1). As in all the ascophoran and anascan species observed to date, the chimney zooids had tentacles which were all much longer than those of other autozooids and which were particularly elongated on the side of the tentacle crown facing the centre of the chimney. In *M. membranacea* the 6-8 distal, lateral and proximal tentacles were most elongated in the proximal, lateral and distal chimney zooids respectively. The autozooids immediately surrounding a chimney also had slightly elongated tentacles in corresponding positions (sec Plate I B). The central zooid of each chimney group also had very elongated distal tentacles, and in contrast to the other species so far observed (see Banta *et al.,* 1974 and Cook, 1977), this zooid frequently protruded its tentacle crown. The central zooid was, however, always the last to protrude its crown during colony-wide feeding, and was the first to withdraw it. All chimney zooids also had very long tentacle sheaths (see Table 1), which when everted, 'leant away' from the central zooid, which itself directed its tentacles distally, not frontally as in other feeding zooids (see Plate 1 A).

Chimney zooids had well developed viscera, and apparently fed like other zooids. The gut, including the caecum, passed up into the everted tentacle sheath in all feeding zooids. The 'leaning' behaviour of the tentacle sheaths of the chimney zooids was not apparently correlated with the attachment of the retractor muscles or the arrangement of the introverted tentacle sheath and viscera when the tentacles were withdrawn. In many species with erect, unilaminar biserial colonies, the position of the withdrawn tentacles and tentacle sheath is regularly to the right or left of the gut and caecum, and is directly related to the position of the zooids to the right or left of their branch. Usually in *M. membranacea* the primary, paired members of bifurcated zooidal rows showed a similar correlation. The left hand zooid (viewed frontally) withdrew its tentacles to the left hand side of the viscera and these relative positions were reversed in the right hand zooid. Bifurcations of zooid rows were not, however, directly related to the occurrence and position of chimney groups (see p. 397) and the relative positions of withdrawn tentacle sheaths and viscera appeared to be randomly arranged in all other zooids.

3. Spacing of chimneys

The centres of distally successive chimneys occurred very regularly at intervals of 7-8 zooids. Laterally, the zooidal series producing chimney groups were spaced 11-13 rows apart. Chimney groups were arranged in regularly alternating series (see Banta *et al.,* 1974, Fig. 2 A. B and see Plate 1 B). This type of spacing was found in areas of unrestricted growth. Where there irregularities in the substratum and where different colonies, or lobes of the same colony were in spatial competition, some elongated tentacle crowns occurred 1-2 zooid generations away from the area of contact at the growing edges. Organized groups of chimney zooids did not, however, occur.

The distances among chimneys in *M. membranacca* (measured from centre to centre) is far greater than that reported for the unnamed species of *Membranipora* observed by Banta *et al.* (1974), and for all the ascophoran species observed by Cook (1977), which varied from l-3mm. This difference is directly related to the large size of the zooids, in this population of *M. membranacca* at least (see Table 1). Zooids figured by Stebbing (1973) are of comparable size, as are those of the majority of preserved specimens examined (BMNH 1934.3.26.2 and 3, Plymouth Sound; 1963.3.26.26, Exmouth and 1963.3.20.209, St. Andrew's). Other specimens including BMNH unregistered, Colwell Bay and those figured by Ryland and Hayward (1977:56, Fig. 19A), have much smaller zooids (Lz 0.40-0.60mm). The population variation of nominal forms of *M. membranacea* has not been investigated, and these differences may be seasonal, environmental or genetic. Even in preserved specimens with small zooids, there is, however, a size variation which is inferred here to be correlated with the occurrence of chimney zooids (see below).

4. Relationships of chimney zooids with astogeny

Zooids of chimney groups were first recognizable from 4-8 zooidal generations proximal to the giant buds (sec Lutaud, 1961) at the growing edge of the colony. In a few cases, partially formed chimneys were seen, in which the distal members had not yet deve--oped fully formed lophophores. The proximal and lateral members of these partially formed chimneys had elongated tentacles and tentacle sheaths which already showed 'leaning' behaviour, however. Active chimneys are therefore the direct result of astogenetic changes (luring primary budding, not the result of later, ontogenetic changes produced by degeneration and regeneration of lophophores and viscera (see p. 394 and Cook, 1977, p. 40). Very young colonies, comprising 20-25 zooids, did not show any evidence of chimney zooids. The first chimney groups were budded 5-7 zooidal generations distal to the twinned ancestrular complex, when the colony comprised approximately 200 zooids. At nearly the same time, a more centrally placed chimney was formed close to the ancestrular area by zooids belonging to one of the fan-shaped series which were budded proximally and eventually surrounded the ancestrular complex. These zooids too are from 5-7 generations from the ancestrular complex.
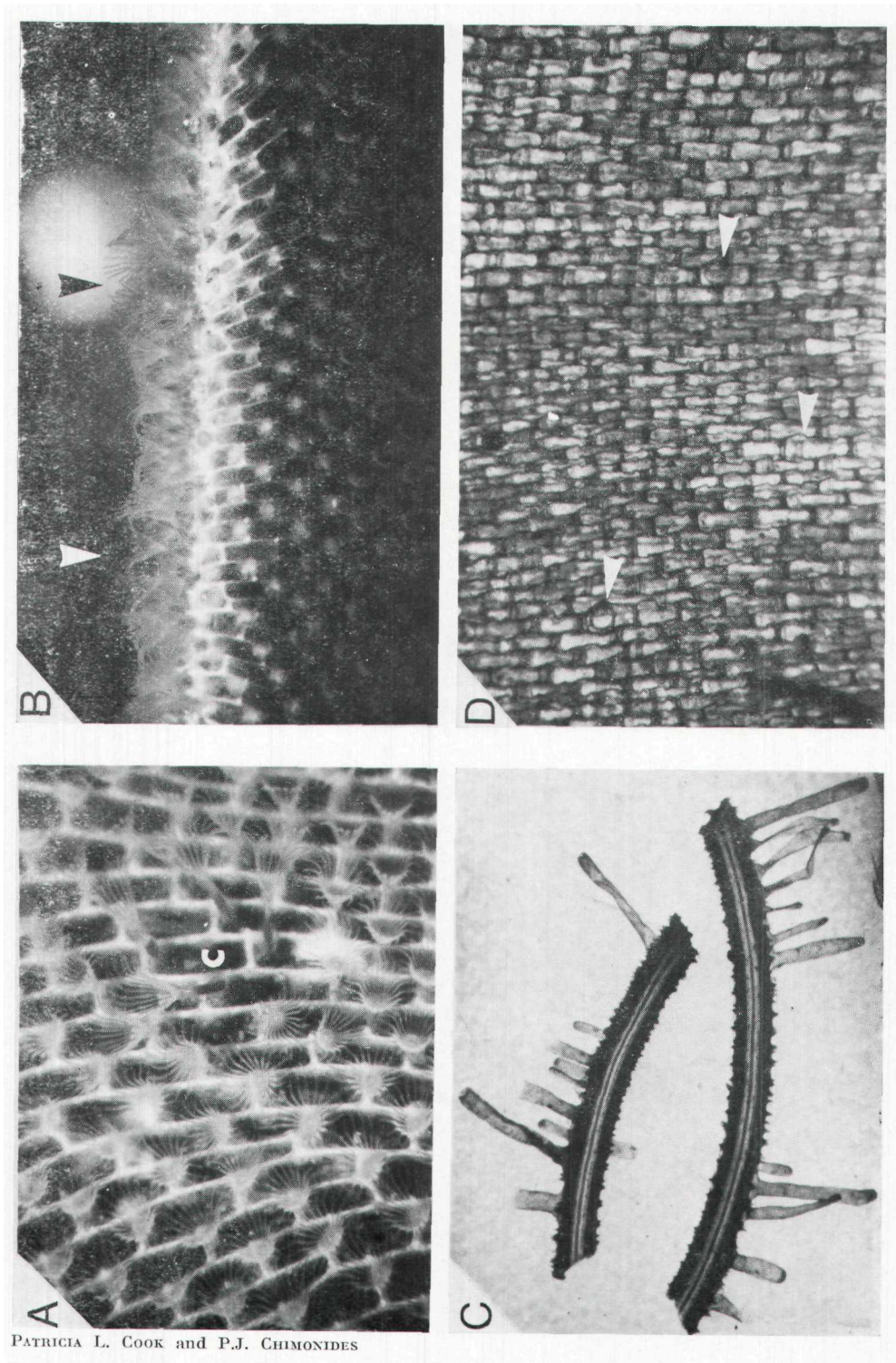
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PLATE 1

Active chimneys and 'tower cells' in *Membranipora membranacea* (Linnaeus)

A: frontal view of a chimney group. Note 'leaning' hehaviour of tentacle sheaths and cenlnl zooid (c) with everted tentacle crown (X 15); B: part of a colony showing colony-wide feeding and two active chimneys (arrowed) (X 12); C: lateral view of preserved 'tower cells', BMNH 1903. 3.20.28, Exmouth (X 6); D: frontal view of part of a preserved colony showing distribution of large and small zooid series and of associated 'tower cell' groups (arrowed), BMXH 1963. 3.26.26, Exmouth (X 10).

The distribution of chimneys is directly related to the size of zooids and to their budding pattern. Although expanses of *M. membranacea* appear to be composed of regularly shaped zooids of identical size, there is a colony-wide pattern of budding which produces alternating, multiserial groups of larger and smaller zooids. These differences in size form an almost continuous series, but the ends of their range of variation are considerable (see Plate 1D). In young colonies, too, there are differences in size among the zooids in the primary zone of astogenetic change, due to the large numbers of bifurcations of zooid rows forming the early, fan-shaped growth pattern. As a result, some zooids are larger than others at the beginning of the zone of astogenetic repetition. Some of these series of larger zooids eventually form chimney groups. Two to three astogenetic generations after a chimney group, one or more of the zooid rows may bifurcate, producing series of smaller zooids. The zooids of other rows remain large for one or two generations and then become rapidly smaller from generation to generation, apparently as a response to indirect spatial pressure. This seems to originate from the nearest, laterally placed series of larger zooids which are potentially able to produce a chimney, and whose zooids are rapidly enlarging from generation to generation. After these last zooids have produced a chimney, the spatial pressure is apparently relaxed and the zooids of the original series often increase in size during the next few generations, more often than not producing another chimney group. Occasionally, the central zooid row of a chimney series may remain larger than surrounding zooids for 20-30 astogenetic generations, after which bifurcation of rows occurs. Generally, there is an alternation of large and small zooid groups sequentially in potential chimney series, but the intervening 10-11 zooid rows laterally are constantly composed of very small zooids (see Plate 1D).

5. Relationships of chimney zooids with ontogeny

The only ontogenetic changes usually occurring in *M. membranacea* once the zooids are fully developed, are the purely cyclic changes of degeneration and regeneration of lophophores and viscera. In the colonies observed alive, no zone of degeneration was present. However, these colonies were young, comprising only 50 zooidal generations and approximately 20,000 zooids. Later in the year, colonies have grown much larger and frequently cover the entire *Laminaria* plant completely on both sides of the fronds. Each frond is then covered by a colony or a complex of colonies, extending over an area of more than $400 cm^2$ and comprising 300-500 zooidal generations and approximately 160,000-200,000 zooids.

In the ontogenetically older (and astogenetically younger) parts of such colonies 'tower cells' are frequent. These consist of zooids in which the cuticular frontal wall is raised to form a cylindrical expansion (see Ryland and Hayward, 1977:58, Fig. 190). The 'tower' is produced by intussuceplive growth of cuticle and underlying epidermis and the zooid has neither orifice nor viscera and is therefore a kenozooid. Preserved specimens show the stages of development of 'tower cells' by ontogenetic change from autozooids. In these

specimens (BMNH 1963.3.24.6, Tresco, Scilly Is; 1934.3.26.3, Ply-
mouth and 1963.3.26.26, Exmouth) groups of 'tower cell' kenozooids
are positively correlated in occurrence with the series of larger
zooids, and are often spaced in an alternating pattern exactly like
that of the chimney groups in living colonies, and at the same
distances apart (see Table 1 and Plate 1D). 'Tower cell' groups
become more extensive as the colony grows older, and also occur
in areas of zoid crowding. These kenozooids are not necessarily
arranged in groups and are sometimes derived from smaller zooids
(sec Ryland and Hayward, 1977, p. 58).

TABLE 1

Measurements in millimetres of active chimney zooids, other autozooids and
'tower cell' kenozooids in *Membranipora membranacea.*

Living colonies	Range	Average
Diameter of chimney	3.50—4.30	3.80
Distance between chimney centres	6.00—8.00	7.00
Vertical height of expulsion of particles	5.00—8.00	7.00
Lz. chimney zooids	0.78—1.10	0.95
lz chimney zooids	0.38—0.50	0.42
Lt chimney zooids (longest)	0.87—0.95	0.92
Lt chimney zooids (shortest)	0.70—0.73	0.71
Lt — sheath chimney zooids	0.80—0.87	0.85
Lz other autozooids	0.65—0.80	0.72
lz other autozooids	0.25—0.38	0.33
Lt other autozooids	0.42—0.45	0.44
Lt —sheath other autozooids	0.30—0.35	0.33
Preserved colonies		
Lz 'tower cell' kenozooids	0.75—1.00	0.90
lz 'tower cell' kenozooids	0.35—0.48	0.43
Vertical height of 'tower cell' kenozooids	6.50—8.40	7.50
Distance between 'tower cell' group centres	5.00—8.00	7.00

Fn order to confirm directly the inference that some active
chimney zooids become 'lower cell' kenozooids in the course of
colony life, living colonies would have to be observed through all
astogenetic and ontogenetic changes. In some preserved specimens
(BMNH 1963.3.26.26 and 28. Exmouth) the zooids surrounding the
'tower cell' groups can be seen to possess lophophores and viscera,
and were therefore capable of feeding when alive. In living colonies,
'tower cell' groups could therefore function as passive chimneys,
focussing excurrent water patterns and directing the currents to their
vertical height of up to 8mm above the colony surface (see Plate 1C),
a comparable distance to that observed in active chimneys (see also
Table 1).

'Tower cell' kenozooids may, of course, combine alternative or
additional functions with those of water current control. One of
these functions may be related to the increased rigidity (rather than
the increased weight) of the algal fronds when they are completely
covered by bryozoan colonies (see also Wing and Clendenning, 1971).
Living 'lower cell' kenozooids are turgid and their cuticle is thick.
They may therefore perhaps have the effect of cushioning collisions

among the algal fronds. A similar function may be postulated for the enlarged, hollow gymnocystal tubercules of *M. tuberculata* (Bosc) and species of the genus *Thairopora* MacGillivray, as well as for the gymnocystal spines of *Electra pilosa.* All these species encrust algae. Additional functions of spines are of course, very probable. Stebbing (1973) correlated their occurrence with spatial competition in *E. pilosa,* and Cook (in press) has noted their efficacy in discouraging nudibranch predators in *E. verticillata* (Ellis and Solander).

DISCUSSION

The presence of colony-wide water current patterns provides evidence of colony control (a high degree of integration) of zooidal function, in contrast to zooidal autonomy (a low degree of integration) (see Cook, 1979). In all bryozoans, the process of colony growth by budding (astogeny) reflects integration whenever there is regular repetition of groups of zooids of discontinuously differing morphologies (see Boardman and Cheetham, 1973). In addition, there may be ontogenetic changes in the morphologies of member zooids during colony life. These changes may be small but continuous (as in subsequent thickening of calcified walls) or cyclical (as in repeated degeneration and regeneration of tentacles and viscera). Some other changes may he considerable, as in the formation of rhizoids in *Euginoma* (see Hayward, 1978) and the 'tower cells' in *M. membranacea* (see above). In all cases, changes may involve a partial or complete difference in zooidal functions, which themselves reflect degrees of colony-wide function and integration. Thus the methods by which chimney zooids are budded and the effects on them of ontogenetic changes, are important in study of integration. In addition, correlations between the observed occurrence of excurrent chimneys and the skeletal morphology and patterning of the zooids concerned, allows assessment of colony integration in fossil species with increasing confidence.

The occurrence of active chimney groups in *M. membranacea* is directly correlated with the size of zooids and thus with small astogenetic changes during budding. At the growing margin, colonies have an extensive peripheral zone of giant buds, which are delineated only by vertical lateral walls. As the colony grows, these buds are partitioned into sequential zooidal rows by the growth of vertical terminal walls. Lutaud (1961) described the astogeny of M. *membranacea* in detail and noted that the large, apical palissade cells of the giant buds oscillated in orientation regularly as the buds extended. Before a bifurcation of zooidal rows, however, the palissade cells became polarized in two differently orientated series (see Lutaud, 1961, p. 254). It would seem probable that the mutual accommodation of zooidal series in alternating large and small sequences is initiated by regular changes in the behaviour of the palissade cells.

Chimney groups are formed by large zooids but not all large zooids develop into chimney groups. There is therefore, in addition,

some inherent potential to produce polymorphic lophophores in some, regularly patterned zooids of the large zooid series. This involves the development of slightly different types of lophophore in each of three to four sequential astogenetic generations, in several, laterally contiguous zooidal rows. Further, the inherent behaviour patterns of the tentacle sheaths of chimney zooids in 'leaning out' from the centre of the chimney is correlated with their position. All these characteristics are indicative of a high degree of colony control. In addition, whether or not the functions of 'tower cell' kenozooids include the formation of passive chimneys, their regular spacing indicates an inherent series of integrated ontogenetic changes, which occur long after the primary astogenetic and ontogenetic processes are completed.

It is possible that the same kinds and degrees **of** differences in zooidal size and budding pattern are correlated with the occurrence of active chimneys in some ascophoran species. Cook (1977) noted that there were varying degrees of correlation between active chimneys and bifurcation of zooidal rows in *Hippoporina porosa* (Verrill), *Schizoporella cornuta* (Gabb and Horn), *Cleidochasma contractual* (Waters) and *Parasmittina nitida* (Verrill). Zooid size may also be **a** contributory factor in these species. It is interesting that Banta (1974) investigated the relationships of size with bifurcation in *Schizoporella nnicornis floridana* Osburn and concluded that although zooid width (as a function of zooid volume) was an important factor, it did not alone decide the occurrence of bifurcations. It should be noted that the differences in zooid widths between chimney zooids and other autozooids in *M. membranacea* are greater proportionally than the differences between zooid lengths (see Table 1).

The relationship between budding pattern and chimney groups in M. *membranacea* also suggests that the apparent absence of integrated excurrent outlets in *Electra pilosa* may be correlated with its totally different and somewhat unusual budding pattern. Encrusting expanses of *E. pilosa* are generally far smaller than those of *M. membranacea,* although, as the size of the zooids and lophophores is also much smaller, there may be as many as 2,500 tentacle crowns feeding simultaneously in a relatively small area (approximately 30cm^2). Some zooids do have larger tentacle crowns, but these do not have unilaterally elongated tentacles and do not occur in patterned groups (see also Cook, 1977). There are no giant buds in *E. pilosa* and colonies tend to grow in star-shaped, diverging series of one to three rows of laterally contiguous zooids which extend the colony by budding distally. Spaces between these series are *filled* in much later in astogeny in two ways. First, each zooid on the outer edge of a row buds a distal-lateral series which itself buds distally. Second, each zooid buds one distal-lateral zooid only, which itself produces one distal-lateral bud. This type of astogeny is essentially derived from a uniserial pattern, and therefore resembles that of the earliest cheilostomes (see Pohowsky, 1973). These forms had a low degree of integration, reflected in all their skeletal characters (see Boardman and Cheetham, 1973). By analogy with similar uniserial living species such as *Pyripora catenularia* (Fleming) and *Aetea anguina* (Linnaeus) (see Ryland and Hayward, 1977), the zooids of these colonies may be

inferred to have had virtually autonomous functions (see Cook, 1979). The lack of chimney zooid groups in *E. pilosa* also allows the inference of a similar, low degree of integration in this species. Although all the colonies observed here were totally encrusting in habit, *E. pilosa* is known to assume a wide variety of erect growth forms under conditions of restricted substratum (see Norman, 1894, pp. 119-122). Erect growth facilitates unrestricted water flow (see Cook, 1977) and might be regarded as a correlated response to still water and restricted substratum. However, Jebram (1970) observed that it occurred in laboratory specimens exposed to a unidirectional current speed of 15cm/sec.

Further observations on *M. membranacea* are needed in order to establish the inferred function of 'tower cell' kenozooids as passive chimneys, and to discover if active chimney groups have any special role in breeding colonies. Spermatozoa are released through the lips of the two distalmost tentacles and congregate in the intertentacular organ (see Silén, 1972), through which fertilized eggs are laid directly into the sea, the larva being of the planktotrophic, cyphonautes typo (sec Ryland and Hayward, 1977. Fig. 11). It would be of interest to know if chimney zooids produce intertentaeular organs and ova and/or spermatozoa, or are non-sexual. All the zooids of *Electra posidoniae* Gautier are capable of producing both ova and spermatozoa, which last are released by all the tentacles. The behaviour of tentacle crowns releasing spermatozoa is distinctive (see Silén, 1966), and resembles that of the polymorphic male zooids of *Hippopodinella adpressa* (Busk), which have specially modified, non-feeding tentacle crowns (see Gordon, 1968). In the genus *Hippoporidra* Canu and Bassler, similar behaviour patterns and modified tentacle crowns are found in male zooids which also form raised, passive chimneys (see Cook. 1968: 1979). The everted tentacle sheaths of all these polymorphic male zooids are extremely elongated. In view of the less apparent, but highly integrated morphological differences of the chimney zooids in *M. membranacea,* it seems possible that they too, may have a specialized sexual function or may, at least, be involved in the efficient dispersal of the sexual products.

Other species of *Membranipora* which are associated with large algal substrata: *M. tuberculata* (Bosc), M. *villosa* Hincks, M. *hyadesi* Jullien and M. *serrilamella* Osburn, together with the algal associated species of *Thairopora,* also require investigation in order to discover whether or not they develop groups of chimney zooids.

Acknowledgments

Summary

The occurrence of active excurrent chimneys has been observed in *Smittoidea reticulata, Parastnittina trispinosa* and *Membranipora membranacea.* In .1/. mem-

branacea the chimney groups are formed by large zooids which alternate in position with smaller zooids. The patterning of 'tower cell' kenozooids, which are developed later in ontogeny, is very similar, and it is inferred that they are derived from active chimney groups, and function as passive chimneys.

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