

Bryozoan Monticules: Excurrent Water Outlets?

Abstract. *Monticules, regularly arranged modified areas on Paleozoic Bryozoa, may represent regions from which water currents produced by lophophores of adjacent feeding zooids escaped. Such circulation patterns have been observed in Recent forms.*

Bryozoan monticules (maculae) are modified groups of zooids distributed more or less evenly over the surface of many Paleozoic stenolaemate Bryozoa (1). Monticules may be elevated or depressed, and they contain modified zooids such as mesopores, enlarged polymorphs, or autozooids more widely spaced than usual (Fig. 1).

Ulrich proposed (2, p. 298) that monticules contained reproductive structures. Ulrich extended the theory of reproductive function to most Paleozoic Bryozoa, even though few possess gonozoid-like polymorphs (3). A second hypothesis is that monticules are centers of budding (4). We examined longitudinal sections of 80 Paleozoic bryozoans; budding within monticules is rarely more pronounced than between monticules (5). This hypothesis therefore can apply to only a relatively small number of Paleozoic Bryozoa.

The following suggest that most or all monticules had a common function.

(i) The distance between monticules is remarkably constant among Paleozoic taxa (6). (ii) Monticules are arranged in a rhombic (hexagonal) pattern in virtually every bryozoan possessing them. (iii) Diameters of monticules are nearly constant within species and vary little among taxa (6). (iv) Monticules are common in many taxonomically unrelated Bryozoa with robust colonies (2, 7). (v) All stenolaemate monticules appear to be modifications of the exozone and not the endozone, and so seem to be associated with functional parts of the colony and not developing parts (8). (vi) Monticules are characteristic of robust colonies and are generally absent on delicate colonies.

We examined the cheilostome *Membranipora* sp. from California and Washington, growing on large algal thalli. When active, most of the colony is covered by extruded polypides (Fig. 2A), but numerous circular blank spaces, called chimneys here, are

formed because lophophores of zooids located beneath the chimneys lean away from the area. Chimneys are consistent in location; if the colony is disturbed, lophophores reexpand in the same pattern. Lophophores bordering chimneys are like other lophophores, except that they have longer necks and the two or three tentacles bordering the chimneys are longer than other tentacles (Fig. 2B). It is virtually impossible to detect the location of chimneys when the lophophores are retracted. Incurrent water passes between tentacles into the space between lophophores and zoecia (neck regions of extruded polypides), passes peripherally, and is exhaled forcefully at the edge of the colony if an edge is nearby, or through chimneys; small colonies lack chimneys. Chimneys are about 0.8 mm in diameter and are distributed in a rhombic pattern about 1.9 mm from nearest neighbors. Small colonies of a phylactolaemate bryozoan have been found to be more efficient than large colonies in that they have higher clearance rates of food cells per lophophore (9). These observations suggest that lophophores in large, robust colonies interfere with each other unless excurrent channels such as chimneys are present.

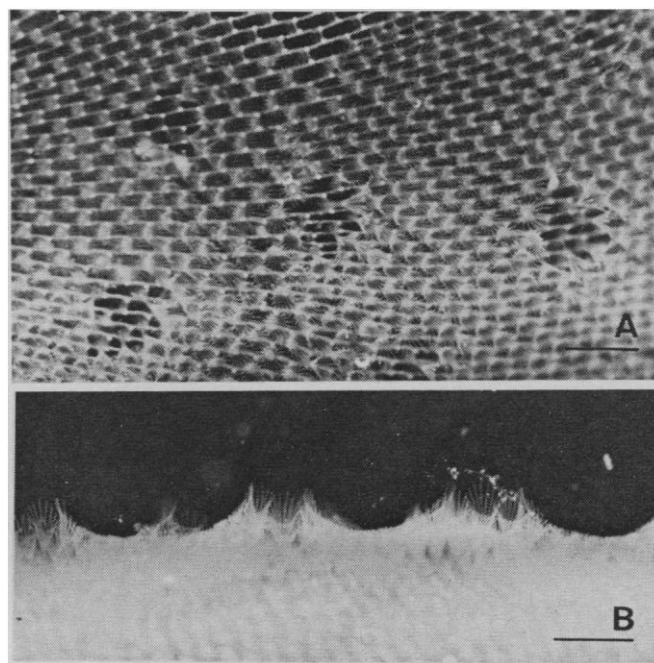
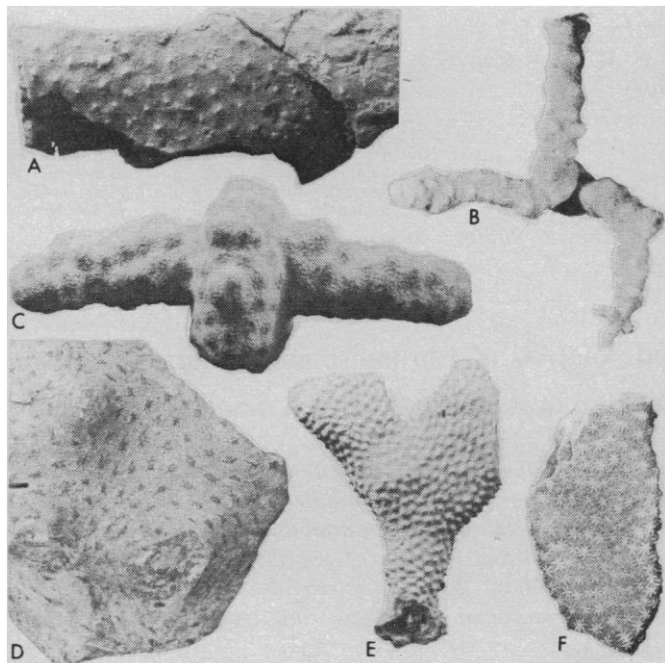


Fig. 1 (left). Paleozoic (A and D to F) and Modern (B and C) bryozoans with monticules. Scale bar, 1 cm. (A) Bifoliate cryptozostome, *Pachydictya splendens*, of the Late Ordovician (Maquoketa Shale), Wilmington, Illinois [U.S. National Museum of Natural History (USNM) specimen 189912]. (B) Branching cheilostome, *Hippoporidra* sp., from Albatross Station 2414, Gulf of Mexico (USNM 189913). (C) Cheilostome, *Hippoporidra* sp., encrusting pagurid-inhabited gastropod shell, Sansibel, Florida (USNM 189914). (D) Cystoporate, *Fistulipora* sp., of the Devonian (Traverse Formation), Thunder Bay River near Alpena, Michigan (USNM 189915). (E) Trepustome, *Monticulipora molesta*, of Late Ordovician (Maysville Group), near Ruckerville, Kentucky (USNM 97779). (F) Cystoporate, *Constellaria florida prominens*, of Late Ordovician (Mt. Hope Formation), Newport, Kentucky (USNM 189916). Fig. 2 (right). Live *Membranipora* sp., from Catalina Island, California. Scale bars, 1 mm. (A) Frontal view of extruded lophophores showing six chimneys. (B) Side view of the same showing elongation of tentacles in lophophores adjacent to chimneys.

The long, flexible neck which makes it possible for a lophophore to bend away from chimneys in cheilostomes is essentially absent in modern stenolaemates, in which the lophophore seldom protrudes far from the skeletal aperture (8). This suggests that if chimneys analogous to those in *Membranipora* exist in stenolaemates, their location would be reflected in some modification of the skeleton.

We propose that monticules in fossil stenolaemate Bryozoa are skeletal reflections of areas in which functional lophophores were absent or modified so as not to resist the excurrent flow of water. This hypothesis would explain a number of observations. (i) The consistency of distances between monticules would be expected if the number of cilia per unit area of colony surface is approximately equal among species possessing monticules. (ii) A rhombic arrangement of monticules would be expected, since water movement would be most facilitated by having lophophores located no farther than some relatively constant distance from a chimney. (iii) The sizes of monticules would be expected to be roughly consistent if assumption (i) is correct. Too big a chimney would take up too much space that could otherwise be occupied by a feeding lophophore; too small a chimney would reduce feeding efficiency. (iv) The heterogeneity of structures comprising monticules among taxa of fossil stenolaemates can be explained because monticules could be comprised of a variety of structures, depending on the evolutionary backgrounds of the taxa. For chimneys to be functional the only requirement is that no zooids effectively resist the excurrent water stream. (v) Monticules would be expected to develop only in the exozone where functional polypides were present. (vi) One would expect monticules to develop some distance from a growing edge, where lophophores were not yet functional and water could escape. Delicate colonies would therefore lack monticules.

Many Recent and fossil cheilostomes with robust colonies possess regularly distributed mammillate areas which resemble monticules in gross appearance. Perhaps such structures represent skeletal reflections of chimneys. One genus with many such protuberances, *Hippoporidra*, was studied by Cook (10), who reported that in some species the areas contain specialized zooids (called "cortical zooids") with reduced aper-

tures. In *H. senegambiensis*, cortical zooids possess only half the usual number of tentacles and lack cilia altogether. This suggests that protuberances are areas in which excurrent water flow is not resisted by functional lophophores. In view of later research (11), it seems likely that such zooids are males which release sperm into the water to be carried to other colonies for fertilization. If the protuberances represent chimneys, male zooids would be in a suitable location for sperm dispersal.

The hypothesis proposed here does not necessarily exclude previous theories. In some species, for example, monticules may have been brooding or budding regions and still represent chimneys.

The hypothesis suggests similar explanations for some Bryozoa with unusual colony forms. Colonies of *Scalariopora*, *Glyptopora*, *Evactinopora*, *Radiofascigera*, *Centronia* (12), and others have regularly arranged regions which apparently lacked functional autozooids in life. These regions may represent avenues for excurrent water, and it may be that providing for efficient water circulation has had an important effect on colony form in Bryozoa.

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5. Photographs of 96 longitudinal thin sections of about 80 species of Paleozoic stenolaemate Bryozoa exhibiting recognizable monticules were examined at random. Eleven specimens (11.4 percent) exhibited budding in monticular regions and were counted as supporting the theory of Anstey and Delmet (4) even if budding was common elsewhere in the section.
6. The distance between monticules (2 to 3 mm) was more nearly constant among Ordovician Trepostomata than among any of 20 other variates measured in 24 species [F. McKinney, *Bull. Am. Paleontol.* 60, 218 (1971)]. We measured numerous specimens from 20 species of cystoporates and cryptostomes chosen at random from the reference collections at the Smithsonian Institution, Washington, D.C. Monticulate diameter is difficult to measure because monticules ordinarily blend into the colony surface without a definite border. Within the limits of precision of measurement (± 0.2 mm), monticulate diameter in any one species is constant; the diameter varies from 1 to 2 mm among taxa in Cystoporata and Cryptostomata.
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Computer-Assisted Analysis of Chromosomal Abnormalities: Detection of a Deletion in Aniridia/Wilms' Tumor Syndrome

Abstract. A chromosome translocation, $t(8p+;11q-)$, in a patient with aniridia and Wilms' tumor, appeared balanced by standard techniques, including trypsin banding. Computer analysis of optical microscope scanning profiles of chromosome pairs 8 and 11 revealed an interstitial deletion of the short arm of 8. Computer analysis coupled to the new banding techniques provides greater resolution for the detection of subtle chromosomal variations not recognized by banding methods alone.

Newly developed chromosomal banding techniques not only permit ready identification of all human metaphase chromosomes, but also assist in the detection of complex chromosomal rearrangements (1-4). However, variation in the state of chromosome con-

traction (or elongation) within and among metaphase preparations may obscure subtle translocations or deletions when they are analyzed by visual scanning alone. Neurath and colleagues (5) have developed a high-resolution microscope scanning system coupled