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Alan H. Cheetham Functional Morphology
and Biofacies
Distribution of
Cheilostome Bryozoa
in the Danian Stage
(Paleocene) of
Southern Scandinavia

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ABSTRACT

Cheetham, Alan H. Functional Morphology and Biofacies Distribution of Cheilostome Bryozoa in the Danian Stage (Paleocene) of Southern Scandinavia. *Smithsonian Contributions to Paleobiology*, number 6, 87 pages, 1971.—Highly diversified assemblages of cheilostome Bryozoa in the Danian Stage of southern Sweden and Denmark represent the culmination of primarily divergent evolutionary trends originating in the first appearance of the group in Early Cretaceous time. Functional relationships between colony and zooid morphology are less likely to have been obscured by vestigial structures and convergent and parallel evolution in these assemblages than in later Cenozoic faunas. The Danian assemblages, then, provide a test of the hypothesis that, in the early evolution of cheilostomes, environmentally correlated variation in the form of colonies depended functionally upon the structure of their component zooids.

Theoretically, the rigidly erect growth form should have an adaptive advantage over the presumed ancestral encrusting form, by virtue of a vastly increased potential zooid density relative to substrate occupied. A rigidly erect colony must be able to resist stresses induced by vertical loading, bending, and twisting and thus appears to require calcified walls, especially on the frontal sides of its zooids. Given the constraints imposed by the cheilostome mode of growing and calcifying zooid walls and of operating the hydrostatic system, zooid morphotypes can be relatively graded for efficiency in structural support of the colony by the degree to which their joint calcification approaches a laterally merging, continuously thickening, distally tapering skeletal mass analogous to the outer walls of an enlarging cantilever beam.

These hypothetical relationships are generally consistent with biofacies distributions of more than 50 species associated with a single middle Danian mound in southern Sweden. This mound is typical of many which accumulated, probably at depths approximating the shelf-edge, in southern Scandinavia during Danian time. It includes three biofacies: (1) the flanks, dominated by bryozoans; (2) the core, rich in octocorals with less abundant colonial scleractinians and bryozoans; and (3) transitional areas, between the two, dominated by octocorals but with abundant bryozoans. Sediments of the three biofacies contain distinctive assemblages of cheilostome species which differ in abundance rather than by presence or absence. The flanks are dominated by species inferred to have had erect colonies and the more complex zooid morphotypes. This group of species constitutes the bulk of the total fauna in weight-abundance but fewer than half the species. Species dominant in the
(Continued on page iv)

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(Abstract—Continued)

core facies make up about half the total number of species and are inferred to have had mostly encrusting colonies with zooids of all morphotypes recognized, including the simplest. The transitional facies includes a mixture in subequal proportions of the two groups of species dominant in the other facies; however, this facies has other distinctive species in abundance and thus may represent an ecotone. Morphologically, the cheilostomes abundant in the transitional facies are intermediate in inferred zooid morphotypes and colony forms.

The relation between abundance and morphology of Danian cheilostomes suggests that attainment of the more advantageous rigidly erect colony form was functionally more probable for zooid morphotypes susceptible of heavy frontal calcification than for others. If a minimum amount of frontal calcification must have been present before the rigidly erect mode of growth could be assumed, then frontal calcification was associated originally with some other function, such as protection of the lophophore. It is possible that the various further advances in zooid morphotype could also have been made as separate prospective adaptations, but it seems more likely that some or all of them represent direct adaptive improvements for the structural support of rigidly erect colonies.

Alan H. Cheetham

Functional Morphology and Biofacies Distribution of Cheilostome Bryozoa in the Danian Stage (Paleocene) of Southern Scandinavia

Introduction

The evolutionary role of selection requires that sustained trends of morphologic change be adaptive, that is, advantageous to the organism or to the conspecific population of which it is a part (Simpson 1953:160, 1958:534). Morphologic differences between taxa, usually resulting from sustained evolutionary trends, therefore suggest differences in adaptation. Within a multispecific assemblage of organisms occupying broadly similar ecologic niches in closely related habitats, the relative abundances of morphologically differing populations thus should reflect differing degrees of adaptation to the general environment (Simpson 1953:161, 1958:523).

Highly multispecific assemblages of cheilostome Bryozoa are known to have occurred from mid-Late Cretaceous time to the present. Since their origin, apparently in late Early Cretaceous time, cheilostomes have increased in diversity almost steadily (Figure 1). This increase reflects morphologic proliferation with respect both to changes between time-successive assemblages of species and to the range of differences among coeval populations. To the extent that this proliferation applies to assemblages of species that lived in similar environments, it can be assumed to express increasing degrees of adaptation.

The morphologic diversity of cheilostomes encompasses many characters, few of which have been considered in terms of both evolutionary trends and relation to the environment. The growth form of the colony has received much attention because of its correlation with substrate type and water agitation, but its evolutionary significance has not been fully considered. On the other hand, the structural features of the zooids, which have been shown to follow an evolutionary trend of increasing structural complexity through the Cretaceous, have not been investigated for their possible adaptive correlation with other characters or with environmental variables. Other characters, such as kinds and distributions of avicularia, ovicells, and the like, are poorly known in terms of both evolutionary trends and relation to the environment.

The present investigation considers relationships among colony form, zooid structure, and environment in assemblages of cheilostomes of Danian age in southern Scandinavia. This fauna is important to the study of adaptations in cheilostomes because it has a high species diversity within a geographically and apparently ecologically restricted area and because it represents the culmination of the first major episode in cheilostome evolution (Figure 1). The seeming pause in taxonomic diversification during Danian time suggests that cheilostomes had reached an adaptive plateau by the end of the Cretaceous, and yet all three major groups of cheilostomes are diversely represented in the Danian

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fauna. The functional relationships between colony and zooid morphology are less likely to have been obscured by vestigial structures and convergent and parallel evolution in these assemblages than in later Cenozoic faunas, which consist predominantly of species with the most complex zooid morphotypes (ascophorans).

The adaptive significance of colony form and zooid structure are inferred here from the general evolutionary history of cheilostome morphology, as presently understood, and by analogy with living species. The hypothetical relationships of colony form, zooid structure, and environment thus proposed are then tested against the relative abundances of Danian species in a series of samples inferred to represent related habitats.

Previous studies of cheilostomes from the Scandinavian Danian deposits, summarized by Berthelsen (1962:43–50), have been primarily taxonomic and have included reports of more than a hundred species from Denmark, Sweden, and glacial erratics in northern Germany and Holland. Cheilostomes from Denmark have been studied extensively by many authors, including Pergens and Meunier (1886), Lang (1921, 1922), Voigt (1923, 1930, 1956, 1968a), Levinsen (1925), Berthelsen (1948, 1962), and Jürgensen (1968). Many species are known from the erratic boulders of Germany primarily through the work of Voigt (1924, 1925, 1928, 1930, 1968a), and several have been recorded from the boulder clays of Holland by Veenstra (1963). Danian cheilostomes from Sweden have received much less attention; 16 species were studied by Hennig (1892, 1894), and a few were included by earlier workers in studies of Cretaceous and Danian faunas in the Scandinavian region. In addition to his taxonomic studies on Danian cheilostomes, Berthelsen (1962:225–256) also determined weight-abundances of cheilostome skeletal material and relative abundances in number of fragments of cheilostome species in samples from eight localities in Denmark. His purpose was to characterize different Danian lithologies in terms of their bryozoan content and to identify stratigraphically distinctive species assemblages.

Most of the data on which the present study is based are from field observations and samples collected in 1964–1965 from a single moundlike structure of middle Danian age in the large cement quarry in the Limhamn district of Malmö, Sweden. Additional material from other sediments in the Limhamn quarry, from other Swedish localities, and from some Danish localities (including the classical exposures along

Stevens Klint and in the quarry at Fakse) was collected and examined in an attempt to extend the relationships inferred from the Limhamn mound. This additional material was not examined in the same quantitative detail as that from the one mound, but the differences between samples from similar parts of different mounds appeared generally to be less than those between different parts of the same mound. Therefore, the quantitative relationships for the Limhamn mounds are thought to apply to all Danian moundlike sedimentary structures in southern Scandinavia.

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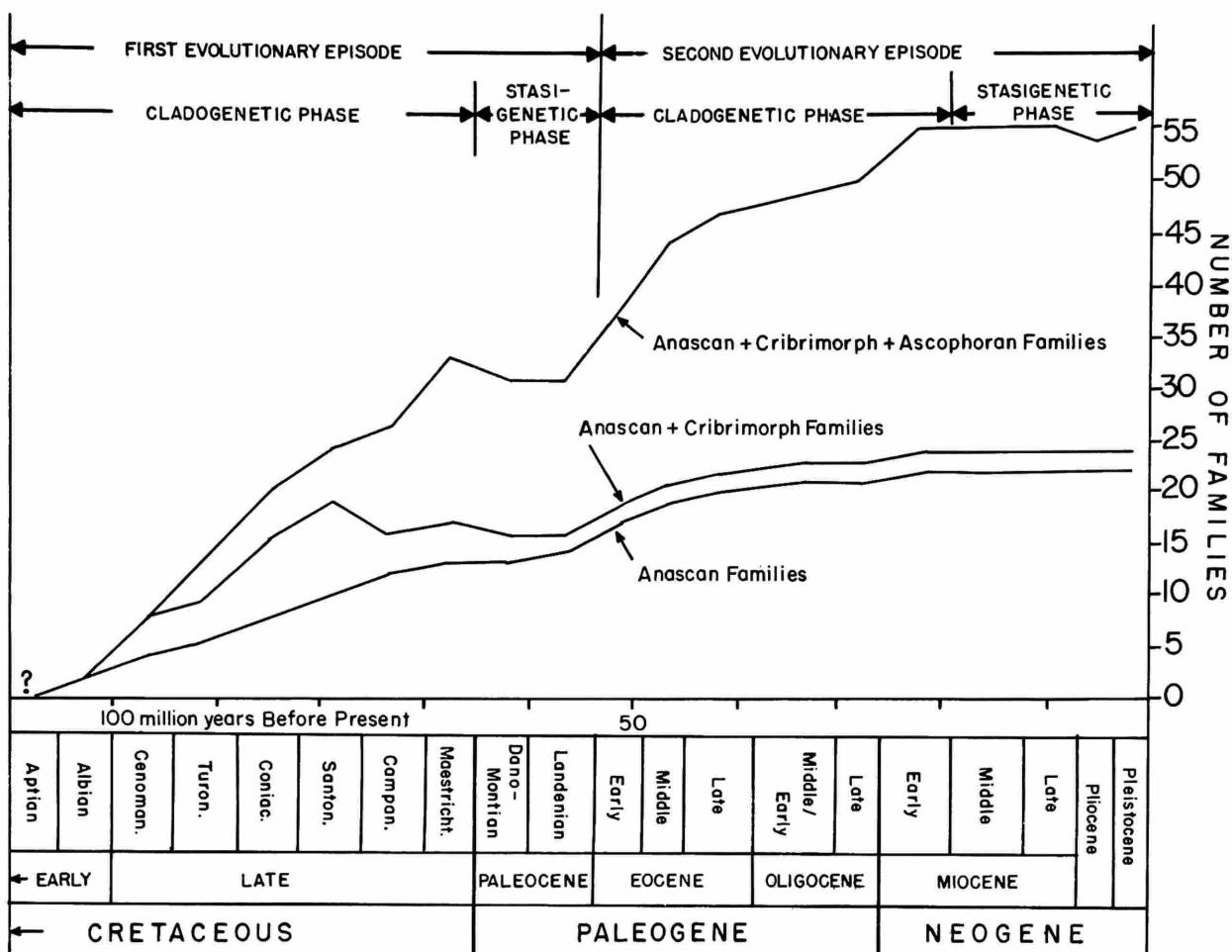


FIGURE 1.—Division of evolutionary history of cheilostome Bryozoa into two major episodes, as suggested by changes in number of families from Early Cretaceous through Pleistocene. Data are from Larwood et al. (1967), and time scale is after Casey (1964) and Funnell (1964). Two roughly sigmoid curves, Albion-Paleocene and Eocene-Pleistocene, are each separated into a phase of rapid diversification (cladogenesis) and a following quiescent phase (stasigenesis). Because of the generally long ranges of families and the nearly equal intervals of time over which the census was taken, it seems inappropriate to calculate frequencies as time-frequencies. Changes in diversity at the family level, as shown here, may be an inadequate expression of evolutionary activity at lower categorical levels. The earlier evolutionary episode shows increase in all three major groups of cheilostomes—anascan, cribrimorph, and ascophoran. Most increase in the later episode has been in the ascophoran cheilostomes. One genus, *Dacryoporella*, included by Larwood et al. (1967) among the ascophorans, has been omitted from consideration of family ranges, as discussed in the text (page 15).

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Functional Morphology of Cheilostomes

ADAPTIVE SIGNIFICANCE OF MORPHOLOGIC DIFFERENCES

The differing states of a morphologic feature can be expected, in general, to differ in adaptive value with respect to any particular environment. In the study of adaptive morphology of fossils, two approaches have been used to infer the relative values of differences in a morphologic feature. In the functional-analysis method (e.g., Rudwick 1968:44), a graded series of states is deduced from the theoretical efficiency of the

morphologic feature in performing a postulated function—this usually having been chosen by analogy with living organisms—and the actual states of the feature in known fossils are then compared with the hypothetical constructs. The second method is empirical and consists simply of grading the actual series of states of the morphologic feature according to the relative abundances of populations within which each state is shown.

Neither method, used alone, can be expected to result in a full understanding of the adaptive significance of morphologic differences in fossils. It is apparent that empirically graded character states are only the results of evolutionary adaption and do not yield its basis. Functional analysis may not yield adaptive significance directly, because conflicts among the functional properties of a feature may require some functions to remain partly or wholly unrealized (Bock and von Wahlert 1965:274). An example of functional conflict in cheilostomes is that between rigidity and flexibility of the frontal wall; the advantage of having that wall completely calcified (except for the operculate orifice through which the lophophore is protruded), to protect the lophophore and associated organs, is partly offset by the necessity of keeping a portion of the wall depressible as part of the hydrostatic system (Harmer 1930: 92–99).

As pointed out by Dobzhansky (1956:346), it is the whole phenotype of the organism, not each of its separate features, aspects, or stages, which is adapted to the environment. Pleiotropic and other forms of genetic correlation between features, aspects, or stages of the phenotype can result in the appearance and continuation in successive populations of states of morphologic features whose functions are never realized because of adaptive conflicts. Thus the adaptive significance of any morphologic feature can be expected to depend on the functions of other features, but to varying degrees (Dullemeyer 1958). The object of functional analysis of fossils, then, is to deduce adaptively graded series of morphologic states which can be tested against their relative abundances in populations.

GENERAL RELATION OF MORPHOLOGY TO ENVIRONMENT

A large part of the variation in skeletal morphology of cheilostome Bryozoa appears to be directly related to the environment. The extent of environmental influence on morphology is suggested by some of the differ-

ences within a colony, either among the individual zooids themselves or among major regions of the colony (Stach 1935). These are the approximately continuous differences that remain after patterns of intracolony variation related to growth stages of the zooids (ontogeny) and generational differences among zooids which have budded at different stages of colony development (astogeny) have been taken into consideration (Boardman et al. 1970). More distinctly discontinuous intracolony variation in zooid form (polymorphism) presumably has a functional basis, such as feeding and reproduction, and therefore is at least indirectly related to the environment, whether or not the polymorphism is directly induced by microenvironmental differences (Silén 1938:646, Powell and Cook 1966). Moreover, each set of a polymorphous series of zooids ordinarily displays a similar remainder of microenvironmental variation after growth differences have been taken into consideration (Cheetham 1966:17–21).

Non-growth variation shown by the zooids of a colony (or by one set of zooids in a colony having polymorphous zooids) may be inferred to reflect environmental influence on morphology because of the general genetic homogeneity of a bryozoan colony (Stach 1935:646, Boardman and Cheetham 1969:208, Boardman et al. 1970). Lacking correlated genetic differences, phenotypic variants of the same ontogenetic, astogenetic, and polymorphic state within a colony must be interpreted as so many physiologic adaptations to varying microenvironments during colony growth. Although such non-heritable variation lacks direct evolutionary significance (Bock and von Wahlert 1965:284), it provides a baseline for recognizing morphologic differences which may be heritable, in separate colonies within or among populations. Although few comparisons between intra- and intercolony variation have been made quantitatively for cheilostomes, the evidence available suggests that these two kinds of variation, expressed as coefficients of variation for the linear dimensions of zooids, may not be significantly different (Boardman and Cheetham 1969:226). The relationship between these kinds of variation is apparently unlike that for some features in other colonial groups (Oliver 1968:27).

Environmentally induced differences within some colonies are expressed by groups of zooids making up major parts of the colony as well by individual zooids. For example, Cook (1968a:124) described a Recent colony of *Membranipora arborescens* (Canu and Bassler) combining broadly encrusting portions with

erect, unilaminar fronds. The zooids on the erect fronds are relatively more elongate than those on the encrusting portions and differ from them in some structural features. Other Recent specimens of *M. arborescens* show one or the other of the colony forms and correlated zooid morphologies (Cook 1968a:124, pl. 1c,d). The correlation of colony form and zooid morphology in this species suggested to Cook (1968a:123) that the two classes of features are a correlated adaptive response to environmental factors, probably differences in availability of suitable substrates. Similarly correlated differences have been described in other species, e.g., *Smittoidea variabilis* (Canu) (Cheetham 1966:70). In many previous studies of the functional morphology of cheilostomes, such as those by Stach (1936, 1937), Voigt (1939), Silén (1942), and Lagaaij and Gautier (1965), it has been inferred that colony form expresses directly the adaptation of the organism to the environment, whereas zooid structure at best reflects adaptations at the individual level of organization. It has even been argued that structural differences in zooid skeletons follow orthogenetic trends of diminishing adaptation (Lang 1916, 1919, 1921). The object of this functional analysis is to deduce some of the possible adaptive relationships between colony form and zooid structure.

COLONY FORM

The general correlation between some environmental factors and the form of colonies in cheilostome Bryozoa was recognized by earlier workers, but Stach (1936, 1937) was the first to systematize the relationship by describing nine basic forms of colonies and adducing the conditions of turbulence and substrate under which each will thrive. Although subsequent authors have made further or different divisions of colony forms, their studies of Recent faunas—such as those of Gautier (1962), Lagaaij and Gautier (1965), Cook (1968b), and Schopf (1969)—have generally verified the relationship described by Stach and therefore have justified its application to the reconstruction of paleoenvironments by Stach (1936) and by others such as Berthelsen (1962), Cheetham (1963), Labracherie and Prud'homme (1967), and Askren (1968).

Stach (1937:80–82) suggested that cheilostomes are divisible into two groups on the basis of their variability in colony form. The first group comprises species, having a stable form, that produce only one colony type regardless of environmental conditions. Adverse conditions simply preclude their occupying that hab-

itat. The particular colony form shown by a species in this group can be inferred to represent a heritable adaptation fixed through evolution. The second group comprises species, having an unstable form, that produce different colony types in various environments. Their ecologic range can therefore be expected generally to be greater than that of stable species. The different colony forms shown by an unstable species, taken together, represent a heritable adaptation, but each form separately is a nonheritable, physiologic modification brought on by particular environmental conditions.

Stable colony form was thought by Stach (1937:80) to be restricted to species developing only the most specialized types of colonies: loosely encrusting (petraliiform); free-living and discoidal or conical (lunulitiform); erect-fenestrate (reteporiform); erect-jointed (cellariiform and catenicelliform); and erect-flexible (flustriform). All species having non-fenestrate, rigidly erect colonies, with either subcylindrical or bilaminar trunks and branches (vinculariiform and eschariform colonies, respectively), or closely encrusting (membraniporiform) colonies were regarded as unstable. This is a consequence of Stach's assumption (1937:82) that any species having vinculariiform or eschariform colonies can become encrusting under adverse conditions of turbulence and that any species having membraniporiform colonies will tend to assume erect growth under favorable conditions.

Studies on Recent faunas—such as those by Gautier (1962), Lagaaij and Gautier (1965), and Cook (1968b)—suggest that even though the great majority of cheilostome species have the colony forms regarded by Stach as unstable, only a small proportion of them assumes more than one of the three major growth forms. Variation, for example, in thickness of trunks and branches in erect forms is common, but this type of variation is also known in so-called stable colony forms (Gautier 1962:386, 387). Therefore, it appears that membraniporiform, eschariform, and vinculariiform colonies may be developed in different species, either as stable forms fixed by evolutionary adaptation or as unstable forms varying plastically through physiologic adaptation.

An alternative grouping of Stach's nine colony forms has been suggested by Lagaaij and Gautier (1965:51) and Schopf (1969:239). Four major groups are based on relation to substrate and the surrounding water: (1) encrusting (membraniporiform and petraliiform), (2) rigidly erect (eschariform, vinculariiform, and retepori-

form), (3) nonrigidly erect (flustriform, cellariiform, and catenicelliform), and (4) free-living (lunulitiform). Each of these groups is susceptible of further or slightly different division than Stach's nine forms (Lagaaij and Gautier 1965:51, Cook 1968b:120, Schopf 1969:239). In the study of morphologic adaptations in cheilostomes, this method of grouping has the advantage of emphasizing the functional, rather than the genetic, basis of colony form.

The adaptations shown by two of the colony-form groups and by parts of the other two, involve specialized colony-wide features. Nonrigidly erect forms have major areas of the colony with reduced calcification; lunulitiform colonies develop specialized zooids or extrazoidal tissue to thicken the basal side; petraliiform colonies have non-calcified attachment tubes; and reteporiform colonies develop calcified anastomoses. The principal morphologic differences between the remaining forms in the other two groups, encrusting and rigidly erect colonies, include the geometric arrangement of zooids. As these colony forms—membraniporiform, eschariform, and vinculariiform—characterize the great majority of cheilostomes, they are of special significance in the functional morphology of the group.

Encrusting and erect colonies differ in several basic adaptations, some of which were recognized by Stach (1937:82). Encrusting colonies are supported directly by the substrate on a zooid-by-zooid basis (Figure 2a). The size of the colony, consideration being given to factors such as competitive growth of other organisms (Boardman et al. 1970), is directly related to the size of the cohesive and relatively smooth surface available for encrustation. Encrusting colonies thus use the habitat virtually two dimensionally, they depend nearly entirely on movement of the surrounding water to increase their exposure to food, and they are highly vulnerable to sedimentation and to limitation of the areal extent of suitable substrate. Erect colonies, on the other hand, are less affected by sedimentation and by substrate limitations because they use the habitat in a more distinctly three-dimensional way, increasing their exposure to the surrounding water and their potential for population density relative to the substrate occupied. Lacking extensive supportive contact with the substrate, however, they must provide most of their own support, ultimately through the architectural properties of their zooids (Figure 2b). Consequently, the size of an erect colony may be directly related to the combined structural strength of its constituent zooids,

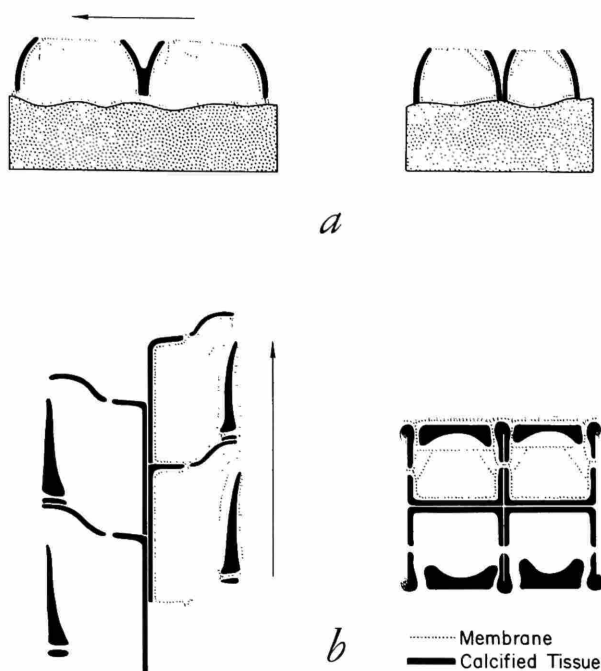


FIGURE 2.—Generalized morphology of zooids in an encrusting (a) and a rigidly erect (b) colony in cheilostomes, shown in diagrammatic sagittal (left) and transverse (right) sections. Lophophores, alimentary canals, and other organs have been omitted for simplicity. The direction of colony growth (distal) is indicated by arrows.

whereas that of an encrusting colony may be almost independent of it.

The inference that the erect colony form is an adaptive advancement over encrusting growth finds some support in the stratigraphic distribution of those cheilostomes whose growth form can be interpreted. The oldest genera known (*Pyripora*, *Rhammatopora*, *Wilbertopora*, and *Charixa*), which occur in rocks of Albian or possibly Aptian age in Europe and North America (Voigt, 1968b:13), all have simple, apparently encrusting (membraniporiform) zoaria. It has not been possible to substantiate the presence of presumed erect cheilostomes in the Albian of Texas, reported by Laughbaum (1960:1186–1189, *Stamenocella* sp. and *Thyracella* sp.; specimens not found in the Southern Methodist University collections, T. E. Williams, personal communication, 1967); on the other hand, erect cyclostomes are abundant in the same Texas Albian rocks that yield encrusting cheilostomes and in rocks of comparable age in Europe (Canu and Bassler 1926). The first erect cheilostomes thus are apparently Turonian species of *Quadricellaria* and *Stamenocella* (Voigt 1959a) having vinculariiform

and eschariform zoaria. The more specialized forms of colonies appeared later in the Cretaceous (lunuliti-form, cellariiform) or in the Tertiary (reteporiform, cateniceform, etc.).

STRUCTURAL ANALYSIS OF RIGIDLY ERECT COLONY

The structural properties of the rigidly erect colony thus are central to understanding adaptation in cheilostomes. As an architectural structure, this colony form seems analogous to a pillar or beam, and an approach to its analysis is suggested by D'Arcy Thompson's (1942:967–985) discussion of the strength of these types of structures. In drawing this analogy, it appears necessary to assume only an economical expenditure of energy in the production of skeletal reinforcement, a minimum amount of which is required for the hydrostatic function of the individual zooids (discussed below); that is, zooecial walls should be thickened in proportion to the stresses distributed through the colony as a result of its subjection to forces in the environment.

Two sets of forces probably act on any rigidly erect cheilostome colony: those due to the weight of the colony itself, and those due to the movement of the water in which the colony grows. Even though these two sets of forces are probably very unequal in magnitude, they are probably both factors in structural response and may be considered separately.

In motionless water, a rigidly erect colony that rises perpendicularly from a horizontal substrate would behave as an evenly loaded pillar if it is either unbranched or symmetrically branched. If the specific gravity of the nonskeletal parts of such a colony can be assumed not to be significantly different from that of sea water, the vertical load on the base of the colony, due primarily to the weight (in water) of the skeleton, increases with the growth in volume of skeletal material in the colony. The increase in load is arithmetically proportional to the increase in total colony volume (skeletal and nonskeletal) in species that calcify zooecial walls only during early ontogenetic stages, but it is exponentially proportional in species that continue to calcify zooecial walls throughout the life of the zooids.

Vertical loads on rigidly erect colonies that grow downward, as from roofs of submarine caves, would be equal to those on identical upright colonies, but

they would induce tensional rather than compressional stress.

The ability of the colonial skeleton (zoarium) to resist stresses set up by the vertical load is proportional to the cross-sectional area of skeletal material. The ratio between the cross-sectional area through weight-supporting structures and the volume of the body is a well-known relationship restricting body size in terrestrial organisms. The restriction of body size is, of

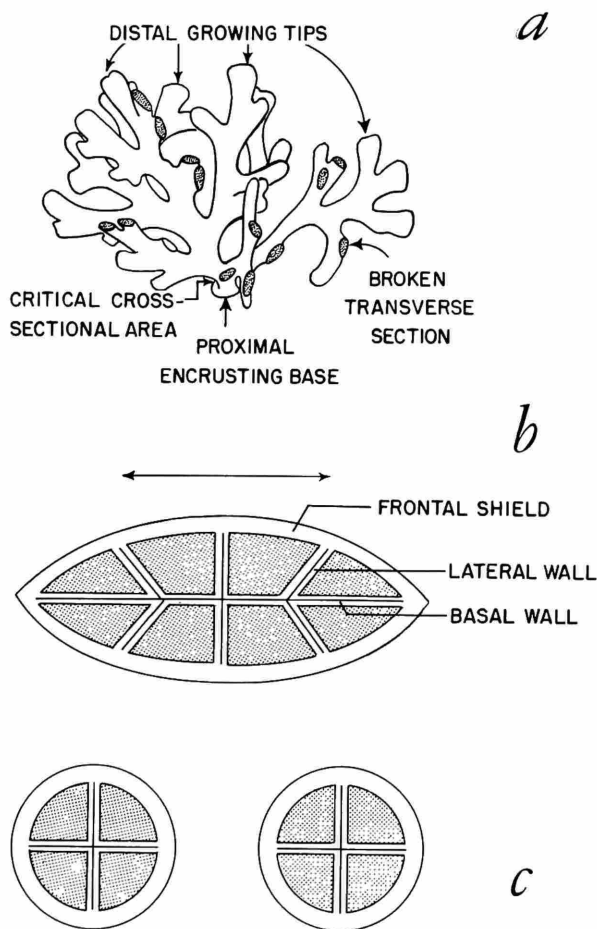


FIGURE 3.—Structure of rigidly erect cheilostome colonies. *a*, Erect bilaminar (eschariform) zoarium of a Recent specimen of *Metrarabdotos* (*Biavicularium*) *tenue tenue* (Busk), showing critical cross-sectional area near proximal base and preferred orientation of branches with long axes roughly parallel to plane of figure (after Cheetham 1968, pl. 9:1). *b*, Transverse section through a bilaminar branch, showing arrangement and relative thickness of zooecial walls and inferred directions (double-headed arrow) of bending moments (see Figure 4). *c*, Transverse section through two cylindrical branches which together have the same number of zooecia of the same volume as in *b*, but only about half the strength.

course, less significant for organisms that live in sea water. Even though the area-to-volume ratio establishes a maximum colony size for any given cross-sectional area through the colonial skeleton of a cheilostome, stresses induced by movement of the surrounding medium probably cause failure at colony sizes far short of the theoretical maximum that can be supported in motionless water. Structural modifications for improving the area-to-volume ratio, however, can be expected to be part of the adaptation shown by rigidly erect cheilostomes. These modifications involve shape changes to increase the cross-sectional area of the colonial skeleton in critical vertical-load supporting regions of the colony.

In any rigidly erect cheilostome colony, there is a critical cross-sectional area through the skeleton at which failure would occur if the colony exceeded its theoretical maximum size. This area is the smallest one having the greatest load distal to it and ordinarily lies near the proximal end of the colony (Figure 3*a*). In species in which zooecial walls do not thicken appreciably after early ontogenetic stages, and in which the zooids have a nearly constant volume, the only way that the critical area can be larger is by including more zooids. In some Eocene and younger cheilostomes, such as *Kleidionella grandis* Canu and Bassler (1920, pl. 78:1–6), zooids were apparently added to the proximal trunk and branches during growth of the colony; this was accomplished by frontal budding from proximal zooids at the same time that distal budding occurred at the growing tips (Boardman et al. 1970:304, fig. 5). The earlier cheilostomes considered here appear not to have had this capability; instead, in some of them, the shape of the whole colony became bilaminar (Figure 3*b*) rather than cylindrical (Figure 3*c*), so as to include a larger number of zooids in the critical zone. Because the cross-sectional area of the combined zooecial walls is greater than in a cylindrical colony having zooids of the same volume, a bilaminar colony has greater vertical-load-bearing strength for any given total colony volume or for any given number of zooids. For the same number of zooids of the same volume, however, a bilaminar colony has either less height or fewer branches than a subcylindrical one and thus does not exploit the rigidly erect mode of growth as effectively as can a subcylindrical one (see discussion above).

Colonies having either bilaminar or subcylindrical form can be more efficiently strengthened for vertical-load bearing by an increase in the proportion of skele-

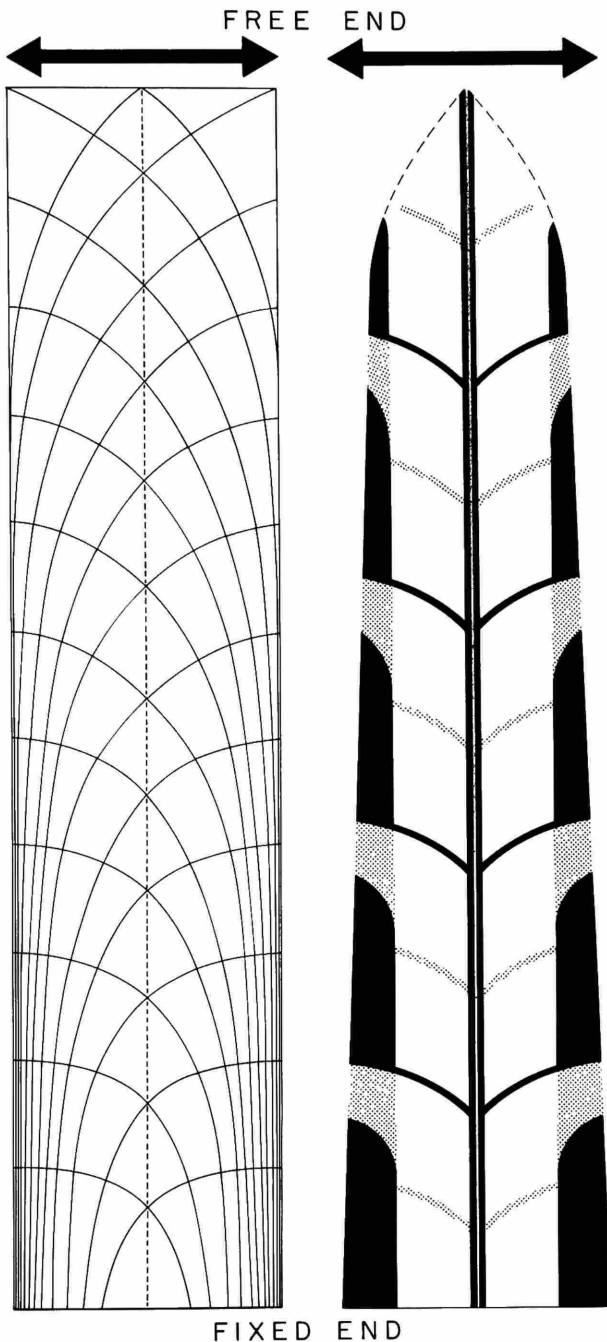


FIGURE 4.—Relation between bending stresses and skeletal construction in a rigidly erect cheilostome colony. Idealized lines of stress (*left*) in a longitudinal section through a cantilever beam fixed perpendicularly to the substrate and subjected to bending moments in either of the directions (double-headed arrow) in the plane of the section (redrawn and modified after Thompson 1942, fig. 460). The parabolic lines converging subparallel to the left and right outer surfaces would alternately express compressional stresses as the load was directed toward the left and right, respectively; simul-

tal to non-skeletal volume during growth. This is achieved in species in which zooecial walls continue to calcify throughout the life of the zooids. Even though a bilaminar form has more skeletal material than a subcylindrical one, the proportion of skeletal material to non-skeletal volume is about the same in distal parts of the colony as in the critical region, unless zooecial walls continue to accrete ontogenetically. Continued accretion concentrates skeletal volume disproportionately nearer the critical support zone where zooids are ontogenetically older (Boardman and Cheetham 1969, fig. 4) and thus minimizes the difference between rates of increase in load and strength.

Most cheilostomes having rigidly erect colonies probably grew in water in which there was appreciable motion (Schopf 1969:236), and therefore the erect colony cannot be regarded simply as an evenly loaded pillar. Bending and torsion moments produced by water movement around the rigid colony set up stresses that are probably much more significant than those induced by the vertical load. The strength to resist bending or twisting is also enhanced by skeletal reinforcement, and if parsimony in the production of skeletal material is assumed, then the form and position of skeletal structures should be such as to diminish the risk of breaking without exceeding the limits of the organism's practical expenditure of energy (Thompson 1942:985, Bowman 1961:151, 229).

The distribution of stresses under bending moments in a rigidly erect colony can be approximated by those in a cantilever beam fixed at one end and free at the other (Thompson 1942, fig. 460; Bowman 1961, fig. 63). Such beams are ordinarily depicted in a horizontal position and evenly loaded, as for example by their own weights (see, for comparison, the vertical cantilever shown on the left side of Figure 4).

taneously, the lines subparallel to the right and left surfaces would express tensional stresses. The generalized skeletal structure of a rigidly erect cheilostome colony (*right*) is shown in longitudinal section. Structures in the plane of section—frontal, basal, and transverse walls of two opposing series of zooids—are shown solid, and those out of the plane of section are stippled. In addition, lateral walls form almost continuous sheets of skeletal material parallel to the plane of section, but are not shown. The frontal walls of the zooecia form flanges which are thickest near the fixed end of the colony where bending stresses are greatest. The flanges thicken in such a way as to leave the zooecial cavity undiminished in volume. The thinner basal, transverse, and lateral walls form a web which takes up the less concentrated stresses in the axial region of the colony.

As a cantilever, the rigidly erect cheilostome colony has its fixed end placed downward, against the substrate, and is subjected to bending moments by loads which may impinge on any of its outer surfaces. Thus, in longitudinal section, as shown in Figure 4 (left), the stress lines subparallel to each outer surface alternately express tension and compression as the bending force alternates in the directions of the double-headed arrow. Concentration of these stresses near the outer surface of the colony suggests that the most efficient arrangement for resistance to bending would place the greatest skeletal reinforcement in this outer region, a reinforcement corresponding to thickening the flanges on an I-beam (Thompson 1942:970). Moreover, because stresses induced by the bending moments are greatest at the proximal base of the colony, and because the moments in this region increase as the length of the beam increases, it would be advantageous for this outer flange to increase in thickness throughout the ontogeny of the zooids. This increase would be most efficiently accomplished by the addition of skeletal material on the outside, thus increasing the distance from the flange to the axis and giving the highest resistance to bending (Nye et al. 1940:116) while keeping zooecial cavities undiminished in size, as shown in Figure 4 (right).

Corresponding to the web connecting the flanges of the I-beam, the generally thinner basal, lateral, and transverse walls of the zooecia (Figures 3 and 4) transmit the stresses across the axial region of the colony. Although these stresses are less concentrated than those in the flanges, they are more evenly distributed along the colony's axis (dashed line on left side of Figure 4) from the fixed proximal end to the free distal end. Thus the most efficient arrangement of skeletal material in the axial region is uniformly thin walls formed ahead of the outer flange to resist the vertical shearing stresses set up along the colony axis (Nye et al. 1940:121). The transverse walls also may take up the shear stresses acting in the transverse sections through the colony due to torsion moments (Nye et al. 1940:153).

If bending and torsion moments of similar magnitude operate in any direction around the colony axis, it would be advantageous to have the outer flange of thickened skeleton form a cylindrical tube around the whole trunk and around each branch (Thompson 1942:970). If significantly greater loads were applied from one direction than from the others, or from two directions at 180°, then a bilaminate form would be more resistant to bending. A tube yields first by flat-

tening perpendicularly to the plane of bending, before it buckles or ruptures (Thompson 1942:971). Resistance therefore is increased by flattening in the opposite direction, that is, in the plane of bending (Figure 3b), because of the increased distance between the flange and the axis (Nye et al. 1940:116). An ability to withstand more powerful bending moments in the direction of flattening could explain the success of bilaminate colonies in more rapidly moving water than that tolerated by subcylindrical ones (Satch 1937:82, Lagaaij and Gautier 1965:52, Schopf 1969:235). The longer axes of the trunk and branches of a bilaminate colony thus could be expected to show a preferred orientation in the direction of prevailing water motion (Figure 3a). In simple cheilostomes lacking extensive skeletal reinforcement on the frontal side of the zooid, the flattening of branches may be even more significant as an adaptation to resist bending than it is in more complex cheilostomes.

In summary, a rigidly erect cheilostome colony could be strengthened to resist bending and twisting caused by water movement in two ways, assuming economy in the production of skeletal material. First, concentration of skeletal reinforcement near the outer surface of the colony would take up the concentrated stress, with the more central, thinner zooecial walls transmitting the more spread-out stress across the colony axis. Second, a flattening of the trunk and branches would maximize resistance to bending in the plane of flattening. Both of these modifications would also strengthen the colony for bearing the load of its own weight.

ADAPTIVE FEATURES OF RIGIDLY ERECT COLONY

The morphologic features of rigidly erect colonies in cheilostome Bryozoa thus seem at least in part to be explicable as adaptations for load bearing and for resistance to bending and twisting. In general, the bilaminate trunks and branches of an eschariform colony offer more resistance to both sets of forces than the subcylindrical ones of a vinculariiform colony do. Even without significant skeletal reinforcement on the outer surface of the colony, eschariform types may grow to appreciably greater volume than vinculariiform ones, especially in more rapidly moving water, if the water movement is essentially in one direction (or in two opposing directions). The volume increase is achieved, however, without a corresponding increase in height above the substrate, and therefore eschariform colonies probably cannot expose themselves as fully to the three-

dimensional habitat as taller, but less voluminous vinculariiform colonies can, and so do not have as high a potential for population density. The vinculariiform colony also appears to be superior in resistance to weak water movement in many directions. Other, more specialized colony forms can also be considered to show adaptations against these forces, but, because of their asymmetrical or one-sided cross sections, they face special problems in the distribution of stresses (Nye et al. 1940:119). The reteporiform colony appears to be able to transmit bending and twisting stresses from branch to branch through struts (anastomoses), thus increasing the number of points of support, and therefore probably is better able to tolerate strong loads from many directions. The various types of non-rigidly erect colonies, also common in shallow, turbulent water, substitute elastic skeletal structures for rigid zoecial walls at intervals throughout the colony; thus they may resist bending and twisting largely through tensile strength and may use the force of water motion to compensate for the loss of load-bearing support. A structural and stress analysis of lunulitiform colonies would be much more complex than the one attempted here for erect forms, because the stresses probably change drastically as the colony is tumbled on the substrate (Greeley 1967).

In the absence of skeletal reinforcement of its outer surface, the power of a rigidly erect colony to resist the forces acting upon it is restricted. With stiffening, a vinculariiform colony can be stronger than an eschariform colony lacking it. Whereas the shape of the colony is determined by growth as a whole, reinforcement of its outer walls is determined by the growth of individual zooids. An important and perhaps even the greater part of colony form thus seems to depend upon morphologic features of the zooids, and, in this sense, it is not an independent functional feature.

ZOOID STRUCTURE

At the zooid level of organization, the functional morphology of cheilostomes is complicated by polymorphism. Although the functions of some polymorphs may be obvious—as, for example, the brooding of embryos by ovicelled zooids—those of others, such as avicularia and kenozooids, require further investigation (see, for example, Kaufmann 1968:54–55).

At least some zooids in every colony, perhaps all of them in some colonies, are autozooids and probably fulfill a variety of roles in the growth, nutrition, reproduc-

tion, respiration, and other processes of the colony. Among the functions of these zooids, those concerned with the movement and protection of the lophophore and associated organs have been discussed most extensively (see, for example, Harmer 1930:92–99; Ryland 1967b:1040–1041).

The similar mode of protruding and retracting the lophophore in living cheilostomes of all types (Marcus 1926:19–21) permits little variation in the general form of most of the walls of the zoecium. The action of the muscles which effect these functions is enhanced by the rigidity of the walls in which they originate. The parietal muscles usually originate in the lateral walls and in most cheilostomes are distributed in multiple pairs on either side of the zooid for most of its length. These muscles insert in the hydrostatic membrane, either the membranous frontal wall or the floor of the ascus, depending on zooid structure (Harmer 1930, figs. 2–4). The medially positioned retractor muscle originates on the distal side of the transverse wall and in many cheilostomes paired lateral occlusor muscles originate on the proximal side. These muscles insert, respectively, in the base of the lophophore and the basal side of the operculum. The seating of muscles must be one-sided on lateral walls but can be two-sided on transverse walls as a consequence (Banta 1968:498–499) of the lineal mode of asexual budding in cheilostomes (Lutaud 1961, figs. 18–19), which is such that each zooid has its own lateral walls (exterior walls of Silén, 1944:470) but shares its transverse walls (interior walls of Silén) with adjacent zooids in the same series.

The transverse and lateral walls of cheilostomes are different as the relatively soft-bodied *Membranipora* (Lutaud 1961) and the robustly rigid-bodied *Metrarabdotos* (Cheetham 1968) are monotonously similar in their general form and degree of calcification. The basal wall (also an exterior wall) may remain uncalcified or may be skeletally reinforced and thus serve as origin for one or more sets of muscles—as for example, the parietals and opercular occlusors in *Steganoporella* and *Labioporella* (Harmer 1926, pl. 17:3; Cook 1964: 57, fig. 4). The greatest variation in the form and extent of calcification, however, is in walls at or near the frontal side of the zooid.

In the protrusion of the lophophore, the obvious advantage of having the hydrostatic membrane exposed at the frontal surface of the zooid has been difficult to correlate with the equally obvious proliferation of calcified frontal structures in cheilostome evolution.

It was apparently this difficulty that led Lang (1916, 1919, 1921) to view the progressive calcification at the frontal side of the zooid and the development of calcareous peri-oral structures as an orthogenetic trend of "uncontrolled super-secretion" amounting to a "disease" to which every "calcareous lineage" must "eventually succumb" (1919:195-196). Although he did not deny the possible momentary usefulness of calcified frontal structures, Lang was convinced of their general inadaptiveness because of the common occurrence in cheilostome colonies of some zooids with completely calcified frontal walls and "the consequent death of the zooid, since even the orifice is sealed up" (1916:76). Most other authors have considered frontal calcification to represent an adaptation for protecting the retracted lophophore and associated organs (e.g., Harmer 1930:94, Silén 1944:41), presumably against predation or mechanical damage. Complete or nearly complete closure of frontally calcified zooids seems to be regarded generally as an individual response to extremely unfavorable environmental conditions (e.g., Canu and Bassler 1920:68). Closed zooids are known, however, to be regularly present in particular parts of the colonies of taxonomically and architecturally different groups of cheilostomes, such as species of *Cupuladria* and *Discoporella* (see Cook 1965:159, 162-163) having lunulitiform colonies with apical and peripheral areas of closed zooids, and species of *Metrarabdotos* (see Cheetham 1968:9, pl. 15:1) having eschariform colonies with proximal trunks composed almost entirely of closed zooids. The regular placement of these groups of closed zooids in the colonial budding pattern and the continued secretion of calcareous material on the frontal sides of the sealed zooids make it unlikely that the process of occlusion in these examples is generally an individual response to an environmental accident. Rather, as Larwood (1969:179-181) has suggested for certain kinds of lattice-like features in cribrimorph cheilostomes—including branched spines, costae, avicularia, and some types of frontal shields—frontal structures grown by zooids may have a colony-wide functional significance beyond that directly related to the "needs" of the zooids themselves.

In investigating the possibility of a general, colony-wide functional role for calcified frontal structures, it is necessary to consider the particular functional properties of the known classes of frontal structures. Attention here is directed to the major wall-forming structures, rather than to branched spines, avicularia, or so-called tertiary frontal walls, some of which Larwood

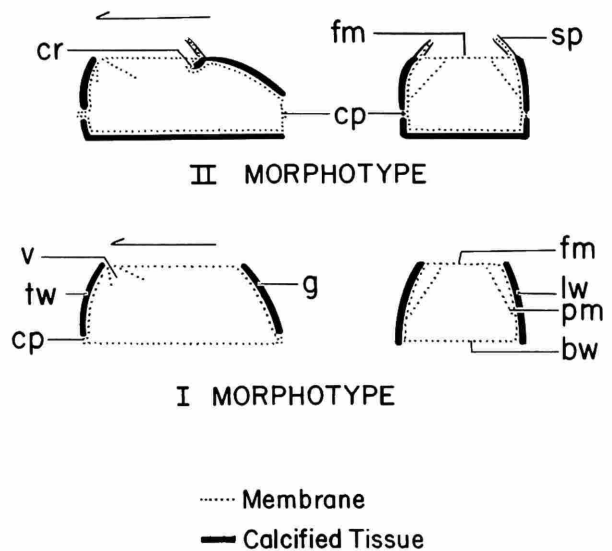


FIGURE 5.—Zooid morphotypes I and II. The relations of skeletal tissues to membranes are shown in diagrammatic sagittal (left) and transverse (right) sections (*bw*, basal wall; *cp*, communication pore; *cr*, cryptocyst; *fm*, frontal membrane; *g*, gymnocyst; *lw*, lateral wall; *pm*, parietal muscle; *sp*, spine; *tw*, transverse wall; *v*, vestibule beneath orifice). Lophophore, alimentary canal, and other organs have been omitted for simplicity; the direction of colony growth (distal) is indicated by the arrows.

In morphotype I (simple membranimorph or flustrine) the frontal wall is entirely membranous or shows slight exterior calcification on its proximal and lateral margins in the form of a short gymnocyst; there are virtually no subfrontal or suprafrontal skeletal structures, but their presence in even rudimentary form results in gradation into type II.

In morphotype II (complex membranimorph or cellularine) the frontal wall is more extensively calcified at its proximal end to form a long gymnocyst whose length is limited only by the necessity for keeping part of the frontal wall membranous and depressible; calcified spines, probably tubular extensions of the gymnocyst containing within their lumina evaginations of the frontal wall, generally project over the frontal membrane from its proximal and lateral margins; from the same margins may project subfrontally a short, shelf-like invagination skeletally reinforced with a cal-

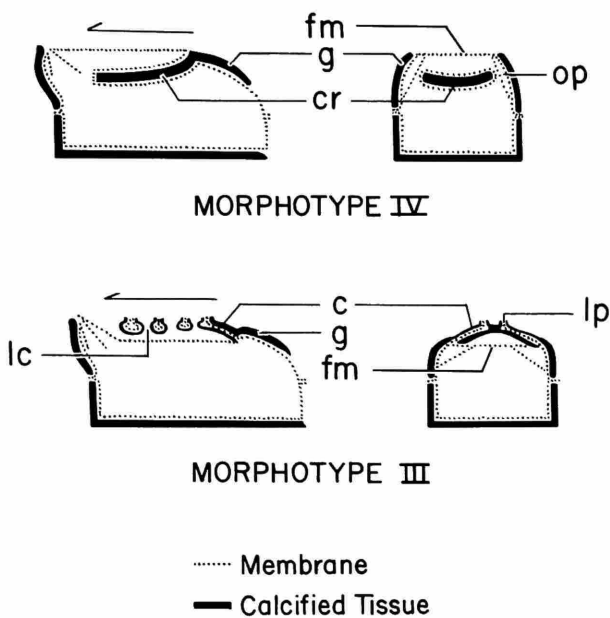


FIGURE 6.—Zooid morphotypes III and IV. Representation as in Figure 5 (*c*, costa; *lc*, lacuna between costae; *lp*, lumen pore; *op*, opesiule; other abbreviations as in Figure 5).

cified cryptocyst. Lacking a cryptocyst, this morphotype grades into type III, and, lacking proximal and lateral spines, into type IV.

In morphotype III (cribrimorph) a major part of the frontal wall, within a short or extensive gymnocyst, is membranous but is overarched by a calcified shield of spine-like costae usually connected to each other with various kinds of processes; the costal lumina are occupied by evaginations of the frontal wall which may be exposed through uncalcified portions of the frontal sides of the costae; an additional wall of solid calcareous tissue of undetermined origin is present above the costal shield in some extinct genera.

In morphotype IV (microporoid) a major part of the frontal wall is membranous but is underlain by an extensive cryptocyst calcified in a subfrontal invagination from the proximal and lateral margins of the frontal membrane; a gymnocyst may be present on the proximal and lateral margins of the cryptocyst; the parietal muscles pass the cryptocyst either beyond its distal margin or through distolateral pores (opesiules).

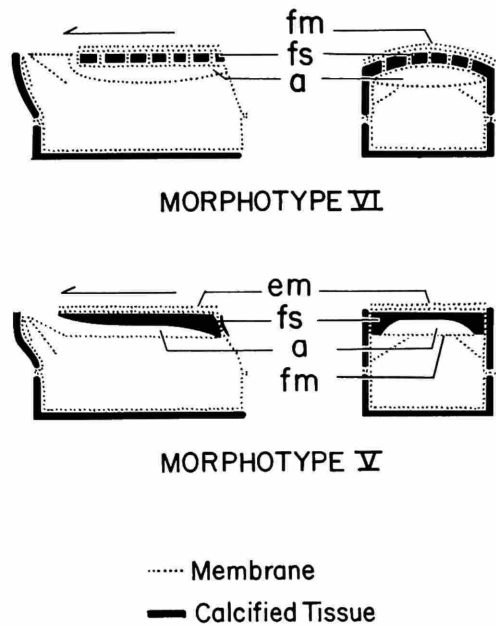


FIGURE 7.—Zooid morphotypes V and VI. Representation as in Figure 5 (*a*, ascus; *em*, epifrontal membrane; *fs*, frontal shield; other abbreviations as in Figures 5 and 6).

In morphotype V (umbonuloid) the frontal wall is membranous but is overarched by a continuous frontal shield calcified on the underside of a suprafrontal evagination from the proximal and lateral margins of the frontal membrane; uncalcified areas may remain, commonly on the lateral and proximal margins of the shield, through which the epifrontal membrane communicates with that on the zooid interior; the space between the frontal membrane and the shield forms an ascus opening to the exterior near the orifice.

In morphotype VI (lepralioid or microporelloid) the frontal wall is reinforced by the development just beneath it of a calcified, continuous shield in an invagination from the proximal and lateral margins of the frontal membrane; uncalcified areas may remain on the margins of the shield and dispersed over its surface; some of these openings provide communication between the frontal membrane and that on the zooid interior (Banta 1970 and personal communication); a new hydrostatic membrane forms as the floor of an ascus invaginated from the frontal membrane under the shield proximally from the orifice.

interpreted as a "coarse outer filter" (1969:180) to keep coarse detritus and organisms from the frontal surface of the colony.

Because of the seeming functional conflict between rigidity and flexibility of the frontal side of the zooid, and because of the external position of calcareous material relative to the epidermis, there are limited possibilities for the arrangement of skeletally reinforced walls in this region. On the basis primarily of the modes of development of calcified walls on the frontal side of the zooids and the concomitant development of the hydrostatic system, Harmer (1902:329–339) grouped living cheilostomes in six major morphotypes (Figures 5–7). To the extent that mode of growth can be interpreted from the morphology and microstructure of the skeleton (Boardman and Cheetham 1969:220–223), these morphotypes are also recognizable among fossil cheilostomes. Criteria specifically applicable to interpretation of Danian cheilostomes are discussed below, in a separate section.

Among living cheilostomes, the generally gradational relationships of the basic zooid morphotypes in two or more series of increasingly anatomically complex forms have been recognized by Harmer (1902, 1930), Silén (1942), and others. One major morphologic series begins with simple membranimorph anascans (morphotype I, Figure 5) having the frontal side of the zooid with a simple, almost entirely membranous frontal wall; progresses through complex membranimorph anascans (morphotype II, Figure 5) having proximally and laterally calcified frontal walls (gymnocysts) with hollow, tubular, calcified extensions (spines) projecting over the membranous part of the frontal wall; continues through cribrimorphs (morphotype III, Figure 6) having frontal shields composed of hollow costae, presumably comparable to spines which have fused medially and usually also laterally; and may culminate in umbonuloid ascophorans (morphotype V, Figure 7) having continuous frontal shields calcified on the underside of a fold-like evagination, presumably comparable to completely fused costae, the upper surfaces of which have failed to calcify. In all of these morphotypes, the hydrostatic membrane is the original membranous frontal wall.

The second major morphologic series also begins with morphotype I; it progresses through microporoid anascans (morphotype IV, Figure 6) having extensive subfrontal shields (cryptocysts) calcified within an invagination into the body cavity in such a way as to permit insertion of the parietal muscles in the mem-

branous frontal wall; and it culminates in lepralioid or microporelloid ascophorans (morphotype VI, Figure 7) having continuous frontal shields developed as cryptocysts beneath which the hydrostatic membrane is invaginated together with attached parietal muscles. In morphotype VI, the position of the hydrostatic membrane relative to the original membranous frontal wall differs from that of all other known cheilostome morphotypes.

A developmental relationship between microporoid anascans (morphotype IV) and lepralioid-microporelloid ascophorans (morphotype VI) was suggested by Harmer (1902:333), in part on the basis of the anatomy of microporoid genera described by Jullien (1881:276–285, in his anascan suborder Diplodermata). Subsequently, Harmer's suggestion was either ignored (Harmer 1930:99, Silén 1942:46) or denied (Ostroumov 1903), but recently it has been corroborated by Banta's (1970, and personal communication) detailed morphologic investigations of the lepralioid genera *Watersipora* and *Schizoporella*.

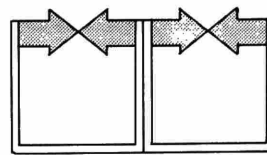
A third morphologic series is at least theoretically possible. This is a progression from anascans of morphotype II, in which the gymnocyst is extensive, to ascophorans through invagination beneath the gymnocyst of a hydrostatic membrane. The genus *Pseudolepralia* has been assumed to be an ascophoran with a gymnocystal frontal shield (Silén 1942:49–54), but the mode of development of the shield (Silén 1941:39, 1942:50) appears to differ from that of a gymnocyst. The original frontal membrane forms the floor of the ascus rather than having been at the level of the "gymnocyst," and the frontal shield of *Pseudolepralia* thus might be comparable to those of umbonuloids (morphotype V), except for calcifying on the upper rather than the lower side of the fold-like evagination. Whether it develops on a fold or on the frontal membrane, the frontal shield of *Pseudolepralia* differs from those of morphotypes V and VI in one respect significant to the following discussion of the possible colony-wide functional role of frontal structures: that is, because it lies exposed at the outer surface of the zooid, without an overlying secretory membrane (Silén 1942, fig. 50), it lacks the potential for continued accretionary thickening.

Although the recognition of zooid morphotypes in fossil cheilostomes is still tentative, the stratigraphic sequence of first appearances of morphotypes appears to be largely in agreement with the two major morphologic series described above. Morphotypes I and II

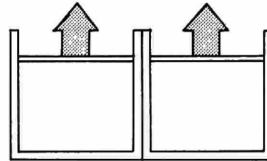
(membranimorphs) appeared in Early Cretaceous time, in the Albian or possibly as early as Aptian (Voigt 1968b:13). Morphotypes III (cribrimorphs) and IV (microporeoids) made their debut soon after the beginning of Late Cretaceous time, in the Cenomanian (Larwood et al. 1967:388, Voigt 1967). The time of origin of morphotypes V and VI (umbonuloid and lepralioid-microporelloid ascophorans) is more doubtful, partly because of the difficulty of distinguishing the two modes of development in fossils, and partly because of the incompleteness with which the morphology of some early genera is known. If it is assumed that supposed porinid genera, such as *Rotiporina*, developed as do the modern species of *Porina*, and that supposed exochellid genera, such as *Balantiostoma*, developed as do the modern species of *Escharoides*, then these morphotypes date at least from the Turonian and Campanian, respectively. The supposed hippothoid genus *Dacryoporella*, which nominally includes species older than Turonian, and which was accepted by Larwood et al. (1967:390) as an ascophoran, could be interpreted as an anascan of morphotype II (see Voigt, 1968b:13); the oldest (Cenomanian) species of this genus, *D. reussi* (Lang) (see Larwood et al. 1967:390) is especially suspect, because Lang (1914:443) only provisionally assigned it to *Dacryoporella* on account of its subcircular (membranimorph-like) zooecial openings. In general, therefore, the graded series of morphotypes appear to have evolutionary significance.

RELATION OF ZOOID STRUCTURE TO COLONY FORM

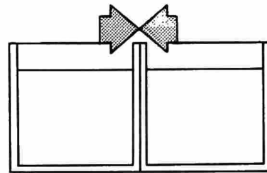
A possible colony-wide function of frontal calcification, which appears not to have been given detailed consideration previously, is architectural support of an erect colony. As discussed above, the strength of an erect colony, under the load of its own weight in sea water and under bending and torsion moments due to water movement and possibly other forces, is especially enhanced by concentration of reinforcing skeletal material near the outer surface of the zoarium (Figure 2b). With regard to the origin and mode of growth of calcareous frontal structures, three steps are involved in the attainment of greatest functional efficiency in this role (Figure 8): (1) if frontal structures become continuous as they extend medially and distally across the zooid, they JOIN the vertical walls together, forming a bridge on the outer surface of the zoarium; (2) if, in growing medially and distally, these structures can



JOINING
intrazooecial walls



THICKENING
zoarial cover



BINDING
interzooecial walls

FIGURE 8.—Possible functional steps in development of calcareous frontal structures for colony support. The steps are cumulative in that during zooid ontogeny, joining is followed by thickening, and thickening by binding.

accrete frontally during a major portion of the life of the colony, they THICKEN the zoarium; and (3) if, in thickening frontally, these structures can also spread laterally over the frontal edges of the lateral walls to merge with frontal structures of adjacent zooids, they BIND the individual zooecia into a unified zoarial structure. These three steps give frontal structures a cumulative significance (Rudwick 1968:46), increasing the functional effectiveness of frontal structures during the ontogeny of the zooids by which they are grown. This cumulative effectiveness is expressed as an increase, greatest near the proximal end and less toward the distal end, in the critical cross-sectional area of the colony, and also as a concentration of mass farther from the colony axis that, again, is greatest near the proximal end and decreases toward the distal end.

Because of limitations imposed by the mode of growth of their frontal structures, not all zooid morphotypes are capable of taking all three functional steps in their ontogeny. Thus, with respect to the postulated function of colony support, the six basic morphotypes can be arranged in a graded series of progressive adaptations for the erect mode of life on the basis of their relative effectiveness in each functional step (Figure 9). In zooecia of morphotype I, the virtual absence of frontal skeletal structures makes their functional importance

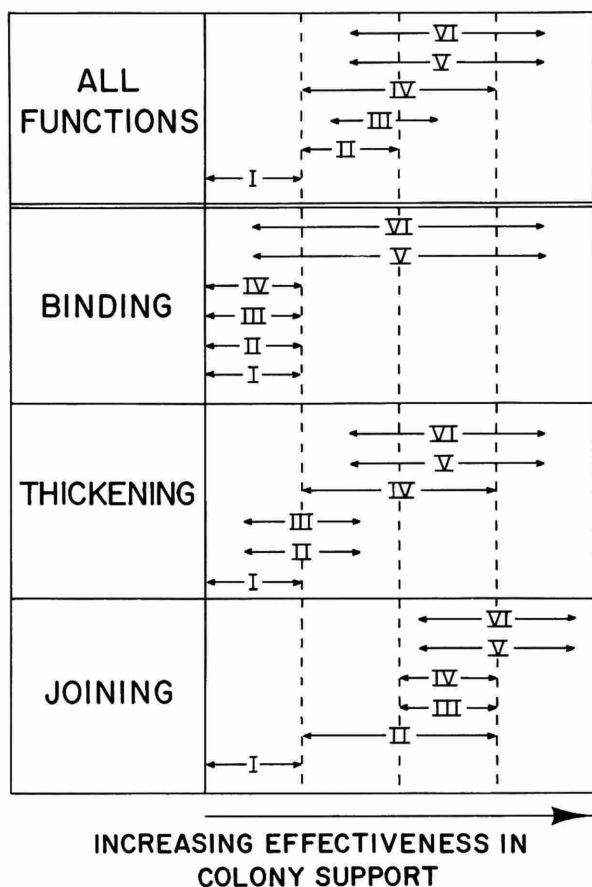


FIGURE 9.—Inferred potential effectiveness of the six zooid morphotypes in three functional steps involved in structural support of the rigidly erect colony. The scale of effectiveness is arbitrary and intended only to illustrate approximate relative differences among morphotypes. The effectiveness in all functions is an approximate average of those for the three steps.

negligible in all aspects of colony support. The extensive gymnocyst of morphotype II places this zooecial type higher on the scale, but the effectiveness of the gymnocyst is subject to two limitations: first, the joining of the lateral walls to each other cannot be as extensive as in more complex morphotypes because of the necessity for keeping an appreciable part of the frontal wall membranous and depressible; and, second, because of the necessity for keeping the body cavity undiminished in size, the gymnocyst, which lies at the exterior frontal surface of the zooid and thus is secreted from within the zooecial cavity, cannot be appreciably thickened ontogenetically or merge with gymnocysts of adjacent zooids. The costal shield of type III zooecia is only slightly more effective than a gymnocyst; even

though costae are effective in joining the lateral walls together for a great proportion of their length, costae like gymnocysts apparently are secreted from within and therefore are not susceptible of appreciable thickening or of merging across lateral walls of adjacent zooids.

The so-called tertiary frontal walls, formed in some Cretaceous cribrimorphs possibly by encroachment of interzooecial tissue over the costal shield (Larwood 1962:33, 40-41), may improve significantly the potential effectiveness of this morphotype, but the mode of formation of this type of structure has not been determined.

In type IV zooecia, the extensive cryptocyst has a joining ability greater than that of a gymnocyst, because the gaps in it, aside from that for passage of the lophophore which occurs in all types of frontal shields, need be only large enough to accommodate the parietal muscles. In addition, its position beneath the secretory epithelium gives the cryptocyst a greatly increased capacity for thickening. Because the cryptocyst lies beneath the hydrostatic membrane, however, it cannot merge with cryptocysts of adjacent zooids without interfering with the hydrostatic system. The greatest capacity for colony support appears to be embodied in the ascophoran structure of type V and VI zooecia. These have a frontal shield which is continuous for much of the length of the zooid and which, because of its position above the hydrostatic membrane but beneath the secreting membrane, can thicken without apparent limit throughout zooid ontogeny and can merge across the lateral walls of adjacent zooids. There is no apparent difference between the two ascophoran morphotypes with respect to the three functional steps.

Thus, on theoretical grounds, the morphotype of the zooid appears to be the primary functional feature on which adaptations, including those expressed in colony form, are based. This hypothesis is tested in the following analysis of cheilostomes from the Danian Stage in southern Scandinavia.

Morphologic Interpretation of Danian Cheilostomes

CHARACTERS RELATED TO COLONY FORM

Measurement of abundances of different colony forms in assemblages of fossil or Recent cheilostomes requires morphologic interpretation of the typically fragmentary specimens incorporated into sediment (see, for example, Maxwell 1968:271). Even though

some specimens in an assemblage are ordinarily preserved well enough to indicate their growth form directly (see, for example, the encrusting zoarium on Plate 1:4 and the rigidly erect, branching zoarium on Plate 11:2), it cannot be assumed that all conspecific colonies had the same form. In addition, some colony forms are nearly always fragmentary in sediments; jointed colonies, for example, can be expected to be found as disarticulated internodes with only their inconspicuous nodal structures to indicate their form. Therefore, the interpretation of colony forms in an assemblage requires the application of indirect criteria of zooecial morphology and its pattern of variation within the zoarial fragments (Cook 1968b:119, Boardman et al. 1970:309).

As remarked upon by Hennig (1899:38–39), the Danian cheilostomes in Scandinavia are typically skeletal fragments rarely larger than 1 cm and ranging down to particles just recognizable as cheilostome skeletal material $\frac{1}{4}$ mm in diameter. For the most part, these fragments appear not to have retained their positions relative to each other or to the substrate (see Plate 17:1–3).

Among the Danian cheilostomes of eastern Denmark, Berthelsen (1962:238) recognized four forms of colonies: vinculariiform, eschariform, membraniporiform, and lunulitiform. The last of these forms is represented by a single species, *Lunulites saltholmensis* Berthelsen, which occurs chiefly in the upper part of the Danian at a few localities (Berthelsen 1962:155). This species and two similar ones, *Lunulites* sp. and *Vibracella* (*Discovibracella*) *oculata* Voigt, have been found in rocks of about the same age, or slightly younger (Dano-Montian), in Poland (Voigt 1964:441–443, Maryanska 1969:112–113). Lunulitiform colonies have not been reported from most of the Danian sediments in Scandinavia (Berthelsen 1962:238), and no zoaria that could be interpreted as lunulitiform were encountered in the present study.

Voigt (1964:457–458, pl. 14:1–3) described and illustrated from the Dano-Montian of Poland specimens of *Pavobeisselina oblita* (Kade) having tapering proximal ends perforated with numerous small openings which he interpreted as indicating "attachment by radicle cells or by a chitinous stalk." Similar interpretations of openings in the proximal ends of zoarial fragments of other species, such as *Onychocellaria rhombea* (Hagenow) and *Smittipora? canalifera* (Hagenow) from the Maestrichtian, have led to the conclusion that such specimens represent segments of jointed

(cellariiform) colonies (Voigt 1957:15–17; 1968:27–29). A proximally tapering shape, even without openings in the proximal end, has been considered evidence of a cellariiform colony in the Maestrichtian species *Micropora transversa* (d'Orbigny) (Voigt 1968b:32). *Pavobeisselina oblita* and a species similar to *Smittipora? canalifera*, *S.? prismatica* (Hagenow), are known from the Danian in Scandinavia but have been interpreted to have had a rigidly erect colony form (Berthelsen 1962:67, 201). Some Danian specimens of *S.? prismatica* (Plate 7:1) have tapering proximal ends occupied by zooecia whose frontal sides are occluded except for a small, suboral pore, or slit. Though these closed zooecia are shown by the presence of opercular scars to have been parts of autozoids, the openings left in them may have held noncalcified tubes. Such tubes, however, are known in living cheilostomes having erect, non-jointed colonies. In *Zeuglopora arctata* Harmer (1957:756), *Siphonocyrtara formosa* Harmer (1957:893), and *Cleidochasma biavicularium* (Canu and Bassler) (Harmer 1957:1048), non-calcified tubes form rootlets anchoring the otherwise rigidly erect colonies to the substrate. In jointed colonies of living and fossil species of *Nellia*, *Poricellaria*, *Cellaria*, *Margaretta*, and other typical cellariiform genera, openings for the tubes connecting internodes are present not only at the proximal end of the internode, but also at the distal end or at some position intermediate between the two ends. Distally placed structures of this sort appear not to have been described from the Cretaceous and Danian fossils discussed here and have not been observed in the present study. Therefore, cellariiform colonies are not inferred to have been present in the Danian fauna, and the zoarial fragments in this study have been classified in the three forms: vinculariiform, eschariform, and membraniporiform.

Vinculariiform Colonies (Plates 7:1–3, 5–6; 11): Zoarial fragments inferred to have been parts of vinculariiform colonies are cylindrical or subcylindrical. Locally, in regions of branching (Plate 11:2–3), the stem may be flattened, and fragments from these regions of a colony might be mistaken for eschariform specimens if some of them did not show gradation into a cylindrical form distally (see Jürgensen's, 1968, pl. 1:3–4, separation of two forms of *Floridina gothica*). On growing tips (Plate 11:1) and in transverse sections (Plate 12:3–4), zooecia are arranged radially. This arrangement is more conspicuous in species in which the zooecia are grouped in verticillate whorls (Plate

11:1-4), than in species in which they are in alternating series (Plate 7:1-3, 5-6). Zooecia typically lack basal walls because their lateral walls reach the axis of the stem (Plates 3:8; 12:3-4). In *Floridina gothica* (d'Orbigny), however, narrow basal walls are present, and the stem axis has a small, triangular hollow (Plate 3:7). This hollow might be the remnant of a soft structure encrusted by the colony in the fashion described by Stach (1936:62) as pseudovinculariiform, but it has a constant size and form in all zoarial fragments of this species and lacks any signs of the patterns normally present on the basal surfaces of encrusting colonies. Moreover, the zoarial form of *F. gothica* seems to be more regular than known pseudovinculariiform colonies in species such as *Metrarabdotos* (*Uniaicularium*) *unguiculatum* Canu and Bassler (Cheetham 1968, pl. 10:2).

Eschariform Colonies (Plates 2; 3:1-5; 7:4, 7; 8-10; 12:5-6): Bilaminate zoarial fragments have been interpreted in this study as parts of eschariform colonies. There is some variation in the width of branches in the bilaminate Danian cheilostomes, but, because of the fragmentary condition of the material, it has not been possible to separate consistently the narrow-branched (adeoniform) colonies from the others. In some species, such as *Pithodella cincta* Marsson, unilaminate fragments commonly occur together with bilaminate ones, and, because of the regularity of both frontal (Plate 2:4) and basal surfaces of these unilaminate specimens, they have been inferred to be parts of eschariform colonies rather than membraniporiform ones. The proximal parts of some bilaminate fragments are subcylindrical (Plates 2:2, 3:5, 8:2), and such specimens might be mistaken for vinculariiform colonies. None of these fragments, however, shows a distalward gradation into subcylindrical shape.

Typical bilaminate arrangement of zooecia can be observed on growing margins (Plates 8:2, 10:4) or in transverse sections (Plates 3:2-3, 5; 9:1, 3; 12:5-6). Most or all of the zooecia have wide basal walls, those of the two layers of zooecia being juxtaposed to form a more or less regular median lamella. Structurally, the median lamella is double-walled, consisting of the basal walls of the two layers of zooecia, and it is discontinuous, being interrupted by the boundaries between lateral walls of each pair of contiguous zooecia. Actually, the basal wall of each zoecium is structurally continuous with its lateral walls, and many of the bilaminate colonies appear to have broken into the two constituent layers of zooecia, with each layer broken

further into lineal series of zooecia. The zooecia within lineal series would tend to resist breaking because of sharing transverse walls.

At the lateral margins of a bilaminate specimen, the zooecia, which may be autozooecia or heterozooecia, either have basal walls essentially like those of the more centrally placed zooecia (Plates 9:3; 12:5-6) and thus continue the median lamella to the lateral margin of the zoarium, or lack basal walls (Plate 3:2-3, 5) and thus cut off the median lamella short of the margins. Subcylindrical portions of colonies having shorter median lamellae (Plate 3:5) closely approximate the vinculariiform arrangement.

Among the zoarial fragments from the Danian in the cement quarry at Limhamn, Sweden, interpreted as vinculariiform and eschariform colonies, specimens preserving growing extremities are common. On the other hand, as with the erect cyclostome Bryozoa from the same locality (Brood 1970, personal communication), specimens showing proximal attachment surfaces are scarce. In any assemblage of large, many-branched colonies, the growing extremities would of course greatly outnumber the attachment surfaces. Moreover, in large, erect colonies, such as in *Metrarabdotos moniliferum* (Milne Edwards) (Cheetham 1968, pl. 15:1-2), the proximal zooecia may be occluded and no longer comparable morphologically with the more distal ones. Comparable ontogenetic differences between zooecia in proximal and distal parts of Danian cheilostome colonies are suggested by fragments of *Coscinopleura angusta* Berthelsen (Plate 8:2-3) and some other erect species. Therefore, many of the eschariform and vinculariiform cheilostomes may have had large colonies despite the small size of the fragments incorporated in the sediments sampled, and the proximal parts of the colonies bearing the attachment surfaces may be included among the unidentified cheilostome fragments in each sample (see Figure 22). Alternatively, the paucity of recognizable attachment surfaces could indicate transportation of colony fragments away from the site of their growth (Brood, personal communication), though evidence discussed below suggests that this is not the case.

Membraniporiform colonies (Plates 1, 4-6): Those unilaminate zoarial fragments which show direct or indirect evidence of adherence to the substrate by their whole basal surface have been inferred in this study to represent membraniporiform colonies. Small zoaria (Plates 5:1a-b; 6:1) may adhere entirely to larger single objects, such as barnacle valves or octocoral

axes. Larger zoaria (Plate 1:2) may remain attached to only one or more small objects, such as echinoderm ossicles. In membraniporiform colonies, the basal wall of each zooid is in contact with the substrate, and in many of the Danian zoaria the basal walls apparently were uncalcified (Plates 1:1-4, 6:1) so that the substrate is visible in frontal view. In others the basal walls were completely calcified (Plates 5:1a; 6:2), and in many of these forms the topography of the basal wall conforms to that of the encrusted object. Where the colony appears to have become detached from its substrate, the basal surfaces of the zooecia may show these topographic characteristics, as in the specimen of *Callopora* sp. (Plate 6:2) having pits suggesting growth on a calcareous sponge. Some zoarial fragments reflect the overall shape of their still adherent substrate by having the whole layer of zooecia roughly conform to it, as the subcylindrical zoarium of *Aechmella pindborgi* Berthelsen (Plate 5:1) on an octocoral axis, the domed specimen of *Onychocella ravni* Berthelsen (Plate 5:2) on a calcareous sponge, or the arched specimen of the same species (Plate 5:3) on the outer ends of the septa of a scleractinian corallite. Still another morphologic expression of substrate topography is the alternation of budding directions in the zoarium of *Micropora hennigiana* Berthelsen (Plate 6:3) on a ribbed brachiopod shell. Many free, unilaminar fragments (Plate 4:1-3) have shapes suggesting growth on these types of substrates.

CHARACTERS RELATED TO ZOOID MORPHOTYPE

Frontal surfaces of zooecia are generally well preserved in Danian cheilostomes, and growing extremities of colonies preserving ontogenetic stages of frontal structures are common. The disappearance of membranes during fossilization, however, makes reconstruction of some zooid morphotypes doubtful. Consequently, it is not possible to group specimens on any single morphologic criterion; emphasis has been placed instead on possession of a majority of characteristics typical of each morphotype.

Morphotype I (Plate 1:1, 3): These zooecia are broadly open frontally within narrow, calcified rims, inferred to represent gymnocysts, which end at distinct, usually grooved zooecial boundaries, assumed to mark the position of the intercalary cuticle between lineal series of zooids. Basal walls commonly are uncalcified; spines, cryptocysts, and adventitious avicularia are virtually lacking.

Morphotype II (Plates 1:2, 4-5; 2; 3:1-5): These zooecia have moderate to extensive frontal calcification in the form of a convex lamella, inferred to represent a gymnocyst. In longitudinal section (Plate 3:1, 4), this lamella has about the same thickness as the other zooecial walls. The mural rim, marking the inner margin of the gymnocyst, commonly supports spine bases, each with a conspicuous lumen (Plate 2:3-4). Within the mural rim, a slightly to moderately developed, depressed shelf, inferred to represent a cryptocyst, may be present (Plate 2:1-4). Adventitious avicularia occur on the gymnocysts of some zooecia (Plate 2:1-2, 4). Zooecial boundaries are usually marked by furrows in frontal view and are discernible in transverse sections as distinct lines, presumably the position of the intercalary cuticles in the living colony, running from the basal wall to the frontal surface of the zoarium (Plate 3:2-3, 5).

Morphotype III (Plate 4:2-5): These zooecia show differing kinds of frontal costation, extending over virtually the whole frontal surface or limited to the central part of it. The costae may be fused only at their medial ends or show numerous lateral fusions. Species of *Tricephalopora* (Plate 4:5) have tertiary frontal walls, but in general these structures are less common in Danian species than in Cretaceous cribrimorphs.

Morphotype IV (Plates 3:6-9; 5-9): These zooecia have extensive frontal lamellae, inferred to represent cryptocysts. These structures are centrally depressed, at least in early ontogenetic stages on zoarial fragments preserving the growing extremities of colonies (Plate 8:2). In specimens inferred to represent later ontogenetic stages, the cryptocyst may be much thicker and not depressed (Plates 8:3, 9:1-3). The boundaries between type IV zooecia, inferred to mark the intercalary cuticles, remain distinct in frontal view, even where the cryptocyst apparently has been greatly thickened ontogenetically (Plate 8:3); however, in transverse sections (Plate 9:1,3) the boundaries may become progressively less distinct frontally, possibly through calcification of the intercalary cuticle (see Banta 1968:499).

The distal part of the cryptocyst in type IV zooecia reflects structurally the passage of the parietal muscles, either through proximolateral indentations in the opesia (Plates 5; 6:4; 7:1, 3-5, 7; 8) or through lateral opesiules proximal to the opesia (Plates 6:1-3; 7:2, 6). In *Floridina gothica* (Plate 7:2-3), zooecia having opesiules appear to occur in the same zoarial fragment with those having indentations in the opesia,

TABLE 1.—General morphologic and distributional characteristics of cheilostome Bryozoa in middle Danian Mound II-N₁, Limhamn Quarry, Sweden. Species are ranked in order of maximum abundance in coarse fraction of any sample. Weight-

Rank	Species	Inferred zoarial form (if more than one, dominant first)	Inferred zoecial morphotype	Total occur- rences	Occurrence in Denmark—Zones		
					B	C	D
1	Coscinopleura angusta BERTHELTSEN.....	ESCHAR	IV	13	x	x	x
2	Floridina gothica (D'ORBIGNY).....	VINC	IV	12	x	x	x
3	Aechmella pindborgi BERTHELTSEN.....	MEMB	IV	16	x	x	x
4	Membraniporidra lacrymoporoides BERTHELTSEN.....	ESCHAR	II	10	x	x	x
5	Callopora spp.....	MEMB + ESCHAR	II	15	?	?	?
6	Columnotheca cribrosa MARSSON.....	VINC	V or VI	13	x	x	x
7	Floridina spp.....	MEMB	IV	16	?	?	?
8	Pithodella cincta MARSSON.....	ESCHAR	II	15	x	x	x
9	Porina salebrosa MARSSON.....	ESCHAR	V or VI	16	x	x	x
10	Onychocella ravni BERTHELTSEN.....	MEMB	IV	15		x	x
11	Aechmella tenuis BERTHELTSEN.....	ESCHAR	IV	14		x	x
12	Porina cylindrica VOIGT.....	ESCHAR	V or VI	11	x	x	x
13	Onychocella? columella BERTHELTSEN.....	ESCHAR	IV	17	x	x	x
14	Pachythecella lundgreni (PERGENS & MEUNIER).....	ESCHAR	V or VI	10	x	x	x
15	Smittipora? prismatica (HAGENOW).....	VINC	IV	11	x	x	x
16	Puncturiella sculpta (D'ORBIGNY).....	VINC + MEMB	IV	11	x	x	x
17	Pachythecella anhaltina (VOIGT).....	ESCHAR	V or VI	17	x	x	x
18	Semiescharinella complanata D'ORBIGNY.....	ESCHAR + MEMB	IV	17	x	x	x
19	Balantiostoma vallata MARYANSKA.....	MEMB	V or VI	14	?	?	?
20	Floridina voighti BASSLER.....	ESCHAR	IV	6		x	x
21	Smittipora? sp.....	ESCHAR	IV	10	?	?	?
22	Membraniporidra huckeana VOIGT.....	MEMB	II	14		x	x
23	Pliophloea spp.....	MEMB	III	13	?	?	?
24	"Cellepora" daniensis VOIGT + spp.....	MEMB	V or VI	13	?	?	?
25	Micropora hennigiana BERTHELTSEN + spp.....	MEMB + ESCHAR	IV	17	?	?	?
26	Ellisina brittanica (BRYDONE).....	MEMB	I	10	x	x	x
27	Crassicellepora voighti BERTHELTSEN.....	MEMB	V or VI	9		x	x
28	Membraniporidra declivis (MARSSON).....	MEMB + ESCHAR	II	12	x	x	x
29	Tricephalopora circumvallata (LEVINSEN).....	MEMB	III	13		x	x
30	Psilosecos angustidens (LEVINSEN).....	MEMB	V or VI	12		x	x
31	Tricephalopora cerberus LANG.....	ESCHAR	III	3	x	x	x
32	Allantopora stomatoporoides LANG.....	MEMB	II	10		x	
33	Anornithopora minuta VOIGT.....	MEMB	III	13		x	x
34	Anornithopora polygona VOIGT.....	MEMB	III	4		x	x
35	"Herpetopora" danica LANG.....	MEMB	I	7		x	
36	Monoceratopora quadrisulcata (HENNIG).....	MEMB	III	11	x	x	x
37	Gargantua parvicella (VOIGT).....	MEMB	IV	14		x	x
38	Membranipora? johnstrupi BERTHELTSEN.....	MEMB	II	4		x	x
39	Aplousina? oedumi BERTHELTSEN.....	MEMB	I	4	x	x	x
40	Onychocella poulsenii BERTHELTSEN.....	MEMB	IV	5	x	x	x
41	Pelmatopora? daniensis VOIGT.....	MEMB	III	2			x
42	Cryptostomella pectinata BERTHELTSEN.....	MEMB	V or VI	2	x	x	
43	Fissuricella fissa (VOIGT).....	MEMB	II	1	x	x	x
44	Pithodella? pristis (LEVINSEN).....	ESCHAR	II	2	x	x	x
45	Tricephalopora robusta BERTHELTSEN.....	MEMB	III	3		x	
46	Systenostoma pontiferum BERTHELTSEN.....	ESCHAR	V or VI	2		x	x
47	Pachydera fissa BERTHELTSEN.....	MEMB	III	3		x	
48	Membranipora? sp.....	MEMB	I	1	?	?	?
49	Phractoporella cordiformis (LEVINSEN).....	MEMB	III	2	x	x	
50	Pliophloea vincularioides VOIGT.....	VINC	III	1		x	x
51	Leptocheilopora laticostata BERTHELTSEN?.....	MEMB	III	1		x	x
Total number of species in samples					24	42	36

equivalent percentages are based on counts of fragments and weights of each size grade for each sample. Assemblages are catalogued USNM 169554-169570. Denmark occurrences from Berthelsen, 1962.

Sample occurrence in weight-equivalent percent of identifiable specimens in coarse fraction ($>500\ \mu$)																		Rank
1	2	3	4	5	6	7	9	10	11	12	13	14	15	16	17	18		
0.26	2.91	—	1.42	0.23	6.78	12.99	—	0.20	1.06	—	—	9.62	15.31	18.17	28.24	34.12	1	
8.28	15.18	21.71	0.14	20.53	10.01	—	—	0.08	—	—	—	0.37	0.29	0.43	2.83	3.76	2	
0.12	0.89	0.19	22.06	—	3.51	6.28	13.21	17.46	16.96	17.23	23.48	9.22	11.02	5.48	2.64	1.02	3	
3.91	6.62	20.62	0.14	7.54	1.63	—	—	—	—	—	—	0.62	0.32	—	0.22	0.46	4	
0.08	—	—	2.24	0.07	2.14	6.40	8.64	20.76	15.79	13.62	11.00	8.92	4.57	5.22	1.17	0.51	5	
11.20	12.64	16.10	1.05	5.38	8.40	1.05	—	—	—	—	0.51	0.70	3.07	9.53	13.28	10.25	6	
0.09	0.72	—	7.76	0.07	4.96	4.71	17.82	15.53	11.46	9.72	9.13	6.65	7.78	5.13	2.87	0.70	7	
12.78	12.53	6.26	4.60	5.78	12.63	7.02	—	0.08	—	0.88	1.52	0.72	5.88	5.25	14.79	13.60	8	
13.36	5.55	8.22	14.63	8.87	6.28	13.84	0.28	—	3.08	9.71	9.94	11.85	3.60	9.76	11.14	10.06	9	
0.22	—	0.38	3.62	—	3.06	8.28	15.66	6.93	15.44	9.60	5.41	6.30	3.43	1.44	0.92	0.28	10	
9.47	11.94	5.57	0.40	6.42	1.90	—	—	0.27	0.18	—	0.65	0.13	0.42	0.67	0.74	1.40	11	
7.27	3.72	2.49	0.14	10.15	8.07	—	—	—	—	—	0.22	—	0.11	1.02	0.50	0.64	12	
0.35	1.39	1.02	2.37	0.43	3.27	4.51	1.45	0.27	0.96	1.21	2.79	11.07	9.90	5.25	6.97	7.24	13	
9.21	4.07	3.13	—	8.88	4.06	0.12	—	0.38	—	—	—	—	0.03	0.34	0.45	—	14	
6.38	8.42	2.43	1.59	4.31	5.96	0.27	—	—	—	—	—	—	0.07	1.86	2.56	1.82	15	
2.40	1.33	1.65	—	7.54	0.28	0.26	—	—	—	—	—	0.41	0.11	0.82	0.09	0.18	16	
4.38	1.15	3.20	6.07	1.38	3.24	3.28	0.56	0.20	3.14	1.21	7.96	7.92	5.61	4.18	1.37	1.46	17	
5.92	3.90	4.79	0.28	6.93	1.35	0.26	0.39	0.20	0.18	1.56	0.65	0.50	0.74	0.67	1.55	2.26	18	
—	0.05	—	6.07	—	0.81	5.99	8.88	8.80	6.57	9.43	5.11	4.52	4.19	2.26	0.51	0.13	19	
—	0.26	—	—	—	—	0.79	—	—	—	—	—	—	0.20	7.68	1.31	3.99	20	
2.63	6.16	1.65	—	0.65	1.63	—	—	—	—	—	—	0.13	0.07	0.29	0.30	1.06	21	
0.06	—	—	3.55	—	1.62	2.85	2.90	8.01	1.32	1.02	1.31	1.11	1.23	0.67	0.16	0.13	22	
—	—	—	1.84	—	0.54	0.94	7.45	2.28	3.55	2.92	1.39	2.74	1.97	1.26	0.37	0.82	23	
—	—	—	0.93	0.22	—	1.20	4.41	3.78	2.96	7.08	6.22	2.18	0.85	1.31	0.59	0.18	24	
0.46	0.21	0.51	4.48	0.87	3.37	3.90	4.41	2.36	5.32	3.07	2.98	2.29	2.70	1.39	0.68	0.33	25	
—	0.15	—	5.13	—	0.26	1.20	1.05	0.76	0.41	—	2.90	0.45	0.30	—	—	—	26	
—	—	—	—	—	0.91	4.55	0.08	0.28	7.70	—	2.09	1.19	3.74	3.46	—	—	27	
0.61	—	—	3.30	2.20	—	2.71	1.45	—	0.55	0.34	—	2.12	3.60	1.12	1.02	1.02	28	
—	—	—	0.75	—	0.26	1.47	3.13	4.60	0.18	1.36	0.43	1.09	1.27	0.97	0.32	0.10	29	
—	—	—	0.80	—	1.35	2.81	2.92	0.46	0.94	4.46	—	1.09	1.22	1.21	0.33	0.36	30	
—	—	—	—	—	—	0.14	—	—	—	—	—	—	1.32	—	—	2.06	31	
—	—	—	0.26	—	—	0.41	1.17	0.54	0.55	2.10	—	1.27	1.69	0.38	0.28	—	32	
0.06	—	—	1.32	0.07	0.54	—	1.13	0.92	0.88	1.22	2.47	0.78	1.24	0.58	0.34	—	33	
—	—	—	1.81	0.07	—	—	—	0.08	—	—	0.51	—	—	—	—	—	34	
—	—	—	—	—	—	0.50	—	1.82	0.26	1.22	0.43	0.51	—	—	0.12	—	35	
—	—	—	0.53	—	0.54	0.41	0.36	1.50	0.18	1.02	0.22	0.99	0.99	0.30	—	—	36	
0.12	0.05	0.07	0.40	0.30	—	0.52	1.06	0.18	0.22	—	0.65	1.38	0.17	0.19	0.08	—	37	
—	—	—	—	—	—	—	1.34	0.78	—	—	—	—	0.14	0.24	—	—	38	
—	—	—	—	—	—	0.26	0.22	0.38	—	—	—	—	—	—	1.06	—	39	
0.26	—	—	0.26	0.07	—	—	—	—	—	—	—	—	0.83	0.44	—	—	40	
0.06	—	—	—	0.80	—	—	—	—	—	—	—	—	—	—	—	—	41	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.48	0.62	—	42	
—	—	—	—	—	0.52	—	—	—	—	—	—	—	—	—	—	—	43	
—	—	—	—	—	—	—	—	—	—	—	—	0.13	—	0.34	—	—	44	
—	—	—	—	—	—	—	—	—	—	—	—	0.22	0.03	0.14	—	—	45	
—	0.17	—	—	—	—	—	—	—	—	—	—	1.01	—	—	—	—	46	
—	—	—	—	—	—	0.12	—	—	0.14	—	—	—	—	0.05	—	—	47	
—	—	—	—	0.14	—	—	—	—	—	—	—	—	—	—	—	—	48	
—	—	—	0.14	—	—	—	—	—	—	—	—	—	—	—	0.08	—	49	
—	—	—	—	0.07	—	—	—	—	—	—	—	—	—	—	—	—	50	
0.02	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	51	
27	23	18	32	27	30	32	24	29	26	21	25	34	38	38	35	28		

although Berthelsen (1962:16) considered the zooecia lacking opesiules in such specimens to have lost them in fossilization.

Morphotypes v and vi (Plates 4:1; 10-12): Zooecia of types v and vi have not been separated in this study. There are at present no known criteria in zooecial morphology that consistently distinguish between fully developed zooids of these two morphotypes. Even though the frontal shield and ascus develop in different relationship to the frontal membrane, as discussed above, the membrane bounding the frontal surface, the frontal shield, and the underlying ascus are arranged similarly in fully developed zooids of the two types (Figure 7). Harmer (1957:645, 662) assumed that zooids in which the proximal part of the operculum is continuous with the membranous floor of the ascus developed by the umbonuloid pattern (morphotype v), whereas those which developed in the lepralioid manner (morphotype vi) should have the proximal margin of the operculum contiguous with the portion of the frontal shield forming the proximal lip of the primary orifice. As pointed out by Banta (1970:52), however, the relation of the membranous floor of the ascus to the operculum is identical in the two modes of development. Therefore, the structure of the zooecial orifice appears not to be a criterion for separating the two morphotypes.

It has been assumed that ascophorans having frontal shields developed by the two major patterns represent two or more distinct phyletic lineages (see, for example, Ryland, 1967a:348). Because the two types cannot now be distinguished in fossils, however, the phylogenetic significance of the difference in development is unknown (Boardman and Cheetham, 1969:229). The difference in development does not seem to involve functional differences in the ability to calcify frontally. Both kinds of frontal shields appear to be susceptible of long-sustained ontogenetic thickening and concomitant merging across the frontal edges of lateral walls of contiguous zooids.

Ascophoran zooecia have convex, usually heavily calcified frontal lamellae commonly lacking zooecial boundaries in zoarial fragments inferred to represent later stages of zooid ontogeny. The frontal shield displays perforations along its margins (Plate 10:4) or scattered over its surface (Plate 11:2-4) or on its midline proximal to the orifice (Plates 10:2-4; 11:2-4). Except by similarity of position in living ascophorans, there is no known way to distinguish between perforations which in life were covered with

membrane (areolae, frontal pores) and those which represent true openings (ascopores, spiramina). In transverse and longitudinal sections (Plate 12), the frontal shield appears convex and much thicker than the basal and lateral walls. In most species, the transverse wall is also appreciably thinner than the frontal shield, but in *Columnotheca cribrosa* Marsson (Plate 12:1-2), it is about as thick as the frontal shield and is perforated with similar tube-like pores. In most species, distinct boundaries are discernible between lateral walls but disappear frontally, suggesting merging of the epifrontal membranes of adjacent zooids. Adventitious avicularia are commonly present on the frontal shield, especially in the vicinity of the orifice. The distal portion of the shield is generally raised around the orifice to form a mucro (Plate 4:1) or a peristome (Plates 11-12).

TAXONOMIC SIGNIFICANCE OF MORPHOLOGIC VARIATION

Even though the objective of this study has been to understand the functional morphology and distribution of Danian cheilostomes rather than their taxonomy, it has of necessity involved the recognition of operational taxonomic units. The basic units of this study are groups of fragmentary specimens inferred to have been parts of approximately contemporaneous, sympatric, morphologically similar colonies. The morphologic differences between any two of these groups of specimens (phena of Mayr, 1969) thus might reflect either intrapopulation variation or taxonomic differences. For nomenclatural convenience and in accordance with taxonomic practice in most previous studies of Danian cheilostomes, these operational units, or phena, are regarded as separate species (Table 1) except where there is evidence of intergradation among coeval assemblages. Intergrading phena are here united in single operational taxa, rather than being regarded as conspecific subspecies as they have in some previous studies. In the absence of evidence for the positions of these operational species in evolutionary lineages, it would be presumptuous to propose formal revisions of the existing taxonomy on the basis of the morphologic variation observed in this material.

Within each of the operational species, those zooecia inferred to represent autozooids belong to a single morphotype. At the distal end of a zoarial fragment preserving the growing extremity of a colony, zooecia may lack or have only incomplete frontal structures

(Plate 8:2). In those few zoarial fragments found to preserve the primary zone of astogenetic change (Plates 1:4, 6:1), all zooecia, including the ancestrula, appear to belong to the same morphotype. Variations in details of morphotype structure, however, are discernible among the zooecia in many zoarial fragments studied. For example, *Floridina gothica* (Plate 7:2-3) has, within the same zoarial fragment, some zooecia with separate opesiules and others with opesiular indentations confluent with the opesia. In *Micropora hennigiana* the opesiules are small, subcircular perforations near the opesia on some specimens (Plate 6:1-2) and more elongate slits placed nearer midlength on others (Plate 6:3), but intermediates between these two extremes are common. A similar gradational series characterizes *Pithodella cincta* (Plate 2:2-4) in which the relative development of spines, cryptocyst, and avicularium are highly variable but overlapping in different specimens. In still other operational taxa, variations in details of zooecial morphology are less distinctly gradational or overlapping, and a number of specific separations might be justified in each. However, the material studied seemed inadequate for making distinctions in the following complexes (Table 1): *Callopora* spp., *Floridina* spp., *Pliophloea* spp., and "*Cellepora*" *daniensis* Voigt + spp.

Zoarial form also appears to be variable within some operational species, but the evidence is less definite than that for zooecial variation. The small size of the fragments might account for the lack of specimens clearly showing more than one colony form. Specimens which show differences in zoarial form but which lack correlated differences in zooecial structure have been included in the same operational species. In this category fall the following (Table 1): *Puncturiella sculpta* (d'Orbigny), *Semiescharinella complanata* (d'Orbigny); *Micropora hennigiana* + spp., *Membraniporidra declivis* (Marsson), and *Psilosecos angustidens* (Levinson). The last species seems to occur in only one form (membraniporiform) in the material studied here, but has previously been found only in another (eschariform).

Paleoenvironments of Danian Cheilostomes

BRYOZOAN MOUNDS

Although Bryozoa occur in southern Scandinavia in several kinds of limestone of Danian age, they are typically associated with mound-like sedimentary

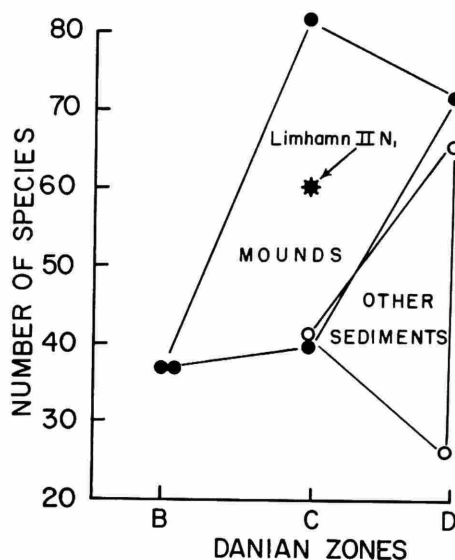


FIGURE 10.—Numbers of species of cheilostome Bryozoa in mound and non-mound facies of Danian (Zones B-D); data from Berthelsen (1962:242-255); zonal classification after Ødum (1926:217). For comparability with other localities, the number of species in samples from Limhamn Mound II-N₁ has been adjusted to the same morphologic basis, i.e., each distinct zooecial or zoarial variant has been counted as a separate species. Therefore, the number of species is greater here than in Table 1 or the analyses (Figures 20-29) based on it.

structures variously referred to in the literature as reefs, bioherms, or banks. Among the localities in Denmark from which Danian cheilostomes were studied by Berthelsen (1962), those having evident mound structure on the average yielded more species than those of the same age showing only evenly bedded limestone (Figure 10). The abundance of cheilostomes at these localities, however, is highly variable but averages about the same in mound and non-mound sediments (Berthelsen 1962, Tables 3, 4). The diversity of mound faunas therefore suggests multiple adaptations within the geographic confines of a single mound.

Typical mounds having well-defined boundaries occur in the lower and middle parts of the Danian (Figure 11) and are best exposed along Stevns Klint, Denmark, and in the quarry at Limhamn, Sweden. The Stevns Klint structures and larger mounds with less distinct limits at Fakse, Denmark, have been described and illustrated in a number of papers summarized by Rosenkrantz and Rasmussen (1960). Those at Limhamn were described and illustrated by Brotzen (1959).

Stratigraphic correlations between the mound sediments of Denmark and Sweden have not been com-

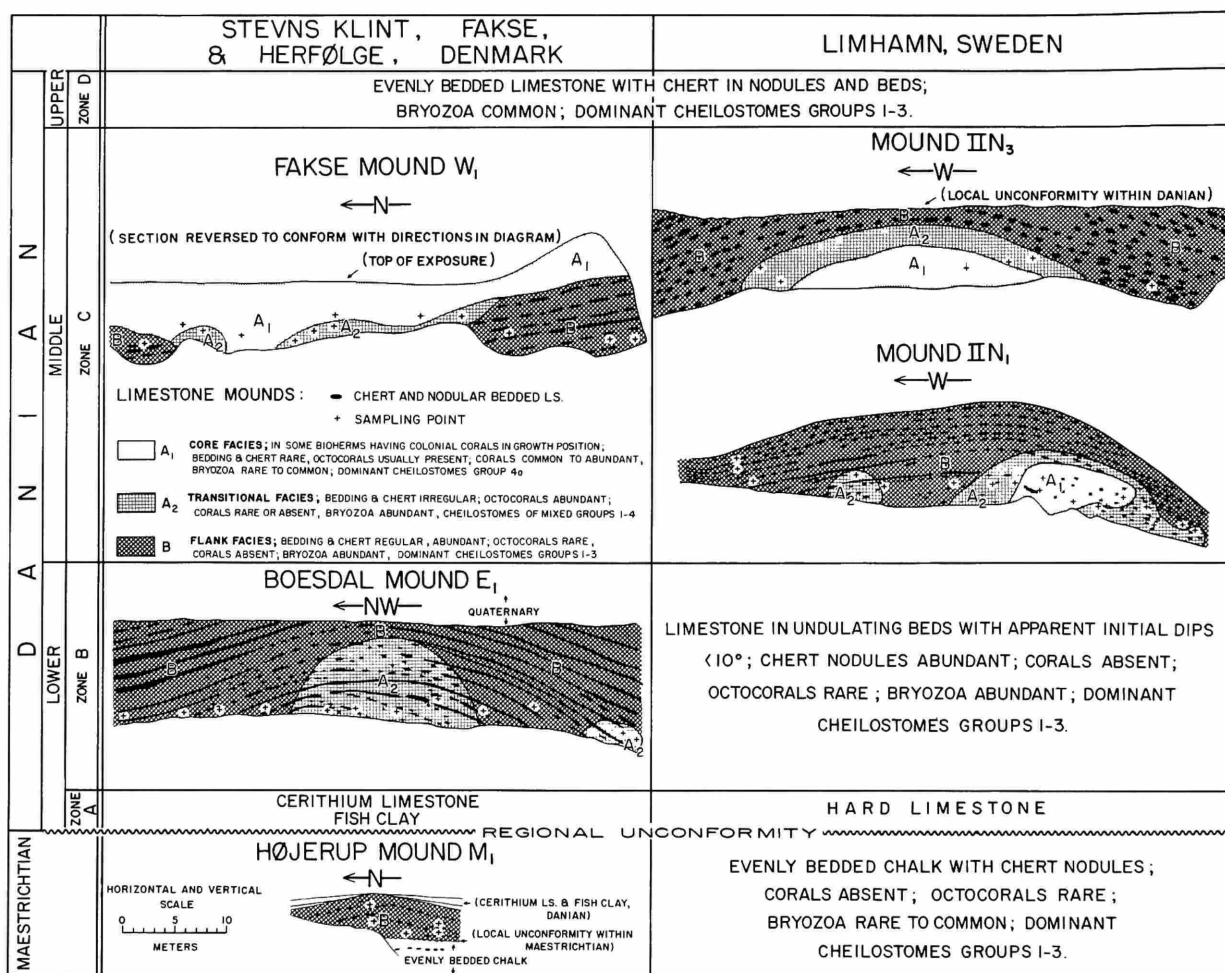


FIGURE 11.—Stratigraphic distribution and general characteristics of bryozoan mounds in Maestrichtian and Danian Stages in southern Scandinavia; zonal classification after Ødum (1926); correlation between Denmark and Sweden in part after Brotzen (1959). Mounds are drawn from field measurements with bedding and lithology shown diagrammatically. Biofacies are generalized from detailed quantitative study of samples from Limhamn Mound II-N₁ (Figure 12) and visual estimates of samples from all other mounds and non-mound sediments. See text (pages 25–35) and Figures 13–28 for detailed description and analysis of mound sediments.

pletely established. In Denmark, mounds are primarily in lower and middle Danian zones named, respectively, B and C by Ødum (1926) and *Tylocidaris oedumi* and *T. abildgaardi* Zones (Zone B) and *T. bruennichi* Zone (Zone C) by Rosenkrantz (1937). The mounds at Limhamn are in middle Danian zones called *T. rosenkrantzi* and *T. bruennichi* Zones by Brotzen who (1959:24) suggested that the *T. rosenkrantzi* Zone of Limhamn is represented by an unconformity between Zones B and C in the area from Stevns Klint to Fakse. Assemblages of cheilostome Bryozoa, as discussed below, indicate that the *T. rosenkrantzi* Zone at Limhamn

may correlate with part of Zone C, and this assignment is shown in Figure 11.

The typical lower and middle Danian mounds are about 50 m across and a maximum of about 15 m thick. There is no intermound facies, so mounds are in contact laterally and vertically (Plates 13:1, 14:3). The less-distinct mounds at Fakse also appear to be laterally and vertically contiguous (Rosenkrantz and Rasmussen 1960, fig. 12).

The limestone and included chert composing the mounds show two kinds of structure, each associated with a different lithology, one being bedded and the

other poorly bedded to massive (Plates 13:2, 14:2). The bedded limestone is light gray and friable, usually shows finely nodular bedding (Plate 15:1), and is abundantly interbedded with nodular or continuous chert layers. In general, the nodular bedding and the chert layers are subparallel. These sediments have generally been called Bryozoan Limestone (Berthelsen 1962:225). Poorly bedded to massive limestone (Plate 15:2) is white and may be either friable or indurated. Zones of finely nodular bedding (Plate 15:2) and isolated nodules of chert (Plate 13:2) are rare. This limestone includes lithologies generally called Coral Limestone.

The boundaries and internal structure of the mounds are discernible principally on the basis of the distribution of these two kinds of sediment. In general, the bedded limestone forms several zones of irregularly wave-like structures. The limestone underlying the wave troughs is bedded throughout, but that underlying the wave crests generally consists of bedded limestone gradationally overlying massive limestone. The massive limestone thus forms the mound cores, from which the bedded limestone dips away at angles as high as 24° to form the flanks.

Massive limestone also overlies bedded limestone in some of the wave troughs. These masses have sharp contacts with the bedded limestones below and gradational contacts with bedded limestones above and lateral to them (Plate 15:3). They thus appear to be the cores of younger mounds superposed on the troughs formed by the oppositely dipping flanks of adjoining older mounds. The troughs between mounds, however, are not invariably overlain by younger mound cores. In both the lower Danian of Stevns Klint (Rosenkrantz and Rasmussen 1960:6, fig. 5) and the middle Danian of Limhamn (Plate 14:3), the flank of one mound may overlap the opposing flank of an adjacent mound, forming an unconformity. In some cases (Plate 14:3), the bedded limestone of the overlapped mound appears to have been truncated, but these angular relationships give way to apparent conformity within a few meters. Continuous unconformities running through the whole of Limhamn Quarry were not observed, nor were zones of induration ("hardgrounds") such as have been reported by Rosenkrantz and Rasmussen (1960:6) at Stevns Klint.

In the quarry at Limhamn and in those along Stevns Klint, vertical faces at approximately right angles expose similar cross sections through the mounds. This suggests that the mounds are roughly radially sym-

metrical. In detail, however, all the mounds studied are asymmetrical, as noted by Rosenkrantz and Rasmussen (1960:6), with steeper dips on their southern or eastern sides (Figure 11).

In the middle Danian mounds of both Denmark and Sweden, the core limestones may contain colonial scleractinian corals which appear to be nearly in position of growth (Plate 14:1), though according to Floris (1967) they are always at least slightly tilted and broken. Other biotic constituents of both types of limestone seem to be invariably broken and incorporated into the matrix with the long axes of the fragments parallel to the obvious bedding, whatever their original growth position relative to the substrate. This orientation is conspicuous for most of the bryozoan and octocoral material in the mound limestones (Plates 16-17). In the lower Danian mounds along Stevns Klint and in some middle Danian mounds at Limhamn, all the visible skeletal material in the core limestones is fragmental and lying parallel to the bedding.

Where, as is usually the case, the material near growth position occurs in minor amounts or is lacking, the core limestone grades upward into bedded limestone. Only in the middle Danian mounds at Fakse, where colonial scleractinians are abundant, does the core limestone seem to dominate, overlap, and replace the bedded limestone vertically upward. Thus the core structure of the mounds appears to become progressively more important from the lower into the middle Danian, and this progression appears to be more rapid in Denmark than in Sweden (Figure 11). In both areas the trend is reversed in the upper Danian with a return to predominantly bedded limestone.

BIOFACIES ANALYSIS OF LIMHAMN MOUND II-N₁

To determine the lithologic and biofacies characters of the mounds and the variation of these properties within one such structure, a series of samples from the middle Danian in the quarry at Limhamn, Sweden, was analyzed quantitatively. The mound sampled (Figure 12) was exposed in 1964 and 1965 on the north wall of the quarry in a situation which made it easily accessible, although it has subsequently been completely removed by quarrying. Its boundaries were well defined, and its core and flanks were distinctive, although none of its biotic constituents were observed to be in position of growth.

This mound, designated Limhamn II-N₁, was in the lower part of Brotzen's (1959:33) Bioherm Group II or *Tylocidaris rosenkrantzi* Zone, a stratigraphic

TABLE 2.—*Determination of aliquot size for analysis of coarse-fraction major biotic constituents of Mound II-N₁.*

Grain size	Sample	Aliquot			Significance of difference
		Number	Weight	Particles	
1000–2000 μ	1	1a	2.4153	1,506	P<0.001
		1b	2.5244	1,787	P<0.001
		1a+1b	4.9397	3,293	P=0.012
		2	5.4240	3,827	P=0.013
	2000 μ	1+2	10.3637	7,120	Total
500–1000 μ	1	1	3.3289	1,192	P=0.14
		2	3.9450	1,353	P=0.16
		1+2	7.2739	2,545	Total
	7	1	1.5095	4,782	P=0.65
		2	0.7177	2,018	P=0.12
		1+2	2.2272	6,800	Total
		1	1.2670	3,055	P<0.001
		2	0.7057	1,731	P<0.001
		1+2	1.9727	4,786	Total

TABLE 3.—*Dry weight of samples processed from Mound II-N₁ and aliquot percent of each size grade used in biofacies analysis (2000 μ =100 percent for each sample).*

Sample	Aliquot (%)		Weight (g)		
	500–1000 μ	1000–2000 μ	>500 μ	>74 μ	Total
1	8.7	100.0	36.6	77.4	236.5
2	5.6	49.2	33.8	82.1	250.9
3	6.5	13.0	40.5	96.2	293.2
4	12.3	22.0	61.4	112.7	308.2
5	5.9	23.2	29.9	74.2	170.7
6	6.7	25.3	39.3	102.8	329.8
7	19.1	50.0	55.9	127.5	436.3
9	13.6	100.0	12.2	58.8	281.3
10	38.2	100.0	33.4	86.5	140.8
11	25.6	100.0	29.4	87.2	391.8
12	12.5	24.8	82.6	128.5	288.2
13	9.1	25.1	59.5	119.1	298.6
14	28.0	52.6	64.3	110.8	358.8
15	30.9	44.9	63.7	109.5	379.2
16	12.3	41.8	81.2	146.2	354.2
17	15.1	37.1	85.5	142.6	354.2
18	12.2	51.7	66.1	115.1	322.6

TABLE 4.—*Major biotic constituents in biofacies analysis of Mound II-N₁.*

Symbol	Category	Description
CHEILO....	Cheilostome bryozoans...	(Data analyzed separately.)
CYCLO.....	Cyclostome bryozoans....	Flat, crust-like; slender, twig-like; and massive, mushroom-like colony fragments.
OCTO.....	Octocorals.....	Smooth to tuberculate, rod-like fragments of axes, with or without calycal pits; small, fusiform, tuberculate spicules.
SCLER.....	Scleractinian corals.....	Slender, branching colony fragments and cup-shaped solitary forms; plate-like fragments of septa, with or without perforations.
ECHIN.....	Echinoderms.....	Mostly disarticulated ossicles of echinoids, asteroids, ophiuroids, and crinoids.
SERP.....	Serpulids.....	Fragments of irregularly coiled, cylindrical tubes, many showing attachment scars or still adherent to other particles.
RETI.....	Calcareous sponges.....	Irregular crusts to sub-spheroidal masses, all with tuberculate surfaces; detached or adherent to other particles.
OTH....	Other constituents (in minor amounts).	Brachiopod valves, mostly fragmentary, usually punctate and plicate. Mollusk shell fragments, including oyster-like and scallop-like forms. Calcareous foraminiferal tests. Bairdiid ostracode valves. Lepadomorph barnacle valves.

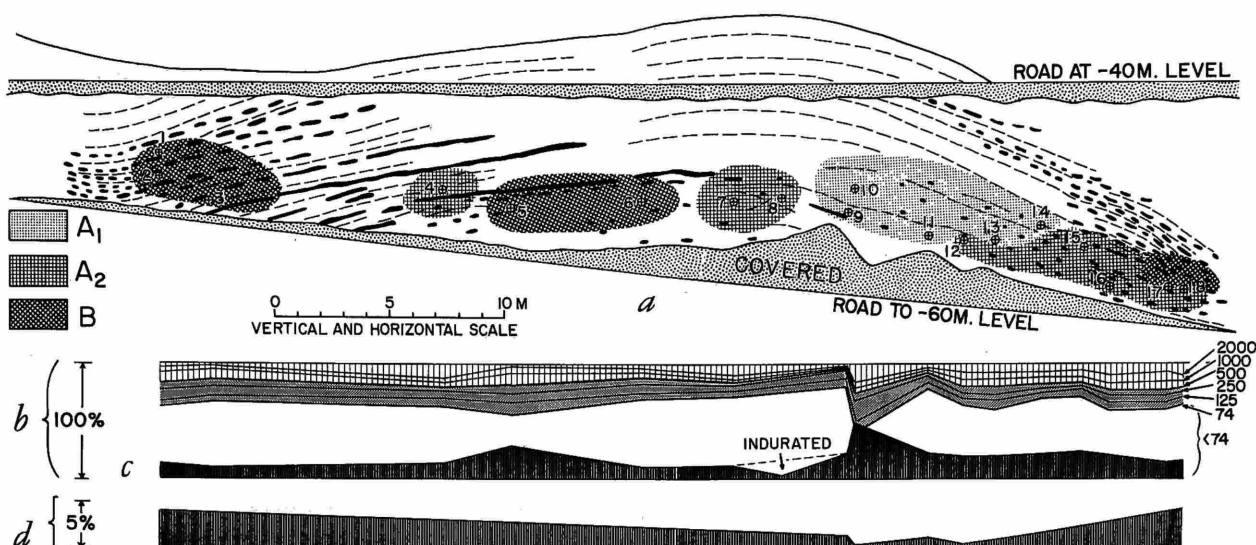


FIGURE 12.—Lithology and biofacies of Mound II-N₁, middle Danian, in the quarry of Skånska Cement A. B., Limhamn, Sweden. Location on north wall of quarry is shown on Plate 13:1.

a, Cross section of mound, constructed in the field by tape, hand-level, and plumbline survey. Since the mound was measured and sampled in 1964–65, quarrying has removed it completely. Location of samples 1–18 is shown by crosses. Biofacies A₁, A₂, and B were delineated by cluster and principal components analysis (see Figures 18–19) of abundances of eight major biotic constituents. Nodular bedding is shown by dashed lines. Chert, indicated in black, was not mapped in the upper third of the mound, but presumably was distributed as shown in Figure 11.

b, Grain size (as dry-weight percentage of sample) obtained by wet-sieving through 74-μ (200-mesh) screen and dry-sieving the residue through a set of 2000, 1000, 500, 250, and 125 μ screens after the larger lumps which would not disaggregate were picked out by hand and subtracted from the original weight. Disaggregation was effected by washing in water, supplemented, where necessary, by alternately freezing and thawing.

c, Moisture loss (as dry-weight percentage of sample) on heating for 48 hours at 102° C (treatment empirically determined to give constant weight). On the assumption that the samples (all from below sea level) were water-saturated when collected, water content is a kind of measure of effective porosity. Sample 8, having a low water content, was indurated.

d, Non-carbonate content (as dry-weight percentage of sample) of eight samples (1, 5, 9–11, 14, 18) determined by digestion of 2 g of powdered sample (with no visible chert) in 1:1 hydrochloric acid.

position suggested by him to be between the lower and middle Danian of Denmark, as mentioned above. The species of cheilostome Bryozoa identified from it (Table 1) compare closely with those listed by Berthelsen (1962) from the middle Danian of eastern Denmark (Zone C). One species in the Mound, *Pelmato-pora? daniensis* Voigt, suggests a younger age, but none has previously been found only in older rocks. The number of species in the Mound also compares favorably with the diversity of other middle Danian localities, if adjusted as in Figure 10. This diversity is higher, in general, than those of lower Danian localities. Therefore, the fauna of the Mound can be considered to be consistent with a middle Danian age, and

there is no suggestion that it might be older than the middle Danian faunas of Denmark.

Mound II-N₁ is slightly asymmetrical, with higher apparent dips (measured up to 24°) on its eastern flank and with the massive core limestone nearer its eastern extremity. The core limestone reaches a maximum thickness of at least 6 m (the lower boundary of the mound was covered with talus at the time measurements were made) and is gradationally overlain by about 7 m of bedded limestone. Colonial scleractinians were found only as fragments out of growth position, although coral masses in growth position might have lain outside the exposed cross section.

Nodules and beds of chert were numerous on the

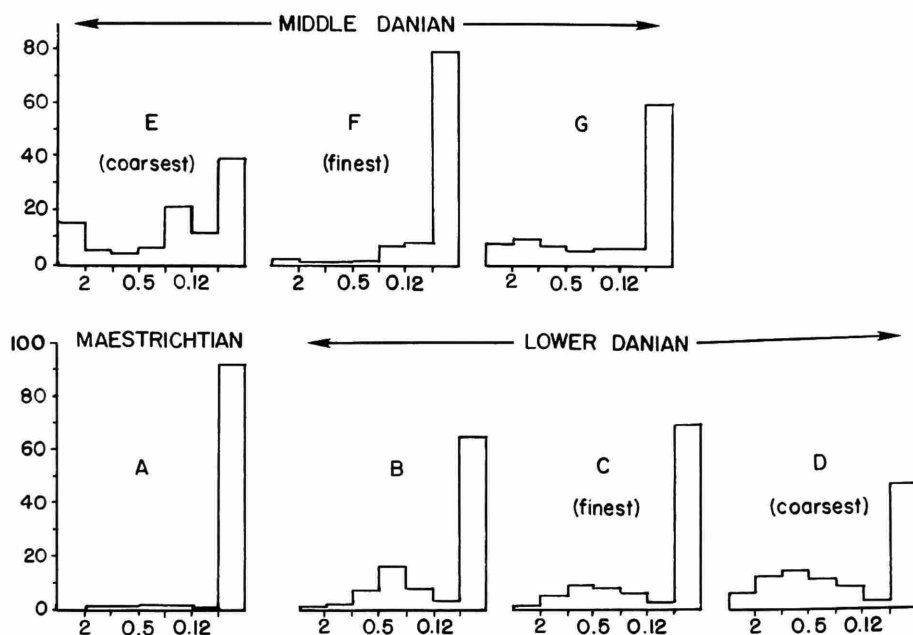


FIGURE 13.—Grain size (as dry-weight percentage of sample) of limestone samples from Maestrichtian and Danian of Sweden and Denmark (size ranges were determined as explained in Figure 12b): A, Uppermost of three similar samples from upper 20 m of Maestrichtian, north wall of Limhamn Quarry. B, Middle of three similar samples from upper 1 m of lower Danian in north wall of Limhamn Quarry. C, Southeast part of core, Mound E₁, Boesdal. D, Southeast flank of Mound E₁. E, Sample 10, core of Mound II-N₁, Limhamn. F, Sample 9, core of Mound II-N₁. G, Sample 17, flank of Mound II-N₁.

flanks of Mound II-N₁, and chert nodules also occurred in the core. For the most part, the chert appeared devoid of fossils, but in some places still-calcareous echinoderm ossicles and other skeletal material could be observed. Some of these skeletal elements were observed to lie partly in the chert and partly in the adjacent limestone. In a few of the limestone samples taken some distance from the obvious chert nodules or beds, siliceous steinkerns of Bryozoa, in some cases with the skeleton also silicified, were found. Most of the samples were chert-free and, with the exception of one (Sample 8, Figure 12), were readily disaggregated.

The limestone composing Mound II-N₁ has variable grain size, but the high proportion of fine particles shown by all samples (Figure 12b) characterizes them as calcilutites (see Plates 16–17). In general, there is a higher percentage of material finer than 500 μ in this mound than in a lower Danian mound in Boesdal Quarry on Stevns Klint (Figure 13; Berthelsen 1962, Table 2). However, the ranges of grain size in the Boesdal and Limhamn mounds overlap. Maestrichtian and lower Danian samples from Limhamn (Figure 13) are also calcilutites, but some middle and upper Danian

sediments analyzed by Berthelsen (1962, Table 2) are calcarenites with as little as 7.4 percent material finer than 500 μ .

The Danian calcilutites from Limhamn and Stevns Klint differ from those of Maestrichtian age at Limhamn in being coarser grained and in showing more than one modal class in the particle sizes analyzed (Figure 13). This composite character is also reflected in the cumulative particle-size distribution (Figure 14A) and results from the occurrence in each sample of several skeletal constituents each having its distinctive size-frequency distribution (Figure 15). The sediment thus is very poorly sorted.

The distribution of grain size across Mound II-N₁ (Figures 12b, 13) suggests that the bedded flank limestones are approximately uniform, whereas the core limestone may be either coarser or finer. This pattern appears to be the result of differences in the distributions of the biotic constituents and thus not the product of physical sorting.

Insoluble residues, consisting of what on visual inspection appears to be chiefly clay, silt-size quartz, mica, and glauconite in the samples of essentially chert-free limestone, are distributed in conformity with

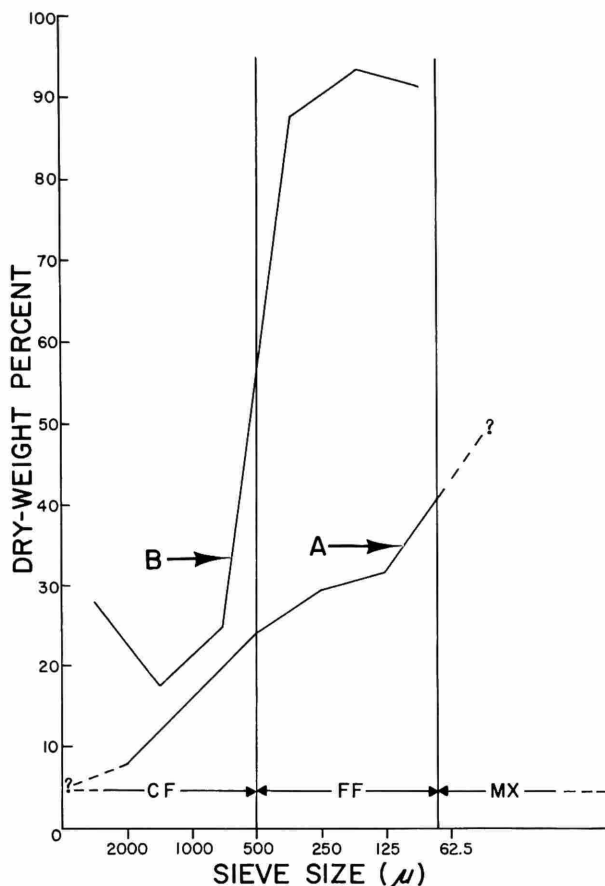


FIGURE 14.—Distribution of grain size and unidentified particles in Sample 17, Mound II-N₁ (CF, coarse fraction; FF, fine fraction; MX, matrix): A, Cumulative grain size by dry-weight percentage of sample. B, Unidentified and composite grains as dry-weight percentage of fraction of sample between each pair of grain sizes.

mound structure (Figure 12*d*), that is, with higher percentages on the flanks than in the core. Concentration of this material in quantities up to 4½ percent of dry weight on the flanks suggests that, if it was available at the same rate over the area of the whole mound, the core limestone accumulated more rapidly than that on the flanks. Also, because the “effective porosity” of the samples (Figure 12*c*) appears to be correlated with grain size rather than strictly with position within the mound, the structure of the mound appears not to be the result of differential compaction.

As the identifiable major biotic constituents of each sample are concentrated in the coarse fraction (>500 μ) of the limestone (Figure 15), biofacies analysis of Mound II-N₁ was limited to this material. Only a few constituents, such as foraminifers and oc-

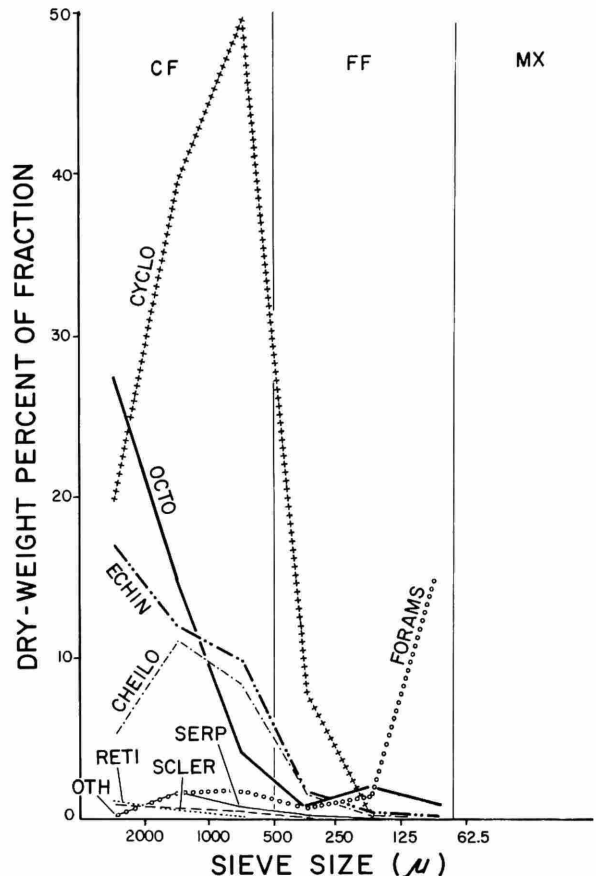


FIGURE 15.—Distribution of major biotic constituents with grain size in Sample 17, Mound II-N₁. Coarse fraction (CF) percentages were calculated from particle counts of aliquots of each of the size fractions. Unidentified and composite grains in each size fraction of Sample 17 are shown in Figure 14. (FF, fine fraction; MX, matrix; other symbols explained in Table 4, on p. 26.)

tocorals (spicules), could be identified in significant amounts in the finer fraction. The coarsest material (>2000 μ) was analyzed in its entirety, but, to reduce sorting time, smaller aliquots were used for the 1000–2000 and the 500–1000 μ material. Very small amounts of these size grades were found to give weight percentages of the constituents which, by chi-square tests based on the number of particles in the aliquot, are significantly different from the whole-fraction values in an appreciable number of cases (Table 2). Therefore, aliquots of 10 g of the 1000–2000 μ fraction and 5 g of the 500–1000 μ fraction were used to minimize this risk. The weight of material processed for each sample and the aliquot percent of that weight in which the biotic constituents were analyzed are shown in Table 3.

The biotic constituents of Mound II-N₁ are divisi-

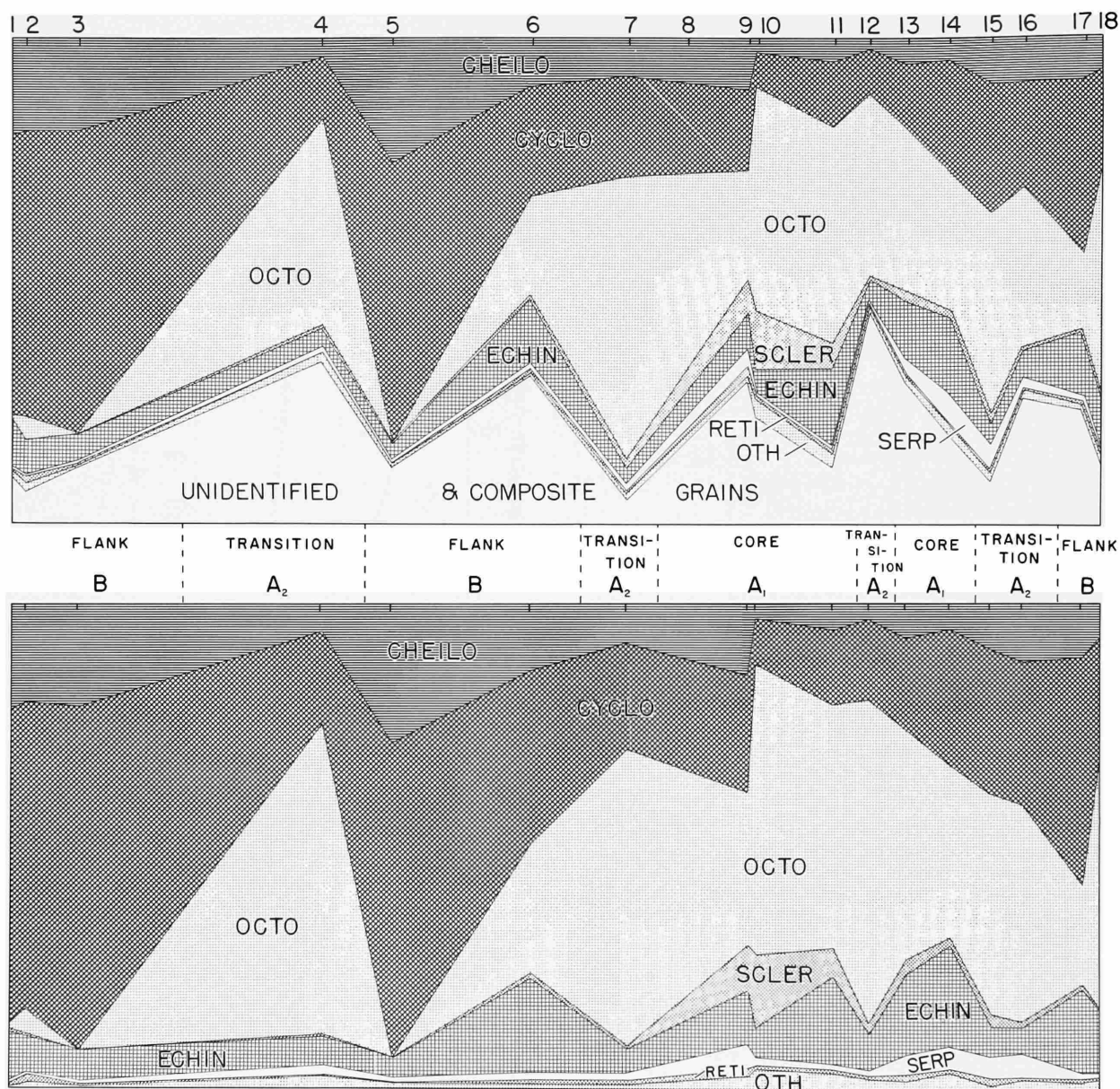


FIGURE 16.—Distribution of major biotic constituents in coarse fraction ($>500\mu$) of limestones from Mound II-N₁. In each diagram, the dry-weight percentages of coarse fraction add up to 100 percent. The lower diagram was constructed without the unidentified and composite grains which were included in the upper diagram. (Symbols explained in Table 4; biofacies classification shown in Figures 18 and 19; location of samples indicated in Figure 12).

ble into eight major categories (Table 4), which can be identified in significant amounts in the coarse fractions of the samples. Most constituents occur generally in fragments (Plates 16–17), but indications of abrasion (Plate 8:1) are rare. Of the constituents, cyclo-

stome and cheilostome bryozoans and octocorals are dominant (Figure 16), together making up at least half of the coarse fraction (or more than three-fourths of the identifiable constituents) of every sample. In general, the two groups of bryozoans vary in abundance

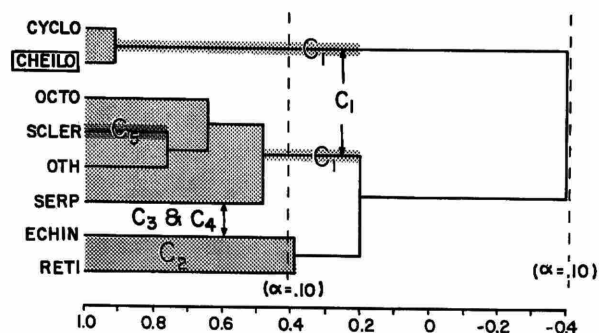


FIGURE 17.—R-mode (constituent-by-constituent) dendrogram of relationships among eight biotic constituents of coarse fraction ($>500\mu$) of the 17 samples from Mound II-N₁ and influence of principal components on clustering. Weighted-pair-group-method clustering is based on correlation coefficients calculated from weight percentages transformed by the arcsine-square-root method recommended by Seal (1964). Unidentified and composite grains were excluded in calculation of percentages. Dashed lines indicate values of correlation coefficient at 10-percent significance level. C₁ through C₈ are the first five factors from Table 5. Identifying and uniting influences are indicated by shading; opposing influences are shown by arrows; abscissa is product-moment correlation coefficient. (Symbols for biotic constituents explained in Table 4.)

in the same way and in opposition to the octocorals. To the extent that the compositional data approximate a two-constituent, closed system, the correlation between bryozoans and octocorals can be expected to approach -1 (Chayes 1960). To investigate this relationship and others not apparent directly from the abundance variation (Figure 16), the weight-

percentage abundances in the 17 samples from Mound II-N₁ were submitted to multivariate analysis. To minimize the constant-sum constraint, percentages were transformed (Seal 1964). Both constituent-by-constituent (R-mode) and sample-by-sample (Q-mode) analyses were made.

Relationships among the eight biotic constituents were investigated by cluster analysis and principal components analysis of the array of product-moment correlation coefficients among all pairs of constituents, the R-mode correlation matrix. Cluster analysis (Sokal and Sneath 1963) arranges the eight constituents in three groups (Figure 17). Within each group, the constituents are positively correlated at about the 10-percent significance level or higher, indicating that their abundances vary together. Cheilostome and cyclostome bryozoans form the most tightly knit group (correlation 0.91), and echinoderms and calcareous sponges the least (correlation 0.39). The remaining four constituents are correlated with each other at values of 0.44 to 0.76. The relationships among the three main clusters of constituents are not as clear as those within them. The echinoderm-sponge group clusters with the group (coral cluster) composed of octocorals, scleractinians, serpulids, and the category "other constituents" at a level not significantly different from zero; the abundances of these two groups therefore appear to vary independently. The cheilostome-cyclostome group shows a negative relationship, significant at about the 10-percent level, to one or both of the other two; thus, bryozoan abundances vary in

TABLE 5.—Principal components analysis of variation in eight major biotic constituents of coarse fraction ($>500\mu$) of 17 samples from Mound II-N₁ based on correlation coefficients calculated from arcsine-square-root transformed weight percentages. $r = \pm 0.41$ significant at $\alpha = 0.10$. Symbols for constituents are explained in Table 4.

Factor	Eigen-value	Variance		Eigenvector (factor loadings)							
		% tot.	Cum.	CHEILO	CYCLO	OCTO	SCLER	ECHIN	SERP	RETI	OTH
C ₁	4.5582	57.0	57.0	-.89	-.96	+.89	+.79	+.25	+.62	+.36	+.92
C ₂	1.3630	17.0	74.0	+.22	+.21	-.31	+.14	+.72	+.22	+.76	-.03
C ₃	0.8109	10.1	84.2	+.34	+.09	-.18	+.37	-.55	+.43	+.14	+.08
C ₄	0.6284	7.9	92.0	+.06	+.02	-.02	-.17	+.26	+.58	-.42	-.06
C ₅	0.4003	5.0	97.0	+.08	-.01	-.22	+.40	+.19	-.19	-.30	+.13
C ₆	0.1708	2.1	99.1	-.02	+.10	-.11	-.16	-.02	-.01	0.00	+.35
C ₇	0.0613	0.8	99.9	+.19	-.10	+.08	-.04	+.03	-.03	-.06	+.05
C ₈	0.0071	0.1	100.0	+.01	+.06	+.05	+.02	+.01	0.00	+.01	+.01
Communality (Factors C ₁ to C ₅)				0.97	0.97	0.97	0.97	0.99	0.99	1.00	0.88

opposition to those of echinoderms and sponges, or the other four constituents, or all six constituents combined.

These relationships are brought out further by principal-components analysis (Seal 1964), which relates the eight intercorrelated constituents to eight uncorrelated (orthogonal) factors (Table 5), of which the first five explain the principal influences on the cluster dendrogram. These factors are mathematical abstractions which together account for nearly all (97 percent) of the total variation and also for nearly all of the variation in each constituent (as shown by the very high communalities calculated from the loadings on the first five factors). The nature of the first five factors and their resulting influence on clustering are suggested by their loadings (significant at about the 10 percent level) on the constituents. (Note that the sixth through eighth factors lack significant loadings as a result of the low eigenvalues attached to each of them.) From the loadings, three kinds of influences are distinguishable: (1) "identifying influences" are shown by factors (e. g., C_5) having a significant loading (either positive or negative) on only one constituent; (2) "uniting influences" are shown by factors (e. g., C_2) having significant loadings of the same sign on two or

more constituents; (3) "opposing influences" are shown by factors (e. g., C_4) having significant loadings of opposite sign on two or more constituents. In these data, the first factor, accounting for more than half the total variance, is both a uniting and an opposing influence and thus explains the general shape of the dendrogram. The significant opposition is between the cheilostome and cyclostome bryozoans on the one hand and the octocorals, scleractinians, serpulids, and the category "other constituents" (the coral cluster) on the other. Cluster analysis, which forces the echinoderms and calcareous sponges into the opposing relationship with the bryozoans, is thus seen to be an over-generalization. The uniting influence of the first factor explains the bryozoan cluster and the coral cluster of the dendrogram. The second factor, accounting for as much variance as the next two put together, unites echinoderms and calcareous sponges at a more significant level than suggested by the dendrogram. The third and fourth factors appear to be mainly a contrast between the echinoderm-sponge cluster and the serpulids. The fifth factor indicates that scleractinians may show some independence of variation, although the significance of the loading is borderline.

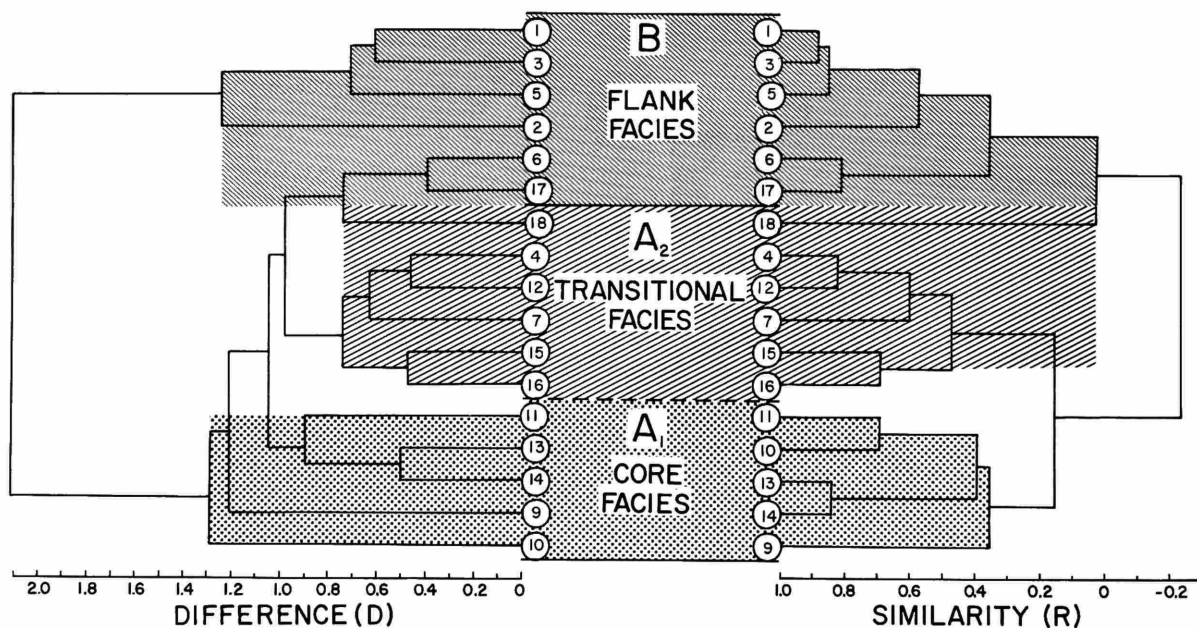


FIGURE 18.—Q-mode (sample-by-sample) dendrograms of relationships among 17 samples from Mound II-N₁ on the basis of eight biotic constituents. Weighted-pair-group-method clustering is based on correlation coefficients (*right*) and distance function (*left*) calculated from arcsine-square-root-transformed weight percentages. The transformed data were standardized by rows (Sokal and Sneath 1963) in the calculation of both correlation coefficients and distances. The biofacies are constituted as shown in Figure 19.

Relationships among samples from Mound II-N₁ were investigated by cluster analysis and by ordination. The cluster analysis, based on two different Q-mode matrices of association coefficients, resulted in slightly differing dendrograms (Figure 18), which are alike, however, in arranging the samples in two major clusters. The dendrogram based on the correlation coefficient groups together samples from both flanks (17 and 18 from the east flank; 1-3, 5, and 6 from the west flank) and, within the cluster consisting of samples principally from the core region (4, 7-16), distinguishes two subclusters. The dendrogram based on the distance function (Sokal and Sneath 1963:147) places samples from the east flank (17 and 18) and one from the west flank (6) with those in the core region. Inclusion of these samples in the core cluster seems to loosen the clustering of samples 9 and 10 with the others in the core and thus to imply more complex relationships. Consequently, biofacies suggested by the correlation dendrogram are more readily mappable than those indicated by the distance dendrogram.

A compromise between the two Q-mode dendrograms in Figure 18 is suggested by ordination of the samples relative to the factors obtained by principal components analysis of the R-mode matrix. This technique (Figure 19) plots the positions of the samples with respect to the orthogonal factor axes thus giving a geometric representation of the relationships among samples. For an almost undistorted representation, all five significant factors (Table 5) are required, but it is not possible to represent more than three factors in one diagram. This is not a serious limitation; the first two factors alone can be expected to approximate these relationships closely, for they account for 74 percent of

the total variation and include the heaviest loadings on the three major constituent clusters—bryozoans, the coral cluster, and echinoderms-sponges (Figure 17). The ordination diagram (Figure 19) shows generally the same relationships that the dendrograms do; the flank samples differ distinctly from those in the core region, and the core samples form two broadly overlapping subgroups. Further, it suggests that samples 6 and 17 are close to the flank cluster, whereas 18 is nearer one of the core subclusters. The facies assignments shown in Figure 19 are used in the following analysis of cheilostome species abundances.

The nature of the biofacies suggested in Figure 19 is brought out in Table 6, which combines the R-mode and Q-mode results. The greatest contrast in composition is between Biofacies B, in general occupying the flanks of Mound II-N₁, and Biofacies A₁ occurring in the core (Figure 12). Biofacies A₂ is transitional between the two but seemingly has more in common with A₁.

Biofacies A₁ and A₂ are characterized by predominance of the coral group (octocorals, scleractinians, serpulids, and the category "other constituents") over bryozoans (cyclostomes and cheilostomes). Octocorals are the single most abundant constituent of these related facies, and bryozoans are second in abundance in both. Biofacies A₁ shows the nearest approach to equal proportions of the constituents, and scleractinians (making up more than 3 percent of the coarse-fraction biota), serpulids, echinoderms, sponges, and the category "other constituents" have their maxima here. Biofacies A₂ shows less than 3 percent scleractinians and intermediate proportions of bryozoans, serpulids, and

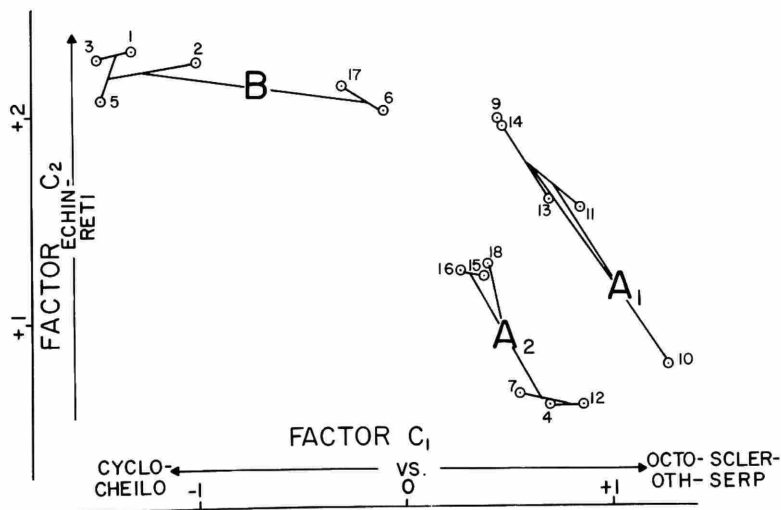


FIGURE 19.—Ordination diagram: distribution of samples from Mound II-N₁ with respect to first two principal components (factors C₁ and C₂, Table 5) of major biotic constituents. Coordinates of samples were obtained by pre-multiplying by the eigenvectors the matrix of arcsine-square-root-transformed abundances. Lines connecting samples are a compromise between the two dendrograms obtained by cluster analysis and shown in Figure 18.

TABLE 6.—*Distribution of biotic constituents (as mean weight percentages for samples clustered as in Figures 18 and 19) in biofacies of Mound II-N₁. Constituents clustered as in Figure 17.*

Q-mode biofacies clusters	R-mode clusters of CF constituents							
	CYCLO	CHEILO	OCTO	SCLER	OTH	SERP	ECHIN	RETI
B { (1-3,5) (6, 17)	66.0	23.1	1.6	0.4	1.0	0.6	7.2	0.5
	41.2	12.6	23.6	1.0	1.4	1.4	18.2	0.8
A ₂ { (4, 7, 12) (15, 16, 18)	19.4	5.5	64.7	0.9	2.2	1.6	5.6	0.3
	28.0	9.5	47.1	1.3	2.1	2.8	8.8	0.4
A ₁ { (9) (10) (11, 13, 14)	24.1	14.7	31.5	9.6	2.9	4.9	10.8	1.4
	9.2	3.3	59.5	15.5	4.3	1.7	5.9	0.6
	20.7	5.8	44.5	3.5	3.2	3.2	18.3	0.7

"other constituents." Echinoderms and calcareous sponges tend to be at their minima.

Biofacies B is characterized by cheilostomes and cyclostomes which together make up more than 50 percent of the coarse-fraction biota. Constituents of the coral group have their minima in this facies, though octocorals are a significant constituent of some samples. Echinoderms and calcareous sponges show a second abundance peak in this facies.

The distribution of these biofacies in Mound II-N₁ (Figure 12) is asymmetrical and slightly more complex than the mound structure alone indicates. Biofacies A₁ is in the core, but slightly displaced eastward or toward the steeper flank relative to the lithology and the attitude of the bedding. Biofacies B occupies the principal parts of the flanks, proportionately more of the long, gentle western flank than the shorter, steeper eastern one. Biofacies A₂ is present on both sides of the mound between A₁ and B and also occurs as outliers within B on both flanks. The differences between biofacies are more distinct on the long western flank than on the short eastern one.

COMPARISON WITH OTHER MOUNDS

The general characteristics of the biofacies of Mound II-N₁ at Limhamn were compared with visual estimates of biotic constituents of samples collected from other mounds in the Limhamn Quarry and in Denmark. The suggested distributions of biofacies in these mounds (shown in Figure 11) are briefly described below.

Mound M₁, at the top of the Maestrichtian exposed in the south end of the sea cliff just below Højerup Church on Stevns Klint, Denmark, is a small structure

apparently lacking a distinct core or transitional facies. Bryozoans appear to be slightly more common in the center of the mound than on its flanks, though nowhere are they as abundant as in the Danian. Octocorals and scleractinians were not observed.

Mound E₁, in the lower Danian exposed in the northeast face of the Boesdal Quarry just behind the sea cliff on Stevns Klint, Denmark, is comparable in size, structure, and lithology to Mound II-N₁, but the core of Mound E₁ appears to be comparable to the transitional facies (Biofacies A₂) of the Limhamn mound in its proportions of biotic constituents. Bryozoans are in general more abundant on both flanks and in the core than they are in Mound II-N₁. Octocorals are common, though not dominant, in samples from the mound center. Also in contrast to the Limhamn mound, cheilostomes are more abundant than cyclostomes in most samples.

Mound II-N₃, in the middle Danian exposed in the north wall of Limhamn Quarry above and to the west of Mound II-N₁, is also comparable to that Mound in size, structure, and lithology and in distribution of biofacies. The greatest difference is the more extensive core facies (Biofacies A₁), which includes numerous masses of colonial scleractinians in, or nearly in, growth position. As in Mounds II-N₁ and E₁, however, the core and transitional limestones grade upward into flank-type limestones. The whole upper part of Mound II-N₃ appears to have been truncated before the deposition of suprajacent mound sediments.

Mound W₁, at about the middle of the Danian section exposed in the west end of the quarry at Fakse, Denmark, differs from all of the mounds described above in having the core facies (Biofacies A₁) dominant so that it appears to have overgrown not only its

own flanks but also those of adjacent mounds. As a result, the boundaries of the mound are indefinite. Also, the core includes abundant colonial scleractinians nearly in growth position, and octocorals are abundant only in the much less extensive transitional biofacies. A richly diversified biota associated with the corals has been described at Fakse (summarized by Asgaard 1968:104), and it includes bryozoans, mollusks, brachiopods, serpulids, echinoderms, and burrows of sponges, crustaceans, and possibly algae (Asgaard 1968:117). The flank limestones are richer in bryozoans than those of mounds described above.

INFERENCES ABOUT MOUND FORMATION

The biofacies study of Mound II-N₁ at Limhamn and comparison with other mounds suggest some general relationships in the formation of these structures:

(1) Differences in content of non-carbonate detritus and in character of bedding are distributed in conformity with mound structure, whereas differences in porosity are less regularly distributed (correlated only with differences in grain size). The structure of the mounds therefore appears to be a primary depositional feature, rather than a product of post-depositional alteration. If this is so, the present structure of the mounds indicates their depositional configuration.

(2) Although most biotic constituents of the mounds occur in all of the samples, differences in their abundances are distributed in conformity with mound structure, whereas differences in grain size are less regularly distributed. Therefore, as inferred by Hennig (1899:38, 39), the biotic constituents for the most part probably accumulated approximately where they grew, rather than having been mechanically sorted. If this is so, the biofacies of the mounds represent different paleoenvironments.

(3) The proportions of fine-grained non-carbonate detritus and fine-grained carbonate sediment vary independently of each other within a mound. The non-carbonate detritus must have been transported into the area of mound deposition, whereas the calcilutite could have been produced near the site of its accumulation. If the difference in distribution indicates a difference in source, Hennig's inference (1899:38, 39) that the calcilutite represents detritus from the activity of predation on the carbonate-producing benthos may be correct.

(4) If the inferences in both (1) and (2) are correct, then the paleoenvironmental differences between biofacies are correlated with depositional topography. In general, the mound core, having abundant octocorals and subsidiary colonial scleractinians and bryozoans, probably stood higher than the flanks, dominated by bryozoans but in places including patches of octocorals.

(5) Because the cores and flanks of each mound probably originated at about the same topographic level, the growth of some or all of the core- or transitional-facies constituents was probably initially responsible for any topographic differences between biofacies, rather than vice versa. If this is so, some or all of the core- or transitional-facies constituents are the essential element in mound formation.

(6) Because both cheilostome and cyclostome Bryozoa have minimum abundances in the core facies, and because they are abundant in non-mound Danian limestones, Bryozoa were probably not the initiators of mounds in the Danian, although they may have had this role in the smaller Maestrichtian mounds. If this is so, octocorals or colonial scleractinians or combinations of these two constituents are the most likely prerequisite for mound formation, and, as the proportion of scleractinians increases, the extent of the core facies and the ultimate size of the whole mound also increase.

(7) Because the spacing of mounds, both laterally and in stratigraphic sequence, is not random, and because octocorals may occur in moderate abundance on the mound flanks without appreciably altering mound structure, factors other than biotic appear to have influenced mound formation by determining the sites and rates of growth of the cores.

(8) Because calcilutite is dominant throughout all the mounds studied, it seems unlikely that the sites of deposition of core and flank sediments differed significantly in resistance to erosion. Intermittent, localized erosion, however, seems to have removed both core and flank sediments from some mounds while adjacent, coeval mounds were the sites of virtually continuous deposition.

(9) If the inferences in (5) to (7) are correct, abundances of cyclostome and cheilostome bryozoans in the Danian mounds in general vary because of factors promoting or inhibiting growth of octocorals or colonial scleractinians or combinations of the two groups. This inference appears to be substantiated by the strong negative correlation in the abundances of

the two bryozoan groups with those of the two coral groups.

(10) The distinct positive correlation between the abundances of serpulids and the category "other constituents" and those of the coral groups suggests a principally epizoid relationship with corals providing the substrate; the smaller size of the bryozoans may have made them a less attractive substrate for epizoids. The less significant positive correlation between the abundances of the corals and those of echinoderms and calcareous sponges suggests that the latter constituents represent a third element of the mound biota, less strongly facies-controlled than the other two.

If all the preceding inferences are correct, the variations in abundances of species of each biotic constituent of the Danian mounds could be expected to reflect differences in adaptations to paleoenvironments represented by the biofacies. The relationship is investigated for cheilostome Bryozoa in the following section (pages 37–47).

These inferences add little to the already extensive interpretations of the physical conditions surrounding the formation of Danian mounds, summarized by Berthelsen (1962:235–245) and Asgaard (1968:116–118). The range of interpretations is indicated by previous usage of the term "reef" for two distinct concepts applied to the Danian mounds. On the one hand, the mounds have been considered to have formed as shallow-water, wave-resistant structures containing crusts possibly produced by calcareous algae and including large amounts of skeletal detritus "detached by . . . breakers and rolled by waves and tide-water" (Hadding 1941:120, 122). On the other hand, the mounds have been thought to represent accumulations "at a depth of more than 50 m and probably more than 100 m" and to have their closest Recent analogues "in coral beds at a depth of 100–300 m" (Hadding 1941:124, 126).

Evidence indicating a shallow-water origin for the Danian mounds has been chiefly from mollusks, brachiopods, some octocorals, and "penetrations of thalphytes . . . probably algal" (Asgard 1968:117). These interpretations, for the most part, place the upper limit for the depths at which mounds were formed at 40 to 50 m, rather than the near-surface environments suggested by the first of the concepts mentioned above.

Evidence indicating a deeper-water origin has been chiefly from scleractinian corals and some octocorals. The Danian scleractinians include both solitary and

colonial forms, all ahermatypic (Floris 1967). Teichert (1958:1087) considered the Danian colonial coral association to be closely analogous with the modern Norwegian deep-water coral banks, and therefore thought that the Danian mounds accumulated at depths greater than 100 m. Floris (1967:151), making the same comparison, concluded that an average depth of 75 m was likely.

Both shallow- and deep-water interpretations have been made for the extensive, coral-dominated mounds at Fakse, in which Floris (1967:151) suggested that depositional relief may have approached 50 m where submarine talus of rounded coral limestone fragments is present. It is unlikely, however, that relief approached this magnitude among the middle Danian mounds at Limhamn or the lower Danian ones on Stevns Klint.

Squires (1964), in consideration of the structure and faunal composition of Recent and fossil deep-water coral mounds, recognized three developmental stages (single colony, thicket, and coppice) leading to the formation of coral banks. Of the Danian mounds, only the largest of those at Fakse, in the middle Danian, probably formed by continued accretion of debris from a living cap of coral together with impaction of mud and thus represent the full bank stage (Squires 1964:905). The largest Fakse mounds thus might be comparable to Recent banks in Norway (Dons 1944, Burdon-Jones and Tambs-Lyche 1960) as suggested by Teichert (1958). The more typical mounds, such as those in the middle Danian at Limhamn, probably represent less-advanced, smaller stages of bank development, that is, thickets or coppices (Squires 1964:905), and thus could be compared with Recent coral mounds on the edge of the European Atlantic shelf from the British Isles to Portugal (LeDanois 1948:161–191). The small amount of recognizable debris of colonial scleractinians in the Limhamn mounds suggests that these structures had not advanced beyond the thicket stage, but the great concentrations of broken calcareous axes of octocorals indicates that an appreciable amount of time was involved in the accumulation of the mound cores. Perhaps the octocorals contributed to mound formation through growth analogous to that of the colonial scleractinians, and in the early Danian mounds on Stevns Klint octocorals may even have been able to produce thickets or coppices without a significant scleractinian component.

If the cores of the typical Danian mounds represent octocoral-scleractinian thickets or coppices, then

some process periodically terminating coral growth must have been responsible for the upward gradation of the core limestone into bedded limestone indistinguishable from that on the mound flanks. Similar termination of thickets in the Miocene and Pliocene in New Zealand was reported by Squires (1964:913-914) and was inferred by him to have been produced by renewed or increased sedimentation which drowned the corals. The sediments enclosing the New Zealand fossil thickets and those impacted in them and in known modern deep-water coral mounds are chiefly terrigenous muds and sands (Squires 1964:909), in contrast to the overwhelmingly carbonate composition of all of the fine-grained sediment associated with Danian mounds. If the calcilutite in the Danian mounds was produced largely in situ through fragmentation of skeletons of benthos by the action of other organisms, as suggested above, this material may have been winnowed from the coarser debris and periodically redeposited over the cores, or it might simply have been produced in greater quantity in the core region. The local unconformities suggest periodic movement of sediment, whereas the distribution of non-carbonate sediment suggests more rapid accumulation of carbonate mud in the cores. Thus both processes may have been involved in the drowning of coral growth.

The Danian mounds contrast with all known modern deep-water coral mounds in the abundance and diversity of their associated bryozoan faunas. From the Norwegian and Celtic regions 55 species of cheilostomes have been reported by LeDanois (1948), Burdon-Jones and Tambs-Lyche (1960), and Ryland (1963), though the number of species within a given area is much smaller (Table 7). The greater number of these species is restricted, according to ranges given by the authors cited, to water more than 50 m deep. With regard to colony form, the Danian and Recent cheilostomes associated with coral mounds are similar, except that the Recent fauna includes a number of species having specialized forms apparently not represented in the Danian, and the Danian includes a proportionately higher number of eschariform species. With respect to zooid morphotype, the two faunas are very different, with a considerable increase in the Recent fauna of species having more complex structure; this change is presumably a continuation of the general evolutionary trend in zooid structure discussed earlier. This change could account for the fact that the two faunas have no genera in common, even if they represent the same environment.

TABLE 7.—Numbers of species of cheilostomes associated with coral mounds in Danian and Recent North Atlantic. Data on Recent faunas are from LeDanois (1948), Burdon-Jones and Tambs-Lyche (1960), and Ryland (1963).

	Danian Lim- hamn II-N ₁	Recent		Total
		Nor- way	European Atlantic	
Total associated with coral mounds:	51+	32	39	55
Restricted to water >50 m deep	11	20	26
Restricted to water <50 m deep	0	3	3
Predominant colony form:				
Membraniporiform	31	22	23	35
Eschariform	15	1	1	2
Vinculariiform	5	4	6	8
Cellariiform, reteporiform, or flustriform	0	5	9	10
Zooid morphotype:				
I	4	3	3	3
II	9	4	3	5
III	12	0	0	0
IV	15	5	4	6
V+VI	11	20	29	41

The Danian paleoenvironment prevalent in southern Scandinavia thus appears generally to have been highly favorable to cheilostome diversity and density. The development of a coral facies within this environment then appears to have provided a secondary increase in cheilostome diversity rather than the primary impetus for it.

Biofacies Distribution of Danian Cheilostomes

DISTRIBUTION IN MOUND II-N₁

If the distribution of cheilostome species in the Danian mounds was controlled by the same factors that produced the biofacies, then the samples from Mound II-N₁ should cluster on the basis of their cheilostome abundances in conformity with the Q-mode dendrogram based on the major biotic constituents (Figure 18). A slight modification of the analytical procedure was required for the cheilostome abundances. The small numbers of minute fragments

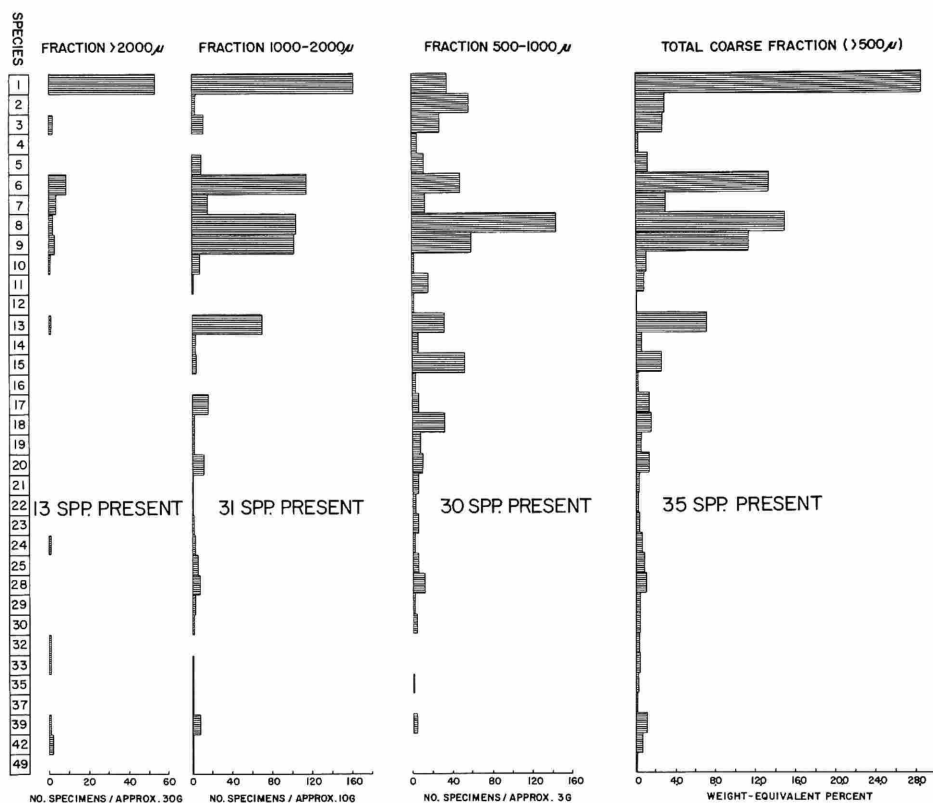


FIGURE 20.—Abundances of cheilostome species and numbers of species present in three size grades and total coarse fraction of Sample 17, Mound II-N₁. Size grades differ from each other and from the total proportions. (Species numbered as in Table 1.)

TABLE 8.—Number of cheilostome specimens counted in coarse-fraction size grades of samples from Mound II-N₁ (total, 18,705). Counts of identifiable specimens were used to calculate weight-equivalent percentages of species listed in Table 1 (id, identifiable; un, unidentifiable).

Size grade		Sample																	
		1	2	3	4	5	6	7	9	10	11	12	13	14	15	16	17	18	
>2000μ	{ id	2	9	23	10	12	20	38	11	10	4	12	5	40	58	32	81	23	
	{ un	0	3	0	0	0	1	6	2	0	0	0	2	8	1	11	7	1	
1000-2000μ	{ id	1277	598	223	110	615	114	353	201	197	313	22	96	291	405	419	678	410	
	{ un	82	42	27	12	20	47	29	50	58	57	11	38	28	24	9	60	50	
500-1000μ	{ id	1127	639	699	261	762	228	286	771	500	516	194	184	318	662	515	599	342	
	{ un	112	48	191	144	24	93	124	285	334	237	111	165	116	63	319	191	147	
CF (>500μ)	{ id	2406	1246	945	381	1389	362	677	983	707	833	228	285	649	1125	966	1358	775	
	{ un	194	93	218	156	44	141	159	337	392	294	122	205	152	88	339	258	198	

recovered for some of the 51 operational species identified from Mound II-N₁ (Table 1) made it impractical to obtain direct weight percentages. Therefore, the particles within each of the coarse-fraction size grades (containing virtually all of the identifiable cheilostomes, as shown in Figure 15) were assumed to be of equal weight, and weight-equivalent percentages were calculated from the particle counts (Table 8). The percentages of species in each of the three size grades are significantly different (Figure 20); as a result the weight-equivalent percentages for all three size grades were combined proportionally. All cluster analyses discussed below are thus based upon weight-equivalent percentages within the entire coarse fraction of each sample.

Some species (numbered 38–51 in Table 1) were found to occur in so few samples and in such small quantities that they were omitted from the comparison. Thus, only the 37 species having at least one abundance of 1.5 percent or greater or occurring in at least six samples were included in the analyses.

In Figure 21 is illustrated the general similarity of the Q-mode cluster analysis based on cheilostome abundances to that based on the major biotic constituents (from Figure 18). The cheilostome composition of the core facies (A₁) is distinct from that of the flank facies (B), and that of the transitional facies (A₂) is more like that of the core. The distributions of the cheilostome species conform even more closely to the structure of the mound than do the major biotic constituents. The samples from each flank (1–3, 5, 6 on the western flank; 16–18 on the eastern one) form distinct subclusters within the flank cluster. The samples from the structural center of the mound (9–12) form a distinct subcluster within the core-transitional cluster. The high degree of conformity of cheilostome species distributions to mound structure suggests an even greater sensitivity to topography-related environmental differences than that displayed by the biota as a whole.

The abundances of individual cheilostome species vary markedly across the mound (Figure 22), but the

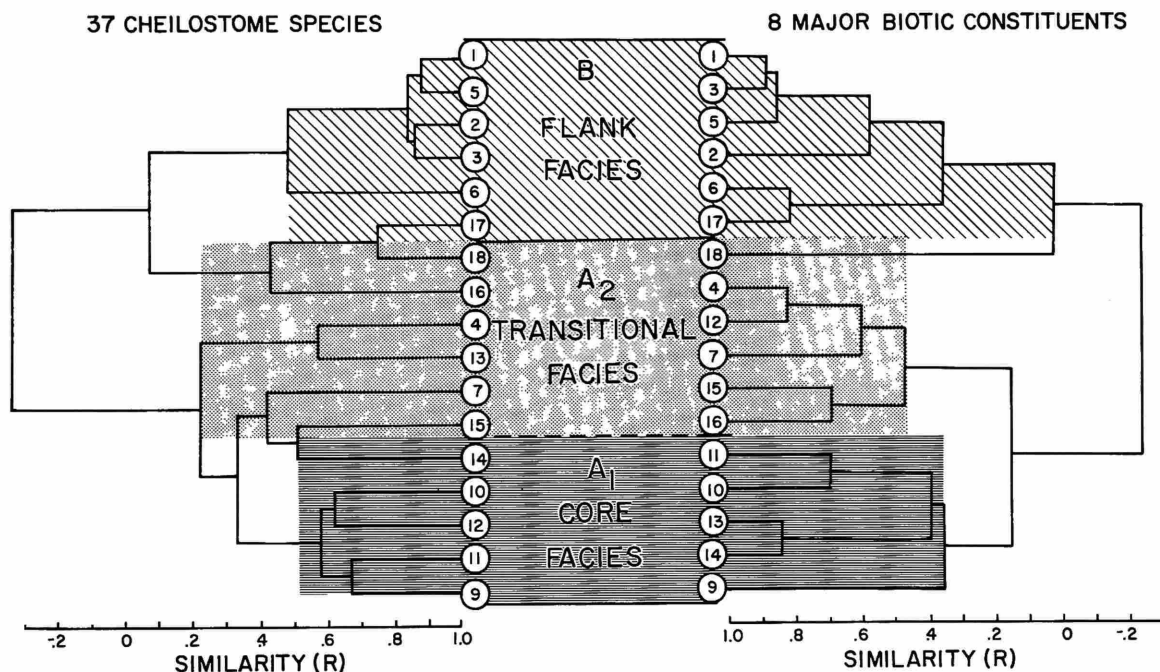


FIGURE 21.—Q-mode dendrograms of relationships among 17 samples from Mound II-N₁ showing general distribution of 37 cheilostome species (*left*) in biofacies based on eight major biotic constituents (*right*). Each dendrogram was formed by weighted-pair-group-method clustering of correlation coefficients calculated from arcsine-square-root-transformed weight percentages, standardized by rows. Biofacies assignments are as shown in Figure 19. Q-mode dendrogram of cheilostome species based upon distance function (not shown) is almost identical to that based on correlation coefficient.

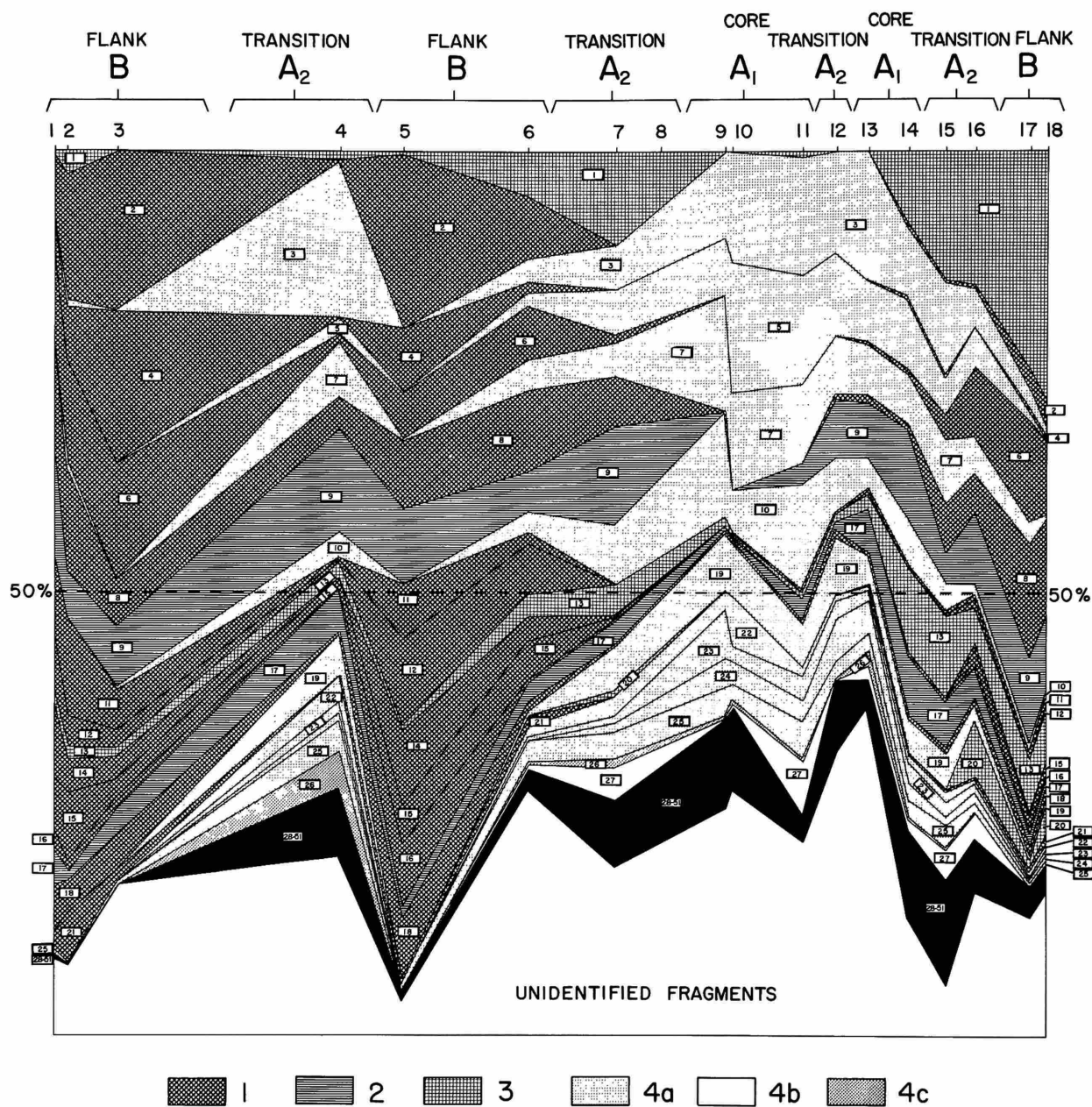


FIGURE 22.—Variation in abundances (as weight-equivalent percentages) of species of cheilostome bryozoans in coarse fraction of samples from biofacies in Mound II-N₁. Species are numbered as in Table 1 in order of maximum abundance in any single sample. Biofacies as in Figure 12. Species 28 to 51, having abundances too small to diagram, have been lumped in the portion of the diagram shaded black. Species groups are in accordance with the R-mode dendrogram of Figure 25 and explained in the text (pages 41–44). Unidentified fragments are represented by the unshaded portion at the bottom of the diagram.

differences in species composition of flank, core, and transitional assemblages are not apparent from the abundances alone. It is not clear, for example, whether there are three distinct assemblages, two distinct assemblages with the third an intermixture, or a more or less continuous gradation from first to third. No species is restricted to any single biofacies, and only two (20 and 31) are absent from even one biofacies (A_1). On the other hand, four species (13, 17, 18, and 25) occur in every sample. The relationships among assemblages should be reflected in both species diversity and density.

The total number of species present in each sample varies from 18 to 38 without apparent pattern relative to the structure of the mound (Table 1). Number of species, however, is probably not an effective measure of species diversity, because it may fluctuate with sample size, and rare species may be present or absent practically at random. The information function

$$H(S) = -\sum_{i=1}^S p_i \log_e p_i,$$

where S is the number of species and p_i is the proportion of the i th species, is used in ecology as a more effective measure of diversity (Buzas and Gibson 1969, and references therein). The information function for the 17 samples from Mound II-N₁ (Figure 23) shows pronounced diversity highs in the transitional facies

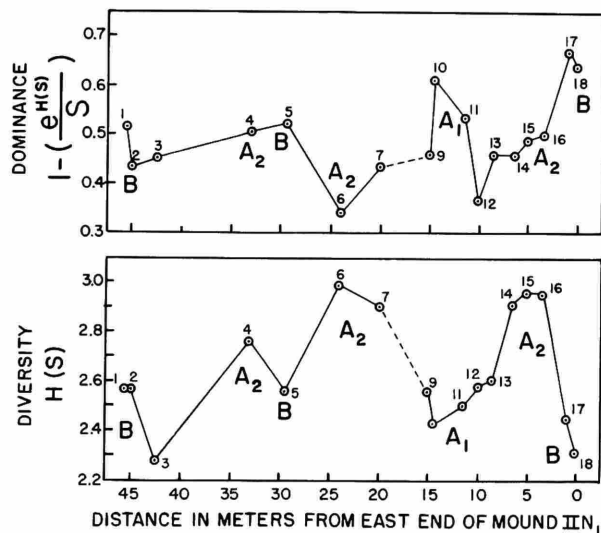


FIGURE 23.—Variation in species diversity (below) and dominance (above) of cheilostome assemblages in the 17 samples from Mound II-N₁. A_1 , A_2 , and B indicate approximate positions of biofacies based on eight major biotic constituents (Figure 19). Numbers 1–18 mark sample locations along horizontal axis of mound exposure.

(A_2) separating a diversity low in the core (A_1) from lows on the flanks (B). Together with the Q-mode dendrogram based on the cheilostome species, the diversity pattern suggests that Biofacies A_2 contains a mixture of two distinctive assemblages which dominate Biofacies A_1 and B. This relationship appears to be borne out by the variation in species dominance across the mound as measured by the function (Buzas and Gibson 1969)

$$1 - \left(\frac{e^{H(S)}}{S} \right),$$

where e is the base of natural logarithms. The low diversities of the core and flank assemblages correspond to high dominance, and the transitional assemblage to low dominance, although the negative correlation is not perfect (Figure 23).

If the cheilostome assemblage of Biofacies A_2 represents an extension of that of Biofacies A_1 by admixture of species of Biofacies B, as the Q-mode dendrogram (Figure 21) and the diversity and dominance profiles (Figure 23) suggest, then the increase in diversity from Biofacies A_1 to Biofacies A_2 should be accompanied by a logarithmic increase in density (Odum et al. 1960). Most of the samples in Biofacies A_1 and A_2 appear to conform to the expected relationship (Figure 24). In contrast, the assemblage in Biofacies B has a much higher density than would be expected from its low diversity and lies distinctly off the trend of the A_1 and A_2 samples; Biofacies B thus represents a more distinctive group of samples.

To identify which species of the 37 characterize each assemblage, the abundance data were submitted to R-mode cluster analysis (Figure 25). Slightly differing results were obtained with unweighted and weighted pair-group clustering (dendrograms on left and right

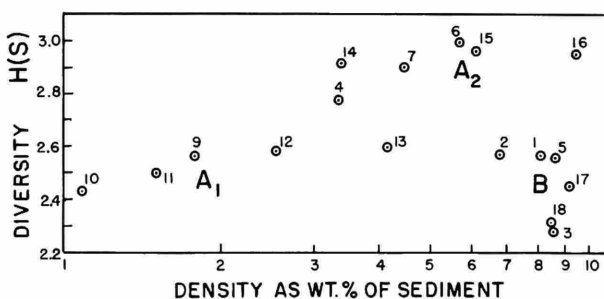


FIGURE 24.—Relation between diversity and density of cheilostome assemblages of the 17 samples from Mound II-N₁. Diversity is shown as in Figure 23. Density is dry-weight percentage of cheilostomes in whole sediment sample.

CORRELATION COEFFICIENT

- > 0.67
- 0.34 to 0.67
- ◐ 0.01 to 0.33
- -0.33 to 0
- ◑ -0.67 to -0.34
- < -0.67

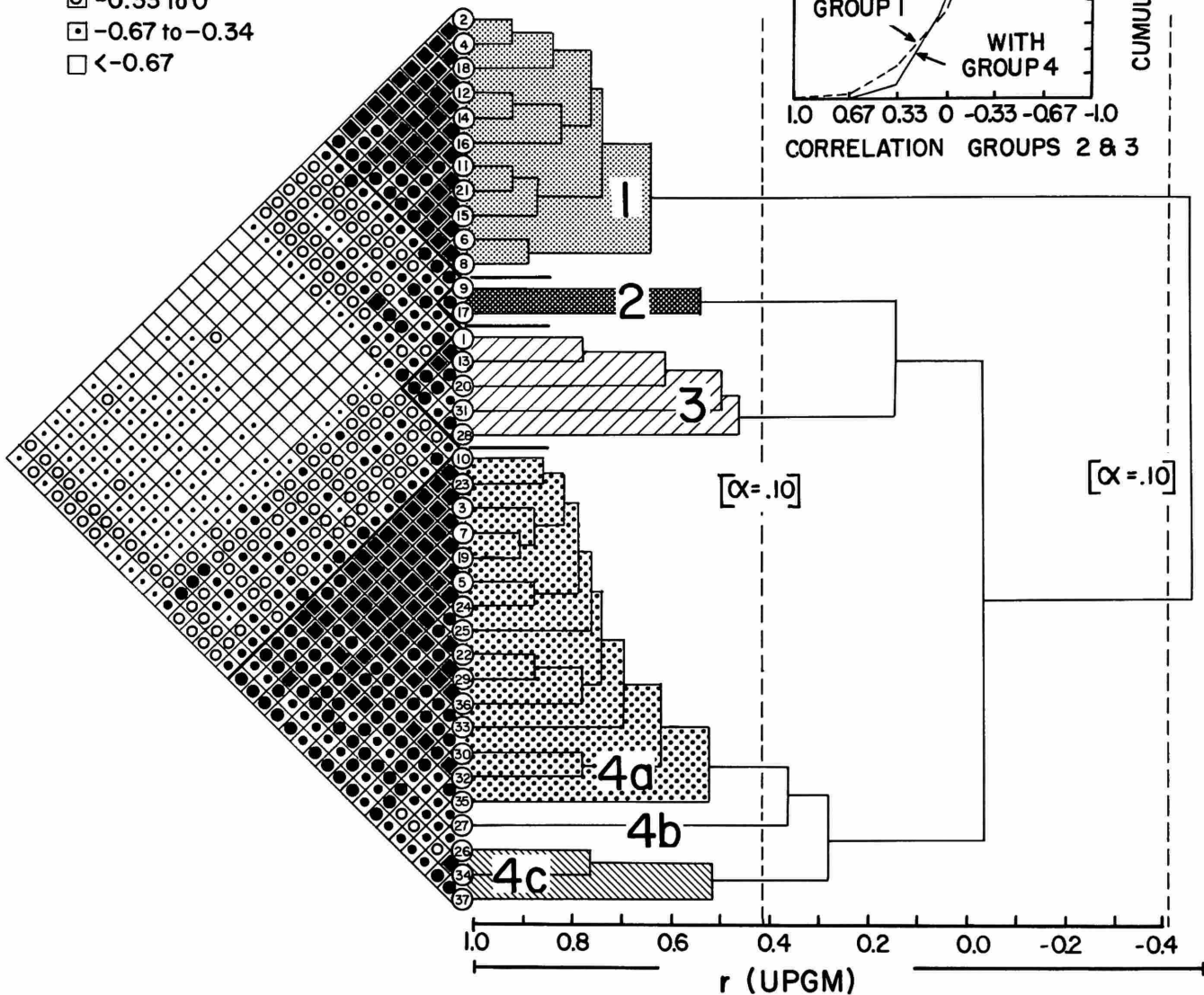
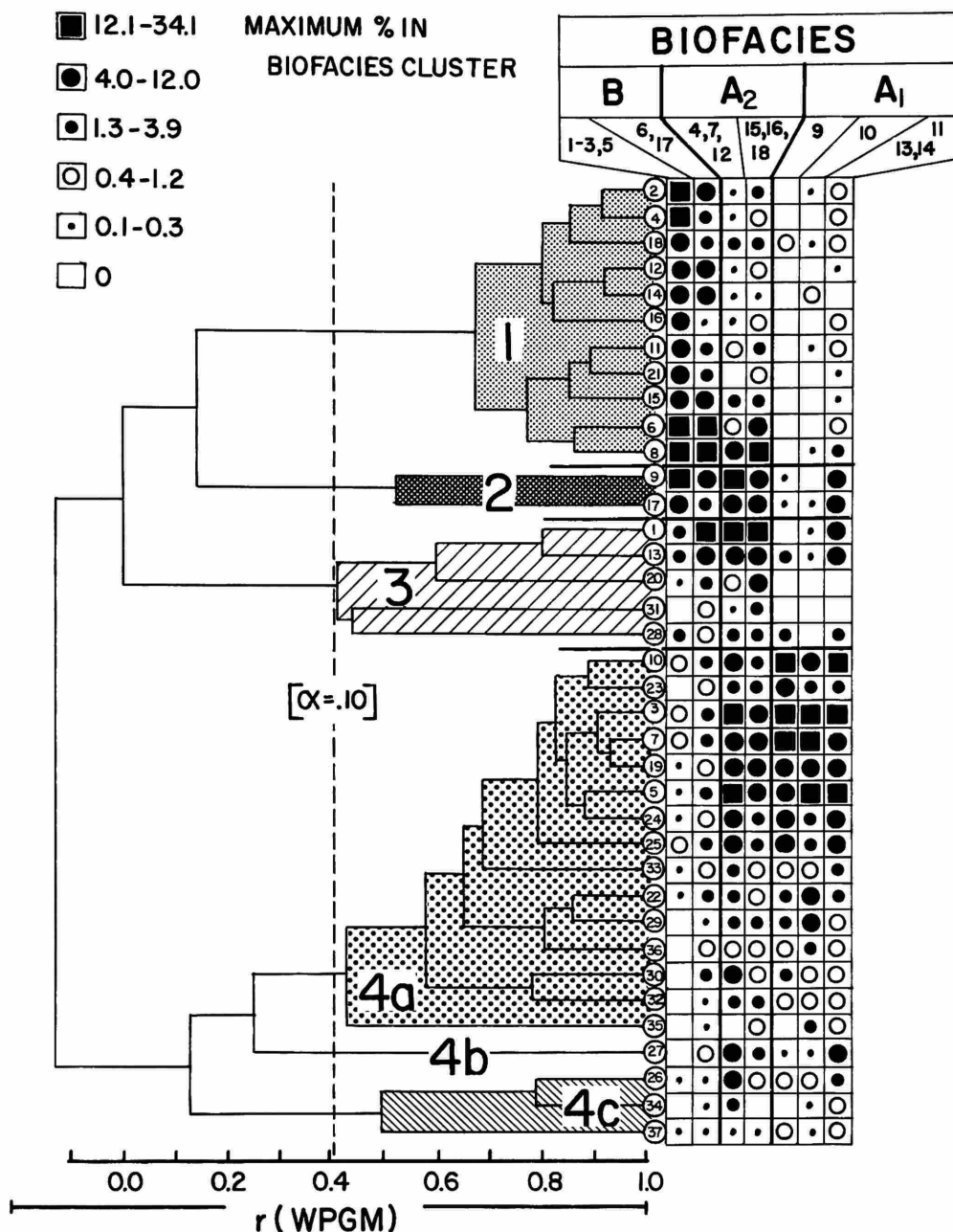


FIGURE 25.—R-mode relationships among 37 cheilostome species in Mound II-N₁ and their distribution in biofacies. Clustering is based upon correlation coefficients calculated from arcsine-square-root-transformed weight-equivalent percentages for each species in the coarse fractions of the 17 samples. Unidentified fragments of cheilostomes were excluded from calculation. Species are numbered as in Table 1.

Left, Dendrogram based on unweighted-pair-group-method (UPGM) clustering (Sokal and Sneath 1963:309) and trellis diagram (shaded similarity matrix; Sokal and Sneath 1963:176) of individual correlations between all pairs of species. Clustering method emphasizes individual correlations at all levels of clustering; thus groups 2 and 3 cluster with group 4, despite several high correlations with group 1 (*inset, at top*). Homogeneity of groups 1 and 4a contrasts with heterogeneity of groups 2, 3, 4b, and 4c, each of which shows conspicuous overlaps with two or more other groups. Correlation coefficients in trellis diagram have been grouped in six equal classes shaded so that density indicates closeness of correlation.



Right, Dendrogram based on weighted-pair-group-method (WPGM) of clustering (Sokal and Sneath, 1963:309) and biofacies distribution of species in each group. Clustering method emphasizes correlations among groups regardless of how many species compose each group; thus groups 1 and 2 have equal weight at the level at which they join, even though they include very different numbers of species. The WPGM dendrogram becomes less like that clustered by UPGM at lower levels of correlation. However, the only significant difference between the two is that 2 and 3 join 1 rather than 4. The membership of each of the six clusters is the same in both dendrograms, and, with the exception of species 33, the species are arranged in identical order. The biofacies distribution of each species is indicated by its maximum weight-equivalent percentage within each of the Q-mode sample clusters based on the major biotic constituents (Figures 18, 19). Within each biofacies, the clusters are arranged from west to east. The abundances are grouped in six classes increasing geometrically and shaded in approximate proportion to density. The biofacies distributions of groups 2 and 3 are slightly more like that of 1 than that of 4.

of Figure 25), but both methods indicate that more than two-thirds (26) of the species belong to one or the other of two contrasting clusters: group 1 with 11 species and group 4a with 15. The correlations between pairs of species within each of these two clusters are high (trellis diagram, left side of Figure 25), and, in this sense, these clusters are homogeneous compared to the other four, each of which includes only five species or fewer.

The abundances of the two main clusters, 1 and 4a, in the biofacies based on major biotic constituents are markedly different (right side of Figure 25). Every species of group 1 has its maximum abundance in Biofacies B, whereas each one in group 4a is most abundant either in Biofacies A₁ (7 species), in Biofacies A₂ (2 species), or subequally in Biofacies A₁ and A₂ (6 species). Regardless of which of the three distributions a species in group 4a has, it is relatively more abundant in Biofacies A₁ than in Biofacies B. Therefore, group 1 appears to characterize the flanks and group 4a the core of the mound. It is noteworthy, however, that every one of the species in both groups occurs in all three biofacies; it is the abundance of species of groups 1 and 4a and not their presence or absence that conforms to the biofacies. The dominance of group 1 in Biofacies B and of group 4a in Biofacies A₁ then accounts for the low diversities and high dominances shown by samples from these parts of the mound (Figure 23).

The opposing abundance gradients of species groups 1 and 4a cross in the transitional areas (Biofacies A₂) between core and flanks. The intermediate abundances of both major clusters of species in Biofacies A₂ thus appear to explain the higher diversity and lower dominance of samples from this facies. Furthermore, the tendency for species of group 4a to maintain higher abundances in this facies than those of group 1 seems to account for its closer resemblance to Biofacies A₁ than to B (Figures 18, 19). The transitional facies is additionally characterized by species groups 2, 3, 4b, and 4c, some species of which are rare or even absent (species 20 and 31) in other facies. The diversity, dominance, and composition of the transitional assemblage thus seem to be an ecological edge effect, and the assemblage probably should be considered an ecotone (Odum 1959:278). If correct, this interpretation would further argue against appreciable post-mortem transportation of the cheilostome fauna.

MORPHOLOGIC BASIS OF DISTRIBUTION

The preceding analysis shows that Danian cheilostome species in Mound II-N₁ are distributed in general concordance with the biofacies that are based upon the major biotic constituents of the sediment, and it suggests that the morphologic differences among the cheilostomes could be expected to reflect differences in adaptation to two principal environments represented by the flank and core facies. Furthermore, because the distributional differences among these species are expressed by variation in abundance rather than by presence and absence, the underlying differences in adaptation to the two principal environments are probably gradational, with the transition facies between the core and the flanks calling for some combination of the adaptive characteristics of the other two.

The two major groups of cheilostome species having the most contrasting patterns of distribution (groups 1 and 4a in Figure 25) also show morphologic differences with respect to inferred colony forms and zooid morphotypes (Figure 26). All the 11 species clustered in group 1 may be inferred to have possessed rigidly erect colonies (7 species eschariform, 4 species vinculariiform), and they include all the inferred vinculariiform species identified from Mound II-N₁ except one rare species omitted from the R-mode analysis (species 50 in Table 1, found in only one sample; as this occur-

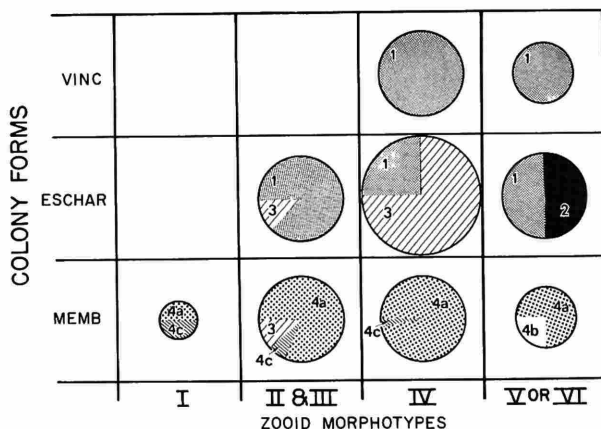


FIGURE 26.—Inferred colony forms (see Table 1) and zooid morphotypes of R-mode groups of cheilostome species in Mound II-N₁. Species belonging to each cluster are identified by number in Figure 25, and their morphology is indicated in Table 1. Circles are approximately proportional to summed maximum abundances of species having each combination of zooid morphotype and colony form, and are divided in approximate proportion to the groups represented. Largest circle, about 80%; next to largest, about 40%; next to smallest, about 20%; smallest, about 10%.

rence is in Biofacies B, this species presumably would sort with group 1). This group of species, as indicated above, dominates the flanks of the mound, where the cheilostome assemblage shows an unexpectedly high density relative to its diversity.

All the 15 species clustered in group 4a appear to have had closely encrusting (membraniporiform) colonies. As indicated above, these species have maximum abundances in the core or transitional facies, and the cheilostome assemblages in these biofacies show the expected direct logarithmic relationship between density and diversity.

The 11 species belonging to the other four groups (2, 3, 4b, and 4c), which characteristically show high abundances in the transitional facies, appear to have had encrusting or eschariform, but not vinculariiform, colonies. With respect to their potential density relative to the substrate, these species may be considered intermediate in adaptation between groups 1 and 4a.

Five species (listed in Table 9) were interpreted to have unstable colony form, including both erect and encrusting phases. Among these species, there is a tendency for the encrusting phase to be replaced by the erect habit from the core to the flanks of the mound, even though the ratio between the two forms differs from one species to another. The same tendency is apparent in the genus *Floridina* (Table 10), which has a vinculariiform species dominating on the flanks, a membraniporiform species dominating in the core, and intermediate proportions of membraniporiform and eschariform species in the transitional facies.

To test the apparent correlation between biofacies distribution and inferred colony form, the abundance data were regrouped from species to colony forms (upper part of Figure 27). These three categories were then substituted for cheilostomes in the data array on

TABLE 10.—Changes in abundance proportions in biofacies of Mound II-N₁ of three species of *Floridina* having different inferred colony forms. Species are numbered as in Table 1; samples are grouped as in Figures 18 and 19.

Species group	Species	Colony form	Biofacies		
			B	A ₂	A ₁
1	2	VINC	89	9	1
3	20	ESCHAR	1	24	0
4a	7	MEMB	10	67	99

which R-mode cluster and principal-component analyses were made. The result (Figure 28) is similar to the original dendrogram, with the erect groups (vinculariiform and eschariform) clustering at a high level and occupying the cheilostome position in the bryozoan cluster of the original dendrogram. The encrusting group (membraniporiform), on the other hand, shifted to a new position far removed from the other cheilostomes, into the coral cluster. This pattern of clustering confirms that the major difference in biofacies is expressed morphologically in colony form.

If the adaptation expressed in colony form is based upon the structure of the zooids—the hypothesis proposed in the theoretical consideration of cheilostome structure above—then the abundance data regrouped by inferred zooid morphotypes (lower part of Figure 27) should also correlate with the biofacies. The distribution patterns in Figure 27 suggest that this correlation is much less conspicuous than that between colony form and biofacies, but the morphotypes cluster with the major biotic constituents (Figure 29) in much the same way that the colony forms do. Morphotypes iv–vi cluster at a high level and occupy the cheilostome position in the bryozoan cluster of the original dendrogram, as do the erect colony forms shown in Figure 28. Morphotype iii, like the encrusting colony form, joins the coral cluster in a position far removed from morphotypes iv–vi. The remaining morphotypes occupy somewhat looser positions, morphotype ii joining the bryozoan cluster at a low level of correlation and morphotype i joining the non-bryozoan groups at a still lower level. The patterns of changes in abundance of these two morphotypes, however, conform in general with that of morphotype iii (Figure 27), that is, with peaks in the core and transition facies.

The reason for the looseness of correlation of biofacies with zooid morphotypes, as compared to that with colony form, is suggested in Figure 26. With the

TABLE 9.—Changes in inferred colony forms (see Table 1) of unstable cheilostome species in biofacies of Mound II-N₁. Ratios are between average weight-equivalent percentages of inferred erect and encrusting phases. Species are numbered as in Table 1; samples are grouped as in Figures 18 and 19.

Species group	Unstable species	Colony forms	Biofacies		
			B	A ₂	A ₁
1	16	VINC/MEMB	100/0	75/25	33/67
	18	ESCHAR/MEMB	99/1	54/46	26/74
4a	25	ESCHAR/MEMB	32/69	0/100	0/100
	5	ESCHAR/MEMB	1/99	0/100	0/100
3	28	ESCHAR/MEMB	1/99	0/100	0/100

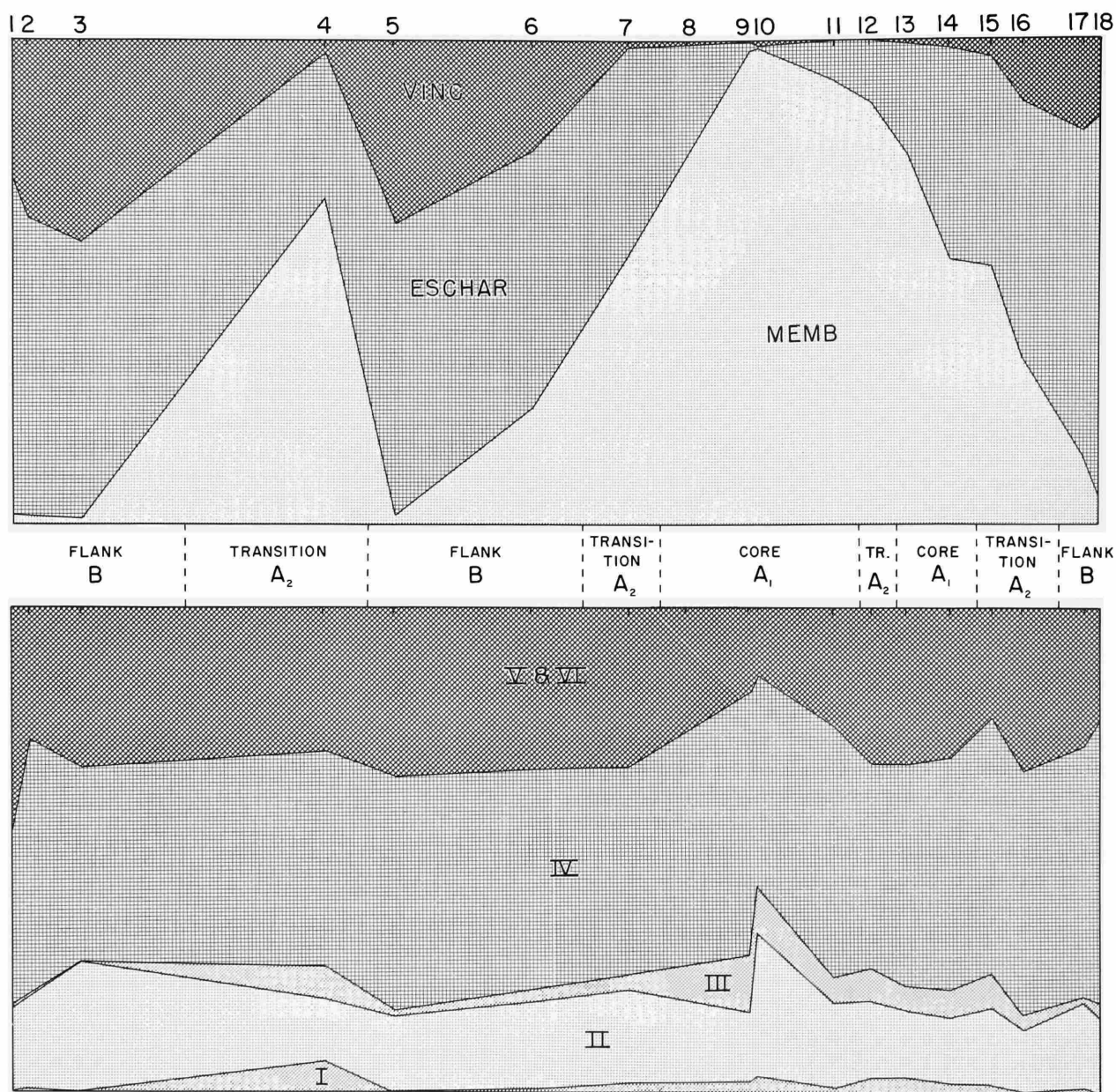


FIGURE 27.—Variation in abundances (as weight-equivalent percentages) of morphologic groups of cheilostome bryozoans in coarse fractions of samples from Mound II-N₁. Abundances shown in Figure 22 for 51 species have been redistributed by morphology, with unidentified cheilostomes omitted. Abundances in each diagram add up to 100 percent. In the distribution of inferred colony forms (*above*) abundances of stable species showing same form have been summed and abundances of unstable species have been divided according to proportions of forms exhibited and the portions added to the appropriate categories. In the distribution of inferred zooid morphotypes (*below*) abundances have been summed for species having the same morphotype.

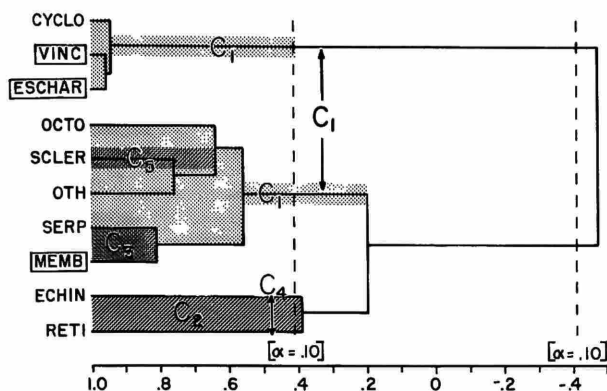


FIGURE 28.—R-mode dendrogram of relationships among major biotic constituents and inferred colony forms of cheilostomes in Mound II-N₁ and influence of principal components on clustering. Dendrogram is similar to that shown in Figure 17, except that cheilostome abundances have been proportionately divided among three colony forms as indicated in Figure 27. Abscissa is product-moment correlation coefficient.

exception of group 2, comprising two species, and 4b, consisting of just one, each of the R-mode groups of species includes a range of inferred zooid morphotypes. In the two major groups of species (1 and 4a) dominating contrasting biofacies, however, the ranges of morphotypes differ. A majority of group 1 species exhibit morphotypes iv–vi, whereas those of group 4a are distributed among all morphotypes with a concentration in groups ii–iv. Group 3 shows an intermediate range of morphotypes, and group 4c is like 4a but excludes morphotypes v–vi. These relations between the Danian species groups and the two sets of morphologic characteristics therefore suggest that the more complex zooid morphotypes are associated with the erect colony habit, whereas the encrusting form of growth may be virtually independent of morphotype.

Conclusions

The marked increase in numbers of cheilostome taxa from Early Cretaceous time to an apparent pause during Danian time reflects morphologic diversification at both colonial and zooidal levels of organization. The diversified and abundant fauna associated with Danian mounds in southern Scandinavia thus represents the culmination of primarily divergent evolutionary trends in cheilostome morphology. The abundances and biofaces distributions of cheilostomes in the Danian mounds are consistent with the hypothesis that, in general, the form of the colony depends upon the structure of the zooids. This is not to say that any

given colony form was restricted to any particular zooid morphotype, but rather that the attainment of a colony form permitting increased zooid densities was functionally more probable for some zooid morphotypes than for others. The correlation between such a functionally specified structural series and observed abundances, of course, establishes only an inferential relationship, and it is with this limitation that the following adaptive relationships are suggested:

(1) The ability of cheilostomes to assume an erect growth habit appears to represent an evolutionary adaptation that vastly increased the potential for zooid density relative to the amount of substrate occupied. The erect colony, compared to the encrusting one, should be much less dependent upon the availability of surfaces suitable for direct adherence, less affected by sedimentation, and exposed more fully to the surrounding water. The advantage of erect growth is suggested in the Danian cheilostome fauna by the overwhelming abundance of forms inferred to have had rigidly erect colonies, even though they account for fewer than half the species present. Furthermore, their negative correlation in abundance with larger constituents of the sediments, which might have provided the surfaces of adherence for encrusting colonies, is consistent with a reduced sensitivity to limitation of substrate.

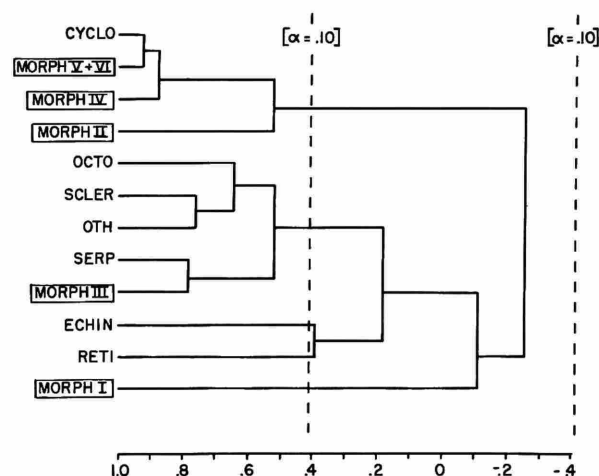


FIGURE 29.—R-mode dendrogram of relationships among major biotic constituents and inferred zooid morphotypes of cheilostomes in Mound II-N₁. Dendrogram is similar to those in Figures 17 and 28, except that cheilostome abundances have been proportionately divided among five categories of zooid morphotypes as indicated in Figure 27. Abscissa is product-moment correlation coefficient.

(2) Although some modern erect forms having flexible (flustriform) colonies may have originated through reduction of zooecial calcification, the primary evolutionary attainment of erect growth appears to have been made possible by reinforcement of zooid walls beyond that present in the earliest cheilostomes known. Calcified basal walls and at least partly calcified walls on the frontal side of the zooid appear to have been the minimal advancements necessary as a prospective adaptation for the structural support of a rigidly erect colony. Among Danian and earlier cheilostomes which can be inferred to have grown erect, zooecia have at least the morphotype II degree of complexity—that is, they possess an extensive gymnocyst, cryptocyst, or frontal shield.

(3) For a growing, rigidly erect, non-fenestrate cheilostome colony, the most efficient means of taking up stresses—due to vertical loading, bending, and twisting—appears to be that of concentrating further calcification, beyond the minimal requirement for erect growth, near the frontal surfaces of the zooids and to do this in increasing proportion toward the proximal end of the colony. To the extent that their joint calcification approaches a laterally merging, continuously thickening, distally tapering skeletal mass analogous to the outer walls of an enlarging cantilever beam, zooids of morphotypes II–VI appear to form a graded series of increasingly efficient building blocks for larger colonies and hence denser populations. Except for the unexpectedly low abundance of morphotype III (cribrimorph), the abundances of morphotypes among Danian species inferred to have grown erect are proportional to their postulated functional efficiencies.

(4) If a zooid structure at least as complex as morphotype II was required for attainment of a rigidly erect growth form, whatever adaptive significance frontal calcification may have had originally must be associated with a function other than colony support, such as protection of the lophophore and associated organs. Some or all of the morphotypes beyond type II could also represent, with respect to rigidly erect growth, prospective adaptations which served a different original function or functions. Such a series of prospective adaptations would account for the presence of the more complex morphotypes in encrusting species among Danian and earlier faunas and in the majority of modern cheilostomes of every colony form except some that are non-rigidly erect (flustriform).

The rarity of inferred erect cheilostomes of morphotype III in the Danian fauna suggests that this morphotype arose as a prospective adaptation. The correlation between abundances of inferred erect species and morphotypes IV–VI in the Danian fauna, however, suggests that evolution beyond morphotype III consisted of direct adaptive improvements for rigidly erect growth. Otherwise, each evolutionary step in adaptation for the other function or functions would have required a parallel increase in prospective adaptation for colony support. There is evidence that some lineages having complex morphotypes started with erect colonies and evolved an encrusting form with concomitant thinning of the frontal shield (Cheetham 1968:10–11). Whether this kind of trend might account for many other encrusting species with complex morphotypes can be determined only by detailed studies of many other lineages.

(5) If the rigidly erect form represents an adaptive type attained during cheilostome evolution, then the ecologic niche or group of niches for which it was suited must have been either vacant or occupied by organisms for some reason competitively inferior to cheilostomes. Among the other constituents of the biota associated with Danian mounds, the cyclostome bryozoans display zoarial forms which can be inferred to approximate the cheilostome rigidly erect (vinculariform and eschariform) growth most closely. Cyclostomes having apparently erect colonies are known from strata throughout the Cretaceous, and some are coeval and sympatric with the earliest known cheilostomes. During Late Cretaceous time, the cyclostomes were progressively overtaken in numbers of genera and species by the cheilostomes (Voigt 1959a:702), which apparently have had a large margin of numerical dominance at these categorical levels throughout the Cenozoic. Whether the relationship between diversities in the two groups is one of negative correlation, suggesting competitive replacement, has not been determined because of the many uncertainties in the ranges of cyclostome taxa (Larwood et al. 1967:385).

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PLATES 1-17

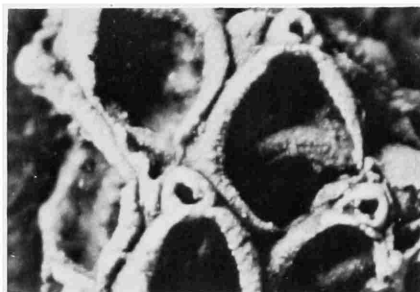
PLATE 1

(All figures $\times 55$; specimens coated with NH_4Cl)

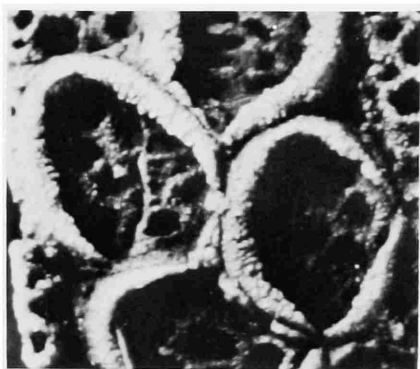
- 1.—*Ellisina brittanica* (Brydone): Frontal view of part of zoarial fragment encrusting basal side of cyclostome zoarium; zooecia have basal and frontal walls apparently uncalcified except for narrow gymnocysts; a small interzooecial avicularium is distal to each zooecium; USNM 169491, Sample 9, Limhamn Mound II-N₁.
- 2.—*Callopora* sp.: Basal view of unilaminate fragment in part encrusting an echinoderm ossicle; basal and frontal walls of zooecia apparently calcified only peripherally so that extensive gymnocysts and small, rim-like cryptocysts (arrow) on proximal ends of frontal sides of zooecia are visible; USNM 169492, Sample 9, Limhamn Mound II-N₁.
- 3.—"*Herpetopora*" *danica* Lang: Frontal view of part of zoarium encrusting frontal side of cyclostome zoarium; basal and frontal walls of zooecia apparently uncalcified except for narrow gymnocyst; USNM 169493, Sample 14, Limhamn Mound II-N₁.
- 4.—*Allantopora stomatoporoides* Lang: Frontal view of small zoarium with ancestrula at lower center, slightly broken, encrusting smooth interior of gooseneck barnacle valve; basal walls of zooecia apparently uncalcified; frontal side of zooecia having extensive proximal gymnocyst supporting ring of spine bases (arrow) on mural rim; narrow, shelf-like cryptocyst within mural rim; USNM 169494, Sample 15, Limhamn Mound II-N₁.
- 5.—*Fissuricella fissa* (Voigt): Frontal view of zoarial fragment encrusting frontal side of unidentified cheilostome; calcified frontal structure interpreted as a gymnocyst (Voigt 1959b:260) shows extreme development; USNM 169495, Sample 6, Limhamn Mound II-N₁.



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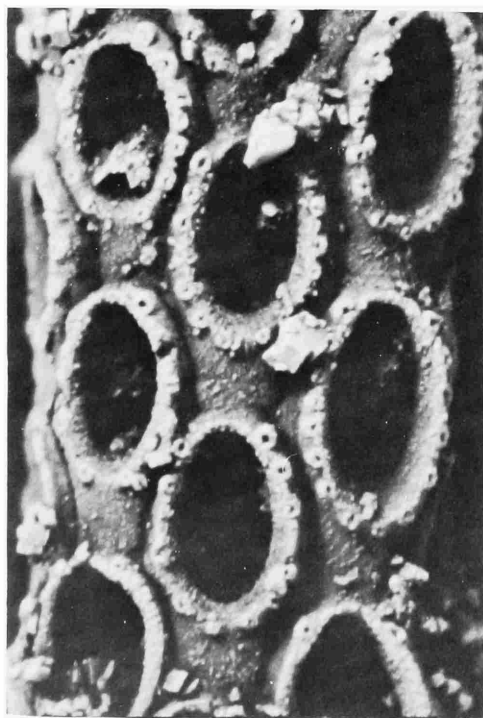
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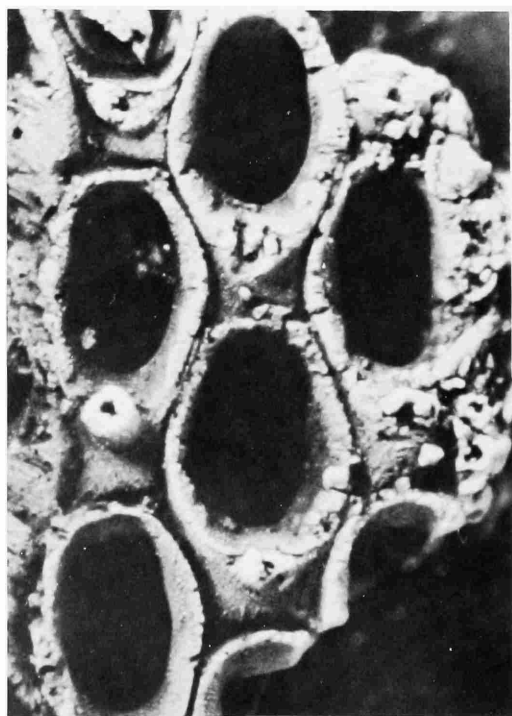
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PLATE 2

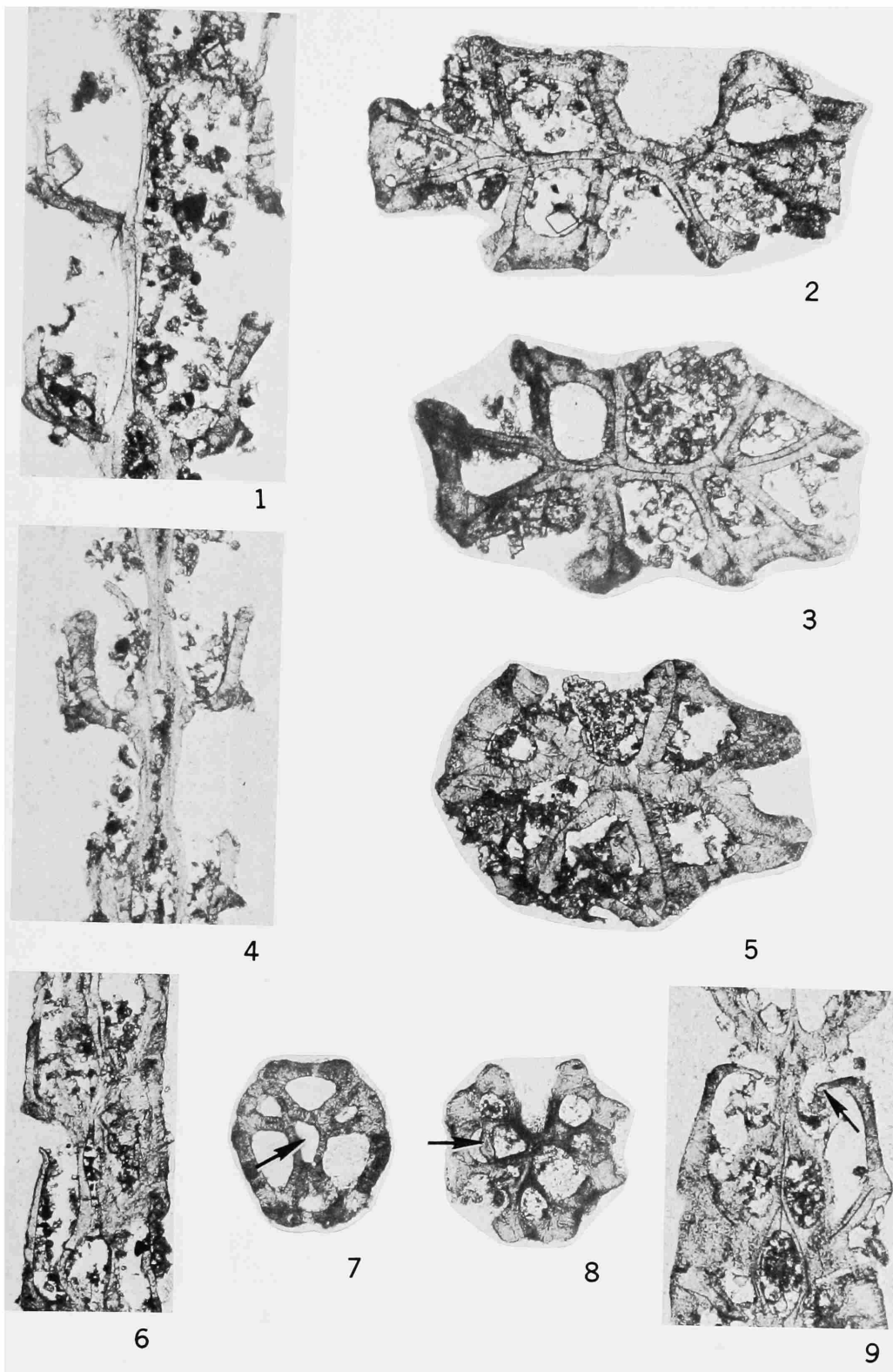
(All figures $\times 55$; specimens coated with NH_4Cl)

- 1.—*Membraniporidra declivis* (Marsson): Zooecia on margin of narrow bilaminate fragment showing wide cryptocysts and small interzooecial avicularium with mandibular bar; USNM 196496, Sample 5, Limhamn Mound II-N₁.
- 2-4.—*Pithodella cincta* Marsson: 2, Frontal view of bilaminate fragment expanding distally from a subcylindrical proximal end; zooecia have broad cryptocysts and large adventitious avicularia on proximal gymnocyts; spine bases lacking; USNM 169497, Sample 1, Limhamn Mound II-N₁. 3, Frontal view of bilaminate fragment showing zooecia having gymnocyts with complete or partial rings of spine bases; cryptocysts narrow; avicularia lacking; USNM 169498, Sample 5, Limhamn Mound II-N₁. 4, Frontal view of unilaminate fragment showing zooecia having scattered, isolated gymnocystal spine bases, narrow cryptocysts, and small avicularia; USNM 169499, Sample 17, Limhamn Mound II-N₁.

PLATE 3

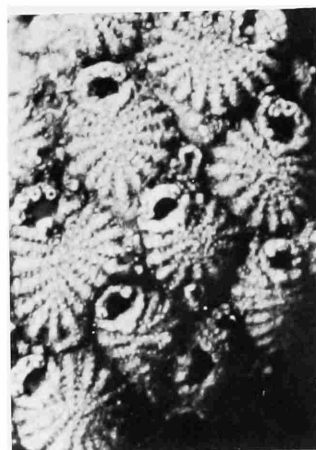
(All figures $\times 55$)

- 1-5.—*Pithodella cincta* Marsson: 1, 4, Longitudinal views of bilaminate fragments having zooecia with extensive gymnocysts of approximately same thickness as other zooecial walls; zooecium on right in 1 is ovicelled; USNM 169500, 169501, Sample 5, Limhamn Mound II-N₁. 2, 3, 5, Transverse views of bilaminate to subcylindrical fragments showing zooecia with continuous basal and lateral boundaries and gymnocysts continuous with lateral walls; USNM 169502-169504, Sample 17, Limhamn Mound II-N₁.
- 6, 7.—*Floridina gothica* (d'Orbigny): 6, Longitudinal view of subcylindrical fragment having zooecia with extensive, concave cryptocysts curved frontally at their distal ends; 7, transverse view of subcylindrical fragment showing radially arranged zooecia all reaching the zoarial axis and their basal walls forming a small, triangular hollow (arrow); lateral and basal boundaries between zooecia are continuous, and cryptocyst is continuous with lateral walls; USNM 169521, 169522, Sample 1, Limhamn Mound II-N₁.
- 8, 9.—*Smittipora? prismatica* (Hagenow): 8, Transverse view of subcylindrical fragment showing radially arranged zooecia lacking basal walls; zooecia are excluded from zoarial axis in their proximal parts (indicated by thick cryptocysts) by widening of zooecia in adjacent rows; recurved distal end of cryptocyst (arrow) is shown in zooecium on left; 9, longitudinal view of subcylindrical fragment showing zooecia with cryptocysts descending steeply into distal part of cavity where their free ends are recurved proximally (arrow); exclusion of proximal ends of zooecia from zoarial axis is shown near bottom of view; USNM 169517, 169518, Sample 5, Limhamn Mound II-N₁.





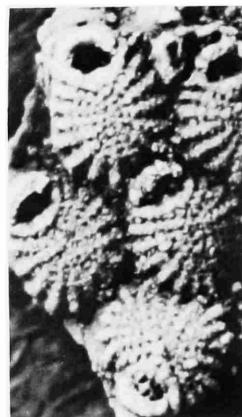
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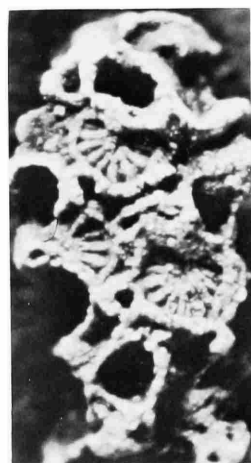
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PLATE 4

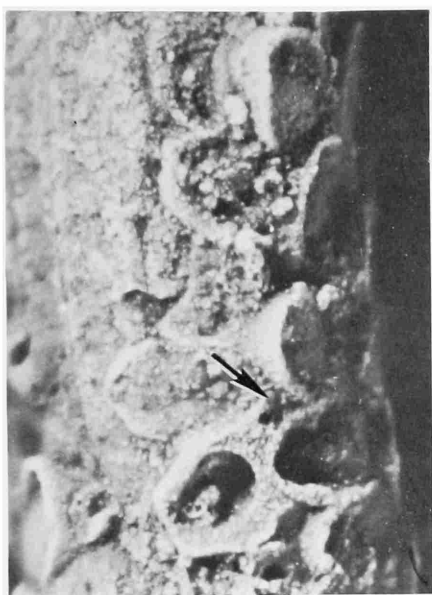
(All figures $\times 55$; specimens coated with NH_4Cl)

- 1.—*Balantiostoma pallata* Maryanska: Frontal view of unilaminate fragment having zooecia with convex, marginally perforate frontal shields which project over the orifice as mucrones; paired distal-oral spine bases are discernible on non-ovicelled zooecia; adventitious avicularia are present on some zooecia; USNM 169505, Sample 14, Limhamn Mound II-N₁.
- 2, 3.—*Anornithopora minuta* Voigt: 2, Frontal view of unilaminate fragment having zooecia with costal shields margined proximally by gymnocysts of varying widths; costae joined by numerous lateral fusions and fused medially in a narrow area; orifices with two to four distal spine bases; several interzooecial avicularia with spatulate rostra are present; USNM 169506, Sample 14, Limhamn Mound II-N₁. 3, Frontal view of unilaminate fragment having zooecia without gymnocysts; orifices with four or five distal spine bases; and an avicularium; USNM 169507, Sample 9, Limhamn Mound II-N₁.
- 4.—*Anornithopora polygona* Voigt: Frontal view of zooecia encrusting a fragment of smooth mollusk shell and in turn encrusted by a cyclostome; costal shields lack gymnocysts and have narrow median areas of fusion; zooecium at center has broken ovicell; USNM 169508, Sample 4, Limhamn Mound II-N₁.
- 5.—*Tricephalopora circumvallata* (Levinsen): Frontal view of unilaminate fragment having zooecia with costal shields margined peripherally by a ridge-like tertiary frontal wall; costae joined only medially; remnants of peristomes bearing adventitious avicularia are present; zooecium on right is ovicelled; USNM 169509, Sample 9, Limhamn Mound II-N₁.

PLATE 5

(All figures $\times 55$; specimens coated with NH_4Cl)

- 1a, b.—*Aechmella pindborgi* Berthelsen: 1a, Frontal view of two growing margins of same colony converging around encrusted, slightly grooved octocoral axis; zooecia and inter-zooecial avicularia (arrow) have incomplete cryptocysts limited to proximal and lateral margins; 1b, frontal view of other side of same zoarium showing zooecia and avicularia with completely developed, concave cryptocysts and opesia with proximolateral indentations; USNM 169510 Sample 9, Limhamn Mound II-N₁.
- 2, 3.—*Onychocella ravni* Berthelsen: 2, Frontal view of dome-shaped zoarium reflecting the shape of the encrusted calcareous sponge; zooecia have concave cryptocysts and opesia with proximolateral indentations; at the bifurcations of lineal series are curved, vicarious avicularia also with cryptocysts; 3, curved zoarium reflecting the shape of the corallite of an encrusted colonial scleractinian coral; USNM 169511, 169512, Sample 11, Limhamn Mound II-N₁.



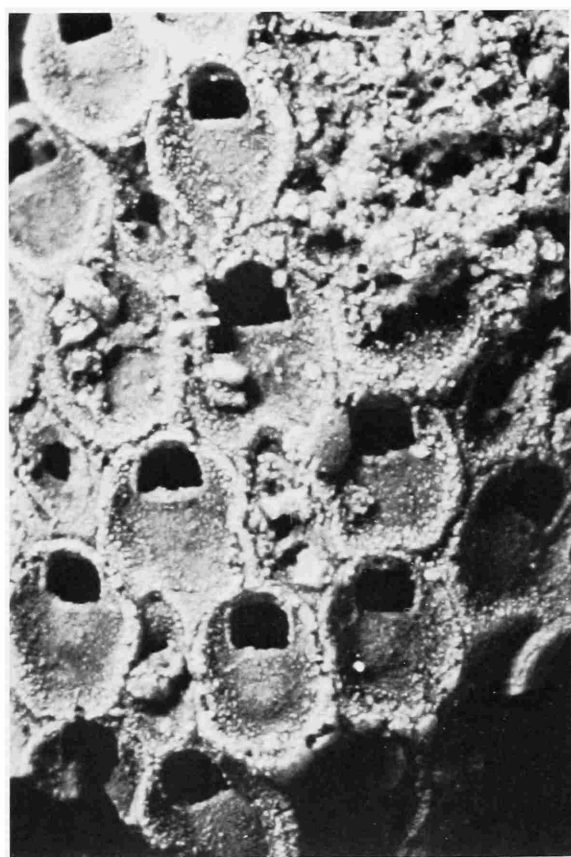
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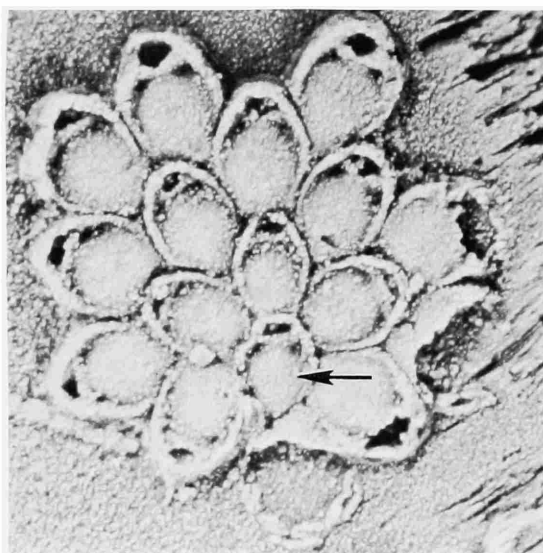
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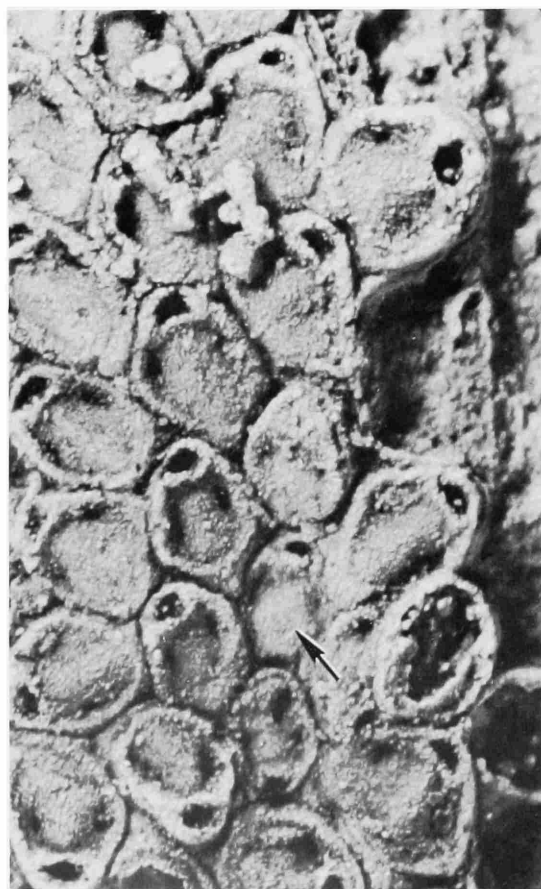
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PLATE 6

(All figures $\times 55$; specimens coated with NH_4Cl)

- 1-3.—*Micropora hennigiana* Berthelsen: 1, Frontal view of small zoarium encrusting smooth interior of same barnacle valve as specimen shown on Plate 1:4; zooecia regularly arranged in triads around ancestrula (arrow), all having concave cryptocysts with opesiules proximolateral to opesia; broken zooecium at bottom of view shows apparent lack of calcified basal wall and presence of dietellae; USNM 169513, Sample 15, Limhamn Mound II-N₁. 2, Frontal view of zoarial fragment encrusting basal side of *Callopora* sp., overlapping its broken edge at upper right; zooecia irregularly arranged on irregularly concave surface, one zooecium on upper left having its morphologic axis reversed; zooecium at extreme right has entozoecial ovicell (arrow); USNM 169514, Sample 11, Limhamn Mound II-N₁. 3, Frontal view of part of a large zoarium encrusting a fragment of ribbed brachiopod shell; ancestrula just below center (arrow); zooecia show regular growth parallel to underlying topographic pattern and irregular growth across it; USNM 169515, Sample 7, Limhamn Mound II-N₁.
- 4.—*Floridina* sp.: Frontal view of part of a large zoarium encrusting a mollusk shell fragment; zooecia and large vicarious avicularia (at left center and upper right) have concave cryptocysts which, in avicularia, continue around distal end of opesia; zoecial opesia have broad proximolateral indentations; zooecia at upper right and at right center show entozoecial ovicells (arrows); a small, closed kenozoecium is present just below center; USNM 169516, Sample 11, Limhamn Mound II-N₁.

PLATE 7

(All figures $\times 55$; specimens coated with NH_4Cl)

- 1, 5.—*Smittipora? prismatica* (Hagenow): 1, Frontal view of proximal portion of subcylindrical fragment showing proximal zooecium with frontal side closed by a calcareous lamella except for a median slit and U-shaped opercular scar (arrow) with deep proximolateral pits; more distal zooecia show thick, but concave cryptocysts separated by distinct mural rims; 5, frontal view of less heavily calcified zooecia with more concave cryptocysts descending steeply toward opesia; opesial indentations are apparently not differentiated from opesia; USNM 169519, 169520, Sample 5, Limhamn Mound II-N₁.
- 2, 3.—*Floridina gothica* (d'Orbigny): 2, Frontal view of subcylindrical fragment showing zooecia with concave cryptocysts and opesiules separated from opesia by cryptocystal bars; USNM 169523, Sample 3, Limhamn Mound II-N₁. 3, Frontal view of subcylindrical fragment showing zooecia with opesiular indentations confluent with opesia; three zooecia have entozoecial ovicells (arrows); USNM 169524, Sample 5, Limhamn Mound II-N₁.
- 4, 7.—*Onychocella? columella* Berthelsen: 4, Frontal view of narrow bilaminate fragment showing zooecia having concave cryptocysts and opesia with notched proximolateral corners; interzooecial avicularium shows distinct mandibular bar; 7, frontal view of subcylindrical fragment showing zooecia (two of which have entozoecial ovicells), avicularia, and a kenozoecium (arrow) closed except for a central perforation; USNM 169525, 169526, Sample 5, Limhamn Mound II-N₁.
- 6.—*Puncturiella sculpta* (d'Orbigny): Frontal view of subcylindrical fragment showing zooecia with concave, perforate cryptocysts, opesiules (arrow) proximal to opesia, and small, interzooecial avicularia in lineal series with zooecia; USNM 169527, Sample 5, Limhamn Mound II-N₁.



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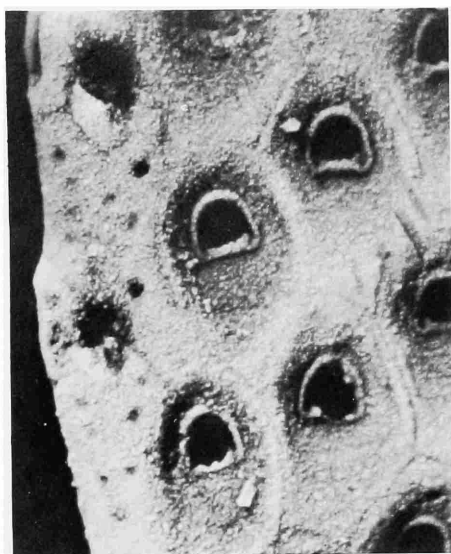
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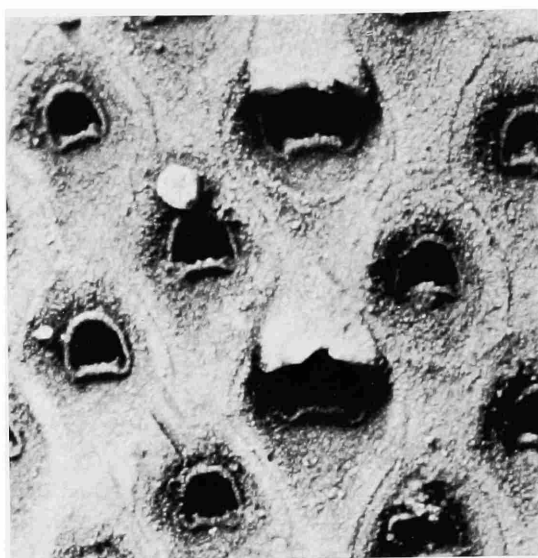
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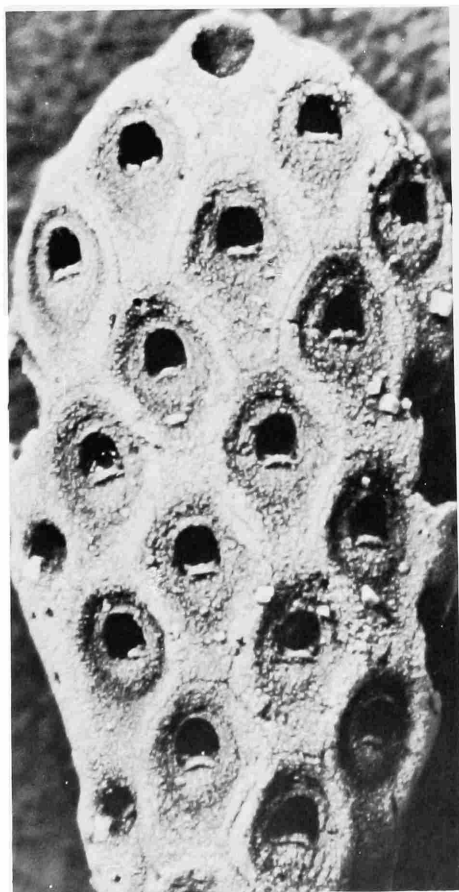
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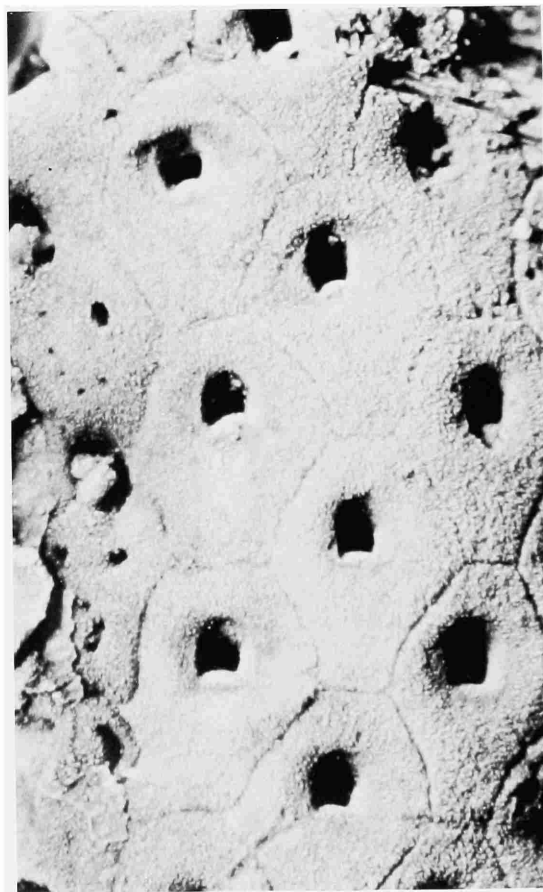
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PLATE 8

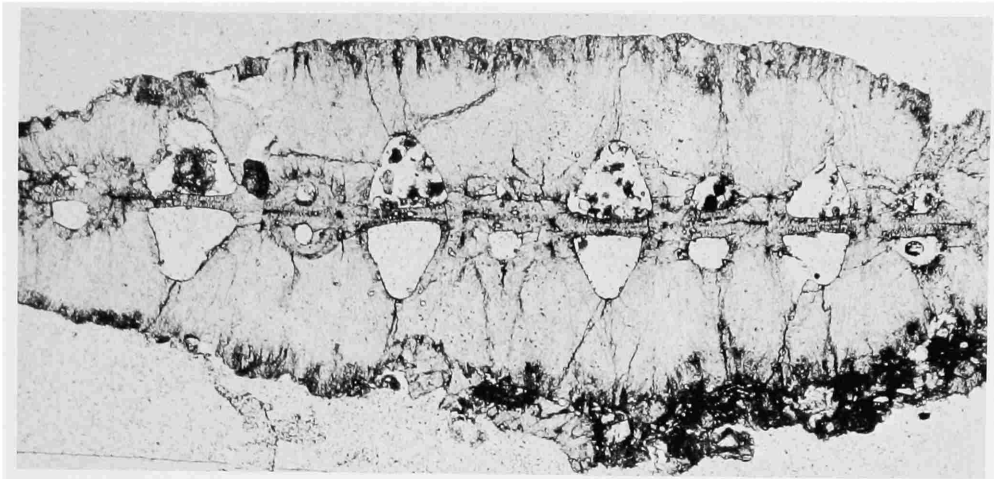
(All figures $\times 55$; specimens coated with NH_4Cl)

- 1-3.—*Coscinopleura angusta* Berthelsen: 1a, Frontal view of lateral margin of large, bilaminate fragment showing zooecia having concave cryptocysts continuous around their opesia, the proximolateral corners of which are notched; large, vicarious vibraculiform zooecia (coscinozooecia) having convex, perforated, probably gymnocystal proximal covers and asymmetrical distal openings are in a series on lateral margin of zoarium; grooves on zooecia at right may have resulted from predation on the soft membranes which presumably covered each zooecium; 1b, frontal view of central part of same fragment showing grooves and two zooecia with entozoecial ovicells; USNM 169528, Sample 7, Limhamn Mound II-N₁. 2, Frontal view of small bilaminate fragment tapering toward proximal end and preserving growing margin at distal end; distalmost zooecium has incomplete cryptocyst; USNM 169529, Sample 14, Limhamn Mound II-N₁. 3, Frontal view of bilaminate fragment apparently from proximal end of large colony showing zooecia with greatly thickened cryptocysts but retaining distinct zoecial boundaries; USNM 169530, Sample 17, Limhamn Mound II-N₁.

PLATE 9

(All figures $\times 55$)

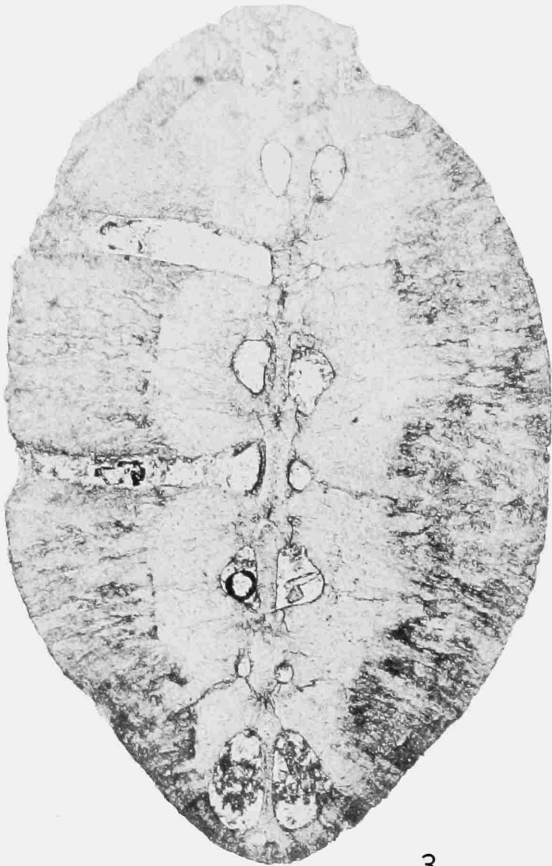
- 1-3.—*Coscinopleura angusta* Berthelsen: 1, 2, Transverse and longitudinal views of wide, bilaminate fragments apparently from distal parts of large colonies showing zooecia having moderately thick, concave cryptocysts; boundaries between zooecia for the most part are not discernible, as a result of alteration or of complete calcification of cuticles; minute open spaces in both views scattered randomly through zooecial walls have no external expression and seem to be products of alteration; 3, transverse view of narrow bilaminate fragment apparently from proximal part of large colony showing zooecia having enormously thickened cryptocysts; zooecial boundaries not discernible, but crude, coarse lamination near frontal surface may be remnant of original skeletal structure; shaft-like opesia are shown in two zooecia on left, suggesting that some lophophores remained functional. USNM 169531-169533, Sample, 17, Limhamn Mound II-N₁.



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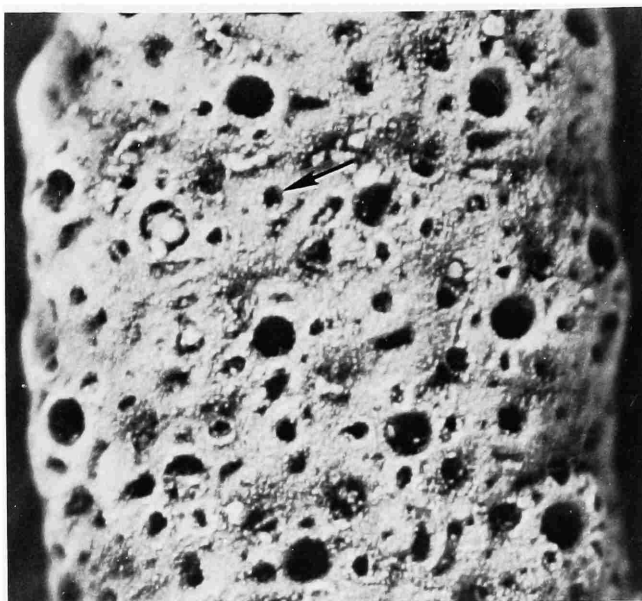
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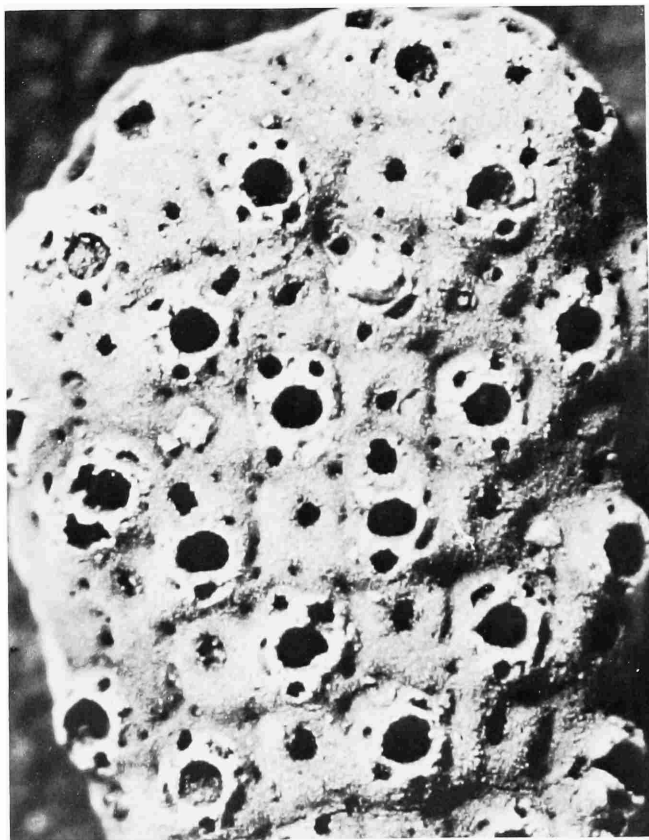
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PLATE 10

(All figures $\times 55$; specimens coated with NH_4Cl)

- 1.—*Pachythecella lundgreni* (Pergens & Meunier): Frontal view of subcylindrical proximal portion of bilaminate fragment showing zooecia lacking boundaries and having thick, apparently imperforate frontal shields upturned around orifice as peristome; zooecium at lower left bears a suboral frontal avicularium (arrow); USNM 169534, Sample 1, Limhamn Mound II-N₁.
- 2-4.—*Porina salebrosa* Marsson: 2, Frontal view of bilaminate fragment apparently from proximal part of colony, showing zooecia lacking boundaries and having thick frontal walls perforated by a large, circular ascopore (arrow) at about midlength and by smaller, scattered pores; portion of shield raised around orifice as a peristome bears numerous small, and rarer large avicularia; USNM 169535, Sample 14, Limhamn Mound II-N₁. 3, Frontal view of subcylindrical fragment showing zooecia with thick frontal shields which have apparently been abraded; 4, frontal view of bilaminate fragment preserving growing margin and showing zooecia having thin frontal shields with prominent ascopores, marginal pores at distinct interzooecial boundaries, and peristomial avicularia at varying stages of development; USNM 169536, 169537, Sample 1, Limhamn Mound II-N₁.

PLATE 11

(All figures $\times 55$; specimens coated with NH_4Cl)

- 1-4.—*Columnotheca cribrosa* Marsson: 1, End view of growing tip of subcylindrical fragment showing radially arranged zooecia having transverse walls perforated by distal ends of interzooecial canals; USNM 169540, Sample 5, Limhamn Mound II-N₁. 2, Frontal view of branched fragment from distal part of zoarium preserving one growing tip showing verticillate arrangement of zooecia; zooecia have frontal shields lacking interzooecial boundaries and bearing small scattered pores; near base of peristome are slightly larger spiramina, which in some zooecia in most fragments examined are paired (arrows), as typical for this species (Voigt 1968a:385); large, adventitious avicularia are near peristomes of few zooecia; USNM 169541, Boesdal Mound E₁. 3, Frontal view of branched fragment apparently from proximal part of zoarium; zooecia have few perforations except for spiramina; avicularia are common; scattered, dash-shaped, shallow grooves arranged in branching uniserial patterns possibly are burrows of ctenostome bryozoans (J. D. Soule, personal communication, 1969); USNM 169542, Sample 1, Limhamn Mound II-N₁. 4, Frontal view of fragment from distal part of zoarium showing zooecia near growing tip with numerous small frontal pores and more proximal zooecia with progressively fewer pores; zooecium just below center on right has paired spiramina (arrows); dash-shaped grooves are common; USNM 169543, Boesdal Mound E₁.



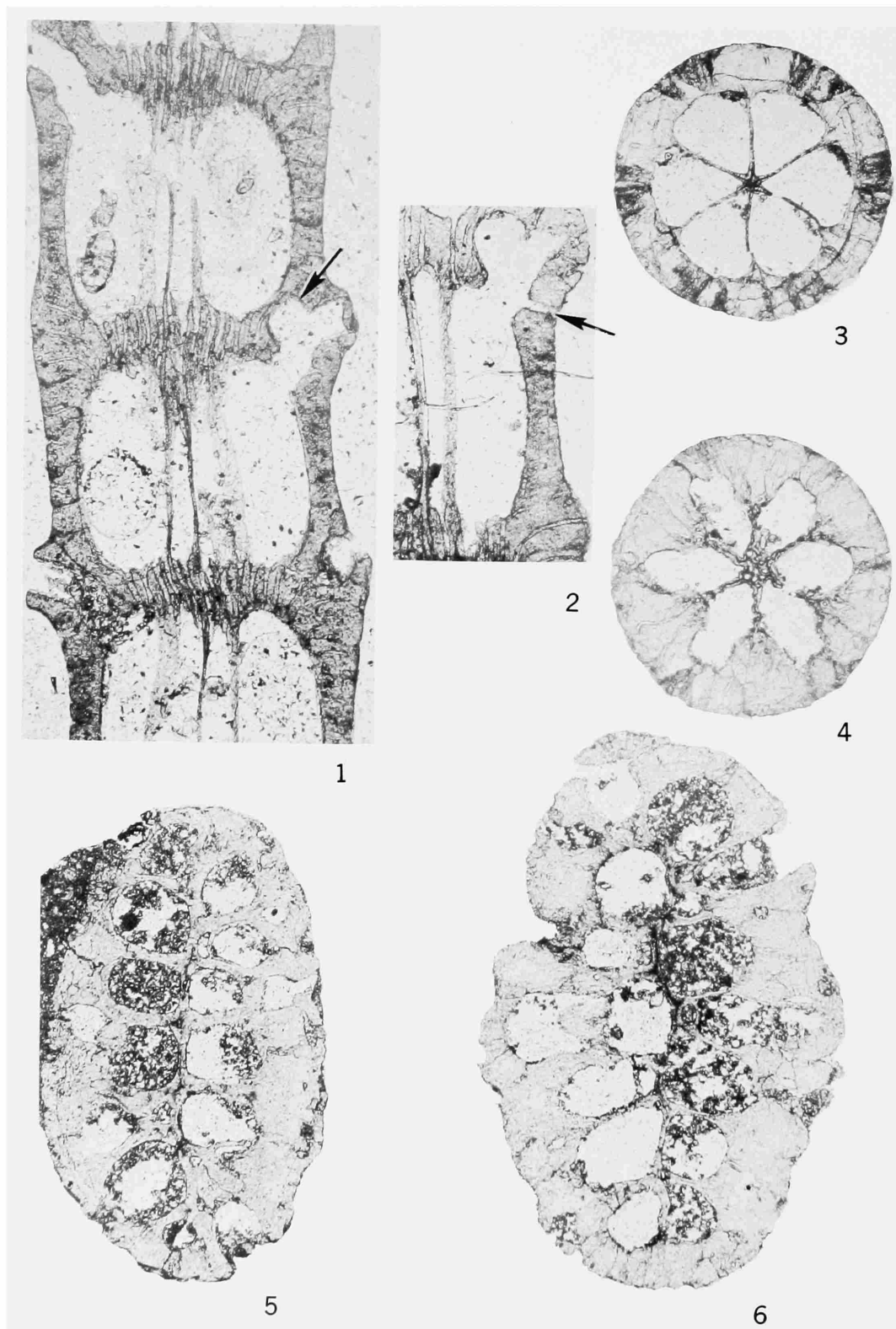


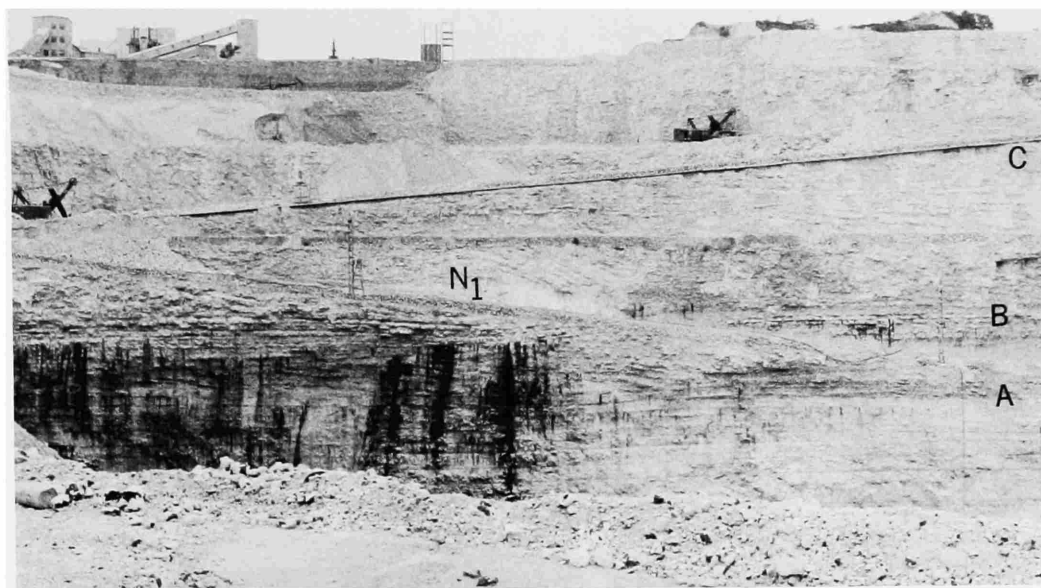
PLATE 12

(All figures $\times 55$)

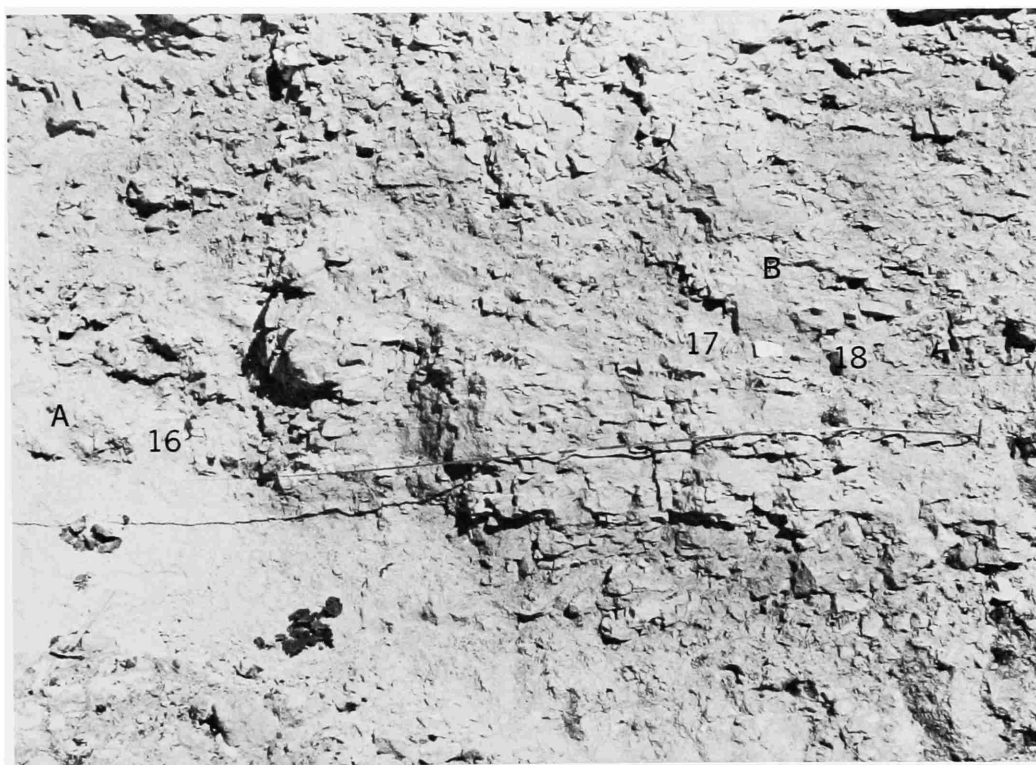
- 1-4.—*Columnotheca cribrosa* Marsson: 1, Longitudinal view of subcylindrical fragment showing zooecia having thick, convex frontal shields perforated by canal-like pores similar to those passing through thick transverse walls; middle zooecium on right has hyperstomial ovicell (arrow) completely hidden externally by development of peristome; USNM 169544, Boesdal Mound E₁. 2, Longitudinal view of ovicelled zooecium showing spiramen (arrow) perforating peristomial wall and opening internally distal to orifice; USNM 169545, Sample 1, Limhamn Mound II-N₁. 3, 4, Transverse views of subcylindrical fragments showing thin lateral zooecial walls with distinct interzooecial boundaries which disappear in the thick frontal walls; the section in one figure (4) passes in part through transverse walls; USNM 169546, 169547, Boesdal Mound E₁.
- 5, 6.—*Porina salebroza* Marsson: Transverse views of bilaminate fragments showing zooecia having thin basal and lateral walls with distinct interzooecial boundaries and thick frontal walls lacking them; USNM 169538, 169539, Sample 14, Limhamn Mound II-N₁.

PLATE 13

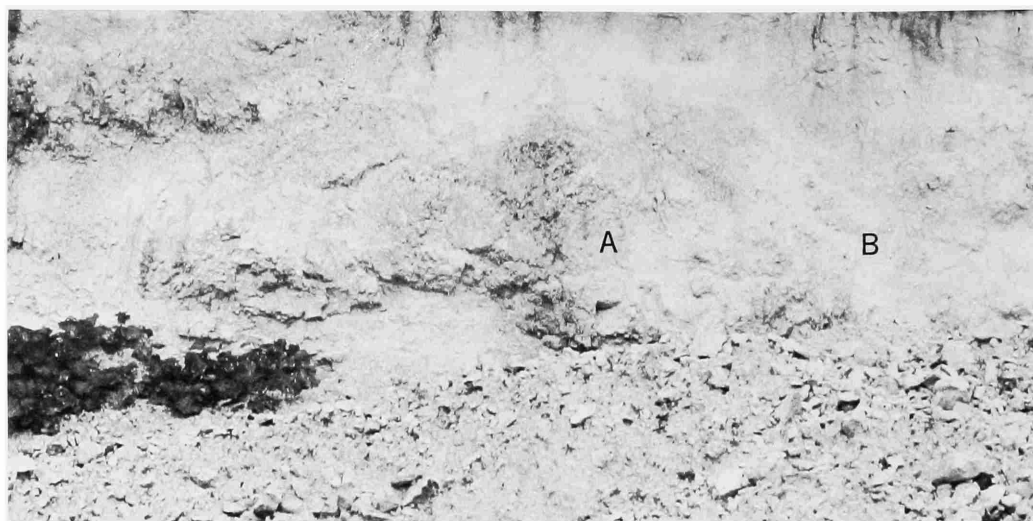
- 1, 2.—North wall of limestone quarry at Limhamn, Malmö, Sweden: 1, View from —40-m level, September 1964; dark vertical stripes are modern algal growths; from —60-m level to bottom of quarry, evenly bedded chalk with chert nodules is exposed; these sediments (belonging to Maestrichtian Stage) are marked at top (A) by major disconformity (Brotzen 1959:15–17); above this level to about —50 m (B), bryozoan-rich limestones with numerous chert nodules form lower zones of Danian Stage as undulating beds which in places are truncated; from top of these undulating beds (Bioherm Group I of Brotzen) nearly to ground level, middle Danian bryozoan-rich limestones with well-developed mounds are exposed; these sediments include Brotzen's Bioherm Groups II and III, the contact between which lies approximately at C; evenly bedded upper Danian limestones exposed above Bioherm Group III in the south wall of the quarry (Brotzen 1959:29) are not shown in this view; Mound N₁, which was sampled in detail, is exposed in lower half of Bioherm Group II and is cut by an access road at the —40-m level and another between the —40- and —60-m levels; Mound N₂ is in upper part of Bioherm Group II, above the —40-m level to left of view. 2, Contact between sediments transitional to core (A) and composing the east flank (B) of Mound II-N₁, middle Danian; transitional sediments are poorly bedded, chalky limestones with sparse chert nodules, some of which appear as dark blobs near 16; flank limestones are light gray, have more abundant chert, and show finely nodular bedding; numbers 16 to 18 mark positions of samples (see Figure 12).



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PLATE 14

- 1, 2.—North wall of limestone quarry at Limhamn, Malmö, Sweden: 1, Contact between core sediments (A) and sediments transitional to the east flank (B) of Mound II-N₃, middle Danian. The core facies consists of indurated white lime-mud filling the space in and around colonial scleractinian corals nearly in position of growth; chert is lacking. The coral mass shown is about 4 m across. The original content of scleractinian skeletons, now either replaced by calcite or represented by molds (Brotzen 1959:21), is much less than in the coral limestone at Fakse, Denmark (Berthelsen 1962:23). Dark material at lower left is modern algal growth. 2, Contact between sediments composing west flank (A) and those transitional to core of Mound II-N₃; flank facies consists of gray limestone with abundant chert; transitional sediments show irregular, discontinuous bands of finely nodular bedding; thickness of interval shown, about 2 m.
- 3.—West wall of Limhamn quarry, just above -40-m level, showing middle Danian sediments of upper part of Bioherm Group II; bedded gray limestones with chert nodules and interbeds intersect in pattern suggesting local unconformities; bedding surface A-B truncates beds on south flank of mound on lower right and appears to be concordant with beds on north flank of partly contemporaneous mound on left; zones of induration, such as have been reported at the contacts between overlapping mounds in the lower Danian of Stevns Klint, Denmark (Rosenkrantz and Rasmussen 1960:6, fig. 5), were not observed here.

PLATE 15

- 1, 2.—Sediments of Mound II-N₁, middle Danian, Limhamn: 1, Flank-facies: gray, bryozoan-rich limestone with finely nodular bedding, west flank; limestone layer, only partly shown here, is about 1 m thick and occurs between two layers of chert nodules; Sample 3 was taken from this location (see Figure 12). 2, Transitional-facies: white, massive limestone with a thin, finely nodular bed containing numerous octocorals, just west of center of mound; Sample 7 was taken from this location (see Figure 12).
- 3.—North wall of Limhamn quarry, just above —40-m level, showing coral-rich core facies (X) of one mound overlying flank limestones (Y) of another mound and grading vertically upward into bedded limestones (Z) like those on its own flanks; middle Danian, Bioherm Group II.



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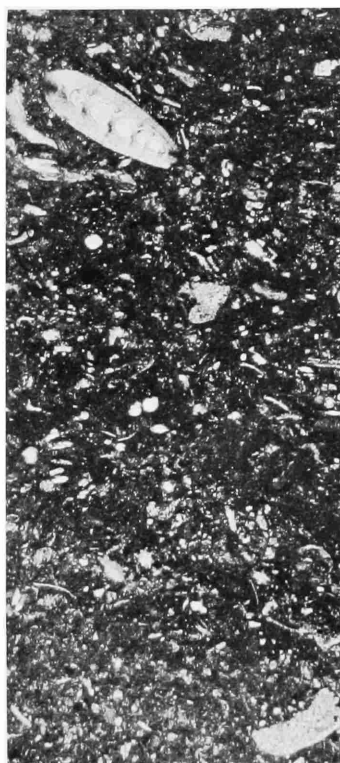
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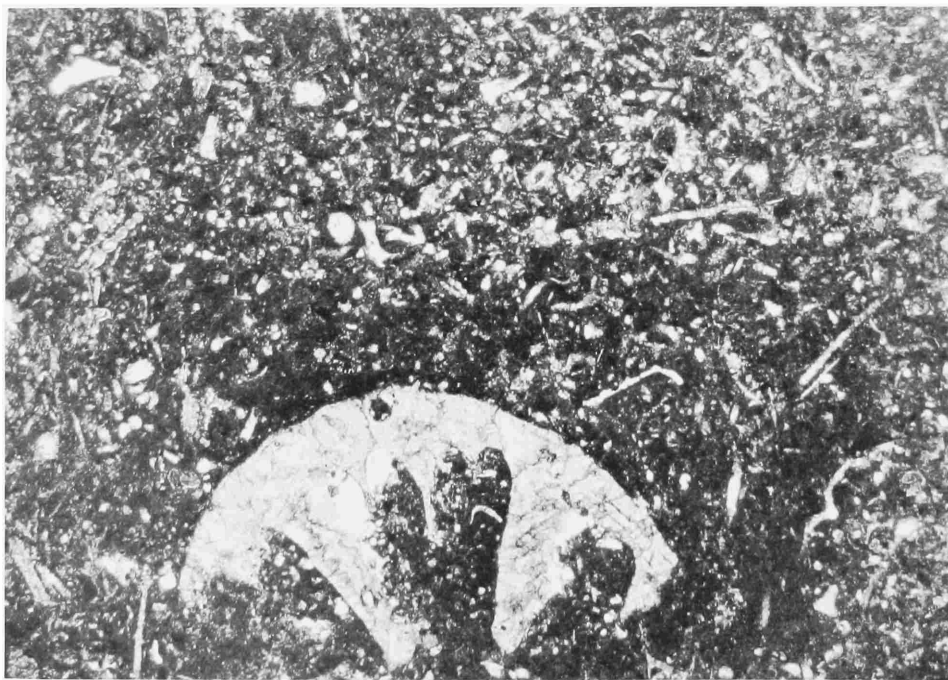
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PLATE 16

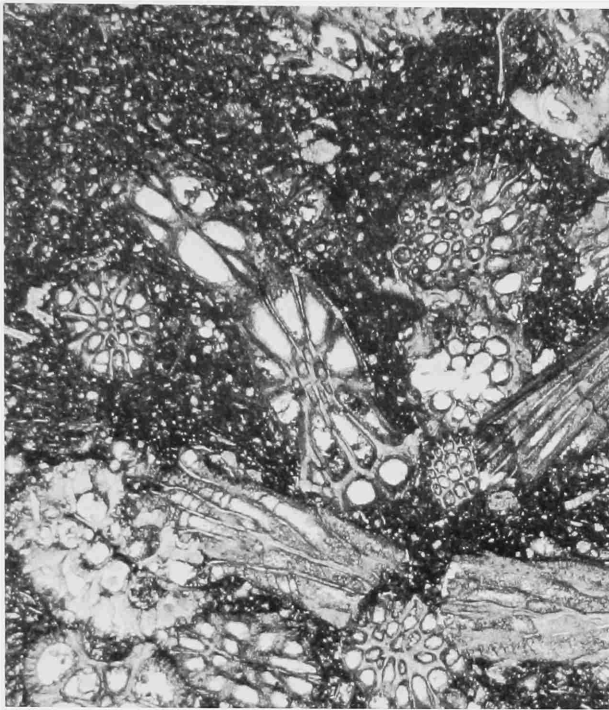
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- 1-3.—Sections transverse to bedding of epon-impregnated, undisturbed sediment, in plane-polarized light, from central part of Mound II-N₁, middle Danian, Limhamn: 1, Biofacies A₂ (transitional facies) with large octocoral fragment encrusted by cyclostome bryozoan, a second cyclostome (left center), abundant echinoderm debris, and fine carbonate matrix; USNM 169548, Sample 7. 2, Biofacies A₁ (core facies) consisting predominantly of fine carbonate matrix with scattered foraminifers and identifiable octocoral (just under foraminifer at upper left) and echinoderm debris; USNM 169549, Sample 9. 3, Biofacies A₁ with more abundant echinoderm debris and foraminifers relative to matrix than Sample 9, and showing a large fragment of scleractinian coral; USNM 169550, Sample 10.

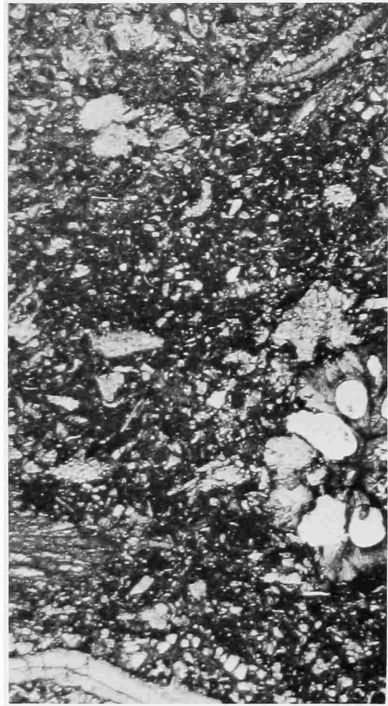
PLATE 17

(All figures $\times 22$)

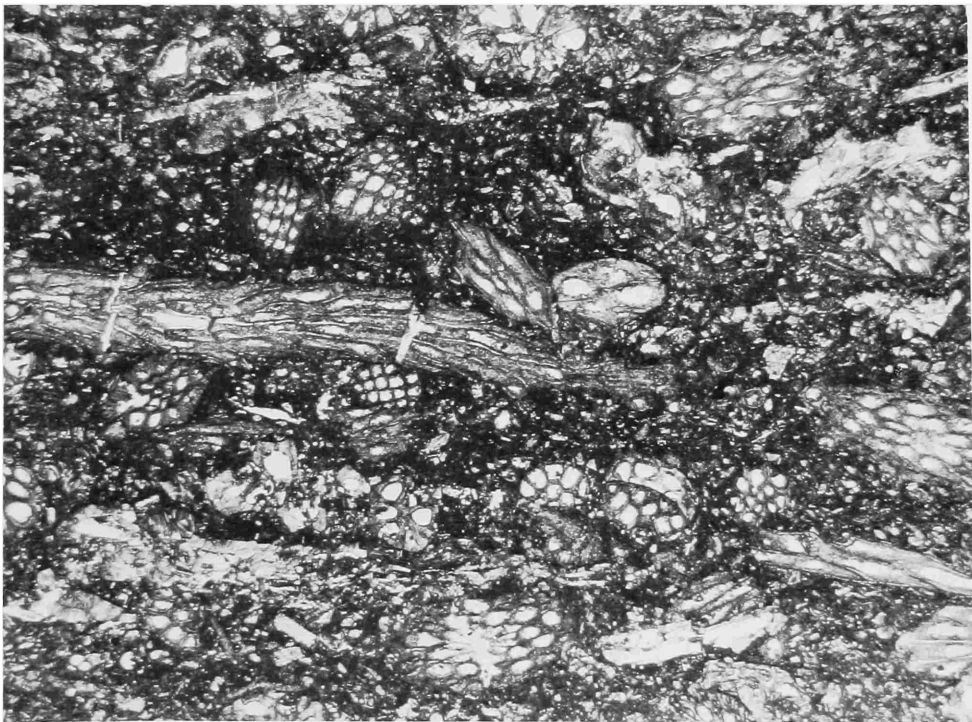
- 1-3.—Sections transverse to bedding of epon-impregnated, undisturbed sediment, in plane-polarized light, from flanks (Biofacies B) of middle Danian mounds at Limhamn: **1**, Abundant bryozoan fragments with long axes approximately parallel to bedding in fine carbonate matrix with scattered debris, mainly of echinoderms. Fragmentary cheilostomes are shown in transverse sections at lower left (*Porina salebroza*) and at upper right (*Coscino-pleura angusta*); most other bryozoans shown are cyclostomes. Across the lower part of the view are two fragments in longitudinal section that are probably separated pieces of the same cyclostome colony; USNM 169551, east flank of Mound II-N₃. **2**, Abundant echinoderm debris, part of a brachiopod (lower left), and bryozoan fragments (cyclostome at left and a cheilostome, *Porina salebroza*, at right) in fine carbonate matrix; USNM 169552, Sample 18, east flank of Mound II-N₁. **3**, Abundant bryozoan fragments, with long axes closely paralleling bedding, in fine carbonate matrix. Cyclostome shown in longitudinal section across middle of view from left has fractures, one of which is partly filled with matrix. Cheilostomes are identifiable in transverse sections at top center (*Floridina gothica*) and near bottom center (*Smittipora? prismatica*); USNM 169553, Sample 1, west flank of Mound II-N₁.



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