PART G
BRYOZOA
REVISED

Introduction, Order Cystoporata, Order Cryptostomata

By R. S. Boardman, A. H. Cheetham, D. B. Blake, John Utgaard, O. L. Karklins, P. L. Cook, P. A. Sandberg, Geneviève Lutaud, and T. S. Wood

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INTRODUCTION TO THE BRYOZOA

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Bryozoa constitute a major phylum of invertebrates. Modern Bryozoa are widely distributed in fresh and marine waters, from high altitudes to abyssal depths. They are a dominant component of the sessile fauna of shelf seas and fouling communities. They are also the most abundant fossils in many sedimentary deposits. The fossil record of the phylum extends over the last 500 million years (Ordovician to Holocene) and is characterized by wide distribution, great abundance, and high diversity throughout most of that time.

The Bryozoa are the only phylum in which all known representatives form colonies. A **colony** can consist of a few to tens of millions of minute members called **zooids**. The numbers of zooids in most bryozoan colonies are comparable to the numbers of individuals in a society of ants or a population of ordinary solitary animals. The zooids in a bryozoan colony differ from members of a population or an insect society in being both physically connected and asexually reproduced, but many of their functions are comparable to those of solitary individuals.

Even though Bryozoa are among the most common marine invertebrates in modern seas and in the fossil record, they are not so likely to be recognized as are members of several other major phyla. A bryozoan colony can be so varied in megascopic appearance (see Fig. 7–9, 13–15) as to be practically indistinguishable from some representatives of such other phyla as hydroids, corals, and algae. The distinguishing characters are generally observable only with magnification.

A bryozoan colony is made up of asexually replicated, physically connected zooids. The asexual origin and physical connection of zooids justifies a basic assumption, that genetic makeup is uniform throughout a colony. Nevertheless, morphologic variation is normal among zooids of a colony because of ontogeny, astogeny, polymorphism, and microenvironment. Because of genetic continuity, these sources of variation can be studied within a colony without the complication of differences in genotype, an advantage not available in solitary animals.

Physical continuity allows some zooids, such as nonfeeding polymorphs, to be highly specialized and parts of colonies to develop structures not possible in solitary animals. Feeding zooids in the same colony may differ so in morphology and other functions that, if not physically connected, they could be considered genetically different; many might be placed in distinct taxa.

Colonies can increase in size and their **growth habits** change in response to environmental pressure without any increase in size or change in basic morphology of feeding zooids. This flexibility is an advantage to species in which competition for substrates requires irregular configurations or erect growth. Commonly, an increase in size or change from encrusting to erect growth habit requires structural support accomplished by development of colony-wide skeletal structures, changes in the morphology of some zooids, or both.

Some aspects of bryozoan morphology, especially those related to the colonial state, have not been fully exploited in the study and application of the phylum. The abundance and wide geographic distribution of Bryozoa from the Ordovician to the present, the flexibility of their colony growth habits in response to environmental pressure, and the availability of many morphologic characters for studying their classification and evolutionary trends make Bryozoa potentially highly significant to the study not only of biostratigraphy but of past and present ecology and zoogeography. In general, but with much overlap, the morphology of zooids tends to reveal genetically controlled char-

acters whereas the form of the colony reflects environmental modifications. The lack of significant transportation after death commonly can be detected for many fossil Bryozoa, especially for erect branching colonies preserved nearly intact.

Taken together, these qualities give promise of considerable success not yet realized in the application of Bryozoa study to geologic and zoologic problems.

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L. B. Isham constructed Figures 2 through 4. Other figures were drafted by JoAnn Sanner, who together with D. A. Dean gave other technical assistance.

CHARACTERISTICS OF BRYOZOA

Bryozoa are colonial, aquatic, generally sessile metazoans, regarded as coelomate, with a retractable lophophore and U-shaped digestive tract.

All Bryozoa form colonies (Fig. 1). Each colony consists of one or more kinds of minute zooids and multizooidal parts, and some colonies include extrazooidal parts. Zooids are physically connected, asexually replicated morphologic units that separately perform such major physiologic or structural functions as feeding, reproduction, or support. **Multizooidal parts** include continuous wall layers grown outside existing zooidal boundaries and their enclosed **body cavities**, which become parts of zooids as colonies develop. **Extrazooidal parts** remain outside zooidal boundaries throughout the life of a colony and include walls with or without skeletal layers, skeleton not parts of body walls, and adjacent body cavities.

A colony interacts with the environment as a complete organism comparable to a solitary animal. Internally, however, the zooid corresponds to a solitary animal in that it has systems of organs or other structures that separately perform the major functions of a colony. Zooids differ from solitary animals in being both physically connected and asexually replicated. Therefore, zooids and other parts of a colony are assumed to be genetically uniform.

Colonies characteristically include enormous numbers of replicated zooids, with some notable exceptions in a few taxa, and may be more than one meter in size. The size and growth habit of colonies commonly are highly variable under environmental influence, but in some taxa growth habit and size of colony appear to be narrowly restricted genetically.

Zooids and other parts of colonies are interconnected by cells, tissues, confluent body cavity, or a combination of these, to nourish developing, injured, and nonfeeding zooids, and other parts of colonies incapable of feeding. It is probable that interzooidal connections function in the coordinated nervous behavior observed in some colonies.

Body walls enclose body cavities of zooids, parts of zooids, and all other parts of colonies. Body walls consist of cellular and noncellular layers. Cellular layers can be continuous or can consist of scattered cells. Cellular layers in two of the three major groups of Bryozoa include an inner **peritoneum** lining the body cavity (considered to be a **coelom**) and an outer **epidermis**. A peritoneum also is reported to be present in the third major group but is not part of the body wall. Noncellular layers include outermost cuticular or

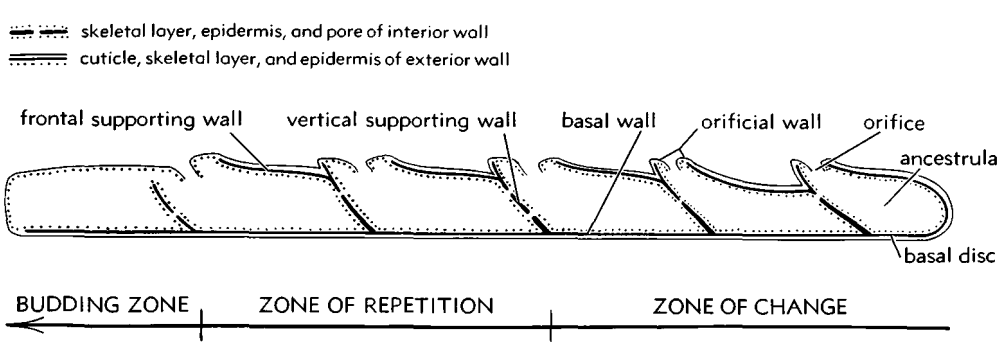

FIG. 1. Characteristics of the Bryozoa. Diagram of a longitudinal section through an encrusting colony of a fixed-wall stenolaemate bryozoan showing zones of astogenetic change and repetition and basic orientation of zooidal walls. Lophophores, digestive tracts, and some other soft parts have been omitted. The zooid at the proximal end of the colony, extreme right, is the primary zooid (ancestrula). As the colony grows, the expanding exterior wall of the budding zone gains enclosed space that is partitioned into zooids by interior vertical walls. The boundary between zooids runs through the middle of the calcareous layer of interior vertical walls. The cuticle is attached directly to skeletal layers of exterior frontal and basal walls.

gelatinous layers, and in most taxa some calcareous material, the skeleton, between the cuticle and epidermis, or in some taxa between layers of the cuticle. Calcareous layers of zooidal walls and any connected intrazooidal calcareous structures form a zooidal **skeleton**, the **zooecium**. Zooecia of a colony together with any other skeletal parts form a colonial skeleton, the **zoarium**. The entire zoarium is secreted on the external side of the epidermis opposite the body cavity. The skeleton therefore is exoskeletal throughout, even though in some places it is deposited by epidermis that is infolded into existing body cavity.

Body walls are basically of two developmental kinds, exterior and interior (SILÉN, 1944a,b). **Exterior walls** extend the body cavity of zooids and the colony; **interior walls** partition preexisting body cavity into zooids or parts of zooids or extrazooidal structures. Exterior walls include an outermost cuticle or gelatinous layer, which is not necessary and commonly not present as a component of interior walls.

All zooids minimally have body cavities enclosed by body walls (Fig. 1). Body walls can be complete or incomplete so zooidal cavities can be partly open to adjacent zooidal or colony body cavities. **Feeding zooids** must be present at some stage in the lives of all colonies and have in addition to body walls and cavities a protrusible lophophore, an alimentary canal, muscles, a nervous system, and **funicular strands** (Fig. 2–4).

Zooids within a colony can differ distinctly in morphology and function at the same stages of ontogeny and in the same sexual generations. Such zooids are termed **polymorphs**. Polymorphs can be specialized to perform sexual, supportive, connective, cleaning, or defensive functions for example, and can even lack feeding organs entirely.

The body walls of feeding zooids include exterior **orificial walls** and **supporting walls** (Fig. 1). The concepts of orificial and supporting walls are based on comparisons of function and position among taxa and do not necessarily imply homology. Orientation of these zooidal walls relative to zooidal and colony growth directions (**distal**) can differ in major groups.

The orificial wall is exterior and terminal or subterminal. It bears or defines the opening (**orifice**) through which the lophophore is protruded into the environment. It is attached through the orifice to a **vestibular wall** leading to the lophophore and gut (Fig. 2–4), and may or may not be attached to other zooidal walls (Fig. 2). Some kinds of

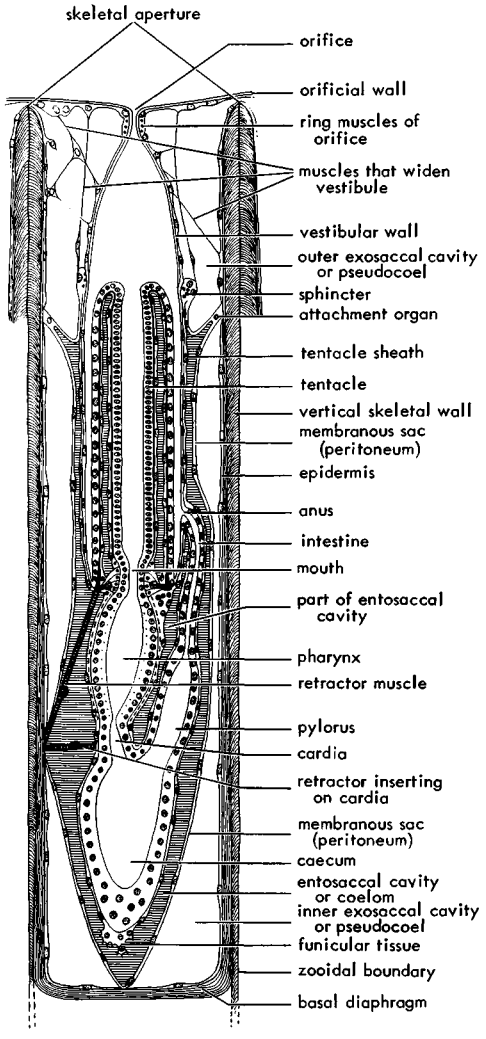

FIG. 2. Characteristics of the Bryozoa. Model of the retracted feeding zooid of a free-walled stenolaemate based on organs of a living tubuliporate (after Nielsen, 1970, fig. 13) and the zooidal living chamber of a Paleozoic trepostomate.

polymorphs lacking feeding organs also have orificial walls or their equivalents.

Supporting zooidal walls (Fig. 1) can be either interior or exterior, or a combination, and several kinds may be recognized by their position and orientation relative to the orificial wall. **Basal zooidal walls** are supporting walls that are opposite and generally parallel to orificial walls. All colonies apparently begin with one or more zooids having exterior basal walls. These basal walls form the encrusting base of the colony either alone or by extending distally as multizooidal walls. Zooids budded above the encrusting base of a colony can have exterior or interior basal walls, or can lack basal walls altogether.

Vertical walls are supporting walls that are entirely or in part at high angles to basal and orificial walls, thus giving depth, length, or both to the zooidal body cavity. Vertical zooidal walls can be exterior or interior, or a combination. Exterior vertical walls originate from multizooidal (Gymnolaemata) or extrazooidal (Phylactolaemata) walls. Interior vertical walls originate from interior or exterior zooidal walls, interior extrazooidal walls, or either interior or exterior walls of multizooidal origin (Stenolaemata, Gymnolaemata). Vertical walls may be attached distally to orificial walls, to intervening frontal walls, or a combination, or may terminate beneath orificial walls.

Frontal walls, where present (see Stenolaemata and Gymnolaemata), are exterior supporting walls that originate as zooidal or multizooidal walls. Frontal walls provide a front side to zooids more extensive than the orificial walls alone. Parts of frontal walls can extend beyond the general colony surface to form **peristomes**, which either carry orificial walls at their outer ends or surround orificial walls at their inner ends.

The walls of the vestibule and lophophore are also parts of body walls. The vestibular wall, lophophore, and alimentary canal (Fig. 2–4) apparently originate by infolding of the exterior wall of the colony or internally from the lophophore and gut of existing zooids (see Phylactolaemata). The vestibular wall surrounds a space of variable extent, the **vestibule**, and connects the orificial wall to the tentacle sheath. The vestibule is the passage through which the lophophore is protruded for feeding.

The tentacle sheath and ciliated, coelomate tentacles together constitute the **lophophore**. In position, the lophophore is that part of the body wall of a feeding zooid that begins at the inner end of the vestibule and

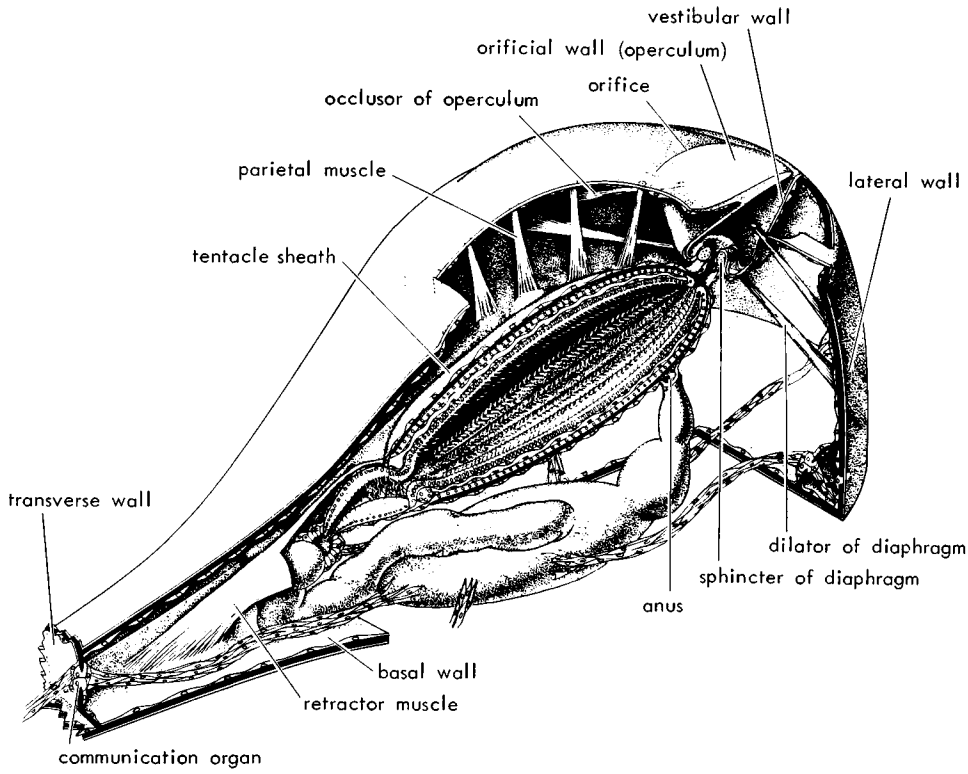

FIG. 3. Characteristics of the Bryozoa. Model of a simple gymnolaemate with the lophophore retracted, based on organs of living cheilostomates (after Nitsche, 1871, fig. 1, 2; Calvet, 1900, pl. 2) and the skeleton of a Mesozoic cheilostomate.

ends at the mouth. The **tentacle sheath** is that part of the body wall that is introverted to enclose the tentacles in the retracted position and is everted to support them in the protruded position (Fig. 3, 4). The boundary between the tentacle sheath and the vestibular wall is generally a sphincter muscle.

A single row of **tentacles** surrounds the mouth in a circular or bilobed pattern. The mouth is opened and closed by muscular action and in a small number of genera is overhung by a fold of body wall (**epistome**). In feeding, the movement of cilia on the tentacles produces currents that concentrate food particles near the mouth.

Protrusion and retraction of the lophophore are accomplished by muscular action. Protrusion involves hydrostatic pressures produced in various ways by muscles modifying the shapes of parts of the body cavity. Retraction is by direct contraction of retractor muscles.

The digestive tract is complete and recurved, so that the anus opens near the mouth. When the tentacles are protruded, the anus opens on either the distal or proximal side of the tentacle sheath wall below the row of tentacles (Fig. 2–4). The nervous system includes a ganglion near the mouth. Nephridia as well as circulatory and respiratory organs are apparently absent.

In almost all taxa, colonies, but not all zooids, are hermaphroditic; gonads form in zooidal coeloms and are ductless, sex products being released through special openings in the body wall. Embryos are commonly brooded, either within or outside body cavities, to produce ciliated **larvae** or other motile stages. Embryonic fission occurs during brooding in some modern taxa (see Steno-

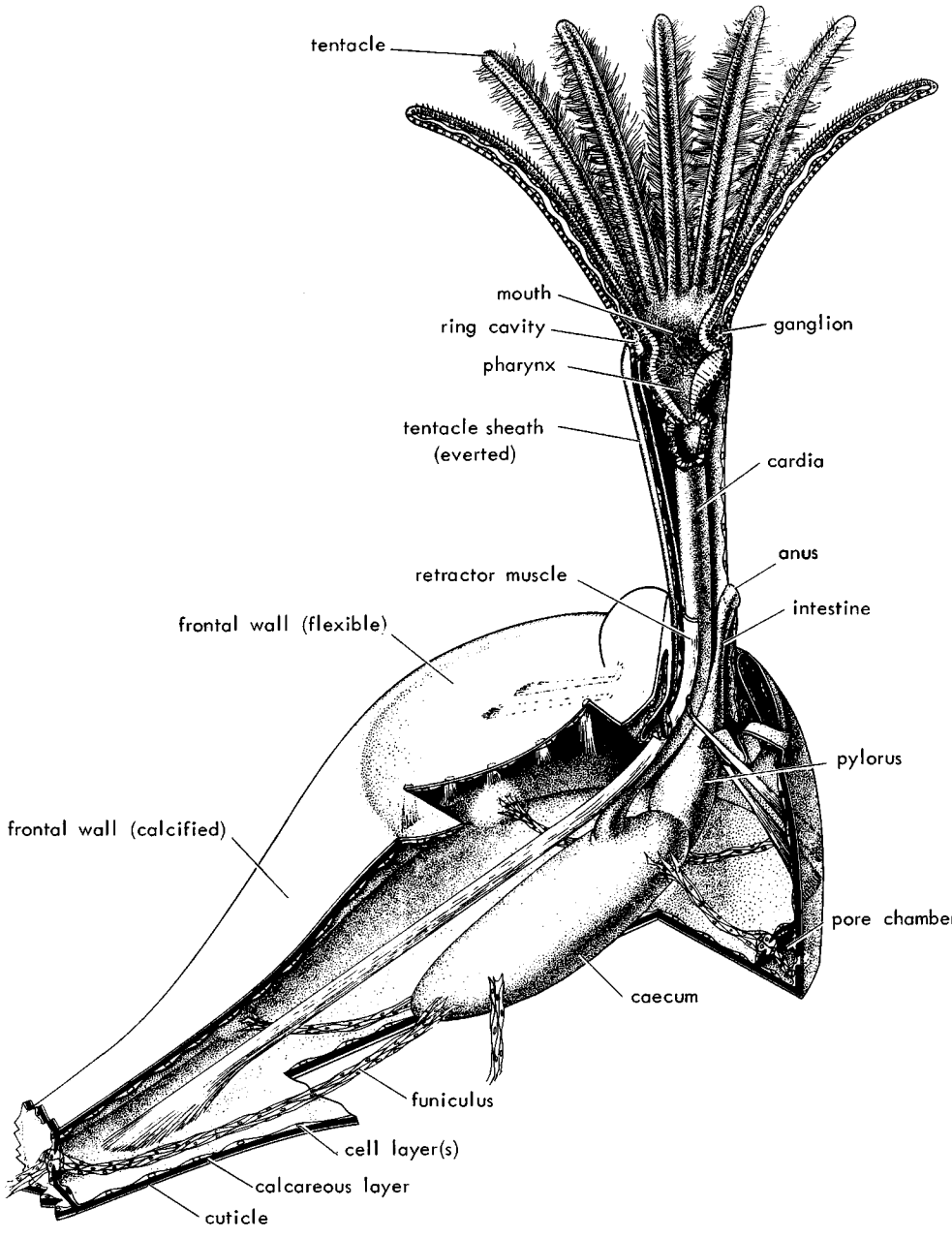

FIG. 4. Characteristics of the Bryozoa. The zooid of Figure 3 with the lophophore protruded.

laemata). Ciliated larvae include bivalve forms with complete digestive tracts and naked forms lacking digestive tracts.

A larva settles on a substrate and undergoes **metamorphosis** with extensive reorganization of tissues, typically to form a single zooid, the **ancestrula** (Fig. 1). Colonies of some taxa also may be produced asexually by **fragmentation** into groups of functional zooids and in a few taxa by the formation of resistant resting bodies. In most taxa, the ancestrula produced by a larva or the first

zooid produced by a resistant resting body differs in size or other morphologic characters from other zooids in a colony. Generally, both types of initial zooids contain feeding organs.

Asexually produced zooids following an ancestrula (Fig. 1) commonly show a morphologic gradient through several generations (**zone of astogenetic change**) leading to one or more kinds of zooids replicated in succeeding generations (**zone of astogenetic repetition**). Newly developing, asexually produced zooids (**buds**) can be initiated either as feeding organs (see Phylactolaemata) or as body walls. Buds initiated as feeding organs can develop from either exterior walls or other developing feeding organs. Buds initiated as body walls develop distally by outward expansion of exterior membranous walls of the colony or of other zooids. Proximally, buds appear as infolds from (1) interior or exterior multizooidal walls, (2) interior walls of other zooids, or (3) interior extrazooidal structures.

Parts of zooids characteristically undergo cyclic phases of degeneration and regeneration in most taxa. Degeneration products commonly form encapsulated masses of degenerating cells, termed **brown bodies**. Parts that degenerate include lophophore, gut, some muscles, and some other nonskeletal parts, varying in different groups.

HISTORICAL REVIEW

The study of Bryozoa has been marked historically by an insufficient number of workers. Approximately 20,000 fossil and living species have been described, but these are undoubtedly a small number in proportion to those that remain to be recognized and investigated. Uneven distribution of studies has left major gaps in our knowledge of Paleozoic and Mesozoic faunas, and a pattern susceptible of interpretation is just emerging from results of work on Cenozoic faunas. Little detailed information is available for the Triassic or Jurassic systems. In North America, there are comparable gaps in the Silurian, Mississippian, Pennsylvanian, Permian, Cretaceous, and upper Tertiary systems. Bryozoa of the Paleozoic Era are relatively well known from the Soviet Union but are generally unknown in Europe. Cretaceous and Cenozoic faunas in Europe have been studied extensively, but revision, synthesis, and comparison with other areas are needed. In southeast Asia, all faunas but those from the Upper Paleozoic are poorly known, and in Australia, faunal studies are scattered throughout most of the Paleozoic and part of the Cenozoic. In South America, Africa, Antarctica, and large parts of Asia, there is little knowledge of any of the fossil record.

Abundant Bryozoa have been found in a few cores of Tertiary sediments in the Atlantic, Pacific, and Indian oceans recovered by the Deep Sea Drilling Project, but the fossil record of Bryozoa in the open oceans is still poorly known.

Living faunas have been investigated extensively throughout the world, but gaps in distributions and the need for revision, synthesis, and comparison of described faunas have delayed an understanding of world biogeographic patterns.

The earliest work in which fossil Bryozoa were described and illustrated is reportedly that of Bassi (1757) (Neviani, 1894; Astrova, 1960a; Annoscia, 1968), but living Bryozoa have been studied for at least 400 years. The early history of the study of Bryozoa (summarized in detail by Harmer, 1930; Hyman, 1959; and Ryland, 1970) was marked by a series of misunderstandings of their nature, resulting in their confusion with plants and coelenterates. The animal nature of Bryozoa seems to have been established with the studies of Ellis (1754, 1755a–c), who considered most of the Bryozoa known to him to be ramified animals, which he called celliferous corallines. Linné (1758), basing his work on Ellis's descriptions and plates, named the Zoophyta as an order of the class

Vermes and considered them to be at least partly of a plant nature. He included bryozoans and coelenterates in this order. The difference between bryozoans and coelenterates was established as the result of observations of a digestive tract with two openings (DE BLAINVILLE, 1820; AUDOUIN & MILNE-EDWARDS, 1828), and of ciliated tentacles (GRANT, 1827). This difference was formalized by establishment of a taxon to which the name Polyzoa of THOMPSON (1830) or Bryozoa of EHRENBERG (1831) was applied. Although the name Polyzoa was published first and a controversy existed for many years (HARMER, 1947; BROWN, 1958), the name has been dropped in most recent literature.

When THOMPSON separated Bryozoa from coelenterates, he placed them with the Mollusca. MILNE-EDWARDS (1843) named the Molluscoidea to include Bryozoa and tunicates, and HUXLEY (1853) added Brachiopoda to this group. The use of Molluscoidea, as either a phylum or a subkingdom, persisted into the twentieth century (CANU & BASSLER, 1920). The most common usage has been as an emended taxon including Bryozoa and Brachiopoda. In some classifications the Phoronida have been included. The names Podaxonia (LANKESTER, 1885), Tentaculata (HATSCHEK, 1888), Vermidea (DELAGE & HEROURARD, 1897), and Lophophorata (HYMAN, 1959) have also been used for varying combinations of these and other phyla.

NITSCHE (1869) distinguished two groups among the Bryozoa as known in the nineteenth century and named them Entoprocta and Ectoprocta. These groups were elevated to phylum rank by HATSCHEK (1888). Some workers (NIELSEN, 1971) still include Entoprocta in the phylum Bryozoa, as was done in the earlier edition of this *Treatise* (BASSLER, 1953). The Entoprocta are excluded from the Bryozoa as recognized here. CUFFEY (1973) included phyla Entoprocta and Ectoprocta in a superphylum Bryozoa.

The shifts in hierarchic level and contents have led some more recent workers to abandon the name Bryozoa for the phylum and to use the name Ectoprocta (HYMAN, 1959; SCHOPF, 1967, 1968; CUFFEY, 1969). The name Bryozoa is used for the phylum as understood here to exclude the phylum Entoprocta. Reasons for this usage were given by MAYR (1968). Controversy over the name of the phylum contributes little to understanding the bryozoans (SOULE & SOULE, 1968).

The relationships of the Bryozoa to the other phyla have not been established on the basis of a fossil record from which evolutionary trends can be interpreted. Necessary evidence for hypotheses of the origin of Bryozoa, such as that from the Phoronida discussed by FARMER, VALENTINE, and COWEN (1973), would be morphologies intermediate between Bryozoa and other groups that existed at the time of the earliest Bryozoa.

Bryozoa have commonly been divided into two major groups, varying slightly in composition according to the morphologic criteria employed. DE BLAINVILLE (1834) distinguished Bryozoa having bilobed lophophores from those having circular lophophores. GERVAIS (1837) named these groups Polypiaria hippocrepia and Polypiaria infundibulata, respectively. VAN BENEDEN (1848) recognized the hippocrepia division in his study of freshwater Bryozoa, and BUSK (1852) used the name Polyzoa infundibulata in his study of marine Bryozoa. ALLMAN (1856) rejected the classification based on the shape of the lophophore as an artificial grouping and named two new groups, the Phylactolaemata and the Gymnolaemata, based on the possession and lack, respectively, of an epistome overhanging the mouth. ALLMAN's names have generally been accepted in the subsequent literature. Two of the genera placed in the Phylactolaemata and one placed in the Gymnolaemata by ALLMAN, however, were removed by NITSCHE in 1869 to form the phylum Entoprocta.

BORG (1926a) named the Stenolaemata as a third group equal in rank to the Phylactolaemata and Gymnolaemata by dividing the Gymnolaemata into two groups, based on shapes of zooids. He retained the name Gymnolaemata for the major group with a more restricted concept. This three-part divi-

sion of the phylum has been used by SILÉN (1944a,b), RYLAND (1970), and BOARDMAN and CHEETHAM (1973).

MARCUS (1938a) and ASTROVA (1960a) retained ALLMAN's two-part division of the Bryozoa into Phylactolaemata and Gymnolaemata as major groups of equal rank. MARCUS further proposed a two-part subdivision of the Gymnolaemata at the next lower taxonomic level and named these groups Stenostomata and Eurystomata. The name Stenostomata was proposed as a replacement for BORG's Stenolaemata; the Eurystomata were proposed as a new group.

CUFFEY (1973) proposed a formal classification in which Phylactolaemata, Gymnolaemata, and Stenolaemata were retained as groups equal in rank, but arranged in a different two-part division of the phylum (called Ectoprocta by CUFFEY). The Phylactolaemata and Gymnolaemata, considered classes by CUFFEY, were united in a new superclass Pyxibryozoa. The Stenolaemata formed the only class of a new superclass Tubulobryozoa.

For reasons discussed in the following section, the Phylactolaemata, Gymnolaemata, and Stenolaemata are retained here as taxa of class rank with no further grouping between class and phylum levels.

BUSK (1852) subdivided the living marine Polyzoa infundibulata (Gymnolaemata of ALLMAN) into the Cyclostomata (here called Tubuliporata),[1] Cheilostomata, and Ctenostomata. The Tubuliporata and Cheilostomata were soon recognized among fossil Bryozoa (BUSK, 1859), and two more divisions were later added, the Trepostomata by ULRICH (1882) and Cryptostomata by VINE (1884). In 1957, ELIAS and CONDRA gave the name Fenestrata to a group they removed from the Cryptostomata, and in 1964, ASTROVA proposed the name Cystoporata for a group she removed from the Paleozoic Tubuliporata, Cryptostomata, and Trepostomata. All seven of these groups are considered here to be orders.

DISTINGUISHING CHARACTERISTICS OF CLASSES

The classification used here at the class level follows the three-part grouping of BORG (1926a), SILÉN (1944a,b), and some subsequent authors. It may well require modification as additional data become available and therefore is used here as an initial basis for discussion.

Phylum Bryozoa
Class Stenolaemata
  Order Tubuliporata
    (=Cyclostomata of BUSK)
  Order Trepostomata
  Order Cryptostomata
  Order Cystoporata
  Order Fenestrata
Class Gymnolaemata
  Order Ctenostomata
  Order Cheilostomata
Class Phylactolaemata

The diagnoses of the classes Stenolaemata and Gymnolaemata are based on our own experience as much as possible. We have relied entirely on the literature and the review by WOOD in this volume for the characteristics of the Phylactolaemata. We have, however, attempted to describe phylactolaemate morphology using terminology consistent with that employed for the other two classes. Characterizations of these classes represent our present understanding and include as many characters as this understanding permits. New characters undoubtedly will be added as revision at the generic level proceeds.

[1] Because of homonymy with the vertebrate order Cyclostomata DUMÉRIL, 1806, *Treatise* policy recommends replacement of the well-known name Cyclostomata BUSK, 1852; however, this replacement is not obligatory under the International Code of Zoological Nomenclature. BUSK listed Tubuliporina without direct author reference as the only synonym of the Cyclostomata (1852, p. 347). Earlier, in 1847, JOHNSTON had clearly defined the name Tubuliporina as a group name to include the modern species of the Tubuliporidae JOHNSTON, 1838, and the Crisiadae JOHNSTON, 1847 (present-day Crisiidae). BUSK renamed the Tubuliporina on the conformation of the aperture rather than any significant change in concept or content. The name Tubuliporina is changed to Tubuliporata JOHNSTON, 1847, to conform to order-level endings and to avoid conflict with the use of Tubuliporina as a suborder. Research on this problem was done by OSBORNE B. NYE, JR.

We have attempted to recognize comparable, potentially homologous, phylum-wide structures in these morphologically different classes in order to employ a consistent language to express relative differences and similarities among taxa. Comparability of structures has been evaluated from their modes of growth, functions, and positional similarities. Homologies (comparability due to common ancestry) of most of these structures have not been tested against the fossil record at these higher taxonomic levels. The significance in phylogenetic classification of characters derived from many of these structures, therefore, has yet to be determined. Some characters, such as presence or absence of extrazooidal parts, of polymorphism, and of frontal zooidal walls, might be shown by future study to incorporate iteratively derived states.

We also have attempted to describe and compare the three classes as polythetically as possible. A polythetic classification (SNEATH & SOKAL, 1973, p. 21) results from clustering colonies, populations, or taxa that possess a majority of character states common to a majority of the members of a cluster. A cluster becomes a potential taxon that can be evaluated from data on occurrence in time and space. No one character state or combination of character states must be present for a group to be included in the taxon. The traditional approach to classification in Bryozoa has been monothetic, that is, all members of a taxon have been required to possess a character state or a combination of character states unique to that taxon. Examples of character states used monothetically at high levels of classification include the presence or absence of an epistome overhanging the mouth and the presence or absence of intrinsic muscle layers in the body wall. The need for polythetic use of characters at the species level has been recognized for a long time. At higher levels the choice of "defining" monothetic characters has been largely arbitrary and has resulted in at least as much instability as such choice has at lower levels.

The rigorous procedures needed to develop polythetic clusters at the class level require more detailed data than are now available. The polythetic characterizations of the Stenolaemata, the Gymnolaemata, and the Phylactolaemata below include states of 48 morphologic characters (Table 1). Of these characters, 37 are reflected directly or indirectly in skeletons or preserved remnants of soft parts in fossil taxa, and 11 are reflected only in soft parts of living taxa.

In this comparison of the three classes, morphologic similarities were estimated for each pair of classes without making detailed counts of included genera, most of which must be restudied before all character states are available. Two estimates were made, one using as many of the 48 characters as applicable (Fig. 5,*A*) on the assumption that soft parts of fossil taxa were like those of living representatives of the same class, and the other based only on the 37 characters reflected in the phylactolaemates and in skeletons or remnants of fossil taxa (Fig. 5,*B*) of the other two classes.

To make the comparison as polythetic as possible, estimates of similarity between each pair of classes were based on the number of character states shared by all taxa in each pair plus the number of states partly shared by overlapping proportions of taxa in each pair. At this stage in our understanding of class characters, the phylogenetic significance of the absence of a character in two of the three classes is not known, so shared absence was given the same weight as shared presence.

Of the 48 characters used to characterize the three classes, 25 provided entirely shared states for a pair of classes and 14 of these characters have unique states in the third class; 21 provided only partly shared states for any pair of classes; and 2 provided only states unique to a class. Fifteen characters provided states partly shared by all three classes.

The proportions of overlap in partly shared states of different characters are estimated to range from few genera to almost all genera within the classes, and these proportions were estimated to the nearest 20 percent (Table 1). The percentages of overlap in four char-

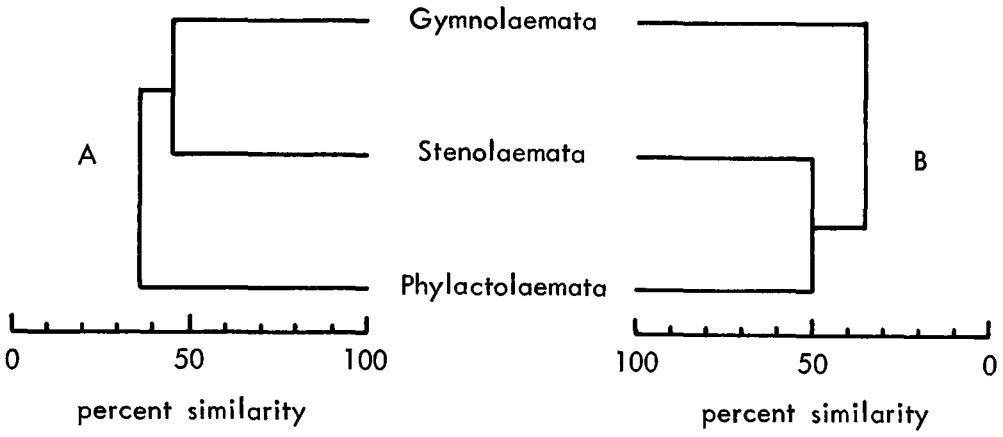

FIG. 5. Distinguishing characteristics of classes. Dendrograms expressing similarities between classes Stenolaemata, Gymnolaemata, and Phylactolaemata based on estimated percentages of morphologically overlapping genera in pairs of classes (Table 1, Fig. 6).——*A*. Dendrogram based on all 48 characters listed in Table 1.——*B*. Dendrogram based on 37 characters, omitting those known only in living genera (indicated by asterisk in Table 1).

acters are illustrated diagrammatically in Figure 6. Percentages were employed to remove the effect of the enormous difference in numbers of genera in classes. To make the similarity estimates comparable (scales of similarity in Fig. 5), the sum of shared states plus percentages of overlap for partly shared states was divided by the number of characters applicable to the comparison of each pair of classes.

If all 48 characters are considered polythetically in comparing the three classes (Fig. 5,*A*), Stenolaemata and Gymnolaemata are more similar to each other than either class is to the Phylactolaemata. This result is apparently in agreement with the two-part arrangement of living taxa employed by MARCUS (1938a) and earlier authors. If the 11 characters that are reflected only in the soft parts of living taxa in all three classes are omitted (Fig. 5,*B*), the similarity between Stenolaemata and Phylactolaemata becomes greater than that of Gymnolaemata to either. These differences in similarity are small; however, that between any pair of classes falls between 29 and 50 percent with either set of characters employed (Table 1). It seems improbable that these results reflect any clear taxonomic grouping between class and phylum levels. The three classes seem best retained as equally distinct taxa until fossil evidence of their phylogenetic relationships to each other becomes available.

If only character states shared by all taxa in a pair of classes are considered (100 percent in Table 1), the results are similar to those of the polythetic comparison, even though this reduces the number of characters to 25. Stenolaemata and Gymnolaemata share states of 9 characters, 4 of which are reflected in skeletons or remnants of fossil taxa. Stenolaemata and Phylactolaemata share 9, 8 of which are reflected in fossil stenolaemates. Phylactolaemata and Gymnolaemata share 7, 5 of which are reflected in fossil gymnolaemates. This monothetic sharing approach to comparison of classes omits characters derived from interzooidal communication organs, confluent coelom, and budding zones, for example. Present understanding does not justify rejection of such characters at this level, although future discovery of phylogenetic evidence in the fossil record may reveal them to be important only at lower taxonomic levels.

Considering monothetically the characters that are unique to a class, the Phylactolaemata and Gymnolaemata are about equally

TABLE 1. *Morphological Comparison of the Three Major Groups of the Phylum Bryozoa.*

(Percentages to the nearest 20 are estimates of component genera with overlapping character states in each pair of groups; see Fig. 6 and text. Overall morphologic similarity is indicated at the foot of the table; see also Fig. 5. A asterisk marks a character known only in living genera; P, present; A, absent; S, saclike; C, cylindrical.)

	Character	Percent Overlap of Character States		
		Stenolaemata–Gymnolaemata	Stenolaemata–Phylactolaemata	Gymnolaemata–Phylactolaemata
1	Outermost layer of exterior walls	100, cuticular	>80, cuticular	>80, cuticular
2	Calcification (P or A)	>80, P	0	<20, A
3*	Composition of skeleton	60, calcite	—	—
4	Growth directions of zooids and colony	0	80[a]	0
5	Erect basal zooidal walls (P or A)	40 (20P, 20A)	80, A	20, A
6	Erect basal zooidal walls exterior or interior	20 (<20 int., <20 ext.)	—	—
7	Vertical zooidal wall orientation relative to zooidal growth direction	0	100	0
8	Vertical zooidal walls exterior or interior or a combination	20 (<20 ext., <20 int.)	<20, ext.	<40 (<20 ext., 20 comb.)
9	Completeness of interior vertical zooidal walls	>80, complete	<20, incomplete	0
10	Vertical zooidal walls with endozone and exozone	<20, A	<20, A	100, A
11	Ontogenetic duration of vertical zooidal wall growth	20, early	20, early	100, developed early
12	Shape of zooidal body cavity (S or C)	40 (20S, 20C)	20, C	20, C
13	Frontal zooidal wall (P or A)	20, P	80, A	0
14	Frontal zooidal wall orientation relative to zooidal growth direction	>80, parallel	—	—
15	Flexibility of frontal zooidal wall	0	—	—
16	Orificial wall orientation relative to zooidal growth direction	0	100, transverse	0
17	Orificial wall terminal or subterminal	<20, terminal	100, terminal	<20, terminal
18	Structure of orificial wall	0	100, single membrane	0
19	Orificial wall free or fixed to other zooid walls	20, fixed	20, fixed	100, fixed
20	Ratio of area of orificial wall to cross section of zooidal body cavity	20, smaller	80, same	0
21	Shape of orifice	0	100, simple pore	0
22	Completeness of skeletal margin of aperture	<20	—	—
23	Interzooidal communication organs (P or A)	40, P	60, A	0
24	Interzooidal communication organs in interior or exterior walls	<20, int. only	—	—
25	Extent of confluent body cavity among fully developed zooids	20, A	80[b]	0
26	Retracted position of lophophore and gut during ontogeny	20, constant	20, constant	100, constant

[a] Varies ontogenetically.
[b] Colony-wide.
[c] Multizooidal.

TABLE 1. *(Continued from preceding page.)*

	Character	Percent Overlap of Character States		
		Stenolaemata–Gymnolaemata	Stenolaemata–Phylactolaemata	Gymnolaemata–Phylactolaemata
27	Regeneration and brown bodies (P or A)	100, P	0	0
28	Membranous sac (P or A)	0	0	100, A
29	Parietal muscles (P or A)	0	100, A	0
30	Intrinsic body wall muscle layers (P or A)	100, A	0	0
31*	Diaphragmatic dilator muscles (P or A)	0	0	100, P
32*	Vestibular dilator muscles (P or A)	<20, P	100, P	<20, P
33*	Tentacle number	100, 8–35	<20, <35	<20, ≤35
34*	Tentacle arrangement	100, circular	<20, circular	<20, circular
35*	Epistome (P or A)	100, A	0	0
36	Polymorphism (P or A)	<80 (60P, <20A)	40, A	<20, A
37	Extrazooidal parts (P or A)	80 (20P, 60A)	40, P	20, P
38	Extrazooidal skeleton exterior or interior	60, int.	—	—
39	Brooding of embryos (P or A)	40 (<40P, <20A)	40, P	>80, P
40	Known brooding within or outside of body cavity	<20, within	100, within	<20, within
41*	Single or multiple embryos per zygote	0	0	100, single
42*	Initial zooids produced from larva or directly from embryo	100, larva	0	0
43*	Encapsulated resistant resting bodies produced from funicular strands (statoblasts) or body walls (hibernacula)	—	—	0
44*	Initial zooids produced asexually (P or A)	>80, A	0	<20, P
45	Primary zone of astogenetic change (P or A)	>80, P	100, P	>80, P
46	Extent of budding zones	20[c]	20[b]	0
47	Initial structures of bud	100, body wall	0	0
48*	Anus on distal or proximal side of tentacle sheath	100, distal	0	0
	Percent similarity of pairs of classes:			
	All characters	45	42	29
	Omitting characters from living genera	39	50	29

distinct. Phylactolaemata all have unique states of 7 characters, 3 of which have contrasting states recognizable in fossil stenolaemates and gymnolaemates (indicated in Table 1 by 0 percent, or 0 percent and "not applicable" under pairs that include the Phylactolaemata). Gymnolaemata have unique states of 6 characters, all of which have contrasting states recognizable in fossil stenolaemates. Stenolaemata have the fewest characters with unique states, 2, one of which is assumed to have a contrasting state in fossil gymnolaemates.

The extreme approach to a monothetic

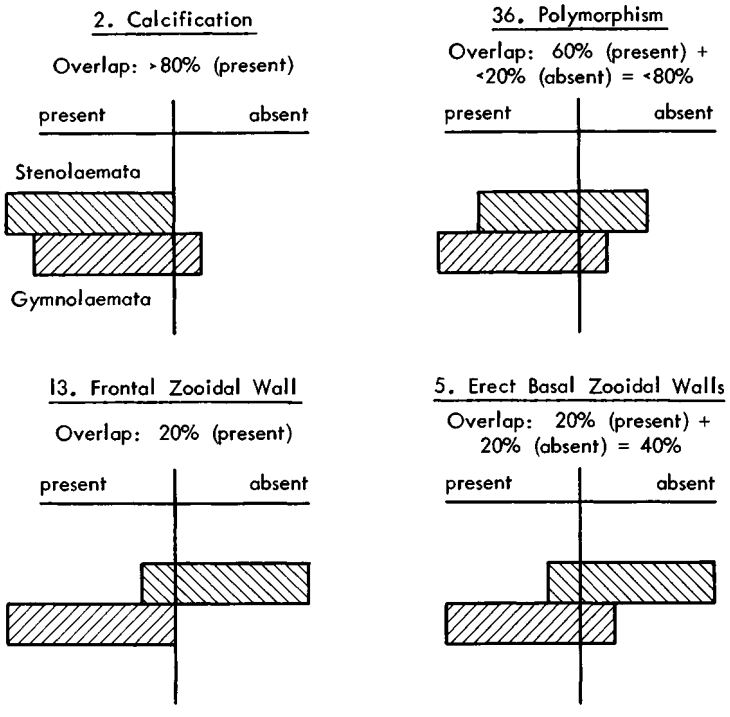

FIG. 6. Distinguishing characteristics of classes. Estimated percentages of stenolaemate and gymnolaemate genera having overlapping states of four morphologic characters (numbered as in Table 1). Bars of equal length represent 100 percent of the genera in classes, even though numbers of genera in classes are unequal. In two characters shown, calcification and frontal zooidal wall, Stenolaemata and Gymnolaemata overlap only in one state. In the other two characters shown, these two classes overlap in both states. In all four characters shown, all phylactolaemate genera have only one state, absent, and thus overlap one or both other classes to different degrees (see Table 1).

classification is the search for the panacea character or characters having states shared by all taxa of each class and being unique to each class. None of the characters used here separates all three classes.

Even though we obtained some minor differences in the comparisons between any pair of classes, depending on the characters used, with both the polythetic and monothetic approaches, our results are all strikingly different from the two-part arrangement proposed by CUFFEY (1973). We found no evidence that Phylactolaemata and Gymnolaemata (forming the superclass Pyxibryozoa of CUFFEY) are more similar to each other than either is to the Stenolaemata (the only class in the superclass Tubulobryozoa of CUFFEY). This major difference in results may be at least partly explained by the number of different characters used, especially the char-

FIG. 7. Stenolaemate colonies.——*1a,b. Hornera* sp., rec., Westernport, Vict., Australia; fenestrate, free-walled colony with branches connected by crossbars of zooids, zooidal apertures on one side of branches only; *a,* lat. view, *b,* growing surface, USNM 220028, ×2.——*2a,b. Discocytis lucernaria* (SARS), rec., Kvaenang Fjord, Nor., depth of 145–180 m; stalked colony, zooids at ends of rays free-walled, stalk covered by smaller, free-walled polymorphs at high angles to zooids and surface of stalk; *a,* lat. view, *b,* growing surface, USNM 220029, ×4.——*3. Plagioecia* sp., rec., Arctic O.; growing surface of bifoliate colony, zooids free-walled in budding zones near edges of medial multizooidal walls, zooids fixed-walled proximally, developing secondary nanozooids of SILÉN & HARMELIN (1974); USNM 220030, ×4.

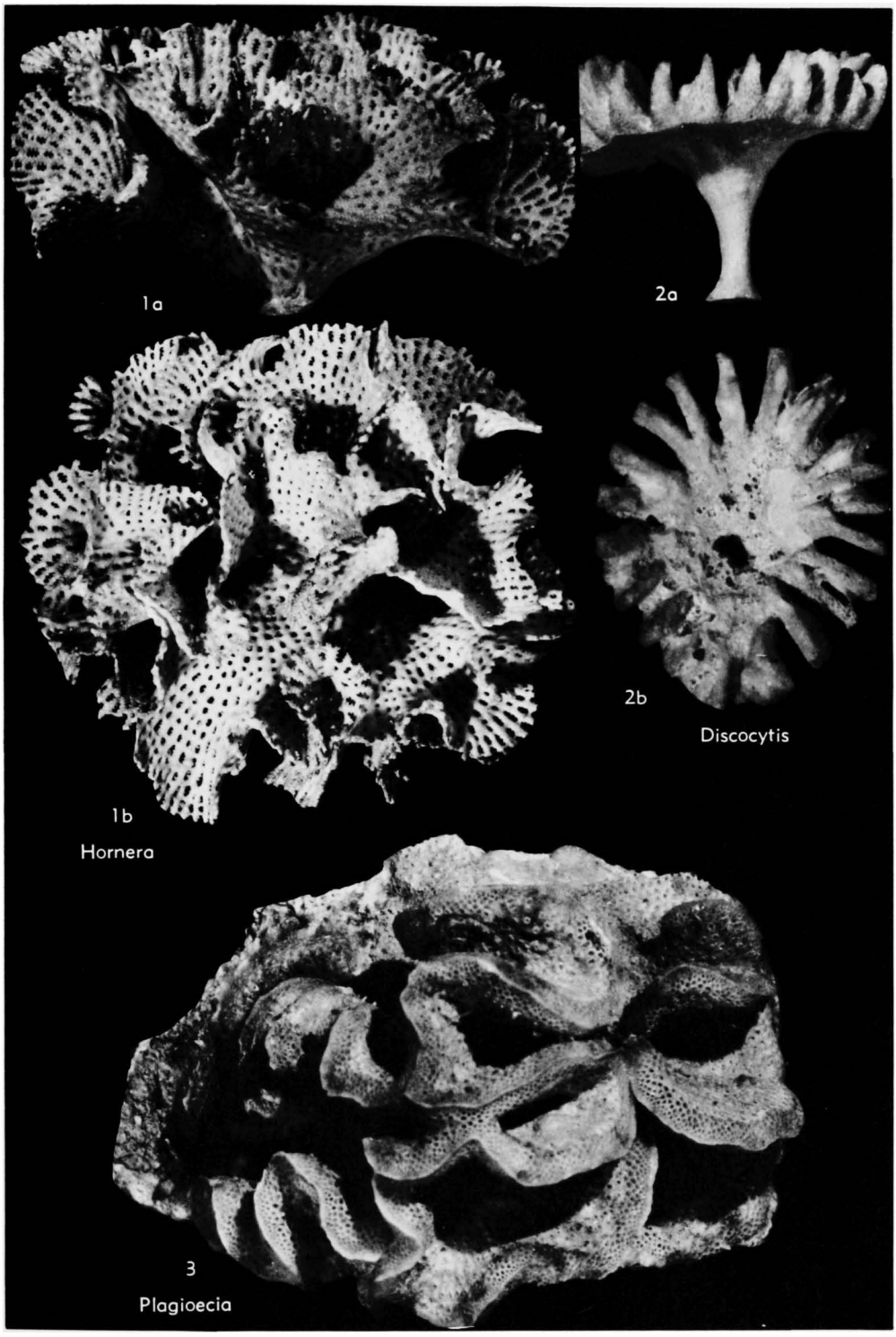

FIG. 7. *(For explanation, see facing page.)*

acters that have become available in the past few years (CUFFEY, pers. commun., 1975). Also, some characters and character states were interpreted differently. Even though CUFFEY derived his classification polythetically using the characters available to him, the verbal description in his classification is monothetic, including only the character states shared by all component taxa of each major taxon (CUFFEY, 1973, p. 553). Without the full set of character states for the CUFFEY classification, a detailed comparison with our results is not possible.

Class Stenolaemata.—The Stenolaemata are exclusively marine and have an extensive fossil record (Fig. 7–9). They constitute the overwhelming majority of bryozoans from the Ordovician into the Cretaceous and occur in large numbers in many Tertiary and modern faunas.

An exterior cuticle forms a complete outermost layer around living colonies and presumably occurred around fossil colonies as well. Encrusting basal colony walls are direct lateral extensions of the exterior walls of basal discs of ancestrulae (Fig. 1) and are exterior, multizooidal, and calcified. All basal, vertical, and frontal zooidal walls (Fig. 1) are calcified. Almost all skeletons are calcitic; a few species in the Triassic are aragonitic.

Basal zooidal walls occur in most colonies as parts of encrusting multizooidal colony walls and so are exterior along colony bases. In erect parts of colonies, basal zooidal walls can be parts of multizooidal walls that are either interior (**bifoliate colonies** and probably some **unilaminate colonies**) or exterior (some unilaminate colonies). In some unilaminate and **dendroid colonies**, basal zooidal walls can be parts of interior walls of other zooids. In erect parts of most dendroid colonies, the inner ends of zooids are pointed and basal walls are absent.

Vertical zooidal walls form elongated conical or tubular shapes. Vertical walls are complete except possibly for those with small skeletal gaps in several Paleozoic species. They are interior walls, except for those in the few uniserial or multiserial species, which are exterior or a combination. Growth directions of vertical walls parallel long axes of zooids (Fig. 10, 11). Zooids can commonly be divided ontogenetically into inner and outer parts. Inner parts (**endozones**) are characterized by one or a combination of growth directions at low angles to colony growth directions or colony surfaces, thin vertical walls, and relative scarcity of intrazooidal skeletal structures. Outer parts (**exozones**) are characterized by growth directions at high angles to colony growth directions or colony surfaces, thicker vertical walls, and concentrations of intrazooidal skeletal structures (Fig. 10, 11).

Frontal zooidal walls (Fig. 1, 11) occur in relatively few stenolaemates, most commonly in species of post-Paleozoic age. They are exterior walls (as in the Gymnolaemata), and so their outermost layer is part of the colony-wide exterior cuticle. Subjacent skeletal layers are structurally continuous with or attached to outermost edges of skeletal layers of interior vertical zooidal walls. Frontal walls range in orientation from nearly parallel with, to perpendicular to, zooidal growth direction in different taxa. Frontal walls in stenolae-

FIG. 8. Stenolaemate colonies.——*1a,b. Neofungella* sp., rec., Albatross Sta. 3212, lat. 54°05′30″ N., long. 162°54′ W., S. of Alaska, depth of 90 m; stalked, free-walled colony with stalk covered by exterior terminal diaphragms; *a,* growing surface, *b,* lat. view, USNM 220031, ×4.0.——*2. Corymbopora* sp., Cret. (Cenoman.), Le Mans, Sarthe, France; stalked, branching colony with free-walled autozooids, stalks covered by small, free-walled polymorphs; lat. view, USNM 220032, ×4.0——*3. Frondipora verrucosa* (LAMOUROUX), rec., Medit. Sea., Oran, Alg.; colony of anastomosing branches with clusters of free-walled zooids surrounded by exterior frontal walls of combined free- and fixed-walled zooids; growing surface except for nonzooidal reverse side of branches in lower part of figure, USNM 220033, ×1.5.——*4. Tretocycloecia* sp., up. mid. Yorktown F., Mio., Rice's Pit, Hampton, Va.; free-walled dendroid colony, many branches anastomosing; growing surface, USNM 220034, ×1.5.

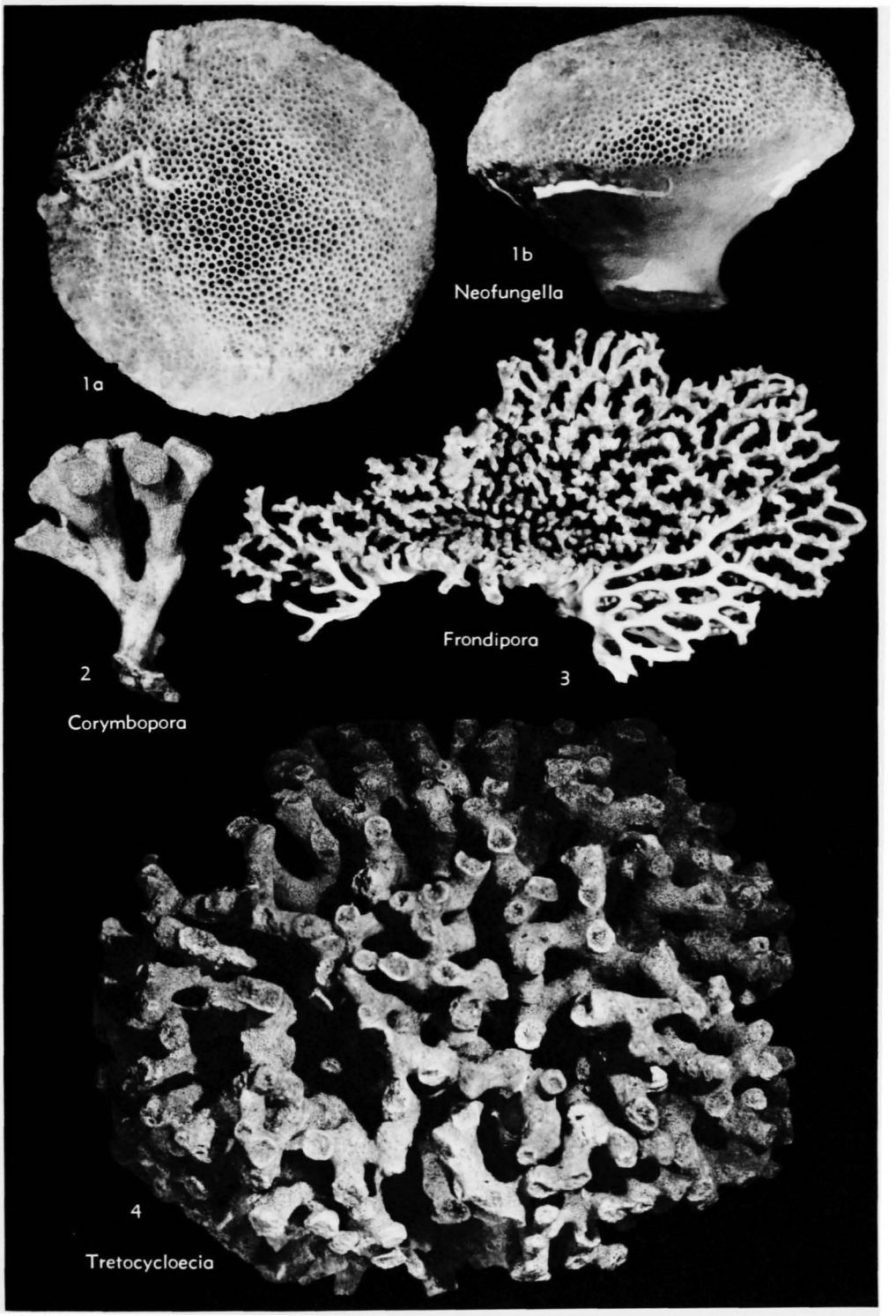

FIG. 8. *(For explanation, see facing page.)*

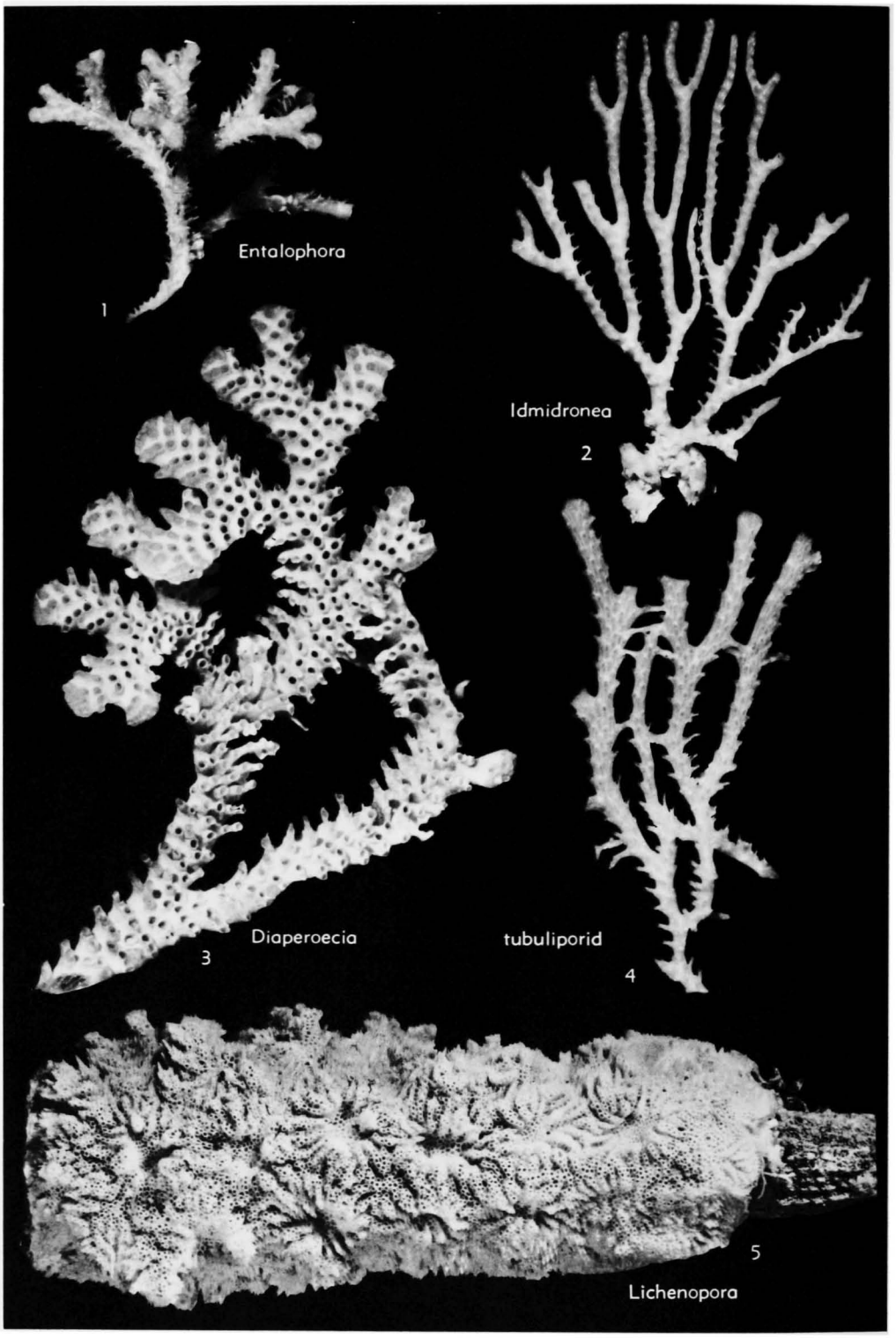

FIG. 9. *(For explanation, see facing page.)*

mates are entirely calcified and so are inflexible in lophophore protrusion.

Zooecial **apertures** (Fig. 2) are the terminal skeletal openings of zooids. They occur in all stenolaemates, have complete margins, and vary in shape in different taxa. They are the terminations of frontal wall skeleton, vertical wall skeleton where frontal walls are absent, or a combination. Zooids typically elongate through most of their ontogeny by growth of zooidal body walls at apertures. In a few fossil taxa, apertures are covered by exterior, skeletal, hinged structures that apparently performed an operculumlike function.

Orificial walls (Fig. 10, 11) are single membranous exterior body walls that cover skeletal apertures and include the simple circular orifices through which tentacles are protruded. Orificial walls are transverse to zooidal growth direction in most taxa and are terminal, except in the few fossil taxa in which operculumlike structures apparently covered them. Similar orificial walls are assumed for fossil taxa because of the general likeness of supporting zooidal walls and simple skeletal apertures among fossil and recent taxa.

The relationships of orificial walls to zooecial apertures of vertical and frontal walls produce three different kinds of colonies, the third kind being a combination of the first two.

1. In most stenolaemate colonies, frontal walls are absent in feeding zooids and vertical walls support membranous orificial walls (Fig. 10) apparently without direct attachment (**free-walled colonies**). In free-walled colonies, orificial walls are parts of exterior membranous walls that completely cover colonies above their encrusted bases. The membranous covering wall of a colony is held in place by attachment organs within the zooids (Fig. 2). With minor exceptions, all skeletal parts above encrusting colony walls are interior in origin in free-walled colonies and are separated from exterior membranous colony walls by confluent outer body cavities. In some post-Paleozoic taxa, colony-wide exterior cuticle is attached to outer sides of skeletal layers of terminal diaphragms and outer walls of brood chambers.

2. In colonies with frontal walls in feeding zooids (Fig. 1, 11) the colony-wide exterior cuticle is attached to outer surfaces of skeletal layers of the frontal walls, and is also the outer layer of orificial walls, as in all Bryozoa. The cuticular layer of the frontal wall, therefore, fixes individual orificial walls directly to zooecial apertures (**fixed-walled colonies**). Exterior walls on feeding sides of fixed-walled colonies consist primarily of orificial and frontal walls of contiguous zooids. The colony-wide outer body cavity of free-walled colonies is therefore eliminated.

3. In some taxa that have feeding zooids arranged in isolated clusters on colony surfaces, free- and fixed-walled morphologies are combined. The clusters are isolated from each other by exterior frontal walls of their outermost zooids. The apertures of the outermost zooids of each cluster are parts of both frontal and interior vertical walls so that their orificial walls are partly fixed and partly free. The apertures of inner zooids of larger clus-

FIG. 9. Stenolaemate colonies.——*1. Entalophora depressa* (SMITT), rec., Albatross Sta. 2407, Gulf of Mexico; dendroid colony of fixed-walled zooids with long peristomes; USNM 220035, ×4.——*2. Idmidronea atlantica* (FORBES), rec., Thatcher's Is. Light, Mass., depth of 60 m; unilaminate, regularly bifurcating colony of fixed-walled zooids with long peristomes of different lengths within a row, some with flaring ends, reverse side of branches covered by exterior multizooidal wall lacking zooids; USNM 220036, ×4.——*3. Diaperoecia* sp., rec., Australia; unilaminate colony of fixed-walled zooids with some anastomosing branches, reverse side of branches covered by exterior multizooidal wall; USNM 220037, ×4.——*4.* Tubuliporid, rec., Gulf of Mexico; unilaminate colony of fixed-walled zooids with some anastomosing of branches and crossbars of single or clustered zooids, reverse side of branches covered by exterior multizooidal wall; USNM 220038, ×4.——*5. Lichenopora* sp., rec., Marcial Point, Gulf of Lower Cal., Mexico; complex of free-walled colonies encrusting stick, radial rows formed by zooids with long interior-walled peristomes; USNM 220039, ×5.

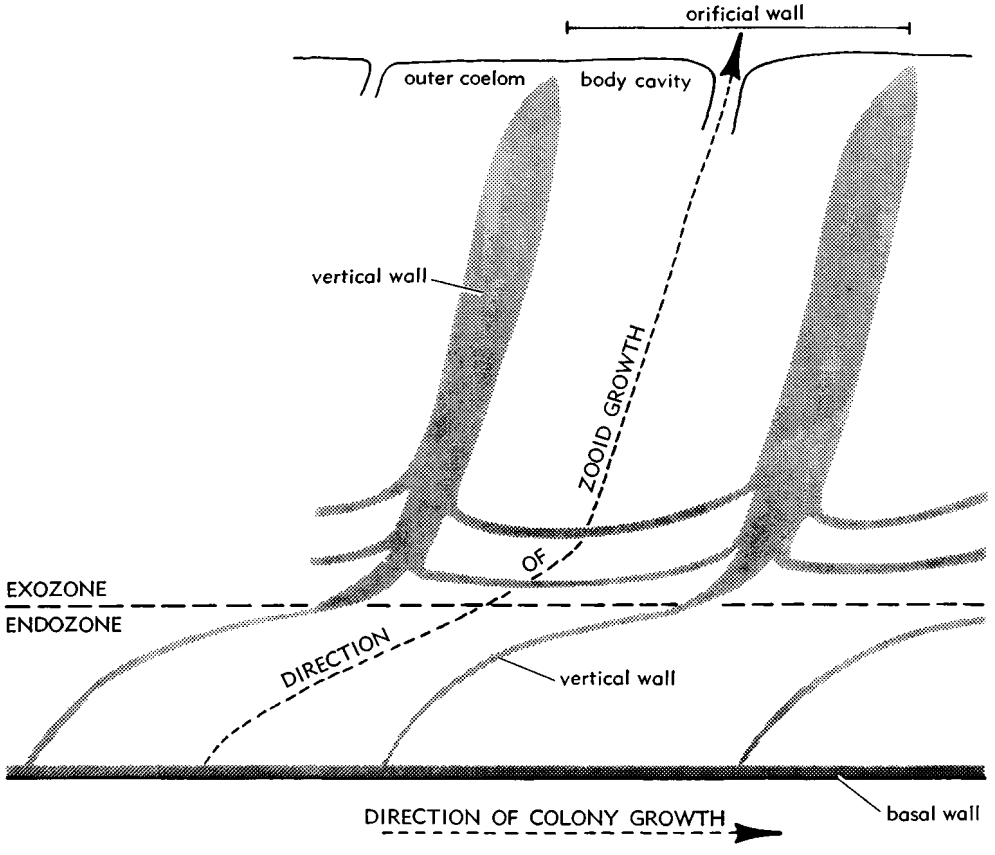

FIG. 10. Stenolaemate colonies. Diagram of a longitudinal section through a zooid of a unilaminate free-walled colony. The frontal wall is absent and the membranous exterior orificial wall is not attached to interior vertical walls (stippled) so that the body cavity is colony-wide around ends of vertical walls. Transverse skeletal diaphragms (stippled) act as floors of the living chamber sequentially with ontogenetic growth. Soft parts are deleted except for the orificial wall and the external cuticle of multizooidal basal wall.

ters are supported entirely by vertical walls so that those zooids are free-walled and an **outer coelomic space** occurs within a cluster. (In Table 1, line 19, the term "fixed" includes both fixed-walled and these combined taxa.)

Physiologic communication among fully developed zooids and between feeding zooids and extrazooidal structures is assumed for all stenolaemates except for a few fixed-walled species of Paleozoic age. Communication must have occurred through confluent outer body cavity around ends of vertical zooidal walls and extrazooidal skeleton in free-walled taxa. In most post-Paleozoic stenolaemates communication is assumed through pores (Fig. 11) in interior vertical zooidal walls. Two means of interzooidal communication, therefore, are assumed for most free-walled taxa of post-Paleozoic age. Additional communication is assumed in a few post-Paleozoic taxa that have communication pores in erect interior median walls, and in a few Paleozoic taxa that have communication pores and gaps in vertical skeletal walls.

In modern stenolaemate species a **membranous sac** (see Fig. 2) surrounds the digestive and reproductive systems in feeding zooids and divides the living chamber into two parts, the **entosaccal cavity** within the

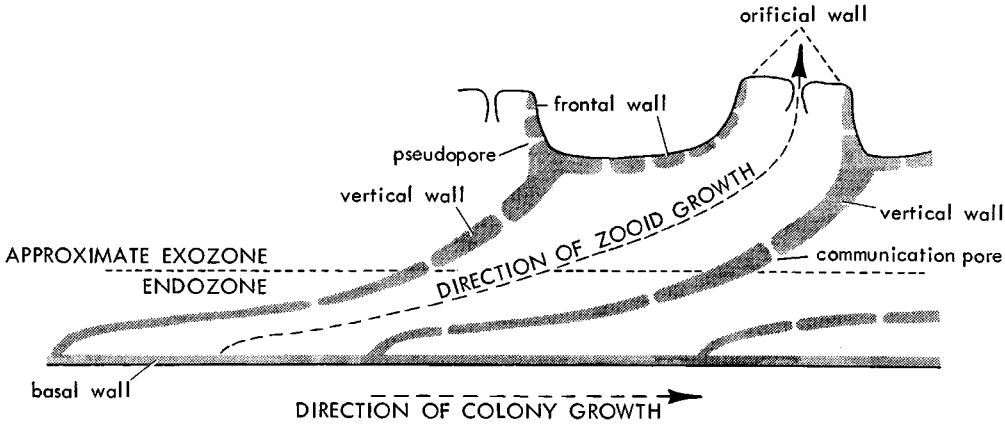

FIG. 11. Stenolaemate colonies. Diagram of a longitudinal section through a zooid of a unilaminate fixed-walled colony. The exterior frontal wall with exterior cuticle attached to skeletal layer (stippled) that contains pseudopores closes interzooidal communication through the outer body cavity of free-walled colonies. Interzooidal communication is assumed through pores in calcified vertical walls. Soft parts are deleted except for the orificial wall and the external cuticle of the multizooidal basal wall.

sac and the **exosaccal cavity** between the membranous sac and the zooidal body wall. A recent study (NIELSEN & PEDERSEN, 1979; first reported by NIELSEN at the 1977 meeting of the International Bryozoology Association) indicates that the membranous sac is peritoneum. Also, body walls of stenolaemates have only one cellular layer, the epidermis (NIELSEN, 1971). Body cavities within sacs, therefore, are surrounded by peritoneum (possibly a mesoderm) and are considered to be coeloms. All body cavities outside of sacs are termed **pseudocoels**, lined either by epidermis or by peritoneum on one side and epidermis on the other.

The membranous sac is attached to the body wall near its inner end by large **retractor muscles** and at its outer end by different kinds of attachment organs or ligaments in different taxa. Membranous sacs contain annular muscles (NIELSEN & PEDERSEN, 1979), which when contracted reduce the volume of the sac, slowly forcing the digestive organs and lophophore outward just far enough to free the tentacles for feeding. The tentacles can be withdrawn quickly by relaxation of the annular muscles and contraction of the powerful retractor muscles.

In feeding zooids of modern species, tentacles are arranged in a circle around the mouth, which has no epistome. Tentacle counts have been made for a few taxa and range from 8 to more than 30. The anus reportedly opens on the distal side of the tentacle sheath when tentacles are protruded.

Degeneration-regeneration cycles, which affect most of the functioning organs, occur after the initial growth of feeding zooids. In most taxa, retracted positions of lophophore and gut advance with zooid elongation, apparently by means of degeneration-regeneration saltations. Outward growth of zooids is generally enough for advancing organs to vacate inner parts of zooidal chambers, which can retain the remains of the degeneration process, generally brown bodies. In some fossil taxa vacated chamber space can be partitioned by transverse skeletal **diaphragms**. The last-grown diaphragm apparently formed the base of the living chamber for regenerated organs. In other taxa retracted positions of regenerated organs are fixed in zooecia and any continued elongation occurs in outermost vestibular walls and their enclosing skeleton.

Polymorphs may be larger or smaller than feeding zooids and may have different shapes. One kind, at least, has a reduced lophophore and gut. In some fossil taxa, polymorphs have

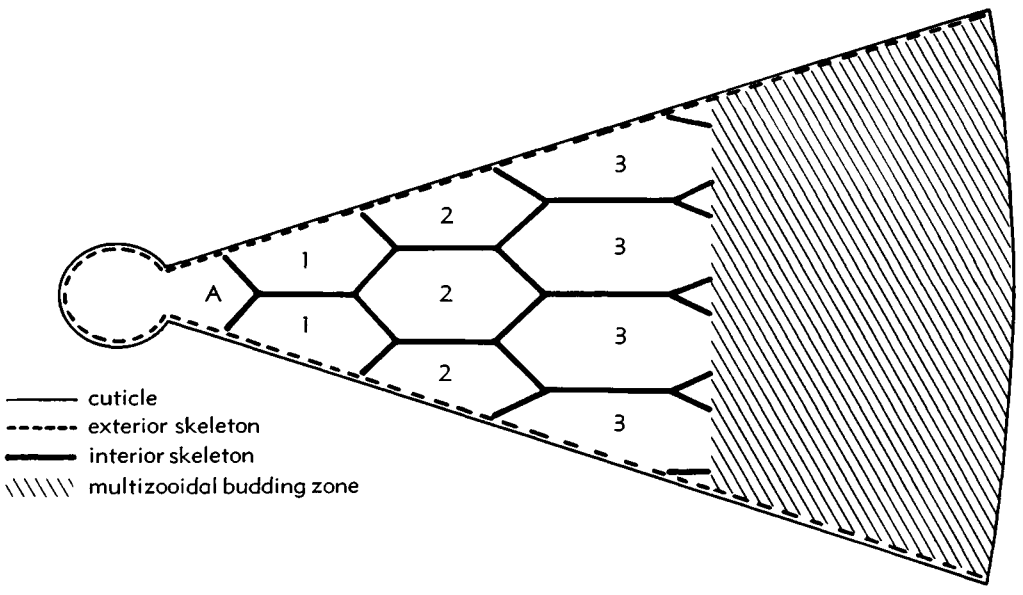

FIG. 12. Stenolaemate colonies. Idealized diagram of a section parallel to the basal layer of an encrusting colony (after Borg, 1926a, fig. 36) showing position and extent of the confluent, multizooidal budding zone around the basal margin. A is the primary zooid (ancestrula). The fourth generation of zooids is just beginning with the formation of proximal ends of vertical walls.

such small living chambers, however, that functional organs were not possible. Polymorphs may be isolated or contiguous with each other between feeding zooids, may cluster into **maculae** among feeding zooids, may surround clustered feeding zooids, or may form continuous layers on nonfeeding sides or on entire supporting peduncles of colonies.

Extrazooidal skeletal structures are grown by many free-walled colonies and can intervene between zooids in exozones or be colony-wide supporting structures. Most extrazooidal skeleton is interior in origin (see next paragraph for exception), that is, it contributes to the partitioning of preexisting colony body cavity. Growth of extrazooidal skeleton occurs in colony pseudocoels outside of zooidal chambers. The pseudocoel and parts of exterior membranous colony wall opposite extrazooidal skeleton are also considered extrazooidal.

In modern species, brooding of embryos occurs within body cavities of zooidal or extrazooidal **brood chambers** of widely varying shapes and modes of growth. Extrazooidal brood chambers have outer skeletal walls that are exterior in some taxa and interior in others. Skeletal structures in fossils that can be compared directly to known brooding structures in modern species are

FIG. 13. Cheilostomate colonies.——*1. Cystisella saccata* (BUSK), rec., N. Atl., U.S. Fish Comm. sta. 121; heavily calcified, rigidly erect colony with narrow, bilaminate branches and small encrusting base; zooidal orifices open on both sides of branches, covered by thick skeletal deposits of kenozooidal origin proximally; USNM 220040, ×4.0.——*2. Bugula neritina* (LINNAEUS), rec., Gulf of Cal., Sonora, Mexico; lightly calcified, flexibly erect colony with narrow, unilaminate branches and basal rootlets; USNM 220041, ×2.0.——*3. Hippoporidra calcarea* (SMITT), rec., Str. of Fla., Albatross Sta. D2640, depth of 100 m; nodular, multilaminate colony built upon and extending from gastropod shell; outer layers formed by budding in frontal direction; USNM 220042, ×2.0.——*4a,b. Parasmittina nitida* (VERRILL), rec., Long Is. Sound; heavily calcified, nodular, multilaminate colony encrusting pebble; outer layers formed by budding in frontal direction; *a*, frontal view, *b*, lat. view, USNM 220043, ×1.5.

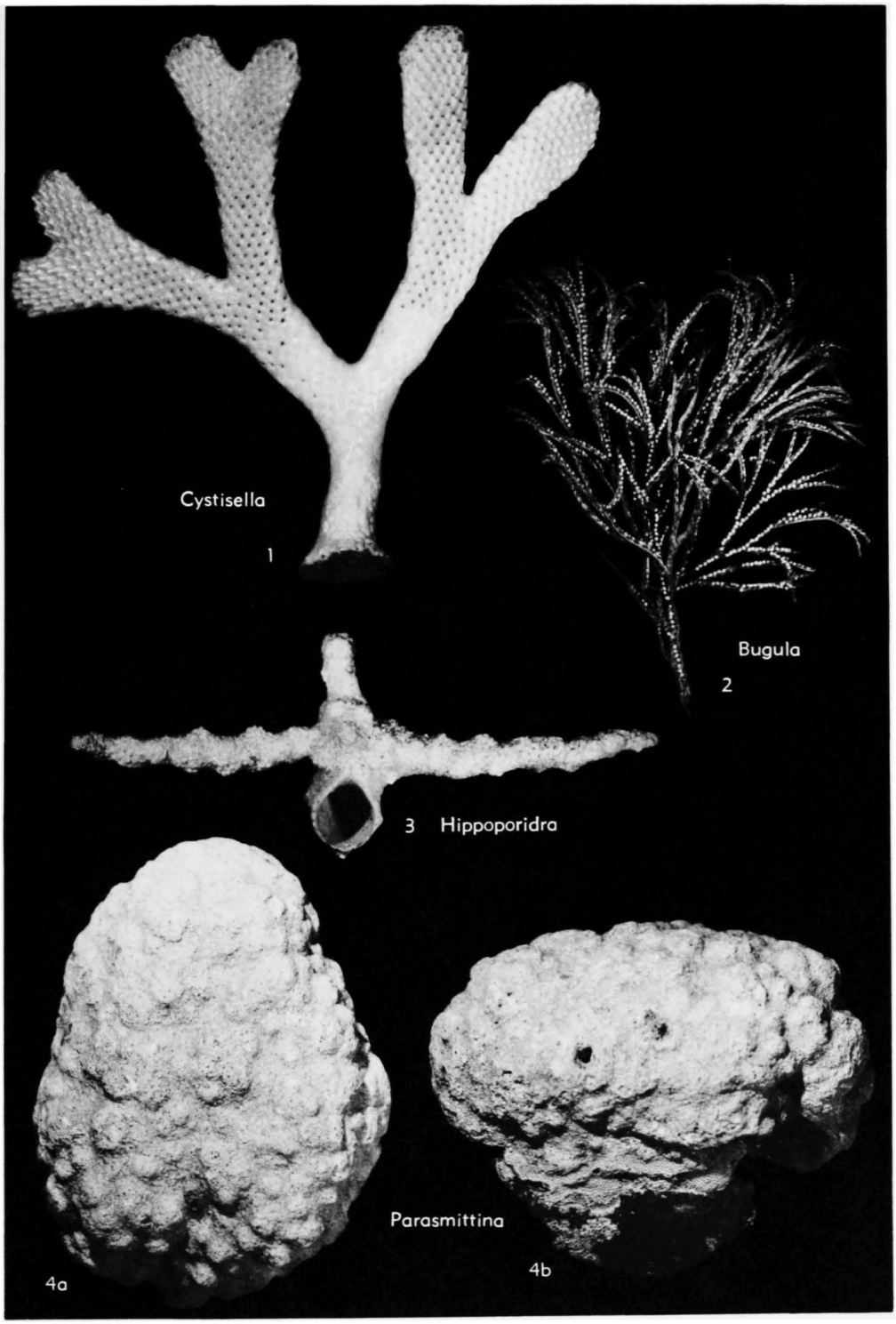

FIG. 13. *(For explanation, see facing page.)*

post-Paleozoic in age. Inferred brood chambers have been reported in a few Paleozoic taxa. Embryonic fission has been reported in modern species in which embryos have been studied. No resistant resting bodies or other asexual generations are known in life cycles.

Metamorphosis of the free-swimming, ciliated, nonfeeding larva in modern species produces the **basal disc**, the encrusting proximal end of the ancestrula (see Fig. 1). The basal disc has an exterior wall calcified from within in most taxa. The ancestrula is completed distally by exterior or interior skeletal walls, or a combination. A single ancestrula occurs in both modern and fossil colonies in species studied. All colonies apparently develop a zone of astogenetic change beginning with the ancestrula and including one to several generations of founding zooids of changing morphology (Fig. 1). The zone of change is followed by a zone of repetition in which similar zooidal morphology is repeated in a potentially endless **zooidal pattern**.

Zooids originate at their inner ends by the appearance of vertical walls growing either from encrusting or erect multizooidal walls, existing walls of zooids, or in a few species from extrazooidal parts. In endozones of both free- and fixed-walled colonies (Fig. 1, 12) vertical walls of most taxa grow into confluent outer body cavities of distal **multizooidal budding zones**. The outermost body walls of these zones are exterior membranous walls grown outside of existing zooids. As colony growth proceeds, multizooidal budding zones advance distally as their proximal regions become parts of zooids, or in many taxa are divided between zooids and extrazooidal parts. In some growth habits of free-walled colonies, budding can occur on all surfaces above encrusting colony walls in both endozones and exozones. In exozones the outer body cavities and outermost exterior membranous walls are parts of established zooids and the confluent cavities available for budding are zooidal. Feeding organs of zooids apparently originate from exterior orificial walls.

Class Gymnolaemata.—The Gymnolaemata include some brackish and freshwater representatives, but the overwhelming majority of members of this class is marine. Gymnolaemates having calcareous body-wall layers produce an abundant fossil record beginning in the Jurassic and extending nearly continuously from the Late Cretaceous onward. Taxa lacking skeletons have been found sporadically distributed as fossils from the Ordovician onward. Late in the Cretaceous, gymnolaemates became the dominant bryozoans in marine communities and remain so in present-day seas.

All exterior body walls have cuticle as the outermost layer in all living gymnolaemate taxa. Cuticles have not been found directly preserved in fossil taxa, but are assumed to have been present. In most taxa calcareous layers occur in some exterior and interior walls of zooids and other parts of zoaria. In a few taxa of major rank, skeletons are lacking, and both exterior and interior walls are stiffened only by cuticular layers, some of which may contain scattered calcareous particles. Where developed, the skeleton may be entirely calcitic or aragonitic or can combine layers of calcite and aragonite within the same zoarium. Zooidal organs are suspended in zooidal body cavities completely enclosed by zooidal body walls (see Fig. 3, 4).

Zooids can be arranged in a great diversity

FIG. 14. Cheilostomate colonies.——*1. Microporina articulata* (FABRICIUS), rec., Bering Sea, depth of 95 m; well-calcified, flexibly erect colony with jointed subcylindrical branches, base with rootlets, zooidal orifices opening all around branches; USNM 220044, ×2.——*2. Myriapora coarctata* (SARS), rec., N. Pac., Albatross Sta. 2877; well-calcified, rigidly erect colony with subcylindrical branches and small encrusting base, zooidal orifices opening all around branches; USNM 220045, ×2.——*3. Cryptosula pallasiana* (MOLL), rec., Long Is. Sound; unilaminate colony encrusting bivalve shell; USNM 220046, ×2. ——*4a,b. Cupuladria biporosa* (CANU & BASSLER), rec., Fish Hawk Sta. 7157; cap-shaped, free-living colony, zooidal orifices opening on convex surface, concave basal surface covered by extrazooidal deposits; *a*, frontal view, *b*, lat. view, USNM 220047, ×4.

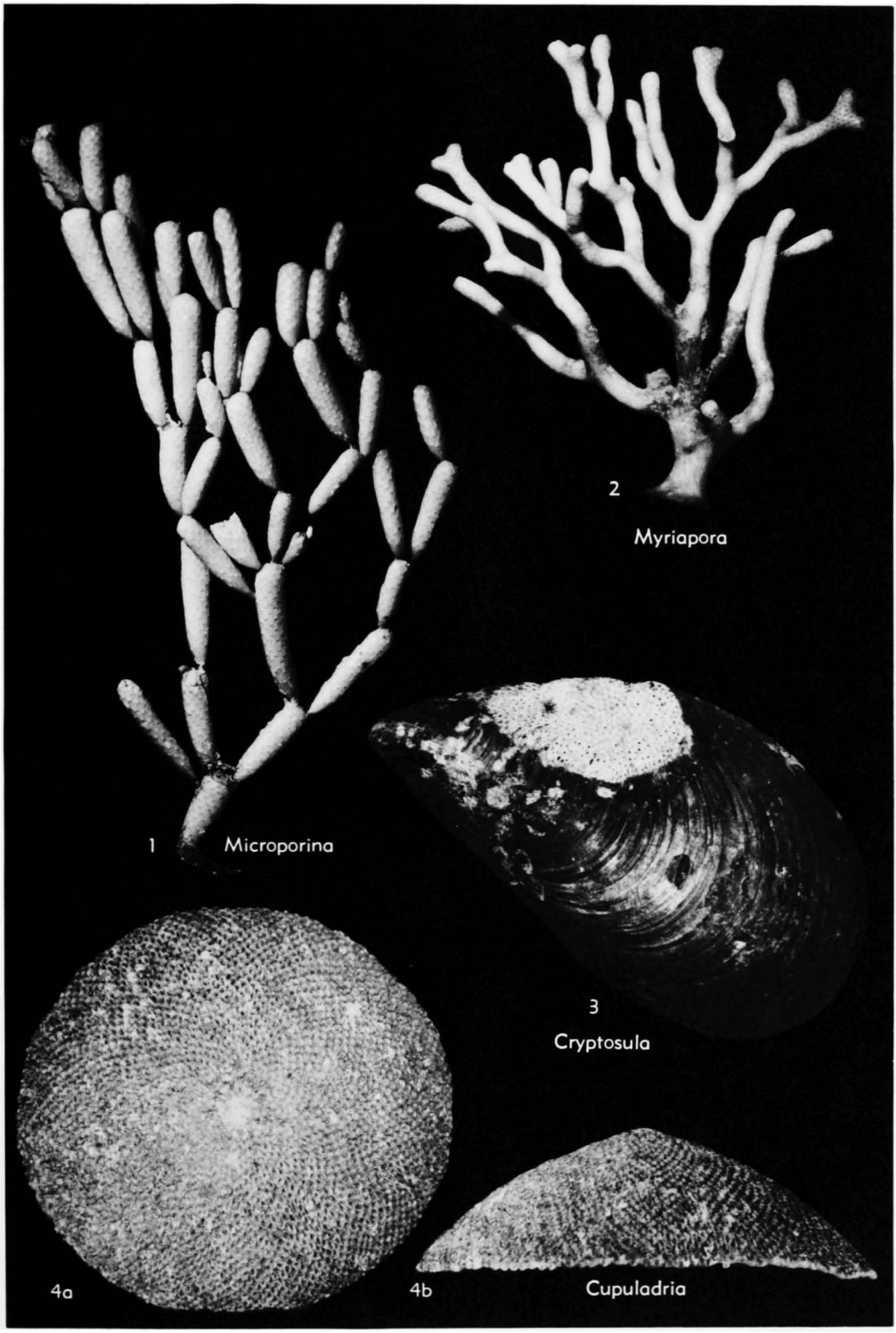

FIG. 14. *(For explanation, see facing page.)*

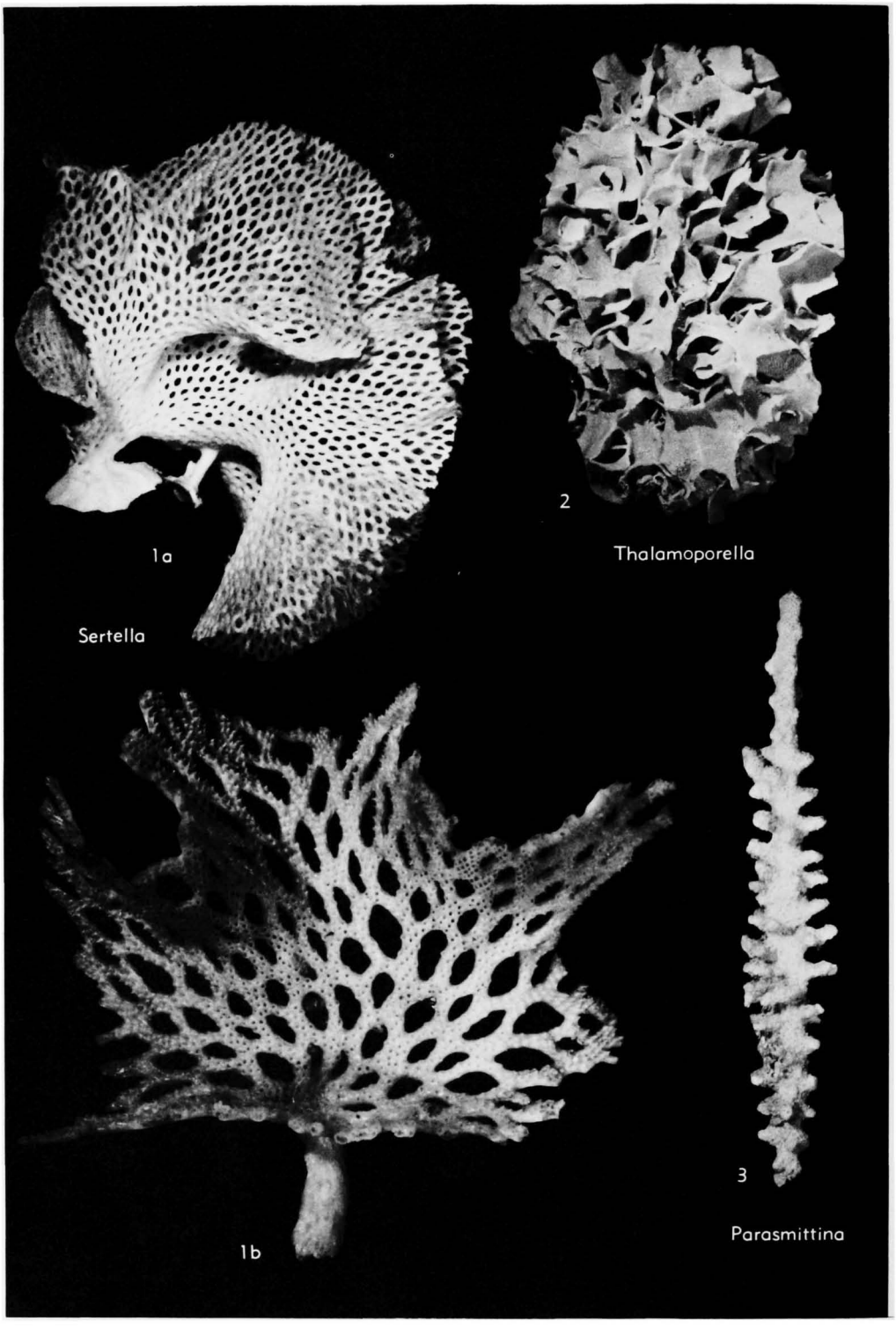

FIG. 15. *(For explanation, see facing page.)*

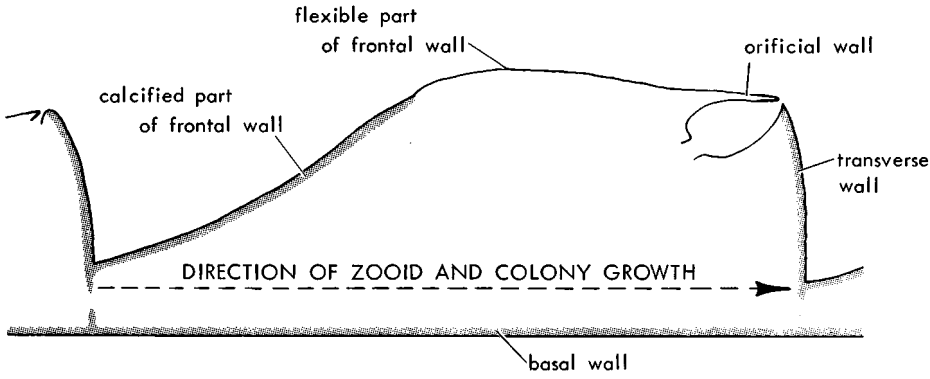

FIG. 16. Cheilostomate colonies. Diagram of a median longitudinal section through body walls of an autozooid of a simple encrusting colony. The exterior frontal wall consists of a calcified proximal part (skeletal layer stippled) protecting zooid organs (not shown, see Fig. 3, 4) and a flexible distal part fixed to the orificial wall and functioning in the hydrostatic mechanism. The exterior basal wall, of multizooidal origin, floors the body cavity. Interior walls are limited to interzooidal communication organs (pore plates) in transverse walls. Soft parts other than cuticle (solid lines) are not shown.

of patterns to form a large variety of colonies. These can include **encrusting** and **free-living colonies** as well as **rigidly erect, flexibly erect**, and **jointed-erect colonies** (Fig. 13–15). Major regions of erect and free-living colonies in some taxa are composed of extrazooidal parts. Principal growth directions of zooids and the colony approximately coincide (Fig. 16, 17).

Basal zooidal walls may be calcified or uncalcified, even within the same colony. In erect unilaminate, bilaminate, or cylindrical branches of colonies, basal zooidal walls most commonly are exterior and include multizooidal layers continuous with those in encrusting bases, but may be interior or absent, with vertical walls meeting at branch axes.

Vertical zooidal walls are calcified in the great majority of taxa and consist of lateral walls elongated subparallel to the direction of zooidal growth and transverse walls oriented subperpendicular to zooidal growth. Zooids budded in specialized directions (for example, frontally budded zooids in subsequent astogenetic zones of some colonies) may have all vertical walls oriented subparallel to the zooidal growth direction. In most taxa lateral walls are exterior and transverse walls include extensive interior components (Fig. 18). In a few taxa vertical walls are all interior, and in a few others having predominantly uniserial growth vertical walls are virtually all exterior. Exterior vertical walls include multizooidal cuticular and, where present, skeletal layers continuous among zooids within a budding series. Interior vertical walls completely separate living chambers of contiguous zooids. Vertical walls are not divided into endozones and exozones and

FIG. 15. Cheilostomate colonies.——*1a,b. Sertella couchii* (HINCKS), rec., Medit.; *a*, Beaulieu-sur-Mer, France, rigidly erect fenestrate colony with narrow, anastomosing branches having zooidal orifices on one side only, opposite sides of branches covered by extrazooidal deposits, small encrusting base (note smaller, subsequently formed additional support on right), lat. view, USNM 220048, ×1.5; *b*, Naples, Italy, frontal view, USNM 220049, ×4.0.——*2. Thalamoporella gothica floridana* OSBURN, rec., Gulf of Mexico, Alligator Point, Fla.; rigidly erect colony with broad, anastomosing, bilaminate branches with zooidal orifices opening on both sides; USNM 220050, ×0.7.——*3. Parasmittina echinata* (CANU & BASSLER), rec., Gulf of Mexico, Cedar Keys, Fla.; nodular, multilaminate colony encrusting seaweed, outer layers formed by budding in frontal direction; USNM 220051, ×1.5.

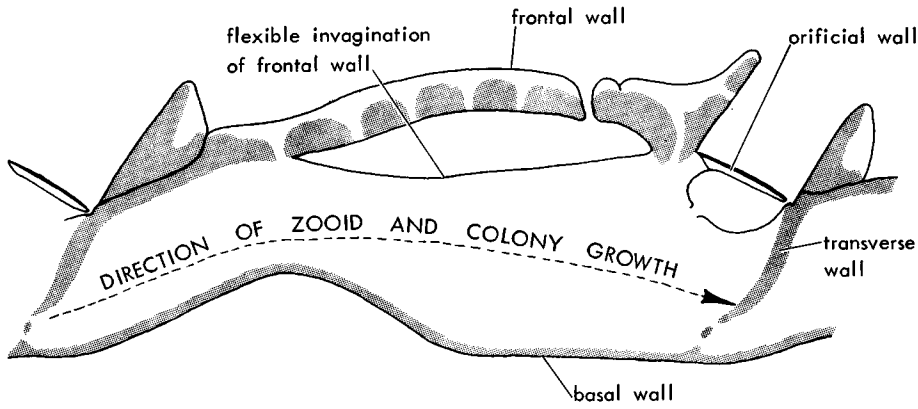

FIG. 17. Cheilostomate colonies. Diagram of a median longitudinal section through body walls of an autozooid of a complex erect subcylindrical colony. The exterior frontal wall consists of three parts. *1.* An outer part is uncalcified except at its proximal end, where it is overlain by the peristome of the proximal zooid. This outer frontal wall is underlain by a separated part of zooidal body cavity and by a protective calcified interior frontal shield (stippled). The frontal shield was formed before invagination of separate cuticle subjacent to it. *2.* A distal extension of frontal wall forms a tubular peristome surrounding and fixed to the orificial wall. The calcified portion of the exterior-walled peristome is structurally continuous with the interior-walled frontal shield. *3.* An invaginated part of the frontal wall has a flexible floor that functions in the hydrostatic system. An exterior basal wall of multizooidal origin floors the principal body cavity. Transverse walls are interior with multiporous pore plates. Soft parts other than cuticle (solid line) are not shown. (For detailed illustrations of this cheilostomate, see Fig. 67; 73; 82,*3*.)

are completed early in ontogeny to establish a maximum dimension for the zooidal living chamber, which ranges in shape from box- or saclike to cylindrical.

Frontal zooidal walls generally elongate subparallel to the direction of zooidal growth are present in all taxa. Frontal walls are exterior, as in the class Stenolaemata, but in some taxa are associated with subparallel calcified interior walls (Fig. 17). In calcified taxa all or part of the frontal wall (Fig. 16), or an infolded sac derived from it (Fig. 17), remains uncalcified and flexible to function in lophophore protrusion. Frontal walls include cuticular and, where present, some skeletal layers that are continuous among zooids in a budding series.

Orificial walls are subterminal in most taxa, terminal in a few, and consist of one or more movable folds of body wall. The outer side of the orificial wall is fixed to, and includes cuticular layers continuous with, the frontal wall (Fig. 3, 4). The inner side includes cuticular layers continuous with those of the vestibular wall. When closed (Fig. 3, 16, 17), the orificial wall is subparallel to the direction of zooidal growth and defines a slitlike or puckered orifice. In most taxa, the orificial wall is a single, distally directed flap, stiffened to form an operculum (Fig. 3, 4, 16, 17). In most calcified taxa, marginally incomplete skeletal openings support distal and, in some, lateral margins of the operculum and coincide with these margins of the orifice. In a few taxa margins of skeletal openings may be complete proximally (Fig. 17) and are apparently analogous to skeletal apertures in the class Stenolaemata. Margins of skeletal openings can be formed by transverse or frontal zooidal walls, by structures associated with frontal walls, or by a combination.

Developing zooids at growing tips of budding series or in multizooidal budding zones can have confluent living chambers, but those of fully developed zooids are not confluent. Communication among fully developed zooids and between zooids and extrazooidal parts where present is through **pore plates**, which in modern species are penetrated by

cells of special form connected to the body wall and to funicular strands (Fig. 3, 4). Communication organs can occur in interior vertical and basal zooidal walls, in exterior vertical, basal, and frontal walls of zooids that are in contact, and in some intrazooidal walls.

Retracted positions of lophophore and gut are approximately constant at all regenerated phases. Degeneration in modern species results in brown bodies that generally are expelled after regeneration, but are retained in living chambers in some species.

Lophophore protrusion involves contraction of two sets of muscles, parietals and dilators (Fig. 3, 4). **Parietal muscles** traverse the body cavity in bilaterally arranged pairs, from lateral or basal walls to the flexible exposed, overarched, or infolded part of the frontal wall. This flexible part of the frontal wall is depressed by contraction of the parietals, causing the lophophore to protrude. Skeletal evidence of parietal muscles has been found in many fossils. **Dilator muscles** are known only in modern species. **Diaphragmatic dilator muscles** traverse the body cavity in bilaterally or radially arranged groups from lateral or transverse walls or both to the diaphragm. In some taxa vestibular dilators are also present. The diaphragm and vestibule are dilated by contraction of the dilators to allow passage of the lophophore during protrusion.

Feeding zooids of modern species have 8 to 35 tentacles arranged in a circle around the mouth, which has no epistome. The anus opens on the distal side of the tentacle sheath.

Polymorphism is known in the great majority of taxa and is generally reflected in skeletons of calcified taxa. A variety of polymorphs may occur in the same colony to perform sexual reproduction, embryo brooding, and other functions. These polymorphs differ markedly in size, shape, and other morphologic characters from ordinary feeding zooids. Polymorphs may lack lophophore and gut, or have organs different from those of ordinary feeding zooids, with or without feeding ability. Some polymorphs communicate with just one other zooid, in the extreme form being almost an appendage of that zooid; some communicate with two or more zooids, either seemingly at random positions in the colony, or in regular positions or clusters.

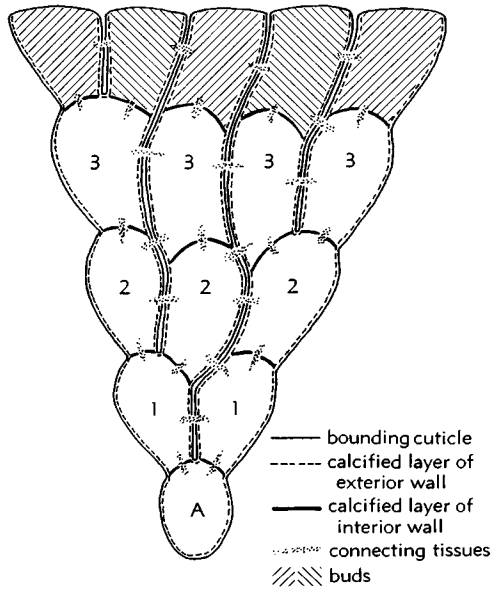

FIG. 18. Gymnolaemate colonies. Idealized diagram of a section parallel to basal walls of zooids in an encrusting or erect colony (after Silén, 1944b; Banta, 1969) showing positions of buds at distal ends of lineal series. Lateral zooidal walls are exterior walls breached by communication organs (connecting tissues). A is the primary zooid.

Extrazooidal parts are known in a few taxa and are apparently limited to calcified groups. Some structures interpreted as polymorphs in uncalcified taxa, however, may prove to be extrazooidal. Proximal parts of rigidly erect colonies in some taxa have outer extrazooidal membranous wall, body cavity, and calcified wall all formed through coalescence of corresponding frontal parts of zooids. Extrazooidal skeletal layers in these taxa succeed, without interruption, zooidal skeletal layers that are parts of either interior or exterior walls. Basal sides of free-living colonies in some taxa and reverse sides of erect colonies in some taxa have outer membranous wall, body cavity, and calcified wall all formed at colony growing edges concurrently with budding of zooids. In some taxa skeletal layers

of these extrazooidal parts are parts of compound walls that include interior basal walls of zooids. In other taxa extrazooidal skeletal layers are parts of exterior walls that are in contact with exterior basal walls of zooids.

In the great majority of modern species, embryos are brooded; and in almost all calcified forms that brood, this function is reflected in varying kinds of polymorphic skeletal structures including recognizable brood chambers. Comparable skeletal evidence of brooding has been recognized in the majority of fossil taxa. Fossil species in which evidence of brooding has not been found most commonly are morphologically similar to modern species in which embryos are not brooded. In all but two of the modern genera in which brooding occurs, embryos are held topologically outside the body cavity within chambers of widely differing size, shape, and position, each partly enclosed by the body wall of one or more polymorphic zooids. Embryos in modern species apparently are each produced from a separate egg. Ciliated larvae are naked and lack digestive tracts in most taxa, but are covered with bivalve cuticular shells and have digestive tracts in a few.

Metamorphosis of a larva is followed by development of one (ancestrula) or more primary zooids, which in the great majority of taxa initiate a primary zone of astogenetic change in turn followed by a primary zone of astogenetic repetition. In a few taxa, primary zooids are part of a zone of repetition, with no astogenetic changes in morphology of zooids. Complex astogenetic zonations are known in colonies of some taxa. Initial zooids of some colonies in a few modern freshwater or marine species can be produced asexually from encapsulated resistant resting bodies (**hibernacula**) developed as inswellings or outswellings from body walls of the parent colony.

Zooids are budded most commonly as localized swellings at distal ends of lineally budded series (Fig. 18) bounded by exterior, lateral, frontal, and basal walls of multizooidal origin. Within lineal series zooidal body cavities become separated by ingrowth of interior components of transverse walls and included pore plates, or of pore plates alone, transforming multizooidal structures into zooidal walls. In taxa having all interior vertical walls, budding occurs in laterally confluent multizooidal budding zones similar to those in the class Stenolaemata (Fig. 12). In modern species, budding initiated by outswelling of exterior walls of preexisting zooids or of multizooidal budding zones is followed by infolding of the lophophore and gut from the exterior orificial wall before it has differentiated from the developing frontal wall.

Class Phylactolaemata.—The Phylactolaemata are exclusively a freshwater class. Resistant resting bodies (**statoblasts**) produced by phylactolaemates have been reported as fossils from the Pleistocene and upper Tertiary, but reports of Cretaceous phylactolaemates are problematical and need to be reinvestigated. The few modern species in the class have intercontinental distributions and are the dominant bryozoans in freshwater communities.

Phylactolaemata have all body walls without skeleton, but soft outer noncellular layers of body walls can have adherent foreign particles in most taxa. In some taxa outermost layers of some exterior body walls are gelatinous and thick. In most taxa outermost layers of all exterior body walls are thin cuticles similar in appearance to those in other bryozoan classes.

Zooidal organs are suspended in confluent body cavity (Fig. 19), which can be continuous throughout the colony or divided by widely spaced **septa**. Zooids open in approximately the same direction on the colony surface, which consists of zooidal orificial and exterior vertical walls together with exterior extrazooidal walls. Opposite surfaces in both encrusting and erect colonies consist of exterior extrazooidal walls to which zooidal organs are attached by retractor muscles and the funiculus. Basal and frontal zooidal walls are apparently absent in all taxa. (Walls to which retractor muscles are attached are considered **colony walls** by authors.) The angle between growth directions of zooids and their colony

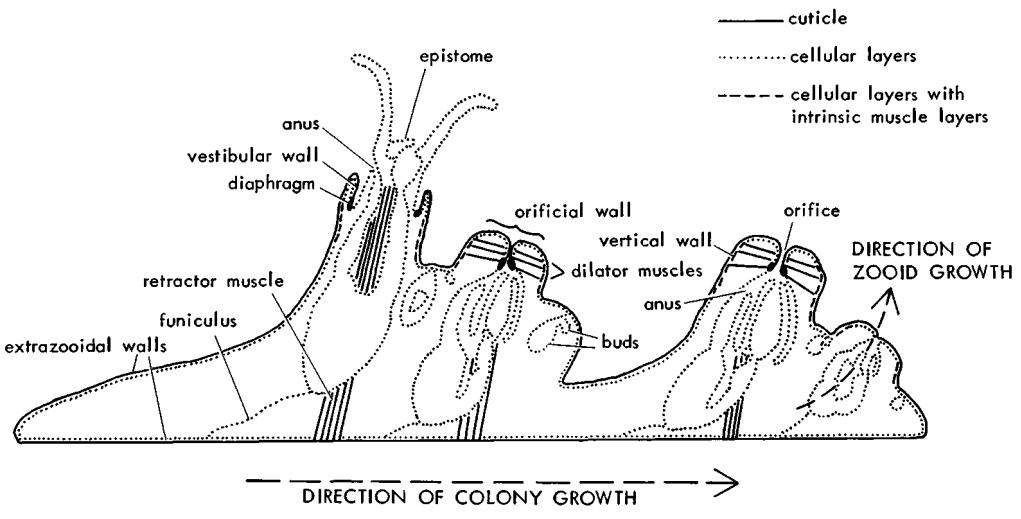

FIG. 19. Phylactolaemate colonies. Diagram of a longitudinal section through generalized encrusting colony with either circular or bilobed lophophore showing interpreted relationships between zooidal and extrazooidal body walls, confluent body cavity, and zooidal organs. The zooid near the proximal end of the colony (left) is one of two or more primary zooids with connected extrazooidal parts, all developed directly from the sexually produced embryo. Primary zooids reportedly do not differ morphologically from more distal, asexually produced zooids toward the right. As the colony grows by distal and outward expansion of the colony body wall, new buds appear as developing zooidal organs both distal to and between preexisting zooids, by infolding from the outer body wall of the colony and from other developing zooidal organs. Orificial and exterior parts of vertical zooidal walls as shown here are subsequently differentiated from the exterior wall of the colony by continued outward expansion to complete the zooid. In some phylactolaemate taxa, incomplete interior vertical zooidal walls (not shown) can grow into the body cavity from the inner ends of exterior vertical walls to separate zooidal body cavities further.

increases ontogenetically to subperpendicular in most taxa. Zooidal and colony body walls include peritoneum as their inner layer. Therefore, body cavities are considered to be coeloms.

Vertical zooidal walls are parallel to the direction of zooidal growth. They are exterior walls in most taxa and a combination of exterior and interior walls in a few taxa (see *Lophopus,* Fig. 141,*2*). Exterior vertical walls are limited to outer ends of zooids (Fig. 19). Interior vertical walls, where present, are incomplete and extend from inner ends of exterior vertical walls, ending in confluent coelom. Vertical zooidal walls are not divided into endozones and exozones, and are developed early in ontogeny to define the outer part of the zooidal living chamber, which is cylindrical in the part enclosed by exterior vertical walls.

Orificial walls are terminal, perpendicular to the direction of zooidal growth, fixed to exterior vertical zooidal walls, and comparable in area to cross sections of zooidal body cavities. Orificial walls are single membranes containing simple porelike orifices.

Communication among zooids and between zooids and extrazooidal parts of the colony is through confluent coelom. Communication organs have not been reported.

Retracted position of lophophore and gut is approximately constant after exterior vertical zooidal walls are developed. Lophophore and gut degenerate completely, and brown bodies and regeneration apparently do not occur (WOOD, pers. commun., 1975).

Lophophores are protruded by contraction of circular and longitudinal **intrinsic body-wall muscles** present in both interior and exterior vertical zooidal walls. A membranous sac and parietal muscles are apparently unnecessary and have not been found. Radi-

ally arranged dilator muscles are attached to vestibular walls (**vestibular dilator muscles**) and to the diaphragm (**duplicature muscles**). Tentacles are arranged in a bilobed row, except for one genus in which the pattern is subcircular. Tentacles range in number from 18 to over 100. The mouth has a movable fold of body wall, the epistome, projecting over it from the anal side. The anus opens on the proximal side of the tentacle sheath (Fig. 19).

Polymorphism has not been reported.

Extrazooidal parts are apparently present in all colonies, developed as exterior colony walls concurrently with budding of zooids.

Embryos are brooded in all taxa within body chambers enclosed by infolds from the extrazooidal body wall of the parent colony. Each embryo is produced from a separate egg.

Brooded embryos develop directly into a ciliated motile colony consisting of two or more zooids and associated extrazooidal parts, without metamorphosis. Motile colonies released from parent colonies settle, lose their external cilia, and continue to grow asexually, apparently without a zone of astogenetic change.

New colonies arise most commonly by asexual reproduction through development of encapsulated statoblasts formed internally on funicular strands of zooids. Colonies developed from statoblasts begin with a zooid that can have some morphologic features different from those budded from it, and it thus initiates a zone of astogenetic change.

Budding is initiated by development of lophophore and gut infolded into the confluent coelom from exterior extrazooidal walls or internally from other developing feeding organs (Fig. 19). Orificial, vertical, and vestibular walls of zooids develop subsequently. Buds occur distal to and between preexisting zooids.

NATURE OF BRYOZOAN COLONIES

A colony in Bryozoa consists of physically connected, asexually replicated member zooids with or without connected extrazooidal parts. In this section we are concerned with theoretical aspects of the colony as expressed throughout the phylum. Further descriptions and examples of bryozoan colonies will be found in review and taxonomic sections in this and following volumes.

SOURCES OF MORPHOLOGIC VARIATION WITHIN A COLONY

The basic assumption in this study of Bryozoa is that the colony is genetically uniform. Within sexually produced colonies, only the primary zooid or group of zooids is produced sexually. All other parts of the colony arise from physically continuous mitotic division of cells and secretion of noncellular parts (LUTAUD, 1961). Because of their assumed genotypic uniformity, zooids in a colony might be expected to be morphologically identical. Zooids in a bryozoan colony, however, can differ in some morphologic features. Intracolony morphologic variation follows patterns attributed to four sources (BOARDMAN, CHEETHAM, & COOK, 1970): ontogeny of zooids and, where present, extrazooidal parts; astogeny of the colony; polymorphism of zooids; and microenvironment.

1. **Ontogenetic variation** arises from changes in a zooid (or any extrazooidal part of the colony) during the course of its development, which may or may not continue throughout the life of the zooid. These changes are recognizable within a colony in most Bryozoa as increases in size or complexity among zooids along a gradient extending in a **proximal direction** from growing extremities toward the primary zooids illustrated on the left of Figure 20. Further development of the colony (right side of Fig. 20) transforms younger, less complex

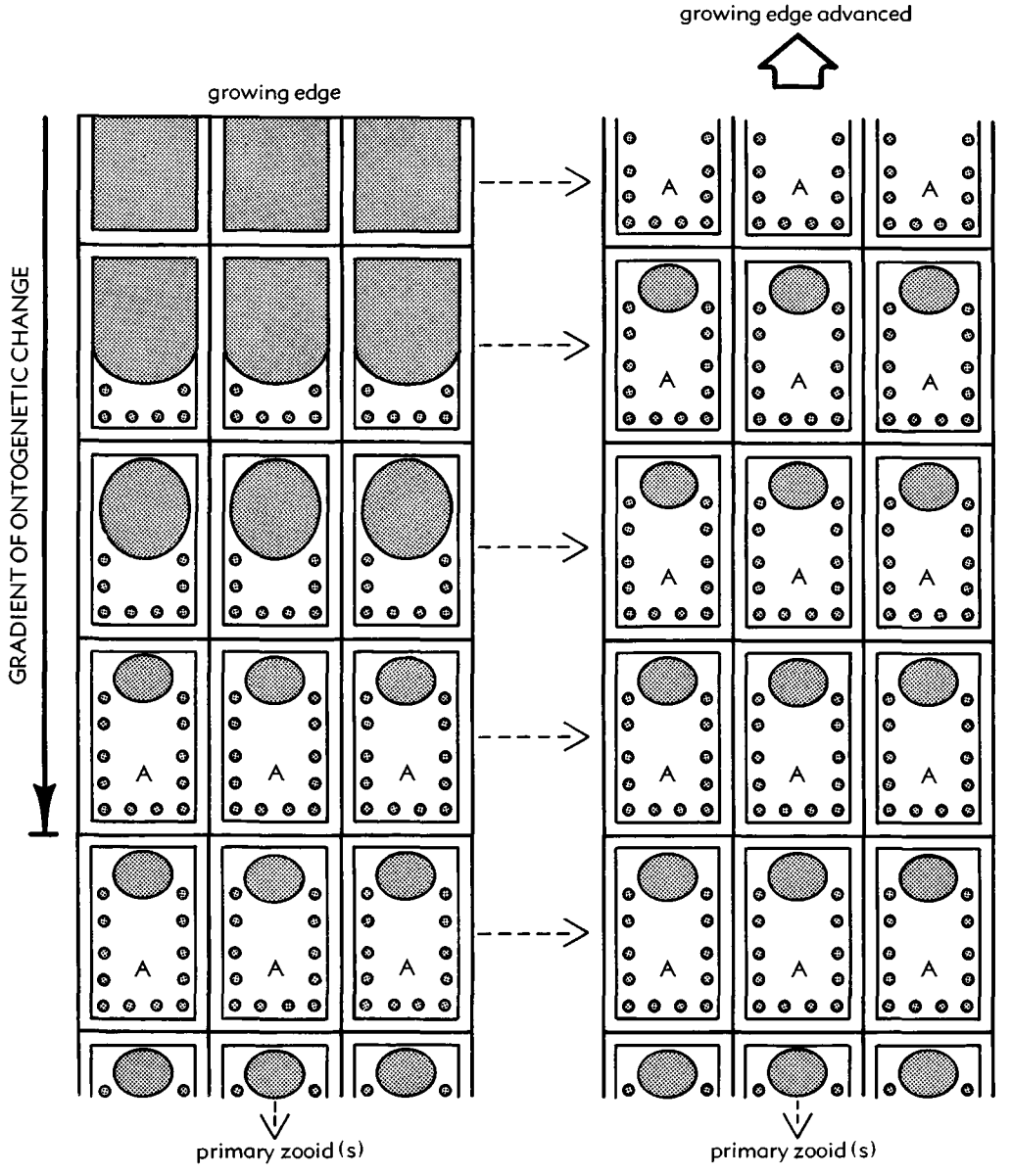

FIG. 20. Colony morphologic variation. Pattern of ontogenetic differences in zooid morphology in the zone of astogenetic repetition of a hypothetical bryozoan colony. In the series shown on the left, zooids have increasing amounts of skeleton from the growing edge to establishment of a fully developed morphology (A) through intermediate morphologies on a gradient directed proximally. Zooids the same distance proximal to the growing edge are identical in morphology, as this diagram assumes no polymorphic or microenvironmental differences. With further growth of the colony, as indicated in the series on the right, zooids of initial and intermediate morphologies have all changed to morphology A, beyond which there is no further ontogenetic change (after Boardman & Cheetham, 1973).

zooids to older, more complex ones (morphology A). Thus, zooids and extrazooidal parts of colonies form a sequential record in proximally directed series of the ontogenetic stages through which the proximal members of a series have progressed.

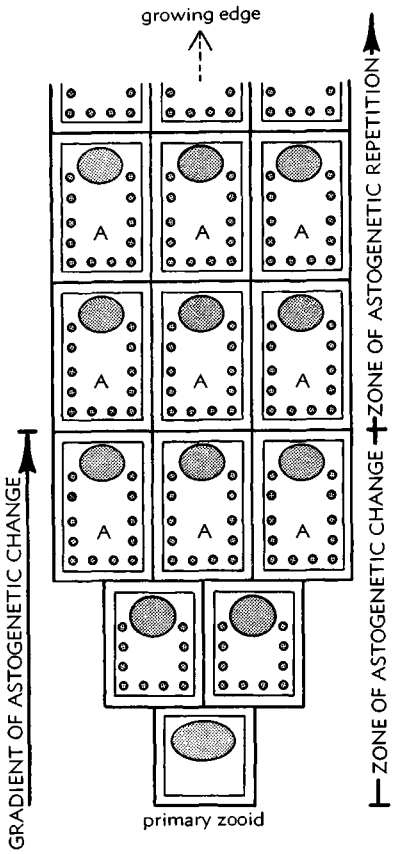

FIG. 21. Colony morphologic variation. Pattern of astogenetic differences in zooid morphology in the zone of change in a hypothetical bryozoan colony. Zooid morphology changes through one asexual generation of intermediate morphology from the primary zooid to morphology A on a gradient directed distally. Zooids belonging to the same generation are identical, as it is assumed in this diagram that there are no polymorphic or microenvironmental differences. With further growth of the colony, zooids in the zone of change retain the morphology characteristic of their generation (after Boardman & Cheetham, 1973).

2. **Astogeny** (CUMINGS, 1905, p. 169) is the course of development of the sequence of asexual generations of zooids and any extrazooidal parts that together form a colony. Most bryozoan colonies are developed from a primary zooid or group of primary zooids generally resulting from metamorphosis of a larva. A relatively few colonies arise from either asexually produced resistant resting bodies or fragmentation. In most Bryozoa, the process of colony founding involves morphologic differences of size and complexity between generations of zooids immediately following the primary zooid or zooids. These differences define a **primary zone of astogenetic change**, which at its distal end develops a pattern capable of endless repetition of zooids (Fig. 21). The primary zone of change comprises the zooids, usually belonging to a few generations, which show morphologic differences from generation to generation in more or less uniform progression distally away from the primary zooids. In a zone of change, therefore, the zooids in each generation in a distally directed series express morphologic characteristics unique to that generation.

The primary zone of astogenetic change is followed distally by a **primary zone of astogenetic repetition** in which large numbers of zooids of repeated morphologies are proliferated, usually through many generations. Morphologic differences attributed to astogeny, therefore, are restricted to zones of change in a colony.

In some Bryozoa, a colony may develop further astogenetic changes in morphology distal to the primary zone of astogenetic repetition. These subsequent zones of change can in turn be followed distally by subsequent zones of repetition in which the morphologic pattern capable of endless repetition is either like or unlike that in the primary zones of repetition. Subsequent zones of change and repetition may be part of the normal budding pattern, as frontal budding in some gymnolaemates (see CHEETHAM & COOK, this revision), or stimulated by microenvironmental accident, as in patches of intracolony overgrowth common to many stenolaemates (see BOARDMAN, this revision).

3. **Polymorphism** is repeated, discontinuous variation in the morphology of zooids within a colony. Polymorphism may be recognized in the same generation of zooids in a zone of astogenetic change, or in any zooids at the same ontogenetic stage in a zone of astogenetic repetition (Fig. 22).

4. **Microenvironmental variation** is vari-

ation within a colony that cannot be inferred to be an expression of ontogeny, astogeny, or polymorphism. The morphologies of zooids within a colony are the result of continuous reaction by the genotype to the microenvironments of the colony, expressed at any particular time and place in the colony throughout colony growth. Differences in microenvironments during growth of the colony can be expected to produce differences in zooid morphologies (Fig. 23). This morphologic variation may occur in one or more regions of the colony or may affect scattered zooids. An environmental change affecting

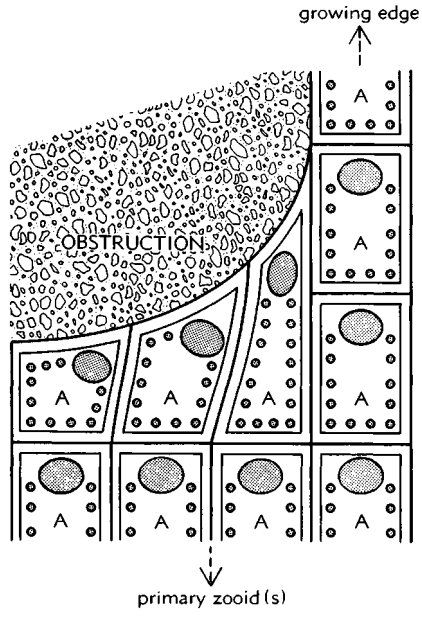

FIG. 23. Colony morphologic variation. Microenvironmental differences in zooid morphology in the zone of astogenetic repetition of a hypothetical bryozoan colony. Zooids belonging to the same generation have slightly differing morphologies, all modifications of the A form. The difference between extremes of morphology is related to growth around the obstruction (after Boardman & Cheetham, 1973).

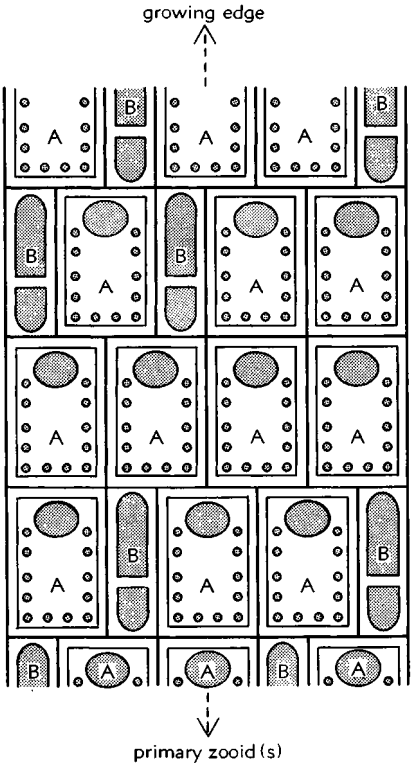

FIG. 22. Colony morphologic variation. Polymorphic difference in zooid morphology in the zone of astogenetic repetition of a hypothetical bryozoan colony. Zooids belonging to the same generation may have either morphology A or morphology B, intermediate morphologies being absent. Polymorphs may also occur in the zone of change in some species (after Boardman & Cheetham, 1973).

the morphology of zooids throughout the colony is a more widespread change than considered here as microenvironmental.

A few of the environmental causes that seem to explain observed morphologic variation within a colony but may also affect the colony as a whole are: crowding by growth of the colony itself or by competitive growth of other organisms, irregularities in the substrate, encrustation by the colony itself or by other organisms, differential turbulence, various forms of breakage, boring, and differential sediment accumulation. Differences in temperature, salinity, light intensity and duration, nutrients, and other environmental factors have been demonstrated to affect morphology, but their effect on intracolony variation is not generally known.

Microenvironmental variation can be recognized as irregular or gradational differences

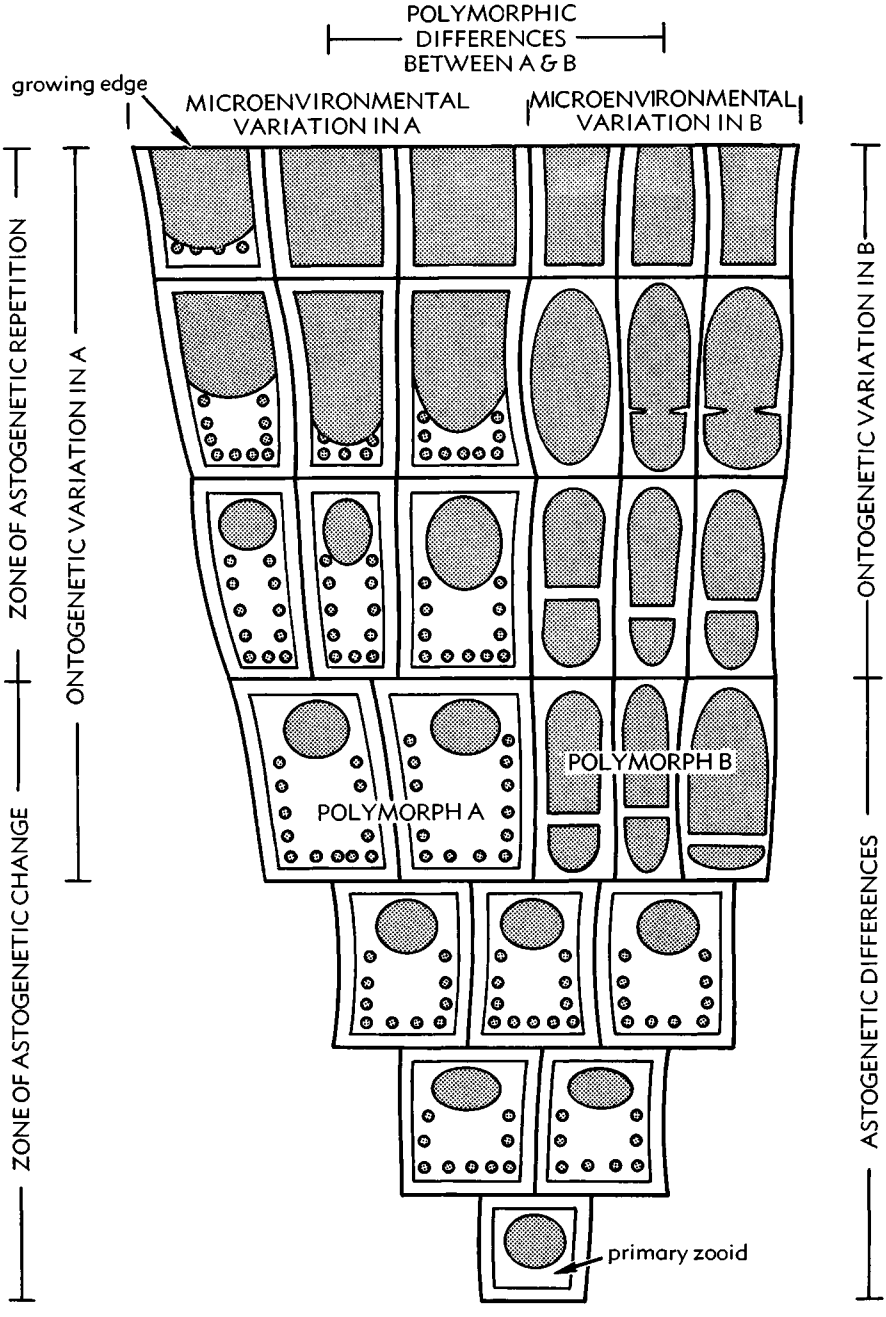

FIG. 24. Colony morphologic variation. Combined patterns of ontogenetic, astogenetic, polymorphic, and microenvironmental differences in zooid morphology in a hypothetical bryozoan colony. Spatial arrangement of polymorphs A and B is for convenience of comparison (although similar to those known in some groups of gymnolaemates); in actual colonies, polymorphs are commonly intermixed in the budding pattern. Note that no two zooids, even those belonging to the same polymorph and the same generation, are identical in the morphologic features shown (after Boardman & Cheetham, 1973).

between zooids; such differences are not necessarily repeated in a colony. Irregular differences can be recognized anywhere in the colony. Gradational differences can be recognized in zooids belonging to the same generation in a zone of astogenetic change, or to the same or different generations (at the same ontogenetic stage) in a zone of astogenetic repetition (Fig. 23).

The artificial restriction of variation within a colony to a single pattern seen in the hypothetical bryozoan colonies of Figures 20–23 is probably never approached very closely in real colonies. All four patterns are commonly combined (Fig. 24), but differences attributable to each source of variation can be separated. As shown in Figure 24, both ontogenetic and **astogenetic differences** in morphology are expressed in a series of zooids parallel to the direction of budding. In most Bryozoa, ontogenetic differences are expressed by generally increasing complexity proximally and astogenetic differences by generally increasing complexity distally. Because of the sequential nature of budding, these differences have relative time significance. Intracolony differences produced by polymorphism and microenvironment are not necessarily sequential.

The hypothetical examples above, and most studies of actual colonies, have emphasized patterns of variation in the morphology of the zooidal body wall, and especially of its skeletal layers. Patterns of variation in the morphology of zooidal organs may not be entirely congruent with those of the body wall. In gymnolaemates and stenolaemates for example, cyclic degeneration and regeneration of the lophophore and associated organs can produce cyclic repetition of ontogenetic gradients, in characters such as tentacle length, proximally from growing extremities. Also, lophophores and other organs may differ with the sex of zooids whose skeletons are not distinguishable (see Cheetham & Cook, this revision). Within most colonies, however, ontogenetic, astogenetic, polymorphic, and microenvironmental differences are all reflected in the skeletons of zooids. These differences therefore can be recognized in fossil as well as living taxa and may be taken into consideration in classification.

COLONY CONTROL OF FUNCTION AND MORPHOLOGY

Physical wholeness and assumed genetic uniformity make the colony the unit that survives and contributes to the gene pool in Bryozoa. The colony responds to the environment through its functions, contributed at any level of organization from the entire colony to its member zooids and extrazooidal parts, to their organs, tissues, and cells. Structures at these levels of organization may respond separately to the environment and therefore are subject to natural selection. The colony, however, is comparable to the solitary animal as the viable unit in the environment.

As far as is known, bryozoan colonies perform the following functions at some stage in their development: sexual reproduction; asexual reproduction of zooids; feeding, digestion, and intracolony dispersion of nutrients; formation and evacuation of feces; structural support by the colony itself; growth, and repair of injury; and degeneration and regeneration of zooid organs. These functions include those essential to solitary animals as well as those unique to colony organization. Functionally, therefore, bryozoan colonies and solitary animals are only partly comparable. Other basic functions, such as respiration and excretion of some metabolic wastes, must be assumed but are poorly understood and not considered here.

If only those functions common to both bryozoan colonies and solitary animals are considered, such as feeding and sexual reproduction, solitary animals compare most closely with the member zooids of colonies. Morphologically, solitary animals also compare most closely with zooids. Therefore, zooids are considered to be the basic morphologic and functional units of Bryozoa that correspond most closely to individual solitary animals.

Comparison between bryozoan zooids and

solitary individuals, however, is not exact. Member zooids are not viable by themselves, but grow and function cooperatively with each other and any extrazooidal parts to form viable colonies. It is therefore impossible to separate completely the morphology and functions of zooids from those of the colony.

The degree to which zooids differ from solitary animals morphologically and functionally because of their membership in a colony expresses the degree of control that the colony has over its member zooids (BOARDMAN & CHEETHAM, 1973). Many functions are speculative or unknown, and can become better known through study of living colonies. However, it is generally possible to assess the degree of **colony control** over zooidal functions by inference from the morphology of zooids and extrazooidal parts, that is, by the extent to which zooids in combination with extrazooidal parts differ morphologically from solitary animals (degree of **integration**). Morphologic features under some degree of colony control commonly can be observed to have grown or can be inferred to have functioned cooperatively with adjacent zooids, or as extrazooidal structures separate from zooids.

Structures contained within **zooidal boundaries** that perform functions similar to those of solitary animals reflect a degree of autonomy retained by zooids within their colonies. These structures may be inferred to reflect a degree of **zooidal control**. It is probable, however, that few, if any, zooidal structures in most Bryozoa are grown without some influence from adjacent zooids, extrazooidal parts, or both.

The degrees of morphologic integration expressing colony control may be interpreted on the basis of the following assumptions.

1. The body cavity of the colony (possibly excluding the portion contained by the tentacles and tentacle sheaths of the zooids) is separated from the external environment by body wall having protective cuticle or gelatinous material as its outermost layer.

2. An imperforate cuticular wall is sufficiently impervious to physiologic exchanges to sustain zooid growth and function.

3. An imperforate calcareous wall is sufficiently impervious to physiologic exchanges to permit further zooid growth.

4. Some zooids in a colony are feeding zooids.

5. Growth of cellular tissue and secretion of noncellular layers require a source of nutrients.

6. Nutrients are dispersed through the colony through either cells in mural pores or confluent coelom.

7. Confluent coelom between zooids or between zooids and extrazooidal parts of a colony permits freer physiologic exchange than do cells in mural pores.

8. Extrazooidal parts and zooids lacking feeding organs have direct or indirect access to nutrients from feeding zooids.

9. Morphologic difference between zooids implies physiologic or functional differences, or both.

10. Colony control of zooids and extrazooidal parts may be local or colony-wide in extent.

11. Correlated cyclic growth within a group of zooids is not necessarily a result of colony control, but may be simultaneous separate responses to a cyclic environment.

Integration of vertical zooidal walls.—The walls between zooidal cavities (most commonly vertical walls) may be either interior or exterior. Exterior walls are comparable in mode of growth and morphology to those bounding a solitary individual. These walls have the capability of separating the zooid from the environment, thus expressing **zooidal autonomy**. Interior walls, in their mode of growth and morphology, express colony control in that they partition existing body cavity and have no apparent potential for separating the zooid from the environment. The following combinations of vertical zooidal wall types occur in Bryozoa and are listed in order of increasing integration as the result of colony control.

1. Walls only exterior (a few stenolaemates, most phylactolaemates).

2. Walls partly exterior, partly interior (a

few stenolaemates, most gymnolaemates, few phylactolaemates).

3. Walls wholly interior (most stenolaemates, a few gymnolaemates).

Integration by interzooidal connection.—Soft-tissue connections are generally lacking among solitary animals. Interzooidal connection by zooidal soft tissues and their assumed function in Bryozoa, therefore, express colony control. Connected body cavities of zooids or extrazooidal parts apparently can exchange physiologic substances, and the nature of the connection expresses the degree of colony control. These states are listed in order of increasing integration.

1. No soft-tissue connections between adult zooids (a few stenolaemates).

2. Connections by cells through mural pores (some stenolaemates, all gymnolaemates).

3. Connections by confluent body cavity around ends of complete, interior vertical walls (some stenolaemates).

4. Connections both through mural pores and around ends of interior vertical walls (some stenolaemates).

5. Connections by confluent body cavity through and around incomplete interior vertical walls (a few stenolaemates, some phylactolaemates).

6. Connections by confluent body cavity, no interior vertical walls (most phylactolaemates).

Integration by extrazooidal hard and soft parts.—The presence of extrazooidal hard and soft parts in a colony is an indication of a degree of colony control of growth, because extrazooidal parts are unique to colonial animals, based on the assumption that a solitary individual is internally comparable to a zooid. The development of extrazooidal parts results in a further loss of zooid autonomy from the condition in solitary animals. In Bryozoa, extrazooidal parts are connective or supportive structures outside zooidal boundaries. Extrazooidal parts known in stenolaemates and gymnolaemates form a transitional morphologic series approaching in its variety that of polymorphic zooids. Extrazooidal parts in phylactolaemates form a transitional morphologic series from identifiable colony body wall to identifiable zooidal vertical walls. The following states, listed in order of increasing integration, are known in Bryozoa.

1. Extrazooidal parts absent (many stenolaemates, many gymnolaemates).

2. Extrazooidal parts formed after budding of zooids through coalescence and resorption of zooidal tissue (some gymnolaemates).

3. Extrazooidal parts formed after budding of zooids, extrazooidal in origin (some stenolaemates).

4. Extrazooidal parts formed at the same time as budding of zooids (some stenolaemates, a few gymnolaemates, all phylactolaemates).

Integration through astogeny.—It is assumed that the morphologic differences among zooids imply physiologic and functional differences. Astogenetic differences between zooid generations in a zone of change therefore can be assumed to have been developing toward a repeatable set of physiologies and functions as well as morphologies. The sequence of morphologic as well as inferred physiologic and functional change is an expression of colony control because it is absent in solitary animals. In Bryozoa, the following states, in order of increasing integration, may be present.

1. All zooids of all generations, including the first zooid, of constant morphology (a few sexually produced gymnolaemates, some asexually produced—by fragmentation—stenolaemates and gymnolaemates, all sexually produced phylactolaemates).

2. First zooid or group of zooids different, all others without generational differences (some sexually produced gymnolaemates, asexually produced phylactolaemates).

3. Generational differences between zooids limited to proximal region of colony; that is, the colony has primary zones of astogenetic change and repetition only (many sexually produced stenolaemates, many sexually produced gymnolaemates).

4. Generational differences between zooids present in proximal regions and at least one

distal region of colony; that is, the colony has both primary and subsequent zones of astogenetic change and repetition (many sexually produced stenolaemates, some sexually produced gymnolaemates).

5. Generational differences between zooids on gradient throughout colony; that is, the colony lacks any zone of astogenetic repetition (a few sexually produced gymnolaemates).

Integration through morphologic differences among polymorphs.—Polymorphic differences are an expression of colony control, for polymorphism is one kind of functional reponse to the environment by the colony. In feeding, reproduction, and other basic processes, zooids in a **monomorphic colony** respond virtually as individuals. The response of a polymorph, however, is through its contribution to the colony as a whole, in direct proportion to its functional specialization. The following states, in order of increasing integration, are known in Bryozoa.

1. All zooids of same generation of constant morphology (all phylactolaemates, skeletally many stenolaemates, a few gymnolaemates).

2. Asexually produced zooids polymorphic, all having feeding and sexual reproductive ability (possibly some stenolaemates, some gymnolaemates).

3. Asexually produced zooids polymorphic, some lacking either feeding or sexual reproductive ability (possibly some stenolaemates, some gymnolaemates).

4. Asexually produced zooids polymorphic, some lacking both feeding and sexual reproductive ability (many stenolaemates, most gymnolaemates).

Integration through positional differences of polymorphs.—Another measure of colony control is expressed by polymorph position and structural dependence on other zooids. Polymorphs intercalated randomly in the colony budding pattern probably contribute their specialized functions as separate operating units. Those assembled in repeated groups of one or more kinds of zooids can carry out their specialized functions jointly. These functions include joint production of currents or brooding of larvae in living colonies. **Intrazooidal polymorphs** (zooids changed in morphology and function during life within the same living chambers) and some **adventitious polymorphs** (appendagelike zooids adding functions to those of the supporting zooids) indicate higher degrees of structural dependence on the supporting zooid than polymorphs intercalated in the budding pattern. The following states, listed in order of increasing integration, are known in Bryozoa.

1. All zooids of same generation of constant morphology (all phylactolaemates, skeletally many stenolaemates, a few gymnolaemates).

2. Asexually produced zooids polymorphic, intercalated in the budding pattern randomly (some stenolaemates, some gymnolaemates).

3. Asexually produced zooids polymorphic, intercalated in the budding pattern regularly (some stenolaemates, some gymnolaemates).

4. Asexually produced zooids polymorphic, in repeated groups (many stenolaemates, some gymnolaemates).

5. Asexually produced zooids polymorphic, intrazooidal or adventitious (a few stenolaemates, many gymnolaemates).

USE OF CHARACTERS IN CLASSIFICATION

Classifications consistent with inferred evolutionary history are essential for application to problems in biogeography, biostratigraphy, and other historical aspects of biology. Therefore, evolutionary classifications of Bryozoa must be attempted, even though no definitive classification is likely to be established. Even if it were possible to know the

evolutionary history of Bryozoa, more than one classification could be consistent with that history. Taxa are segments of a lineage or grouping of lineages, and the boundaries between taxa can only be placed arbitrarily through the continuum, even if some lineages evolved so rapidly that few generations of intermediates existed. The only nonarbitrary rule for the placement of taxonomic boundaries is that a taxon must not combine lineages having separate evolutionary histories as inferred from their distribution in time and space. Given these restrictions, evolutionary classifications can only be approximations that are subject to improvement.

The evolutionary significance of a classification increases with increased use of genetically controlled characters. This does not mean that characters of unknown genetic significance, such as the presence or absence of polymorphism, cannot be used in a classification, but only that those inferred to lack genetic control, such as the irregular two-dimensional shapes of individual encrusting colonies on rough substrates, should not be used.

In bryozoans, taxonomic characters are derived from morphologic features that must reflect varying proportions of genetic and environmental control. Estimates of the proportions of genetic and environmental control are among the most difficult interpretations to make in evolutionary taxonomy. The only direct and convincing approach to the problem seems to be through experimentation with the breeding and growing of colonies, ideally in their natural habitat. Until studies of living colonies are accomplished for many taxa in many environments, the taxonomist must continue to approach the matter indirectly. For many fossil taxa, of course, such approaches will always be indirect.

All modern classifications or proposed evolutionary arrangements of Bryozoa have been based on morphologic differences expressed as states of taxonomic characters. Some have used only morphologic characters of living forms (e.g., Borg, 1926a; Marcus, 1938a; Silén, 1942), or of living and fossil forms without reference to the independent evidence of position in time (Cuffey, 1973). One classification is based on inferred position in time of soft-part morphology not available in the fossil record (Jebram, 1973b). Some proposed evolutionary classifications have considered morphologic differences in a time-space framework (e.g., Bassler, 1953; Astrova, 1960a; Ryland, 1970).

Classifications that attempt to express evolutionary relationships depend on the nature and number of characters used as well as the independent evidence of position in time. Improved evolutionary arrangements and new classifications can be achieved by the addition of taxa and taxonomic characters, by improved understanding of stratigraphic relationships, and by new approaches to character analysis and taxonomic philosophy. Material that has not been employed in classifications of the Bryozoa is now available in each of these areas. The procedure for taxonomic character analysis suggested below is based on a new synthesis of the nature of the bryozoan colony and an evolutionary taxonomic philosophy that has not been tried in classifications of Bryozoa.

TAXONOMIC CHARACTER ANALYSIS

In all groups of Bryozoa, the high level of organization of both zooids and colony makes available many morphologic characters for taxonomic study. A character having potential taxonomic importance has states, which are morphologic properties by which organisms differ. Characters may show many states, a wide variety of differences, or few, the simplest being the two-state character of "present" or "absent."

The taxonomic process begins with observations of the more obvious intracolony and intercolony morphologic differences in structures that are initially assumed to be comparable. Initial observations are followed by a three-part character analysis, which tests the evolutionary potential of all available

morphologic differences, using biologic processes, assumptions, and principles. In addition to expressing morphologic differences, evolutionary characters and their states should satisfy three major requirements. First, a character should be morphologically independent to the extent that its observable states are not partly determined by states of other characters within the taxon being considered. Second, a character influenced by ontogeny, astogeny, or polymorphism should have separable states that are comparable from colony to colony. Third, a character should be genetically controlled to the extent that its observable states correlate with genetic differences among colonies.

Biological analysis.—The first step in obtaining characters of evolutionary significance is to recognize as many characters as possible that are morphologically, but not necessarily genetically, independent of each other. Morphologic independence of many characters generally adds detail and sensitivity to the resulting classification while guarding against redundancy of characters and morphologic ambiguity of character states. Independent characters are most likely to be recognized by detailed study of the morphology of the whole colony and its parts, and interpretations of mode of growth and function of that morphology. It is generally assumed that morphologic features have biological significance in growth and functions of the colony. Some structures possibly have changed or lost their original function during evolution, but direct evidence of vestigial structures has not been recognized in Bryozoa.

Characters appropriate to any level of the taxonomic hierarchy may be derived from morphologic features at organizational levels of cell, tissue, organ, zooid, unified grouping of zooids, extrazooidal part, or entire colony. Whether characters are independent can be determined only by comparison among colonies and taxa of the character states of comparable, potentially homologous morphologic structures. Improvement in our understanding of the comparability of structures will result only from application of the most revealing study techniques available to comparative morphology, and from more detailed interpretations of mode of growth and function. At this stage in the study of Bryozoa, advancements in biological analysis generally will result in an overall increase in the number of morphologically independent characters to be considered in classifications.

Morphologic features from which independent characters can be derived include orificial and frontal walls in most gymnolaemate bryozoans. These features are morphologically continuous (Fig. 3), but perform different functions and therefore form the basis for two separate sets of characters. In stenolaemate bryozoans, vertical walls may be distinguished from frontal walls in zooids by their microstructure and mode of growth, and by partial functional differences (Fig. 11), allowing them to be recognized as separate features providing separate sets of independent characters.

Intracolony analysis.—The second step in taxonomic character analysis in Bryozoa is to recognize, for each independent character, states that have been separated from, or have taken into account, intracolony variation. A set of separated states of characters must be recognized and expressed for each colony. These may come from the generally recognizable morphologic patterns of ontogeny, astogeny, polymorphism, and narrowly determined microenvironmental modifications within each colony (Boardman, Cheetham, & Cook, 1970). Character states separated into major stages of these patterns can be compared directly from colony to colony (see Sources of Morphologic Variation).

It is obvious that all morphologic variations within a colony must fall within the potential range of expression of the presumed uniform colony genotype, and in this sense all morphologic variation is genetically based. Genetically controlled variation as used here, however, applies only to morphologic differences that reflect differences in genotype. Because of the asexual mode of growth of the colony, variation due to differences in geno-

type is assumed not to occur within a colony but only among colonies, except for somatic mutations, which have not been recognized in Bryozoa.

Intracolony analysis begins with recognition of whether zooids are monomorphic or polymorphic. Each set of polymorphs has a set of character states at least partly different from the sets of other polymorphs. Each character is studied for astogenetic and ontogenetic changes. Some characters change from generation to generation in zones of astogenetic change, but others may be constant from generation to generation whether in a zone of change or a zone of repetition. Similarly, some characters change continuously throughout the life of a zooid, but others are either constant throughout life or may become constant at different ontogenetic stages. The characters that are constant ontogenetically and astogenetically (and as nearly as determinable, microenvironmentally) may be expressed as one state for each polymorph in each colony. Some but not all of these characters may also be constant for all polymorphs in the colony. For example, constant microstructure of vertical walls throughout a colony is a single state representing the entire colony. Likewise, constant calcitic or constant aragonitic composition of all calcified walls in a colony are single states representing entire colonies.

Characters that change in generational patterns indicating either ontogeny or astogeny can be expressed as series of states for each colony. Intervals of these series then serve as the separated states for the colony. For example, maximum extent of vertical walls can be reached early in zooid ontogeny, or these walls can increase throughout the life of the zooid. Aragonite layers may be added to initial calcite wall layers during zooid ontogeny. The size of zooids can increase from generation to generation in a zone of astogenetic change. Thus, the ontogenetic extension of vertical walls, the mixed composition of calcareous walls, and the astogenetic increase in zooid size can be divided into separated character states.

Young living colonies, or modern or fossil colonies that died in early stages of life, commonly show only parts of the series of separated character states present in fully developed colonies. States characteristic of zones of astogenetic repetition or of later stages of zooid ontogeny may be missing. If certain polymorphs or extrazooidal parts are present only in zones of astogenetic repetition or after zooids have reached a certain ontogenetic stage, these too may be missing in young colonies.

Fragments of colonies also commonly lack parts of series of separated character states. In different fragments of a colony, one may find states of different ontogenetic or astogenetic stages, of different sets of polymorphs, or of extrazooidal parts characteristic of the whole colony. If a sufficient number of fragments presumably from the same population is available, their overlapping patterns of variation permit at least tentative reconstruction of the separated character states of whole colonies. In many fossil bryozoan taxa, reconstruction from colony fragments has provided the only basis for recognition of separated character states.

Intercolony analysis.—The third step in taxonomic character analysis in Bryozoa is to attempt to recognize, for each independent character, states that more nearly express genetic rather than environmental difference between colonies. The first two analyses reduce the sources of variation to genetic and environmental differences between colonies. Unfortunately, environmental variation cannot be accounted for in the comparison of colonies to the same degree as ontogenetic, astogenetic, and polymorphic differences. Different colonies, even within the same community, may have been subject to differing environments and therefore record different morphologic reactions. Some species exhibit encrusting growth on an "unlimited" substrate and erect growth where the extent of substrate is or becomes severely limited; an example is illustrated and described by Cook (1968a, p. 124, pl. 1, fig. c,d). A colony growing in a changing environment may combine both modes of growth (Cook,

1968a, p. 124), which demonstrates that the variation between colonies can be of the same kind as that within a colony. Environmental differences thus produce two kinds of morphologic variation in Bryozoa: that expressed by the colony as a whole (colony-wide environmental variation) and that observable within a colony (microenvironmental variation).

Recognition of direct environmental modification of the states of a character does not necessarily rule out the use of that character in deriving a classification. The limits within which the states of a character can express direct environmental modification are assumed to be genetically controlled. Differences of limits within the same range of environments can be inferred to reflect genetic differences of potential taxonomic value. For example, two species might exhibit different but overlapping series of growth habits developed within the same range of environments. The growth habit most commonly developed within each species in the same environmental range, moreover, could fall within the overlap between species and that modal growth habit could be under genetic control. The observed differences between the growth habits of individual colonies themselves, however, would not be directly correlated with genetic differences and thus would have no evolutionary significance as a basis for further taxonomic subdivision.

Proportions of genetic and colony-wide environmental control of many single morphologic characters may be estimated indirectly based on the following assumptions.

1. Characters are assumed to be closely controlled genetically if they remain relatively constant through significant intervals of geologic time, or if their patterns of transitional change are not significantly modified by inferred environmental changes through intervals of geologic time. In either case, inference of genetic control is strengthened by increased independent evidence that the bryozoan successions were subjected to changing environments. Of course, a character that changed through a significant interval of time in correlation with environmental changes can also be closely controlled genetically, but this genetic control would be difficult to distinguish from environmental modification.

2. Some characters derived from structures grown within exterior walls are assumed to reflect increased degrees of genetic control because they are sheltered from some kinds of environmental interference by the comparative stability of the internal environment of the body cavity.

A corollary is that because colony-controlled (integrated) structures are commonly grown within exterior walls, many characters derived from these structures also show greater degrees of genetic control.

3. Microenvironmental modifications are generally recognizable and serve as a basis for estimating the kinds of morphologic differences that might be caused by colony-wide environmental differences.

4. The colony growth habit of many species varies and is assumed to be closely controlled by environment within genetically set limits. Parts of zooids and extrazooidal features that are affected by changes of growth habit can also be assumed to be directly modified by the environment. Environmental modifications are assumed to be especially pronounced in features that are structural in function, relating to the strength of colonies in the different growth habits.

5. Environmental control is assumed for certain modifications of characters not necessarily associated with differences in growth habits of colonies. Such modifications are observable in colonies subjected to environmental changes of short duration relative to colony life, or in colonies that lived in more than one environment. It is assumed that structures in which modifications independent of colony growth habit are observable can be interior or exterior, or colony controlled or zooid controlled. If these modifications are developed throughout whole colonies and are comparable to those developed microenvironmentally in other closely associated colonies, the inference of environmen-

tal influence is more convincing (assumption 3 above).

6. It is assumed that the proportions of genetic and environmental control of any potential taxonomic character can be different in different taxonomic groups under similar environmental circumstances.

Development of increasing colony control appears to have conferred a selective advantage, as suggested by the trend in some stocks toward higher degrees of integration. Some early forms in evolving stocks of major taxonomic rank exhibited so low a degree of integration that member zooids may have functioned nearly as solitary animals (e.g., corynotrypids in stenolaemates, BOARDMAN, this revision; and *Pyriporopsis, Arachnidium,* and similar forms in gymnolaemates, CHEETHAM & COOK, this revision). Evolution of some of these forms can be inferred to have proceeded toward higher degrees of integration. Study of the major branch of gymnolaemates, the cheilostomates, has suggested an increase in colony integration from the Jurassic to the present (BOARDMAN & CHEETHAM, 1973, p. 178–191). Body walls of the earliest cheilostomates were almost entirely exterior, immediately adjacent to the environment. Through time, other cheilostomates appeared with greater proportions of interior vertical walls. The concept of interior zooidal walls in Bryozoa requires that these walls grow under the protection of the colony and not the immediate influence of the environment. Features of their internal construction, therefore, such as lack of cuticle in stenolaemates and microstructure of zooecial boundaries and skeleton, may be less dependent on the environment and more reflective of the genotype.

Physiologic communication among zooids and between zooids and extrazooidal structures of a stenolaemate colony apparently can be through pores or around ends of interior vertical walls, under the protection of the exterior wall and within the body cavity of the colony. The two kinds of connections are used separately or together, in different combinations with other structures for apparent selective advantage, expressed by the functional performance of the colony as a whole. Characters of communicational function in a colony, therefore, might well show more genetic than environmental control and be subject to natural selection in the evolutionary process.

In all but the simplest gymnolaemates, contiguous exterior walls are breached by interzooidal communication organs. Some colonies with significant proportions of exterior vertical walls can therefore have a higher degree of integration than the simplest uniserial forms. Communication organs in both exterior and interior walls are within the body of the colony and thus should show more genetic than environmental control.

Astogenetic differences leading to an ever-repeatable budding plan and functions are expressions of colony control. Astogenetic development of the zone of repetition has selective advantage in that it allows colonies to become larger without increasing the size of member units. The general sequential patterns in zones of change to zones of repetition for a species are constant enough to suggest genetic control. In the gymnolaemate order Cheilostomata, evolutionary trends toward development of increasingly complex astogenetic change further suggest genetic control.

The diversification of functions made possible by the development of polymorphic zooids provides a selective advantage, especially in uniform environments (SCHOPF, 1973). In the gymnolaemate order Cheilostomata, the development and refinement of polymorphs in many evolving stocks appears to be an expression of this selective advantage.

Extrazooidal parts are generally structural in function and add to the strength or flexibility of a colony. They are therefore probably subject to considerable modification from the immediate environment, even though they form under direct colony control. Extrazooidal parts may well provide colony protection for zooids, however, so that zooidal characters can be relatively independent of envi-

ronmental influence and more nearly reflect the genotype. The regularity of arrangement of zooids in cupuladriid cheilostomates may reflect this kind of control.

Examples of characters in stenolaemates assumed to be environmentally modified without change in colony growth habit include such small variations in growth characteristics of zooidal and extrazooidal structure during their ontogeny as in thickness of different skeletal layers of walls, in overall thickness of wall segments, or in spacing and thickness of basal diaphragms. These modifications appear to be based on growth rates controlled by short-term environmental changes during the life of the colony. These changes are microenvironmental if they are restricted to parts of colonies. If similar-appearing growth changes are colony-wide, they are generally considered to be environmentally controlled, but with less certainty.

Summary.—The aim of the three-part character analysis is to obtain genetically controlled states for as many independent characters as possible for each colony. At the end of this procedure, the list of states for each colony will include some for which the degree of genetic control has been inferred with a high degree of confidence. Others, for which the degree of genetic control has been inferred with less confidence, may or may not be used in classification on the judgment of the investigator.

The effort to distinguish between genetic and environmental control of character states is greatly facilitated by application of the concept of colonies in bryozoans as opposed to the concept of solitary animals. The ability to recognize separately those morphologic differences in bryozoan colonies that result from ontogeny, polymorphism, and microenvironment means that character states controlled by these variables can be "cleanly" removed from consideration without overlapping morphologic confusion with the genetic and colony-wide environmental effects being studied.

GENERAL FEATURES OF THE CLASS STENOLAEMATA

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The Stenolaemata are here considered to make up one of three classes of the phylum Bryozoa. Members of the class are characterized by feeding zooids with complete interior vertical walls (Fig. 25, 26) that are commonly elongated to enclose tubular, conical, or sac-shaped body cavities. Vertical walls are elongated parallel to the direction of zooidal growth. Vertical walls of all zooids have skeletal layers, as do basal and frontal walls (Fig. 26) where they occur. In most taxa, zooids open at high angles to colony surfaces, and zooecial apertures are comparable in area to cross sections of living chambers. Zooecial apertures and the terminal membranous orificial walls that cover them in living colonies are transverse to zooidal length. Tentacles are protruded through circular porelike orifices by the action of a membranous sac that surrounds the lophophore and gut in recent stenolaemates.

The class Stenolaemata produced virtually all of the vast accumulation of fossil bryozoans from the Early Ordovician into the Early Cretaceous, a time interval lasting nearly 400 million years. During that interval the class Gymnolaemata is represented by a few scattered species of ctenostomates beginning in the Ordovician and of cheilostomates beginning in the Jurassic (see CHEETHAM & COOK, this revision, General Features of the Gymnolaemata). Stenolaemates are the most abundant fossil group in many rock units throughout the stratigraphic column and the continuity of their stratigraphic occurrences is comparable to that of other major groups of fossils. During the Late Cretaceous, the stenolaemates began to lose their predominance within the phylum to the class Gymnolaemata. Stenolaemate numbers and diversity have apparently been on a slow decline since the Cretaceous. Stenolaemates can be found living in large numbers, however, in many marine communities (e.g., the Mediterranean Sea; HARMELIN, 1974, 1976).

The class includes four (Blake, this revision) to six (SHISHOVA, 1968) orders, depending on the classification used. Five orders are recognized here. The Trepostomata, Cystoporata, Cryptostomata, and Fenestrata all appeared during the Ordovician, all were prolific at times during the Paleozoic Era, and all are generally considered to have become extinct during or just after the Permian. The Tubuliporata (formerly Cyclostomata) also appeared in the Ordovician, but remained unimportant in numbers and diversity until the Mesozoic and Cenozoic eras, when they occurred in large numbers.

Unfortunately, the Paleozoic and post-Paleozoic taxa have been studied using different preparation techniques and taxonomic characters. The present literature tests neither the assumed Permian and Triassic extinctions of Paleozoic stocks, nor the generally accepted monophyletic origin of the post-Paleozoic Tubuliporata. One of the questions of highest priority to improved understanding of the class Stenolaemata is the piecing together of its evolutionary history across the Paleozoic-Mesozoic boundary, using modern taxonomic procedures and as many taxonomic characters as are available.

Stenolaemate bryozoans apparently have been entirely marine throughout their history. In Paleozoic rocks their numbers are largest in calcareous shales, mudstones, and some limestones. Colonies that grew erect are commonly preserved broken but unscattered in shales and mudstones, indicating little or no transportation after death (e.g., BOARDMAN, 1960).

Growth habits of colonies of many species of bryozoans have long been assumed to be modified significantly by different environments (e.g., ULRICH, 1890; STACH, 1936). A thorough review of the literature of steno-

laemate ecology and paleoecology was published by DUNCAN (1957). Experimental studies are just beginning to emphasize the effects of different environments on colony growth habits and correlated changes of internal morphology within the same species of living stenolaemates (for examples, see HARMELIN, 1973, 1974, 1975, 1976).

Details of skeletal structures are commonly well preserved in fossil stenolaemates of all ages and provide many taxonomic characters that can be inferred to be genetically controlled. Skeletal structures furnish evidence of modes of growth, functional morphology, and intra- and intercolony morphologic variation, especially where their relationships with soft parts can be inferred with confidence.

A surprising number of indications or actual fragmentary remains of soft parts occur throughout the fossil record of the stenolaemates and some very general comparisons can be made with the complete soft parts of modern species. Unfortunately, the soft parts of most modern species and their growth and functional relationships with skeletal counterparts are poorly known. For example, recent sectioning of a few randomly selected taxa has revealed four different morphologies affecting the protrusion of tentacles (BOARDMAN, 1973, 1975). Only one of these had previously been reported. Most of the character states derived from soft parts that are assumed to be characteristic of the order Tubuliporata are known from relatively few species and therefore should be investigated further.

Independent, apparently genetically controlled taxonomic characters within colonies that are carefully collected from vertical sequences commonly show transitional changes. Not enough of these detailed studies have been published, however, to demonstrate many evolutionary patterns and detailed morphologic trends. Unfortunately, the study of stenolaemate bryozoans has not been advanced enough for a general realization of their potential value in applied problems of ecology, zoogeography, and biostratigraphy.

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HISTORICAL REVIEW

CLASSIFICATION

The concept of tubular Bryozoa, now the class Stenolaemata, began formally with the establishment of the Tubuliporina JOHNSTON (1847, p. 265), placed under Polyzoa infundibulata, and based on studies of recent Bryozoa only. The group was characterized by JOHNSTON as "Polypidoms calcareous, massive, orbiculated or lobed or divided dichotomously; the cells long and tubular, with a round prominent unconstricted aperture." The characterization was accompanied by a drawing of an unmistakable tubuliporid and descriptions of a number of appropriate taxa.

Later, BUSK (1852, p. 346) established the Cyclostomata as a suborder, basing the name on recent Bryozoa ". . .having a round, simple opening to the cell. . . ." BUSK recognized

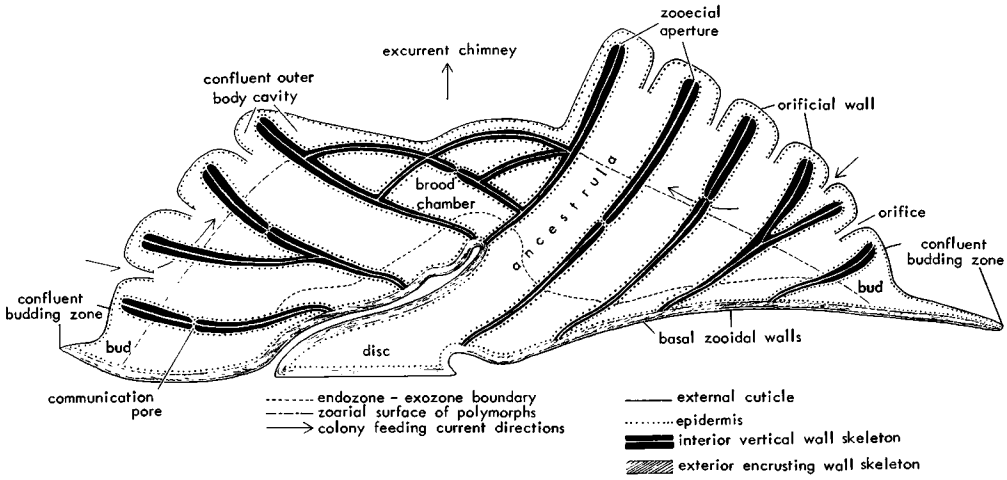


FIG. 25. General features of the Stenolaemata. Diagram of a longitudinal section through the center of a free-walled lichenoporid colony. The plane of section lies within feeding zooids radially arranged in both directions from the colony center. Polymorphs (not shown) are in radial rows between rows of feeding zooids and form a part of the zoarial surface at the lower level indicated by the unevenly dashed line. Arrows parallel the flow of feeding currents past orifices, up to the center of the colony on the polymorph surface, and out through the chimney in the center of the colony. The basal encrusting colony wall is multizooidal, originating in the multizooidal budding zone, which is confluent around the outer margin of the colony. In lichenoporids, budding of most zooids occurs from basal colony walls in endozones in the confluent budding zones. A few zooids are budded from zooidal walls of exozones into confluent outer body cavities, as indicated by bifurcations of vertical walls. (In exozones outer body cavities are divided into zooids so that budding space is zooidal, not multizooidal.) Zooids growing to the right of the colony center form a wedge in the primary direction of encrusting growth. The fold on the left side of the disc provides encrusting colony wall for a wedge of zooids growing in the secondary encrusting growth direction. White lines in the center of interior vertical walls depict zooidal boundaries, indicating that vertical walls are compound.

his suborder as ". . .coinciding very nearly with the Tubuliporina. . ." of JOHNSTON. Unfortunately, BUSK's name Cyclostomata had earlier been used in the classification of fishes (DUMÉRIL, 1806). Nevertheless, the name Cyclostomata has been adopted in the classification of both living and comparable fossil tubular bryozoans and Tubuliporina has been ignored. *Treatise* policy recommends that the name Cyclostomata BUSK, 1852, be considered a junior homonym. To replace it, the name Tubuliporina is changed here to Tubuliporata JOHNSTON, 1847, to conform to order-level endings and to avoid conflict with the use of Tubuliporina as a suborder.

Many of the first tubular bryozoans of Paleozoic age to be described were thought to be corals by some paleontologists (e.g., NICHOLSON, 1879, 1881; VINE, 1884, p. 182; WAAGEN & WENTZEL, 1886, p. 885). Others considered some of the same genera to be bryozoans (e.g., ROMINGER, 1866; LINDSTRÖM, 1876; DOLLFUS, 1875; and ZITTEL, 1880). The controversy was so confused by inadequate understanding of the taxa considered to be critical to the problem that the arguments are nearly impossible to follow in detail. Most of the genera of Paleozoic age involved in the controversy were considered to be bryozoans and placed in the new suborder Trepostomata by ULRICH (1882, p. 151). Trepostomates were finally accepted as bryozoans based largely on the work of ULRICH (from 1882 through 1893), CUMINGS (1912), and CUMINGS and GALLOWAY (1915).

CUMINGS' work was especially convincing. He based his interpretation on the shape of the zooecium of the ancestrula and the

arrangement of the first few zooids. Similarities of ancestrulae in the trepostomate colonies of Paleozoic age and in species of undoubted tubuliporate bryozoans placed in the genus *Heteropora* (CUMINGS, 1912, p. 366) suggested that tubuliporates were the ". . .recent Bryozoa most closely related to the Paleozoic Trepostomata. . ." (CUMINGS & GALLOWAY, 1915, p. 350).

GREGORY (1909, p. 122–126) recognized some of the same morphologic features in both the Paleozoic trepostomates and post-Paleozoic tubuliporates and therefore placed some Mesozoic and Cenozoic tubuliporates in the Trepostomata. These similarities, which are now considered to characterize the class Stenolaemata, include long, tubular, parallel zooecia; size of zooecial cross section; presence of zooecial bends; and thicker walled outer segments of zooecia.

BORG (1926a, p. 489) argued that the Cyclostomata (including the Trepostomata and what is here called Tubuliporata), Phylactolaemata, and Gymnolaemata (including the Paleozoic Cryptostomata of this revision) probably had common ancestors but no ". . . lineal relation to one another." For that reason, he raised the Cyclostomata to the same taxonomic level as his Phylactolaemata and Gymnolaemata rather than leaving them in the next lower hierarchical level with the Cheilostomata, Ctenostomata, Cryptostomata, and Trepostomata as interpreted by earlier authors. BORG (1926a, p. 490) concluded that ". . . it seems to me necessary to form a new order for the Cyclostomata, coordinate with the two older orders [now considered classes] Gymnolaemata and Phylactolaemata. I propose that this new order should be termed Stenolaemata." He diagnosed the order as follows:

"Zooids narrow, cylindrical, tapering proximally, with terminal opening; cystids with calcified walls; polypide enclosed in a membranous sac acting as a hydrostatic apparatus, embryonic development within the membranous sac of a fertile polypide which itself degenerates, either in gonozoids, or in a coelomic space between the zooids; polyembryony."

BORG's (1926a, p. 490) classification included three orders, Phylactolaemata, Stenolaemata, and Gymnolaemata. The order Gymnolaemata contained three suborders: Cryptostomata, Cheilostomata, and Ctenostomata.

BORG suggested that the Stenolaemata should be divided into two suborders, the newly restricted Cyclostomata and the Trepostomata; however, he did not actually divide them until 1944 (p. 18, 19), when he reclassified genera and families so that his restricted Cyclostomata included only fixed-walled species (simple-walled species of BORG, single-walled species of subsequent authors, and fused-walled species of BOARDMAN, 1975; see Fig. 26). His Trepostomata apparently included all free-walled stenolaemates of all ages (the double-walled forms of BORG and subsequent authors; see Fig. 25) minus the cryptostomates. BORG's classification within the Stenolaemata has not been followed by subsequent authors.

The Paleozoic order Cryptostomata was defined by VINE (1884, p. 196) to include small ribbon-shaped bifoliate genera and small dendroid (branches circular in cross section) genera that were thought to have "orifice of cell surrounded by vestibule, concealed." This inferred inner position of the orifice was thought to be near the **hemisepta** (shelflike skeletal structures within the zooecia) that occur in some of the included genera. The presumed inner orifice caused the cryptostomates to be compared with the cheilostomates (ULRICH, 1890, p. 333; CUMINGS, 1904, p. 76; BORG, 1926a, p. 481; BASSLER, 1953, p. G119) and to be placed in the same grouping with the cheilostomates and ctenostomates (BORG, 1926a, p. 490). Evidence from modern tubuliporates with similar appearing hemiseptumlike structures (see Fig. 39,*4*) suggests that the orifice was not at the inner position of the hemiseptum but at the outermost zooecial aperture (Fig. 25). The remainder of the skeleton and the inferred mode of growth are comparable with those of free-walled stenolaemates, and transi-

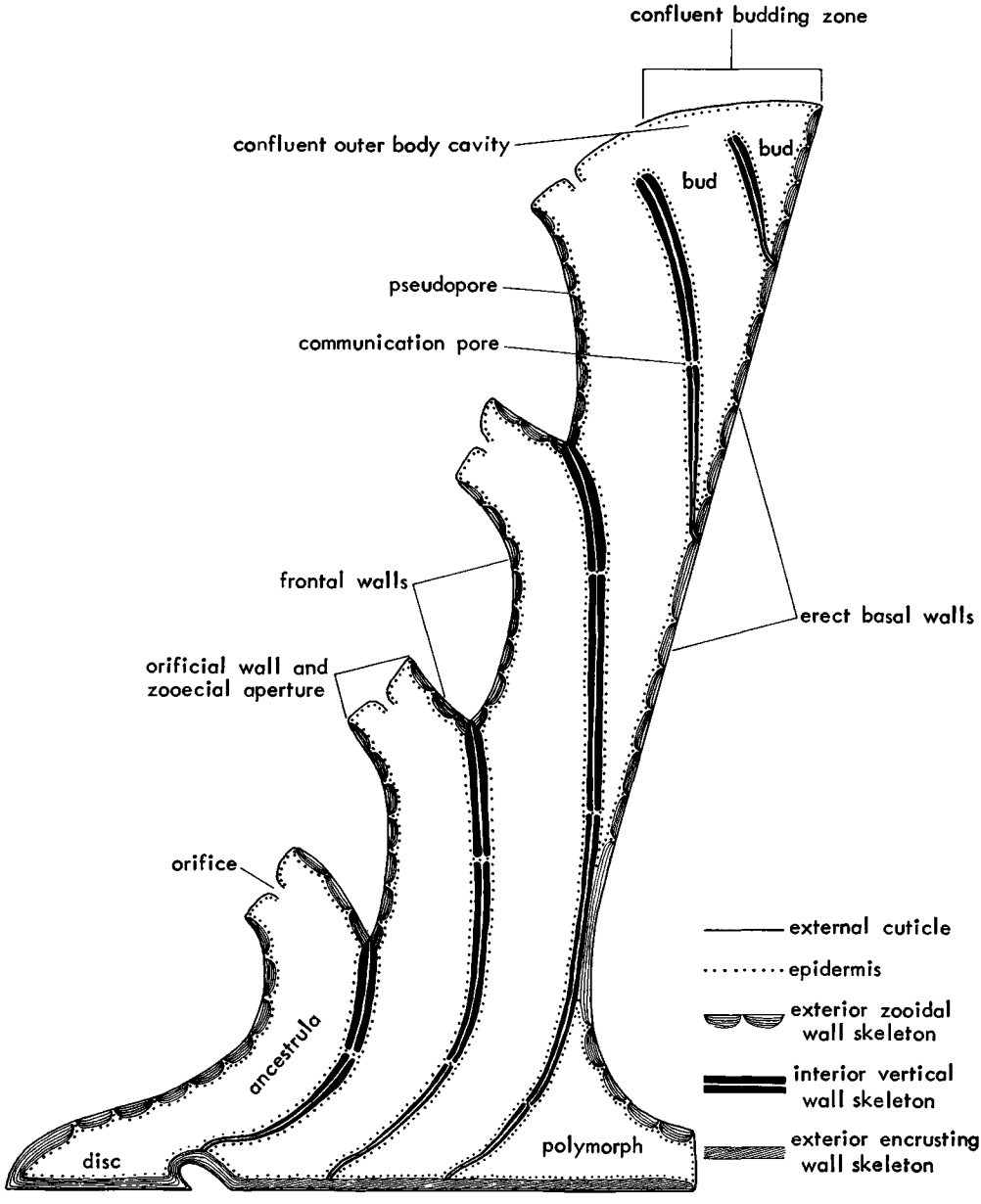


FIG. 26. General features of the Stenolaemata. Diagram of a longitudinal section through an idealized erect fixed-walled tubuliporate colony. The basal encrusting colony wall is multizooidal at least until it reaches basal polymorphs. The confluent budding zone in the distal end of the erect part of the colony includes outer confluent body cavity, covering exterior membranous wall, and the buds themselves. Calcification of exterior frontal walls at outer ends of interior vertical walls eliminates the outer body cavity of budding zone. Pseudopores in exterior walls do not penetrate exterior cuticle; most communication pores in interior vertical walls are open. The white line in the center of interior vertical walls depicts the zooidal boundary, indicating that vertical walls are compound. Peristomes are the outermost extensions of exterior frontal zooidal walls beyond more general colony surface.

tional morphology is a source of taxonomic confusion in distinguishing some cryptostomates from some trepostomates. The cryptostomates, therefore, have now been placed in the Stenolaemata (BOARDMAN & CHEETHAM, 1969; RYLAND, 1970).

In 1890 ULRICH (p. 349–362) removed the fenestrate (reticulate growth habit) genera of Paleozoic age from the tubuliporates and placed them in the Cryptostomata with the small bifoliate and dendroid forms. ELIAS and CONDRA (1957, p. 35) suggested a return to VINE's original two-part concept of the cryptostomates and elevated the fenestellids to the order Fenestrata. SHISHOVA (1968) removed the dendroid forms from the cryptostomates and made them an order, the Rhabdomesonata. In 1964 ASTROVA removed most of the Paleozoic genera from the Tubuliporata, added some genera that had been in the Trepostomata and Cryptostomata, and combined those genera into a new order, the Cystoporata (see UTGAARD, this volume).

As considered here, the class Stenolaemata [=Stenostomata MARCUS, 1938a] includes the following orders: order Tubuliporata JOHNSTON, 1847; order Trepostomata ULRICH, 1882; order Cryptostomata VINE, 1884 (see BLAKE and KARKLINS, this revision); order Fenestrata ELIAS and CONDRA, 1957; and order Cystoporata ASTROVA, 1964 (see UTGAARD, this revision).

METHODS OF STUDY

Students of the Stenolaemata may be divided into two schools based on preparation techniques and the resulting taxonomic characters employed. The earlier school relied primarily upon those characters that can be observed from outer surfaces or broken sections of zoaria. A second and later school uses characters occurring throughout zoaria. The second school began with the preparation of thin sections cut through zoaria of Paleozoic age in orientations standardized relative to the zooecia. Thin sections reveal morphologic details of colony interiors, adding greatly to the number of potential taxonomic characters.

Reliance on external characters.—The almost exclusive use of external characters has persisted in western studies of fenestellids (Paleozoic in age), and remains dominant in the taxonomy of post-Paleozoic and recent stenolaemates, the Tubuliporata. CANU and BASSLER, as early as 1920, published drawings and photographs of sections of zoarial interiors of many species of the Tubuliporata at low magnifications. Because they used only generalized zooecial shapes and arrangements from sections and relied mostly on external morphology, little taxonomic advantage was achieved. Only some of the most recent taxonomic papers on the Tubuliporata have employed thin sections more fully (e.g., VISKOVA, 1972, 1973; HARMELIN, 1974; HINDS, 1975; TILLIER, 1975; and NYE, 1976).

Use of external and internal characters.—Early sectioning techniques of the second school have provided the basis for modern sectioning refinements that, in combination with greatly improved light and electron microscopes, produce detailed information on the entire colony. Advantages of the use of sectioning include: first, the potential availability of all taxonomic characters of complete stenolaemate zoaria; second, the relative increase in numbers of characters from internal morphology of zooids and extrazooidal structures over characters concerning colony growth habit; and third, the availability of biological evidence concerning such subjects as mode of growth, functional morphology, reproduction, and feeding.

Oriented sections were first used by NICHOLSON (1876, 1879, 1881) in Scotland and DYBOWSKI (1877) in Russia. It was immediately recognized that new taxonomic characters derived from zooarial interiors differentiated many new taxa from specimens that were either externally poorly preserved, embedded in a hard rock matrix, or had similar colony surfaces.

Sectioning was adopted immediately by ULRICH, whose major monographs of American Paleozoic Bryozoa (1882, 1890, 1893), together with NICHOLSON's monographs,

established the necessity for deriving taxonomic characters from both external and internal morphology in Paleozoic Bryozoa. Likewise, NEKHOROSHEV and NIKIFOROVA began work in the early 1900's (ASTROVA in SARYCHEVA, 1960) and established, with the help of other workers, the oriented-section approach to Paleozoic Bryozoa in Russia.

Details of colony interiors, as seen in sections of Bryozoa of Paleozoic age, were especially effective in providing information on zooecia. The importance of zooecial characters was recognized immediately by the first taxonomists to make sections. As a result, taxonomic emphasis shifted from zoarial characters to zooecial characters. "Paleontologists, indeed, have now universally recognized that, in such difficult forms as the Monticuliporoids, the microscopic structure is the chief element in the determination of species; since surface characters may not be recognizable, or may vary greatly according to the state of preservation of the specimens, or other similar circumstances, while mere external form is a more treacherous and delusive guide" (NICHOLSON, 1881, p. v). And ". . .it cannot be questioned that differentiations in the cell or actual home of the polypide are more trustworthy structural variations than the form of the zoarium" (ULRICH, 1890, p. 326).

In an exchange of letters in *Science* in 1887 and 1888 between JAMES and FOERSTE, FOERSTE (1887, p. 225) presented philosophical arguments for the "new" study of internal characters of Paleozoic Bryozoa, which are as challenging today as they were then. "Theoretically development has proceeded in two lines,—one internal, to accommodate itself to the needs of internal function; and one external, to accommodate itself to environment, to the world with which the being comes in contact. Variations of function are far less frequent than those of environment: hence internal structure may still be very similar when external features have already extensively varied. Hence internal structure usually furnishes the reliable characters, which distinguish genera and higher groups; external features are used for specific determination. . . . It remains to be seen what characters of specific importance cannot be shown in microscopic slides."

The earliest study of thin sections of skeletons was done at relatively low magnifications. ULRICH and BASSLER routinely used hand lenses instead of the microscopes that were available to them. Their observations were necessarily deficient in the description of small-scale characters and their biological interpretations were restricted. Nevertheless, their work and that of their contemporaries on Bryozoa of Paleozoic age was a major improvement because of the addition to the classification of many internal characters.

Another practice commonly employed in this early use of thin sections was based on the assumed correlation between external and internal characters. Often, free specimens from a stratigraphically and geographically restricted fauna were sorted into "species" groupings on external appearance. Only one to several fragments of colonies were actually sectioned from each of those groupings. Early descriptions emphasized internal characters observed from those few sections and were thought to be adequate to distinguish species. Subsequent sectioning of the unsectioned paratype suites of trepostomate species commonly reveals several taxa at the genus and species level because of the prevalence of external homeomorphy. Also, ranges of transitional morphologic variation within species commonly appear greater than first supposed.

An unfortunate result of the thin-sectioning technique itself is the still common custom of describing character states as seen in the two dimensions of thin sections without conversion to their actual three-dimensional condition. Much confusion and misinformation have resulted, adding to the difficulty of biologic understanding and taxonomic application.

At the turn of the century, lack of knowledge of living species was a formidable handicap to biological interpretation of fossil stenolaemates of all ages. CUMINGS (1904,

1905, 1912) and CUMINGS and GALLOWAY (1915), using standard microscopes of that time, worked out some ingenious approaches to biologic interpretation for Paleozoic stenolaemates, which can be applied inferentially. They unfortunately were not followed until the 1960's when their approaches furnished the foundation for many of the present-day refinements of biologic interpretation of stenolaemates of Paleozoic age.

Beginnings were made on the study of soft parts of stenolaemates in early papers, especially by HARMER (1896, 1898). Later, papers by BORG (e.g., 1926a, 1933, 1944) on recent tubuliporates developed much new information with evidence from enough taxa to indicate the general applicability of some basic features for the entire class. BORG, however, did little work on the skeletons overall (see BORG, 1933, for an exception) and their more detailed relationships to corresponding soft parts. Unfortunately, these excellent beginnings to the study of soft parts of modern stenolaemates have not been continued by zoologists.

A large gap exists between the philosophies and procedures employed in most existing taxonomy of stenolaemates and those philosophies and procedures that have been available beginning in the early 1940's. The selection and treatment of stenolaemate characters at higher taxonomic levels have been based on a minimum of biologic interpretation and are largely arbitrary. Many structures and their characters, both external and internal in colonies, are those most readily observed and described. The taxonomic value of a newly recognized structure or character is commonly judged in proportion to its visual prominence, without inquiring into its possible mode of growth, functional significance, degree of inferred genetic control, or possible occurrence in known taxa that might be related.

Even with use of too few fragments of colonies and too few characters at the species level, it is possible to differentiate some species within local faunas of living stenolaemates or local fossil faunas through restricted time intervals. Many taxonomists have necessarily concentrated on relatively local faunas, and relatively few characters and character states have seemed adequate. Each species recognized, however, should be distinct from all others of the world through time. This seems an overwhelming and perhaps impossible goal that can only be approximated, with each generation hopefully adding improvements.

APPROACH TO TAXONOMIC CHARACTERS

All modern methods for constructing phylogenetically based classifications begin with as many independent taxonomic characters as possible. Although these taxonomic characters should be largely genetically controlled, in practice, they are derived from morphologic structures that initially must be assumed to reflect varying proportions of genetic and environmental control. Unfortunately, estimates of degrees of genetic and environmental control expressed by taxonomic character states are among the most difficult interpretations to make in taxonomy.

Such estimates in modern stenolaemates rely upon some understanding of the biology of the entire colony, including its mode of growth, detailed morphology, astogeny, ontogeny, polymorphism, functional morphology, and environmental modifications. The most convincing estimates are arrived at through study and experimentation with living colonies in their natural habitats. Relatively little is known about the basic biology of living stenolaemates, and that little has yet to be applied to classifications to improve their phylogenetic content. Extrapolations of comparable biologic and taxonomic approximations backward into geologic time require study of as much of the fossilized skeleton of the colony as possible.

COMPARATIVE STUDY OF RECENT AND FOSSIL STENOLAEMATES

The major approach to biologic interpretation of extinct stenolaemates is basically uniformitarian morphologic comparison with living species. The assumptions of the uniformitarian approach used here are listed below.

1. Comparable morphology in fossil and living taxa is assumed to indicate similarity in function and mode of growth. Conversely, different morphologies are generally assumed to indicate modified or different functions. In general, the older the fossil taxa being compared with living species and the greater the morphologic differences, the less assured is the correctness of the biologic interpretation.

2. A few similar functions can be carried on by different morphologies in living colonies, and restricted numbers of these functions can be inferred for fossil taxa. For example, **excurrent chimneys** are localized currents, created by colonies, which carry water and rejected particles away during the feeding process (Fig. 25). They can be set in motion by a number of different morphologies on colony surfaces (see below).

3. Differences in morphology of hypothetical soft parts of fossil taxa should be expected at least to the degree that they occur in comparable living taxa. For example, the general morphology of feeding organs of an exceptionally preserved fossil specimen should not be assumed for its entire family or order if corresponding organs are of several kinds in living species within families or orders (see below).

4. Modes of growth and functions unknown in living species can be expected to have occurred in extinct taxa and can be usefully suggested if the fossil evidence is convincing. Many biologic interpretations unknown in living forms, however, will be necessarily speculative in fossil taxa in proportion to degree of departure from living analogues.

The correctness of many biological interpretations of fossil taxa based on morphologic comparison with recent taxa seems unknowable. These interpretations, therefore, must remain open to question and can change as additional evidence is obtained.

PREPARATION TECHNIQUES

Published preparation techniques make it possible to describe interiors of bryozoan colonies with as much accuracy and detail as exteriors. Three-dimensional relationships and microstructural details of both skeletons and preserved tissues and organs in living position can be determined with certainty.

The time and effort to prepare standard thin sections of skeletons has been cut in half by the use of slides of standard glass-slide thickness made entirely of cellulose acetate (Boardman & Utgaard, 1964). Ground surfaces of specimens are oriented, given a high polish, etched lightly with formic acid, dried thoroughly, flooded with acetone, and placed gently on a blank slide. The impression that is left is a replica that is suitable for qualitative and quantitative studies, records of serial sections, light photography if thin sections cannot be made, identification of small fragments as in well cuttings (Merida & Boardman, 1967), and scanning-electron microscopy (F. M. Bayer, pers. commun.).

Epoxy resins have greatly improved the quality of thin sections (Nye, Dean, & Hinds, 1972). The resins permit a tighter bonding between highly polished specimens and glass slides. More importantly, thin solutions of the resins can impregnate preserved specimens in a vacuum so that hard and soft parts can be sectioned together in living positions in stenolaemates (see Fig. 39, 40, 43–45; Boardman, 1971, 1973, 1975; Boardman & Cheetham, 1973; Boardman & McKinney, 1976; Harmelin, 1976).

The quickest method to determine most three-dimensional relationships within a colony is to use thicker sections with a stereoscopic microscope and transmitted light (e.g., Boardman & Cheetham, 1969, pl. 29, fig. 1). This is especially useful for seeing zooidal

patterns or studying structures parallel to zooidal length in **longitudinal sections** where it is difficult to determine if a structure actually ends or merely passes out of the plane of the section. Another useful method for three-dimensional observation retains the chambers and removes the skeletons so that the general arrangements of colony interiors can be observed through the voids that were formerly walls (HILLMER, 1968).

Electron microscopy provides more sensitive and detailed information than can be obtained from light microscopes, especially for investigating modes of skeletal and soft part growth (SANDBERG, this revision; BROOD, 1972; TAVENER-SMITH & WILLIAMS, 1972).

MAJOR PARTS OF COLONIES

ASTOGENETIC ZONES

Stenolaemate colonies can be divided into at least two parts (Fig. 27) based on overall colony development (astogeny). The first or founding part of a colony includes the ancestrula (Fig. 25, 26) and one or more generations of asexually produced founding zooids. The morphology of each generation of founding zooids differs to some extent from the last, and so the first part of a colony is the primary zone of astogenetic change (BOARDMAN, 1968; BOARDMAN, CHEETHAM, & COOK, 1970).

The second part of a colony is attained by the generation that first repeats the morphology of the zooids of the preceding generation. Generations in the second part display morphologically comparable zooids of one or more kinds, which appear in one or more patterns capable of endless repetition. This second part is the primary zone of astogenetic repetition and constitutes the larger part of most stenolaemate colonies.

In most stenolaemates the founding zooids of the zone of change are covered by subsequent generations of zooids (see Fig. 53). The morphology and patterns of founding zooids, therefore, are relatively difficult to determine. Detailed studies of stenolaemates with covered zones of change (e.g., CUMINGS, 1904, 1905, 1912; BORG, 1933, text-fig. 28; 1941; BOARDMAN, & MCKINNEY, 1976; MCKINNEY, 1977c) are few, and taxonomic characters from zones of change generally are not included in classifications. Most of the morphology discussed here is from zones of astogenetic repetition.

ZOOIDS AND MULTIZOOIDAL AND EXTRAZOOIDAL PARTS

Stenolaemate colonies are made up of zooids and multizooidal parts, and many have extrazooidal parts. Zooids within a colony are of two or more kinds, the sexually produced ancestrula, asexually produced feeding zooids, and in many taxa, asexually produced polymorphs.

Minimally, zooids include body walls that enclose body cavities (BOARDMAN & CHEETHAM, 1973, p. 124). In recent colonies, feeding zooids have, in addition to body walls and body cavities, a protrusible lophophore, an alimentary canal, a membranous sac surrounding the alimentary canal and lophophore in retracted position, muscles to move the lophophore in and out, a nervous system, and, apparently, funicular strands (Fig. 2). In the zone of change, the founding zooids include feeding zooids that show some morphologic change from generation to generation. In a zone of repetition, feeding zooids generally have the same morphology at comparable ontogenetic stages, unless disturbed by microenvironmental differences.

Polymorphs are zooids that differ distinctly in morphology and function from ordinary feeding zooids at the same stage of ontogeny and in the same generation within a colony. Polymorphs may or may not be feeding zooids and can occur both in zones of change and zones of repetition.

In fossil stenolaemates, skeletons (zooecia) of feeding zooids can be identified with reasonable accuracy. Within the order Tubuliporata, zooecia of most living species are

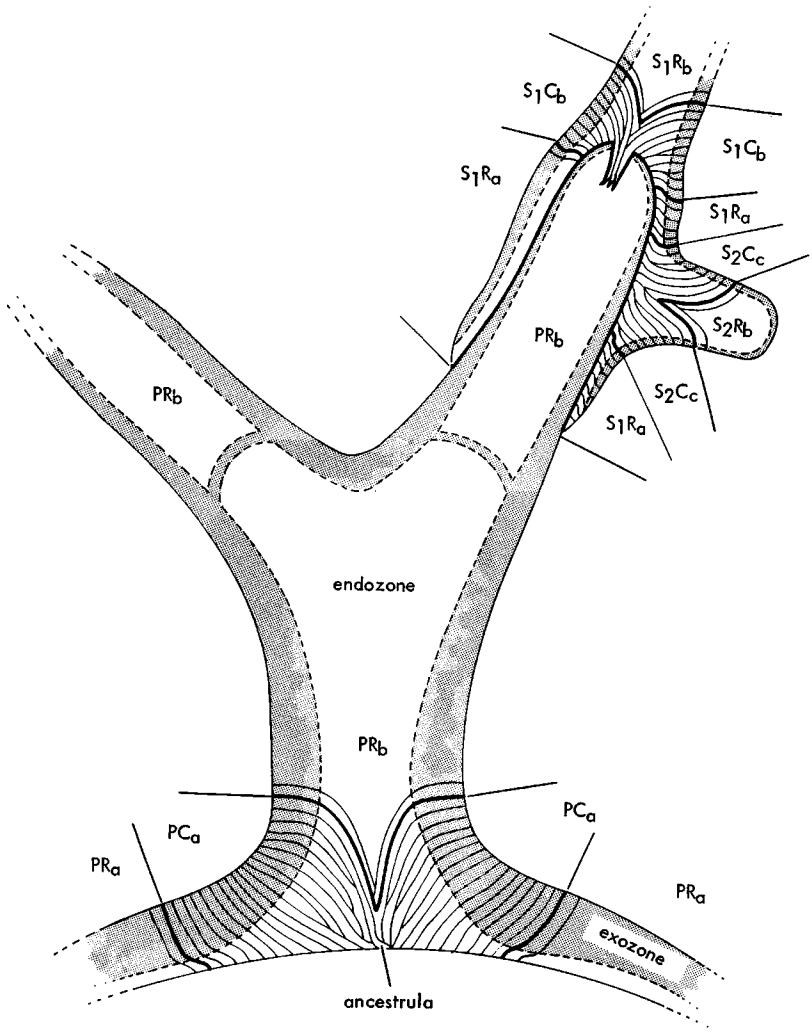
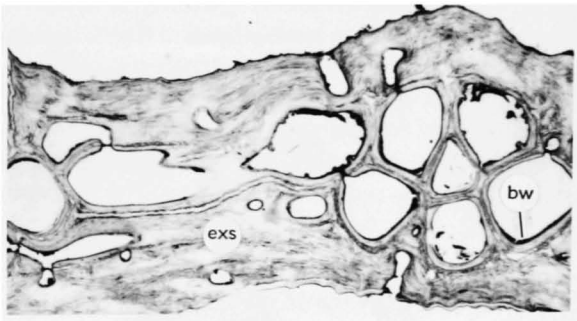


FIG. 27. Major parts of colonies. Idealized diagram of a hypothetical stenolaemate colony in longitudinal section illustrating the concepts of ontogeny and astogeny. Zooids are drawn in critical regions only. ASTOGENY. The primary zone of astogenetic change, PC_a, includes the ancestrula and succeeding generations of zooids of progressively changing form, which give rise concurrently to two primary zones of repetition: the encrusting growth habit at the base of the colony, PR_a, and the erect growth habit, PR_b. Survival of few zooids in a localized region suffering microenvironmental interruption can give rise to a subsequent zone of change, S_1C_b, which is produced asexually and lacks an ancestrula. The subsequent zone of change in erect colonies commonly produces two subsequent zones of repetition, one encrusting to form an intracolony overgrowth, S_1R_a, and one erect to continue extension of the branch, S_1R_b. A second type of subsequent zone of change, S_2C_c, can develop asexually within an encrusting overgrowth to provide transition to zone of repetition of another branch, S_2R_b. ONTOGENY. Progressively older ontogenetic stages are generally expressed by increasing lengths of zooids. Operationally, ontogenetic stages within a colony are proportional to widths of exozones, the outer regions shown in gray. Widths of exozones generally decrease progressively from the oldest zooids of the colony in the primary zone of change, PC_a, and are in approximate proportion to growth time. The exozone under intracolony overgrowth is narrower than the uninterrupted exozone of the left branch. The narrow exozones crossing endozones of the two branches depict abandoned growing tips, typical of most trepostomates.



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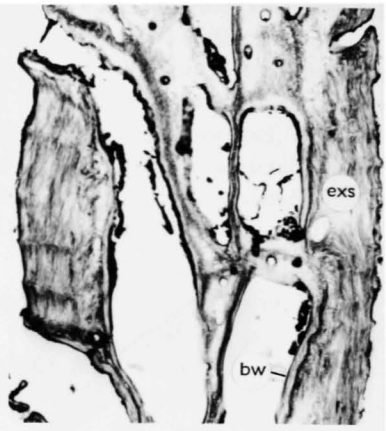

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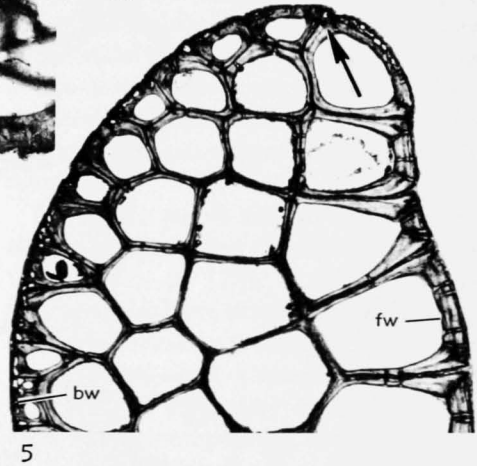

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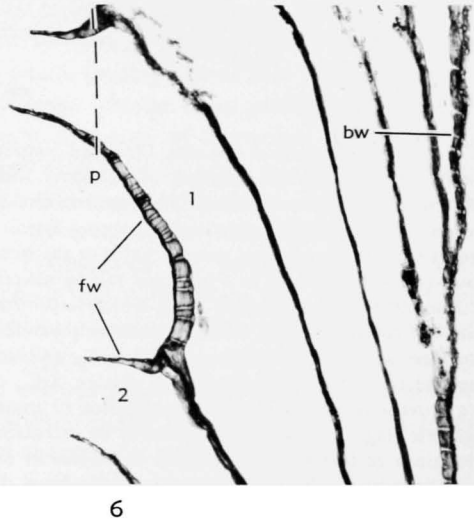

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FIG. 28. *(For explanation, see facing page.)*

comparable to those of fossil species, and there is little doubt as to which kind of zooecium in fossil species contained the feeding organs.

In Paleozoic species, zooecia of feeding zooids of many taxa are not directly comparable morphologically to those of living species. In Paleozoic species with monomorphic zooecia in zones of repetition, some of those zooids must have contained feeding organs for at least a part of their ontogeny. Operationally, all of the zooecia in monomorphic colonies are considered to have been skeletons of feeding zooids. In Paleozoic colonies containing two or more kinds of zooecia, the commonly occurring kind that compares most closely with the zooecia of related monomorphic forms is considered to have contained feeding organs. Further, living chambers of assumed feeding zooids of Paleozoic species are comparable in number, diameter, and in length to living chambers of feeding zooids of living species. In living species, the most common kind of larger zooid contains the feeding organs. Generally, nonfeeding polymorphs are smaller than feeding zooids. The assumption is made that the same was generally true for Paleozoic species, although many taxa have polymorphs in maculae (regularly spaced clusters of polymorphs, see Fig. 59) which are larger than zooecia of assumed feeding zooids between maculae.

The second kind of structural part of stenolaemate colonies is the multizooidal structure, which is grown outside of zooidal boundaries, can be colony-wide in extent, and eventually becomes part of a zooid or zooids. The most common multizooidal structures in stenolaemates are **confluent budding zones** of clustered buds and the **encrusting colony walls** from which zooids bud (Fig. 25, 26).

The third kind of structure is the extrazooidal part, which is also grown outside of zooidal boundaries but remains outside of zooidal boundaries throughout the life of a colony. Extrazooidal parts are generally larger than single zooids, and occur in many stenolaemate taxa, commonly providing at least structural support.

MORPHOLOGY AND FUNCTION OF ZOOIDS

Zooids contain complexes of both skeletal and soft parts. Differentiation of parts of skeletons is attempted here so that a set of independent taxonomic characters can be obtained from each part.

BASAL ZOOIDAL WALLS

Basal zooidal walls are body walls at inner ends of zooids opposite orificial walls (Fig. 25). They occur in most colonies as parts of

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FIG. 28. Stenolaemate morphology.——*1a,b. Hornera* sp., rec., Flinders Is., Vict., Australia; erect, unilaminate, fenestrate colony with basal zooidal walls (bw) covered by laminated extrazooidal skeleton (exs) on reverse sides of branches; *a,b,* transv., long. secs. of same specimen, USNM 250057, ×100.——*2. Lichenopora* sp., rec., Medit. Sea, Oran, Alg.; granular microstructure in both encrusting colony wall (ecw) and vertical zooecial walls; long. sec., USNM 250058, ×100.——*3. Lichenopora* sp., rec., Galapagos Is.; laminae in encrusting colony wall (ecw) dip proximally toward ancestrula to left, requiring simultaneous edgewise growth; long. sec., BMNH specimen, ×150.——*4. Archimedes* sp., Miss. (Chester.), near W. Lighton, Ala.; laminated extrazooecial skeleton (exs) surrounding granular zooecial skeleton (gs); long.-transv. sec., USNM 182789, ×100.——*5. Idmonea californica* D'ORBIGNY, rec., Pac. O. at La Jolla, Cal.; erect unilaminate zoarium with exterior basal zooidal walls (bw) and exterior frontal zooidal walls (fw); arrow at junction of basal zooidal walls to left and frontal walls to right, transv. sec., USNM 186545, ×50.——6. *I. californica,* same data as *5*; indicated frontal zooidal walls (fw) belong to zooecia 1 and 2, peristome (p) to left of dashed vertical line, long. sec., USNM 186546, ×50.

encrusting multizooidal colony walls. In erect parts of colonies, basal zooidal walls (erect basal walls of Fig. 26) may originate from multizooidal colony walls or walls of older zooids. The part of a multizooidal or zooidal wall subsequently enclosed by a developing zooid forms the basal wall of that zooid.

Encrusting colony walls originate as single structures grown by the colony generally distal to developing buds at growing colony margins (see Fig. 39,*5*; 60,*1–4*). Encrusting colony walls become multizooidal as they are divided into basal zooidal walls by zooids spreading outward as colonies develop encrusting growth habits or basal attachments. Encrusting walls are simple exterior walls that occur in most taxa. These walls extend body cavities of colonies (exterior walls) and are consequently calcified on edges and inner surfaces only (**simple skeletal walls**). They consist of an outermost cuticle, skeletal layers, and epidermis.

Most encrusting colony walls have a laminated structure in skeletal layers in which the laminae dip proximally back toward the ancestrula (Fig. 25; 26; 28,*3*). This direction of dip requires that all of the laminae at the growing edges are calcified simultaneously by **edgewise growth** (addition of calcite on edges of crystals and individual laminae; Fig. 29,*2,3*; Boardman & Towe, 1966; Boardman & Cheetham, 1969, pl. 28). A few taxa show different microstructures in encrusting colony walls (Fig. 28,*2*) and such differences have taxonomic value. **Pseudopores** (Fig. 33) typical of calcified layers of other exterior walls have not been found in encrusting colony walls.

Electron microscopy has revealed that in some species, at least, the calcified part of the encrusting wall has two microstructural layers (Tavener-Smith, 1969b; Tavener-Smith & Williams, 1972).

Erect basal zooidal walls can be simple and exterior in some unilaminate colonies (Fig. 26) and compound and interior in others. **Compound skeletal walls** are calcified on edges and both sides simultaneously (Fig. 29,*1–3*), and so they are necessarily interior body walls that partition preexisting body cavity.

Unilaminate colonies with erect exterior basal zooidal walls (Fig. 26) are apparently restricted to post-Paleozoic taxa. These erect walls (Fig. 28,*5,6*) apparently are multizooidal in origin. Many of these taxa form unilaminate colonies in early stages of ontogeny near growing tips and subsequently develop overgrowing layers of polymorphs on reverse sides proximally towards colony bases (Hinds, 1975).

Unilaminate colonies with compound interior basal zooidal walls in erect parts occur in both Paleozoic and post-Paleozoic taxa. Most of these basal walls appear to be zooidal rather than multizooidal in origin. The Paleozoic order Fenestrata is partly characterized by zooidal walls of nonlaminated skeleton (Fig. 28,*4*). Laminated skeleton covers nonlaminated zooecia, is generally continuous over at least the reverse sides of fenestrate fronds, and is extrazooidal. Recent hornerids have the same relationship of erect interior basal zooidal walls (Fig. 30,*2*), which on reverse sides of colonies are covered by an outer layer of extrazooidal skeleton proximally in later growth stages (Fig. 28,*1a,b*).

In bifoliate colonies erect basal zooidal walls originate as multizooidal compound interior walls that extend bladelike through the centers of colonies beyond zooidal boundaries distally (Fig. 30,*3,4*). These **median walls** provide budding surfaces for vertical zooidal walls on both sides so that feeding zooids are back to back to form colonies of generally flattened branches or expansions of different shapes (see Karklins and Utgaard, this revision).

Evidence indicating that median walls of bifoliate colonies are interior walls includes intermittent development of median walls with interior vertical zooidal walls within colonies (Fig. 30,*1*) and apparent lack of connections between exterior cuticle and median walls. Connections between exterior cuticle and median walls seem unlikely because of gaps between exterior encrusting walls and proximal ends of median walls in some gen-

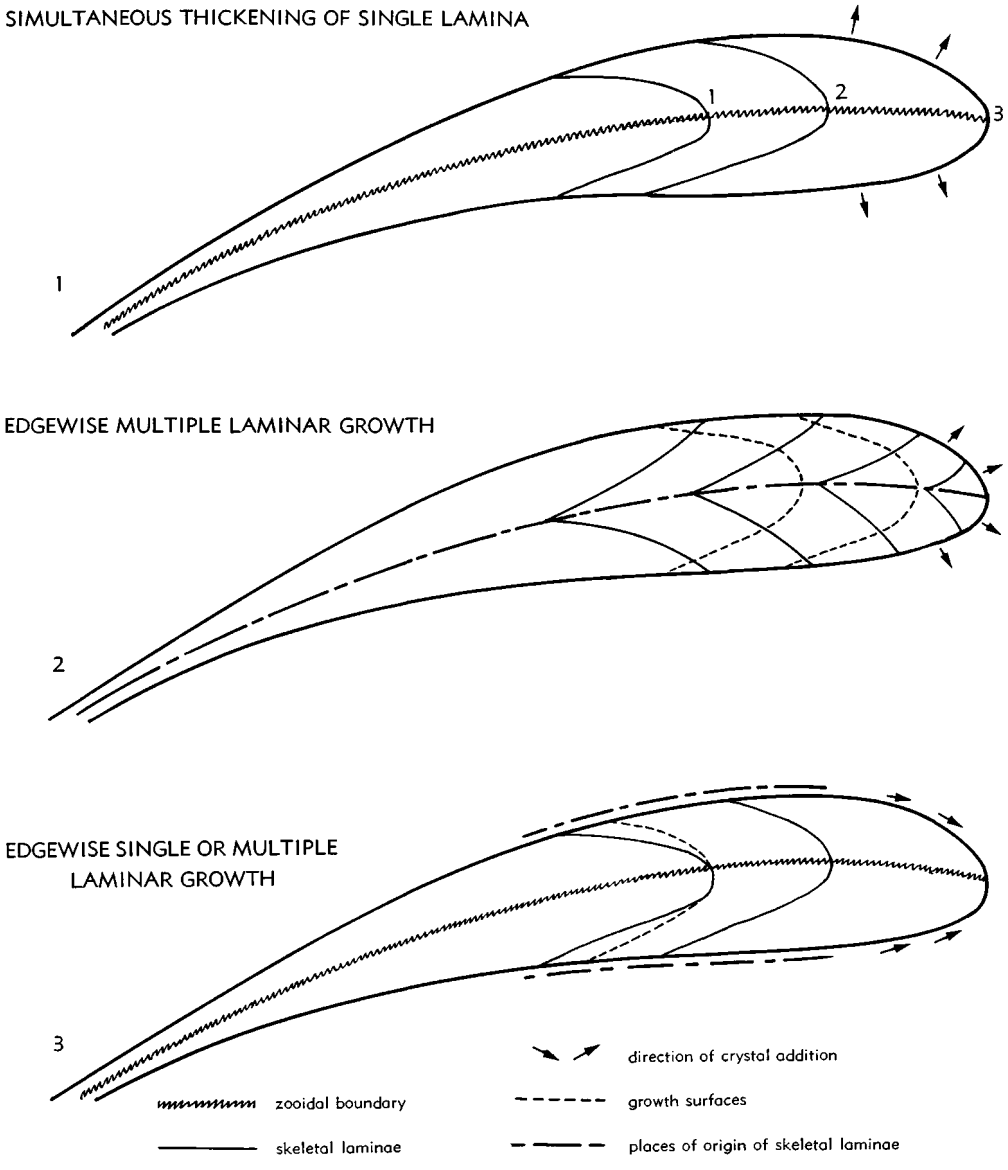


FIG. 29. Stenolaemate morphology. Diagrams of single vertical skeletal walls of adjacent zooids in longitudinal section illustrating hypothetical patterns of calcification.——*1.* Compound wall with laminae arched convexly in direction of growth to right in figure. Laminae grow singly on outermost skeletal surface adjacent to depositing epidermis so that laminae 1 and 2 are parts of a continuous series of laminae that reflect growth surfaces of earlier ontogenetic stages. Places of origin of skeletal laminae and growth surfaces are identical.——*2.* Compound wall with laminae pointing opposite to direction of growth. Walls extend in length by growth of laminae simultaneously on outer edges. Laminae are at high angles to depositing epidermis on skeletal surface and so are not growth surfaces. Places of origin of skeletal laminae are at inner ends of laminae near zooidal boundaries.——*3.* Compound wall with laminae arched convexly in direction of growth. Laminae theoretically can grow singly or several simultaneously by growth of laminae on outer edges. Growth surface (dashed line) is not quite parallel to laminae if laminar growth is multiple. Places of origin of skeletal laminae are at inner ends of laminae at skeletal surfaces.

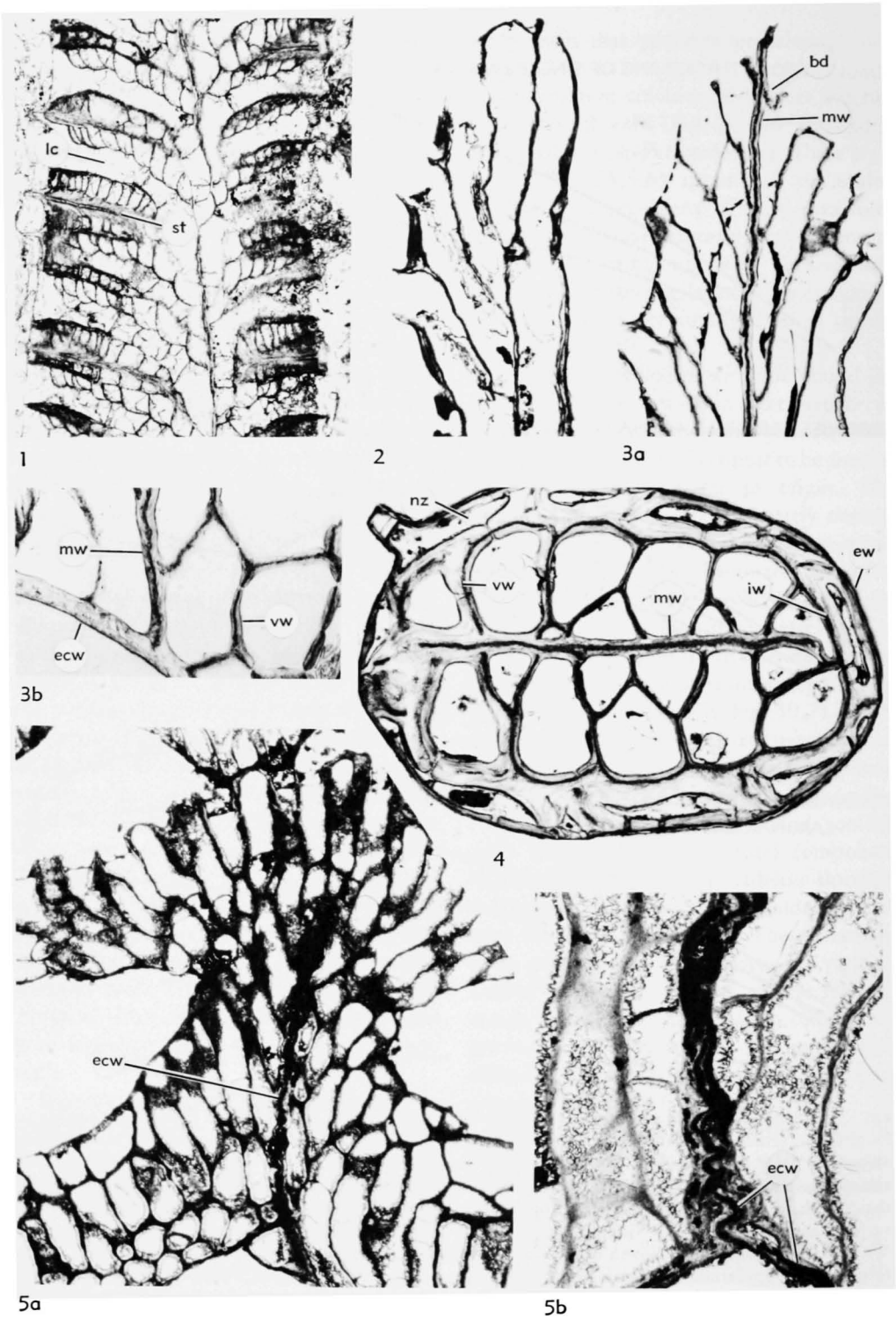


FIG. 30. *(For explanation, see facing page.)*

era (KARKLINS, this revision), skeletal layers of encrusting walls between basal cuticle and median wall at colony bases in other genera (Fig. 30,*3b*), and intervening skeletal layers of exterior zooidal walls at colony margins (Fig. 30,*4*).

The Oligocene-Pliocene genus *Alveolaria* forms subspherical colonies consisting of an open network of thin encrusting layers and cone-shaped expansions (Fig. 30,*5a*). Abutting encrusting layers bend and project vertically for short invervals in a sinuous, back-to-back contact simulating median walls (Fig. 30,*5b*). The colonies, therefore, appear externally to be bifoliate, but their irregular internal structure with the ever-present exterior basal colony wall suggests that they would be more accurately described as a complex of encrusting and cone-shaped growth habits.

VERTICAL ZOOIDAL WALLS

Vertical zooidal walls are body walls that grow parallel to the long axes of zooids to form either elongate conical or tubular body cavities or shorter sac-shaped body cavities. Thus, they provide the depth and length to zooid living chambers (Fig. 25, 26). Vertical walls have an epidermis but apparently no peritoneum (NIELSEN, 1971). The skeletal layers of vertical walls are continuous except for small skeletal gaps and communication pores in one Paleozoic suborder (see UTGAARD, this revision), and communication pores in most post-Paleozoic species (Fig. 25, 26).

Most vertical walls are interior, that is, they partition existing body cavity of colonies. Vertical walls that are exterior, or a combination of exterior and interior, occur only in the few uniserial and multiserial encrusting species (Fig. 31,*1–4*). Vertical walls generally bud from encrusting or erect multizooidal colony walls or from vertical walls of existing zooids. Vertical walls bud from extrazooidal structures in a few cystoporates (see UTGAARD, this revision) and from exterior walls of peristomes (Fig. 26) in a few tubuliporates (HARMELIN, 1976, fig. 7).

Zooids can commonly be divided into: (1) inner parts (endozones) characterized by growth directions at low angles to that of the colony or to the colony surface, thin vertical walls, and relative scarcity of intrazooidal skeletal structures; and (2) outer parts (exozones) characterized by growth directions at high angles to that of the colony or to the colony surface, thicker vertical walls, and concentrations of intrazooidal skeletal structures (Fig. 25).

Vertical zooidal walls are contiguous in most taxa and microstructure of the combined skeletal layers of two contiguous zooids in sections displays bilateral symmetry (Fig. 31,*5–7a*; 32,*1–4*). Exceptions include acanthocladiid fenestratids (GAUTIER, 1972, 1973) and the development of lunaria in cystoporates (UTGAARD, this revision). Bilateral symmetry is interpreted to mean that the walls are compound, that is, that they were grown cooperatively on edges and both sides from chambers of adjacent zooids. Zooidal bound-

FIG. 30. Stenolaemate morphology.——*1. Peronopora decipiens* (ROMINGER), lectotype, Corryville Mbr., McMillan F., Ord. (Cincinnat.), Cincinnati, Ohio; cystiphragms are the overlapping curved partitions in series above each living chamber (lc) and styles (st) project beyond zoarial surface into overgrowth to left; long. sec., UMMP 6676-3, ×30.——*2. Hornera* sp., rec., Arctic O.; growing tip of unilaminate, free-walled colony; long. sec., BMNH, Blacken Coll. 2.6, ×50.——*3a,b. Plagioecia* sp., rec., Pac. O. at La Jolla, Cal.; *a,* growing tip of bifoliate colony with median wall (mw) and developing buds (bd), long. sec., USNM 250059, ×50; *b,* junctions between encrusting colony wall (ecw), erect median wall (mw), and vertical walls (vw) showing microstructure, long. sec. same colony, ×100.——*4. Diplosolen intricaria* (SMITT), rec., depth of 200–240 m, Barent Sea, 60 mi. N. of North Cape; bifoliate colony showing interior walls (iw) between end of median wall (mw) and outermost exterior wall (ew), microstructure of vertical walls (vw), and nanozooids (nz) around margin of colony; transv. sec., BMNH specimen, ×100. ——*5a, b. Alveolaria semiovata* BUSK, Plio., Broom Hill, Suffolk, Eng.; exterior encrusting colony walls (ecw) in sinuous, back to back contact; *a,b,* long. secs., USNM 250060, ×30, ×100.

aries, therefore, are necessarily within compound vertical walls between adjacent zooidal body cavities and extend generally along centers of bilateral symmetry.

Zooidal boundaries or boundary zones of vertical walls (Fig. 25; 26; 29,*1,3*) are indicated microstructurally by abutting laminae from contiguous vertical walls (Fig. 31,*5*); thin, organic-rich partitions (Fig. 32,*1–4*); or thicker zones of granular appearing admixtures of organic material and small calcite crystals (Fig. 30,*3b,4*; 33,*1*). Some contiguous vertical walls, however, may have undifferentiated laminate or granular microstructure extending across centers of bilateral symmetry so that zooidal boundaries are not indicated microstructurally (Fig. 31,*6,7*) and must be located arbitrarily. Boundary zones of vertical walls lack the longitudinal canals or spaces that Ross (1976, p. 353) suggested ". . .provide the framework for growth and resorption of the body wall. . . ."

Organic-rich partitions occur at zooidal boundaries of interior vertical walls in a number of modern and fossil species of stenolaemates (e.g., Fig. 32,*1–4*; 33,*3*; 34; 42,*5,6*; 44,*4a,b*). In thin sections under a light microscope the partitions appear to be noncellular organic membranes or cuticles. The partitions have been recognized by HARMELIN (1974; 1976, pl. 16, fig. 4, 8) as surfaces of discontinuity. Otherwise, organic partitions, membranes, or cuticles have not been reported in interior vertical walls of stenolaemates (e.g., BORG, 1926a, p. 192; BROOD, 1972, p. 28; BOARDMAN & CHEETHAM, 1973, p. 138).

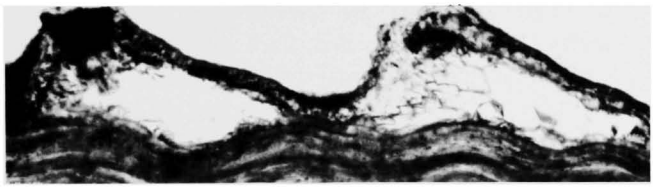
Organic-rich partitions in vertical walls of stenolaemates are parts of interior walls formed within body cavities of colonies and are considered to be interior in origin, as contrasted with exterior cuticles, which are the outermost layers of exterior walls and are adjacent to the environment. Extensive investigation using electron microscopy is necessary to determine the exact nature of the interior partitions.

FRONTAL ZOOIDAL WALLS

One of the major evolutionary advances of many post-Paleozoic tubuliporates is the more extensive skeletal reinforcement of exterior walls. Such reinforcement provides structural advantages and makes possible a greater variety of colony growth habits in post-Paleozoic species. Calcified layers of exterior walls are attached to inner surfaces of parts of colony-wide exterior cuticles. These structurally reinforced exterior walls form basal zooidal walls at inner ends of zooids on reverse sides of some erect unilaminate species, and frontal zooidal walls at outer ends of zooids (Fig. 26) of many species of several different growth habits.

The calcified layers of frontal walls are

FIG. 31. Stenolaemate morphology.——*1,2. Corynotrypa inflata* (HALL), Bellevue Mbr., McMillan F., Ord. (Cincinnat.), Cincinnati, Ohio; *1,* uniserial zoarium showing connecting pore between zooecia, long. sec., USNM 186554, ×100; *2,* exterior vertical wall (evw), arrows indicate connecting pores to younger zooecia at bifurcation of uniserial zoarium, sec. parallels base of zoarium, USNM 186553, ×100.——*3,4.* Stomatoporid tubuliporates; *3,* Bellevue Mbr., McMillan F., Ord. (Cincinnat.), Cincinnati, Ohio; encrusting, single-layered zoarium with exterior (evw) and interior (ivw) vertical walls, small circles are pseudopores in frontal walls, external apertural view, USNM 186556, ×100; *4,* Waynesville F., Ord. (Cincinnat.), Oregonia, Ohio; arrow points to zooecial boundary between interior vertical walls; sec. parallel to zoarial base, USNM 186558, ×100.——*5. Amplexopora septosa* (ULRICH), Mount Hope Sh. Mbr., Ord. (Cincinnat.), Covington, Ky.; compound vertical walls showing bilateral symmetry about zooecial boundary (zb) of abutting laminae, living chamber (lc) intact, protected by overgrowth (ov) and floored by basal diaphragm (bd); long. sec., USNM 138287, ×100.——*6. Rhombotrypella* sp., 9 m above Torpedo Ss. Mbr. of Ochelata F., Penn., Washington Co., Okla.; zooecial boundaries not indicated microstructurally in vertical walls; long. sec., USNM 204859, ×50.——*7a,b. Siphodictyum irregularis* CANU & BASSLER, Cret. (Apt.), Faringdon, Eng.; zooecial boundaries not indicated microstructurally in vertical walls, smaller zooecia polymorphs; *a,b,* long., tang. secs., USNM 248243, ×100.



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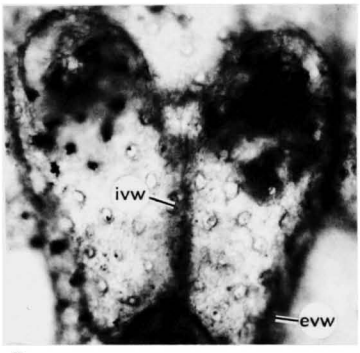

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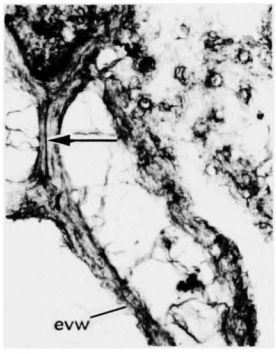

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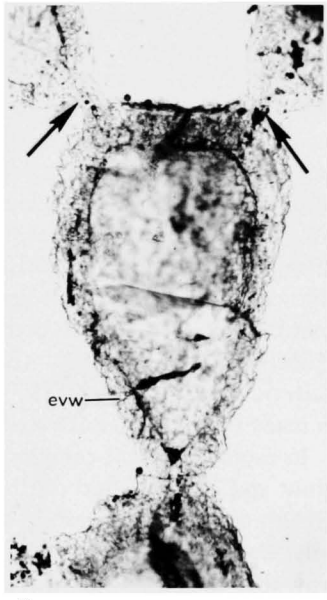

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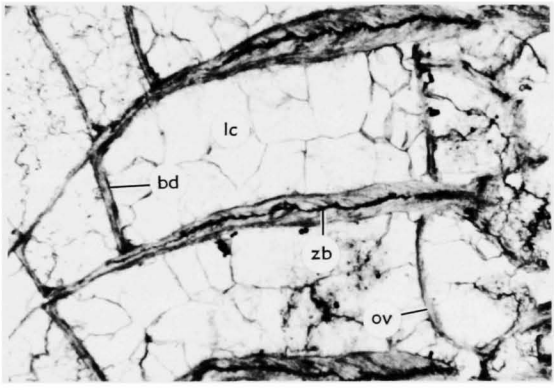

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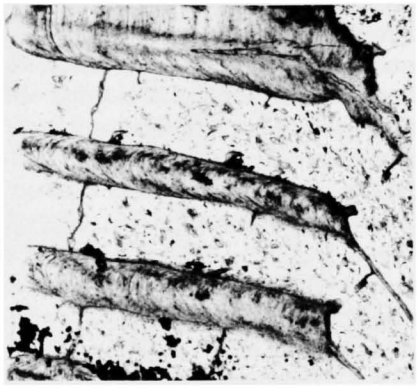

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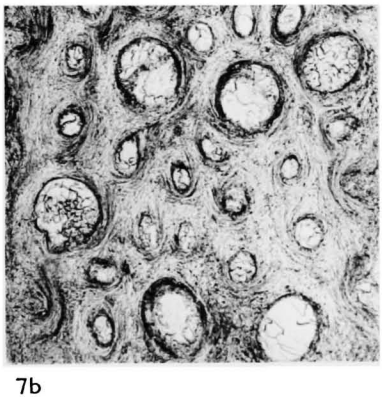

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FIG. 31. *(For explanation, see facing page.)*

structurally continuous with or attached to outer ends of one or more calcified layers of the supporting vertical walls of single zooids. Like vertical walls, frontal walls reportedly have an epidermis and no peritoneum. Outer ends of frontal walls are zooecial apertures. Most commonly, calcified layers of frontal zooidal walls are restricted as structural units to single zooids (Fig. 28,*5,6*), and their calcification is considered to be largely zooidally controlled. Frontal walls occur in the few Paleozoic tubuliporates (BOARDMAN & CHEETHAM, 1973; BROOD, 1973, 1975b) and in many tubuliporates of post-Paleozoic age.

In zooids of recent colonies, frontal walls grow and calcify after the termination of growth of supporting vertical walls. Reportedly, the epidermis of the vertical walls joins with that of the exterior membranous walls (BORG, 1926a, p. 322) at proximal ends of budding zones. After that contact, the epidermis produces zooidal skeletal layers on inner sides of the exterior cuticle to form frontal zooidal walls. Calcification of frontal walls takes place on edges and inner sides only (edgewise growth of simple walls; Fig. 34,*1d*), and so their skeletal microstructure lacks bilateral symmetry (Fig. 32,*1*; 35,*4*).

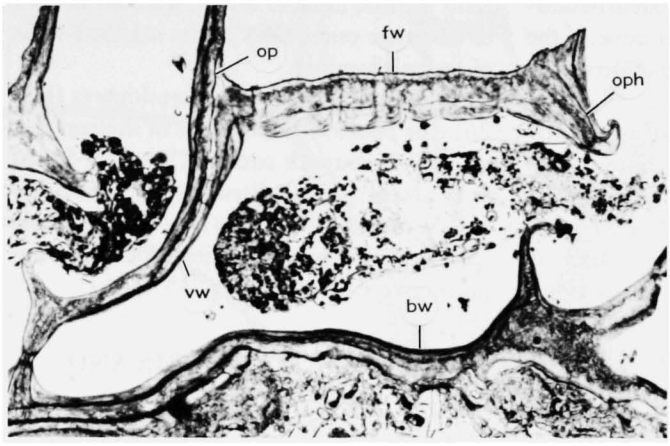
In a few taxa, calcified layers of frontal zooidal walls form continuous units extending across all of the feeding zooids of colonies proximal to distal budding zones (Fig. 33,*4,5*). Terminated vertical walls abut inner calcified surfaces of the frontal walls. Calcification of these continuous frontal walls apparently takes place from individual living chambers after zooids have established their vertical walls. The colony-wide frontal walls, therefore, are considered to have been zooidally controlled. Each zooid has an aperture in these frontal walls.

In a few forms, the juncture between vertical and frontal walls is of a type apparently transitional between connections indicating zooidal frontal walls and connections indicating colony-wide frontal walls. The vertical walls nearest zooidal boundaries apparently reached exterior cuticles, and some inner skeletal layers of the vertical walls abut layers of the frontal walls (Fig. 36,*2,4a*).

The microstructure of skeletal layers of frontal zooidal walls is commonly correlated with that of supporting vertical walls. If the vertical wall of a zooid has an outer calcified granular layer in the zooidal boundary zone and a laminated layer lining its zooecial chamber (the basic tubuliporidean wall of BROOD, 1972, p. 33; HINDS, 1975, p. 877), the vertical bilaterally symmetrical compound walls of adjacent zooids divide in half at the frontal zooidal walls (Fig. 32,*2*; 33,*1*). Each half extends into the calcified parts of the frontal walls of adjacent zooids so that the skeletal portion of the frontal zooidal wall includes an inner laminated skeletal layer and an outer granular skeletal layer. In some taxa with frontal walls the granular layer is replaced by a laminated skeletal layer with the laminae oriented at high angles to growth surfaces (Fig. 33,*2,3*).

A very different kind of frontal wall is formed in at least one species in which only the calcified zooecial linings of the vertical walls extend outward to form the peristomes that make up most of the frontal walls (Fig. 34,*1a,c*).

FIG. 32. Stenolaemate morphology.——*1. Diaperoecia indistincta* CANU & BASSLER, rec., 28–30 m, Medit. Sea off Riou Is., Marseille, France; short living chamber with constant retracted position during ontogeny, basal zooidal wall (bw), vertical wall (vw), frontal wall (fw), organic-rich partitions in both vertical walls (op) and hemisepta (oph); long. sec., USNM 250062, ×150.——*2. Idmonea californica* D'ORBIGNY, Pleist., Dead Man Is., San Pedro, Cal.; organic partition (op) in vertical wall (vw), frontal wall (fw); long. sec., USNM 250063, ×150.——*3,4. Cinctipora elegans* HUTTON, rec., 110 m, off Otago Heads, South Is. N.Z.; organic-rich partition (op) in vertical walls; *3*, transv. sec., USNM 250064, ×100, *4*, long. sec., USNM 250065, ×50.——*5a,b. Hornera* sp., rec., a fjord in East Finmark, Nor., 215 m; vertical walls (vw) with laminae convex outward to right (*5a*), extrazooidal skeleton (exs) between zooids; *a,b*, long., tang. secs. same colony, BMNH, Norman Coll., ×100.



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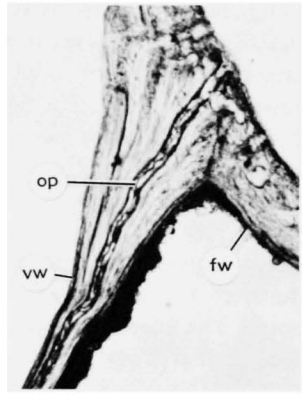

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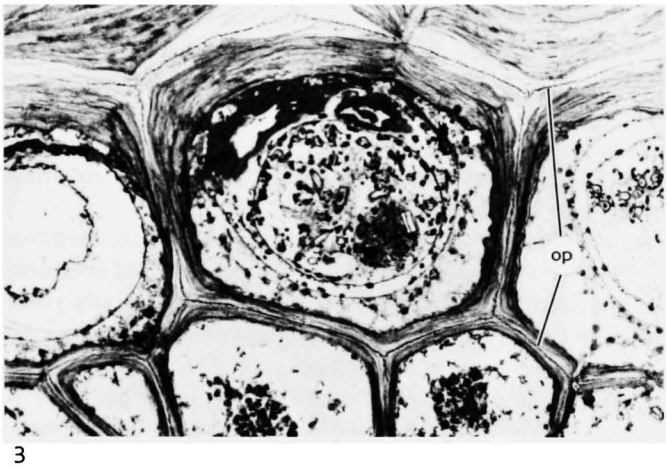

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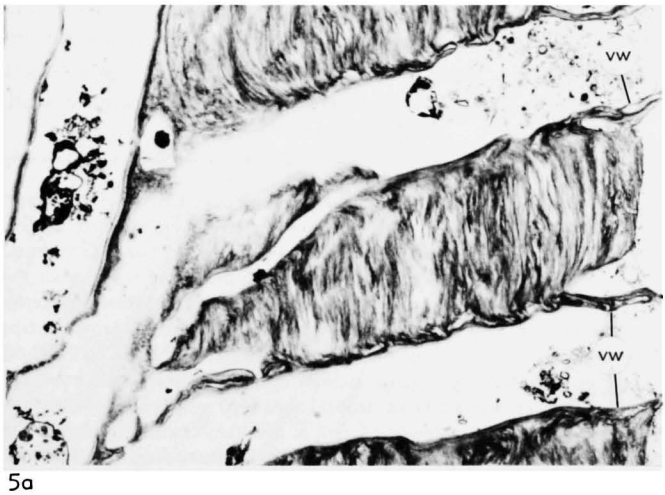

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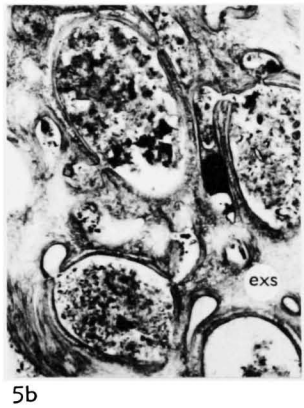

5b

FIG. 32. *(For explanation, see facing page.)*

Organic-rich partitions at zooidal boundaries of vertical walls occur with most of the variations of frontal wall microstructure illustrated here (e.g., Fig. 32,*1,2*; 33,*3*; 34; 55,*4,5*). The interior partitions apparently attach to exterior cuticles at junctions of vertical and frontal walls.

Taxa may be arranged in a morphological series showing transitional differences in length of frontal walls restricted to single zooids. The shortest frontal walls are little more than terminal diaphragms containing apertures (Fig. 33,*4,5*). Longer frontal walls commonly occur with peristome extensions (Fig. 28,*6*; 33,*1*). The longest frontal walls of single zooids may extend virtually along the entire length of an erect colony (Fig. 35,*1,3a,b*). (Exterior walls on the right sides of Fig. 35,*3a,b* are frontal walls or terminal diaphragms because zooids budded from the center of the branch and grew in all directions so that the exterior walls on the right sides of the figures are attached to outer ends of vertical walls of zooids. In contrast, the exterior wall at the bottom of Fig. 35,*2* is an erect basal wall from which zooids budded).

The lengths of single frontal walls from their proximal margins to the bases of possible peristomes are largely determined by the angles that vertical walls of zooids make with surfaces of colonies. The shortest diaphragm-like frontal walls are formed by zooids whose vertical walls intersect the surface of a colony nearly at right angles. As the surface angles of vertical walls decrease, lengths of frontal walls increase because frontal walls are needed to complete outer sides of the calcified walls of living chambers.

Most frontal walls have pseudopores (Fig. 26) that penetrate all or parts of skeletal layers but not exterior cuticles (Tavener-Smith & Williams, 1972). Pseuodpores can be few and scattered (Fig. 33,*1*) or more closely spaced than communication pores of supporting vertical walls (Fig. 35,*4*).

ZOOECIAL APERTURES AND ORIFICIAL WALLS

Zooecial apertures are generally simple terminal skeletal openings of zooecia that are oriented transverse to zooidal growth directions. They terminate frontal wall skeleton (Fig. 26), vertical wall skeleton in taxa in which frontal walls are absent (Fig. 25), or a combination of both. Zooids elongate through most of their ontogeny by growth at apertures.

Orificial walls (Fig. 25, 26) are membranous body walls that cover zooecial apertures, and they are therefore also generally transverse to zooidal growth direction. They are the outer terminal part of the complete zooid (Fig. 37), except in the few fossil taxa in which orificial walls were apparently covered by operculumlike structures. In living species orificial walls are single membranous walls that contain simple circular pores (the orifices) through which tentacles are protruded. Orificial walls are part of the exterior walls

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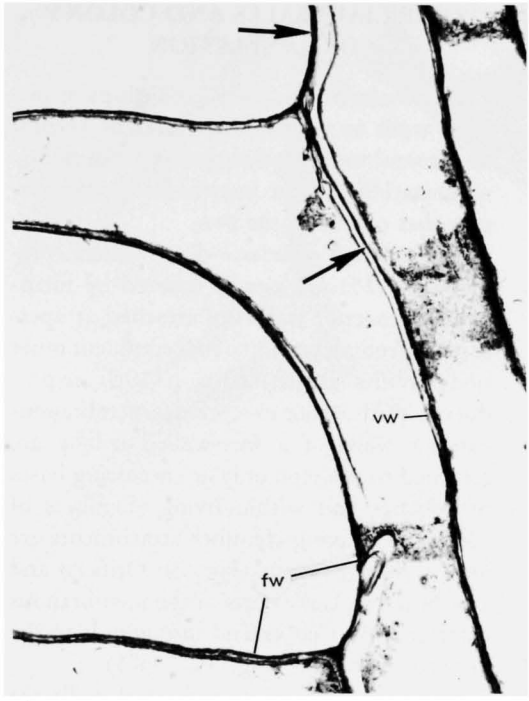
Fig. 33. Stenolaemate morphology.——*1.* Idmoneid tubuliporate, rec., Kara Sea, USSR; vertical walls (vw) with thicker boundary zones of organic-rich granular calcite (arrows) continuing as outer skeletal layers of frontal walls (fw); long. sec., USNM 186552, ×100.——*2. Spiropora verticellata* (Goldfuss), Cret. (up. Maastricht.), Stevns Klint, Seeland, Denm.; vertical (vw) and frontal (fw) walls with two skeletal layers of laminae oriented at high angles to growth surfaces, small tubes cut transversely at center of branch are inner ends of zooecia at bud stage, indicating central grouping of buds at growing tips; transv. sec., USNM 250066, ×100.——*3.* Fixed-walled tubuliporate, rec., 280 m, 51°22.52′ S., 73°8.64′ E., Kerguelan Ridge, S. Indian O.; vertical wall showing organic-rich partition (op) at zooidal boundary and skeletal laminae oriented at high angles to growth surfaces, frontal wall (fw) with pseudopores (ps); long. sec., USNM 186551, ×150.——*4,5. Diplocava incondita* Canu & Bassler, Cret. (Valangin.), Ste Croix, Switz.; *4,* showing frontal walls (fw) containing pseudopores apparently extending across ends of granular vertical walls (vw), restricted aperture (ap); long. sec., USNM 216475, ×100; *5,* showing restricted aperture (ap) formed by frontal wall (fw) with pseudopores; tang. sec., USNM 216476, ×100.



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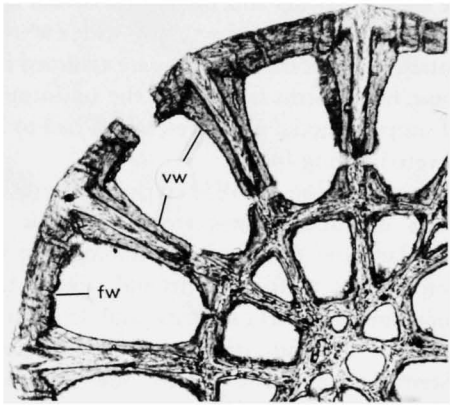

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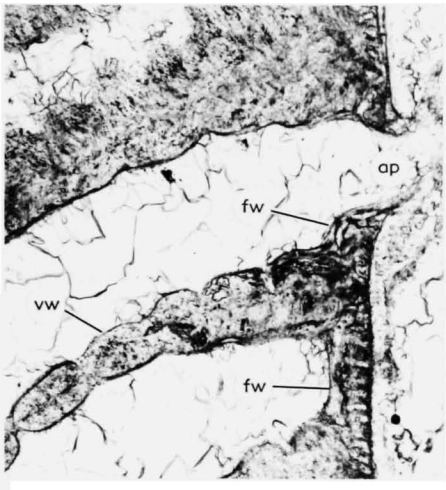

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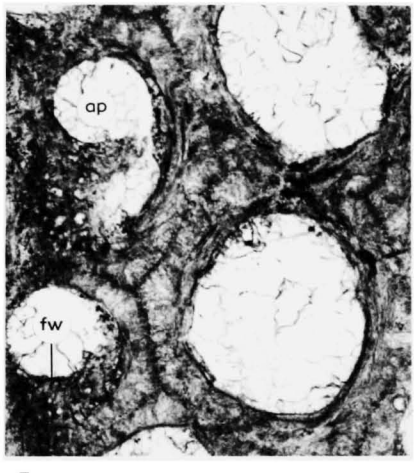

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FIG. 33. *(For explanation, see facing page.)*

of feeding zooids and the cuticle of the orificial walls is part of the colony-wide exterior cuticle. Similar orificial walls are assumed for most fossil forms because of the uniformity of simple zooecial apertures, which had to be covered during life.

BORG (1926a, p. 483) considered orificial walls of tubuliporates (terminal walls of stenolaemates in BORG's terminology) to be homologous to the ". . .frontal side of the zooid in the Cheilostomata and Ctenostomata. . . ." Similarities in general position, extent, and mode of growth, however, suggest that until more is known about the evolution between orders and classes, frontal walls as defined above for the stenolaemates are more nearly analogous to frontal walls of cheilostomates and ctenostomates.

In a few Jurassic and Cretaceous tubuliporates (the meliceritidids) apertures are closed by calcareous plates (Fig. 36,*2–4*) interpreted to have been **opercula** (LEVINSEN, 1912). Apertures of all feeding zooids except those in growing tips of branches are covered by the plates. The plates, therefore, must have been hinged to open when zooids were feeding (Fig. 38). The opercula were most likely hinged on their straight proximal margins to the stationary parts of frontal walls. In some colonies opercula have longitudinal ridges on inner sides (Fig. 36,*4b*), possibly for some kind of muscle attachment.

The opercula apparently were developed as parts of frontal walls because the outer sides of the opercula and stationary parts of the frontal walls are aligned. The opercula are exterior structures and some have what appear to be pseudopores, a common feature of frontal walls.

ORIFICIAL WALLS AND COLONY ORGANIZATION

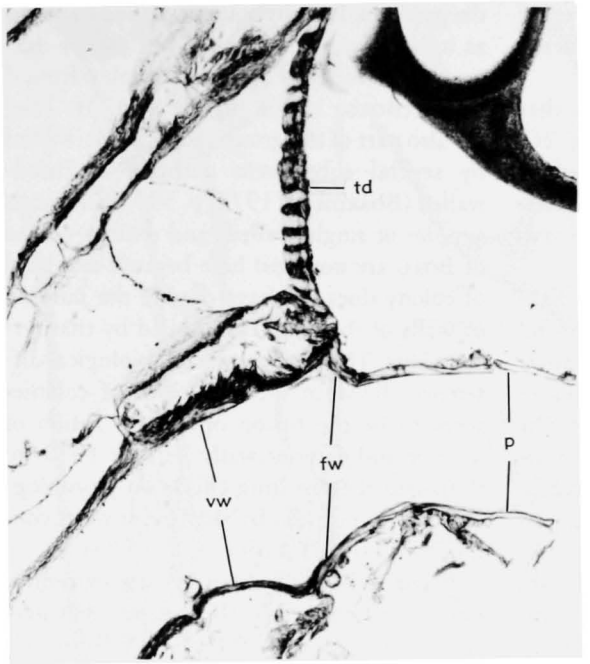
In stenolaemates, the relationships of orificial walls to zooecial apertures of vertical and frontal walls produce two types of colony organization and an intermediate organization that combines the two.

Free-walled colonies.—Free-walled colonies (Fig. 25) are loosely covered by membranous exterior walls not attached at apertures of feeding zooids so that confluent outer body cavities (BORG, 1926a, p. 196) are produced. With minor exceptions, membranous exterior walls of a free-walled colony are attached to skeleton only at encrusting bases of colonies and within living chambers of zooids. The living chamber attachments are at attachment organs (Fig. 2). Orificial and vestibular walls are parts of the membranous exterior walls that extend into zooids to the attachment organs (Fig. 39,*1–3,5*).

In free-walled colonies skeletal walls are largely interior above encrusting colony walls; as they grow they partition colony-wide body cavities established by the advancing membranous exterior walls. Exceptions include calcified exterior walls of terminal diaphragms and brood chambers that interrupt confluent outer body cavities in some post-Paleozoic tubuliporates.

Apparent advantages of the free-walled arrangement include colony-wide distribution of nutrients through confluent outer body cavities (BORG, 1926a, p. 204; BOARDMAN & CHEETHAM, 1969, text-fig. 1; 1973, p. 132) and the possibility of growth of all outer skeletal surfaces throughout colony life. Parts of colonies suffering accident are commonly

FIG. 34. Stenolaemate morphology.——*1a–d. Heteropora? pacifica* BORG, rec., 21–25 m, vicinity of Middleton Is., S. Alaska; *a,* zooecial lining of vertical wall (vw) extended outward to form frontal wall (fw) and peristome (p), terminal diaphragm (td) with closely spaced pseudopores; *b,* frontal wall (fw) similar in microstructure to terminal diaphragm (td); *c,* frontal wall formed distally by extension of zooecial lining (zl) and proximally by combination of thicker wall (arrow) microstructurally comparable to terminal diaphram (td) and zooecial lining; *d,* external cuticle (c) and partly grown skeletal layers of terminal diaphragms (td); all long. secs. from same colony, USNM 186549, all ×100 except *a* ×150.



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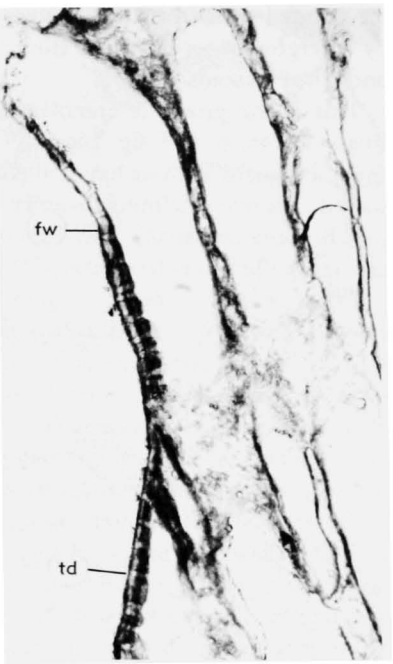

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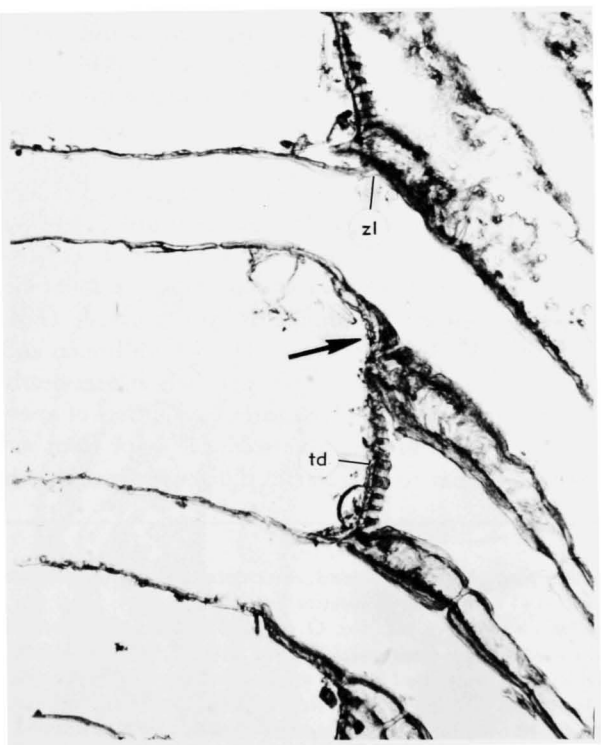

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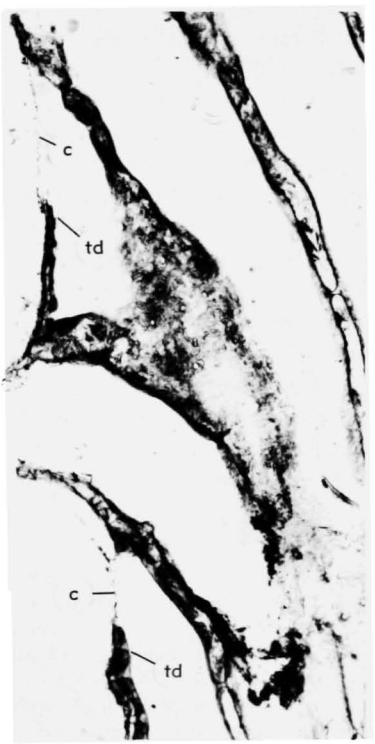


1d

FIG. 34. *(For explanation, see facing page.)*

regenerated under the membranous covering by overgrowth originating from adjacent undamaged zooids.

This is the group of stenolaemates that BORG (1926a, p. 473, fig. 55; 1933, fig. 26) and subsequent authors have called double-walled. The overwhelming majority of Paleozoic Bryozoa and many post-Paleozoic taxa are free-walled stenolaemates.

Fixed-walled colonies.—Stenolaemate colonies are termed fixed-walled if orificial walls of feeding zooids are attached at apertures so that confluent outer body cavities between zooids are eliminated (Fig. 26). The great majority of fixed-walled stenolaemates has frontal walls. Skeletal layers of frontal walls are attached at outer ends of vertical zooidal walls and terminate at apertures. The outermost cuticles of fixed-walled colonies are attached to outer surfaces of the calcareous layers of frontal walls up to apertures, which eliminates outer confluent body cavities.

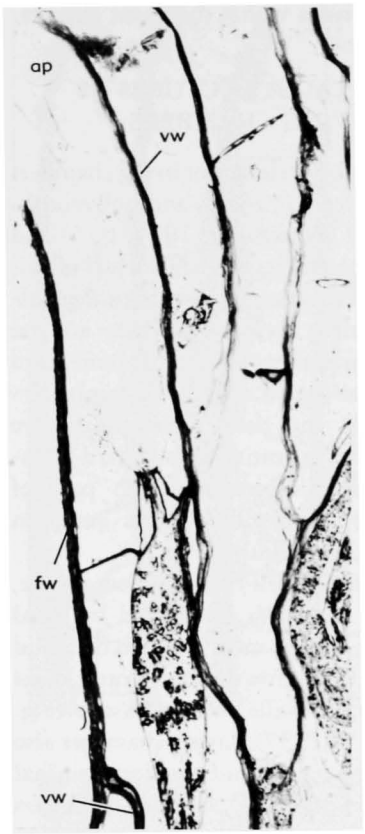
Communication among feeding zooids of fixed-walled colonies apparently can occur only through pores in vertical walls. Feeding zooids in species without communication pores therefore are presumably without physiologic connection after their zooecia are completed. A probable advantage is gained, however, by the skeletal reinforcement of exterior walls (BOARDMAN & CHEETHAM, 1973, p. 158, 159). The exterior walls on feeding sides of most fixed-walled colonies consist of membranous orificial walls, calcified frontal walls of contiguous zooids (some can be polymorphs) and in many colonies, outer brood-chamber walls.

Fixed-walled stenolaemates are a part of the group of Tubuliporata described by BORG as having simple walls, without clearly designating which walls were simple (frontal walls) (BORG, 1926a, fig. 1, p. 473). They are also part of the group called single-walled by several subsequent authors, or fused-walled (BOARDMAN, 1975, p. 598). The terms simple- or single-walled, and double-walled of BORG are not used here because one kind of colony does not have double the number of walls of the other, as implied by that terminology. The most significant biological differences between the two kinds of colonies seem to be the fusion or lack of fusion of interior and exterior walls (HINDS, 1975, p. 876) and the resulting effects on physiological communication by the free or fixed condition of orificial walls.

Fixed-walled tubuliporates are extremely rare in the Paleozoic (BOARDMAN & CHEETHAM, 1973, p. 159; BROOD, 1975b, p. 69) and common in post-Paleozoic bryozoan faunas.

Combined free- and fixed-walled colonies.—Some feeding zooids in colonies of a few post-Paleozoic tubuliporates have orificial walls that are partly free and partly fixed (BOARDMAN, 1975, p. 601). The combined free- and fixed-walled morphology occurs in colonies of taxa in which apertures of feeding zooids are clustered and the clusters are surrounded by the combined frontal walls of the outermost zooids in the clusters (Fig. 35,*3a,b*). In these colonies both frontal and vertical walls are generally long and are nearly parallel to colony surfaces. Clusters of apertures vary in cross-sectional shape from circular to irregular in different taxa and may

FIG. 35. Frontal walls.——*1. Fasciculipora* sp., rec., McMurdo Sound, Antarctica; zooid with aperture (ap) consisting partly of exterior frontal wall (fw) and partly of interior vertical wall (vw); long. sec., USNM 179007, ×50.——*2. Idmonea californica* D'ORBIGNY, rec., Pac. O. off La Jolla, Cal.; erect zoarium with buds starting from exterior basal zooidal walls (bw); transv. sec., USNM 250067, ×50. ——*3a,b. Frondipora verrucosa* LAMOUROUX, rec., Naples Bay, Italy; budding of vertical walls (vw) from central region of branch outward in all directions so that all exterior walls are frontal (fw), clusters of combined free- and fixed-walled zooecia open to left; *a,b,* transv., long. sec. from same zoarium, USNM 250068, ×30.——*4.* Fixed-walled tubuliporate, rec., 285 m, 51°22.52′ S., 73°8.64′ E., Kerguelan Ridge, S. Indian O.; communication pores (cp) in interior vertical walls and pseudopores (ps) in exterior frontal walls; long. sec., USNM 186551, ×150.



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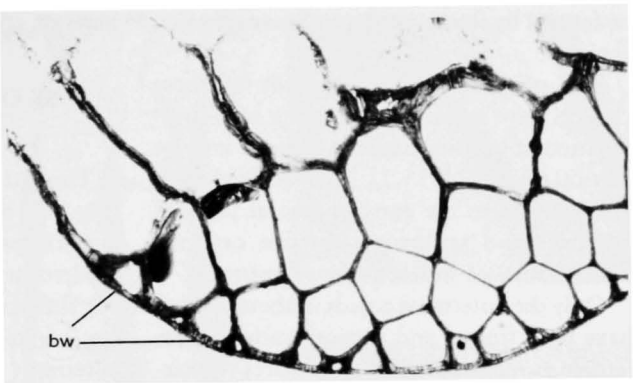

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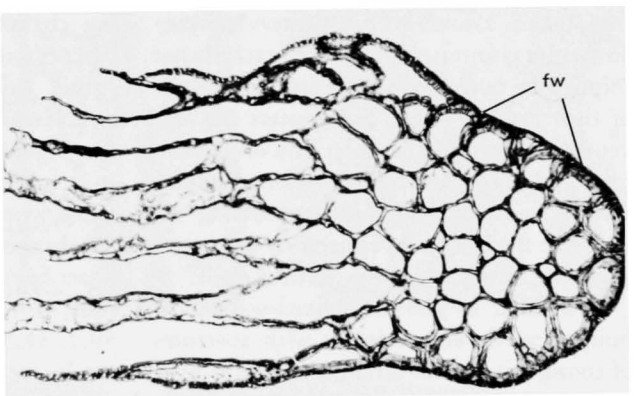

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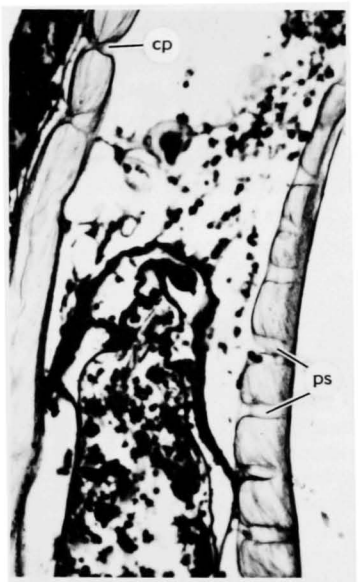

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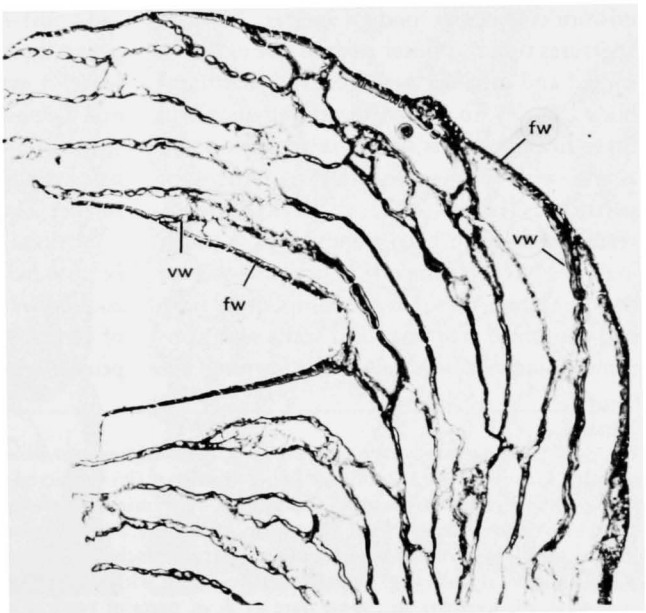

3b

FIG. 35. *(For explanation, see facing page.)*

be formed by few to many contiguous feeding zooids.

The outermost feeding zooids of these clusters have apertures consisting of a combination of exterior frontal walls and interior vertical walls (Fig. 35,*1*). Their orificial walls are attached to the exterior frontal parts of apertures and apparently are free over the interior vertical-walled parts of apertures.

Only the outermost zooids of these clusters have both frontal and vertical walls. Zooids farther inside clusters have apertures consisting entirely of interior vertical walls and are free-walled. Zooids within clusters can presumably communicate with each other through the outer body cavity around the ends of their vertical walls, but clusters are prevented from communicating with other clusters in this manner by intervening exterior frontal walls. Communication among all zooids in these colonies apparently can occur, however, through pores in vertical walls.

A number of genera of fixed-walled tubuliporates develop colonies with apertures of contiguous zooids arranged singly in rows (see Fig. 61,*4a*). Frontal walls of the zooids within a row are extended into peristomes in unworn colonies of modern species. Zooecial apertures occur at outer ends of the exterior-walled and calcified peristomes so that outer body cavities do not occur among zooids in these linear clusters. Zooecia in some fossil zoaria with similar zooecial patterns lack peristomes (HINDS, 1975, p. 881). The peristomes may have been removed by wear or may not have developed. If peristomes were not developed, these fossil colonies could have had combined free and fixed walls with contiguous interior vertical walls forming the parts of apertures within the linear clusters.

SKELETAL STRUCTURES OF LIVING CHAMBERS

The enclosing skeletons of living chambers (Fig. 37) of feeding zooids and polymorphs in both fossil (BOARDMAN, 1971, p. 5) and modern stenolaemates can be the parts of colony skeletons that reveal most about the biology of colonies. **Living chambers** are the outermost parts of zooidal body cavities into which zooidal organs retract. Certainly, living chambers and their skeletons deserve description as an entity in standard taxonomic works. Unfortunately, no part of stenolaemate colonies of all ages has been more ignored historically.

In free-walled fossil taxa of Paleozoic age, many living chambers are floored by **basal diaphragms** and are most likely to be found intact behind overgrowths that protect outer ends of vertical walls from abrasion (Fig. 30,*1*; 31,*5*; 36,*1*; 37). Living chambers also can be recognized behind interior **terminal diaphragms** (see Fig. 43,*2,3*; also discussion of terminal structures).

In post-Paleozoic taxa, living chambers are generally recognizable because of the prevalence of exterior terminal diaphragms. Skeletal terminal diaphragms in post-Paleozoic species have a different microstructure than basal diaphragms and apparently terminate further zooidal growth (Fig. 34,*1a,c*).

Skeletal structures of living chambers can be divided into: basal structures, including zooidal walls or diaphragms that act as floors of living chambers and any structures that project from them; lateral structures, which

FIG. 36. Stenolaemate morphology.——*1. Amplexopora pustulosa* ULRICH, Waynesville Sh., Ord. (Richmond.), Hanover, Ohio; complete living chambers (lc) protected by encrusting overgrowth, abandoned living chambers within zooecia (alc) capped by terminal diaphragms; long. sec., USNM 250069, ×50. ——*2,3. Meliceritites* sp., Cret. (Cenoman.), Le Mans, Sarthe, France; *2,* part of vertical wall (vw) abutting frontal wall (fw), funnel-shaped structure partly attached to operculum (o), long. sec., USNM 250070, ×100; *3,* frontal walls (fw) and opercula (o), both with pseudopores, tang. sec., USNM 216480, ×100. ——*4a,b. Meliceritites* sp., same data as *2*; *a,* parts of vertical walls (vw) abutting frontal walls (fw), opercula (o), long. sec.; *b,* transv. sec. showing spiral arrangement of zooecia around axial cylinder in center of branch, opercula (o) with ridges on inner sides; USNM 216481, ×100.

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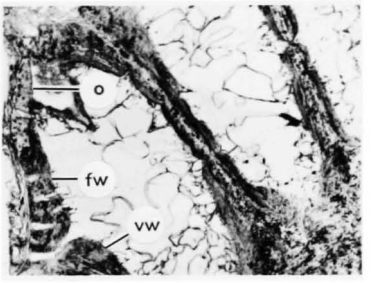

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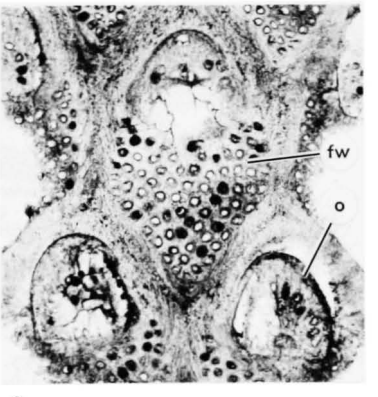

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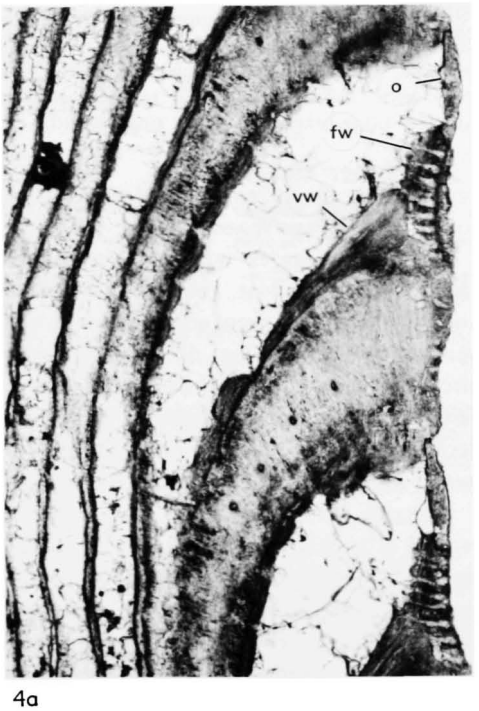

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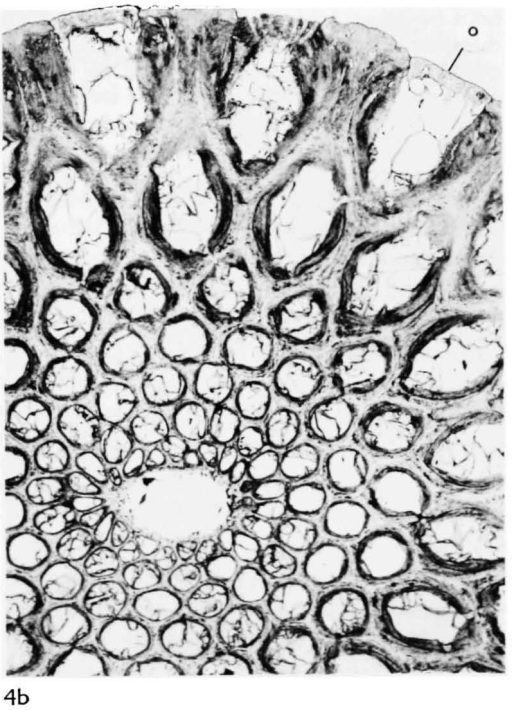

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FIG. 36. *(For explanation, see facing page.)*

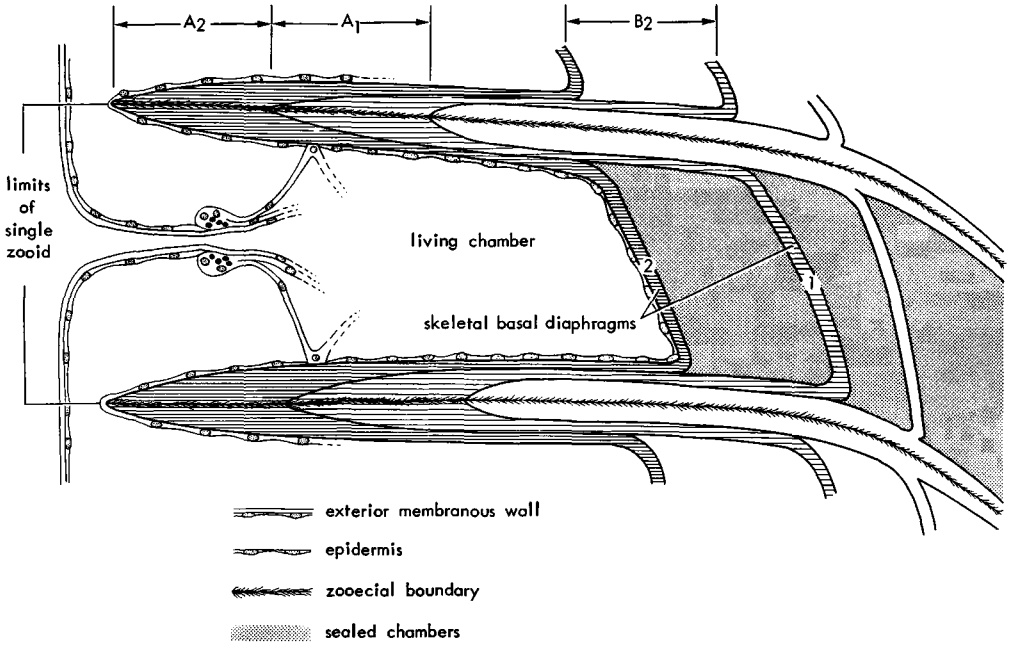

FIG. 37. Stenolaemate morphology. Diagram of a longitudinal section through the exozone of the hypothetical zooid of a free-walled Paleozoic trepostomate; growth direction is to the left, and laminae (not shown) from adjacent zooids point in that direction. The ontogenetically oldest part of skeleton is to the right; the youngest part, which both lines and extends living chamber, is to the left. The youngest basal diaphragm (2) forms the floor of the living chamber and it and older diaphragms seal off abandoned chambers that presumably lacked living tissue. A_1 and A_2 are the hypothetical extent of vertical wall growth during the degeneration part of the last two cycles. B_2 is the resulting displacement of the base of the latest living chamber (see text for further explanation). Zooid includes the terminal exterior membranous wall (orificial wall), body cavity, and skeleton (see brackets defining single zooid).

occupy positions opposite feeding organs as they move in and out, including structures that project from vertical or frontal zooidal walls; and terminal or subterminal diaphragms, which seal living chambers from the environment.

Basal structures and ontogeny.—In those taxa having relatively short zooidal chambers, retracted positions of feeding organs are constant throughout colony life. Inner ends of these shorter chambers can be made up of vertical walls, or combinations of vertical and basal walls (Fig. 32,*1*). Any elongation of short zooids occurs in outermost membranous vestibular walls and at outer ends of enclosing vertical or frontal walls. Brown bodies, which are encapsulated degenerated cells resulting from the cyclic degeneration of most of the organs of zooids (Fig. 40,*3b*), presumably would be disposed of regularly for lack of storage space.

In stenolaemates with longer zooidal chambers, in contrast, the living chambers and retracted positions of organs advance with skeletal elongation (Fig. 40,*3a,b*), presumably by means of degeneration-regeneration saltations. Outward ontogenetic growth of zooids is enough for advancing organs to vacate inner parts of zooidal chambers.

In many free-walled fossil taxa, vacated regions of zooidal chambers are partioned by transverse basal diaphragms in ontogenetic series (Fig. 31,*5*; 36,*1*; 37). Diaphragms are membranous or skeletal partitions that extend across entire zooidal chambers. The outermost basal diaphragm of a zooid must have acted as the floor of the living chamber for the functional organs of the last regenerated

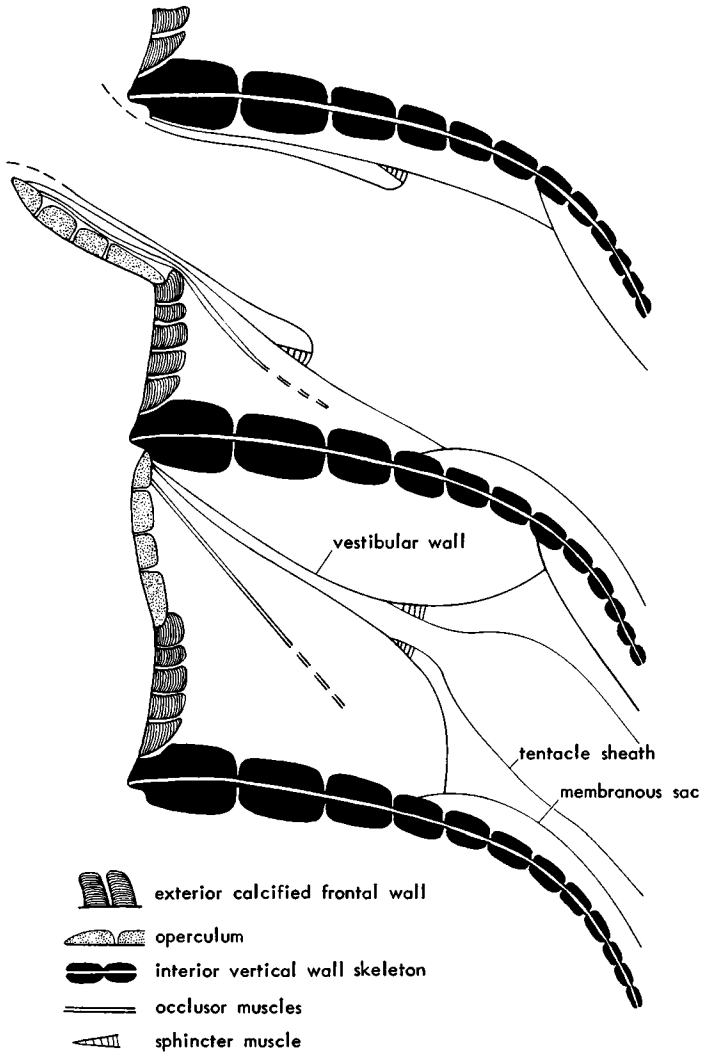

FIG. 38. Zooecial apertures and orificial walls. Reconstruction of a longitudinal section through the outer parts of two zooids of a meliceritid tubuliporate showing hypothetical relationship between opercula of meliceritid and generalized vestibular walls and tentacle sheaths, based on recent tubuliporates. The lower zooid shows the operculum in the closed position seen in fossil specimens (Fig. 36,*4a*). The upper zooid shows a hypothetical open position when tentacles (not shown) were protruded. There is no direct evidence of occlusor muscles to close the operculum. Exterior cuticle presumably covers outer calcified surfaces of frontal walls, opercula, and outer exposed ends of vertical walls.

part of the cycle. Basal diaphragms bend outward where they join enclosing vertical zooecial walls to be continued as skeletal linings, of varying thickness and extent, of living chambers. This outward bend indicates that the diaphragms were deposited by an epidermis on their outer sides at living chamber bases. Paleozoic taxa lacking basal skeletal diaphragms could have had basal membranous diaphragms of similar function, which were not preserved (BOARDMAN, 1971, p. 11).

Both the outward shift of zooidal organs and the spacing of basal diaphragms ontogenetically are apparently results of the

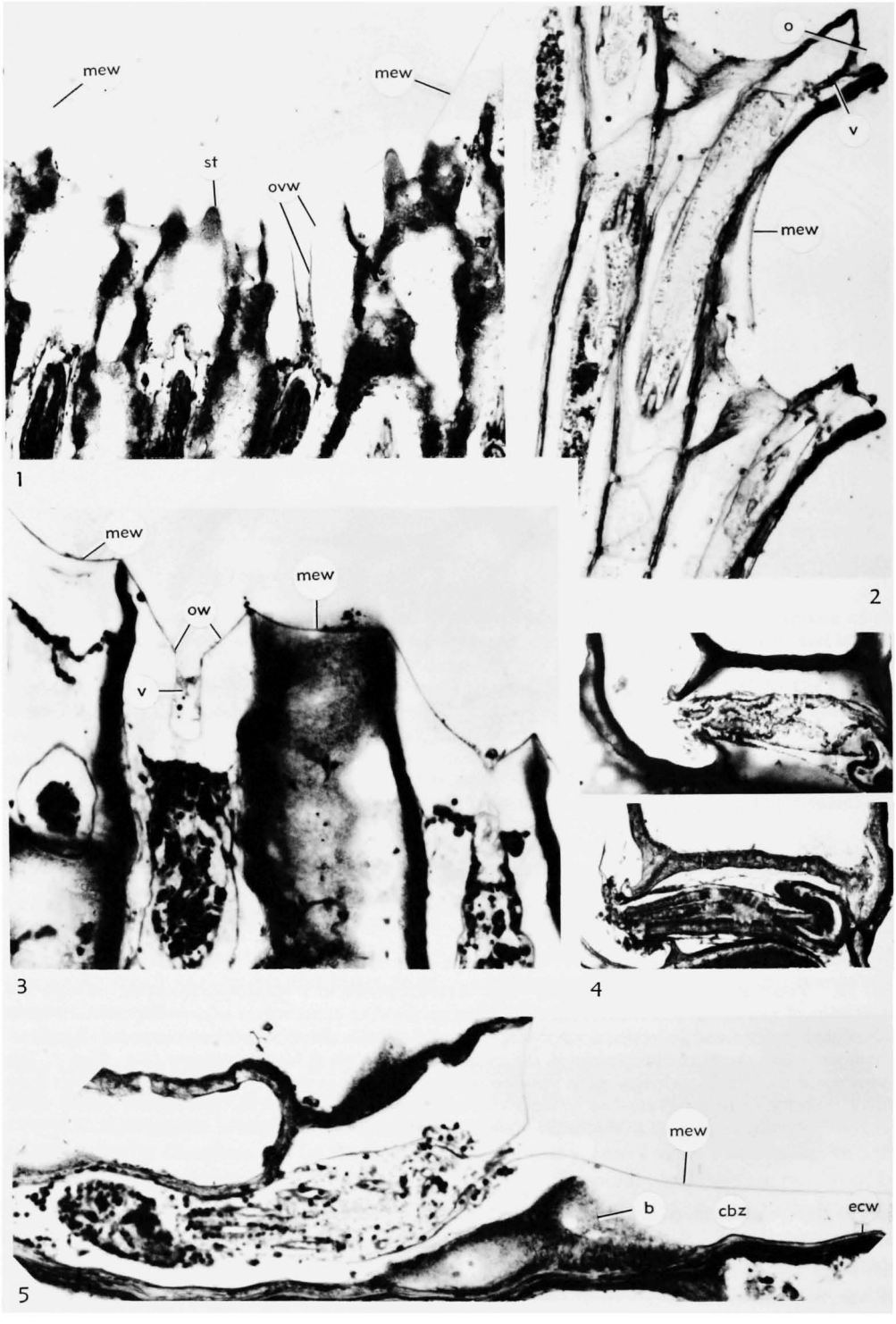

FIG. 39. *(For explanation, see facing page.)*

degeneration-regeneration cycle of feeding zooids (BOARDMAN, 1971, p. 18). More or less continuous growth of vertical zooidal walls during periods of degeneration is assumed. As illustrated in Figure 37, the laminated skeletal microstructure indicates that the newest growth of a vertical wall (A_2) and the outermost diaphragm (2) grew simultaneously as a single skeletal unit. The distance (B_2) between the last two diaphragms (1 and 2) is equal to the distance (A_1) that the vertical wall grew in the previous cycle. When the new organs regenerated they were displaced outward by the distance (A_2) that the vertical wall grew during the newest cycle.

In free-walled fossil taxa lacking communication pores in vertical walls, segments of zooecial chambers enclosed by skeletal diaphragms are assumed to have been sealed physiologically and to have lacked living tissue (Fig. 37). Nutrients for continued growth of vertical walls at outer ends of degenerated zooids presumably would come through the outer body cavity from other feeding zooids of the colony, or were stored within the degenerated zooids themselves. In post-Paleozoic free-walled forms, outer body cavities, and in most taxa, communication pores in vertical walls are both apparently available for transfer of nutrients to regenerating zooids.

In support of the interpretation of the relationship between the spacing of basal diaphragms and the degeneration-regeneration cycle, a few exceptionally preserved specimens of Paleozoic age have a one-to-one relationship between basal diaphragms and presumed fossilized brown bodies (Fig. 40,*1*). Recent tubuliporates have not been found as yet with calcified basal diaphragms in regularly spaced ontogenetic series, but their accumulated brown bodies in inner ends of living chambers can be as many as twenty or more (Fig. 40,*3b*), which compares in number with basal diaphragms in ontogenetically older zooecia of many Paleozoic trepostomates (see Fig. 27 for distribution of ontogenetic stages in a colony).

Lateral skeletal projections.—**Lateral skeletal projections** in living chambers occupy positions opposite feeding organs and are structures of chamber walls that generally reduce or contort living space available to feeding organs. Lateral projections can be shelflike, spinose, or cystose.

Shelflike skeletal projections have been designated by different terms depending on their number and relative position in zooecia. Shelves may be calcified from one or both sides. **Hemisepta** are shelves that generally occur singly on the proximal sides of zooecia or in one or two pairs in alternate positions on proximal and distal sides of zooecia. Proximal and distal hemisepta commonly have different dimensions. Hemisepta have been one of the main polythetic characters (occurring in some taxa but not in others) in the cryptostomates (see BLAKE, this revision) and have only recently been discovered in living (HARMELIN, 1976) and fossil (HINDS, 1973,

FIG. 39. Membranous walls of tubuliporates.——*1. Densipora corrugata* MACGILLIVRAY, rec., 5-m wave-cut platform, Western Port Bay, W. end Phillip Is., Australia; membranous exterior wall (mew) of free-walled colony supported by skeletal styles (st) leading to orificial-vestibular wall (ovw) of feeding zooid; long. sec., USNM 250071, ×100.——*2. Mesonea radians* LAMARCK, rec., Great Barrier Reef, Low Is., Australia; free-walled colony showing membranous exterior wall (mew), vestibule (v), and orifice (o); long. sec., BMNH specimen, ×150.——*3. Plagioecia dorsalis* (WATERS), rec., 70 m, off Riou Is., Marseille, France; membranous exterior wall (mew) of free-walled colony, orificial wall (ow), vestibule (v); long. sec., Harmelin Coll., ×200.——*4. Diaperoecia indistincta* CANU & BASSLER, rec., 25–35 m, Port Cros, La Palud, France; retracted position of feeding organs behind hemisepta, gut bends in opposite directions in two zooids from same colony; long. sec., Harmelin Coll., ×100.——*5. Plagioecia* sp., rec., 22 m, off Riou Is., Marseille, France; confluent budding zone distal (to the right, and extending well beyond right margin of figure) of feeding zooid, including multizooidal encrusting colony wall (ecw), confluent budding zone (cbz), membranous exterior wall (mew), and developing bud (b); long. sec., Harmelin Coll., ×200.

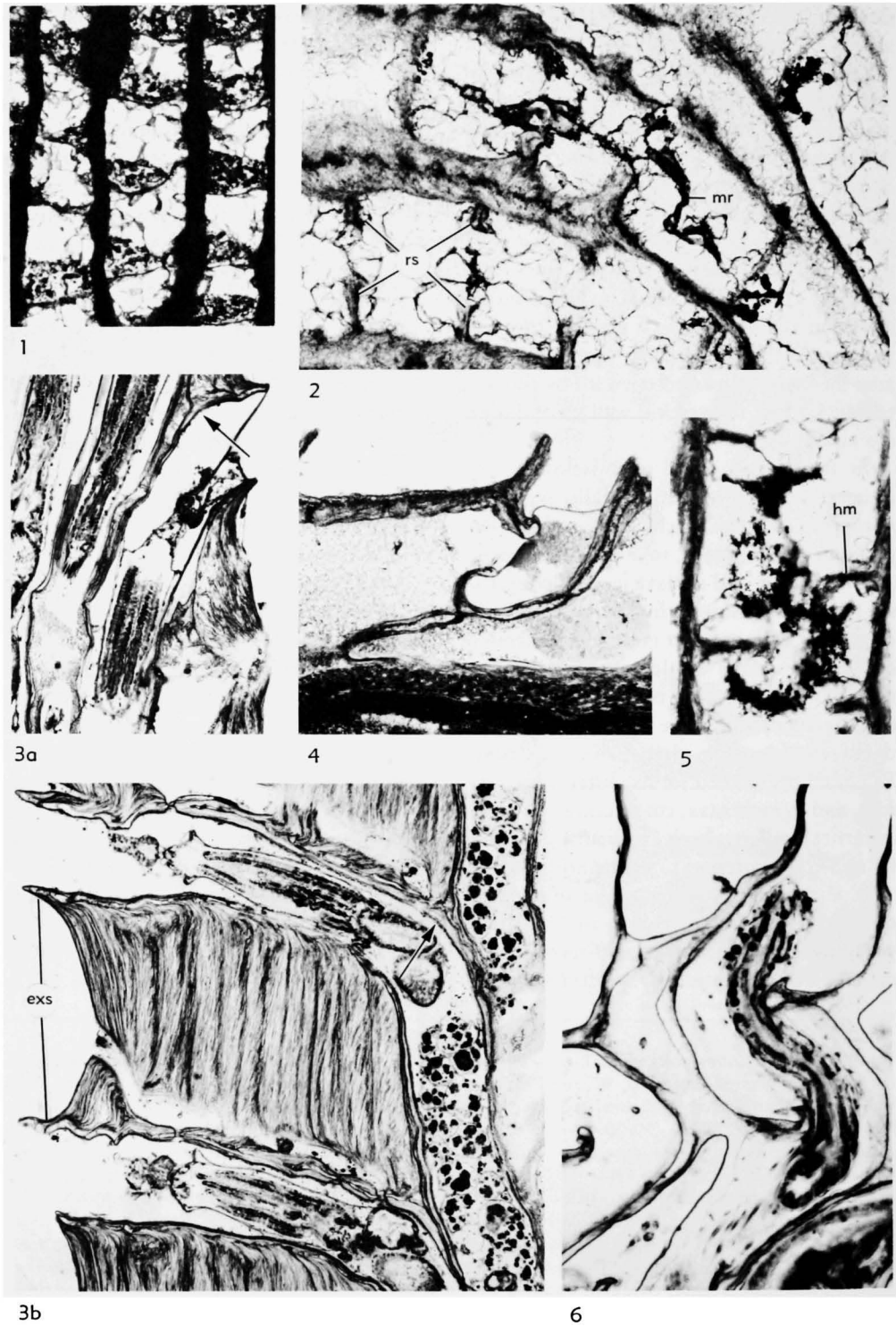

FIG. 40. *(For explanation, see facing page.)*

p. 302) tubuliporates. Retraction of feeding organs behind hemisepta (Fig. 39,*4*) makes it evident that retracted positions are constant in these short zooecia during their ontogeny. Also, openings between hemisepta are covered by a thickened, apparently protective organic diaphragm during degenerated stages (Fig. 40,*4*).

Hemiphragms are skeletal shelves of comparable dimensions within a zooid, which alternate in ontogenetic series from opposite sides of chamber walls. In modern species, comparable structures demonstrate how active feeding organs can bend around the projections as they move in and out of living chambers (Fig. 40,*6*). Fossilized indications of inferred feeding organs have the same relationships to comparable skeletal projections (Fig. 40,*5*).

Ring septa are centrally perforated diaphragms (Fig. 31,*6*; 40,*2*) that have been found in only a few Paleozoic taxa. They originate as lateral structures, outward from basal diaphragms. As ontogeny continues, however, the openings in ring septa may be closed skeletally, suggesting that they eventually acted as living chamber floors (Gautier, 1970, p. 9).

Protection from predation might be a function of the chamber constrictions caused by hemisepta, hemiphragms, and ring septa during either the feeding or degenerated state. A lateral shelflike structure projects inward from the frontal and vertical walls of feeding zooids of a tubuliporate of Cretaceous age, which could serve this same function (Fig. 41,*5a–c*).

Inward-projecting **mural spines** from zooidal chamber walls are common in stenolaemates of all ages. They may be scattered without noticeable pattern or aligned in rows parallel to zooidal growth (Fig. 41,*2*). Mural spines may be of different shapes, and more than one shape may occur in the same zooid (Fig. 41,*4*). The use of spines is not clear (Harmelin, 1976). In one tubuliporate colony they serve as skeletal supports for presumed attachment ligaments (Fig. 41,*1*), but this does not seem to be generally true, especially for randomly scattered spines. Spines also occur in brood chambers (Fig. 41,*3*); Brood, 1972, p. 70). Certainly more than one function is possible.

Skeletal **cystiphragms** form inwardly curved cysts or collars that extend partly or entirely around living chambers in some Paleozoic taxa. Cystiphragms are calcified on their outer surfaces only, and so are simple partitions. Cystiphragms generally are overlapping in repeated ontogenetic series in zooidal body cavities, causing living chambers to be roughly cylindrical or funnel-shaped and greatly reduced in diameter (Fig. 30,*1*). Overlapping cystiphragms are closed and show no indication of enclosed soft parts (Cumings & Galloway, 1915, p. 354). Cystiphragms have not yet been found in modern species, so no function other than reduction

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Fig. 40. Stenolaemate morphology.——*1. Trachytoechus* sp., Dev. (Erian, Petoskey Ls.), Petoskey, Mich.; one-to-one ratio between basal diaphragms and presumed fossilized brown bodies; long. sec., USNM 37518, ×30.——*2. Tabulipora ramosa* (Ulrich), Glen Dean F., Miss. (Chester.), Falls of the Rough, Grayson Co., Ky.; ring septa (rs) and remains of membrane (mr), possibly of membranous sac; long. sec., USNM 167706, ×100.——*3a,b.* Hornerid tubuliporate, rec., Arctic O.; ontogenetic variation showing increase in width of exozone and outward shift of retracted position of feeding organs with increased age within one colony; arrow in each figure points to zooecial bend position, which remains fixed during ontogeny; for intermediate growth stage from same colony, see Figure 44,*5*; laminated skeleton between zooids is extrazooidal (exs); *3a,* long. sec., *b,* accumulation of brown bodies in base of living chamber, another indicating of advanced growth stage, long. secs., both BMNH specimen, ×100. ——*4. Diaperoecia indistincta* Canu & Bassler, rec., 110 m, Medit. Sea, Levant, Magaud, France; opening between hemisepta covered by organic diaphragm during degenerated stage; long. sec., Harmelin Coll., ×100.——*5. Hemiphragma* sp., Maquoketa Gr., Ord. (Richmond.), Wilmington, Ill.; brown granular deposit with flask shape typical of feeding organs bending around hemiphragms (hm); long. sec., ×100. ——6. *Tubulipora ziczac* Harmelin, rec., 30 m, Port Cros, Gabinière, France; tentacles of feeding zooid bending around hemiphragms; long. sec., Harmelin Coll., ×100.

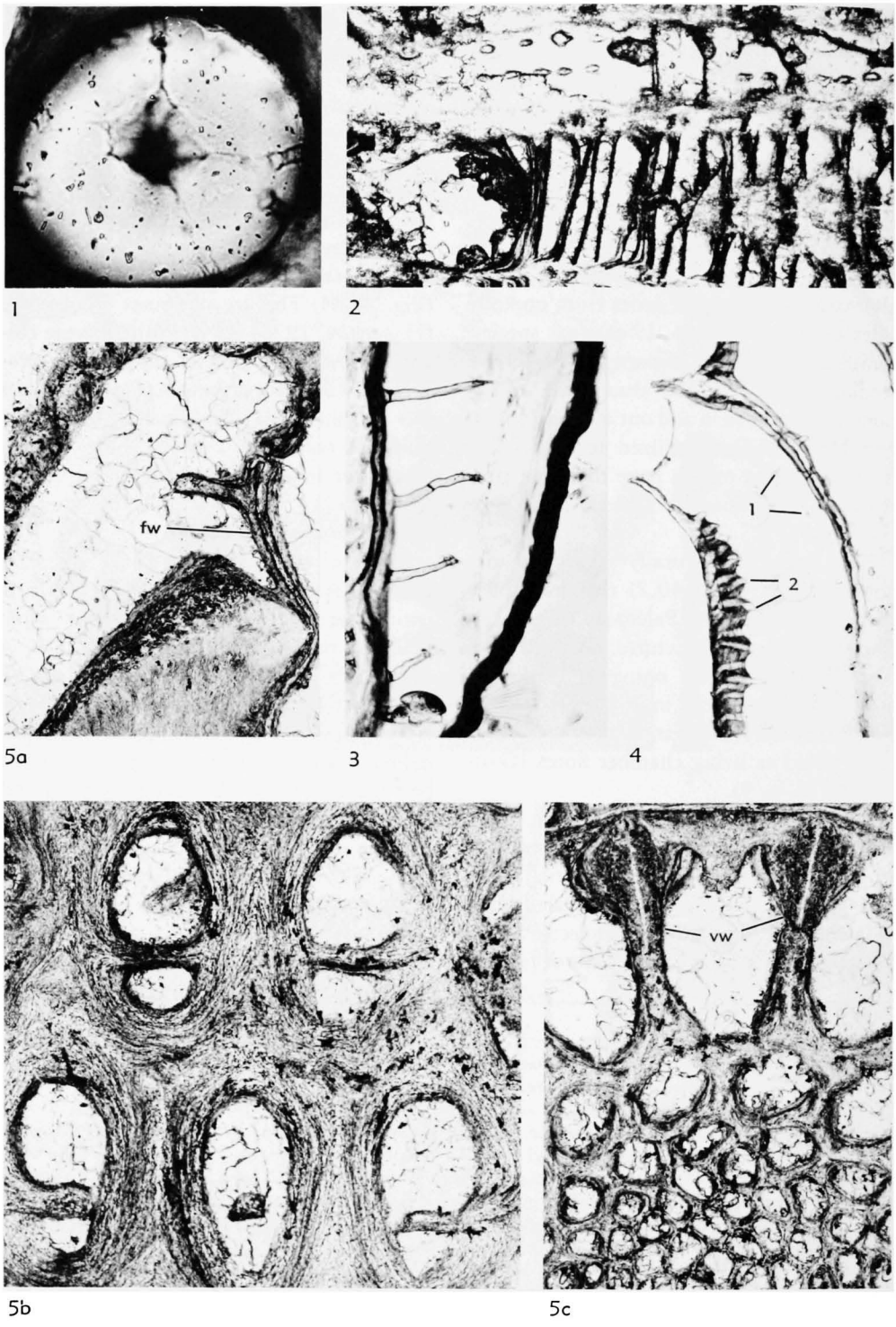

FIG. 41. *(For explanation, see facing page.)*

of living chamber volume is suggested.

Terminal structures.—Membranous or skeletal terminal and subterminal diaphragms seal living chambers from the surrounding environment because of their position at or near skeletal apertures. Terminal diaphragms are calcified from one side only. It is assumed from examples in a few modern specimens (Fig. 34,*1d*) that skeletal structures calcified on one side are positioned by earlier formed membranes of similar configuration upon which subsequent calcification takes place. Edgewise calcification seems to be the method of skeletal growth.

In post-Paleozoic stenolaemates it is assumed that zooids sealed by terminal diaphragms are in a degenerated state. Growing zooids in the degenerated state of the normal degeneration-regeneration cycle are routinely closed at apertures by membranous terminal diaphragms, which presumably are readily removed by the succeeding regeneration part of the cycle. It also seems probable that the growth of calcified terminal diaphragms terminates the feeding and outward growth of zooids. No indications have been seen of resorption of terminal calcified diaphragms and continued outward growth of vertical walls.

In post-Paleozoic stenolaemates, calcified terminal and subterminal diaphragms bend inward at junctions with vertical walls of chambers (Fig. 42,*5,6*), indicating that skeletal growth occurs on inner sides of membranous diaphragms within closed living chambers. Calcified terminal diaphragms are exterior walls because they wall off body cavity from the external environment. As in other exterior walls, the skeletal layers are fastened directly to inner sides of outermost cuticles. Apparently, communication pores in vertical walls allow transfer of nutrients among zooids so that degenerated zooids can grow calcified diaphragms after their apertures are closed by membranous diaphragms. Pseudopores are generally abundant in calcified layers of terminal diaphragms but may be few or lacking. Membranous diaphragms can be many near skeletal apertures (Fig. 42,*5*), and more than one can be calcified in a zooid in reverse order, the inner one later (Fig. 42,*6*). Apparently, multiple terminal diaphragms indicate that the active outer boundary of a zooid is retreating inward.

In some post-Paleozoic taxa calcified layers of exterior terminal diaphragms are continuations of calcified layers of interior vertical walls just as they are in some frontal zooidal walls (Fig. 42,*2*). Also, some terminal diaphragms form continuous structural units extending across apertures of a number of zooids (Brood, 1972, fig. 30B). Vertical zooidal walls abut the subsequently formed calcified exterior walls of the terminal diaphragms (Fig. 42,*1*). The essential morphologic difference between these exterior terminal diaphragms and frontal walls, which can also form structural units across a number of zooids (see above), is the lack of apertures in the terminal diaphragms.

In Paleozoic taxa, diaphragms that are terminal or subterminal to zooidal living chambers (Boardman, 1971, p. 18) bend outward at junctions with vertical walls of chambers

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Fig. 41. Lateral skeletal projections.——*1. Lichenopora* sp., rec., Pac. O. off La Jolla, Cal.; dried specimen showing feeding zooid in which membranes attach membranous sac to mural spines; thick tang. sec., USNM 250072, ×400.——*2. Hallopora* sp., Waldron F., Sil. (Niag.), Nashville, Tenn.; alignment of transversely cut mural spines parallel to direction of zooidal growth in zooidal chamber; long. sec., USNM 167698, ×200.——*3. Mecynoecia delicatula* (Busk), rec., 28–30 m, Medit. Sea off Riou Is., Marseille, France; interior of brood chamber of gonozooid with large spines; long. sec., USNM 250073, ×100.——*4. Pustulopora* cf. *P. purpurascens* Hutton, rec., 36 m, off Poor Knights Is., N.Z.; two kinds of mural spines (1 and 2) in living chamber of feeding zooid; long. sec., USNM 216483, ×100.——*5a–c.* Salpinginid tubuliporate, Cret. (Cenoman.), Essen, W. Ger.; shelflike projections connected to both frontal (fw) and vertical walls (vw) in living chambers, cluster of inner ends of zooecia in centers of branches indicate buds clustered centrally at growing tips of branches; *a–c*, long., tang., transv. secs., USNM 213325, ×100.

(Fig. 43,*3*) and communication pores of vertical walls are lacking. As a result, skeletal growth is assumed to have occurred only on outer sides of membranous diaphragms where nutrients are available from adjacent zooids. Because these terminal diaphragms are calcified on their outer surfaces, they are interior structures that formed within outer body cavities protected by outermost membranous exterior walls of free-walled colonies.

Terminal and basal diaphragms in Paleozoic taxa have comparable microstructure and generally differ only in function and position relative to the skeletal aperture when developed. Continued zooidal growth is common beyond terminal diaphragms, so that irregular alternations of basal and terminal diaphragms are found in older zooecia, and abandoned living chambers can be difficult to distinguish (Fig. 36,*1*; 43,*2*; BOARDMAN & MCKINNEY, 1976, p. 66). In most taxa having numerous diaphragms in zooecia, living chambers are generally longer than the spacing between successive basal diaphragms (Fig. 37). Spacing comparable to living chamber length suggests that outer diaphragms of those intervals may have originally been terminal. Some terminal diaphragms appear to serve as basal diaphragms after vertical chamber walls have grown outward enough to house new feeding organs (Fig. 43,*2*).

Communication pores or larger gaps occur in vertical walls in one suborder of early Paleozoic age. Correlated with such communication potential are diaphragms in two genera that bend inward at vertical wall junctions, indicating growth on inner diaphragm surfaces (UTGAARD, this revision) and implying transfer of nutrients through communication pores. Some of these diaphragms could have served as terminal diaphragms (UTGAARD, 1968b, p. 1446) although they are subterminal or intermediate in position along zooecial length. Apparently they are interior in origin.

Sequential skeletal growth.—The relative time of formation of laminated basal, lateral, or terminal skeletal structures during the ontogeny of the same or adjacent zooecia can be determined by structural continuity of skeletal structures with each other or with the enclosing laminated zooecial walls (BOARDMAN, 1971, p. 14, 15).

Relative time of formation of skeletal structures that abut others can generally be concluded by determining which of the two, the abutting or the abutted, is the supporting structure. In most tubuliporates terminal diaphragms of separate zooids abut supporting vertical zooidal walls and are formed after the vertical walls (Fig. 42,*5,6*). In other tu-

FIG. 42. Stenolaemate diaphragms.——*1. Diplocava incondita* CANU & BASSLER, Cret. (Valangin.), Ste Croix, Switz.; vertical walls (vw) abut subsequently formed terminal diaphragms (td) and frontal walls (fw); long. sec., USNM 250074, ×50.——*2. Diplosolen intricaria* (SMITT), rec., 200–235 m, 100 km N. of North Cape, Barent Sea; extension of vertical wall (vw) forms calcified terminal diaphragm (ctd), membranous terminal diaphragm (mtd) at zooidal aperture; long. sec., BMNH specimen, ×100.——*3. Hemiphragma* sp., Bromide F., Ord. (Champlain.), Spring Cr., Arbuckle Mts., Okla.; laminae of hemiphragms (hm) extend outward and become part of vertical wall (vw) for interval of two to three diaphragms (md) in adjacent mesozooecium; all mesozooecial diaphragms having at zooecial boundary laminae abutting laminae connected to a hemiphragm are outward in position (to right) from that hemiphragm; long. sec., USNM 167709, ×100.——*4. Leptotrypella* (*Pycnobasis*) *pachyphragma* BOARDMAN, Wanakah Sh. Mbr., Ludlowville Sh., Dev. (Erian), Deep Run, Canandaigua Lake, N.Y., paratype; superposition of laminae in zooecial lining attached to sequence of progressively younger diaphragms to right in figure; long. sec., USNM 133919, ×50.——*5.* Heteroporid tubuliporate, rec., Pac. O.; laminae from calcified diaphragm (cd) turn inward at junction with vertical wall, membranous diaphragms (md) in closely spaced cluster outward from calcified diaphragm; long. sec., BMNH specimen, ×150.——*6. Heteropora? pelliculata* WATERS, rec., Neah Bay, Wash.; laminae from calcified diaphragms (cd) turn inward at junctions with vertical walls, superposition of laminae at junctions with vertical walls indicates that inner diaphragm developed after outer diaphragm in same zooid; long. sec., USNM 186550, ×100.

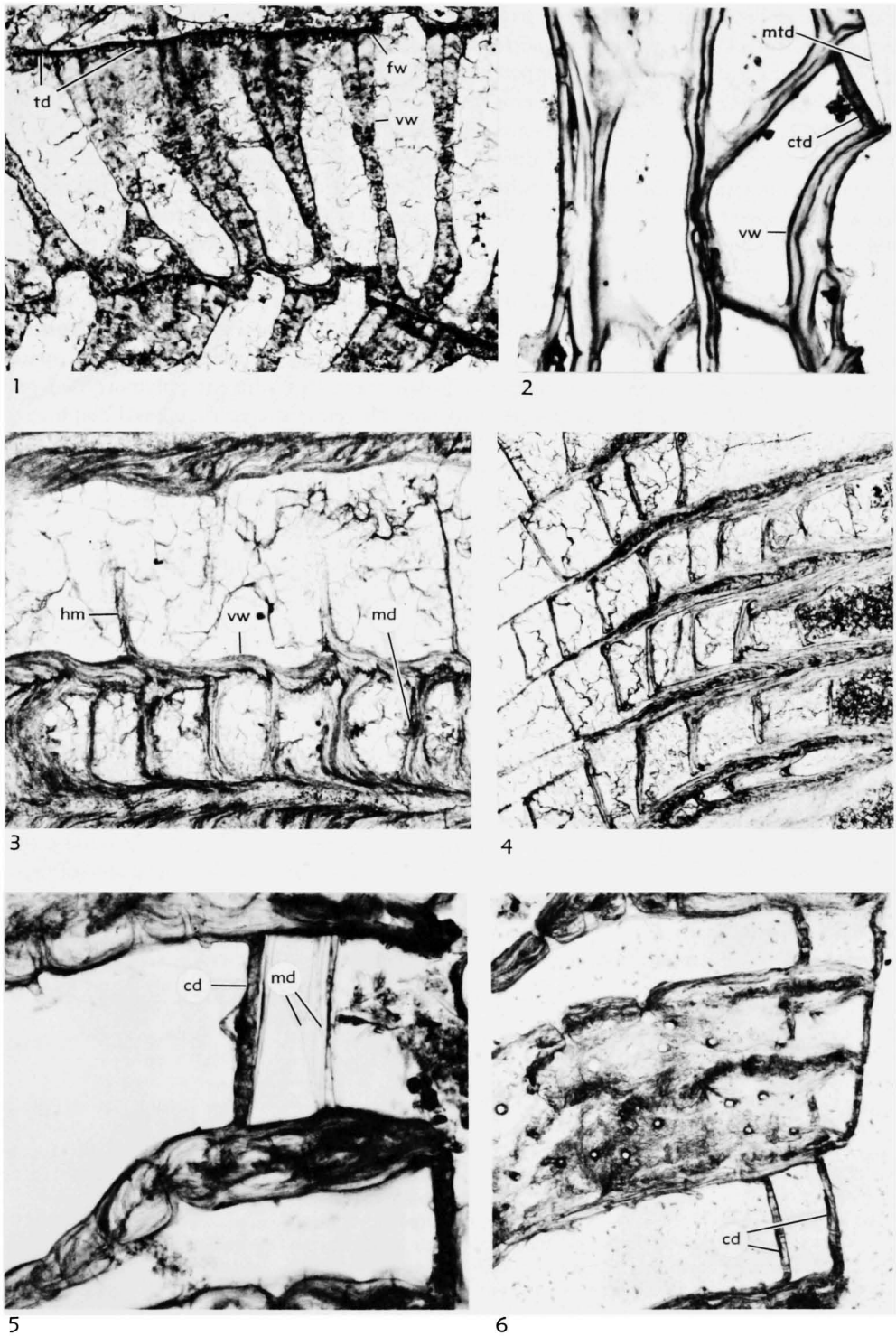


FIG. 42. *(For explanation, see facing page.)*

buliporates terminal diaphragms extend across apertures of a number of adjacent zooids and the previously formed supporting vertical walls abut the younger diaphragms (Fig. 42,*1*). The mode and sequence of growth of this combination is more difficult to understand, and growing tips that actually show the sequence of formation would be helpful.

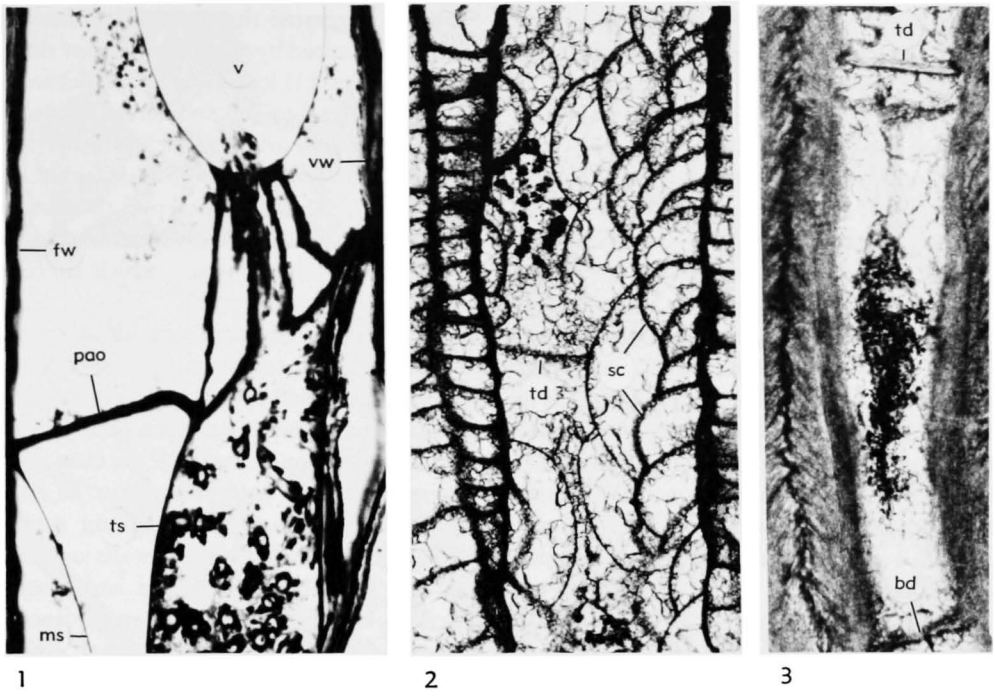
Superposition in zooecial linings of layers of skeletal laminae attached to skeletal structures within zooecial chambers necessarily indicates relative time of formation of the structures. Basal diaphragms calcified on outer surfaces in zooecia of Paleozoic age (Fig. 42,*4*) are progressively younger outwardly as indicated by superposition of laminae of attached linings. Superposition of layers connected to terminal diaphragms calcified on inner surfaces, however, indicates that terminal diaphragms can be relatively younger inwardly (Fig. 42,6) in zooecia of post-Paleozoic age.

Relative time of formation can be determined for skeletal structures within zooidal chambers that are connected by zooecial wall laminae to zooecial boundaries in the same or adjacent zooecia. The outward growth of zooecial walls results in the outward migration of skeletal apertures at zooecial boundaries. If one structure connected to wall laminae intersects the zooecial boundary farther out than another structure in the same or an adjacent zooecium, the one farthest out was developed later. In application, if basal diaphragms of feeding zooids are coordinated with degeneration-regeneration cycles, nonalignment of diaphragm laminae of adjacent zooecia along their common boundaries indicates that the cycles were not in unison in those zooids and a degree of zooidal control is expressed. Other structures that can be aligned at zooecial boundaries with basal diaphragms, such as cystiphragms, ring septa (GAUTIER, 1970, pl. 4, fig. 2), or hemiphragms in most Paleozoic species, are also interpreted to be expressions of degeneration-regeneration cycles. Regularly spaced diaphragms in adjacent polymorphs, which are differently spaced than basal diaphragms or hemiphragms, would be controlled by some other cycle, or perhaps be more strongly controlled by environment (Fig. 42,*3*).

BODY CAVITIES AND FEEDING ORGANS OF ZOOIDS

Organs of feeding zooids and polymorphs are the least-known parts of recent stenolaemates. The most detailed coverage of functional organs of a relatively few species are available in papers by BORG and by NIELSEN. Additional information included here is made possible by a sectioning technique (NYE, DEAN, & HINDS, 1972) that produces thin sections containing both skeletal and soft parts in place. Approximately 45 different kinds of tubuliporates have been sectioned. The morphologic differences in soft parts among

FIG. 43. Zooidal soft parts.——*1. Fasciculipora* sp., rec., McMurdo Sound, Antarctica; membranous sac (ms), tentacle sheath (ts), perimetrical attachment organ (pao), and vestibule (v) within vertical (vw) and frontal (fw) walls of zooid; long. sec., USNM 179007, ×150.——*2. Prasopora simulatrix* ULRICH, Ord. (Trenton.), Can.; flask-shaped chambers with calcified walls below and above diaphragm (td), which could have served as both terminal and basal diaphragm, skeletal cystiphragms (sc) reduce volume of living chambers; long. sec., USNM 167688, ×100.——*3. Tetratoechus crassimuralis* (ULRICH), Maquoketa Gr., Ord. (Richmond.), Wilmington, Ill., paralectotype; brown granular deposit in the general shape of feeding organs in living chamber floored by basal diaphragm (bd) and protected by terminal diaphragm (td); long. sec., USNM 204875, ×100.——*4.* Tubuliporid tubuliporate, rec., washed in at Manomet Bay, Cape Cod, Mass.; membranous sac (ms) and tentacle sheaths (ts) in two feeding zooids of a narcotized colony; the tentacle sheath is attached to the membranous sac at points 1 and to the base of the tentacles at points 2; in the zooid to the right, tentacles are protruded far enough that point 2 has moved outward past point 1, causing tentacle sheath to turn inside out; points 1 and membranous sac appear to remain in place; long. sec., USNM 216485, ×150.——*5. Diaperoecia indistincta* CANU & BASSLER, rec., 30 m, Medit. Sea, Port Cros, Gabinière, France; tentacles partly protruded past hemisepta, minute strands connecting membranous sac (ms) to zooecium; long. sec., Harmelin Coll., ×150.



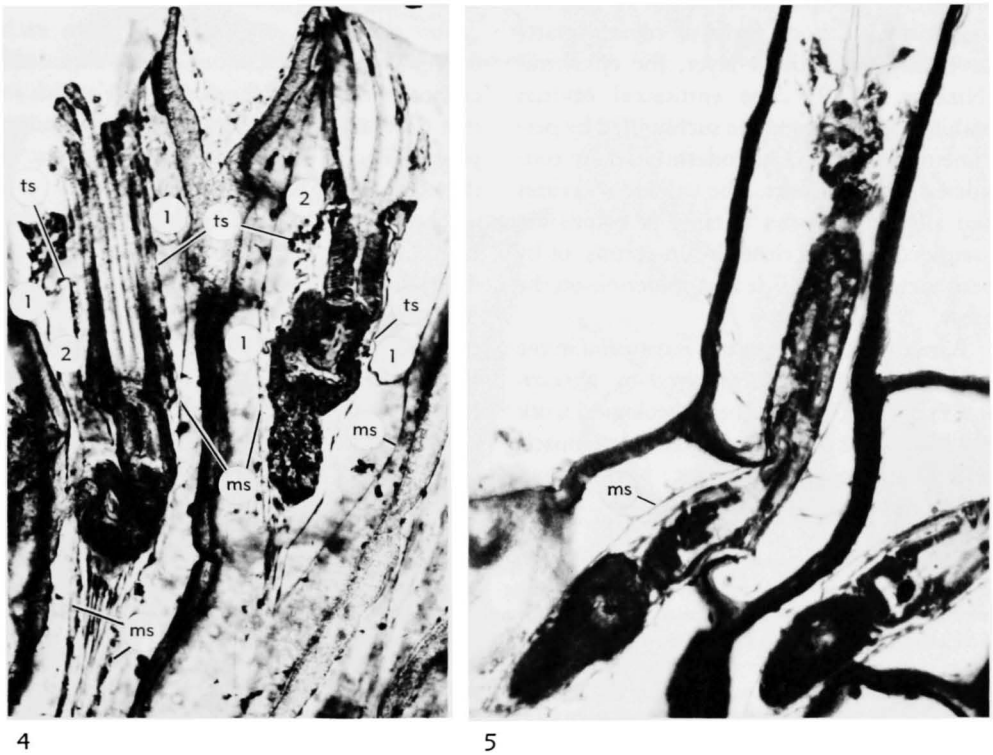


FIG. 43. *(For explanation, see facing page.)*

taxa are striking (Fig. 39, 40, 43–45). The degree of correlation between skeletal and soft-part morphology is an especially important question for classification and that question has yet to be investigated.

All tubuliporates sectioned to date have a membranous sac (BORG, 1926a, p. 207). The sac divides the body cavity into two parts, the entosaccal cavity surrounding the digestive and reproductive systems, and the exosaccal cavity between the membranous sac and the zooidal wall (see Fig. 2). Membranous sacs are attached to the skeletal walls of living chambers near their inner ends by the inner ends of large retractor muscles. The sacs also are attached to skeletal walls of chambers at or near their outer ends and to membranous vestibular walls, which continue out to orificial walls.

A recent study (NIELSEN & PEDERSEN, 1979; first reported by NIELSEN at 1977 meeting of International Bryozoology Association) interpreted the membranous sac to be peritoneum. Also, body walls of stenolaemates have only one cellular layer, the epidermis (NIELSEN, 1970). The entosaccal cavities within sacs, therefore, are surrounded by peritoneum (possibly a mesoderm) and are considered to be coeloms. The exosaccal cavities and all body cavities outside of zooids are pseudocoels, lined either by epidermis, or by peritoneum on one side and epidermis on the other.

A mechanism for tentacle protrusion in the genus *Crisia* was also reported by NIELSEN and PEDERSEN (1979). Their histological work has revealed a series of fine annular muscle cells in the membranous sac. NIELSEN and PEDERSEN suggested that tentacle protrusion in *Crisia* is caused by the contraction of three sets of muscles: (1) longitudinal muscles from the orificial wall to the sphincter muscle at the base of the vestibule, which pull the orificial wall inward; (2) longitudinal muscles in the tentacle sheath, which pull the mouth end of the gut outward; and (3) annular muscles of the membranous sac, which squeeze the feeding organs outward.

The presence of membranous sacs surrounding feeding organs in all preserved tubuliporates studied to date suggests that the sac with its annular muscles is a basic part of tentacle protrusion throughout the class. The system of tentacle protrusion must be confined to living chambers of feeding zooids because all vertical and frontal walls are skeletal and inflexible in the class and cannot enter into zooidal volume changes as frontal walls do in gymnolaemates. Further, living chambers in most stenolaemates, because of outer body cavities and/or open communication pores, are not sealed off from each other. The living chamber, itself, therefore, cannot confine body fluids to single zooids so that differential pressures can be produced to push tentacles out. The membranous sac is the obvious confining organ.

The presence of feeding organs and membranous sac in a large brood chamber (Fig. 45,*1*) also provides a bit of presumptive evidence. Presumably the tentacles were able to protrude, regardless of what the soft parts were doing there. Certainly, volume restriction and control by the membranous sac in an otherwise oversized chamber must have been a necessary factor in the process.

FIG. 44. Feeding organs.——*1,2. Lichenopora* sp., rec., Galapagos Is.; *1,* radially arranged ligaments attaching top of membranous sac to zooecium, tang. sec., BMNH specimen, ×200; *2,* orificial-vestibular wall (ov), ligament (lg), and mass of eggs (e), long. sec., BMNH specimen, ×150.——*3. Idmidronea atlantica* (FORBES), rec., 24 m, Medit. Sea off Riou Is., Marseille, France; vertical wall (vw) and frontal walls (fw) enclosing outer ends of tentacles and horney cap (hc); long. sec., Harmelin Coll., ×200.——*4a,b.* Crisinid tubuliporate, rec., 320 m, Nausen Is., W. Palmer Penin., Antarctica; *a,* horny cap (hc) rotated a few degrees, presumably to provide an exit (arrow) for tentacles; *b,* horny caps (hc) in presumed fully retracted position, organic-rich partitions (op) in interior vertical walls; long. secs. from same colony, USNM 216489, ×150.——*5.* Hornerid tubuliporate, rec., Arctic O.; membranous sac (ms) and enclosed retracted feeding organs form flask shapes comparable to flask-shaped chambers of species of Paleozoic age (see Fig. 46); long. sec., BMNH specimen, ×150.

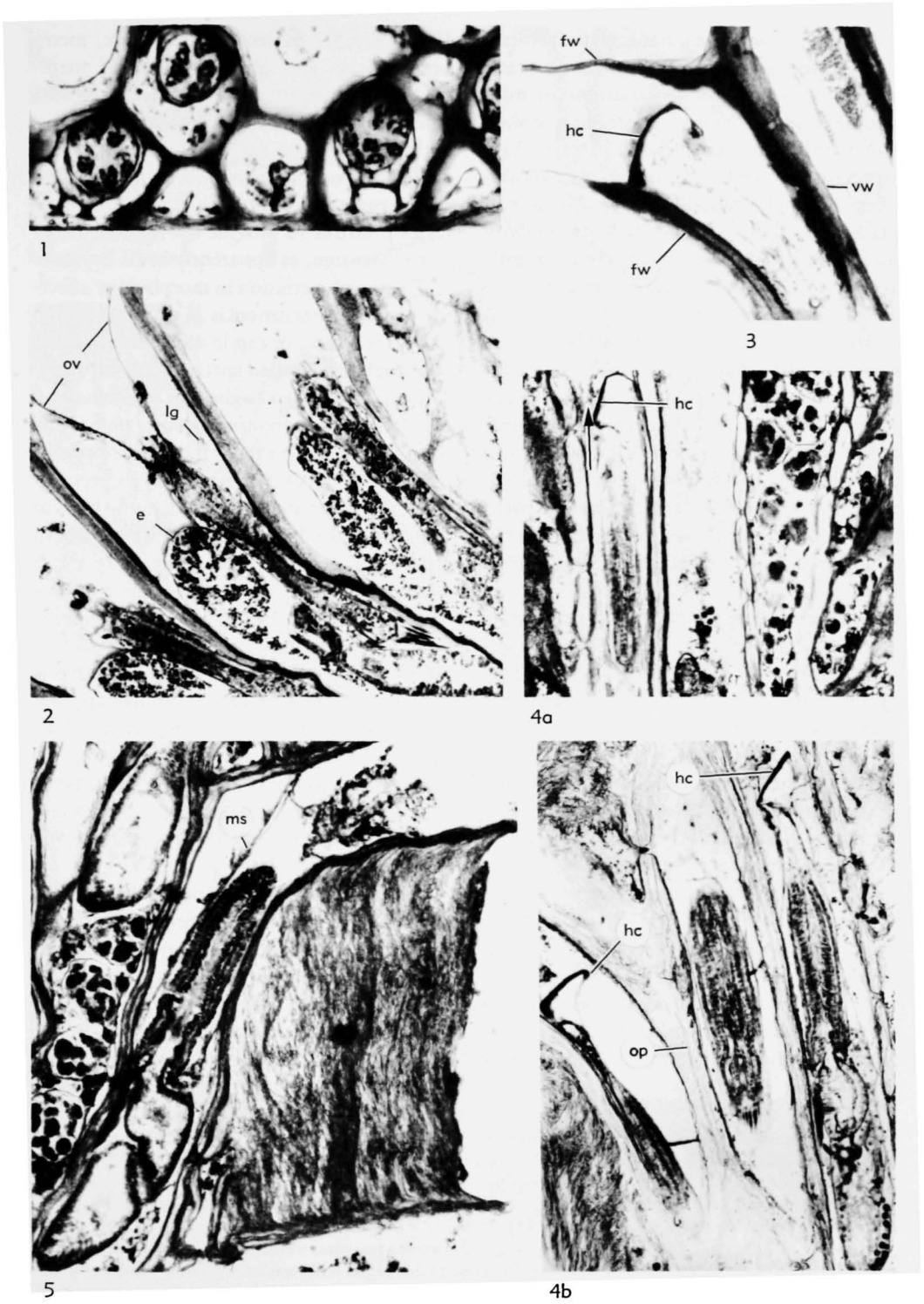


FIG. 44. *(For explanation, see facing page.)*

The region near the outer end of the membranous sac and the fixed end of the tentacle sheath has at least four variations in morphology and attachment of soft parts to skeleton in different taxa. BORG (1926a, p. 209) reported that this attachment was accomplished by eight radially arranged ligaments placed just inward from the outer ends of membranous sacs (Fig. 44,*1*). He apparently assumed that the eight ligaments were present throughout the order.

Most of the colonies sectioned here, however, including both free- and fixed-walled species, have membranous sacs and tentacle sheaths attached by single collarlike membranes (Fig. 43,*1*). These membranes, termed **perimetrical attachment organs** (BOARDMAN, 1973, p. 235), are attached at their inner perimeters to tentacle sheaths and at outer perimeters both to outer ends of membranous sacs and to skeletal body walls. In some species, at least, the attachment organ is attached to walls by many very short ligaments (Fig. 45,*2–4*), most easily detected by the narrow gap between the attachment organ and skeletal wall in longitudinal sections (Fig. 45,*3*).

The perimetrical attachment organ divides the exosaccal body cavity of a zooid transversely into inner and outer portions (Fig. 2). BORG's inferences on tentacle protrusion (1926a, p. 241) were based on exchange of body fluid from outer to inner parts of the exosaccal cavity through spaces between radial ligaments.

In a few fixed-walled species, membranous sacs are attached to chamber walls by a number of minute strands at many different levels (Fig. 43,*4,5*). As tentacles protrude, membranous sacs and orificial-vestibular membranes stay in place. The tentacle sheath surrounds the tentacles in the retracted position and is attached at the base of the tentacles and outer end of the membranous sac. The sheath turns inside out (Fig. 43,*4*) as the tentacles protrude to provide the necessary outward extension, as apparently in all Bryozoa.

The fourth variation in morphology affecting tentacle protrusion is a stiffened horny, uncalcified valve or cap in each feeding zooid of a single free-walled species (Fig. 44,*4a,b*). The cap is attached to the tentacle sheath on one side and apparently the outer end of the membranous sac on the other. No prominent attachment organ has been seen so presumably the membranous sac is attached to chamber walls by minute strands. The cap must act as a flutter valve by rotating about a central axis to allow space for the tentacles to protrude (Fig. 44,*4a*). Normal membranous vestibular walls pass under an indentation in the cap margin when the valve is closed. An apparent cap of similar appearance (Fig. 44,*3*) has been reported (HARMELIN, 1976, pl. 32, fig. 4–7) from a single fixed-walled species; however, subsequent sectioning of other specimens of the species from the same locality has failed to reveal others.

In all Bryozoa, the anus opens through the tentacle sheath below the ring of tentacles. In the classes Stenolaemata and Gymnolaemata the anus reportedly opens on the distal side (toward the colony growing direction) when the tentacles are protruded (e.g., BORG, 1926a, p. 219; JEBRAM, 1973b) and on the

FIG. 45. Zooidal soft parts.——*1. Lichenopora* sp., rec., "Crab Ledge" E. of Chatham, Mass.; feeding organs surrounded by membranous sac (ms) in large brood chamber; long. sec., USNM 250075, ×100. ——*2–4. Cinctipora elegans* HUTTON, rec., 110 m, off Otago Heads, South Is., N.Z.; *2,* membranous sac (ms), tentacle sheath (ts), sphincter muscle (sm), section cuts perimetrical attachment organ (pao) through short ligaments shown in *4,* long. sec., USNM 250064, ×150; *3,* section cuts perimetrical attachment organ between ligaments, indicated by narrow gap between organ and vertical wall (vw) on both sides, long. sec., USNM 250076, ×100; *4,* perimetrical attachment organ removed from zooid showing approximately 24 short ligaments, USNM 250077, ×150.——*5a–c. Discocytis lucernaria* (SARS), rec., Kara Sea; *a,* sphincter muscle (smm) of mouth at base of tentacles (t); *b,* membranous sac (ms), tentacle sheath (ts), perimetrical attachment organ (pao), sphincter muscle (sm) at top of tentacle sheath; *c,* extreme length of feeding organs of species; all long. secs., USNM 250078, *a,b,* ×150, *c,* ×50.

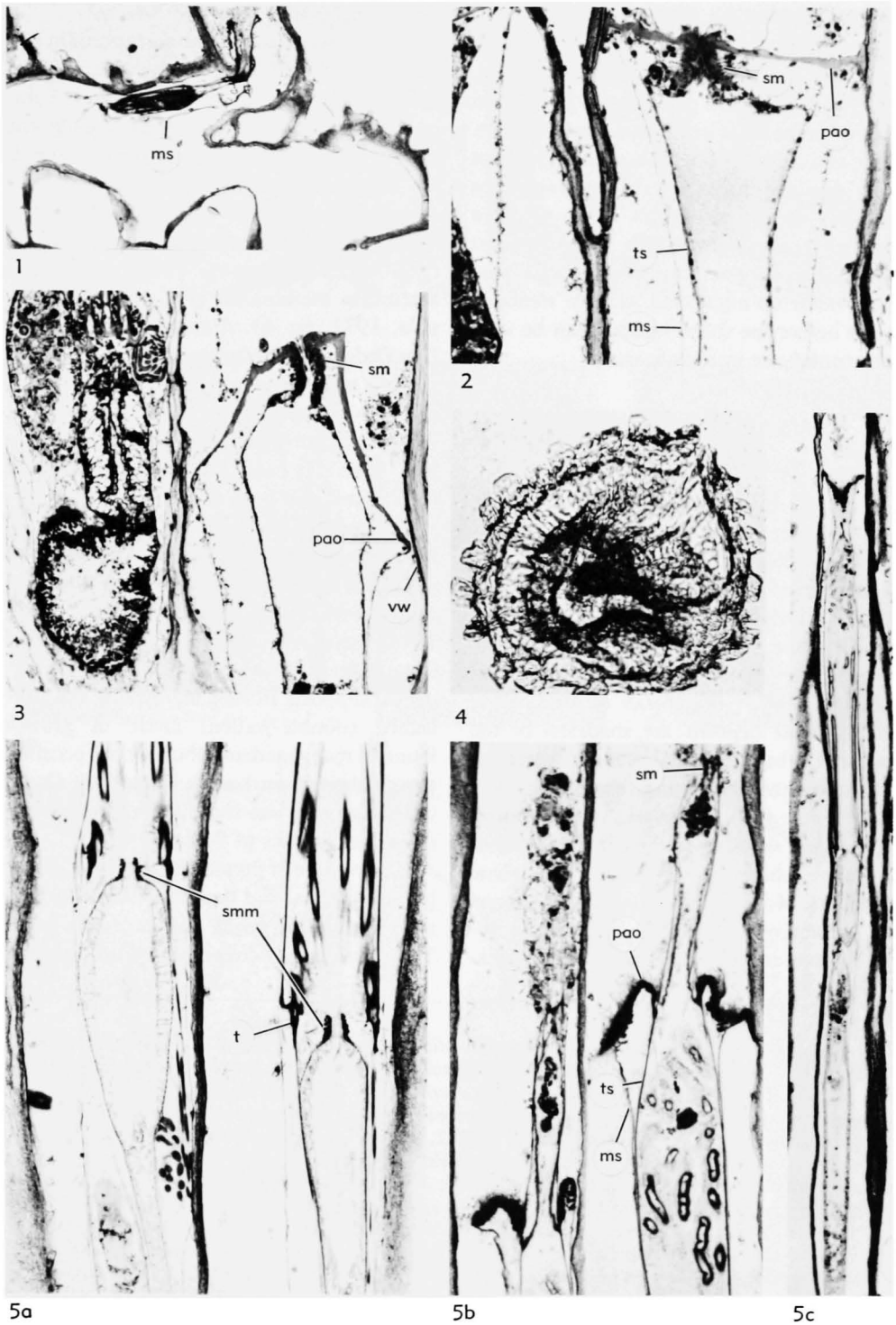


FIG. 45. *(For explanation, see facing page.)*

proximal side in the freshwater Phylactolaemata (WOOD, this revision). In two zooids from the same stenolaemate colony (Fig. 39,*4*), however, the gut appears to bend in opposite directions in the retracted position. If so, and if one of the lophophores does not twist during protrusion, the anal openings will be on opposite sides when the two lophophores are protruded. This apparent discrepancy suggests that observations need to be made on additional modern stenolaemates before the character state can be used with confidence in classification.

FOSSIL INDICATIONS OF SOFT PARTS

Granular brown deposits of iron oxide and some deposits of pyrite presumably represent remains of organic material and have been reported in a number of Paleozoic Bryozoa (e.g., DYBOWSKI, 1877, p. 76, pl. 2, fig. 46; CUMINGS & GALLOWAY, 1915; BOARDMAN, 1971; CORNELIUSSEN & PERRY, 1973; UTGAARD, 1973; BOARDMAN & MCKINNEY, 1976). Most deposits are shapeless or too scattered to be interpreted usefully. Some can be interpreted as having been functional organs (Fig. 40,*5*; 43,*3*; 46,*1,4a*) or brown bodies (Fig. 40,*1*) of feeding zooids depending upon shape and position in skeletal chambers. Most deposits occur under protective skeletal overgrowths or in skeletally isolated, abandoned chambers between diaphragms.

Remains of actual membranes occur in colonies of stenolaemates throughout most of the Paleozoic and are noticeably more common in later Paleozoic species. Again, the majority of membranous remains in zooids are fragmentary and provide little evidence of their biological significance; however, a few could represent the walls of membranous sacs (Fig. 40,*2*; MCKINNEY, 1969) or orificial-vestibular membranes (Fig. 46,*5*; BOARDMAN, 1971, fig. 6). A single zooecium of a Late Ordovician specimen shows what appears to be a transverse section across a retracted tentacle crown bearing 10 tentacles (Fig. 46,*2*; compare with tentacle crown of modern species, Fig. 46,*3*; BOARDMAN & MCKINNEY, 1976, p. 65).

The most biologically significant finds of membranous remains in colonies of Paleozoic age are of exterior membranous walls of free-walled colonies (Fig. 46,*4a–c*; BOARDMAN, 1973; BLAKE, this revision). The presence of these delicate walls, added to the skeletal evidence, supports BORG's theory that the free-walled (double-walled) mode of growth found in many modern tubuliporates occurred also in the earliest known Bryozoa of Ordovician age and was the mode of growth for the great majority of Paleozoic taxa.

A third type of preserved indication of soft parts is skeletal and therefore has the potential for retaining living shapes of soft parts. These skeletal structures occur within zooecia

FIG. 46. Fossilized soft parts.——*1. Dittopora colliculata* (EICHWALD), Ord. (Wassalem Beds, D3), Uxnorm, Est.; granular brown deposit presumably reflecting generalized shape of feeding organs; long. sec., USNM 250079, ×50.——*2. Tetratoechus crassimuralis* (ULRICH), Maquoketa Gr., Ord. (Richmond.), Wilmington, Ill.; ring of 10 inwardly tapered wedges of brown granules interpreted as tentacles cut transversely by section; tang. sec., USNM 204872, ×150.——*3.* Heteroporid tubuliporate, rec., Pac. O.; tentacles cut transversely by section; tang. sec., BMNH specimen, ×150.——*4a–c.* Dendroid trepostomate, Waynesville F., Ord. (Richmond.), Hanover, Ohio; *a–c,* remnants of exterior membranous walls (arrows), brown granular deposit in generalized shape of feeding organs in *4a*; long. secs., USNM 179006, ×100.——*5. Leptotrypella? praecox* BOARDMAN, Horlick F., L. Dev., Ohio Ra., Antarctica, holotype; remnants of soft parts, probably an orificial-vestibular wall; long. sec., USNM 144807, ×200.——*6. Leptotrypella furcata* (HALL), Windom Mbr., Moscow F., Dev. (Erian), Menteth Cr., Canandaigua Lake, N.Y.; flask-shaped chamber containing granular brown deposits; long. sec., USNM 133901, ×100.——*7. Prasopora grayae* NICHOLSON & ETHERIDGE, Craighead Ls., Ord., Craighead Quarry near Girvan, Ayrshire, Scot.; flask-shaped chamber containing granular brown deposits; long. sec., RSM 1967-66-406, ×100.

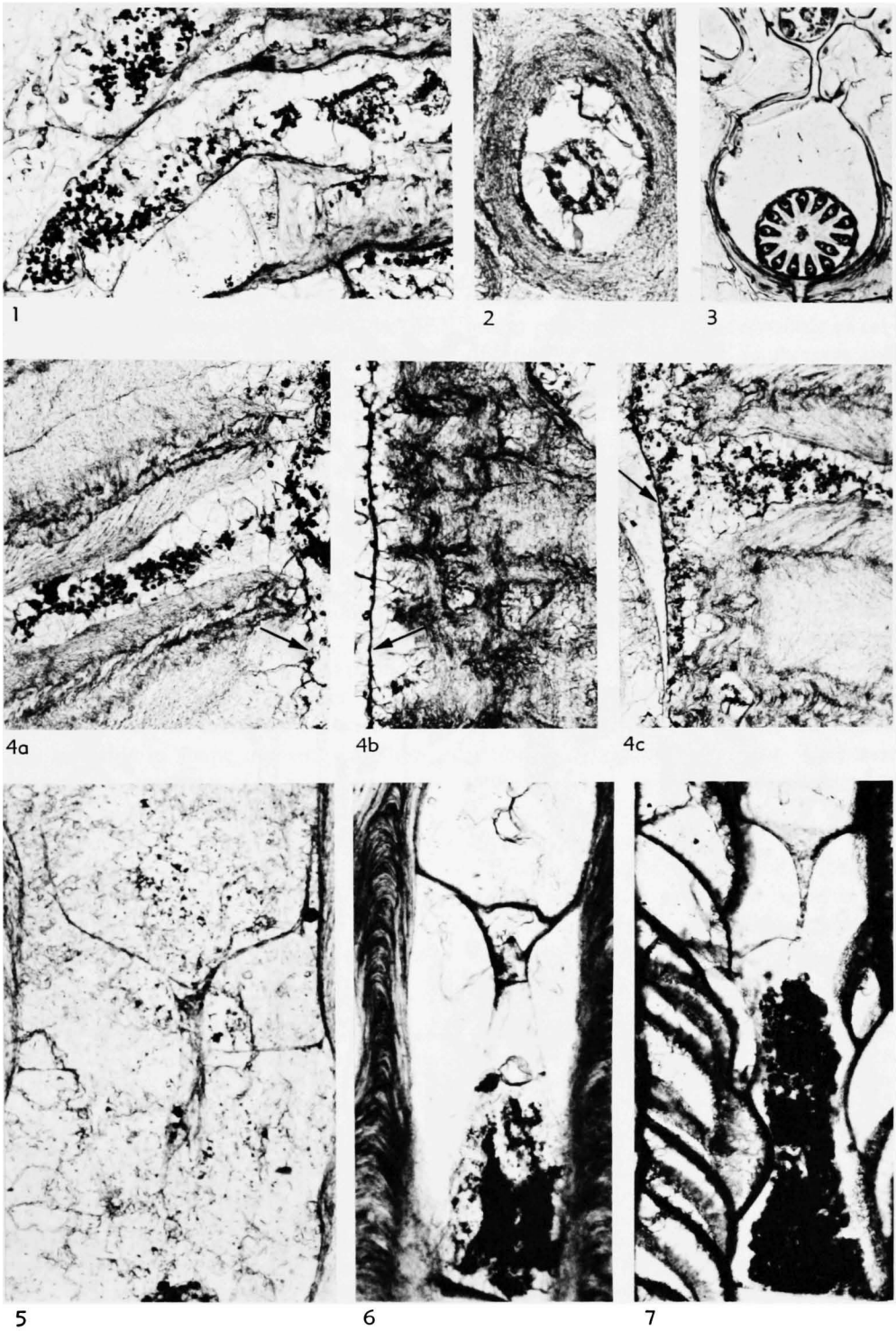


FIG. 46. *(For explanation, see facing page.)*

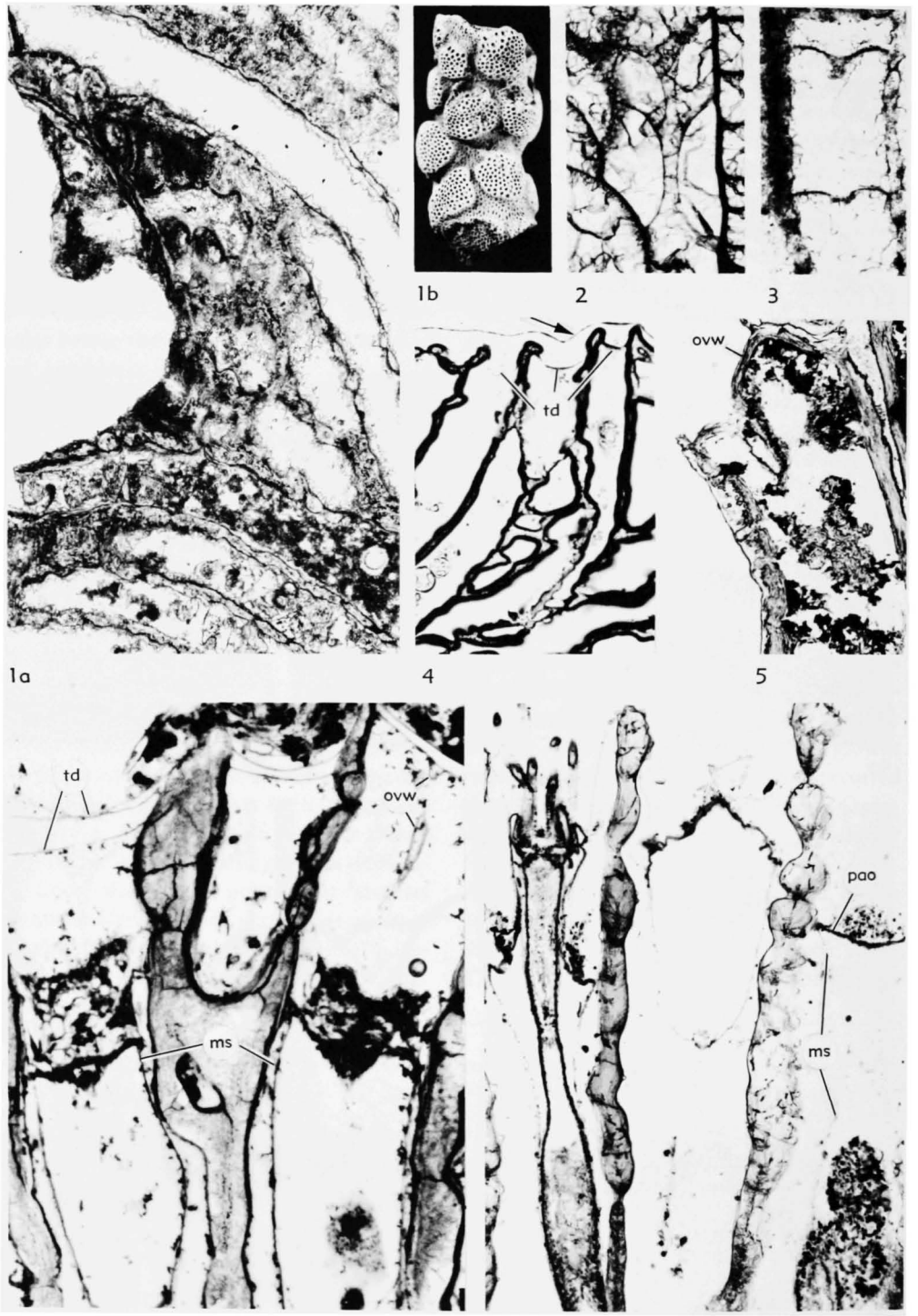


FIG. 47. *(For explanation, see facing page.)*

and generally form inner **flask-** or **funnel-shaped chambers** containing granular brown deposits (Fig. 43,*2*; 46,*6,7*). The calcareous laminae of the walls of the flask-shaped chambers continue into surrounding zooecial walls as do the laminae of other skeletal structures within zooidal chambers. The chambers are commonly floored by basal diaphragms and covered by terminal diaphragms.

CUMINGS and GALLOWAY (1915, p. 354) interpreted flask-shaped chambers to be products of degeneration. Walls of the chambers were thought to be new skeletal body walls housing the shrunken nonfunctional remains of the degeneration process. BOARDMAN (1971, p. 26), CORNELIUSSEN and PERRY (1973, p. 159), and UTGAARD (1973, p. 339) interpreted the walls of the chambers to be skeletal body walls of smaller regenerated intrazooidal polymorphs formed after the organs of the original feeding zooids had degenerated.

A third interpretation (BOARDMAN & MCKINNEY, 1976, p. 66) suggests that the flask shapes were not chambers, but were what they resemble in shape in living tubuliporates, that is, remnants of orificial-vestibular walls (Fig. 39) or membranous sacs (Fig. 44,*5*; 53,*3*) of normal feeding zooids in more or less retracted positions.

Evidence for the third interpretation begins with the discovery that in modern tubuliporates orificial-vestibular walls and membranous sacs retain their functional shapes during at least part of the degeneration process (Fig. 47,*6,7*). It is possible, therefore, that in taxa of Paleozoic age, orificial-vestibular walls, membranous sacs, and attachment organs could also have remained in place during part of the degeneration process. These organs then would have been nonfunctional and the zooids dormant so that loss of flexibility due to calcification would not be a problem. Calcification on these static membranes presumably occurred similarly to calcification of membranes of diaphragms and cystiphragms and would have been attached to calcified layers of enclosing zooidal walls in the same manner.

Further evidence for the degeneration hypothesis was found by WALTER and POWELL (1973) in a fixed-walled tubuliporate species of Jurassic age. Their specimens were interpreted to contain calcified orificial-vestibular walls (compare Fig. 39 and 47,*5*). Comparison with modern tubuliporates leaves no reasonable doubt that the calcified funnels in the Jurassic specimens are calcified orificial-vestibular walls, and that the walls had ceased to function in the feeding process. They were probably acting as terminal diaphragms to protect the living chambers after zooidal growth was completed.

Two skeletal structures similar in shape to orificial walls have since been found in the same zooecium of a tubuliporate species of Cretaceous age (Fig. 47,*3*). Considering the

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FIG. 47. Soft-part morphology.——*1a,b. Plethopora verrucosa* (HAGENOW), Cret. (Maastricht.), St. Pietersberg, Neth.; smaller polymorphs surrounding circular clusters of feeding zooids; *a*, long. sec., *b*, external view, USNM 250080, ×50.0, ×3.5.——*2. Prasopora simulatrix* ULRICH, Ord. (Trenton.), Trenton Falls, N.Y.; double-funneled flask-shaped chamber; long. sec., USNM 167685, ×100.0.——*3. Defranciopora neocomiensis* CANU & BASSLER, Cret. (Valangin.), Ste Croix, Switz., syntype; tops of two calcified funnels shaped like orificial walls; long. sec., USNM 250081, ×100.0.——*4. Disporella neopolitana* (WATERS), rec., 21 m, Medit. Sea, Plane, near Marseille, France; colony-wide membranous exterior wall (arrow) above degenerated zooids covered by membranous terminal diaphragms (td); long. sec., peel USNM 204876, ×50.0.——*5. Mesenteripora wrighti* HAIME, M. Jur., King's Sutton, Northamptonshire, Eng.; calcified orificial-vestibular wall (ovw) closing aperture of zooid; long. sec., OUM, Walford Coll., ×150.0.——*6. Disporella separata* OSBURN, rec., South Coronados Is., Baja Cal., Mexico; partly degenerated zooids with membranous terminal diaphragms (td), orificial-vestibular walls (ovw), and membranous sacs (ms); long. sec., USNM 167679, ×200.0.——*7. Neofungella* sp., rec., 133 m, off Victor Hugo Is., W. coast Palmer Penin., Antarctica; intact feeding zooid with tentacles partly protruded on left, partly degenerated zooid to right showing membranous sac (ms) and perimetrical attachment organ (pao) forming a flask-shaped chamber; long. sec., USNM 250082, ×100.0.

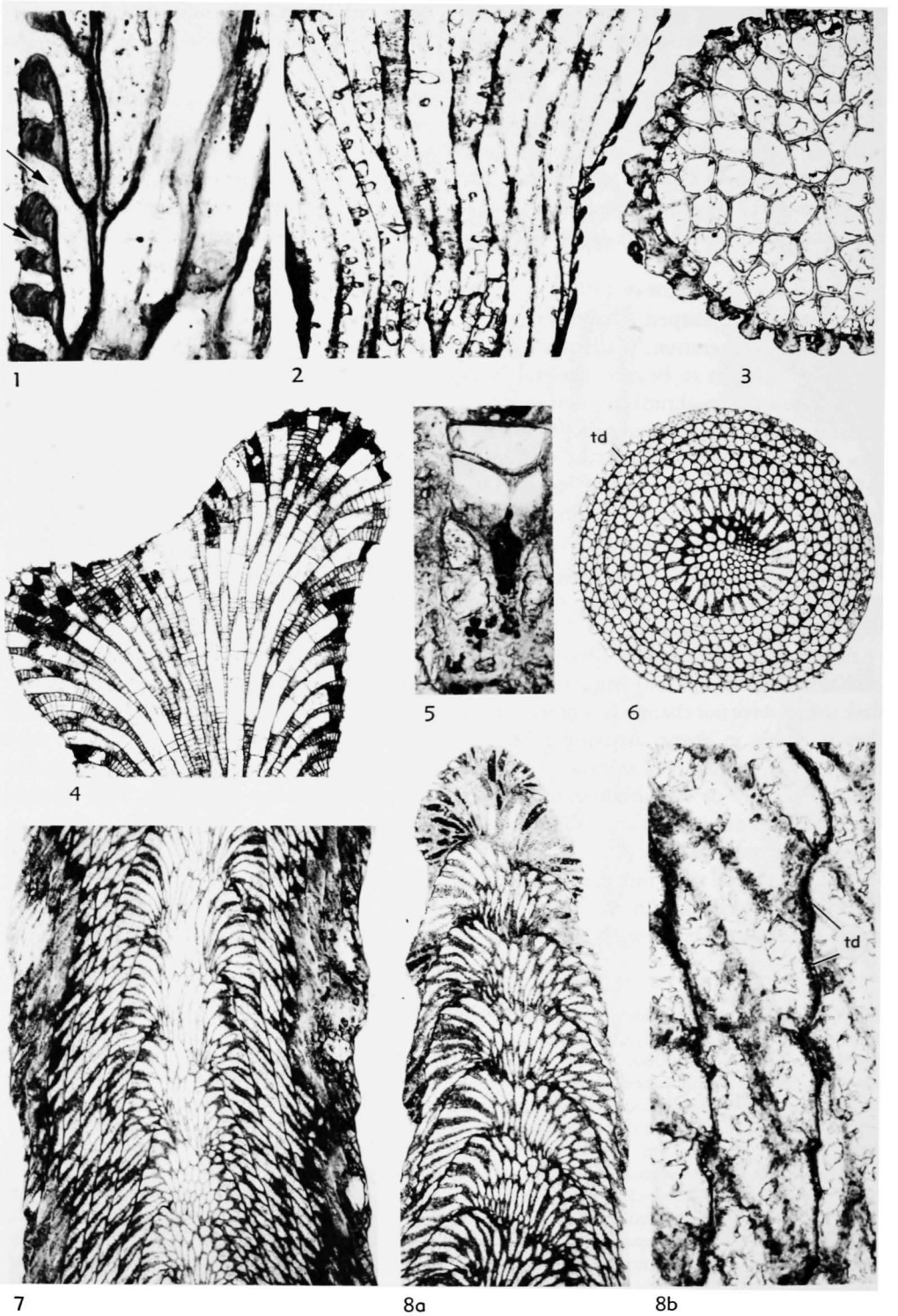

FIG. 48. *(For explanation, see facing page.)*

flexibility displayed in stenolaemates, the inner structure could well have functioned as a basal diaphragm for the organs of the next cycle represented by the outer structure.

The major difference between flask-shaped structures of Paleozoic and those of Jurassic age is that calcification took place on the outer sides of membranes that were originally either exterior or interior in Paleozoic colonies and on inner sides of exterior cuticle in Jurassic species. The Paleozoic flask-shaped walls were interior walls at the time of calcification and the Jurassic walls were exterior. In Jurassic fixed-walled species (Fig. 47,*5*), communication pores in the vertical walls provided the possibility, at least, for a continuing supply of nutrients within otherwise dormant zooids so that calcification within living chambers could occur. In most Paleozoic free-walled species communication pores are lacking. Body cavities and exterior membranous walls necessarily occurred outward from the membranes being calcified and nutrients presumed necessary for continued growth apparently came from other regions of the colonies through outer body cavities (Fig. 1; 46,*4a–c*). The exterior membranous walls were probably colony-wide (BOARDMAN & MCKINNEY, 1976, fig. 13), similar to the exterior wall in the dormant free-walled recent colony (Fig. 47,*4*).

It is not clear for most flask-shaped structures in Paleozoic colonies whether the walls of the flasks represent orificial-vestibular walls or the membranous sacs attached at their outer ends to form the flask shapes. Either possibility produces comparable shapes in some recent tubuliporates (compare Fig. 39,*3,5* with 53,*3*). Also, the best explanation for the occasional multiple funnels in Paleozoic colonies with mostly single-funnel flasks (Fig. 47,*2*) has been found in only one zooid of a recent tubuliporate (BOARDMAN, 1971, pl. 1, fig. 5a). In that single zooid a double orificial-vestibular wall developed a similar configuration to double funnels interpreted to be membranous in a Devonian specimen (BOARDMAN, 1971, pl. 1, fig. 2) and to the numerous multiple calcified funnels of Paleozoic age.

POLYMORPHISM

In stenolaemates many taxa have polymorphs and other taxa are entirely monomorphic, at least skeletally. Polymorphs may be isolated or contiguous with each other between feeding zooids and may be numerous enough to isolate feeding zooids from each other (Fig. 31,*7a,b*). Polymorphs can be arranged regularly (see Fig. 55,*4a,b*) or irregularly relative to feeding zooids. Polymorphs of one or more kinds may be clustered into maculae (see Fig. 59 and related text) surrounded by feeding zooids, or polymorphs may surround clusters of feeding zooids (Fig. 47,*1a,b*). Polymorphs cover reverse sides of colony branches or entire supporting stalks (Fig. 48,*1–3*). Intrazooidal polymorphism occurs where polymorphs

FIG. 48. Polymorphism.——*1.* Crisinid tubuliporate, rec., Philippines expedition of the Albatross, loc. D5559, coll. 1909; small pores (shorter arrow) and polymorphs (longer arrow) on left, feeding zooids open to right; long. sec., USNM 186566, ×150.0.——*2,3. Corymbopora menardi* (MICHELIN), Cret. (Cenoman.), Le Mans, Sarthe, France; small polymorphs on outside of main supporting stalks of zoarium, larger feeding zooids within stalk; *2,* long. sec., USNM 213332, ×30.0; *3,* transv. sec., USNM 213331, ×50.0.——*4,5. Hallopora elegantula* (HALL), Rochester Sh., Sil. (Niagar.), Rochester, N.Y.; *4,* mesozooecia indicated by closely spaced diaphragms and small cross-sectional areas, followed intrazooidally by larger feeding zooecia and widely separated diaphragms, long. sec., USNM 250083, ×7.5; *5,* flask-shaped skeletal structure in small exilazooecium, long. sec., USNM 250084, ×100.0.——*6–8. Terebellaria ramosissima* LAMOUROUX, Jur. (Bathon.), Ranville, France; *6,* spiral budding pattern and connected terminal diaphragms (td), transv. sec., USNM 250085, ×7.5; *7,* terminal diaphragms covering outer ends of zooecia in older part of colony, long. sec., USNM 250086, ×7.5; *8a,b,* tip showing zooecia growing proximally over older zooids in progressively younger cycles and zooecia from same colony with terminal diaphragms (td), long. secs., USNM 250087, ×7.5, ×50.0.

develop within zooecia of regular feeding zooids, either before or after zooids were capable of feeding.

Polymorphs vary widely in morphology and function in stenolaemates. Terms applied to differentiate kinds of polymorphs have been based primarily on soft-part morphology and assumed function in some modern tubuliporates (e.g., nanozooid, kenozooid, gonozooid), or skeletal morphology and position within the colony in both modern and fossil stenolaemates (e.g., dactylethra, firmatopore, nematopore, tergopore, mesozooecium, exilazooecium). Unfortunately, morphology and function together are not well enough known or defined for some of these terms to be used to advantage.

The term **kenozooid,** for example, was defined as a polymorph lacking lophophore and gut, muscles, and orifice (LEVINSEN, 1902, p. 3; 1909, p. v). BORG used the term for any polymorph that functioned as a rhizoid or spine (1926a, p. 239), or later (1933) for any smaller polymorph with aperture that was open or covered by a calcified terminal diaphragm regardless of its soft parts (Fig. 49,*8*) or possible function.

Dactylethrae (GREGORY, 1896, p. 12) are defined as aborted, shorted zooecia closed externally, as in the Jurassic genus *Terebellaria.* They have been interpreted as a type of kenozooid (e.g., BASSLER, 1953, p. G9; BROOD, 1972, p. 49). Sections of topotypes of the type species, *T. ramosissima,* suggest that they are zooecia of feeding zooids covered by terminal diaphragms forming continuous skeletal walls across apertures (Fig. 48,*6–8*).

Nanozooids (Fig. 49, *5–7,9*) are exceptionally well known both morphologically and functionally. Nanozooids were named and their soft parts described by BORG (1926a, p. 188, 232–239) from the recent genus *Diplosolen.* BORG reported a lophophore with a single tentacle, muscular system, reduced alimentary canal, membranous sac, and no reproductive structures. The single tentacles are relatively long and have been observed cleaning colony surfaces (SILÉN & HARMELIN, 1974).

In *Diplosolen,* nanozooids are restricted to an outer position in the colony and occur singly between feeding zooids (Fig. 30,*4*; 49,*5*). Nanozooids bud in distal confluent budding zones where the compound interior vertical walls of contiguous feeding zooids divide into two compound walls (Fig. 49,*5*). The outer walls of both feeding zooids and nanozooids are simple exterior frontal walls. The frontal wall of a nanozooid grows distally from its vertical wall, which is contiguous with the vertical wall of the proximal feeding zooid. The nanozooid tentacle protrudes through a small aperture in the frontal wall.

FIG. 49. Polymorphism.——*1. Meliceritites* sp., Cret. (Santon.), Coulommiers, France; two polymorphs in profile, which together form aviculariumlike structure in *3,4*; upper polymorph closed off by opercular shelf (os), lower polymorph apparently produced opercular shelf and large operculum (missing) hinged on frontal wall (fw); long. sec., USNM 216482, ×50.——*2–4. Meliceritites* sp., Cret. (Coniac.), Villedieu, France; *2,* opercular shelf (os) and living chamber (lc) of lower polymorph, frontal wall, and operculum removed by sectioning, tang. sec., USNM 216479, ×50; *3,* polymorph at zoarial surface minus operculum, external view, USNM 216477, ×30; *4,* polymorph with operculum in place, external view, USNM 216478, ×30.——*5. Diplosolen* sp., rec., Popoff Str., Alaska; budding position of nanozooid (nz) at division of interior vertical walls (vw) of two supporting feeding zooids; corresponding walls of distal supporting zooids where nanozooids not formed are parts of exterior frontal walls (fw); long. sec., USNM 250088, ×100.——*6. Plagioecia dorsalis* (WATERS), rec., 70 m, off Riou Is., Marseille, France; intrazooidal nanozooid formed subsequently in outer end of feeding zooid; long. sec., Harmelin Coll., ×200.——*7. Plagioecia* sp., rec., Pac. O. at La Jolla, Cal.; intrazooidal nanozooids with small apertures at outer ends; long. sec., USNM 250059, ×100.——*8.* Heteroporid tubuliporate, rec., Pac. O.; smaller polymorphs (pm) on either side of feeding zooid; long. sec., BMNH specimen, ×100.——*9. Diplosolen intricaria* (SMITT), rec., 200–235 m, 100 km N. of North Cape, in Barents Sea; sequence of growth of walls of feeding zooids (fz) and nanozooids (nz) at growing tip; buds (bd); long. sec., BMNH specimen, ×50.

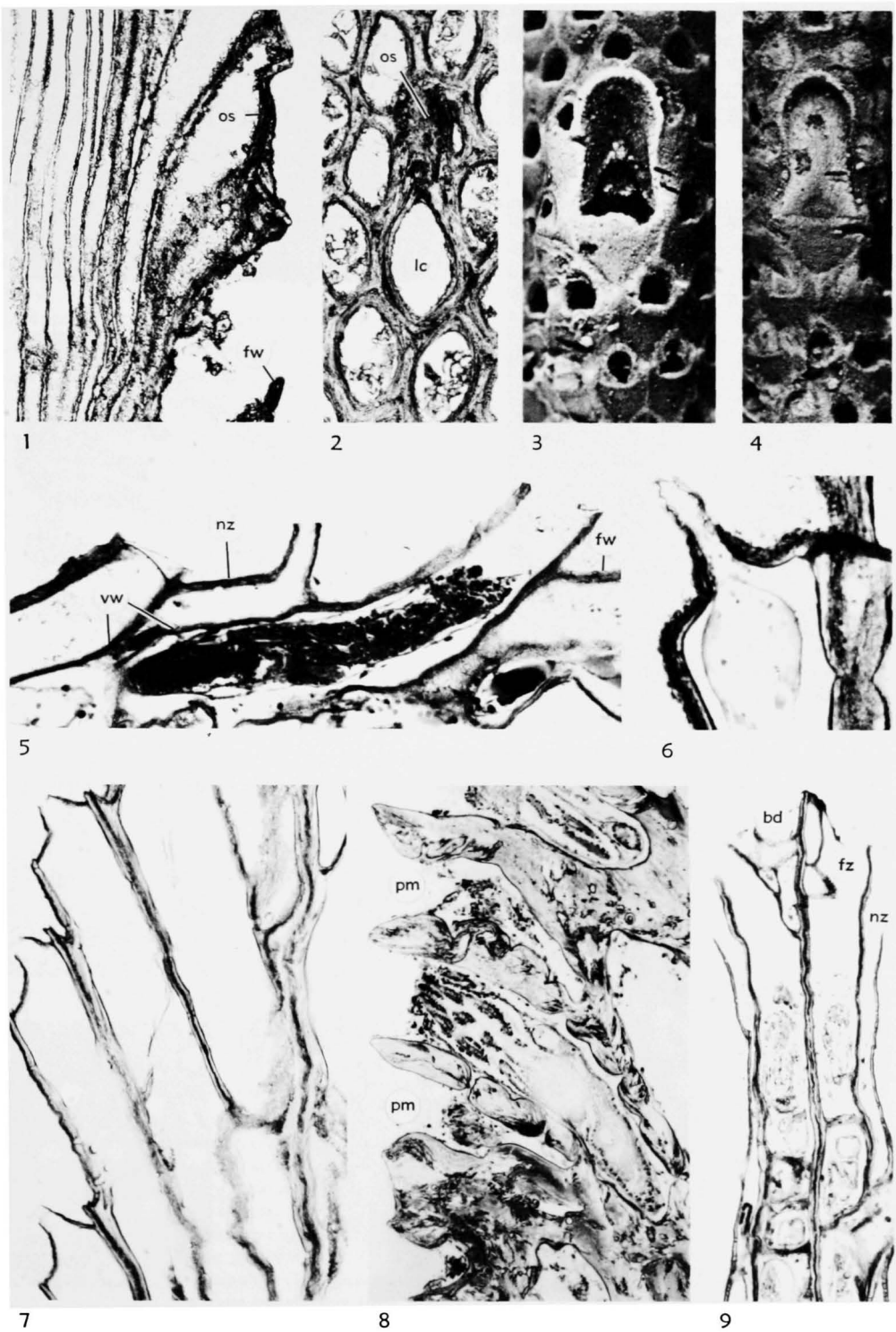

FIG. 49. *(For explanation, see facing page.)*

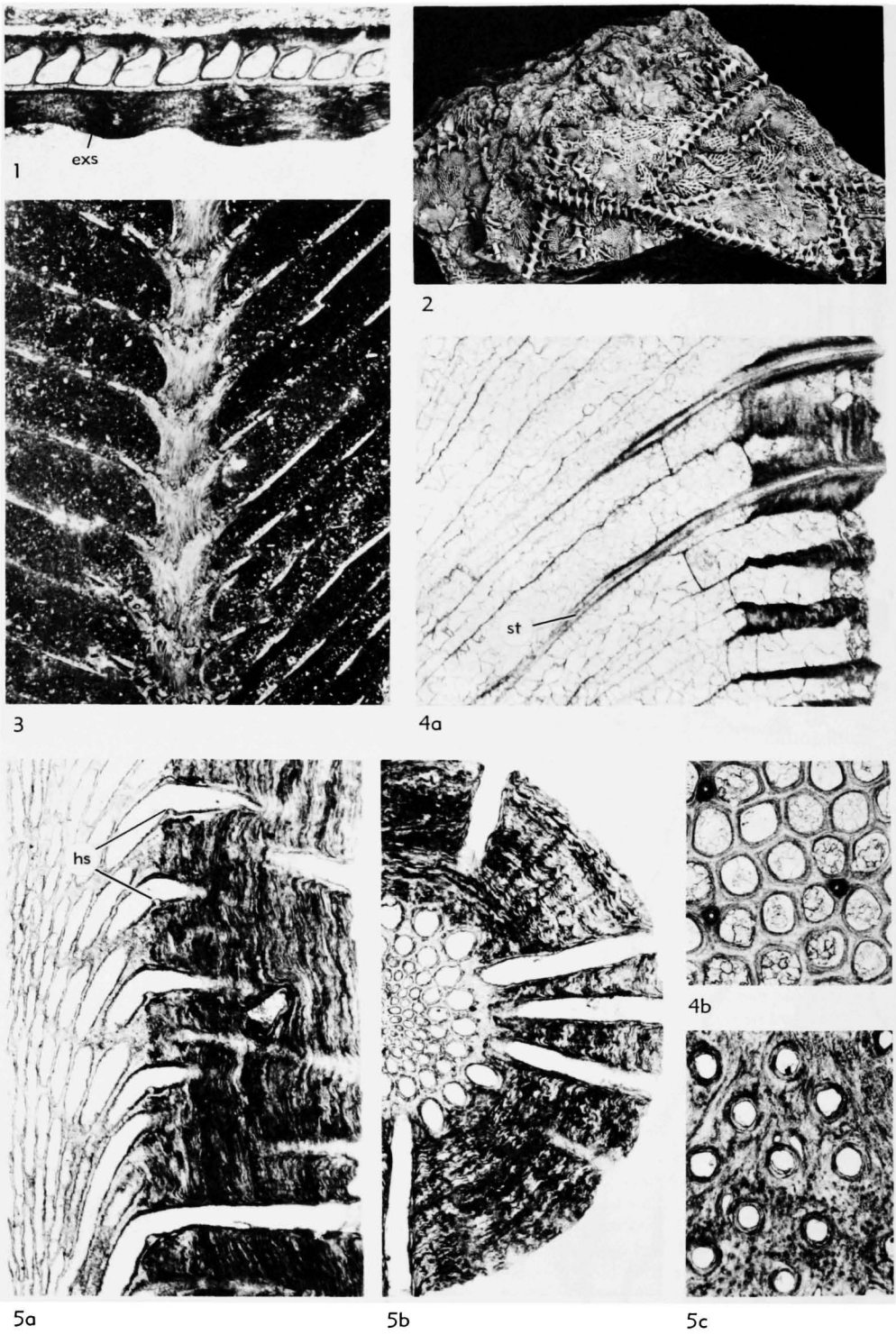

FIG. 50. *(For explanation, see facing page.)*

Two other types of nanozooids have been discovered (SILÉN & HARMELIN, 1974) in another genus, *Plagioecia*. The one of more general interest develops within the zooecium of a degenerated feeding zooid (Fig. 49,6,7) and is an example of intrazooidal polymorphism. An exterior frontal wall develops in the skeletal aperture of the feeding zooid much like a terminal diaphragm except that it contains the smaller aperture of the nanozooid.

Mesozooecia provide another example of intrazooidal polymorphism in a few of the many Paleozoic trepostomates in which they occur. Mesozooecia are skeletons of **mesozooids**, generally small, space-filling polymorphs between zooecia of feeding zooids in exozones. They are closely tabulated out to their distal ends (Fig. 42,*3*) so that no room is available for functional organs. In one group, the halloporids, zooids bud as mesozooids in endozones at growing tips, are transformed to feeding zooids intrazooidally (Fig. 48,*4*), and in later growth stages can revert to mesozooids.

Exilazooecium is a term used for skeletons of polymorphs in colonies of Paleozoic age that have few or no basal diaphragms in their chambers. The available chamber space allows for possible organs. A flask-shaped skeletal structure occurring in one of the few exilazooecia seen in the genus *Hallopora* (Fig. 48,*5*) suggests that at least some **exilazooids** did have functional organs.

In some species of the meliceritidis occur operculate polymorphs that superficially resemble the avicularia of cheilostomate Bryozoa (Fig. 49,*3,4*). Each polymorph occupies two enlarged zooidal spaces on colony surfaces in these species, and internally, at least two polymorphs were involved, one above the other. The more proximal polymorph grew a thickened interior vertical wall that covered the upper polymorph and functioned as an opercular shelf, apparently for the operculum to close against (os, Fig. 49,*1,2*). The operculum was hinged on the frontal wall (fs, Fig. 49,*1,3,4*) of the more proximal polymorph, so apparently was produced by the polymorph. These operculate tubuliporates are extinct and the function of the polymorphs is unknown.

EXTRAZOOIDAL PARTS

Parts of colonies formed outside of zooidal boundaries are considered either multizooidal or extrazooidal. Body cavities or walls that are formed outside of zooidal boundaries and subsequently become parts of zooids are termed multizooidal. Body cavities or structures that develop outside of zooidal boundaries and remain outside of those boundaries throughout the life of a colony are termed extrazooidal.

Extrazooidal parts occur in many stenolaemates and range from small spinelike skeletal growths between zooidal walls to structures that are virtually colony-wide. Because

FIG. 50. Extrazooidal parts.——*1. Archimedes wortheni* (HALL), Warsaw Ls., Miss. Warsaw, Ill., lectotype; extrazooidal skeleton (exs) on reverse side of fenestrate branch; long. sec., AMNH 7525, ×30.0. ——*2. Archimedes proutanus* ULRICH, Miss. (Chester.), Sloans Valley, Ky., syntypes; spiral axial supports of colonies surrounded by broken fronds of this and other species of fenestrates; external view, USNM 43737, ×0.5.——*3. Archimedes* sp., Miss. (Chester.), 19 km S. of West Lighton, Ala., near Fox Trap Cr.; section through a spiral extrazooidal support showing relationship with fenestrate fronds extending distally outward; long. sec., USNM 182789, ×4.0.——*4a,b. Dekayia aspera* MILNE-EDWARDS & HAIME, Fairmount Ls. Mbr., Fairview F., Ord. (Maysvill.), Covington, Ky.; *a,* beginning of style (st) in endozone, long. sec.; *b,* three styles cut transversely from same zoarium, tang. sec.; both USNM 250089, ×30.0. ——*5a–c. Pustulopora verrucosa* ROEMER, Cret. (Santon.), Crosz Bülten, Ger.; laminae of extrazooidal skeleton concave outward between zooecial walls and minute styles, hemisepta (hs); *a–c,* long., transv., tang. secs., all USNM 250090, ×30.0.

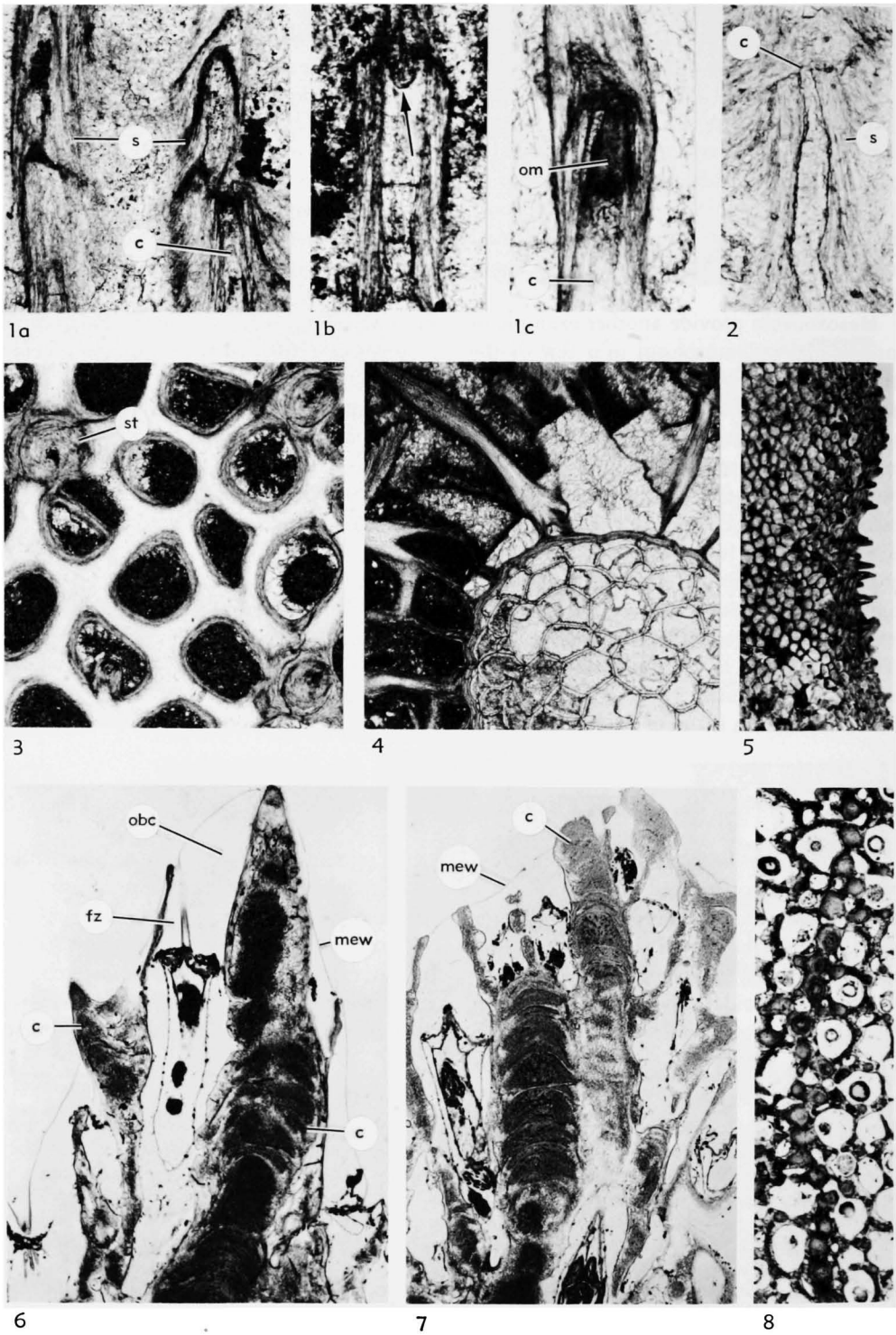

FIG. 51. *(For explanation, see facing page.)*

they are not parts of feeding zooids, their growth depends upon transfer of nutrients. Apparently most extrazooidal skeletal structures in stenolaemates are interior in origin; however, outer skeletal walls of extrazooidal brood chambers in many post-Paleozoic taxa are exterior walls. Interior extrazooidal parts are connected to zooids by outer body cavities protected by exterior membranous walls. The outer body cavities and exterior membranous walls opposite extrazooidal skeleton are also considered to be extrazooidal.

In some taxa, extrazooidal skeleton provides supports for erect colonies, for example on the reverse sides of free-walled unilaminate colonies such as recent hornerids (Fig. 28,*1a,b*) and Paleozoic fenestellids (Fig. 50,*1*), as cross supports to form fenestrules in some fenestrate growth, or as massive marginal (McKINNEY, 1977a) or axial (Fig. 28,*4*; 50,*2,3*) colony-wide supports in other fenestellids (see BLAKE, KARKLINS, UTGAARD, this revision, for many examples of extrazooidal skeleton).

In some taxa, extrazooidal skeleton intervenes between zooids in exozones, either in irregular patches, in spaces longitudinally along colonies distally, or completely surrounding the zooids. This intervening extrazooidal skeleton can be either vesicular or solid (Fig. 32,*5a,b*; 40,*3a,b*; 50,*5a,b*). The distinction between zooidal and extrazooidal skeleton is evident where microstructural boundaries of zooids are apparent (Fig. 32,*5a,b*). Where zooidal boundaries are not clearly indicated microstructurally, extrazooidal skeleton between zooids can be distinguished by reversals in orientation of laminae from convex outward in zooidal walls to concave outward in extrazooidal skeleton (Fig. 40,*3a,b*; 50,*5a–c*). The controlling criterion for distinguishing extrazooidal skeleton is that it was calcified by epidermis that cannot be associated with a particular zooid.

Styles (acanthopores of authors; acanthostyles of BOARDMAN & McKINNEY, 1976, p. 28; stylets of BLAKE, this revision) are elongate rodlike structures that form spinose projections on zoarial surfaces of many Paleozoic stenolaemates and at least one modern free-walled genus. Styles extend approximately parallel to zooecial walls and have their origin in exozones (Fig. 30,*1*), or less commonly in endozones (Fig. 50,*4a,b*). Styles form spinose projections throughout ontogenetic development and extend in length at growth rates comparable to or exceeding those of surrounding vertical zooidal walls.

Styles are interpreted to have had central skeletal cores in living colonies. The cores are nonlaminated in most taxa but may be laminated or a combination in some (Fig. 51). Cores are centered on zooecial boundaries or are surrounded by extrazooidal skeleton, and are considered to be extrazooidal. Nonlaminated cores are commonly continuous rods (BLAKE & TOWE, 1971) but in some taxa may be divided into segments by laminae from

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FIG. 51. Stenolaemate styles.——*1a–c. Leptotrypella? praecox* BOARDMAN, Horlick F., L. Dev., Ohio Ra., Antarctica, holotype; styles showing nonlaminated granular cores (c), laminated sheaths (s); *a*, ×100; *b*, laminated zooecial wall grown on broken style (arrow), ×200; *c*, organic matter (om) at end of core, followed by subsequent outward growth of style, ×200; all long. secs., USNM 144807.——*2. L.? praecox*, same data as *1* but paratype; broken style with core (c) extending beyond sheath (s); USNM 250091, ×200. ——*3. Polycylindricus asphinctus* BOARDMAN, Wanakah Sh. Mbr., Ludlowville F., Dev. (Erian), Elma, N.Y., holotype; large styles (st) with laminated cores; tang. sec., USNM 133916, ×50.——*4. Polycylindricus clausus* BOARDMAN, Centerfield Ls. Mbr., Ludlowville F., Dev. (Erian), Paines Cr., Cayuga Lake, N.Y., paratype; long styles with laminated cores; transv. sec., USNM 133922, ×30.——*5. P. asphinctus*, same data as *3* but Big Tree Shale Pit, Erie Co., N.Y.; surface expression of styles; USNM 158321, ×5.——*6–8. Densipora corrugata* MACGILLIVRAY, rec., 5-m wave-cut platform, Western Port Bay, W. end Phillip Is., Australia; *6*, styles with sparsely laminated cores (c) covered by membranous exterior walls (mew), outer body cavity (obc), feeding zooid (fz), long. sec., USNM 250092, ×100; *7*, styles with cores (c), membranous exterior wall (mew), long. sec., USNM 250071, ×100; *8*, ridge of large styles, tang. sec., USNM 250093, ×50.

surrounding sheaths or zooidal skeleton (BLAKE, 1973b).

Laminated sheaths surround the skeletal cores and in most taxa the sheaths are microstructurally continuous with adjacent zooecial walls or extrazooidal skeleton. Laminae of the sheaths bend outward against the cores to form cone-in-cone patterns (Fig. 51,*1a,2*), so that both cores and enclosing sheaths extend beyond zooecial walls to form spines on colony surfaces. Style sheaths in some taxa can be considered extrazooidal, but because of microstructural continuity with zooidal walls, sheaths in many taxa are not clearly either zooidal or extrazooidal.

Styles were first interpreted to have been hollow tubes during colony life, hence the term "acanthopore." More recently, authors have interpreted the cores as filled with skeletal material during life (e.g., TAVENER-SMITH, 1969b; ARMSTRONG, 1970; BROOD, 1970; BLAKE, 1973b). For recent interpretations of styles as hollow tubes and kenozooids during colony life, see ASTROVA (1971, 1973).

There is much evidence for the interpretation of style cores as skeletal in living colonies.

1. Styles are present as long spines beyond the ends of zooecial walls (Fig. 30,*1*; 51,*3–8*).

2. Laminae of sheaths extend outward against the cores of styles. Laminae are added to outer surfaces of sheaths as indicated by progressive thickening of sheaths toward the bases of styles and by structural continuity with surrounding zooidal walls or extrazooidal skeleton. A solid projecting core of some kind would appear necessary to deflect the depositing epidermis outward beyond zooidal walls to form the sheaths. In recent taxa, laminae surrounding demonstrable pores turn not outward but inward, into the pores relative to direction of thickening of surrounding wall (Fig. 35,*4*).

3. The microstructure of nonlaminated style cores is relatively constant, and it compares with the microstructure of such skeletal parts as most lunaria in cystoporates and zooecial walls of fenestellids. Microstructures of styles differ from those of fillings of adjacent abandoned chambers (Fig. 50,*4a,b*). In addition to being commonly nonlaminated, many cores contain minute pyrite crystals in varying proportions thought to be indications of organic-rich skeletal material. The chemical composition of the cores in two species of *Stenopora,* a trepostomate, is more complex than that of the secondary calcite of living chambers (ARMSTRONG, 1970, p. 584), presumably reflecting the differences in microstructure.

4. In well-preserved specimens of Devonian age containing membranous structures (BOARDMAN, 1971, p. 9), many styles were either broken or stopped growing for some less obvious reason. The outer ends of many cores of terminated styles contain brown material, suggesting a concentration of organic matter at core ends (Fig. 51,*1a,c*) and progressive calcification inwardly. Laminated skeleton of a vertical zooidal wall rests on the nonlaminated core of one broken style, which apparently was present when wall growth was renewed (Fig. 51,*1b*). Another style broke, leaving the core extending beyond the laminated sheath (Fig. 51,*2*).

5. Zoaria of Paleozoic age are commonly preserved in terrigenous mudstones or shales. Many styles are broken or worn off at zoarial surfaces. If they had been hollow tubes they would certainly have been routinely filled with terrigenous material after death, just as are open chambers of zooecia. Terrigenous material has not been observed in cores of styles by the author. (For contrasting observations, see ASTROVA, 1973, p. 7.)

Colonies of the recent free-walled tubuliporate genus *Densipora* develop sinuous ridges supported by single rows of large styles (Fig. 51,*6–8*). The styles consist mostly of laminated cores. Several smaller styles with granular cores occur at each zooecial aperture. Unfortunately, the zooecial walls appear granular rather than laminated and intergrowth relationships are not clear.

Sections of *Densipora* with soft parts intact provide some insight into the mode of growth

and function of styles in colonies of Paleozoic age. The styles of *Densipora* are part of the interior skeleton and are within the exterior membranous walls of the colonies (Fig. 51,*6,7*). In order to grow in length, styles throughout the history of the phylum necessarily have had epidermis and outer body cavity between their outer ends and exterior colony walls. With intervening body cavities there is no evidence that exterior colony walls could have been fastened to or held in place by styles, as has often been suggested.

The only suggested function of styles is to raise exterior membranous walls above zooecial apertures and skeletal surfaces. The raising of membranous walls (Fig. 39,*1*; 51,*6,7*) increases the volumes of outer body cavities and, presumably, colony-wide communication through those cavities. Outer body cavities obviously provided adequate communication in colonies of Paleozoic age that lacked both styles and communication pores in vertical walls. The apparent disappearance of styles when communication pores developed in post-Paleozoic stenolaemates, however, suggests that there might have been some communication advantage associated with styles.

MODE OF GROWTH, MORPHOLOGY, AND FUNCTION OF COLONIES

SEXUAL REPRODUCTION

Colonies are reportedly bisexual, in modern tubuliporates as in other bryozoan classes. Zooids within many colonies are also bisexual but apparently in some taxa are unisexual. Both male and female reproductive cells originate in the peritoneum of confluent budding zones. Both kinds of cells become attached to zooids and develop within body cavities (Borg, 1926a, p. 336–343).

Sperm cells begin multiplication inside membranous sacs of feeding zooids within a thin peritoneum attached to the funiculus near the inner end of the gut. In some species, concentrations of spermatozoa are large and expand outward along the gut (Fig. 44,*2*) or inward to the funiculus. Release of spermatozoa occurs through the ends of tentacles in at least two species of tubuliporates, a method of sperm release more generally observed in gymnolaemates (Silén, 1972). After the spermatozoa escape, zooidal feeding organs degenerate (Borg, 1926a, p. 336–341).

Eggs that do not become associated with zooids degenerate in confluent budding zones. Only one or two eggs attach to a single zooid and, within a colony, most of those also degenerate. In fertile zooids, eggs are surrounded by a thin peritoneum and begin development inside membranous sacs. In some species feeding organs of fertile zooids never fully develop and never become functional (Borg, 1926a, p. 410–416).

Eggs are fertilized internally, within the membranous sacs. How released sperm enter body cavities of maternal zooids is not known. Cross breeding is generally assumed. As soon as eggs are fertilized, the feeding organs of maternal zooids degenerate (Borg, 1926a, p. 412–419).

The embryology of modern stenolaemates is characterized by **embryonic fission (polyembryony)** in the species studied. One or rarely two primary embryos develop in a fertile zooid. Primary embryos divide to form secondary embryos, and in some species tertiary embryos are developed, presumably all with the same genetic makeup (Harmer, 1893). Embryonic fission counteracts the reproductive disadvantage of a small number of primary embryos and necessitates large brood chambers, some of which reportedly can hold as many as 100 embryos at one time.

Brood chambers are all coelomic cavities and have many forms and modes of development in tubuliporates. In many taxa they are single inflated polymorphs (gonozooids) large enough to accommodate the developing embryos (Fig. 52,*8*; Borg, 1926a, p. 345–

357; 1933, fig. 27). In many tubuliporates one or more fertile zooids give rise at their distal ends to large, highly inflated extrazooidal brood chambers on colony surfaces (Fig. 52,*5,7*; BORG, 1926a, p. 357–396). In some taxa middle segments of body walls of several adjacent fertile zooids are resorbed allowing eggs to escape into the space produced by the resorption (Fig. 52,*1*; BORG, 1933, fig. 28). In a few taxa these extrazooidal chambers formed by resorption can be floored by zooidal diaphragms and roofed by undisturbed outer ends of zooidal walls so that the chambers are not visible on colony surfaces (BORG, 1933, fig. 29).

The outer walls of extrazooidal brood chambers are simple calcified exterior walls in fixed-walled and many free-walled tubuliporates (Fig. 52,*3,4,6*). In some taxa of free-walled colonies the skeletal walls of brood chambers are interior walls with an outer body cavity and membranous exterior walls outward from the interior skeletal wall (Fig. 52,*1,5,7*; BORG, 1926a, fig. 92). Brood chamber apertures are developed for release of larvae (Fig. 52,*1,6–8*).

In Paleozoic stenolaemates skeletal indications of inferred brood chambers have been reported in a few taxa of two orders, the Cystoporata (see UTGAARD, this revision) and the Fenestrata (e.g., TAVENER-SMITH, 1966; STRATTON, 1975). In both orders the inflated chambers are skeletal blisters attached to outer ends of zooecia, similar in position to generally larger brood chambers of most post-Paleozoic tubuliporates.

Yet to be investigated is whether or not all modern tubuliporates have large gonozooids or brood chambers, and if not, whether they undergo polyembryony. If it were found that large brood chambers are necessary to accommodate the multiple embryos resulting from polyembryony, as it would seem, fossil taxa such as most Paleozoic species that lack skeletal indications of comparably large chambers could be assumed to have not undergone polyembryony in their reproductive cycles.

According to NIELSEN (1970), the released larvae are rounded, radially symmetrical, lack a gut, and are ciliated. They swim for a short period, apparently measured in minutes to a few hours. At metamorphosis, a posterior evagination produces an adhesive organ in contact with the substrate and an anterior evagination brings the exterior cuticle to the surface. The ciliated outer layer is turned inward by the evaginations and the ciliated cells disintegrate. The exterior cuticle covers the body, calcification begins on the inner sides of the body, and the basal disc of the first adult member of the colony, the ancestrula, is formed.

The ancestrula, the primary zooid of stenolaemate colonies (Fig. 25, 26), generally begins with an encrusting hemispherical or disc-shaped body (Fig. 52,*2*). Basal discs have exterior walls consisting minimally of an outermost cuticle, epidermis, and peritoneum.

FIG. 52. Brood chambers.——*1. Lichenopora* sp., rec., "Crab Ledge," E. of Chatham, Mass.; feeding zooid (fz), extrazooidal brood chamber (bc) with embryos in sac (es), interior skeletal wall (isw), and brood chamber aperture (bca); long. sec., USNM 250094, ×100.——*2.* Tubuliporid tubuliporate, rec., Manomet Pt., Cape Cod Bay, Mass.; young colony showing basal disc (bd) of ancestrula; sec. parallel to encrusting colony base, USNM 250095, ×30.——*3. Densipora corrugata* MACGILLIVRAY, rec., 5-m wave-cut platform, Western Port Bay, W. end Phillip Is., Australia; feeding zooid in middle of brood chamber, which has exterior outer walls (ew); long. sec., USNM 250093, ×100.——*4. Plagioecia sarniensis* (NORMAN), rec., 28–30 m, Medit. Sea off Riou Is., Marseille, France; brood chamber, its exterior outer wall (ew), and aperture (bca); long. sec., USNM 250096, ×150.——*5. Hornera* sp., rec., Poor Knights Is., N.Z.; extrazooidal brood chamber with interior skeletal wall (isw) on reverse side of colony, feeding zooids (fz); long. sec., USNM 250097, ×50.——*6. Mecynoecia delicatula* (BUSK), rec., 28–30 m, Medit. Sea off Riou Is., Marseille, France; brood chamber with exterior wall (ew) and aperture (bca); long. sec., USNM 250073, ×50.——7. *Hornera* sp., rec., Flinders Is., Vict., Australia; brood chamber showing pattern of interior skeletal wall and aperture in upper right center, centered on fenestrule; exterior view, USNM 250098, ×7.5.——*8. Crisia* sp., rec., low-tide level, Eng. Channel, Roscoff, France; brood chamber with aperture (bca) and exterior walls; long. sec., USNM 250099, ×100.

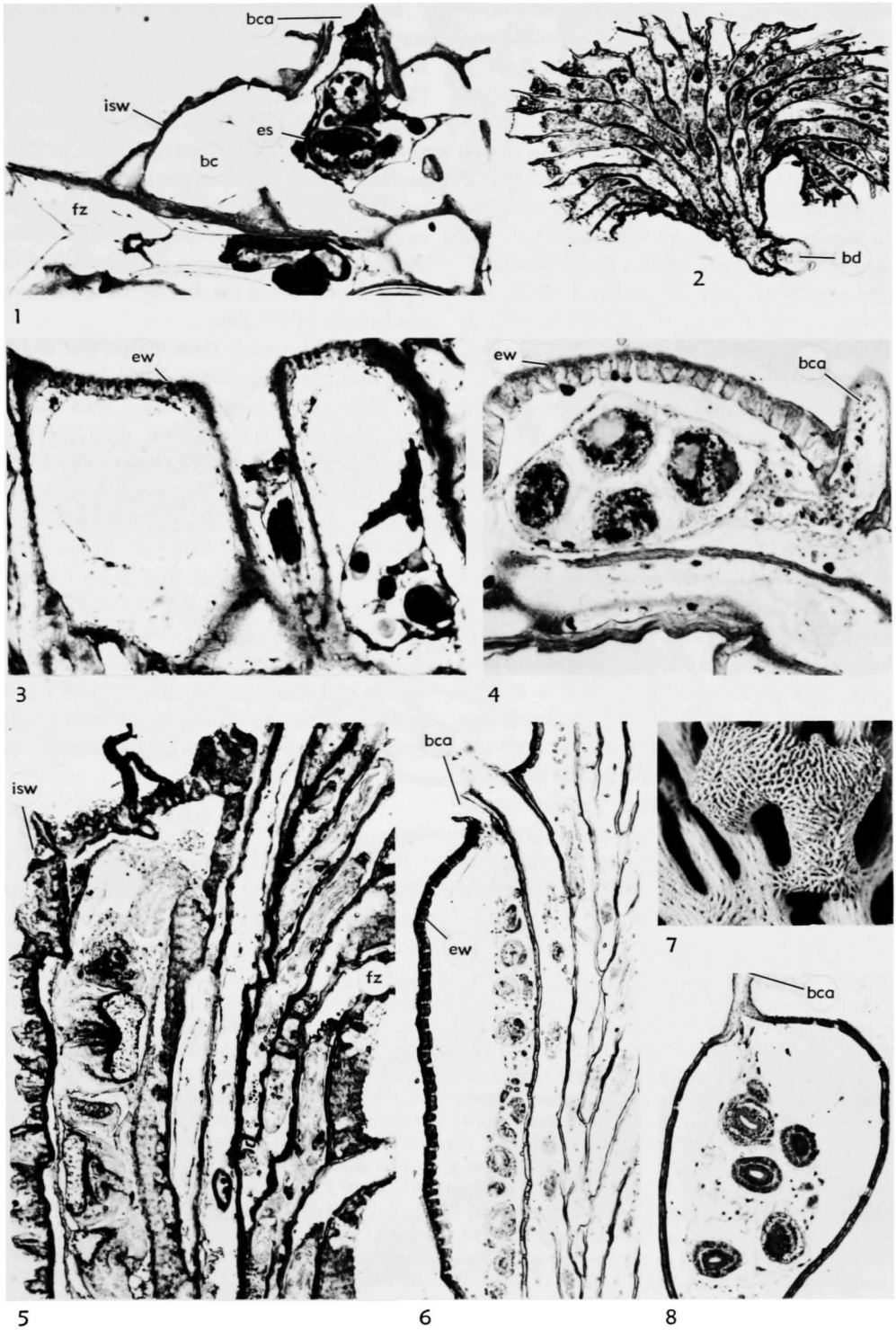


FIG. 52. *(For explanation, see facing page.)*

Most basal discs also have a skeletal layer (Fig. 53,*1,3,7*) calcified by the epidermis from within the disc. The skeletal layer is simple, that is, calcified on its growing edges and inner surfaces only.

The basal disc is generally larger in diameter than the diameter of the distal extension of the ancestrula and the diameters of living chambers of associated feeding zooids. In some Paleozoic species, however, the proximal part of the disc is smaller and may be nearly pointed (Fig. 53,*2*; BOARDMAN & MCKINNEY, 1976, pl. 7, fig. 3; CUMINGS, 1912, pl. 19, fig. 3, 4, 11, 12).

Continued growth of the simple exterior wall of the disc does not complete the skeleton of the ancestrula, but extends the wall laterally to produce the encrusting basal wall of the colony in most taxa (Fig. 25; 26; 53,*3,6,7*). The ancestrula is completed distally by skeletal body walls that are either simple and exterior as in the uniserial corynotrypids (Fig. 31,*1,2*; BOARDMAN & CHEETHAM, 1973, fig. 33A, B), compound and interior (Fig. 25; 53,*1,4,6,7*) or a combination (Fig. 26; 53,*3*). (Compound walls are calcified on edges and both sides and are, therefore, necessarily interior walls that partition existing body cavity.) The few ancestrulae of preserved colonies studied contain a feeding lophophore and gut, which retract down into the basal disc (Fig. 53,*3*; NIELSEN, 1970).

In at least some taxa of the order Fenestrata, the encrusting wall of the basal disc is reportedly not calcified from inside the disc (TAVENER-SMITH, 1969a; GAUTIER, 1972). As reconstructed, a circular flap of ectodermal epithelium (TAVENER-SMITH, 1969a, p. 295) projected from the aperture of the basal disc and folded over so that the flap rested on the exterior cuticle of the outer surface of the disc. A calcified layer was then deposited on the outer surface of the disc by the ectodermal epithelium of the flap.

It should be made clear that in this reconstruction, the hypothesized flap has to be a complete exterior membranous wall enclosing body cavity. It is assumed, therefore, that the folding places the exterior cuticles of the basal disc and flap back to back (questioned by GAUTIER, 1972). The skeletal wall of the disc is here interpreted to be an exterior wall, equivalent to the basal colony wall folded over on top of the basal disc in a lichenoporid (left basal side, Fig. 25). The distal neck of the ancestrula and skeletons of subsequent zooids and extrazooidal structures of fenestrates are interior in origin, surrounded by epidermis and body cavity on all sides.

ASEXUAL GROWTH

The aperture of the basal disc of the ancestrula is covered by an exterior membranous wall consisting of an outermost cuticle and

FIG. 53. Ancestrulae.——*1,2. Orbipora distincta* (EICHWALD); *1,* Kuckers Sh., Ord. Kohlta, Est., basal disc (bd), encrusting colony wall (ecw), primary wedge to right, secondary wedge to left, long. sec., USNM 250100, ×30; *2, Echinospherites* Ls., Ord., Reval, Est., exterior view of underside of zoarium showing small, nearly pointed basal disc, USNM 250101, ×4.——*3.* Fixed-walled tubuliporate, rec., Popoff Str., Alaska; ancestrula with feeding organs surrounded by membranous sac (ms) and retracted into basal disc (bd), perimetrical attachment organ (pao), distally wall of basal disc connected to encrusting colony wall (ecw), outer walls of ancestrula both exterior (ew) and interior (iw); long. sec., USNM 186542, ×150. ——*4,5. Eridotrypa briareus* (NICHOLSON), Ord. (Trenton.); *4,* Cynthiana F., ancestrula (a), notch or fold, which initiates secondary wedge (n_2), direction of growth of secondary wedge (arrow), exterior encrusting wall of secondary wedge (ew), long. sec., USNM 250102, ×50; *5,* Catheys Ls., 3.2 km SE. Mt. Pleasant, Tenn., ancestrula (a), notch or fold of secondary wedge (n_2), exterior encrusting wall folded over (ew), direction of growth of secondary wedge (arrow), deep sec. parallel to encrusting colony wall, USNM 250103, ×50.——*6–8. Lichenopora* sp., rec., Galapagos Is.; ancestrula (a), basal disc of ancestrula (bd), exterior wall of ancestrula (ewa), notch or fold of primary wedge of zooids (n_1), notch or fold of secondary wedge of zooids (n_2), direction of growth of secondary wedge (arrow), exterior encrusting colony wall (ecw), exterior encrusting colony wall of secondary wedge (ew_2, ecw_2), feeding zooids (fz), polymorphs (pm), vertical walls (vw); *6,* long. sec., ×75, *7,* long. sec., ×300, *8,* deep sec. parallel to encrusting colony layer, ×100, all BMNH specimens.

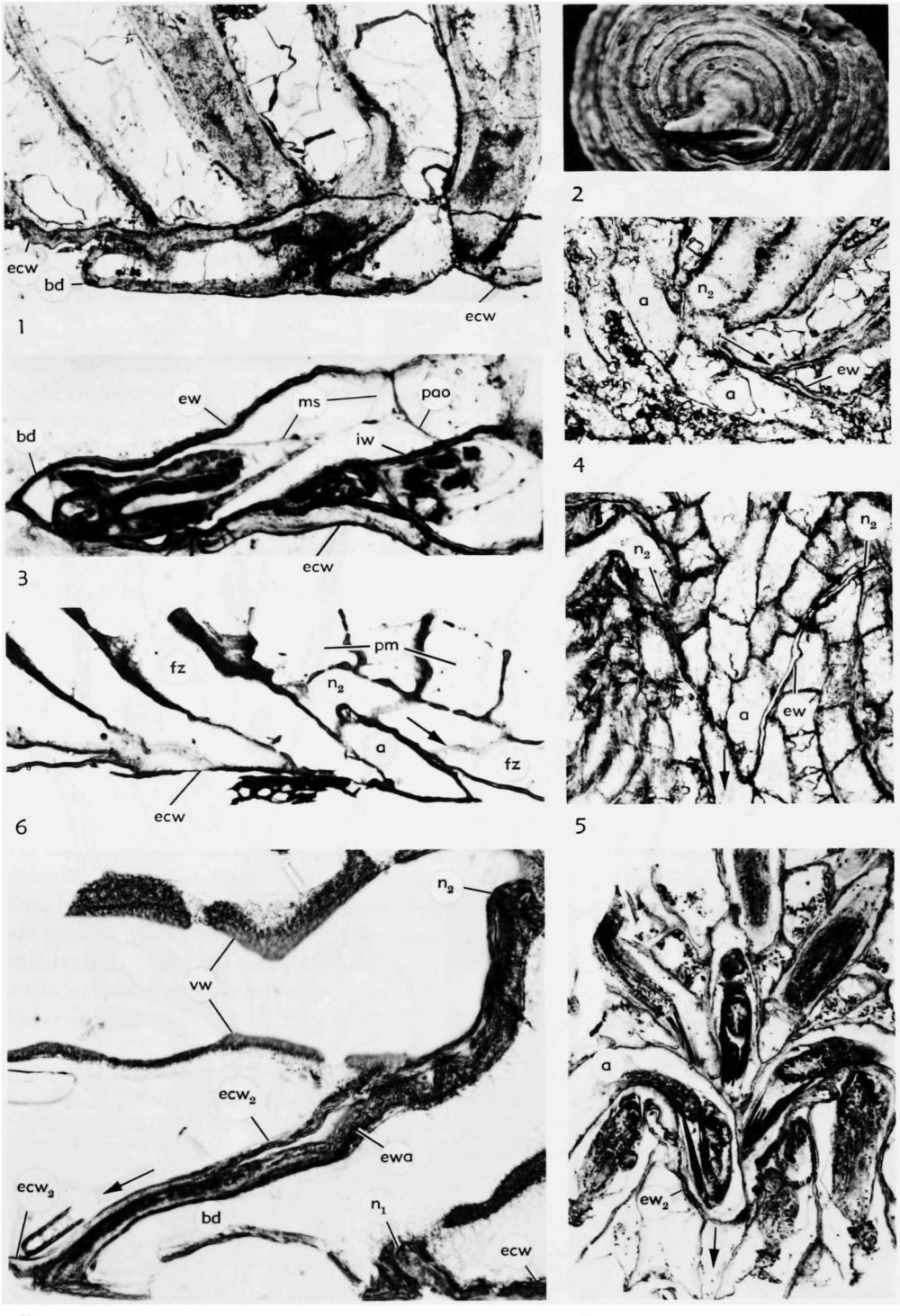


FIG. 53. *(For explanation, see facing page.)*

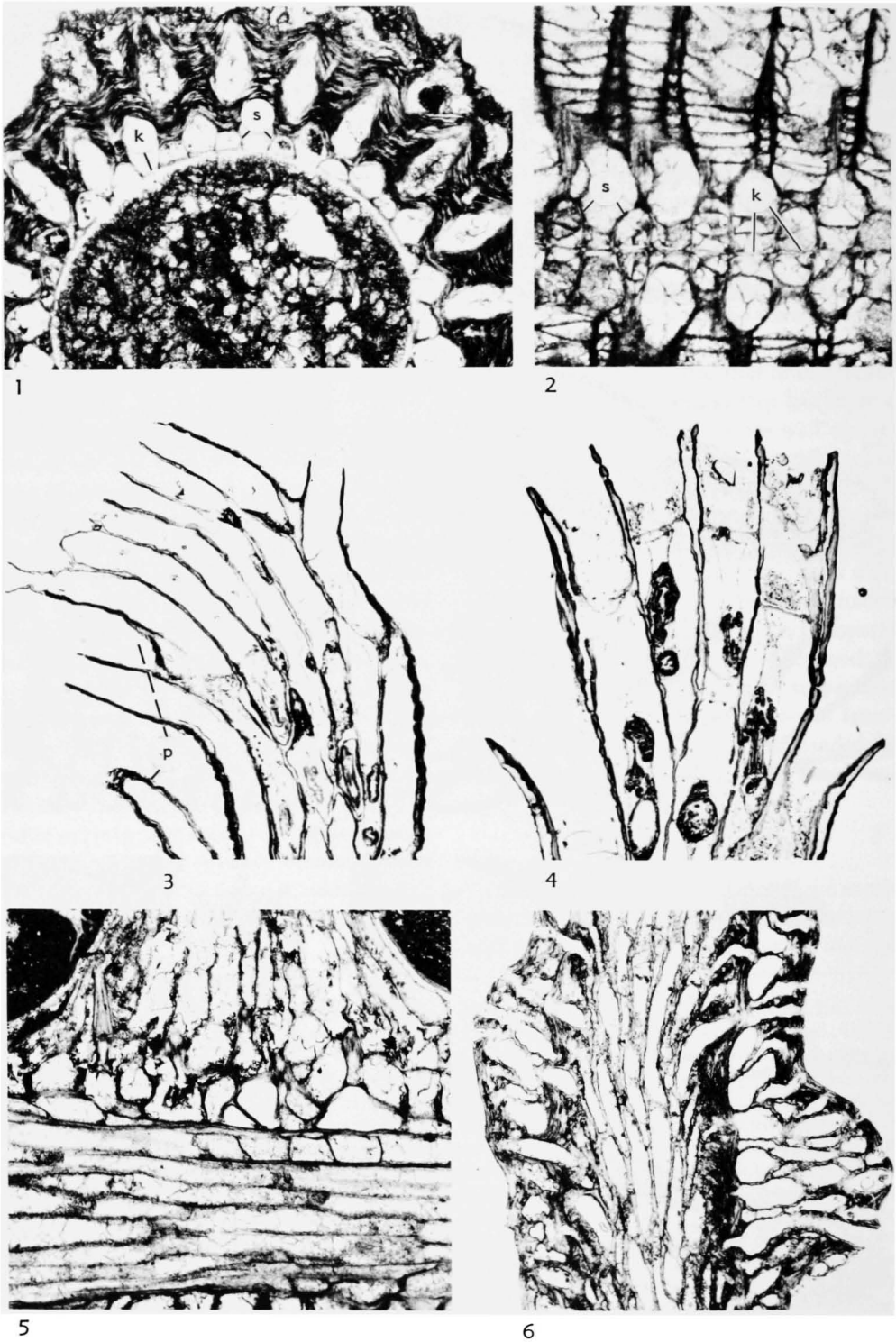


FIG. 54. *(For explanation, see facing page.)*

epidermis. The cuticle is expanded from within itself by multiplying epidermal cells, and this growing cuticle apparently is present in all exterior walls.

Zooidal wall development and confluent budding zones.—In stenolaemate bryozoans, asexual reproduction of zooids (**budding**) begins by the growth of interior vertical walls into existing confluent body cavities. Interior vertical walls of buds are initiated by localized growth produced by infolding into existing body cavity of epidermal cell layers from established skeletal surfaces (BORG, 1926a, p. 322). Skeletal layers of vertical walls (and the entire skeleton of stenolaemate colonies) are, therefore, secreted on outer sides of the epidermis and are exoskeletal throughout. (For an endoskeletal interpretation of vertical wall growth, see Ross, 1976.)

Vertical walls of buds grow from: (1) encrusting basal walls of colonies that are exterior and multizooidal in origin (Fig. 25; 39,*5*), (2) erect walls of colonies that are exterior and multizooidal in origin (reverse walls of many unilaminate colonies; Fig. 26; 28,*5,6*), (3) erect walls of colonies that are interior and multizooidal (median walls of bifoliate colonies, Fig. 30,*1,3a*; possibly reverse walls of some unilaminate colonies), (4) walls of zooids that are interior (dendroid colonies, Fig. 48,*4*; some unilaminate colonies, Fig. 28,*1a,b*), (5) extrazooidal parts that are interior (few cystoporates, see UTGAARD, this revision), and (6) peristomes of fixed-walled zooids that are exterior (few tubuliporates, HARMELIN, 1976, fig. 7).

Most budding is interzooidal, that is, it occurs outside of living chambers of zooids. Buds commonly are centered on growing edges or corners of interior vertical zooidal walls that are necessarily shared by 2 to 4 older supporting zooids. The growing edges of vertical walls of buds and contiguous supporting zooids are grown cooperatively and advance evenly into confluent budding spaces. Therefore, these buds never occupy spaces within living chambers of supporting zooids, regardless of whether the buds are centered on walls or centered on the living chamber of older zooids on encrusting colony walls. In the great majority of taxa, therefore, buds can not be related to single parent zooids.

Intrazooidal budding does occur where buds develop from within established living chambers of single supporting zooids. The budding of subcolonies in some multilaminate stenolaemates (HILLMER, 1971, p. 27, fig. 4, 5, 25, 26) is an example. (For a different concept of intrazooidal budding, see MCKINNEY, 1977b.)

Exterior membranous walls and enclosed confluent body cavities precede budding distally, apparently in all but uniserial stenolaemates. Confluent budding spaces connect body cavities of a few to many existing buds or combinations of buds and zooids. The entire confluent budding zone (apparently the common bud of authors) includes the confluent body cavity, enclosing membranous exterior walls, and any exterior multizooidal basal wall that is present (Fig. 25; 26; 39,*5*).

Confluent multizooidal budding zones

FIG. 54. Asexual growth.——*1. Ceramophylla vaupeli* (ULRICH), Ord. (Eden.), Brown Street, Cincinnati, Ohio, paralectotype; sinuses (s) and keels (k) in recumbent endozones on basal colony walls of hollow-branched zoarium; transv. sec., USNM 245040, ×30.——*2. Peronopora decipiens* (ROMINGER), Corryville Mbr., McMillan F., Ord. (Maysvill.), Cincinnati, Ohio, lectotype; sinuses (s) and keels (k) developed irregularly from median wall; transv. sec., UMMP 6676-3, ×50.——*3. Mecynoecia delicatula* (BUSK), rec., 35 m, Grand Salaman, Marseille, France; growing tip of branch of fixed-walled colony with feeding zooids opening into confluent budding space, peristomes (p); long. sec., Harmelin Coll., ×50.——*4. Cinctipora elegans* HUTTON, rec., 110 m, off Otago Heads, South Is., N.Z.; growing tip of branch of free-walled colony with confluent zooidal budding zone; long. sec., USNM 250064, ×30.——*5. Polycylindricus clausus* BOARDMAN, Centerfield Mbr., Ludlowville F., Dev. (Erian), Paines Cr., Cayuga Lake, N.Y.; secondary branch (projecting upward) grown from exozone of supporting branch without an overgrowing basal encrusting wall; long. sec., USNM 250104, ×20.——6. Free-walled tubuliporate, Paleocene, Vincentown, N.J.; secondary branch to right; long. sec., USNM 250105, ×30.

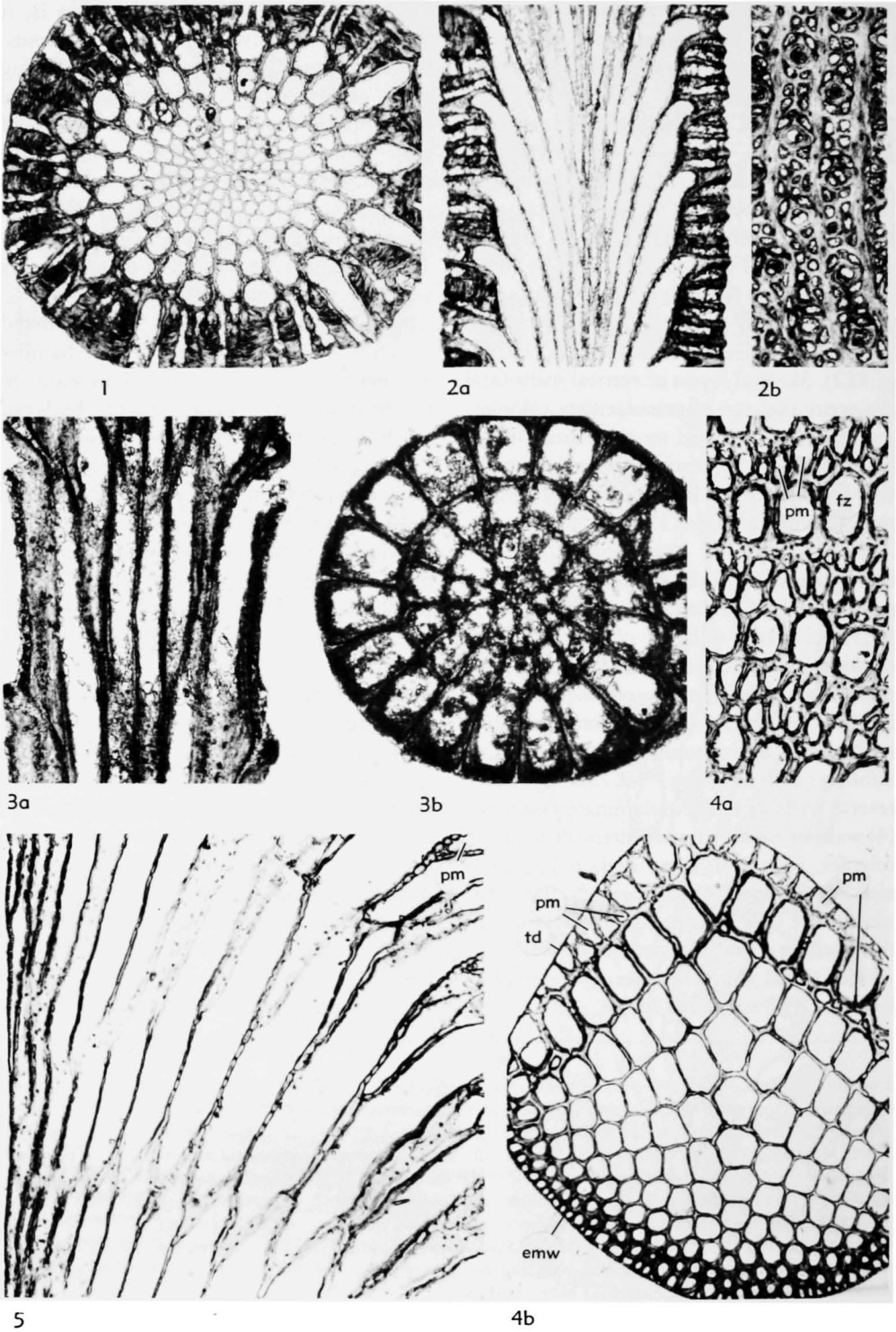


FIG. 55. *(For explanation, see facing page.)*

occur opposite endozones that contain only buds (Fig. 32, 33). The confluent budding space and enclosing exterior walls originate and are at the time of budding outside of zooidal boundaries. As colony growth proceeds and budding zones advance distally, proximal parts of confluent multizooidal budding spaces and enclosing walls become parts of zooids.

Confluent zooidal budding zones occur where buds are interspersed with fully developed zooids (Fig. 54,*3,4*). The budding zone is considered zooidal because the available confluent spaces and enclosing exterior walls are parts of established zooids (Fig. 37) before budding begins. As buds develop, the interspersed zooids share the expanding confluent space with the intervening buds. The relative concentrations of fully developed zooids and buds in distal budding zones can be determined by zooecial patterns in sections cut through more proximal parts of many colonies.

Buds develop in endozones from basal encrusting walls of both free- and fixed-walled colonies and grow into multizooidal body cavities, which are peripherally confluent around margins of colony bases (Fig. 25; 39,*5*; 60,*1–4*).

In free-walled colonies, growing regions of both endozones and exozones are potential budding zones because outer body cavities are confluent over both regions. Budding in exozones generally occurs in confluent zooidal spaces because zooids are fully developed there and all confluent spaces are either parts of zooids or are extrazooidal (Fig. 25). Endozonal budding occurs in multizooidal budding zones in distal ends of erect parts of some taxa of free-walled colonies of unilaminate (Fig. 55,*4,5*), bifoliate (Fig. 54,*2*), and dendroid (Fig. 50,*5a,b*; 55,*1,2*) growth habits. Endozonal budding occurs in zooidal confluent budding zones containing interspersed feeding zooids and buds in the distal ends of erect free-walled colonies of some unilaminate (Fig. 30,*2*) and dendroid (Fig. 54,*4*; and possibly Fig. 48,*4*) taxa.

In fixed-walled colonies, confluent budding zones and budding occur only in the most distal regions of colonies, at growing margins and tips. Most budding in fixed-walled colonies, therefore, occurs in endozones and not in exozones. In some taxa of erect fixed-walled colonies, buds are grouped at distal ends and grow into multizooidal budding spaces (Fig. 26; 30,*3a*; 33,*2*; 36,*4a,b*; 41,*5c*; 55,*3a,b*). In other fixed-walled taxa buds are interspersed with established feeding zooids and grow into zooidal budding spaces (Fig. 54,*3*).

Zones of astogenetic change.—The ancestrula and the one to several asexually produced generations of founding zooids commonly differ morphologically from more distally placed zooids. Some of these differences are sequential by generation, are not entirely assignable to ontogeny or polymorphism, and are generally too constant from colony to colony of the same species to be interpreted as microenvironmental in origin. These sequential differences occur as regular developmental features of colonies and, therefore, are assumed to be expressions of astogeny.

The sequential changes of the earliest generations of a colony provide a morphologic transition between the single ancestrula and the complex of zooids and extrazooidal structures that are either repeated or continued

FIG. 55. Zooidal patterns.——*1,2. Petalopora* sp., Cret. (Coniac.), Villedieu, Loire-et-Cher, France; *1*, zooecia arranged radially, grown from multizooidal budding zone around branch axis, transv. sec., USNM 216468, ×30; *2a,b*, polymorph small tubes in exozones, *a*, long. sec., *b*, polymorphs and feeding zooecia of same zoarium cut transversely, tang. sec., both USNM 250106, ×30.——*3a,b. Spirentalophora* sp., Cret. (Coniac.), Villedieu, Loire-et-Cher, France; spiral zoarial pattern, budding at axis into multizooidal budding zone; *a,b*, long., transv. secs., USNM 213321, ×50.——*4,5. Tennysonia* sp., rec., Algoa Bay, S. Afr.; feeding zooecia (fz) budded from exterior multizooidal wall (emw) on reverse side of zoarium, small polymorphs (pm) bud in outer exozone, apertures of polymorphs covered by terminal diaphragms (td); *4a,b*, tang., transv. secs., USNM 216467, ×30; *5*, long. sec., USNM 216466, ×30.

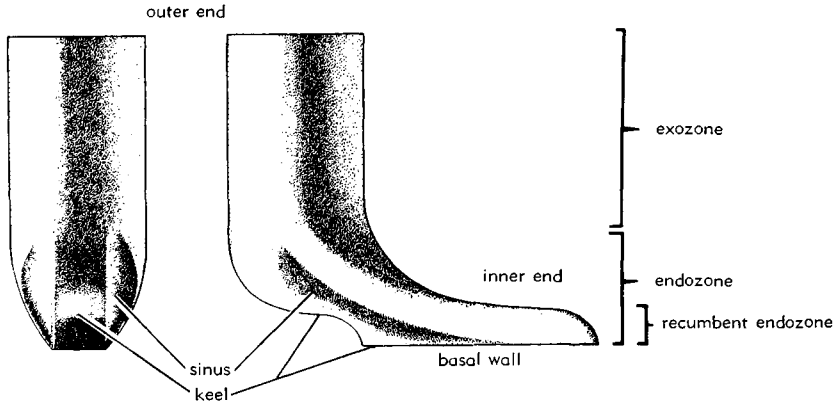


FIG. 56. Zooidal patterns. Idealized drawing of single zooecium from encrusting or bifoliate colony showing generalized shape, including keel and lateral sinuses.

during the growth of colonies. The ancestrula and the one or more transitional generations of a colony are together called the primary zone of astogenetic change (Fig. 21, 27).

In zones of change of many stenolaemates, the exterior wall of the basal disc of the ancestrula grows laterally to become the basal encrusting exterior wall of the colony. Many colonies, initially at least, grow in one general direction from the ancestrula along the substrate, here called the **primary direction of encrusting growth** (Fig. 25, 26, right of disc). The wall of the basal disc develops a small fold (Fig. 53,7) on the primary-growth-direction side, which takes the wall of the disc down to the substrate to be continued laterally as the encrusting colony wall. The distal part of the ancestrula commonly bends toward the primary direction of growth. Zooids of the first encrusting generations bud from the encrusting colony walls into confluent budding zones and zooids of many species display a subparallel orientation to form generally wedge-shaped young colonies of variable proportions (Fig. 52,2), the **primary wedge of encrusting zooids**.

If the downfold of the wall completely encircles the colony (Fig. 25, left side, and 53,6,7), the encrusting colony wall can grow laterally and support progressively younger generations of zooids in all directions from the ancestrula. This encircling exterior wall provides a basal colony wall for a **secondary wedge of encrusting zooids** growing opposite to the primary direction of growth (Fig. 25, left side; 53,6, right side; CUMINGS, 1912; BOARDMAN, 1971, pl. 3, fig. 4; BOARDMAN & MCKINNEY, 1976, pl. 7, fig. 2a,b). Contacts between primary and secondary wedges of zooids produce a typical discordant pattern as seen in deep sections parallel and perpendicular to encrusting colony bases in some stenolaemates of all ages (Fig. 53,*1,4–6,8*).

The number of generations of zooids in both primary and secondary wedges that constitute primary zones of astogenetic change varies in different taxa. Other arrangements of zooids and multizooidal structures in the zone of change have not been described in detail.

Zones of astogenetic repetition.—Zooids commonly develop in repeated patterns and extrazooidal structures are extended to establish colony growth habits distal to zones of change in colonies. These distal parts of colonies are termed zones of astogenetic repetition (Fig. 27). A zone of repetition begins with the first generation of zooids that repeats the morphologies of zooids of the preceding generation. Zooidal patterns and repeated maculae and subcolonies described below are from zones of repetition.

Zooidal patterns.—Zooidal patterns are the three-dimensional shapes and interrela-

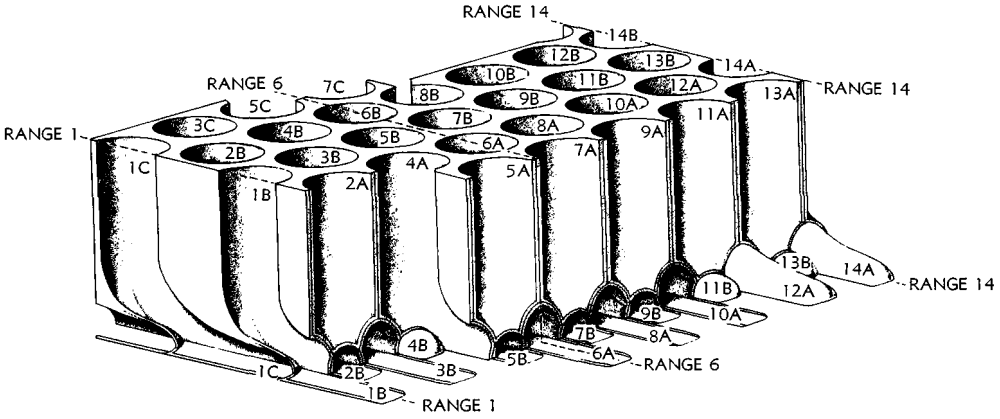


FIG. 57. Zooidal patterns. Idealized cutaway diagram of part of an encrusting colony, showing zooecia similar in shape to the one in Figure 56 arranged in the basic rhombic pattern of zooids in stenolaemate colonies. Recumbent segments of zooecia are long enough in this specimen for adjacent zooecia to overlap in numbered range as seen in longitudinal section. The longitudinal section is cut along the left front side, the transverse section along the right front side.

tionships of zooids within colonies. They are particularly useful in understanding the modes of growth of colonies and in differentiating taxa. Most of the more common growth habits of colonies as described externally can be produced by several different internal patterns of zooids. The common arrangement of zooids in rhombic patterns on colony surfaces in stenolaemates can be produced by a number of different internal zooidal patterns (see discussion of *Petalopora* and *Meliceritites* below). Patterns of zooids and their positional relationships with multizooidal and extrazooidal skeletal structures provide character states that are generally constant enough in occurrence to suggest a high degree of genetic control, and can be expected to produce a more detailed classification.

Factors that are basic to understanding zooidal patterns in three dimensions include: (1) **budding patterns**, that is, shapes of buds and their relative positions on supporting structures; (2) the three-dimensional shapes of zooids during their ontogeny; (3) the manner in which zooids or zooids and adjacent skeletal structures fit together; and (4) the position of depositing epidermis relative to skeletal microstructures.

Three-dimensional regularity of zooidal patterns is indicated by regularity in patterns of oriented two-dimensional sections. It is necessary to convert the two-dimensional patterns to three-dimensional reconstructions to understand fully zooidal patterns and the way zooids fit together to form colonies (for example, see BOARDMAN & MCKINNEY, 1976).

Zooids in many taxa develop **sinus** and **keel** configurations in recumbent endozones (Fig. 56–58; BOARDMAN & UTGAARD, 1966, p. 1083) of encrusting colonies or erect bifoliate colonies. The sinus and keel shape of the zooids allows their narrow recumbent portions (Fig. 54,*1,2*) to fit together in a generally rhombic arrangement and to expand into the full cross-sectional size of zooids in exozones. Variations in this basic pattern can be caused by a number of factors, including differing lengths of recumbent zones, intervening extrazooidal skeleton modifying zooecial shapes, patterns other than rhombic for relative budding positions, and irregular substrates.

In a species of *Tennysonia,* a free-walled tubuliporate (Fig. 55,*4,5*), feeding zooids bud from exterior multizooidal walls on the back side of a unilaminate colony without

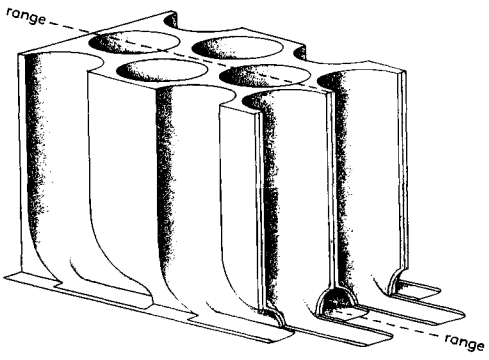


FIG. 58. Zooidal patterns. Idealized cutaway diagram of part of an encrusting colony in which recumbent segments of zooecia are short enough that adjacent zooecia do not overlap in range. Note lack of the mushroom shape caused in transverse section of Figure 57 by zooecial overlap.

developing the sinus and fold. The six-sided zooids fit together in a rhombic pattern and increase in cross-sectional area ontogenetically toward the front of the colony (Fig. 55,*4b*, top). Small polymorphs are budded (pm) near the front surface of the colony in transverse rows, forcing feeding zooids out of the rhombic pattern and into an alternating transverse pattern with the polymorphs (Fig. 55,*4a*). The outermost row of zooids in the transverse section (Fig. 55,*4b*) contains the polymorphs that are covered by terminal diaphragms.

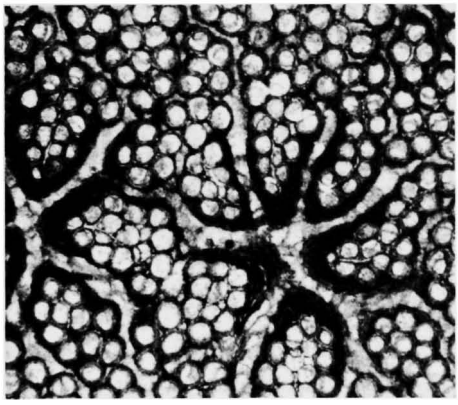
In a species of *Petalopora,* a free-walled tubuliporate (Fig. 55,*1,2*), feeding zooids bud from an axial region with the buds positioned so that the six-sided zooids remain in a rhombic pattern as they extend radially to the surface. The numerous small polymorphs are restricted to the outer exozone.

Spiral zooidal patterns are formed when bud locations occur in a spiral about an axial structure or region. A simple spiral pattern occurs in a species of *Spirentalophora,* a fixed-walled tubuliporate. The buds of feeding zooids are spaced spirally about a linear axis (Fig. 55,*3a,b*) so that the four-sided zooids are aligned radially in transverse section. The outer sides of the zooids at any one level combine to form a continuous outwardly spiraling wall as the zooids develop ontogenetically. Apparently the zooids vary progressively in length because the zooidal apertures are arranged in annular rings at the colony surface, giving little external indication of a spiral budding pattern.

In some species of *Meliceritites* the buds of feeding zooids are arranged spirally about an axial cylinder (Fig. 36,*4a,b*) and are so closely spaced that the transverse view suggests two alternatives. Either the zooids grew radially out to the exozone in a rhombic pattern, or the zooids themselves curved in a clockwise direction part way around the branch axis as they grew. The zooids remain in profile throughout their length in a longitudinal plane through the center of the branch (Fig. 36,*4a*), demonstrating that the zooids are radially arranged in the rhombic pattern that shows on the colony surface. (For another spiral pattern of different origin, see Fig. 48,*6–8.*)

Maculae.—Maculae (monticules of some authors) occur in the exozones of many Paleozoic genera and have been reported in

FIG. 59. Maculae.——*1,2. Constellaria* sp., Catheys F., Ord. (Mohawk.), E. side Harvey Knob, N. of Liberty Pike about 8 km E. of Franklin, Tenn.; *1,* radial or stellate maculae surrounded by feeding zooecia, tang. sec., USNM 250107, ×20.0; *2,* limb of macula cut transversely showing solid to vesicular skeleton and feeding zooecia (fz) on either side, long. sec., USNM 250108, ×20.0.——*3. Constellaria florida prominens* ULRICH, Mount Hope Sh. Mbr., Fairview F., Ord. (Maysvill.), reservoir near Newport, Ky.; star-shaped maculae in relief; external view, USNM 189916, ×1.5.——*4a,b. Amplexopora* sp., Mount Auburn Sh. Mbr., McMillan F., Ord. (Maysvill.), Cincinnati, Ohio; macula in exozone surrounded by feeding zooecia (fz) showing some budded polymorphs of irregular shape; *a,b,* long., tang. secs. of same zoarium, USNM 250109, ×30.0.——*5,6. Crepipora venusta* (ULRICH), Economy F., Ord. (Eden.), river quarries, W. Covington, Ky., paralectotypes; macula of small tabular polymorphs surrounded by feeding zooecia (fz) with lunaria (lu); *5,* tang. sec., USNM 159707, ×30.0; *6,* long. sec., USNM 213295, ×30.0.



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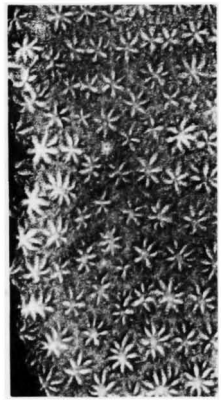

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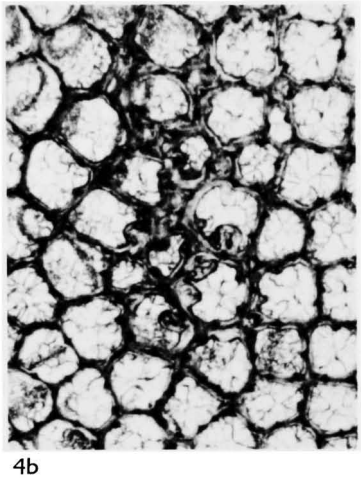

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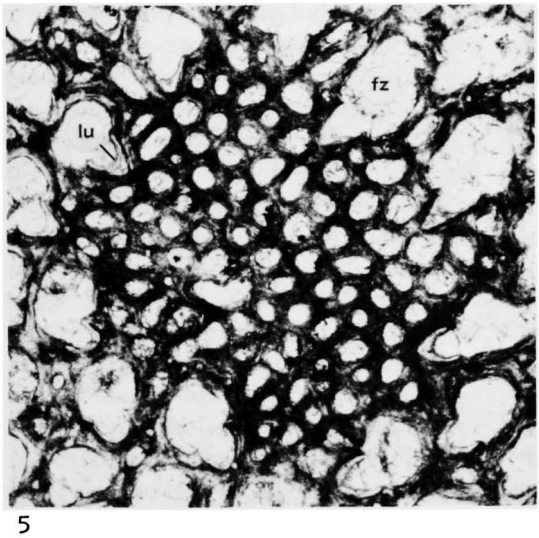

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FIG. 59. *(For explanation, see facing page.)*

post-Paleozoic tubuliporates (e.g., TILLIER, 1975; NYE, 1976, pl. 13, fig. 1b, pl. 20, fig. 1b; TAYLOR, 1975). Maculae are generally small equidimensional clusters of polymorphs, or polymorphs in combination with possible feeding zooids, extrazooidal skeleton, or both. They are isolated from each other by areas dominated by assumed feeding zooids and are more or less regularly spaced on colony surfaces (Fig. 59,*3*). They commonly form prominences, or less commonly their surfaces are flush with or depressed below the colony surface. The word macula is used here instead of monticule because its more general definition better satisfies empirical requirements as expressed on colony surfaces, that is: any of various anatomical structures having the form of a spot differentiated from surrounding tissues.

Some of the common skeletal details that distinguish maculae from surrounding regions of feeding zooids include: differences in size and shape of zooids; increased zooecial wall thicknesses; changing distinctness of zooecial boundaries; different intrazooidal structures such as basal diaphragms and cystiphragms, or differences in their spacing, configuration, or both; increased size and concentration of extrazooidal styles; and central masses of extrazooidal skeleton.

The prominence of maculae on zoarial surfaces attracted attention to them and their possible function or functions early in the study of Paleozoic Bryozoa. A reproductive function was suggested by ULRICH (1890, p. 940), which has been referred to by many subsequent authors. ULRICH compared the large polymorphs occurring in most maculae with the gonozooids of living stenolaemates. Gonozooids are large enough to brood several embryos and therefore much larger than associated feeding zooids. The relative differences in size, however, between feeding zooids and macular polymorphs in many Paleozoic species is less than size differences between feeding zooids and gonozooids of living tubuliporates. Moreover, the character is not constant; some species within genera and even some colonies within species have maculae, and other congeneric species or conspecific colonies do not (e.g., BOARDMAN & MCKINNEY, 1976, p. 60). In some cystoporate genera (UTGAARD, this revision) colonies have both blisterlike skeletal structures on distal ends of some zooecia, which appear to be brood chambers, and maculae with large polymorphs. The reproductive hypothesis for larger polymorphs in maculae of taxa of Paleozoic age should be viewed as speculative until better evidence is available.

Budding of polymorphs occurs in maculae of some taxa. Both maculae and included smaller polymorphs, commonly mesozooecia or exilazooecia (Fig. 59,*5,6*) are restricted to exozones, so that the smaller polymorphs occurring in maculae are necessarily budded there. In most taxa in which maculae occur, however, budding in maculae produces few polymorphs as large as associated feeding zooids. Relatively narrow exozones typical of erect colonies generally provide little opportunity for budding of the larger polymorphs within maculae (Fig. 59,*4a,b*). In erect parts of colonies the great majority of both feeding zooids between maculae and larger polymorphs within maculae are budded in endozones at growing tips.

In the larger **massive** and **hemispherical colonies,** endozones can be relatively narrow on basal colony layers and exozones can be many times wider. Exozones can be either uninterrupted throughout most of a colony, or interrupted by endozone-exozone cycles. The cycles are produced by intracolony overgrowths indicated by basal encrusting walls, or rejuvenations in which zooidal chambers are continuous between cycles except for possible basal diaphragms or abandoned chambers. Maculae have more opportunity to contribute polymorphs in the wider exozones of massive and hemispherical colony, and distally these polymorphs can become feeding zooids between maculae in a few species (ANSTEY, PACHUT, & PREZBINDOWSKI, 1976). In massive and hemispherical colonies zooids are budded in varying proportions from basal colony walls, basal walls of overgrowths, other zooids between maculae, and from other

zooids within maculae.

There seems to be no morphologic evidence that deregulation of the budding rate of a macula can produce a branch in an erect colony as suggested by ANSTEY, PACHUT, & PREZBINDOWSKI (1976, p. 144). Most branching stenolaemates have uninterrupted endozones from supporting stalks to branches, without intervening maculae at branch bases. A necessary function of endozones is the asexual reproduction of zooids in budding zones at distal ends of colony branches. Budding and more rapid growth of the thinner zooid walls in endozones produce the distal lengthening of branches. Maculae, where present, develop proximal to distal ends in exozones and grow relatively slowly and laterally at right angles to branch length. Certainly maculae are not necessary for branching because many branching species lack maculae.

Branches grown from exozones proximal to growing tips occur in a few species. These secondary branches are generally smaller in diameter at bifurcations than supporting branches and grow at right angles by rejuvenation on supporting branch exozones (Fig. 54,5,6). Two trepostomate species that developed secondary branches (see *Polycylindricus* BOARDMAN, 1960, p. 67) do not have recognizable maculae and the branches arose by rejuvenation from outer surfaces of supporting branch exozones without skeletal interruption of living chambers and with little or no budding. The secondary branches have both endozones and exozones.

See the following section on feeding currents for further discussion of possible functions of maculae.

Feeding currents and subcolonies.—Recent observations of colony-wide feeding currents in several species of stenolaemate suggest that feeding currents produced by ciliated tentacles of zooids were also colony-wide in many fossil species. Colony growth habit and spatial patterns of different kinds of zooids and extrazooidal skeleton on colony surfaces are major factors in the production of colony-wide feeding currents.

As has long been known, feeding currents of a zooid are incoming toward the mouth and surrounding colony surface. They are produced by motion of cilia on the tentacles. The tentacles themselves are nearly motionless in an expanded feeding position unless struck by larger particles. To reject such particles, one to several tentacles bat the particles out of the incoming current and away from the mouth area. Rejected particles can be bounced from zooid to zooid until they are finally taken beyond the colony. (For detailed discussion of morphology and feeding behavior of bryozoans, see WINSTON, 1978.)

Some basic assumptions can be made relative to the formation of colony-wide feeding currents and to the reconstruction of hypothetical feeding currents for fossil colonies. Surely more assumptions will be suggested as more living colonies of stenolaemates are observed.

1. The prevailing directions of incoming currents of feeding zooids are presumably parallel to the central axes of the outermost lengths of zooidal living chambers. **Tentacle crowns** in recent stenolaemates do not extend far enough beyond skeletal apertures for lophophores to bend independently of zooidal walls. As a result, current directions set up by zooids presumably must parallel their axes. This assumption is more speculative in taxa of Paleozoic age because lengths of extensions of tentacle crowns are unknown.

In contrast, tentacle crowns of cheilostomates can bend in different directions, causing changes in current direction. For example, in a broad unilaminar cheilostomate genus the tentacle crowns of clusters of a few zooids lean away from the centers of the clusters to form excurrent chimneys that permit unopposed outflows of water. No indications of chimneys are reflected in zooidal skeletons (BANTA, MCKINNEY & ZIMMER, 1974).

2. Colonies with broad interrupted surfaces dominated by feeding zooids presumably have some method that permits incoming water to escape from colony surfaces without passing out through actively feeding tentacle crowns and thereby opposing incoming currents. This assumption is supported

partly by observations of different methods employed to release water from colony surfaces in living species, only a few of which are discussed below.

3. Any colony surface area that lacks feeding zooids or in which feeding zooids are not feeding, and which is large enough to be unaffected by surrounding incoming currents, will function as an excurrent chimney because outflow is unopposed.

4. Skeletal apertures of feeding zooids in many taxa are raised by peristomes above the colony surface so that water can escape to colony margins or excurrent chimneys along colony surfaces between peristomes and under tentacle crowns (Fig. 54,*3*; 61,*1*,*4a*).

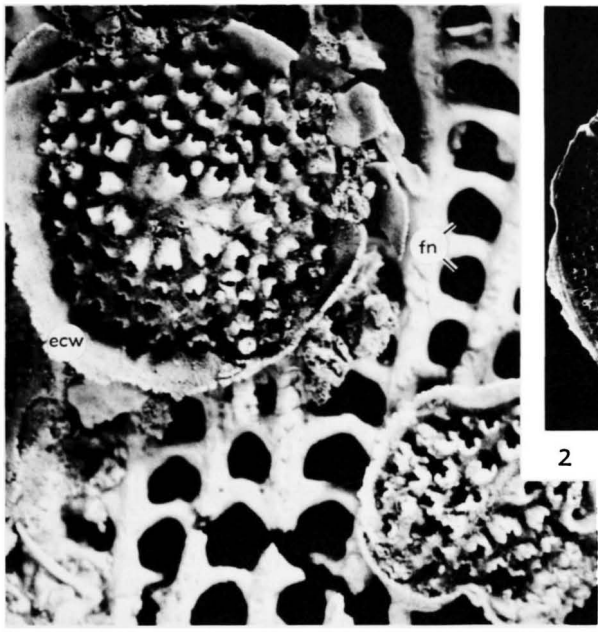
5. In some taxa, spacing between skeletal apertures of adjacent feeding zooids can be wider than tentacle crowns so that unopposed excurrent space surrounds single zooids. Wider spaces between skeletal apertures may result from sparse budding patterns, the thickening of vertical walls in exozones, intervening extrazooidal skeleton, the growth of frontal walls, diverging peristomes, or presence of interspersed nonfeeding polymorphs. These spacing factors are expressed skeletally but are difficult to evaluate in most fossil colonies because of lack of evidence of diameters of tentacle crowns. It can be generally assumed, however, that lengths of feeding tentacles will be less than axial lengths of their living chambers, because tentacles of living stenolaemates are more or less straight in retracted positions.

6. Colonies of slender branches of one to several feeding zooids at any one level apparently need no special arrangements for water removal because water apparently can flow past branches relatively unimpeded. Unilaminate **fenestrate colonies** are a growth habit modification in which slender branches separated by rectangular open spaces called **fenestrules** are arranged in a reticulate pattern to form broad fronds (Fig. 60,*1*). In living fenestrate cheilostomates, feeding tentacle crowns pump incoming water through fenestrules and out past the nonzooidal or reverse sides of the fronds. It is assumed that this is also the normal feeding current direction for fenestrate stenolaemates of all ages (e.g., McKinney, 1977a).

Most recent species of the free-walled tubuliporate genera *Lichenopora* and *Disporella* are small, circular, convex colonies in which feeding zooids are arranged in radial rows and have long interior-walled peristomes (Fig. 60,*2–4*). Polymorphs occur between rows of feeding zooids. The polymorphs are without tentacles and form a general zoarial surface (Fig. 25) below peristome apertures and therefore below feeding tentacle crowns (Fig. 60,*3*, left side). The lower surfaces formed by polymorphs rise toward high central areas consisting of brood chambers or polymorphs, both lacking feeding tentacles.

In this radial growth habit, walls of feed-

Fig. 60. Feeding currents.——*1*. Cystoporatid encrusting reverse side of fenestellid, Road Canyon F., Perm. (Leonard.), 2.4 km N. 19° W. of Hess Ranch House, Hess Canyon Quandrangle, Texas; radial arrangement of feeding zooecia with lunaria budded from encrusting colony wall (ecw); fenestrules (fn) provided passageway for feeding currents through frond of colony; exterior view, USNM 250110, ×10.——*2*. *Disporella* sp., rec., Jamaica; feeding zooids arranged radially around large central area of polymorphs lacking tentacles; external view, USNM 250111, ×8.——*3*. *Disporella* sp., rec., off Riou Is., Marseille, France; polymorphs (pm) on left side of section rise to central area (ca) of colony and form lower zoarial surface at general level of dashed line, feeding zooids (fz) with peristomes (p), encrusting colony wall (ecw); long. sect., USNM 250112, ×30.——*4*. *Lichenopora* sp., rec., 10–20 m, between Rotones and Caribe Is., Puerto Rico; radially arranged feeding zooids around central brood chamber with large aperture at upper right; external view, USNM 250113, ×15.——*5,6*. *Prasopora* sp., Ord. (Trenton.), Trenton Falls, N.Y.; *5*, feeding zooecia with cystiphragms (c) surrounding living chambers (lc) radially arranged on sides of zooecia nearest center of macula (m), consisting of smaller mesozooecia, tang. sec., USNM 250114, ×20; *6*, macula (m) in center indicated by smaller, closely tabulated mesozooecia, surrounded by feeding zooecia containing cystiphragms (c) and living chambers (lc) that change in position from center of zooecia at 1 to sides nearest maculae at 2, long. sec. USNM 250115, ×10.



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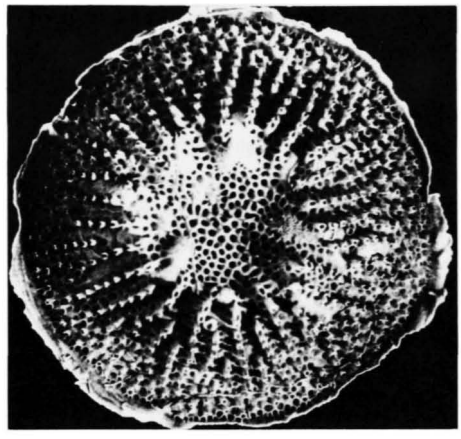

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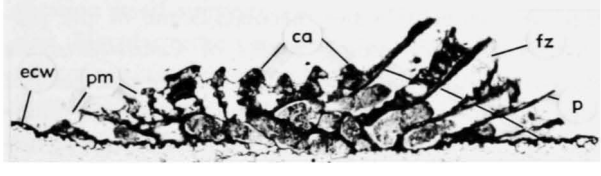

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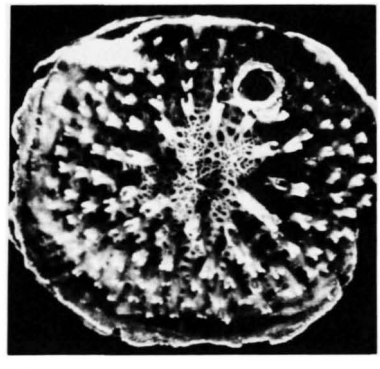

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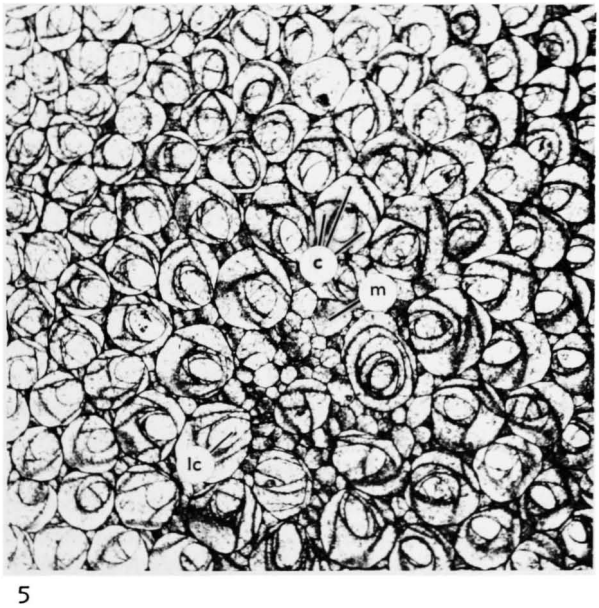

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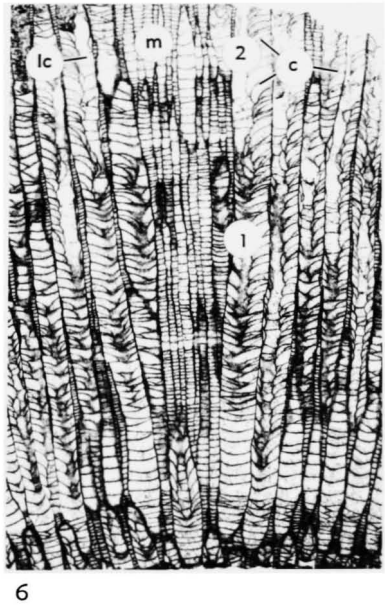

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FIG. 60. *(For explanation, see facing page.)*

ing zooids commonly bend away from colony centers distally (Fig. 60,*3*) so that incoming zooidal feeding currents (Fig. 25) that pass between tentacles and tentacle crowns are directed (assumption 1) along the lower surfaces formed by the polymorphs (assumption 4). These currents are reflected up to colony centers, apparently because of the inward-facing obtuse angles between peristome axes and the lower surfaces. In colony centers excurrent chimneys are formed because there are not feeding zooids to set up incoming currents to oppose outflow (assumption 3). For a contrasting analysis of the origin of feeding currents of *Lichenopora,* see COOK (1977).

Outgoing currents from centers of lichenoporid colonies are strong, rising several colony thicknesses above the colonies, where any lateral currents of surrounding environments could carry rejected debris away. The colony-wide currents also have the advantage of keeping colony surfaces free of moderate amounts of settling mud in quiet-water environments. Presumably this kind of cooperative action among feeding zooids of a colony is more efficient than zooids acting individually in both food intake and colony cleaning. These may be reasons why the radial growth habit has developed independently many times in stenolaemate history. For examples of comparable colonies of tubuliporate species of Cretaceous age, see BROOD (1972, pl. 45–47, 50).

A cystoporate species of Permian age (Fig. 60,*1*) has radial surface features comparable to those of recent lichenoporids, suggesting similar colony-wide currents. Several of these colonies occur on the reverse side of a large, erect fenestrate frond. If both lichenoporid and fenestrate colonies were alive at the same time, the feeding currents passing through the fenestrules may have been reversed and captured in the feeding currents of the smaller radial colonies.

Larger colonies in some species of *Lichenopora* develop several radial centers (see Fig. 9,*5*). Each of these centers presumably develops radially incoming feeding currents and central excurrent chimneys. Repeated morphologic groupings on colony surfaces of many recent and fossil taxa suggest the concept of subcolonies. **Subcolonies** are groupings of zooids and any extrazooidal structures within colonies, which may or may not be skeletally identifiable, but which carry out most or all of the functions of whole colonies. In many taxa containing subcolonies, the subcolonies develop in exozones of zones of repetition. It is not implied here that subcolonies are necessarily independently budded units.

Among fossil stenolaemates, many maculae apparently were subcolonies. In *Constellaria,* a cystoporate genus of Ordovician age (Fig. 59,*1–3*), the distinctive radial maculae compare closely with the radial subcolonies of recent species of *Lichenopora.* Species of *Constellaria* range from small circular colonies of one macula to erect branching colonies of many maculae. Some of the presumed feeding zooids of *Constellaria* are radially arranged in the stellate maculae but do not develop isolated peristomes. Thin-walled, closely tabulated mesozooecia or vesicles, both lacking living chamber space, form the interrays. The interrays can be lower than, flush with, or above apertural levels of the feeding zooids (UTGAARD, this revision), so that excurrent chimneys might have been at the center of the macula as in *Lichenopora,* or over the stellate nonfeeding interrays. For examples of comparable maculae of post-Paleozoic age, see HILLMER (1971, pl. 22, fig. 9) and NYE (1976, pl. 13, fig. 1b).

The concept of many types of maculae as subcolonies or centers of subcolonies is suggested in some taxa of Paleozoic age by the radial orientation of eccentrically placed living chambers on sides of feeding zooids either nearest to (Fig. 60,*5,6*), or farthest from (BOARDMAN & UTGAARD, 1966, p. 1094), centers of the nearest maculae. In monticuliporid trepostomates, cross-sectional areas of living chambers of feeding zooids are considerably reduced from areas of entire zooecia by skeletal cystiphragms. Living chambers are on proximal sides of zooecia and cysti-

phragms are concentrated on distal sides in early growth stages near endozonal-exozonal boundaries. As maculae developed during ontogeny in a few monticuliporids, living chambers and cystiphragms of some of the zooids both within and surrounding the maculae twisted around zooidal axes so that living chambers were nearest to centers of the nearest maculae (Fig. 60,6). The amount of twisting was variable and controlled, resulting in living chambers of nearby zooids being radially oriented around macular centers in later growth stages. In some species it is possible to divide most feeding zooids into groups surrounding adjacent maculae based on radial orientation of living chambers in later growth stages.

Maculae and surrounding zooids with radially oriented living chambers such as those in the monticuliporid trepostomates are interpreted as subcolonies because that orientation itself suggests a cooperative function. Macular centers in these species generally consist of clustered mesozooecia. The best functional inference presently to be made is that these macular centers resulted in excurrent chimneys (assumption 3). The eccentricity of living chambers in some monticuliporids may not have affected feeding currents because in other monticuliporid species, living chambers remained on proximal sides of feeding zooids throughout their ontogeny and no radial orientation developed.

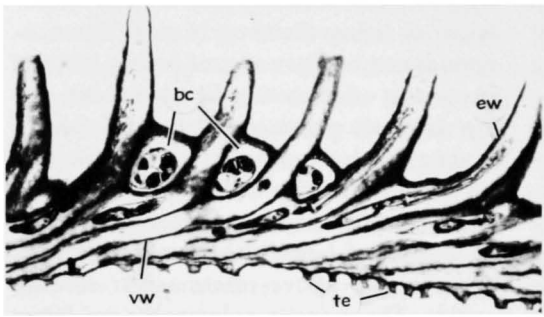
Maculae of many Paleozoic species consist of clusters of larger polymorphs that form prominences above intermacular feeding zooids. The macular polymorphs are larger than adjacent feeding zooids and have larger living chambers. At present there is no evidence that these larger polymorphs lacked tentacles, that they were not extended when surrounding zooids were feeding, or that their cilia created outgoing currents. There seems to be no evidence, therefore, that these maculae formed excurrent chimneys. Nevertheless, these maculae commonly occur in large colonies that should have had some provision for outgoing currents. Observations of large living stenolaemate colonies having closely spaced feeding zooids may suggest methods of forming excurrent chimneys not necessarily reflected in skeletons.

GENETIC AND ENVIRONMENTAL CONTROL, COLONY INTEGRATION, AND CLASSIFICATION

The procedure preferred here for obtaining character states for use in phylogenetic classifications is described in the introduction to this revision in the section on taxonomic character analysis. The goal of character analysis is to obtain states of morphologically independent characters that are largely genetically controlled.

A character should be morphologically independent to the extent that its observable states are not partly determined by states of other characters within the group of taxa being classified. Independent characters can be derived from morphologic units ranging organizationally from single cells to entire colonies. Such characters are determined to be independent only by comparisons among potentially homologous morphologic structures. These structures are generally similar in mode of growth and most have some functions in common. For example, frontal walls of gymnolaemates and stenolaemates are potentially homologous. They are exterior in origin in both classes. At class level the flexibility of frontal walls in tentacle protrusion is an independent character whose states separate the two classes, flexible in gymnolaemates and inflexible in stenolaemates.

Dependent characters are not considered in the classification. These are of at least two types, redundant and ambiguous. Ambiguous characters can produce equivocal results because they combine states of two or more characters, which can vary independently from specimen to specimen. For example, a commonly cited character of Paleozoic stenolae-



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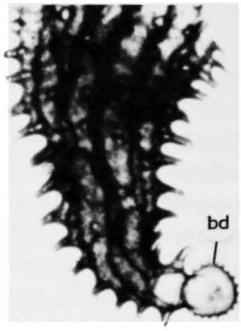

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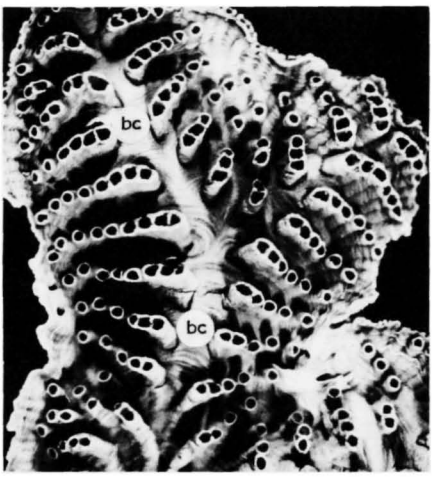

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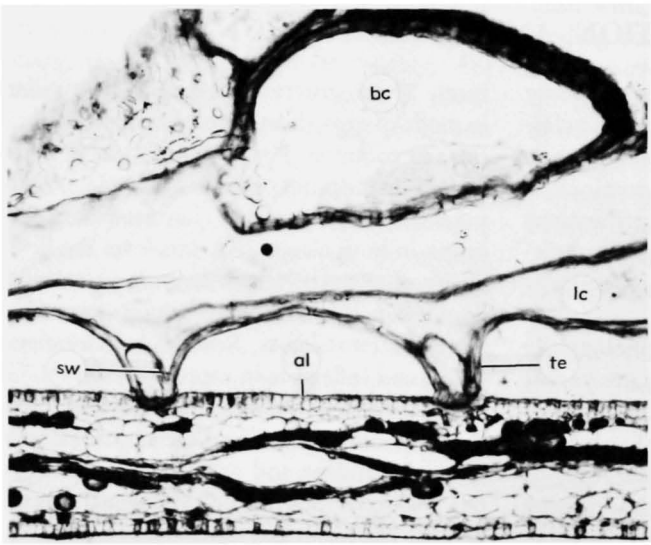

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FIG. 61. *(For explanation, see facing page.)*

mates is the number of zooecia of feeding zooids in a standard area or length. Several independent characters of different morphologic units are combined in these counts: the diameter of zooecial chambers, thickness of zooecial walls, and dimensions of any intervening polymorphs or extrazooidal skeleton. The same counts can be obtained from colonies with large living chambers and thin walls and colonies with small living chambers, thick walls, and intervening polymorphs or extrazooidal skeleton. If such a count is presented as the major statement of zooecial size in a description, it could be misleading. If presented as measures of zooecial spacing, however, such counts would be independent character states.

Redundant characters are those whose states are necessarily determined by other characters. For example, in stenolaemates the presence of frontal walls necessarily determines that orificial walls are fixed (attached to the frontal wall) and that confluent outer body cavity between fully formed zooids is absent. Within stenolaemates, therefore, two of the three characters are redundant. Among all three classes of Bryozoa, however, not all orificial walls are fixed to frontal walls (phylactolaemates) and confluent body cavity is present because vertical walls are incomplete or lacking (phylactolaemates). At the class level, therefore, the three characters are independent.

Genetic control of taxonomic characters is expressed to the extent that their observable states correlate with genetic differences among colonies (BOARDMAN, CHEETHAM, & COOK, this revision). Some character states vary within colonies. These are largely controlled by ontogeny, astogeny, polymorphism, and microenvironment, and are increasingly recognizable in stenolaemates as study techniques improve. Character states that vary within colonies are subject to intracolony analysis and are presented as stages of series or as limits of variation in order to be in a form that can express possible genetic control. Other character states appear to be uniform within colonies and intracolony analysis is not necessary. Both variable and uniform character states of colonies apparently can express different proportions of genetic and environmental control.

Degrees of environmental control of taxonomic characters are expressed by morphologic differences of character states in response to environmental differences within essentially constant gene pools. Environmentally controlled character states, therefore, should correlate closely with environmental differences, although such correlations do not necessarily rule out taxonomically significant degrees of genetic control.

Morphologic limits of environmentally controlled states of characters are presumably genetic, and so these states have taxonomic significance as expressed by their limits. Further division of a taxon, however, based on environmentally controlled states of characters within those limits would have no genetic significance and, therefore, no validity in phylogenetic classifications.

Environmentally controlled character states that are colony-wide or community-wide are

FIG. 61. Microenvironmental modification.——*1–5. Tubulipora anderssoni* BORG, rec., 12 m, Bay of Islands, N.Z.; *1,* tubular extensions (te) in encrusting colony wall, interior vertical walls (vw) and exterior frontal walls (ew) of feeding zooids; extrazooidal brood chamber (bc) between rows of feeding zooids, long. sec., USNM 250116, ×30; *2,* proximal end of colony showing small spines at base of basal disc (bd) and lateral positions of some tubular extensions, USNM 250117, ×60; *3,* underside of colony with evenly distributed tubular extensions, USNM 250118, ×15; *4a,b,* views of *a,* upper side of colony showing distribution of feeding zooids and elongated brood chamber (bc), *b,* underside of same colony with tubular extensions in proximal region only, both USNM 250119, ×15; *5,* underside of colony with tubular extensions unevenly spaced, USNM 250120, ×15.——*6. Tubulipora* sp., rec., intertidal, Leigh Cove, N.Z.; tubular extensions (te) with skeletal wall (sw) projecting into soft algal substrate (al), living chambers of feeding zooids (lc), brood chamber (bc); long. sec., USNM 250121, ×150.——7. *T. anderssoni,* same data as *1*; pattern of tubular extensions from within colony; sec. parallel to encrusting colony layer, USNM 250122, ×30.

most difficult to recognize because they could equally well be genetically controlled. Experimentation with the same living stenolaemate colonies in different natural environments is the obvious approach to distinguishing the effects of changes of environment on character states. A presently available but less satisfactory alternative is the series of indirect assumptions concerning both genetically and environmentally controlled character states, which are listed under the section on intercolony analysis (BOARDMAN, CHEETHAM, & COOK, this revision). The assumptions are useful both as a means of making interpretations and of indicating new questions to be investigated.

ENVIRONMENTALLY CONTROLLED CHARACTERS

Environmentally controlled modifications of parts of colonies are termed microenvironmental and are caused by local environmental differences within a colony. The morphologic limits of microenvironmentally controlled states of a character are set by the constant genetic makeup of the colony and those limits can be valid parts of taxonomic descriptions. Intermediate morphologies or virtually the entire range of morphologic variation can be displayed within a single colony. Colonies exhibiting microenvironmental differences can aid in distinguishing environmentally controlled morphologic states that might be uniform in other colonies of the species and therefore more difficult to recognize (assumption 3, BOARDMAN, CHEETHAM, & COOK, this revision).

Some microenvironmental modifications demonstrate how colonies repair themselves after environmental accidents or reveal something about the environment itself. Many modifications are the results of fortuitous accidents or occurrences and are so trivial that their description adds nothing to the concepts of taxa in phylogenetic classifications.

Modifications involving exterior walls.—An example of a microenvironmentally controlled modification as an aid to the recognition of colony-wide environmental differences (assumption 3) can be inferred in the concept of the species *Tubulipora andersonni* BORG, 1926a. Colonies of this and some other species of *Tubulipora,* which grow on kelp and other soft algae, develop tubular extensions of exterior encrusting colony walls (Fig. 61). These function as basal attachments to the algae, leaving their impressions on the algal surfaces when colonies are removed (Fig. 61,6). The ends of the tubes are only partly calcified. The spaces within the tubes of *T. andersonni* are confluent with body cavities of living chambers of feeding zooids (Fig. 61,*1*) that bud from the encrusting colony walls. The tubes, therefore, are apparently not polymorphs (kenozooids) as suggested by BORG (1944, p. 46), and as they appear to be externally. In other species of *Tubulipora* (Fig. 61,6) skeletal walls are present between the tubes and feeding zooids, but not enough material is available to determine whether the tubes are entirely sealed off.

Within *T. anderssoni,* BORG (1944, p. 46) also included colonies that grow on hard substrates and that have comparable morphology except for the lack of basal tubes. Recently collected colonies from New Zealand presumably belong to the same species and have their encrusting surfaces either partly (Fig. 61,*4b*) or entirely (Fig. 61,*3,5*) covered with basal tubes. The converse of assumption 2 apparently applies here, that exterior walls grown adjacent to the environment can reflect greater degrees of environmental modification than interior walls protected by the body cavity of the colony.

Tube distribution is apparently microenvironmentally controlled in colonies with tube development restricted to parts of encrusting walls. These intermediate states within colonies support BORG's interpretation that the presence or absence of tubes under entire encrusting surfaces of particular colonies is environmentally controlled within a broad species concept. If so, the limits of tube distribution can be considered to be a genetically controlled taxonomic character state of that species and partial distribution that is

microenvironmentally controlled in conspecific colonies is a valid part of the species description.

Colonies of many free-walled taxa of Paleozoic age are especially susceptible to interruptions of growth of localized groups of zooids. The interruptions appear to be fortuitous because of irregularities in the position and numbers of zooids in the localized groups. Repair of these growth interruptions is generally by the development of **intracolony overgrowths.** The overgrowths (Fig. 27; 36,*1*) originated from adjacent surviving zooids and were initiated by simple basal encrusting walls, which presumably were exterior and had exterior cuticles.

One can only speculate about causes of Paleozoic growth interruptions. Rupture of exterior membranous colony walls is commonly indicated by debris-filled living chambers of the overgrown zooecia (Fig. 62,*5,6*). Accidental rupture of the membranous walls, therefore, might have been a cause of zooids being killed in parts of colonies. These interruptions and repairs primarily involving exterior walls are so common in some species occurring in calcareous mudstones and shales that it is difficult to find wider uninterrupted exozones of advanced growth stages for description and illustration. Descriptions of these overgrowths in some species could possibly establish genetically controlled limits to some of their environmentally controlled character states.

In some post-Paleozoic stenolaemates, cyclic intracolony overgrowths apparently are the normal colony growth pattern (Fig. 62,*7*; Hillmer, 1971). Thus, a mode of colony growth that started as a means of injury repair may have evolved into a more genetically controlled growth habit not initiated by fortuitous environmental factors. In a few taxa, a number of overgrowths can start simultaneously on a colony surface and develop subcolonies, so that each cycle of intracolony overgrowth consists of adjacent subcolonies (Hillmer, 1971, p. 27, pl. 11, 12).

Intracolony overgrowths form subsequent, more distal zones of astogenetic change and repetition (Fig. 27). These subsequent zones of change, which are produced asexually, lack ancestrulae.

Another indication of accidental rupture of exterior membranous colony walls is the presence of obviously foreign organisms within free-walled colonies. Tubuliporate colonies commonly react by growing simple exterior skeletal walls around the foreign organisms (Fig. 62,*1,4*), presumably to contain their advance and to protect surrounding living zooids. The protective exterior skeletal wall can conform to the most minute patterns on surfaces of foreign bodies to provide an apparently tight seal (Fig. 62,*1*). This kind of fortuitous microenvironmental interruption is useful in demonstrating methods of colony repair but adds little to taxonomic concepts.

Exterior frontal walls serve to complete the skeletal living chambers of the zooids because of their outermost positions in fixed-walled colonies. In that role frontal walls necessarily compensate for minor irregularities of size and shape of supporting vertical walls in order to establish apertures in more or less regular external patterns.

For example, within one colony of *Heteropora pacifica* Borg, 1933, p. 317, the most common frontal walls of feeding zooids are exterior-walled peristomes formed by outward extensions of thin zooecial linings from interior vertical walls (Fig. 34,*1a*). In adjacent polymorphs (also *1a*), thick terminal calcified diaphragms containing closely spaced pseudopores form a second kind of skeletal exterior wall. The two kinds join in a few feeding zooids of the colony to form frontal walls (Fig. 34,*1c,* upper zooecium). In a fourth zooecium near the growing tip of the branch (Fig. 34,*1b*) the vertical wall makes a smaller angle with the colony surface than those of most of the other zooecia so that the thicker exterior wall necessarily forms a longer frontal wall in order to complete the living chamber before growing the presumed peristome. Inclusion of these largely microenvironmental variations in the species description seems both valid and useful and

conceivably could establish genetically controlled limits of variation.

Modifications involving interior walls.—Examples of microenvironmental modifications of interior walls of colonies (Fig. 62,*2*) generally seem to be either less common or less obvious than examples for exterior walls. If true, this tentative generalization supports assumption 2, that structures grown within body cavities are more sheltered from some kinds of environmental interferences than are exterior walls. For example, the interior vertical walls of *Tubulipora andersonni,* described above, are apparently not affected by the presence or absence of basal tubes in exterior encrusting walls. Likewise, interior vertical walls of the colony of *Heteropora pacifica* (above) show less variation in construction than exterior frontal walls, except perhaps for the obvious angle difference of the vertical walls in the zooecium (Fig. 34,*1b*).

Body-cavity protection (assumption 2) apparently can be overcome by environmental changes of short duration relative to colony life, which affect either interior or exterior structures, or both (assumption 5). For example, the erect part of the skeleton of a bifoliate trepostome colony is of interior origin. Zooecia of one side of one of these colonies (Fig. 62,*3,* right side) are shorter than on the other, the exozonal walls are thicker, and the cystiphragms and diaphragms are more closely spaced. Some directional microenvironmental factors must have caused these differences. Although morphologic differences within colonies are rarely so pronounced, theoretically these different states could be produced by different colony-wide environments and a thin-walled population of this species might well be conspecific with a thick-walled population from another environment (assumption 3).

In many erect forms of Paleozoic age, colony branches are extended by a series of growth cycles of interior vertical walls of zooids (Boardman, 1960, p. 38). A cycle starts with the establishment of exozones around growing tips, followed by resorption of the outermost segments of zooecia in the exozones leaving behind traces of exozonal position of that cycle, followed by rejuvenation and growth of thin endozonal walls, followed again by growth of exozones at the new growing tips. In a large colony many of these growth cycles combine to form a branch. Distances between remnants of growing tips commonly vary from cycle to cycle within a branch (Fig. 62,*6*) or from branch to branch within the same colony. Skeletal walls in both endozones and exozones are interior in origin so that body-cavity protection (assumption 2) is again overcome by environmental changes of short duration (assumption 5).

Modifications involving colony growth habit.—The most comprehensive taxonomic study of fixed-walled tubuliporates relative

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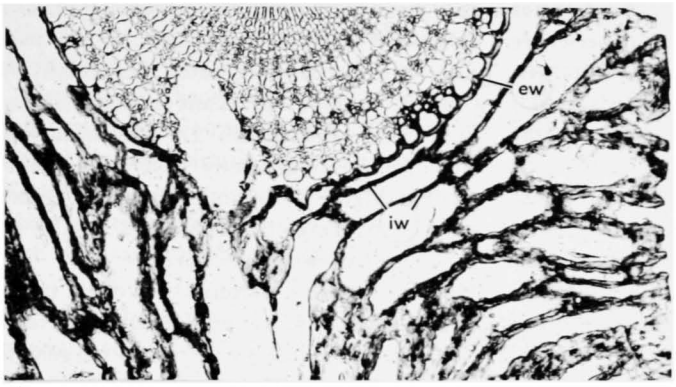
Fig. 62. Microenvironmental modification.——*1.* Heteroporid tubuliporate, rec., Neah Bay, Wash.; colony with exterior skeletal wall (ew) fitted precisely to minute pattern of echinoderm spine, interior vertical walls (iw) of feeding zooecia; long. sec., USNM 250123, ×30.——*2. Orbignyella* sp., Bellevue Ls. Mbr., McMillan F., Ord. (Maysvill.), Cincinnati, Ohio; region of zoarium apparently injured during life and partly filled with cystiphragms (c) to reestablish living chamber (lc); transv. sec., USNM 167689, ×50.——*3. Peronopora decipiens* (Rominger), Corryville Sh. Mbr., McMillan F., Ord. (Maysvill.), quarry at Dent, W. of Cincinnati, Ohio; walls thicker and cystiphragms more closely spaced on narrower exozone to right than in exozone to left; long. sec., USNM 250124, ×20.——*4. Densipora corrugata* MacGillivray, rec., 5-m wave-cut platform, Western Port Bay, W. end Phillip Is., Australia; protective exterior wall (ew) around foreign growth, interior vertical walls (iw); long. sec., USNM 250125, ×100.——*5. Atactotoechus fruticosus* (Hall), Windom Mbr., Moscow F., Dev. (Erian), Kashong Cr., Seneca Lake, N.Y.; living chambers filled with terrigenous material under overgrowth (arrow); long. sec., USNM 133941, ×2.——*6. Leptotrypella asterica* Boardman, Kashong Mbr., Moscow F., Dev. (Erian), Little Beards Cr., Leicester, N.Y., paratype; living chambers filled with terrigenous material under overgrowth (arrow), remnant of growing tips, cycles 1 to 6; long. sec., USNM 133895, ×5.——*7. Atagma macroporum* (Hamm), Cret. (Maastricht.), S. of Mons, Belg.; remnants of cyclic growing tips and related overgrowths; long. sec., USNM 186564, ×7.



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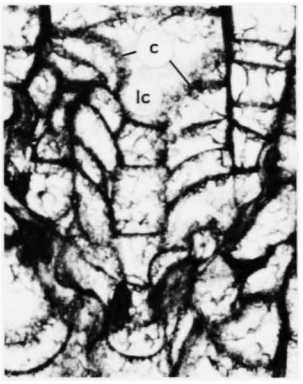

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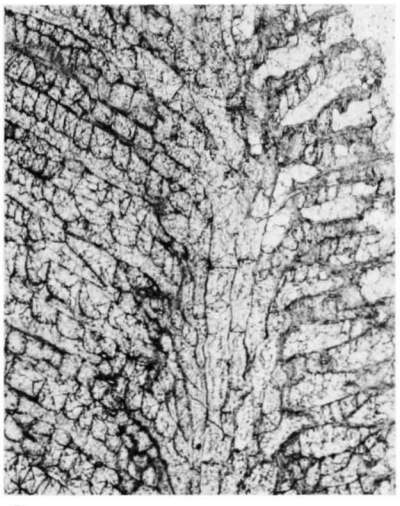

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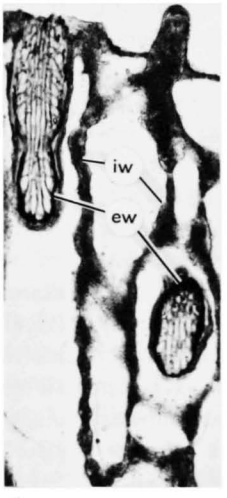

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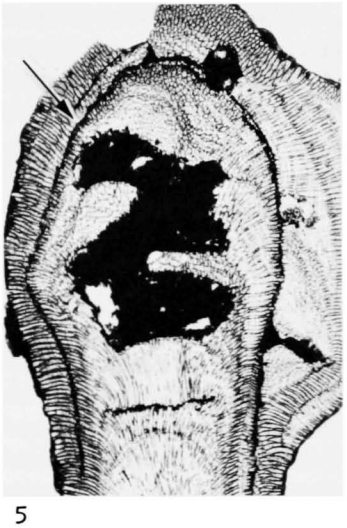

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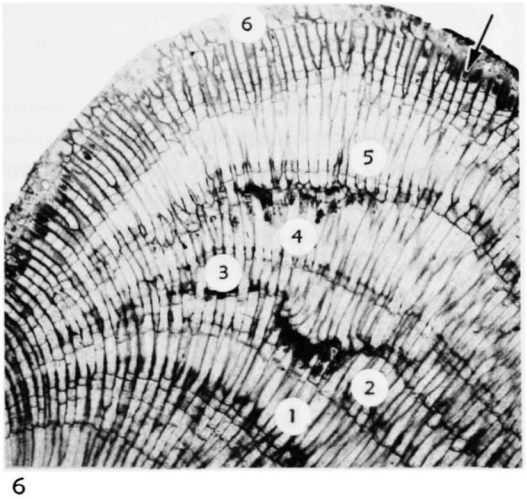

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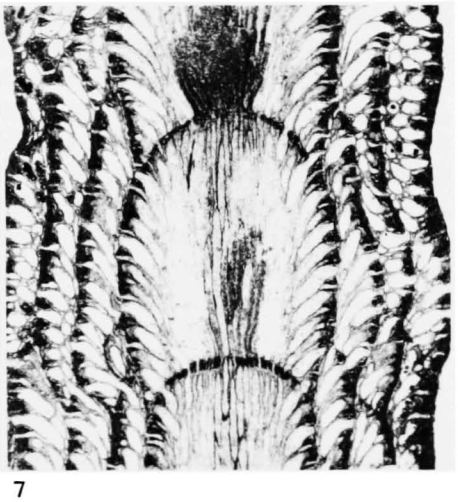

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FIG. 62. *(For explanation, see facing page.)*

to environments (HARMELIN, 1976) indicates that colony growth habits of many species are environmentally controlled (assumption 4). Character states derived from exterior frontal walls, such as wall thickness and peristome length and diameter, are correlated with changes in growth habit and therefore those states are interpreted to be environmentally controlled. Within the same species, microstructure of frontal walls, including the density and size of pseudopores, is relatively constant in different environments, so some character states of exposed exterior walls can be assumed to be more nearly genetically controlled (assumption 1). Skeletal structures of HARMELIN's species such as hemisepta, hemiphragms, and some mural spines are grown within zooidal body cavities and are relatively constant in occurrence in different environments. These are interpreted here to be largely genetically controlled (assumption 2).

Summary.—Many characters of exterior structures appear to be largely environmentally controlled and many characters of interior structures appear to be largely genetically controlled. Just the reverse can be true, however, for other characters. From the examples above, body-cavity protection (assumption 2) seems to cause some reduction in microenvironmental and environmental modifications. Some variations of characters apparently caused by environmental changes of short duration (assumption 5), especially those reflecting amounts or rates of growth, can occur within colonies. There seems to be no universally reliable group of indirect approaches to the recognition of all environmental modifications. Reasonable approximations can be achieved for some characters, however, resulting in improvements in attempts at phylogenetic classifications.

GENETICALLY CONTROLLED CHARACTERS

A number of taxonomic characters have been used in the classification of stenolaemates of Paleozoic age. Although generally unexpressed, it apparently has been assumed that these characters were largely genetically controlled because their states, or the patterns of their changing states, were relatively constant through significant intervals of geologic time (assumption 1). Longer lasting character states generally have been evaluated at higher taxonomic levels and more rapidly changing character states tend to be used at lower taxonomic levels.

Microstructural patterns of skeletal layers of interior vertical walls are a major source of taxonomic characters inferred to be genetically controlled. Wide experience by many workers with thousands of stenolaemate specimens of Paleozoic age has produced many different patterns of microstructure in vertical walls (see discussion above). Microstructural patterns are distributed within colonies, among colonies, and among taxa with such high degrees of constancy (assumption 1) that their genetic control has generally been assumed. As a result, different aspects of microstructure have been used in the classification of Paleozoic forms at most hierarchical levels. Microstructure of vertical walls has the added advantage of being present in all specimens except those that are modified diagenetically. The nature of zooecial boundaries within vertical walls is correlated to different degrees with wall microstructure and is also assumed to be largely genetically controlled. Body-cavity protection (assumption 2) is assumed to be a factor in genetic control of vertical zooidal walls.

In post-Paleozoic stenolaemates the microstructures of both interior vertical walls and exterior frontal walls give promise of comparable usefulness in classifications. Sectioning has not been a standard part of the study of post-Paleozoic stenolaemates, the Tubuliporata, however, and no significant amount of information exists in the literature on the taxonomic characters of their vertical walls. We have sectioned approximately two hundred kinds of post-Paleozoic tubuliporates, including both fossil and modern species. This preliminary survey reveals a wider range of microstructural patterns in vertical walls (e.g., Fig. 32,*1–4*; 33,*1–3*;

42,*1,5,6*) than has been discovered in Paleozoic forms, indicating later evolutionary developments.

Laminae of adjacent zooecia form patterns that are convex outward (Fig. 29,*1,3*) in Paleozoic taxa, indicating that surfaces of the laminae were approximate growth surfaces. Many post-Paleozoic species have laminae with that same orientation (e.g., Fig. 31,7; 32,5; 50,5; 55,*1,2*; Nye, 1976, pl. 15, 36, 40, 45). The similarity of orientation and generally comparable microstructures of vertical walls of Paleozoic and many post-Paleozoic taxa suggest the possibility of phylogenetic relationships between the two groups (Boardman, 1973, 1975). (For contrasting interpretations, see Brood, 1976.)

In many other post-Paleozoic species, including both fixed-walled taxa and free-walled taxa, the direction of inclination of laminae of compound vertical walls is reversed (Boardman & Towe, 1966, p. 2; Boardman & Cheetham, 1969, p. 211) from convex outward to convex inward (Fig. 29,*2*; 33,*2,3*; 42,*5,6*). This reversal necessarily places the laminae at high angles to growing surfaces, requiring edgewise growth of all laminae simultaneously as vertical walls are extended.

The geometric perfection of patterns of vertical zooidal wall arrangements in endozones of many taxa, especially if they remain unchanged in communities having different environments, suggest that zooidal patterns (see above) can be genetically controlled. Most stenolaemates have less regular zooidal patterns; however, it is possible that genetic control, suggested by regularity of zooidal patterns in some taxa, is just as strong in taxa with less regular patterns. All zooidal patterns should be described in detail in taxonomy until more direct evidence of genetic and environmental control is available.

The presence of basal and lateral skeletal structures that project into zooidal body cavities, such as diaphragms, cystiphragms, hemiphragms, hemisepta, and mural spines, generally has been assumed to be genetically controlled, judging from their use in classification. They have been given approximately the same taxonomic weight as vertical wall microstructure in many taxa, possibly because they are attached to vertical walls.

Enough differences in the distribution of projecting skeletal structures and vertical wall microstructure have been recognized to suggest that projecting structures should be independently evaluated in different taxa. In some cryptostome taxa, hemisepta occur in virtually all zooecia of feeding zooids and are apparently genetically controlled. In other taxa, however, hemisepta occur in some zooecia and not in others in the same zoarium. This irregular intrazoarial distribution could be interpreted as an indication of polymorphism. It seems best interpreted as the result of microenvironmental control, however, because of a general lack of other observable morphologic differences between the two kinds of zooecia.

Variation in the distribution of hemisepta within colonies is comparable in Paleozoic species and in the few post-Paleozoic species that have them. One species (Harmelin, 1976) apparently has hemisepta in all feeding zooids and another species of Cretaceous age (Fig. 50,5) lacks them in many zooids. This variation suggests that their presence is subject to significant degrees of environmental control at lower taxonomic levels (assumption 3). The variation also illustrates the assumption that proportions of genetic and environmental control of a potential taxonomic character may differ in different taxa (assumption 6).

Cystiphragms are the single monothetic character defining the family Monticuliporidae Nicholson, 1881, in the order Trepostomata (see Bassler, 1953, p. G94). Cystiphragms are generally present in all assumed feeding zooecia in the zoaria of most included genera, so their presence can be considered to be genetically controlled (assumption 1), although they can vary at least microenvironmentally in spacing and thickness (assumption 3).

The problem of noncorrelation of occurrences of apparently genetically controlled character states is illustrated by the Monti-

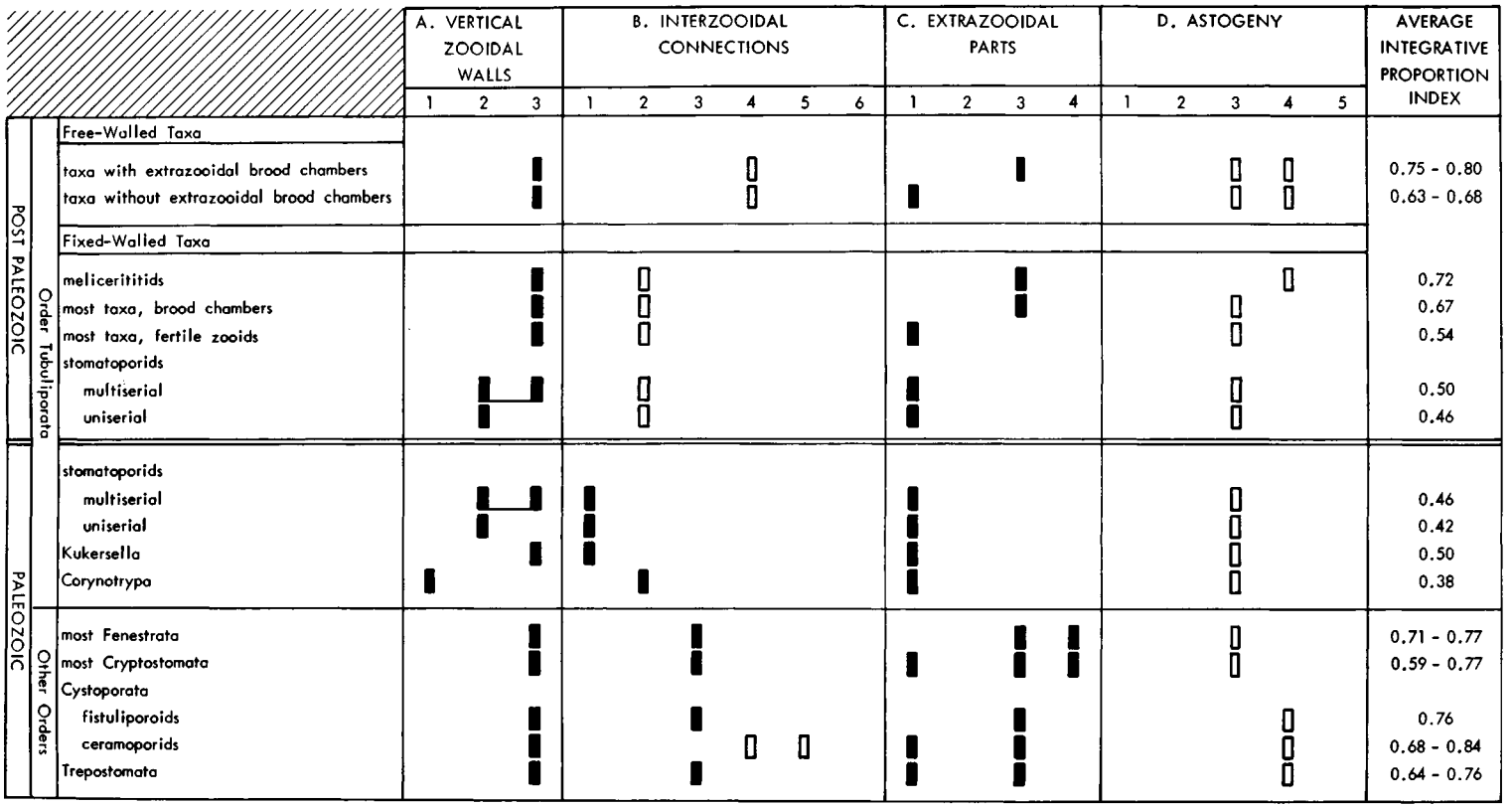

FIG. 63. Colony integration. Summary of integrative states of stenolaemate Bryozoa directly or indirectly discussed in text. Numbered states for each character, A through D, are described by Boardman, Cheetham, and Cook (colony control of function and morphology, this revision). Higher numbers of states and of average integrative proportion indexes indicate higher degrees of integration. Vertical position of groupings of bryozoans within Paleozoic and post-Paleozoic intervals have no relative time significance. The chart merely shows that Paleozoic tubuliporates are not as highly integrated as most post-Paleozoic tubuliporates. Observed states are indicated by black rectangles; inferred states are indicated by open rectangles. Two rectangles of same grouping joined by horizontal line indicate both states in same colony.

culiporidae. Several different vertical wall microstructures and other presumably genetically controlled morphologic differences occur with the cystiphragms in the Monticuliporidae. Certainly, a family with a single diagnostic character is suspect. Noncorrelation of the states of presumably long-lasting characters thought to be genetically controlled suggests that more natural family groupings might be achieved by using all of the available characters in a polythetic approach.

The taxonomic application, especially in higher categories, of the presence or absence of frontal walls and the resulting concepts of free, fixed, or combined orificial walls seems unpredictable until detailed study of colony interiors is carried out on a significant number of genera. The first division of the stenolaemates into fixed- or free-walled groups as suggested by BORG (1944, p. 18) should be tested because comparable vertical wall structures (compare Fig. 29 with 32,*2* and 33,*3* with 42,*5,6*) and different methods of forming frontal walls (contrast Fig. 33 and 34) suggest the possibility of several independent origins of free- and fixed-walled taxa. If true, BORG's monothetic grouping is polyphyletic.

COLONY INTEGRATION AND GENETIC CONTROL

The concept of the integration of colonies is based on morphologic and associated functional characteristics that occur in colonies and not in solitary animals. It assumes that feeding zooids of bryozoan colonies are more nearly comparable to solitary animals than are whole colonies. Degrees of integration of colonies depend on the extent to which zooids in combination with any extrazooidal parts differ morphologically from solitary animals. States of characters of colonies ranging from nonintegrated to highly integrated provide the basis for the integration series presently recognized (see section on colony control of function and morphology, BOARDMAN, CHEETHAM, & COOK, this revision).

A corollary to the assumption of body-cavity protection of structures of interior origin (assumption 2) states that many integrated structures are grown within the protection of the body cavity and so are relatively sheltered from the environment. Therefore, they can display character states more nearly reflecting genetic control. For example, vertical body walls of zooids in most stenolaemates are integrated structures because they are interior body walls grown cooperatively by adjacent zooids within the body cavity. Similarly, body-cavity connections among zooids through and around vertical walls are integrated features. Neither interior cooperatively grown body walls nor body-cavity connections are possible between solitary animals.

To the extent that integrated structures are interior in origin the two concepts of integration and body-cavity protection are overlapping. Either one or both might be a source of genetically controlled characters. The concept of integrated structures, however, extends beyond wholly interior structures to include structures that are at least partly exterior in origin. For example, basal encrusting colony walls are multizooidal in origin and therefore express a degree of integration although they are exterior walls. Covering walls of many extrazooidal brood chambers are exterior walls but express a degree of integration because extrazooidal structures are not possible in solitary animals.

The concept of integration becomes important to the classification of bryozoans if integrated characters as a group provide a measure of genetic control. A significant proportion of genetic control would be indicated by an apparent development of and selection for integrated structures and associated functions during the evolutionary history of bryozoans. The earliest taxa of the Cheilostomata exhibit low degrees of integration, which increase progressively through time in major evolving stocks of the order (CHEETHAM & COOK, this revision). The stenolaemates are less well known and comparable detail is not available, especially concerning polymorphs (Fig. 63).

Paleozoic tubuliporates have the lowest

integration indices among the stenolaemates and are unique to the phylum because they are fixed-walled colonies with calcified frontal walls and apparently no communication pores in interior vertical walls. Once the zooidal walls were calcified, therefore, no interzooidal connections existed and except for being physically connected the zooids lived like solitary animals. The few Paleozoic tubuliporates known produced small colonies suggesting a minimum of success.

The great majority of post-Paleozoic tubuliporates evolved communication pores in interior vertical walls. Fixed-walled taxa, therefore, had presumed interzooidal connections and were more highly integrated in that character than fixed-walled taxa of Paleozoic age.

Free-walled stenolaemates of Paleozoic age apparently all had interzooidal connections through confluent outer body cavity around ends of vertical walls. They were more highly integrated, therefore, than the few fixed-walled species of the same age.

Free-walled post-Paleozoic tubuliporates were more highly integrated in interzooidal communication than free-walled Paleozoic stenolaemates because, in addition to confluent outer body cavities, they developed communication pores (only the few ceramoporids had communication pores in the Paleozoic). It is possible that some free-walled Paleozoic stocks continued into the post-Paleozoic. If so, stenolaemates evolved toward more means of interzooidal communication and higher integration indices through time.

The phylogenetic relationships of post-Paleozoic free-walled taxa with fixed-walled taxa of equivalent ages can not be inferred convincingly because of lack of evidence to date, so no claim is made here that one or several stocks of fixed-walled forms evolved communication pores and free walls (see Brood, 1976) resulting in increasing interzooidal communication and integration.

The most highly integrated free-walled stenolaemates are the ceramoporids (Fig. 63). They were highly integrated partly because they had communication pores in vertical walls when they first appeared in the Ordovician. They apparently became extinct in the Devonian (Utgaard, this revision), and communication pores of post-Paleozoic stenolaemates were evolved independently. The other orders presently considered to be restricted to the Paleozoic also were highly integrated when they first appeared. Perhaps the tubuliporates are the only stenolaemate order that has its earlier fossil record available so that patterns of integration can be studied throughout its existence.

The few functional interpretations available of integrated characters suggest that there is increasing functional cooperation among zooids and extrazooidal parts of colonies as degrees of morphologic integration increase. Functional cooperation of the kinds that should prove advantageous to colony survival presumably would be selected for over long periods of time. If future work indicates that integrated structures increased in number and degree of integration with time, many of their character states can be inferred to have been selected for in the evolutionary process and many integrated characters can be assumed to be genetically controlled.

As now understood, steps in the integration series (Boardman, Cheetham, & Cook, this revision) for stenolaemates (Fig. 63) express long-lasting character states and associated functions that define generalized evolutionary stages of development in taxa of the higher categories. Long-lasting character states suggest genetic control (assumption 1), whatever the underlying reasons.

Steps in the integration series, however, are only a few of the many character states derived from integrated structures. Many others are relatively short-lived. Unfortunately, it does not seem possible to assume that all characters which can be derived from integrated structures are largely genetically controlled. Examples described above of states of integrated structures interpreted to be environmentally controlled include: (1) the distribution of tubes in encrusting walls of multizooidal origin within colonies of *Tubulipora andersonni*; (2) the variable lengths of

growth of vertical walls in endozones between cyclical, abandoned, branch tips within colonies; and (3) the variable thickness of vertical walls in the exozones within colonies of many taxa.

Examples of integrated structures having character states that apparently are either genetically or environmentally controlled suggest that it is too early to predict the ultimate importance of the concept of colony integration as an independent source for genetically controlled characters in the classification of stenolaemates.