GENERAL FEATURES OF THE CLASS GYMNOLAEMATA

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The Gymnolaemata are here considered to be one of three classes of the phylum Bryozoa. Distinguishing characteristics of the class are given by BOARDMAN, CHEETHAM, and COOK in this revision (p. 26).

The Gymnolaemata include a great diversity of morphologies, ranging from simple uncalcified and partly calcified genera to elaborately integrated soft-bodied and complexly calcified genera. Among living Bryozoa, the Gymnolaemata are the dominant class in abundance and number of species, and the only class with representatives that live in fresh, brackish, and marine waters. The fossil record of the class extends more that 400 million years, beginning in the Late Ordovician; however, the record is sparse before the Late Cretaceous, approximately 100 million years ago. Proliferation of the Gymnolaemata beginning in the Late Cretaceous coincided with the decline in the Stenolaemata (VOIGT, 1972b; BOARDMAN, this revision), the only other bryozoan class with a significant fossil record. Numerical dominance in marine environments was achieved by the Gymnolaemata toward the close of the Cretaceous and has increased through the Cenozoic.

The class Gymnolaemata comprises two orders, the Cheilostomata and the Ctenostomata. Most fossil evidence of gymnolaemate history has been produced by the Cheilostomata, which have body walls with continuous calcareous layers that can be readily preserved and from which the morphology of soft parts can generally be interpreted. The body walls of Ctenostomata have only scattered or no calcareous parts, and fossils confidently assigned to this order occur sporadically as external molds.

Fossil Cheilostomata are abundant in many calcareous marine deposits of late Mesozoic and Cenozoic age from throughout the world. In some Upper Cretaceous limestones in Europe, and in some limestones, calcareous sands, and calcareous clays of Tertiary and Quaternary age in Europe, North America, and Australia, cheilostomates are the most abundant remains of megascopic invertebrates. Some cheilostomates having microscopic colonies outnumber even Foraminifera of similar size in some deposits. Similar high abundances of Cheilostomata have recently been reported in cores taken by the Deep Sea Drilling Project in the Atlantic, Pacific, and Indian oceans from deposits of Paleocene to Pleistocene age (CHEETHAM & HÅKANSSON, 1972; WASS & YOO, 1975; CHEETHAM, 1975a; LABRACHERIE & SIGAL, 1975). The oldest deposits from which cheilostomates have been reported are of Late Jurassic age (POHOWSKY, 1973).

Fossils that have been confidently assigned to the Ctenostomata are much rarer than fossil cheilostomates and are distributed sporadically in marine deposits of Paleozoic, Mesozoic, and Cenozoic age. All Paleozoic and many younger fossils that have been closely compared with living ctenostomates are shell-penetrating forms. **Borings** made by these ctenostomates in calcareous substrates are molds reflecting the external morphology of zooids and the budding patterns of colonies and are comparable to those of living shell-penetrating representatives of the order (VOIGT & SOULE, 1973; POHOWSKY, 1974).

The only fossils of nonpenetrating ctenostomates comparable in morphologic detail to borings of shell-penetrating species are external molds produced by overgrowth of the soft-bodied colonies by such shelled organisms as oysters (VOIGT, 1966, 1968, 1971a). Nonpenetrating ctenostomates are known from deposits as old as Middle Jurassic (VOIGT, pers. commun., 1976). Other fossils of earlier Mesozoic and Paleozoic age, which historically have been interpreted as

nonpenetrating ctenostomates, seem not to be comparable in morphology with living representatives of the order or in mode of preservation with younger fossils and so remain problematical. One Jurassic genus, *Vinelloidea,* previously assigned to the Ctenostomata, has recently been demonstrated to belong to the Foraminifera (VOIGT, 1973).

The abundance and wide distribution of fossil Gymnolaemata are equaled by those of living representatives of the class. Gymnolaemates have been reported from the Arctic to the Antarctic and from freshwater lakes and streams to the abyssal depths of the oceans. A number of gymnolaemate species are important components of fouling communities in fresh, brackish, and marine habitats, and many of these species are cosmopolitan. Many nonfouling gymnolaemate species also have wide geographic distributions. Circumtropical distributions of shallow water species and tropical submergence of shallow to deepwater species have been reported (distributions summarized by CHEETHAM, 1972; LAGAAIJ & COOK, 1973, and references listed therein).

Even though many more living than fossil Ctenostomata are known, the number of living species of Cheilostomata apparently far exceeds that of Ctenostomata. Living species of Cheilostomata are found in brackish to marine water, some in water of variable salinity. The great majority is limited to marine water of shelf depth. Ctenostomates are found in fresh as well as brackish and marine water. Marine representatives of both orders have been found at abyssal depths (SCHOPF, 1969b; D'HONDT, 1975), but only cheilostomates have been reported from depths exceeding 5,000 meters.

Marine Gymnolaemata seem to be most abundant and diversified where available firm substrates and low turbidity and turbulence permit encrusting and erect growth. Less favorable conditions, such as those in intertidal zones, commonly permit habitation by some species with encrusting or flexible growth forms, some of which may be highly specialized in modes of growth. The most specialized growth forms appear to be the free-living, partly mobile colonies of some cheilostomate and ctenostomate species adapted for life on or in unstable seafloor sediments. (For a variety of cheilostomate growth forms, see Fig. 13–15.)

The variety of simple to specialized growth forms in differing combinations with a high diversity of zooidal and, where present, extrazooidal morphologies limits the number of character states shared by all members of the Cheilostomata and Ctenostomata. The few shared states recognized are related to orientation of zooid walls and to the soft parts (see Table 1). Even this small number of states has become recognized only gradually during the long history of gymnolaemate studies.

Different combinations of states of numerous morphologic characters, inferred to reflect independently more genetic than environmental control, provide a rich basis for classification of the two orders. Although a greatly increasing amount of detailed information on morphology and functions of living gymnolaemates and their closely similar fossil relatives has become available during the past 100 years, attempts to generalize about modes of growth and to base classifications on monothetic hierarchies of drastically limited numbers of key characters have produced much instability in taxonomy and conflicting interpretations of phylogenetic relationships. As modern studies confirm and extend the diversity of modes of growth and functions of living gymnolaemates suggested by some earlier workers, a new polythetic basis is being developed to evaluate the multitude of fossil and living genera now included in the class. The detail in which many morphologic features known in diverse groups of living gymnolaemates can be recognized in fossil representatives of the class suggests that comparisons based on all available morphologic characters can be closely approached. By testing such comparisons against the stratigraphic record of the class, a fuller understanding of the evolutionary history of this major group of Bryozoa should be

achieved.

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HISTORICAL REVIEW

The abundance and wide distribution of Gymnolaemata in modern seas and in late Mesozoic and Cenozoic marine sediments assured that members of this class were available for even the earliest studies of Bryozoa. Among the five living Mediterranean species of Bryozoa catalogued and illustrated (as Pori) nearly 400 years ago by Imperato (1599), four are now recognized as members of the gymnolaemate order Cheilostomata and one as a member of the stenolaemate order Tubuliporata (=Cyclostomata of Busk). Of the eight species of Bryozoa included (as Zoophita) in the work of Bassi (1757) on Pliocene invertebrates of Italy, reportedly the first publication in which fossil bryozoans were described and illustrated, seven are now assigned to the Cheilostomata and one to the Tubuliporata (Annoscia, 1968).

In North America, the first Bryozoa to be reported (as Polypi) were three species from the Paleocene of New Jersey (Morton, 1829, 1834) and four species from the Eocene of Alabama (Lea, 1833), all but one of which are now assigned to the Cheilostomata.

Pioneer observations of morphology and functions of living Bryozoa during the late eighteenth and early nineteenth centuries were made largely on marine species now assigned to the Gymnolaemata. Ellis's studies establishing the animal nature of Bryozoa, synthesized in a major work (1755c), included many cheilostomates and a few ctenostomates. Grant's (1827) detailed observations of the arrangement and movement of tentacular cilia were made on cheilostomates. The classic demonstrations of anatomical differences between bryozoans and coelenterates (Audouin & Milne-Edwards, 1828; Thompson, 1830) were based on gymnolaemates. Lister (1834) and Farre (1837) provided further detailed descriptions and illustrations of lophophores, retractor and parietal muscles, and other organs, together with observations on their functions, in several species of cheilostomates and ctenostomates. The independent establishment by Thompson (1830) and Ehrenberg (1831) of the phylum as now recognized was based on studies of Ctenostomata.

Freshwater Gymnolaemata, comprising a few geographically widespread living genera, are all now assigned to the Ctenostomata. They apparently went unnoticed until nearly 100 years after the first freshwater Bryozoa (members of the class Phylactolaemata) were described by Trembley (1744). Since their discovery by Ehrenberg (1831), freshwater ctenostomates have commonly been included in studies of freshwater Bryozoa. Indeed, Allman's establishment (1856) of the Gymnolaemata and Phylactolaemata as orders of Bryozoa was based on his anatomical comparisons of freshwater genera belonging to both groups.

By the middle of the nineteenth century enough was known about the morphology of Bryozoa for Busk (1852) to establish Cheilostomata, Ctenostomata, and Cyclostomata (called Tubuliporata in this revision) as sub-

orders of living marine Bryozoa (Table 2), partly paralleling taxa above the family level previously recognized by JOHNSTON (1847). ALLMAN (1956) placed BUSK's suborders, together with freshwater ctenostomates (suborder Paludicellea of ALLMAN) and freshwater entoprocts (suborder Urnatellea of ALLMAN), in the Gymnolaemata (Table 2). BUSK (1859) followed ALLMAN in considering the freshwater ctenostomates to be a suborder of the Gymnolaemata separate from the Ctenostomata, but did not include entoprocts in the Gymnolaemata (see BOARDMAN, CHEETHAM, & COOK, this revision). It was not until late in the nineteenth century that freshwater gymnolaemates were assigned to the Ctenostomata (KRAEPELIN, 1887) and in the twentieth century that the Tubuliporata (=Cyclostomata of BUSK) were removed from the Gymnolaemata (BORG, 1926a).

D'ORBIGNY (1851–1854), in his large monograph of the post-Paleozoic Bryozoa of France, proposed a different classification based principally on study of fossil species but also including numerous living species. Most genera now assigned to the Cheilostomata he placed in an order Bryozoaires cellulinés (1851, p. 23), and a few genera of cheilostomates were placed with the tubuliporates in an order Bryozoaires centrifuginés (1853, p. 585). Each of D'ORBIGNY's orders was divided into suborders on colony forms (1852, p. 318; 1853, p. 591). This classification gained little following, even among paleontologists. GABB and HORN (1862) employed the D'ORBIGNY classification in monographing the fossil Cenozoic Bryozoa of the United States, but BUSK's suborders have been adopted throughout subsequent paleontologic literature.

Fossil species were assigned to the Cheilostomata soon after the suborder was established (BUSK, 1859). As early as 1851, REUSS arranged his descriptions of numerous Tertiary species of Bryozoa so that the species now assigned to the Cheilostomata all preceded those now assigned to the Tubuliporata (=Cyclostomata of BUSK). By 1864, REUSS employed BUSK's subordinal names for this arrangement.

Fossils now assigned to the Ctenostomata were first described and illustrated near the middle of the nineteenth century (D'ORBIGNY, 1839; FISCHER, 1866). However, these species were not distinguished from cheilostomates, and definite assignment of fossil species to the Ctenostomata apparently was not made until late in the nineteeth century (ULRICH, 1890). The anatomy of living shell-penetrating ctenostomates, on which interpretation of much of the fossil material of Ctenostomata depends, remained virtually unknown until nearly the middle of the twentieth century (MARCUS, 1938b).

Most paleontologists have assumed that the morphology and functions of whole zooids and colonies can be inferred from the study of fossil gymnolaemates and by comparison with living species. Only a few paleontologists (for example, BRYDONE, 1929, p. 5–6) have thought that skeletal evidence is generally insufficient for making such inferences and have advocated separate classifications for fossil and living taxa. Recently, it has been proposed that ctenostomates known only from their borings should be classified as ichnotaxa (BOEKSCHOTEN, 1970; BROMLEY, 1970; HÄNTZSCHEL, 1975), but bryozoan workers contend that such borings preserve sufficient evidence of zooid morphology and budding patterns to be compared with living shell-penetrating taxa (VOIGT & SOULE, 1973; POHOWSKY, 1974). No major classification of the Gymnolaemata has been proposed for fossil species alone.

BUSK's subordinal classification emphasized zooid morphology and thus stimulated more detailed observation of both living and fossil gymnolaemates. At lower levels BUSK (1859, 1884, 1886) continued to rely upon colony form and zooid arrangement, but late ninteenth century and early twentieth century workers produced much information on morphology, modes of growth, and functions of zooids with which the classification continued to be refined.

SMITT (1865, p. 115; 1866, p. 496; 1867, p. 279) raised BUSK's suborders to ordinal

TABLE 2. *Major Classifications of the Class Gymnolaemata above the Superfamily Level.*

(Boldface indicates a taxon now wholly included; italic, a taxon now partly included; subtaxa of now-excluded taxa are omitted. Author and date are footnoted for taxa the earliest reference to which is not shown, as are some usages of other authors. Correlations are approximate and informal.)

BUSK (1852)	ALLMAN (1856)	SMITT (1865–1868)	JULLIEN (1888a)	GREGORY (1893)
Order *Polyzoa Infundibulata*[a]	Order *Gymnolaemata*	Tribe *Infundibulata*		Subclass *Gymnolaemata*
Suborder **Cheilostomata**	Suborder **Cheilostomata**	Order **Cheilostomata**	Order *Cheilostomata*	Order **Cheilostomata**
Multiserialaria			Suborder *Diplodermata*[d]	Suborder **Stolonata**[i]
Inarticulata		Suborder **Flustrina**	Tribe *Monopesiata*[e]	
Articulata		Suborder **Cellularina**		Suborder **Cellularina**
Uniserialaria				Suborder **Athyriata**
			Tribe **Opesiulata**	
			Tribe **Anopesiata**	
		Suborder **Escharina**[b]	Suborder **Monodermata**[d]	
			Tribe **Inovicellata**	
		Suborder **Celleporina**[b,c]	Tribe **Subovicellata**[f]	Suborder **Schizothyriata**
			Tribe **Superovicellata**[f]	Suborder **Holothyriata**
	Suborder **Paludicellea**		Order **Paludicellea**	
Suborder **Ctenostomata**	Suborder **Ctenostomata**	Order **Ctenostomata**	Order **Ctenostomata**	
			Suborder **Halcyonellina**	
			Suborder **Utricularina**	
			Tribe **Orthonemida**[h]	
			Tribe **Campylonemida**[h]	
Suborder Cyclostomata	Suborder Cyclostomata	Order Cyclostomata		Order Cyclostomata
	Suborder Urnatellea			

[a] GERVAIS, 1837.
[b] Used as family names by EHRENBERG, 1839.
[c] JOHNSTON, 1847.
[d] JULLIEN, 1881.
[e] =*Opesiata*.
[f] JULLIEN, 1882.
[g] see HARMER column.
[h] HINCKS, 1880.
[i] BUSK, 1884.

TABLE 2. *(Continued from preceding page.)*

LEVINSEN (1909)	HARMER (1915–1957)	SILÉN (1942)	BASSLER (1953)	RYLAND (1970)
	Tribe *Gymnolaemata*[k]	Order *Gymnolaemata*	Class *Gymnolaemata*	Class Gymnolaemata
Order Cheilostomata	Order Cheilostomata[l]	Suborder Cheilo-Ctenostomata[p]	Order Cheilostomata	Order Cheilostomata
Suborder Anasca	Suborder Anasca		Suborder Anasca	Suborder Anasca
Division Malacostega[j]	Division Inovicellata	Section Inovicellata	Division Inovicellata	
	Division Malacostega	Section Protocheilostomata	Division Malacostega	
		Section Membranidea		
		Division Scrupariina		
		Division Malacostega		
	Division Cellularina	Division Cellularina	Division Cellularina	
		Section Cryptocystidea		
Division Coilostega[j]	Division Coelostega	Division Coelostega	Division Coilostega	
Division Pseudostega	Division Pseudostega	Division Pseudostega	Division Pseudostega	
	Division Cribrimorpha[m]		Division Cribrimorpha	Suborder Cribrimorpha
Suborder Ascophora	Suborder Ascophora	Section Spinocystidea	Suborder Ascophora	
	Division Ascophora imperfecta			Suborder Gymnocystidea
		Section Gymnocystidea		
	Division Ascophora vera			Suborder Ascophora
	Order Ctenostomata[l]		Order Ctenostomata	Order Ctenostomata
		Section Carnosa		Suborder Carnosa
	Group Paludicellea	Division Paludicellea	Suborder Paludicellea	
	Group Carnosa[n]	Division Halcyonellea[b,s]	Suborder Carnosa	
		Section Stolonifera	Suborder Stolonifera	Suborder Stolonifera
	Group Vesicularina[c]	Division Vesicularina	Suborder Vesicularina	
	Group Stolonifera[o]	Division Valkeriina		
			Order Cryptostomata[q]	
	Order Cyclostomata[l]	Suborder Cyclostomata	Order Cyclostomata	
			Order Trepostomata[r]	

[j] LEVINSEN, 1902.
[k] Order in 1915.
[l] Suborder in 1915.
[m] Following informal usage of LANG, 1916.
[n] GRAY, 1841.
[o] EHLERS, 1876.
[p] Following informal usage of BORG, 1926.
[q] VINE, 1884.
[r] ULRICH, 1882.

rank and within the living Cheilostomata established a series of suborders based upon the assumption that ontogenetic and astogenetic gradients recapitulate phylogeny (SMITT, 1868; transl. SCHOPF & BASSETT, 1973). SMITT's suborders (Table 2) ranged from simple, slightly calcified cheilostomates, compared by him to the Ctenostomata, to increasingly complexly calcified cheilostomates. Some of SMITT's suborders were readily adopted for fossil species (KOSCHINSKY, 1885). Recognition of a broad evolutionary trend of increasingly complex calcification among fossil cheilostomates led GREGORY (1893) to propose a series of suborders (Table 2) for both living and fossil species partly paralleling those of SMITT. As more detailed understanding of modes of growth and functions emerged around the turn of the century, however, the SMITT and GREGORY classifications were soon superseded.

Early histologic studies by NITSCHE (1869, 1871), VIGELIUS (1884), OSTROUMOV (1886a, b), DAVENPORT (1891), and others provided detailed evidence of the arrangement of cellular and noncellular layers of body walls and of the structure of interzooidal communications in a number of cheilostomates and ctenostomates. These studies are the foundation for modern understanding of modes of growth in the Gymnolaemata, but emphasis was on taxa in which body walls are uncalcified or only slightly calcified and zooids are relatively simple in morphology. Information on more complex taxa was gained more slowly.

As modes of growth of more complex gymnolaemates were studied, attention was directed to modifications of the frontal structure of zooids, and especially to the hydrostatic system for everting the lophophore. The morphology and function of the hydrostatic system in the Ctenostomata and simple, lightly calcified Cheilostomata had been known at least from the time of FARRE (1837). As frontal structures of more complexly calcified cheilostomates were compared with those of simple gymnolaemates, new characters became available not only for classification within the Cheilostomata but also to establish basic morphologic similarities between cheilostomates and ctenostomates. The diversity of morphologies in the Cheilostomata, however, makes these relationships complex.

Around the turn of the century, it was realized that the hydrostatic function in many of the more complexly calcified cheilostomates is performed by an inner compensating sac or ascus, instead of the exposed flexible frontal wall to which parietal muscles are attached in ctenostomates and simple cheilostomates (see Morphology and Mode of Growth, below). The concept of the ascus is generally attributed to JULLIEN (1888b,c), who did not, however, distinguish its method of operation. Further, JULLIEN applied this and other morphologic concepts heterogeneously in his taxonomic studies and derived a classification (1888a, p. 7) that bears little resemblance to twentieth century classifications based upon his discoveries (Table 2). JULLIEN's suborders were employed by CANU (1900) in revising D'ORBIGNY's Cretaceous species of Cheilostomata, but the JULLIEN classification gained little following.

The first detailed evidence of the arrangement of cuticular, calcareous, and cellular layers on the frontal sides of zooids in more complex gymnolaemates was presented in a major work by CALVET (1900) on the comparative histology of species of cheilostomates, ctenostomates, and tubuliporates. Some of JULLIEN's concepts were clarified and refined at the histologic level, but CALVET (1900, p. 166) did not distinguish between different modes of growth of similar frontal structures (see Morphology and Mode of Growth, below). Further, CALVET (1900, p. 278) rejected the concept of the ascus, believing the parietal muscles to be attached to calcareous frontal structures. Despite this denial, CALVET presented evidence for an ascus in at least two genera (1900, p. 168–169; fig. 21, pl. 7, fig. 1).

The first major comparison of modes of growth of structures on the frontal sides of simple to complex gymnolaemate zooids was presented by HARMER (1901, 1902). HAR-

MER recognized JULLIEN's concept of the ascus and presented evidence for two different methods by which it is formed (1902, p. 280–281, 294–295). Each mode of ascus formation was thought by HARMER to correlate with a particular mode of growth of the overlying calcified wall, although he (1902, p. 333) suggested two possibilities for the origin of one wall type. In both developmental types, HARMER recognized parietal muscles that insert on the flexible ascus floor, thereby establishing a morphologic comparison with the hydrostatic system of nonascus-bearing gymnolaemates.

HARMER suggested that differences in mode of ascus formation provide a basis for classification within the Cheilostomata (1902, p. 294) but did not then propose formal taxa. Perhaps because HARMER did not formalize his ideas, some were countered almost immediately. LEVINSEN (1902, p. 4) accepted one concept (HARMER, 1902, p. 280–281) but considered this mode of growth to apply to all ascus-bearing genera. LEVINSEN thus seems to have rejected the other concept (HARMER, 1902, p. 294–295), although his later description of one species (LEVINSEN, 1909, p. 18, 33) agrees with HARMER's in some respects. An entirely different, but in many ways unclear concept (see BANTA, 1970, p. 50) was thought by OSTROUMOV (1903) to apply to ascus-bearing taxa.

Attempts to generalize and simplify ideas on development of gymnolaemate frontal structures obscured the important point made by HARMER that features such as the ascus can develop differently in major groups of Gymnolaemata. This point was ignored until 40 years later, when SILÉN (1942) developed a classification of largely new groupings within a combined cheilostomate-ctenostomate taxon (Table 2). Even then, it was assumed that some features, such as parietal muscles and the membranous walls on which they insert, are developmentally homologous throughout these groups (SILÉN, 1942, p. 44).

As a consequence of his attempt to generalize development of certain morphologic features, LEVINSEN proposed a classification (Table 2) in which all ascus-bearing cheilostomates were assigned to one taxon (Camarostega LEVINSEN, 1902; suborder Ascophora LEVINSEN, 1909) and all cheilostomates lacking an ascus to another (suborder Anasca LEVINSEN, 1909). LEVINSEN regarded some lightly calcified anascans as providing a link between the Cheilostomata and Ctenostomata (1909, p. 92, 95) but did not propose a taxonomic revision to reflect this link. Relationships stated or implied in the LEVINSEN classification have been widely accepted by twentieth century workers on fossil and living gymnolaemates.

The LEVINSEN classification, like its nineteenth century predecessors, relied at higher taxonomic levels on the monothetic use of a few morphologic characters. Most discussions of the basis of classification in both the nineteenth and twentieth centuries have concerned the characters selected for monothetic arrangements at each taxonomic level (see HINCKS, 1887, 1890). LEVINSEN, however, recognized with WATERS (1913, p. 460) that a character too variable for taxonomic use in some taxa can be relatively consistent in others. LEVINSEN therefore avoided a strict monothetic adherence to a hierarchy of characters below subordinal level. Indeed his diagnoses of some taxa, for example the Coilostega (LEVINSEN, 1909, p. 161), are quite polythetic.

CANU and BASSLER (1917, 1920, and later works), in a widely used modification of the LEVINSEN classification, returned to more consistently monothetic arrangements in both the Cheilostomata and Ctenostomata, with no close relationship suggested between the two orders. This classification was used with some modifications in the first edition of this *Treatise* (BASSLER, 1953; see Table 2). Diagnoses at all hierarchic levels became severely abbreviated. The hierarchic arrangement of characters was attempted in correlation with essential functions. However, observations on which the functional significance of some characters can be interpreted were not available to CANU and BASSLER, and the ideas of NITSCHE, CALVET, HARMER, and others on

modes of growth were not taken fully into account in the hierarchy of functions. Although CANU and BASSLER established numerous taxa at familial and lower levels, their higher level taxa, such as the cheilostomate division Hexapogona, have been little used.

In his large monograph of living Bryozoa of Indonesia, HARMER (1915–1957) synthesized a classification (Table 2) incorporating many features of the Levinsen classification, some of Harmer's earlier ideas, and some new revisions. LEVINSEN's cheilostomate suborders were retained, and HARMER (1926, p. 187) suggested that lightly calcified anascans gave rise independently to two groups of Ctenostomata, the Stolonifera and Carnosa. However, HARMER did not propose taxonomic revisions to reflect this inferred diphyly, or the suggested close phylogenetic relationship between cheilostomates and ctenostomates. Some taxa, such as the Cellularina reintroduced by HARMER (1926), were emended on at least a partly polythetic basis. Other taxa, such as HARMER's divisions of the Ascophora, however, are monothetically based. Unfortunately, HARMER's concepts of ascophoran divisions remained incomplete when he died in 1950 (HASTINGS in HARMER, 1957), and polythetic and phylogenetic evaluation of these groupings is only beginning.

Despite a growing realization that the Cheilostomata and Ctenostomata have certain strong similarities in zooid morphology and mode of growth apparently not shared with other bryozoan orders, the monothetic basis of the Gymnolaemata (ALLMAN, 1856) to include stenolaemate bryozoans continued to be followed by early twentieth century workers. Fundamental works on embryology, larval morphology, and metamorphosis by BARROIS (1877, 1882), REPIACHOFF (1880), VIGELIUS (1886, 1888), KRAEPELIN (1892), HARMER (1893), BRAEM (1897), and CALVET (1900) further emphasized resemblance between living cheilostomates and ctenostomates. Eventually, study of living Tubuliporata (=Cyclostomata of BUSK) by BORG (1926a) revealed striking contrasts with cheilostomates and ctenostomates and led him to remove the Tubuliporata from the Gymnolaemata (see BOARDMAN, this revision). However, BORG held the traditional view that the Cryptostomata are closely related to the Cheilostomata and left both taxa, together with the Ctenostomata, in the emended Gymnolaemata. An extreme application of this view was BASSLER's (1935) assignment of a Paleozoic cryptostomate genus to the Cheilostomata. It has only been in the last few years that the stenolaemate characters of the Cryptostomata have been recognized and this order removed from the Gymnolaemata (see BOARDMAN, this revision).

MARCUS (1938a) and SILÉN (1942) proposed different means of formalizing the similarities between Cheilostomata and Ctenostomata while retaining the older concept of Gymnolaemata to include the Tubuliporata.

MARCUS (1938a, p. 116) established an order Eurystomata to include suborders Cheilostomata and Ctenostomata. His concept of the Eurystomata was based on embryologic similarities between the Ctenostomata and both anascan and ascophoran Cheilostomata (1938a, p. 123), and morphologic similarities including a generally wide orifice relative to the size of the zooid (1938a, p. 116).

SILÉN (1942, p. 3) went a step farther than MARCUS, by rejecting the concepts of Cheilostomata and Ctenostomata altogether and merging their component taxa in a suborder, which he named Cheilo-Ctenostomata following an informal usage of BORG (1926a, p. 482). Later, SILÉN (1944a, p. 98; and subsequent papers) followed BORG in removing the Tubuliporata from the Gymnolaemata, which SILÉN then regarded as an order including only cheilostomates and ctenostomates. In this later revision, SILÉN continued to reject Cheilostomata and Ctenostomata as taxa.

SILÉN's concept of the Gymnolaemata (=Cheilo-Ctenostomata) and its component taxa (Table 2) was based on a series of phylogenetic inferences from the morphology of living genera, and on the morphology of the feeding apparatus, which ". . .does not show

any differences of importance but is surprisingly monotonous throughout the two groups" (SILÉN, 1942, p. 2). SILÉN (1942, p. 52–58) assigned all ctenostomates to two groups, the Stolonifera and Carnosa, which he inferred to have evolved separately, a conclusion similar to that of HARMER (1926). The hypothetical gymnolaemate ancestor of these two groups was inferred by SILÉN to be similar morphologically to a living genus for which he proposed the taxon (section) Protocheilostomata. The Protocheilostomata were regarded by SILÉN as the central gymnolaemate stock leading to five major taxa (sections) of cheilostomates (see Table 2). These include three for anascans and two for ascophorans, although LEVINSEN's suborders were also rejected in the SILÉN classification. SILÉN's ascophoran taxa were based on modes of growth of the calcified wall overlying the ascus. However, SILÉN (1942, p. 43–44) considered the ascus to originate the same way in both groups. His concept of ascus formation appears to correlate with that of HARMER's Ascophora imperfecta.

Some aspects of SILÉN's classification have been incorporated in current classifications of the Gymnolaemata (for example, PRENANT & BOBIN, 1966; MAWATARI, 1965; RYLAND, 1970; see Table 2). RYLAND (1970), BANTA (1971), and indeed SILÉN (1942) himself have emphasized the highly tentative state of some groupings established on virtually monothetic criteria. Emendations of SILÉN's major gymnolaemate taxa have included: (1) rearrangement of component genera (SOULE, 1954; SOULE & SOULE, 1969; RYLAND, 1970); (2) recombination of parts of different taxa (assignment of ascophoran genera of the Spinocystidea to the Gymnocystidea by RYLAND, 1970; assignment of some ascophoran genera to the Cryptocystidea by BANTA, 1970, 1971; new groupings of ctenostomates proposed by JEBRAM, 1973a); and (3) reintroduction of taxa apparently excluded from SILÉN's classification (Ascophora as emended by RYLAND, 1970).

Most subsequent workers have not followed SILÉN in rejecting intermediate level taxa between the Gymnolaemata and these major groupings, however. Cheilostomata and Ctenostomata are generally retained as orders following the usage of SMITT more than 100 years ago, even though POHOWSKY (1975) has suggested the possibility that the Cheilostomata as well as the Ctenostomata may be polyphyletic.

In contrast, BANTA (1970, 1971) has elevated the emended Cryptocystidea to ordinal rank within a subclass Cheilostomata. As phylogenetic relationships become better understood, the diversity of morphologies embraced by the Gymnolaemata, especially within the Cheilostomata, may well justify significant increases in the categorical ranks of component taxa. Here, however, the Cheilostomata and Ctenostomata are tentatively retained as taxa of ordinal rank.

Some workers still retain the broader concept of Gymnolaemata to include the stenolaemates, and follow MARCUS in recognizing Eurystomata (=Eurylaemata of MAWATARI, 1965) as an intermediate level taxon. Reasons for not employing this two level classification are presented by BOARDMAN, CHEETHAM, and COOK (this revision).

The concept of the Gymnolaemata followed here is that of SILÉN (1944a), RYLAND (1970), and some other authors. A tentative phylogenetic basis for this concept is given below (Possible Evolutionary Relationships). To suggest taxonomic emendations within the Gymnolaemata or to review the many fundamental works on lower level taxa, principally at superfamilial and familial rank, would obviously be premature before restudy of the approximately 1,000 nominal gymnolaemate genera has been completed. These reviews will appear in subsequent volumes of this revision of the *Treatise*.

A single example will perhaps serve to illustrate the extensive internal rearrangements in classifications of the Gymnolaemata that have been brought about by changing morphologic emphasis in the predominantly monothetic use of characters. The Cribrimorpha, comprising genera with frontal shields composed of fused spinelike costae

(see Morphology and Mode of Growth, below), are now usually considered to be a suborder of the Cheilostomata (BUGE, 1957; RYLAND, 1970; and others). These genera were placed by LEVINSEN (1909) in the morphologically simplest of his divisions of the suborder Anasca, emphasizing their simple membranous frontal walls underlying costal shields. HARMER (1926) considered the Cribrimorpha to be morphologically the most complex division of the Anasca, forming a link with the Ascophora, because of the structure of their frontal shields. CANU and BASSLER (1920) placed the cribrimorph genera in the Ascophora, and BASSLER (1935) considered the Cribrimorpha to be a division of the Ascophora, emphasizing the ascuslike cavity between frontal wall and frontal shield. SILÉN (1942) included the cribrimorphs with some ascophorans in his section Spinocystidea on the basis of phylogenetic inferences. The current subordinal position of the cribrimorphs thus seems to be a compromise between more extreme assignments. The systematic positions of this and other major taxa of the Gymnolaemata can only become better known through detailed comparisons of component living and fossil genera, considering all available morphologic characters and the distribution of their states in time and space (for example, LARWOOD, 1969).

Uneven progress over the past 125 years in deriving a stable classification of the Gymnolaemata, at the levels of class, orders, suborders, and lower level taxa, has resulted partly from the sheer number of genera to be understood morphologically and distributionally, as well as from repeated changes in the monothetic bases of classification. However, another, human factor also seems to have been involved. Some of the most significant morphologic discoveries have been ignored, rejected, or misrepresented, often to emphasize shifts in monothetic criteria, and so rediscovered decades later. Some misunderstandings have doubtless been encouraged by a confusing manner in which interpretations were expressed, especially if in a new and complex terminology, or by a failure to present sufficient supporting evidence: "these heroic attempts. . .made without facts to bear them out. . .are usually ignored, and so bring their own punishment" (WATERS, 1889, p. 3). However, over the years the prevalence of such rejections, or worse yet misrepresentations, must make many bryozoologists sympathize with SMITT's (1872, p. 246, 247) comment on contemporary misunderstanding of his work: "Thus I could not think that any one should impute to me such a thought. . .such an opinion would be an absurdity."

MORPHOLOGY AND MODE OF GROWTH

Colonies in the Gymnolaemata range from a few zooids in the free-living ctenostomate *Monobryozoon* to estimated tens of millions of zooids in multilaminate encrusting species of such cheilostomates as *Membranipora* and *Schizoporella*. Major parts of colonies in some taxa are extrazooidal. Principal growth directions of zooids and of major parts of most colonies approximately coincide. Zooids within colonies are commonly polymorphic. **Autozooids** (zooids having protrusible lophophores, some with feeding ability and others without) have orificial walls consisting of one or more movable folds, the outer sides of which are continuous with an elongated frontal wall (Fig. 64). When closed, the orificial wall generally lies subparallel to the frontal wall and to the principal direction of zooid growth. Part or all of the frontal wall, or an infolded sac derived from it, is flexible by means of attached parietal muscles and functions in the **hydrostatic system** for protruding the lophophore. A variety of supportive and protective structures may be associated with the frontal wall. Other supporting zooid walls include lateral walls, and in most taxa basal walls, elongated generally subparallel to the principal direction of zooid

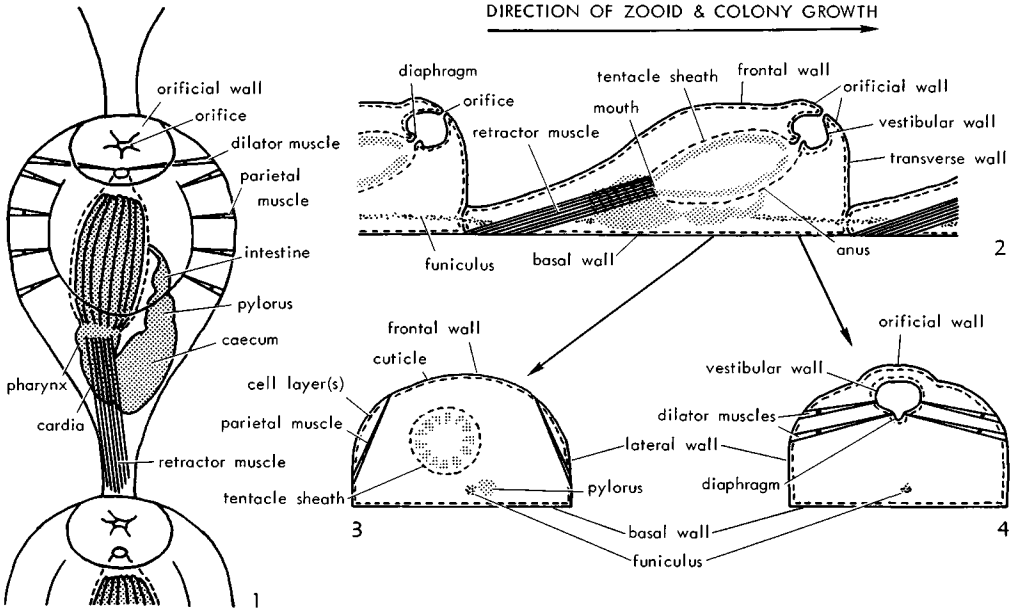


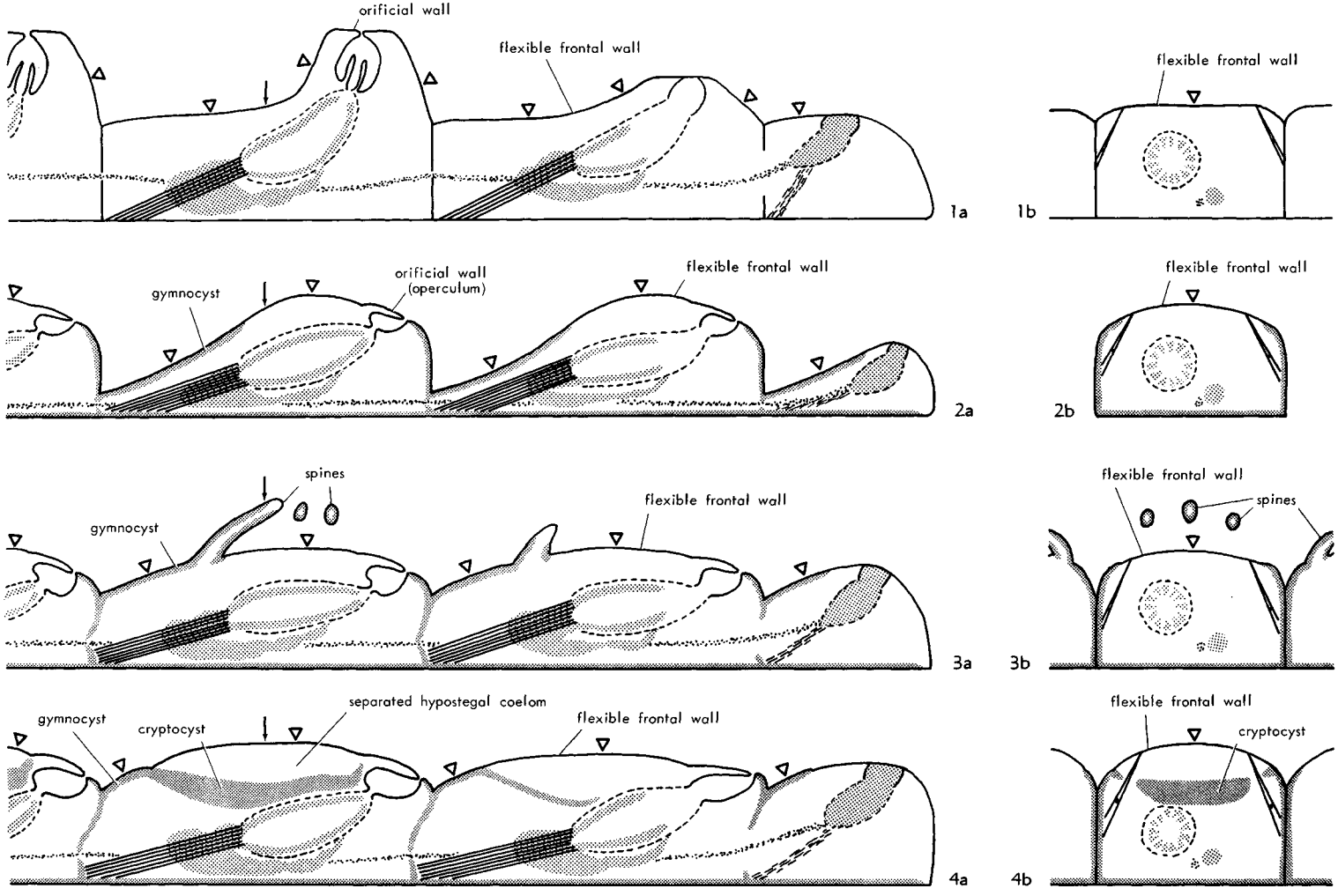
FIG. 64. General features of the class Gymnolaemata. Diagrams of the autozooid of a generalized, uncalcified, encrusting gymnolaemate bryozoan, based on a ctenostomate morphologically comparable to the earliest cheilostomates. Body walls of zooid are virtually entirely exterior walls.——*1.* Frontal view, showing retracted feeding organs and muscles through transparent frontal and orificial walls (compare with Fig. 3, 4).——*2.* Median longitudinal section, showing orientation of basal, transverse, frontal, and orificial walls relative to principal growth direction of zooid and colony.——*3.* Transverse section through frontal wall, retracted lophophore, and gut, showing parietal muscles that depress part of frontal wall in lophophore protrusion.——*4.* Transverse section through orificial wall, vestibule, and diaphragm, showing muscles that dilate vestibule and diaphragm in lophophore protrusion.

growth, and transverse walls oriented subperpendicular to the principal growth direction. A plane of bilateral symmetry bisects the orificial, frontal, transverse, and basal walls, but some contained zooid organs as well as some body wall structures may be markedly asymmetrical.

In this section some characters of the Gymnolaemata are considered in expanded form to explain and illustrate some of the great diversity of morphologies in taxa included in the class. To facilitate correlation of this discussion with the distinguishing characteristics of the class as listed by BOARDMAN, CHEETHAM, and COOK (this revision), characters are considered in approximately the same sequence here, but not all are discussed. Throughout this discussion, an attempt is made to emphasize those characters that have recognizable states in both the Ctenostomata and the Cheilostomata. However, the highly unequal diversity of morphologies in the two orders and their even more unequal representation in the fossil record result in considerable emphasis going to character states, and also some characters, known only in the Cheilostomata. Emphasis on the Cheilostomata is particularly apparent in the sections on calcification, the frontal wall and associated structures, and extrazooidal parts.

CALCIFICATION

The Gymnolaemata apparently comprise the only bryozoan class that includes both uncalcified taxa (Ctenostomata) and calcified taxa (Cheilostomata). In the Cheilostomata, mineral composition and microstructure of



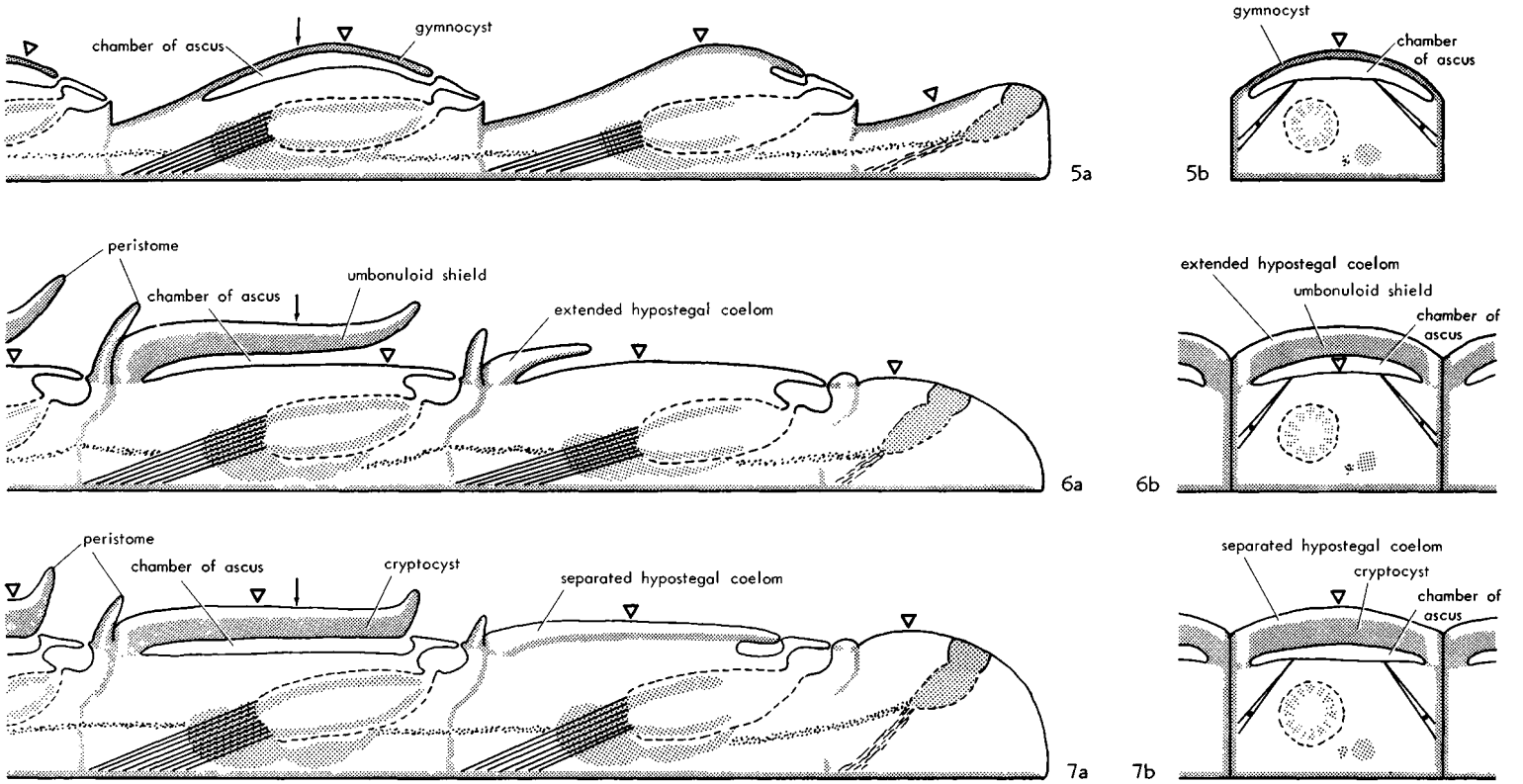


FIG. 65. General features of the class Gymnolaemata. Diagrams of median longitudinal (left) and transverse (right) sections through developing autozooids at and near growing edges of unilaminate (or one layer of bilaminate) simple to complex encrusting or erect colonies. Zooids at more advanced ontogenetic stages lie toward left of longitudinal sections, growing tips at right. Frontal walls of zooids (indicated by open triangles) originate as exposed membranous walls at growing tips and are retained in nearly unmodified form or are modified in various ontogenetic patterns. In all patterns, frontal walls are exterior walls, whether calcified or uncalcified. (Representation as in Fig. 64,*2–4*, but cellular layers of body walls omitted. Calcareous layers finely stippled. Lophophore and gut more coarsely stippled. Positions of transverse sections indicated by vertical arrows.)——*1*. Carnose ctenostomate, showing uncalcified body walls and peristomelike frontal-wall prominence on which orificial wall becomes elevated.——*2*. Simple anascan cheilostomate, showing frontal wall calcified proximally and laterally to form protective shield of

(Continued on p. 153.)

skeletal walls also seem to be more variable than in other calcified Bryozoa (Stenolaemata). If the Cheilostomata evolved from the Ctenostomata, as their comparative morphology and stratigraphic records suggest, calcareous skeletons in the Stenolaemata and the Gymnolaemata evolved independently. (See DZIK, 1975, for a contrasting interpretation of separate evolutionary origins of the Ctenostomata and the Cheilostomata from the Stenolaemata, and inferred close relationship of skeletons in cheilostomates and stenolaemates.)

Body walls in the Gymnolaemata consist of cellular layers and more or less stiffened noncellular layers. The great majority of Ctenostomata has body walls stiffened only by cuticular layers (Fig. 64; 65,*1*; 66,*1–3*), but scattered calcareous particles have been reported in the cuticle of one freshwater species (KRAEPELIN, 1887). With few possible exceptions (BANTA, 1975), Cheilostomata have some body walls of zooids and, where present, of extrazooidal parts reinforced with continuous calcareous layers, in addition to the less stiffened cuticular layers. These calcareous layers collectively form the skeleton of a colony (zoarium). Zooid skeletons (zooecia) in the Cheilostomata can include few, thinly calcified walls (Fig. 65,*2*), or most zooid walls can be calcified; some zooid skeletons continue to receive calcareous deposits throughout zooid life (Fig. 65,*6,7*). A variety of ontogenetic patterns of calcification have been described between these two extremes (see section on the frontal wall and associated structures; and SANDBERG, this revision).

Calcareous layers of both interior and exterior body walls in the Cheilostomata are all exoskeletal, deposited outside the adjacent epidermal cells on the side away from the body cavity (Fig. 67,*1b*). Epidermal cells of different shapes adjacent to cuticular and skeletal layers have been reported to possess secreting structures (TAVENER-SMITH & WILLIAMS, 1972). No morphologic differences have been observed between epidermal cells adjacent to skeletal layers of different mineral composition in the same skeleton (BANTA, 1971). Skeletal layers of both interior and exterior walls have been reported to lie between noncellular organic sheets and to contain noncellular organic networks continuous in places with these sheets (BANTA, 1969). The cuticular nature of outer organic sheets on calcified parts of exterior walls and of the whole sequence of organic sheets on uncalcified parts of exterior walls suggests that the cheilostomate skeleton can be regarded as **intracuticular** (BANTA, 1969).

Skeletons in the Cheilostomata are composed of either calcite or aragonite (**monomineralic skeleton**), or a combination (**bimineralic skeleton**). At present, the Cheilostomata are the only order in the phylum in which bimineralic skeletons are known. The generally consistent results obtained in analyzing cheilostomate species from different geographic areas suggest that skeletal composition is closely controlled genetically (POLUZZI & SARTORI, 1975). In some bimineralic species, there is evidence that aragonite : calcite ratios may increase in populations living in warmer water (RUCKER & CARVER, 1969), but the ratio can be strongly affected by ontogenetic gradients within colonies (CHEETHAM, RUCKER, & CARVER, 1969; SANDBERG, 1971).

More than 150 cheilostomate species have been analyzed (POLUZZI & SARTORI, 1975, and references listed therein), over 80 percent from recent specimens only. Of the analyzed species about 50 percent have all skeletal layers composed of calcite, about 40 percent include both calcite and aragonite, and about 10 percent have only aragonite. In bimineralic species in which intracolony distribution of skeletal components has been studied, calcite and aragonite are present in discrete layers. In many of these species, aragonite layers succeed calcite layers ontogenetically in some zooecial walls, whereas other walls in the same zooecium remain entirely calcitic throughout ontogeny (Fig. 67,*1c*; 68,*1d,1e,2*) (SANDBERG, 1971). In a few species, zooecial walls have been found to be calcitic and associated with aragonitic extrazooidal skeleton

in the same zoarium (GREELEY, 1969; RUCKER & CARVER, 1969).

At higher taxonomic levels, there appears to be less consistency in skeletal composition than within species. The species analyzed are distributed in more than 80 genera, of which only 33 include more than one analyzed species. Of these 33 genera, 11 include only calcitic species and 3 only aragonitic species. Monomineralic skeletons thus appear to be in a slight minority (about 40 percent) among analyzed genera, in contrast to their majority (about 60 percent) among analyzed species. The 19 bimineralic genera analyzed appear to be of two kinds. In 11 genera all species analyzed are bimineralic. The remaining 8 genera include some species of entirely calcitic composition and some of either mixed or entirely aragonitic composition. Examples of all four compositional types of genera are known among both anascan and ascophoran Cheilostomata. Calcite is apparently dominant among anascan species (47 species calcitic, 4 aragonitic, 10 mixed), and the earliest cheilostomates known are morphologically similar to modern anascan species having entirely calcitic skeletons. Bimineralic and aragonitic compositions are more common among ascophoran species, but a large proportion of ascophorans retain calcitic skeletons (36 species calcitic, 20 aragonitic, 41 mixed). The oldest fossil cheilostomates in which aragonite has been reported are of Late Eocene age (GREELEY, 1969; RUCKER & CARVER, 1969). Even diagenetically altered fossil cheilostomate skeletons have been found to contain relic inclusions and textural evidence of their original composition and microstructure (SANDBERG, 1975a), and so it is at least theoretically possible to interpret stratigraphic distribution of skeletal composition in cheilostomate lineages.

Diversity in skeletal composition in the Cheilostomata is paralleled by, but not precisely correlated with, a variability in skeletal microstructure (SANDBERG, 1971, 1973). Calcitic skeletal layers can assume a variety of structures, from laminated subparallel to wall surfaces (Fig. 68,*1a–c*; 69,*1d–f*; 70,*1a–*

FIG. 65. *(Explanation continued from page 151.)*

exterior origin (gymnocyst) and exposed and flexible distally and medially to form hydrostatic membrane to which parietal muscles are attached.——3. Complex anascan, showing frontal wall as in *2*, but with flexible part overarched by calcified tubular exterior-walled outpocketings (spines) forming a protective (costal) shield. Spines contain extensions of body cavity of zooid.——*4*. Complex anascan, showing frontal wall as in *2*, but with the flexible part underlain by a frontal shield of interior origin (cryptocyst) protecting feeding organs. The cryptocyst grows between layers of epidermis folded into the body cavity of the zooid, partitioning the cavity into an overlying hyposteegal coelom and an underlying principal body cavity. The cryptocyst is thickened ontogenetically by addition of skeleton to its frontal surface by epidermis underlying hypostegal coelom.——5. Simple ascophoran cheilostomate, showing frontal wall calcified, except at the proximal margin of the operculum, to form a protective shield of exterior origin (gymnocyst), beneath which the ascus becomes infolded from the proximal margin of operculum. Parietal muscles are attached to the flexible floor of the ascus (compare with the simple anascan in *2*).——6. Complex ascophoran cheilostomate, showing the flexible frontal wall, with attached parietal muscles, forming the floor of the ascus overarched by a protective shield of exterior origin (umbonuloid shield). The umbonuloid shield grows on the basal side of a double-walled outfold, within which is the extension of the zooid body cavity (hypostegal coelom), and it is attached to vertical walls by interior wall segments. The umbonuloid shield is thickened ontogenetically by addition of skeleton to its frontal surface by epidermis underlying the extended hypostegal coelom. The calcified layer of peristome is an extension of umbonuloid shield (compare with complex anascan in *3*).——7. Complex ascophoran cheilostomate, showing exposed uncalcified frontal wall underlain by cryptocyst grown as in *4*, protecting feeding organs. However, the cryptocyst is underlain by an ascus infolded from the proximal margin of the operculum, as in *5*. Parietal muscles are attached to the floor of the ascus. The cryptocyst is thickened ontogenetically by addition of skeleton to its frontal surface by epidermis underlying separated hypostegal coelom. The calcified layer of the peristome is continuous with the cryptocyst, but of exterior origin, formed after attachment of the rim of the cryptocyst to the membranous frontal wall (compare with complex anascan in *4*).

c,2) to fibrous parallel or transverse to wall surfaces (Fig. 71,*1a–d*). Most aragonitic layers are fibrous either parallel or transverse to wall surfaces (Fig. 67,*1c–e*; 68,*1d,1e*; 72,*1,2*), but more blocky textures have recently been recognized in aragonitic cheilostomates (for further discussion, see SANDBERG, this revision).

BODY WALLS OF AUTOZOOIDS

In living gymnolaemate colonies, some or all zooids can be observed to possess body-wall features associated with protrusible lophophores and thus be recognized as autozooids. In colonies of many taxa all autozooids are capable of feeding at some stages of their ontogeny. In colonies of a few taxa, some autozooids concerned with sexual reproduction, and possibly other functions, remain incapable of feeding. Nonfeeding sexual autozooids have recognizable body-wall differences from feeding autozooids in all but a few species. Colonies in most gymnolaemate taxa also have nonfeeding polymorphs without protrusible lophophores and with distinctive body wall features reflecting this major difference from autozooids.

Body walls expressing morphology by which autozooids can be recognized in the Gymnolaemata are principally the orificial wall defining the orifice through which the lophophore is protruded and the frontal wall and associated structures functioning in the hydrostatic system for protruding the lophophore. In the Cheilostomata, this morphology commonly is reflected in the skeleton. Basal and vertical walls of autozooids may be different from or similar to those of polymorphs and thus are less significant in recognizing the major functional organization of a colony.

Basal walls.—Basal walls generally are present in gymnolaemate autozooids and serve to enclose basal sides of body cavities, to support vertical walls, and to provide attachment for some muscles or organs. Zooids may lack basal walls in some taxa having erect cylindrical colony branches, along the axes of which lateral walls of zooids meet directly to enclose zooids basally (CHEETHAM, 1971, pl. 12, fig. 1–4). Zooids may also lack basal walls in some taxa in which autozooids were budded frontally from hypostegal coeloms of subjacent autozooids and are enclosed basally by frontal structures of subjacent zooids.

Most commonly basal walls of autozooids are exterior walls, which extend the body of the colony (Fig. 64; 65; 68,*1a*). Exterior basal walls may be present in both encrusting and erect parts of colonies. Exterior basal walls of zooids most commonly form the surfaces by which encrusting colonies adhere to other objects (Fig. 69,*1a–c*; 71,*1a–d*; 72,*1,2*) or to overgrown parts of the same colony (Fig. 68,*1a–e*). Encrusting bases of erect colonies and of initial portions of free-living colonies can also adhere to objects by means of exterior basal walls of variable numbers of founding zooids (HÅKANSSON, 1973, pl. 2, fig. 4). Medial surfaces of erect **bilaminate** branches in colonies of many taxa and of subcylindrical branches in colonies of some taxa are formed by exterior basal walls of zooids adherent back to back (Fig. 70,*1a*; 73,*1a,b,2a,c*). Reverse surfaces of unilaminate branches in colonies

FIG. 66. Carnose ctenostomates.——*1,2. Elzerina blainvilli* LAMOUROUX, rec., S. Afr.; *1,* Port Alfred, Pondoland, erect branching colony composed of alternating rows of autozooids (az) and kenozooids (kz), BMNH 1922.8.23.1, ×9; *2a,b,* Durban, *a,* autozooids with operculumlike orificial wall (ow), flexible frontal wall (fw), tentacles (te), and retractor muscle (rm), embryos (emb) brooded in diverticulum of tentacle sheath (ts), diaphragm marked by pleated collar (pc), long. sec., *b,* autozooids flanked by kenozooids (kz), parietal muscles (pm) of autozooids originating on cuticular lateral walls (lw) and inserting on frontal wall (fw), transv. sec.; both BMNH 1942.8.6.25, ×120.——*3. Alcyonidium nodosum* O'DONOGHUE & DE WATTEVILLE, rec., S. Afr.; autozooid with orificial wall (ow) slightly elevated on frontal wall (fw) to which parietal muscles (pm) are attached, diaphragm marked by pleated collar (pc), diaphragmatic dilator muscles (dm) originating on cuticular transverse wall (tw); long. sec., BMNH 1942.8.6.1, ×120.

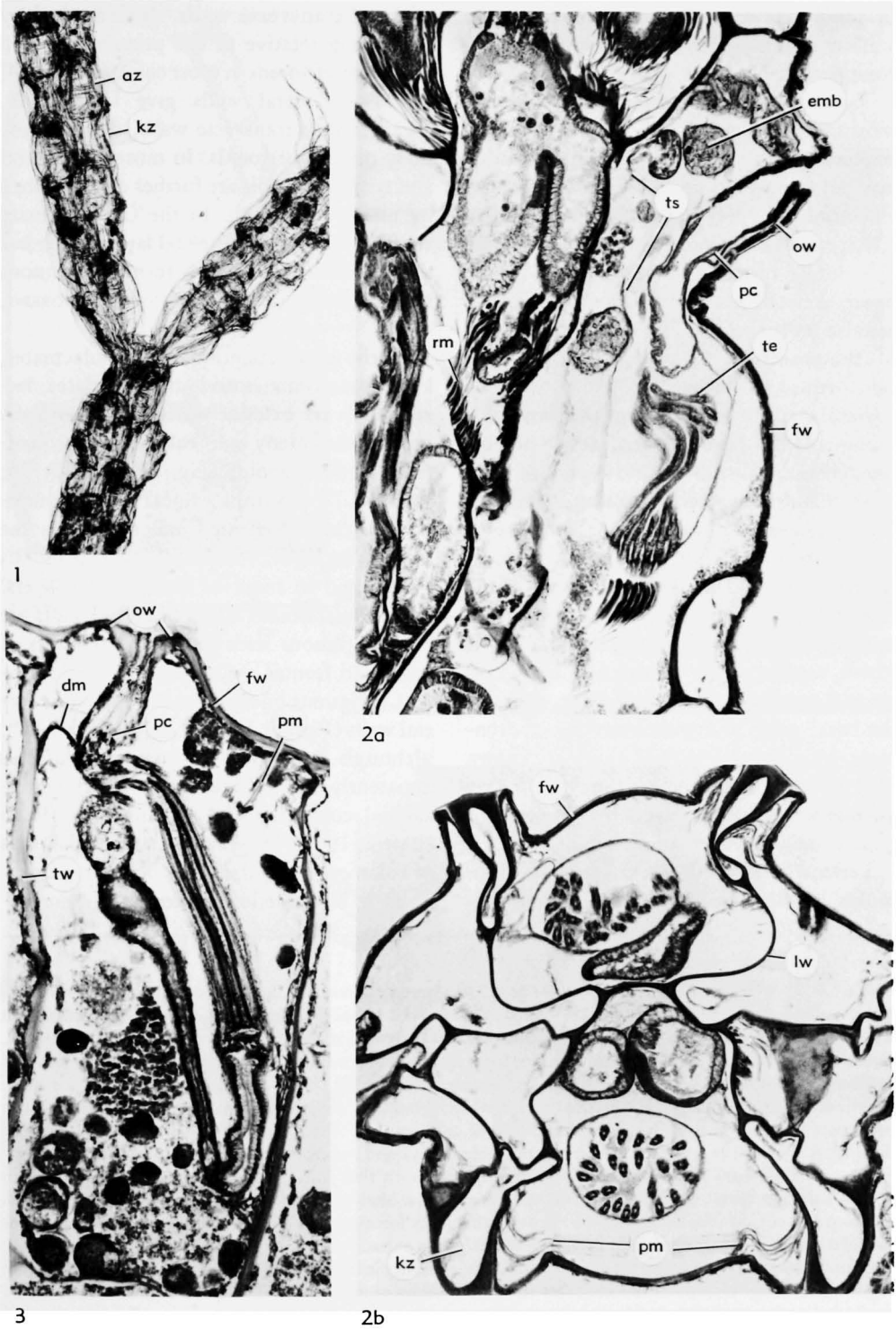


FIG. 66. *(For explanation, see facing page.)*

of some taxa are formed by exterior basal walls of zooids in direct contact with the environment.

Exterior basal walls have at least outermost cuticular layers continuous from zooid to zooid within a budding series (**multizooidal layers**). In the Cheilostomata, exterior basal walls may be calcified (Fig. 68,*1a–e*; 71,*1a–d*) or wholly or partly uncalcified (Fig. 69,*1f*; **basal window** of BANTA, 1968). Some skeletal layers of calcified basal walls are also multizooidal (Fig. 69,*1d*; basal plate of BOARDMAN & CHEETHAM, 1969; **basal platform** of SANDBERG, 1971).

Basal walls of zooids in parts of some free-living colonies beyond initial adherent portions (HÅKANSSON, 1973) and in parts of some erect colonies beyond encrusting bases (see Fig. 78,*1a–c*) are interior walls, which partition preexisting body cavity of the colony. In free-living and unilaminate erect colonies (see Fig. 78,*1a–c*), interior basal walls of zooids adjoin interior extrazooidal walls which, together with extrazooidal body cavity and exterior extrazooidal walls, separate the basal walls of zooids from the environment. Interior basal walls of zooids are known only in the Cheilostomata, in which they include some skeletal layers that are continuous among zooids (multizooidal).

Vertical walls.—Vertical walls of autozooids in the Gymnolaemata comprise **lateral** and **transverse walls**, distinguished by orientation relative to the principal growth directions of zooids in most colonies (Fig. 64, 65, 74). Lateral walls give length and, together with transverse walls, depth to the body cavities of zooids. In most taxa lateral and transverse walls are further distinguished by modes of growth. In the Cheilostomata vertical walls include skeletal layers, some but not all of which commonly form a continuous structural unit (zooecial lining of SANDBERG, 1971).

In the great majority of gymnolaemates, both ctenostomates and cheilostomates, lateral walls are exterior walls that extend the body of the colony in **lineal series** of sequentially budded zooids (Fig. 65; 66,*1,2*; 75; 76,*1–4*; 77). Within a lineal series, bounding cuticles and, in the Cheilostomata, some skeletal layers of lateral walls are continuous from zooid to zooid as multizooidal layers. Some multizooidal layers of lateral walls are also continuous with multizooidal layers of basal and frontal walls (Fig. 69,*1f*; 73,*1a–c*). Contiguous lineal series have separate lateral walls (Fig. 69,*1f*; 70,*1,2*; 71,*1c,d*; 72,*2*), although contiguous bounding cuticles apparently can be breached to form interzooidal communication organs (Fig. 70,*2*) (BANTA, 1969) or confluent extrazooidal parts of colonies (Fig. 70,*1b*; see below).

In a few cheilostomates and ctenosto-

FIG. 67. Ascophoran cheilostomate.——*1a–e. Margaretta cereoides* (ELLIS & SOLANDER), rec., Naples, Italy; *a,* growing tip (gt) with distalmost membranous wall of lineal series nearly intact, distal zooid with walls nearly complete, but outer part of transverse wall (tw) not calcified and operculum not formed, cryptocyst (cry) nearly complete, but without underlying ascus, proximal part of frontal wall (fw) calcified to form gymnocyst (gy), the shape of which reflects future brood chamber to be roofed by peristome of proximal zooid (compare *d*), proximal zooid with operculum (op) and ascus (fa, floor of ascus), but peristome little developed, long. sec.; *b,* detail of cryptocyst of distal zooid with adjacent epidermis on both sides, outer side overlain by hypostegal coelom (hy) and membranous frontal wall (fw), long. sec.; *c,* cryptocyst of more proximal zooid in same segment with thin initial skeletal layer (il) nonstaining in Feigl's solution (presumed calcitic) and thick superficial skeletal layer (sl) staining in Feigl's solution (aragonitic), cuticle of frontal wall (fw) heavier than that forming roof of ascus (ra) immediately adjacent to underside of cryptocyst without intervening epidermis or body cavity, hypostegal coelom (hy) extending into funnel-shaped depression (fd) at base of which is uncalcified spot (un) in initial skeletal layer (compare Fig. 82,*3b*), long. sec.; *d,* brood chamber (bch) floored by gymnocyst (gy) of distal zooid and roofed by outfolded peristome (of) surrounding operculum (op) of maternal zooid, long. view; *e,* ordinary autozooid with heavily reinforced operculum (op) supported circumferentially by skeleton and surrounded by outfolded peristome (of), opening to ascus (oa; fa, floor of ascus) passing through frontal wall (fw) and cryptocyst (cry), long. sec. (for diagram of zooid, see Fig. 7); USNM 242573, *a,d,e,* ×100, *b,c,* ×300.

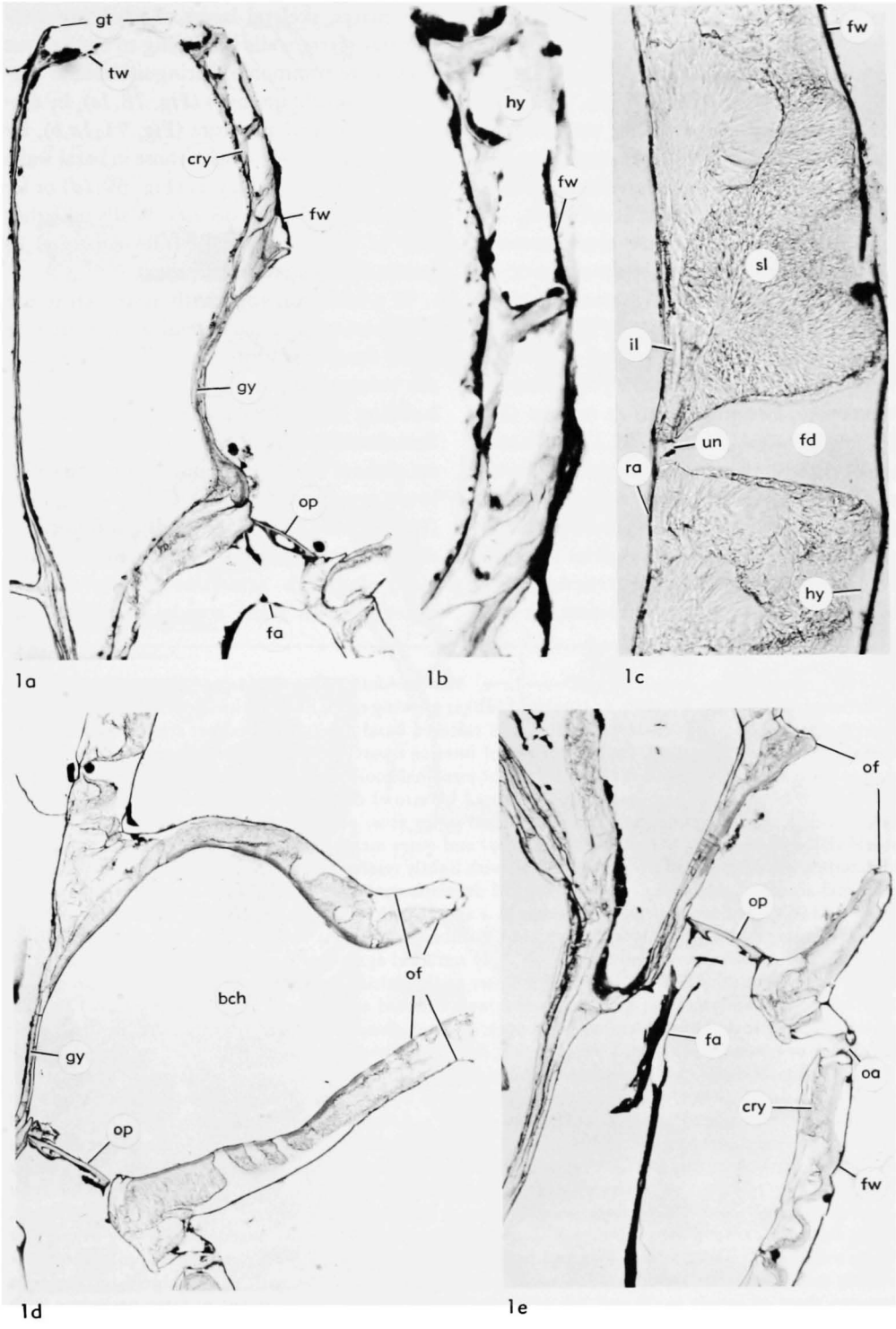


FIG. 67. *(For explanation, see facing page.)*

mates, transverse walls are also largely exterior, formed as extensions of lateral walls enclosing distal ends of zooids (Fig. 64; 65,*2*; 69,*1e*; 74,*1*; 75,*1–6,8*; 77,*1a*). Near basal margins of transverse walls, small interior walls extend from inner surfaces to form pore plates of communication organs, separating zooid body cavities within lineal series.

Transverse walls in most cheilostomates, and apparently in most ctenostomates, are developed principally as extensive interior walls, completely partitioning body cavities within lineal series (Fig. 65,*1,3–7*; 74,*2*; 75,7). These walls contain pore plates of interzooidal communication organs (Fig. 67,*1e*; 68,*1a,b,e*; 71,*1a,b*; 78,*1a,e*). Basally, laterally, and frontally, interior transverse walls are attached to inner surfaces of multizooidal layers of exterior walls (Fig. 68,*1a–e*; 69,*1d,e*). Parts of these exterior walls can become incorporated in the transverse walls by expansion in a frontal direction. In cheilostomates, skeletal layers of adjoining interior transverse walls belonging to contiguous zooids are commonly distinguishable at distinct organic boundaries (Fig. 78,*1e*), by distinctive skeletal structure (Fig. 71,*1a,b*), by continuity of laminae with those in basal walls above multizooidal layers (Fig. 69,*1d*) or by a combination (Fig. 68,*1d*). Walls on either side of a boundary vary from subequal to markedly unequal in thickness.

In a few taxa, apparently restricted to the Cheilostomata, both lateral and transverse walls develop as interior walls partitioning the colony body cavity within multizooidal budding zones similar to those in the class Stenolaemata (Fig. 74,*3*; 75,9). Skeletal layers of these walls form a unit continuous with interior basal walls (Fig. 78,*1a–c*) (HÅKANSSON, 1973). Frontally, interior vertical walls are attached to multizooidal cuticles, although attachment may remain incomplete on some zooidal margins in at

FIG. 68. Ascophoran cheilostomates.——*1a–e. Metrarabdotos* (*Uniavicularium*) *unguiculatum cookae* CHEETHAM, rec., Ghana, W. Afr.; *a,* distal bud (db) at growing tip of lineal series of encrusting intracolony overgrowth, membranous frontal wall (fw) and calcified basal (bw) and proximal transverse (tw) walls enclosing body cavity of bud, frontal portion of interior transverse wall attached to outer membranous wall to form skeletal rim for orificial wall (ow) of proximal zooid, calcified exterior peristomial wall (now collapsed, original position of inner end indicated by arrow) continued from transverse wall as part of distal bud; *b,* next proximal zooid in same lineal series as *a,* with extensive, thin umbonuloid frontal shield (fs), and overlying hypostegal coelom (hy) and outer membrane, all overarching proximal portion of membranous frontal wall (fw), orificial wall with lightly reinforced operculum (op) complete, but more proximal organs of zooid (dev) in early stage of development; *c,* proximal part of zooid just proximal to distal bud in a lineal series neighboring that in *a* and *b,* with frontal shield (fs) and associated soft parts in an early stage of development, overarching membranous frontal wall (fw); *d,* fully developed zooid just proximal to zooid in *b,* with lophophore fully retracted against proximal transverse wall by retractor muscle (rm), tentacle sheath (ts) attached at outer end to calcified shelflike extension of distal transverse wall beneath operculum (op), distal transverse wall attached at outer end to orificial wall (ow) to form skeletal rim, frontal shield extending over operculum to complete peristome, which has denticles (pd) that check operculum, when open, from closing chamber between frontal shield and membranous frontal wall (fw), frontal shield two-layered, with initial layer (il) of calcite and superficial layer (sl) of aragonite, hypostegal coelom (hy) communicating with principal body cavity of zooid through pore plate (ppl) plugged with cells placed at margin of frontal shield; *e,* fully developed zooid, third proximal to zooid in *c,* with thickened superficial aragonitic layer (sl) of frontal shield, occlusor muscle (om) at lateral margin of calcified distal shelf (see *d*) inserting on operculum (op), funicular strand (fu) attached to cells passing through pore plate (ppl) in transverse wall; all long. secs., USNM 243229, ×100.——*2. Metrarabdotos* (*Uniavicularium*) *unguiculatum unguiculatum* CANU & BASSLER, rec., Norseman Sta. 348, off Bahia, Brazil, 50 m; encrusting colony with distal bud (db; compare with *1a*) and autozooids near growing edge; right distal zooid with transverse wall (tw) and frontal shield (fs) with marginal pore plates (ppl), at approximately same stage of development as zooid in *1c,* left central zooid with frontal shield intermediate between those of zooids in *1b* and *1d,* with initial calcitic layer (il) extended to form peristome with denticles (pd), proximal zooids on left and right at comparable stages to zooid in *1e,* with frontal shields and peristomes covered by superficial aragonitic layer (sl), adventitious avicularia (av) with pivotal bars (piv) for mandibles partly or completely developed; frontal view, USNM 243230, ×50.

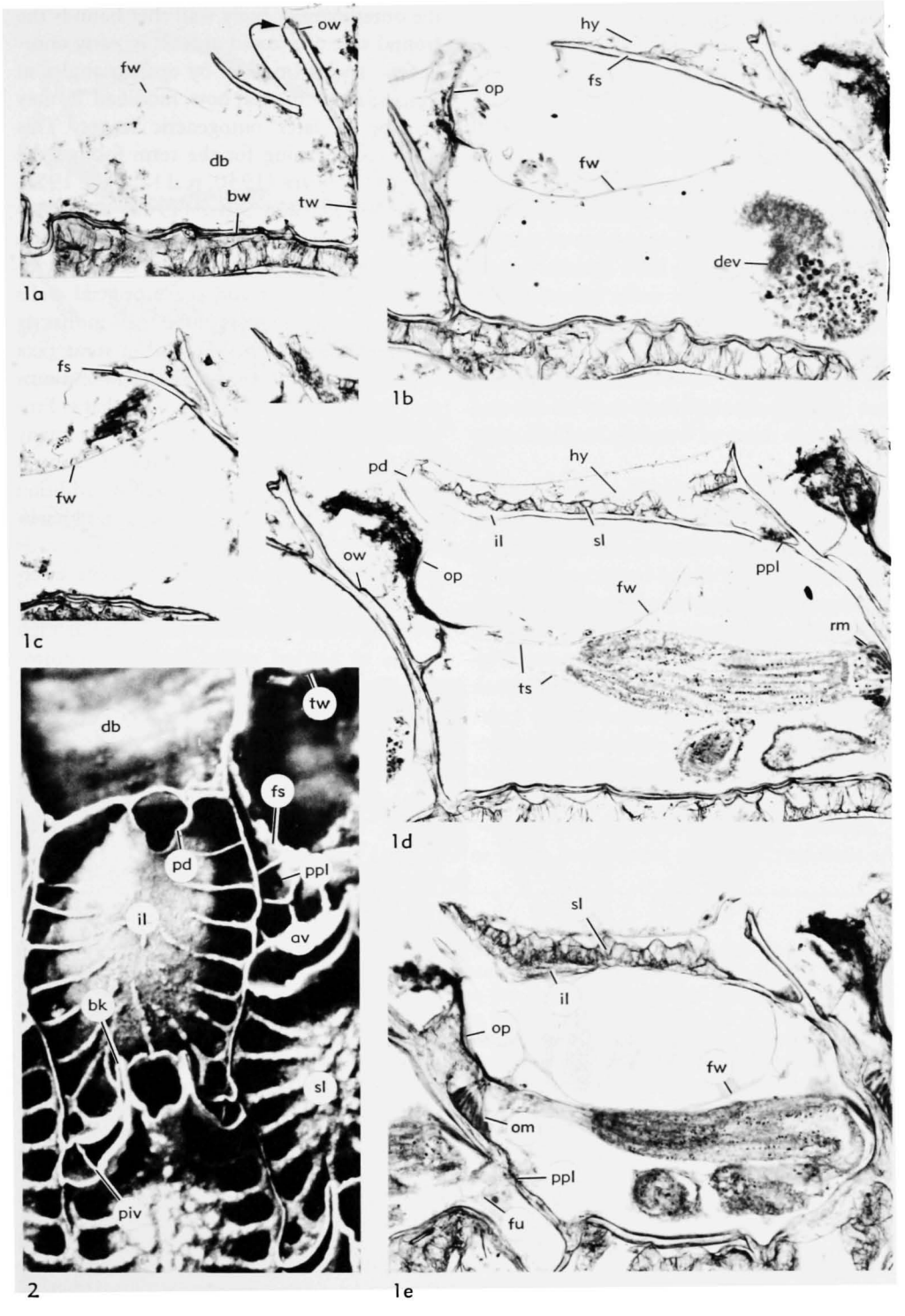


FIG. 68. *(For explanation, see facing page.)*

least one genus (Fig. 78,*1c*).

In a few cheilostomates, autozooids in subsequent zones of astogenetic change and repetition have all exterior vertical walls, which extend the body of the colony in a frontal direction (Fig. 79,*3*; **frontal budding**). In some taxa, these frontally budded zooids originate from hypostegal coeloms of underlying zooids in the primary zone of astogenetic repetition, which have exterior lateral and interior transverse walls oriented with respect to zooidal growth direction as in most other cheilostomates (BANTA, 1972). Vertical walls of some adventitious polymorphs (see below, polymorphism) may be oriented similarly to those of frontally budded autozooids.

Interior vertical walls are grown cooperatively by contiguous zooids, as indicated by microstructure of skeletal (Cheilostomata) or cuticular (Ctenostomata) layers and by complementary configuration (Fig. 74,*3*) (both orders). Configurations of exterior walls of zooids may suggest either autonomous (Fig. 74,*1*; 76,*1–4*; 77,*1,2*) or cooperative growth (Fig. 74,*2*; 80,*2*). Development of interzooidal communication organs in both interior and exterior vertical walls in most taxa also involves cooperative growth.

Frontal walls and associated structures.—As used here, the term frontal wall refers to the outer exterior body wall that bounds the frontal side of a zooid at least in early ontogenetic stages (marked by open triangles in Fig. 65), no matter how modified it may become in later ontogenetic stages. This restricted meaning for the term follows the usage of HARMER (1930, p. 112, 113; 1957, p. 655–657) and SILÉN (1942, p. 5), although several different usages are common in the literature. Frontal walls in the Gymnolaemata support and space orificial walls of autozooids, function directly or indirectly in lophophore protrusion, and in some taxa can be partly calcified to increase colony support and protect retracted zooid organs. Protective and supportive structures in many taxa, however, form a complex of features associated with the frontal wall in addition to any forming parts of the frontal wall itself.

Frontal walls characterize autozooids throughout the Ctenostomata and the Cheilostomata (Fig. 65). In most taxa frontal walls are subparallel to orificial walls and at high angles to vertical walls. In some ctenostomates and a few cheilostomates that have erect tubular autozooids arising from stolonlike bases, frontal walls are at high angles to orificial walls and subparallel to vertical walls. In these taxa, few of which are known as fossils, the distinction between frontal and vertical walls may be arbitrary.

FIG. 69. Ascophoran cheilostomate.——*1a–f. Hippothoa hyalina* (LINNÉ), rec., Cape Cod Bay, U.S. Fish Comm., 1879, 50 m; *a,* growing tip of lineal series with distal bud (db) and autozooid with operculum (op), calcified frontal wall (gy, gymnocyst) and partly formed organs, but no ascus, long. sec.; *b,* next proximal, feeding autozooid with fully formed organs and ascus reaching nearly to proximal end (oa, opening of ascus; fa, floor of ascus), frontal buds (fb) with exterior basal walls (bw) present on both feeding autozooids, long. sec.; *c,* still more proximal, feeding autozooids with partly (fb) and fully developed, frontally budded maternal autozooids, fully developed maternal zooid with ascus (fa, floor of ascus; oa, opening to ascus), brood chamber (bch) enclosed by part of maternal zooid outfolded (of) from distal wall, upper side of brood chamber roof protecting embryo (emb) calcified but with uncalcified spots (un), long. sec.; *d,* junction of basal (bw) and transverse (tw) walls of contiguous zooids in lineal series (distal to top), initial skeletal layers (il) of basal wall continuous between zooids (multizooidal), long. sec.; *e,* distal bud (distal to right) with cuticular and skeletal layers of frontal wall (gy, gymnocyst) continuous with layers of transverse wall of proximal zooid, long. sec.; *f,* laterally contiguous and frontally budded (fb) zooids with bounding cuticles and skeletal layers continuous from basal to lateral to frontal walls (gy, gymnocyst), skeletal layers pinching out medially in basal wall of zooid to right (bw), some basal and lateral wall laminae continuing into interior wall partitioning pore chamber (pch) from principal body cavity (coel) of zooid, transv. sec.; all USNM 242568, *a–c,* ×100, *d,f,* ×800, *e,* × 300.——*2. H. hyalina,* New England coast; encrusting colony with feeding autozooids (az), frontal buds (fb), female autozooids with brood chambers (bch), and male autozooids; frontal view, USNM 242569, ×50.

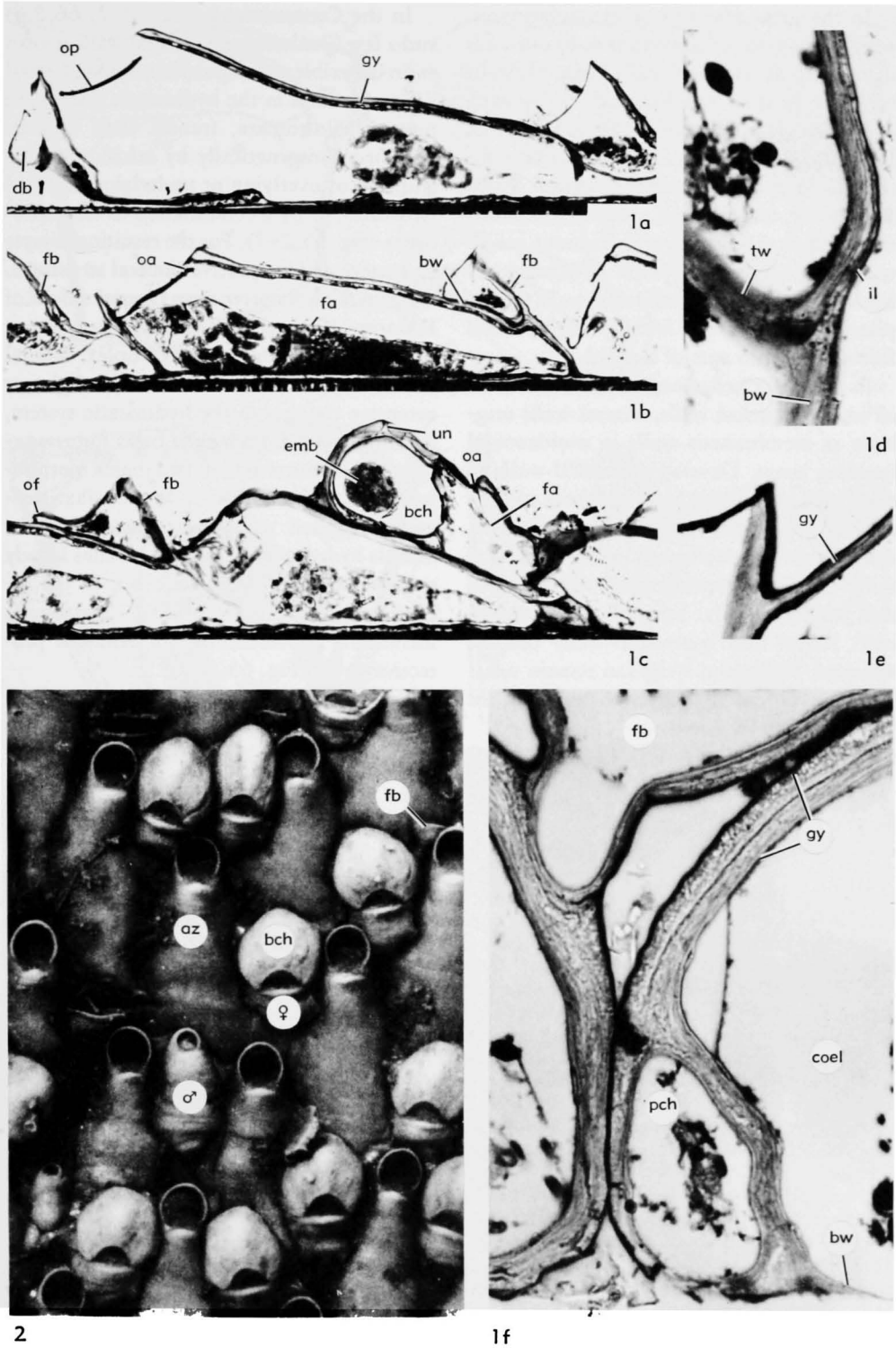


FIG. 69. *(For explanation, see facing page.)*

In the great majority of gymnolaemates, which have some or all vertical walls of zooids developed as exterior walls, frontal walls originate as membranous walls at growing tips of lineal budding series (Fig. 65; 68,*1a*). Laterally, frontal walls in these taxa are continuous in part with exterior vertical walls. Proximally, frontal walls are initially continuous with frontal walls of contiguous zooids within the same lineal series. Attachment of interior components of transverse walls or pore plates transforms the initially multizooidal frontal wall into part of a zooid.

In the few Cheilostomata known to have all interior vertical walls, frontal walls originate as membranous walls in multizooidal budding zones. Developing frontal walls in these taxa are continuous with those of contiguous zooids both laterally and proximally. Attachment of developing interior vertical walls transforms multizooidal frontal walls into parts of zooids. In most of these taxa, both lateral and transverse walls become attached, but lateral walls can remain unattached and parts of body cavities confluent laterally (Fig. 78,*1a–c*).

In the Ctenostomata (Fig. 65,*1*; 66,*2,3*) and a few Cheilostomata, frontal walls remain entirely flexible and exposed throughout zooid life to function in the hydrostatic system. In most Cheilostomata, frontal walls become modified ontogenetically by calcification, by addition of overlying or underlying calcified structures, or by a combination of these processes (Fig. 65,*2–7*). For the resulting diverse protective and supportive skeletal structures, the general descriptive term **frontal shield** of HARMER (1902, p. 282) is employed here.

Growth of simple to complex frontal shields is partly correlated with slight or extensive changes in the hydrostatic system, conventionally forming the basis for arranging the Cheilostomata in two major morphologic groups (see Table 2). In most taxa generally assigned to the anascan group, the flexible hydrostatic membrane remains largely to partly exposed (Fig. 65,*2–4*). In the ascophoran group, the flexible hydrostatic membrane is overlain by a continuous protective cover (Fig. 65,*5–7*).

Frontal shields in the Cheilostomata comprise skeletal layers of either exterior or inte-

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FIG. 70. Ascophoran cheilostomate.——*1a–c. Metrarabdotos* (*Biavicularium*) *tenue tenue* (BUSK), rec., Caroline Sta. 68, off NE. coast of Puerto Rico, 20 m; *a,* ordinary autozooid just proximal to growing edge of erect bilaminate colony, basal (bc) and lateral (lc) cuticles of calcified exterior walls forming boundaries with zooids in adjacent lineal series, membranous exterior frontal wall (fw) attached by parietal muscles (pm) to lateral walls, overarched by umbonuloid frontal shield (fs) with overlying hypostegal coelom (hy) and outer membranous wall (compare with Fig. 68,*1a–c*), communication between principal body cavity of zooid and hypostegal coelom through pore plate (ppl), section at midlength of zooid; *b,* part of same colony about 2.5 cm proximal to *a,* ordinary autozooids and adventitious avicularia (av) occluded by extrazooidal skeleton (exs), initial calcitic layer of frontal shield (il) overlain by superficial layer (sl), also calcitic, in turn succeeded without interruption by calcitic extrazooidal skeleton, extrazooidal skeletal layers continuous from zooid to zooid, terminating lateral walls (lc, lateral cuticle) so that hypostegal coelom (hy) confluent around circumference of branch; *c,* part of same colony between *a* and *b,* with ordinary autozooids and adventitious avicularia (av), frontal shield of autozooid with superficial layer (sl) within cuticular boundaries; all transv. secs., USNM 243231, ×100.——*2. M.* (*B.*) *t. tenue,* same data as *1*; brooding autozooid about 0.5 cm from growing edge of erect bilaminate colony, embryo (emb) contained in chamber (bch) outside body cavity of colony, surrounded by inner membranous wall (im) and calcified frontal shield (fs), uncalcified spots (un) in frontal shield of brood chamber open into hypostegal coelom (hy); transv. sec., USNM 243232, ×100.——*3a,b. M.* (*B.*) *t. tenue,* same data as *1*; *a,* part of erect bilaminate colony about 1 cm from growing edge, with ordinary and brooding autozooids (bch, brood chamber) and two forms of adventitious avicularia, smaller avicularia (av) similar to those in *1b* and *1c* and with simple pointed mandibles, larger avicularia with rounded, bilobed mandibles (md), cuticular boundaries (lc, lateral cuticle) discernible between some but not all zooids; *b,* some of same zooids as in *a* with outer membranous walls and avicularian mandibles removed, pointed and bilobed beaks (bk) conforming in shape to mandibles, both types of avicularia with complete pivotal bars (piv) for mandibles; both frontal views, USNM 243233, ×50.

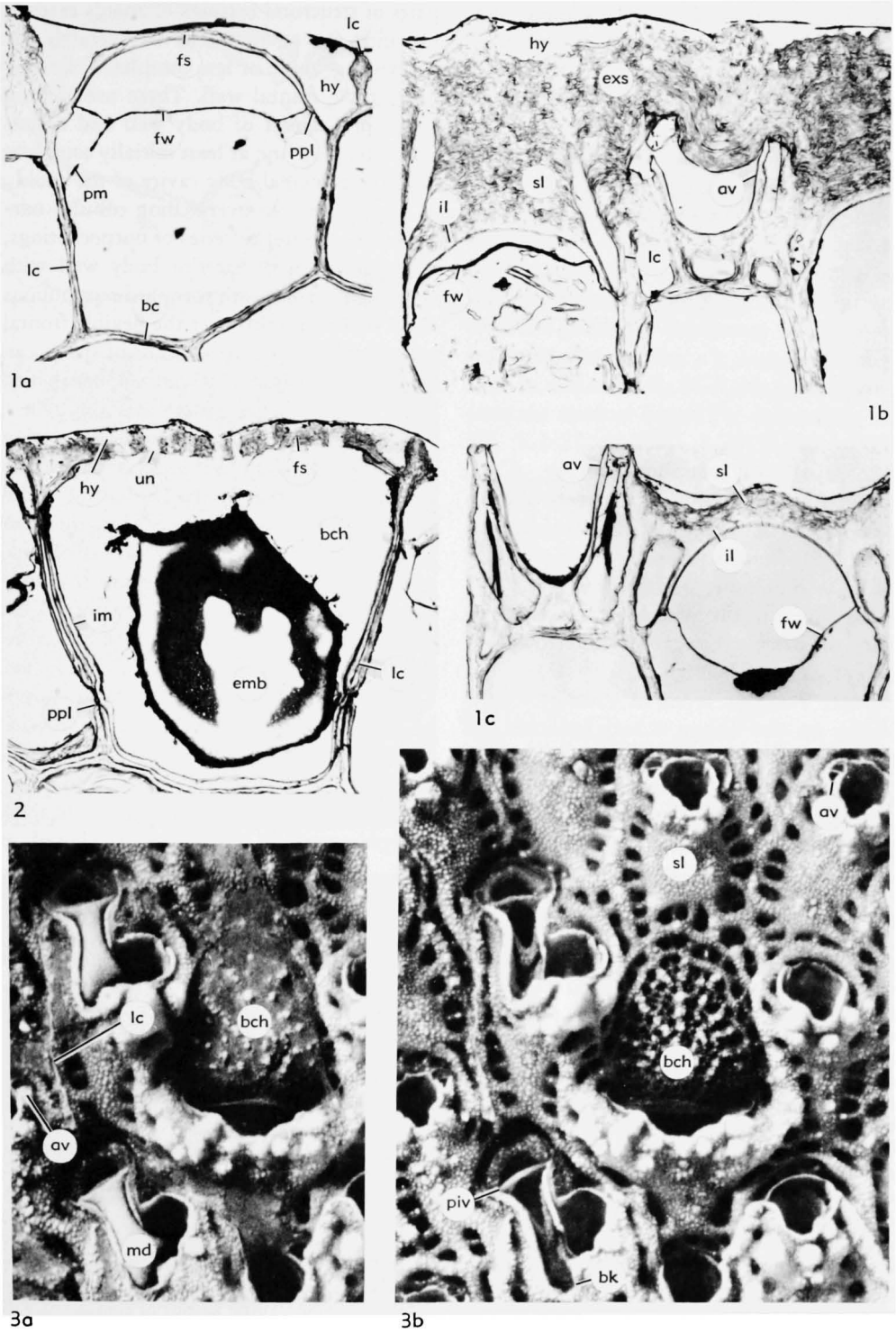


FIG. 70. *(For explanation, see facing page.)*

rior walls. In some taxa (for example, Fig. 65,*4*) a frontal shield can combine both exterior and interior elements. The ultrastructural characteristics of exterior and interior frontal shield elements are discussed and illustrated by SANDBERG (this revision).

The simplest type of frontal shield is part of the exterior frontal wall itself (**gymnocyst** of HARMER, 1930, p. 113). As the membranous frontal wall develops at a colony growing tip, calcification follows just proximally to produce a gymnocyst extending from the proximal margin of a zooid varying distances distally (Fig. 65,*2–5*). Gymnocysts of similar appearance are found in both anascans (Fig. 65,*2–4*; 72,*4*; 76,*1–4*; 77,*1,2*; 80; 81,*1,2,4*) and ascophorans (Fig. 65,*5*; 67,*1a,d,e*; 69). Prominent transverse growth banding is commonly evident on outer surfaces of gymnocystal shields (Fig. 69,*2*; 76,*1,2*) (SANDBERG, 1976, pl. 2, fig. 1, 2). Relationship of the gymnocyst to the hydrostatic membrane, however, is different in the two groups (see below).

More complex types of exterior frontal shields are also known in both anascans and ascophorans. These shields differ in the two groups, not only in relation to the hydrostatic system, but also in morphology. In both groups complex exterior frontal shields are parts of structural features of zooids extending into the environment to overarch the preexisting, more or less completed, flexible part of the frontal wall. These overarching extensions consist of body wall and a contained body cavity, at least initially confluent with the principal body cavity of the zooid.

In anascans, an overarching tubular outpocketing (**spine**) or series of outpocketings, each consisting of exterior body wall with contained coelom, can form a discontinuous cover (**costal shield**) over the flexible frontal wall (Fig. 65,*3*). Exterior walls of spines can be entirely calcified, or contain uncalcified spots, or be calcified except in a ring where attached to the frontal wall of the supporting zooid. Body cavities of spines can be broadly confluent with that of the supporting zooid (Fig. 71,*1c,d*) or have openings into the zooidal coelom constricted by body wall (SILÉN, 1942a), in that case being difficult to distinguish from some kinds of polymorphs. In fossils, unfused spines are rarely preserved intact, but **spine bases** are commonly recognizable where they emanate from continuous skeletal structures (Fig. 77,*2*). In some taxa, spines can be fused at medial ends and intermittently along lengths to produce a more nearly continuous costal shield (**cribrimorph** structure; Fig. 71,*1–3*). Fused or

FIG. 71. Cribrimorph cheilostomates.——*1,2. Figularia figularis* (JOHNSTON), rec., Medit.; *1a–d,* Oran, Alg., 100 m; *a,* maternal autozooid with heavily reinforced operculum (op) continuous with membranous frontal wall (fw; collapsed proximally); overarching costal shield (cs) composed of internally thickened spinelike costae, brood chamber (bch) floored by gymnocyst (gy) and roofed by part of costal shield (cs) of distal autozooid, long. sec., ×100; *b,* communication organ in thinned portion (ppl, pore plate) of transverse wall (distal to left), initial granular layer (il) marking boundary between zooids in lineal series and approximately reaching bounding cuticle of basal wall (bc), long. sec., ×300; *c,* brood chamber (bch) floored by gymnocyst (gy) and roofed by costal shield (cs) with narrow central cavities (ccc) opening into body cavity (coel) of autozooid distal to maternal zooid, transv. sec., ×100; *d,* contacting lateral walls of zooids in contiguous lineal series, bounding cuticles (lc) continuous with bounding cuticle of basal wall (bc), narrow central cavities of costae (ccc) opening into body cavities of zooids, all skeletal layers nonstaining in Feigl's solution (presumed calcitic), transv. sec., ×300, all USNM 242565; *2,* Naples, Italy, encrusting colony with autozooids having costal shield (cs) margined by gymnocyst (gy) and interzooidal avicularium with complete pivotal bar (piv) for mandible, autozooids with condyles (cd) for hinging operculum, frontal view, USNM 242566, ×50.——*3. Figularia figularis* (JOHNSTON)?, rec., specimen labeled Albatross Sta. D3987, presumably from Hawaiian Is., 100 m; encrusting colony with maternal and nonmaternal autozooids having dimorphic opercula (op) and interzooidal avicularia having elongate mandibles (md) and smaller membranous postmandibular area (pmd), costal shields of autozooids with openings (ofc) between fused costae and uncalcified spots (un) near peripheral ends of costae (covering cuticle broken in proximal zooid), covering of brood chamber (bch) part of costal shield of autozooid distal to maternal zooid; frontal view, USNM 242567, ×50.

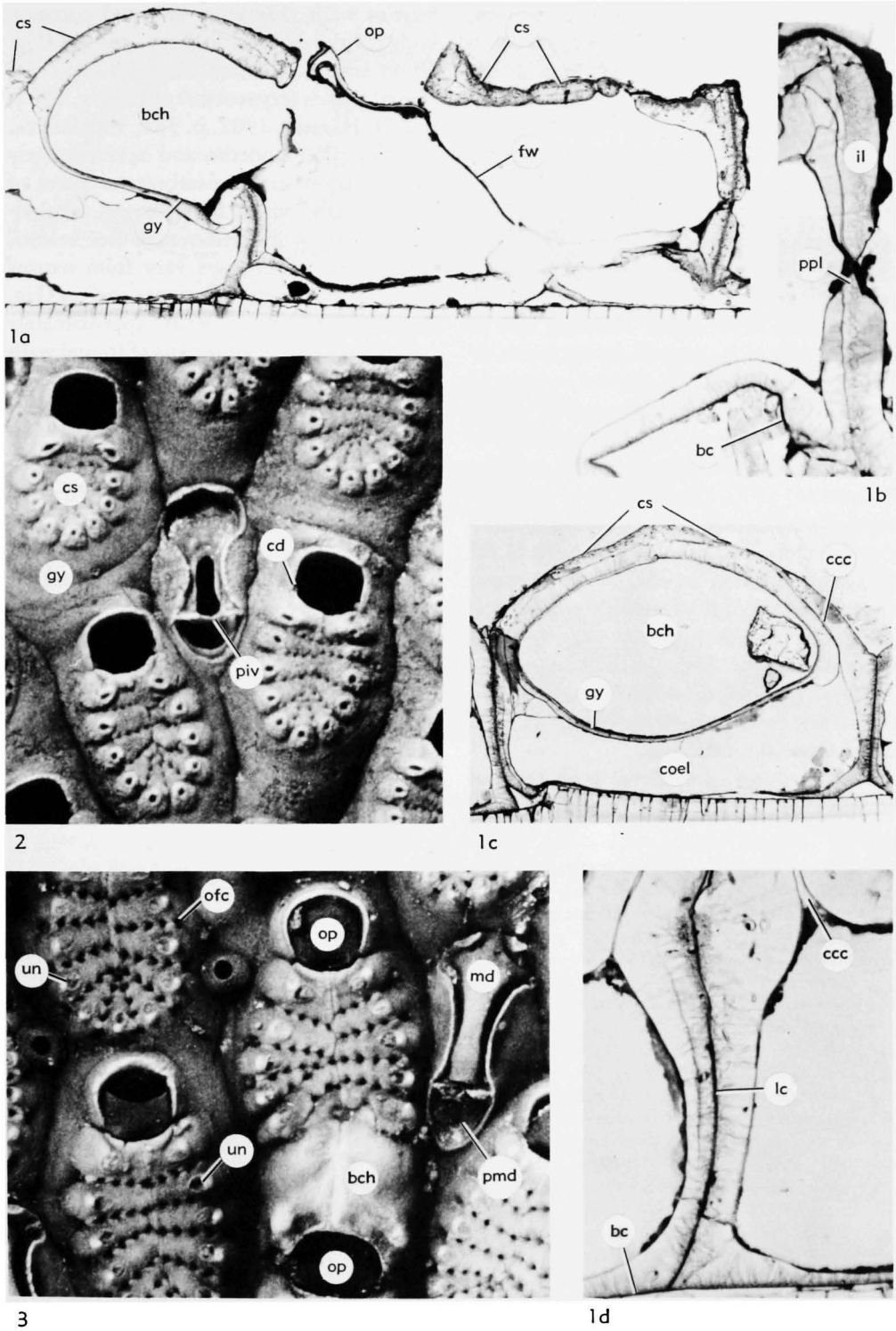


FIG. 71. *(For explanation, see facing page.)*

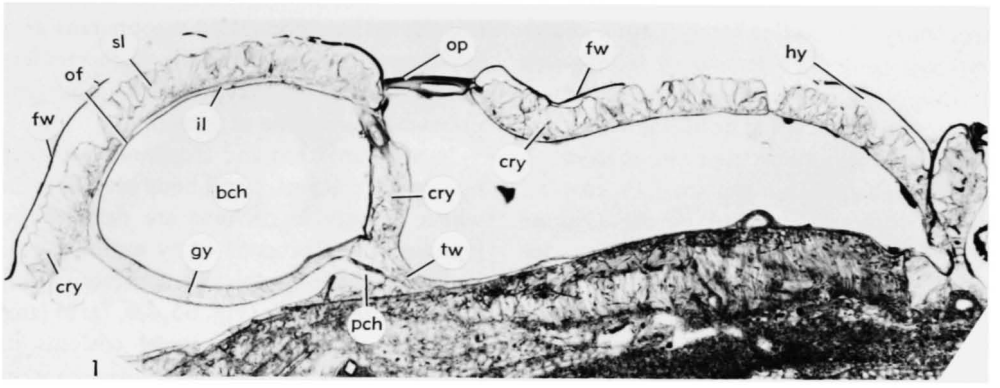
unfused spines in these anascans emanate from a marginal gymnocyst of variable extent, with which their skeletal layers are structurally continuous (Fig. 71,*1c,d*) (Tavener-Smith & Williams, 1972, p. 111).

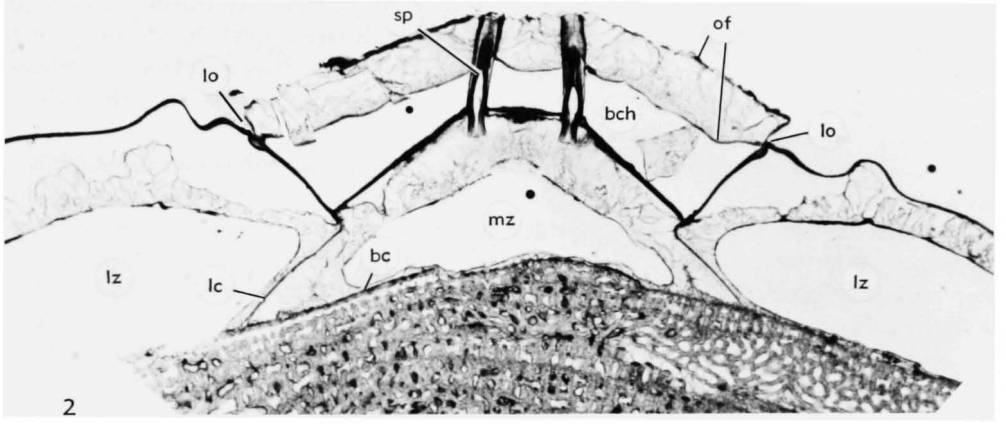
In ascophorans, a double-walled exterior outfold with contained coelom can overarch the flexible frontal wall from its proximal and lateral margins (Fig. 65,6; 68,*1b–e*; 70,*1a–c*). The overarching outfold isolates the frontal wall laterally and proximally from the vertical walls of the zooid. The body wall on the basal side of the outfold, facing the membranous frontal wall, is calcified to form an exterior frontal shield (**umbonuloid shield** of Harmer, 1902, p. 332), the underside of which can show prominent growth banding (Sandberg, 1976, pl. 1, fig. 2–4; this revision). An umbonuloid shield is attached laterally and proximally to vertical walls of the zooid by calcified interior wall segments (Sandberg, 1976; this revision) forming pore plates of communication organs (Fig. 68,*1b,d,e*) or more extensive walls (Sandberg, 1976, pl. 1, fig. 2). Body wall on the exposed frontal side of the overarching outfold remains uncalcified (Fig. 68,*1b–e*).

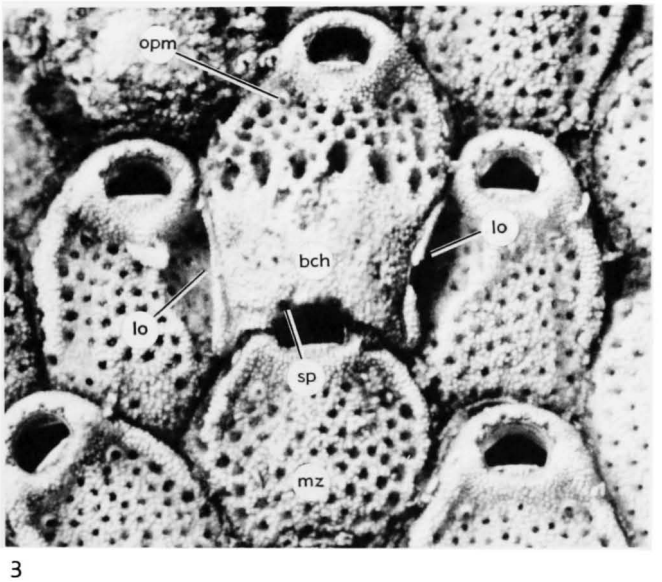
Frontal shields also develop as parts of interior walls that grow into and partition body cavities of zooids in both anascans (Fig. 65,*4*) and ascophorans (Fig. 65,7). These frontal shields (**cryptocysts** of Jullien, 1881, p. 274; Harmer, 1902, p. 331, 333; Banta, 1970, p. 39) underlie and approximately parallel preexisting, membranous parts of frontal walls, which bear varying relationships to the hydrostatic system (see below). In anascans, cryptocysts vary from narrow proximal and lateral calcareous shelves (Fig. 80,*3*) to calcareous walls approximately coextensive with flexible parts of frontal walls (Fig. 72,*1,3,4*). In ascophorans, cryptocysts are all approximately coextensive with uncalcified parts of frontal walls (Fig. 67,*1a*; 73,*1a,c*; 78,*1a*). In both anascans (Fig. 72,*1–3*; 81,*3*) and ascophorans (Fig. 78,*1a,c*) cryptocysts can be attached directly to vertical walls laterally and proximally. In many anascans (Fig. 80,*3*) cryptocysts are attached to marginal gymnocysts of varying extent. Some ascophorans (Fig. 67,*1a*) also can have gymnocysts to which cryptocysts are attached proximally.

Different types of frontal shields in anascan and ascophoran cheilostomates differ in potential for ontogenetically increasing in

Fig. 72. Anascan cheilostomate.——*1–4. Monoporella nodulifera* (Hincks), rec., Jolo Light, Jolo, Philip., 40 m; *1,* Albatross Sta. D5142, maternal autozooid with heavily reinforced operculum (op) attached to flexible frontal wall (fw) overlying hypostegal coelom (hy) and cryptocyst (cry), cryptocyst with membranous attachment to frontal wall just proximal to operculum, distal part of cryptocyst continuous with inner calcified part of transverse wall (tw) and subparallel to outer membranous part of transverse wall, which faces brood chamber (bch), brood chamber enclosed by parts of distal zooid, floored by proximal gymnocyst (gy) and roofed by outfold (of) originating at junction of gymnocyst, cryptocyst (cry), and membranous frontal wall (fw), lower side of outfold calcified, its initial skeletal layer (il) continuous with gymnocyst and superficial layer (sl) continuous with cryptocyst, all of which stain in Feigl's solution (aragonitic), zooids communicating through pore chambers (pch), long. sec., USNM 242561, ×100; *2,* Albatross Sta. D5142, cluster of polymorphic autozooids forming brooding structure; brood chamber (bch) roofed by outfold (of) from distal zooid through openings in which spines (sp) on distal margin of maternal zooid (mz) protrude, membranous frontal walls of laterally adjacent zooids (lz) fitted into lateral openings (lo) of brood chamber, lateral cuticles (lc) separating zooids, are continuous with basal cuticle (bc), transv. sec., USNM 242562, ×100; *3,* Albatross Sta. D5142, encrusting colony with cluster of polymorphic autozooids forming brooding structure, brood chamber (bch) part of zooid distal to maternal zooid (mz), from which spines (sp) project through brood-chamber roof, cryptocysts of laterally adjacent zooids with shapes reflecting lateral openings (lo) of brood chamber, cryptocysts of all polymorphic autozooids with distolateral openings for parietal muscles (opm), frontal view, USNM 242563, ×50; *4,* Albatross Sta. D5137, self-encrusting part of colony with growing edge having brood chamber in early stage of development, distal bud (db) with gymnocyst (gy) to form floor of brood chamber, gymnocysts lacking in other zooids, lateral opening of brood chamber reflected in shape of cryptocyst of lateral zooid with opening for parietal muscle (opm) deeply set, zooids communicating through pore chambers (pch); frontal view, USNM 242564, ×50.







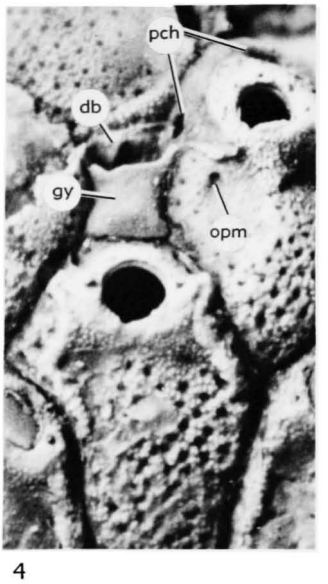


FIG. 72. *(For explanation, see facing page.)*

complexity. Depending on the nature of soft parts overlying their frontal surfaces, some kinds of frontal shields undergo little ontogenetic change except at or near growing tips of colonies, and others continue to undergo extensive changes far proximal to growing tips. With respect to this potential, some exterior frontal shields are similar to interior frontal shields, even though differing in their initial mode of growth.

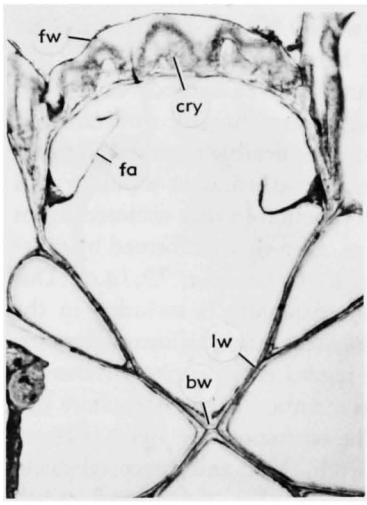
Gymnocysts and costal frontal shields are covered frontally only by contiguous outermost cuticle (Fig. 69,*1e*; 71,*1a,c*). Cuticles and most or all calcareous layers are continuous with those of vertical walls to which the shields are attached (Fig. 69,*1f*; 71,*1c*). Like the calcareous layers of vertical walls, these frontal shields cease to be deposited relatively early in zooid life and characteristically remain relatively thin.

Cryptocysts and umbonuloid frontal shields are overlain frontally by cellular layers and intervening body cavity, with outermost cuticle (Fig. 67,*1b,c*; 68,*1b–e*; 70,*1a–c*; 73,*1a,c*; 78,*1a–c*). The body cavity overlying a cryptocyst is a separated part of the original body cavity of a zooid (Fig. 65,*4*,7), and it is to this structure that the term hypostegia or **hypostegal coelom** was originally applied by JULLIEN (1881, p. 276). The latter term has been broadened, however, to include an extension of the original body cavity of a zooid overlying an umbonuloid frontal shield (BANTA, 1970, p. 39; TAVENER-SMITH & WILLIAMS, 1972, p. 110) (see Fig. 65,*6*). Earlier, CALVET (1900, p. 166) also regarded this cavity in umbonuloid ascophorans as a hypostegal coelom, but termed the underlying frontal shield a cryptocyst, without distinguishing its mode of growth.

In most anascans and ascophorans having hypostegal coeloms, zooid body cavities from which hypostegal coeloms are derived (by ingrowth of cryptocysts or by outfolding of body wall) are completely separated from those of other zooids (Fig. 65,*4*,*6*,7). In later ontogenetic stages, hypostegal coeloms in some ascophoran genera may coalesce to form extrazooidal parts (see below) and in other ascophoran genera may expand to become frontal buds (see below). In one ascophoran (Fig. 78,*1c*) hypostegal coeloms overlying cryptocysts are confluent laterally throughout ontogeny.

Cryptocysts and umbonuloid frontal shields have initial layers that are continuous with some skeletal layers in vertical walls, marginal gymnocysts, or interior wall segments attached to vertical walls (Fig. 68,*1b–e*). Initial layers of anascan and some ascophoran cryptocysts clearly show deposition on both basal and frontal sides (TAVENER-SMITH & WILLIAMS, 1970, 1972; BANTA, 1970, 1971; SANDBERG, 1973), but in ascophorans deposition on the basal surface is soon cut off by development of the ascus (see below). The thin initial layer of some ascophoran cryptocysts shows little evidence of basal deposition (Fig. 67,*1a–e*; 73,*1c*; 78,*1a*). Initial layers of umbonuloid shields, which are of exterior origin, are deposited from the frontal side only (Fig. 68,*1b,c*). (For further discus-

FIG. 73. Ascophoran cheilostomate. *Margaretta cereoides* (ELLIS & SOLANDER), rec., Naples, Italy.——*1a–c*. Walls; *a*, fully developed autozooid about 0.5 cm proximal to growing tip of branch, with membranous frontal wall (fw) intact and overlying completed cryptocyst (cry); floor of underlying ascus (fa) complete but broken; zooid contacting three others at branch axis along its basal (bw) and lateral (lw) walls, and two others outward from axis along its lateral walls, transv. sec., ×100; *b*, detail of basal wall–lateral wall junctions at axis of branch near growing tip, zooid contact along cuticles of basal (bc) and lateral (lc) walls, transv. sec., ×300; *c*, detail of frontal wall–lateral wall junctions in proximal part of zooid near growing tip of branch, cryptocyst (cry) fully developed but proximal to end of ascus, cuticles of lateral walls (lc) continuous with outer cuticular layer of frontal wall (fw), transv. sec., ×300; all USNM 249641.——*2a–c*. Walls; *a*, detail of basal wall–lateral wall junctions at axis of branch near growing tip, with cuticles of basal (bc) and lateral (lc) zooidal walls, gold-plated polished etched transv. sec., SEM, ×1,000; *b*, lateral walls of two contacting zooids, same section as *a*, ×1,000; *c*, detail of *a*, ×6,600; all USNM 249642.



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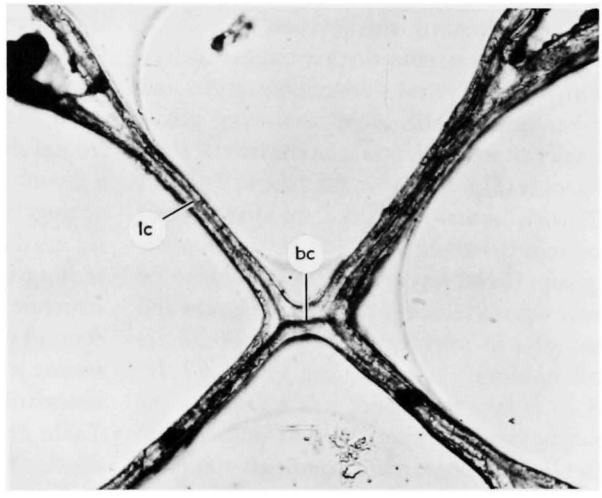

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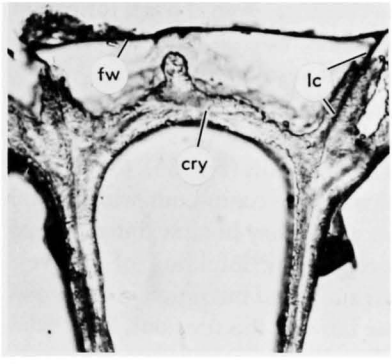

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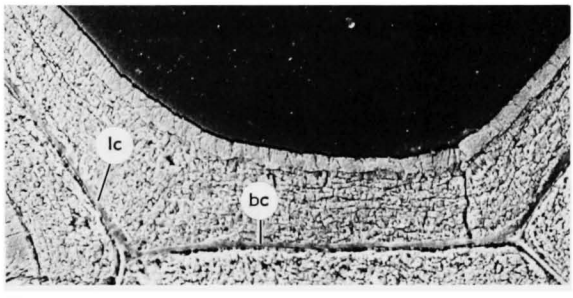
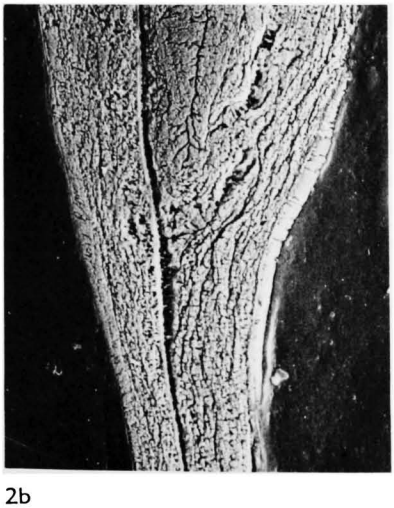


2a



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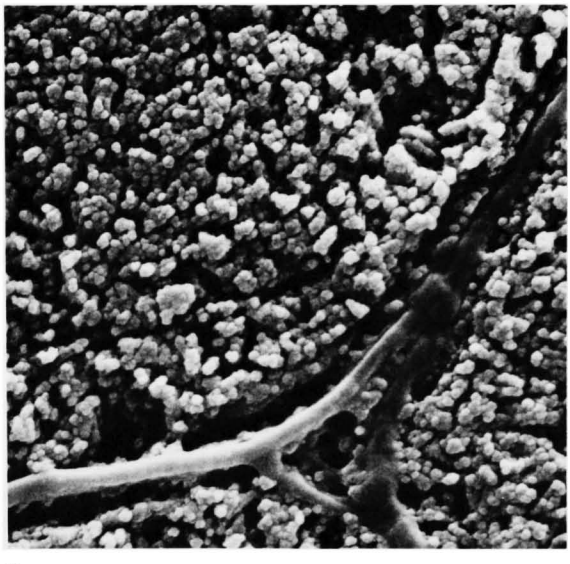


2c

FIG. 73. *(For explanation, see facing page.)*

sion, see SANDBERG, this revision.)

Cellular layers and the hypostegal coelom overlying the frontal sides of cryptocysts and umbonuloid shields allow continued accretion of calcareous deposits on the frontal sides of zooids (Fig. 67,*1a–e*; 68,*1d,e,2*; 70,*1b,c*; 82,*3a,c*), in many species long after deposition in other zooid walls has ceased. Resulting **superficial layers** of these shields can be many times as thick as their **initial layers** and can differ in microstructure (Fig. 70,*1b,1c*) and mineral composition (Fig. 67,*1c*; 68,*1d,e*) (see SANDBERG, this revision). The morphology of cryptocysts and umbonuloid shields can become correspondingly complex, with markedly differing appearance in proximal and distal parts of a colony. With the formation of an ascus, fully formed zooids having cryptocysts and umbonuloid shields can become almost identical in appearance (Fig. 65,6,7) (COOK, 1973b).

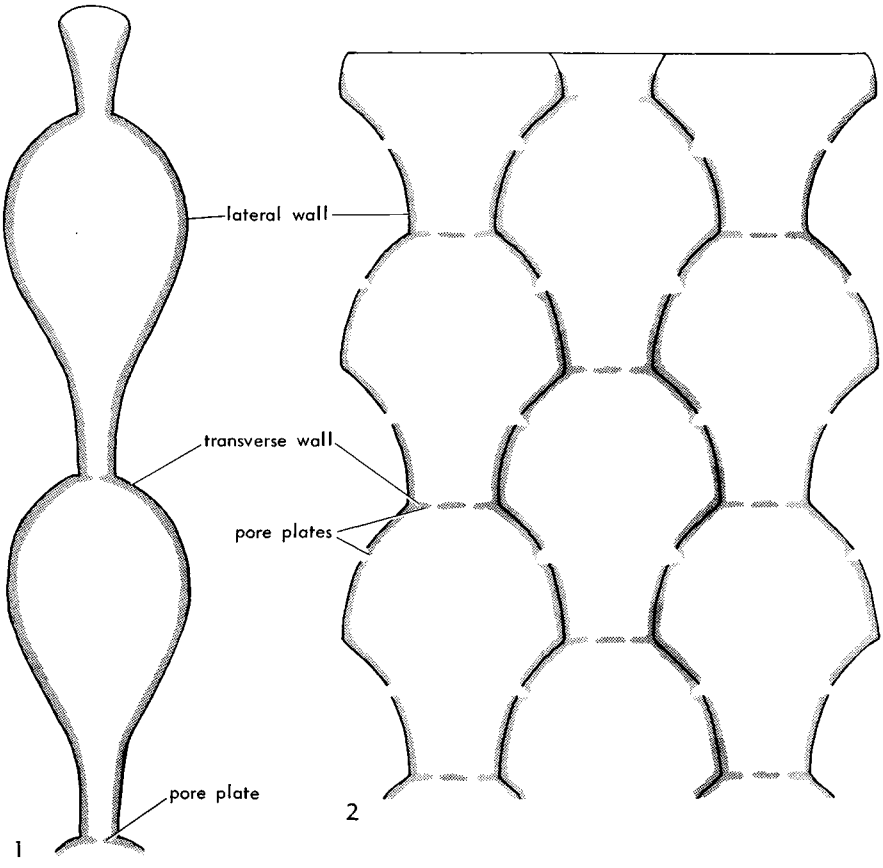
In ascophorans having gymnocysts and cryptocysts part of the membranous frontal wall becomes infolded beneath the shield after initial calcification is completed. Infolding can occur at the proximal margin of the orificial wall (Fig. 65,5,7; 69,*1a,b*; 78,*1a*) or proximal to the orificial wall on the frontal wall (Fig. 67,*1e*). Infolding forms an exterior-walled, flexible-floored sac, the **ascus** (Fig. 65,5,7), which opens to the exterior to function in the hydrostatic system. In most species examined, the cuticular roof of the ascus is subjacent to the calcareous frontal shield (Fig. 67,*1c,e*) or possibly lacking (TAVENER-SMITH & WILLIAMS, 1970), the intervening cellular layers apparently having migrated with the proximally advancing edge of the developing ascus. In a few species, the roof of the ascus is separated wholly (COOK, 1975) or in part (Fig. 78,*1a*) from the frontal shield by cellular layers and intervening body cavity.

In cheilostomates having umbonuloid frontal shields, the flexible frontal wall floors a chamber nearly identical in topology and analogous in function to that enclosed by an infolded ascus, even though formed by overarching (Fig. 65,6; 68,*1d,e*; 70,*1a,c*). This structure conventionally is included in the concept of the ascus, and cheilostomates possessing it are regarded as ascophorans but not necessarily as members of the Ascophora (see Table 2). The corresponding space between the flexible frontal wall and the costal shield in some anascans (Fig. 65,*3*) and cribrimorphs (Fig. 71,*1a*) is not generally regarded as an ascus chamber, even though formed in much the same way as the chamber in umbonuloid cheilostomates.

Orificial walls.—In all gymnolaemates, autozooids have orificial walls at or near distal ends of frontal walls (Fig. 65). Outer sides of orificial walls are continuous with frontal walls, from which they become differentiated during ontogeny by infolding of the vestibular wall and distal migration in the growing bud (see LUTAUD, this revision). Inner sides of orificial walls are continuous with vestibular walls (Fig. 66,*2a*).

In most ctenostomates and a few cheilostomates, an orificial wall consists of a radial series of body-wall folds, or a single continuous ringlike fold (Fig. 64). When closed, the orifice is slitlike or puckered and contained within the margins of the orificial wall. In the overwhelming majority of cheilostomates and in some ctenostomates (Fig. 66,*2a*), an orificial wall consists principally

FIG. 74. Cheilostomate vertical walls. Diagrams of sections through vertical walls of developing zooids at and near colony growing edges. Outermost cuticles are represented by solid lines, calcareous layers are stippled, and cellular layers and other soft parts are omitted.——*1.* Uniserial cheilostomate having virtually all exterior vertical walls except for pore plates of communication organs (compare with Fig. 65,*2,5*). ——*2.* Multiserial cheilostomate having interior transverse and exterior lateral walls, and lateral as well as transverse pore plates. Each zooid of a laterally contiguous pair has a separate bounding cuticle shown as a single line (compare with Fig. 65,*3,4,6,7*).——*3.* Multiserial cheilostomate having entirely interior vertical walls.



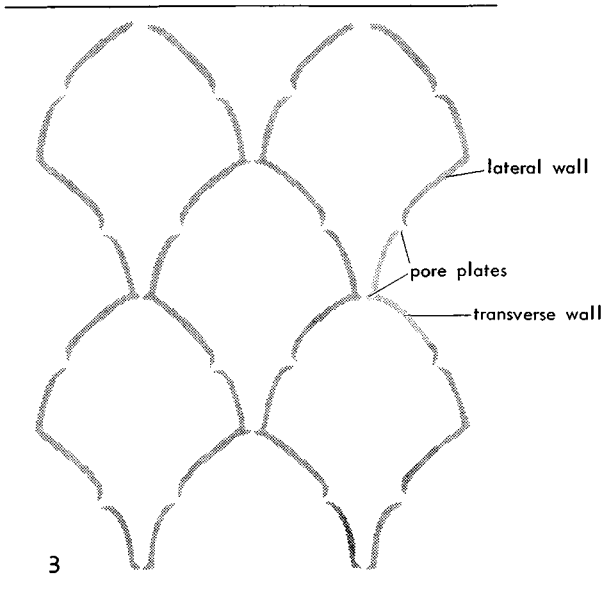


FIG. 74. *(For explanation, see facing page.)*

of a distally directed flaplike fold. When closed, the orifice in these taxa is a crescentic slit defined by the distal and lateral margins of the orificial wall. A weaker, opposing distal flap of wall can be present in a few ctenostomates (Fig. 66,*2a*) and cheilostomates (Fig. 68,*1b,d*),

In most cheilostomates and a few ctenostomates, the distally directed flap is stiffened peripherally or over its whole outer (and in some, inner) surface to form an operculum (Fig. 67,*1d,e*; 68,*1b–e*; 71,*1a*; 72,*1a*; 78,*1a*). Opercula are calcified in a few cheilostomates, but in the great majority stiffening is entirely cuticular. Traces (**opercular scars**) of originally cuticular opercula are known in some fossil cheilostomates in autozooids that lost functioning lophophores with development of calcareous **frontal closures** (Fig. 76,*3*), which are seemingly analogous to terminal diaphragms in fixed-walled members of the class Stenolaemata. Preserved calcareous opercula have been reported in two Cretaceous genera assigned to the Cheilostomata (VOIGT, 1974; TURNER, 1975).

In Ctenostomata orificial walls are supported entirely by membranous frontal walls or membranous vertical and frontal walls. Commonly, orificial walls are elevated above the frontal surface at outer ends of more or less elongate peristomelike extensions of frontal wall (Fig. 65,*1*; 66,*3*). When the lophophore is everted, the diaphragm, which bears a pleated membranous **collar** (Fig. 66,*2a,3*), is exposed at the frontal surface.

In Cheilostomata orificial walls also can be supported entirely by membranous frontal walls (Fig. 80,*2*). In most taxa, however, distal and lateral margins of the operculum or the distal unstiffened part of the orificial wall (Fig. 68,*1b,d,e*) are supported by a skeletal rim generally corresponding in form to the orifice. This skeletal rim comprises the frontal edge of a calcified transverse wall (Fig. 67,*1a,d,e*; 69,*1a*; 78, *1a*), calcified parts of the frontal wall (Fig. 72,*1*), or a combination (Fig. 76,*1–3*). In most cheilostomates the orificial wall is attached proximally to membranous frontal wall (Fig. 68,*1b,d,e*; 71,*1a*; 72,*1a*) or to the floor of an infolded ascus (Fig. 69,*1b*; 78,*1a*), and the skeletal rim of the orifice is thus incomplete (Fig. 65,*2–7*). In those having the opening of the ascus removed from the orificial wall (Fig. 67,*1e*), the skeletal rim is completed proximally by the margin of the frontal shield, and apparently then is analogous to skeletal apertures in fixed-walled members of the class Stenolaemata.

Peristomes are commonly developed in ascophoran Cheilostomata as tubular outfolds of body wall and contained coelom, which together surround the operculum at their inner ends (Fig. 67,*1e*) (BANTA, 1970). Peristomial skeleton is part of the exterior body wall facing inward around the operculum. Proximally and laterally, peristomial skeleton is continuous with the frontal shield and commonly is included in frontal accretion of superficial skeletal layers (Fig. 67,*1d,e*; 68,*1d,e,2*). Distally, peristomial skeleton can be part of an exterior body wall of a distal zooid (Fig. 68,*1d,e,2*) (see SANDBERG, this

FIG. 75. Cheilostomate vertical walls. Diagrams of sections through vertical walls of zooids in early astogenetic stages of encrusting colonies developed from single (a = ancestrula) or multiple (p) primary zooids. Budded generations of zooids are numbered, bud origins are indicated by arrows, outermost cuticles are represented by solid lines, and calcareous layers are stippled.——*1–6*. Uniserial cheilostomate, showing distal budding from ancestrula (*1,2*) to produce single lineal series (*); distal and distolateral budding from ancestrula (*3*) and from budded zooid (*4*) to produce branched lineal series; and other budding sites on the ancestrula (*5*) and budded zooid (*6*) found in some colonies.——*7*. Multiserial cheilostomate with combination of exterior and interior vertical walls and combination of budding directions similar to those in *8*.——*8*. Multiserial cheilostomate with virtually all exterior vertical walls, showing combination of distal, distolateral, and proximolateral budding, and zooids produced by fusion of buds.——*9*. Multiserial cheilostomate with all interior vertical walls, showing circumferential multizooidal budding zone.

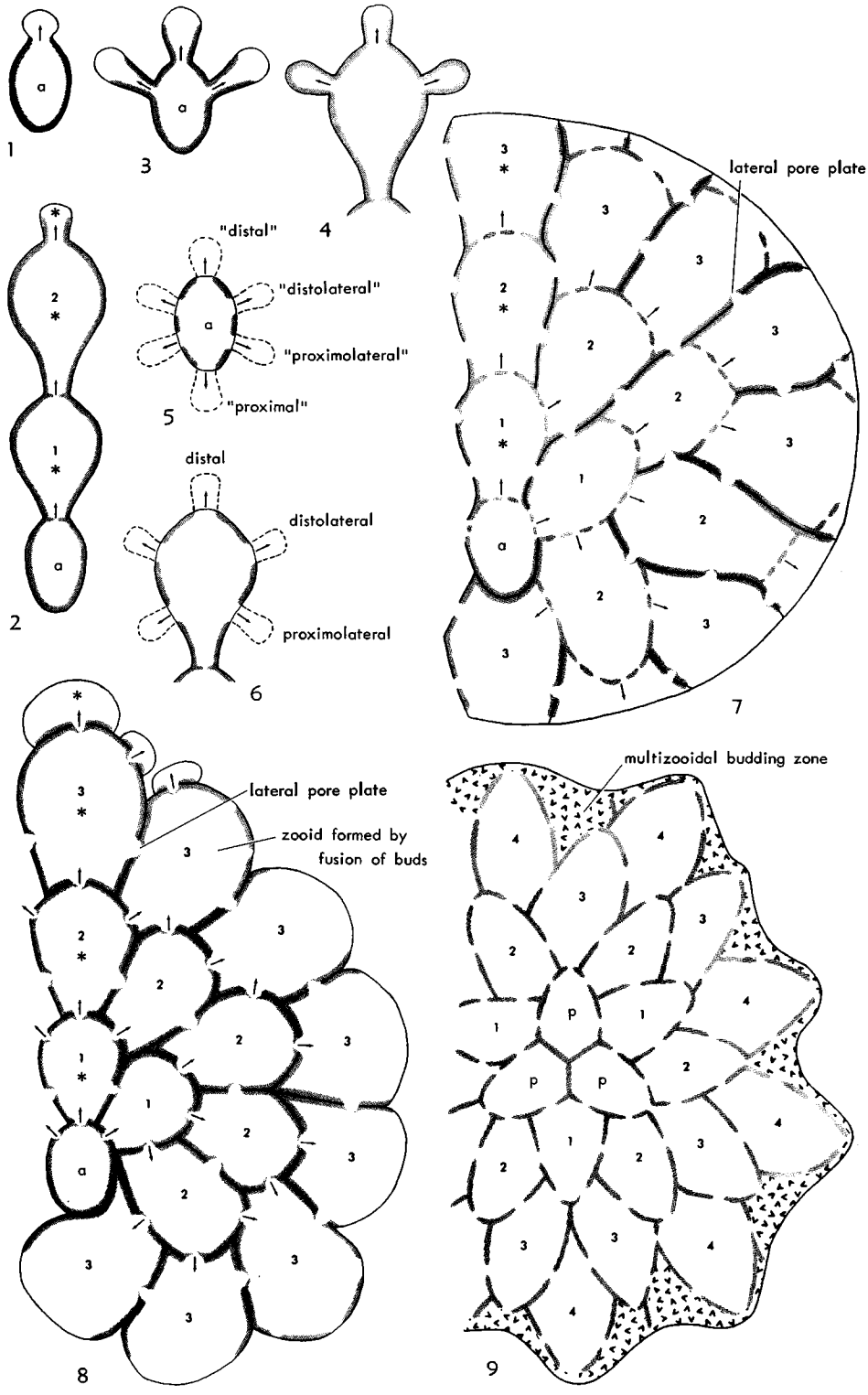


FIG. 75. *(For explanation, see facing page.)*

revision). In some ascophorans, the opening of the ascus is proximal to the peristome (Fig. 67,*1d,e*; 82,*3b,c*). In others, the ascus opens within the peristome into a proximal peristomial channel (Fig. 68,*2*) or a separate opening on the proximal side of the peristome (Fig. 83,*1–3*).

Various elevated structures around orificial walls in both anascan and ascophoran cheilostomates can be similar in appearance to peristomes but be produced by closely spaced spines or adventitious avicularia.

BODY CAVITIES OF AUTOZOOIDS AND CONTAINED ORGANS

The perigastric or **principal body cavity** of a gymnolaemate autozooid is generally enclosed by basal, vertical, and orificial walls, and frontal wall, cryptocyst (and adjacent inner cellular layer), or floor of the ascus (Fig. 65). This body cavity varies markedly in shape in both the Ctenostomata and the Cheilostomata from box- or saclike to cylindrical. Whatever its shape, the principal body cavity of an autozooid in most taxa tends to remain relatively fixed in its dimensions after completion of the vertical walls early in zooid ontogeny. Early completion of the cavity provides a relatively constant position for retracted organs through any later changes in zooid morphology, such as those associated with the frontal wall (Fig. 68,*1a–e*).

The principal body cavity is occupied almost fully by retracted organs and muscles, except in autozooids that have degenerated. These contained structures include (Fig. 66,*2,3*; 68,*1d,e*; 69,*1b,c*): protrusible lophophore, with or without feeding capability; functional or rudimentary alimentary tract; muscles concerned with protrusion and retraction of lophophore; funicular strands; parts of communication organs; and, in some zooids, structures concerned with sexual reproduction. In the Cheilostomata, some of these structures are reflected directly or indirectly in the skeleton.

Protruded, the lophophore characteristically extends far beyond the orifice, carrying the tentacle crown on an elongate neck (Fig. 4). This **lophophore neck** is formed by the everted tentacle sheath, turned inside out to produce a flexible structure capable of individual or cooperative movement to concentrate exhalant currents away from feeding lophophores (Banta, McKinney, & Zimmer, 1974; Cook, 1977). Cooperative current production by groups of zooids may or may not be reflected in skeletons in the Cheilostomata. The presence of elongate tubular peristomes in some presumably restricts movement of the lophophore neck because the orifice remains at the inner end of the peristome.

Lophophore protrusion involves contraction of parietal muscles to depress the hydrostatic membrane of the autozooid and cause pressure in the principal body cavity (Fig. 3, 4). Bilaterally arranged parietal muscles (Fig. 66,*2b*; 70,*1a*) traverse the cavity in one to several pairs, or rarely are arranged unilaterally in highly asymmetrical zooids in a few

Fig. 76. Anascan cheilostomates.——*1,2. Pyriporopsis? catenularia* (Fleming), rec., Brit. Is.; *1a,b,* Plymouth, Eng.; *a,* encrusting colony with uniserially arranged, predominantly distally and laterally budded autozooids, several injuries repaired by growth of distally and "proximally" budded autozooids (rz); *b,* autozooids and distal bud (db) at growing tip of lineal series, with uncalcified spots on lateral walls (un) opening into pore chambers (pch); both frontal views, USNM 242555, ×30, ×60; *2,* Hastings, Eng.; autozooids, proximal one with frontal and orificial walls completely calcified to form frontal closure preserving traces (scars) of operculum (op) and parietal muscle insertions (pm); frontal view, USNM 242556, ×50.——*3,4. Pyriporopsis? texana* (Thomas & Larwood), Fort Worth F., Cret. (Alb.), Fort Worth, Texas; *3,* encrusting colony with distally budded, uniserially arranged autozooids, one zooid with frontal closure preserving trace (scar) of operculum (op), frontal view, USNM 216139, ×30; *4,* autozooids with uncalcified spots on lateral walls (un); frontal view, USNM 216138, ×50.——*5. P.? catenularia,* same data as *1,2* except exact locality unknown; proximal region of encrusting colony with presumed primary zooids attached by proximal extremities; frontal view, BMNH 1847.9.18.107, Johnston Coll., ×30.

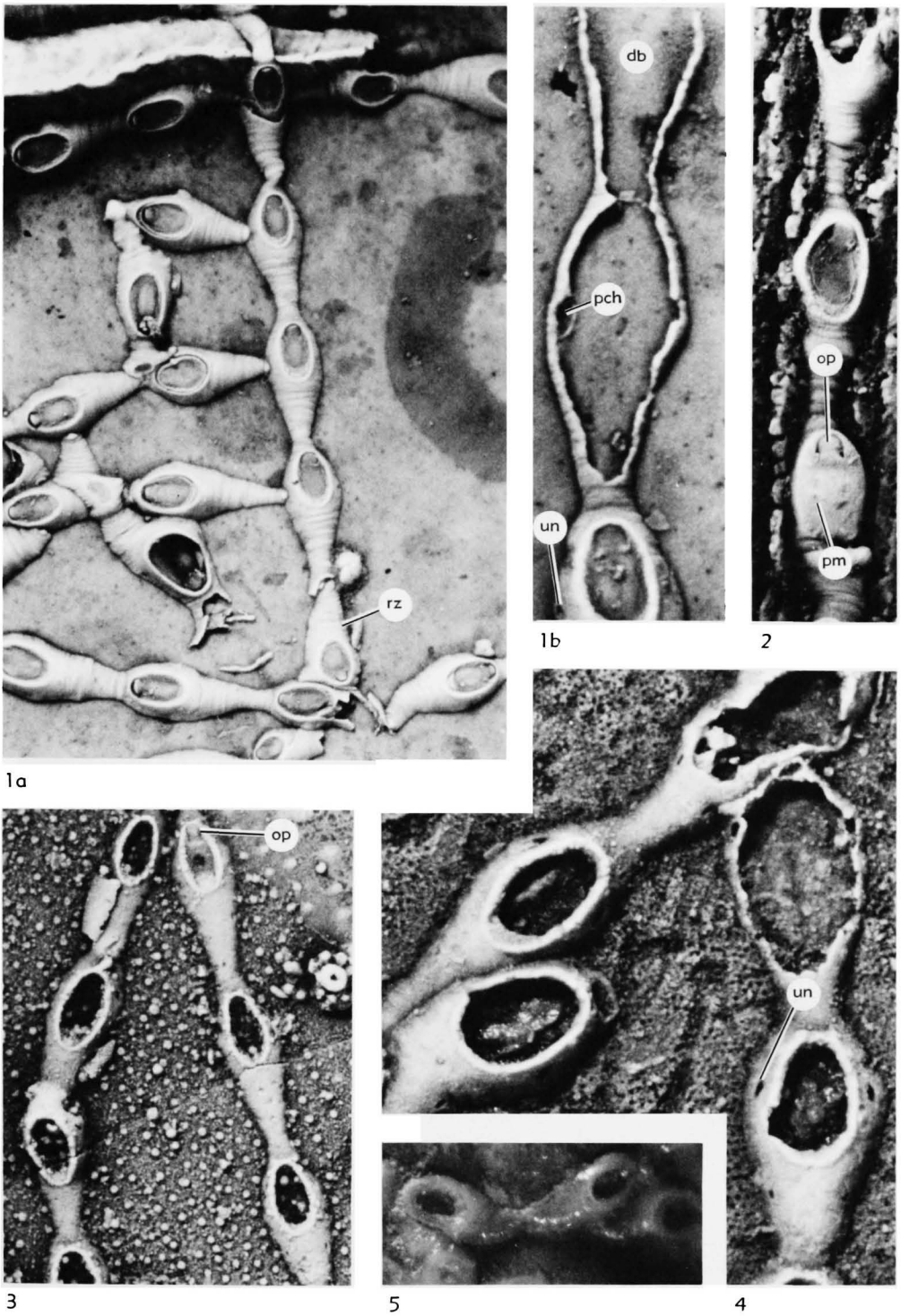


FIG. 76. *(For explanation, see facing page.)*

anascan genera. Parietals originate on lateral walls or on lateral margins of the basal wall and insert on the flexible part of the frontal wall or on the floor of the ascus. In cheilostomates having extensive cryptocysts and no ascus, parietals commonly pass from the principal body cavity into the hypostegal coelom through pores or notches in the lateral margins of the cryptocyst (Fig. 81,*3b*). In one genus, LEVINSEN (1909, p. 162) reported parietals to originate on the frontal side of the cryptocyst. Calcified frontal closures preserving traces of opercula can also have traces of parietal insertions (Fig. 76,*2*).

Parietal muscles may develop in different groups of living gymnolaemate genera at different ontogenetic stages relative to formation of other muscles (SOULE, 1954) or to calcification of a frontal shield, where present. In all Gymnolaemata, parietals develop before the lophophore can be protruded. In cheilostomates having an infolded ascus, parietal muscles grow to insert on the ascus floor as it develops proximally beneath the frontal shield (HARMER, 1902). In those having an overarched frontal wall, parietal muscles may develop before the frontal shield has formed.

During lophophore protrusion, the diaphragm at the outer end of the tentacle sheath is dilated by radially or bilaterally arranged muscles (Fig. 66,*3*) that originate on vertical walls. In some ctenostomates additional radially or bilaterally arranged dilators insert on the vestibular wall (Fig. 64). In some cheilostomates a pair of muscles in series with the parietals is attached to the proximal margin of the operculum to form **divaricator muscles** for opening the operculum. Evidence of dilator and opercular divaricator muscles has not been reported in fossil cheilostomates. MEDD (1964) inferred that depressions on the inside of basal walls of avicularia of some Upper Cretaceous cheilostomates are scars of mandibular divaricators.

Lophophore retraction is accomplished by contraction of the retractor muscle, as in the other bryozoan classes. In a cheilostomate genus, the retractor muscle has been measured to have one of the fastest contraction rates known in animals (THORPE, SHELTON, & LAVERACK, 1975a). The origin of the retractor muscle can be on the proximal part of the basal wall or on the proximal transverse wall (Fig. 68,*1d*). No traces of retractor muscles have been reported in fossil cheilostomates.

As the lophophore is retracted, the operculum in cheilostomates closes, generally by contraction of a pair of opercular **occlusor muscles**. Opercular occlusors extend from lateral walls or the proximal side of the distal transverse wall to insert on the proximobasal side of the operculum (Fig. 3; 4; 68,*1e*). Various skeletal expressions of occlusor attachments have been reported (HARMER, 1926; MEDD, 1964; CHEETHAM, 1968).

In living Gymnolaemata, connections between principal body cavities of fully developed zooids and between zooids and extrazooidal parts are limited to **interzooidal communication organs** (Fig. 67,*1e*; 68,*1e*; 70,*2*; 71,*1b*). Even in ascophoran cheilostomates in which hypostegal coeloms remain confluent laterally, principal body cavities of zooids communicate with each other and with their hypostegal coeloms only by means of communication organs (Fig. 78,*1a*).

FIG. 77. Anascan cheilostomate.——*1,2. Allantopora irregularis* (GABB & HORN), Vincentown F., Paleoc., Noxontown Millpond, Del.; *1a,b,* primary zone of astogenetic change of encrusting colony with uniserially arranged, distally and laterally budded zooids; *a,* ancestrula (an) produced bud distally only, size and shape of zooids change from ancestrula through successive generations of budded zooids in zone of change (db, distal bud; lb, lateral bud), frontal view, ×30, *b,* ancestrula with extensive proximal gymnocyst (gy), frontal view, ×50, both USNM 242557; *2a–c,* autozooids in zone of astogenetic repetition, all have spine bases (sp) ringing inner margin of gymnocyst, some have distal brood chambers (bch) preserved in various states of completeness; *a–c,* all frontal views, USNM 242558, ×50.

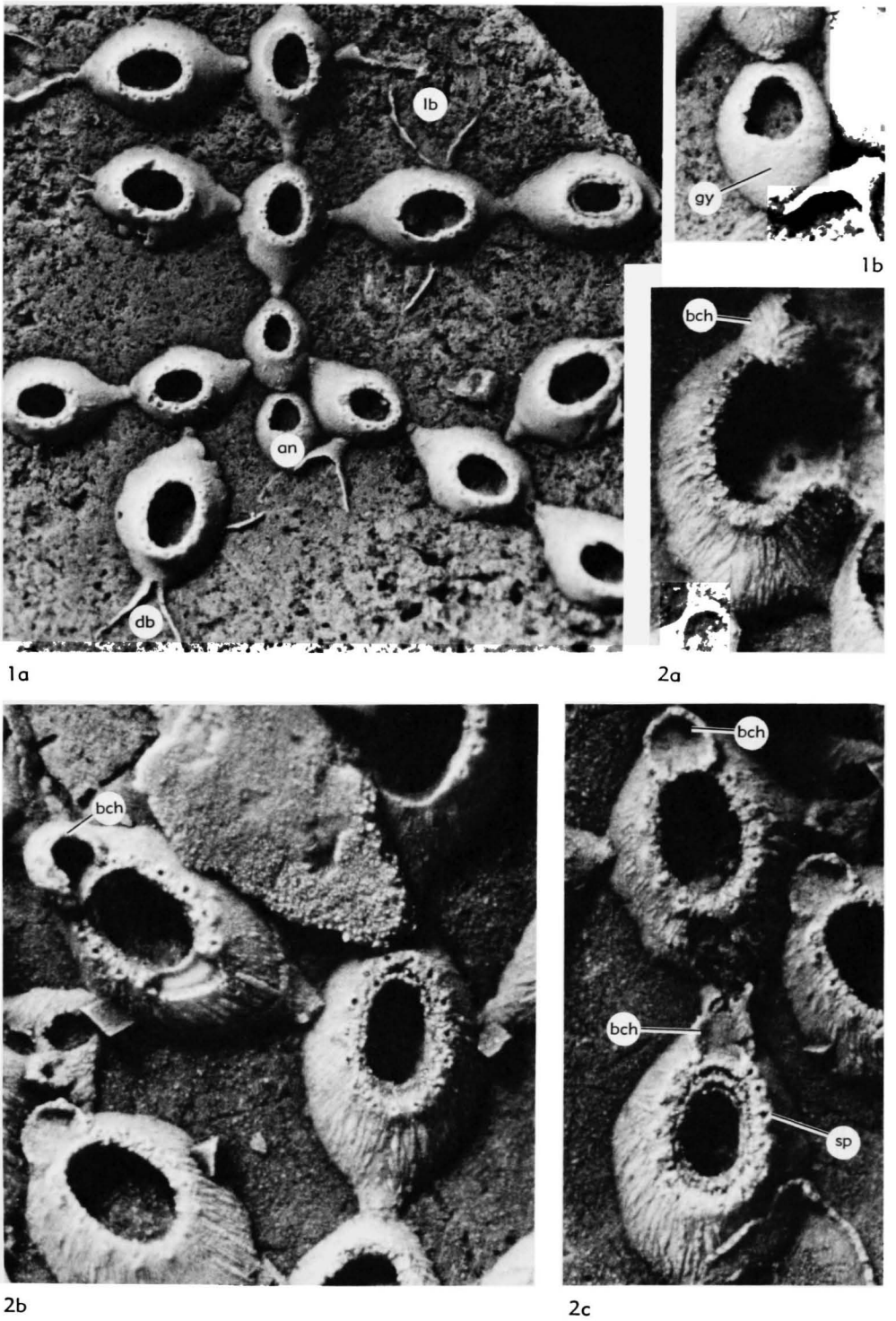


FIG. 77. *(For explanation, see facing page.)*

Throughout the Gymnolaemata, communication organs therefore appear to form the only means of transporting nutrients from feeding autozooids to nonfeeding polymorphs and extrazooidal parts, except possibly those at growing tips of colonies. BOBIN (1964, 1971) presented direct biochemical evidence that nutrients are transferred through cells that make up communication organs.

A **communication organ** consists of a complex of interdigitating cell types together with a cuticular or calcareous pore plate bearing one or more communication pores (BOBIN & PRENANT, 1968; BANTA, 1969; BOBIN, 1971; GORDON, 1975). Cells of special form extend through communication pores to provide the actual interzooidal connection. Communication organs occur on open expanses of walls or on parts of walls partly enclosed within **pore chambers** (Fig. 69,*1f*; 76,*1b*; 80,*1*). Interzooidal communication organs occur in vertical walls of zooids, whether interior or exterior, and can also be present in basal walls and frontal shields. Development of communication organs in preexisting exterior walls that are in contact involves cooperative dissolution of bounding cuticles (BANTA, 1969). Communication organs similar to those connecting zooids occur intrazooidally in cryptocysts of ascophorans (BANTA, 1970, 1971) and around margins of umbonuloid shields of ascophorans (Fig. 68,*1b,d*), to connect the hypostegal coelom with the principal body cavity.

POLYMORPHISM

In the overwhelming majority of living species in both the Cheilostomata and the Ctenostomata, zooids within a colony may differ discontinuously in morphology and function at the same stages of ontogeny and in the same asexual generations. This polymorphism is most commonly reflected in skeletons in the Cheilostomata and therefore is generally recognizable in fossil species. A few examples of **soft-part polymorphism** without apparent skeletal expression have been reported in living cheilostomates (for example, GORDON, 1968). These include sexual dimorphism of lophophores, differences in vestibule structure for brooding embryos, and differences in tentacle length for producing exhalant water currents, all of which are correlated with skeletal differences in some other species. In some examples, soft-part polymorphs apparently alternate within the same body cavity during degeneration-regeneration cycles.

Polymorphs in the Gymnolaemata include autozooids, which differ from ordinary feeding autozooids in size, shape, tentacle num-

FIG. 78. Ascophoran cheilostomate.——*1a–e. Euthyrisella obtecta* (HINCKS), rec., Queensl., Australia; *a,* autozooids and adjacent extrazooidal parts of colony (exp), autozooids with heavily reinforced dimorphic opercula (op), extensive hypostegal coeloms (hy), membranous frontal walls (fw), and cryptocyst (cry) underlain by ascus (fa, floor of ascus; ra, roof of ascus) opening (oa) at proximal margin of operculum, ascus roof in contact with cryptocyst except at distal end, where small body cavity intervenes, skeletal layers of zooid and extrazooidal walls very thin throughout colony, organic sheets (os) form boundaries between basal walls of zooid (bw) and inner wall of extrazooidal parts, membranous basal wall (bm) of extrazooidal parts attached to calcified inner wall by membranous filaments (arrows) that may be calcified at inner ends, long. sec., ×100; *b,* growing tip (gt) with outer membrane intact but shriveled, interior walled zooecia and extrazooidal skeleton fragmented but entirely within colony body cavity, proximal zooid with ascus (fa, floor of ascus), ascus lacking in distal zooid, long. peel, ×50; *c,* autozooids with calcified lateral walls (lw) not reaching membranous frontal walls so that hypostegal coeloms (hy) are confluent, frontal wall (fw) attached to cryptocyst (cry) by filaments (arrow) similar to those in extrazooidal parts, injured membranous basal wall (bm) of extrazooidal parts replaced inwardly by a second membrane with foreign particles in intervening space, transv. sec., ×100; *d,* erect colony with autozooids having continuous membranous frontal walls and dimorphic opercula (op), frontal view, ×50; *e,* communication organ (ppl, pore plate) in transverse walls of contiguous zooids (distal to left), organic sheet (os) marking boundary between zooids, floor of ascus (fa) reaching to transverse wall which is continuous with cryptocyst (cry), long. sec., ×300; all USNM 242577.

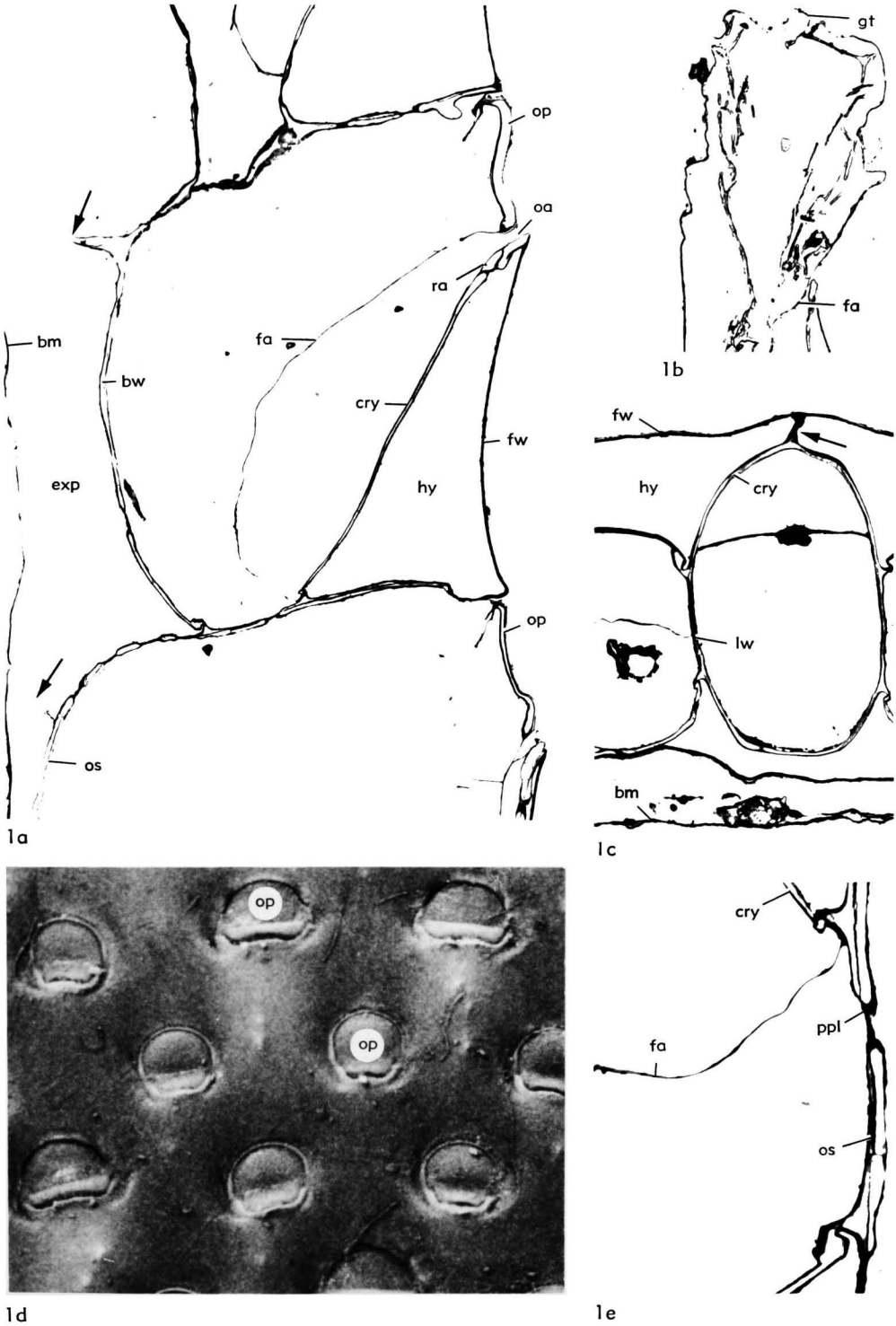


FIG. 78. *(For explanation, see facing page.)*

ber, and other features, but retain protrusible lophophores with or without feeding capability; and **heterozooids**, which have nonprotrusible or no lophophores (and therefore no apparent feeding capability), different or no musculature, and specialized organs present or lacking. Different combinations of polymorphic autozooids and heterozooids can differ so in appearance that were they not in the same colony, they might be placed in different taxa (heteromorphy of VOIGT, 1975) (Fig. 84,*1*). Autozooidal and heterozooidal polymorphs lacking feeding ability presumably are nourished through interzooidal communication organs that connect them directly or indirectly to feeding autozooids.

Polymorphs may communicate with just one other zooid (adventitious polymorphs) (Fig. 68,*2*; 70,*1b,c,3*; 79,*2,3*; 82,*1,2*; 83,*2,3*; 84,*1–3*), in the extreme form being almost a structural appendage of that zooid. Polymorphs may also be intercalated within budding series and communicate with two or more zooids or with extrazooidal parts of colonies. **Interzooidal polymorphs** (Fig. 71,*2,3*; 81,*1,2*) are intercalated in spaces smaller than those occupied by ordinary feeding autozooids. **Vicarious polymorphs** (Fig. 79,*3*; 81,*3,4*) are intercalated in spaces subequal to or larger than those occupied by ordinary feeding autozooids. Interzooidal and vicarious polymorphs may be arranged among ordinary feeding autozooids either regularly or seemingly at random. Regularly arranged polymorphs may occur at isolated positions among ordinary feeding autozooids or in clusters. Clusters of polymorphs may be restricted to one part of a colony, such as a basal stalk, or may recur throughout a colony. A cluster can consist of one kind of polymorph (Fig. 82,*3a*) or a variety of polymorphs (Fig. 70,*3*; 72,*1–4*) either keyed to a single function (such as reproduction, brooding of embryos, support of the colony, or connection of other zooids) or serving a broad spectrum of functions (including, for example, feeding and defense with other functions).

Diversity in morphology of polymorphs throughout the Gymnolaemata is at least as great as that in ordinary feeding autozooids. However, taxa having autozooids of quite different appearance can have similar heterozooids (compare Fig. 70,*3*; 71,*2*; 79,*3*).

Other than ordinary feeding autozooids, the only kind of zooid that is present virtually throughout the class is the kenozooid (Fig. 66,*1,2b*; 85,*3*). Kenozooids in the Gymnolaemata have body walls enclosing body cavities containing funicular strands and parts of communication organs, but empty of alimentary canal and, in most, of musculature. Kenozooids therefore are all heterozooids apparently incapable of feeding. Basal and vertical walls of kenozooids, and frontal walls of some (including presence of parietal muscles), are comparable in some characters with those of autozooids in the same colony. The function of these parietal muscles must be different from that of parietals in autozooids, which act to protrude the lophophore. Kenozooids lack orifices and orificial walls, and the structures associated with frontal walls, such as cryptocysts, may also be quite different from those of autozooids or lacking.

Adventitious kenozooids much smaller than, and placed in consistent positions upon autozooids can be difficult to distinguish from zooidal structures such as spines. This difficulty is increased if, as suggested by SILÉN (1942), wall constrictions at spine bases correspond to pore plates of communication organs. Frontal structures of some ascophorans containing hypostegal coeloms that communicate with principal body cavities of autozooids only by means of communication organs are distinguishable from kenozooids, only by their possession of a part (frontal wall) of the supporting functional autozooid. Vicarious kenozooids larger and less regular in shape than autozooids can be difficult to distinguish from some kinds of extrazooidal parts. Distinction of some basic morphologic and functional units in the Gymnolaemata, because of this morphologic continuity throughout a colony, is unavoidably arbitrary.

Most species in the Cheilostomata possess

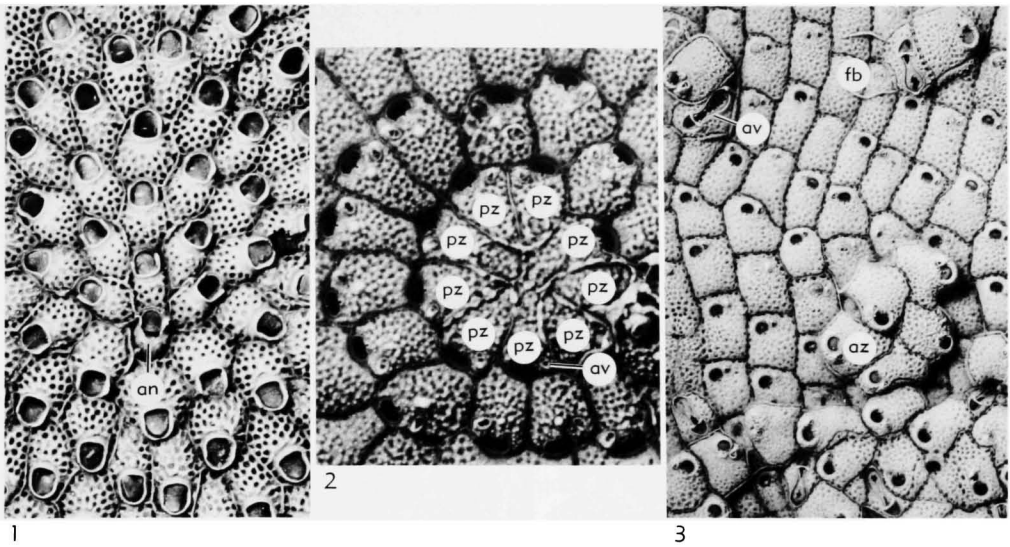


FIG. 79. Ascophoran cheilostomates.——*1. Cryptosula pallasiana* (MOLL), rec., Monterey, Cal., 30 cm below lowest tide; primary zone of astogenetic change of encrusting colony with multiserial budding throughout, size and other characters of autozooids change from ancestrula (an) through successively budded generations, zooid proximal to ancestrula belongs to third asexual generation (compare with Fig. 75,7); frontal view, USNM 242581, ×17.——*2,3. Stylopoma spongites* (PALLAS), rec.; *2,* Atl., Fowey Light, 24 km S. of Miami, Fla., 80 m; small encrusting colony with primary zone of astogenetic change beginning with central group of nine primary autozooids (pz) smaller than those of succeeding budded generations, primary zooids supporting adventitious avicularia (av) like those in succeeding generations; frontal view, USNM 242583, ×34; *3,* Discovery Bay, Jamaica, West Bull no. 1, 30 m; encrusting colony with autozooids (az) and vicarious avicularia (av) of discontinuous secondary zone of astogenetic change budded frontally from hypostegal coeloms of autozooids (fb, frontal bud) in primary zone of astogenetic repetition, frontally budded autozooids less regular in shape and orientation than those in primary zone of repetition, small adventitious avicularia present on frontal shields of autozooids in both zones, vicarious avicularia also present in primary zone of repetition, not shown; frontal view, USNM 242582, ×17.

another kind of polymorph, the **avicularium**, which itself can occur in two or more distinct forms within a colony (Fig. 70,*3*; 79,*2*). Avicularia are zooids in which the equivalent of the orificial wall, the **mandible,** is relatively larger and more intricately reinforced than orificial walls (opercula) of ordinary feeding autozooids (Fig. 70,*3a*; 71,*3*; 81,*3a*; 84,*3*). The mandible is opened and closed by greatly augmented divaricator and occlusor muscles (Fig. 70,*1c*). In some living cheilostomates, avicularia can be autozooids with feeding organs, but much more commonly are heterozooids with only a nonprotrusible rudiment of lophophore and nondigesting rudiment of alimentary canal. Movement of the mandible is apparently at least partly independent of feeding and in some species has been inferred to play a role in cleaning (COOK, 1963; GREELEY, 1967) and defense (for example, KAUFMANN, 1971, and references therein). Vertical and basal walls of avicularia tend to resemble those of ordinary feeding autozooids, but in some species may be elongated to form stalks that attach the avicularia to other zooids (for example, HASTINGS, 1943). The skeletal rim supporting the free tip and lateral edges of the mandible, the **beak**, may (Fig. 70,*3*; 71,*3*; 84,*3*) or may not (Fig. 81,*3*) closely approximate the mandible in shape. A partial or complete rim may form the **condyles** or **pivotal bar** on which the fixed edge of the mandible is hinged (Fig. 68,*2*; 70,*3b*; 71,*2*; 79,*2,3*; 81,*3b*; 83,*2,3*; 84,*1–3*). The frontal wall is relatively smaller than that of ordinary

feeding autozooids, typically forming only a small membranous **postmandibular area** (Fig. 71,*3*; 84,*3*) on which the mandibular divaricator muscles are inserted.

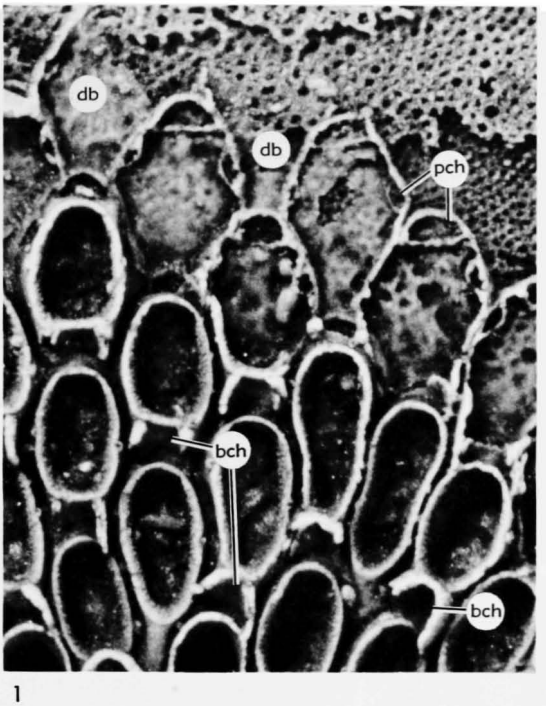
Polymorphism associated with sexual reproduction is highly diverse in the Gymnolaemata. Sex cells are produced by zooids, sperm most commonly on funicular strands and eggs on parts of the body wall within the principal body cavity. Sexes may be combined within single zooids, but not necessarily at the same time. There may be a distinct tendency for zooids to be male at earlier stages and female at later ones (SILÉN, 1966), without skeletal expression of sex change. In many species production of eggs is limited to zooids associated with brooding structures with a great diversity of polymorphic expression. Both sperm- and egg-producing zooids are autozooids with protrusible lophophores that may or may not be capable of feeding (RYLAND, 1976, and literature cited therein). In some species **sexual zooids** are distinct feeding polymorphs (Fig. 70,*3*; COOK, 1973a). In others, they are nonfeeding polymorphs, with or without skeletal expression of their functional specialization (Fig. 69,*2*) (MARCUS, 1938a; GORDON, 1968; COOK, 1968c).

EXTRAZOOIDAL PARTS OF COLONIES

In most Gymnolaemata parts of colonies proximal to growing tips or margins consist entirely of morphologically distinguishable zooids of one or more morphologic kinds. At growing tips zooids originate as buds or as parts of multizooidal budding zones that have some (multizooidal) body wall layers continuous with those of other zooids. These walls of multizooidal origin become parts of zooids early in ontogeny, through the completion of the bounding walls of zooids. In a few taxa, apparently limited to the Cheilostomata, major parts of colonies commonly many times as large as autozooids are extrazooidal, with continuous body walls enclosing unpartitioned body cavity devoid of feeding and reproductive organs and musculature, although probably transversed by funicular strands (LUTAUD, pers. commun., 1976). Extrazooidal parts can be restricted to more proximal regions of colonies or can extend from proximal regions to growing tips. Once developed, extrazooidal parts lie outside boundaries of zooids throughout the life of the colony. Extrazooidal body cavities are connected to body cavities of zooids by communication organs similar to those connecting zooids to each other. It is through these connections that extrazooidal tissues apparently are nourished.

Some structures interpreted as extrazooidal parts in cheilostomates may intergrade morphologically with some kinds of polymorphic zooids. It is also possible that structures interpreted as polymorphs in ctenostomates (such as masses of rootlets or basal

FIG. 80. Anascan cheilostomates.——*1. Wilbertopora mutabilis* CHEETHAM, Grayson F., Cret. (Cenoman.), Roanoke, Texas; growing edge of encrusting multiserial colony with staggered lineal series (db, distal buds); autozooids with pore chambers (pch) and some with partly developed brood chambers (bch) distal to maternal zooids; frontal view, USNM 216141, ×50.——*2. Aplousina gigantea* CANU & BASSLER, rec., Bogue Sound, Beaufort, N. Car., 6 m; encrusting colony with apparently coordinated lineal series forming smooth growing edge (ge; db, distal buds); autozooids have membranous frontal walls margined by narrow gymnocysts (gy) and continuous distally with lightly reinforced operculum (op); frontal view, USNM 242559, ×50.——*3. W. mutabilis,* holotype, same data as *1* except Fort Worth F., (Alb.), Krum; primary zone of astogenetic change of encrusting colony; ancestrula (an) produced buds distally and distolaterally to initiate multiserial arrangement evident throughout colony, size of zooids increasing from ancestrula through successive generations of budded zooids in zone of change; zooecia with narrow cryptocysts (cry) attached to marginal gymnocysts (gy); frontal view, LSU 4500, ×50.——*4. W. mutabilis,* same data as *1* except Pottsboro; primary zone of astogenetic change of encrusting colony; ancestrula (an) produced bud distally only, in initially uniserial arrangement, lateral and distal budding in following generations resulted in multiserial arrangement throughout remainder of colony; some zooecia with frontal closures preserving trace (scar) of operculum (op); frontal view, USNM 216140, ×50.



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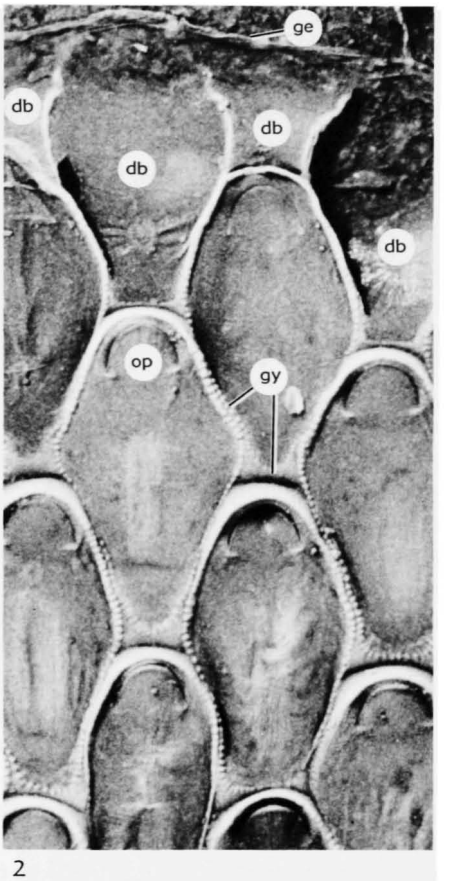

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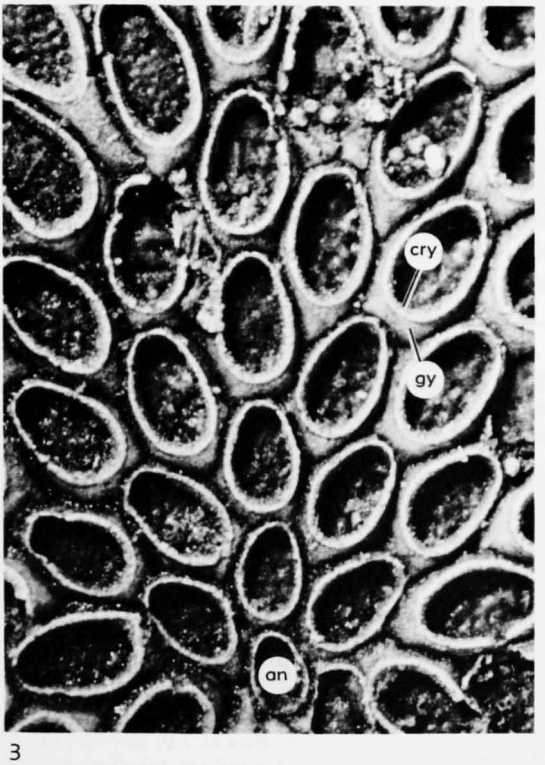

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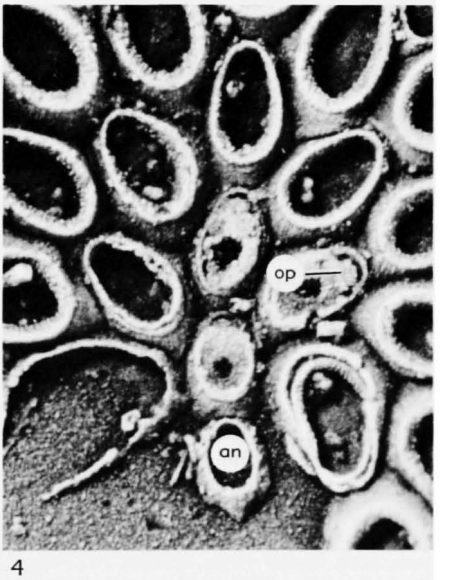

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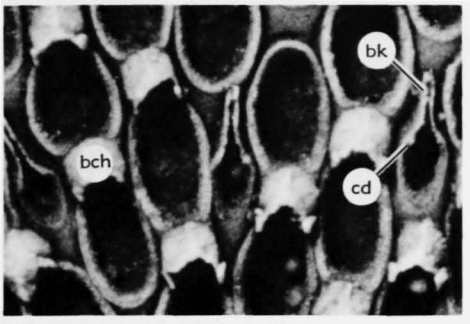
FIG. 80. *(For explanation, see facing page.)*

stalks) may be extrazooidal, as suggested by HARMER (1915, p. 61).

Extrazooidal parts limited to proximal regions of colonies are found in some ascophorans having autozooids with hypostegal coeloms overlying frontal shields of either exterior (umbonuloid; Fig. 70,*1–3*) or interior (cryptocystal) origin. Extrazooidal parts in these taxa are apparently formed by coalescence of hypostegal coeloms and associated body walls of contiguous preexisting zooids. The first step in this process is apparently dissolution of cuticles at frontal margins of vertical walls; this dissolution of vertical wall cuticles seems similar to that occurring in the formation of some communication organs (BANTA, 1969). Ontogenetically thickened frontal shields with zooid boundaries marked on their frontal surfaces by bounding cuticles (Fig. 70,*1a*; 83,*3*) then are succeeded without interruption by calcareous layers that are continuous across zooid boundaries (Fig. 70,*1b*; 83,*2*). The next step is overgrowth, by these continuous layers, of orificial walls and other structures such as adventitious avicularia (Fig. 70,*1b*); similar overgrowth by zooidal skeleton has been reported in the formation of frontally budded zooids from hypostegal coeloms (BANTA, 1972, suprapercular space). Coalesced extrazooidal coeloms continue to communicate with some underlying zooidal body cavities through communication organs originally filling marginal openings in frontal shields. At proximal ends of colonies, these openings may also become covered with extrazooidal skeleton, but more distal ones apparently remain functional. The extrazooidal coelom is apparently confluent throughout, so that its more proximal parts can continue to be nourished through connection of its distal parts with feeding zooids.

Extrazooidal skeleton produced by coalesced body walls originally bounding zooidal hypostegal coeloms is especially prominent in ascophorans having erect colonies (Fig. 13,*1*; 83,*1*). These deposits are thickest at the most proximal ends of erect colonies, where they cover the ontogenetically oldest zooids. As growing tips of a colony advance distally, extrazooidal skeleton not only thickens at the proximal end of the colony, but also encroaches distally over zooidal frontal shields, as more zooidal hypostegal coeloms and associated body walls become coalesced. The colony thus can be strengthened as it grows (CHEETHAM, 1971), but at the expense of feeding and some other functional abilities earlier possessed by its more proximal zooids. In anascans and some ascophorans having erect colonies and zooidal frontal shields overlain by hypostegal coeloms, skeletal thickening can occur entirely within zooid boundaries (Fig. 82,*3a*,c)

FIG. 81. Anascan cheilostomates.——*1,2. Wilbertopora mutabilis* CHEETHAM, Cret., Texas; *1,* Grayson F., (Cenoman.), Salado, encrusting colony with autozooids and interzooidal avicularia budded distally and distolaterally, most autozooids provided with brood chambers (bch) that are parts of zooids distal to maternal zooids (see Fig. 80,*1*), avicularia with pointed beaks (bk) and condyles (cd) for hinging mandible, frontal view, USNM 216143, ×50; *2,* Kiamichi F., (Alb.), Fort Worth, encrusting colony with ordinary autozooids and interzooidal avicularium-like polymorph (av) budded distolaterally, frontal view, USNM 216142, ×50.——*3a,b. Smittipora levinseni* (CANU & BASSLER), rec., Atl., 33°41.6′ N., 76°42.4′ W., 70–87 m; *a,* encrusting colony with autozooids and vicarious avicularia having membranous frontal walls, opercula (op), and mandibles (md) intact; membranous mandibles with strongly reinforced central axes are in open (right) and closed (left) positions; postmandibular walls of avicularia (pmd) are similar to frontal walls of autozooids; *b,* autozooids with membranes removed, showing extensive cryptocysts notched (opm) for parietal muscles; small brood chambers (bch) roofed by skeleton continuous with cryptocysts of zooids distal to maternal zooids; vicarious avicularium, budded distolaterally, divided by pivotal condyles (cd) into rounded mandibular part, much shorter than mandible, and postmandibular part; both frontal views, USNM 242560, ×50.——*4. W. mutabilis,* same data as *1,2,* and Fort Worth F., (Alb.), Fort Worth; encrusting colony with ordinary autozooids and vicarious avicularia budded distolaterally; avicularia with rounded beaks (bk) and condyles (cd) for mandible; frontal view, USNM 186572, ×50.



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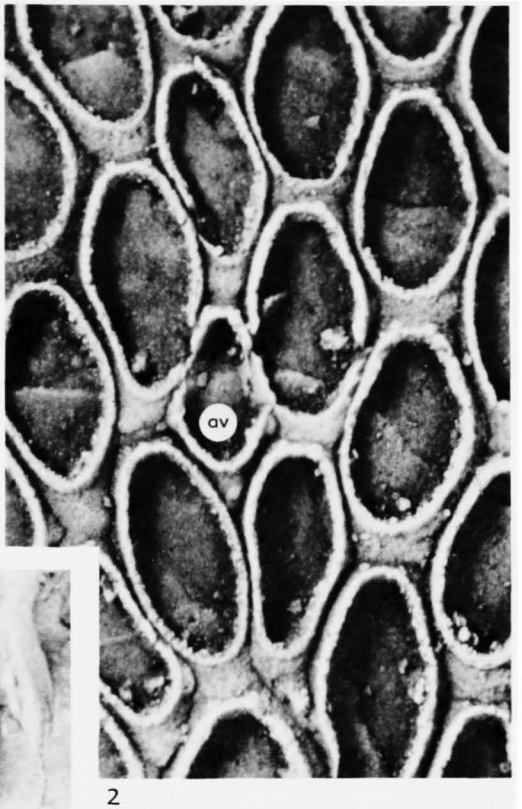

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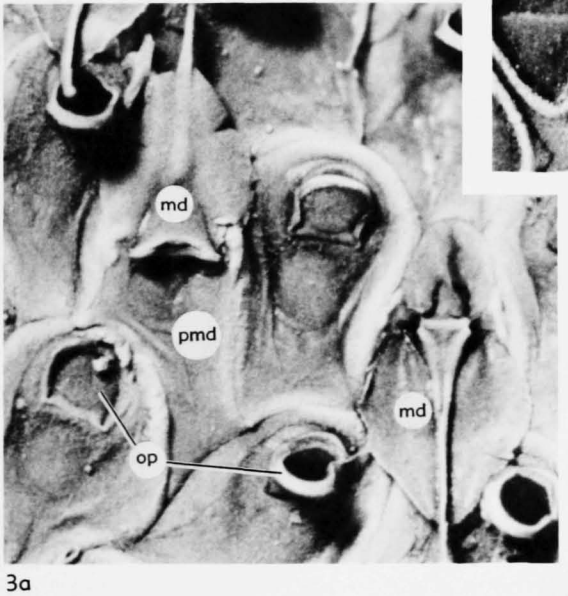

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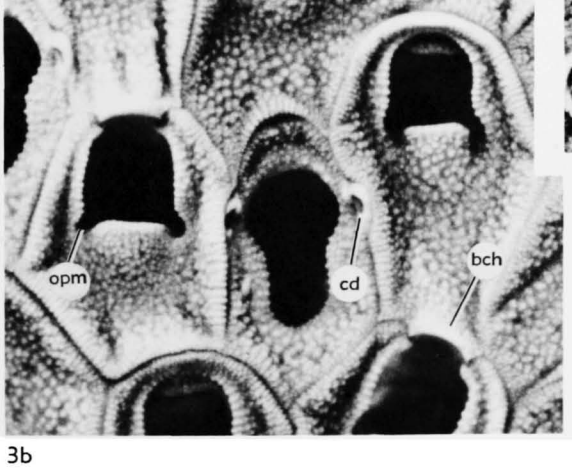

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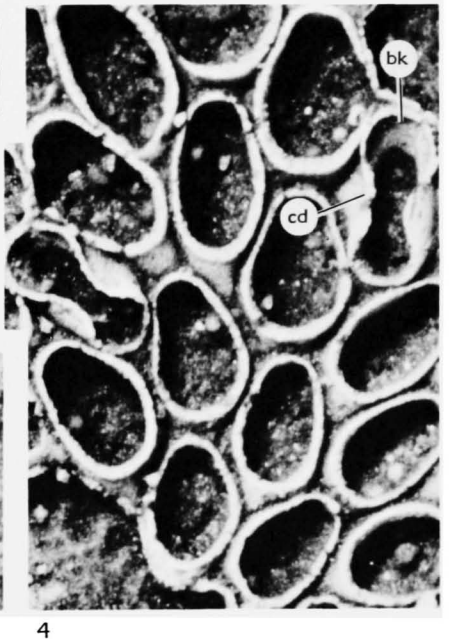

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FIG. 81. *(For explanation, see facing page.)*

(CHEETHAM, 1971, pl. 8, 9), without extrazooidal coalescence. In some of these colonies, proximal zooids also apparently lost their feeding function with overgrowth by zooidal skeleton of their orificial walls (Fig. 82,*3c*). Presumably communication with feeding zooids then can be maintained through underlying principal body cavities of zooids.

Extrazooidal parts developed at growing tips or margins of colonies concurrently with budding of zooids are known in a few anascans and ascophorans having all interior vertical walls (HARMER, 1902; HÅKANSSON, 1973). These structures form one side of free-living and unilaminate erect colonies. It was for this type of structure that HARMER (1901, p. 16) proposed the term extrazooecial. Calcareous layers of extrazooidal walls in these taxa are parts of interior walls shared with basal walls of contiguous zooids (Fig. 78,*1a–c*). Communication between extrazooidal body cavity and principal body cavities of zooids is through communication organs in interior basal walls of zooids and through confluence with body cavities of developing zooids at the growing tip or edge of the colony (Fig. 78,*1b*).

BROODING AND LARVAE

Embryos are brooded in the great majority of Cheilostomata and in most Ctenostomata. In two genera of Ctenostomata brooding is reportedly within the body cavity (HARMER, 1915; RYLAND, 1970), as in the classes Phylactolaemata and Stenolaemata, but in other brooding gymnolaemates, embryos are held topologically outside the body cavity of the colony within water-filled brood chambers (Fig. 66,*2a*; 69,*1c*; 70,*2*) partly enclosed by the body walls of one or more kinds of polymorphs. In cheilostomates that brood, this function is generally reflected in the skeleton even though walls enclosing brood chambers are not invariably calcified.

Body walls enclosing brood chambers in the Gymnolaemata most commonly are parts of zooids but can comprise, together with contained coelom and parts of interzooidal communication organs, a whole zooid (polymorph). In the Ctenostomata and many Cheilostomata, the enclosing walls are apparently entirely part of the **maternal zooid** that deposits eggs in the brood chamber. In many other Cheilostomata the enclosing walls are parts of one or more zooids distal or distolateral to the maternal zooid. If part of a maternal zooid, enclosing walls can lie internally, as for example a diverticulum of the vestibule or tentacle sheath (Fig. 66,*2a*), or can extend distally from the zooid, as for example a double-walled outfold from the distal transverse wall. The outer surface of such outfolded enclosing walls may be exposed at the surface of the colony (Fig. 67,*1d*; 69,*1c,2*; 70,*3*; 77,*2a–c*; 82,*3b*), or hidden beneath the surface of the distal zooid (Fig. 81,*3b*). If distal to the maternal zooid, a brood chamber can be enclosed by body walls of a kenozooid (WOOLLACOTT & ZIM-

FIG. 82. Anascan and ascophoran cheilostomates.——*1,2. Setosellina* aff. *S. folini* (JULLIEN), rec., Gulf of Mexico, 28°51′ N., 88°18′ W., Albatross Sta. D2385, 1,500 m; *1*, free-living colony with proximal autozooid apparently broken from preexisting colony, autozooids products of left distolateral budding, each with a distally budded adventitious avicularium (av); setiform mandibles of avicularia, which pivoted on small condyles (cd), missing, frontal view, USNM 242570, ×75; *2*, free-living colony with right distolaterally budded autozooids, uncalcified spots (un) present on left lateral walls, frontal view, USNM 242571, ×75.——*3a–c. Margaretta cereoides* (ELLIS & SOLANDER), rec., Naples, Italy; *a*, distal segment of erect, jointed colony with growing tip, ordinary and maternal (bch, brood chambers) autozooids (forming proximal cluster) with relatively thin frontal shields and dimorphic peristomes; *b*, detail of same segment with ordinary and maternal autozooids having dimorphic peristomes and distinct cuticular boundaries (lc), frontal shields with numerous funnel-shaped depressions (fd) similar in appearance to opening to ascus (oa) (compare Fig. 67,*1c,e*); *c*, proximal segment of same colony with frontal shields of autozooids greatly thickened, funnel-shaped depressions nearly filled, and peristomes sealing off underlying opercula, cuticular boundaries (lc) and opening to ascus (oa) still distinct; all frontal views, USNM 242572, *a,c*, ×30, *b*, ×50.

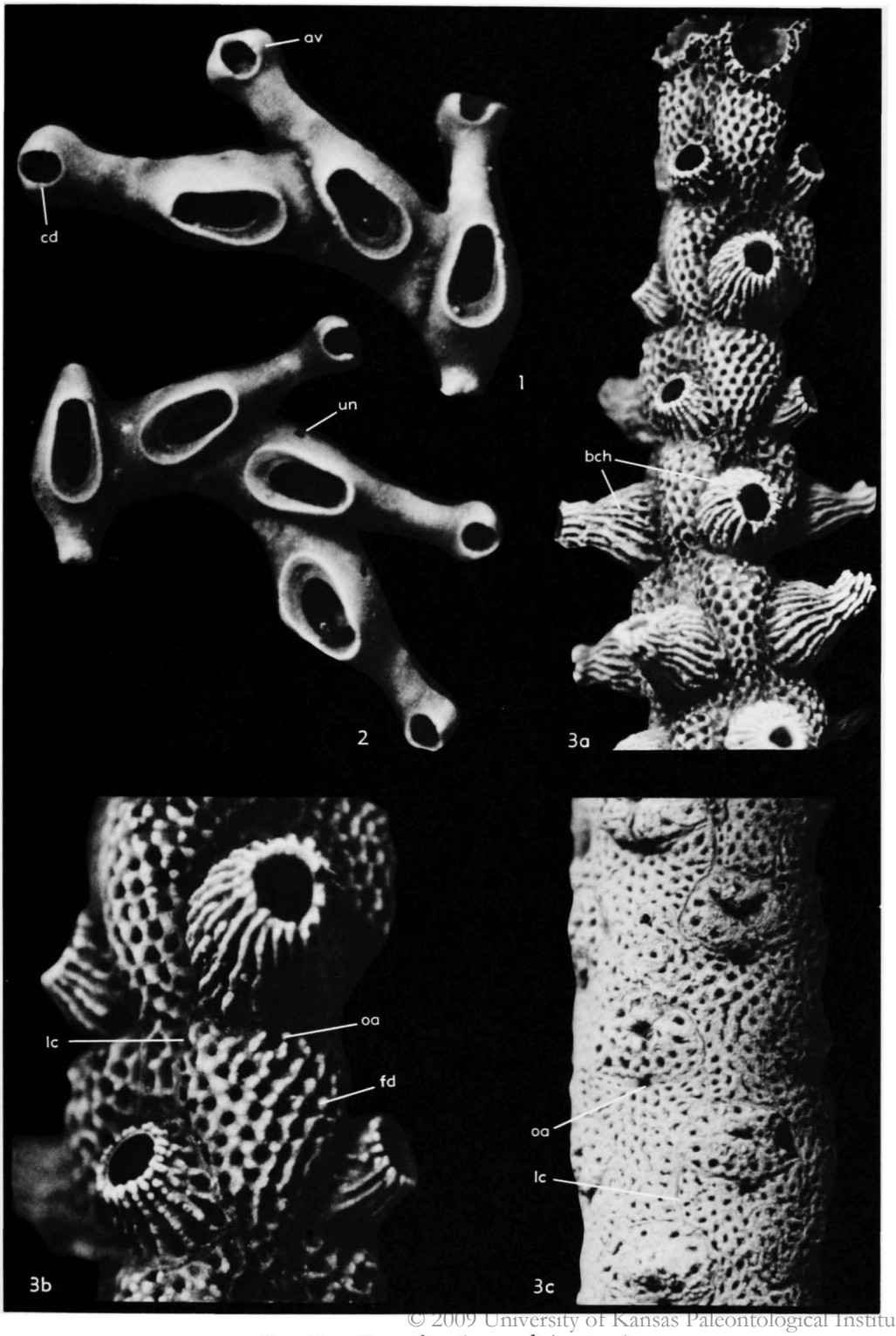


FIG. 82. *(For explanation, see facing page.)*

MER, 1972a) or by exposed or hidden parts of one or more autozooids or heterozooids (Fig. 71,*1a,c,3*; 72,*1–4*). In the Cheilostomata, varying combinations of exposed and hidden walls enclosing brood chambers can be calcified, and especially for brood chambers that have some calcareous enclosing walls the term **ovicell** is commonly used (see RYLAND, 1976, for alternative usage). Whatever its origin, a brood chamber opens near the orifice of a maternal zooid that commonly but not invariably differs in size, shape, or both from nonmaternal ordinary feeding autozooids, and therefore commonly is a polymorph (Fig. 70,*3*). Brood chambers formed by clusters of polymorphic zooids can have multiple openings (Fig. 72,*1–4*). Clusters of brood chambers around the orifice of a maternal zooid have been reported in two species, but only one chamber at a time in such clusters has been observed to be occupied by an embryo (POWELL, 1970).

Maternal zooids must at some ontogenetic stage be female autozooids, provided with protrusible lophophores through which eggs are extruded into the brood chamber. Except in a few living species, maternal lophophores bear tentacles and most such zooids appear to be capable of feeding. An egg produced on the body wall of the maternal zooid makes its way through the body cavity to the lophophore. Fertilization has not been observed in brooding gymnolaemates (RYLAND, 1976), but, as in nonbrooding genera, sperm has been reported to be released through tips of tentacles of male or hermaphrodite zooids (SILÉN, 1966, 1972; RYLAND, 1976, and literature cited therein). Thus, a mechanism for interzooidal or intercolony fertilization appears to be common if not universal in the Gymnolaemata (RYLAND, 1976). Once fertilized, an egg is extruded by the maternal zooid into the brood chamber through a pore in the wall of the lophophore below and between the distal pair of tentacles. After deposition of a fertilized egg in the brood chamber, the maternal lophophore may degenerate.

Except in a few living species, only one egg undergoes embryonic development in a brood chamber at a time, but additional eggs may occupy the same brood chamber sequentially. Embryonic fission is unknown in the Gymnolaemata. In a number of anascan and ascophoran cheilostomates, embryos have been observed to increase in size during development (RYLAND, 1976, and literature cited therein). In one such species, in which embryos may increase tenfold in diameter, evidence has been presented that nutrients are transferred to the developing embryo through a membranous outfold of the maternal zooid occupying the opening of the brood chamber (MARCUS, 1938a, p. 120; WOOLLACOTT & ZIMMER, 1972a,b, 1975). Membranous walls of maternal zooids occupy openings of or face into brood chambers in other species (Fig. 72,*1*), thus providing possible mechanisms for nutrient transfer. In still other species, membranous walls appear to be lacking (Fig. 67,*1d*), and the developing embryo may be physiologically isolated from its maternal zooid. In species in which there is no embryonic size increase, brooded embryos apparently subsist on yolk in the egg (**lecithotrophic development** of RYLAND, 1976). Apparently, both lecithotrophic development and nourishment of brooded embryos can occur within a genus (RYLAND, 1976).

FIG. 83. Ascophoran cheilostomate.——*1–3. Tessaradoma boreale* (BUSK), rec.; *1,* near Georges Bank, small erect colony thinly calcified near growing tips (gt) of branches, thickly calcified with nearly occluded peristomes near encrusting base (eb), USNM 242574, ×20; *2,* Caribb. Sea, 15°24′40″ N., 63°31′30″ W., Albatross Sta. D2117, 1,350 m, thickly calcified proximal part of colony with zooid boundaries covered by extrazooidal skeleton within which peristomes and adventitious avicularia (av) are immersed, USNM 242575, ×50; *3,* Albatross Sta. D2117, thinly calcified more distal part of colony with distal zooids having cuticular boundaries (lc) exposed distally and peristomes and adventitious avicularia (av) not immersed, USNM 242576, ×50.

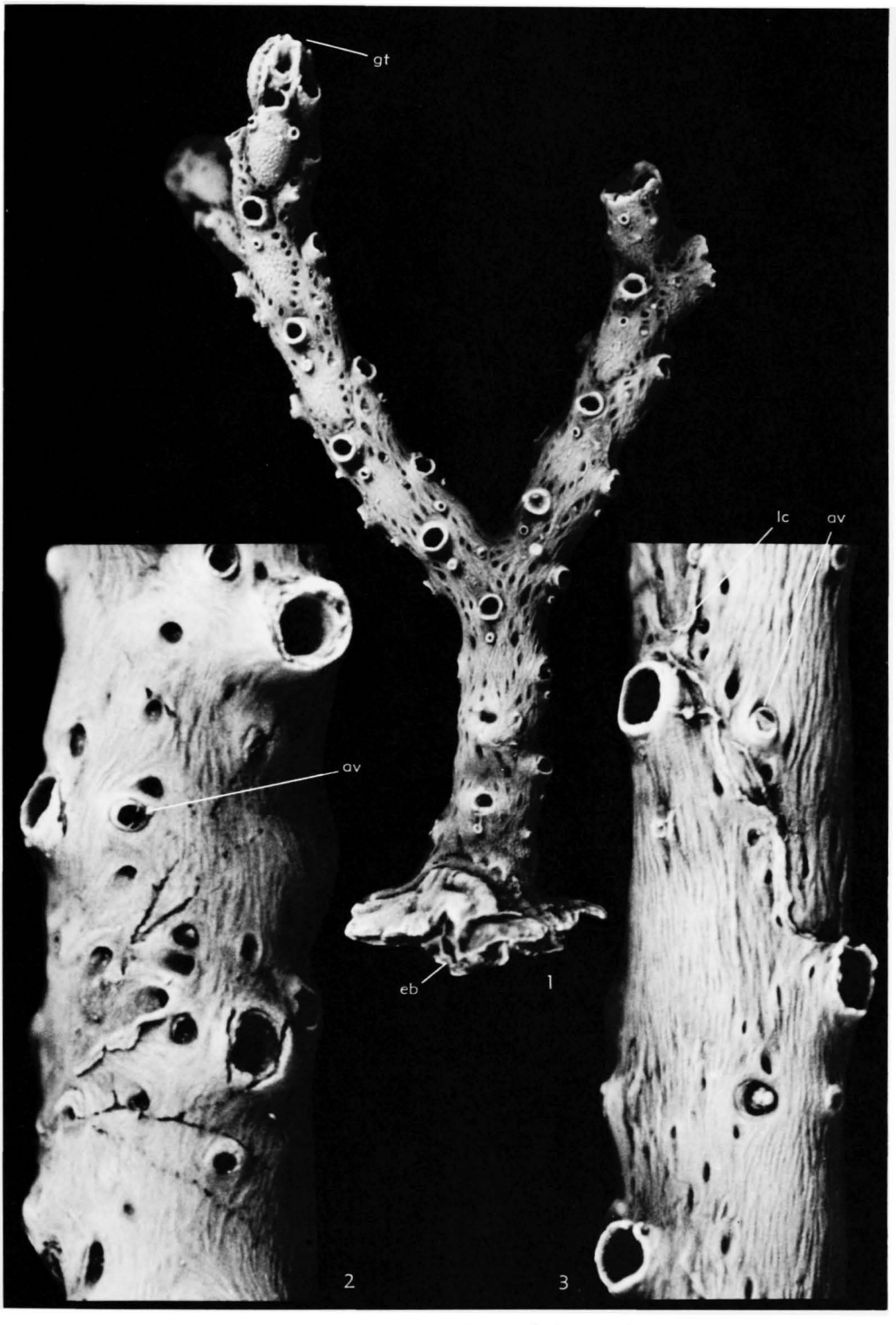


FIG. 83. *(For explanation, see facing page.)*

Larvae produced by most brooding gymnolaemates lack a digestive tract and after their release from brood chambers continue to subsist entirely on nutrients provided by maternal zooids before or during development (RYLAND, 1970, and references cited therein). These larvae are naked and have variable but relatively short motile stages before metamorphosis.

Even though brooding is widespread in the Gymnolaemata, nonbrooding species are known among both the Cheilostomata and the Ctenostomata. The ctenostomate genera *Alcyonidium* and *Flustrellidra* include both brooding and nonbrooding species. Commonly, fossil cheilostomates that lack evidence of brooding are morphologically similar to living species that do not brood; however, no skeletal evidence of production of nonbrooded larvae is known in either living or fossil gymnolaemates. The presence of nonbrooded larvae in fossil species, therefore, is inferential.

Nonbrooding gymnolaemates release fertilized eggs, commonly in great numbers, directly into the water through a pore at the end of an elongate **intertentacular organ** (absent in all but a few brooding gymnolaemates). The intertentacular organ is on the distal side of the lophophore beneath the tentacle bases in the same position as the pore through which eggs are extruded in brooding species. Lophophores provided with intertentacular organs for releasing eggs apparently can alternate in degeneration-regeneration cycles with lophophores lacking these organs, and no skeletal expression of this soft-part dimorphism is known.

Nonbrooded embryos undergo extensive development after release, and most of their lengthy motile stage is passed as larvae (Fig. 85,*4*) with fully functional digestive tracts (planktotrophic) and in most, a bivalved cuticular shell. Both digestive tract and shell are lost in metamorphosis. **Planktotrophic larvae** of gymnolaemates have generally been termed **cyphonautes,** because they were originally described under this name as a genus of planktonic animals.

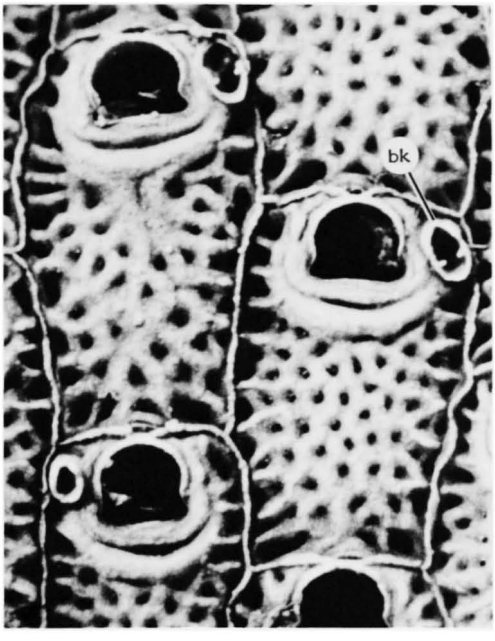
In a few species larvae developed from brooded embryos have digestive tracts and other morphologic features, including bivalved shells in some, that are similar to those of planktotrophic larvae. The digestive tracts are not functional, however, so that these larvae are not planktotrophic even though included within the concept of cyphonautes.

In one freshwater ctenostomate, larvae have been reported to contain much yolk and to lack a digestive tract, even though not brooded (BRAEM, 1896).

ASTOGENY

The Gymnolaemata apparently include the widest variety of astogenetic patterns known in the phylum. The number of primary zooids formed by metamorphosis of a larva, the presence or absence of a primary zone of asto-

FIG. 84. Ascophoran cheilostomates.——*1a,b. Hippopetraliella marginata* (CANU & BASSLER), rec., Gulf of Mexico, 28°45′ N., 85°02′ W., Albatross Sta. D2405, 60 m; *a,* repaired part of loosely encrusting colony with autozooids having wider orifices and smaller adventitious avicularia with pointed beaks (bk) placed in distolateral corners of frontal shields; *b,* uninjured part of same colony, about same distance from growing edge, with autozooids having narrower orifices and larger adventitious avicularia with rounded beaks (bk) placed nearer middle of lateral margins of frontal shield, avicularia with complete bars (piv) for hinging mandible; both frontal views, USNM 242578, ×50.——*2,3. Petraliella bisinuata* (SMITT), rec., Gulf of Mexico; *2,* 28°45′ N., 85°02′ W., Albatross Sta. D2405, 60 m, loosely encrusting colony with autozooids and adventitious avicularia communicating through frontal shield with underlying principal body cavity of zooid, pivotal bar (piv) separating mandibular (bk) and postmandibular regions of avicularium, frontal view, USNM 242579, ×75; *3,* 22°18′ N., 87°04′ W., Albatross Sta. D2365, 50 m, autozooids and adventitious avicularia with membranous frontal walls, opercula (op), and mandibles intact, mandible (md) hinged to pivotal bar, behind which is postmandibular membranous area for attachment of divaricator muscles (pmd), frontal view, USNM 242580, ×50.



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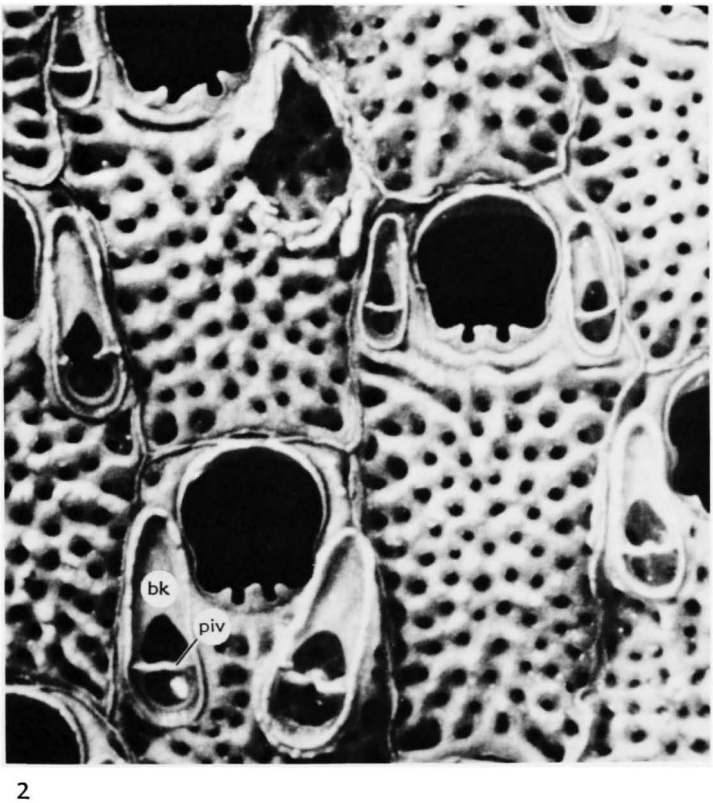

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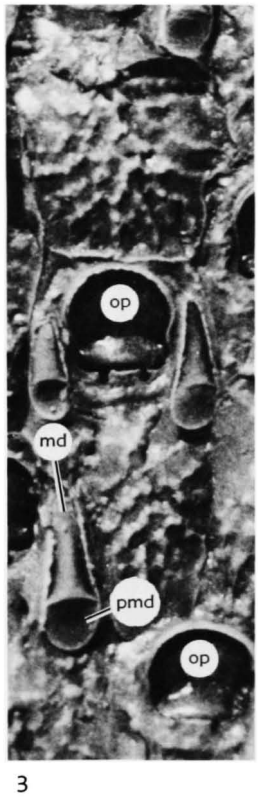

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FIG. 84. *(For explanation, see facing page.)*

genetic change, the magnitude and generational duration of astogenetic differences in zooid morphology, and the presence or absence of subsequent zones of astogenetic change and repetition—all can differ between taxa, and some can differ within species.

The soft-bodied sac formed by extensive reorganization of larval tissues becomes the body wall of one or more primary zooids. Usually a single primary zooid (ancestrula) is formed (Fig. 75,*1–8*; 77,*1*; 79,*1*; 80,*3,4*), but in some cheilostomates two or more primary zooids are partitioned simultaneously by interior walls (Fig. 75,*9*; 79,*2*) (EITAN, 1972; COOK, 1973a; HÅKANSSON, 1973). Localized, broad or circumferential swelling of the outer wall of the sac (Fig. 75,*1–3,5,7–9*) is followed by ingrowth of interior walls or pore plates to cut off the primary zooids from buds.

Primary zooids, whether multiple or a single ancestrula, most commonly are smaller and morphologically simpler than autozooids subsequently produced by budding in the same colony (Fig. 77,*1*; 79,*1*). Most have basal, lateral, and distal transverse walls similar to those of succeeding autozooids. The proximal end of an ancestrula commonly includes a more extensive exterior component than those of succeeding zooids (Fig. 75,*1–3,7,8*; 79,*1*). Orificial and frontal walls of an ancestrula commonly differ at least in proportions from those of succeeding zooids, but can also differ in structure. Some ascophoran species, for example, have an ancestrula with frontal structure like that of anascan autozooids. In living species, an ancestrula typically has feeding and alimentary organs, developed by infolding of exterior walls, but lacks sex cells. In a few genera of both Cteno-stomata and Cheilostomata, the ancestrula is a kenozooid (HARMER, 1926; RYLAND, 1976).

In a few morphologically simple cheilostomates and ctenostomates, a zone of astogenetic change is apparently lacking, with the primary zooid or zooids having the same morphology as subsequently budded zooids. In most gymnolaemates, primary zooids initiate a primary zone of astogenetic change that extends through one to several asexual generations of zooids of intermediate morphology and ends with a generation of repeatable morphology (Fig. 77,*1a*; 79,*1*; 80,*3*).

In a few morphologically complex cheilostomates a zone of astogenetic repetition is apparently lacking, with zooids continuing to show generational changes throughout colony life (COOK & LAGAAIJ, 1976). In most cheilostomates and ctenostomates primary zones of astogenetic repetition typically consist of numerous generations of one or more kinds of zooids.

In some species of both Cheilostomata and Ctenostomata **subsequent zones of astogenetic change** and **repetition** are developed (BOARDMAN, CHEETHAM, & COOK, 1970). These subsequent zones can be distal or frontal (Fig. 79,*3*) to zooids in primary zones of repetition. Subsequent astogenetic zones may provide renewed growth or a different form of concurrent growth in some colonies and restrict or end further growth in others (COOK & LAGAAIJ, 1976). In ascophorans having cryptocysts or umbonuloid frontal shields, frontally budded subsequent zones of astogenetic repetition can produce massive nodular multilaminate growth from initially encrusting colonies (Fig. 13,*3,4*).

FIG. 85. Carnose and stoloniferous ctenostomates, cheilostomate cyphonautes larva.——*1,2. Arachnidium clavatum* HINCKS, rec., Eng.; *1*, Northumberland, encrusting colony with uniserially arranged, distally and laterally budded autozooids, irregular anastomoses (ana) between lineal series common, frontal view, BMNH 1913.7.10.3, ×16; *2*, locality unknown, proximal region of encrusting colony with presumed primary zooids (pz) attached by proximal extremities, frontal view, BMNH 1898.5.7.182, Norman Coll., ×18.——*3. Terebripora* sp., rec., Bay of Santos, Brazil; polyester cast of boring in shell with autozooids (az) connected by stolonlike kenozooids (kz); oblique basal view, ×21 (photograph courtesy R. A. Pohowsky).——*4. Electra pilosa* (LINNÉ), rec., River Crouch, Essex, Eng.; cyphonautes larva; right lateral view, ×215.

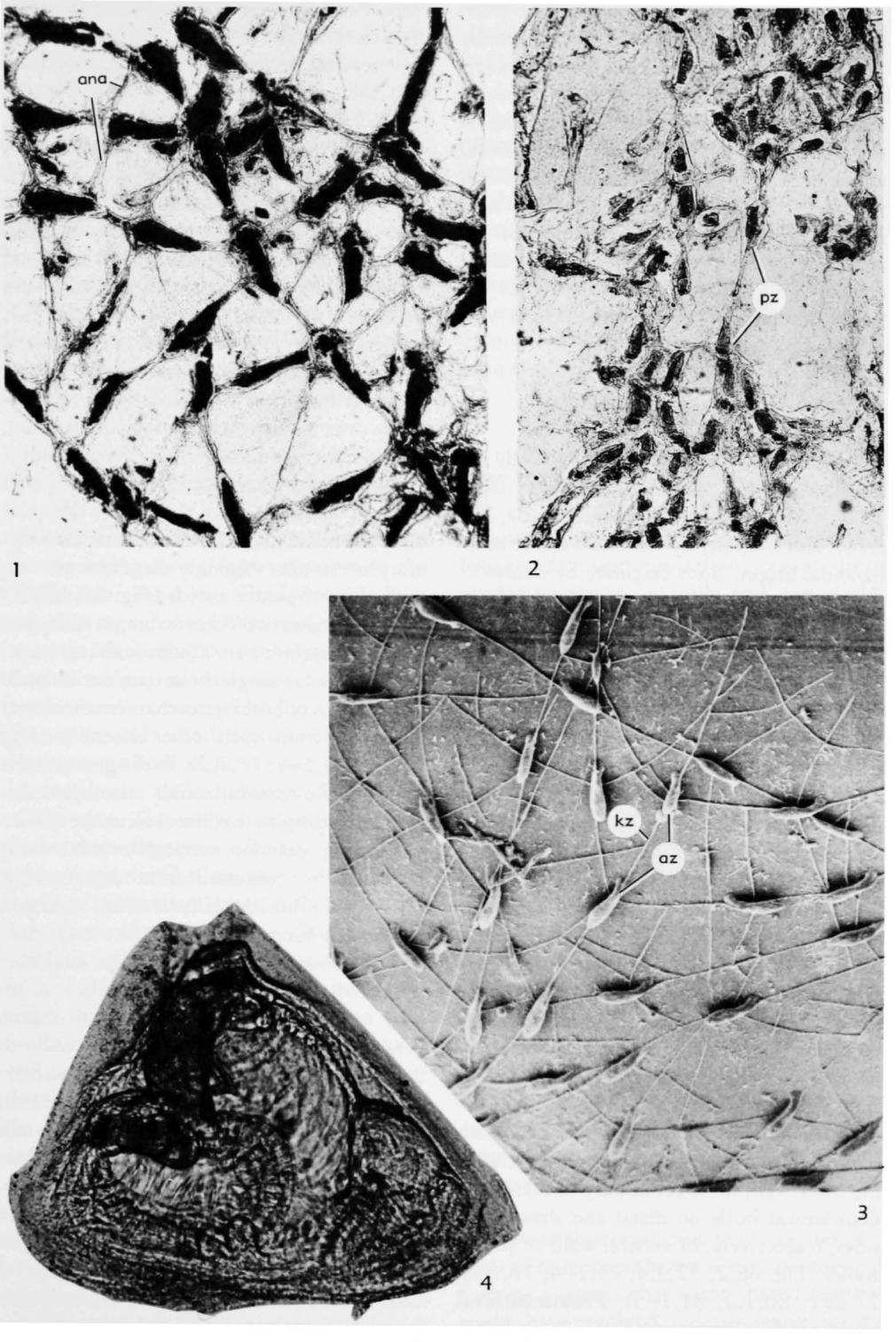

FIG. 85. *(For explanation, see facing page.)*

Some colonies in a few species of both freshwater and marine ctenostomates (JEBRAM, 1975) are produced asexually from encapsulated resistant resting bodies (hibernacula) that develop by inswelling or outswelling of the body walls of parent colonies. Similar asexual reproductive bodies have been reported in a marine cheilostomate (SIMMA-KRIEG, 1969). These colonies may form attached to or detached from the dead parent colony, and unlike colonies produced by fragmentation, have been noted to begin with zones of astogenetic change.

BUDDING

Zooids in the Gymnolaemata typically are budded at distal ends of lineal series (Fig. 74,*1,2*; 75,*1–8*), each bounded basally, laterally, and frontally by exterior walls of multizooidal origin. Buds originate by outswelling of these multizooidal walls (Fig. 68,*1a,2*; 76,*1b*; 77,*1a*; 80,*1,2*). As or after a bud swells, ingrowth of an interior wall separates the newly developing zooid body cavity from that of its proximal asexual parent (Fig. 68,*1a*; 75,*1,2*). Further lengthening of the bud is followed by ingrowth of a second, more distal interior wall that separates the now developed zooid body cavity from that of the next distal bud in the series (stage approximating that of zooid in Fig. 68,*1b*). Facing portions of the two interior walls are the transverse walls, or parts of the transverse walls, of the zooid, and their completion transforms exterior multizooidal walls to basal, lateral, and frontal zooidal walls. Further growth of walls and organs of the zooid takes place from or within these zooidal walls (Fig. 68,*1b,d,e*).

In the Cheilostomata, outswelling to initiate budding occurs on uncalcified parts of the body wall, most commonly as **distal** and **distolateral buds** on distal and distolateral sides, respectively, of vertical walls of parent zooids (Fig. 68,*2*; 72,*3,4*; 75,*1–4*; 76,*1–4*; 77,*2b,c*; 80,*1,2*; 81,*1–3*). **Proximolateral buds** are less common (Fig. 77,*1a*; 79,*1*; 80,*3,4*), and **proximal buds** arising from ends of zooids appear to be limited to repair of broken zooids (Fig. 76,*1a*) and to **periancestrular budding** in a few species (possibly the one shown in Fig. 76,*5*; note that periancestrular budding indicated in Fig. 75,*7,8* does not include "proximal" budding).

Budding in the Cheilostomata can also be initiated on basal walls of zooids in erect, unilaminate colonies and on frontal walls and associated structures in both anascans and ascophorans (Fig. 68,*2*; 69,*1b,c,f,2*; 70,*1b,c,3*; 79,*3*; 83,*2,3*; 84,*1–3*). Frontal buds most commonly produce such adventitious polymorphs as avicularia, communicating only with the underlying parent zooid, but can also produce ordinary feeding autozooids that communicate with each other through vertical walls (Fig. 79,*3*) (POUYET, 1971; BANTA, 1972). Adventitious polymorphs can also originate distally from vertical walls of parent zooids (Fig. 82,*1,2*).

In some genera of Ctenostomata and anascan and ascophoran Cheilostomata, most zooids arise as single buds (**uniserial budding**) at tips of lineal series that remain mostly separated from each other laterally (Fig. 75,*1,2*; 76,*1–4*; 77,*1,2*). In the great majority of Cheilostomata, zooids arise by **multiserial budding** so that lineal series are in contact along exterior vertical zooidal walls breached by communication organs (Fig. 75,*7,8*). In multiserially budded colonies, zooids can form by fusion of two or more buds emanating from different asexual parent zooids (Fig. 75,7) (GORDON, 1971a, b). The interzooidal communication organs breaching exterior vertical zooidal walls in multiserially budded colonies have also been regarded by some workers (SILÉN, 1944b; BANTA, 1969) as buds fused with zooids, and their formation involves much the same process as bud fusion.

In some cheilostomates, buds can become multizooidal by a lag in formation of interior walls leaving two or more zooid lengths of each lineal series unpartitioned. The relative lengths of such multizooidal buds (*Grossknospen* of NITSCHE, 1871; *bourgeons géants*

of LUTAUD, 1961), however, may be controlled more by environmental conditions than by genetic differences (LUTAUD, 1961; this revision).

In the few genera of cheilostomates presently known to have all interior vertical walls (Fig. 74,*3*), zooids are budded in multizooidal budding zones (Fig. 75,*9*) with body cavity confluent laterally around the colony periphery (HÅKANSSON, 1973) or at distal ends of colony branches (Fig. 78,*1b*). These budding zones are similar to those in the class Stenolaemata. Relationships between asexual parent and descendant zooids are less distinct in these colonies, and lineal budding series are not recognizable. However, ontogenetic gradients in zooid morphology proximally from growing tips are discernible (Fig. 78,*1a,b*), as in colonies with lineal series.

Budding in the Ctenostomata, in which the uncalcified walls are apparently predominantly exterior, could be expected to be more flexible than that in the calcified Cheilostomata. However, budding sites in the Ctenostomata tend to be similar in position to those of cheilostomates having similar growth forms (BANTA, 1975). In some major groups of the Ctenostomata, autozooids are budded only from kenozooids (Fig. 85,*3*).

POSSIBLE EVOLUTIONARY RELATIONSHIPS

Similarities in morphology and mode of growth among living representatives of the Ctenostomata and the Cheilostomata have long been regarded as evidence of a close phylogenetic relationship between the two orders. The following similarities form a major basis for the modern concept of the class Gymnolaemata, and include features expressed in development both of larvae and of colonies (see summary and discussion by BANTA, 1975). (1) The only nonbrooded larvae known in the Bryozoa are found in the Ctenostomata and the Cheilostomata (cyphonautes larvae). (2) Brooded larvae in the two orders ". . .seem impossible to distinguish. . . unless the adult is known" (BANTA, 1975, p. 574). (3) Embryological development in both orders leading to both brooded and nonbrooded larvae proceeds similarly (MARCUS, 1938a; RYLAND, 1970) and is less "aberrant" than in the other bryozoan classes (ZIMMER, 1973). (4) Autozooids in both orders have parietal muscles traversing the coelom to insert on flexible body walls to form the hydrostatic system for protruding the lophophore. (5) Reinforced, distally directed orificial wall flaps form opercula or operculumlike structures in some, but not all genera in each order. (6) Where present, opercula or operculumlike structures are closed by paired occlusor muscles in series with parietals. (7) Interzooidal communication organs form similar complexes of cells and noncellular structures in the two orders (BOBIN, 1964, 1971; BOBIN & PRENANT, 1968; BANTA, 1969, 1975; GORDON, 1975). (8) Budding in both orders commonly is in lineal series between which communication organs are formed in exterior walls in all but a few genera.

In addition, certain features that apparently are present in one order but not in the other can vary markedly in expression where present (BANTA, 1975). For example, the pleated membranous collar on the diaphragm of ctenostomate autozooids varies among genera, from rudimentary to prominent. Continuous calcareous layers in body walls of cheilostomates vary from a few lightly calcified zooecial walls to extensive heavily calcified zooecial walls and extrazooidal skeleton. Characteristic cheilostomate polymorphs, such as avicularia, are absent in many cheilostomate genera of diverse morphologies.

The variable expression in the Gymnolaemata of numerous shared as well as unshared features suggests that some shared features could have evolved independently in the Ctenostomata and the Cheilostomata.

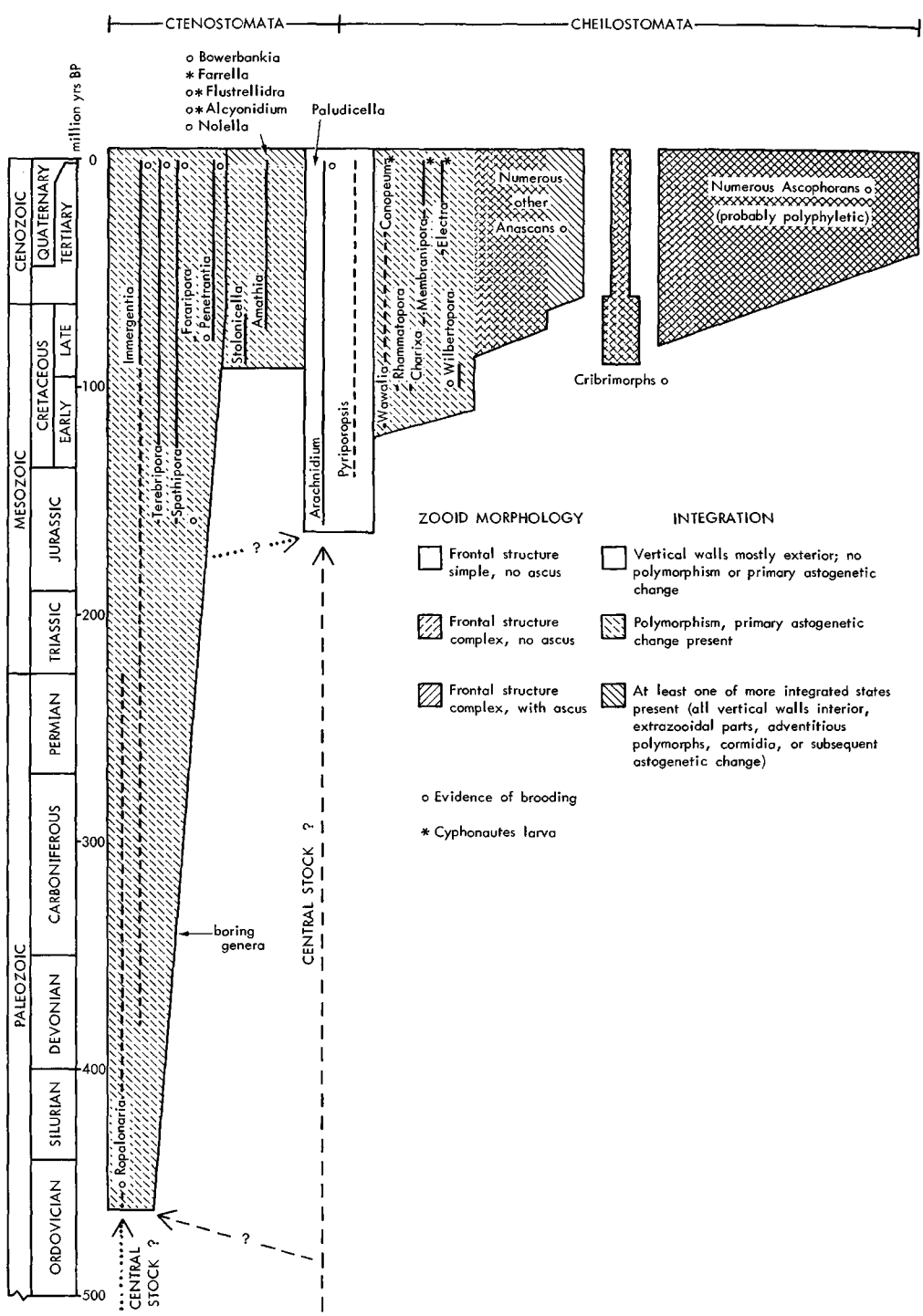

FIG. 86. *(For explanation, see facing page.)*

Cyphonautes larvae have been reported in ctenostomate genera that, on the basis of morphologies of zooids and colonies, are considered not to be closely related (BANTA, 1975, p. 574). Two ctenostomate genera include species having brooded and cyphonautes larvae. Cheilostomate genera in which cyphonautes larvae have been found are generally similar morphologically, but also show much morphologic similarity, except in reproductive structures, to some brooding genera. Morphology associated with brooding is variable in both orders.

If features considered to be characteristic of the Gymnolaemata, such as cyphonautes larvae, brooding, polymorphism, or interzooidal communication through exterior walls, could have evolved convergently, then the Cheilostomata and the Ctenostomata might have entirely separate evolutionary origins (DZIK, 1975). The question of whether the two orders should form a higher level taxon (class Gymnolaemata) in a phylogenetic classification cannot be answered by comparing morphology of living representatives alone. Evolutionary trends in the morphology of each order through time must be considered in order to suggest how the two orders might be phylogenetically linked.

Phylogenetic inference in the Gymnolaemata is hampered by the sporadic fossil record of the Ctenostomata, inadequate knowledge of distributions of more complex morphologies in the Cheilostomata, and low correlation between characters in both orders. A more precise delineation of major evolutionary stocks within the Cheilostomata can be attempted after restudy of the nearly 1,000 described nominal genera now assigned to the order is completed. Current understanding of early gymnolaemate morphology and of its apparent relationships to morphology of later gymnolaemates of both orders provides a starting point to suggest a tentative evolutionary basis for the class Gymnolaemata. This understanding has recently been increased by discoveries of new material and modern interpretations of modes of growth.

Phylogenetic relationships of the Cheilostomata and the Ctenostomata to the Stenolaemata or the Phylactolaemata are no less important to an evolutionary concept of the Gymnolaemata, but are more speculative. Significant overlaps occur in mode of growth between the Stenolaemata and some genera of the Cheilostomata (for example, cupuladriids, *Euthyrisella*) in which zooids have all interior vertical walls that grow into confluent body cavities in multizooidal budding zones. These groups of cheilostomate genera, however, seem to have appeared too late in gymnolaemate history (Late Cretaceous to Cenozoic) to provide a phylogenetic link between the Cheilostomata as a whole and representatives of the class Stenolaemata. Moreover, cheilostomates having this mode of growth have zooid morphologies and other characters closely comparable to those of different groups of anascans ranging from simple to complex, to which the cheilostomates seem to be phylogenetically related. Similarities in zooid shape and degree of "frontal" calcification once thought to imply a close phylogenetic relationship between cheilo-

FIG. 86. Possible evolutionary relationships among commonly recognized major morphologic groups of gymnolaemate bryozoans. Groups to right, under Cheilostomata, include many more genera than those to left, under Ctenostomata. Groups of genera are marked with two patterns, representing zooid morphology and integration level. The simplest state of each set of characters is indicated by absence of pattern, the most complex state by solid cross-hatching. Simple ctenostomates and cheilostomates are considered to have zooids with simple frontal structure and low degrees of integration (absence of both patterns). Other ctenostomates also are considered to have zooids with simple frontal structure, but can vary in integration from simple to complex (single pattern). Other cheilostomates vary from simple to complex in both zooid morphology and integration (intersecting patterns). Ranges of a few critical genera, discussed in text, are plotted, including all reported fossil genera confidently assigned to the Ctenostomata. Dotted and dashed arrows indicate two hypotheses of evolution in the Ctenostomata, discussed in text.

stomates and fenestellid cryptostomates (ULRICH, 1890; BASSLER, 1911) are now interpreted as a heterochronous convergence (TAVENER-SMITH, 1971).

Overlaps with the Phylactolaemata, such as lack of calcification in almost all ctenostomates and development of resistant resting bodies by some freshwater ctenostomates and some marine ctenostomates and cheilostomates, seem more difficult to evaluate because of the scarcity or lack of a fossil record in these groups of genera. Furthermore, JEBRAM (1973b) has suggested that early stenolaemate as well as early gymnolaemate and phylactolaemate stocks may have been uncalcified and thus may not be preserved in the fossil record. If this hypothesis is correct, phylogenetic relationships among the three bryozoan classes may remain speculative, unless exceptionally preserved material is eventually discovered.

Even within the Gymnolaemata, in which fossil evidence is available for some uncalcified as well as calcified taxa, study of the phylogenetic significance of such features as presence or absence of larval brooding, monomorphism or polymorphism of zooids, and different budding sites and directions has been based mostly on comparative morphology and development of living representatives of the class. Assumptions that certain states of these features are primitive and others derived are only beginning to be checked against fossil morphology (BANTA, 1975). Some genera that have been considered to link the Cheilostomata and the Ctenostomata, or the Gymnolaemata to other classes, either are not represented in the fossil record at all or have not been found in Mesozoic and older deposits, from which evidence of early gymnolaemate history must come to be convincing (Fig. 86).

The broad outlines of evolutionary relationships in the Gymnolaemata tentatively suggested below emphasize the rich fossil record of the Cheilostomata. As presently understood, evolutionary trends within the Cheilostomata support the inferred close phylogenetic relationship with the Ctenostomata. Even though much less adequate than that of the Cheilostomata, the fossil record of the Ctenostomata also supports this inferred relationship, and the two records thus provide some evolutionary basis for the modern concept of the Gymnolaemata. The ctenostomate record, however, seems inadequate to provide a choice between alternative hypotheses of evolutionary trends within that order (Fig. 86), and thus seems to shed little light on the origin of the Gymnolaemata. Major improvements in our understanding of early gymnolaemate history probably will require new discoveries and interpretations of more Paleozoic and early Mesozoic Ctenostomata.

EVOLUTIONARY TRENDS IN CHEILOSTOMATA

Phylogenetic inference in the Cheilostomata begins conveniently with the observation that the group of species having the oldest reported occurrence in the fossil record also has the simplest combination of morphologic features apparent in the order (Fig. 86). This group of species seems to be referable to a single genus, *Pyriporopsis,* and to include *P. portlandensis* POHOWSKY from the Upper Jurassic of England, one or more species of intermediate age, and the living North Atlantic species *P.? catenularia* (FLEMING). In Lower Cretaceous deposits a few genera in addition to *Pyriporopsis* have been reported. These genera are slightly more complex in morphology but, like *Pyriporopsis,* are comparable to some living species. In Upper Cretaceous and younger deposits, an increasing diversity of simple to complex morphologies leads to the numerous groups of living species of Cheilostomata.

Morphologic similarities between fossil and living species in each of the major groups of Cheilostomata permit a high degree of biologic interpretation of the morphology of the order. No major group of Cheilostomata, above the family level, appears to have become extinct. Most morphologic features found in fossil cheilostomates can be studied

in living colonies. However, some important questions in the biology of early cheilostomates, such as presence or absence of brooding and functions of different types of avicularia, still remain to be answered, at least in part through further studies of living representatives of their groups.

Earliest cheilostomates.—Morphologic simplicity of Jurassic to recent *Pyriporopsis* is expressed by a low level of integration of zooids in colonies and by lack of structural complication of zooids, particularly in features associated with the frontal wall and hydrostatic system.

Almost entirely exterior-walled zooids in *Pyriporopsis* are budded for the most part uniserially in series that branch irregularly to form encrusting colonies (Fig. 76,*1–5*). Basal walls of zooids, which may be either calcified or uncalcified in the same colony, adhere directly to the substrate, with no tendency to be partly immersed in calcareous substrates as are some stratigraphically younger cheilostomates with similar colony forms (for example, *Electra, Hippothoa*).

Zooids have only slight contact along vertical walls. Within lineal series, contact is through pore plates or pore chambers at the narrowed proximal extremities of zooids. Lateral contacts are irregular and less frequent in the generally open areas between lineal series. Even though the calcified lateral walls of zooids have uncalcified gaps opening into pore chambers (Fig. 76,*1b,4*), these gaps do not match where zooids contact laterally (Pohowsky, 1973; Banta, 1975). Interzooidal communication thus appears limited to zooids within lineal series. Uncalcified spots in lateral walls appear to serve only as incipient budding sites (Banta, 1975).

Frontal walls in *Pyriporopsis* include calcified and flexible portions. An extensive gymnocyst margins a simple, flexible hydrostatic membrane proximally and laterally (Fig. 76,*1,2*). This membrane, commonly preserved in both fossil and modern colonies by formation of frontal closures (Fig. 76,*2,3*), was apparently entirely exposed and unprotected in fossils as it is in modern colonies and demonstrates the simple anascan structure of the genus. Frontal closures preserve traces (scars) of bilateral series of parietal muscle insertions and the simple flaplike operculum reinforced only on its distal and lateral margins (Fig. 76,*2*) (Pohowsky, 1973, fig. 1). Cretaceous and living *Pyriporopsis* have narrow cryptocysts within the margins of the gymnocyst, and the Cretaceous species has a pair of minute spine bases flanking the orifices of some zooids. Both spines and cryptocyst are lacking in Jurassic *Pyriporopsis* (Pohowsky, 1973).

Zooids in *Pyriporopsis* apparently are entirely monomorphic, at least skeletally and in the morphology of the hydrostatic membrane and operculum. This apparent monomorphism and the presence of structures reflecting protrusible lophophores (Fig. 76,*2,3*) suggest that all fully developed zooids in *Pyriporopsis* colonies, except when lophophores and associated organs were degenerate, were able to feed. All fully developed zooids also may have been able to produce sex products, but there is no direct evidence for this known from either living or fossil colonies. It is not known whether living *Pyriporopsis* broods embryos or releases them directly. Modern species of *Electra, Conopeum,* and *Membranipora,* which have similar zooid morphology and only slightly higher levels of integration (Fig. 86), all produce nonbrooded cyphonautes larvae. However, such other genera as *Allantopora* (Fig. 77) appear equally similar to *Pyriporopsis,* except for having skeletally reinforced brood chambers. Genera that are known to brood embryos without apparent skeletal expression of this function, such as *Steginoporella* (Cook, 1964), are morphologically much less similar to *Pyriporopsis.* It therefore seems likely that *Pyriporopsis* is not a brooder.

Astogenetic differences in zooid morphology also appear to be lacking in *Pyriporopsis.* Differences in zooid size and shape reported in Jurassic colonies (Pohowsky, 1973) appear to be gradational within generations and related to different budding sites. Primary zooids have not been recognized in fossil *Py-*

riporopsis, but a few modern colonies have been found with proximal ends intact. In most fossil and modern colonies, the frequency of regenerative budding, commonly from proximal ends of broken zooids (Fig. 76,*1a*), obscures the proximal region. In intact colonies a pair of proximal zooids, having the same size and shape as those of succeeding generations, are joined by their narrowed "proximal" extremities (Fig. 76,*5*). Whether one zooid is the ancestrula from which the other budded "proximally" (see Fig. 75,*5*) or both grew simultaneously at opposite poles of a postlarval sac has not been determined. Both "proximal" budding (*Conopeum*) and simultaneous differentiation of twinned primary zooids (*Membranipora*) are known in living cheilostomates with generally similar zooid morphology. However, these genera all have primary zones of astogenetic change in which zooids show progressive generational increases in size and changes in other morphologic characters.

Other early cheilostomates.—All four or five other genera that have been reported from the Lower Cretaceous (Dzik, 1975; Larwood, 1975) show one or more increases in morphologic complexity over *Pyriporopsis* (Fig. 86). The fewest changes are evident in *Rhammatopora* and *Wawalia* and the most in *Wilbertopora.* These changes are not strictly progressive, however, but rather show the beginnings of a mosaic evolutionary pattern that typifies Upper Cretaceous and stratigraphically younger cheilostomates (Boardman & Cheetham, 1973).

All genera known from the Lower Cretaceous retained an encrusting growth form generally similar to that in *Pyriporopsis.* Cheilostomates with erect and other specialized colony forms are found in Upper Cretaceous and younger deposits. In the Lower Cretaceous *Rhammatopora,* uniserial budding of zooids was also retained, but other genera are characterized by multiserially budded zooids. In *Wawalia* and most colonies of *Wilbertopora* (Fig. 80,*3*) budding produced multiserial arrangements throughout, beginning at the ancestrula. In some colonies of *Wilbertopora* (Fig. 80,*4*), one or more generations of zooids initially budded uniserially, and these were followed by generations of zooids arranged like those in fully multiserial budded colonies (Cheetham, 1975b). Some modern species of *Conopeum* and *Electra* also show this pattern. Winston (1976) found that uniserial or multiserial budding in cultured colonies of *Conopeum* can be controlled by varying the kind of food. Variation in arrangements of zooids in *Wilbertopora* may also have been environmentally controlled and related to the low degree of integration, especially in the largely exterior vertical walls of zooids, in this genus.

Multiserial budding represents an advance in integration in that growth of adjacent lineal series is more or less coordinated and thus apparently less autonomous than uniserial growth. Gaps in calcified lateral walls match pore plates or pore chambers in laterally adjacent zooids (Fig. 75,*7,8*; 80,*1*) to provide interzooidal communication between lineal series. Such lateral communications occur in *Wawalia* (Dzik, 1975) and in *Wilbertopora* (Banta, 1975). Growing edges preserved in some *Wilbertopora* colonies (Fig. 80,*1*) show that adjacent lineal series were slightly staggered, suggesting less coordination of growth than in many stratigraphically younger cheilostomates that have smooth growing edges (Fig. 75,*7*; 80,*2*).

Within lineal series, multiserially budded zooids are also more extensively in contact than uniserially budded ones. Increased contact in Lower Cretaceous multiserial cheilostomates is generally produced by widening of proximal extremities of zooids, a shape change that is also common in multiserial parts of predominantly uniserial colonies. In *Wilbertopora* widening of proximal extremities of zooids was achieved by folding back the exterior vertical wall upon itself without greatly increasing the amount of interior wall (Fig. 75,6) or changing most of the zooidal outline from the elongated, distally inflated shape common in uniserial colonies (Cheetham & Lorenz, 1976). In this respect *Wilbertopora* remained significantly less integrated than stratigraphically younger multiserial cheilostomates in which broad

intraseries contact is along extensive interior transverse walls (Fig. 75,7), generally to produce more squat, uninflated zooid outlines.

Frontal and orificial walls of zooids in these Lower Cretaceous cheilostomates appear to be only slightly different from those in coeval *Pyriporopsis*. In *Rhammatopora* and *Charixa* a row of spine bases rings the inner margin of the gymnocyst. Spines presumably protected the hydrostatic membrane and the orifice, as in living genera such as *Callopora*. A few spine bases, in addition to the pair flanking the orifice, occur in some specimens of *Wilbertopora*. More extensive cryptocysts are evident in the Lower Cretaceous species compared by LARWOOD (1975) to *Conopeum*, in *Wawalia*, and in *Wilbertopora* (Fig. 80,*3*). There is no evidence, however, of fused spines, cryptocysts extensive enough to reflect passage of parietal muscles, or an ascus in any Lower Cretaceous species. Evidence of a simple frontal wall and operculum similar to those of *Pyriporopsis* has been reported in *Rhammatopora*, *Wawalia*, and *Wilbertopora*.

Polymorphism has been recognized in *Rhammatopora* and *Wilbertopora*. In *Rhammatopora* polymorphs are limited to kenozooids that occur sporadically between autozooids in the uniserial colonies (THOMAS & LARWOOD, 1960). In *Wilbertopora*, colonies with varying combinations of polymorphs that can be interpreted as kenozooids, avicularia, and zooids with brood chambers, together with ordinary autozooids, occur in the same populations as colonies in which zooids were apparently monomorphic (CHEETHAM, 1975b). Structures interpreted as avicularia and brood chambers (Fig. 81,*1,2*) have been reported from the earliest known *Wilbertopora* populations and thus could have evolved approximately simultaneously in this genus. However, broken brood-chamberlike structures have also been reported in a poorly preserved multiserial anascan that is slightly older stratigraphically (PITT, 1976).

Avicularia in *Wilbertopora* are all interzooidal or vicarious and follow a graded sequence of increasing morphologic difference from ordinary autozooids (Fig. 81,*1,2,4*). The most differentiated avicularia (Fig. 81,*1*) are found only in the stratigraphically youngest *Wilbertopora* populations, which also include colonies having less differentiated or no avicularia. The similarity in shape of the less differentiated avicularia (Fig. 81,*2,4*) to ordinary autozooids in the same colonies suggests that these avicularia may have had feeding organs, as in such living genera as *Crassimarginatella*. It seems unlikely that the most differentiated avicularia had feeding organs because of diminished width of the orificial wall (mandibular) area relative to the frontal wall (postmandibular and gymnocystal) area (Fig. 81,*1*). More highly differentiated avicularia of adventitious position, which are common in Upper Cretaceous and Cenozoic cheilostomates, have not been found in Lower Cretaceous genera (BOARDMAN & CHEETHAM, 1973).

The polymorphism evident in Lower Cretaceous cheilostomates, especially in *Wilbertopora*, can be inferred to represent at least some separation of functions and therefore a significant advance in the level of integration over the earliest cheilostomates, which appear to have been monomorphic. The apparent variability in polymorphism (presence or absence within a colony, degree of morphologic differentiation of polymorphs, and number of kinds of polymorphs) within *Wilbertopora* populations again suggests that integration was less rigidly controlled than in most stratigraphically younger cheilostomates (CHEETHAM, 1975b).

Astogenetic differences in zooid morphology are commonly preserved in *Wilbertopora*, and similar astogenetic differences have been reported in *Wawalia* (DZIK, 1975). With some variation in arrangement (Fig. 80,*3,4*), an ancestrula, smaller than but otherwise similar in morphology to distal zooids, is followed by a few generations of distally and generally distolaterally budded zooids of gradually increasing size (CHEETHAM & LORENZ, 1976). Numerous following generations of ordinary autozooids, and commonly polymorphs, form the primary zones of astogenetic repetition. The morphologic

difference between the ancestrula and autozooids of repeated morphology is small compared to that in many stratigraphically younger cheilostomates probably because of the low level of morphologic complexity of zooids in *Wilbertopora*. The level of integration through astogeny shown by *Wilbertopora* thus seems similar to that shown by many, perhaps even the majority of stratigraphically younger cheilostomates.

In summary, the stratigraphic sequence of increasing morphologic complexity among Lower Cretaceous cheilostomates seems to be: (1) development of cryptocysts in autozooids and of primary zones of astogenetic change and multiserial budding of zooids in colonies, with concomitant establishment of interzooidal communication through exterior walls of zooids in adjacent lineal series (*Wawalia*); (2) development of spines on gymnocysts of autozooids and differentiation of kenozooids (*Rhammatopora, Charixa*); and (3) development of brood chambers and differentiation of avicularia (*Wilbertopora*). The Early Cretaceous record of the Cheilostomata is probably not well enough known, however, to attach much significance to the exact order of appearance of new morphologic features in this sequence. The possibility of brood chambers in the poorly preserved multiserial anascan slightly older than *Rhammatopora, Charixa,* and *Wilbertopora* (PITT, 1976) already suggests that revisions in this sequence will be forthcoming as further studies are made. It does seem apparent even from this tentative sequence that autozooidal frontal structure and colony integration increased approximately simultaneously and at least partly independently in the early evolution of the Cheilostomata. For example, gymnocystal spines and cryptocysts are present both in better integrated genera such as *Wilbertopora* and in poorly integrated ones such as *Rhammatopora.*

Mosaic evolution in younger cheilostomates.—The many hundreds of genera of Cheilostomata known from deposits of Late Cretaceous and Cenozoic age display a range of morphologic differences markedly increased over that shown by Early Cretaceous representatives of the order. This diversification involved progressive appearances of major groups of genera having autozooids with more complex frontal structure, colonies with higher states of integration, or both (Fig. 86).

At least some changes in zooid morphology and colony integration in the Cheilostomata appear to be functionally linked to evolution of more specialized growth habits (CHEETHAM, 1971; BOARDMAN & CHEETHAM, 1973). In contrast to the exclusively encrusting habit of Jurassic and Early Cretaceous cheilostomates, younger representatives of the order exhibit an increasing variety of growth habits, eventually to include: (1) encrusting colonies of unilaminate, multilaminate, and loosely attached form; (2) erect colonies of rigid, flexible, jointed, and fenestrate form; and (3) free-living colonies of discoid and conical form. (See Fig. 13–15 for growth habits in living representatives of the Cheilostomata.) The earliest evidence of rigidly erect, jointed erect, and free-living colonies in the Cheilostomata has been found in Upper Cretaceous deposits (VOIGT, 1959, 1972b). These and other specialized growth habits numerically dominate fossil and living Cenozoic marine bryozoan assemblages (STACH, 1936; CHEETHAM, 1963; LAGAAIJ & GAUTIER, 1965; COOK, 1968b; LABRACHERIE, 1973; see SCHOPF, 1969a, for a review). However, the simpler growth habits also continue to be represented in many assemblages and even to dominate some of them.

For approximately 100 years, frontal structure of autozooids conventionally has been regarded as providing the most significant morphologic characters for phylogenetic interpretation of the Cheilostomata. This assumption has been inadequately tested on a polythetic basis against the fossil record; however, available evidence continues to suggest that increasing complexity of frontal structure is the apparent evolutionary trend, with the most obvious sequence of intermediate morphologies in the Cheilostomata (Fig. 86). Considered against the trend in frontal structure, characters derived from colony growth form and levels of integration form patterns suggesting uneven rates of evolution

or parallel or convergent trends in the several major evolutionary stocks within the order.

Characters expressing growth habit seem particularly to have been subject to parallel or convergent evolution. The most highly specialized growth habits, such as jointed erect and free-living colonies, are found in groups of genera ranging from simple anascans *(Nellia, Cupuladria)* to complex ascophorans *(Margaretta, Mamillopora)*. Numerous examples of simple encrusting to more specialized growth habits are known within the same genus, also in groups ranging from simple anascans (*Membranipora*) to complex ascophorans (*Metrarabdotos*). Observed environmental plasticity of growth habits within species, and even within some colonies (Cook, 1968a), further suggests that some similarities in colony form among otherwise morphologically distinct genera may be induced directly by the environment (Stach, 1936).

The generally increasing level of integration evident in the stratigraphic record of the Cheilostomata appears to have proceeded at uneven rates (Fig. 86), partly but not entirely correlated with specialization in colony form. For example, both encrusting and erect species of *Metrarabdotos* and *Schizoporella* have similar high levels of integration in their combination of interior and exterior vertical zooid walls, transverse and lateral communication organs, brooding autozooids, and adventitious avicularia. Erect species of *Metrarabdotos* have extensive extrazooidal skeleton, which is only partly or not developed in the encrusting species, and thus a higher level of integration. However, encrusting species of *Schizoporella* have subsequent zones of astogenetic change and repetition not found in erect species of this genus, and thus are the more highly integrated.

Some integrative characters reached peak states in groups of cheilostomate genera having increasingly different types of frontal structure and either high or low levels of other integrative characters. Some peak states occur in genera so different in other morphologic characters that convergence in integrative characters seems highly probable. Convergence seems especially probable in integrative characters with states associated with differences in environment. For example, species possessing avicularia in stable environments can lack them under unstable conditions of salinity or temperature (Schopf, 1973). In colonies that are either uniserial or multiserial under the influence of different foods (Winston, 1976), it seems likely that integrative characters of zooid walls and interzooidal communication may suffer direct environmental modification.

Detailed review of the combinations of states of integrative and frontal characters can be made only when all the genera now assigned to the Cheilostomata have been restudied. The following examples are intended to show a few of the extreme combinations that have been reported previously (as reviewed by Boardman & Cheetham, 1973), or are illustrated in this section.

Genera having extensive interior vertical walls include anascans (*Cellaria,* Banta, 1968; Sandberg, 1971; cupuladriids, Håkansson, 1973) and ascophorans (*Euthyrisella,* Fig. 78; Harmer, 1902; *Myriapora, Mamillopora,* and conescharellinids, Sandberg, 1973), with erect colonies of jointed, flexible, or rigid form and free-living colonies. The erect *Euthyrisella* and free-living cupuladriids are further integrated in having extrazooidal parts formed concurrently with budding of zooids. Extrazooidal parts are apparently absent in other genera in this group. Some cupuladriids are even more highly integrated through the presence of subsequent zones of astogenetic change and repetition (Boardman, Cheetham, & Cook, 1970). Some genera with erect or free-living habit (*Myriapora, Mamillopora,* conescharellinids) have highly specialized polymorphs (avicularia) adventitious upon autozooids or in clustered arrangements. Others also erect or free-living (*Cellaria,* cupuladriids) have interzooidal or vicarious avicularia in irregular or regular, nonclustered arrangements. Still others (*Euthyrisella*) lack highly specialized polymorphs but have dimorphic autozooids in apparently random intermixtures.

TABLE 3. *Comparison of Some Morphologic Characters of Early Gymnolaemata.*

Character	Paleozoic–Early Mesozoic (Boring) Ctenostomates	Cretaceous *Amathia, Stolonicella*	Jurassic–Early Cretaceous *Arachnidium*	Jurassic *Pyriporopsis*	Early Cretaceous Cheilostomates
Form of colony	Totally immersed in calcareous substrates	Encrusting to erect, not immersed	Encrusting, not immersed	Encrusting, not immersed	Encrusting, not immersed
Budding and communication	Uniserial, lateral fusions regular	Uniserial, lateral fusions irregular or absent	Uniserial, lateral fusions irregular	Uniserial, no lateral fusions	Uniserial-multiserial, lateral fusions generally regular
Vertical zooid walls	Virtually all exterior, uncalcified	Virtually all exterior, uncalcified	Virtually all exterior, uncalcified	Virtually all exterior, calcified	With significant interior components, calcified
Frontal zooid walls	Entirely flexible but protected by immersion in substrate	Entirely flexible and exposed	Entirely flexible and exposed	Flexible portion exposed, but reduced by rigid gymnocyst	Flexible portion largely exposed, but commonly protected by spines or underlain by cryptocyst, and reduced by gymnocyst
Orificial walls	Probably radially disposed, unreinforced folds[a]	Ringlike or radially disposed, unreinforced folds	Ringlike, unreinforced fold	Operculum reinforced distally and laterally	Operculum reinforced distally and laterally
Polymorphism	Generally present, integral to budding pattern	Present, integral to budding pattern	Apparently absent	Apparently absent	Generally present
Brooding	Generally present	Probably present	Probably present	Possibly absent	Generally present
Astogenetic change	Primary zone present	Probably present	Probably absent	Probably absent	Primary zone generally present

[a] Excludes Cretaceous *Penetrantia*.

Highly specialized adventitious and clustered interzooidal or vicarious polymorphs are commonly found among the numerous cheilostomate genera that retained extensive exterior vertical walls. These genera include anascans (*Monoporella,* Fig. 72; *Setosellina,* Fig. 82,*1,2*) and ascophorans (*Hippothoa,* Fig. 69; *Tessaradoma,* Fig. 83; *Hippopetraliella,* Fig. 84,*1*; *Petraliella,* Fig. 84,*2,3*; *Stylopoma,* Fig. 79,*2,3*; *Metrarabdotos,* Fig. 68,*2*; 70,*1b,c,3*) with a wide variety of growth habits. The specialized adventitious or clustered polymorphs include brooding and other sexual zooids (for example, *Monoporella, Hippothoa,* and *Metrarabdotos*) and avicularia. Some ascophoran genera in this group develop extrazooidal parts through coalescence of parts of zooids (*Tessaradoma, Metrarabdotos*), and others have subsequent zones of astogenetic change and repetition formed by frontal budding from hypostegal coeloms (*Stylopoma*). Some anascans in this group can also have subsequent astogenetic zones formed by distal budding (*Nellia*; *Poricellaria,* Boardman, Cheetham, & Cook, 1970).

A great diversity of Late Cretaceous, Tertiary, and living genera include species that have frontal structures of moderate to high complexity but have not reached peak states of any integrative characters considered here. These genera even include relatively complex ascophorans (*Margaretta,* Fig. 67; 73; 82,*3*; *Cryptosula,* Fig. 79,*1*) with both specialized and simpler growth habits.

Flexibility of different integrative morphologic features in combination with different zooidal frontal structures may well have provided the broad adaptability in growth habit evident in late Mesozoic and Cenozoic Cheilostomata, and consequently assured the increasing evolutionary success of the order (Boardman & Cheetham, 1973). Despite the great numbers of elaborately integrated and morphologically complex species present in modern faunas, however, even the simplest morphology, as represented by *Pyriporopsis* and similar forms, continues to have its niche in present seas.

POSSIBLE LINKS BETWEEN CHEILOSTOMATA AND CTENOSTOMATA

There has been no convincing evidence reported of the existence of calcified Cheilostomata before Late Jurassic time. The earlier Mesozoic and Paleozoic fossil record of the uncalcified Ctenostomata, however fragmentary, provides strong evidence that representatives of this order considerably preceded the earliest cheilostomates in time (Fig. 86).

Present understanding of gymnolaemate morphology makes it appropriate to seek the ancestry of the Cheilostomata among Ctenostomata approximately coeval with and similar in morphology to early, simple, *Pyriporopsis*-like cheilostomates (Banta, 1975). Three groups of ctenostomate genera have been reported from Mesozoic or earlier deposits (Fig. 86): genera that penetrate calcareous substrates (boring genera), stoloniferous nonboring genera (*Amathia, Stolonicella*), and a carnose genus (*Arachnidium*). These genera show different degrees of morphologic similarity to *Pyriporopsis* (Table 3).

Similarities between *Pyriporopsis* and some simple uniserial stenolaemates of Paleozoic age (corynotrypids) led Dzik (1975) to propose that the Cheilostomata and the Ctenostomata each separately evolved from the Stenolaemata. This hypothesis requires that basic features shared by zooids throughout the Cheilostomata and Ctenostomata—such as flexible frontal walls or their derivatives, parietal muscles, and the folded structure of the orificial wall, together with negative features such as the absence of a membranous sac—all evolved convergently. These convergences would be in addition to those that possibly produced cyphonautes larvae, extracoelomic brooding, or polymorphism in the two gymnolaemate orders.

Nonboring carnose ctenostomates.—Although lacking calcification and possessing typical ctenostomate features such as unreinforced orificial walls, *Arachnidium* is closely similar in morphology to *Pyriporopsis* (Table 3). As in other carnosans, autozooids bud

directly from other autozooids. Predominantly uniserial colonies lack apparent zones of astogenetic change and begin with a pair of proximally opposing zooids (Fig. 85,*2*). Irregular tubular extensions connect some zooids in neighboring lineal series (Fig. 85,*1*). Zooids are monomorphic and similar in shape to those of *Pyriporopsis*. Living species brood embryos in diverticula of vestibules of otherwise unmodified zooids. Although *Arachnidium* is marine, hibernacula have been reported in one species (JEBRAM, 1975).

Arachnidium thus appears to be more specialized reproductively and slightly more advanced in integration than *Pyriporopsis,* even though occurring in slightly older deposits (Middle Jurassic; VOIGT, pers. commun., 1976). Simpler ctenostomates might have existed before the earliest cheilostomates, but there is as yet no fossil evidence. The morphologic similarities are enough, however, to make a close phylogenetic relationship between *Arachnidium* and *Pyriporopsis* likely.

Other carnosans, none known as fossils, display differing but higher levels of integration. Genera such as the freshwater *Paludicella* are similar to *Arachnidium*. At the upper end of the scale are genera such as *Flustrellidra, Elzerina,* and *Alcyonidium* (Fig. 66,*1–3*) with clustered arrangements of autozooids and kenozooids and some other features paralleling those of advanced cheilostomates (Fig. 86). The reproductive features of these genera display a pattern seemingly best interpreted as the result of convergence.

Nonboring stoloniferous ctenostomates.—Colonies of stoloniferous ctenostomates are comparable in levels of integration to most complex carnose genera. Autozooids in **stoloniferans** are budded entirely from kenozooids. Budding patterns typically include lineal series of kenozooids forming stalks or encrusting networks from which regularly grouped clusters of autozooids arise. This highly organized budding pattern seems to exclude stoloniferous genera from consideration as a possible link to early cheilostomates.

Boring ctenostomates.—Even though boring ctenostomate genera have a long fossil record preceding the earliest known cheilostomates (Fig. 86), their morphology and mode of life suggest that they did not include the direct ancestors of the Cheilostomata.

A few modern boring genera penetrate noncalcareous substrates, apparently by mechanical means (SOULE & SOULE, 1969). None of these genera is known from fossils. Colonies of fossil boring genera are completely immersed in calcareous substrates. Most of these genera have living representatives (VOIGT & SOULE, 1973) found exclusively, or nearly so, in calcareous substrates. Growth of colonies in calcareous substrates is accomplished by some chemical means of penetration not well understood (SOULE & SOULE, 1969, p. 801). SILÉN (1947) presented chemical evidence that in *Penetrantia* dissolution of mollusk shell may be accomplished by secretion of phosphoric acid. In some cheilostomates (*Electra, Hippothoa*) basal walls of zooids in encrusting colonies may be immersed in calcareous substrates to produce pits, which in some respects seem comparable to ctenostomate borings (PINTER MORRIS, 1975). However, there is no evidence that the earliest cheilostomates or their modern representatives produced such pits.

Within calcareous substrates, zooids of boring ctenostomates are connected in lineal series and laterally by a complex system of elongate, anastomosing tubes to form colonies with relatively widely spaced autozooidal orifices (Fig. 85,*3*). In all but one genus (*Immergentia*) the connecting tubes are kenozooids separated from autozooids by pore plates so that the autozooids themselves are widely separated. This arrangement is similar to that in some nonboring stoloniferans, to which most boring genera are considered to be related.

Polymorphs in addition to connective kenozooids have been reported in a number of Paleozoic and Mesozoic genera (VOIGT & SOULE, 1973; POHOWSKY, 1974, 1975; RICHARDS, 1974). In a Cretaceous species, these polymorphs have been compared in shape and position to brooding autozooids in

living species of the boring genus *Penetrantia.* Living species of other boring genera all brood embryos without apparent modification of autozooidal size or shape.

The complex budding patterns and polymorphism of boring ctenostomates thus represent a significantly higher level of integration than that reached by early cheilostomates. Even though one boring genus, *Penetrantia,* has features such as opercula and associated musculature similar to those in the Cheilostomata (SOULE & SOULE, 1975), it shares the high level of integration of other boring genera. Moreover, reinforced flaplike orificial walls even more similar to the opercula of early cheilostomates also occur in other groups of ctenostomates (for example, *Elzerina*; Fig. 66,*2a*). If *Penetrantia* should be assigned to the Cheilostomata (SOULE & SOULE, 1969), its ctenostomate features probably indicate convergence (possibly through adoption of the boring mode of life), rather than a phylogenetic link between the orders.

Summary.—Even though other groups of ctenostomates also occur in deposits older than those containing earliest (Late Jurassic) *Pyriporopsis,* Middle Jurassic to Early Cretaceous *Arachnidium* is most comparable morphologically to early cheilostomates. Simple *Arachnidium*-like ctenostomates therefore seem likely to have been the mid-Mesozoic ancestors of the Cheilostomata and to provide a phylogenetic basis for the class Gymnolaemata.

NATURE OF EARLY CTENOSTOMATA

Evolutionary relationships of simple *Arachnidium*-like ctenostomates both to more highly integrated boring and nonboring genera of the Ctenostomata, and to representatives of other bryozoan classes, are much more difficult to infer from available evidence. Critical to such an inference is whether nonboring ctenostomates existed during Paleozoic and early Mesozoic time and, if so, whether they were as highly integrated as Paleozoic and early Mesozoic boring genera or possessed a low level of integration comparable to that of *Arachnidium.* Problematical Paleozoic fossils historically interpreted as nonboring ctenostomates have not yielded morphologic evidence that permits comparison with living ctenostomates (DZIK, 1975). The nature of early Ctenostomata thus remains speculative, with only the few boring ctenostomate genera providing stratigraphic evidence for the early history of the group.

If nonboring ctenostomates of the *Arachnidium* type did not evolve until mid-Mesozoic time, as the sporadic Paleozoic record of Ctenostomata suggests, the central gymnolaemate stock would likely have lain among relatively highly integrated forms of boring and perhaps nonboring habit (dotted arrows on left side of Fig. 86). Evolution of *Arachnidium*-like ctenostomates then would have involved a decrease in integration through loss of polymorphism and simplification of astogeny and budding patterns. Such a decrease would be in contrast to prevailing evolutionary trends toward higher levels of integration in the Cheilostomata.

Conversely, if trends increasing integration could be assumed to have characterized the class Gymnolaemata as a whole, then simple *Arachnidium*-like ctenostomates would have existed throughout much of Paleozoic and early Mesozoic time as the central gymnolaemate stock (dashed arrows, center of Fig. 86). Ctenostomates within this hypothetical central stock should have been similar in some morphologic features to the ancestors of the Gymnolaemata.

Although the ancestry of the Gymnolaemata must now be the most speculative inference of all, the morphology of the class as a whole is slightly more similar to that of the Stenolaemata than to that of the Phylactolaemata (Table 1), even allowing for convergence in some modes of growth. Some uniserial stenolaemates of early Paleozoic age (corynotrypids) are comparable, especially in level of integration, to gymnolaemates of the *Arachnidium-Pyriporopsis* type (BOARDMAN & CHEETHAM, 1973, p. 144; DZIK, 1975; BANTA, 1975; see BOARDMAN, this revision). In contrast, no close comparison between boring ctenostomates and any group of stenolaemates seems to have been suggested.

AUTOZOOID MORPHOGENESIS IN ANASCAN CHEILOSTOMATES

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Modes of growth and subdivision of initial buds of zooidal series, as well as ontogenetic folds of the undifferentiated wall of the bud, are fundamental manifestations of the diversification of species in Bryozoa. It is necessary therefore to coordinate structural observations on the temporal evolution of zooid shape and of skeletal deposits with biological observations on the underlying cellular layers and their capacity for proliferation and organization. The zooecium is not a simple tegumental protection for the feeding organ, or **polypide**. It is the persistent and physiologically active organ of the entire functional zooid.

Early anatomists, notably Braem, Calvet, Claparède, Nitsche, Seeliger, and Smitt, established in the late nineteenth and early twentieth centuries the biological details of the phylum. These are: the community of the body wall within a colony, which results from a continuous process of asexual reproduction by budding and implies an incomplete anatomical and physiological autonomy of zooids; and internal budding and periodic renewal of the polypide from the parietal layers of the **zooecial compartment**, which implies that the **digestive epithelium** in the adult does not derive directly from the larval endoderm, but from a secondary invagination of zooecial epithelium.

In adult zooids of any shape and functional adaptation, the bryozoan wall includes a pavemental **epithelium** externally covered by its cuticular and skeletal secretions (Fig. 87), and an inner peritoneal lining limiting the body cavity and including several cellular categories. In stenolaemates and cheilostomates, the superficial **cuticle** is reinforced by an underlying deposit of calcium carbonate within an organic matrix (Fig. 87,*2*). Undifferentiated epithelium is **columnar** in the bud and restricted areas of tissue proliferation in the adult wall. Both epithelium and peritoneum are present and mitotically active in the bud wall.

Confusion in terminology arose from use of the terms **ectocyst** and **endocyst** with different meanings in early descriptions of zooecial wall structure. According to different authors, ectocyst may mean either cuticle only, or include epithelium, or epidermis, and its cuticular and skeletal protection. Endocyst has been used to mean both cellular layers or only the peritoneum. More recent authors have preferred the terms **ectoderm** and **mesoderm** to designate epithelium and peritoneum. Although this is justified by the organogenetic potential of the two layers in the bud, ectoderm and mesoderm are embryologic terms that cannot be directly applied to budding and adult tissues before the precise relationship between these tissues and larval layers throughout metamorphosis is established. The general term **mesenchyme** for a comprehensive designation of subepithelian tissues is simply descriptive of their destiny during morphogenesis, and more appropriate than mesoderm. Here, cellular layers of the wall are designated by the terms epithelium and peritoneum, which account for their cytological character, function, and relative situation in the bud, zooecial wall, and polypide.

The bryozoan wall has a propensity to proliferate whenever space is free and energy is supplied. **Primary buds** around the ancestrula arise as hollow outward expansions of the parietal layers from distal and lateral areas in the ancestrular wall, which locally retain undifferentiated characters. In gymnolaemates, buds grow in a linear direction and by the development of lateral areas of proliferation that may or may not be able to expand

depending on specific budding patterns, physiological and trophic regulations, and intrinsic or incidental obstacles.

Fundamental phylogenetic options based on evolution of zooid shape and colony construction will not be discussed here. However, for a better understanding of the basic process of proliferation, which will be described for Anasca, it is noted that colony construction is regulated by specific differences in relative intensity of distal and lateral budding, and by rhythms of the transverse and longitudinal subdivisions of buds. In the simplest colonial pattern of such ctenostomates as *Arachnidium,* or of such uniserial Anasca as *Pyropora,* new zooids are formed one after another in divergent series from equal distal and lateral buds borne by successive zooids. In Stolonifera, the distal portion of the **stolon**, or stolonal bud, grows in a rapid linear progression while lateral buds are formed with a specific periodicity. Lateral buds develop into autozooids, which are separated from the stolon by a basal septum. Other transverse septa separate segments along the stolon. Division of the stolon at the **growing tip** leads to branching. In Carnosa and some Anasca, multiserial colonies are built when new zooidal series formed from the longitudinal division of the bud are kept together by reciprocal pressure and by adherence of the cuticular and skeletal layers of adjacent series. Lateral proliferation is then inhibited, or restricted to the formation of rows of heterozooids, kenozooids, and pore chambers. Thus, a phylogenetic and morphogenetic difference is apparent between longitudinal and transverse partitions. According to SILÉN (1944a), a unique peripheral evagination, or "common bud," would have first appeared around a solitary ancestral zooid. Then, this "common bud" would have been subdivided by peripheral indentations of the "exterior wall," as a consequence of the formation of several polypides when space became sufficient for their development. Transverse septa, or "interior walls," would have secondarily separated successive zooids along zooidal lines. Longitudinal partitions are now universally interpreted as the contiguous lateral walls of adjacent zooidal series growing together. Transverse partitions are formed from an invaginated fold of the parietal cellular layers, in the middle of which a skeletal lamina is secreted.

Two principal modes of colonial construction occur among encrusting cheilostomates (HARMER, 1931; BOARDMAN & CHEETHAM, 1969). In the simplest colonial pattern, linear series of zooids in concordant or alternate rows are regularly produced, first from peripheral buds around the ancestrula, then by growth of distal buds of linear series at the periphery of the colony. The formation of lateral buds is inhibited. With increase in surface area and circumference of the growing colony, buds tend to enlarge until their normal width is reestablished by longitudinal subdivision (LUTAUD, 1961). In some species, the longitudinal subdivision occurs earlier and young peripheral zooids bear two distal buds. In species of quincuncial or spiral pattern, every new zooid is formed between two preceding zooids from an axillary bud, which may be either a dominant lateral bud or a distal bud of distorted orientation. The colonial pattern is often complicated by partial development of distal and lateral buds that build an intercalary range of pore chambers around the anterior portion of every fully developed zooid. Then, new zooids are formed from distal or lateral buds arising from distal or lateral pore chambers (*Fenestrulina,* GORDON, 1971a,b). Only the simple mode of **lineal growth** will be taken into account in the following description of the budding process in Anasca.

In bilaminate and encrusting cheilostomates of lineal growth mode, new zooids are formed from the proximal portion of the bud, which is separated from the proliferating distal portion by formation of a new transverse septum. The proximal portion absorbed during the formation of every new zooid varies in length according to the speed of proliferation and to specific zooecial dimensions. The rhythm of transverse divisions depends on both genetic regulation and the abundance

of metabolites transmitted by preceding feeding zooids and accumulated in the parietal tissues of the bud. It is a general rule in Anasca that rapid colony growth, with increase in number of feeding units, leads to an increase in length of buds. Growth, being proportional to the number of cells participating in mitosis, is intensified in long buds (LUTAUD, 1961). In slowly growing species, in young colonies, or in unfavorable conditions, buds are not much longer than the average size of a zooid. Except for the tip, they are almost entirely absorbed in the formation of every successive zooid. Rest periods while metabolites are consumed by organogenesis may interrupt proliferation, and budding then is discontinuous. In large colonies, when nutrition and climate are good, proliferation becomes so rapid that the formation of transverse partitions and the organization of newly formed zooids are delayed in comparison to the progression of buds along the substrate. This growth acceleration reaches an exceptional potential in large colonies of *Membranipora membranacea* (LINNÉ), which cover many square feet of kelp frond. In large tongue-shaped colonies, a thick margin of **giant buds** is progressively developed in a dominant growth direction. Several rows of incomplete zooids showing the successive phases of organogenesis extend behind the growing margin. Moreover, the frontal wall without a gymnocyst is simple and transparent. The systematic position of the group, near the divergence of the orders Ctenostomata and Cheilostomata, indicates that this species offers the best possibility to observe basic organizational processes of cellular wall layers before generic diversification introduces parietal superstructures. These are the reasons for choosing this particular species for a study of autozooid morphogenesis in Anasca.

BUD PROLIFERATION IN MEMBRANIPORA MEMBRANACEA

EPITHELIUM AND SECRETION OF CUTICLE

Sagittal sections through a bud of the growing margin in *Membranipora membranacea* show decreasing thickness of the epithelium from tip to proximal septum. Epithelial cells are columnar and high at the tip, as in the bud of other cheilostomates, and become progressively lower in the median region of the bud; epithelium becomes abruptly flat and pavemental in the clearing proximal region, which will be absorbed during formation of a new zooid. At equal distance from the tip, epithelium is thicker on the basal wall than on the frontal wall.

Normally, parietal epithelium in invertebrates is one-layered with a determinate polarity in the orientation of its secretory activity, and with the ability to secrete an external cuticular coating.

Cytological features of columnar epithelial cells at the tip of the bud indicate their intense secretory activity and their participation in the construction of the cuticle (LUTAUD, 1961; TAVENER-SMITH & WILLIAMS, 1972). Density of the cytoplasm and its affinity for standard histological dyes correspond to the development of granular **endoplasmic reticulum**. Mitochondria are abundant around a median nucleus with large multiple nucleoli. These are the normal characters of any embryonic epithelium; however, this cytological aspect in *M. membranacea* corresponds to a relatively stable region of the bud (see Fig. 88,*2*). In live and preserved specimens, the cytoplasm of the columnar apical cells clears abruptly a short distance beneath the fragile cuticular coating already protecting the tip of the bud (Fig. 88,*1*). The loose cytoplasmic web of the external pole of the cells beneath the cuticle contains granular secretions and a vesicle of diffuse substances. An important **Golgi apparatus** lies next to this vesicle. Positive reactions to such histochemical tests as the PAS, controlled by the reversible acety-

lation reaction, indicate that mucopolysaccharides are dominant in the subcuticular secretions and in the internal layer of the cuticle. However, the secretory activity of the cells is diversified. Part of the granular secretions, intermixed with diffuse secretions in the external pole of the cells, shows affinities for stains of proteins. Concomitant protein and polysaccharide secretions, produced by undifferentiated columnar stages of the epithelium at the tip of the bud, are consistent with the hypothesis that the glycoprotein frame of the cuticle is built at this level (see Fig. 88,*2*). Supple cuticular coating would be later hardened by one of the tanning processes that are known to occur in the superficial organic pellicle of the exoskeleton in other invertebrates.

TAVENER-SMITH and WILLIAMS (1972) studied the structure of the wall by transmission and scanning electron microscopy in the adult and in the bud of *M. membranacea* and of a few other Anasca. According to their observations, the cuticle, which they called "periostracum," is externally bounded by a "triple-unit membrane" consisting of an electron-light layer between two dense layers. The "triple-unit membrane" is internally reinforced by a thicker fibrillar formation.

The cuticular coating cannot be confused with a basal limit of the epithelium. Although no differentiated membrane separates the parietal epithelium from the peritoneal lining, there is no doubt that the basal pole of the cells is their internal extremity, in direct contact with the underlying peritoneal tissues, in the adult as well as in the bud. The implications of this fundamental orientation of the polarity of epithelium must be taken into account when interpreting the superposition of calcified layers in the skeleton of higher cheilostomates. A reversal of the orientation of activity of the epithelial cells would be the adaptation of their external border to an absorption function, as is the case in the digestive tract and in the tentacle sheath.

HYMAN (1958), using the chitosan test of CAMPBELL, found evidence of glycosaminic components of chitin in the organic substrate of the exoskeleton of several cheilostomates and ctenostomates. SCHNEIDER (1963) estimated that chitin represented approximately 10 percent of the exoskeleton in *Bugula,* considering together the cuticle and the organic matrix of the calcified deposits. JEUNIAUX (1963, 1971), using a precise method of enzymatic digestion by chitinolases, confirmed the presence of chitin in the cuticle and in the matrix of various Anasca, at the rate of 3 to 6 percent of the organic material; in cheilostomates, 1.6 percent of this would be free chitin, and the rest would be combined with a glycoprotein substrate.

SUBTERMINAL GROWTH OF THE BUD

Cinematographic observations showed the feeble adhesion of the columnar apical cells to the thin cuticular membrane at the tip of the bud. SCHNEIDER (1958), in a cinematographic study of the phototropic orientation of growth of the autozooidal bud in *Bugula,* observed that the positive response beneath the cuticle was due to displacement of apical cells toward the light source. In *M. membranacea* cultured on glass slides, the progression of the bud, gliding forward along the smooth experimental substrate, is accompanied by a slow but perpetual horizontal oscillation of the columnar epithelial cells at the tip (LUTAUD & PAINLEVÉ, 1961). This movement stirs permanently the fluid secretions of the external poles of cells beneath the cuticle.

Colored markers of vital dye have been applied on the frontal wall of the giant bud of *M. membranacea,* at various levels between the tip and the proximal partition. Change of the marks during growth shows that bud elongation is preapical and that the apex does not proliferate as a **blastema**, where cellular multiplications would be localized and from which new cells would be added to preceding tissues (LUTAUD, 1961). Marks applied at the tip remain concentrated in place. Marks applied in median and proximal portions of the bud are dispersed both by cellular mul-

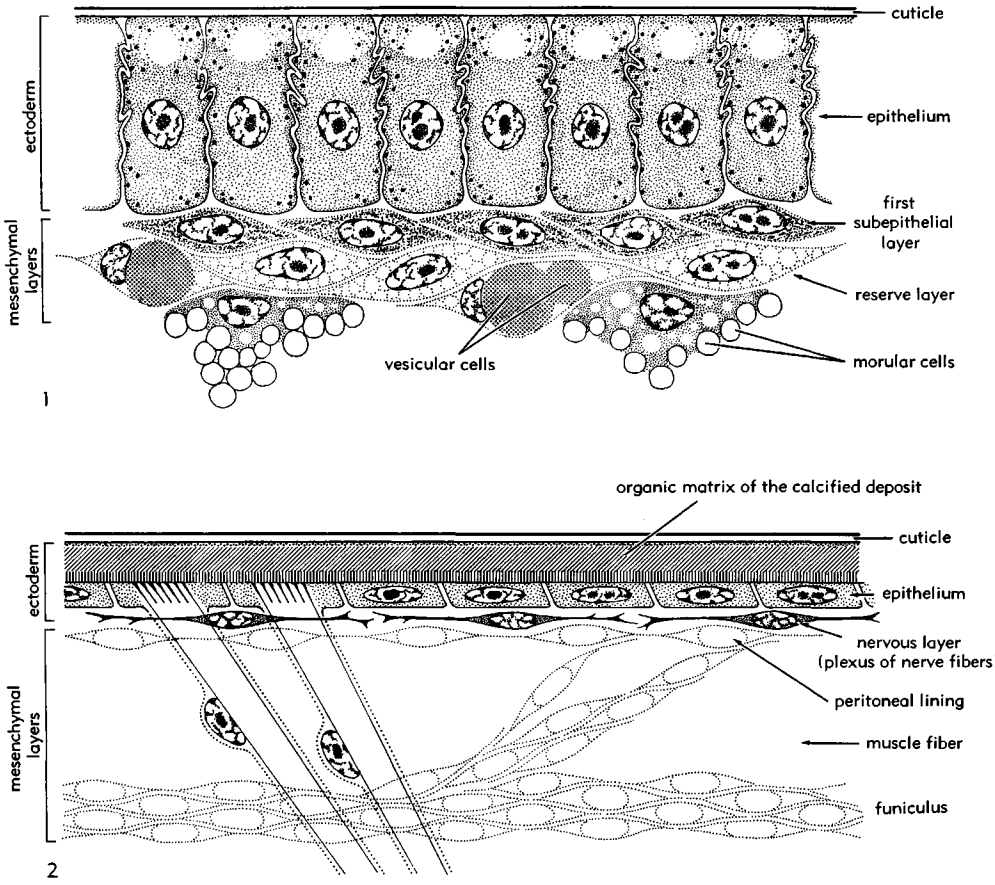

FIG. 87. Cellular layers of the zooecial wall in Anasca.——*1.* Structure of the undifferentiated wall of a bud.——*2.* Organization of parietal tissues in the wall of an adult zooid.

tiplication and by pavemental spreading of the epithelium. Analysis of the distribution of mitoses by precise counts shows that cellular multiplication occurs in the epithelium along the entire length of the bud. However, mitotic activity is maximal in the median region for the frontal wall, and in the anterior half of the bud for the basal wall. It is significantly minimal among the columnar apical cells, which participate to a lesser extent in bud elongation. This means that the tip of the bud is pushed forward by proliferation of the preceding regions and by general spreading of parietal tissues in the proximal region. The apical cells that TAVENER-SMITH and WILLIAMS called "archaetype cells" show a remarkable stability of their undifferentiated character and corresponding secretory features. This preapical mode of growth implies a permanent stretching of the preexisting cuticular membrane at the tip of the bud where the secretion of the primary glycoprotein frame of cuticle is presumed to take place. The precise process of cuticle extension at the tip of the bud, under the pressure of growing subjacent tissues, is unknown. According to TAVENER-SMITH and WILLIAMS (1972) ". . .the existing central apical zone of periostracum is gradually pushed aside as newly secreted material displaces it, either physically or by longitudinal impregnation of an adjustable protein-chitin fabric that has not yet polymerized. . . ."

In the giant bud of *M. membranacea,* the

proliferating region behind the apex is extensive. The mitotically active zone, between the tip and the proximal septum, is more restricted in shorter buds of lateral zooidal series diverging from the dominant direction of growth, or in normal buds of other species. The maintenance or appearance of a group of columnar epithelial cells actively secreting glycoprotein substances characterizes any region in the wall capable of proliferation or temporary dedifferentiation. A localized group of columnar cells is formed at the growing tip of spines, in healing areas after a wound, around the ancestrula at the origin of initial buds, at the origin of communication chambers, and, in Stolonifera, at the origin of lateral autozooidal buds.

EVOLUTION OF EPITHELIAL SECRETIONS DURING DIFFERENTIATION

In *M. membranacea,* the progressive lowering of epithelium, from the columnar stages at the tip of the bud to a steady pavemental state in the wall of the adult zooid, is accompanied by a reduction of granular endoplasmic reticulum, by a reduction of the length of mitochondria, and by migration of the Golgi apparatus toward the basal pole (LUTAUD, 1961). Mucopolysaccharides and protein granules are still actively produced by the differentiating epithelium. However, these cytological modifications correspond to an evolution in the nature or proportions of organic substances that first reinforce the primary cuticular membrane, then are deposited on the inner surface of the cuticle and form the organic substrate of the skeleton in calcified regions. Secretion of this organic matrix and concomitant deposition of calcium carbonate persist in the pavemental epithelium of the adult, and the skeleton is reinforced in young adult zooids.

Organic matrix of calcified deposits always remains after cautious decalcification. The matrix shows the histochemical affinities of mucopolysaccharides. Observed with the transmission electron microscope on ultrathin sections through lateral walls in *M. membranacea,* and through the frontal gymnocyst or basal and lateral walls in *Electra pilosa* (LINNÉ), the matrix appears as a thick fibrillar formation lying beneath the internal fibrillar layer of cuticle. The matrix itself consists of two unequal layers differing in the density and orientation of their **fibrillation**: the thickest, next to the cuticle, shows a looser web and would correspond to a primary deposit of calcium carbonate; the internal layer of the matrix next to the epithelium may correspond to newly secreted material. According to TAVENER-SMITH and WILLIAMS, this stratification of matrix indicates that two successive phases occur in the deposit and crystallization of calcite.

In study of *M. membranacea* by polarized light, calcite crystals in lateral walls are first detected in the proximal region of buds, in front of the first transverse partition. In *Bugula,* calcification proceeds on the basal and lateral walls by continuous growth of a calcified lamina, and later extends to the frontal wall to form the gymnocyst (CALVET, 1900). According to SCHNEIDER (1963), who did not discriminate cuticle and matrix, organic fibers and calcite crystals grow together by preapical construction behind the group of columnar apical cells. The frontal wall of a newly formed zooid undergoes invagination of the polypide and development of the tentacle sheath (see Fig. 90,*3*). Of course, a coherent shield of calcite cannot solidify in the frontal wall while the underlying cellular layers are still undergoing morphogenetic movements, and the extension of calcification to the frontal wall is normally delayed. Consolidation of a calcified layer requires mechanical stabilization of the epithelium.

Without entering into a fundamental discussion of skeletal evolution, and of the significance of the superposition of calcified layers in the frontal wall of Ascophora, an open question of bryozoan biology is how calcium carbonate is produced at the cellular level. Modern cytochemical techniques that are now used in the study of animal secretion of calcium carbonate in other phyla have not been

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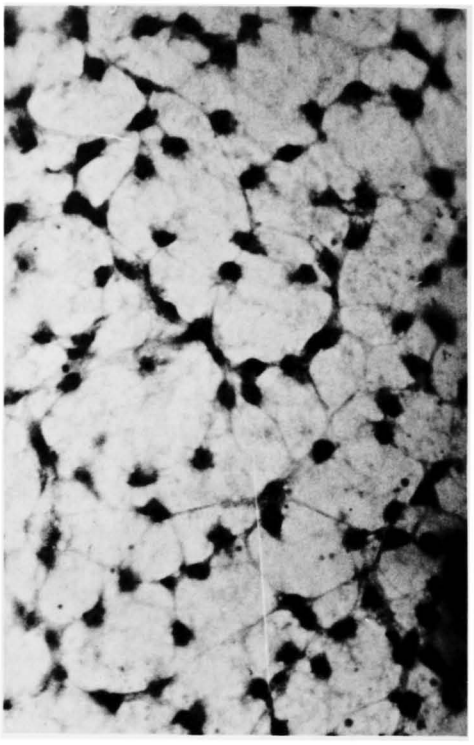

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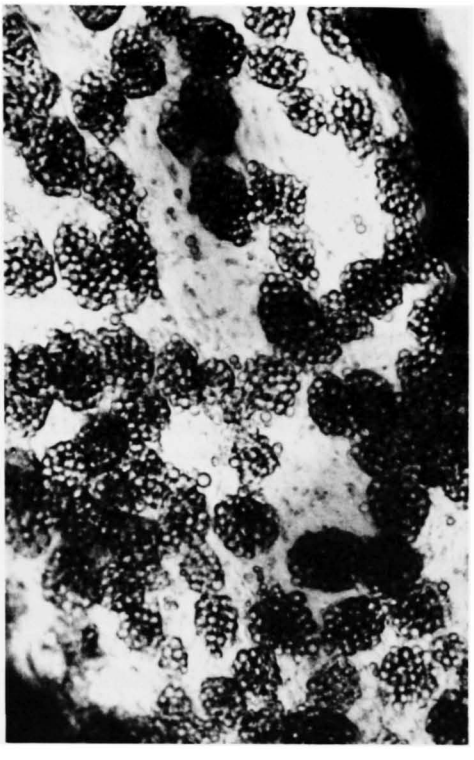

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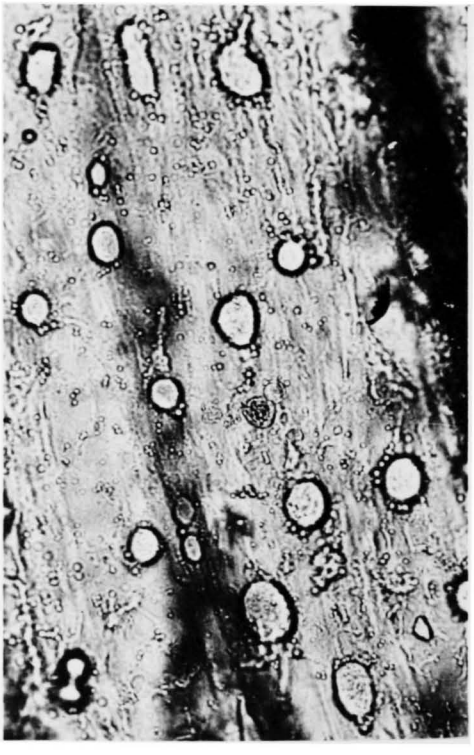

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FIG. 88. *(For explanation, see facing page.)*

applied to Bryozoa (Vovelle, 1972). The secretory or eliminative process in cellular metabolism, which releases calcium carbonate, is unknown. It has not been established whether organic substances of the matrix and calcite were simultaneously produced and interwoven, or whether ionic calcium carbonate impregnates a preformed organic frame and then precipitates. The evolution in epithelial metabolism within gymnolaemates, which induces calcification in Anasca, then its reinforcement in Ascophora, is entirely unknown.

SUBEPITHELIAL CELLULAR LAYERS

In the adult zooid, peritoneum lining the inner surface of the epithelium in basal, lateral, and frontal walls is a thin network of stellate cells (Fig. 87,*2*; 88,*2*). Diffuse endings of parietal funicular strands could be intermixed with the peritoneal network. The peritoneum of the wall includes various cellular categories, among which are mucocytes presumed to liberate acid mucopolysaccharides into the body cavity, and different cells carrying protein granules, granular glycogen, globular glycoprotein inclusions, or lipid droplets (Calvet, 1900; Lutaud, 1961; Bobin & Prenant, 1972). Two kinds of predominant cells, attached to the peritoneal network and to funicular strands, occur in all ectoprocts. These are cells occupied by a voluminous vesicular inclusion, called **vesicular cells** (Fig. 87,*1*; 88,*4*), and cells filled with a cluster of refringent spherules, called **morular cells** (Fig. 87,*1*; 88,*3*). Amoeboid **phagocytes** are are also liberated into the body cavity (Bobin & Prenant, 1957, 1972).

Sections through a bud of *M. membranacea* show that a thick lining of undifferentiated tissue lies beneath the epithelium (Fig. 87,*1*), extending from the tip to the clearing proximal region, where it is dissociated into longitudinal strands. Subepithelial tissues in the bud are composed of two distinct superposed layers (Lutaud, 1961; Tavener-Smith & Williams, 1972). An external, first subepithelial layer (Fig. 87,*1*), lying against the epithelium in cellular membrane to membrane contact, is composed of spindle-shaped cells poor in inclusions. An internal reserve layer (Fig. 87,*1*) is thicker, especially in the basal wall. It is multistratified and composed of large vacuolated cells carrying chains of lipid droplets and glycoprotein inclusions of various sizes, which tend to concentrate into large globular vesicles.

Vesicular cells, or "vesicular leucocytes" of Calvet, are simply distended cells occupied by a voluminous vesicle showing a positive reaction to the PAS test (Fig. 87,*1*). This vesicle results from the confluence of smaller glycoprotein droplets in the reserve layer. Vesicular cells are dispersed along peritoneal strands in the clearing proximal region of the bud. They are usually abundant in the basal and lateral walls of newly formed zooids (Fig. 88,*4*). They are partly consumed during development of the polypide. They appear in adult zooids under high nutrient conditions. Vesicular cells have specific shapes and are commonly subdivided.

Morular cells (Fig. 87,*1*) are quite different in structure and significance. At the inner surface of the reserve layer, protruding cells of irregular shape are formed. Their dense cytoplasm is progressively invaded by growing vacuoles. Condensation of the vacuolar contents forms spherules that protrude at the periphery of the cells and that deplete the cytoplasm. Finally, a small residual area of cytoplasm, including a distorted nucleus, remains against the cluster of spherules retained within a cytoplasmic film. Morular

Fig. 88. Parietal tissues in *Membranipora membranacea* (Linné).——*1*. Epithelium in the frontal wall of an adult autozooid; silver impregnation, ×150.——*2*. Peritoneum in the frontal wall of an adult autozooid; decalcified whole mount, stained with hematoxylin, ×250.——*3*. Morular cells in the wall of a bud; live specimen, ×200.——*4*. Vesicular cells in the basal wall of a newly formed zooid, live specimen, ×200.

cells are probably liberated into the body cavity at the end of their cytological development. They have not been found in mitotic division, and are probably formed from divisions of other elements in the reserve layer. CALVET (1900) interpreted morular cells as coelomocytes, which he called "leucocytes spherulaires"; however, the nature of the spherules and their function are unknown. The term morular cells, used by BOBIN and PRENANT (1957) because of their shape, seems preferable to leucocyte, which has precise physiological implications. Spherules are refractory to most usual histochemical stains, including PAS. They might be sclerotized proteins, comparable to pigments. Morular cells are numerous in the bud (Fig. 88,*3*). They are still produced in the wall of the adult zooid. They may be related in some way to metabolism of parietal tissues, particularly active during proliferation. Shape and refringence of the spherules are specific characters.

CALVET (1900) presumed that mesenchymal cells were produced at the tip of the bud from divisions of the columnar apical cells. Superficial observation of live or preserved specimens might give the impression that mesenchymal cells detach from the epithelium at the tip of the bud. However, this interpretation implies that a parietal sheet is formed in the bud during asexual reproduction, after metamorphosis of the larva, and is contradicted by more recent observations. Sections through the bud of *M. membranacea* show that the two subepithelial layers are already present at the tip of the bud, and that mitoses occur in subepithelial tissues from the tip to the proximal partition (LUTAUD, 1961). It seems more probable that epithelium and peritoneum both participate in evagination of initial buds around the ancestrula, and proliferate concomitantly further.

FORMATION OF INTERZOOIDAL WALLS

LONGITUDINAL DIVISION OF THE BUD

Parallel buds of the growing margin in *M. membranacea* grow rapidly in a linear progression while successive zooids are individualized from their proximal extremity by the formation of new **transverse partitions** at regular intervals (Fig. 89,*1*). However, with increase in colony size, longitudinal divisions occur occasionally in certain enlarged buds in favorable locations, particularly in rounded margins of the colony (Fig. 89,*2*).

A **longitudinal partition** begins at the tip of the bud as a median notch (Fig. 89,*3,4*). Cinematographic observation showed that the initial indentation was preceded by a local disturbance in regularity of the apical epithelial cells when the width of the bud exceeded an average dimension (LUTAUD & PAINLEVÉ, 1961). Colored marks applied on the initial notch remained concentrated as the tips of newly formed buds issued from the longitudinal division. Marks applied along more developed partitions were dispersed in the same way as marks of similar level on the frontal wall of undivided buds (LUTAUD, 1961). This means that lateral double walls do not grow from the tip of the bud to the proximal septum, but elongate distally from their origin by the parallel growth of the two new buds that they separate. This is confirmed by the presence of two contiguous layers of cuticle in the middle of the calcified skeleton, with sand, bacteria, and dirt particles enclosed between.

The consequence of this mode of construction is that interzooidal communications are secondarily pierced in lateral walls (SILÉN, 1942b; LUTAUD, 1961; BANTA, 1969; BOBIN, 1977). In *M. membranacea,* zooidal rows generally alternate. Two pairs of lateral communications are formed in the clearing proximal region of the bud, a little in front of every newly formed transverse partition. The formation of a pore plate is prepared by a

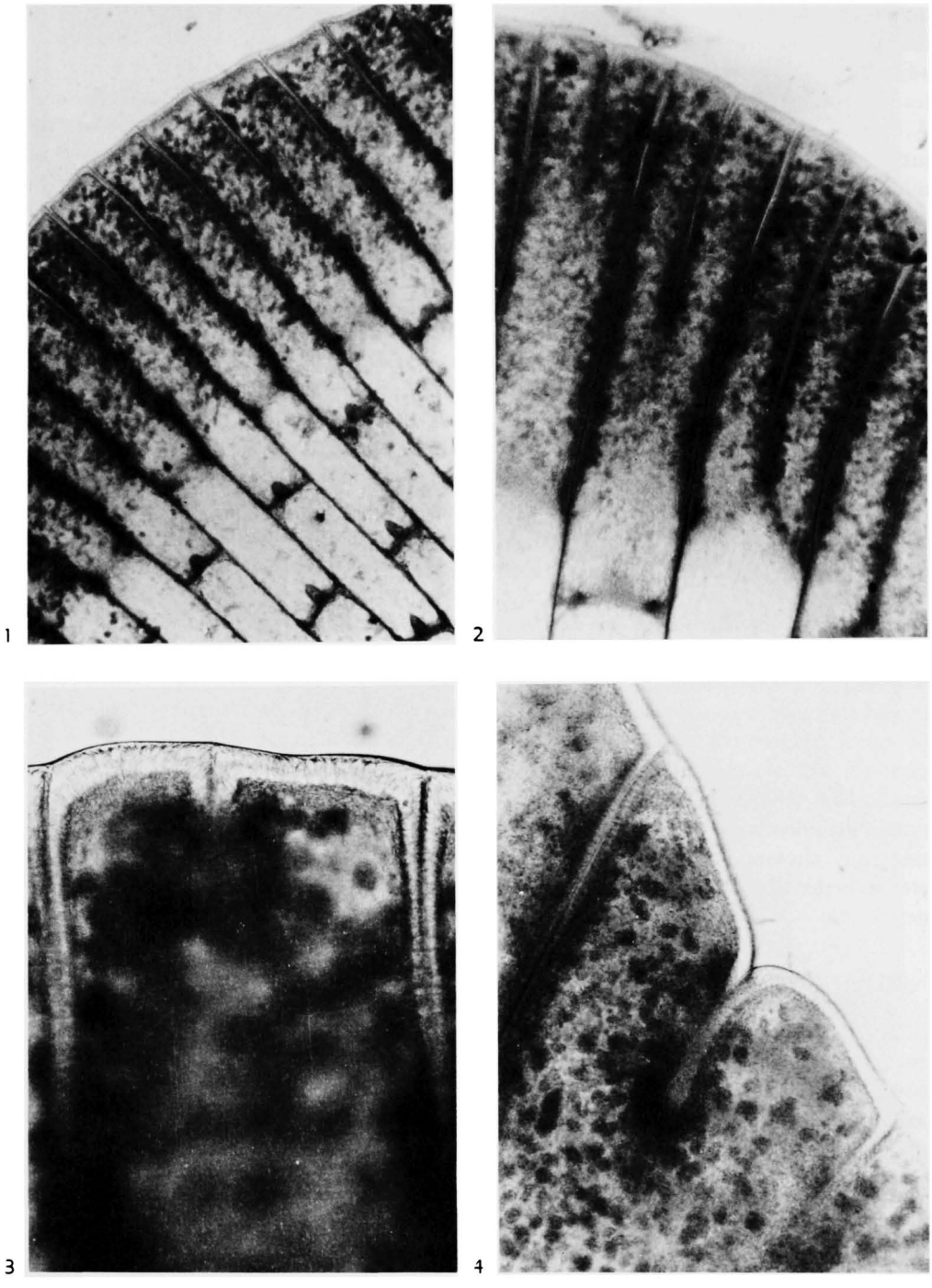


FIG. 89. Longitudinal division of the bud in *Membranipora membranacea*; all live specimens.——*1*. Buds in the growing margin of the colony, ×25.——*2*. Formation of longitudinal partitions, ×40.——*3*. Initiation of a longitudinal partition at the tip of the bud, ×100.——*4*. Further stage in development of a longitudinal partition, ×80.

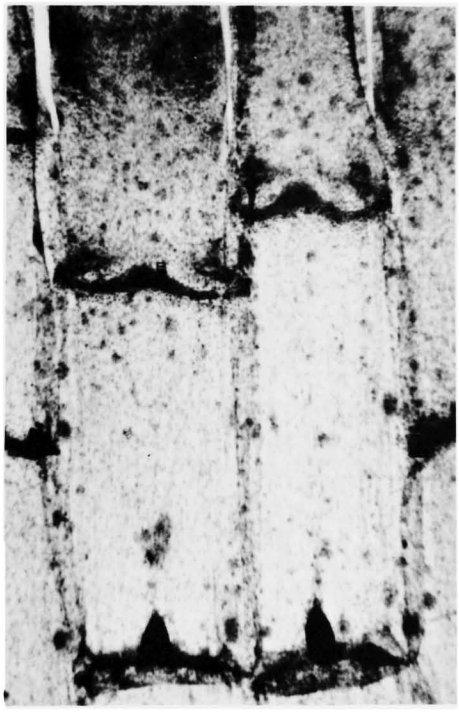
unilateral lenticular concentration of epithelial cells, slightly bulging into the wall of the adjacent bud. The opposite wall immediately reacts by a coinciding epithelial thickening. According to BANTA, in *Watersipora* the **intercalary cuticle** is then dissolved in the middle of the double epithelial thickening. A complete pore plate is later secreted in the perforated area during differentiation of pedunculate cells of an organ called a **rosette**, which obstructs every pore in the adult (see Fig. 98,*1–3*). SILÉN (1944b) analyzed the alternation of communications chambers, or **septulae**, in several anascans of quincuncial colonial pattern (*Electra, Flustra,* and *Callopora*). According to his interpretation, communication chambers would have the significance of lateral buds stopped in their development by the presence and tissue reaction of the adjacent obstructing wall. Development of normal autozooidal buds from septulae, after accidental or experimental destruction of adjacent zooids, is often observed in *Electra,* and has been recorded in various other cheilostomates. Alternation of communication chambers, originating on opposite sides of the common double wall of two zooidal series, might induce an alternation in the orientation of rosettes across pores and, thus, alternation of the direction of lateral exchange from a zooid on one side to the next on the other side.

AUTOZOOID INDIVIDUALIZATION

In *M. membranacea,* the length of buds in the growing margin of medium-sized colonies is 2 to 5 mm. Daily progression under experimental conditions on the substrate is approximatively twice the length of the buds (LUTAUD, 1961). As the average length of a zooid is between 0.8 and 1.2 mm, a new transverse partition separates a new zooidal compartment every 4 to 6 hours.

CALVET working with *Bugula,* and earlier authors working with other eurystomes, described the formation of a transverse partition between a new zooid and the distal bud. The partition proceeded from an annular invagination of the cellular layers of the wall, closing like an iris diaphragm. Accelerated cinematography showed that the beginning of the septal invagination in *M. membranacea* coincides with a maximum contrast of density in the wall between the distal proliferating portion and the proximal clearing portion of the bud (LUTAUD & PAINLEVÉ, 1961). A localized disruption in thickness of parietal tissues may have a part in the initiation of the partition. The initial annular fold is asymmetrical and begins on the basal and lateral walls, later extending to the frontal wall. This slight asymmetry in dynamic development of the transverse partition in an encrusting anascan is related to the unequal thickness of the basal and frontal walls in the bud, to their divergent organogenetic evolution in the new zooidal compartment, and to the concomitant formation of a polypide on the distal side of the closing partition (Fig. 90). According to recent observations on skeletal growth (BOARDMAN & CHEETHAM, 1969), this asymmetrical development of the transverse wall is more pronounced in higher cheilostomates, in which the partition grows from the basal to the frontal wall.

Interzooidal communications in a transverse wall are formed during closure of the annular septal fold. Pores, either irregular in their distribution or grouped in pore plates, are maintained through the epithelial layers and median skeletal deposit of the closing partition when peritoneal tissues, grouped in the center, are intersected by the epithelial fold. In *M. membranacea,* peritoneal strands are grouped in the center of the closing partition in two bundles from which the main funicular branches are formed. Rosette cells are differentiated from elements of the funicular strands surrounded by epithelium (LUTAUD, 1961). According to BOBIN (1958a,b), in Stolonifera, undifferentiated mesenchyme and accumulated mucoid substances first obstruct the central hole of the growing septum, which separates the autozooidal bud from the stolon. Then, special cells differentiate unilaterally and insert



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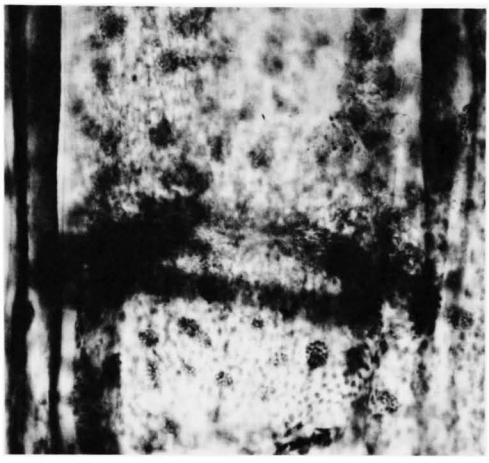

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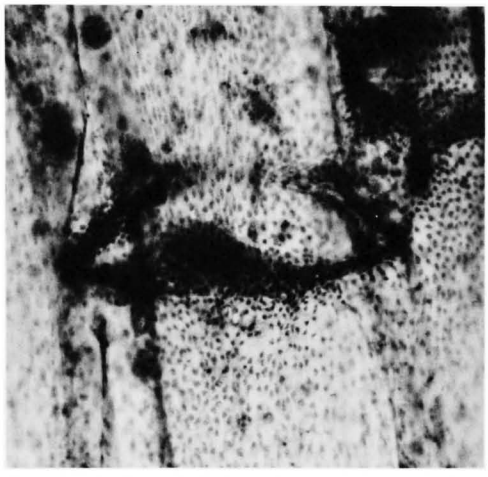

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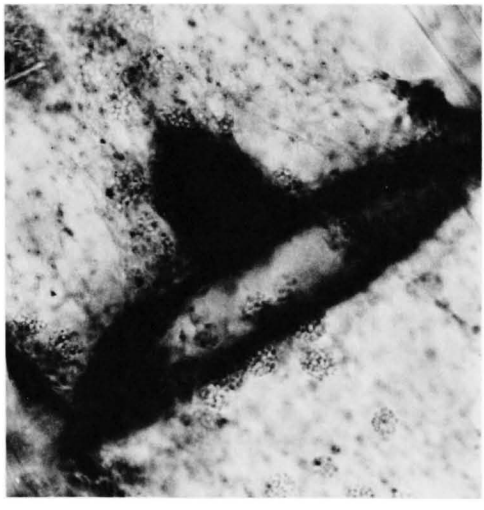

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FIG. 90. Individualization of the autozooid in *Membranipora membranacea*; all decalcified whole mounts, stained with hematoxylin.——*1*. Formation of transverse partitions at the rear of the buds, ×50.——*2*. Separation of a new zooid, ×100.——*3*. Early stage of formation of the transverse partition, ×125.——*4*. Formation of the polypidean bud, ×125.——5. Closure of the transverse partition, ×150.

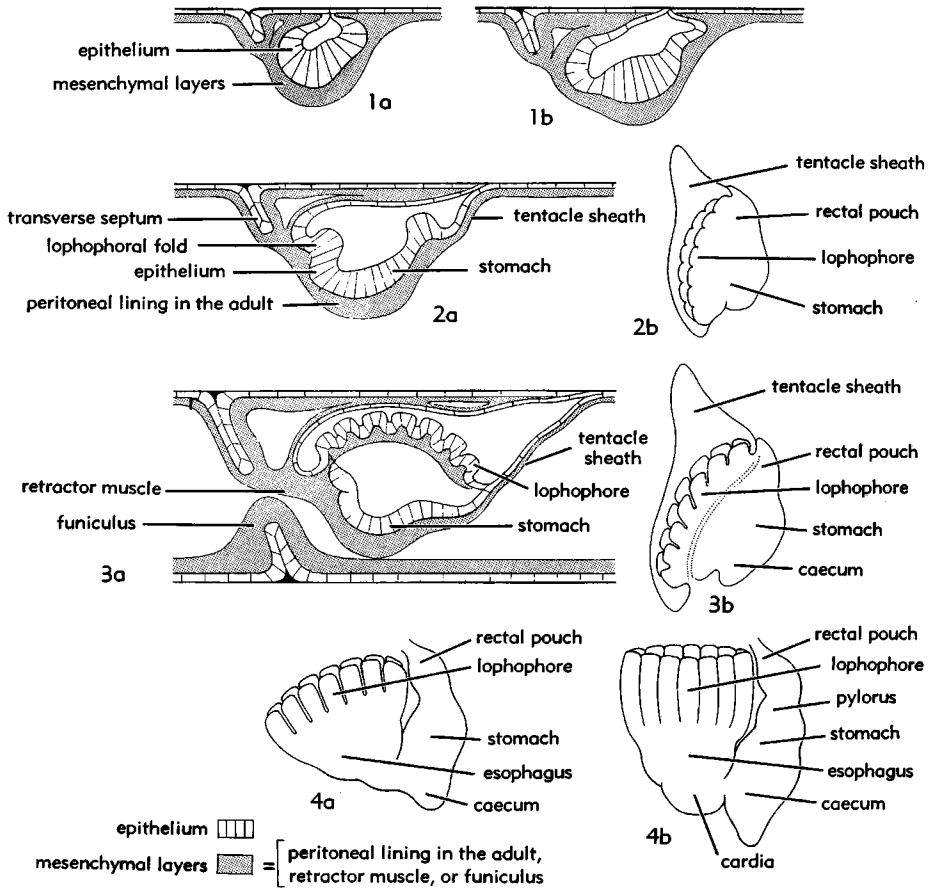

FIG. 91. Development of the polypide in *Membranipora membranacea,* an encrusting Anasca; based on histological sections and whole mounts.——*1a,b.* Early formative stages of a polypidean vesicle, in section. ——*2a,b.* Formation of the atrial bag, lophophoral fold, and digestive pouch; *a,* in section, *b,* in profile. ——*3a,b.* Differentiation of the tentacle sheath, tentacles, and retractor muscle; *a,* in section, *b,* in profile. ——*4a,b.* Allometric development of the lophophore and subdivisions of the digestive tract, both in profile.

pedunculate prolongations between the epithelial cells of the septal fold, thus impeding locally the secretion of cuticle. In cheilostomates, the manner in which peritoneal strands are invested by the epithelial fold during closure of the partition, and correlatively the number and distribution of pores or pore plates, are specific characters. In some anascans, a single funicular bundle is formed, attached to a central pore plate. In *M. membranacea,* two main funicular strands are attached to two pore plates. In *Electra,* funicular strands are spread across the partition through a range of single pores.

Histological and ultrathin sections show that transverse walls, like longitudinal walls, include two opposite sequences of epithelium and peritoneal lining on either side of the median skeleton. However, structural differences in the skeletal deposits may correspond to morphogenetic differences in the moment and modalities of the initiation of transverse and lateral partitions. Recent observations show that cuticle is lacking in the middle of the transverse wall, and that the calcareous layer is homogeneous, at least in certain species. This might be related to the occurrence of transverse and lateral partitions at

different stages of secretory evolution of the epithelium: a lateral double wall begins at the level of columnar stages in the epithelium where secretion of cuticle is presumed to be particularly active, and grows forward between the tips of adjacent buds. Transverse partitions are formed later and grow inward, at the beginning of differentiation of parietal tissues and shortly before calcification.

FORMATION AND LOCATION OF THE FIRST POLYPIDIAN BUD

At the beginning of septal invagination, a cluster of epithelial cells rapidly condenses at its frontal edge and distal side (Fig. 90,*3,4*). This is the **polypidian bud** of the next autozooid invaginating into the body cavity with the internal edge of the closing partition. The initial epithelial cluster, surrounded by the subepithelial layers, quickly increases in volume by cellular multiplication. Then a central lumen is formed by cavitation with the concentric alignment of the epithelial cells (Soule, 1954; Lutaud, 1959a). By this time, the polypidian bud has become a double-layered **polypidian vesicle**. An internal epithelium is oriented toward the central cavity and is enclosed by a thickened mesenchymal envelope where lipid and glycoprotein droplets accumulate (Fig. 91,*1*). A constriction separates the epithelial vesicle from the parietal epithelium. However, the polypidian vesicle remains attached to the internal edge of the contiguous partition by the continuity of its mesenchymal envelope with the parietal peritoneal lining.

Simultaneous formation of the transverse partition and the first polypidian bud is fundamental in gymnolaemates. The origin of regenerated polypidian buds during cyclic renewals of the polypide is not precisely established. A regenerated polypidian vesicle is usually found next to a brown body.

Experimental dissociation of the polypidian bud from the concomitant partition has been attempted in *M. membranacea* to understand in detail the determinism of their coinciding formations (Lutaud, 1961). A reversed orientation of bud proliferation is obtained by removing all recently formed zooids behind the growing margin of the colony. If sufficiently rich in reserves, isolated buds resume growth and formation of transverse divisions after healing of the wound. When an incision is made behind proximal bud partitions, growth goes on in the initial direction. When an incision is made in front of proximal partitions, newly formed buds of reversed orientation are regenerated from the cut, on the proximal side of the next partition. A single polypidian bud is borne on one or the other side of this partition separating the operated bud from the proximal regenerated bud. Of course, traumatism is important. One or several partitions may abort, and a giant zooidal compartment is formed. This does not impede the formation of polypidian buds at regular intervals. Such monstrous zooids are occupied by two or three successive polypides of similar or opposite orientations, each with a normal aperture and tentacle sheath. The retractor muscle of polypides formed without a partition is inserted on a lateral wall. The formation of a polypide depends first on the available space, as suggested by Silén (1944a). The formation of a partition and of a polypidian bud occurs at the same moment as differentiation of parietal tissues. The orientation of the polypide is the immediate consequence of the orientation of bud growth.

AUTOZOOID ORGANIZATION

EARLY DEVELOPMENTAL STAGES OF THE POLYPIDE

Development of the polypide has been precisely studied by Calvet (1900) in *Bugula simplex* Hincks, and by Herwig (1913) in *Alcyonidium gelatinosum* (Linné). These classical descriptions have been corroborated

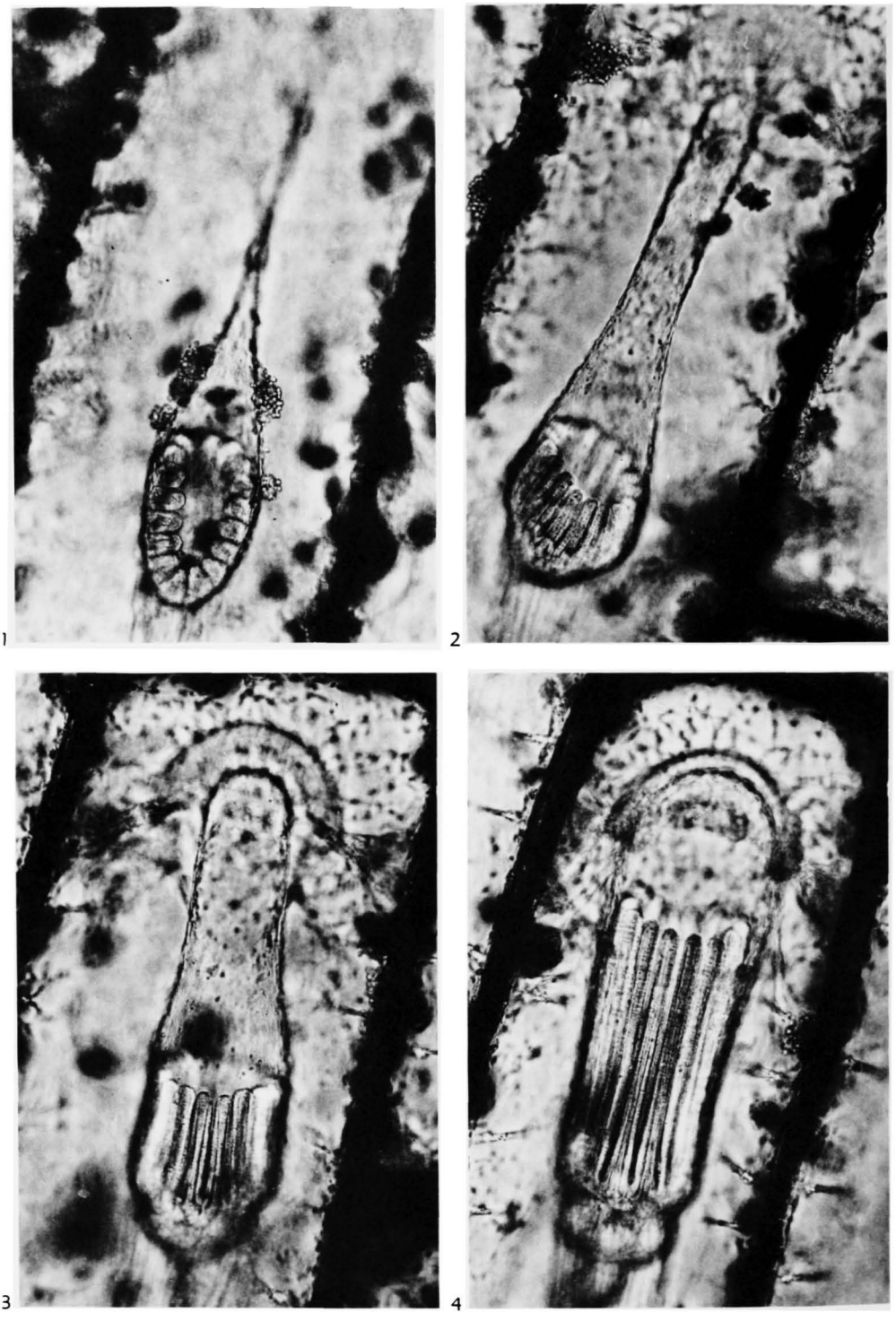

FIG. 92. Development of the polypide in *Membranipora membranacea*; all live specimens, ×125.——*1*. Early stages in differentiation of the lophophore and tentacle sheath.——*2*. Development of the tentacle sheath and orientation of the lophophore.——*3,4*. Elongation of the tentacles and formation of the operculum.

by SOULE (1954) in Carnosa and Stolonifera, and by LUTAUD (1959a,b, 1961; LUTAUD & PAINLEVÉ, 1961) in *Membranipora membranacea* by histological and cinematographic observations.

In *M. membranacea,* under experimental conditions, complete development of the polypide, tentacle sheath, and aperture requires approximately two days. The first step in organization of the polypidian vesicle is the development of a central lumen with the rapid multiplication and concentric orientation of internal epithelial cells (Fig. 91,*1a*). The next step is the asymmetrical development of the polypidian vesicle, still attached to the frontal wall and to the contiguous transverse partition; the superior, or frontal, region tends to spread while the bottom, or dorsal, region thickens (Fig. 91,*1b*). This is a determinant morphogenetic stage initiating the differentiation of an **atrial bag** from which the tentacle sheath is formed, and of a dorsal pouch from which the digestive tract is formed. Very soon, a slight constriction delimits more clearly the two unequal regions differing in the height of the epithelium, and subdivides the central cavity into a lophophoral atrium and a digestive lumen.

A protuberance next appears at the limit of the atrial and digestive regions. This is the **lophophoral fold** into which the peritoneal layers of the polypidian vesicle penetrate (Fig. 91,*2a*). Meanwhile, the digestive pouch is unequally subdivided by a new constriction into a distal rectal pouch and a stomach pouch (Fig. 91,*2b*). The atrial region extends into a conical bag arising from the base of the lophophoral fold. This atrial bag elongates unilaterally toward the distal end of the zooid along a median tract induced on the frontal wall by invagination of the polypidian bud (Fig. 90,*2*).

The slightly oblong polypidian vesicle has then acquired the shape of a coffee bean, with the furrow of the intestinal lumen opening between the symmetrical pads of the lophophoral fold (Fig. 92,*1*). The tentacle sheath, lophophore, and digestive tract are already clearly delimited. The polypidian vesicle is now enclosed in a bag becoming the tentacle sheath, which derives from the frontal portion of the polypidian vesicle and is ontogenetically a polypidian organ. The mesenchymal layers of the polypidian vesicle follow the epithelium in all its successive folds and constrictions; their continuity with the peritoneal lining of the wall is never interrupted during development of the polypide.

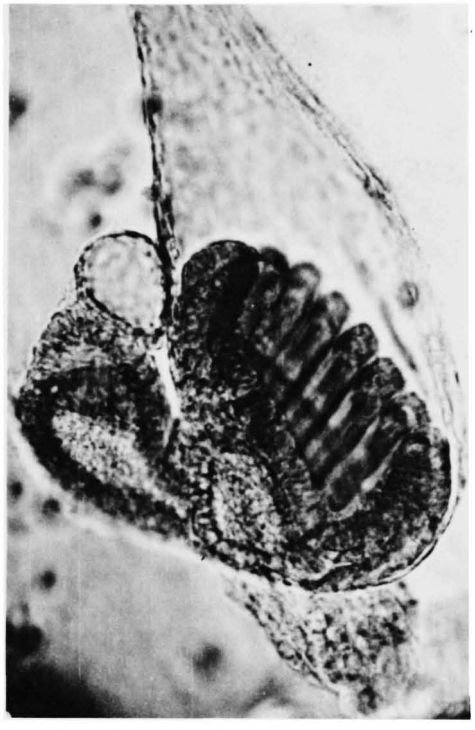

FIG. 93. Differentiation of the digestive tract in *Membranipora membranacea*; live specimen, ×350.

DEVELOPMENT OF LOPHOPHORE AND DIGESTIVE TRACT

The next period is characterized by two simultaneous morphogenetic movements, migration of the polypidian vesicle toward the center of the zooecium and orientation of the lophophore toward the apertural area (Fig. 92,*2*). Tentacular stubs are separated by regular slits between secondary folds in the lophophoral protuberance, and then elongate within the atrial bag (Fig. 91,*3*; 92,*3,4*). The

FIG. 94. The adult polypide in *Membranipora membranacea*; decalcified whole mount stained with hematoxylin, ×100.

peritoneal layers, infiltrated into the lophophoral fold, penetrate further into the internal interstice of each tentacular stub. Meanwhile, successive constrictions delimit the different organs of the digestive tract (Fig. 91,*4*; 93).

In an adult cheilostomate, the successive regions of the digestive tract, from the mouth at the base of the lophophore to the anus opening through the tentacle sheath into the **tentacular atrium**, are the **esophagus**, **cardia**, stomach, **pylorus**, and **rectal pouch** (Fig. 91,*4*; 94). The esophagus is sometimes mentioned as the **pharynx**, although the term pharynx is usually restricted to the transitional area of the oral constriction. The esophagus is characterized by a vacuolated myoepithelium, which contracts strongly during ingestion (MATRICON, 1973). The esophagus opens into a curved cardial tube, itself opening into the stomach. In certain ctenostomates, an additional **gizzard** is differentiated from the stomach portion of the cardia. The stomach is prolonged by a blind **caecum**, in which food remains for some time, and opens into a ciliated pylorus. In the pylorus, the remnants of digestion are agglutinated with mucins into a whirling **stylet** by vibratile cilia, before being expelled into the rectal pouch.

The first constriction in the dorsal pouch of the polypidian vesicle separates the rectal pouch from the stomach (Fig. 91,*2b*). The thick mesenchymal connection that persists between the polypidian vesicle and the contiguous partition, and from which the great retractor muscle of the polypide is formed, retains the posterior portion of the stomach pouch, which elongates into a posterior caecal prolongation (Fig. 91,*3b*). Meanwhile the esophagus bulges slightly at the base of the lophophore (Fig. 91,*4a*). Then, the transitional area between esophagus and stomach elongates into a cardial tube, while the pylorus is differentiated from the subrectal portion of the stomach (Fig. 91,*4b*). Thus, the early subdivisions of the digestive pouch are the esophagus, rectum, and stomach, which have different cytological characters in the adult. The caecum, cardia, and pylorus are localized parts of the stomach pouch. All these subdivisions occur early during development of the polypidian vesicle, while the lophophore develops into a low tentacle crown, and are completed when the young polypide reaches its definitive position in the center of the zooecium. Its further development consists simply of allometric growth of the different organs to their final shape and proportions (Fig. 93, 94).

TENTACLE SHEATH AND FORMATION OF THE APERTURE

The zooidal aperture is secondarily pierced as a result of tension exerted on the frontal wall by development of the tentacle sheath of the first polypide. The aperture is lacking when the polypidian bud aborts, and two apertures are formed in abnormal zooids with

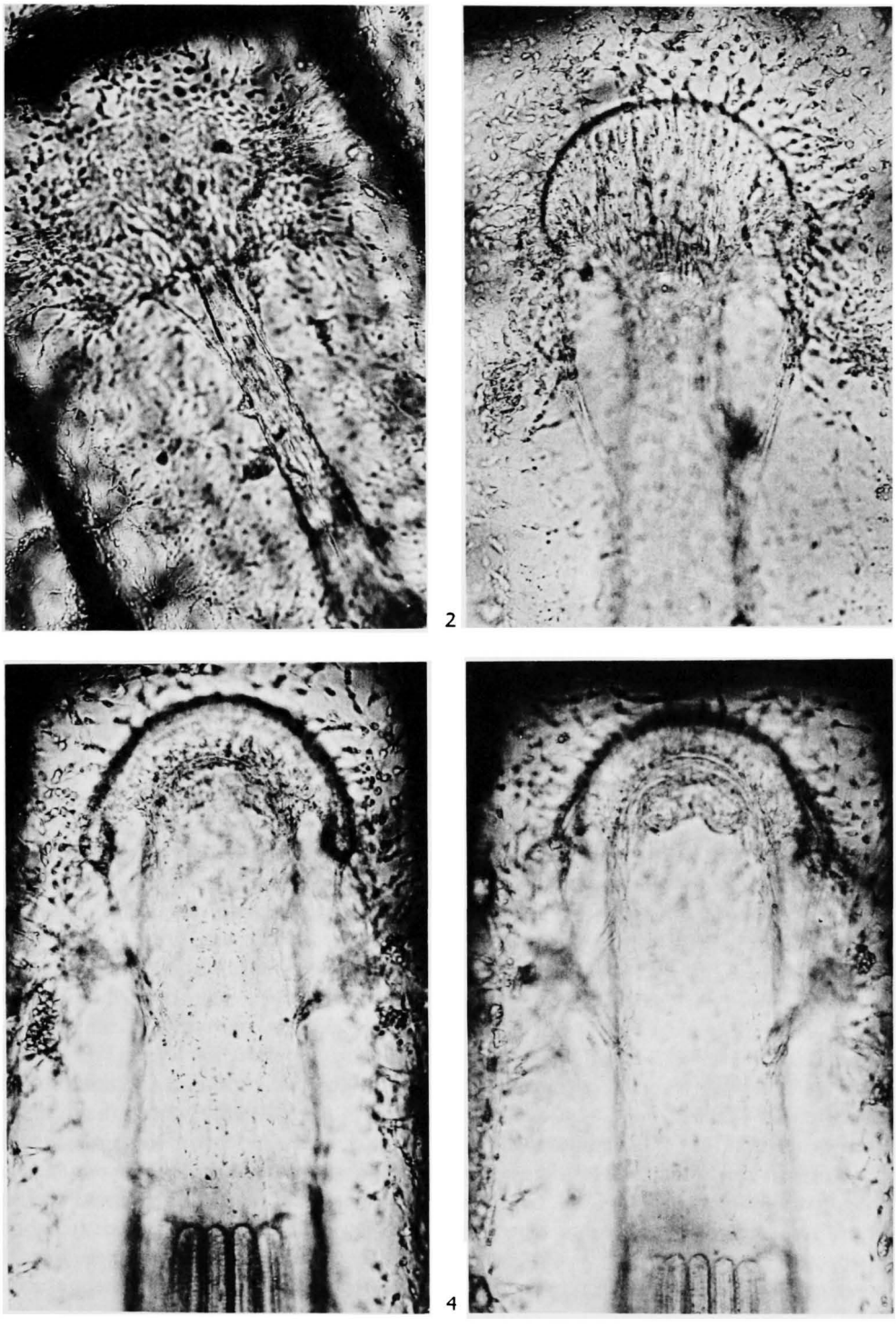

FIG. 95. Formation of the aperture in *Membranipora membranacea*; all live specimens, ×150.——*1*. Orientation of parietal tissues around the top of the embryonic tentacle sheath.——*2*. Junction of the tentacle sheath with the frontal wall and secretion of the edge of the operculum.——*3*. Differentiation of the vestibule.——*4*. Differentiation of the diaphgram.

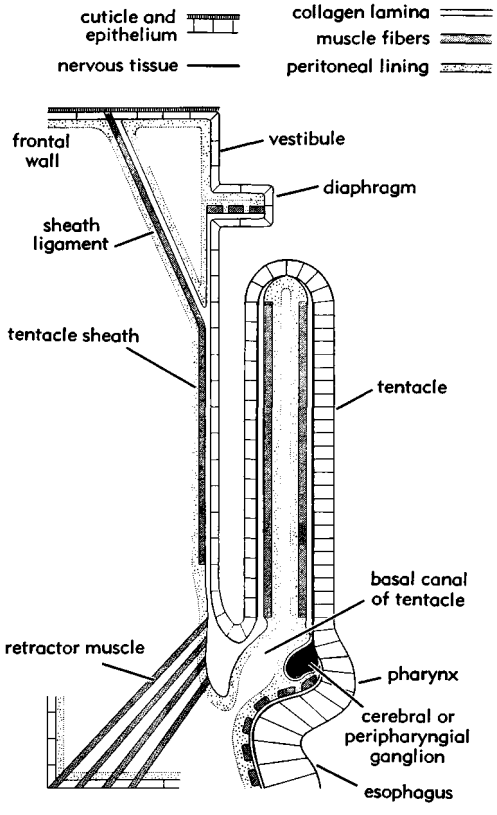

FIG. 96. Continuity of cellular layers in the wall and polypide of adult cheilostomates.

twin polypides.

Displacement of the top of the atrial bag along the median tract, which prolongs it on the frontal wall, is the mechanical consequence of invagination and growth of the polypidian bud. It is not known whether elements from the cellular layers of the frontal wall are absorbed in the growing sheath. Organization of the vestibule, between the brim of the aperture and the muscular diaphragm that closes the tentacular atrium at the top of the sheath, is complex. It has long been presumed that the vestibule, between the operculum and diaphragm, derived from invagination of the frontal wall in the apertural area as a result of traction exerted by the embryonic sheath.

Cinematographic observation of live specimens in *M. membranacea,* confirmed by stained whole mounts, shows that a special sutural process occurs between the conical top of the growing sheath and a subapertural epithelial thickening. The first step in organization of the aperture is the concentric alignment of epithelial cells around the top of the sheath in the distal region of the frontal wall (Fig. 95,*1*). Then this semicircular area, delimiting the shape of the future operculum, thickens by cellular concentration. A refringent line, corresponding to a localized hypersecretion of cuticle on the surface of the opercular area, appears at the periphery (Fig. 95,*2*). Cuticle is reinforced at the edge. Meanwhile, the conical top of the growing sheath adheres to the subopercular epithelial pad. The suture proceeds from the center tothe corners of the operculum while the sheath enlarges with the elongation of the tentacles (Fig. 95,*3*). At the end, a double epithelial ring, from which the diaphragm is formed, appears at the precise level of the suture (Fig. 95,*4*). In the adult, the diaphragm consists of two upper and lower fans of epithelial folds enclosing peritoneal cells, mucocytes, and the fibers of a sphincter muscle. By the time that operculum, vestibule, and diaphragm are completed, the adult polypide is already active and striving for protrusion. A slit appears along the hardened edge of the operculum, which bursts open under repeated pressure from the lophophore (LUTAUD & PAINLEVÉ, 1961).

The relative positions of epithelium, musculature, and peritoneum in polypidian organs result from the ontogenetic continuity of parietal and polypidian layers (Fig. 96). The wall of the tentacle sheath includes the complete sequence of epithelium on the atrial side, muscle fibers, and peritoneal lining on the coelomic side. At its junction with the base of the lophophore, the epithelium of the tentacle sheath is in continuity with the aboral cellular rows of the tentacular epithelium; the oral rows of the tentacular epithelium are in continuity with the digestive epithelium in the pharyngeal area. In the polypide and in the tentacle sheath, the epithelium is supported by an elastic lamina of collagen that

does not exist in the zooecial wall. The collagen lamina is not a basal membrane of the epithelium, for collagen is presumed to be of mesenchymal origin in invertebrates. The collagen lamina is reinforced at the insertion of the great retractor muscle on the base of the lophophore and inside tentacles, where it forms an elastic tube limiting the internal tentacular canal. The peritoneal lining forms a continuous envelope in the tentacle sheath and digestive tract, and joins the reticular peritoneal lining of the wall at the aperture. Annular and longitudinal muscle fibers in the digestive tract, and longitudinal muscle fibers in the tentacle sheath, lie on the coelomic side of the collagen lamina. Muscle fibers are imbedded in the peritoneal lining.

In tentacles, musculature and peritoneal lining penetrate into the collagen tube (Fig. 96). Peritoneal tissues fill the internal space, except for a narrow central lacuna. Muscle fibers lie against the collagen in two oral and aboral groups, in prolongation of muscle fibers of the digestive tract and tentacle sheath. The internal lacunae of all tentacles open at the base into a circumoral lacuna called the **basal canal** of the lophophore. The tentacular and basal lacunae derive from the initial space of the lophophoral fold of the polypidian vesicle, and are enclosed within the peritoneal lining. They are prolongations of the body cavity into the lophophore. The question arises whether the basal canal of the lophophore is closed in the adult, or freely communicates with the body cavity. Communication occurs at least during breeding periods for the passage of eggs and spermatocytes, which are formed in the body cavity and liberated into the tentacular atrium by means of the lophophoral canals.

In the tentacle sheath, tentacles, and digestive tract, the epithelium has lost cuticle and acquired **microvilli** on the external border of cells, which indicate a potential absorption function. It acquires also vibratile cilia in specialized regions of the tentacles and digestive tract. A fundamental function of epithelium in Bryozoa is the secretion of mucoid substances, which form the substrate of the cuticle and matrix in the exoskeleton. In the vestibule, epithelium is still protected by a supple cuticular coating. In polypidian organs, the epithelium liberates mucopolysaccharides on the outer surface of the tentacles and into the lumen of the digestive tract. These function in prey capture, protection of tentacles, and digestion. The tentacle sheath is more than a tissue connection between the polypide and the wall. Because of its absorbent or secretory potential, it may have important functions in the physiology of the entire zooid, particularly in respiratory or excretory exchanges between seawater and the coelomic cavity.

FIG. 97. Funiculus in the autozooid of *Electra pilosa* LINNÉ; decalcified whole mount stained with hemalun, ×90.

FORMATION AND FUNCTION OF THE PERITONEAL-FUNICULAR SYSTEM

Two functionally and topographically distinct tissues derive from differentiation of the

two subepithelial layers of the bud wall, the peritoneal-funicular system and the musculature.

In adult zooids, a **funiculus** comprises thick funicular strands (Fig. 87,*2*), which extend across the body cavity and join the digestive tract to every interzooidal communication in the transverse and lateral walls. In Stolonifera, the funiculus is a simple axial strand in stolons, with branches to the basal septum of autozooids; in autozooids, it joins the basal septum to the stomach and caecum. In multiserial cheilostomes, funicular strands are multiple and ramified (Fig. 97). The main funicular ramifications, attached to pore plates, extend from proximal to distal partitions. They lie between the digestive tract and basal wall, and wrap the stomach, caecum, and pylorus along the way. Divergent branches join every pore plate in lateral walls. In adjacent zooids, correspondent ramifications attach to the other side of the pore plates. Thus, the funicular system extends throughout the colony across interzooidal pores (Fig. 98,*1,2*). Funicular ramifications are present in heterozooids and kenozooids. Parietal funicular strands extend and ramify in the wall of the zooid. In encrusting Anasca, particular parietal strands of funiculus run in vertical walls at the periphery of the zooid, from one pore plate to the next. Funicular ramifications in the wall and across the body cavity persist during cyclic renewals of the polypide.

Funicular strands are made of spindle-shaped cells (Fig. 98,*4*) of feeble cohesion, free to diverge and join crossing or adjacent strands. At their junction with the polypide, they simply fuse with the peritoneal lining of the digestive tract, of similar nature and origin. Funicular cells are characterized by coiled formations of granular endoplasmic reticulum, which indicate an intense synthesis activity. They carry lipid droplets and diffuse glycoprotein substances. In *M. membranacea,* the peripheral parietal strand, at the base of vertical walls, is so charged with diffuse reserves that it becomes a canal with the formation of a central lacuna filled with glycoprotein material (Lutaud, 1961). This phenomenon of accumulation occurs in other species in rich nutrient conditions, or at certain periods of the life cycle.

The funicular system is presumed to transmit metabolites from the digestive tract to the wall and from one zooid to another through interzooidal pores. The rosettes (Fig. 98,*3*), which obstruct every pore, consist of a group of dumbbell-shaped cells. The nucleated portion of these special cells is on one side of the pore plate and extends into a narrow pedunculate prolongation; the cell extends through the pore and swells on the other side into an anucleated blister in the adjacent zooid (Banta, 1969; Bobin, 1977; Gordon, 1975). In *Membranipora, Electra,* and *Watersipora,* two special cells occupy every pore. In Stolonifera, a single rosette of several special cells occupies the central perforation of each stolonal or autozooidal partition. Rosettes are surrounded on both sides by a semicircular row of limiting cells by which funicular strands are attached to pore plates. Within this cellular boundary, diffuse glycoprotein material accumulates in a lacuna around the nucleated portion of the special cells. These special cells would absorb metabolites by the microvillous border of their nucleated portion, which is presumed to be on the transmitting side of the pore plate. Metabolites are released on the anucleated side of the special cells. According to Bobin (1958a,b), orientation of the special cells may be reversed when the direction of need for

Fig. 98. Structure of funiculus and interzooidal communications in *Electra pilosa.*——*1.* Funicular strands and their junction with pore plates in a lateral wall; decalcified whole mount stained with hematoxylin, ×200.——*2.* Pore plate in lateral wall; decalcified whole mount stained with hemalun, ×350.——*3.* Rosette cells through a range of pores in a transverse partition; silver impregnation, ×500.——*4.* Structure of funicular tissue; histological section stained with hematoxylin, ×500.

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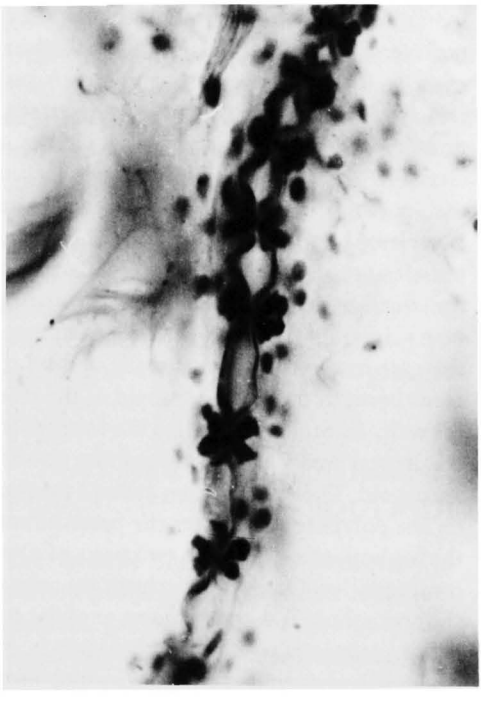

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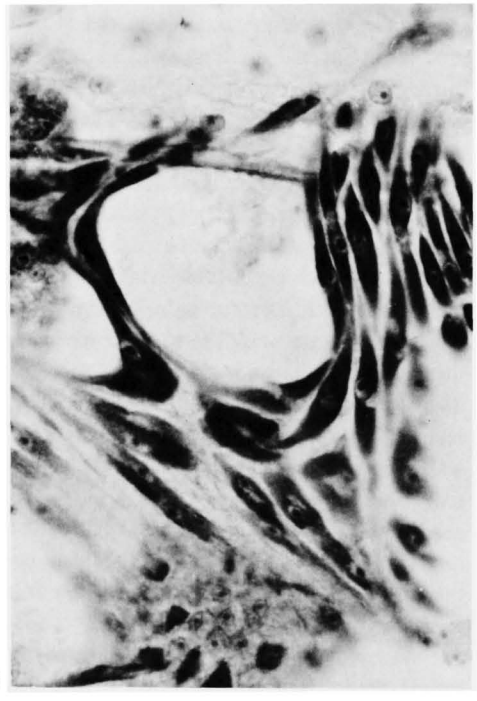

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FIG. 98. *(For explanation, see facing page.)*

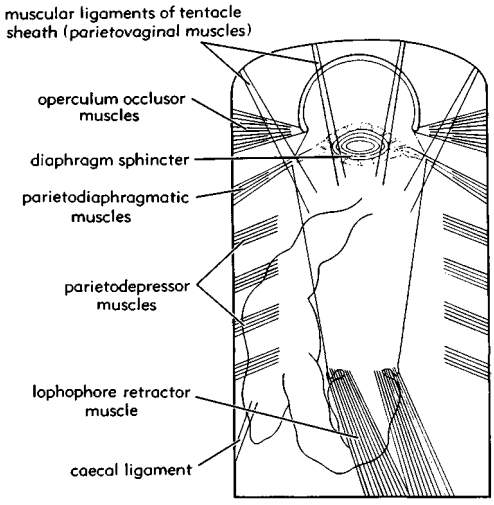

FIG. 99. General external muscle pattern in encrusting cheilostomates.

energy changes between adjacent zooids.

Funicular strands are formed from the reserve layer of the undifferentiated wall of buds (Fig. 87,2). In *M. membranacea,* the cells of the two subepithelial layers are segregated into separate strands in the clearing proximal region of the bud, which is absorbed during formation of a new zooid. Different thickness of the basal and frontal walls in the bud results in a different organization of subepithelial tissues in basal and frontal walls of the zooid. Segregation of peritoneal strands is multidirectional in the frontal wall under combined developmental tensions of the tentacle sheath and aperture; the peritoneal lining becomes reticular. On the basal wall, the thicker reserve layer is dissociated into bundles of anastomosing, longitudinal, funicular strands, which are partly detached from the wall by partitions. The junction of the digestive tract and funiculus occurs early, proceeding either by simple adhesion of the bottom of the polypidian vesicle to the underlying funicular bundles or by fusion of the dorsal funicular bundles with peritoneal strands in the mesenchymal connection that attaches the polypidian vesicle to the center of the proximal partition. The precise destiny of the first subepithelial layer and its contribution to the peritoneal network of the wall are not clearly established; however, reserve cells, vesicular cells, and morular cells, originating from the reserve layer, are attached to the peritoneal lining of the adult wall.

FORMATION OF MUSCULATURE

CALVET (1900) and earlier authors described how fibers of the retractor muscle, inserted on the proximal partition and at the base of the lophophore, are formed from **myocytes** in the mesenchymal connection that persists between the polypidian vesicle and the partition. Myocytes are stretched and separated from peritoneal-funicular strands during growth of the polypidian vesicle toward the center of the zooecium. According to CALVET, a muscle fiber is formed from two associated myocytes. The retractor muscle is contractile early in development, and the young polypide is capable of sudden retractions before differentiation and elongation of the muscle fibers are completed.

The general muscle pattern in gymnolaemates includes **external muscles** inserted on transverse or lateral walls and polypidian muscles formed within the polypidian vesicle. External muscles include the retractor muscle of the polypide and the parietal muscles (Fig. 99). The parietal muscles include the **parietodepressor** and the **apertural muscles**. In Anasca, the parietodepressor muscles are inserted on lateral walls and on the flexible frontal membrane, at regular intervals around the opesia. In Ascophora, they are inserted on lateral walls and on the ascus beneath the calcified shield of the frontal wall. In Stolonifera, they are inserted on the lateral and abanal sides of the tubular autozooid. Their contraction exerts a pressure on the polypide and incites the protrusion of the lophophore. There are two pairs of apertural muscles. One is the occlusor muscles of the operculum in cheilostomates or of the collar in ctenostomates. The other pair is the **parietodiaphragmatic muscles**, which insert on lateral walls and on the diaphragm at the junction of the tentacle sheath and vestibule.

In *M. membranacea* and *E. pilosa,* fibers of the retractor, parietodepressor, and apertural muscles are not striated; however, in the avicularia and vibracula of other species, homologues of the occlusor muscles of the operculum, which animate the mandible or seta, are striated.

Parietodepressor muscles originate at the periphery of the opesia from small groups of myocytes at the corner of the lateral and frontal walls. Myocytes are stretched and detached from the wall by development of the tentacle sheath and aperture. Apertural muscles are formed from similar groups of myocytes at the level of the apertural area. Occlusor muscles of the operculum are formed from a distal pair of thick mesenchymal bridges stretched between lateral walls and the base of the opercular area. Parietodiaphragmatic muscles are formed from minor groups attached at the junction of the conical top of the embryonic sheath with the frontal wall; their frontal insertion is later drawn in during development of the vestibule.

The polypidian muscles adhere to the collagen lamina along their entire length. In adults, the esophagus is surrounded by an almost continuous layer of large annular muscle fibers. In the pharynx, muscle fibers form a sphincter around the mouth (Fig. 99). Thinner annular muscles, overcrossed by longitudinal fibers, surround other subdivisions of the digestive tract.

In the tentacle sheath, the muscular layer consists of parallel longitudinal fibers arising at some distance from the base of the lophophore, and of a few annular fibers grouped in the sphincter of the diaphragm. Longitudinal muscle fibers of the tentacle sheath are collected below the diaphragm into suspending ligaments attached at the base of the distal transverse partition, and on the frontal wall near the aperture. Ligaments of the tentacle sheath have been designated by CALVET (1900) as **parietovaginal muscles**. In ligaments, muscle fibers are imbedded in collagen within a tubular peritoneal envelope; epithelium is lacking (Fig. 96). Ligaments are formed from early mesenchymal anastomoses between the top of the embryonic sheath and the wall. Their contraction lifts the polypide toward the aperture during protrusion, and completes the action of the parietodepressor muscles. Another ligament of identical structure links the caecum to the nearest lateral wall and retains the digestive tract during protrusion.

In *M. membranacea* and *E. pilosa,* annular muscle fibers of the esophagus and intracellular myofibrils of the esophageal epithelium are striated (MATRICON, 1973). Internal muscles of the tentacles are also striated. Longitudinal and annular muscle fibers in the tentacle sheath, sheath ligaments, and diaphragm are smooth.

The precise origin of muscle fibers during differentiation of parietal and polypidian organs is not established; however, in all polypidian organs, the position of muscles between the epithelium and peritoneal lining suggests that myocytes are formed from the first subepithelial layer of undifferentiated mesenchyme of the bud.

NERVOUS COORDINATION OF PARIETAL AND POLYPIDIAN ORGANS

The tentacle sheath is the substrate of important **peripheral nerves** that arise from the cerebral ganglion at the base of the lophophore and serve the aperture and zooecial wall. Motor and nonmotor nerve endings, or nerve cells, are found in extensive or restricted dispersion in the free, external, zooidal wall. Two coexistent pathways of parietal innervation, of different degree of differentiation, occur in Bryozoa. They are either clearly separate in their topographical pattern or intermixed in their connectives to or from the cerebral center. The first consists of motor and sensory endings borne by parietal branches of the great

mixed nerves of the tentacle sheath, which exist in all gymnolaemates. The second is a nerve net, or plexus, of more primitive character, which has been found at present in the wall of phylactolaemates and gymnolaemates. A similar plexus has been found by HILTON (1923) in the body wall of entoprocts.

CEREBRAL CENTER AND INNERVATION OF THE POLYPIDE

The **cerebral ganglion** lies in the oral constriction between the base of the lophophore and the esophagus on the anal side of the polypide. An annular ganglionic belt, called the **peripharyngeal ganglion**, lies between the basal canal of the lophophore and the epithelium of the pharynx. The cerebral ganglion and its circumoral prolongation, as well as lophophoral and visceral nerves, are basiepithelial and lie between the epithelium and the collagen lamina (Fig. 96). The cerebral and peripharyngeal ganglia are formed early in the polypidian vesicle from a secondary fold of reversed orientation at the base of the lophophoral fold.

In *Electra,* the cerebral ganglion includes 40 to 50 cells, among which are neurons of different kinds, secretory cells, and investing nonnervous elements (LUTAUD, 1977). Neurons are arranged in a fixed pattern around a deep core of intermixed fibers and intracerebral connectives. Arrangement of the cerebral cells is constant in *Electra*; however, specific variations occur in different cheilostomate families. Nevertheless, three areas always remain distinct: (1) a central aggregate with topographical potential for general cerebral coordination; (2) the distal brim where chains of neurons in the peripharyngeal ganglion are initiated and sensory nerves from the lophophore are received; and (3) symmetrical proximal clusters including giant neurons from which the main peripheral nerves arise.

Two pairs of sensory and motor nerves along every tentacle arise at regular intervals from the peripharyngeal ganglion (Fig. 100,*2*). Twin nerves arise from branched intertentacular stems on either side, and converge to run along the oral edge of every tentacle. These are presumed to be sensory nerves to which sensory cells in the tentacular epithelium would be sporadically attached (MARCUS, 1926). They run beneath two rows of monociliated epithelial cells along the oral edge of the tentacle, which are presumed to have a tactile function (LUTAUD, 1973). Another pair of median oral and median dorsal nerves arise in the axis of the tentacle. Although they lie on the epithelial side of the collagen lamina, their pathway coincides with the position of the internal tentacular muscles, and they are presumed to be either motor or mixed.

The digestive tract is served by a median dorsal visceral nerve along the esophagus, and by a pair of branched lateral visceral nerves arising from a small group of ganglionic cells below the cerebral ganglion (Fig. 100,*2*). Short connectives and anastomoses link the visceral stems to nervous strands of the peripharyngeal ganglion, and provide a plausible pathway for coordination of lophophore activity and of contractions and peristaltic waves of the digestive tract.

INNERVATION OF THE APERTURE AND FRONTAL WALL

In gymnolaemates, two pairs of peripheral nerves arise from the proximal cellular clusters of the cerebral ganglion, and emerge together through lateral openings. They first diverge, then meet again and fuse on their way toward the aperture along the tentacle sheath (Fig. 100,*1*). Equivalent peripheral nerves, of slightly different pathway, exist in phylactolaemates. The peripheral nerves run in the tentacle sheath on the peritoneal side of the collagen lamina, imbedded in the peritoneal lining. They are, on either side, a thick fibrillous strand directly joining the aperture and a thin three-branched motor nerve, called the **trifid nerve** (BRONSTEIN, 1937). The three branches of this motor nerve are: (1) a branch around the pharynx to the insertion of the

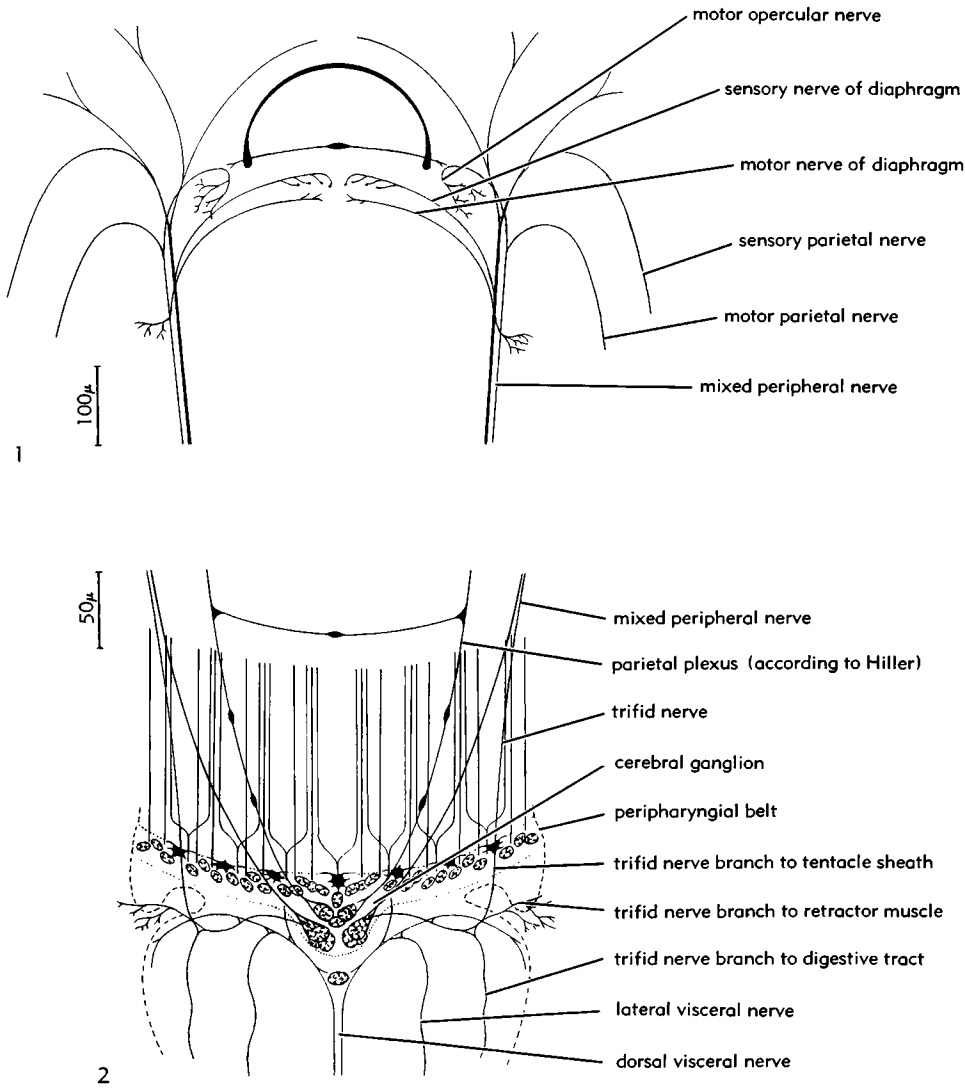

FIG. 100. Main nervous pathways in anascan cheilostomates.——*1.* Parietal and apertural branches of main peripheral nerves; frontal view.——*2.* Cerebral ganglion and innervation of the polypide, dorsal view.

retractor muscle; (2) a visceral branch bending down to the esophagus; and (3) an axial branch bending up along the sheath and joining the **direct nerve**. Below the junction, an annular ramification of the axial branch surrounds the tentacle sheath at the level of the basal extremities of the longitudinal muscle fibers of the tentacle sheath and sheath ligaments.

In Anasca, the great **mixed nerves**, formed by conjunction of the direct and trifid nerves on either side, ramify at the top of the sheath into three couples of motor and sensory branches (Fig. 100,*1*). A motor ramification innervates first the parietodiaphragmatic muscle, then joins the sphincter in the diaphragm; a corresponding sensory ramification develops arborizations in the upper folds

of the diaphragm. Parietal ramifications join the zooecial wall next to the aperture. At this level, an opercular motor branch to the occlusor muscles of the operculum diverges, while a transverse nonmotor ramification follows the hinge of the operculum. Twin proximal ramifications around the opesia, or motor parietal nerves, run through frontal insertions of all parietodepressor muscles. In Electridae, parallel nonmotor branches around the opesia expand into diffuse fibers with terminal knobs or cells at the base of every marginal spine (LUTAUD, 1977). Distal fibers with peculiar cellular endings of undetermined function join the base of the distal partitions. Nerve strands in the zooecial wall run between the epithelium and the peritoneal lining.

Thus, the main nerves of the tentacle sheath carry motor impulses to all muscles working together during lophophore protrusion and retraction. They are also the probable pathways of an unelaborate perception of the environment at the level of the free external wall and at the entry of the tentacular atrium. However, it is not established whether superficial endings of nonmotor parietal nerves are nerve cells or epithelial receptors.

HYPOTHETICAL PATHWAYS OF COLLECTIVE INTERZOOIDAL INFORMATION

The observations of GERWERZHAGEN (1913) and MARCUS (1926, 1934) brought evidence of the existence of a nerve net in the body wall of ectoprocts. In phylactolaemates, both GERWERZHAGEN in *Cristatella* and MARCUS in *Lophopus* observed a network of large multipolar cells, selectively stained by the vital methylene-blue dye after ERLICH, in the tentacle sheath and external wall. MARCUS found a similar plexus in the wall of tubular zooids of the stoloniferan ctenostomate *Farella repens* (FARRE), spreading from a nonmotor parietal ramification of the main tentacle sheath nerves. This parietal nerve net has been recently observed again in the autozooids and stolons of *Bowerbankia gracilis* LEYDI (LUTAUD, 1974). The large meshes of the network, which is probably continuous all over the colony across interzooidal pores, are brightly stained by methylene blue in orthochromatic tones and cannot be confused with the underlying peritoneal network of quite different appearance and affinity for the stain. According to BRONSTEIN (1937) a similar plexus would exist in the external wall of all gymnolaemates. However, in the encrusting carnosan *Alcyonidium polyoum,* as well as in *Electra pilosa* and other malacostegans, this unorganized network is replaced in the frontal wall by a more differentiated set of nerve fibers spreading from the sensory branch of the parietal nerve, with cellular endings around the orifice and at the periphery of the frontal area (LUTAUD, 1981).

Another form of methylene-blue positive network coexisting with the superficial developments of the parietal nerve in the frontal wall was discovered by HILLER (1939) in *Electra pilosa* (confirmed by LUTAUD, 1969). In Electridae and other encrusting anascans, methylene-blue staining reveals a linear chain of bipolar cells running at the base of the interzooidal partitions (Fig. 101). This internal pathway around the basal wall is linked to prominent cells in the central cellular cluster of the cerebral ganglion by twin connectives of similar structure running on the dorsal side of the tentacle sheath to join the peripheral plexus filament at the distal corners of the zooid. Short transverse branches penetrate into every septular chamber on its concave side. Interzooidal bonds, which are made of a modified plexus cell replacing a rosette across one pore of every lateral pore plate and certain pores in transverse partitions, periodically link the parallel filaments running on both sides of the common partitions of adjacent zooids (LUTAUD, 1979). Ultrastructural investigation confirms the nervous nature and cellular structure of the network. No homologous nervous pathway in a similar location was found in the carnosan *Alcyonidium polyoum.*

Thus, the differentiation of two separate pathways of parietal innervation is observed in encrusting cheilostomates. One is a group

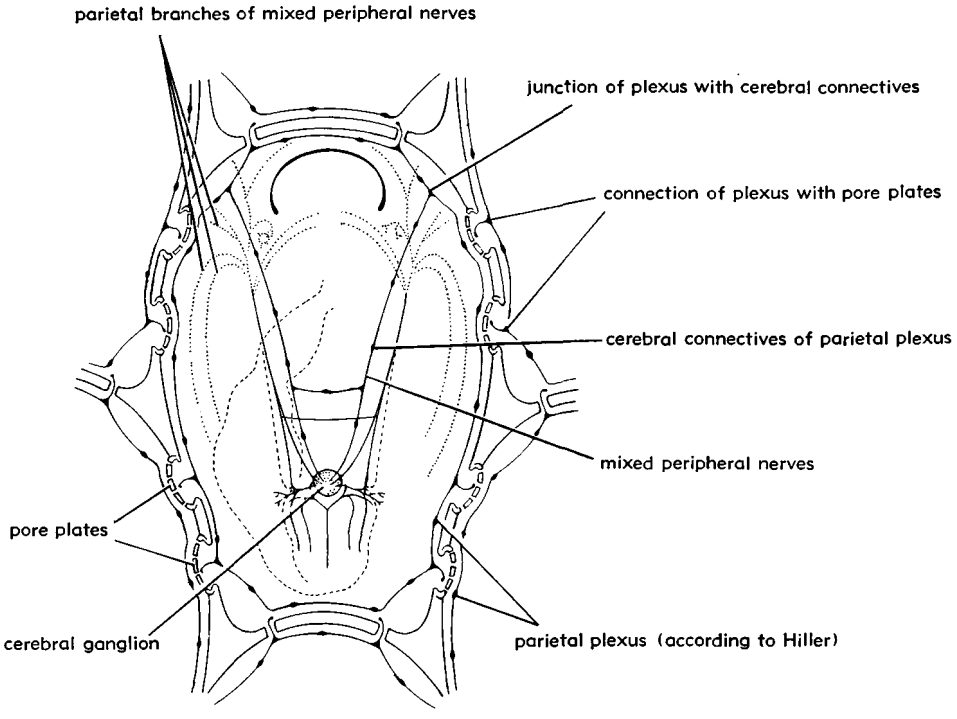

FIG. 101. Pathways of parietal innervation in *Electra*; dorsal view.

of nerve fibers with sensory endings in the frontal area, which informs the nervous center of each polypide about external variations. The other is a dorsal pathway of plexus structure along interzooidal partitions. By its colonial continuity across certain pores in communication organs and its connection with the cerebral centers of all the polypides, the plexus is the most probable pathway for a primitive collective communication among groups of zooids within a colony. The interzooidal transmission of experimental stimuli in all directions along zooidal rows was recently demonstrated in malacostegans by electrophysiological experimentation (THORPE, SHELTON, & LAVERACK, 1975b). However, the colonial plexus cannot be interpreted from its cytological features as a colonial nerve, which would imply oriented impulses from one zooid to the next and the incomplete autonomy of the cerebral center of a polypide. Colonial coordination should rather be understood as a simple consequence of the morphogenetical continuity of cellular layers of the wall in bryozoans, and as response to a diffuse collective perception of the general activity of polypides, which might be reinforced or counterbalanced by individual perceptions of the medium at the level of the frontal wall.

CONCLUSIONS

The complete succession of soft tissues in the wall of the adult zooid, from exoskeleton to body cavity, is epithelium, nervous layer (either diffuse peripheral endings or plexus), musculature, and peritoneal-funicular strands. Muscles and funiculus are partly detached from the wall by formation of partitions and by development of the polypide.

Except for exoskeletal layers secreted by epithelium, a similar succession is present in all organs of the polypide as a result of its formation from an investigation of soft layers of the wall. The body cavity and its prolongations into the lophophore, with the function of a coelom, are enclosed by mesenchymal tissues.

Except for musculature that is differentiated after individualization of the autozooid, all layers of the wall contribute to functional coordination of the colony. Continuity of epithelium is not interrupted during the formation of partitions. Coalescence of exoskeletal layers in transverse and double lateral walls maintains the mechanical cohesion of zooidal units. Nervous coordination of the colony might be possible by the ontogenetic continuity of a parietal nerve net, closely associated with epithelium, which is already present in the wall of the bud. Interzooidal continuity of the funiculus is the consequence of the initial continuity of subepithelial tissues in the bud, maintained or secondarily reestablished during formation of septal folds and during longitudinal division of the bud.

The peritoneal-funicular system, with a trophic function, does not have an equivalent in other invertebrates. Constant interaction of its different organs regulates the equilibrium between individual and colonial energy needs. The funiculus carries excess metabolites from feeding autozooids toward regions in the colony where the claim for energy is maximal, such as the growing margin, rows of active heterozooids, or rows of autozooids during renewal of their polypides. Orientation of the filtering apparatus in communication pores is related to directions of budding and to changing needs of zooids. Funicular pathways are the means of the colonial community of reserves. The transit of metabolites is not the only function of the peritoneal-funicular system. The peritoneal lining is also presumed to have the function of wall nutrition and of storage of reserves, in the adult zooid as well as in the bud. Intensity of proliferation and secretory activity of the epithelium, and therefore the metabolism of calcification, depend on the availability of these reserves. The peritoneal lining and funicular tissues also contribute to secretion and equilibrium of the coelomic medium by such specialized elements as mucocytes, phagocytes, and morular cells.

The zooecial wall contributes to physiological regulation of the entire zooid by its secretions toward external and internal media, and by storage and utilization of reserves. There are presumptions that it has also a function in respiration, either through the flexible frontal membrane in Anasca, or through frontal pores, or through uncalcified developments of the frontal wall in Ascophora. It is also the durable organ of the entire zooid. Persistence of its organogenetic potential allows renewal of the polypide when it becomes poisoned by waste products of its own digestive function. When the polypide degenerates, resorption of the tentacle sheath interrupts the continuity of parietal and polypidian tissues at the level of the aperture. The retractor and parietodiaphragmatic muscles are destroyed; the opercular occlusor and parietodepressor muscles remain. Funicular ramifications surround the brown body formed by encysted remnants of the degenerated polypide; they are later reconnected with a new polypidian vesicle. The early stages of a regenerating polypidian vesicle, and the restoration of the junction of a new tentacle sheath with the preexisting aperture and opercular muscles, have not been closely investigated. The superficial plexus of the ctenostomates, and the internal plexus of *Electra,* persist during renewal of the polypide; however, their connectives to the cerebral ganglion are broken. Plexus, nerve endings, or epithelial receptors in the wall are secondarily reconnected with the new peripheral nerves arising from the cerebral ganglion of the regenerated polypide.

Individuality of the autozooid is maintained by the occurrence of a polypide and by the presence of a central nervous system. Although it is not necessary to the survival and nutrition of the zooecium, the polypide

is more than a feeding organ, for it includes the cerebral center, which coordinates the functional activity of zooecial and polypidian organs, and controls all relations with the environment. Nervous extensions are everywhere present in the wall and in the polypide with the same ubiquitous dispersion as in any other animal. The zooecial wall is not inert, and parietal innervation is controlled by the cerebral ganglion. The plexus structure of part of the parietal innervation in certain families, and the absence of any protective sheath around nerve bundles, are primitive characters that may have some phylogenetic value. The parietal plexus, when it exists, shows a tendency to form linear pathways related to shape of the zooid and to pattern of colonial construction. Perception is elementary, by means of dispersed or ordered nerve endings or epithelial receptors in the wall and lophophore. Although rudimentary in its organization, the cerebral center shows delimited districts of innervation that are found in distinct ganglionic lobes in other lophophorates. Potential for integration of individual perceptions of the environment may overcome, compensate, or reinforce interzooidal information, and allow autonomous behavior of the zooid.

Anatomical pathways of the functional unity of the autozooid have been described here in Anasca with their ontogenetic relationships. These structures are fundamental in the gymnolaemates, with minor specific variations; and, based on the soft parts, the group appears homogeneous. Fundamental characters now used in classification are: (1) laws of colony construction; (2) presence or absence of calcification with correlative modification of the chitinous protection of the aperture, collar (in ctenostomates), or operculum (in cheilostomates); and (3) degree of calcification of external walls, with displacement of parietal muscle insertions on a compensative internal fold of epithelium when calcification extends to the frontal wall. Less apparent variations in soft parts are observed in different orders, families, and genera, which could be used for systematic differentiation. The most evident are the subdivisions of the stomach and the number of tentacles. An increasing complexity of the funiculus and variations in direction of the transit of reserves may be determinant in evolution of the budding mode. From Stolonifera to higher cheilostomates, an increasing complexity in structure of the cerebral ganglion and in nervous ramifications is also noticed. In ctenostomates, and in different families of cheilostomates, evolution of cellular categories of mesenchyme, particularly of protein inclusions, is observed. Modifications in epithelial metabolism are at the origin of skeletal evolution.