Why Bryozoans Have Avicularia — A Review of the Evidence

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ABSTRACT

This review summarizes the evidence for alternative functions of avicularia and vibracula. In the present paper I review the history of speculation on the adaptive function of avicularia and evaluate the evidence for the various functions suggested for them: defense, food-gathering, creation of water currents, respiration, cleaning, and nutrient storage. Then I suggest some alternative views and ways in which they might be tested. Early workers believed that their function might be defense of the colony, and since Darwin's time this function has become tied in with a selectionist argument in which increasing polymorphism of colonies, specialization of zooids for feeding, reproduction, and defense leads to increasing success.

In only a few cases has the function of avicularia and vibracula been empirically established. The pedunculate *Bugula* type of avicularia has the ability to capture possible enemies. The vibracula of some lunulitiform colonies are used in locomotion and cleaning. No defensive or other function has been demonstrated for other avicularia and in fact, observations on their morphology, behavior, and position in the colony are incompatible with the hypothesis that they act in defense of the colony.

INTRODUCTION

In cheilostome bryozoans the problem of the function of the zooid polymorphs known as avicularia has intrigued biologists for over 200 years. All speculations on avicularia since Busk's and Darwin's time have had at their core the idea that avicularian zooids are specialized to perform some function more efficiently than other zooids. Other specialized zooid functions have been adequately documented. Embryos have been seen to be brooded in ovicells and gonozooids and rhizozooids have been observed to attach colonies to substrata. Evidence that avicularian zooids serve an adaptive function, either by defending the colony, or by performing any other function suggested for them is, however, lacking except in a few cases.

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THE NATURE OF AVICULARIA

The presence of avicularia in bryozoan colonies was first reported by John Ellis, who figured the "bird's head coralline" (*Bugula avicularia*). His account stated, "On the outside of each cell we discover, by the microscope, the appearance of a bird's head, with a crooked beak, opening very wide" (1755, p. 36).

Darwin (1845) made detailed observations of these structures in other species from Tierra del Fuego and the Falkland Islands, noting that there were various types:

> The organ, in the greater number of cases, very closely resembles the head of a vulture; but the lower mandible can be opened much wider, so as to form even a straight line with the upper. The head itself possesses considerable powers of movement, by means of a short neck. In one zoophyte the head itself was fixed, but the lower jaw free; in another it was replaced by a triangular hood, with a beautifully fitted trap door, which evidently answered to the lower mandible. A species of stony Eschara had a structure somewhat similar. . . . I might mention one other kind of structure quite as anomalous. A small and elegant Crisia is furnished, at the corner of each cell, with a long and slightly curved bristle, which is fixed at the lower end by a joint.

Krohn (1843) also recognized that these structures varied, having three basic forms: 1) the stalked bird's head type which he likened to a pair of pliers on a handle, corresponding in action to a crab's claw; 2) the second, or forceps, type being a modification of the first in which the basal part is not movable and the handle is lacking, and 3) the third formed by more or less arch-shaped bristles or spines.

Modern workers still recognize these three general types. All can be recognized as modifications of autozooids that usually lack functional polypides and in which the operculum is modified into a mandible (avicularium) or seta (vibraculum).

The basic zooid structure in cheilostomes includes the calcified side walls and calcified basal walls, forming a box filled with coelomic fluid, cells, and internal organs, and covered by a frontal wall which is more or less calcified, but has either some membranous portion or a membranous sac leading from it. In autozooids (fig. 1A, D, E) there is a hinged flap (the operculum) in the distal part of the frontal wall. An opening behind it (the orifice) leads into the vestibule and thence to the tentacle sheath of the retracted polypide (lophophore and gut portion). The operculum is closed by a pair of muscles (the occlusor muscles), and opened by hydrostatic pressure in the coelom, which may be aided by a pair of divaricator muscles. The rest of the autozooid is filled with musculature associated with polypide movement and functioning of the hydrostatic system, and in sexual zooids by gonads. In most cheilostomes embryos are brooded in polymorphs or parts of polymorphs (ovicells), but in some species they are brooded in internal ovisacs, and in a few others released without brooding.

The simplest type of avicularium (fig. 1A, B, C) has an operculum altered into a mandible, which is also hinged to the frontal wall. As illustrated in figure 3 the space beneath the closed mandible equivalent to the orifice or vestibular area is called the palate. In the center of the palate is a round depression marking the opening of the polypide rudiment. In most avicularia this structure lacks tentacles and gut and consists only of a saclike body, sometimes with two additional sacs attached. The coelomic cavity contains no other organs, but much of its volume may be filled by enlarged occlusor muscles (mandible adductors). One or two pairs of abductor muscles (probably equivalent to the divaricator muscles of the autozooid) may also occur. Beneath the hinge area of the mandible two underlying skeletal projections (often
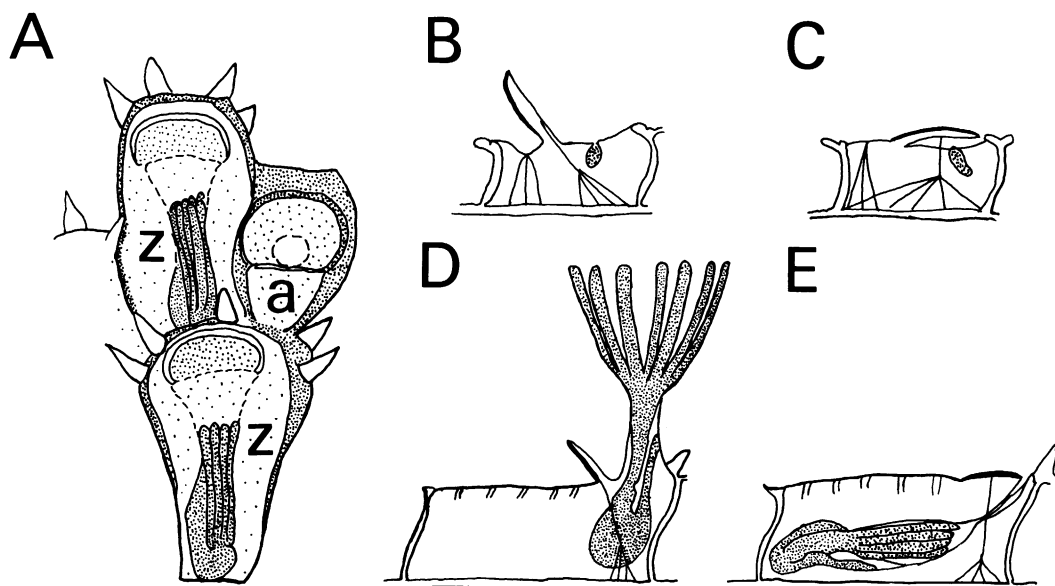
FIG. 1. Autozooids and avicularia. (A) Frontal view of two autozooids and a vicarious avicularium of *Flustra foliacea*. Diagrammatic longitudinal section of such an avicularium with mandible open (B) and mandible closed (C) showing arrangement of muscles and polypide rudiment and its correspondence with autozooid structure. Diagrammatic longitudinal view of autozooid with operculum open (D) and operculum closed (E) showing arrangement of muscles and polypide. Figure 1A redrawn after Ryland and Hayward (1977); figure 1B–E based on diagrams in Banta (1973a) and Silén (1977).

joining in a bar) may reinforce the hinge. Behind the hinge area the frontal membrane continues to the proximal end of the avicularium. This area may also have skeletal reinforcement.

Special terms are used by bryozoologists to distinguish types of avicularia based on their position and shape. Vicarious avicularia are those which replace an autozooid in position (fig. 4). Smaller avicularia, squeezed between autozooids, but still on the same level with them are called interzooidal (figs. 5, 10, 12), whereas the avicularia that develop on lateral, frontal, or basal walls are called adventitious (figs. 5, 6, 9, 11, 13).

The bird's head avicularia (figs. 2, 7), although they were the first to be noticed, are actually the most complex and derived forms. In these the proximal portion of the zooid (fig. 2) is drawn out into a peduncle, whereas the basal portion forms the curved upper surface, terminating in a beak or rostrum, and the frontal wall (with mandible, palate, frontal membrane) has become ventral. Large muscles and skeletal reinforcement of the

walls result in a design structurally suited to grasping, whereas the polypide rudiment contains a large tuft of sensory bristles (Kaufmann, 1971).

Polymorphs with very long and slender mandibles are called vibracula (fig. 8). These have a more elaborate mandibular articulation than the previous forms. The notched base of the mandible, or seta, swings between two skeletal projections, and the addition of a pair of lateral gyrator muscles allows some lateral or rotary motion, as well as back and forth motion. Bryozoologists disagree about whether the vibracula represent a category distinct from avicularia because of the differences in articulation. The term avicularian polymorphs refers to both groups, unless otherwise indicated.

EVOLUTION OF IDEAS ON AVICULARIAN FUNCTION

In Darwin's original (1845) observations on avicularia he also noted their behavior: "Their movements varied according to the
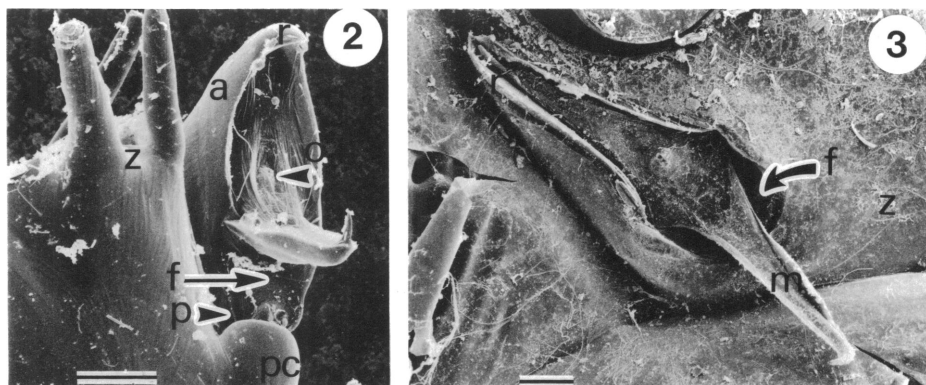
FIG. 2. Pedunculate (bird's head) avicularium of *Bugula stolonifera.* z = autozooid, a = avicularium, r = rostrum, m = mandible, o = opening of setiferous organ (polypide rudiment), f = frontal membrane, p = peduncle, pc = peduncle cushion (scale = 40 μm).

FIG. 3. Adventitious avicularium of *Hippopodina feegeensis.* m = open mandible, f = frontal membrane, o = opening of polypide rudiment, r = rostrum, pa = palate (scale = 40 μm).

species: in some I never saw the least motion; while others, with the lower mandible generally wide open, oscillated backwards and forwards at the rate of about five seconds each turn; others moved rapidly and by starts. When touched by a needle the beak generally seized the point so firmly, that the whole branch might be shaken." However, at that time Darwin made no speculations on their function.

Johnston (1847) summarized the results of the observations of his contemporaries on avicularia. Van Beneden (1845) studied them "without obtaining any clue as to their usefulness or purpose in the economy of the polype." Reid (1845) conjectured that they might "assist in circulating water along the canals in the different processes of the cell." Johnston himself admitted that "the use of them to the polypes is merely conjectural," but went on to speculate that, "By those formed in the model of pincers the polype may seize circumfluent animalcules, for although they are too short to hand the prey to the mouth, yet retained in a certain position, and enfeebled or killed by the grasp, the currents set in motion by the ciliated tentacula, may then carry it within reach. The hair-like bristles are more probably organs to drive away injurious particles or animalcules that might seek an entrance into the cells."

In 1854 George Busk considered their structure and function. He gave the term

avicularium to the pincer-like form and vibracula to the bristle-like form, and he realized that however diverse their appearance, they were all constructed on the same general design. He emphasized their importance as systematic characters, particularly in the encrusting calcified forms then lumped together under *Lepralia,* for which he claimed, "In fact without them it would have been a most difficult task to marshall into order such an irregular and mutinous host." With respect to their function, however, he stated that up to that time only speculation had been offered. As they appeared to be shaped for grasping, he made a case for the primary function being defense, with those of the bird's head type being considered the most highly developed.

Darwin discussed avicularia again in the sixth edition of the *Origin of Species* (1872) in the chapter on "Miscellaneous Objections to the Theory of Natural Selection." By that date Darwin was referring to the bird's head type of avicularia as being "the most perfect condition" of these structures. Although he cited some of his own earlier observations he relied for the most part on Busk's work to make his points. Darwin's critic Mivart (1871) believed that the avicularia of bryozoans were similar to the pedicellariae of echinoderms, and he used them together with pedicellariae to exemplify one of his objections to Darwin's theory—that such complex and similar
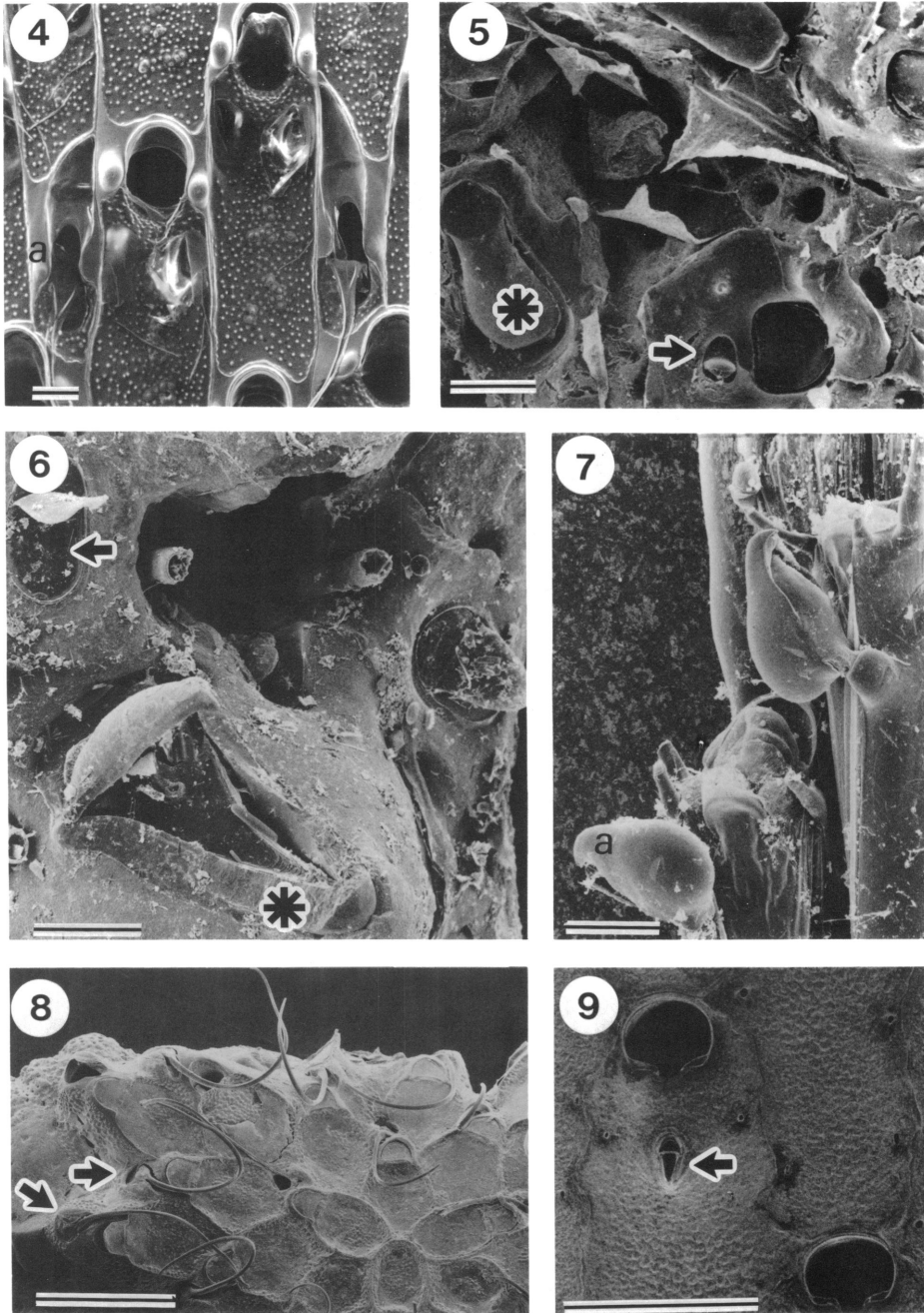
FIG. 4. *Thalamoporella falcifera* (Florida), showing two vicarious avicularia (a) (scale = 100 μm).

FIG. 5. *Trematooecia aviculifera* (Belize), showing suboral adventitious avicularium (arrow) and interzooecial avicularium with spatulate mandible (*) (scale = 200 μm).

FIG. 6. *Sertella frigida* (Antarctica), showing small elliptical (arrow) and large triangular (*) avicularia (scale = 100 μm).

FIG. 7. *Bugula stolonifera* (Long Island Sound), showing position and orientation of pedunculate avicularia (a) (scale = 100 μm).

FIG. 8. *Discoporella umbellata* subsp. *depressa* (Florida) (scale = 400 μm).

FIG. 9. *Isoschizoporella tricuspis* (Antarctica), showing suboral adventitious avicularia (arrow). This is one of the common positions for this type of avicularium (scale = 400 μm).
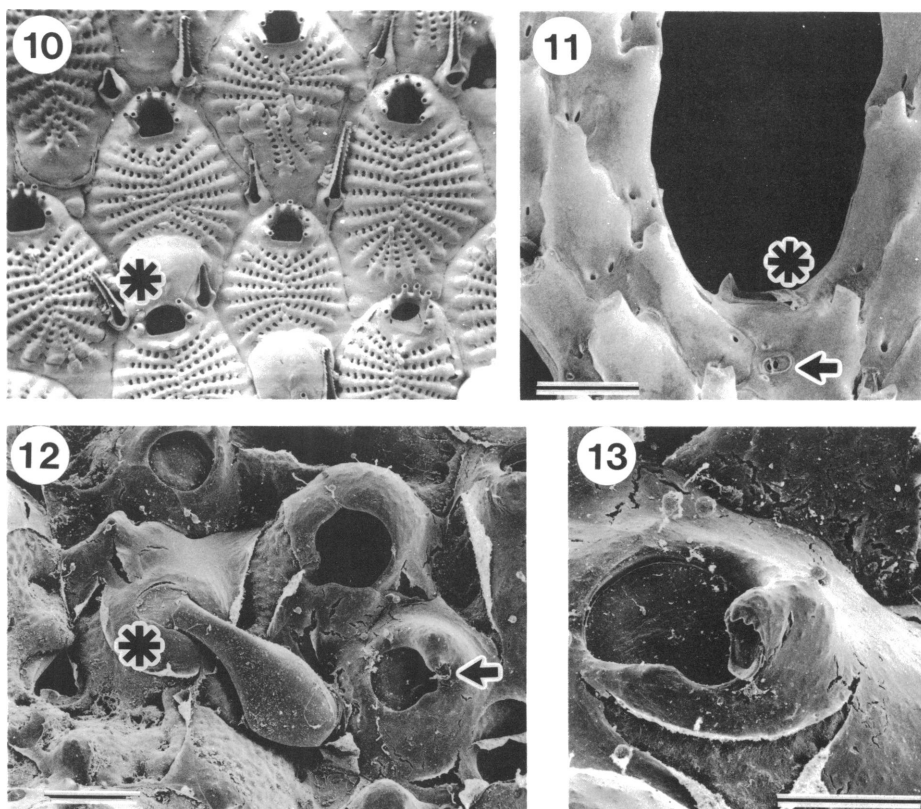
FIG. 10. *Cribrilaria radiata* (Jamaica), showing small interzooecial avicularia (*) with elongated mandibles and serrate rostra (scale = 200 μm).

FIG. 11. *Hippellozoon hippocrepis* (Antarctica), showing small oval avicularia (arrow) and large triangular avicularia (*) located at the base of a fenestra between two branches (scale = 400 μm).

FIG. 12. *Celleporaria albirostris* (Belize), showing two types of avicularia, a large interzooecial avicularium with a spatulate mandible (*) and a much smaller suboral avicularium (arrow) (scale = 200 μm).

FIG. 13. *Celleporaria albirostris:* Enlarged and tilted view of suboral avicularium of figure 12 showing its perpendicular orientation on the side of the suboral umbo and its serrated rostrum (scale = 100 μm).

organs could not have originated from "minute, fortuitous, indefinite variations . . ." (p. 93). Darwin based his refutation of Mivart's objection on the conclusion (still acceptable) of contemporary bryozoologists (Smitt, Busk, Nitsche) that avicularia and vibracula were homologous with zooids. Though no intergradations had been found between avicularia and zooids Busk had informed Darwin that avicularia did grade into vibracula, and Darwin based his argument on that evidence:

This view of the vibracula, if trustworthy, is interesting; for supposing that all the species provided with avicularia had become extinct; no one with the most vivid imagination would have thought that the vibracula had originally existed as part of an organ, resembling a bird's head or an irregular box or hood. It is interesting to see two such widely different organs developed from a common origin: and as the movable lip of the cell serves as a protection to the zooid, there is no difficulty in believing that the gradation, by which the lip becomes converted, first into the lower mandible of the avicularia and then into an elongated bristle, likewise served as protection in different ways and in different circumstances (pp. 217–218).

Darwin gave his support (p. 217) to the defense hypothesis: "The avicularia, like the vibracula, probably serve for defense, but they
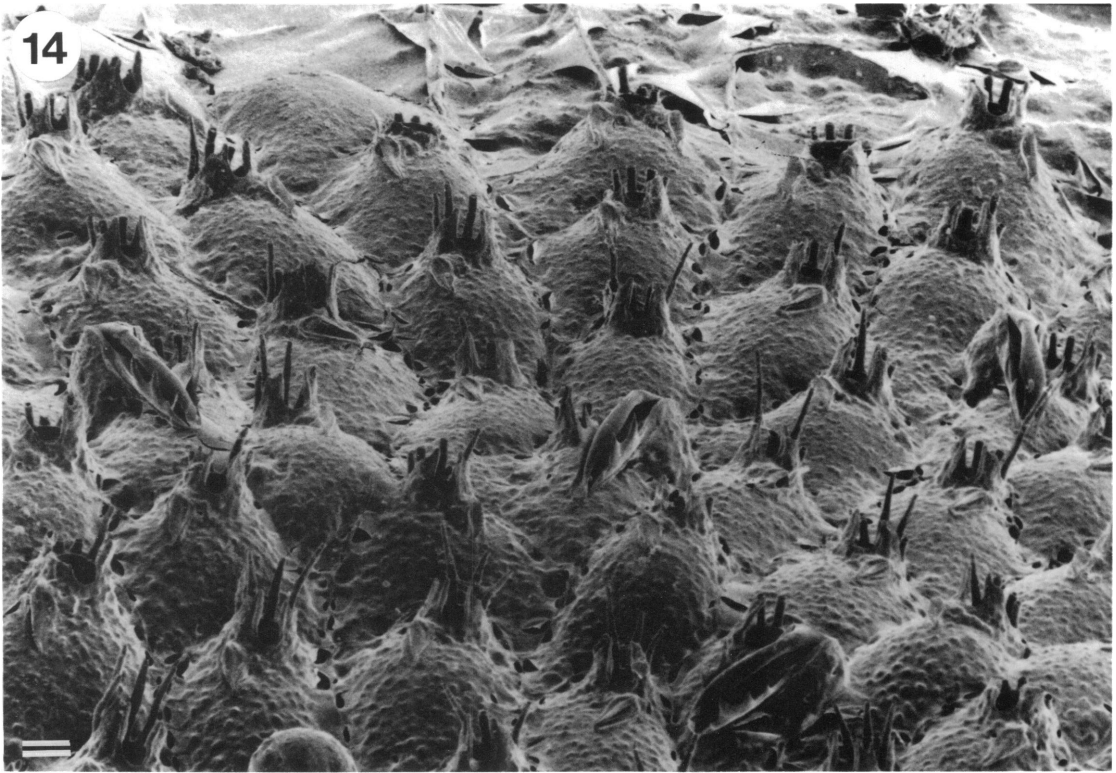
FIG. 14. Perspective view of an area of a colony of *Parasmittina serrula* (Jamaica), showing avicularian orientation with respect to surface topography (scale = 100 μm).

also catch and kill small living animals, which it is believed are afterwards swept by the currents within reach of the tentacula of the zooids."

Thus, by conjecture repeated by various authorities, the defensive function of the avicularia and their role in selection had become well established by the time S. F. Harmer delivered the 1908 presidential address to the British Association for the Advancement of Science (Harmer, 1909). In recognition of the fiftieth anniversary of the presentation of Darwin's and Wallace's papers on natural selection before the Linnaean Society, Harmer spoke of the development of interest in problems of heredity and variation, and the still-unanswered questions, turning for examples to the group with which he was most familiar—the Polyzoa: Harmer believed that avicularia, like the pedicellariae of echinoderms, had a defensive function. Ordinary unmodified opercula might have the

same function in many cases, but in these modified zooids the defensive function of the opercula might have been made more efficient.

After describing observations on avicularia of the *Bugula* type, Harmer admitted that in the majority of Cheilostomata the avicularia are not of the stalked type but occurred scattered over colonies in a considerable variety of positions and forms, usually rigidly connected to the walls of the zooecia. The assumption of an active protective function or functions fits the finding that avicularia were modified in a number of ways, but the patterns of their distribution within and between species could not be so easily explained.

Avicularia might be completely absent in a genus, in some species of a genus, in some subspecies of a species, or in some colonies of a species that normally has them, or they might be lacking on some zooids of a colony though present on some or most others. They

might also vary considerably in position on individual zooids. In a single species all avicularia might be of the same type, or two or more kinds might occur, distinguishable by size or shape.

Thus, while avicularian characters had long been used by systematists in distinguishing species, no hypothesis had explained their numerous modifications.

> The difficulty of understanding the evolutionary significance of the avicularia arises in part from the fact that the occurrence and distribution of these structures appear in many cases to give but slight indications of affinities. It cannot, for instance, be assumed, without further evidence, that two species possessing an identical type of avicularium are nearly related. The complete absence of avicularia in a particular species is not sufficient reason for removing that species from an assemblage of forms in which avicularia are always present. And lastly, there may be good grounds for believing that two forms with entirely different types of avicularia are closely related, and in some cases may even belong to the same species (Harmer, 1909, pp. 723–724).

Harmer could not explain why vicarious avicularia, by their position and structure so easily comparable with autozooids and usually supposed to represent an initial stage of the evolution of avicularia, occurred in a sporadic way in unrelated genera, nor could he explain the association in one and the same colony of an avicularium of the simplest type with one of the most specialized morphology, or the fact that each kind of avicularium occurs in some species, but not all species of many distinct and not closely related genera, or the significance of the fact that certain species of a genus normally provided with avicularia may completely lack them.

Harmer speculated that the answers to these questions might come through the new science of genetics—that the variable presence and morphology of avicularia might be explained genetically by recessive alleles, by recombination, or by a combination of "allelomorphs." Harmer did not believe that the answers to his speculations would be easily obtained due to the difficulties of determining male parentage of colonies (and in fact in the recent successful breeding experiments carried out on marine bryozoans [Maturo, 1973] only the maternal parent is known).

Although Harmer's speculations on Mendelian inheritance of avicularian characteristics had little impact, later workers carried on the tradition that the motivating force for the development of such an amazing variety of form must have been natural selection, total colony function becoming more efficient by the development of zooids specialized for different functions: defense, feeding, reproduction.

The idea that specialization leads to greater efficiency in colony-level function is behind all ideas on the development of polymorphism and on increasing colony integration as an evolutionary trend in bryozoans (Boardman and Cheetham, 1969, 1973; Schopf, 1973, 1977; Cook, 1979). Much recent work on bryozoans (including my own) has focused on these ideas. However, to show that a specialization-selection argument is correct, it must first be shown that there are functions which avicularia perform more efficiently than other zooids. I review the evidence for specialized function in the next section.

REVIEW OF EVIDENCE ON AVICULARIAN FUNCTION

DEFENSE AGAINST PREDATORS

CRUSTACEANS AND POLYCHAETES: Kaufmann (1968, 1971) analyzed the bird's head avicularia of *Bugula* species, showing they should be biomechanically effective in seizing organisms either 0.5–4 mm long with many appendages, or with wormlike bodies less than 0.05 mm in diameter. He observed that the most frequently captured animals were the gammarid amphipods that commonly built their mud tubes on the lower senescent portions of colonies. The protective function, then, might be to keep the active parts of the colonies free from tube-building activities. In his observations, capture of the amphipods reduced the amount of tube building. Obviously, it would be detrimental if tubes smothered the active parts of the colonies, but how much the amphipods damage bryozoan colonies has not been demonstrated. Many of these bryozoan-inhabiting crustaceans, especially gammarid and caprellid amphipods, may be found, like those

inhabiting sea grasses or algae, to graze on epiphytes or on the particulate detritus or diatoms adhering or resting on the colonies (e.g., Keith, 1969; Zimmerman, Gibson, and Harrington, 1979). Thus, the crustaceans may actually be grooming or cleaning the colonies to their benefit rather than to their detriment.

Even avicularia seemingly well designed for grasping objects of a certain size behave inefficiently when confronted with such objects. For example, Harmer (1901) reported that he saw a colony of *Bugula calathus* capture a small nereid polychaete while holding an isopod and an amphipod crustacean with several of its avicularia. "Curiously enough, however, an avicularium did not necessarily close even when part of a captured animal was actually in its mouth. The avicularia made no attempt to place themselves in an advantageous position for catching fresh parts of the *Nereis* which they might easily have done. . . ."

PYCNOGONIDS: Though Kaufmann (1971) did not find pycnogonids on his colonies he thought the *Bugula* avicularia would be able to capture their appendages. The work of Wyer and King (1973), however, shows that while pycnogonids treat the large avicularia of *Flustra foliacea* with care, moving rapidly sidewise away from them if they move, the presence of the avicularia does not prevent the pycnogonids from feeding on the *Flustra,* which they do by facing the proximal end of the colony so that the proboscis is located between the two distal spines of the zooid just above the hinged lid of the operculum. As the operculum starts to open, the pycnogonid thrusts the tip of its proboscis into the opening and with the jaws at the proboscis tip bites bits off the internal organs of the autozooid. Wyer and King also found that the pycnogonids they observed did not feed on *Bugula,* but rather on detritus found on the colonies—when placed near an active avicularium the pycnogonid generally withdrew its palps and proboscis tips before they contacted the avicularium. When forced into contact, avicularia grasped these parts but soon released them without apparent damage; a terminal claw was caught but also released, while other appendages were too long to be grasped. The authors concluded that the avicularia did not seem to be a defense

against pycnogonids. Some pycnogonids were observed to feed on detritus in the lower senescent regions of *Bugula* colonies where avicularia are inactive; the detritus aggregates particularly around these inactive avicularia.

NUDIBRANCHS: There is no evidence that avicularia provide any defense against nudibranchs—the elaborate mandibles may prevent the avicularium from being attacked, but the attacking organism then moves over to an area of autozooids. Cook (personal commun. in Ryland, 1976) reported that avicularia of *Trematooecia* species were not stimulated by contact with nudibranchs, nor were the nudibranchs deterred by them or by the large bird's head avicularia of *Beania magellanica.*

LARVAE: Harmer (1909) thought that certain types of avicularia (those with duck-bill or spatulate mandibles, or with scissor-like mandibles with hooked ends, or mandibles of knife-blade shape) would be particularly effective against larvae of other species of bryzoans or other epifaunal organisms (serpulids, vermetids, foraminifera, sponges, ascidians, etc.). His evidence for this was that active areas of colonies of many species are clean, while senescent areas are fouled by colonies of other bryozoans, or by tubes, shells, or colonies of other organisms. However, avicularia are not necessarily inactive in senescent areas (Waters, 1889, 1904). In addition, similar patterns of fouled versus unfouled area exist in species without avicularia as well, tending to indicate that a chemical activity of the surface, or the feeding activity of zooids, or even the relative newness of the surface might discourage fouling.

Kaufmann (1971) discussed the potential of *Bugula*-type avicularia against potential foulers, concluding that they could not defend against larvae effectively, either because the larvae are small enough (1 mm or less) to avoid contact with the avicularia or because they have few appendages that could be grasped by the avicularia. He noted that for a *Bugula* avicularium to grasp the round soft body of a bryozoan larva (0.5 to 2 mm in diameter) its jaws would have to open wider than 90 degrees, severely limiting its grasping strength. This mechanical restriction would probably apply to the other avicularia indicated as well. I know of no observations

FIG. 15.   Shell of juvenile vermetid gastropod (*) which had settled on a living colony of *Parasmittina serrula* despite the presence of numerous large and small avicularia (fig. 16) (scale = 1 mm).

on interactions of avicularia with larvae except the experiments performed by Kaufmann (1971) in which he forced bryozoan larvae against a branch of a *Bugula simplex* colony. None were caught or hindered by avicularian mandibles, but some were drawn to lophophores and forcibly ejected. In fact, lophophores seemed to be more effective in discouraging larvae than avicularia.

Against shelled larvae like those of vermetids, avicularia seem particularly ineffective. Vermetid larvae (*Serpulorbis* sp.) occurring on panels in Kingston Harbour, Jamaica, were observed to drag their shells across colonies of *Parasmittina serrula* and regardless of avicularia or opercula to settle and attach (example shown in fig. 15). This association may, in fact, have benefited both parties by increasing current production, and thus, food supply. At any rate, the presence of a vermetid on *Parasmittina* colonies was very common (Winston, unpubl. data).

LARGER PREDATORS: The efficiency of avicularia as defense against larger predators or trespassers is questionable. Kaufmann's (1971) study indicates that organisms larger than 5 mm would probably escape because of their strength or because the diameter of their appendages would be too great to fit within the jaw of the avicularia.

Day and Osman (1981) have shown that juvenile bat stars (*Patiria miniata*) digested colonies of the cyclostome *Tubulipora* down to the bare skeleton, but never damaged neighboring cheilostomes. They suggest that the avicularia of the cheilostomes might have irritated the tender everted stomach of the asteroid, and the opercula (which cyclostomes lack) then protected the autozooids. But they showed no evidence that the starfish stomach was damaged by the mandibles of the avicularia. In addition, stomach tissue of an Australian *Patiria* placed on a colony of *Celleporaria fusca* (with avicularia very sim-

ilar to those of fig. 12) did not cause any reaction by the avicularia (Day and Winston, unpubl. observ.). Perhaps opercula alone provide enough protection.

Against the larger armored grazers like fish or echinoids (important predators of bryozoans according to Ryland, 1976) avicularia would be useless.

EMBRYO PREDATORS: Predation on bryozoans has been assumed to be autozooid predation, but embryos of bryozoans might also be preyed upon. Egg predation is a problem to other marine invertebrates, many of which have developed behavioral or physical methods for the protection of developing eggs. In bryozoan species which brood embryos in autozooids or gynozooids the embryos are protected by the operculum, as are embryos brooded in cleithrate ovicells (those which open to the outside through the operculum of the maternal zooid). Many other species, however, have acleithrate ovicells, protected only by a membrane. Harmer (1909) pointed out that adventitious avicularia are especially common just below and beside the operculum; the need to protect embryos as well as autozooids might explain their distribution. In many species these avicularia seem less variable in size, shape, and orientation than do those in other areas of zooids, and it is tempting to assume that this regularity is linked with an anti-predator function. But from what predators could such structures defend? Though the thick serrated edges of the rostra of these avicularia appear quite threatening (fig. 13) they are very small. Probably the only organisms such avicularia could defend against would be nematodes, very small nemerteans, or protozoans. The distributions of these organisms on bryozoan colonies, much less their tastes for embryos, are pretty much unknown (it should be noted here that in the same colony of Celleporaria whose large avicularia showed no activity against stomach tissue of Patiria, a small suboral avicularium was seen to have captured a nematode. This nematode escaped one time, was caught again, and firmly held in the mandibles for approximately three hours after which time observations were discontinued).

FOOD GATHERING: Johnston (1847) speculated that avicularia might gather food by seizing trespassing animals. This idea seemed unlikely to Hincks (1880) who argued that lophophores alone are quite effective at seizing food particles, but, in any case, the avicularia could not catch particles of the size bryozoans feed on (chiefly phytoplankton). Even if avicularian mandibles could grasp potential food objects, avicularia are located below the level of the lophophore bases, where feeding currents would be moving away from the lophophores rather than entering them. In fact, Hincks had nothing but scorn for the whole idea: "they would certainly lead a precarious existence if dependent on the chance supplies of the avicularian commissariat."

No one since then has seriously advanced the idea of a food-gathering function for avicularia, although Forbes (1933) indicated that avicularia of Bugula responded to mussel juice by an increase in the number of closures.

CLEANING

Another function that has been suggested for vibracula, as well as for avicularia with mandibles that do not appear capable of grasping, especially those that have elongated bristle-like (setiform) mandibles, is cleaning the colony. In certain genera, e.g., Scrupocellaria and Caberea, vibracula occur on every branch. They have been observed to move in unison, and it is true that the movement of these bristles in unison would be effective in cleaning the colony of large particles. In branching colonies of this type, the expanded lophophores create a strong unidirectional current through the colony branches, but large particles snagged on the lophophore bearing surfaces are usually effectively cleared by joint retraction of adjacent lophophores (Winston, 1978, 1979). In the course of several hours of observation of Florida and California species of Scrupocellaria, I observed the vibracula to move in unison many times, but never saw any object triggering that response (Winston, unpubl. observ.). This agrees with similar observations by others (e.g., Marcus, 1926).

Setiform avicularia are less common in encrusting species but they do occur, for example, in some Microporella and Escharina species. As Silén (1977) has pointed out, the long mandible and the absence of a rigid maxilla make it impossible for them to function

effectively as graspers. These avicularia have been observed occasionally to move (Cook, 1979; Jackson, personal commun.) and it is possible that they sweep particles off the colony surface.

A cleaning function has definitely been observed for the vibracula in one group of bryozoans, the free-living forms whose dome-shaped colonies are found on sandy or muddy bottoms. Cook (1963) observed that colonies of *Discoporella umbellata* (fig. 8) used the joint action of vibracula to clear the sloping colony surface of sand grains.

SUPPORT AND LOCOMOTION

Though Cook's work (1963) showed no support for the old hypothesis that lunulitiform species can row through the water using their vibracula as oars, the vibracula of this group definitely serve to support and position the colony. Colonies of *Discoporella* use their vibracula to maintain themselves above the surface of the substratum, and to return to the surface after having been buried in sediment. I have also observed that Florida colonies of *Discoporella umbellata depressa* being kept in an aquarium were able to move short distances, staying partially burrowed in the sand and leaving a furrowed trail behind them. Colonies of *Selenaria maculata* were found by Cook and Chimonides (1978) to be even more active, moving rapidly toward a light source, and even climbing over other colonies in their path.

The evidence of the previous sections indicates that avicularian polymorphs:

(1) Have never been observed to function actively in one of the activities attributed to them: capturing food for the colony. Of course, this hypothesis actually has had very limited support, though it was mentioned by Darwin (1872).

(2) Two other functions, defending and cleaning colonies have been supported in the literature for the past century, but, with the exception of the bird's head type, avicularia have not been observed to function in active mechanical defense of bryozoan colonies against trespassers or predators.

(3) Even for those of the bird's head type the efficiency of their grasping actions or

movements as a defense against predators is questionable. Probably, as Hincks (1880) suggested, they are more like the scarecrows of the colony than its weapons. Their activity might frighten away a percentage of possible predators, but their numbers are too low (in proportion to autozooids) and their movements too erratic to be very effective protection.

(4) With the notable exception of the clearing of lunulitiform colonies of sand grains, there is no evidence to show that avicularian polymorphs are as effective in cleaning colonies of debris as is the action of water currents created by the lophophores, or perhaps even the grooming activities of the small crustaceans they have been supposed to protect against.

What do avicularia do then? Previous authors have assumed their specialized function was related to active opening and closing of the mandible in response to some need of the colony, but behavioral observations on Caribbean species (see Appendix) as well as the negative evidence accumulated in the literature suggests that avicularian mandibles stay open, unless they must close to protect the avicularian zooid itself, and that once closure has occurred they reopen as rapidly as possible. All observations on living colonies were, of course, made when either no or only a few lophophores were expanded, as when all lophophores of the colony are expanded, the avicularia, being below the lophophore bells, are invisible from above. It is still possible, therefore, that avicularia perform only when lophophores are expanded (in which case no one has observed their true behavior). When lophophores are expanded observations on avicularian behavior would be very difficult, though it should be possible to position colonies at an angle in a flat-sided glass or plastic tube, so that avicularia could be observed in side view at the necessary 50 to 100× magnification. However, both *Bugula*-type avicularia and vibracula perform their movements readily when the lophophores are retracted, and it seems reasonable to assume that other types of avicularia do the same.

If the position in which the avicularia perform their colony role is with mandible open, then several activities compatible with this

behavior should be considered further: nutrient storage, respiration, chemical defense, and enhancement of water flow.

NUTRIENT STORAGE

Cook (1979) suggested storage of nutrients as an additional or alternative function for zooid polymorphs. For avicularian polymorphs there is no evidence regarding this hypothesis. Avicularia of a few species possess functional polypides and presumably do their share to feed the colony directly. There are no reports of avicularia containing the granular starchy-looking material that has been noted in some autozooids of overwintering or oversummering colonies of certain species (Winston, 1982). Communication pores connect the avicularia with other zooids. It has been observed that under severe environmental conditions (e.g., starvation) all but a few functional polypides of a colony may degenerate, leaving zooids empty except for a brown body (Dudley, 1974; Cummings, 1975). There is no reason why the contents of avicularia could not be distributed to other areas of the colony under such conditions, but there is no evidence that they are.

RESPIRATION

A respiratory function for avicularia has been suggested several times. Waters (1889, p. 27) stated that, "It has always seemed to me that we must look for the explanation of the function of the avicularium in the mass of parenchym or endosarc [=the polypide rudiment and funiculus], for the avicularia remain in activity when the polypides have all disappeared, and in this way the tissues of the colony are indirectly in communication with the surrounding water, so that oxygenation takes place and the colony is kept alive." Waters developed this idea further in 1904:

> The polypide dies down from time to time, and a colony may be left with few or no active polypides. It remains in vigor, through the avicularian organs retaining vitality, and thus keeping the protoplasmic parenchyme in indirect communication with the external surrounding . . . the vitality of the colony will, both in times of full and diminished vigor be increased by the avicularia; for the constant snapping of the man-

dibles often continues when the polypides are not extending themselves out of the zooecia, and, as said before, even when there are few or no polypides. Sections often show the avicularia in unchanged condition, when the zooecia only show hydrolysed remains of polypides.

Obviously, any membranous surface would aid respiration, but there is no evidence for avicularia flapping back and forth like gills to promote respiration, and though Waters does not mention what species his histological sections were from, only the bird's head avicularia show such constant snapping.

Canu and Bassler (e.g., 1920, p. 61; 1928, p. 37) elaborated this respiratory function into a hydrostatic function—but what they meant by this is unclear as there is no way in which avicularia could affect the action of the hydrostatic system that I can see. In *Reptadeonella,* one of the examples they give, though the mandible of the open operculum covers the opening (the spiramen) to the hydrostatic system, its closure and opening had no relationship to polypide movement (Appendix and fig. 23).

CHEMICAL DEFENSE

Chemical defense has been suggested by Lutaud (1969) and Schopf (1977). The little work that has been done on chemicals produced by bryozoans suggests that they may indeed produce powerful substances. Christophersen and Carlé found that *Flustra foliacea* colonies contained an allelochemical mixture of monoterpenes, as well as a mixture of brominated alkaloids (Christophersen and Carlé, 1978; Carlé and Christophersen, 1979, 1980).

Marine alkaloids are uncommon (Fenical, 1982), but probably very active. If avicularia produced such substances they might be released slowly and constantly into the water as a warning to approaching predators (as has been suggested for toxins produced by other groups of marine organisms, e.g., sponges [Green, 1977]). A slow release of a noxious chemical in the vicinity of embryos and lophophores might make them less inviting to predators.

Monoterpenes have been shown to have some anti-insect (and therefore anti-arthro-

pod, e.g., crustaceans and pycnogonid), antiseptic, antibacterial properties. The presence of such compounds in *Flustra foliacea* is especially interesting in view of the work of Al-Ogily and Knight-Jones (1977) who found antibiotic activity in its fronds. This antibacterial activity did not occur at the growing edge of the frond, but was usual in its older portions. (Note that Stebbing [1971] showed the larvae of *Scrupocellaria reptans* to settle preferentially on the distal ends of *Flustra* fronds.)

Recent histological work by Lutaud suggests the possibility that chemical production could be localized in avicularia. Waters (1889) was the first to observe, in the suboral avicularia of a species collected by the *Challenger* Expedition, *Lepralia margaritifera,* the occurrence of two glandlike bodies. He described these features further in later papers (1892, 1904, 1909). On the basis of microscopic sections they appeared to him to be hollow bodies attached to the sheath containing the polypide rudiment. Waters considered the avicularian glands homologous to the suboral glands he had described in autozooids of a number of species, but did not speculate on their function. Lutaud (1964, 1965, 1969) studied both autozooidal vestibular glands and avicularian glands using modern histological methods. She found that they consist of thin cellular pouches derived from an outpocketing of the tentacle sheath of the polypide or polypide rudiment. The inside of the glands is filled with a protidic or mucoidic substance, considered to be a product of the gland itself, and also contains rodlike or threadlike bacteria. According to Lutaud, these bacteria are nonpathogenic and species specific. They occur in many anascan and ascophoran cheilostomes. They do not occur in cellularines, but in many cellularines there are "funicular bodies"—cellular pouches filled with bacteria and attached to the strands of the funiculus (Lutaud, 1969).

In some coelenterates host-specific bacterially produced toxins have been identified. Sea anemones produce cytolytic toxins (presumably derived from nematocysts) which resemble certain bacterial toxins (Bernheimer and Avigad, 1976). Recently the structure of one of the most deadly coelenterate toxins, palytoxin, was isolated (Moore and

Bartolini, 1981). A 1981 National Science Foundation press release reported that Dr. Gregory Patterson discovered that the toxin, which occurs in a Hawaiian zooanthid, is produced by bacteria that live symbiotically with the zooanthid. Whether the host-specific bacteria found in vestibular or avicularian glands also produce cytolytic toxins remains to be seen. There has been no work on isolation of such substances from bryozoans.

LARVAL INOCULATION

In fact, avicularian bacteria may not be used to produce toxins at all, but may play a quite different role. Woollacott (1981) reported that larvae of *Bugula* carry their own bacteria with them, dumping them out to prepare the substratum surface as they settle upon it. A possibility, especially for the suboral or circumoral avicularia, might be that they host such bacteria. As the developing egg passed from the body cavity of the fertile zooid into the ovicell it could be inoculated with its own supply of bacteria from the adjacent avicularian glands.

CURRENT BAFFLES/TRASH CHUTES

If many frontal avicularia acted merely to enhance current flow, their lack of strongly grasping mandibles, their normally gaping position, their often sporadic (both within and between species) distribution, and their variable positioning would be explained. The chief problem with this hypothesis is that most avicularia do not reach the level of the lophophores. Instead they lie beneath the lophophore funnels among the introvert stalks that bear them, and it is difficult to see how they could channel incoming currents. Anyway, these currents seem to be handled quite efficiently by the lophophores themselves, as well as by the topographic patterning of raised and hollowed surfaces of the skeleton (as pointed out by Cheetham, 1968; Cook, 1977; Winston, 1978, 1979).

However, Lidgard (1981) has shown the existence of strong currents just above the colony surface, created by the force of water exiting between the tentacle-bases of the lophophores. This water, carrying with it rejected food particles, fecal pellets and debris, passes over the colony surface and exits at
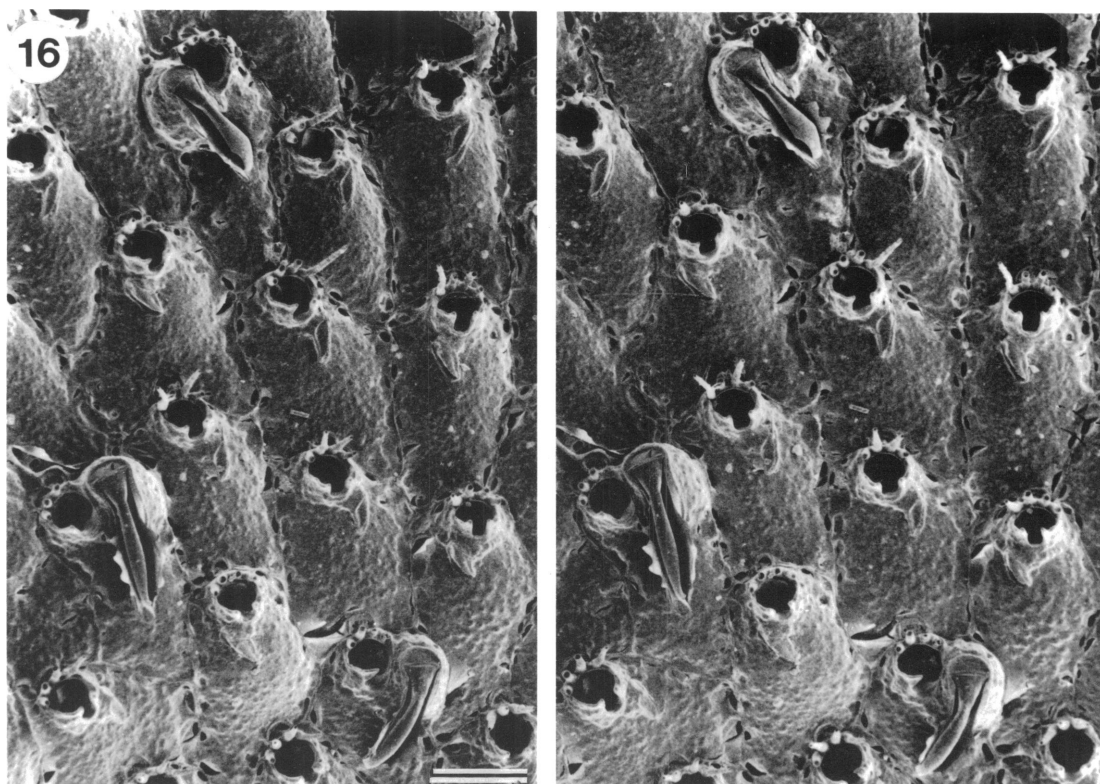
FIG. 16.   Stereo pair of small area of a colony of *Parasmittina serrula* (Jamaica), showing pinball positioning of avicularia (scale = 200 μm).

colony margins and excurrent chimneys with considerable velocity.

Thus, it is possible that avicularia act as current baffles, turning these sub-lophophoral pathways into more efficient trash chutes—keeping colony surfaces clean, preventing pile-ups of debris, and perhaps shuttling trespassers and potential predators more rapidly along, so that they are removed from the colony before causing any damage. Cheetham (1968) thought avicularia of *Metrarabdotos* species might function in zoarial sanitation. Examination of the colony surface of some encrusting species (e.g., *Parasmittina*, fig. 16) cannot help but evoke the same point of view—the knobs of the avicularia resemble those of an old-fashioned pinball machine, and seem well placed to create current channels. While it would be difficult to test this current baffle hypothesis, it should be possible to do so, either by microcinematography or by enlarged models in flow tanks.

DISCUSSION

The traditional view has been that avicularian polymorphs must be defensive structures. The evidence gathered here indicates that many observers failed to see them performing active defensive functions, and presents other possible functions based on their observed behavior. At present, however, while observations support some of these possibilities, no direct experimental evidence compels us to believe that they perform any of those putative functions. Avicularia are such varied and beautifully complex structures that it is difficult for a biologist not to believe that their design must in some fashion better equip the colony for survival. Kaufmann's study of *Bugula* and Cook's work on *Discoporella* and *Selenaria* have shown uses for two types of polymorphs. More careful studies of avicularian behavior in living colonies will no doubt elucidate uses of some

other types of avicularia. The fact remains, however, that only for the vibracula of lunulitiform bryozoans and the pedunculate avicularia of *Bugula* is there good evidence for an adaptive function (and in the case of *Bugula* it does not seem to be carried out with much efficiency). With respect to other types of avicularia (and that means most avicularia known) our understanding has not advanced since Darwin's or Harmer's time.

Recent controversy has made it more difficult for biologists to argue that all evolutionary phenomena can be explained by natural selection, or that because all organisms have evolved by natural selection they are all adapted, or that all their characters are equally well adapted, or that if one or the other is poorly adapted, it is due to some kind of trade off—some "optimal compromise," necessitated by genetic or developmental pathways. As Reed (1981) pointed out this consequence could not follow from natural selection unless the ability to use environmental resources in itself necessitated increased reproductive success—and vice versa, a necessity not implied in the theory of natural selection. Since the adaptationist approach to avicularia has shown so little result, rather than exhorting people to go out and try to demonstrate the ways that avicularia make bryozoan colonies better adapted, I would like to recommend an alternative approach.

The general pattern of production of avicularia may not be a direct adaptation at all, but instead might be better understood as a fabricational phenomenon (in the sense of Seilacher, 1970, 1972, and of Gould and Lewontin, 1979), resulting from architectural constraints implicit in the budding method of bryozoans. Avicularian polymorphs may occasionally be used to beneficial effect (as the exaptations of Gould and Vrba, 1982), but their presence and pattern cannot be understood by viewing the secondary adaptations as the reason for the pattern itself.

One of the fundamental characteristics of bryozoans is that their colonies are produced by asexual budding of new zooid units from the first sexually produced unit (the metamorphosed larva). In budding the connections between new units are not through open holes (as in coelenterates), but are tissue-mediated, through communication pores, pore plates, and pore chambers (which according to the opinions of some authors (Silén, 1977; Gordon, 1971) are themselves zooid polymorphs). Much of this potential for budding must be suppressed entirely or the developing colony would force itself chaotically apart. If a zooid buds a little, the result is a fluid and funicular-thread filled bubble called a kenozooid. If the bud gets a little larger (and perhaps if some other factor is triggered), the result is an avicularium. In other words, *bryozoans make avicularia because avicularia are what bryozoans can make,* or in more general terms because buds are what bryozoans can make.

Silén (1977) pointed out that the distolateral or primogenial budding which predominates in gymnolaemate bryozoans results in the basic quincunx or brick-work arrangement, whereby in each row of zooids each of the zooids has its distal half on the level of the proximal half of the zooids in adjacent rows. When the growing colony widens, however, and there is space for a row to divide, the last zooid in the undivided row buds one distal daughter zooid of normal length and a more lateral zooid which is dwarfed to a varying degree. This pattern restores the quincuxial arrangement. In many cases in encrusting bryozoans the smaller distolateral zooid becomes a polymorph, therefore, in bryozoans, "asexual polymorphs resulting in dwarf zooids are induced regularly by genetically fixed laws of astogeny."

Silén (1938, 1977) found that in *Flustra foliacea,* buds down to a certain size became avicularia. Those below that size became kenozooids. With increasing restriction of body-volume either the polypide bud and associated organs were not formed at all, resulting in a kenozooid or were hampered and transformed, resulting in an avicularium.

According to Silén, essentially the same phenomenon takes place in even more strictly programmed erect colonies. All zooid rows have the potential to form new lateral rows. The development of a particular colony form depends on the suppression of a certain number of rows—either completely or partially, in which case the dwarfed buds produced differentiate as kenozooids or avicularia.

Frontal avicularia, which have seemed to some authors to be very far removed from

normal zooids, can also be explained as functions of budding (Banta, 1973a, 1973b; Silén, 1977). This budding, a form of the frontal budding which emanates from the hypostegal coelom in species with complex frontal skeletons, also appears linked with the production of adventitious avicularia. Banta (1973b) has shown two ways in which these avicularia might have evolved, either suddenly, as a consequence of frontal budding, or slowly, by the gradual reduction in size of the interzooecial avicularium just distal to a zooid row bifurcation and its removal up the transverse wall of the parent autozooid, the primogenial bud in this way dividing into two buds. That avicularia produced in this manner would be located in the very common lateral-oral position is evidence for this hypothesis, but both methods might have evolved in various cheilostome lineages.

Avicularia may have become secondarily adapted to perform various functions with varying degrees of efficiency. Avicularium-like structures are not necessarily the best that could be constructed for cleaning and defense, but cheilostome bryozoans are limited to structures composed of zooid components. Their colonies cannot produce brooms, or garbage trucks, or build better crustacean-traps—they can only make avicularia.

Two authors (Silén, 1977; Banta, 1973a, 1973b) have come close to stating this hypothesis. In fact what Silén said of the interzooids could apply also to avicularia, "Are all these complicated arrangements . . . expressions purely of laws of colonial architectures. To speculate: Might such expressions represent a primary necessity of the ordinary zooid to form buds along the sides of its distal half? Whereby the possibility remains that each bud is capable of forming a complete zooid if space permits" (Silén, 1977, p. 207).

What evidence is there that avicularia are a consequence of the basic body plan of cheilostome bryozoans? Budding is basic to the bryozoan body plan in general, and budding with the development of communication pores is basic to the gymnolaemates (ctenostomes and cheilostomes). One of the basic innovations of the cheilostomes is the operculum, the hinged trapdoor above the tentacle-sheath. As kenozooid formation is a consequence of budding, avicularium formation may be a consequence of budding once an operculum has been integrated into the system.

To parallel Seilacher's (1972) arguments for the divaricate pattern of mollusks being the result of architectural constraints, *the necessary consequences* of the materials and design involved in their basic body plan, the following arguments can be made for bryozoans:

FIELD OBSERVATIONS

Both (a) those observations that have shown lack of supposed functions for avicularia, or their positioning in the colony in places where they could not carry out those functions, or where their carrying out the functions would be of no use to the colony; and (b) those which have shown many or all avicularia of a colony to be completely non-functional in the sense that mandibles are lacking and the frontal area is completely membranous. Many examples could be cited, e.g., *Phylactellipora aviculifera* (fig. 19) which in spite of its name has a sub-oral chamber with a membranous covering and no hinge or mandible (Winston, 1982) or *Nellia tenella,* in which, except for the subspecies *N. t. quadrilatera,* the avicularia often lack mandibles (Harmer, 1926) or several *Reptadeonella* species in which autozooids have avicularia with mandibles, but gonozooids have more often just membrane-covered pockets (Winston, unpubl. data).

PRESENCE IN OLD OR PATHOLOGICAL INDIVIDUALS: Hincks (1880) gives an illustrated example of a case in which an avicularium developed ovicells. Other cases have been noted of avicularia budding avicularia or developing inside a broken zooid (Levinsen, 1907). Figure 18 illustrates an area of a colony of *Orthoporidra compacta,* an Antarctic cheilostome, in which tubular peristomial avicularia have sealed off autozooid orifices. Colonies of this species often have large portions of their total area blocked in this inexplicable fashion.

APPEARANCE IN RESPONSE TO INJURY (ACCIDENTS IN REGENERATION): Avicularia often appear where the morphogenetic program has gone wrong—in response to substratum disturbance or to injury. In such cases they are
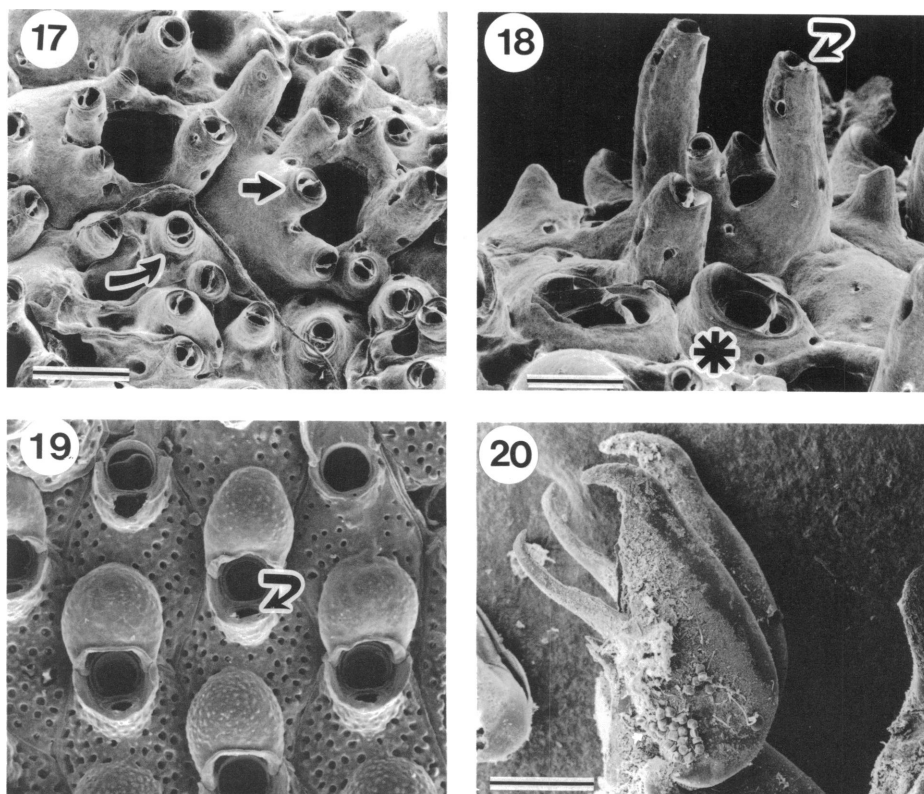
FIG. 17.   *Orthoporidra compacta* (Antarctica), showing autozooid orifice surrounded by tubular peristomial avicularia (arrow) with masses of avicularia of the same type filling in and obliterating other autozooid orifices (scale = 200 μm).

FIG. 18.   *Orthoporidra compacta:* Side view of tubular avicularia of same colony (arrow) and larger interzooecial avicularia (*) (scale = 200 μm).

FIG. 19.   *Phylactellipora aviculifera* (Florida), showing openings (arrow) of mandible-less suboral "avicularia" (scale = 100 μm).

FIG. 20.   *Beania magellanica* (Antarctica), showing twinning of a pedunculate avicularium (scale = 200 μm).

functional in the sense of repairing and maintaining the integrity of the colony surface, but totally nonfunctional in any adaptive sense. Sometimes the patterning of such areas seems to have gone hopelessly awry, as in the colony of *Reptadeonella bipartita* illustrated in figures 21 and 22, in which zooid fragments without orifices or spiramens have regenerated numerous avicularia.

VARIABILITY IN PATTERN AND MORPHOLOGY: Many authors have remarked on the variability of avicularia both in morphology and distribution within and between colonies, e.g., Harmer (1909), as quoted earlier. Such "excessive variability compared with much reduced variability when the same structure assumes a form judged functional on engineering grounds" (Gould and Lewontin, 1979) has been judged evidence for a nonadaptive pattern (Seilacher, 1972; Gould and Lewontin, 1979). This variability could turn out to be environmentally induced (e.g., Powell and Cook, 1966), but as Silén (1977) remarks, "this deformation of polymorphs by extrinsic forces is a secondary phenomenon, occurring as it does only in forms also possessing the same polymorph types induced by the regular forces inherent in the colony structure."
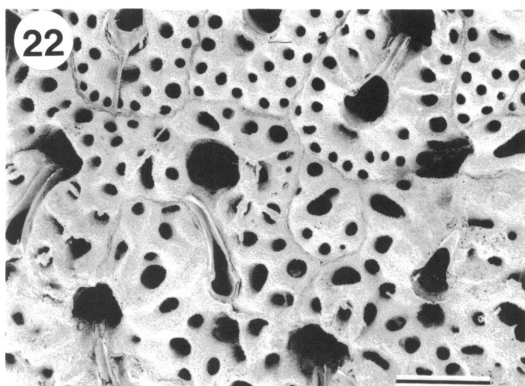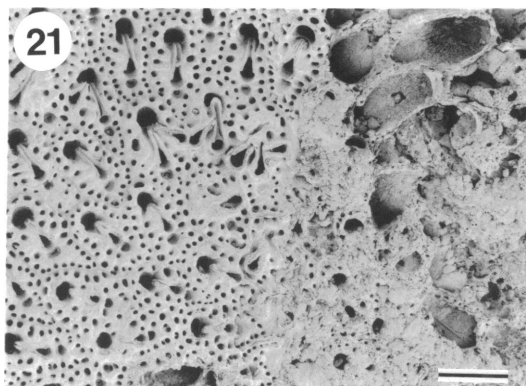
Waters (1900) commented on the vari-

FIG. 21.   *Reptadeonella bipartita* (Puerto Rico): Portion of an injured and partially regenerated colony showing proliferation of avicularia in other than normal position during the repair process (scale = 400 μm).

FIG. 22.   *Reptadeonella bipartita:* Closeup of another area of the same colony showing mistakes during repair. From left to right—slightly enlarged and distorted autozooid, small kenozooid with no orifice or avicularium, larger kenozooid with avicularium but no orifice and (upper right) undamaged autozooid with suboral avicularium in normal position (scale = 200 μm).

ability of avicularian mandibles in contrast to the invariability of opercula. Opercular (orificial) measurements seem to be both less variable than other skeletal parameters and highly correlated with lophophore characters (Winston, 1981). Cheetham (1966) found length of avicularia in Eocene cheilostomes to be so variable as to be almost taxonomically useless, but, in these fossils, some of the variability may have been due to breakage.

TESTS OF HYPOTHESES

Many aspects of avicularian polymorphs make it seem that their general pattern of morphology and distribution may not be directly adaptive at all. Avicularia may not, or may only rarely, be directly important in optimizing survival of cheilostome bryozoan colonies. They may, rather, be best understood as fabricational phenomena resulting from fundamental architectural (developmental) constraints on the budding process. Studies of these constraints are essential if we are to understand the evolution of polymorphs in cheilostome bryozoans and if avicularia are to become useful characters in a phylogenetic systematics of bryozoans. There are questions we can ask to test that assumption, but before those questions can be considered there is basic information we

need in order to evaluate the importance of either hypothesis.

Our knowledge of avicularian development and morphology is still based on very few studies. One of the first priorities is a broad comparative study of the internal and external morphology of the various types of avicularia that have been described. Even now the terms vicarious, interzooecial, and adventitious are used in different ways by different authors. A clear understanding of the different types of avicularia can only come through an understanding of the way in which they are formed (budded) by the colony. Vicarious avicularia are produced by the basic distolateral budding process, but there may be a real difference between those vicarious avicularia that are smaller than autozooids and lack polypides, and those that are larger and possess them (e.g., *Steginoporella* spp., *Membranipora annae*). The term interzooecial has been used for various intermediate forms. "Interzooecial" avicularia of the *Cribrilaria* type (fig. 10) might actually be an innovation of "reticulum zooids." Jebram (1978) has shown how the reticulum zooids of *Conopeum reticulum* can become enlarged and develop opercula and feeding polypides under a certain nutritional regime. Other "interzooecial" avicularia found in ascophoran colonies (e.g., fig. 12) are produced by frontal

budding. In these avicularia and in adventitious avicularia a reversal of polarity compared with the zooid from which they are budded may occur—but is this reversal of polarity only possible with frontally budded avicularia? Finally, there are exceptional avicularia in which no connection with any communication pore has been discovered (Silén, 1977). How can these be explained?

The next step is the analysis of the pattern of occurrence of avicularia within the various groups of cheilostomes, in particular to distinguish those cases in which avicularia vary little in occurrence, position, size, and orientation from those in which they are variable.

We also need to analyze the development of these polymorphs over time. Morphological studies on Recent forms should make it possible to deduce some information about mandible morphology from skeletal remains—by study of muscle scars left by mandible muscles of different shapes and sizes. In spite of arguments postulating gradual evolution of more and more specialized avicularia reaching their greatest perfection in the pedunculate type, several types of avicularia did appear very early in cheilostome history (Dzik, 1975). Interzooecial avicularia did occur first, but both interzooecial and adventitious types were present by the upper Cretaceous. Spatulate and triangular shapes appear quite early in cheilostome evolution. It may turn out that similar avicularia rather than developing gradually more specialized patterns originated separately in a number of lineages. Studies by Cheetham (1968, 1973) have shown that within some Late Cretaceous–Tertiary lineages polymorphism has increased over time, whereas in others it has decreased, and in some it has first increased and then decreased. It was especially puzzling to Cheetham (1973) why lineages with increasing and decreasing polymorphism commonly are found together in the same habitats. To learn the distribution of such patterns and what meaning they might have, more studies of this nature are necessary.

Very few cheilostomes lack avicularia entirely and even those that do almost universally retain the ability to form kenozooids, though their production may be rare or sporadic (Boardman and Cheetham, 1973).

Maybe we should be asking what are the genetic constraints on the development of polymorphism. In what cases is production of avicularia genetically controlled? Can their presence be eliminated by breeding experiments or mutations? It should be possible (though certainly not easy) to test genetic constraints on polymorphism. Bryozoan breeding experiments present difficulties (due to the fact that cheilostome colonies have many eggs, all of which might be fertilized by sperm from a different colony, making only knowledge of maternal inheritance possible), yet progress has been made with such studies (Maturo, 1973).

Tests of developmental constraints might also be possible. In rotifers three female morphotypes, differing in size, shape, behavior, physiology, and ecology are produced by genetically identical females. This extreme polymorphism has been shown to depend on amounts of tocopherol (vitamin E) in the diet (Gilbert, 1980). Investigation of changes produced in cheilostome colonies by different levels of metabolically active chemicals are certainly feasible, and considering the effects of diet on colony morphology that have already been demonstrated (Winston, 1977; Jebram, 1978) would probably be productive.

Another so far unutilized approach is morphogenetic analysis of the changes in shape that take place in the transition from autozooid to avicularium. How much variation can be accounted for allometrically, and how much necessitates an additional factor? The question of the origin and meaning of round or triangular mandibles has been argued for years (Harmer, 1909; Schopf, 1973, 1977), but it might be more productive to investigate the developmental allometry of kenozooidal-avicularial budding and mandible production, rather than postulating adaptively derived integration series and then attempting to make the observed variation fit the scheme. Or maybe we should be asking not why avicularian mandibles are so varied in shape and size, but why opercula are so little variable? Does the occurrence of regularly patterned and sized avicularia (as with many of the pedunculate or lateral-oral types) indicate an adaptive function for them? In summary, the adaptationist orientation of most bryozoologists over the last hundred

years, though often productive with regard to other problems, has produced little evidence to explain the occurrence of avicularia in cheilostome bryozoans. Perhaps the basis of the polymorphism is not ecological but developmental. Developmental constraints seem, as Gould and Lewontin (1979) stated, to be "a most powerful subcategory of phyletic distinctions," and a thorough evaluation of their role in the evolution of avicularian polymorphs is long overdue.

APPENDIX: OBSERVATIONS ON CARIBBEAN SPECIES

Cook's work (1963) demonstrated that *Discoporella* vibracula respond rapidly to mechanical stimuli, light pressure of a brush causing them to close strongly on brush hairs so that the colony could be lifted above the water surface. The colonies also showed considerable colonial integration of this response. However, observations on living avicularian polymorphs of other types appeared to be quite limited. An obvious step seemed to be to test avicularia for response to mechanical stimuli: light pressure of brush, sharp point pressure of needle, and response to contact by motile organisms, including possible predators.

A two-week stay at the Smithsonian Institution field station at Carrie Bow Cay, Belize, gave me the opportunity to make observations on the avicularia of common species from reef and mangrove environments.

The animals and their substrata were collected by SCUBA diving and placed in holding tanks. Observations were made within one to six hours of collection. As I was previously successful in observing feeding behavior in living colonies of bryozoans (including some of the same species) I expected to see a great deal of activity. The results showed something quite different.

Reptadeonella sp. (fig. 23): The suboral adventitious avicularia of *Reptadeonella* have a very delicate and flexible mandible. In living colonies the normal undisturbed position of the avicularia was open and motionless, with mandible held at about a 15-degree angle from the colony surface. Rapidly brushing a colony with the bristles of a camel's hair brush caused all the avicularia to close. They stayed closed only a few seconds, then slowly opened. A needle prick sometimes caused a mandible to close, but closure did not consistently occur. Closure was more readily triggered when the needle touched the junction between mandible and frontal membrane than when it touched the outer part of the mandible or the frontal membrane itself. These avicularia did not seem to have sensory bristles of the *Bugula* type.

A few motile organisms were observed on *Reptadeonella* colonies. A nematode skirted the margin of one colony and ostracodes crept around the zooid surfaces, but none made contact with avicularia. A small transparent polychaete crawled on zooid surfaces, starting over an open avicularium (which did not move), then turning around. On a second colony an artificial worm (a piece of thread tied to a stick) was dragged over zooid surfaces, but caused no movement of avicularia. A small orange polychaete placed on the colony crawled back and forth over the surface (including the avicularia), but did not trigger movement. *Reptadeonella* sp. zooids have hoodlike peristomes around the orifices. These are frequently inhabited by bright orange harpacticoid copepods. When the copepods leave the peristome and crawl over the colony surface they move chiefly in the crevices between zooids, but even when they crawl over an avicularium it does not close.

A sharp vibration (made by moving the coral substratum or by jarring the lab bench on which the dish and microscope stood) sometimes caused closure, but the effect was not consistent.

In summary, closure of the avicularia of *Reptadeonella* was difficult to effect except by a direct jab at the junction of mandible and frontal membrane. When the mandible lies open it covers the spiramen, the opening to the hydrostatic system of this species. If the presence of the open mandible protects the spiramen area this could explain its closing only under extreme duress. The movements of polypides, however, were not connected to movements of the avicularia.

Hippopodina sp. (fig. 25): Zooids possess one or two lateral-oral adventitious avicularia with very thin delicate triangular mandibles. In the colonies examined these remained in an open position, and closure was even more difficult to trigger mechanically than in *Reptadeonella*.

Cleidochasma porcellanum (fig. 24): The adventitious avicularia are very small (about 50 × 100 μm). No movement of mandibles could be detected when the colony was bumped or jarred, or when avicularia were jabbed with a needle.

Trematooecia aviculifera (fig. 5): This species possesses two types of avicularia, small adventitious avicularia which occur suborally, and at least in old frontally budded colonies, may also be found immersed in the heavy calcification of the frontal wall. Larger interzooecial avicularia are scattered
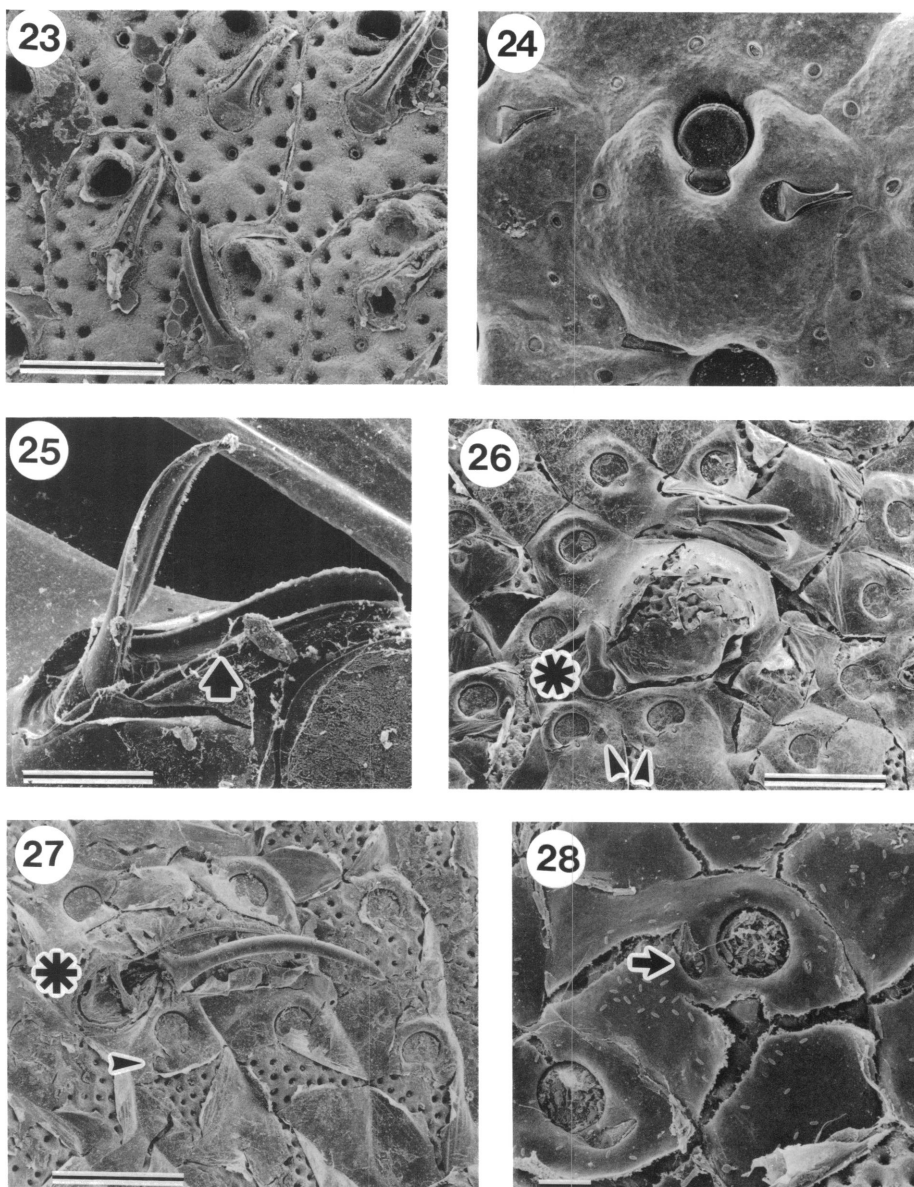
FIG. 23. *Reptadeonella* sp., showing delicate and flexible mandibles (partially destroyed here even though processed by critical point drying). In life mandible lies open over spiramen as in zooid at left (scale = 400 μm).

FIG. 24. *Cleidochasma porcellanum*, showing triangular adventitious avicularium (scale = 200 μm).

FIG. 25. *Hippopodina feegeensis*, showing lateral-oral avicularium with curved mandible and fringed edge (scale = 100 μm).

FIG. 26. *Stylopoma spongites*, showing two spatulate avicularia (*) located near an ovicell (center), and small triangular adventitious avicularia (arrow) (scale = 400 μm).

FIG. 27. *Stylopoma spongites*, showing scimitar-shaped interzooecial avicularium (*) oriented perpendicular to the growth direction of the colony and small adventitious avicularia (arrow) (scale = 400 μm).

FIG. 28. *Schizoporella pungens*, showing small lateral-oral adventitious avicularia. Though outer cuticle has cracked in processing, convexity of surface surrounding avicularium can still be seen (scale = 100 μm).

between autozooids. On these I was able to trigger closure in response to both brush and needle, but movement was sluggish. Rapid brushing of the small avicularia caused them to close, but otherwise mandibles stayed open, not flat against the frontal membrane of the socket, but slightly raised. In this species the opening to the ovicell is not protected by the operculum of the fertile zooid, and there is a membranous window in the center of the ovicell roof; this membrane was easily torn with a needle and the embryo punctured and squashed without provoking any reaction from the surrounding avicularia.

Stylopoma spongites (figs. 26, 27): Three types of avicularia occurred in *Stylopoma* colonies. Two types were interzooecial, one having a very long triangular mandible and one with a spatulate mandible. Very small adventitious avicularia usually occur beside orifices. Some colonies also have tiny avicularia on the surface of the ovicell, but these were not present in the colonies examined. The spatulate (fig. 26) avicularia had strongly chitinized mandibles which curved under at the sides like claws. A spot on the frontal submandibular palate next to the hinge-line had an orange tinge and protruded a bit. It may have marked the opening to the sheath of the polypide rudiment or a sensory tuft. These avicularia closed on a needle when sharply jabbed in the vicinity of this spot, and the grasp was almost strong enough for the colony to be lifted from the bottom of the dish (coral substratum and all), but mandibles released almost immediately, returning to an open position. Holding the brush tip down and allowing the ends of the bristles to dance lightly up and down (in imitation of polychaete setae) eventually caused mandibles to close, but they opened again immediately. Dragging one or several hairs of the brush across the avicularia did not cause movement. A nematode, a polychaete, and a small copepod walked over the colonies without triggering any action from the avicularia.

The small avicularia of *Stylopoma* (figs. 26, 27) could not be observed using the dissecting scope; it was not possible even to tell if they normally remained open or shut.

The spatulate avicularia were oriented parallel to the colony margin, suggesting a possible current baffle function. Even putting pressure directly on the frontal membrane did not trigger closure of these avicularia.

Smittipora levinseni: The avicularia of *Smittipora* were the only ones observed that did react rapidly to disturbance. Brushing the colony surface or jarring the colony caused a whole group of avicularia to reverse direction simultaneously. Closure could also be induced by a needle point, and the pressure did not have to be adjacent to the hinge area to be effective. Poking in the operculum of a fertile zooid twice caused the mandible of the nearest avicularium to swing over and catch the needle. Though the embryo being brooded just below the operculum was destroyed both times, a smaller predator might have been trapped by this method.

Schizoporella pungens (fig. 28): This species was obtained from mangrove roots at Twin Cays. Though it forms massive frontally budded colonies, its structure was fragile in comparison with those of undercoral species (Best and Winston, MS.). The calcification was like ice crust, brittle and easily crushed, and the outer membrane was very delicate, easily punctured and torn with a needle, and as it tore, opercula and avicularian mandibles were ripped off with it.

Small avicularia occurred on either side of the orifice. These closed in response to rapid brushing; they responded reluctantly to needle jabs and jarring of the colony. Two size groups of harpacticoid copepods occurred on the colonies. The small ones moved chiefly in the grooves between zooids, the larger ones moved across the zooids. The copepods, ostracodes, small gastropods, and ciliates walked across the zooids, and accordion-chains of diatoms moved back and forth in the grooves and on zooid surfaces. None of the motions of these organisms triggered closure of the avicularia. When a colony was alive, its outer membrane was quite inflated, and avicularia were sunken in this inflated surface so that they were themselves protected; an animal would have had to step or fall right into one in order to trigger it. In the growing margin zooids were relatively flat-surfaced and lacked avicularia. In the adjacent inner region avicularia were present. Avicularia were larger around the raised bumps marking excurrent chimneys. Areas of secondarily frontally budded upright zooids with ovicells did not generally have avicularia.

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