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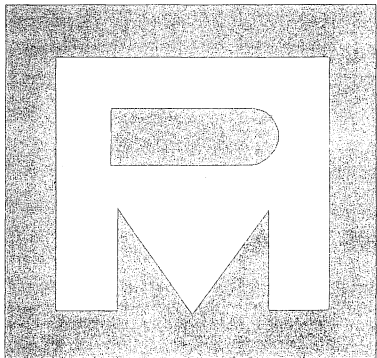
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**THE FORM AND FUNCTIONS OF THE
AVICULARIA OF BUGULA (PHYLUM
ECTOPROCTA)**

KARL W. KAUFMANN





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THE FORM AND FUNCTIONS OF THE AVICULARIA OF *BUGULA* (PHYLUM ECTOPROCTA)*

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ABSTRACT

The most important function of the bird's head avicularium of *Bugula simplex* and *B. stolonifera* is that of reducing the tube-building activities of amphipods. These avicularia would probably also be effective in reducing predation by animals of such a size and shape that could be readily seized. That the avicularium is well adapted to such functions is indicated by:

- 1) the structurally sound design that maximizes the force that can be applied for the least amount of material;
- 2) the arrangement of the musculature that increases the ability to grasp objects of small diameter;
- 3) the reaction to mechanical stimuli, namely, nodding and closing the mandible;
- 4) the placement of avicularia on the colony in positions where they can easily seize crawling organisms. Animals effectively seized by avicularia are those that crawl over the colony and are 0.5 to 4 mm long with either many appendages or wormlike bodies less than 0.05 mm in diameter. Most animals outside this range of size and shape, including most potential predators and larvae of fouling organisms, are inhibited very little by *Bugula*-type avicularia.

*Publication No. 85 from the Center for Marine and Environmental Studies, Lehigh University.

INTRODUCTION

Avicularia are modified individuals of an ectoproct colony; they have greatly enlarged opercula and greatly reduced polypides. They are confined to the Cheilostomata, the most diverse of the three Recent ectoproct orders, where they occur in a majority of the families. There is a great diversity of types of avicularia. The shapes of the mandibles vary from broad and spatulate to narrow and pointed, and may vary in size by a single order of magnitude (Fig. 1). Even for similarly shaped mandibles, the form of the entire avicularium may vary drastically (Fig. 2).

Three primary functions have been suggested for avicularia of all types (Table 1): food gathering, defense and the creation of water currents. Some of the references have been to specific types of avicularia, commonly to those found on *Bugula*, but often all types were implied to have the same function. Hincks (1880, p. lxxviii)

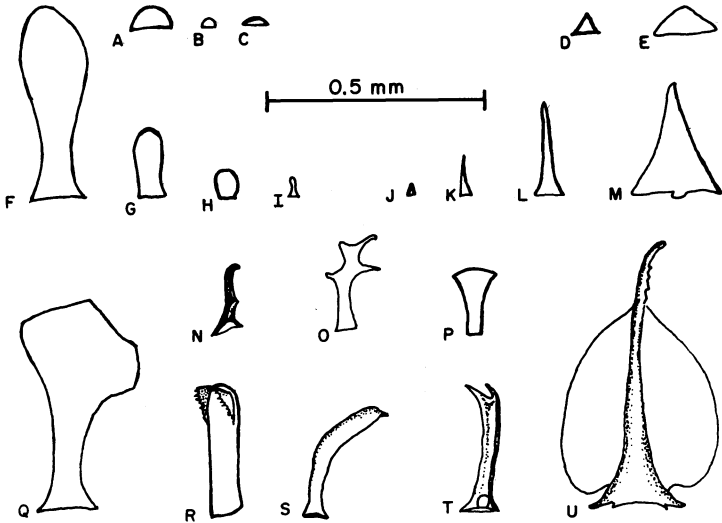


FIG. 1. Types of mandibles found on avicularia. Note the large range in size and shape; F, G, H and E, J, O were on the same colonies. [A, E, J, K, M, O, P, Q, V after Harmer, 1926, pls. xviii, xxv, xxv, xxiii, xxi, xxv, xviii, xxii, xvi respectively; B, C after Harmer, 1934, pl. xxxix, D, F, G, H, I, L, N, R, S, T after Harmer, 1957, pls. lxxx, lxv, lxv, lxv, lxxiii, lxiii, lxii (fig. 67 on p. 721), lxv, lxx respectively.]

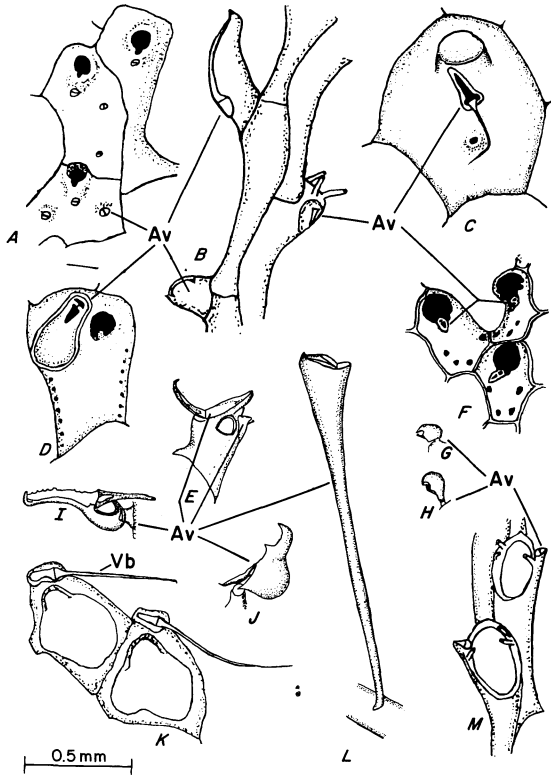


FIG. 2. Various types of avicularia found on Cheilostomata Ectoprocta. K shows two vibracula (*Vb*), polymorphic structures similar to avicularia (*Av*). (B, G, H, I, J, K, L, M after Harmer, 1926, pls. xxiii, xxvii, xxviii, xxviii, xxxii, xvi, xxix, xxiv respectively; F after Harmer, 1934, pl. xxxvi; A, C, D, E after Harmer, 1957, pls. lxii, liv, lxiii, l respectively.)

and Marcus (1926, p. C 56) dispelled the food-gathering hypothesis by noting, among other things, that no type of avicularium could possibly capture the phytoplankton that ectoprocts eat. Harmer (see Table 1) provided the strongest support for the defense hypothesis. He concluded that avicularia would be especially effective against larvae of fouling organisms, particularly larvae of other ectoprocts, and against intruders crawling over the colony. Marcus (1926, p. C 58) noted that the large spacing of avicularia on the colony allowed many small epizoans to become established on the colony. The third primary function, the creation of water currents,

TABLE 1. SUMMARY OF THE LITERATURE ON THE FUNCTIONS OF ALL TYPES OF AVICULARIA

FOOD GATHERING	DEFENSE	CREATION OF WATER CURRENTS	MISCELLANEOUS
<p>Krohn, 1843 (p. 72) Johnston, 1847 (p. 334) Busk, 1849 (p. 118) ——— 1854a (p. 28) ——— 1854b (p. 105) Sars, 1872 (p. 22) Herwig, 1915 (p. 156) Canu and Bassler, 1920 (p. 61)</p>	<p>Krohn, 1843 (p. 72) Busk, 1854a (p. 28) ——— 1854b (p. 105) Sars, 1872 (p. 22) Hincks, 1880 (p. ixix) Harmer, 1896 (p. 486) ——— 1909 (p. 719–722) ——— 1931 (p. 134–136) Herwig, 1915 (p. 156) Hyman, 1959 (p. 330)</p>	<p>Calvet, 1900 (p. 69) Canu and Bassler, 1920 (p. 61, 64) ——— 1929 (p. 360) Gautier, 1961 (p. 385) Cheetham, 1968 (p. 19)</p>	<p>Ellis, 1755 (p. 56) Ellis and Solander, 1786 (p. 20) Nordmann, 1840 (p. 685) Dalyell, 1847 (p. 245) Jullien, 1888 (p. 90)</p>

has been described as aiding in respiration, washing away excretory products or driving the prey toward the tentacles. Hincks (1880, p. lxxvii) made the important observation that the large variation in mandible types indicates that not all avicularia have the same functions. However, the implicit assumption that a particular avicularium has only one function is common. While this may be true under a broad definition of the presumed function, such an approach obscures the possibility that the structure is a compromise resulting from many selective forces acting concurrently. Thus the most fruitful question to ask is *not* what is the function of an avicularium, but rather what are the selective forces that have been most important during the evolution of the avicularium. The answer may then be phrased in terms of causes rather than results. To ask such a question, one must separate what the structure can do, and is thus *available* for selection, from what the structure actually does while interacting with the environment. In a careful analysis of functional morphology, Bock and Von Wahlert (1965) made this distinction and explained that although a structure may have many faculties (the ability to do many things), only a few of these may be important to the animal. ("Faculty," as used here, is nearly equivalent to Bock and Von Wahlert's use of the term. "Function" is equivalent to their term, "biological role.")

This paper first examines the faculties of the avicularia of *Bugula*, and then evaluates the selective forces associated with these avicularia. It amplifies an earlier preliminary report (Kaufmann, 1968).

TERMINOLOGY

The terms, "ventral" and "dorsal," are used by analogy to the autozoid where the ventral side is the side of the opening into the interior, through which the lophophore projects. The various parts of the avicularium (Figs. 3, 4 and 5) will be referred to as follows:

- adductor muscle support — the prominent, bulbous part to which the adductor muscles are attached
- rostrum — a beaklike projection attached to the distal part of the adductor muscle support
- peduncle — the portion proximal to the adductor muscle support
- peduncle cushion — the rounded projection from the autozoid

mandible — the appendage attached to the ventral part of the avicularium

cryptocyst — a horseshoe-shaped partition between the rostrum and the adductor muscle support which continues into the peduncle and forms a strut across the ventral part of the peduncle

Reference is to the avicularia of both *Bugula stolonifera* and *B. simplex* unless otherwise specified.

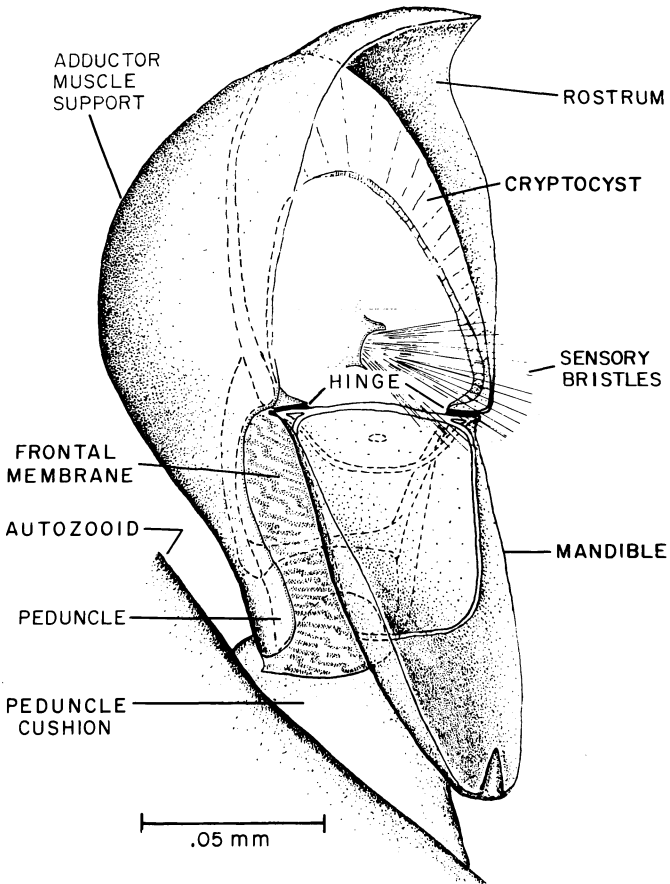


FIG. 3. Avicularium of *Bugula simplex*. Only the chitinous and calcitic parts and the sensory bristles are shown.

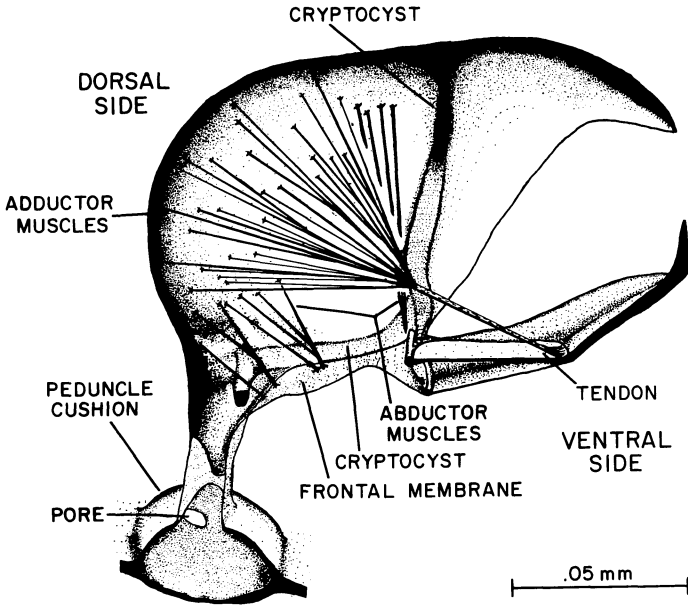


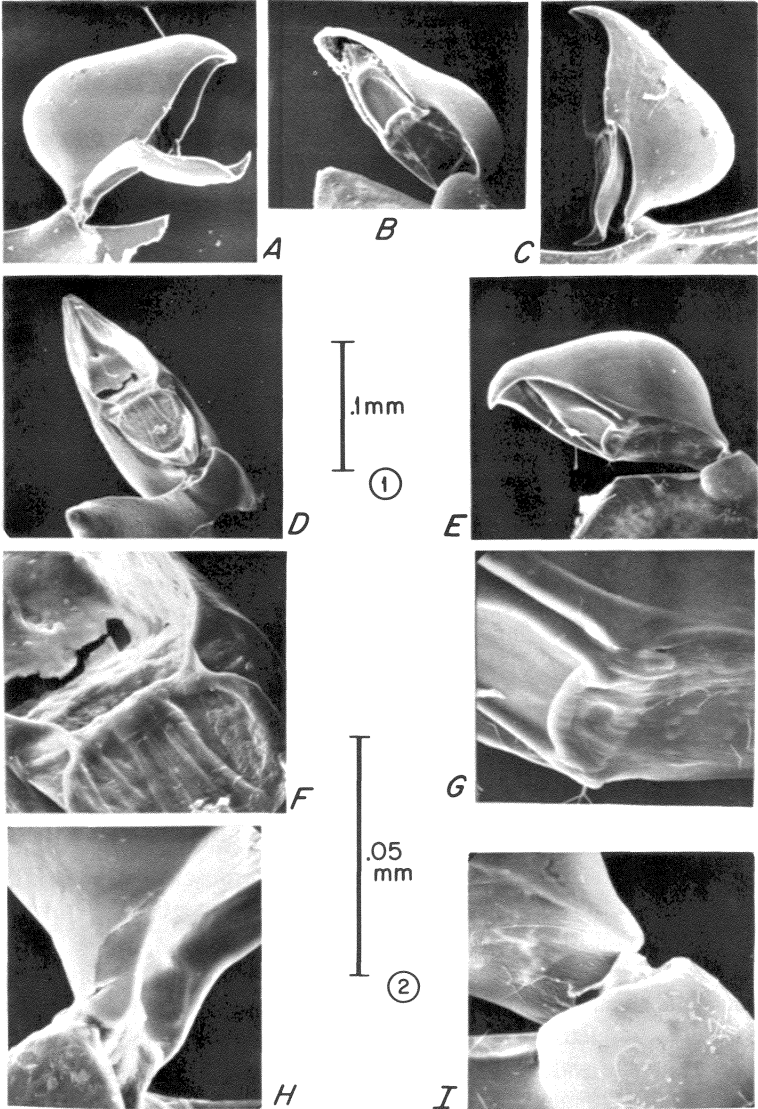
FIG. 4. Cutaway view through a sagittal section of an avicularium of *Bugula simplex*. The sensory bristles and soft parts other than the muscles have been omitted.

MATERIALS AND METHODS

Avicularia were studied in live specimens and in dried and mounted material. All of the colonies of *Bugula simplex* and *B. stolonifera* used for observational and experimental work were collected from the supply department dock in Eel Pond of the Marine Biological Laboratory at Woods Hole, Massachusetts. The majority of the colonies came from two tires suspended from floating docks and covered primarily with ectoprocts, tunicates, barnacles, sponges and hydroids.

Avicularia were dried or mounted in Lakeside Cement. Mounted specimens were cleared in a series of alcohols and xylene and stained in carmine red or methylene blue. Specimens observed with the scanning electron microscope were dried and coated with 200 Å

FIG. 5. Photographs of dried avicularia of *Bugula simplex* taken with a scanning electron microscope. A. The mandible is partially open. B. The mandible is closed and the strut across the peduncle cushion is visible where the membrane has been pressed around it. C. The mandible is open to its maximum extent. D. The mandible is completely open and the ventral surface is facing upward. E. The mandible is closed; note the rounded ventral edge of the rostrum. F. Detail of D; the hinge is best seen in the lower left corner. The tendon appears as a broad ribbon passing over the support between the hinges. G. Detail of E; the membrane attached to the curved support on the mandible has been pressed into the pore in the proximal part of the peduncle. Note the attachment of this membrane to the rim of the peduncle. H. Detail of E; note the shrunken membrane between the peduncle and the peduncle cushion. I. Detail of E; note the attachment of the membrane over the peduncle to the rim of the peduncle. Scale 1 applies to B, C, D, E. Scale 2 applies to F, G, H, I. A is reduced 20% relative to Scale 1.



of gold and palladium. A motion picture of the movement of avicularia was made. Measurements of wall thickness were determined partially by direct measurement and partially by observing differences in interference colors under polarized light.

FORM AND STRESS ANALYSIS OF THE AVICULARIUM

The form of an avicularium is a strong one for dealing with stresses that result from the grasping of an object between the mandible and the rostrum (Fig. 6A, B). Parts that must withstand compressional stresses are calcified and shaped so that shear stresses and bending moments are minimized, thus reducing the amount of skeletal material needed, whereas parts that must withstand shear stresses and bending moments, in addition to compressional stresses, are thicker and contain even more calcite. Those parts that must withstand tensional stresses have little calcite and a large proportion of chitinous matrix.

The wall material consists of a chitinlike matrix with varying amounts of calcite. Calcite, like most minerals, has high compressional strength and low tensional strength. Its brittleness and ease of cleavage indicates that it is comparatively weak under bending moments and shear stresses. It is reasonable to hypothesize that the organic matrix has a higher tensional strength than calcite, although I know of no work on the structural properties of the matrix.

The adductor muscle support (Fig. 3) is shaped like a portion of slightly flattened sphere. The wall is thin (about 0.0024 mm) compared to other parts of the avicularium. The adductor muscles (Fig. 4) close the mandible. Their insertions are evenly distributed over the rounded portion of the adductor muscle support. The muscle fibers join and merge into successively larger bundles toward the attachment to the tendon.

The nearly spherical shape of the adductor muscle support reduces the shear stresses and bending moments that develop (Fig. 6) when the adductor muscles contract, so that the major remaining stresses in the wall material are compressional. The shear stresses and bending moments are at a minimum under the following condition. The direction of the vector sum of the forces exerted by the muscles passes through both the center of the arc described by the adductor muscle support in sagittal section (Fig. 7, M) and the

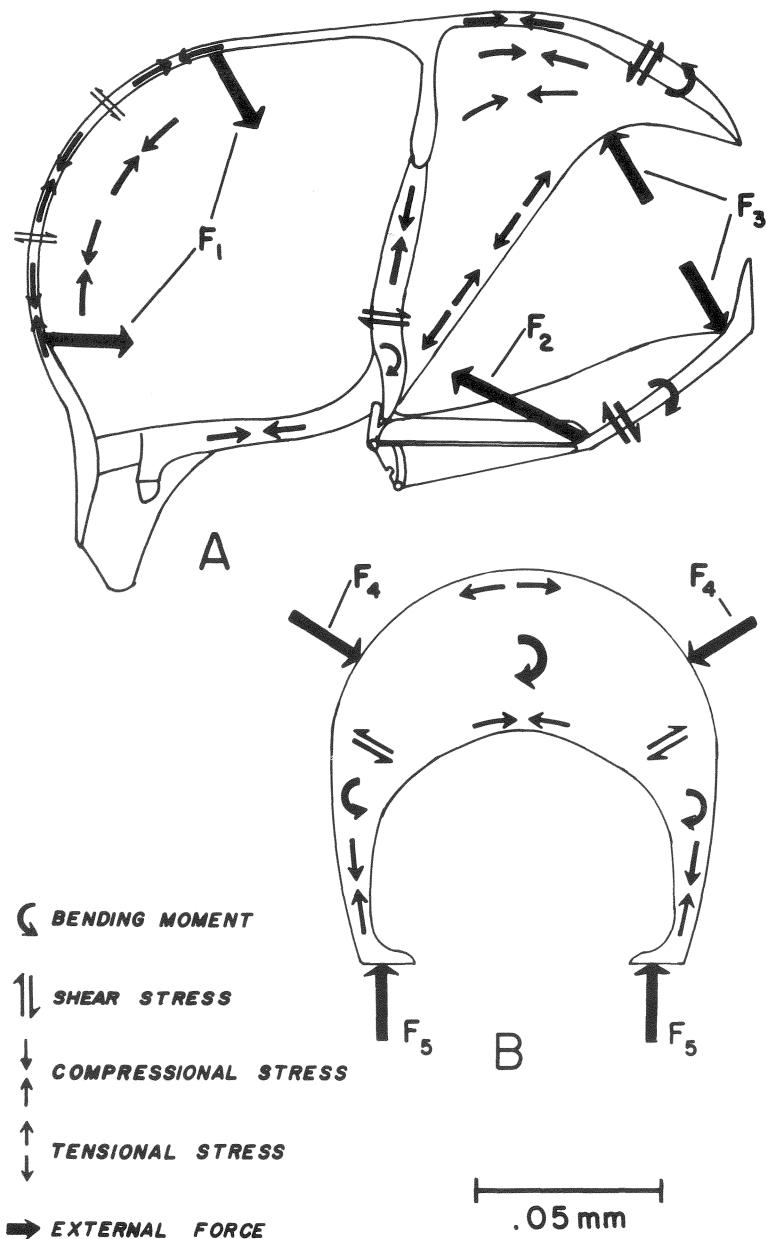


FIG 6. Distribution of stress that would result if the avicularium grasped an object with the mandible open 50° . Only the components of the forces that are parallel to the plane of the diagrams are shown. A. Cutaway view of a sagittal section. Note that several of the symbols are on the part of the avicularium behind the plane of the section. F_1 — Force on the adductor muscle support from the adductor muscles. F_2 — Force on the mandible from the adductor muscles. F_3 — Reaction forces on the rostrum and mandible from the object that is grasped. B. Plane view of the distal part of the cryptocyst. F_4 — Forces on the cryptocyst from the adductor muscles. F_5 — Forces on the fulcrum of the cryptocyst from the mandible.

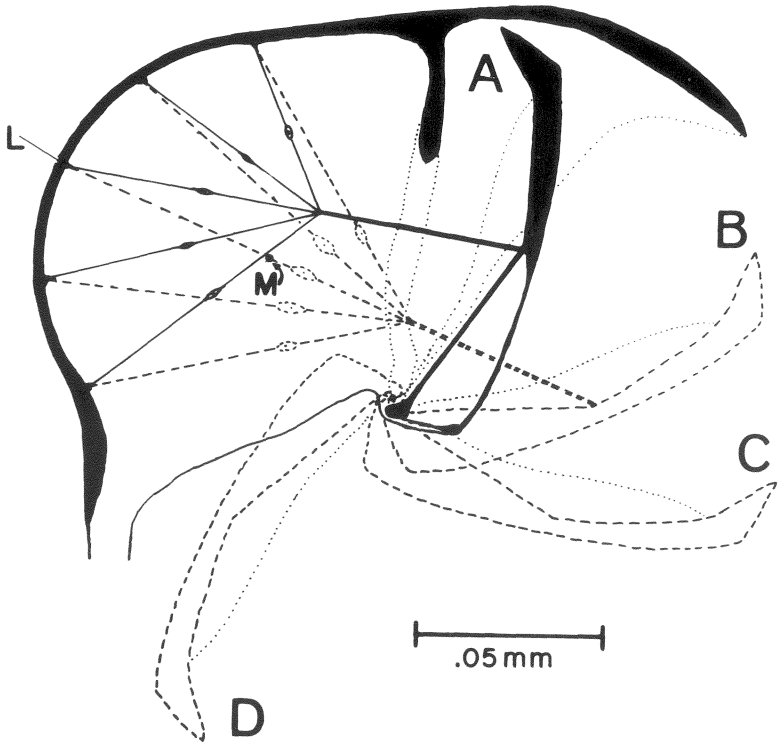


FIG. 7. Sagittal section of *Bugula simplex* showing the mandible and adductor muscles in several positions. In Position A, the mandible is completely closed. Position B (50° from A) is the point at which the adductor muscle support can withstand the greatest force from the muscles in an isometric contraction. Position C (90° from A) is the point at which the tendon (not shown) first touches the hinge line. Position D (180° from A) is the maximum extent of opening. Point L is the center of distribution of the adductor muscles. Point M is the center of the circle describing the arc of the adductor muscle support. The muscle strands are diagrammatic, but show the most proximal and distal limits of attachment.

center of distribution of the adductor muscles (Fig. 7, L). This direction is parallel to the tendon attached to the mandible. Such is the case when the mandible is opened 50° (Fig. 7, Position B).

The shape of the dorsal margin of the rostrum is similar to that of the curved compressional stress trajectories developed in a rectangular beam constrained at one end with zero degrees of freedom and loaded at the other with a force perpendicular to the long axis

of the beam. Such stress trajectories are shown by Thompson (1917, p. 678) in his analysis of the form of bones. Using the same analogy to a beam Bock (1966) analyzed stresses in birds' beaks some of which are shaped much like the rostrum. I conclude then, that the dorsal part of the rostrum, like the adductor muscle support, sustains minimal shear force and bending moment when an object is grasped as shown in Figure 6. Thus, the amount of calcite required, and hence the thickness of the wall, is minimized. The distal part of the rostrum which is considerably thicker is an exception. But here, both shear forces and bending moments would be concentrated if some live and actively struggling animal were grasped.

The tensional forces that develop when an object is grasped are concentrated along the ventral edges of the rostrum. As can be seen in the photographs taken with the scanning electron microscope (Fig. 5B, G), these edges are rounded rather than knifelike as noted by Harmer (1909, p. 720). When observed under a polarizing microscope, however, the isochromes are first-order grey, a fact indicating that a very small amount of calcitic material is present and that the ventral edges are mostly chitinlike.

Forces exerted by the adductor muscles to close the mandible would collapse the adductor muscle support if it were not reinforced distally and proximally. Reinforcement is provided by the cryptocyst (Figs. 3, 4). The distal part is a heavily calcified, horseshoe-shaped structure that separates the rostrum from the remainder of the avicularium. Two fulcrums about which the mandible rotates are found on the ventral end of this portion of the cryptocyst. From the two fulcrums, the cryptocyst extends proximally into the peduncle and is continuous with a strut across the ventral portion of the peduncle (Figs. 4, 5B). The thickness and heavy calcification of the cryptocyst greatly increase its ability to withstand the shear forces and bending moments that develop when the mandible closes upon an object (Fig. 6A, B).

The form of the peduncle (Figs. 3, 4) is perhaps the most difficult part of the avicularium to distinguish with certainty. It consists of a thickened semicircular wall to which is attached a flexible membrane on the ventral surface. The membrane extends from the curved ventral and proximal support of the mandible to the peduncle cushion. It is attached to the edge of the wall of the cryptocyst. The proximal part of the peduncle at the attachment to the peduncle cushion is flexible around the entire area of attachment. This can easily be seen in a motion picture taken of a live avicularium.

The peduncle cushion (Figs. 3, 4) to which the peduncle is attached is a rounded flexible knob that projects from the rim of the lateral wall of the autozoid just below the orifice. The flexible nature of the peduncle cushion reduces the shear stresses that would develop at the point of attachment of the avicularium if the avicularium were pulled or twisted violently. The major stresses that remain at the point of attachment are tensional. Such pulling and twisting moments occur when a large organism is caught and struggles violently. If the avicularium were attached directly to the autozoid without the cushioning effect of the peduncle cushion, then a force parallel to the longitudinal axis of the autozoid would set up shear stresses at the relatively small area of attachment instead of transferring them to the much larger perimeter of the peduncle cushion.

The mandible (Figs. 3, 4), unlike the rest of the avicularium, is lightly mineralized, but still rigid. The proximal part is supported by a bow-shaped structure covered by a membrane with a small pore in the center. A flat sheet extending from the strut across the hinge line to the place of attachment of the tendon, further reinforces the distal half of the mandible. On the distal end is a short spike that inserts into the rostrum when the mandible is closed. The part of the U-shaped channel that extends from the spike to the attachment of the tendon is thickened along the ventral portion, thus increasing the amount of bending moment and shear stress it can withstand. Just proximal to the spike, the sides of the U-shaped channel form a rounded notch. The spike can prevent an object from slipping out past the end of the mandible as it closes; it can also puncture objects, but such objects would have to be small enough to fit between the tip of the rostrum and the tip of the spike.

The mandible is opened by means of two sets of abductor muscles (Fig. 4). One set depresses the frontal membrane of the peduncle, causing the mandible to rotate on its hinge, as shown by Silén (1950, p. 355, fig. 4) for *Bugula flabellata*. This set of muscles consists of 7–10 strands that extend from the thickened part of the peduncle wall to the frontal membrane. Some strands converge to a small region halfway between the peduncle cushion and the mandible. The other set, which opens the mandible to its maximum extent, consists of a pair of muscle bundles, each with about five strands. The bundles are inserted on the adductor muscle support on either side of, and distal to, the adductor muscle and extend to the frontal membrane. I could not determine whether they were attached to the

frontal membrane, as shown by Silén (1950) or to the bow-shaped support of the mandible, as shown by Calvet (1900, p. 50, fig. 9) for *B. sabatieri* [Calvet's *B. sabatieri* is synonymous with *B. simplex* (Ryland, 1960, p. 97)]. The position of the avicularium with respect to the autozoid determines the maximal opening (about 180°) of the mandible. When the avicularium nods back and forth, the mandible opens and closes slightly as it brushes against the surface of the autozoid.

Sensory bristles project outward from a point just above the hinge line (Fig. 3). When the mandible is completely open, 50–100 bristles extend as far as an imaginary line drawn from the tip of the rostrum to the tip of the mandible. Stimulation of the bristles causes the mandible to snap shut. Often whatever touches the sensory bristles is caught between the mandible and the rostrum, and is lodged in the rounded notch just proximal to the spike of the mandible. If such an object remains still, it is released after a few seconds, but if the object is continually agitating, the grasp will not be released.

FORM OF THE COLONY

The branches of colonies of *Bugula simplex* (Fig. 8A) are 3–5 zooids wide and arranged in fanlike clusters of about five branches per cluster. Bunches of these clusters are, in turn, arranged in conical groups that may consist of several concentric layers. The ventral surface of each zooid from which the polypide projects faces inward. The overall appearance of the colony is that of a tightly packed ball of thick branches, as high as 3 cm and several centimeters in diameter. Prominent holes appear between the branches.

Colonies of *Bugula stolonifera* (Fig. 8B) have the same rounded appearance as *B. simplex*, but the branches are biserial rather than multiserial and are not arranged in conical groups. Consequently, the individual zooids are more evenly dispersed over the region occupied by the colony and there are no large "holes" in the colony, as exist in *B. simplex*.

Avicularia are attached to the lateral margins of each branch in such a way that their nodding motion carries the tip of the rostrum into the space between branches. There is a space of about 0.5 mm between avicularia on branches of both species.

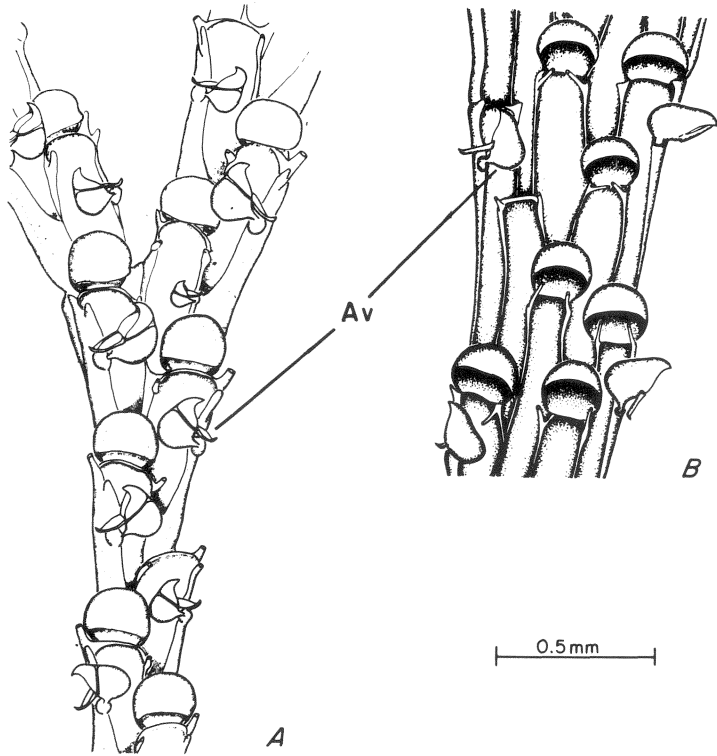


FIG. 8. Branches from colonies of *Bugula stolonifera* (A) and *B. simplex* (B). Note the presence of avicularia (Av) on every zooid of the biserial branch of *B. stolonifera*, but only on the outer zooids of *B. simplex*. (A) from Maturro, 1966, p. 572, fig. 12; (B) from Ryland, 1960, p. 92, fig. 13.

THE FACULTY OF GRASPING

The faculty of grasping can best be assessed if the diameter of an object that can be held securely can be determined. The ultimate force with which the mandible can close upon an object placed between it and the rostrum depends upon the size and position of the object and the moment that the muscles exert through the tendon about the hinge.

The length of the moment arm as a function of the angular opening of the mandible (Fig. 9) may be calculated by making the fol-

lowing assumptions. The first assumption is that the resultant of the force of the adductor muscles acting on the mandible will always be along a line passing through the center of distribution of the adductor muscles (Fig. 7, Point L). Observations of live avicularia show that this is nearly true for all positions of the mandible. The second assumption is that the muscles all converge at one point, where they are attached to the end of the tendon. The region of convergence is small enough to make this assumption reasonable.

The moment arm is at its maximum when the mandible is closed (Fig. 9). It decreases rapidly to half when the mandible is opened to 50° and to less than $1/20$ of the maximum when the mandible opens 90° . Between 90° and 180° opening, the tendon wraps around the hinge line and the moment arms becomes just as long as the distance between the axis of rotation and the slightly bowed strut across the hinge line.

The tension developed in a muscle during an isometric contraction is not the same at all extensions of the muscle. Mostly vertebrate muscles have been studied; for these there is one muscle length, the normal length of the muscle in the body, at which the maximum

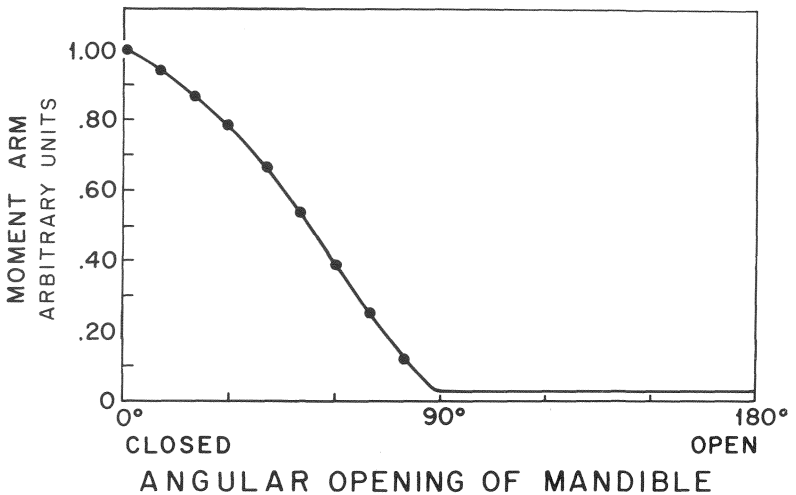


FIG. 9. Graph of the length of the moment arm between the hinge line and the tendon as a function of mandible opening. Values are expressed as a fraction of the maximum moment that exists when the mandible is completely closed.

tension can be developed. At greater or lesser lengths, the tension is less (Prosser and Brown, 1961, p. 433). From a purely morphological analysis, it is difficult to determine the length of maximum tension for the adductor muscles. Because some of the muscles vary considerably in length as the mandible closes, it cannot be assumed that the tension remains constant. The muscles that are inserted most distally in the adductor muscle support must contract almost 50% to close the mandible, and those near the center of distribution of the muscles (Fig. 7, Point L) must contract about 35%. The muscles that are most proximal appear to lengthen slightly while the mandible rotates from 90° open to 50° open and then contract about 10% in closing the mandible from there.

However, in spite of the lack of knowledge about the changes in muscle tension relative to length, a more than twentyfold increase in the moment arm as the mandible closes makes it reasonable to assume that the force that can be exerted upon an object with the mandible partially closed is substantially greater than the force that can be exerted when the mandible is open 90° or more. When the mandible is opened more than 90°, the avicularium cannot grasp objects securely because the mandible and rostrum are not sufficiently opposed in this position.

When the mandible is opened to 50°, the moment arm is half the maximum and an object 0.05 mm in diameter could fit into the space between the rostrum and the mandible. When it opens to 90°, the object size that can be grasped increases to only 0.1 mm while the moment arm is reduced to its minimum. The moment arm, then, gives the avicularium the faculty of grasping most securely objects which are at least 0.1 mm and preferably less than 0.05 mm in diameter.

THE FACULTY OF NODDING

The nodding motion of the avicularium consists of oscillation back and forth in an arc of nearly 180° in the plane of a sagittal section. It increases the effective area over which the sensory bristles can come in contact with an object. If the colony is undisturbed, the avicularia nod infrequently; *Bugula simplex* is less active than *B. stolonifera* in this respect.

Stimulation of the sensory bristles of a single avicularium of

B. stolonifera causes it to nod forward and snap shut. By nodding forward when an object touches the sensory bristles, the avicularium prevents the object from slipping past the distal end of the mandible before it closes completely. If nothing is caught, the avicularium continues nodding vigorously about once a second. Prodding the avicularium with a needle without touching the sensory bristles increases the nodding rate less than actually touching them. Stimulation of the tentacles of the individual to which the avicularium is attached causes no increase in nodding rate, but sticking a needle into the autozoooid or removing the branch from the water briefly causes all avicularia on the branch to start nodding vigorously. Moving the branch around under water increases the nodding slightly.

Rey (1927) and Forbes (1933) found many chemical stimuli that affect the nodding rate, but the relevance of these to the natural environment is not clear.

Silén (1950, p. 350–358), working with *Bugula flabellata* and four other species of *Bugula*, hypothesized that the adductor muscles were responsible for nodding. These muscles pull on the membrane covering the peduncle, causing the avicularium to nod dorsally while using the lateral sides of the peduncle as a pivot. The resiliency of the dorsal part of the peduncle near the peduncle cushion causes the avicularium to nod ventrally when the muscles relax. This model required that the membrane on the ventral side of the peduncle be attached below the dorsal edge of the peduncle.

Avicularia of *Bugula stolonifera* and *B. simplex* do not fit Silén's model. In *B. stolonifera*, the membrane remains limp throughout the nodding motion and becomes taut only when the mandible snaps shut. Thus, the membrane cannot take part in the nodding. In addition, rather than the lateral sides of the peduncle acting as a pivot, the avicularia are separated from the peduncle cushion by a thin membrane around the periphery of attachment (Figs. 3, 4 and 5H). The ventral edge of the peduncle is compressed inward at a point near the peduncle cushion as the avicularium nods ventrally. This deformation was seen clearly in a motion picture of live avicularia of *B. stolonifera*; however, the orientation of the avicularia on *B. simplex* prevented a clear view the peduncle of this species being deformed. Photographs of both species taken with a scanning electron microscope indicate that the membrane is attached to the ventral edge of the peduncle (Fig. 5B, E), although the photographs are difficult to interpret because of shrinkage and deformation which

may occur when the specimens are dried. These changes could cause the membrane to be pulled inward and appear attached below the rim of the peduncle in some (Fig. 5A) but not all (Fig. 5 I) photographs.

As far as I could determine, Calvet's (1900, p. 53) explanation of the nodding motion in *Bugula simplex* is correct. This explanation implies that the peduncle deforms with both ventral and dorsal movements of the avicularium, instead of only with the dorsal movement as implied by Silén. However, I could not find the extensor and flexor muscles described by Calvet in the peduncle.

INTERACTION OF AVICULARIA WITH THEIR ENVIRONMENT

Many have observed the strength of avicularia. They can grab a needle "so firmly the branch might be shaken" (Darwin, 1839, p. 259), or capture various small organisms (Harmer, 1896, p. 485), but no one has evaluated the strength of avicularia in terms of the frequency of capture and ability to hold organisms commonly found on the colony.

A wide variety of organisms inhabits colonies of ectoprocts collected in the field. Among the more common were nematodes, gammarid amphipods, and copepods. The gammarid amphipods (*Corophium insidiosum* and *Jassa falcata*) range in size from 0.5 mm to 4.5 mm and build tubes composed partly of ectoproct fecal material in the lower parts of the colonies where the polypides have degenerated into brown bodies. In late summer, when most of the polypides have degenerated, amphipods may have tubes covering the colony. I have counted as many as 100 amphipods inhabiting tubes or crawling about on a colony of *B. simplex* 2 cm high. Less common animals include triclad flatworms less than 1 mm long, pycnogonids and marine mites. Ciliates, hydroids, and more rarely tunicates, sponges and several species of ectoprocts, are also attached to colonies.

The interaction between larger organisms and avicularia is quite remarkable. I have observed gammarid amphipods (*Corophium insidiosum* and *Jassa falcata*) 4 mm long, not counting the antennae, caught repeatedly by avicularia no longer than 0.2 mm. The few amphipods larger than 4 mm escape from avicularia readily, and those that remain in their tubes are not captured. Most often amphi-

Pods are caught by one of the hairs on their appendages and escape after two or three minutes of struggle. Occasionally an amphipod is caught by one of the terminal segments of the antennae and held as long as 37 hours. The larger amphipods (1–4 mm) wandering about on the colony, spend more than half their time trying to free themselves from the avicularia. By far the most frequently captured animals are amphipods. When present, nematodes larger than 1 mm and smaller than 3 mm long are also readily captured. A pycnogonid, 10 mm across the legs, is held securely by an avicularium. Smaller nematodes, marine mites and flatworms are rarely captured.

Harmer (1909, p. 720) claimed that avicularia discourage the settlement of larvae by crushing or puncturing them. Another possibility is that larvae are prevented from settling because either the avicularia or the lophophores brush them away as they approach the colony. To test this hypothesis and to determine whether anything unusual happens in the presence of larvae, I observed the interaction between ectoproct larvae and *Bugula*-type avicularia.

Sixteen ectoproct larvae were placed in a shallow fingerbowl containing a brush of *Bugula simplex* oriented with its lophophores extended upward. Many attempts were made to use the phototactic response of the larvae to maneuver them toward the branch, but very few actually made contact with anything but the lophophores. Often, a larva was drawn into a lophophore and held for a short time (as long as a full second) by curling the tips of its tentacles around the larva. It would then be ejected as is normally the case for a particle too large to be ingested. No larvae were caught or hindered by the mandible of the avicularium. Thus, the lophophores are a far more effective instrument for discouraging the settlement of larvae than the avicularia.

DISCUSSION OF THE FACULTIES AND THEIR FUNCTIONS

The best developed faculty of the *Bugula*-type avicularium is that of grasping objects about 0.05 mm or less in diameter. The forms of the individual parts, particularly the adductor muscle support, the cryptocyst, and the large moment arm for objects less than 0.05 mm in diameter, are structurally very sound for applying great force through the mandible. The intermittent nodding motion, the reaction to tactile stimuli by snapping the mandible shut and the spike on the mandible aid in capturing animals. The flexibility of the peduncle

cushion prevents the avicularia from being twisted off by animals that are caught.

The limitations of the faculty of grasping animals can be determined if the placement of the avicularia on the colony is considered. First, the manner in which avicularia move in a plane parallel to the surface of the branches means that animals crawling on the surface are more easily caught, and animals swimming above the surface less easily caught, than if the avicularia moved in a plane perpendicular to the surface. Swaying into the holes in the branches of colonies of *B. simplex* increases the probability that the avicularium will come in contact with an animal crawling about on the colony, because such an animal must invariably crawl through these holes. Second, the spacing of about 0.5 mm between avicularia along the branches permits small animals to crawl about with a low probability of encountering an avicularium, whereas larger animals, particularly those that are longer than the spacing between avicularia, will be caught more frequently. Factors other than size and mode of movement which determine the frequency that animals come in contact with avicularia are the number of appendages suitable for being grasped, and the amount of commotion an organism makes in moving over the colony. Amphipods are usually grasped by one of the terminal segments of an appendage. Nematodes smaller than 1 mm are captured infrequently, presumably because of their lack of appendages, while those larger are captured regularly because their violent twisting movement causes their bodies to cover a large area in their progress over a colony.

The ability of the larger amphipods to escape can be attributed both to their strength and to the increased diameter of the terminal segments on their appendages. The upper size limit for the capture of many organisms of the same general shape as amphipods is probably about the same. Small annelids with many small hairs and spindly pycnogonids, although larger than 4 mm, could probably be captured.

In comparison, the faculty of creating water currents and of brushing larvae or sediment off the colony is very poorly developed in *Bugula*-type avicularia. The compact form of the avicularium and the pointed tip of the mandible could not move water nearly as efficiently as a broad spatulate mandible (Fig. 1F), nor is the sporadic nodding motion capable of creating a continuous flow. In species of *Bugula*, at least, lophophores create a much stronger current flow through ciliary action. For brushing larvae and sediment

away, a long narrow mandible or a vibraculum (Fig. 2) would be much more effective than a compact avicularium covering a limited part of the colony.

Because the faculty of grasping is so well developed, there must have been strong selective pressures for it. The most obvious function for the faculty of grasping is that of defense. Some animals may harm the colony but are either too small (ciliates), too large (fish and most molluscs), or are not the right size to be captured often enough to reduce their threat to the colony and be affected by the avicularia. Small snails have very few appendages and do not move actively about the colony.

Smaller annelids, nematodes and crustaceans may crawl about on the colony, but just this alone does not appear to damage the colonies. Pycnogonids (Barnes, 1963, p. 377) and tanaid amphipods (Smith, 1906, p. 335) are predators of ectoprocts, but I observed few pycnogonids and no tanaids on the colonies I studied. Avicularia could be valuable controls of these predators where they are more common.

Larvae deserve special mention because many workers have suggested that avicularia of most species aid in discouraging their settlement. The avicularia studied here cannot defend against larvae effectively. Most common fouling organisms have larvae that are less than 1 mm long and would as often find a place to settle between avicularia or on the dorsal surface of the colony as come in contact with an avicularium. More important, most larvae of fouling organisms have few appendages suitable for being grasped, and are too large to be grasped by the body. The larvae of most ectoprocts, for example, are 0.15–0.2 mm in diameter with only short cilia protruding from their bodies. For an avicularium to grasp the entire body, it would have to open wider than 90° (Fig. 5, Position C) and the moment arm would then be reduced to its minimum. Nodding would certainly prevent larvae from settling within the small range of movement of the avicularia, but because the nodding movement is closely associated with the faculty of grasping, its separate use for the function of brushing away larvae would appear incidental to its function of increasing the probability that the sensory bristles will come in contact with an animal.

Only the amphipods, *Corophium insidiosum* and *Jassa falcata*, do extensive damage through building their tubes in the colonies, thus preventing the lower parts of the colonies from regenerating new polypides and producing larvae. Avicularia do reduce the

amount of tube building by capturing and holding amphipods that leave their tubes. Holding the amphipods for varying periods of time does not cause the amphipods to leave, but it does cut, by at least half, the time that they have available for building more tubes.

CONCLUSION

Grasping and retaining small organisms crawling over the colony are the most highly-developed faculties of the avicularia of *Bugula simplex* and *B. stolonifera*. These faculties reduce the tube-building activities of amphipods and can reduce the harm done by other organisms, such as predators of ectoprocts, provided shape, size and activity on the colony allow them to be caught frequently. Avicularia on other species of *Bugula* appear to have an equally well-developed faculty of grasping and probably have similar functions.

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