

Victims of Avicularia

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With 1 figure

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Abstract. The function of the sessile "trap-door" avicularia of cheilostome bryozoans has been the subject of much speculation but relatively little observation. During studies of reef dwelling cheilostomes, avicularia of this type were seen to capture syllid polychaetes. This diverse group of small predatory worms, commonly found in the same habitats as bryozoan colonies, may be important factors in bryozoan ecology and evolution.

Problem

The polymorphism displayed by zooids of cheilostome bryozoans has long intrigued biologists. In recent years bryozoan workers have used the theories of polymorphism developed by students of social insects (WILSON, 1968) to explain the evolutionary success of the cheilostomes as well as patterns of cheilostome diversity (SCHOPF, 1973; MOYANO, 1977). Yet, in spite of such speculation the function of the most exaggerated zooid polymorphs, avicularia, remains a mystery. In this paper I describe observations on the behavior of avicularia that may have widespread significance with regard to avicularian morphology, function, and evolution.

Two variations of avicularian polymorphs have been studied in some detail. *Vibracula* (polymorphs with long bristle-like mandibles) of several free-living species forming small mobile colonies were studied by COOK (1963) and COOK & CHIMONIDES (1978). Their functions include cleaning colony surfaces of sediment, raising colonies above the sand surface for feeding, and colony locomotion (both to regain the surface after burial in sediment and for lateral movement or migration).

The biomechanical properties of the stalked bird's head or *Bugula*-type avicularia were investigated by KAUFMANN (1968, 1971), who showed that such structures should be effective against organisms with appendages or bodies within certain dimensions. The avicularia he studied captured the tube-building amphipods that inhabited the lower portions of the colonies.

Yet *Bugula*-type avicularia are found in only nine cheilostome families. The distribution of vibracula is even more limited. They occur (in various forms, not all of which may be homologous) in only 4 families.

In most cheilostomes, avicularian polymorphism is limited to the so-called "sessile" non-stalked avicularia. These are modified, usually smaller, versions of autozooids in which the operculum is enlarged into a trap-door like mandible which may be spade-, spoon- or blade-shaped. Such avicularia may be (1) 'vicarious', replacing an autozooid in position; (2) 'interzooidal', smaller but still positioned between autozooids, or (3) 'adventitious', perched on lateral or frontal walls of zooids, or on colonial basal walls.

Fifty of 78 cheilostome families have avicularia of one or more of these types. Biogeographic surveys also demonstrate their dominance. According to SCHOPF (1973) about 75 % of tropical Western Atlantic cheilostomes have at least one avicularium or vibraculum, while MOYANO (1977) gives data for Antarctic species indicating that 80 % have at least one avicularium. For 61 % of the tropical Atlantic cheilostomes and 64 % of the Antarctic cheilostomes these are of the non-stalked, sessile type.

Yet it is for these widespread sessile avicularia that we have no idea of function (WINSTON, 1984 a). That it was possible for careful observers to document behaviour in two kinds of polymorphs (COOK, 1963; KAUFMANN, 1971) suggests that the behaviour of the other types should also be explicable through an observational approach. Specifically, the capture of organisms by sessile avicularia – the first step in proving the active defense hypothesis – could be documented by this approach.

The range of organisms avicularia could capture is limited. Large grazers, *e. g.* sea urchins, starfish, chitons, and limpets may have important effects on cheilostome populations (RYLAND, 1976), but these animals damage large areas of colonies or destroy entire colonies. With the possible exception of everted starfish stomachs (see DAY & OSMAN, 1981) or tube feet the above grazers have no structures small or soft enough to be affected by avicularian actions.

Smaller predators which attack a single bryozoan zooid at a time, and whose bodies or appendages are in the size range of avicularian mandibles (typically 50–500 μm in length) are more likely victims. Pycnogonids, known predators of bryozoan zooids, have been suggested, but the little evidence available is inconclusive. Sessile avicularia do not react to non-living objects of the approximate dimensions of sea-spider legs. Although an avicularium could be forced to close upon such an object, it would not remain closed (WINSTON, 1984 a). These observations agreed with the reactions to living pycnogonid appendages observed by WYER & KING (1973), who found that claws, palps and proboscis tips were caught, but released, while legs were too large to be caught.

Interestingly, avicularia do not react to nudibranchs, many species of which are also known to be bryozoan predators. The only published observations regarding interactions of nudibranchs with avicularia document the lack of such a response (COOK quoted in RYLAND, 1976). This may in part be due to the fact that while nudibranchs are single zooid predators, most nudibranchs are rather large bodied relative to most bryozoan zooids and avicularia.

Thus, none of the above organisms appear to represent the type of aggressor against which avicularia could provide an effective defense. The characteristics

of possible aggressors and victims could be defined as follows:

- 1) they should represent a major group of marine organisms, one that is itself diverse (considering the diversity of avicularian structure);
- 2) members should be found primarily on hard substrata;
- 3) they should have a widespread distribution, perhaps with peak abundance and diversity in the tropics or the Antarctic (areas in which bryozoans show a high degree of avicularian polymorphism according to SCHOPF, 1973 and MOYANO, 1977);
- 4) they should be of a morphology susceptible to the biomechanical properties of the trap-door-like sessile avicularia. That is, they should be soft-bodied, possibly somewhat flattened, of a flimsy or compressible construction, with a diameter (of whole or parts) in the 0.05–0.5 mm range and a length between 0.5 mm and 2 mm. Large or hard-shelled creatures cannot be restrained by avicularia, and smaller soft-bodied organisms (ciliates, copepods, *etc.*) seem to be able to perform most of their activities on colony surfaces without triggering, or usually even encountering, avicularia (WINSTON, 1984 a).

Material and Methods

The species used in this study encrusted coral rubble and undersurfaces of platy corals collected from patch-reef and forereef environments at Carrie Bow Cay, Belize, during October, 1984. Reef zonation at Carrie Bow Cay has been described by RÜTZLER & MACINTYRE (1982). The bryozoan species discussed are described and illustrated in WINSTON (1984b). Specimens were collected in depths between 8 and 20 m by SCUBA diving and transferred to the laboratory where they were maintained in running seawater until they could be examined under the dissecting microscope (usually within 12 h of collection).

Results

Syllid polychaetes are a group of organisms which fulfill all the criteria for an avicularium-sensitive predator. In the colony of *Reptadeonella costulata* shown in Fig. 1, one zooid has trapped such a polychaete. In Fig. 1. a. the body of the worm (with characteristic proventricle visible) is to the left. It is clamped firmly just behind its tentacled head by the median adventitious avicularium of the *Reptadeonella* zooid. Fig. 1. b. is a line drawing of Fig. 1. a. illustrating how the worm is clamped by the avicularium mandible.

During observations on avicularia of coral reef bryozoans carried out at Carrie Bow Cay, Belize, I observed several captures of syllids by avicularia of bryozoan colonies. A spatulate interzoecial avicularium of a *Celleporaria albirostris* colony was seen to close with a very rapid spring-like action on one worm. Closure of these avicularia can be triggered mechanically, either by a sudden sharp vibration or water current (as from a syringe), but they then reopen (a much slower motion) almost immediately (WINSTON, 1984 a). The avicularium that had closed on the worm did not reopen even when subjected to jarring or water currents. It remained closed on the polychaete for 12 h; mechanical probing then detached part of the worm, but the rest remained trapped for at least 24 h.

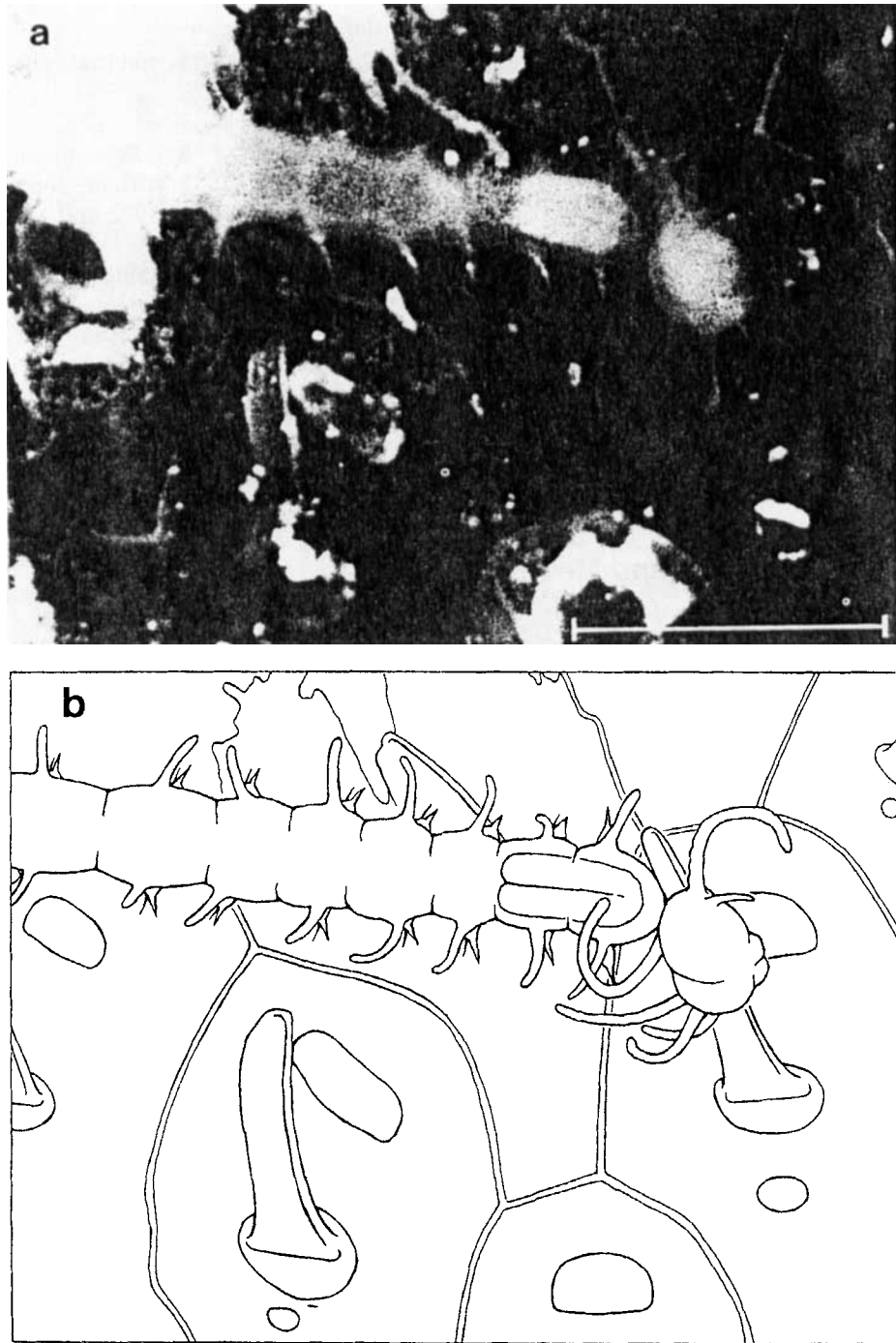


Fig. 1. a. Side view of syllid caught by avicularium of a *Reptadeonella* zooid.
b. Diagram of syllid and bryozoan zooid showing how the worm is clamped to the zooid surface by the avicularian mandible (same view as 1. a). Scale bar = 400 μm .

Syllids were also caught by colonies of *Reptadeonella costulata*. One trapped worm broke when prodded with a needle, the head-section remaining stuck under the avicularium, the tail-section moving rapidly away with a sinusoidal swimming motion. This motion triggered adjacent avicularia, while slow probing motions by implements or animals did not. Unlike the spatulate avicularia of *Celleporaria*, the adventitious avicularia of *Reptadeonella* respond minimally to probing, although they do close rapidly in response to rapid brushing, after which they slowly reopen (WINSTON, 1984 a).

Another colony (that illustrated in Fig. 1) had caught two of these worms before the observation period started. One became detached in a preliminary attempt at photographic documentation; the other remained trapped through fixation and transportation from Belize to New York.

Discussion

These observations show only that syllids may be captured by avicularia – not that their presence is harmful to the colony. Whether any are predators on these two species of bryozoans remains to be studied.

The polychaete family *Syllidae* fulfill all the criteria established for the hypothetical predator group. The *Syllidae* contain over 600 species of small slender-bodied worms. Many are less than 10 mm in length, a considerable number less than 2 mm. Syllids are errant polychaetes, although certain species build mucous tubes. They are often associated with hard substrata, where they are cryptic in habit, and are often very abundant on sponges, corals, algae, hydroids, oysters, gravel, pilings, etc. (FAUCHALD, 1977; UEBELACKER, 1984). They are especially common on coral reefs (KOHN & LLOYD, 1973; HUTCHINGS, 1981; HUTCHINGS & MURRAY, 1982), and abundant in the Antarctic (HENDLER, pers. commun.). Syllids have been reported to feed on hydroids (OKADA, 1928; HUGHES, 1975), bryozoans (MALAQUIN, 1893), sponges (FAUCHALD & JUMARS, 1979), and diatoms, detritus or algae (JONES, 1961; HUGHES, 1975). FAUCHALD & JUMARS (1979) hypothesized that all members of the subfamilies *Autolytinae* and *Syllinae* will be found to be “carnivores feeding on hydroids, bryozoans and other colonial invertebrates”.

Syllids are suctorial feeders, using pharyngeal teeth to break open the integument of the prey and then sucking out the body contents; the digestive system is characterized by a cylindrical eversible pharynx, followed by a muscular structure termed a proventricle, used to pump out the prey's body contents (FAUCHALD & JUMARS, 1979). This mode of attack is strikingly similar to the feeding methods of nudibranchs and pycnogonids, the known single zooid predators of bryozoans.

If syllids are bryozoan predators then both the damage they do to colonies as well as the damage inflicted by the colonies must be quantified. The effects of single zooid predation on bryozoan colonies has been little studied. Work by PALUMBI & JACKSON, (1982) indicates that small lesions regenerate more rapidly than large lesions. Regeneration requires energy, and damage will no doubt diminish the fitness of colonies. The result may be, in a situation analogous to that of a tree losing leaves to caterpillars, a lowering of fecundity. Ecological

studies of bryozoans, thus far, have looked mainly at larger scale interactions (on the level of the community or the individual substratum), examining the role of competition or grazers. Syllid-bryozoan interactions may offer a manipulable system for the study of colony-scale processes.

Summary

Observations on living colonies of reef-dwelling cheilostome bryozoans included several instances of capture of syllid polychaetes by polymorphic zooids known as avicularia. The size and morphology of many syllids makes them susceptible to being trapped by these structures and provides evidence supporting a defensive value of avicularia to bryozoan colonies. Syllids, a diverse family of small predatory worms, are commonly found in the same habitats as bryozoans and contain species known to feed on colonial animals. They may prove to be important agents in cheilostome ecology and evolution.

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References

- COOK, P. L., 1963: Observations on live lunulitiform zoaria of Polyzoa. *Cah. Biol. Mar.*, **4**: 407-413.
- & P. J. CHIMONIDES, 1978: Observations on living colonies of *Selenaria* (*Bryozoa*, *Cheilostomata*); 1. *Cah. Biol. Mar.*, **19**: 147-158.
- DAY, R. W. & R. W. OSMAN, 1981: Predation by *Patiria miniata* (*Asteroidea*) on bryozoans: prey diversity may depend on the mechanism of succession. *Oecologia*, **51**: 300-309.
- FAUCHALD, K., 1977: The polychaete worms. Definitions and keys to the orders, families and genera. *Nat. Hist. Mus. Los Angeles Cty. Contrib. Sci., Ser. no. 28*: 1-188.
- & P. A. JUMARS, 1979: The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Annu. Rev.*, **17**: 193-284.
- HUGHES, R. G., 1975: The distribution of epizoites on the hydroid *Nemertesia antennina* (L.). *J. Mar. Biol. Assoc. U. K.*, **13**: 275-294.
- HUTCHINGS, P. A., 1981: Polychaete recruitment onto dead coral substrates at Lizard Island, Great Barrier Reef, Australia. *Bull. Mar. Sci.*, **31**: 410-423.
- & A. MURRAY, 1982: Patterns of recruitment of polychaetes to coral substrates at Lizard Island, Great Barrier Reef an experimental approach. *Aust. J. Mar. Freshwater Res.*, **33**: 1029-1037.
- JONES, M. L., 1961: A quantitative evaluation of the benthic fauna of Point Richmond, California. *Univ. Calif. Publ. Zool.*, **67**: 219-320.
- KAUFMANN, K., 1968: The biological role of *Bugula*-type avicularia (*Bryozoa*). *Atti Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat. Milano*, **108**: 54-60.
- , 1971: The form and functions of the avicularia of *Bugula* (Phylum *Ectoprocta*). *Postilla*, **151**: 1-26.
- KOHN, A. J. & M. C. LLOYD, 1973: Polychaetes of truncated reef limestone substrates on eastern Indian Ocean coral reefs: diversity, abundance and taxonomy. *Int. Rev. ges. Hydrobiol.*, **58**: 369-399.
- MALAQUN, A., 1893: Recherches sur les Syllidiens. *Mém. Soc. Sci. Arts, Lille; ser. 4, no. 18*; 477 pp.

- MOYANO, H. I., 1977: Bryozoa from Antarctic Bays: some ecological aspects. In: G. P. LARWOOD & M. B. ABBOTT (Eds.), *Advances in bryozoology*. Academic Press, London: 303–401.
- OKADA, Y. K., 1928: Feeding organs and feeding habits of *Autolytus edwardsi* St. Joseph (Studies on the Syllidae, I). *Q. J. Microsc. Sci.*, **72**: 219–245.
- PALUMBI, S. & J. B. C. JACKSON, 1982: Ecology of cryptic reef communities. II. Recovery from small disturbance events by encrusting *Bryozoa*: the Influence of “host” species and lesion size. *J. Exp. Mar. Biol. Ecol.*, **64**: 103–119.
- RÜTZLER, K. & I. G. MACINTYRE, 1982: The habitat distribution and community structure of the barrier reef complex at Carrie Bow Cay, Belize. In: K. RÜTZLER & I. G. MACINTYRE (Eds.), *The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, I*. Smithsonian Institution Press, Washington, D. C.: 9–45.
- RYLAND, J. S., 1976: Physiology and ecology of marine bryozoans. *Adv. Mar. Biol.*, **14**: 285–443.
- SCHOPF, T. J. M., 1973: Ergonomics of polymorphism: Its relation to the colony as the unit of natural selection in species of the phylum *Ectoprocta*. In: R. S. BOARDMAN, A. H. CHEETHAM & W. A. OLIVER (Eds.), *Animal colonies*. Dowden, Hutchinson and Ross, Stroudsburg, Pa: 247–294.
- UEBELACKER, J. M., 1984: Family *Syllidae*. Chapter 30. In: J. M. UEBELACKER & P. G. JOHNSON (Eds.), *Taxonomic guide to the polychaetes of the northern Gulf of Mexico*, vol. 4. Barry A. Vittore Assoc., Inc., Mobile, Alabama; 7 vols.
- WILSON, E. O., 1968: The ergonomics of caste in the social insects. *Am. Nat.*, **102**: 41–66.
- WINSTON, J. E., 1984 a: Why bryozoans have avicularia – a review of the evidence. *Am. Mus. Nat. Hist. Novit.*, no. **2789**: 1–20.
- –, 1984 b: Shallow-water bryozoans of Carrie Bow Cay, Belize. *Am. Mus. Nat. Hist. Novit.*, no. **2799**: 1–38.
- WYER, D. W. & P. E. KING, 1973: Relationships between some British littoral and sublittoral bryozoans and pycnogonids. In: G. P. LARWOOD (Ed.), *Living and fossil Bryozoa*. Academic Press, London: 199–207.