

Sipunculans Associated with Coral Communities

MARY E. RICE

Reprinted from MICRONESICA, Vol. 12, No. 1, 1976
Printed in Japan

Sipunculans Associated with Coral Communities¹

MARY E. RICE

*Department of Invertebrate Zoology, National Museum of Natural History
Smithsonian Institution, Washington, D.C. 20560*

INTRODUCTION

Sipunculans occupy several habitats within the coral-reef community, often occurring in great densities. They may be found in burrows of their own formation within dead coral rock, wedged into crevices of rock and rubble, under rocks, or within algal mats covering the surfaces of rocks. In addition, sand-burrowing species commonly occur in the sand around coral heads and on the sand flats of lagoons. Only one species of sipunculan is known to be associated with a living coral. This is *Aspidosiphon jukesii* Baird 1873 which lives commensally in the base of two genera of solitary corals, *Heteropsammia* and *Heterocyathus*. This review will consider first the mutualistic association of the sipunculan and solitary coral and then the association, more broadly defined, of the rock-boring and sand-burrowing sipunculans as members of the coral reef community.

MUTUALISM OF SIPUNCULAN AND SOLITARY CORAL

The rather remarkable mutualistic association between the sipunculan *Aspidosiphon jukesii* and two genera of ahermatypic corals, *Heteropsammia* and *Heterocyathus*, is a classical example of commensalism (Edwards and Haime, 1848a, b; Bouvier, 1895; Sluiter, 1902; Schindewolf, 1958; Feustel, 1965; Goreau and Yonge, 1968; Yonge, 1975). The *Aspidosiphon* inhabits a spiral cavity in the base of the coral and, through an opening of the cavity on the under surface of the coral, the sipunculan extends its introvert into the surrounding substratum pulling the coral about as it probes and feeds in the sand (Figs. 1-4). Through this association, the sipunculan is provided with a protective habitat and, by movements of the sipunculan, the coral is maintained in an upright position on the surface of the substratum and transported about to different feeding areas.

Heteropsammia and *Heterocyathus* with the associated *Aspidosiphon* are distributed both inside and outside of the limits of hermatypic corals from the Cape of Good Hope eastward to the Great Barrier Reef to Japan and New Caledonia.

¹ Contrib. No. 22 of the Smithsonian Institution IMSWE (Investigations of Marine Shallow Water Ecosystems) Project; Contrib. No. 30, Harbor Branch Foundation. Paper presented at a Symposium on "Animal associates on coral reefs", International Symposium on Indo-Pacific Tropical Reef Biology, Guam and Palau, June 23-July 5, 1974.

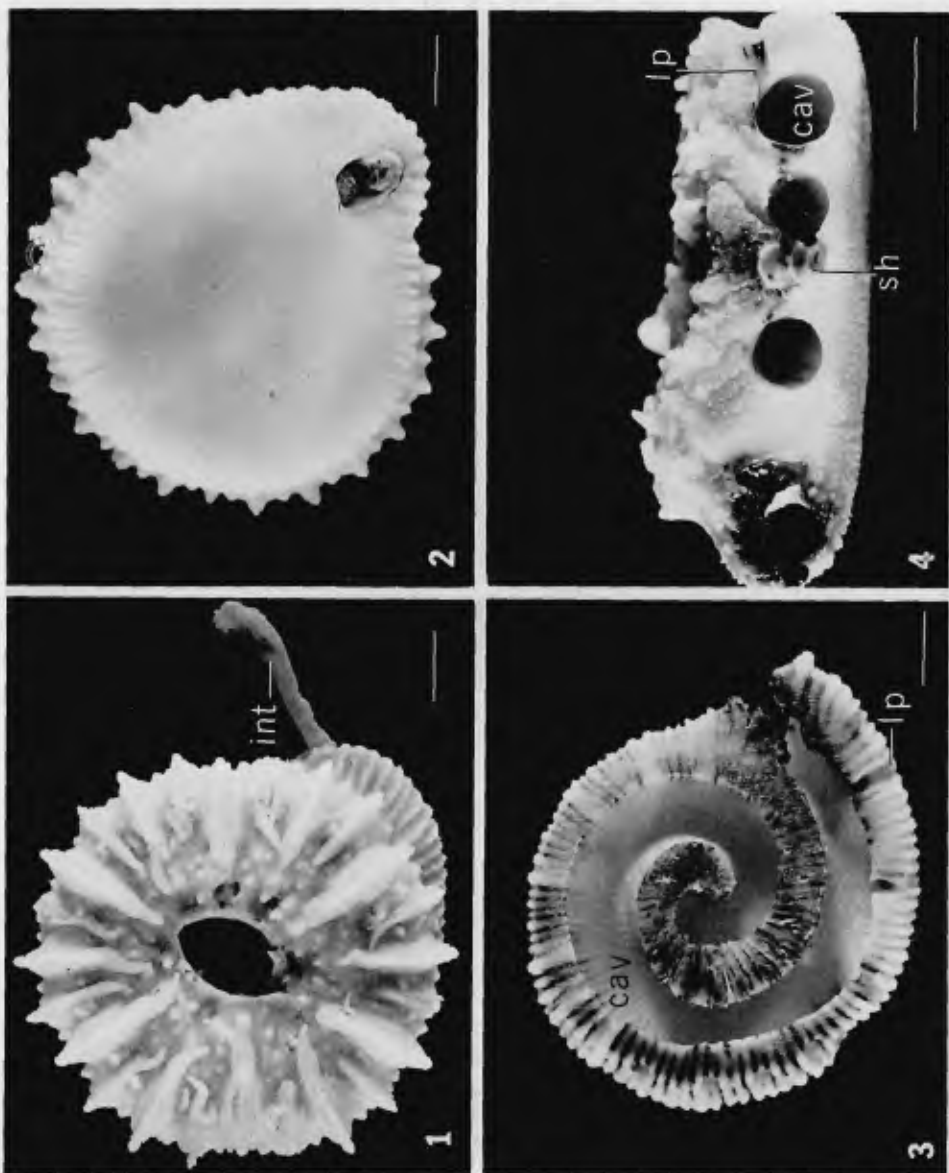


Fig. 1-4. Specimens of the solitary coral, *Heterocyathus sp.*, collected from Addu Atoll, Maldives Islands. Scale, 2 mm.

- Fig. 1. *Heterocyathus sp.*, oral view, with introvert (int) of associated sipunculan, *Aspidosiphon jukesii*, extended from basal aperture of coral.
- Fig. 2. Under surface of *Heterocyathus sp.*, showing aperture of the sipunculan's cavity. The shield of the enclosed *Aspidosiphon* is visible within the aperture.
- Fig. 3. A cross section through the coral to show the spiral cavity of the sipunculan (cav) and the lateral pores (lp). The sipunculan has been removed.
- Fig. 4. A median section of the coral, *Heterocyathus sp.*. Note remnants of the gastropod shell (sh) in the center and sections through the sipunculan cavity (cav) and lateral pore (lp).

They occur on a substratum of muddy sand at depths from 9 to 73 meters (Vaughan and Wells, 1943).

The association was first noted in 1848 by Edwards and Haime in their descriptions of the two coral genera. Sluiter (1902) gave the first complete description of the sipunculan and designated it as a new species, *Aspidosiphon corallicola*. He concluded that the sipunculans from both genera of corals belonged to one species. However, Sluiter overlooked an earlier brief report by Baird (1873) of a sipunculan described as *Aspidosiphon jukesi* from solitary coral in a collection from the Great Barrier Reef, Australia. In a recent redescription of Baird's type specimens, Sluiter's species was synonymized with *Aspidosiphon jukesi* Baird 1873 (Rice and Stephen, 1970). The latter name, being the senior subjective synonym, has priority.

The two genera of ahermatypic corals in which the sipunculan occurs are included in different suborders: *Heterocyathus* in Suborder Caryophylliida and *Heteropsammia* in Suborder Dendrophylliida (Vaughan and Wells, 1943; Yonge, 1975). Six species of *Heteropsammia* are recognized, and 4 species of *Heterocyathus*.

Although widely separated in taxonomic position, the forms of *Heterocyathus* and *Heteropsammia* are similarly modified in response to the presence of the sipunculan. Individuals of both genera are 1 to 2 cm in diameter with a column 1 to 2 cm in height, surmounted by a polyp. The entire corallum is covered by a ciliated coenosarc and its lateral walls are perforated by a series of pores opening into the canal of the sipunculan (Figs. 3, 4). Feustel (1965) has described the canals as lined with endoderm of the coral and proposed that they may serve in the irrigation of the sipunculan burrow. The base of the coral is usually not circular, but is elongated in the region of the terminal opening of the canal of the sipunculan (Fig. 2). Thus the presence of the sipunculan may confer a secondary bilaterality to the form of the coral (Schindewolf, 1958).

From the publications of Bouvier (1895) and Feustel (1965), the developmental history of the association between the sipunculan and coral is known in considerable detail. The juvenile *Aspidosiphon*, when 1 mm or less in length, enters an empty gastropod shell, usually a small *Cerithium*. A coral planula settles on the shell, overgrowing and eventually enclosing it. Only those planulae settling on shells occupied by sipunculans have any chance of survival. Growth of the coral and sipunculan is well synchronized, the sipunculan actively enlarging its cavity as a spiral tube in the base of the growing coral while maintaining an opening of the tube on the underside of the coral. As growth continues, the position of the opening moves in a spiral direction, while small openings, the lateral pores, are pinched off from the terminal opening. Feustel (1965) suggested that the sipunculan enlarges the lumen of its burrow through mechanical attrition by the anal and posterior shields as the animal moves back and forth within its burrow. Others have proposed that the burrow may be excavated through a secretion of the epidermal glands of the *Aspidosiphon* (Schindewolf, 1958; Sluiter, 1902). The small gastropod shell, although sometimes eroded, is usually still evident in fully grown corals at the apex of the spiral burrow of the sipunculan (Fig. 4).

In observations in the field and laboratory of living specimens of *Heteropsammia michelini* and *Aspidosiphon jukesii* from depths of 10–14 meters off Lizard Island, Great Barrier Reef, Australia, Goreau and Yonge (1968) noted that sipunculans, with introverts extended from the basal aperture in the coral, pulled corals over the surface of the substratum and that they were able to upright an overturned individual. It was proposed that the corals feed on particles and organisms suspended in the water and possibly, by extending tentacles over the substratum, on the organic sediment on the surface of the sand. It was further pointed out that the coral does not compete for food with the sipunculan which feeds on the subsurface sediment (Goreau and Yonge, 1968; Yonge, 1975).

The association of coral and sipunculan is frequently extended to include other symbionts which occupy the cavity of the sipunculan. A small bivalve, *Jousseaumiella heteropsammiae* was first seen by Bourne (1906, 1907) and more recently by others (Cutler, 1965). In a collection from the Maldive Islands, the author has found not only the erycinacean bivalve, but also two species of copepods in the cavity of the sipunculan, representing the orders Harpacticoidae and Cyclopoidae (Illg, 1975).

SIPUNCULANS IN THE REEF COMMUNITY

The significance of sipunculans as members of the coral reef community was first reviewed by Gardiner (1903a). In a discussion of boring and sand-feeding organisms on reefs of the Maldive Islands, he listed boring sipunculans along with certain sponges, molluscs, and polychaetes as the "main destructive agents of reefs". He further describes the sipunculans as "prominent forms in breaking up almost any large block of coral from any position on the reefs or from any depth found on them..." (Gardiner, 1903a, p. 336). According to Gardiner (1903b) the first organisms to penetrate the reef are the boring algae and then the sponges. The next invaders are polychaetes, the most numerous of which belong to the family Eunicidae, followed by the sipunculans such as *Aspidosiphon* and *Phaseolosoma*, and finally, the boring molluscs and barnacles. The corals, weakened by the boring organisms, "break of their own weight or the motion of the sea" (Gardiner, 1903a, p. 333). Gardiner traces the further breakdown of the coral fragments into fine sand or mud, pointing to the role of the sand-triturating organisms such as holothurians, echinoids, enteropneusts, sipunculans (especially *Sipunculus*) and echiurans in this process. Describing the biology of the reef at Funafuti atoll, Finckh (1904) depicts a sipunculan of the genus *Aspidosiphon* as chief destroyer of the *Lithothamnion* rock. Other more recent articles alluding to the role of sipunculans in the reef community are Otter, 1937, Rice, 1969 and Rice, 1975.

Systematics and Morphology

Although widespread and relatively abundant benthic animals, sipunculans are a group with limited diversity. In the most recent classification of the phylum, Stephen and Edmonds (1972) have recognized 4 families, 17 genera and approxi-

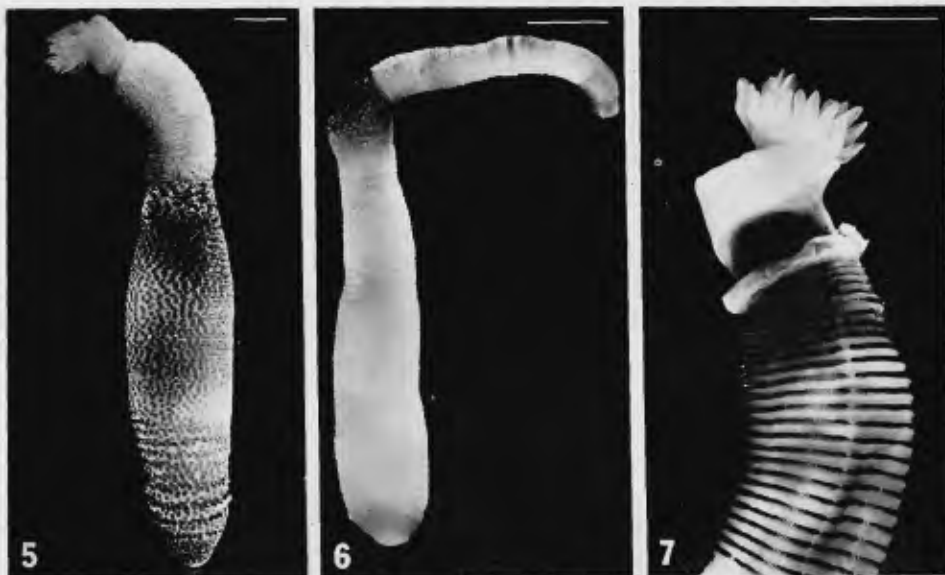


Fig. 5. *Phascolosoma antillarum*. From intertidal calcarenite boulder, Cabo Rojo, Puerto Rico. Scale, 2.5 mm.

Fig. 6. *Paraspidosiphon steenstrupi*. From coral rubble at depth of 35 feet, Key Largo Reef, Florida. Scale, 2.5 mm.

Fig. 7. Introvert of *Phascolosoma perlucens* showing terminal tentacles and rows of small hooks. From intertidal coral rubble, Tiladummati Atoll, Maldives Islands. Scale, 2.5 mm.

mately 321 species. In the coral reef communities the following six genera are represented in burrows in coralline limestone: *Aspidosiphon*, *Paraspidosiphon*, *Cloeosiphon*, *Lithacrosiphon*, *Phascolosoma* and *Themiste*. Species of *Sipunculus* and *Siphonosoma* are sand-burrowers found in the lagoon of the reef or in sand under rocks and rubble. A few representatives of the genus *Golfingia* are found in the reef community either in sand or in cavities of rock.

The body of sipunculans is comprised of a relatively wide and thick posterior trunk and a thinner anterior region, the introvert, which is retractable into the trunk (Figs. 5, 6). Tentacles, surrounding or dorsal to the mouth are usually present at the anterior extremity of the introvert. Frequently the introvert is armed with small, non-chitinous hooks and spines (Fig. 7). The anus is at the base of the introvert and in tube-dwelling species fecal pellets are deposited outside the mouth of the burrow. Cuticular papillae are characteristic for the group, but differ among species and genera in their construction, degree of development, and distribution over the body. In *Sipunculus* the introvert is covered with distinctive papillae, uniquely shaped as triangular, squamiform protuberances, frequently overlapping. The papillae of *Phascolosoma* are typically prominent and densely packed at the anterior and posterior ends of the trunk (Fig. 5). Aggregations of modified papillae in the genera *Aspidosiphon* and *Paraspidosiphon* form thickened horny elaborations,

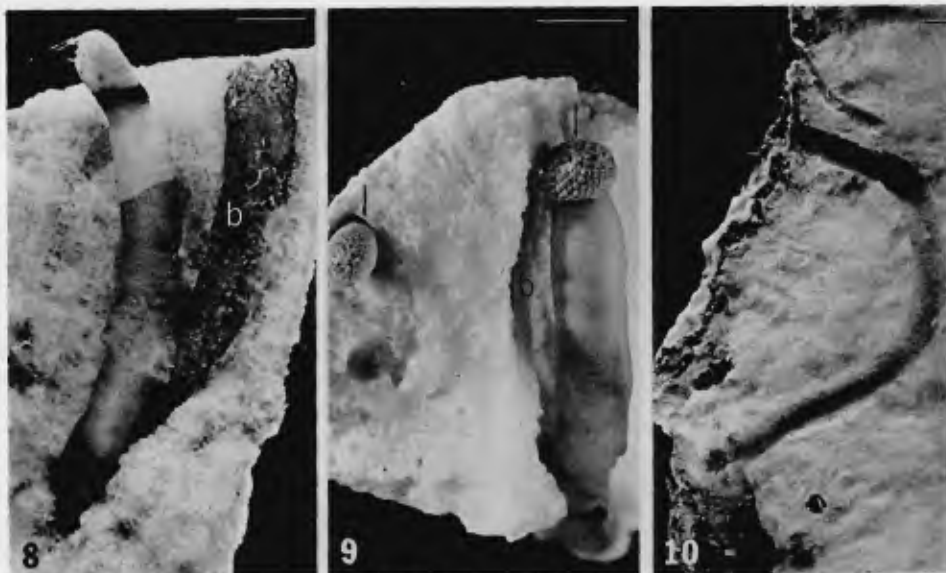


Fig. 8. *Lithacrosiphon gurjanovae* in *Porites astreoides* rock from Carrie-Bow Cay, Belize. Rock is fractured to expose burrow (b); sipunculan is partially dislodged to show wall of burrow. Scale, 2.5 mm.

Fig. 9. *Cloeosiphon aspergillum* in fossilized coralline limestone from Palau Islands. Anterior calcarous shields (arrows) of two specimens are visible. Rock is fractured to expose burrows of one specimen. Scale, 2.5 mm.

Fig. 10. Burrow of *Paraspidosiphon steenstrupi* in *Porites astreoides* rock from Carrie-Bow Cay, Belize. Scale, 2.5 mm.

referred to as shields, at the anterior and posterior extremities of the trunk (Fig. 6). The introvert is somewhat displaced by the anterior shield and extends out at an oblique angle from the trunk. *Cloeosiphon* and *Lithacrosiphon* lack the posterior shield and are characterized by unique variations in the structure of the anterior shield. The anterior shield of *Lithacrosiphon* is a calcareous cone-shaped structure covered by a thickened cuticle (Fig. 8). In *Cloeosiphon* the shield appears as an anterior calcareous knob, composed of small, spirally arranged platelets, each with a central pore which opens from the duct of an epidermal gland (Fig. 9).

Sand-Burrowing Species

Sand-burrowing species of the genera *Sipunculus* and *Siphonosoma* are common throughout the coral communities. Animals in these genera are usually of large size, cylindrical in shape, with short, well-defined introverts. A common tropical species is *Sipunculus indicus*, reported in large numbers on nearly every sand flat in the Maldivé Atolls (Gardiner, 1903a), as well as in coralline sand off the shore of Zanzibar (Stephen and Robertson, 1952), and in various localities throughout the Indo-Pacific (Stephen and Edmonds, 1972). *Sipunculus nudus* is worldwide in distribution and is found not only in tropical waters near coral reefs, but also in

northern temperate waters (Stephen and Edmonds, 1972). Gardiner (1903a) is of the opinion that the activity of sand-burrowing sipunculans is of considerable significance in the conversion of coral sand into mud. From observations on coral reefs of the Maldivé Islands, he found that "animals of the genus (*Sipunculus*) are extraordinarily abundant on all coral reefs in certain positions, such as under dead corals or masses of rock. The quantity of sand that passes through their guts must be considerable, but much of it seems to be retained for a long period—The castings are relatively both small and fine in texture. The quantity of sand passing through the gut does not appear to be great, but what passes through is much triturerated. Perhaps therefore the total action of these animals may be of more importance than that of any other group" (Gardiner, 1903a, p. 341).

Sand-inhabiting sipunculans appear to ingest sand as they burrow. Edmonds (1962) in a study of *Sipunculus nudus* at Morgat, Brittany, France, showed that there was no selectivity in intake of sand but that the granulometric composition of the sand in the gut was approximately the same as that in which the animal lived. He concluded that at least some of its food was organic matter in the sand. Studies of the same species in Quamoy, China (Chin and Wu, 1950) demonstrated large numbers of diatoms in the intestinal contents along with sand and it was concluded that diatoms constituted the main source of nutrition in this locality.

Rock-Boring Species

Rock-boring sipunculans occupy a wide variety of habitats within the coral reef community. They occur in burrows in beachrock, fossil coralline limestone, recent coral rocks and boulders, highly eroded coral rock, coral rubble, and the dead portions of living coral colonies. They are often present in considerable densities, riddling the rock with their burrows. I have measured densities as great as 800 specimens per square meter of coral rock on the barrier reef at Carrie-Bow Cay off the coast of Belize in the Caribbean Sea. Sipunculans reported most commonly in coralline limestone are species of *Phascolosoma*, *Aspidosiphon*, *Paraspidosiphon*, *Lithacrosiphon*, and *Cloeosiphon*.

Of the 60 recognized species of *Phascolosoma* (Stephen and Edmonds, 1972) 82 percent are predominantly tropical in distribution. It is probable that most, if not all, are associated with coral reefs. However, information on habitats is frequently lacking in taxonomic literature. In a collection of sipunculans from coralline limestone and beachrock in the Caribbean Sea *P. perluceus* and *P. antillarum* comprised 46 percent and 16 percent respectively of the total rock-dwelling specimens (Rice, 1975). *Phascolosoma perluceus* was found throughout the Caribbean where it occurred in burrows in all types of rock from friable, highly eroded limestone boulders to hard, compact, and dense recent and fossil coral rock. This species is widely distributed in tropical waters and has been often reported in the Indo-Pacific (Selenka *et al.*, 1883; Sluiter, 1891; Fisher, 1952). *Phascolosoma antillarum*, the second most abundant in the collections from the Caribbean, was also found in burrows within coralline limestone and usually in the same rocks as *P. perluceus* but in fewer numbers. *Phascolosoma antillarum* is absent in the Indian

Ocean and Eastern Atlantic. In the Western Atlantic it has been found at Surinam and Brazil and in several locations in the Pacific (Fisher, 1952). A third species of *Phascolosoma* in the Caribbean collections, *P. varians*, constituted 0.4% of the total specimens. This species was commonly found in crevices of coralline limestone boulders, wedged between branches of *Porites* rubble or buried in a substratum of coarse sand and coral rubble. Only rarely did it occur in burrows and then solely in soft and friable rocks. *Phascolosoma varians* is centered in the Caribbean but has been reported in a few localities in the Indo-Pacific (Stephen and Edmonds, 1972). Species of *Phascolosoma* commonly reported in collections from the Indo-Pacific are *P. nigrescens*, *P. pacificum*, and *P. scolops*. All have been recorded as occurring in dead coral, but whether they are in their own burrows or fissures in the rock is not always clear (Edmonds, 1956, 1971; Sato, 1935; Sluiter, 1891; Stephen and Robertson, 1952).

The combined number of species in the genera *Aspidosiphon* and *Paraspidosiphon* is 48 (Stephen and Edmonds, 1972) and of these approximately 77 percent live in the tropical and subtropical seas where they are usually associated with coral reefs (Shiple, 1899; Sluiter, 1891). In a collection from the Caribbean *A. brocki*, *P. fischeri* and *P. steenstrupi* were the most abundant species of these two genera (Rice, 1975). *Aspidosiphon brocki* has also been reported from the Indo-Pacific, whereas *P. fischeri* is endemic to the Caribbean. *Paraspidosiphon steenstrupi* has been reported, with the exception of the Eastern Pacific, in tropical waters around the world and is considered one of the commonest sipunculans in the Indo-Pacific (Shiple, 1903; Sato, 1939). *Aspidosiphon elegans*, another common Indo-Pacific species, appears to be the first sipunculan to have been reported to inhabit coral rock (Chamisso and Eysenhardt, 1821).

Cloeosiphon and *Lithacrosiphon* occur exclusively in tropical and subtropical seas as borers in calcareous rock, usually coralline limestone. *Cloeosiphon*, a monotypic genus with the single species *C. aspergillum*, is found only in the Indo-Pacific. Five species of *Lithacrosiphon* have been reported from the Caribbean and four from the Indo-Pacific (Stephen and Edmonds, 1972). In a collection from the Caribbean, *L. gurjanovae* comprised 15 percent of the total specimens and was found in great densities at one station in Curacao in intertidal *Porites* rubble (Rice, 1975).

Five of the 25 known species of *Themiste* are tropical to subtropical in distribution. Although they have often been reported in coralline limestone it is not certain whether they form the holes in which they live (Stephen and Robertson, 1952).

At least two patterns of feeding behavior appear prevalent in rock-dwelling sipunculans. Those species with long, extensible introverts and short, digitiform tentacles feed by extending the introvert from the mouth of the burrow, grazing the surface of the surrounding environment. Exemplifying this feeding pattern, *Phascolosoma perlucens*, maintained in the laboratory in intact burrows, has been observed to feed from the surface of the rock on sediment and detritus (Rice, 1975). Some particles adhere directly to the tentacles while others seem to be scraped off

of the rock by the small hooks on the introvert (Fig. 7). Such material is engulfed when the introvert is retracted, presumably being directed into the mouth by ciliary activity of the tentacles. Examination of gut contents of *P. perlucens* has revealed fragments of rock, unidentified fine particulate matter, algal strands, diatoms, foraminifera and a few small crustaceans (Rice, 1975). A second mode of feeding is exhibited by rock-inhabiting species with well-developed, long, filiform tentacles and relatively short introvert such as *P. antillarum* (Fig. 5) and *Themiste lageniformis*. These species feed by a ciliary-mucus mechanism. The tentacular crown is extended above the mouth of the burrow and particles adhering to the sticky tentacles are directed by ciliary currents into the digestive tract. Examination of gut contents of *P. antillarum* has revealed fine particulate matter with a few small fragments of rock and a few strands of algae (Rice, 1975). In studies of *T. lageniformis* the food has been reported as microorganisms and organic debris mixed with sand (Awati and Pradhan, 1935).

It has long been assumed that sipunculans form their own burrows within calcareous rock. This assumption has been based on the exact fit of the animal within its burrow and the smooth lining of the wall of the burrow (Sluiter, 1891). The shape of the burrow has been noted, moreover, to reflect the shape and activity of the species which inhabits it (Rice, 1969). For example, burrows of *Lithacrosiphon* are usually short and straight, those of *Phascolosoma perlucens*, *Paraspidosiphon steenstrupi* and *Cloeosiphon aspergillum* are long, narrow, and sinuous and those of *Phascolosoma antillarum* are straight and wide, terminating in a typically cup-shaped blind end (Figs. 8, 9, 10). Even when sipunculans are densely concentrated within a rock, the burrows rarely intersect.

The mechanisms utilized by sipunculans in the formation of their burrows in calcareous rock have been a subject of much conjecture. Some authors have presumed that boring may be accomplished by chemical secretions (Sluiter, 1891; Shipley, 1890) while others have supposed the burrows to be formed by the abrasive action of cuticular papillae, hooks, anterior and posterior horny shields or anterior calcareous shields (Gardiner, 1903a; Otter, 1937; Yonge, 1963).

A recent review of possible boring structures of sipunculans has cast doubt on the assumption that anterior shields and hooks of the anterior introvert are involved in mechanical excavation of the burrow (Rice, 1969). Observations on living animals in the field have demonstrated that the sipunculan is situated in its burrow with anterior end always directed toward the mouth of the burrow. Thus, in this position, it is likely that the anterior shield functions primarily as an operculum to close the burrow. Further indication that the anterior shield is not involved in abrasive action is the frequent occurrence of algal growth on the shield (Fig. 8). Rather than functioning in formation of the burrow, hooks on the introvert appear to be utilized in securing food. When the introvert is extended over the surface of the rock the hooks pick up a variety of particles which are then ingested. The position of the posterior shield at the blind end of the burrow suggests a possible role in elongation of the burrow. The posterior shield is a thickened cuticular elaboration

comprised of small platelets encompassing the posterior extremity (Fig. 6). In *Paraspidosiphon steenstrupi* the posterior shield of animals removed from burrows has been observed to assume a variety of shapes by extension and contraction. By such movements of the shield against the walls of the burrow, attrition of a relatively friable rock could conceivably occur. In those rock-boring species which lack shields, such as species of *Phascolosoma*, cuticular papillae are usually well-developed in the posterior region and could perform a similar function.

Some authors have suggested that the epidermal glands, opening through the papillary pores of the cuticle, may secrete a substance which is effective in the chemical breakdown of the rock (Sluiter, 1891; Rice, 1969). Little is known of the nature or function of the secretory products of these glands, but they should be considered a possible source of solvents for dissolution of calcareous substrates.

It is difficult to evaluate sipunculid boring experimentally since formation of the hole appears to be a slow process, and animals, once removed from the rock, do not form another burrow under laboratory conditions. Attempts to study the boring mechanism have been confined thus far to an examination of the burrows themselves. Rice and Macintyre (1972) studied thin sections of rock through burrows of several sipunculids from the Caribbean: *Paraspidosiphon steenstrupi*, *P. khunzingeri*, and *Phascolosoma antillarum*. Microscopic examination of the linings of the burrows suggested that both mechanical and chemical processes could be involved in burrow formation. Indications of mechanical abrasion in burrows in coral fragments with sediment infill were found in the finely comminuted carbonate skeletal grains in pockets of the walls of the burrows. However, the source of the comminuted material was uncertain. Indication of chemical activity was found in the alteration of the microstructure of components of the rock at the edge of the burrow.

In an examination of burrows with the scanning electron microscope, Williams and Margolis (1974) similarly concluded that both mechanical and chemical activities were involved in sipunculid boring. In burrows of *Themiste lageniformis* in dead coral rock they found that crystals within the lining of the burrow were etched, pitted, and eroded. Similar alterations were induced by treatment with dilute concentrations of different acids and EDTA. In addition, they reported aggregates of etched and disrupted crystals in spaces between corallite walls in the burrow lining. From these findings they concluded that after weakening of intercrystalline bonds by chemical secretions the crystals within the walls of the burrow could be displaced by mechanical abrasion and deposited in skeletal cavities.

Evidence of chemical etching has also been noted in scanning electron micrographs of the burrows of *Paraspidosiphon steenstrupi* and *Lithacrosiphon gurjanovae* in coral rock (Rice, unpublished). In freshly fractured coral rock adjacent to the burrow, the surface was found to be composed of tightly interlocking crystals of calcium carbonate (Fig. 11, 12), whereas crystals within the lining of the burrow were etched and eroded (Fig. 13). Around the edges of the cavities within the skeletal framework of the coral, the presence of fracture lines indicated a weakening

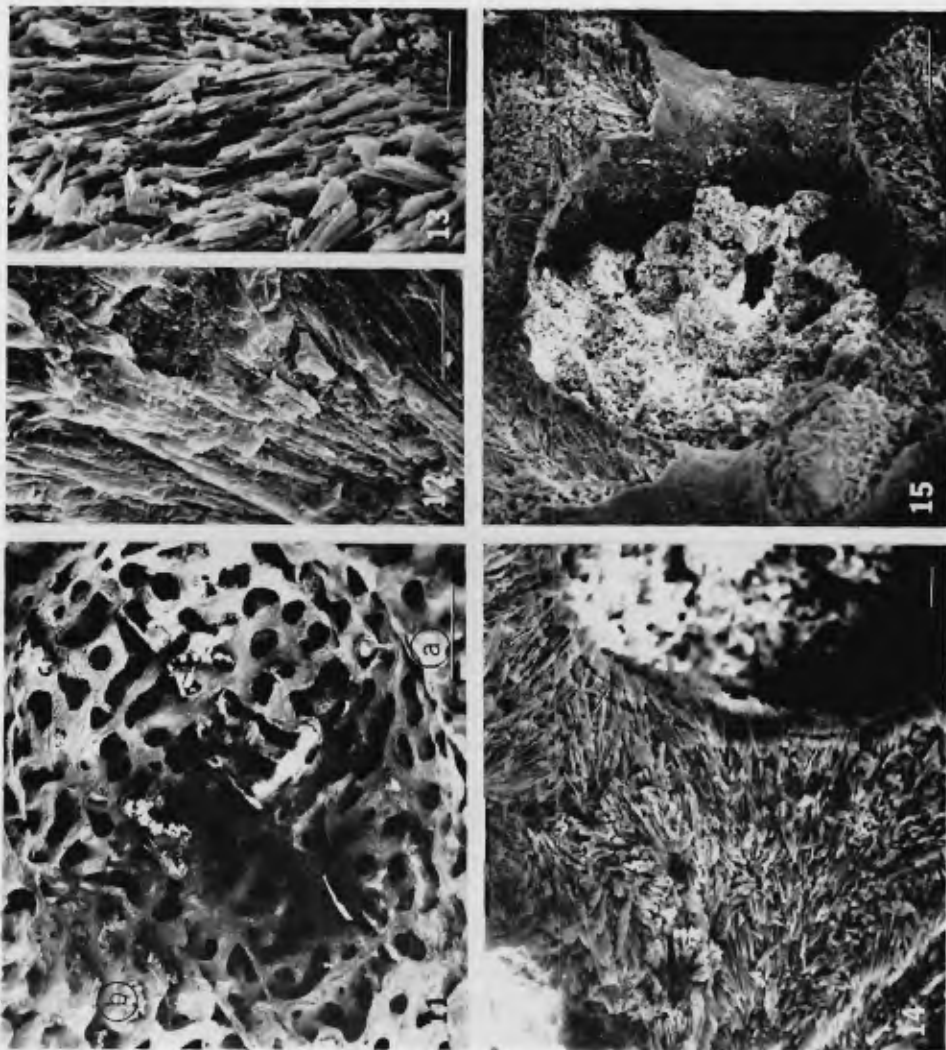


Fig. 11-15. Scanning electron micrographs of burrow of *Paraspidosiphon steenstrupi* in *Porites astreoides* rock from Carrie-Bow Cay, Belize.

Fig. 11. Burrow of *Paraspidosiphon steenstrupi*. The concavity is the blind posterior end of the burrow. Skeletal cavities of the coral are apparent. Scale, 500 μm .

Fig. 12. Freshly fractured surface of the rock outside of burrow, region a, Figure 11. Note tightly interlocking crystals. Scale, 5 μm .

Fig. 13. Lining of burrow; higher magnification of Figure 14. Crystals are etched and eroded. Scale, 5 μm .

Fig. 14. Within burrow. Note fracture lines around edge of skeletal cavity (arrows). Scale, 10 μm .

Fig. 15. Skeletal cavity with sediment infill in lining of burrow. Region b, Figure 11. Only areas of high relief are etched. Scale, 5 μm .

of the skeletal structure in the lining of the burrow (Fig. 14). It is likely that such weakened portions would be readily abraded by movement of the animal within the burrow. Surfaces of low relief in depressions of skeletal cavities were smooth, in marked contrast to the etched surfaces of areas of high relief (Fig. 15). Since the body of the sipunculan when in situ would be touching the areas of high relief, a probable explanation is that etching occurs in response to body contact.

Although adult sipunculans, once removed from their burrows, have not been observed to form new burrows, boring has been affirmed in the laboratory in the case of juveniles of an unknown species of *Aspidosiphon*. The juvenile worms, reared from oceanic planktonic larvae, entered small holes in coral rock and, during a six-month period of observation, the holes were slowly enlarged as the worms increased in size. It is postulated that in its natural environment a sipunculan enters a crevice or cavity in a rock as a juvenile and that, with growth, it enlarges the hole to form a burrow which it inhabits for the duration of its existence.

No estimates are available of the relative contribution of boring sipunculans to carbonate breakdown in coral reefs, but their abundance in reef communities suggests that their activity may be a significant factor in reef erosion. The presence of sipunculan burrows, along with those of other boring organisms, in the dead basal portions of living coral colonies weakens the attachment of the coral, increasing its susceptibility to breakage and dislodgement. The accumulation of rubble and the eventual breakdown of a reef are at least in part the result of the action of boring sipunculans associated with the reef community.

Acknowledgments

I am indebted to Dr. Ian Macintyre, Department of Paleobiology, Smithsonian Institution, for advice and help in the examination of sipunculan burrows by scanning electron microscopy. Mr. Douglas Putnam, Harbor Branch Foundation Science Laboratory, Fort Pierce, Florida, is gratefully acknowledged for his assistance in the collections and observations on the reefs of Belize, Caribbean Sea. I also thank Mr. William Davenport, Harbor Branch Foundation Science Laboratory, for photographic aid. Observations and collections of Indo-Pacific species were made on the Te Vega Expeditions, Cruise B, International Indian Ocean Expedition.

REFERENCES CITED

- Awati, P. R., and L. B. Pradhan. 1935. The anatomy of *Dendrostoma signifer* Sel. et de Man 1883. Part 1. J. Univ. Bombay 3: 102-113.
- Baird, W. B. 1873. Descriptions of some new species of Annelida and Gephyrea in the collections of the British Museum. J. Linn. Soc. (Zool.) 11: 94-97.
- Bourne, G. C. 1906. Report on *Jousseaumia*, a new genus of Eulamellibranchs commensal with corals *Heterocyathus* and *Heteropsammia*. Rep. Pearl Oyster Fish. Manaar, Roy. Soc., 5: 243-264.
- . 1907. Notes. Proc. Malac. Soc. Long. 7: 260.

- Bouvier, E. L.** 1895. Le commensalisme chez certaines polypes madréporaires. *Annls. Sci. nat. Zool.* 20: 1-32.
- Chamisso, A., and C. G. Eysenhardt.** 1821. De animalibus quibusdam e classe vermium linneana etc. *Nova. Acta Acad. Caesar Leop. Carol* 10: 343-374.
- Chin, T. G., and C.S. Wu.** 1950. Diatoms in the intestine of Amoy Sipunculids (Annelida Gephyrea). The food of Sipunculida. *Lingnan Sci. J.* 23: 43-52.
- Cutler, E. B.** 1965. Sipunculids of Madagascar. *Oceanographie* 3(4): 51-63.
- Edmonds, S. J.** 1956. Australian Sipunculoidea. 2. The genera *Phascolosoma*, *Dendrostomum*, *Golfingia*, *Aspidosiphon* and *Cloeosiphon*. *Aust. J. Mar. Freshwat. Res.* 8: 82-97.
- . 1962. Some notes on the abundance, environment and nutrition of *Sipunculus nudus*. L. (Sipunculoidea) at Morgat, Brittany. *Cah. Biol. Mar.* 3: 183-190.
- . 1971. Some sipunculans and echiurans, chiefly from Guam (Sipuncula and Echiura). *Micronesia* 7(1-2): 137-151.
- Edwards, M. and J. Haime.** 1848a. Recherches sur les polypiers. II. Monographie des Turbinolides. *Ann. Sci. Natur. (Ser. 3, Zool.)* 9: 211-344.
- . 1848b. Recherches sur les polypiers. III. Monographie des Eupsammides. *Ann. Sci. natur. (Ser. 3, Zool.)* 10: 65-114.
- Feustel, H.** 1965. Anatomische Untersuchungen zum Problem der *Aspidosiphon-Heterocyathus*-Symbiose. *Verh. der Deutsch Zool. gesell. Jena* 1965: 131-143.
- Finckh, A. E.** 1904. Biology of the reef-forming organisms at Funafuti Atoll. *Rep. Roy. Soc. London, Coral Reef Comm.* 1904: 125-150.
- Fisher, W. K.** 1952. The sipunculid worms of California and Baja California. *Proc. U.S. Natn. Mus.* 102: 371-450.
- Gardiner, J. S.** 1903a. The Maldive and Laccadive Groups, with notes on other coral formations in the Indian Ocean. *The Fauna and Geography of the Maldive and Laccadive Archipelagoes*, 1, 333-341.
- . 1903b. The origin of coral reefs as shown by the Maldives. *Amer. J. Sci.* 16: 203-213.
- Goreau, T. F. and C. M. Yonge.** 1968. Coral community on muddy sand. *Nature* 217: 421-423.
- Illg, P. L.** 1975. Copepod associates of Sipuncula and Echiura. *Proceedings of the International Symposium on the Biology of the Sipuncula and Echiura.* In Press, Nauco Delo Press, Belgrade.
- Otter, G. W.** 1937. Rock-destroying organisms in relation to coral reefs. *Brit. Mus. (Nat. Hist.) Great Barrier Reef Expedition 1928-29.* 1(12): 323-352.
- Rice, M. E.** 1969. Possible boring structures of sipunculids. *Am. Zoologist* 9: 803-812.
- . 1975. Survey of the Sipuncula of the coral and beachrock communities of the Caribbean Sea. *Proceedings of the International Symposium on the Biology of the Sipuncula and Echiura.* In Press, Nauco Delo Press, Belgrade.
- Rice, M. E., and I. G. Macintyre.** 1972. A preliminary study of sipunculan burrows in rock thin-sections. *Carib. J. Sci.* 12(1-2): 41-44.
- Rice, M. E., and A. C. Stephen.** 1970. The type specimens of Sipuncula and Echiura described by J. E. Gray and W. Baird. *Bull. Brit. Mus. (Nat. Hist.) Zool.* 20(2): 49-72.
- Sato, H.** 1935. Sipunculoidea and Echiuroidea of the West Caroline Islands. *Sci. Rep. Tohoku Univ. Ser. 4*, 10: 229-329.
- . 1939. Studies on the Echiuroidea, Sipunculoidea, and Priapulidae of Japan. *Sci. Rep. Tohoku Univ. Ser. 4*, 14: 339-460.
- Schindewolf, O. H.** 1958. Würmer und Korallen als Synöken. Zur Kenntnis der Systeme *Aspidosiphon/Heterocyathus* und *Hicetes/Pleurodictyum*. *Akademie der Wissensch. u. Lit. Mainz. Abh. Math. Nat. Klasse* 6: 1-70.
- Selenka, E., J. G. De Man and C. Bülow.** 1883. Die Sipunculiden. *Reisen im Archipel Philippinen von Dr. C. Semper.* Leipzig and Wiesbaden, pt. 2, 4(1): 1-133.
- Shipley, A. E.** 1899. A report on the Sipunculoidea collected by Dr. Willey at the Loyalty Islands and in New Britain. (In) *A. Willey, Zool. Res.* 2: 151-160.

- . 1903. Report on the Gephyrea collected by Prof. Herdman at Ceylon in 1902. Herdman Rep. Pearl Oyster Fishery 1(3) suppl.: 169-176.
- Sluiter, G. P.** 1891. Die Evertebraten aus der Sammlung des königlichen naturwissenschaftlichen Vereins in Niederländisch Indien in Batavia. Zugleich eine Skisse der Fauna des Java-Meeress mit Beschreibung der neuen Arten. *Natuurk. Tijdschr. Ned. Indie* 50: 102-123.
- . 1902. Die Sipunculiden und Echiuriden der Siboga-Expedition, nebst Zusammenstellung der Ueberdies aus den indischen Archipel bekannten Arten. *Siboga-Expedition. Monographic* 25: 1-53.
- Stephen, A. C., and S. J. Edmonds.** 1972. The phyla Sipuncula and Echiura. British Museum (Nat. Hist.), London, 528 pp.
- Stephen, A. C., and J. Robertson.** 1952. A preliminary report on the Echiuridae and Sipunculidae of Zanzibar. *Proc. R. Soc. Edinb.* 64, sect. B(22): 426-444.
- Vaughan, T. W., and J. W. Wells.** 1943. Revision of the suborders, families and genera of the Scleractinia. *Geol. Soc. Amer., Spec. Pap.* 44, xv+363 pp.
- Williams, J., and S. V. Margolis.** 1974. Sipunculan burrows in coral reefs: evidence for chemical and mechanical excavation. *Pacific Science.* 28 (4): 357-359.
- Yonge, C. M.** 1963. Rock-boring organisms, p. 1-24. In R. F. Sogannaes (ed.), *Mechanisms of hard tissue destruction.* Publ. No. 75. Amer. Assoc. Advan. Sci. Washington, D. C.
- . 1975. A note on mutualism between sipunculans and scleractinian corals. *Proceedings of the International Symposium on the Biology of the Sipuncula and Echiura.* In Press. Naučno Delo Press, Belgrade.



