

THE ROLE OF PSAMMOBIONTIC SPONGES IN THE REEF COMMUNITY

Klaus Rützler

Department of Invertebrate Zoology, National Museum of Natural History
Smithsonian Institution, Washington, D.C. 29560, U.S.A.

ABSTRACT

Unconsolidated carbonate sediments are a substantial part of reefs where they alternate with the coral framework and form the surrounding sea floor. Although most sponges are occupants of solid substrata, a few species have pioneered into sand habitats by developing morphological and ecophysiological adaptations for anchoring and endobenthic existence. The Caribbean staghorn sponge *Spheciospongia cuspidifera* (Clionidae) is discussed as an example. The hitherto known "sponge" is primarily its large incurrent siphon complex, which is photosynthetic owing to the presence of zooxanthellae. The main functional part of the sponge, containing water-propelling choanocyte chambers, reproductive cells, and exhalant canal system, is entirely buried in the sand substratum. Psammobiontic sponges contribute by consolidating, venting, and enriching reef sands and by generating patch-reef communities on sandy bottoms.

INTRODUCTION

Sponges are sessile filter feeders with a free-swimming larva (e.g., parenchymula, in demosponges). The larva stays close to the bottom, swims badly and only for a few hours or days, and, after a brief crawling phase, settles

unstable and subject to new deposits and scouring action by storms. In the calmer environments of back reefs and lagoonal patch reefs, similar sand and rubble substrates shift only during periods of strong water agitation and allow colonization by seagrasses and build-up of miniature reefs on substrate pieces as small as single dead coral branches and snail shells, including a few fast-growing sponges.

In the Caribbean, these sand flats may be colonized by conspicuous clusters of 30 cm tall, slender, light brown columns, commonly branching and tapering toward the top (Fig. 1). Based on the abundant and dense siliceous spicules, these "staghorns" were long identified as sponges, *Spheciospongia cuspidifera* (Lamarck) (Clionidae, Hadromerida) [misinterpreted but well described as *Xestospongia tierney* (de Laubenfels) by Wiedenmayer, 1977:117], although they do not show oscula, usually prominent features of sponges that size.

During the late 1980s, while studying systematic and ecological aspects of West Indian *Spheciospongia*, I took a special interest in *S. cuspidifera*, a species that is common on sand substrate between patch reefs near Carrie Bow Cay, on the barrier reef of Belize. By trying to collect intact specimens for aquarium observations, I

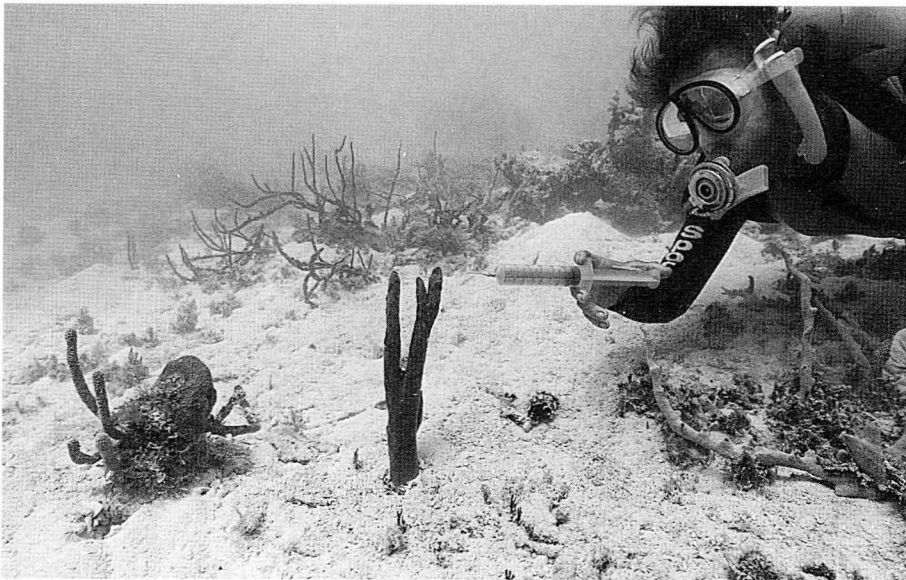


Fig. 1: Typical specimen of *Spheciospongia cuspidifera* at the perimeter of a lagoon patch reef in southern Belize. Diver is holding syringe with fluorescent dye used in current flow experiment.

readily on most non-toxic substrates that have been submerged in seawater for some days and developed a coating of biofilm. While larval swimming and settlement behavior does not appear to be influenced by substrate chemistry, in vitro experiments clearly show effects of light, water movement, and gravity and that these factors may cause different responses in different stages of development. This textbook knowledge (Sarà and Vacelet 1973, Bergquist 1978) can be demonstrated by anyone working with readily available demosponge larvae.

Laboratory observations indicate considerable propagule waste from irreversible attachment to unsuitable substrates. Yet most coral reef habitats are occupied by a characteristic species complement of sponges, suggesting that some selection processes are at work and are aided by the poor dispersal capabilities of sponge larvae.

Sandy patches or grooves on shallow (to 10 m) exposed fore-reef zones are devoid of sponges and other slow-growing sessile organisms because the sand is highly

discovered that this species has developed a special mode of life that is unusual for sponges but a highly efficient adaptation to the sand habitat.

MATERIAL AND METHODS

Voucher specimens of *Spheciospongia cuspidifera* examined during this work are deposited in the sponge collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Systematic description and discussion were part of another study (Vicente et al. 1991). Observations were made by scuba on a series of patch reefs, 4-10 m deep, situated on the barrier-reef platform, outer Belize lagoon, SSW of Carrie Bow Cay (16 48'N, 88 05'W; Rützler and Macintyre 1982). Sponge pumping and other water movements were traced with fluorescent dye dissolved in seawater. Histological fixation for light and transmission electron microscopy was in 1.5% glutaraldehyde buffered in 0.2 M cacodylate with 0.1 M sodium chloride and 0.4 M sucrose (2 h at 4 C), followed by 2% osmium tetroxide in the same buffer (1 h at 30 C room temperature).

RESULTS

Morphology and growth habit

The basic shape of *Sphaciospongia cuspidifera* is that of a single, tapering column reminiscent of an inverted icicle. Larger specimens branch near the top or halfway down the column and may look like a staghorn, or become thickened and club-like in the upper portion. Clusters of differently-shaped specimens are often encountered. Total height, from substrate level to top, is typically 20-30 cm, the largest specimen measured was 36 cm tall. The diameter just above the substrate is 2-8 cm, branches either taper to 1.5-2.5 cm or, in club-shaped specimens, may thicken terminally to 8 cm. The crown diameter of an elaborately branched specimen (7 branches, observed maximum) does not exceed 12 cm. The trunk is cylindrical, subcylindrical, or somewhat angular and flattens along its length in the plane of branches. The surface is lipistomous, looks smooth, and feels like fine sandpaper. In many specimens it becomes tuberculate or rugose or develops convoluted ridges near the upper parts of the column; in places these structures appear rough, almost frayed, possibly zones of new growth. Consistency is firm, almost hard, but elastic and tough; it compares well to solid cork. The color of light-exposed column varies from light walnut to deep chestnut brown; it fades to tan and white below the surface layer and where the trunk enters the sandy substrate. The inside of the entire specimen is hollow, with some longitudinal dividing walls and membranes in the trunk portion. The outer wall measures 5-16 mm in thickness at the base and becomes gradually thinner toward the blind-ending top. There are no obvious openings through the wall except for rare, healed bites (by fishes or sea turtles) and, in some specimens, abundant barnacle burrows.

Most museum specimens, many collected by myself, are frayed at the base, obviously broken near the substratum level. Efforts to retrieve the entire buried portion require the use of digging tools but reveal a semiglobular or conical base that expands from the trunk to several centimeters below the sand surface. This basal mass is grayish white in color, heavily incrustated with sand and shell, and extends large-diameter (5-12 mm) tubes and root-like outgrowths. The inner portions of the mass, too, contains incorporated sand and pieces of rubble. Maximum penetration into the substrate is usually less than 30 % of the height of the column, about 5-12 cm. Clusters of 2-5 or more specimens were found with bases connected underground. Excavation of some sponges revealed that their bases were not only permeating or incorporating sand and shell particles but that they also bored through large pieces of solid coral rock.

Fine-structure anatomy and symbionts

The epibenthic columns of *Sphaciospongia cuspidifera* are supported by a strong, three-dimensional reticulation of thick spicule tracts forming the outer skeleton layer, confused spicule bundles throughout the center portion, and a two-dimensional net with enhanced longitudinal strands lining the inner cavity. Megascleres grade from tylostyles to strongyles. Membranes of longitudinally oriented spongin are sandwiched between skeleton layers. Incurrent pores and canals are abundant, particularly near the top of branches. Pinacocytes, lining surfaces and canals, spherulous cells, archeocytes, and zooxanthellae are the principal cell components (Fig. 2a). The spherical zooxanthellae measure 8-9 μ m in diameter and are always intracellular, one per sponge cell, two if they are daughter cells from recent division. The host cells containing the algae tend to cluster in groups (6-20 per cross section). A choanosome could not be detected in any part of the sponge columns but extensive search of light-microscope sections revealed a few isolated choanocyte chambers among the spicule strands.

The pale-colored underground basal mass off the sponge is cavernous from large exhalant canals and sand grains and shell particles are incorporated throughout. It contains spicules in diffuse tracts and in crisscross fashion. Abundance of choanocyte chambers in dense groups between spicules, sand, and canals indicates that this is choanosome (Fig. 2b). Each measures 15-20 μ m in diameter and shows 4-6 choanocytes per cross section. Central cells (able to control water flow from the chamber) and periplagellar sleeves (of uncertain function) are present; they are common features of Hadromerida.

Spherulous cells and archeocytes are also abundant and several reproductive cells were seen.

Ecology and pumping activity

Sphaciospongia cuspidifera is widely distributed throughout the Caribbean; confirmed records include the Bahamas, Hispaniola, Puerto Rico, Cuba, Belize, Nicaragua, Panama, and Colombia. Typical habitats are sand areas on or near storm-protected reefs, 2.5-20 m deep. The sponges are always anchored in sand and even though they bore through pieces of buried rubble they were never found protruding from rock or coral surfaces, like the similar-looking but smaller fistulas of the unrelated excavating sponge *Aka* (= *Siphonodictyon*) spp. (Haplosclerida). Two other but less conspicuous sponges in the same habitat are the mostly buried *Oceanapia* (= *Foliolina*) *peltata* (Schmidt) and *Tectitethya* (= *Cryptotethya*, *Tethya*) *crypta* de Laubenfels (Hadromerida). Three types of symbionts regularly associated with *S. cuspidifera* are the aforementioned zooxanthellae, the polychaete *Branchiosyllis oculata* Ehlers which inhabits the surface of the columns, and the burrowing barnacle, *Membranobalanus declivis* (Darwin), which produces circular openings that can be misinterpreted as oscula. No field observations are available on predation but in feeding-choice experiments with the starfish *Oreaster reticulatus* (L) it was eaten only 4 out of 23 times it was offered (Wulff 1995).

The apparent lack of aquiferous openings through the wall of the sponge columns suggested to track the water-flow through the sponge by applying fluorescent dye dissolved in seawater. During slack tide on a calm day we released dye from a syringe in small clouds along the column of one specimen and were surprised to see it disappear through the porous wall into the lumen of the sponge. As the dye did not reappear, we applied more, and more. To our surprise, after 10-15 sec, the sand bottom surrounding the sponge to a radius of 40 cm started "steaming" dye for several seconds. It became clear that the sponge had pumped water through the cylindrical epibenthic structures into the buried base from where it exited and passed through the sand and gravel of the substrate.

Other psammobiontic reef sponges

In the study area, only three other sponges were found regularly and sometimes deeply embedded in sand substratum. *Sphaciospongia vesparium* Lamarck, the closest relative to the species studied, forms large, cake-shaped masses but starts out as small chimneys, typically 8 cm tall and 4 cm in diameter, deeply anchored in sand or rock. Oscula in this type are the openings on top, ostia are grouped sieve-like on special swellings or protuberances at the base. This type of *S. vesparium* was previously called habit b (Wiedenmayer 1977); it is also known as a limestone-excavating stage (Rützler 1974). The tethyid *Tectitethya crypta* has most of its large, conical to hemispherical body covered by sand except for the distinctive oscular cone. The 1 mm ostia occur in clusters along the flank of the sponge and may be covered by sand. The oscula, 20-25 mm in diameter, are located on top of the cone and can be contracted. *Oceanapia peltata* is barely visible, except for its 5-15 cm tall, 10 mm thick incurrent fistulas that protrude from the sand surface, end blind, and are ornamented with characteristic disk-like ridges along their sides; these siphons are overgrown by encrusting sponges (e.g., *Artemisia* sp.), milleporid hydrocoral, and algal turfs. Below ground, the fistulas extend twice or more of the surface portion and 5-8 of them enter one spherical body of 5-10 cm diameter. Opposite the ostial fistulas are fewer, shorter and thinner, root-like tubes.

Applying dye to *Sphaciospongia vesparium* and *Tectitethya* showed the expected typical current flow, from ostia (some buried) to osculum. Dye squirted toward the *Oceanapia* fistulas disappeared and resurfaced from the sand substrate, identifying the root tubules as oscular structures and the flow direction downward into the sand, just as in *Sphaciospongia cuspidifera*. It may be of interest to mention here that upon TEM examination of the bulb, *O. peltata* turned out to be a bacteriosponge, with about 50% of the cell mass composed of bacterial symbionts. This sponge was first described as *Foliolina peltata* in 1870, but for almost 120 years it was only known from the small, epibenthic portions of its "pagoda"-like incurrent siphons tubes. Our study in Belize and a survey off Nicaragua revealed the first complete specimens, the latter described by Zea (1987)

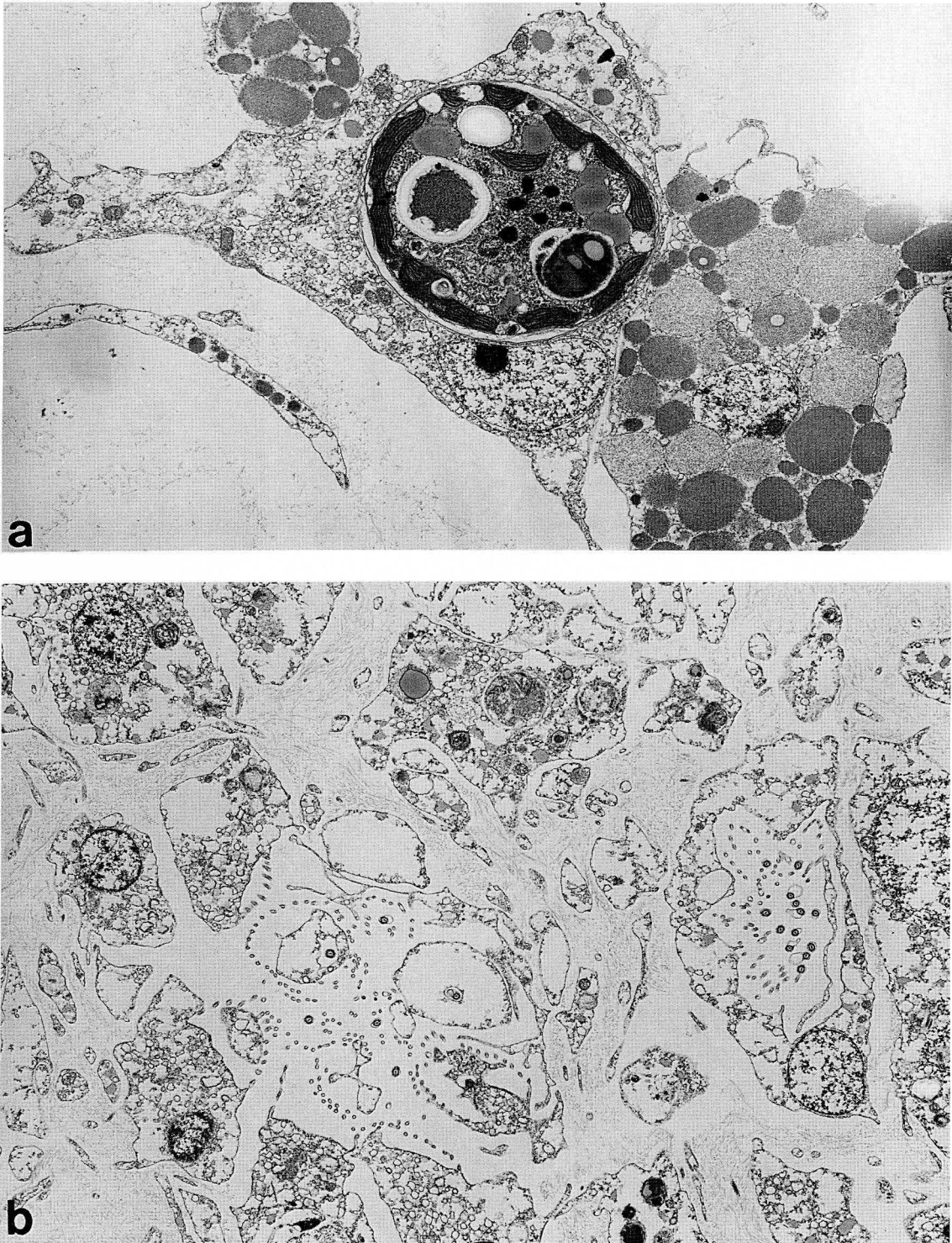


Fig. 2: Transmission electron micrographs of *Spheciospongia cuspidifera*. a Epibenthic ectosome (near top of staghorn) showing spherulous cell and intracellular zooxanthella (x3000). b Endofaunal choanosome with choanocyte chambers; note flagellae and microvilli protruding through lumen of central cell at left (x2500).

who also suggested correctly that *Foliolina* should fall to *Oceanapia*.

DISCUSSION

Organization and function of *Spheciospongia cuspidifera*

Histology and dye observations make it clear that the epibenthic columns or staghorns of *Spheciospongia cuspidifera* are nothing but elaborate incurved siphons, comparable to those of *Aka* (= *Siphonodictyon*) and some

Oceanapia. However, they can also be interpreted as important photosynthetic structures, sun-exposed greenhouse extensions of the underground organism. Understanding this organization, it is not surprising that no choanosome was found in the epibenthic columns although they constitute a substantial part of the biomass in this species. It appears that, because of the presence of zooxanthellae, these "fistulas" are nutritionally quite independent of filter feeding although some food particles could still be retained from

the stream of water passing through the walls. The few isolated choanocyte chambers detected in that region may aid in the trapping and absorption of particles and serve the local transport of oxygen and waste. The zooxanthellae resemble in fine structure *Symbiodinium* (= *Gymnodinium*) *microadriaticum* Freudenthal, the dinoflagellate symbionts ubiquitous in hermatypic corals and other cnidarians (for instance, Trench 1987) and also known in some clionid sponges (Rützler 1990).

The buried, choanosomal sponge mass provides for anchoring, water pumping, and reproduction. The course of water transport is unusual for it goes from the water column through the entire sponge and into the sediment substrate from where it percolates up, back into the open water. Other sponges with pronounced siphons and buried or excavating basal mass, such as *Aka siphona* (de Laubenfels) and *A. coralliphaga* (Rützler), have blind-ending incurrent tubes and open oscular siphons next and parallel to each other (Rützler 1971) allowing direct communication with the surrounding water. *Spheciospongia vesparium* and *Tectitethya* function similarly, except that pores and pore sieves are not raised on tubes and may be buried in sand. *Oceanapia peltata*, on the other hand, produces a water-flow pattern much like *S. cuspidifera* but lacks the elaboration and functional importance of the incurrent siphons demonstrated by the staghorn sponge. The fistulose habit of *Petromica ciocalyptoides* (van Soest and Zea), a little known sponge found in Colombia and Panama, suggests that it too might be functionally comparable to *S. cuspidifera* (J. Wulff, pers. comm.).

Comparison with other sediment-dwelling sponges

Several other sponge species are known to occupy sandy substrates, some having a special body plan to facilitate this life style. *Biemna ehrenbergi* (Keller) (Poecilosclerida) lives attached to sand-buried beach rock in the Red Sea (Ilan and Abelson 1995). Its ostia are located along the wall of the conical sponge (topped by the osculum) and below the substrate surface, thus taking in interstitial water. This mechanism is similar to that of buried *Tectitethya* and of mangrove sponges (e.g., *Haliclona*, *Biemna*, *Ircinia* spp.) that may fall off their stilt-root substrate and survive for many months covered almost entirely by fine sediments (Rützler, unpublished). *B. ehrenbergi* is a bacteriosponge, just like *Oceanapia peltata* described above. The life habit of the latter species, and its relative *O. oleracea* Schmidt, both from Colombia, were analyzed by Werding and Sanchez (1991) who also determined the pumping direction through oscular root tubes into the sediment substrate. *T. crypta*, part of a series of detailed ecophysiological studies in Jamaica, is capable of strong body contraction and complete closure of the osculum (e.g., Reiswig 1971), both valuable attributes for living in sandy habitats.

Much less conspicuous infaunal forms are species of *Tribachium*, *Tethyopsis*, *Monosyringia*, and *Kapnesolenia*, with a small, spherical body and one long, tapering oscular tube, and of *Disyringia*, with a similar choanosome and two opposite siphon structures, one blind and one open ending. More than a century ago, Sollas (1888), describing representatives of the two morphological types, started a controversy about function of the tubes, inhaling versus exhaling, and, indirectly, about the position of these sponges in their substrate. In case of the *Tribachium* type, its position in sand was clarified by divers who observed the bulb buried 5-6 cm below the surface of muddy sand (Fry and Fry 1979). But, without experimental or histological evidence, the latter authors excluded the possibility of water intake through pores on the surface of the buried bulb and suggested that ostia seen at the base of the oscular tube served this function. *Disyringia*, where no direct observations are available, was suspected by Sollas (1888) to bring in water through the large opening of the single-duct tube (which he drew pointing downward) and expel it through smaller pores situated along the opposite, blind-ending, four-duct tube. Fry and Fry (1979) rejected this interpretation and, based on a hydrodynamic model, suggested that both current flow and position in the substrate had to be reversed, closed tube with ostia (and bulb with choanosome) buried, open oscular tube protruding from the substrate. This view was opposed by Werding and Sanchez (1991) who considered intake of interstitial water from sand unlikely and proposed that the current flow had to be reversed: intake through the large opening on top, exit through small pores below.

Although observations on *Oceanapia* support the concept of flow direction from water column into sediment, there is no evidence in Porifera that water enters through one large opening and exits through many small pores. In fact, the *Oceanapia* and *Spheciospongia cuspidifera* examples would rather suggest that the closed (ostial) siphon is on top, the oscular tube buried, which is the forth and last possible hypothesis regarding position and flow direction in *Disyringia*. The Fry and Fry (1979) model, however, is just as likely and strengthened by the examples of other species with sand-covered ostia, particularly that presented by Ilan and Abelson (1995). We await the first in situ observation with great curiosity.

Community benefits

It is possible that in Porifera morphological and physiological adaptations for living in sediment bottoms depend on the nature of the substratum, its grain size, content of organic matter, and exposure to currents. Fine sand with organics may be stable in protected environments and provide ample food in its interstitial water but would not allow a strong oscular flow; it is likely to be inhabited by sponges with buried ostial and free oscular structures. Coarse sand under conditions of moderately strong water movement can be settled by robust species that incorporate and stabilize sediments and discharge their waste water through siphons, hollow stolons, and other anchoring structures. The underground flow stimulates water circulation through the bottom sediments and may provide nutrients for bacteria and other organisms, thus benefiting the interstitial community. There is also evidence (Rützler 1974; unpublished) that both species of *Spheciospongia* are efficient limestone excavators, a physiological adaptation that aids anchoring and may contribute to lithification processes and build-up of sponge bioherms, as described by Wiedenmayer (1978) from the Bahama bank.

Psammobiotic sponges create microhabitats of stabilized, vented, and nutrient-enriched sediment and attract other organisms to live in, on, or near them. They are seed and center of new patch-reef communities, islands in a sea of sand.

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