Siliceous Sponge Spicules in Coral Reef Sediments

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Abstract

Experimental etching with hydrofluoric acid indicated that silica deposition occurs in a recognizable pattern in common sponge microscleres. The postdepositional alteration of these spicules has previously been generally unrecognized or misinterpreted in the literature. Early stages of postdepositional etching of sponge spicules were observed in the acid insoluble fraction of sediments from the West Atlantic barrier reef near Carrie Bow Cay, Belize. Preliminary data on silica distribution in the Belize barrier reef show that concentrations in fine sediment (<0.25 mm) increase landward of the main reef tract. Sponge spicules are the main component of particulate silica in sediments of the reef and fore-reef where sponge populations abound, whereas grains prevail in the back-reef lagoon deposits. Recycling of locally dissolved silica appears to be important for the growth of many off-shore reef sponges.

Introduction

"The spicule which has lived, has to decay, and may live again in another form." (Duncan, 1881).

Sponges contribute to reef sediments in two ways: (1) excavating species (e.g. clionids) produce quantities of carbonate silt by eroding coral rock, mollusk shells and similar substrates (Neumann, 1966; Rützler, 1975; Moore and Shedd, 1977); (2) the majority of sponge taxa (main exception, order Keratosa) form spicules that are liberated when the animals decay. Sponges use two mineral materials to produce skeletal spicules. In the class Calcarea, the simple diactines, triactines and tetractines are composed of calcite. Calcareous sponges make up only a small percentage of the sponge biomass in reefs. Members of all other sponge classes (Demospongea, Sclerospongea, Hyalospongea) produce spicules of opaline silica.

In the sea, diatoms, radiolarians, sponges and silicoflagellates participate in the mineralization of silica. Although substantial sponge spicule mats 2 m thick and larger have been observed in Antarctica (Koltun, 1968; Dayton *et al.*, 1974), on a worldwide basis such deposits rank behind accumulations such as Antarctic diatoms or deep-sea radiolarian oozes. In coral reefs, sponges are known to be quantitatively important (Rützler, 1978), yet no information is available about their participation in cycling silica. Therefore, we examined the distribution and origin of silicious sponge spicules in a modern coral reef complex near Carrie Bow Cay, Belize (Central America) and studied the effect of postdepositional alterations on their morphology. We attempted to reproduce patterns of suspected dissolution in the laboratory and searched the literature on recent and fossil deposits for documentation of similar occurrences. Finally, we looked for sources of dissolved silica needed for mineralization processes in growing sponges.

Materials and Methods

Clean siliceous spicules were separated from sponge tissues by boiling in concentrated nitric acid and thorough rinsing in distilled water. Sterrasters were obtained from *Geodia cydonium* (Jameson) (Adriatic Sea) and *G. neptuni* (Sollas) (Belize), spherasters from *Chondrilla nucula* Schmidt (Belize) and selenasters from *Placospongia carinata* (Bowerbank) (Gulf of

Mexico). Scanning electron microscope preparations were made by drying spicules on small circular cover slips which were mounted on stubs, coated with carbon and, subsequently, with platinum. A Cambridge Stereoscan Mark II A was employed at 100 x to 8000 x primary magnifications.

Sections of spicules were made by grinding and polishing material embedded in epoxy. These were etched for 30 sec or 5 min in 6% hydrofluoric acid (HF), with gentle agitation. Whole spicules were also etched for 5 min and 30 min in 24% HF.

Sediment samples were taken at 10 locations near Carrie Bow Cay (Fig. 6), using a 5 cm diameter hand corer to a depth of 5 cm. Triplicate cores from each station were pooled, the interstitial sea water drained through filter paper, and sediment and water carried separately to the laboratory in plastic containers. Sand was rinsed in fresh water and dried (60°C) for storage. For further processing, 3 to 5 g portions were soaked in 10% sodium hypochlorite overnight to remove organic matter. After thorough rinsing, they were oven-dried to constant weight (60°C), sieved through 250 μm mesh, and the two fractions weighed again to 1 mg. The samples were then decalcified in 10% hydrochloric acid and the insoluble portions rinsed, dried and weighed. Percentage estimates of the siliceous main components were made under a high power stereomicroscope.

Reactive silica in interstitial sea water was determined in the field using commercial test kits with 0.1 to 1.0 mg and 1 to 40 mg SiO_2 1-1 ranges (Hach Chemical Company, USA), calibrated against a graded series of standards. The standards were prepared from synthetic sea water with dried sodium silicofluoride (Strickland and Parsons, 1968).

Results and Discussion

Structure and Origin of Sponge Spicules Common in Reef Sediments

Classification of sponges, from classes to subspecies, is based primarily on their skeleton, which is the only component preserved in most fossils and many older museum collections. Spongin fibers and mineral spicules, separate or in combination, are the main constituents of the sponge skeleton. After death, the collagenous fibers resist decay much longer than the cellular tissue but, be-cause of their low specific gravity, they are readily washed away and eventually, after periods of weeks or months, they are degraded by bacterial action. Spicules, on the other hand, after having been freed from organic binding substances, sink to the bottom and become part of the sediment.

The great variety of forms exhibited by sponge spicules has led to a complex terminology of some 100 names that express size, shape and symmetry conditions (Reid, 1968). Comparatively large megascleres, which form the main skeletal architecture, are distinguished from small microscleres scattered throughout the tissue or concentrated in an ectosomal layer (cortex). Megascleres are grouped according to the number of their axes: monaxons, triaxons and tetraxons. Monaxons and tetraxons occur in reef sponges, whereas triaxons are restricted to the glass sponges (Hyalospongea) of the deep sea. Microscleres have been separated into three major groups: polyactines (astrose), diactines (sigmatose) and microrhabds (Dendy, 1921a; Brien, 1973); all occur in reef sponges.

Spicules are intracellular secretions by single scleroblasts. Ultrastructural studies of their formation have been confined to monaxon forms in which silicic acid ($H_2Si_3O_7$) is deposited in concentric layers around a non-collagenous proteinic axial filament. The concentric stratification has been explained by the presence of organic lamellae (Garrone, 1969) and by differences of hydroxylation caused by periodic pauses in growth (Schwab and Shore, 1971). Factors such as pH, temperature, SiO_2 and CO_2 concentration and available surface area are thought to govern the rate of spicule growth (Jørgensen, 1944; Elvin, 1971; Pé, 1973).

Microscleres exhibit an almost unlimited variety of shapes and, where present, are of great diagnostic value for demosponge classification (Reid, 1968). Unfortunately, because of their small size and delicate structure they are less well preserved in sediments and also more easily overlooked than most of the more uniform megascleres. Exceptions are two types of microscleres: sterrasters and selenasters. Although their structure and origin differ, they are both spherical or subspherical, massive and comparatively large. Unlike most microscleres they play an important part in skeleton formation and, subsequently, in the composition of reef sediments. This study is concerned principally with the structure and postdepositional alteration of these two types of microscleres.

Sterrasters

Sterrasters, which range from 40 to
300 μm in diameter, are characteristic
of the choristid genus *Geodia* (Geodi—
idae), in which they form a densely
packed cortex several millimeters thick.
They represent an extreme development of
astrose spherical or subspherical spic-
ules of almost solid silica, densely
covered by short projections that termi-
nate with recurved spines (Fig. 1: *1* and
2). The sterrasters originate as eu-
asters with globular centrum and numer-
ous pointed rays (Fig. 1: *3*). Our pol-
ished and slightly etched cross-sections
(Fig. 2: *1-6*) illustrate, by the pres-
ence of radiating axial canals, that sil-
ica deposition started on the surface of
a multirayed proteinic structure compa-
rable to the axial filament of monaxon
megascleres. Silica continues to be de-
posited around the rays and eventually
fills the space between them to form a
bluntly spined spheraster. Deposition of
the final 5 to 15 μm layer of opaline
silica, including the ornamentation of
the spines by star-like projections, is
a secondary process apparently unrelated
to the axial filaments of the rays (Fig.
2: *3* and *5*). At one point on the surface
the pattern is interrupted by a depres-
sion (hilum) (Fig. 1: *1*) that marks the
position of the scleroblast nucleus (Sol-
las, 1888).

A related type of spicule is the
spheraster, a common microsclere among
members of the choristid suborder Astro-
phorina and the only spicule type of *Chon-
drilla* spp. (Chondrosiidae), a group of
uncertain systematic position close to
the Hadromerida. It is similar in shape
to an earlier stage of sterraster, but
the spherical center supports only a few
low rays rather than numerous spines
(Fig. 1: *4*). Aspidasters of *Erylus* spp.
(Geodiidae) are also homologous to sterr-
asters, with the same surface ornamenta-
tion, but have flattened oval or lozenge
shapes. Spicules similar to spherasters
of sponges are also produced by didemnid
tunicates, but should not be mistaken
for sponge spicules since they consist
of calcium carbonate.

Selenasters

These spicules, which at maturity mea-
sure 75 μm x 60 μm in average, occur ex-
clusively in the family Placospongiidae
(Hadromerida) and, like sterrasters,
form a cortical armature. They are ovoid
to bean-shaped, have a hilum on the con-
cave surface, and are covered by low
spines — the free distal points of other-
wise solidly cemented rays. The spines
are interconnected by ridges, or trabe-
culae (Fig. 1: *5*). Selenasters differ
basically from sterrasters in their de-
velopment from a monaxial microsclere
with a straight axis covered by minute
spines (Fig. 1: *6* and *7*). They have also
been named sterrospirae (spinispirae,
for early stages) to express the super-
ficial resemblance of sterrasters and
the common origin with spirasters, a
spiny sclere with spirally twisted axis
(Vosmaer and Vernhout, 1902). Although
concentric layering of silica can be
made visible by etching (Fig. 2: *7, 8, 9*),
there is no trace of radiating axial ca-
nals. Apparently the mineral is depos-
ited directly onto a primordial spiny
rod of silica. Selenasters are the only
sponge spicules known in which a varying
percentage is colored (reddish to brown).
The nature of the stable pigment, compa-
rable to that found in calcareous spic-
ules of alcyonaceans, and the way it is
incorporated in the opal, are not known
(Vosmaer and Vernhout, 1902).

Silica Dissolution and its Effect on Spicule Morphology

With an average concentration of 1 mg Si
l^{-1} sea water, the oceans contain only
2% of the soluble amount of this element.
Values are higher in nearshore waters
where terrestrial run-offs are rich in
silicon, and in other areas where par-
ticulate silica abounds, e.g. intersti-
tial water of siliceous sediments and
deep-sea habitats (Riley and Chester,
1971).

The unstable skeletal opal, if not
protected, dissolves quickly after death
of the producing organisms, with the
more delicate forms like silicoflagel-
lates and diatoms disappearing first (Ar-
rhenius, 1963; Hurd, 1972). This process
is delayed in sediments with intersti-
tial water that is <u>enriched</u> with respect
to dissolved silica, a condition that
depends on the presence of particulate
silica and on the rate of water exchange.

Friedman *et al.* (1976) observed that
quartz particles are corroded during ce-
mentation in Red Sea reefs and that high
micro-environmental pH values which
largely control carbonate precipitation
might well be responsible for quartz
etching. They estimated that physiologi-
cal activity of algae could create thin
alkaline water films exceeding pH 10.
Similarly, Macintyre (1977) noted that
the extent of alteration of the surfaces
of selenasters collected from cores in
the fringing reef off Galeta Point (Pa-
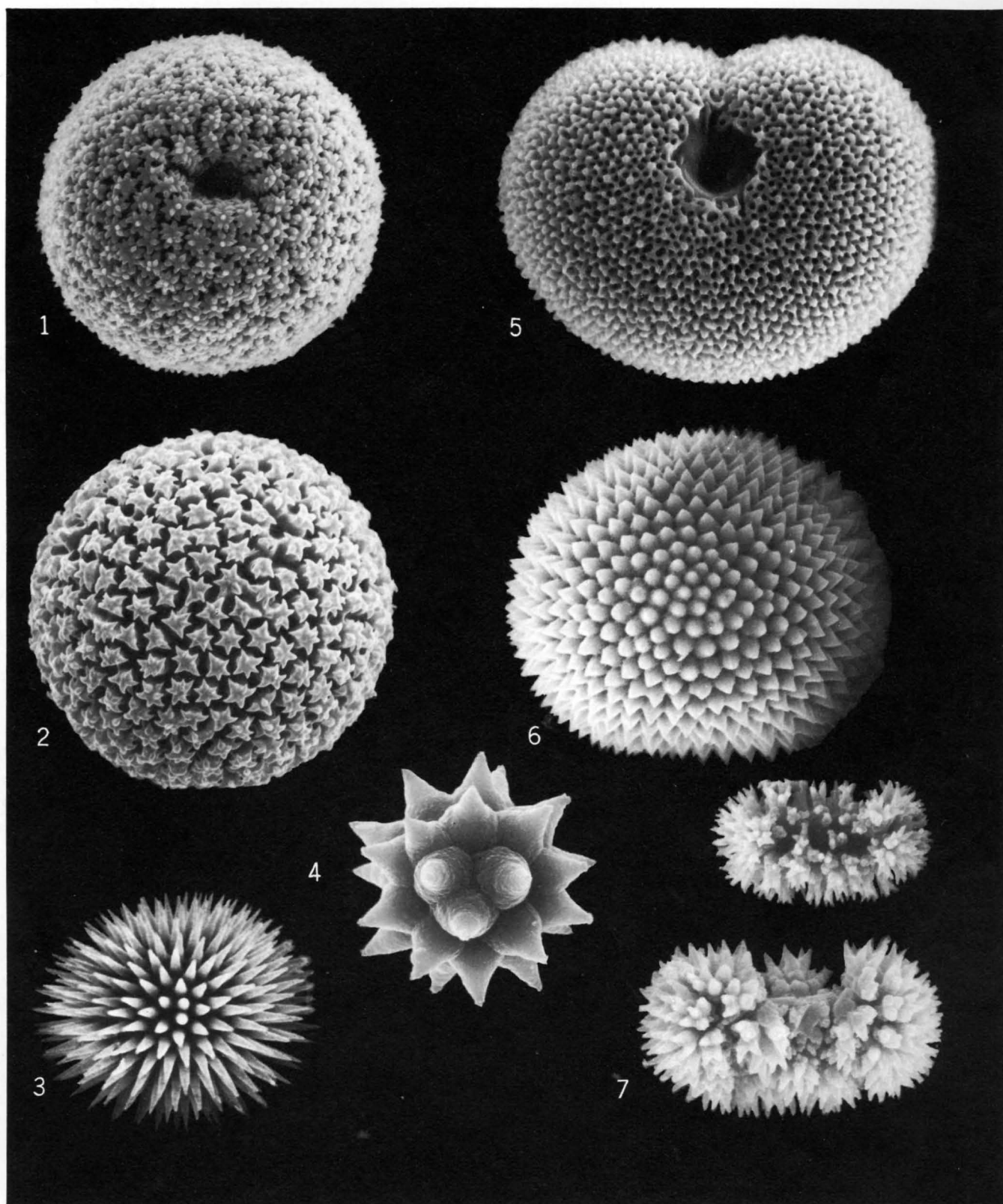namá) is related to the degree of sub-

Fig. 1. Scanning electron micrographs of fresh sponge microscleres. *1*: Sterraster from cortex of *Geodia cydonium* (1000 x). *2*: Sterraster, *G. neptuni* (1000 x). *3*: Immature sterraster (euaster-stage), *G. neptuni* (1000 x). *4*: Spheraster, *Chondrilla nucula* (1200 x). *5*: Selenaster from cortex of *Placospongia carinata* (1000 x). *6*: Immature selenaster, *P. carinata* (1000 x). *7*: Two early stages (spinispirae) of selenasters, *P. carinata* (1500 x)
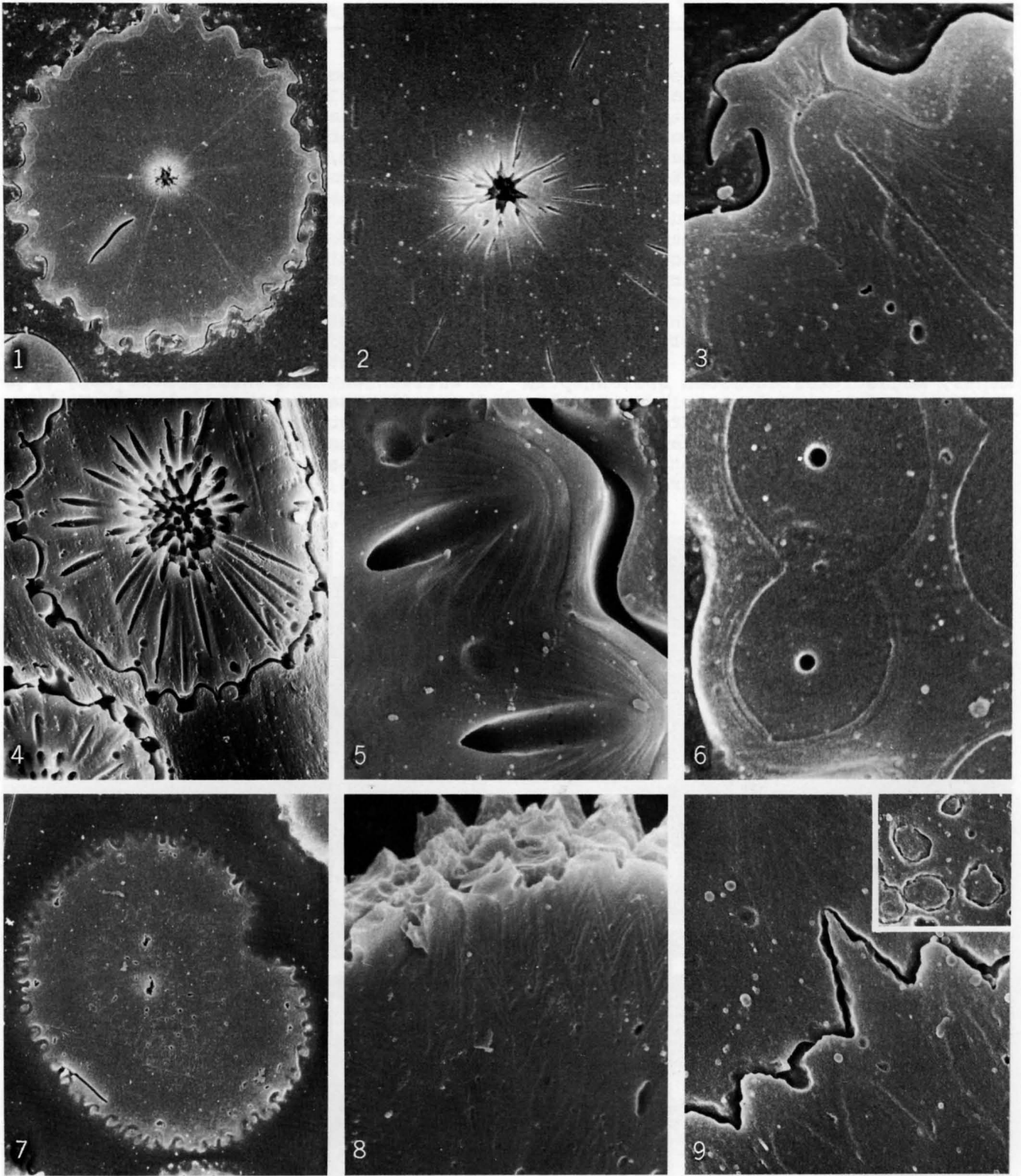
Fig. 2. Ground and polished cross-sections through sterrasters and selenasters (*1-3, 7* and *8*:
etched 30 sec in 6% hydrofluoric acid, HF; *4-6, 9*: etched 5 min in 6% HF). *1*: Sterraster, *Geodia
neptuni*; the crack is an artifact from grinding (1100 x). *2*: Enlarged center and radiating canals
(3000 x). *3*: Enlarged spine with central canal showing stratified silica deposition and separate
surface ornamentation (6500 x). *4*: Enlarged radiating canals by increased etching (1300 x). *5*: De-
tail of distal portion with distinct stratification; most of the surface ornamentation is lost
(6100 x). *6*: Tangential section through sterraster; note two fused rays with central canals and
stratified silica filling spaces between rays (9000 x). *7*: Selenaster from *Placospongia carinata*
sectioned through hilum; cracks and pits are artifacts from grinding (1000 x). *8*: Stratified silica
deposition; note absence of axial canals (3800 x). *9*: Strong etching and mechanical stress during
grinding caused the silica to crack along one layer, outlining shape of original spine (7600 x);
inset: tangential section through similar area (5600 x)

marine lithification of the surrounding reef sediments. In carbonate sands of a Jamaican reef complex, Land (1976) found less biological silica in fore-reef sediments (0.3%) than in carbonate mud behind the fringing reef (1.6%). He observed a higher number of etched spicules in the fore-reef and suggested that the variation in silica content was related to higher opal destruction in environments that favor submarine carbonate cementation.

Most sponge spicules are still recognizable even when extensively eroded by dissolution. In high-energy reef sediments, megascleres are soon broken up to short cylindrical fragments (occasional forked pieces derived from tetraxons). They appear symmetrical, glassy clear in transmitted light, and have an axial canal (Fig. 3: *1* and *2*). In fresh, un-

etched demosponge spicules, this canal is triangular in cross-section, and reflects the shape of the axial filament as well as potential symmetry development (Reiswig, 1971). The original diameter of the canal varies with the systematic position of the sponge between approximately 0.5 and 3 μm, and does not exceed 10% of the spicule diameter. Etching occurs both inside and on the surface of a fragmented sclere, and the rate of dissolution can be related to the ratio of spicule to axial canal diameters.

As a result of physiological defects or certain environmental conditions, spicule erosion can be observed even in live sponges. Resorption of siliceous spicules within a sponge (Dendy, 1921b, p. 64) or in the dense aragonitic skeletons of sclerosponges (Hartman and Goreau, 1970)
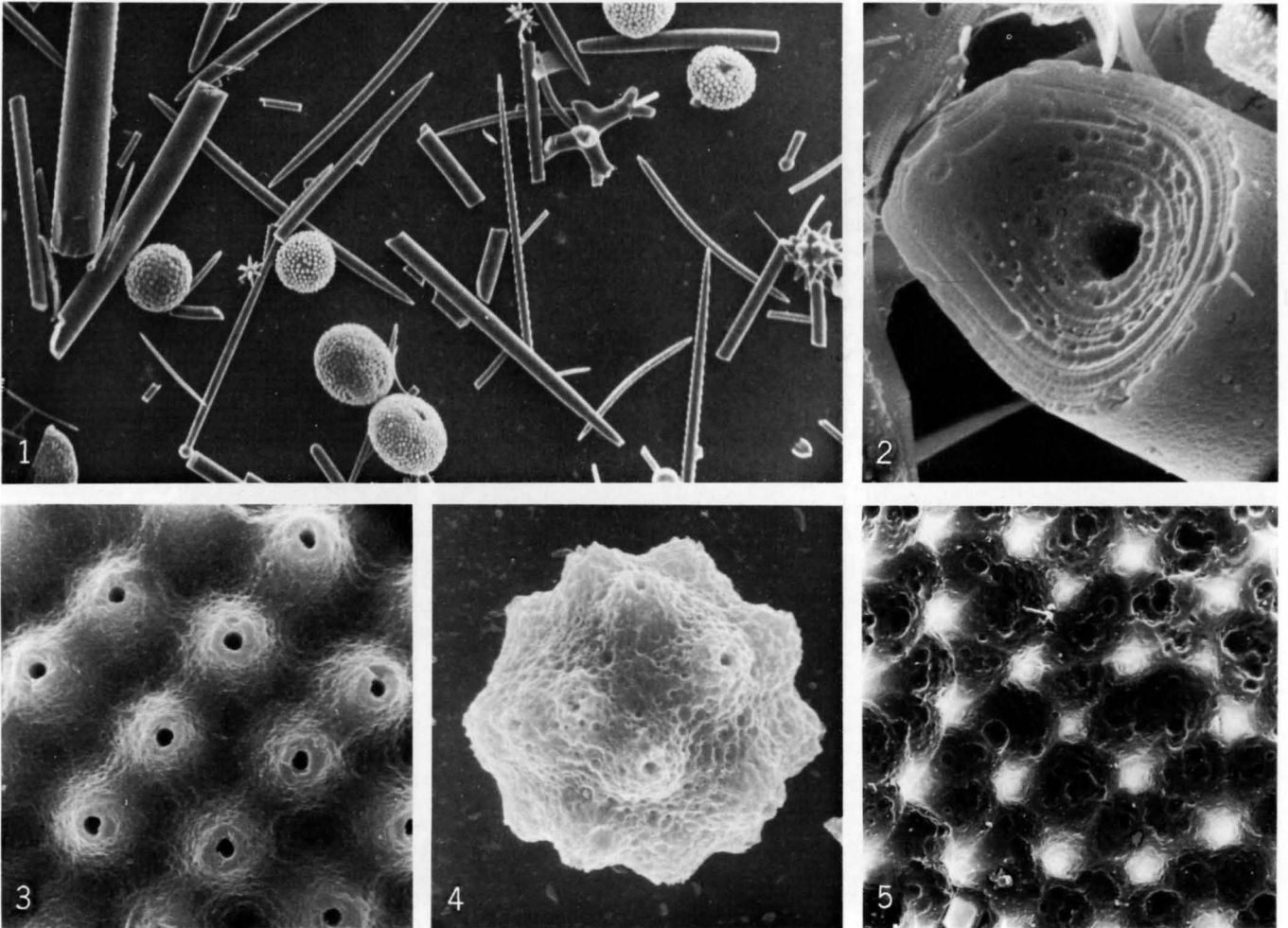

Fig. 3. Sponge spicules in reef sediments. *1*: Typical acid-insoluble residue from Carrie Bow Cay fore-reef, Station 1; *Geodia* sp. sterrasters, some smaller asters and fragments of monaxon and tetraxon megascleres are evident (1300 x). *2*: Broken monaxon spicule showing fair amount of etching (enlarged axial canal, enhanced stratification) (3500 x). *3*: Surface detail of etched sterraster; surface ornamentation is removed, axial canals are exposed (3200 x). *4*: Similar stage of spheraster (4000 x). *5*: Similar stage of selenaster (3200 x)

occurs within the living organism and is unrelated to degradation of loose spicules in reef sediments.

Among the microscleres only spherasters, sterrasters and selenasters survive to serve as a measure of opal destruction in a given sediment or facies because their shape and size render them quite resistant to mechanical destruction. We have determined morphological changes caused by etching in fresh spicules exposed to dilute hydrofluoric acid. The resulting erosion patterns can be compared with those commonly found in spicules from reef sediments (Fig. 3: *3*, *4*, *5*; Fig. 4; Fig. 5). The true asters first lose their surface ornamentation and tips of rays, thus exposing axial canals that become enlarged as erosion progresses (Fig. 3: *3*, *4*; Fig. 4). Heavily etched sterrasters are easily crushed in shallow agitated waters (Fig. 4: *3*, *4*). Selenasters soon lose their surface

ridges and become increasingly pitted (Fig. 3: *5*; Fig. 5). They decrease in size as the surface is eroded but, because they lack radiating axial canals to promote dissolution, they are probably the sturdiest of all biogenic opal in the sea. As mentioned earlier, Macintyre (1977) found both slightly corroded *Placospongia* sp. selenasters in unlithified sediments and strongly etched ones in cemented sections in a modern reef off Galeta Point (Panamá). Similarly, Weaver and Beck (1977, their Figs. 52 and 82) showed unaltered and partially dissolved sponge spicules from Middle Miocene clay sediments (SE United States), including fragmented megascleres and "bean-shaped microscleres" which are *Placospongia* sp. selenasters.

These etched and corroded *Placospongia* spp. selenasters have, however, given rise to some taxonomic confusion. Although recent *Placospongia* species and
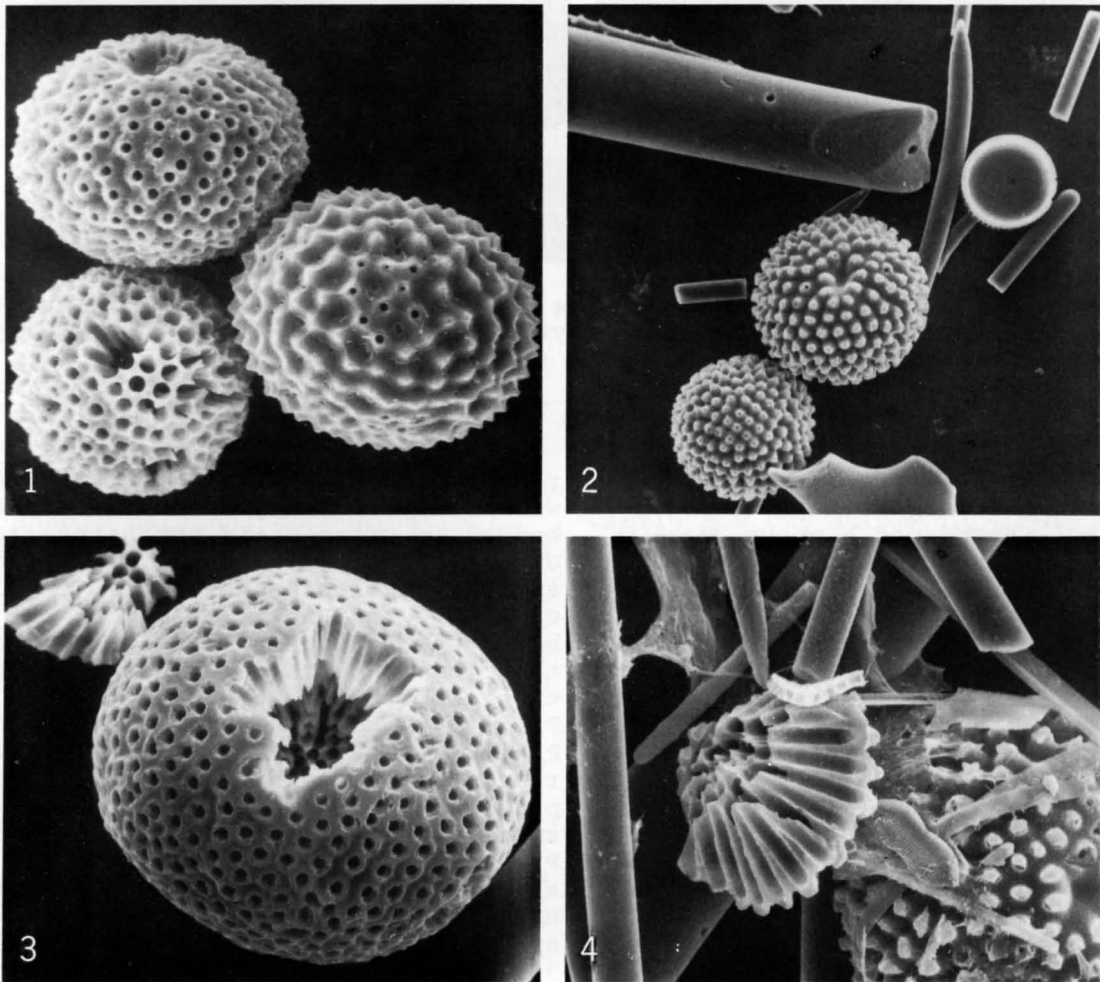

Fig. 4. Corrosion patterns of *Geodia neptuni* sterrasters. *1*: Three stages of HF etched spicules; total exposure time was 5 min in 24% HF, different degree of etching is due to inadequate mixing (800 x). *2*: Similar stages from reef sediment, Carrie Bow Cay fore-reef Station 1 (300 x). *3*: Advanced stage of etching from sediment (700 x). *4*: Heavily etched fragment from sediment (800 x)
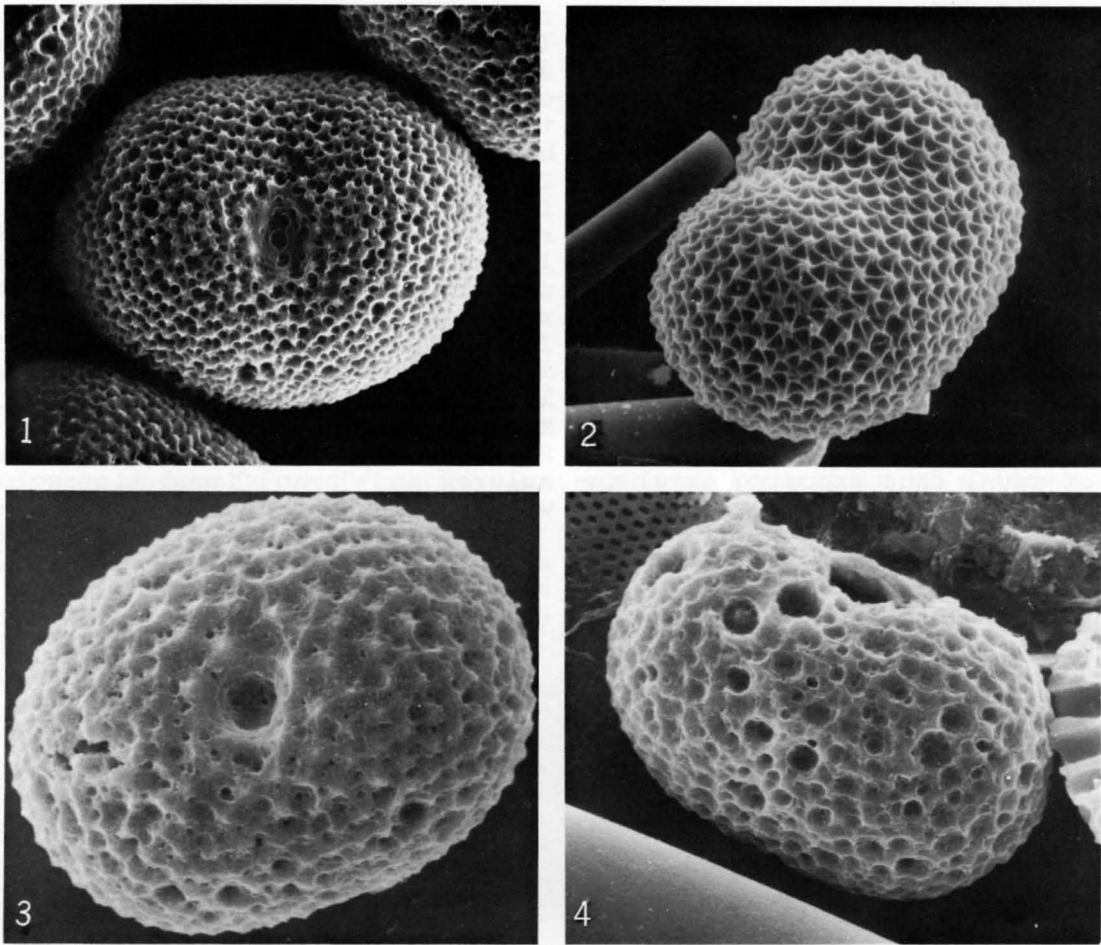
Fig. 5. Corrosion patterns of *Placospongia carinata* selenasters. *1*: Etched 5 min in 24% HF (850 x). *2*: Similar stage from reef sediment, Carrie Bow Cay fore-reef Station 1 (950 x). *3*: Etched 30 min in 24% HF (1400 x). *4*: Similar stage from sediment (1400 x)

their characteristic microscleres had already been described (Gray, 1867), Hinde (1890) introduced a genus *Rhaxella* for Jurassic sponge fragments containing bean-shaped microscleres with smooth to verrucose surfaces. Schrammen (1936) illustrated rock-forming rhaxes, together with spherasters, from Swalian bedded facies (his Plate 19, Figs. 13, 15, 18), and speculated that they might be carriers of reproductive material. Working on the same facies, Reif (1967) considered rhaxes a special form of sterrasters, without rays, and noted particularly the radial structure and verrucose surface of comparative material from the Eocene of Barbados. He also illustrated spherasters (his Plate 15, Figs. 14 and 15) and a "sterraster" (his Plate 15, Fig. 18). The latter looks more like a verrucose ball, or sterrospheraster, as it occurs in recent representatives of the genus *Aurora* (Ancorinidae), but it may be a true sterraster having a cor-

roded surface ornamentation. Schindewolf's (1967) study of microfossils embedded in craspeditid ammonites from the Upper Jurassic of Russia reported mainly sponge spicules, spherasters (possibly carbonate and therefore almost certainly belonging to didemnid tunicates), and radiolarian tests. Of the sponge spicules reported by Schindewolf (1967: his Plate 3, Figs. 2-4; Plate 4, Figs. 1-3; Plate 9, Fig. 14; Plate 12, Fig. 2a), rhaxes are certainly selenasters or impressions left by this spicule type. A smooth sphere (Schindewolf, 1967: his Plate 9, Fig. 15) could be similar to the spheres that occur in the recent genus *Caminus* (Geodiidae), or a corroded spheraster. Other "spheres" (his Plate 9, Figs. 16 and 17) are etched sterrasters or spherasters. Spherasters (his Plate 10, Figs. 6-12) closely resemble those of recent chondrillids or didemnids (the nature of the original material is unknown). Spherical forms with hol-
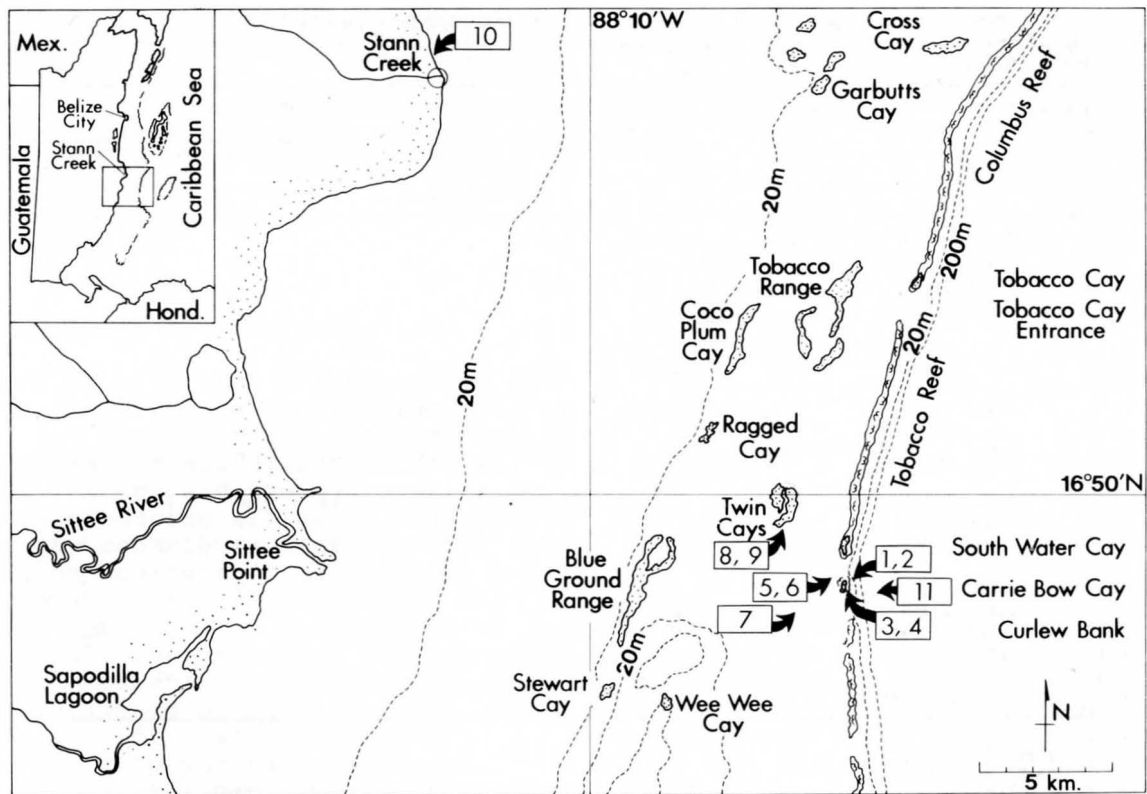
Fig. 6. Map of Belizean barrier reef and lagoon near Carrie Bow Cay. Sample numbers correspond with those in Table 1, and sampling stations are described in text

low centers and radiating tubes (Plate 12, Figs. 1-4; Plate 13, Figs. 3-5) identified by Schindewolf (1967) as "Radiolaria or spheres of Porifera" cannot be accepted as sponge spicules because they show a distinct outer double wall. The taxonomic affinity of rhaxes is still debated among paleontologists (F. Wiedenmayer, Basel, personal communication). Our present findings leave no doubt that they are etched selenasters of placospongiids.

Spheroid opaline bodies, commonly associated with sponge spicules in Miocene and Recent sediments of Japan and termed "OST" shells by Japanese workers, were described as a laracariid radiolarian, *Hataina ovata* Huang (1967). Inoue and Iwasaki (1975) debated the radiolarian nature of OST shells and pointed to the striking similarity with sterrasters of *Geodia* spp., although the inner structure of superficially fractured sterrasters appeared solid under the scanning electron microscope and did not show the radial "tubules" of OST. The outer portion of axial canals in sterraster rays are almost completely filled and can only be made clearly visible by slight etching (Fig. 2: *1* and *3*). Our observations now

confirm the nature of OST as eroded geodiid sterrasters.

Silica Distribution in Shallow-Water Sediments of the Barrier Reef Shelf near Carrie Bow Cay, Belize

Carrie Bow Cay (formerly Ellen Cay) is a small islet (120 m x 35 m) composed of reef sand and rubble located on the outer edge of the Belizian barrier reef (formerly British Honduras), 22 km southeast of Stann Creek (Dangriga). The nearest land is Sittee Point, 18 km due west, where the Sittee River empties into the lagoon. The closest island inside the lagoon is Twin Cays, 2.6 km north-west of Carrie Bow Cay. Ten samples of bottom sediments were taken and analyzed for dissolved (reactive) and particulate silica (Fig. 6, Table 1) from: (1) sand trough, outer fore-reef; (2) spur and groove zone, inner fore-reef; (3) reef crest; (4) reef flat, between reef crest and Carrie Bow Cay; (5, 6) outer lagoon, west shore of Carrie Bow Cay; (7) outer lagoon patch reef; (8, 9) inner lagoon, east shore of Twin Cays; and (10) mainland beach, north of Stann Creek Town.

Table 1. Distribution of silica in Carrie Bow Cay sediments. Terr.: terrigenous sand; Sterr.: sterrasters, selenasters; Mega.: large fragments of megascleres, >50 µm x 20 µm; Misc.: miscellaneous small debris

Sample no.	Location and depth	Reactive Si (as mg SiO_2 l^{-1})	Sediment size (dry weight %)		Particulate silica (dry weight % of <250 µm fraction)	Silicious components (estimated %)			
			>250 µm	<250 µm		Terr.	Sterr.	Mega.	Misc.
1	Fore reef trough, 24 m	0.9	79.2	20.8	1.4	0	27	53	20
2	Fore reef groove, 4 m	0.2	97.3	2.7	1.1	0	33	35	32
3	Reef crest, 1 m	0.3	96.0	4.0	0.7	0	25	35	40
4	Reef flat, 0.5 m	0.4	96.5	3.5	0.6	0	23	29	48
5	Outer lagoon, intertidal	0.3	97.6	2.4	0.8	91	0	1	8
6	Outer lagoon, 0.5 m	0.2	98.4	1.6	0.5	60	0	5	35
7	Outer lagoon patch reef, 4 m	0.5	77.1	22.9	2.0	13	30	30	27
8	Inner lagoon, 1 m	1.5	86.6	13.4	3.0	92	1	2	5
9	Inner lagoon, intertidal	1.2	81.3	18.7	3.7	87	1	5	7
10	Mainland beach, intertidal	3.0	84.8	15.2	98.7	99	0	0	1
11	Outer reef, surface water	0.3	0	0	0	0	0	0	0

For comparison, silica in surface water (11) over the outer reef was also determined.

Undersaturation of surface and interstitial seawater in respect to reactive silica is evident in all samples (Table 1). In the lagoon, terrestrial influence extends to Twin Cays, 16 km from the nearest mainland shore. Outer reef surface water contained 0.3 mg SiO_2 per liter, compared to 0.2 to 0.9 mg for interstitial water in the same area, 0.2 to 0.5 mg in the outer lagoon, and 1.2 and 1.5 mg in the inner lagoon near Twin Cays. Mainland shore water (high-energy quartz beach sand) contained 3.0 mg SiO_2 per liter. Sample number and frequency were insufficient to determine whether local variations were due to mixing of low silica ocean and enriched lagoon waters or if stagnant interstitial water had picked up silica by dissolution of skeletal silicic acid. The latter mechanism must be considered the cause of the comparatively high value (0.9 mg) in the deeper fore-reef (Sample No. 1). This possibility was confirmed by exposing pure sponge spicules (acid-boiled sterrasters from *Geodia neptuni* cortex) to silica-free artificial sea water (pH 5.7) as a 4% suspension in a plastic bottle. The sea water picked up 0.55 mg SiO_2 l^{-1} h^{-1} (a total of 11 mg l^{-1} in 20 h). This indicates that even under open cycle conditions in the sea interstitial water can be considerably enriched during periods of low water exchange rates. Dif-fusion of silica dissolved from interstitial particles in sediments is considered an important input also in the deep sea (Fanning and Pilson, 1974).

Particulate silica of whole samples varied from 0.02 to 0.29% dry weight for reef sands, 0.01 to 0.69% for lagoon sediments. Microscope examination showed that most fragments (96 to 100%) were less than 250 µm in diameter. It follows that the content of particulate silica in whole samples greatly depends on the size distribution of reef sediments (i.e., the proportion of grain sizes above and below approximately 2 phi), which may explain Land's (1976) high concentration of silica in the muds of Discovery Bay (1.6%) and Florida Bay (1.0%). We therefore determined the opal weight percentages of the sediment fractions that pass through a 250 µm mesh sieve and consider these to be a more objective measure of distribution. Qualitative composition of siliceous particles indicates their origin (Table 1). In our reef sediments, sponge spicules accounted for most of the siliceous material. Values were highest in the fore-reef (1.4 and 1.1%), where sample locations were close to large sponge populations. In lagoon deposits, silica increases shoreward of the main reef towards the mainland, but most of the material is terrigenous — except for a patch-reef station with massive sponges nearby.

Although the postdepositional solution of siliceous spicules affects the

distribution of silica in reef sediments, the degree of control in various parts of the reef habitat could not be assessed relative to other controlling factors — including the removal or introduction of spicule-rich fine deposits by wave and current action, or the *in situ* production of carbonate and siliceous skeletal material.

Role of Sponges in Recycling Reef Silica

Abundance of silica in a reef mainly depends on the distance from terrestrial inputs, the current regime determining the dispersal of all dissolved and particulate matter, and the aggregation of organisms producing siliceous skeletons. Diatoms may contribute significantly to some lagoon habitats (P. Hargraves, personal communication), but sponges are the chief component in the cycling of this mineral. The amount of silicic acid required to maintain a sponge population depends on sponge biomass, species composition, and mineralization rates.

Standing crop and composition of sponge communities vary greatly in different parts of the Carrie Bow reef complex. In the shallow lagoon, suitable conditions exist where breaks in the reef barrier permit flow of strong tidal current without the destructive action of large waves or swell. There we distinguish a soft-bottom community, 1 to 6 m deep, dominated by *Thalassia testudinum* seagrass and by a few species of large sponges (*Ircinia* spp., *Spheciospongia vesparium*), and patch reefs, 3 to 5 m deep, composed of large scleractinian coral heads, gorgonians and sponges. In the high-energy shallow back-reef, reef-crest and fore-reef zones, the sponge fauna is restricted to small incrusting, excavating or cryptic forms. In the deeper part of the inner fore-reef (spur and groove zones, 4 to 12 m) and on the outer fore-reef (12 to 60 m), the sponge fauna becomes increasingly more diverse and important in biomass. A preliminary census of standing crop of siliceous sponges in these habitats shows a range of 1 to 2000 g wet weight per m^2 suitable substrate (Rützler, in preparation). Using conversion factors averaged for 10 common species, we estimate dry weight as 20% of wet weight (Rützler, 1978), and spicule content as 28% of dry weight (Table 2). Hence, skeletal silica contained in live reef sponges can range between the orders 0.1 to 100 g m^{-2}. Land (1976) estimated several grams of silica in sponges per square meter of living reef. More accurate biomass calculations for two siliceous species were given by

Table 2. Spicule content of 10 species representing the most common silicious sponges at Carrie Bow Cay

Species	Spicule content (% of dry weight)
Haliclona rubens (Pallas)	20.8
Xestospongia muta (Schmidt)	57.6
Gelliodes ramosa (Carter)	22.4
Callyspongia vaginalis (Lamarck)	3.8
Agelas conifera (Schmidt)	19.3
Neofibularia nolitangere (Duchassaing & Michelotti)	17.1
Iotrochota birotulata (Higgin)	2.5
Hemectyon ferox (Duchassaing & Michelotti)	13.4
Spheciospongia vesparium (Lamarck)	58.7
Geodia neptuni (Sollas)	67.1
Average	28.3

Reiswig (1973) for a Jamaican reef. From his figures we calculate the standing crop of *Mycale* sp. as 0.4 g dry weight per m^2 acceptable substrate and for *Tethya crypta* as 13.3 g m^{-2} (1 m depth) and 25.4 g m^{-2} (3 m depth). Weights of spicules contained in these sponges are 0.01 g m^{-2} for *Mycale* sp., 3.4 g m^{-2} and 6.5 g m^{-2} for *T. crypta*.

Rate and efficiency of silica deposition in marine sponges is virtually unknown. Experimental data from freshwater sponges (*Ephydatia muelleri*) show that 1 mg SiO_2 l^{-1} water is sufficient for spicule formation, although higher deposition rates are obtained with the "normal" (ambient) 5 mg concentration (Elvin, 1971). Another spongillid (*E. fluviatilis*) from a 15 mg SiO_2 l^{-1} habitat produced higher spicule numbers with reduced dimensions in impoverished (1.5 mg) culture water, and a smaller number of thicker spicules in an enriched (60 mg) medium (Pé, 1973). These observations were made during time spans of hours to a few days after germination of gemmules. Field studies of older and more established populations from lakes and streams in Wisconsin (USA) demonstrated that silicon requirements are species-dependent (Jewell, 1935). Some forms do not thrive in water with less than 2 mg SiO_2 l^{-1}, others have strongly reduced skeletons if growing in concentrations of less than 0.7 mg. Conditions in fresh water, however, can be more fluctuating and extreme than in the sea because reduction of silicon may well be paralleled by low levels of other important elements. If the requirements of marine species are similar to those of spongillids, growth of off-shore coral reef sponges is highly dependent on recycling locally dissolved silicic acid. Marine

sponges may also have retained a more efficient silicon metabolism in a medium that is more chemically balanced. Reduced dimensions and erosion of spicules inside live marine sponges do occur, but have yet to be correlated with ambient silicon levels.

In situ pumping activity, growth rate and skeletal silica in a sponge give a measure of silica uptake, but reliable data are scarce. The best example is a detailed study of a population of *Tethya crypta* in Jamaica (Reiswig, 1973). This species contains spicules amounting to 26% of total dry weight. Observation of 30 individuals over a period of 11 months showed that an average specimen (0.8 l volume) produces 2 g skeletal silica per year. An individual of this size is able to pump at least 3.5 m^3 water through its body each day. A calculation using the lowest level of reactive silicon in Carrie Bow reef waters (0.2 mg SiO_2 l^{-1}) shows that, during a year, *T. crypta* circulates water through its body containing 126 times the amount of silicic acid used for skeleton mineralization. Experimental work with marine species is needed to learn how much of this quantity can actually be converted to spicules.

Conclusions

Siliceous spicules (megascleres, microscleres), important for classification, are produced by sponges as part of their skeleton (main exception, Calcarea, Keratosa), and are released to form sediment grains. Etching and dissolution, aided by mechanical abrasion of free spicules, occur after death and decay of the sponge owing to silicon undersaturation of shallow reef waters.

Two kinds of sponge microscleres — sterrasters and selenasters — were found to be reliable indicators of silica erosion in recent and fossil sediments. Both are abundant, massive, and comparatively large, and reflect differential etching by revealing patterns of original silica deposition. Structural changes observed in sediment samples could be replicated with fresh spicules exposed to hydrofluoric acid. Sterrasters from the cortex of choristid sponges (*Geodia* spp.) are the extreme development of astrose (polyactine) spicules. Etched sterrasters, previously misidentified as radiolarians ("OST"), expose radiating axial canals. Selenasters of hadromerid *Placospongia* spp. develop from a spiny diactin to a bean-shaped spicule without radiating canals. Corroded selenasters showed a characteristic pitted surface structure and were proved identical with rhaxes, an important microfossil of hitherto debated origin.

Because of their size, the sponge spicules are restricted to the fine sediment fractions (less than 250 μm). Particulate silica in this fine fraction ranges from 0.4 to 2% dry weight in the reef habitats, and from 3.0 to 3.7% in lagoon mud. High values occur in the reef near large sponge populations, where silica consists predominantly of sponge spicules, whereas terrigenous sands make up most of the noncarbonate material in the lagoon.

The distribution of dissolved silica in interstitial water samples from the barrier reef near Carrie Bow Cay showed SiO_2 values of 0.2 to 0.9 mg l^{-1} for the seaward reef, and 1.2 to 3.0 mg l^{-1} for lagoon habitats. Differences are attributed to terrestrial inputs, to local dissolution of solids, and to mixing with impoverished oceanic surface water.

Data on SiO_2 requirements for spicule formation are available only for freshwater sponges, but suggest that marine sponges in off-shore reefs might depend on recycling locally dissolved silica unless they have a higher metabolic efficiency in extracting SiO_2 from the water they pump.

Standing crop of the population on the Carrie Bow reef tract varies between 1 and 2000 g wet weight per m^2 suitable substrate. An estimated 0.1 to 100 g siliceous spicules per m^2 are contained in live sponges.

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