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The Caribbean spicule tree : a sponge-imitating foraminifer (Astrorhizidae)

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Abstract

An unusually large agglutinated foraminifer was found to be common in semishaded habitats on Caribbean coral reefs. The tree-shaped organism attains 50 mm in height and builds its test using siliceous sponge spicules exclusively. A new genus and species, *Spiculidendron corallicolum,* are established in the Textulariina family Astrorhizidae. The new taxon is characterized by a complexly branching tubular test that is attached to hard substrate and has a simple wall lacking septae and apertures. Electron microscopy shows a spongin-like organic cement and various cell organelles and inclusions, including dinophycean symbionts. Cytoplasm resides in substrate cavities and in the hollow base of stem and branches that form the test. Observations suggest that in life cytoplasm flows also outside the test along its thin distal branches where it cements new spicules in place and takes up food (pseudopodia).
Keywords : Caribbean, coral reef, *Spiculidendron corallicolum*, agglutinated foraminifer.

Résumé

Un foraminifère agglutiné de taille exceptionnellement grande a été trouvé dans des habitats semi-ombragés de récifs des Caraïbes. L'organisme de forme arborescente atteint 50 mm en hauteur et construit son test exclusivement à l'aide de spicules d'éponges. Un nouveau genre et espèce, *Spiculidendron corallicolum*, est crée dans les Textulariina, famille Astrorhizidae. Le nouveau taxon est caractérisé par un test tubulaire à arborescence complexe qui est fixé au substrat dur et qui présente une paroi simple dépourvue de septa et d'ouvertures. La microscopie électronique révèle un ciment organique comparable à de la spongine et différents organites cellulaires et des inclusions parmi lesquelles des dinophycées symbiotiques. Le cytoplasme est localisé dans les cavités du substrat et dans la base creuse du tronc et des branches qui forment le test. Des observations suggèrent que le cytoplasme se répand aussi à l'extérieur du test, le long de ses fines branches distales où il cimente de nouveaux spicules et capture la nourriture (pseudopodes).
Mots-clés : Caraïbes, récifs coralliens, *Spiculidendron corallicolum*, foraminifère agglutiné.

Introduction

Sponge systematists are routinely recipients of enigmatic specimens sent to them for identification. Senders of such material (even some biologists can be included here) are rarely aware that even cursory microscope examination would reveal the identity of the sample that oftentimes has no poriferan affinity but may include all kinds of things, from rock to chordate. For instance, pumice stone, often found washed ashore, has been sent as sample of the excavating sponge *Cliona,* gelatinous balls formed by certain cyanobacteria (blue-green algae), genus *Phormidium,* were mistaken for similarly shaped *Tethya* or *Cinachyrella,* and certain colorful, cushion-shaped or crustose polyclinid *(Diplosoma)* or didemnid *(Didemnum, Trididemnum)* Ascidiacea have tricked many experts into considering them as sponges. An added complication is that didemnids have astrose spicules, some resembling those in the sponge genus *Chondrilla* except that they are calcareous instead of siliceous in composition, as can easily be determined by applying an acid or by examination in polarized light. On the other hand, although presence of siliceous spicules generally points to sponges, many invertebrates (including sponges) incorporate foreign mineral particles such as sponge spicules to serve as skeletal support. Spicule condition (corrosion, breakage), orientation, combination of morphological types, and position within the organism will usually indicate their true origin.

Despite experience and skepticism, several sponge workers, including one of us (K.R.), have been initially misled by a coral-reef organism that superficially resembles a hydroid colony or even a gorgonian *(Trichogorgia viola;* F.M. BAYER, personal communication) but is made up entirely by siliceous sponge spicules cemented together like the skeleton of a raspailiid sponge. In some specimens, even the spicule complement resembles a raspailiid although others point to entirely different sponges. To our knowledge, this organism was first discovered at the roof of a reef-cave entrance in 24 m off Scotts Head Bay, Dominica, West Indies (RÜTZLER, unpublished, 11 June 1966). Since then, several specimens were observed on reefs in Colombia and dubbed "spicule trees" (M. KIELMAN, R.M.W. VAN SOEST, personal communication), and elsewhere in the Caribbean, such as Cayman Islands, Bahamas, Honduras, and Belize (P.H. HUMANN, personal communication; present material). More careful examination of several samples from different locations and subsequent detailed light and electron microscope study clearly show that the spicules were taken up from the sediment and cemented together to support a tiny mass of protoplasm, an agglutinated, arborescent member of Foraminifera.

Material and methods

Specimens available for this study were collected by scuba in 27-35 m on reefs off San Salvador, Bahamas (24°00' N, 74°30' W) and Carrie Bow Cay, Belize (16°48' N, 88°05' W). Bahamas material was photographed *in situ* (courtesy P.H. HUMANN), broken off at the substrate level and partly dried and partly preserved in alcohol. Belize specimens were pried off the coral rock with pieces of substrate still attached. They were returned to shore submersed in fresh seawater, examined and photographed by microscope (Wild M3 stereo-microscope), and fixed immediately for light and electron microscopy. Primary fixatives were 10 % formalin in seawater and 1.5 % glutaraldehyde in 0.2 M cacodylate buffer with 0,1 M sodium chloride and 0.4 M sucrose pH 7.2). The material was kept in this prefixative at 4° C for four days. Upon return to Washington, samples for scanning electron microscopy (SEM) were rinsed in buffer, dehydrated in ethanol, and sublimation-dried using Peldri II (Ted Pella, Inc., Redding, California); they were gold-coated and photographed with a Cambridge Stereoscan 100 microscope. Samples for transmission electron microscopy (TEM) were decalcified in 10 % EDTA in water, rinsed and postfixed in 1 % osmium tetroxide in the above buffer solution (1 h, 4° C), desilicified in 5 % hydrofluoric acid in buffer, and rinsed and dehydrated. Epoxy-resin embedded material was sectioned for light and electron microscopy, the latter stained in uranyl acetate (saturated alcoholic solution), and examined with a Jeol 1200 EX microscope at 2000 x - 30000 x primary magnification. Sub-samples of desilicified material were stained with the fluorochrome 4',6-Diamidino-2-Phenylindole (DAPI).

Systematic description

Suborder **Textulariina** DELAGE & HÉROUARD

Foraminiferida with test composed of agglutinated foreign matter held by various cements
(LOEBLICH & TAPPAN, 1964 : C184; 1988 : 19).

Superfamily **Astrorhizacea** BRADY

Includes forms, as the present one, with tubular, branching, nonseptate test; agglutinated simple wall, simple aperture(s) at the end of tubes or without apertures
(LOEBLICH & TAPPAN, 1964 : C184; 1988 : 19).

Family **Astrorhizidae** BRADY

Includes forms, as the present one, with attached test, simple wall with pseudochitinous inner and agglutinated outer layer; without aperture (LOEBLICH & TAPPAN, 1964 : C184; 1988 : 19). These authors also recognize several subfamilies, including one relating to the present species, the Dendrophryinae, with test attached, commonly branching or occurring in clusters
(LOEBLICH & TAPPAN, 1964 : C192; 1988 : 24).

Genus ***Spiculidendron*** gen. nov.

TYPE SPECIES

Spiculidendron corallicolum sp. nov.

DIAGNOSIS

Arborescent, attached astrorhizid foraminifer with tubular branches of the test gradually tapering, without apertures, into solid growth tips that support pseudopodia. Base of test attached to rock, open at the bottom and connecting with crevices or burrows in the substrate. Simple agglutinated wall supported by spongin-like organic cement.

ETYMOLOGY

Derived from the type-species' field name, spicule tree.

COMMENTS

Of the approximately 10 known genera of agglutinated arborescent Foraminifera (LOEBLICH & TAPPAN, 1964; DELACA *et al.*, 1980; LOEBLICH & TAPPAN, 1988; SHIRES *et al.*, 1994) only species of three are attached to hard substrate and morphologically similar to *Spiculidendron*. The genus *Halyphysema* BOWERBANK differs by having a subdivided, spreading basal expansion, a clavate, possibly bifurcating chamber, and a terminal aperture. Most of the tree-like appearance is due to a pseudopodial network partly supported by single agglutinated sponge spicules; both multinucleate and uninucleate individuals have been reported (HEDLEY, 1958). Dendronina has an arborescent test, with terminal apertures from which a "corona" of sponge spicules may radiate (HERON-ALLEN & EARLAND, 1922 : 78; LOEBLICH & TAPPAN, 1964 : C 192; 1988 : 25). *Dendrophyra* WRIGHT (which has recently been synonymized with *Psammatodendron* by JONES, 1994 : 36) has a nonseptate branching test but the ramifications are few

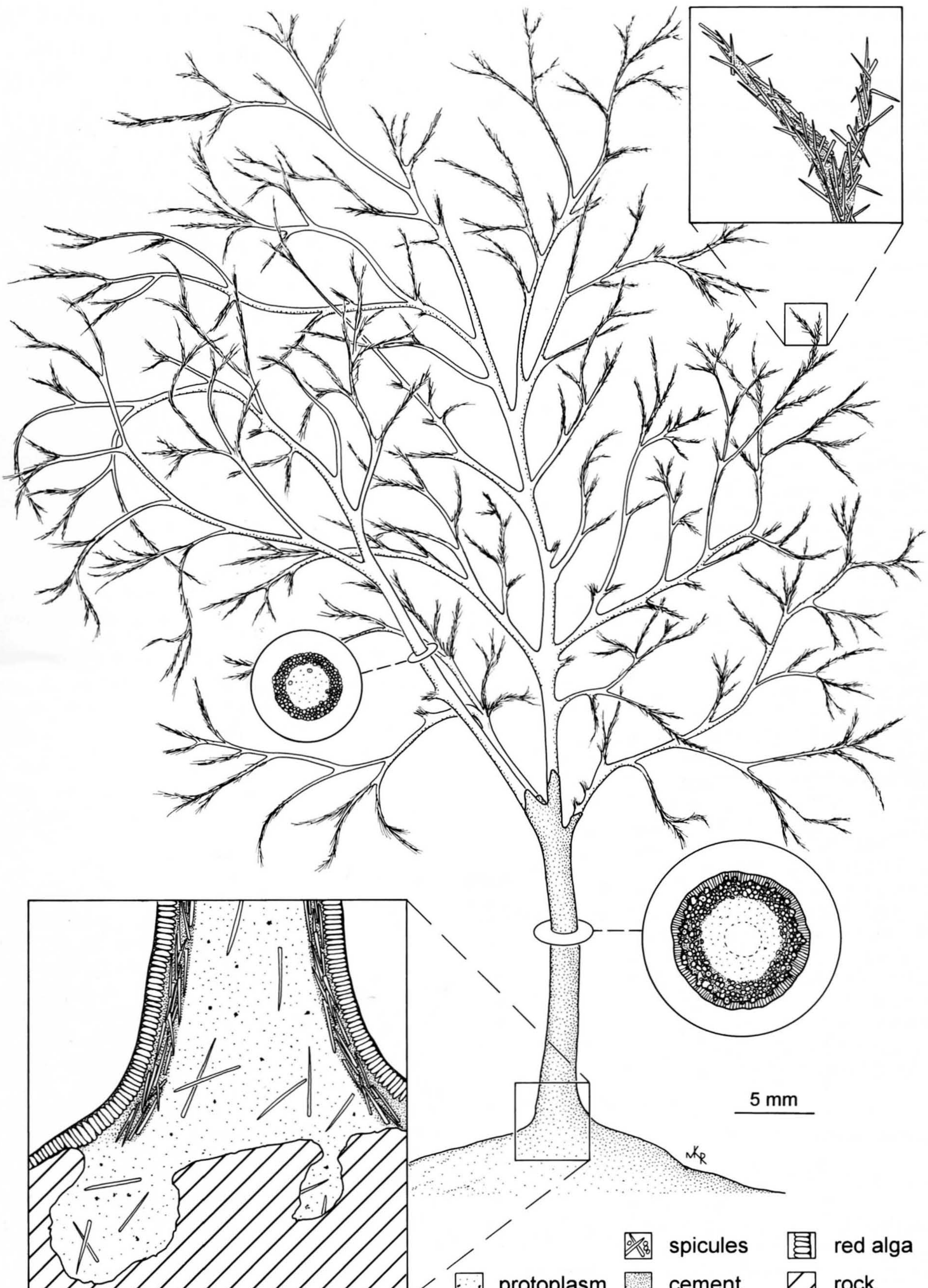

Fig. 1. - *Spiculidendron corallicolum*, new species, habit. (Details are enlarged x 5).

and coarse and there are apertures at the ends of the tubular branches (LOEBLICH & TAPPAN, 1964 : C192; 1988 : 24). Similar tree-shaped species from soft bottoms belong to three genera : *Pelosina* BRADY (Astrorhizidae), *Notodendrodes* DELACA, LIPPS, & HESSLER (Notodendrodidae), and *Arborammina* SHIRES, GOODAY, & JONES (Arboramminidae). All three of these differ from *Spiculidendron* by having root structures which are adaptations to life anchored in sediment bottoms. *Pelosina* also has apertures at the ends of branches that are closed by detrital plugs (CEDHAGEN, 1993). *Notodendrodes* has a subcentral bulb with double-layered wall separating the arborescent portion from the root complex (DELACA *et al.*, 1980 : 210). *Arborammina* tests are solid, without lumen, and the sparse protoplasm may reside within globigerinacean tests that are incorporated near the base (SHIRES *et al.*, 1994 : 150).

Spiculidendron corallicolum sp. nov.
(Figs. 1-3)

DIAGNOSIS

Test tree-shaped, complexly and delicately branched, up to 50 mm tall and composed entirely of sponge spicules joined by spongin-like organic cement; agglutinated spicules densely aligned longitudinally except in the distal growth portions of the test where they are arranged loosely and often perpendicularly to the growth axis; occurs in abundance in shaded fore-reef habitats below 20 m throughout the Caribbean.

TYPE MATERIAL

Holotype USNM 47817 (Belize) and paratypes USNM 47818 (Belize), 47819 (Bahamas), are deposited in the Protozoa collection of the Department of Invertebrate Zoology, National Museum of Natural History, Washington, DC.

TYPE LOCALITY

Fore-reef slope off Carrie Bow Cay, Belize (RÜTZLER & MACINTYRE, 1982 : 33-37); 16°48' N, 88°05' W; cave entrance ceiling, 30 m, collected 18 May 1994.

ETYMOLOGY

Named for the species' habitat, living on coral.

SHAPE AND DIMENSIONS

The shape of *Spiculidendron corallicolum* test is arborescent but most of the branching takes place in one plane (Fig. 1). Studied specimens were 25-61 mm (means = 39.4 mm, n = 10) in height, 4-29 mm (13.7 mm) in width, but only 2-7 mm (4.1 mm) in depth; the holotype, which is still attached to a piece of its substrate, measures 23 x 10 x 5 mm. The size and overall appearance resembles some hydroids, such as species of the genus *Eudendrium*. The stem near the base measures 0.7-1.9 mm in diameter; it is circular to slightly oval in cross section. The stem is firmly attached to the coral-rock substrate. Branches start about 10 mm (4-21 mm) above the substrate. They taper consistently and bifurcate several times, with additional smaller limbs branching off along the way. The stem wall near the attachment base is 0.2-0.4 mm thick, leaving an average lumen of ca. 0.5 mm. Half-way up the tree, a branch measuring 70 µm in diameter has a wall thickness of only 16-19 µm and a lumen of 35 µm. Near the pointed ends the branches become solid, the lumen disappears. The tips may be only the width of 1-3 cemented sponge spicules although in places additional spicules are (temporarily) attached in perpendicular or oblique fashion (Fig. 2a-d).

COLOR

Glassy to white, owing to the refraction of light from the sponge spicules that make up the test. Areas near the base have a brownish tinge from fouling diatoms, the stem may be tan to reddish brown from encrusting tests of other (dead) foraminifers and crustose red algae.

TEST STRUCTURE

The test consists entirely of siliceous sponge spicules. At the growth zones near the tips of branches various carbonate sand grains were seen temporarily attached but these do not become part of the test. Spicules are tightly cemented together in parallel and arranged longitudinally (Fig. 2a and 2d). A few minute circular and oval pores (5-30 µm) through the organic cement between the spicules were seen in the apical parts of the test (Fig. 2f). Only monaxon megascleres and a few microscleres were found in macerated preparations, primarily oxeas, strongyles, styles, acanthostyles, diods, and tylotes (some microspined), rarely sigmas and toxas, obviously derived from different demosponges (possibly *Halichondria, Petrosia,*

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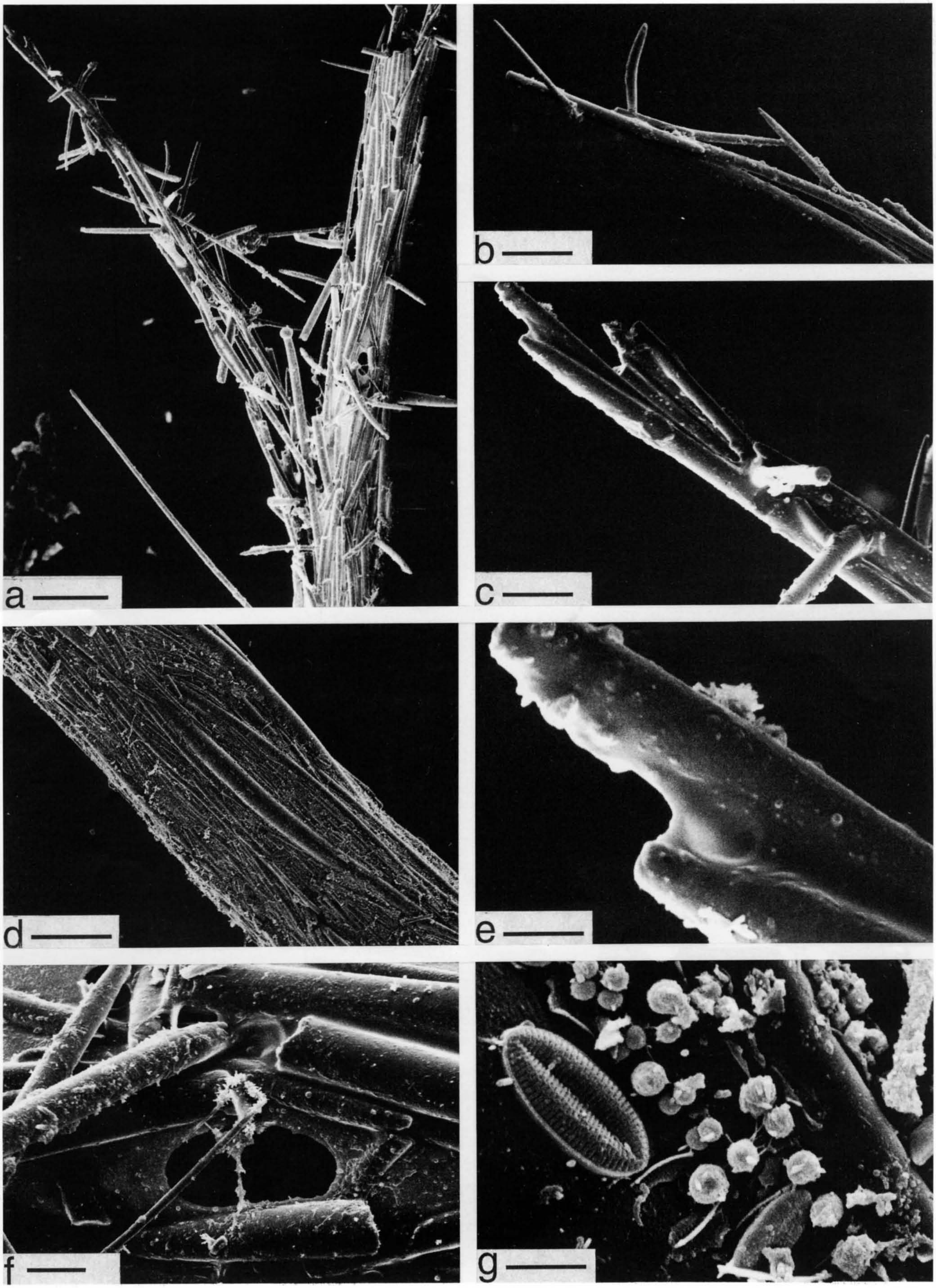
Fig. 2. - *Spiculidendron corallicolum* sp. nov., SEM views of morphology. - a. Two branches of test (scale : 100 µm). - b - c. Sponge spicule arrangement at branch tip (scale, b : 50 µm; c : 20 µm). - d. branch near stem (scale : 200 µm). - e. Cytoplasmic material coating spicules at branch tip (scale : 5 µm). - f. Pores in organic material connecting spicules at distal portion of a branch (scale : 10 µm). - g. Diatom and bacteria adhering to exposed cytoplasm near branch tip (scale : 5 µm).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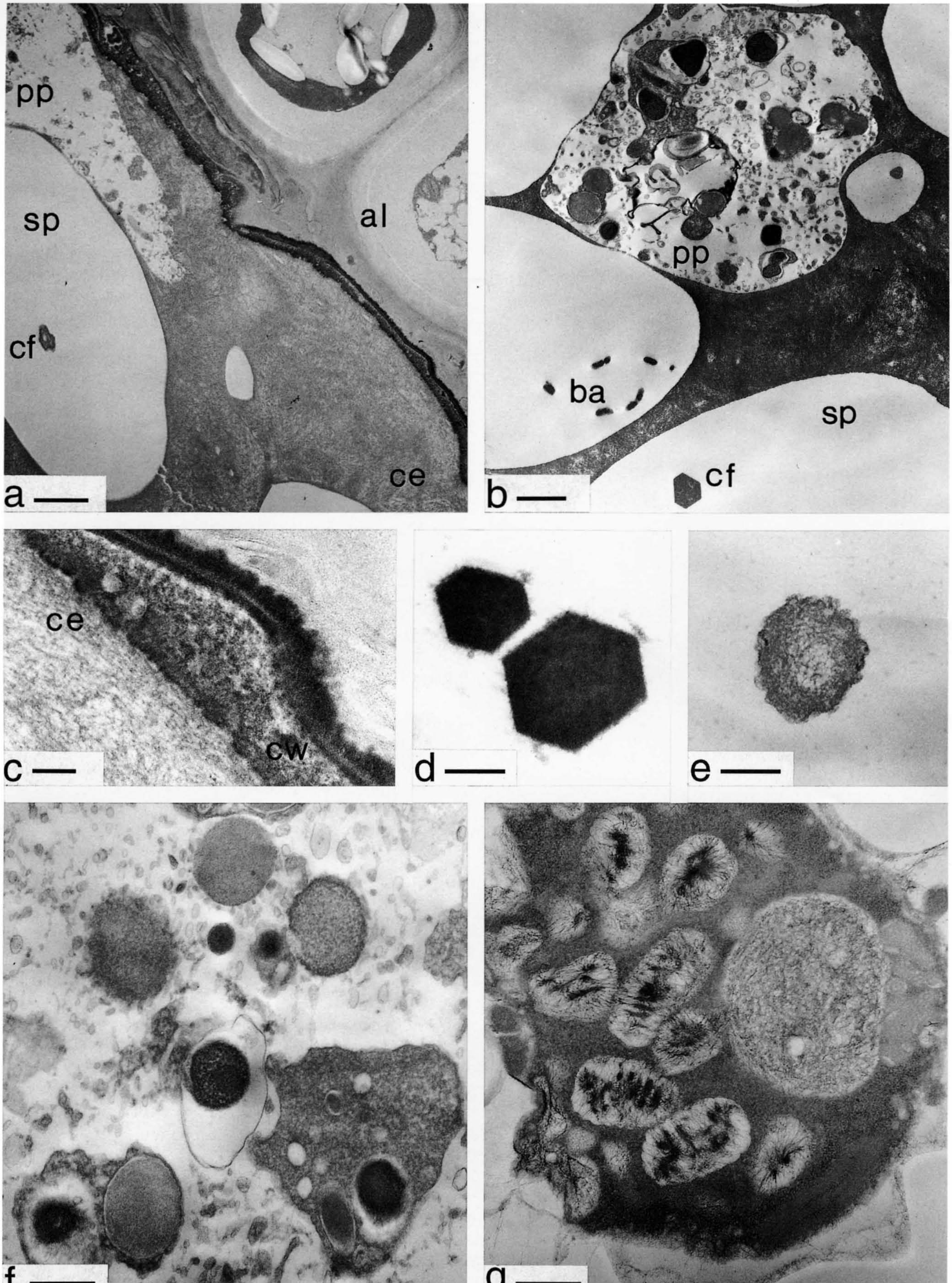
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Eurypon, Cliona, Plakortis, among others). Many spicules are broken or eroded, their size range is large, ca. 7-2000 µm. Occasional calcareous spicules found in preparations derived from small *Sycon* spp. growing on the test. The organic cement appears in electron micrographs as a dense fibrillar substance similar to the spongin that held these spicules in place inside the sponge that produced them (Fig. 3a-c). In desilicified material, many of the original central filaments of the spicules are clearly present (Fig. 3a, b, d, e); some similar structures may be the result of secondary invasion by foraminiferan cement into central canals exposed by erosion. The cement also coats the inner surface of the test and forms the bond to rock substrate and to organisms encrusting the base of the stem, such as red algae (Fig. 1), other Foraminifera, and an occasional syconoid sponge and serpulid polychaete. Distal surface areas of the test show numerous bacteria and diatoms adhering to an organic coating among the cemented spicules (Fig. 2g).

CYTOPLASM

Cavities in the substrate rock and the lumen of the test base are filled with protoplasm, with loose sponge spicules dispersed at random. In the upper stem and branch region cytoplasm occurs in sheets and strands not entirely filling the lumen, at least not in fixed material. More distally and near the tips, cytoplasm is seen between the spicules of the test. Several organelles and inclusions (Fig. 3f) can be distinguished, such as mitochondria and lipid droplets, but identification was not always possible and may have to await specially fixed material (in preparation). No nucleus was found in the sections and there is not enough material with substrate base attached to continue a destructive search in that area. Whole-mount staining with DNA-specific fluorochrome (DAPI) of cytoplasm from inside the test (tree) portion of one specimen of *Spiculidendron* revealed only nuclei of microalgae.

SYMBIONTS

Several types of unicellular microalgae can be distinguished in the cytoplasm, ranging in diameter from 15 x 15 µm to 20 x 12 µm. They were seen in TEM sections (Fig. 3g) and DAPI- stained whole mounts of cytoplasmic strands and were determined to be members of the Dinophyceae (M. FAUST, personal communication).

HABITAT AND DISTRIBUTION

Spiculidendron corallicolum occurs singly or in clusters in semishaded clear-water reef locations, 20-30 m and below. The species is common just inside the entrance of crevices and caves, under ledge overhangs, and along vertical walls where sediment exposure is low. Common associates are crustose red algae, sponges, and foraminifers, reteporid bryozoans, algal turfs, and hydroids. Smaller specimens are difficult to detect in the field because they blend well with similarly structured algae and invertebrates. Distribution of the species is presumed to be Caribbean-wide; so far it has been found in the Bahamas (San Salvador), Turks & Caicos Islands, Leeward Islands (Dominica), Colombia, Honduras (Roatán), Belize (Carrie Bow Cay, Lighthouse Reef), and Cayman Islands.

Discussion

Spiculidendron corallicolum may well be one of the largest species of Foraminifera - indeed of Protozoa - ever recorded. The tallest test among the type specimens measures 61 mm, not counting the portion of the organism that resides in cavities of the substrate. Tests of comparable species in the Astrorhizidae are shown as 1-7 mm in height (LOEBLICH & TAPPAN, 1964 : Fig. 108), *Notodendrodes antarctikos* attains 38 mm (DELACA *et al.*, 1980 : 205), *Arborammina hilaryae* reaches 20 mm (SHIRES *et al.*, 1994).

The placement of *Spiculidendron corallicolum* within the classification of Foraminifera follows the scheme of LOEBLICH & TAPPAN (1964; 1988).

In a more recent paper, LOEBLICH & TAPPAN (1989) restructured the suborder Textulariina and reestablished the suborder Astrorhizina JÍROVEC with the definition that agglutinated foreign particles are held in place only by organic cement (as is the case in our new species). In contrast, the suborder Textulariina *sensu* LOEBLICH & TAPPAN (1964; 1988) encompasses species where agglutinated foreign particles, although encased in organic coating, are held in biogenically deposited low-magnesium calcite cement. We do not consider it appropriate to follow this separation. Other Foraminifera with tests composed of agglutinated particles held together by organic cement, such as the genus *Miliammina*, have been shown to be

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Fig. 3. - *Spiculidendron corallicolum* sp. nov., TEM images of cytology. - a. Cross section at stem portion of test with encrusting red alga (al); sponge spicule (sp), surrounded by organic cement (ce) and some protoplasm (pp), was dissolved in acid leaving behind the central filament (cf) (scale : 2 µm). - b. Cross section of distal branch of test containing protoplasm (pp) surrounded by organic cement and spicules (sp) (now dissolved) with central filaments (cf); bacteria (ba) may be contaminants (scale : 1 µm). - c. Detail of organic cement (ce) attached to cell wall (cw) of encrusting red alga shown in *a* (scale : 200 nm). - d. Cross sections of two hexagonal central filaments typical of demosponge spicules (scale : 200 nm). - e. Cross section of foraminiferal cement that infiltrated the exposed central canal of an eroded sponge spicule (scale : 500 nm). - f. Cytoplasmic inclusions (scale : 500 nm). - g. Dinophycean microsymbiont (scale : 500 nm).

closely related to taxa that secrete calcareous tests (FAHRNI *et al.*, in press). Because the ability to biomineralize may have been lost independently in a number of species we consider it justified to maintain the suborder Textulariina as defined in the earlier papers.

The ultrastructure of the bioadhesive (BOWSER & BERNHARD, 1993) or organic cement (designated in the older literature also as "chitinous lining" and "pseudochitin") appears in electron micrographs as a dense fibrillar substance, similar to spongin, the collagen-like protein that forms intercellular matrix and fibers in Porifera (GARONNE, 1978). Indeed, in a study of a comparable species in the Genus *Halyphysema* (HEDLEY & WAKEFIELD, 1967) the structural similarity of the cement with collagen has been confirmed.

After desilicification the original axial filaments of the sponge spicules are clearly visible. They are triangular or hexagonal in cross section (Fig. 3d), as is typical for demosponges (REISWIG, 1971; SIMPSON *et al.*, 1985). Some however are circular (Fig. 3e) and of the same structure as the surrounding organic matrix. We assume therefore that protozoan cement was deposited secondarily inside the small spaces of the central canals of broken and eroded spicules.

Selectivity for materials used in building tests was studied experimentally using several species of live agglutinated foraminifers (BENDER, 1989). This work showed that the organisms were able to distinguish between shape and size but not chemistry of the particles. This is contrary to our observation that *Spiculidendron corallicolum* is clearly chemoselective for silica and incorporates a considerable size range of sponge spicules. In the habitats studied, calcareous sediment is plentiful in a great size range (from *Cliona*-excavated chips of a few µm to *Halimeda*-derived plates of several mm) but never accepted for test building although small carbonate particles initially attach to pseudopodia in the distal branch region of the test. Other siliceous materials, such as terrigenous quartz grains, are not available in this environment (RÜTZLER & MACINTYRE, 1978).

This is the first report of an agglutinated foraminifer containing dinophycean endosymbionts. All previous descriptions of symbiotic microalgae in Foraminifera were based on species, both benthic and planktonic, that secrete calcareous tests (LEUTENEGGER, 1984; HEMLEBEN *et al.*, 1989; LEE & ANDERSON, 1991).

Spiculidendron corallicolum is somewhat unusual because it does not have distinctive apertures where pseudopodia extrude to capture food. Although live observations are not yet available, we presume that minute pores through the spicule cement in distal areas of branches (Fig. 2f) serve as an exit for cytoplasm for obtaining food and trapping spicules for expanding the test.

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References

BENDER, H., 1989. Gehäuseaufbau, Gehäusegenese und Biologie agglutinierter Foraminiferen (Sarcodina, Textulariina). *Jahrbuch der Geologischen Bundesanstalt,* 132 : 259-347.

BOWSER, S.S. & BERNHARD, J.M., 1993. Structure, bioadhesive distribution and elastic properties of the agglutinated test of *Astrammina rara* (Protozoa : Foraminiferida). *Journal of Eukariotic Microbiology,* 40 : 121-131.

CEDHAGEN, T. , 1993. Taxonomy and biology of *Pelosina arborescens* with comparative notes on *Astrorhiza limicola* (Foraminiferida). *Ophelia,* 37 : 143-162.

DELACA, T.E., LIPPS, J.H. & HESSLER, R.R., 1980. The morphology and ecology of a new large agglutinated Antarctic foraminifer (Textulariina : Notodendrodidae *nov.*). *Zoological Journal of the Linnean Society,* 69 : 205-224.

FAHRNI, J.F., PAWLOWSKI, J. RICHARDSON, S., DEBENAY, J.P. & ZANINETTI, L., (in press). Actin suggests *Miliammina fusca* is related to porcellaneous rather than agglutinated Foraminifera. *Micropaleontology.*

GARONNE, R., 1978. Phylogenesis of connective tissue. Morphological aspects and biosynthesis of sponge intercellular matrix. *In* : ROBERT, L. (Ed.), Frontiers of Matrix Biology, vol. 5. S. Karger, Basel, 250 pp.

HEDLEY, R.H., 1958. A contribution to the biology and cytology of *Halyphysema* (Foraminifera). *Proceedings of the Zoological Society of London,* 130 : 569-576.

HEDLEY, R.H. & WAKEFIELD, J.ST.J., 1967. A collagen-like sheath in the arenaceous foraminifer *Haliphysema* (Protozoa). *Journal of the Royal Microscopical Society,* 87 : 474-481.

HERON-ALLEN, E., & EARLAND, A., 1992. Protozoa, Part II, Foraminifera. *British Antarctic ("Terra Nova") Expedition, 1910, Zoology,* 6 (2) : 25-268.

JONES, R.W., 1994. The Challenger Expedition. Oxford University Press, Oxford & New York, 149 pp.

HEMLEBEN, C., SPINDLER, M. & ANDERSON, O.R., 1989. Modern Planktonic Foraminifera. Springer-Verlag, New York, 363 pp.

LEE, J.J. & ANDERSON, O.R., 1991. Symbiosis in Foraminifera. *In* : LEE, J.J. & ANDERSON, O.R. (Eds), Ecology of Foraminifera. Academic Press, San Diego, pp. 157-220.

LEUTENEGGER, S., 1984. Symbiosis in benthic Foraminifera : specificity and host adaptations. *Journal of Foraminiferal Research,* 14 : 16-35.

LOEBLICH, A.R., JR. & TAPPAN, H., 1964. Sarcodina, chiefly "Thecamoebians" and Foraminiferida. *In* : MOORE, R.C. (Ed.), Treatise on Invertebrate Paleontology. Part C, Protista 2. Geological Society of America, The University of Kansas Press, 900 pp.

LOEBLICH, A.R., JR. & TAPPAN, H., 1988. Foraminiferal genera and their classification. Van Nostrand Reinhold Co., New York, 2 volumes, 1182 pp.

LOEBLICH, A.R., JR. & TAPPAN, H., 1989. Implications of wall composition and structure in agglutinated foraminifers. *Journal of Paleontology,* 63 : 769-777.

REISWIG, H.M., 1971. The axial symmetry of sponge spicules and its phylogenetic significance. *Cahiers de biologie marine,* 12 : 505-514.

RÜTZLER, K. & MACINTYRE, I.G., 1982. The habitat distribution and community structure of the barrier reef complex at Carrie Bow Cay, Belize. *In* : RÜTZLER, K & MACINTYRE, I.G. (Eds), The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I : Structure and Communities. Smithsonian Contributions to the Marine Sciences, 12. Smithsonian Institution Press, Washington, DC, pp. 9-45.

RÜTZLER, K & MACINTYRE, I.G., 1978. Siliceous sponge spicules in coral reef sediments. *Marine Biology,* 49 : 147-159.

SHIRES, R., GOODAY, A.J. & JONES, A.R., 1994. A new large agglutinated foraminifer (Arboramminidae n. fam.) from an oligotrophic site in the abyssal northeast Atlantic. *Journal of Foraminiferal Research,* 24 : 149-157.

SIMPSON, T.L., LANGENBRUCH, P.-F. & SCALERA-LIACI, L., 1985. Silica spicules and axial filaments of the marine sponge *Stelletta grubii* (Porifera, Demospongiae). *Zoomorphology,* 105 : 375-382.

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