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A new deep sea coralline sponge from Turks and Caicos Islands : *Willardia caicosensis* gen. *et* sp. nov. (Demospongiae : Hadromerida)

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Abstract

A new coralline sponge, *Willardia caicosensis*, assigned to the family Timeidae, is described from the deep fore reef off the Turks & Caicos Islands, tropical western Atlantic Ocean, where it is common at depths ranging from 100 to 119 m. Individuals vary up to 15-20 cm in width. The relatively thin aragonitic skeleton is covered with delicate pillars up to + 1 mm. The living tissue is restricted to the spaces between pillars and a thin sheet lying above the calcareous skeleton. Exhalant canals converge upon regularly spaced central oscules on the sponge surface. Siliceous spicules include tylostyles and amphiasters which are secondarily embedded in the aragonitic moiety of the skeleton. In addition, ultrastructural characters of the choanocytes, such as periflagellar sleeves are typical of the Order Hadromerida. Two types of cells with dense spherules are abundant in the mesohyl : spherulous cells packed with large heterogeneous inclusions, protruding at the surface of the sponge, and glycocytes with smaller ovoid corpuscles, mainly grouped along the basal calcareous skeleton. Rough collagen fibrils extend in tracts from the base of the sponge to the ectosome. Sparse bacteria are scattered in the mesohyl.
Keywords : Porifera, sclerosponge, Timeidae, coralline sponge, Atlantic Ocean, new genus, new species, TEM, SEM.

Résumé

Une nouvelle éponge à squelette hypercalcifié est décrite, *Willardia caicosensis*, attribuée à la famille des Timeidae, récoltée sur le tombant récifal externe au large des îles Turks et Caïcos, dans l'Océan Atlantique, où elle est abondante entre 100 et 119 m. La taille des individus varie de 15 à 20 cm dans leur plus grande largeur. La surface du squelette d'aragonite assez mince se caractérise par de fines digitations d'environ 1 mm de haut. Le tissus vivant est limité aux espaces entre ces digitations et une fine pellicule de surface. Les canaux exhalants convergent en surface en des oscules régulièrement espacés. Les spicules de silice, tylostyles et amphiasters, sont secondairement inclus dans le squelette calcaire. De plus, les caractères ultrastructuraux des choanocytes, comme le manchon periflagellaire, sont caractéristiques de l'ordre des Hadromerida. Deux types cellulaires à sphérules denses abondent dans le mésohyle : des cellules sphéruleuses bourrées de grandes inclusions hétérogènes qui font hernie à la surface de l'éponge, et des glycocytes, chargés de plus petits corpuscules ovoïdes, principalement groupés le long du squelette calcaire basal. Des fibrilles de collagène rugeux s'étendent de la base de l'éponge à l'ectosome. Quelques rares bactéries sont réparties dans le mésohyle.
Mots clés : Spongiaires, sclérosponge, Timeidae, éponges coraux, Océan Atlantique, nouveau genre, nouvelle espèce, MET, MEB.

Introduction

Although Recent sponges with a solid calcareous basal skeleton of calcium carbonate have been found in the early century (*Astrosclera willeyana* LISTER, the first to be named in 1900), the extent of their diversity on Recent coral reefs has only been known in the last two decades (HARTMAN, 1969, 1979; HARTMAN & GOREAU, 1970, 1972, 1975, 1976; VACELET, 1977 a, 1977 b, 1979 a, 1979 b, 1980, 1984). Coralline sponges with siliceous spicules were initially erected as a separate class, the Sclerospongiae (HARTMAN & GOREAU, 1970), a view widely accepted among neontologists (LÉVI, 1973; BERGQUIST, 1978). However, a variety of similarities with Recent sponges lacking a calcareous skeleton led to their incorporation into pre-existing groups of Demospongiae (VACELET, 1981, 1983 a, 1983 b, 1985; VAN SOEST, 1984).

To date, about 15 species belonging to 2 classes, 4 subclasses, 8 families and 11 genera are known. They generally live in shaded recesses of reefs easily accessible by scuba diving at depths ranging from shallow water to 30-40 m (SCOFFIN & HENDRY, 1984). Deeper explorations using research submersibles demonstrated their abundance on exposed surfaces of some deep fore reefs, as in Jamaica, between 60 and 120 m (LANG *et al.*, 1975). Here we describe a new genus of sclerosponge, first recorded from the deep fore reef off Turks and Caicos Islands, tropical western Atlantic Ocean, using a manned submersible. Ultrastructural description of the skeleton and soft tissue provide further confirmation of the polyphyletic nature of "sclerosponges".

Material and Methods

SAMPLE COLLECTION

Specimens were collected by the Harbor Branch Oceanographic Institution JOHNSON-SEA-LINK I manned submersible off Turks and Caicos Islands, at depths ranging from 100 to 119 m, between November 11 and 24, 1994 . Specimens were photographed and video taped on collection (Fig. 1). After collection, specimens were either fixed in 10% buffered formalin for four weeks and then preserved in 70% ethanol, fixed for electron microscopy (as described below), or heat dried.

TISSUE PREPARATION

Ground sections for light microscopy were prepared from vouchers fixed in 10% buffered formalin, dehydrated through a graded ethanol series, stained in 100% ethanol saturated with acid fuchsin for 1 h, rinsed in 100 % ethanol and embedded with ERL 4206 according to SPURR (1969). Thick sections were obtained with a low speed diamond saw (Bennet Labcut 1010) prior to grinding. Photomicrographs were taken with a Nikon Optiphot 2 microscope.

Observations in transmission electron microscopy (TEM) were made on small fragments removed and fixed with attached skeleton, from the periphery of sponges, immediately after collection according to a modification of the "low osmium pre-fixative" technique of EISENMAN & ALFERT (1981) previously described (WILLENZ & HARTMAN, 1989). Ruthenium red was added to the fixative (50 mg per 100 ml) (LUFT 1971a, 1971b). Specimens were decalcified for 3 to 4 weeks at 4 °C in a 4.1% solution of disodium ethylenediaminetetraacetate (EDTA), adjusted to pH 6.8 with NaOH, supplemented with 5% polyvinyl pyrolidone (PVP) (FULLMER, 1966) and 12% sucrose to give a final osmotic pressure of 1142 mOsM. Samples were postfixed for 2 h in 1% osmium tetroxide in 0.2 M sodium cacodylate and 0.3 M NaCl. Prior to dehydration through a graded ethanol series, siliceous spicules were dissolved with 15% hydrofluoric acid in 0.2 M sodium cacodylate and 0.3 M NaCl for 1 to 2 h. Samples were then embedded in ERL 4206. Thin sections, double contrasted with uranyl acetate and lead citrate according to REYNOLDS (1963), were examined with a Phillips EM 300 at 80 kV. Semithin sections, from the same embeddings, stained with toluidine blue, were used for choanocyte chamber measurements in light microscopy.

For scanning electron microscopy (SEM), samples were fixed and decalcified as described, omitting ruthenium red. After dehydration through a graded ethanol series, they were cryofractured in liquid nitrogen, thawed in 100% ethanol at ambient temperature and dried by the critical point method from carbon dioxide (Balzers CPD 030). They were finally sputter-coated with gold-palladium, and observed with an ISI DS 130 SEM at 20 and 25 kV.

SPICULE PREPARATION

Spicules were measured from nitric acid preparations, using a calibrated stage micrometer. SEM preparations were made on microscope slide coverglasses mounted on stubs and sputter-coated as above.

MINERALOGICAL ANALYSIS

The aragonitic nature of the calcareous skeleton was determined by X-ray diffraction analysis (Philips P.W. 1729 X-ray generator).

ABBREVIATIONS USED IN THE TEXT

BMNH = Natural History Museum (London), HBOI = Harbor Branch Oceanographic Institution Inc. (Fort Pierce, Florida), RBINS = Royal Belgian Institute of Natural Sciences, YPM = Yale Peabody Museum of Natural History (New Haven, Connecticut).

Systematics

Order **Hadromerida** TOPSENT, 1894
Family **Timeidae** TOPSENT, 1928
Genus ***Willardia*** gen. nov.

DIAGNOSIS

Timeidae of irregular shape, secreting a thin basal skeleton of aragonite, attached to the substratum by a broad peduncle, with edges extending freely above substratum and curled downward. Aragonite surface is ornamented with thin finger-like processes up to ± 1 mm high, ± 250 µm apart. There is no vertical calicle extending into the calcareous skeleton. Megascleres are tylostyles arranged in fanned brushes at the surface with distal ends protruding, forming a velvet-like surface. Microscleres are amphiasters primarily located beneath the surface and around the main aquiferous canals. Siliceous spicules are occasionally covered by aragonite as the basal calcareous mass grows upward.

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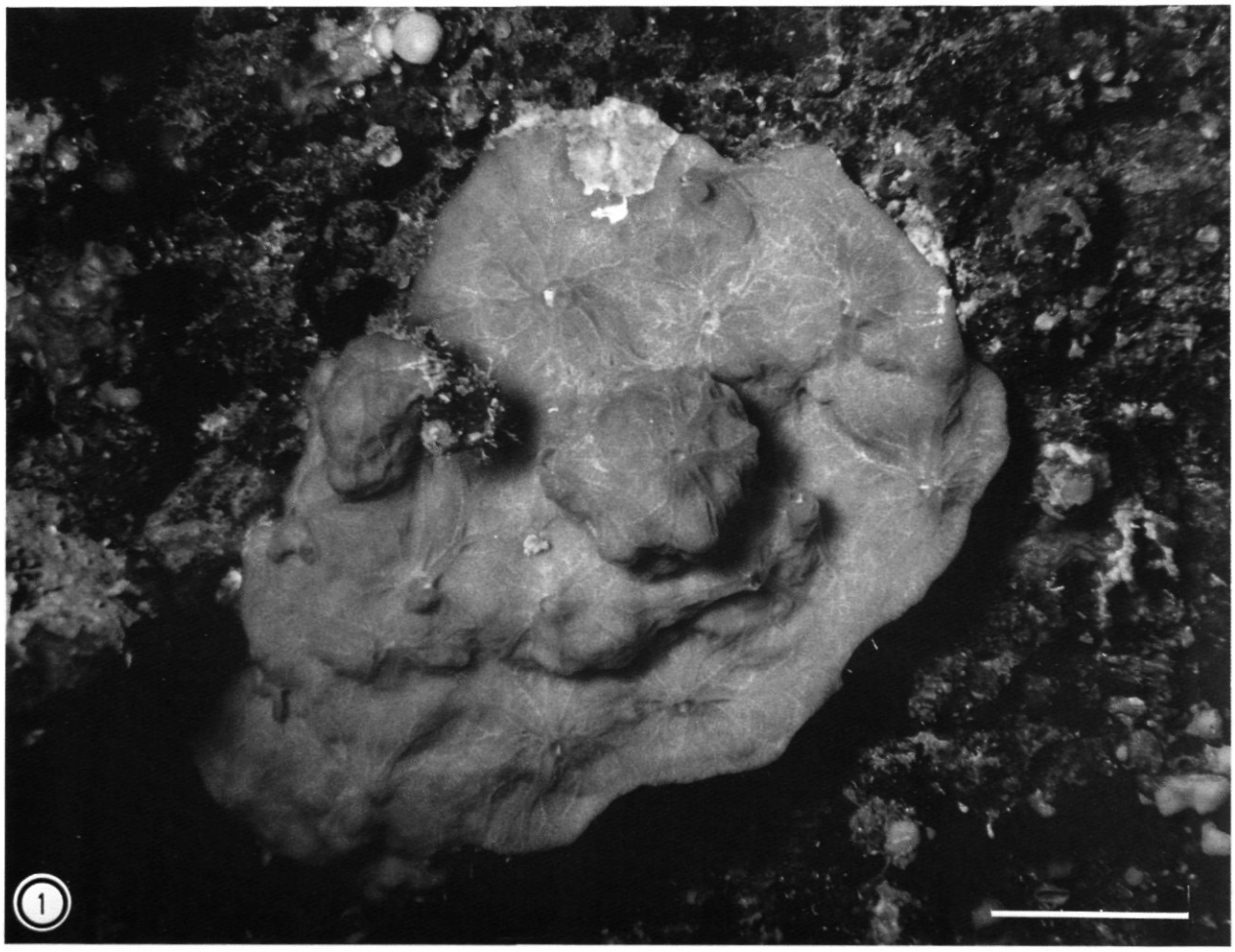
Fig. 1. - *Willardia caicosensis* gen. *et* sp. nov. Holotype (19-XI-94-3-13) *in situ*, NE tip of Grand Turk Island, lat 21°31'59"N, long 71°07'97"W, at 114 m on rocky wall (scale bar = 5 cm).

Fig. 2. - Surface of sponge with radially arranged tylostyles (SEM, scale bar = 500 µm).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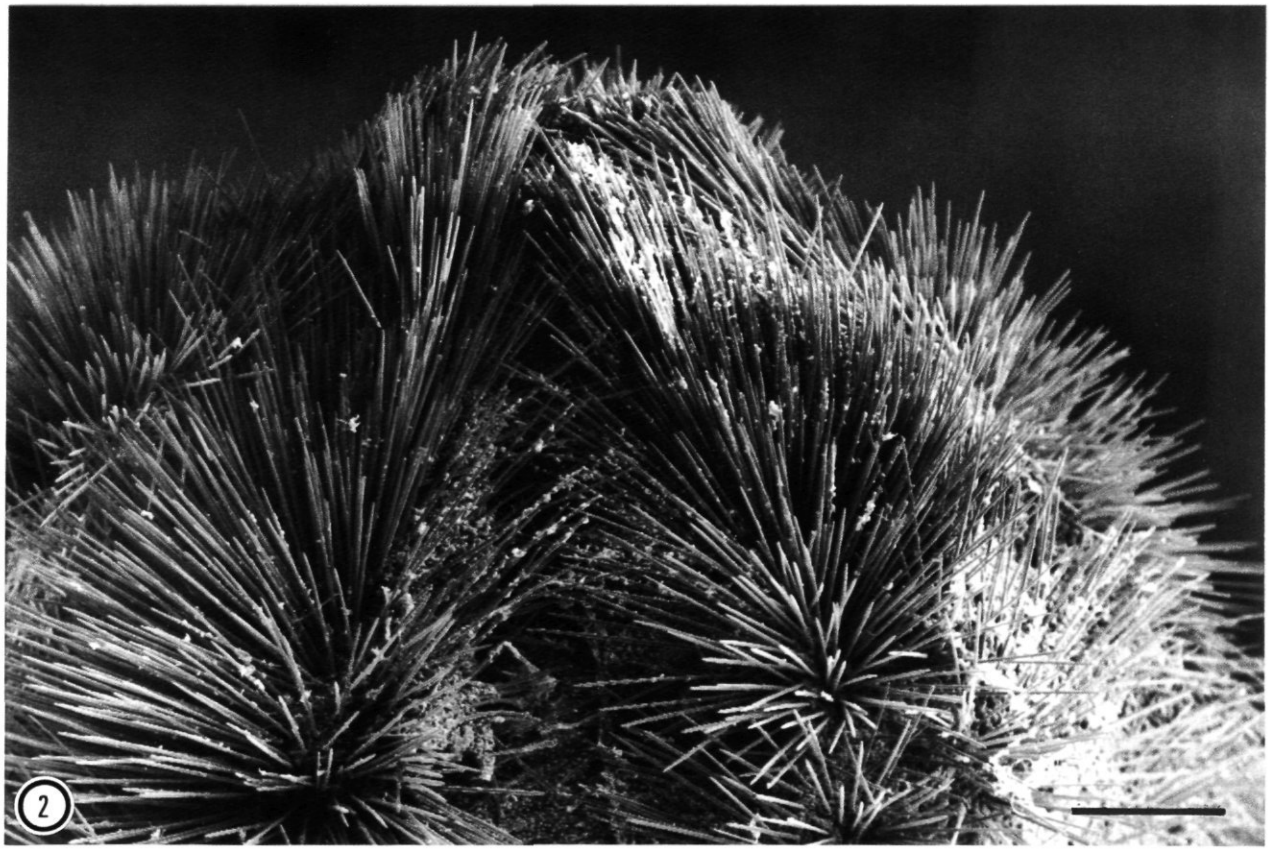
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Living tissue is a thin veneer filling the irregular spaces between erect calcareous processes. Oscules with convergent excurrent canals are located on prominences of the calcareous skeleton.
Type species : *Willardia caicosensis* gen. *et* sp. nov.

Etymology
Generic name honors Prof. Willard D. HARTMAN, Yale Peabody Museum of Natural History, who pioneered the expansion of knowledge on coralline sponges.

Willardia caicosensis sp. nov.

TYPE MATERIAL

Holotype : RBINS-POR. 49 : NE tip of Grand Turk Island, lat 21°31'59"N, long 71°07'97"W, 114 m, 19 Nov. 1994, coll. nr HBOI-19-XI-94-3-13, (Fig. 1), dry, ethanol voucher and EM fixations.
Paratypes : RBINS-POR. 50 : West of Providenciales, lat 21°49'85"N, long 72°20'65"W, 119 m, 13 Nov. 1994, coll nr HBOI-13-XI-94-2-6, ethanol; RBINS-POR. 51 to 55 (5 different specimens) : N tip of Grand Turk Island, lat 21°31' 62"N, long 71°08'04"W, 100 to 111 m, 24 Nov. 1994, coll. nr HBOI-24 -XI-94-1-7, ethanol; HBOI-11-XI-94-3-5 : North of North Caicos Island, lat 21°58'75"N, long 71°57'53"W, 115 m, 11 Nov. 1994, ethanol; BMNH : 1995.11.3.1 : NE tip of Grand Turk Island, lat 21°31'59"N, long 71°07'97"W, 119 m, 13 Nov. 1994, coll. nr HBOI-19-XI-94-3-12, ethanol; YPM 9360 : NE tip of Grand Turk Island, lat 21°31'59"N, long 71°07'97"W, 119 m, 13 Nov. 1994, coll. nr HBOI-19-XI-94-3-12, ethanol.

HABITAT

Vertical rock walls around Turks and Caicos Islands, tropical western Atlantic Ocean, at depths ranging from 100 to 119 m.

DESCRIPTION

Shape and size
Sponge is plate-like, with calcareous basal mass attached to the substratum at its center, reaching 4 to 5 mm in thickness. The edges, not attached to the substratum, are thinner, seldom exceeding 2 to 3 mm, usually curled downward and form an irregular bristled fringe. Individuals reach 15 to 20 cm in width.

Color
Yellow to tan orange in life (Fig. 1), dark to pale brown in alcohol.

Table 1:
Variation of tylostyles sizes among 10 specimens of *Willardia caicosensis* (measurements in μm).

Specimen nr	Length			Width		
	Range	Mean	(std dev)	Range	Mean	(std dev)
RBINS - POR. 49	444 - 1080	785.8	(174.6)	7.8 - 13.2	10.4	(1.4)
RBINS - POR. 50	322 - 725	507.5	(108.6)	4.7 - 15.5	10.0	(2.7)
RBINS - POR. 51	360 - 1140	693.6	(225.3)	6.2 - 15.5	12.0	(2.0)
RBINS - POR. 52	279 - 825	477.2	(138.3)	4.7 - 12.4	7.4	(1.7)
RBINS - POR. 53	254 - 806	455.3	(120.2)	4.7 - 12.4	6.9	(1.7)
RBINS - POR. 54	341 - 880	647.5	(129.0)	4.7 - 15.5	11.0	(2.2)
RBINS - POR. 55	353 - 1023	612.9	(147.4)	4.7 - 15.5	11.3	(2.3)
HBOI-11-XI-94-3-5	303 - 949	573.6	(147.3)	6.2 - 14.0	10.5	(1.9)
BMNH : 1995.11.3.1	310 - 1004	596.4	(182.4)	4.7 - 15.5	10.6	(2.5)
YPM 9360	273 - 775	431.3	(103.7)	4.7 - 12.4	7.9	(1.6)

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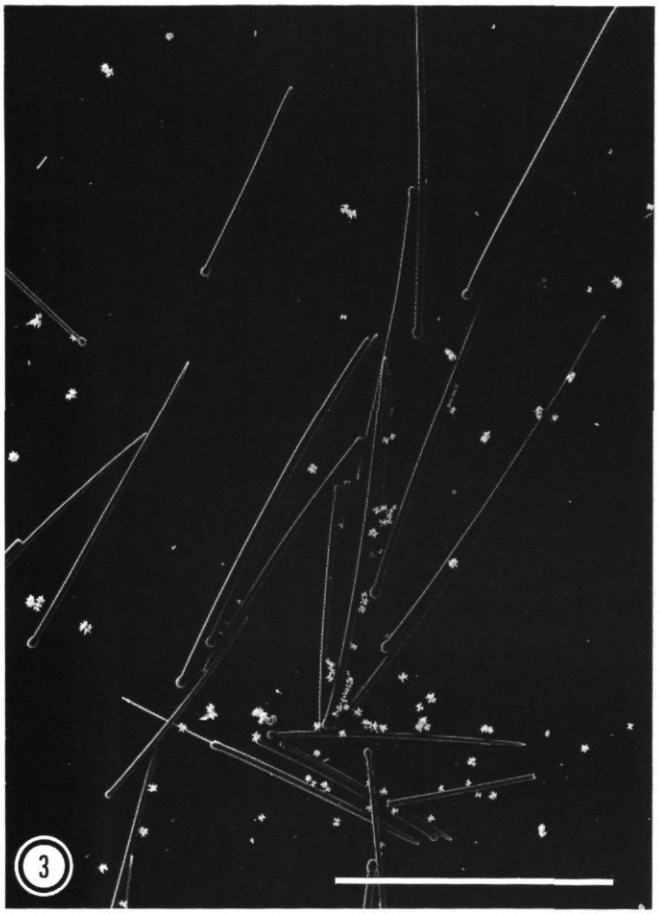
Fig. 3. - Tylostyles and amphiasters (SEM, scale bar = 500 μm).
Fig. 4. - Amphiasters (SEM, scale bar = 10 μm).
Fig. 5. - Surface of calcareous skeleton with pillar shaped processes (SEM, scale bar = 1 mm).
Fig. 6. - Tylostyle protruding from aragonitic skeleton and amphiasters settled on surface during sample preparation (SEM, scale bar = 50 μm).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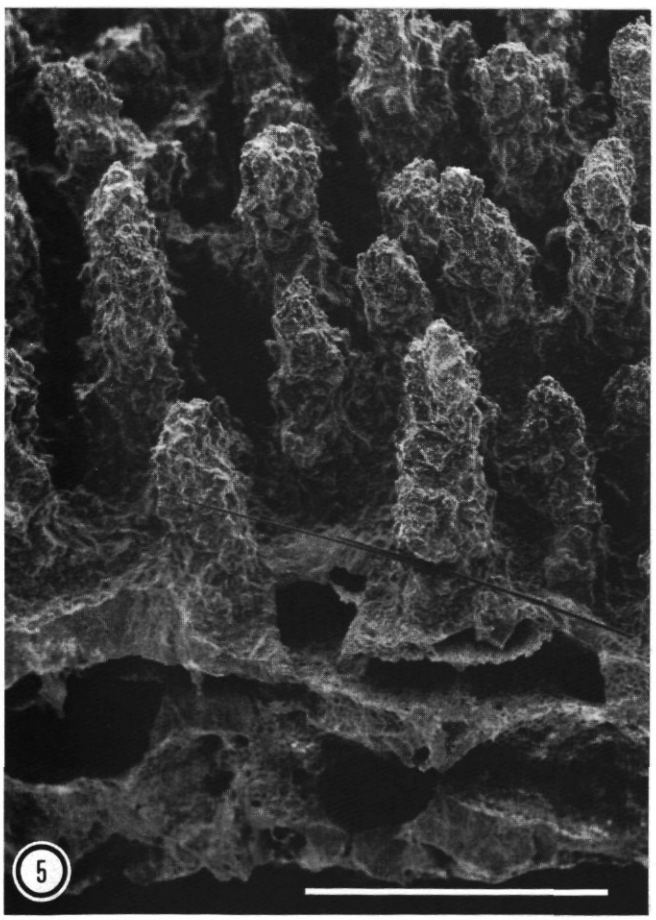
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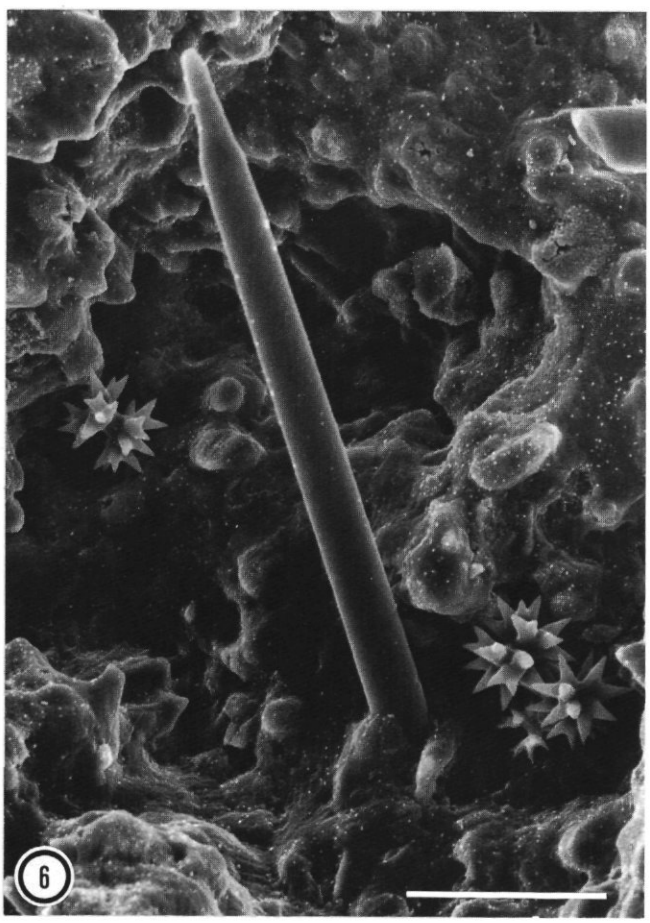
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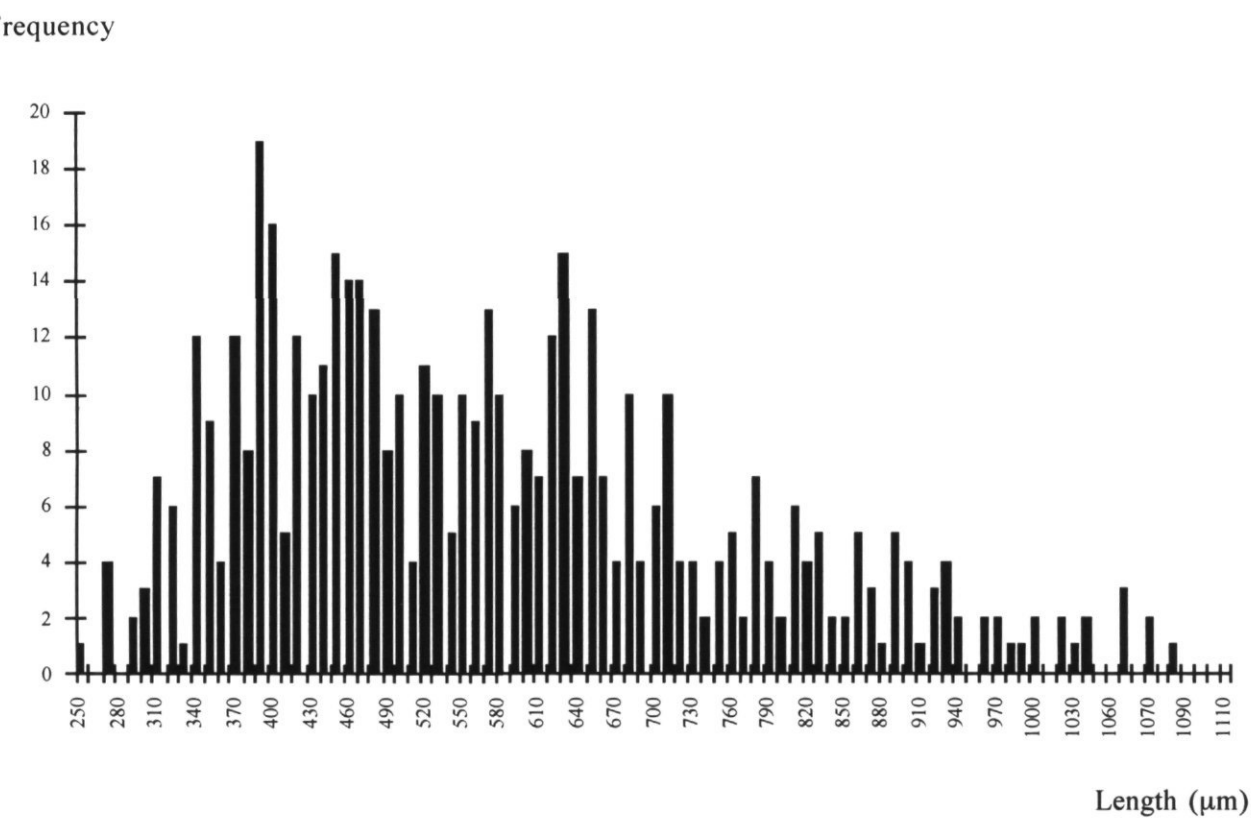
Diagram 1 :
Frequency distribution of tylostyle length among 10 specimens.



Surface
Oscules are evenly distributed over the surface, 3-4 mm wide, receiving raised transparent anastomosed excurrent canals (Fig. 1). Ostia are not readily apparent on preserved specimens or in life. The surface of the living tissue has a velvet-like appearance, due to the abundance of megasclere brushes protruding through the dermal membrane (Fig. 2).

Spicules
Megascleres. (50 measurements of 10 specimens in light microscopy), (Fig. 3).
Tylostyles, straight or slightly curved, length 254-1080 μm ($\bar{x}$ = 577 μm ± 183), width 4.7-15.5 μm ($\bar{x}$ = 9.8 μm ± 2.6). Table 1 and Diagram 1 indicate that two size categories occur.

Microscleres. (50 measurements of 2 specimens in light microscopy), (Fig. 4).
Amphiasters, one size category, length 15.50-21.70 μm ($\bar{x}$ = 17.64 μm ± 1.67), width 10.85-20.15 μm ($\bar{x}$ = 15.84 μm ± 1.60).

Siliceous skeleton
Tylostyles are arranged in fanned brushes at the surface of the sponge, with distal ends protruding beyond ectoderm. (Figs 2 & 16). Basal ends are embedded in collagen tracts extending down to the base of the sponge (Fig. 16).
Amphiasters are located under the exopinacocytes of the outer surface and alongside the endopinacocytes lining the main aquiferous canals (Figs 10 & 11).

Calcareous skeleton
The basal skeleton is aragonitic, with only a small number of both siliceous spicule types entrapped (Figs 6 & 9). The surface is composed of delicate

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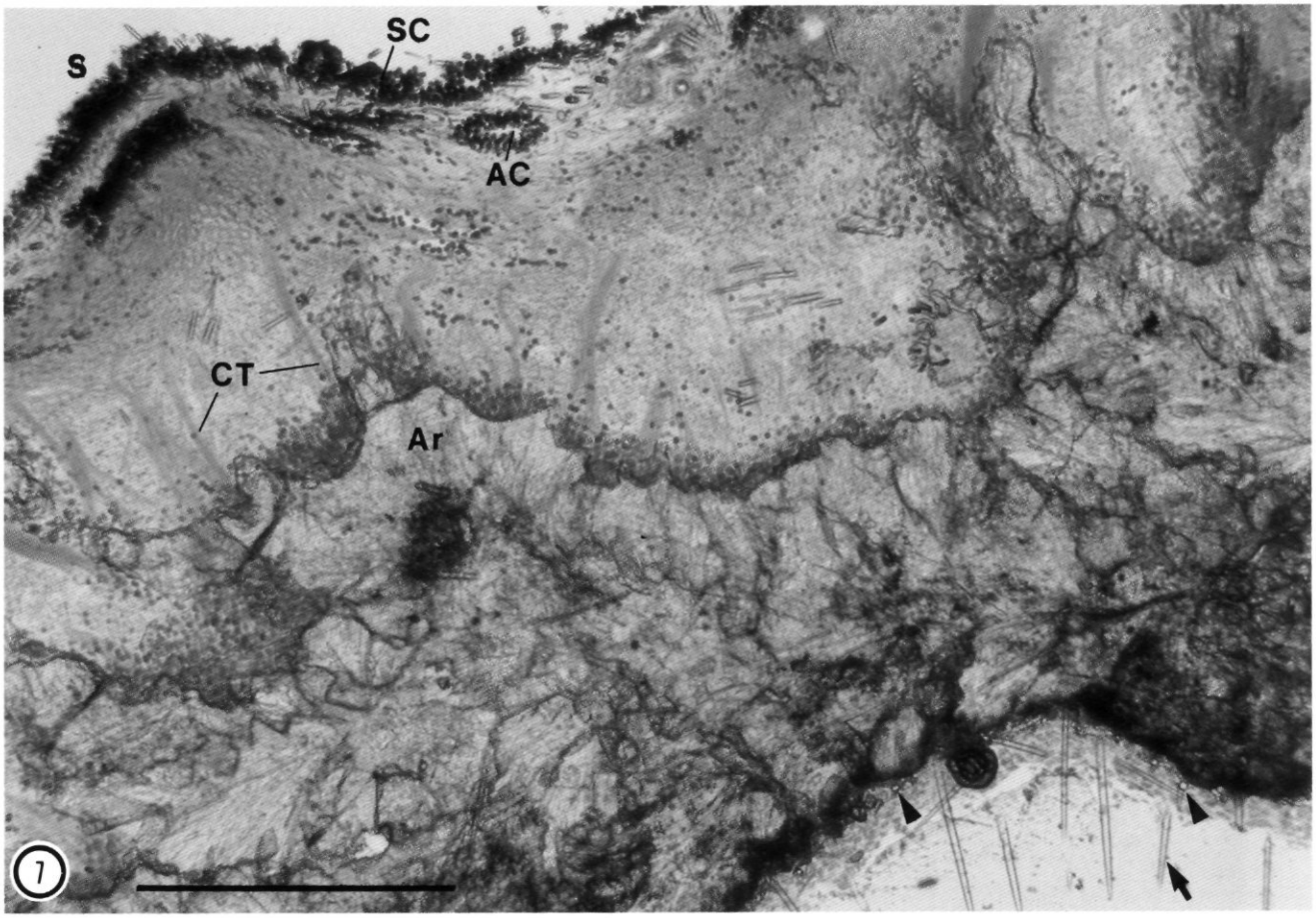
Fig. 7 - 9. - Ground section perpendicular to the surface of *Willardia caicosensis* gen. *et* sp. nov. : living tissue stained with acid fuchsin. A = amphiasters; AC = aquiferous canal; Ar = aragonite skeleton; cc = choanocyte chambers; CT = collagen tracts; G = glycocytes; S = surface; SC = spherulous cells; T = tylostyles. 7 : *Lithobubaris sp.* forms a thin film on lower surface of some specimens (lower right). Arrowheads indicate desmas; arrow indicates tylostyles (light microscopy, scale bar = 500 μm). 8 : Abundant spherulous cells accumulate at and protrude from sponge surface (scale bar = 100 μm). 9 : Concentration of acidophilic glycocytes at basal margin of mesohyl (scale bar = 100 μm).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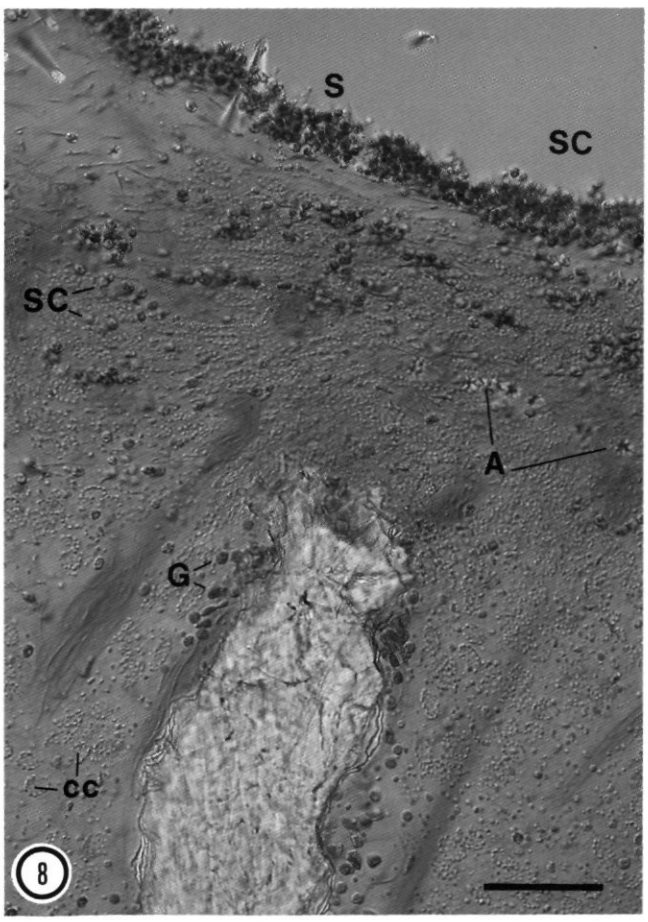
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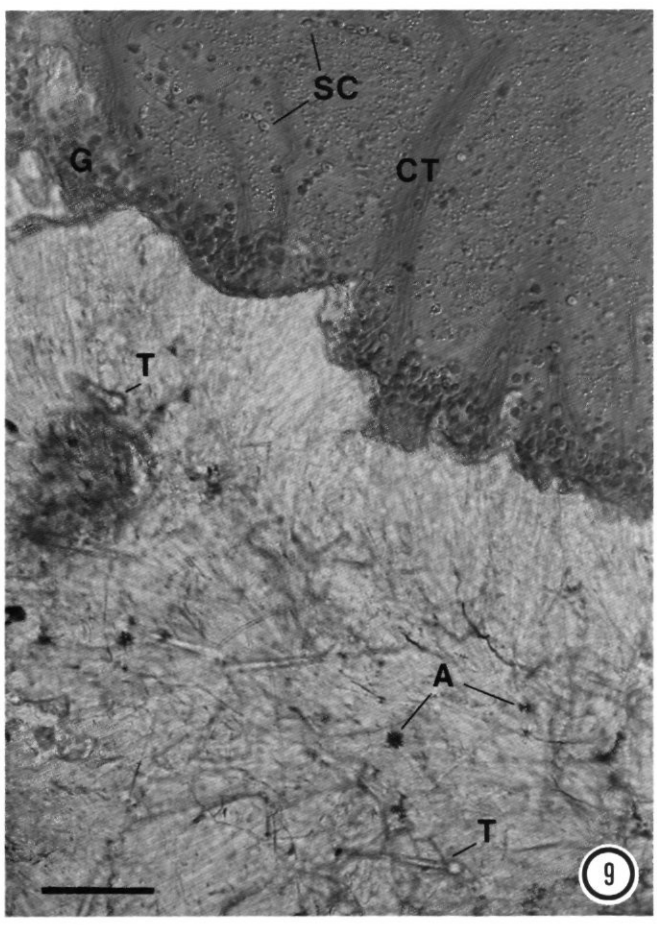
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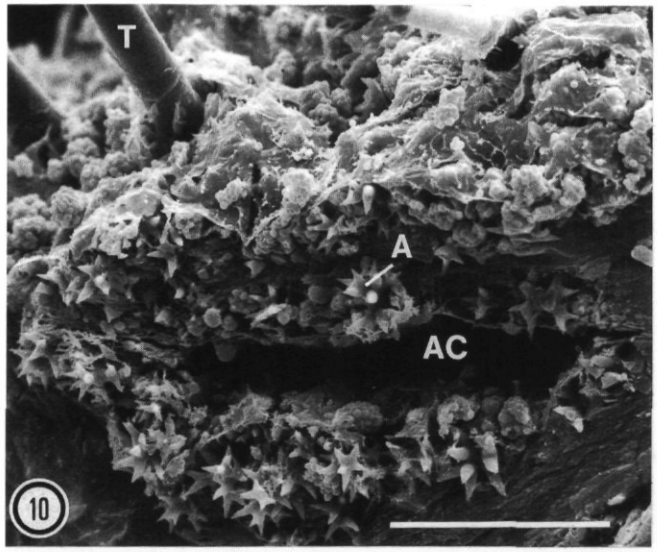
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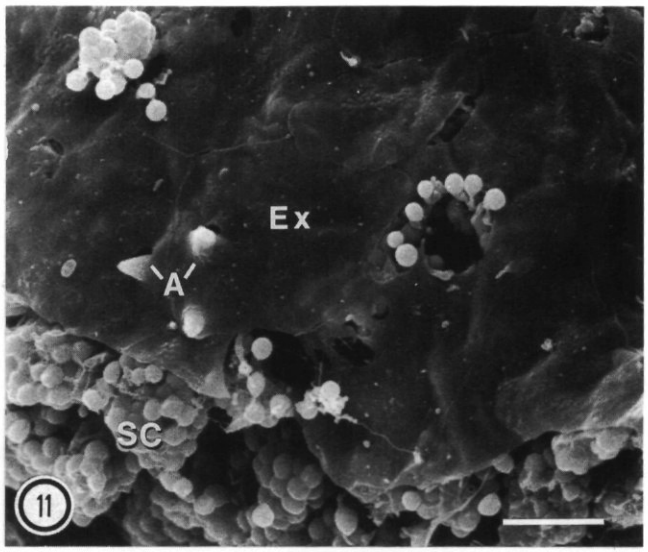
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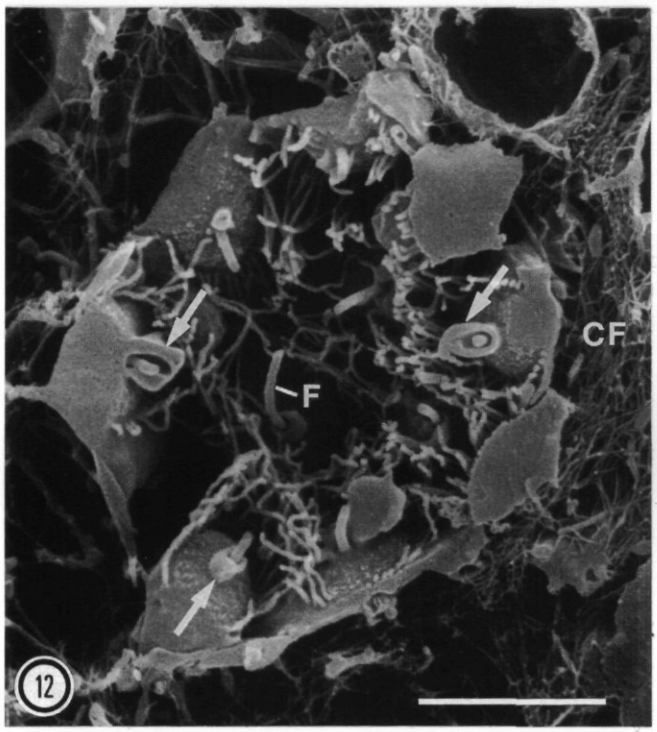
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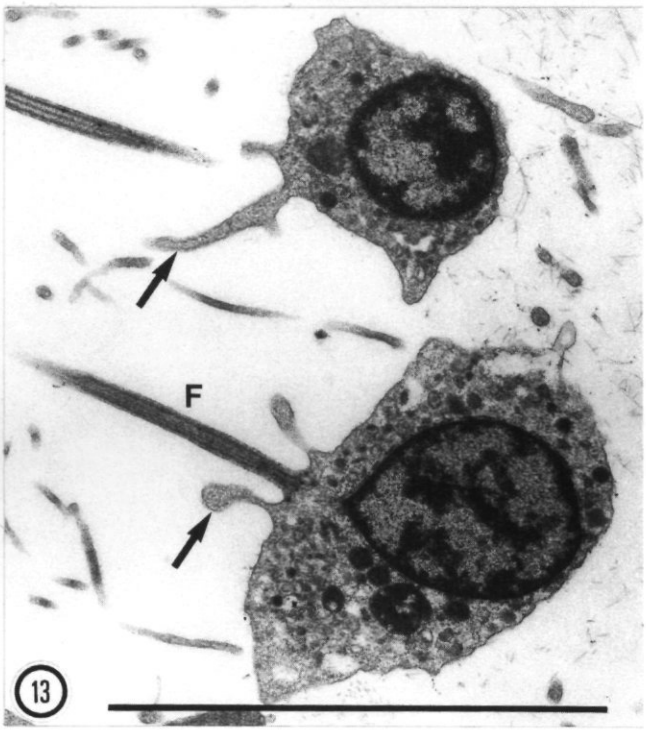
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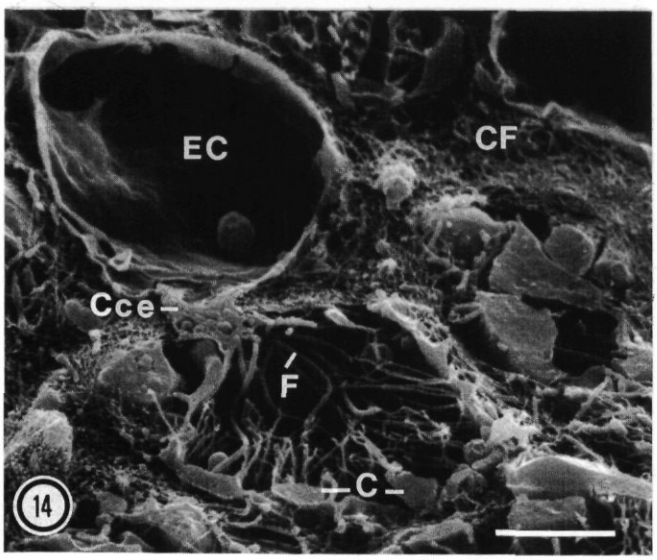
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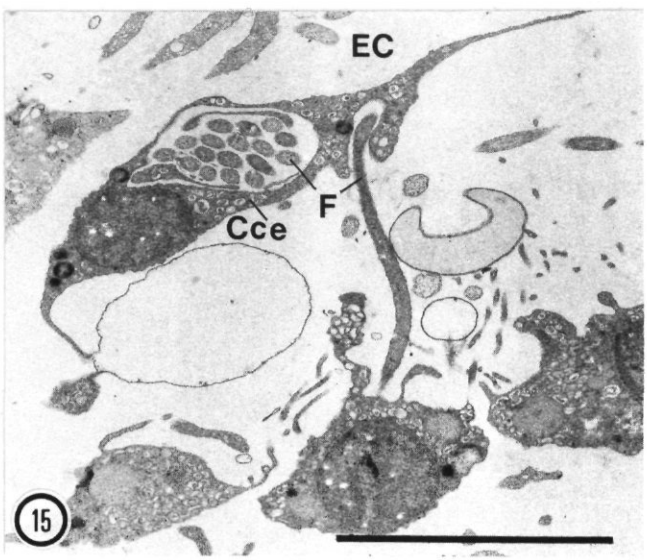
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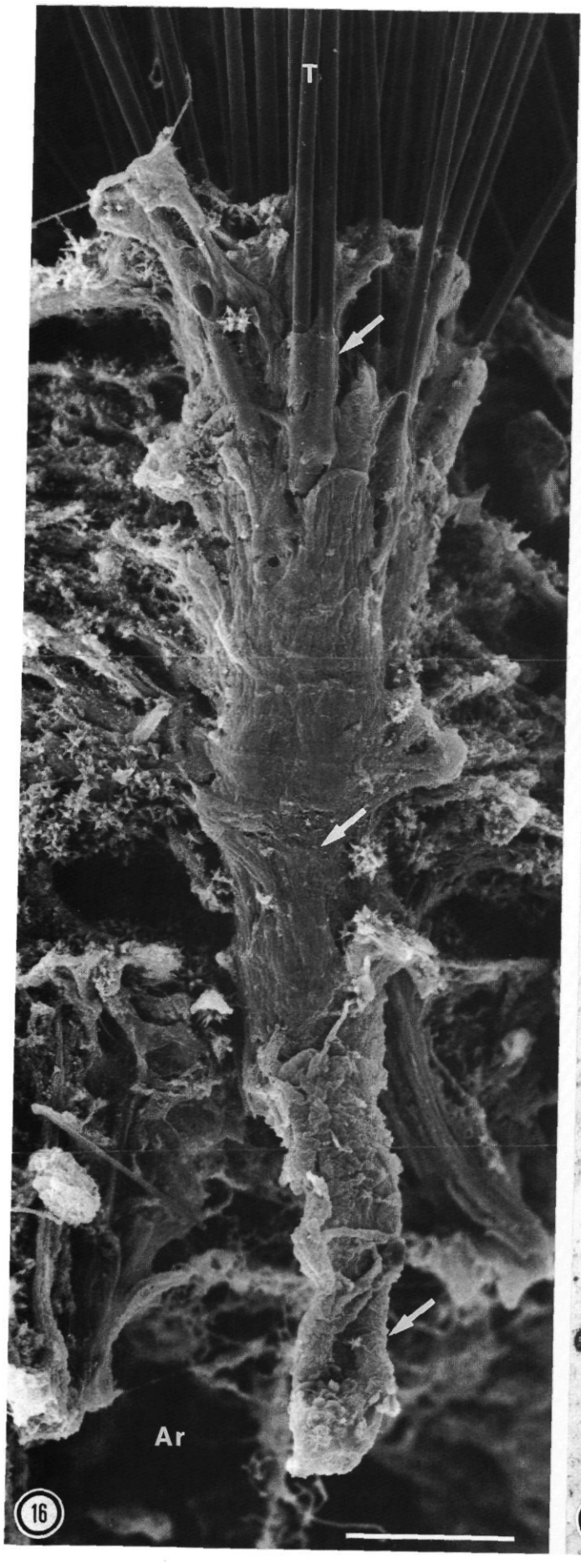
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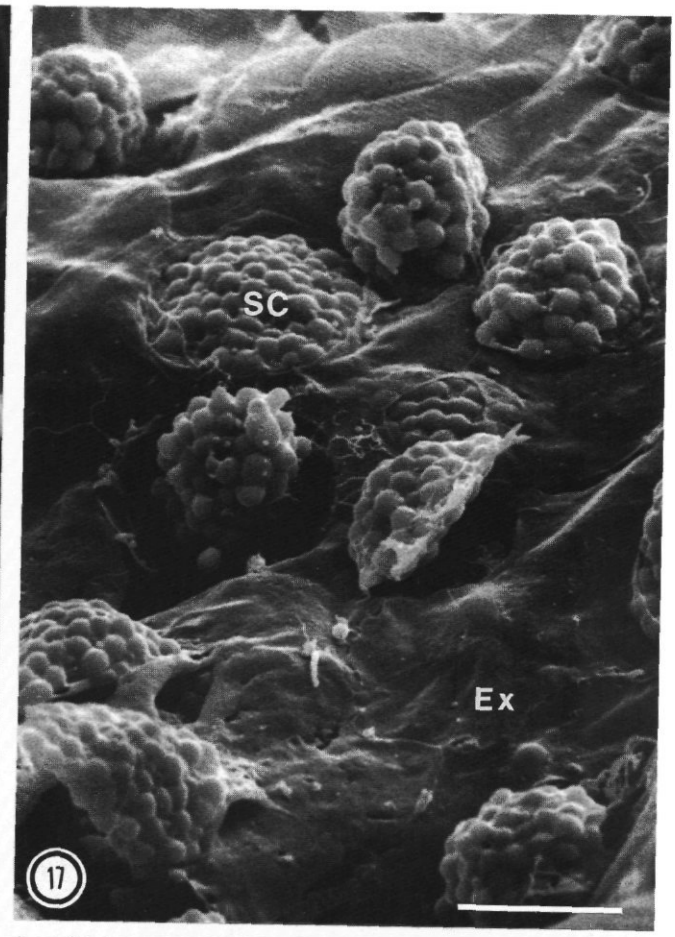
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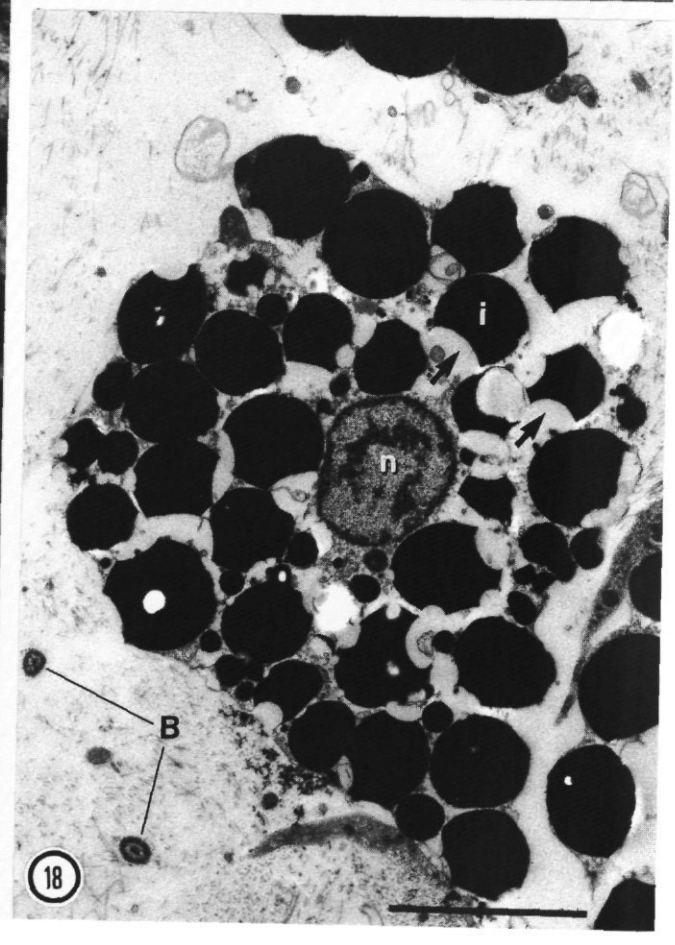
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pillars up to ± 1 mm, ± 250 µm apart (Fig. 5). The microstructure of the aragonitic skeleton is of the peniciliate spherulitic type : the needle-like, crystalline units radiate from centers of calcification (Fig. 7).

Cytology

The living tissue forms a thin sheet of ± 0.1 to 0.5 mm over the surface of the calcareous skeleton (Fig. 7). The ectosome, mostly hidden under the abundant protruding tylostyles, consists of a single layer of flat superficial exopinacocytes (Figs 11 & 17). The choanosome has a higher density of choanocyte chambers in the central zone (Figs 7 & 19). Eurypylous, spherical choanocyte chambers are small, with a mean diameter of 16.8 ± 1.9 µm (n = 50). Choanocytes are oblate with an equatorial annular-shaped expansion, a large nucleus and a long flagellum surrounded at the base by a periflagellar sleeve, typical of the Order Hadromerida (Figs 12 & 13). A central cell, with cytoplasmic processes encircling several flagella, controls the aperture of the apopyle toward the exhalant canals (Figs 14 & 15). The mean number of choanocytes per chamber is approximately 20, as estimated by dividing the mean area of a chamber by the mean basal surface of one choanocyte (RASMONT & ROZENFELD, 1981). The choanocyte chambers lie in a mesohyl rich in collagen fibrils (Figs 12 & 14).

Two different types of cells with dense inclusions occur : spherulous cells and glycocytes.

(I) Spherulous cells are densely concentrated beneath the exopinacocytes and around the large aquiferous canals. They remain unstained after treatment with acid fuchsin (Figs 7, 8 & 9) and protrude from the surface of the sponge (Fig. 17). Around the central nucleus, the cytoplasm is packed with abundant osmiophilic spherical inclusions (2.8 µm in max diameter) bearing peripheral electron-lucent lenses (Fig. 18, arrows).

(II) Glycocytes containing acidophilic and osmiophilic ovoid inclusions (1.9 x 3.3 µm in max diameter) in a dense cytoplasm are particularly abundant at the base of the sponge, close to the basopinacocytes (Figs 8, 9, 19, 20, & 21). The nucleus is anucleolate and glycogen rosettes can be observed.

Bundles of rough collagen fibrils, characterized by a distinct banding pattern with a periodicity of 58 nm, appear at the base of the sponge, close to the calcareous skeleton, anchored deep within the spaces formed between growing aragonitic crystals (Figs 21 & 22); the same fibrils extend upward through the mesohyl and envelope the base of radiating tylostyles (Fig. 16). Neither spongin fibers nor perispicular spongin occur. A single layer of thin basopinacocytes lines the calcareous skeleton (Figs 19, 20, 21 & 22). An organic matrix is revealed as an irregular fibrillar network when the aragonite is dissolved by treatment with EDTA (Figs 21 & 22). Intercellular bacteria are sparsely distributed in the mesohyl (Figs 18 & 21).

Associated fauna

Another sponge, *Lithobubaris* sp., detected by light microscopy, formed a thin encrusting sheet on the underneath surface of some specimens, in close contact with the aragonitic skeleton (Fig. 7).

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Fig. 10. - Cryofractured specimen with amphiasters (A) around aquiferous canal (AC) and beneath surface. T = tylostyle (SEM, scale bar = 50 µm).

Fig. 11. - Exopinacocytes of dermal membrane (Ex) with protruding amphiasters (A) and spherulous cells (SC) (SEM, scale bar = 10 µm).

Fig. 12-13. - Sections through choanocytes. Arrows indicate periflagellar sleeves. CF = collagen fibrils; F = flagellum. 12: Cryofracture (SEM, scale bar = 5 µm). 13 : Detail in longitudinal section (TEM, scale bar = 5 µm).

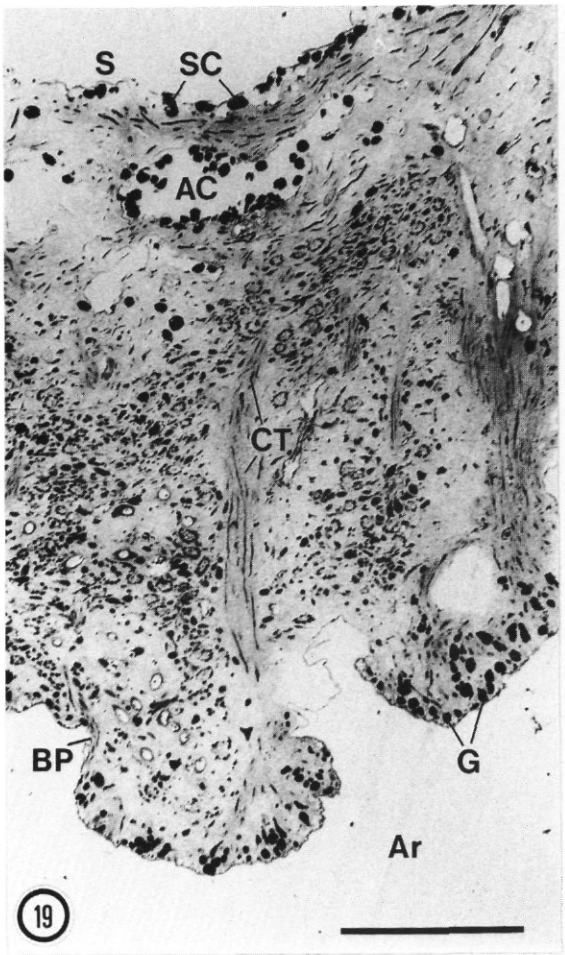
Fig. 14-15. - Choanocyte chambers with free ends of flagella gathered in central cell (Cce). C = choanocyte; CF = collagen fibrils; EC = exhalant canals; F = flagellum. 14 : Connection of chamber with exhalant canal (SEM, scale bar = 5 µm). 15 : Detail in section (TEM, scale bar = 5 µm).

Fig. 16. - Cryofracture perpendicular to surface of decalcified specimen. Radiating tylostyles (T) are clearly embedded in collagen tracts extending down to base of sponge (arrows). Ar = Space filled with aragonite prior to decalcification (SEM, scale bar = 100 µm).

Fig. 17. - Spherulous cells (SC) protrude abundantly at surface between exopinacocytes (Ex) (SEM, scale bar = 10 µm).

Fig. 18. - Spherulous cell packed with heterogeneous inclusions (i) with electron-lucent lenses (arrows). B = bacteria; n = nucleus (TEM, scale bar = 5 µm).

Fig. 19 - 22. - Cross section through decalcified sample of *Willardia caicosensis* gen. *et* sp. nov. AC = aquiferous canal; Ar = space filled by aragonitic skeleton prior to decalcification; ArC = ghost of aragonitic crystals; B = bacteria; BP = basopinacocyte; CT = collagen tracts; G = glycocytes; M = skeletal organic matrix; SC = spherulous cells; S = surface. 19 : Semi-thin section (light microscopy, scale bar = 500 µm). 20 : Cryofracture at base of living tissue (SEM, scale bar = 50 µm). 21 : Section at base of living tissue. Arrow indicates collagen fibrils near glycocyte (TEM, scale bar = 5 µm). 22 : Enlargement of Fig. 21, collagen fibrils apperar as rough fibrils with regularly spaced banding pattern at base inserted between aragonitic crystals (arrowheads) and extend into mesohyl (TEM, scale bar = 1 µm). ▷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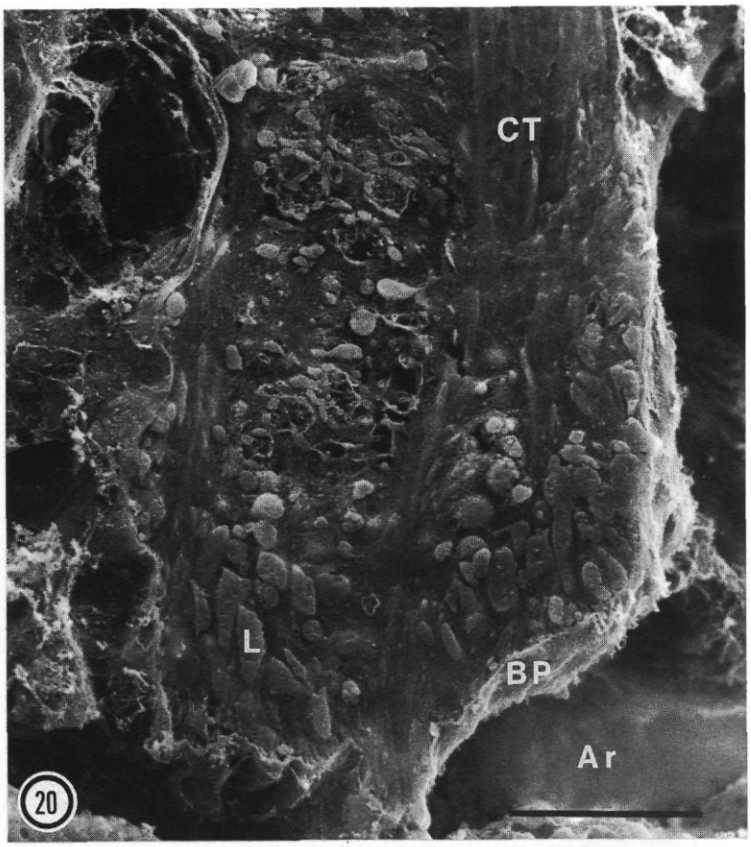
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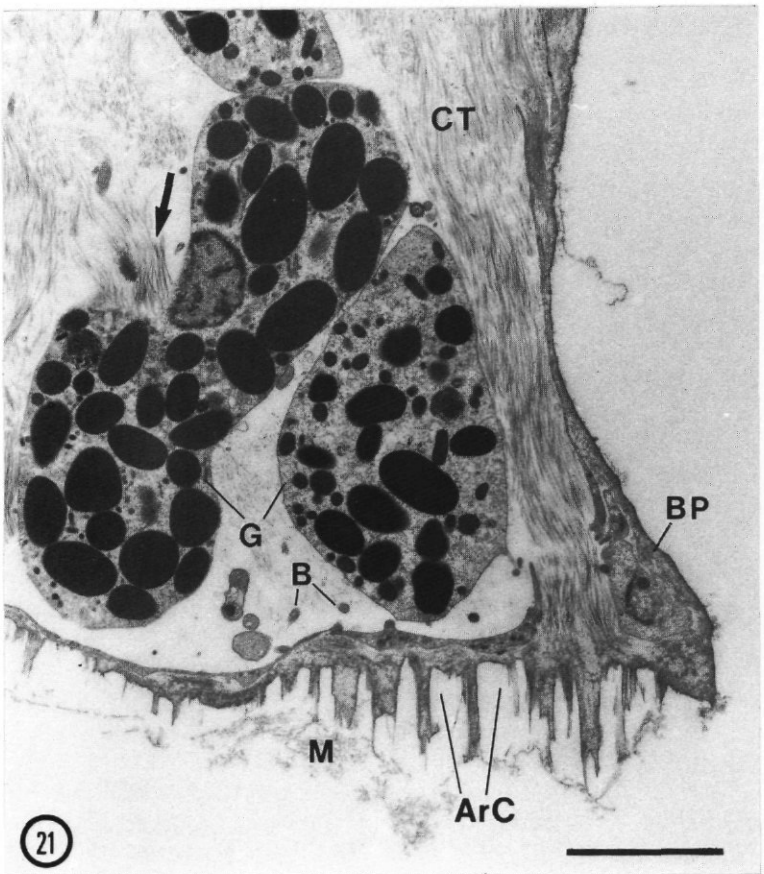
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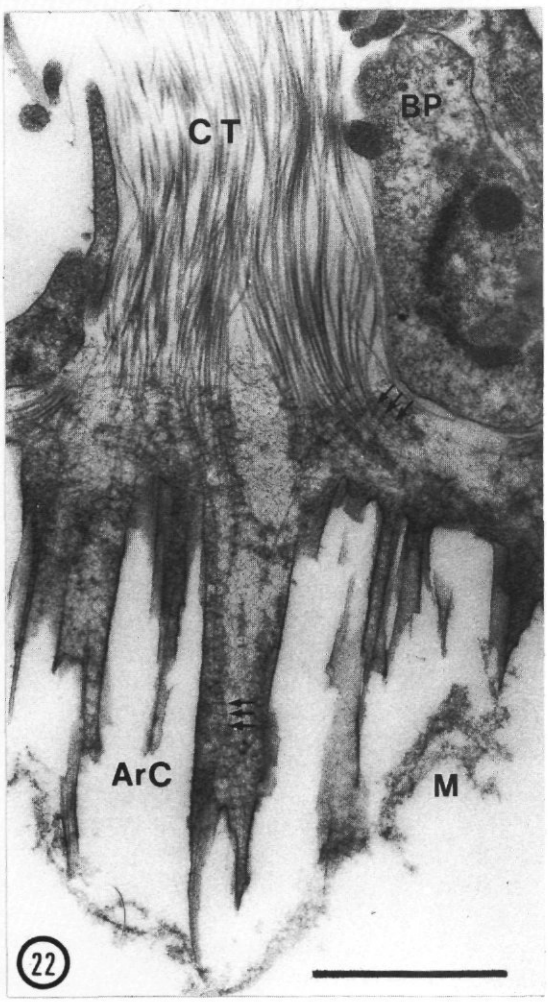
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Etymology
Specific name refers to the locality at which the species was first discovered.

Discussion

Willardia caicosensis gen. nov. *et* sp. nov. clearly belongs to the Order Hadromerida based on its skeletal architecture : radially arranged tylostyles with pointed ends protruding above the surface and numerous peripheral amphiasters. Abundant intercellular collagen fibrils and absence of a well-formed network of spongin fibers are also characteristic of this order (HARTMAN, 1982). The uniqueness of the aragonitic nature of the skeleton of *W. caicosensis* within the Hadromerida forms the basis for erecting a new genus of coralline sponge. There is one other described hadromerid sclerosponge, *Acanthochaetetes wellsi* (HARTMAN & GOREAU, 1975), recently transferred from the family Acanthochaetidae to the family Spirastrellidae (REITNER, 1991). However, several characters differentiate the new genus *Willardia* from *Acanthochaetetes*. Most significantly, the basal calcareous skeletons differ in mineralogy and structure : calcite for *Acanthochaetetes* and aragonite for *Willardia*; a massive formation with superficial contiguous vertical tabulate pseudocalicles for *Acanthochaetetes* and only irregularly arranged protruding pillars for *Willardia.* Next, the asters in *W. caicosensis* are clearly amphiasters, whereas *A. wellsi* has spirasters (HARTMAN & GOREAU, 1975; REITNER, 1991). Finally, no asexual budding rooted in the calcareous skeleton, as described for *A. wellsi* (VACELET, 1983, 1990), has been observed in any sample of *W. caicosensis.* Interestingly, the aragonitic skeleton of the new genus presents similarities with the Family Ceratoporellidae, the largest family of coralline sponges, comprising 4 genera and 6 species. The microstructural organization is of the peniciliate (VACELET, 1985) or elongate (WOOD, 1991) spherulitic type, with siliceous spicules becoming entrapped in the aragonite as the calcareous skeleton grows upwards, secreted by a basal pinacoderm. However, no further comparison can be made with the Family Ceratoporellidae, which has spicule and soft-tissue affinities with the Family Agelasidae.

Features of the siliceous skeleton of *Willardia* are more closely related to the Family Timeidae. The single layer of erect, radial tylostyles is typical of the family. The most closely related, non-coralline Timeidae is the genus *Diplastrella*, whose amphiasters show a striking resemblance to those of *Willardia.* However, *Willardia* can be differentiated from *Diplastrella* on the basis of not only its calcareous skeleton, but also its siliceous skeletal characters. *Diplastrella bistellata* (BMNH.1877.3.25.31) and *Diplastrella gardineri* (BMNH.1936.3.4.491; BMNH.1936.3.4.99) have two size classes of amphiasters, whereas *W. caicosensis* lacks the larger category of amphiasters which are characteristic of *Diplastrella*. Moreover, examined specimens of *Diplastrella* contained euasters, which are not present in *W. caicosensis.*

Although skeletal characteristics are the most convenient way to identify sponges, the significance of cytological characters in systematics is widely accepted (BOURY-ESNAULT *et al.*, 1984, 1990; WILLENZ & HARTMAN, 1989). The small size of the choanocyte chambers of *W. caicosensis* is consistent with previous records published for hadromerids, considering the possible differences in fixation procedures and artifacts that can affect the contraction of the tissues : 21 x 18 µm to 24 x 20 µm for *A. wellsi* (in HARTMAN & GOREAU, 1975), 22 x 28 µm (mean measures) for *Suberites massa* NARDO (CONNES *et al.*, 1972), and 16.8 $\pm$ 1.9 µm for *W. caicosensis*. The number of cells per chamber as estimated herein lies among the smallest values reported in the phylum (BOURY-ESNAULT *et al.*, 1984; reviewed in SIMPSON, 1984). The presence of periflagellar sleeves is a common feature of all Hadromerida having been described at the ultrastructural level, such as *S. massa* (CONNES *et al.*, 1971; DIAZ, 1979); *S. domuncula* OLIVI, *Ficulina ficus* JOHNSTON and *A. wellsi* (BOURY-ESNAULT *et al.*, 1990).

A broad variety of spherulous cells have been reported within the Porifera (for review, see SIMPSON, 1984). They are characterized by their highly variable morphology and chemistry. The abundance of spherulous cells filled with large granules around exhalant aquiferous canals and beneath the exopinacocytes, and their protrusion from the surface of *Willardia* suggest an intense secretory or excretory function. Although these samples of *Willardia* have not yet been evaluated for cytotoxicity, production and storage of secondary metabolites used for chemical defense are functions that have been suggested for spherulous cells of some species (THOMPSON *et al.*, 1983; URIZ *et al.*, 1996). Spherulous cells are much more abundant in *Willardia* than as reported for *A. wellsi* (VACELET, 1990). Moreover, the gemmular, archaeocyte-like, crypt cells found in *A. wellsi* (VACELET, 1990) are not observed in *W. caicosensis*. Conversely, glycocytes have not been reported for *A. wellsi* (VACELET, 1990), but are observed in *W. caicosensis*, concentrated near the basopinacocyte layer. This is consistent with their role in the storage and transfer of glycogen to areas of high metabolic activity (BOURY-ESNAULT & DOUMENC, 1978), such as the deposition of aragonitic skeleton.

The occurrence of rough collagen fibrils in *W. caicosensis* is taxonomicaly important, since it is not in agreement with GARRONE's (1978) views, according to which smooth collagen fibrils would be characteristic of tetractinomorphs whereas rough ones would occur in most ceractinomorphs. Among other characters, VACELET & GARRONE (1985) have confirmed the affinities of *A. wellsi* with the members of the Subclass Tetractinomorpha by reporting the presence of smooth intercellular collagen

fibrils. Although an additional collagen fibril organization occurs in *A. wellsi*, with anchoring bundles bearing a "faintly visible transverse striation", no rough collagen fibrils have been described (VACELET & GARRONE, 1985).
Another feature separates the two genera at this level : although collagen fibrils extend between growing aragonite crystals in *Willardia*, they do not enter the skeleton as deeply as the anchoring bundles of *Acanthochaetetes* reported by VACELET & GARRONE (1985).

In conclusion, the discovery of *Willardia caicosensis*, a new genus and species of coralline sponge, showing very clear affinities with non-coralline Hadromerida, provides additional evidence of the polyphyletic nature of the sclerosponges.

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