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Family Astroscleridae Lister, 1900

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Astroscleridae Lister (Demospongiae, Agelasida) contains five nominal genera all considered valid, and six described species from coral reef caves and deep-fore reefs from tropical Indo-Pacific and West Atlantic regions. The relationship of the family with Agelasidae is indicated by a spiculation of verticillately spined styles and by biochemical characters. The family is characterized by the presence of a basal calcareous skeleton made of spherulitic or clinogonal sclerodermites in aragonite, more or less similar to the skeleton of various fossil taxa such as stromatoporoids and chaetetids.
Keywords: Porifera; Demospongiae; Agelasida; Astroscleridae; *Astrosclera*; *Ceratoporella*; *Goreauiella*; *Hispidopetra*; *Stromatospongia*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Astroscleridae Lister, 1900. Ceratoporellidae Hartman & Goreau, 1972.

Definition

Agelasida with verticillately spined styles, occasionally smooth styles, and a basal calcareous skeleton made of spherulitic or clinogonal sclerodermites in aragonite.

Diagnosis

Encrusting or massive subspherical growth forms. Basal skeleton composed of a mass of aragonitic sclerodermites, which are either spherulitic and intracellularly secreted, or clinogonal and extracellularly secreted. Living tissue organized as in typical Demospongiae, forming a veneer on the surface of the basal skeleton and extending down into calicular skeletal units, cylindrical, meandroid or irregular in form. No tabulae between the tissue-filled external skeleton and the interior interskeletal spaces, which are generally filled in solidly with secondary calcium carbonate deposits. Siliceous spicules styles or strongyles with verticillate spines, more rarely smooth styles, sometimes secondarily lost, secondarily entrapped into the calcareous skeleton.

Scope

Astroscleridae contains five nominal genera, all considered valid: *Astrosclera, Ceratoporella, Goreauiella, Hispidopetra* and *Stromatospongia*.

History and biology

Astrosclera willeyana is the first discovered Recent demosponge with a basal calcareous skeleton. Although the first description was very accurate (Lister, 1900), its sponge nature has been contested (Weltner, 1910) due to the similarity of the basal skeleton to that of cnidarians. Another representative of the family, *Ceratoporella nicholsoni* (Hickson, 1911) has long been ignored by spongologists because it was wrongly classified in Cnidaria (Hickson, 1911) until its rediscovery (Hartman & Goreau, 1966). Astroscleridae are the main representatives of the calcified demosponges that were classified in a special class of sponges, Sclerospongiae (Hartman & Goreau, 1972), which has been shown to be polyphyletic (Vacelet, 1985). The family has affinities with extinct reef builders such as chaetetids and stromatoporoids (Hartman & Goreau, 1972). An exact correspondence with fossil genera or families, however, is difficult to establish. The inclusion of possible fossil representatives is not attempted in the present paper. It appears that true Chaetetidae are more closely related to the calcified demosponges of the genus *Merlia* (Gautret *et al.*, 1991). *Astrosclera willeyana* incubates embryos of parenchymella-type. The reproduction of the other genera has not been observed. The family has a circumtropical distribution, with *Astrosclera* largely distributed in the Indo-Pacific area and the other genera predominantly Caribbean. These calcified demosponges are localized in submarine caves and epibathyal cliffs, where they could replace corals as main reef builders.

Taxonomic remarks

The affinity of *Astrosclera* with Agelasidae is clearly confirmed by chemo-taxonomic studies (review in Wörheide, 1998), cytological characters and molecular sequences (Chombard *et al.*, 1997). The monophyly of the family, however, is presently not well established. The five genera here included in Astroscleridae share the verticillately spined styles and a basal calcareous skeleton made of aragonitic sclerodermites. However, the basal skeleton of *Astrosclera* is spherulitic, the spherules being of intracellular origin, whereas the other genera have a clinogonal structure, with extracellularly secreted sclerodermites. *Astrosclera* is viviparous, and its embryos have been frequently observed, whereas the embryology of the other genera is unknown (with a faint indication of viviparity in *Stromatospongia*), which could mean that they are oviparous as Agelasidae. It is thus possible that future studies will indicate that the family has to be split in Astroscleridae, with *Astrosclera*, and Ceratoporellidae, with the four other genera.

KEY TO GENERA

(1) Calcareous skeleton with spherulitic microstructure ..... ***Astrosclera***
Calcareous skeleton with clinogonal microstructure 2
(2) Calcareous skeleton with regular calicular units ..... ***Ceratoporella***
Calcareous skeleton irregular or meandriform 3
(3) Siliceous spicules smooth styles ..... ***Hispidopetra***
Siliceous spicules verticillately spined styles or strongyles 4
(4) Encrusting on serpulid tubes ..... ***Stromatospongia***
Pedunculate and auriculiform, non associated with serpulid ..... ***Goreauiella***

ASTROSCLERA LISTER, 1900

Synonymy

Astrosclera Lister, 1900.

Type species

Astrosclera willeyana Lister, 1900 (by monotypy).

Definition

Astroscleridae with a reticulate secondary skeleton composed of spherulitic sclerodermites in aragonite and marked with an astrorhizal system.

Diagnosis

Massive growth form. Meandroid or reticulate calcareous skeleton in aragonite, composed of spherulitic sclerodermites of intracellular origin and further epitaxial growth. Living tissue inside the irregular lacunae of the superficial calcareous skeleton. Superficial canals etching an astrorhizal system on the surface of the calcareous skeleton. Siliceous styles of variable shape, often echinating the calcareous skeleton, sometimes absent.

Previous review

Wörheide, 1998.

Description of type species

Astrosclera willeyana Lister, 1900 (Fig. 1).

Synonymy. *Astrosclera willeyana* Lister, 1900: 459.

Material examined. Holotype: BMNH 1900.10.19.1. Other material. Numerous specimens from Red Sea (Djibouti), Madagascar (Tuléar), Europa Island, Comoro Islands, La Réunion, Philippines (Cebu), New Caledonia, French Polynesia.

Description. Massive, globular, bulbous, cushion-shaped or cylindrical. Young specimens encrusting, growing upwards into a cylindrical structure, with a dead stalk and a living "head" progressively becoming rounded and larger than the stalk (bulbous shape). In largest specimens, shape subspherical with a stalk hidden by the head margins growing down towards substratum. Growth rings visible, but without any trace of regeneration or budding. Bathyal specimens mostly cylindrical. Size usually 0.5–2.5 cm, up to 25 cm in diameter. Texture stony. Colour orange. Surface smooth, irregularly mammillate in some large specimens. Oscules small, 2–5/cm^2, in the centre of an astrorhizal system etched into the skeleton. Living tissue located at the surface and inside the irregularly reticulated lacunae of the superficial (1–8 mm thick) calcareous skeleton. No special ectosomal differentiation. Choanocyte chambers small, ca. 15 μm in diameter. Exhalant canals bearing a valvule near the aphodus. Tissue containing a high density of morphologically diverse intercellular bacteria. No well defined spherulous cells. Basal calcareous skeleton in aragonite, alveolar in surface and with an organisation more or less similar to that of the fossil stromatoporoids, solid in the backfilled central parts. Tabulae absent. Basal parts externally covered by an epitheca. Microstructure spherulitic, built up of sclerodermites 10–60 μm in diameter, with crystal fibres, 1–3 μm in diameter, arranged in a radiate structure. Sclerodermites intracellularly secreted as granules which pass through a spheraster-like stage and are incorporated into the superficial parts of the solid skeleton when their size is 20–25 μm. Siliceous styles dispersed in the living tissue. In some specimens, styles entrapped by their basis within the calcareous skeleton, obliquely echinating the basal skeleton. Styles usually with a swelling in the basal third, but highly variable in shape, size and abundance according to the geographic distribution. In the Indian Ocean, styles 42–87 × 2.5–11 μm, with verticillated spines generally well developed; spines absent in the Red Sea. In West Pacific, acanthostyles 47–164 × 1.7–10.5 μm, sometimes vestigial or absent, with an irregular spination. Siliceous spicules absent in Central Pacific. Reproduction viviparous, by incubated parenchymella. Growth rate of the skeleton: ca. 0.2 mm/y (Wörheide, 1998).

Distribution and ecology. Indo-Pacific tropical area: Red Sea, Indian Ocean (Madagascar, Seychelles, Comoro islands, Christmas island, Mascarene islands), Pacific (Philippines, Indonesia, Great Barrier Reef, New Caledonia, Guam, Enewetak, French Polynesia, Japan). Common on undersurfaces of coral rubble, reef cavities, caves, deep cliffs, 1–185 m depth.

Remarks. In the recent species of Astroscleridae, the affinities with the Agelasidae indicated by the spicules are confirmed by the chemistry of secondary metabolites and by cytology. Agelasidae differ, however, by a well developed spongin skeleton and by oviparity. A similar spherulitic structure of aragonitic sclerodermites is observed in Permo-Triassic fossils belonging to various grades of organization (chaetetid, stromatoporoid, sphinctozoid and other), indicating possible affinities (Gautret, 1986). A triassic sponge, *Astrosclera cuifi* Wörheide, 1998 has been described as a fossil representative of the genus (Wörheide, 1998). There are questionable affinities with Middle Ordovician genus *Lapidipanis* Paquette *et al.*, 1983 in which the spherules are considerably larger (Paquette *et al.*, 1983). Specimens from various geographical locations differ by the shape, spination, size and abundance of the siliceous spicules, showing six different geographical groups. Although an initial genetic study based on

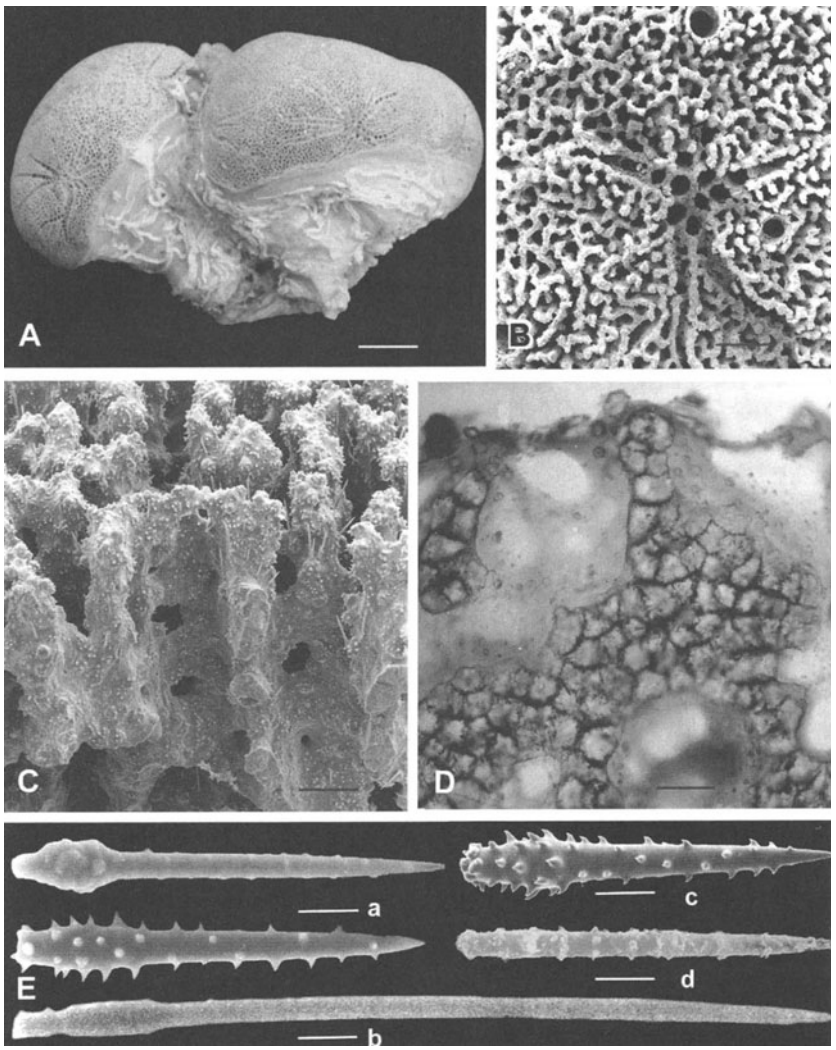

Fig. 1. *Astrosclera willeyana* Lister, 1900. A, specimen from Philippines (scale 4.4 mm). B, SEM photo of the surface of the skeleton showing astrorhizal processes, specimen from Philippines (scale 720 μm). C, SEM photo of a fracture in the skeleton, with echinating verticillately spined styles, specimen from Philippines (scale 140 μm). D, section through the skeleton and the living tissue, including intracellular calcareous spherules, specimen from Glorieuses Islands (Indian Ocean) (scale 100 μm). E, SEM photos of verticillately spined styles: a, specimen from Indonesia (scale 10 μm); b, specimen from Palau (scale 8.3 μm); c, specimen from Philippines (scale 11 μm); d, specimen from Glorieuses Islands (scale 6.5 μm); a, b & c from Wörheide, 1998.

RFLP-PCR of ITS rDNA did not detect any significant differences between some of these populations (Wörheide, 1998), a more detailed examination using ITS rDNA sequences provided strong support for the presence of at least two additional cryptic species, in addition to *Astrosclera willeyana s.s.* (Wörheide *et al.*, 2002).

Distribution

As for type species.

CERATOPORELLA HICKSON, 1911

Synonymy

[*Ceratopora*] Hickson, 1911.

Type species

Ceratopora nicholsonii Hickson, 1911 (by monotypy).

Definition

Astroscleridae with basal skeleton superficially organized in polygonal calicles and verticillately spined styles.

Diagnosis

Massive growth form; basal skeleton made of sclerodermites with a clinogonal microstructure, superficially organized in polygonal calicular units; styles with regular whorls of spines free in the tissue or obliquely echinating the calicle walls.

Previous reviews

Hartman & Goreau, 1970, 1972; Willenz & Hartman, 1989.

Description of type species

Ceratoporella nicholsoni (Hickson, 1911) (Fig. 2).

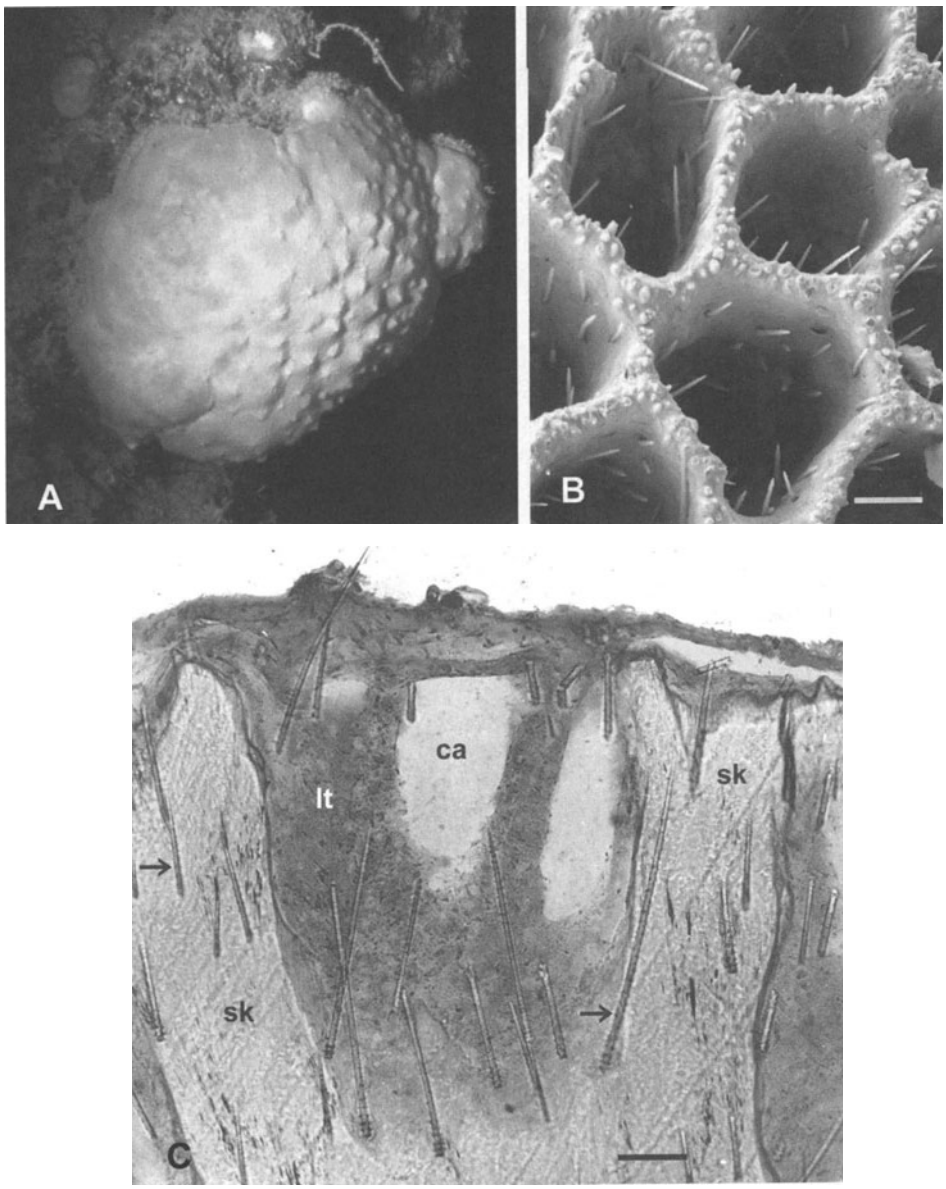

Fig. 2. *Ceratoporella nicholsoni* (Hickson, 1911), specimens from Jamaica. A, underwater photograph of a specimen about 15 cm in diameter. B, SEM photo of the skeleton (scale 84 μm). C, section through the skeleton and the living tissue; arrows: siliceous styles; sk: calcareous skeleton; ca: canal; lt: living tissue (scale 54 μm).

Synonymy. *Ceratopora nicholsonii* Hickson, 1911: 200.

Material examined. Holotype: not seen, Caribbean. Other material. Numerous specimens from Jamaica and Bahamas.

Description. Massive, mound-shaped when mature, with regularly spaced mamelons; young individuals cone-shaped or pedunculate. Colour orange in life. Mound-shaped specimens up to 100 cm in diameter and 50 cm in thickness on deep fore-reef, extraordinarily tough and heavy. Basal and lateral surfaces of the skeletal mass covered by an epitheca showing growth lines. Superficial parts of the basal calcareous skeleton marked by closely spaced calicles, 0.2–0.4 mm across and 1–1.2 mm deep, irregularly polygonal, ranging from 150 μm–300–400 μm in diameter. The lumen of the calicles are filled in with aragonite in the inner part of the basal skeleton. Basal skeleton made of sclerodermites with a clinogonal microstructure, consisting of closely packed crystalline units that diverge at a low angle. Siliceous spicules styles, 206–298×3.1–4 μm, bearing regular whorls of spines, free in the living tissue or obliquely entrapped in the calicle wall by their basis surrounded by collagen microfibrils. Entrapped siliceous spicules progressively dissolved within the basal calcareous skeleton. Living tissue forming a thin veneer at the surface of the calcareous skeleton and extending downwards into each calicle; total thickness of the living tissue 1.5 mm. Each calicular unit corresponds to a single inhalant and exhalant canal. Canals bearing special valvules. Choanocyte chambers small, 20.7 μm in mean diameter. Exhalant collecting system leaving stellate depressions (astrorhizae) on the surface of the skeleton. Intercellular symbiotic bacteria abundant and highly diverse in shape. Growth rate of the skeleton 0.21–0.23 mm/y in Jamaican caves (Willenz & Hartman, 1999). Depth range: 8–184 m.

Remarks. The regular calicular structure of the skeleton is reminiscent of the calcified demosponges *Merlia* Kirkpatrick, 1908, family Merliidae and *Acanthochaetetes* Fischer, 1970,

family Spirastrellidae. The genus, however, is easily distinguished from these by the microstructure and composition of the skeleton and by the spicule complement.

Distribution

Monotypic, endemic to Caribbean.

GOREAUIELLA HARTMAN, 1969

Synonymy

Goreauiella Hartman, 1969.

Type species

Goreauiella auriculata Hartman, 1969 (by monotypy).

Definition

Pedunculate, auriculiform Astroscleridae with verticillately spined strongyles and with basal skeleton superficially covered with arborescent processes.

Diagnosis

Auriculate or saucer-like form, attached to the substratum by a broad peduncle. Siliceous spicules with verticillate spines, strongyles or truncated styles. Aragonitic basal skeleton with superficial arborescent processes, with raised patterns forming astrorhizae running to the edge of the skeleton.

Description of type species

Goreauiella auriculata Hartman, 1969 (Fig. 3).

Synonymy. *Goreauiella auriculata* Hartman, 1969: 17.

Material examined. Holotype (not seen): YPM 6858 – Caribbean. Other material. One specimen from Jamaica.

Description. (from Hartman, 1969; Hartman & Goreau, 1970 and new material). Auriculate or saucer-like form, with the edges upturned or curled downward, attached by a broad peduncle. Colour light yellow in life. Size up to 16 cm in diameter and 3 mm in thickness. Basal skeleton thin, made up of aragonitic scleroderm-ites, with numerous arborescent, spinose processes, 0.5–1.1 mm in height, and multibranching patterns of higher processes draining to the edge of the skeleton. Siliceous spicules strongyles bearing whorls of spines, 35–124 × 1.3–1.9 μm (mean 60–68 × 2.3–2.7 μm, becoming embedded in the basal skeleton first by one end provided with rounded knobs. Living tissue forming a thin veneer filling the space between the superficial processes of the basal skeleton. Oscules 300 μm in diameter, opening out along the edge of the sponge. Eurypylous choanocyte chamber 18–20 μm in diameter. Occasionally associated with zoanthids that induce the formation of processes in the calcareous skeleton. Depth range: 8–70 m in caves and deep fore-reef.

Distribution. Monotypic, endemic to Caribbean.

HISPIDOPETRA HARTMAN, 1969

Synonymy

Hispidopetra Hartman, 1969.

Type species

Hispidopetra miniana Hartman, 1969 (by monotypy).

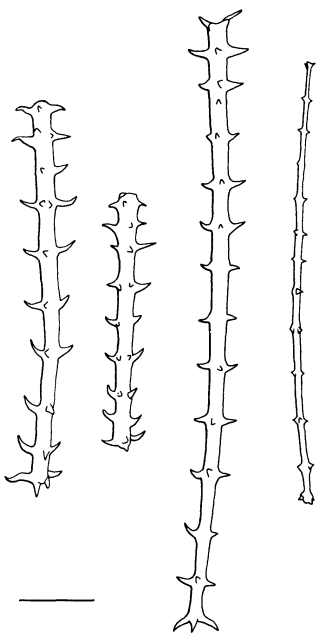

Fig. 3. *Goreauiella auriculata* Hartman, 1969. Siliceous strongyles (scale 12.3 μm), from Hartman (1969).

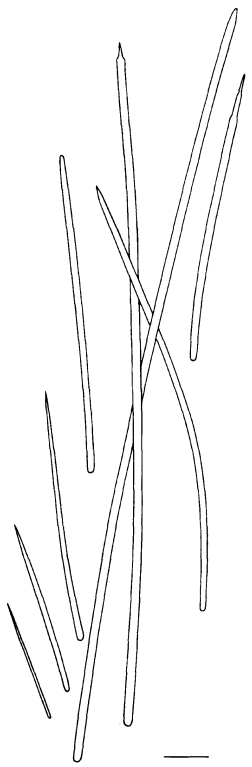

Fig. 4. *Hispidopetra miniana* Hartman, 1969. Siliceous styles (scale 62.5 μm), from Hartman (1969).

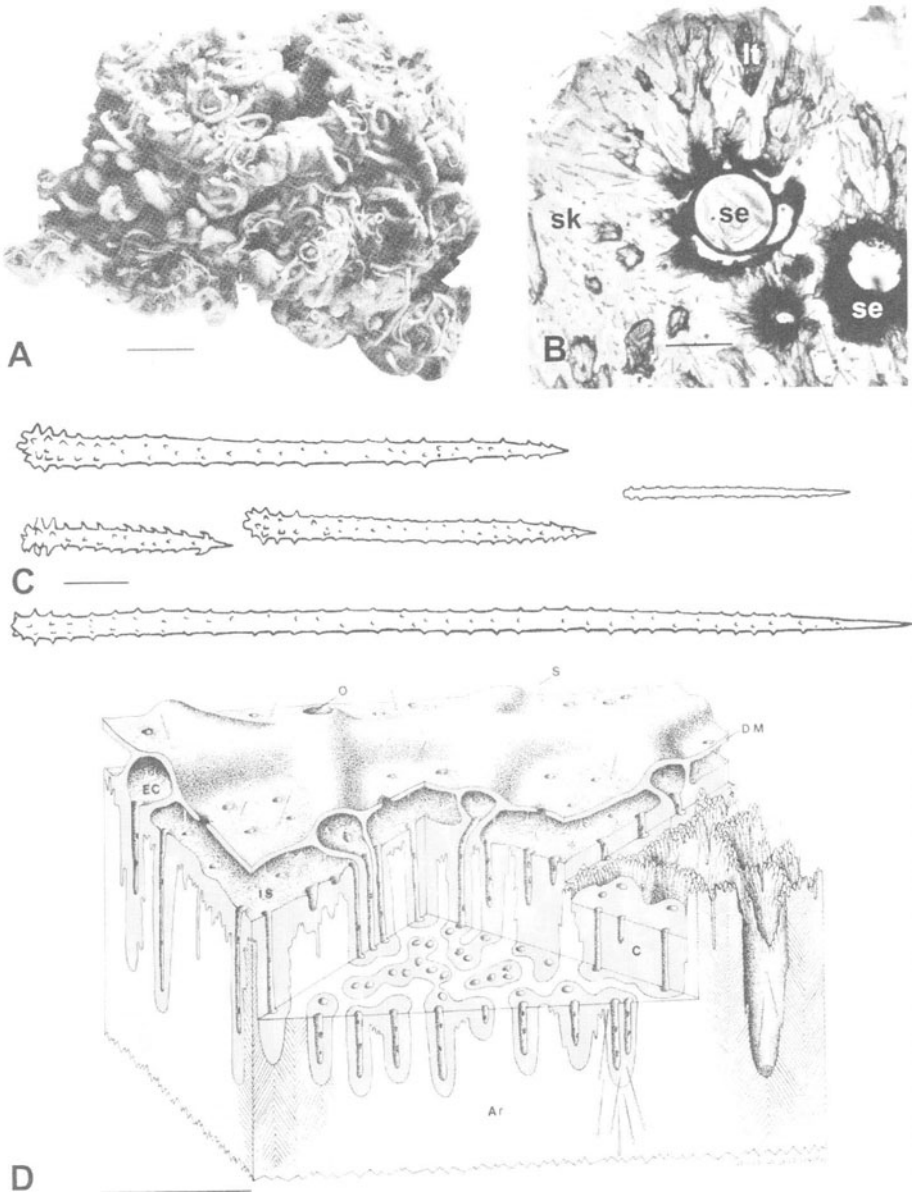

Fig. 5. *Stromatospongia vermicola* Hartman, 1969. A, holotype YPM 6376 (scale 16.5 mm), from Hartman (1969). B, polished section through a specimen from Jamaica; lt: living tissue; se: tube of serpulid worms; sk: calcareous skeleton with siliceous verticillately spined styles (scale 312 μm). C, acanthostyles (scale 30 μm), from Hartman (1969). D, three dimensional schematic representation; Ar: aragonitic skeleton; c: choanosome; DM: dermal membrane; EC: exhalant canal; IS: inhalant space or vestibule; O: osculum; S: spicule (scale 1 mm), from Willenz & Hartman (1989).

Definition

Encrusting to massive Astroscleridae with smooth styles and basal skeleton bearing long superficial processes.

Diagnosis

Encrusting to dome-shaped or massive. Siliceous spicules smooth styles, partially or totally embedded in the calcareous skeleton. Basal skeleton devoid of astrorhizae, with surface covered with conspicuous spinose processes up to 7 mm high.

Description of type species

Hispidopetra miniana Hartman, 1969 (Fig. 4).

Synonymy. *Hispidopetra miniana* Hartman, 1969: 12.

Material examined. Holotype (not seen): YPM 6853 – Caribbean. Other material. One specimen from Jamaica.

Description. (from Hartman, 1969; Hartman & Goreau, 1970 and new material). Encrusting to massive. Colour carmine to vermilion in life. Size reaching 15 cm in diameter and 3 cm in height. Basal skeleton made up of aragonitic sclerodermites, with superficial arborescent processes, up to 7 mm high, with rounded spines and protruding siliceous spicules, without astrorhizae. Spicules smooth styles, range of means 269–301 × 5.4–7.4 μm, with an overall range 125–818 × 1.3–10.4 μm, partially (by the head) or totally entrapped in the basal skeleton. Eurypylous choanocyte chambers, 6–18 μm in diameter. Frequently overgrown by serpulid worms. Depth range: 10–95 m in caves and deep fore-reef.

Remarks. Well characterized among other astrosclerids by its vermilion colour, smooth styles and well developed superficial processes.

Distribution

Monotypic, endemic to Caribbean.

STROMATOSPONGIA HARTMAN, 1969

Synonymy

Stromatospongia Hartman, 1969.

Type species

Stromatospongia vermicola Hartman, 1969 (by original designation).

Definition

Encrusting to massive Astroscleridae with verticillately spined styles, associated with calcareous tubes of serpulid worms.

Diagnosis

Encrusting to massive, with an aragonitic basal skeleton associated with the calcareous tubes of serpulid worms. Siliceous spicules with verticillately spined styles more or less completely entrapped in the basal skeleton. Surface of the basal skeleton ornamented with processes 0.8 to 2 mm high. Living tissue forming a thin veneer in the spaces between the processes of the basal skeleton.

Description of type species

Stromatospongia vermicola Hartman, 1969 (Fig. 5).

Synonymy. *Stromatospongia vermicola* Hartman, 1969: 3.

Material examined. Holotype (not seen): YPM 6376 – Caribbean. Other material. Several specimens from Jamaica.

Description (from Hartman, 1969; Hartman & Goreau, 1970; Willenz & Hartman, 1989 and new material). Encrusting, always growing in association with tangled masses of serpulid worms. Colour apricot to light salmon pink in life. Size up to 40 cm in diameter and 10 cm in height. Basal skeleton intimately mixed with serpulid worm tubes, superficially marked by numerous upright, multibranched processes, 1.5–2 mm high, with the living tissue extending down into irregular spaces left between the processes. Sclerodermites with aragonite crystals radiating in all directions from centers of calcification usually located around spicule heads. Siliceous verticillately spined styles, 75–519 × 3.3–13 μm with a mean of 165–187 × 6.2–8 μm, with whorls of spines on the shaft, more or less completely overgrown by the aragonite. Living tissue forming a thin veneer between the processes of the surface of the basal skeleton. Eurypylous choanocyte chambers, 16–20 μm in diameter. The association with serpulids appears obligatory. Depth range: 10–95 m under overhangs of deep fore-reefs.

Remarks. The association with serpulids, which appears to be a good distinctive character for the Caribbean species, is less characterized for the Pacific representative (Hartman & Goreau, 1976), and the genus is possibly synonym with *Ceratoporella* (Hartman & Goreau, 1972; Willenz & Hartman, 1989). Its superficial skeleton, however, is devoid of the regular calicles highly characteristic of *Ceratoporella*.

Distribution

Mostly Caribbean. One species described from the Central Pacific (Hartman & Goreau, 1976).