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***Vansoestia caribensis* gen. nov., sp. nov.: first report of the family Ianthellidae (Verongida, Demospongiae) in the Caribbean**

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Abstract

A thin fiber-less sponge from Caribbean reefs (Bocas del Toro, Panama) with close genetic affinities (based on 18S and 28S nuclear ribosomal RNA gene sequences) to large fan-shaped fiber-bearing sponges (*Ianthella* and *Anomoianthella*) from the Indo-Pacific Ocean is here presented. We describe its overall external morphology, histological features, and ultrastructure. Its genetic distance from the only previously known fiber-less verongid genus, *Hexadella*, prompted the need to erect a new genus to classify this species. This novel species constitutes the first record for a member of the family Ianthellidae in the Caribbean. The characterization of the family Ianthellidae (*sensu* Cook and Bergquist, 2000) is here modified by: i) highlighting the cavernous nature of the choanosome, with many lacunae and channels reported for all genera included in the family; ii) extending the family distribution to the Caribbean; and iii) adding a fourth genus to the group of verongids with eurypylous chambers. The possession of a cellularized cortex (10–300 µm in thickness) is here proposed as a potential synapomorphic character of the *Ianthella*–*Anomoianthella*–*Vansoestia* clade. The main issues regarding the suprageneric classification of verongids are discussed.

Key words: *Ianthella*, *Anomoianthella*, sponges, cortex, synapomorphy, clade

Introduction

The order Verongida (Bergquist, 1978) comprises approximately 90 marine species with tropical to temperate distributions, with nine genera that possess a characteristic fiber skeleton composed of chitin and spongin (Bergquist and Cook, 2002a), and one fiber-less genus (*Hexadella* Topsent, 1896). Verongid species are found in various growth forms, such as fans (up to a few meters in diameter), tubes, branches (single or in clusters; erect or repent), and thin or thick crusts. Species of Verongida are conspicuous components of the benthic fauna on both exposed and cryptic hard substrates on coral reefs, reef walls, and other rocky substrates (Díaz *et al.*, 2013; Bergquist and Cook, 2002 a, b, c, d). All verongid sponges produce complex brominated tyrosine-derived compounds, which have generated interest in the pharmaceutical industry and promoted several scientific investigations (Wu *et al.*, 1986; Erwin and Thacker, 2007; Erpenbeck and van Soest, 2007; Reveillaud *et al.*, 2012).

Recent studies using a molecular phylogenetics approach (including gene sequences of mitochondrial cytochrome oxidase subunit I [COI] and the small [18S] and large [28S] subunits of nuclear ribosomal RNA) have challenged traditional taxonomic and phylogenetic interpretations within this order, and shed new light on its relationships with other orders of Demospongiae (Erpenbeck *et al.*, 2012; Redmond *et al.*, 2013; Thacker *et al.*, 2013). Erpenbeck *et al.* (2012) suggested that molecular information (28S and COI), and the morphology of

choanocyte chambers are the most robust sets of data for re-evaluating suprageneric verongid taxa and their phylogenetic relationships. These authors found phylogenetic support for two distinct putative clades of choanocyte chamber morphology (taxa possessing eurypylous vs. diplodal chambers), independent of the presence of a fiber skeleton or the skeleton's structural arrangement (anastomosing or dendritic). Therefore, COI and 28S datasets have supported two distinct clades among verongids: i) the Ianthellidae family, containing sponges that possess sac-shaped to ovate-elongate shaped eurypylous choanocyte chambers (20–50 μm in diameter), which includes three genera (*Hexadella*, *Ianthella*, and *Anomoianthella*); and ii) a group that contains the genera previously placed into three separate families: Pseudoceratinidae, Aplysinellidae and Aplysinidae (*sensu* Bergquist and Cook, 2002b, c, e), all possessing much smaller, round diplodal choanocyte chambers (<10–20 μm in diameter).

Analyses of 18S and 28S rRNA gene sequences in the largest dataset of demosponge genera ever studied, showed that *Chondrosia* (previously classified in its own order, Chondrosida) was the sister group to all Verongida (Redmond *et al.*, 2013; Thacker *et al.*, 2013). Redmond *et al.* (2013) amended the definition of the order Verongida in order to include the skeleton-less genus *Chondrosia*, and suggested thus the resurrection of the family Chondrosiidae Schulze, 1877 to include this genus. These analyses also supported the distinction of the subclass Myxospongiae proposed by Maldonado (2009), which includes the amended order Verongida (*sensu* Redmond *et al.*, 2013) and a newly erected order Chondrillida Redmond *et al.*, 2013, which contains the families Halisarcidae and Chondrillidae.

Morphological and genetic (18S rRNA) studies of undescribed verongids from the Caribbean and the Central Pacific island of Moorea revealed the existence of non-*Hexadella* fiber-less verongids, expanding the phylogenetic nature and diversity of the skeleton-less condition within the order (Díaz *et al.*, 2013). Prior to this study, all verongid taxa possessing large eurypylous choanocyte chambers were considered to belong to a monophyletic group, family Ianthellidae. The analyses of Redmond *et al.* (2013) suggested that verongid taxa with eurypylous choanocyte chambers were paraphyletic and positioned in two separate clades. The first clade is sister to the rest of the Verongida (*sensu* Bergquist and Cook, 2002a) and contains at least three *Hexadella* species, while the second clade contains two fiber-bearing genera, *Ianthella* and *Anomoianthella*, in addition to a recently discovered fiber-less species from the Caribbean (Díaz *et al.*, 2013).

The present study aims to describe taxonomically this fiber-less species from the Caribbean. Analyses of 18S and 28S rRNA gene sequences indicated that it is more closely related to fiber-bearing ianthellids from the Pacific Ocean than to the fiber-less *Hexadella* species (Redmond *et al.*, 2013; Thacker *et al.*, 2013). We describe the overall habit of this species, along with some histological and ultrastructure features and their phylogenetic affinities, and erect a new genus of Verongida. The current views of Ianthellidae and the phylogeny of Verongida in light of this novel taxon are also discussed.

Methods

External morphology and histology. Observations of living specimens (color, shape, size, surface features, oscules, and consistency) and under-water photographic records were used to describe the external morphology and habitat of this reef-dwelling, fiber-less verongid from Bocas del Toro, Panama. Five individuals have been collected during various expeditions, and preserved either in ethanol 70% or in a glutaraldehyde solution in cacodylate buffer (2.5 %). Two specimens were prepared for histological studies, USNM 1133773 (P67 from Redmond *et al.*, 2013) and P12x403 from Redmond *et al.*, 2013. Samples were dehydrated in a series of ethanol washes (70%, 75%, 80%, 90%, 97%, and 100%) (Muricy & Pearse 2004) and final clearing was performed in three changes of xylene (100%), 1 min each. The samples were embedded in paraffin and sections (10–30 μm thickness) were made. The sections were deparaffinized and stained according to a hematoxylin-eosin protocol, and permanently mounted in Permount.

Ultrastructure observations. Sample P12x402 (from Redmond *et al.*, 2013) preserved in glutaraldehyde 2.5%, was processed using a standard protocol for cytology and transmission electron microscopy (Reveillaud *et al.*, 2012). Ultrastructural details could be clearly observed, such as various cells containing inclusions, choanocytes, collagen fibril strands, archaeocytes, and bacteria. Material from sample P12x402, and P12x403 fixed in glutaraldehyde were consumed in histological and TEM preparations.

Results

Taxonomic descriptions

Class Demospongiae Sollas 1885

Order Verongida Bergquist 1978 (*sensu* Redmond *et al.*, 2013)

Family Ianthellidae Hyatt 1875 (modified after Bergquist and Cook 2002d)

Verongida with a strongly collagenous dermal/cortical region (cortex), a cavernous choanosome with abundant subdermal lacunae and channels, eurypylous choanocyte chambers, abundant spherulous secretory cells, complex brominated, tyrosine-derived compounds among the secondary metabolites, and a strongly anastomosing skeleton, when present, with fibers containing pith and bark elements which incorporate cellular elements. Known species in life range from typical verongid sulfur yellow through deep orange to deep purple (Bergquist, 1980). All show the characteristic oxidation reaction upon damage or death, with final colorations that range from dark brown to deep purple.

Three genera were recognized by Bergquist and Cook (2002d), extending from the Mediterranean to the British Isles and the eastern Pacific. We expand the family distribution to the Caribbean, adding a fourth genus to the family.

Vansoestia, gen. nov.

Diagnosis. Ianthellidae represented by individuals with a thin (1–4 mm) encrusting growth form that presents a cellularized cortex of variable thickness (10–200 μm) composed of a collagenous matrix and various types of cells with inclusions (i.e. granular, spherulous, and/or vacuolar). Abundant subdermal canals and lacunae are found immediately underneath the cortex. The choanosome consists of numerous aquiferous canals, a mesohyl where two or three types of cells with inclusions can be distinguished, and oval eurypylous choanocyte chambers 20–50 μm , all supported with abundant fibrillar collagen.

Type species: *Vansoestia caribensis* gen. nov. sp. nov.

Material examined. All specimens studied were found in coral reefs from Bocas del Toro, Panama, between 10–20 m in depth. This species grows over dead coral and other organisms, in open and cryptic reef habitats.

Holotype : USNM 1133773, Buoy 19 (N9°18.11, W 82°17.66), Bocas del Toro, Panama (P67), 10 m deep, coll: M.C. Díaz and R.W. Thacker; 7/18/2009

Paratypes: USNM 1133782, Buoy 19 (N9°18.11, W 82°17.66), Bocas del Toro, Panama (P76), 15 m deep, coll: M.C. Díaz and R.W. Thacker; 7/18/2009; USNM 1204851 (P12x342), Punta Caracol (N9°22.66, W 82°18.19), 15 m deep, coll: M.C. Díaz and S.A. Pomponi, 8/8/2012.

Additional material. P12x402, and P12x403 were consumed in histological, or TEM preparations.

Etymology. The species is named in honor of Dr. Rob van Soest, an essential contributor to the understanding of Demospongiae, including Verongida, in the Caribbean and worldwide.

Description. External morphology: The sponge is soft, thinly encrusting (1–4 mm thick), orange to yellow in color internally and externally. Color turns slowly brown to purple in ethanol. The sponge grows over dead coral or over other organisms, particularly other sponges (Figure 1). Its surface is dominated by thin reticulated subdermal canals (3–8 mm wide) that branch and decrease in width away from the oscules (0.5–1 cm wide). Small ostia (0.4–0.8 mm wide) are dispersed between subdermal canals. The soft and fragile consistency of this sponge reflects the lack of a reticulate fiber skeleton.

Internal morphology (Figures 2–4). There is a clear separation between ectosome and choanosome (Figure 2A). The ectosome is a collagenous cortex of variable thickness (10–200 μm), with collagen in the form of an amorphous matrix containing loose cells with inclusions (Figure 2A, B), and an external cuticle (Figure 3A). Large channels and lacunae (subdermal spaces) are observed immediately underneath the ectosome (Figure 2A). The choanosome consists of densely arranged oval-shaped choanocyte chambers (20–40 μm in diameter) (Figure 2A,

C), and a mesohyl reinforced by collagen fibrils arranged in strands (Figure 3B, C), packed with various types of cells with inclusions, and with abundant aquiferous canals. The chambers are densely and homogeneously distributed in some areas (Figure 2A, C), and rare in others that are instead densely packed by conglomerates of cells (Figure 3D). Choanocytes (4–6 μm in diameter) appear oval to triangular in shape (Figure 2D). Larger cells with inclusions of various shapes and sizes (4–12 μm in diameter) can be observed in both the mesohyl and the ectosome (Figures 2–3). The largest cells with inclusions (Ci1) are widespread in the mesohyl, in the cortex, and lining canals (Figure 3B and 3D). There are some canals lined by these large cells with inclusions (Figure 3D), and others without them (Figure 3C).

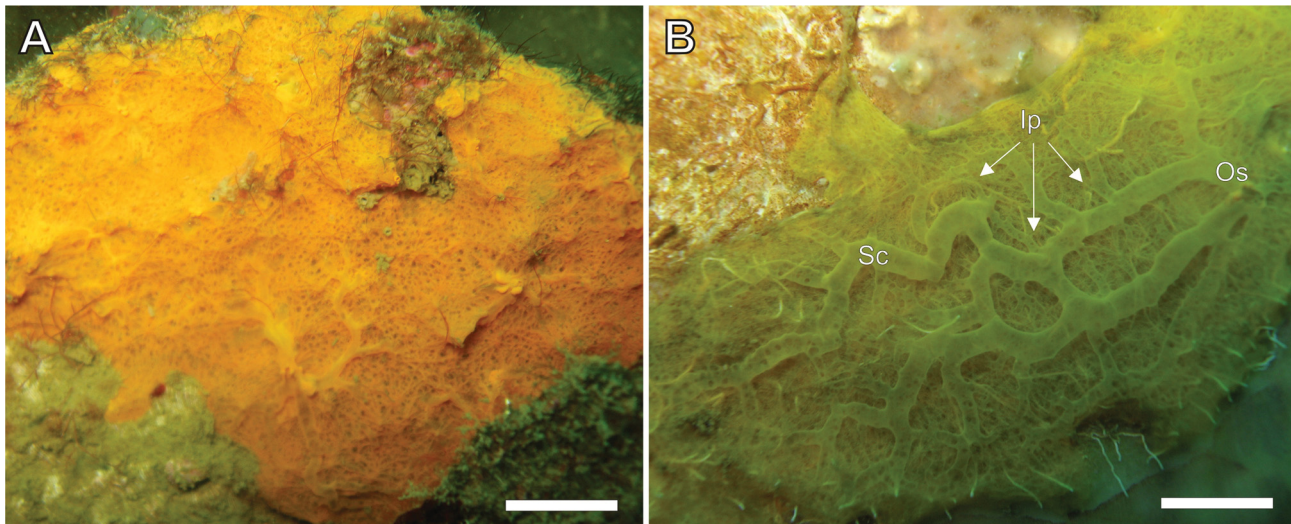


FIGURE 1. *Vansoestia caribensis* gen. nov. sp. nov. growing on the edge of a dead plate coral. A. General habit showing its overall growth form, with algae and polychaete calcareous tubes mingled within the body. Scale bar = 2 cm. B. Close-up view of a more relaxed specimen showing the subdermal canals (Sc), 3–8 mm wide, and the profusely abundant pores. Scale bar = 1.2 cm

TEM sections allowed further distinction of the various types of cells with inclusions, and the observation of archaeocytes, choanocytes, and collagen fibrils. Spherulous cells 1 (Figure 4A, B and D) are ovoid to roundish slightly deformed (6–10 μm in diameter) with spherules (0.7–2 μm wide), containing microgranular inclusions that are dense but grey or black in color (0.06–0.15 μm in diameter), with a clear round nucleus (1.3–2 μm in diameter). By the size and distribution of spherules, these cells probably correspond to the cells with inclusions 1 (Sc1) observed in the histological cross sections (Figures 2–3). Spherulous cells 2 (Figure 4B) are similar in size and shape of Sc1, but their spherules are larger and ellipsoid in shape (0.1–0.3 μm in diameter), and electron dense dark. These cells might represent a different stage of the spherulous cell 1. A third type, which seems like vacuolar cells (Figure 4C), occurs with variable shapes, smaller size (5–8 μm in diameter), and containing a single round, dark dense granule (0.4–0.8 μm in diameter) within each vacuole (1–1.5 μm in diameter). By the shape and size of the granules, these cells likely correspond to the cell with inclusion 2 observed in the histological cross sections. Finally, a microgranular cell with membrane-bound inclusions with striated content, was observed once (Figure 4D). A thick layer of collagen fibrils (Co) with loose bacteria surrounds the choanocyte chambers and long cytoplasmic projections could be seen in some choanocytes (Figure 4E). One choanocyte with a basal nucleolated nucleus was observed (Figure 4F).

Remarks. The delicate and thin specimens of *Vansoestia caribensis* have been found in Bocas del Toro, Panama, since 2006; however, only the slow oxidation observed when specimens were placed into alcohol suggested an affinity to verongids. Due to the lack of a fiber skeleton, we initially affiliated this sponge to the genus *Hexadella*. Histological observations corroborated its ianthellid nature (large, sac-shaped choanocyte chambers), but its distinct identity and closest affinity to the known sequences of fiber-bearing ianthellid genera from the Western Tropical Pacific appeared after analyzing 18S and 28S ribosomal gene sequences (Redmond *et al.*, 2013; Thacker *et al.*, 2013). Its genetic distance from the only previously known fiber-less verongid genus, *Hexadella*, prompted the need to erect a new genus to classify this species. This biological record constitutes the first member of family Ianthellidae ever encountered in the Caribbean Sea.

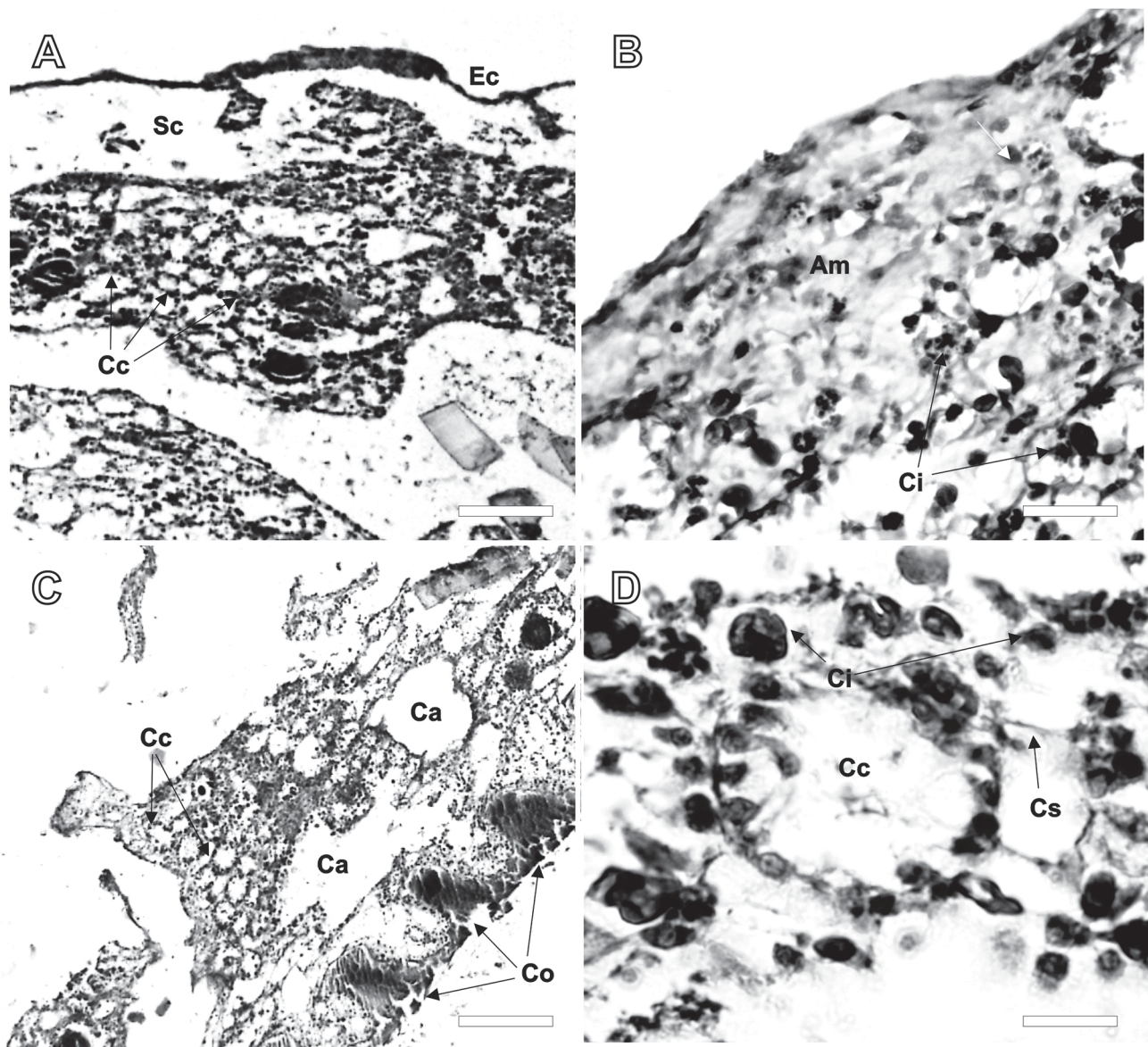


FIGURE 2. Photomicrographs of *Vansoestia caribensis* gen. nov. sp. nov. histological cross sections. A. Upper body region showing a thin ectosome (Ec) followed by wide subdermal canals (Sc) and the choanoderm with densely arranged choanocyte chambers (Cc). Scale = 110 μ m. B. Detail of an area of the ectosome showing a dense “amorphous matrix” (Am) of collagen with dispersed dark stained cells with inclusions (Ci), Scale = 30 μ m; C. Basal region where the sponge is attached to the substrate. Note the corallites (Co) of the dead coral where the sponge was growing, the choanocyte chambers (Cc) and canals (Ca), Scale = 200 μ m. D. Detail of choanocyte chamber with more than 20 choanocytes (oval to triangular in shape). Notice at least two types of cells with inclusions (Ci) and collagen strands (Cs) in between the chambers and the cells, Scale = 15 μ m.

There is a striking similarity between *V. caribensis* gen nov. sp. nov. and the external appearance of *Hexadella pruvoti* Topsent, 1896 (Reveillaud *et al.*, 2012), particularly with respect to the abundant subdermal canals converging in a wide oscule, and its yellowish coloration. However, 18S and 28S gene sequence analyses confirmed the very distinct nature of these two species. A cellularized cortex of variable thickness (10–200 μ m thick) composed of amorphous collagen and various types of cells is present in *V. caribensis* gen. nov. sp. nov. and forms an important morphological difference between these two genera, since *Hexadella* possesses a thinner cortex with a 1 μ m thick cuticle. A well-developed cellularized cortex might represent a potential synapomorphy between *Vansoestia* gen. nov., *Ianthella*, and *Anomoianthella* (Bergquist, 1980, 1995; Bergquist and Kelly-Borges, 1995; Bergquist and Cook, 2002; present study). Indeed, Bergquist, (1995) and Bergquist and Kelly-Borges (1995) described a collagenous ectosome (70 to 300 μ m thick) containing cells for all *Ianthella* species and a cellularized

cuticle for *Anomoianthella* species (Bergquist, 1980). Together with the presence of a collagen-reinforced cortex combined with a cuticle, the high degree of reinforcement of the choanosome with collagen is also a characteristic shared by *Vansoestia* gen. nov., *Ianthella* and *Anomoianthella*.

Some similarities among the spherulous cells of *V. caribensis* gen. nov. sp. nov., and other verongids were also noticed (Vacelet, 1967). The cells with striated membrane-bound bodies are very similar to cells observed in *Aplysina aerophoba* by Maldonado (2009). The dark granules found in cells of *Vansoestia* gen. nov. might represent glycogen granules (Maldonado, 2009), or they might contain brominated compounds (Thompson, 1986) like has been found for microgranular and spherulous cells of two different *Aplysina* species. The large diversity of cells with inclusions, and their similarities with species of *Hexadella* and other verongid genera invites continued research to understand the morphology and physiological functions of these cells and their products.

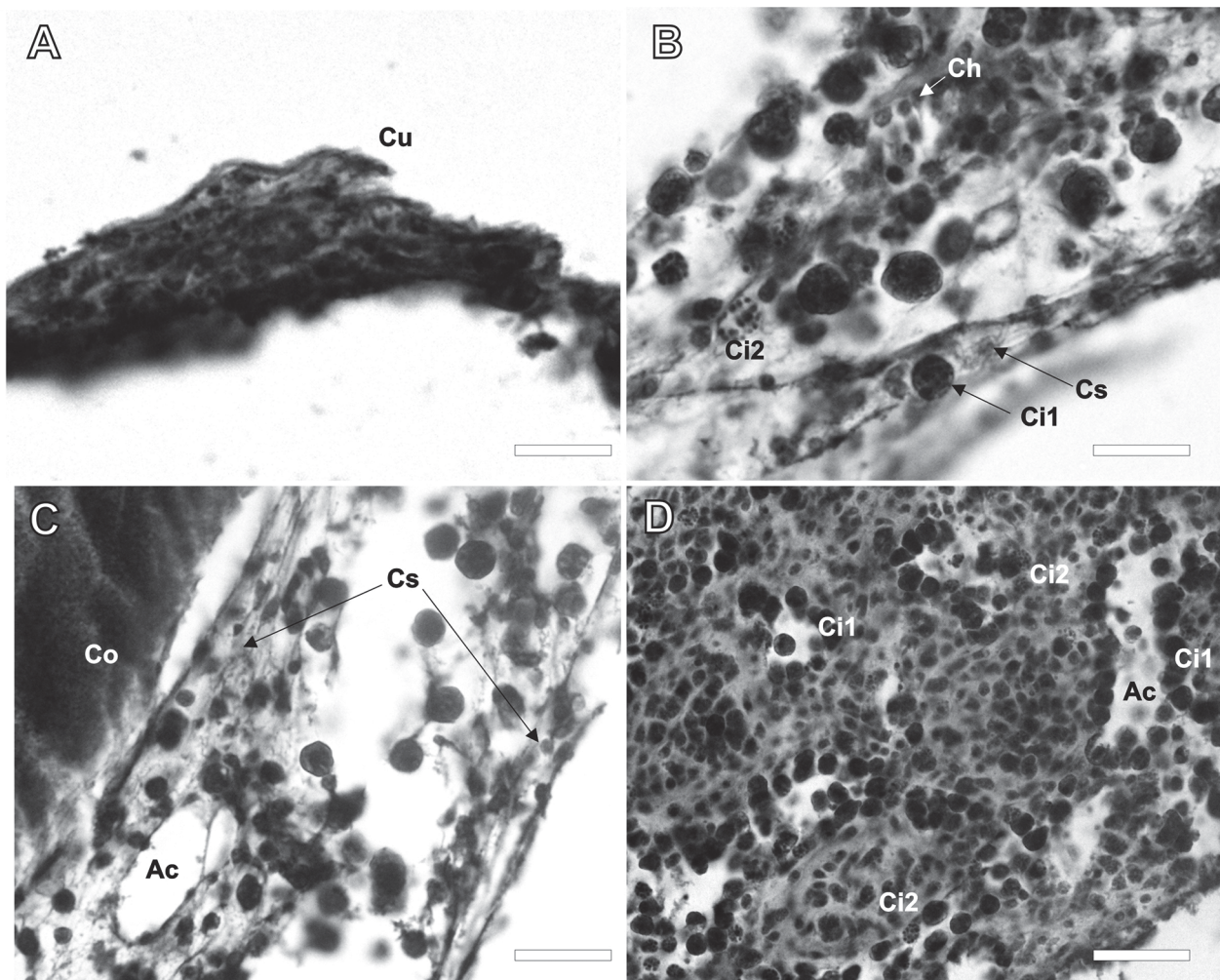


FIGURE 3. Detail of the internal morphology of *Vansoestia caribensis* gen. nov. sp. nov. at 400–600 X. A. Ectosomal cellularized cortex, where a 1 µm cuticle (Cu) lining the outer surface of the sponge is evidenced, Scale = 13 µm. B. Various cells with inclusions (Ci1, Ci2) and smaller choanocytes (Ch) embedded in a mesohyl with abundant strands of collagen (Cs), Scale = 16 µm. C. Portion of the sponge body in contact with the substrate (Co), showing abundance of collagen strands (Cs), and cells. Notice an aquiferous canal (Ac) that is not lined by larger cells with inclusions, Scale = 25 µm. D. Detail of the mesohyl showing an aquiferous canal that is lined by cells with inclusions type 1, and “cell conglomerates” and other types of cells, Scale = 32 µm.

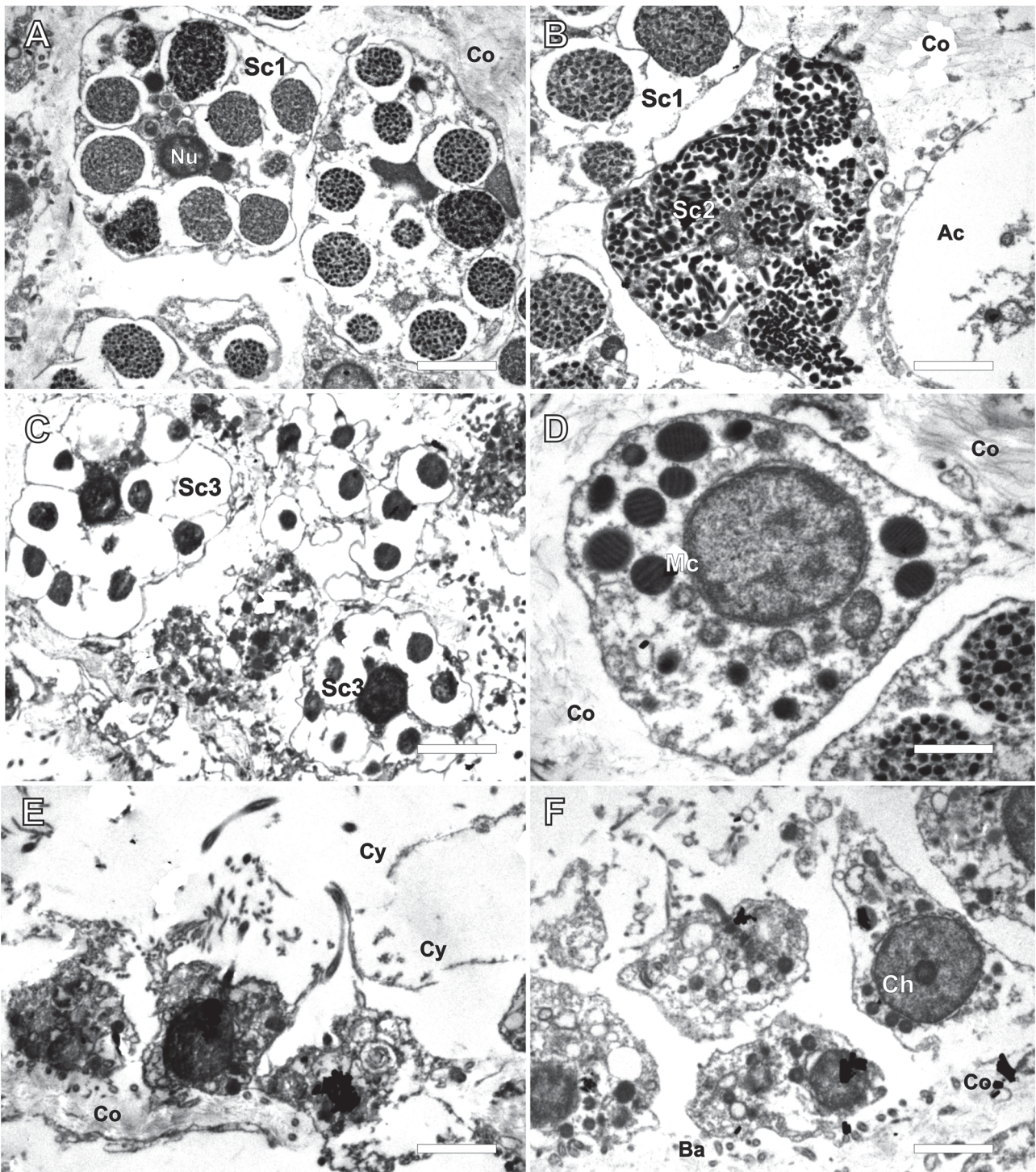


FIGURE 4. TEM sections of *Vansoestia caribensis* gen. nov. sp. nov. A. Roundish to ovoid Spherulous cells type 1 (Sc1) with nucleus (Nu) bearing round spherules containing light and dark inclusions, and abundant collagen fibrils (Co), Scale = 2.5 μm . B. Spherulous cell type 2 with electron dense dark granules, and bacteria within it, close to an aquiferous channel (Ac), Scale = 2 μm . Bacteria can be seen in the interior of the channel. C. Vacuolar cells (Sc 3) seen in the mesohyl close to an aquiferous channel, Scale = 2 μm . D. A microgranular cell (Mc) with striated membrane-bound bodies, among spherulous cells 1, and 2. Note the presence of abundant collagen fibrils (Co) between the cells, Scale = 1.3 μm . E. Portion of a choanocyte chamber where main body of the choanocytes can be seen, some with cytoplasmic projections (Cy). A collagen fibril layer (Co) is found surrounding all choanocyte chambers, Scale = 1.6 μm . F. A triangular shaped choanocyte (Ch) with a basal nucleolated nucleus, contiguous to a layer of fibrillar collagen (Co) containing bacteria (Ba), Scale = 1.3 μm .

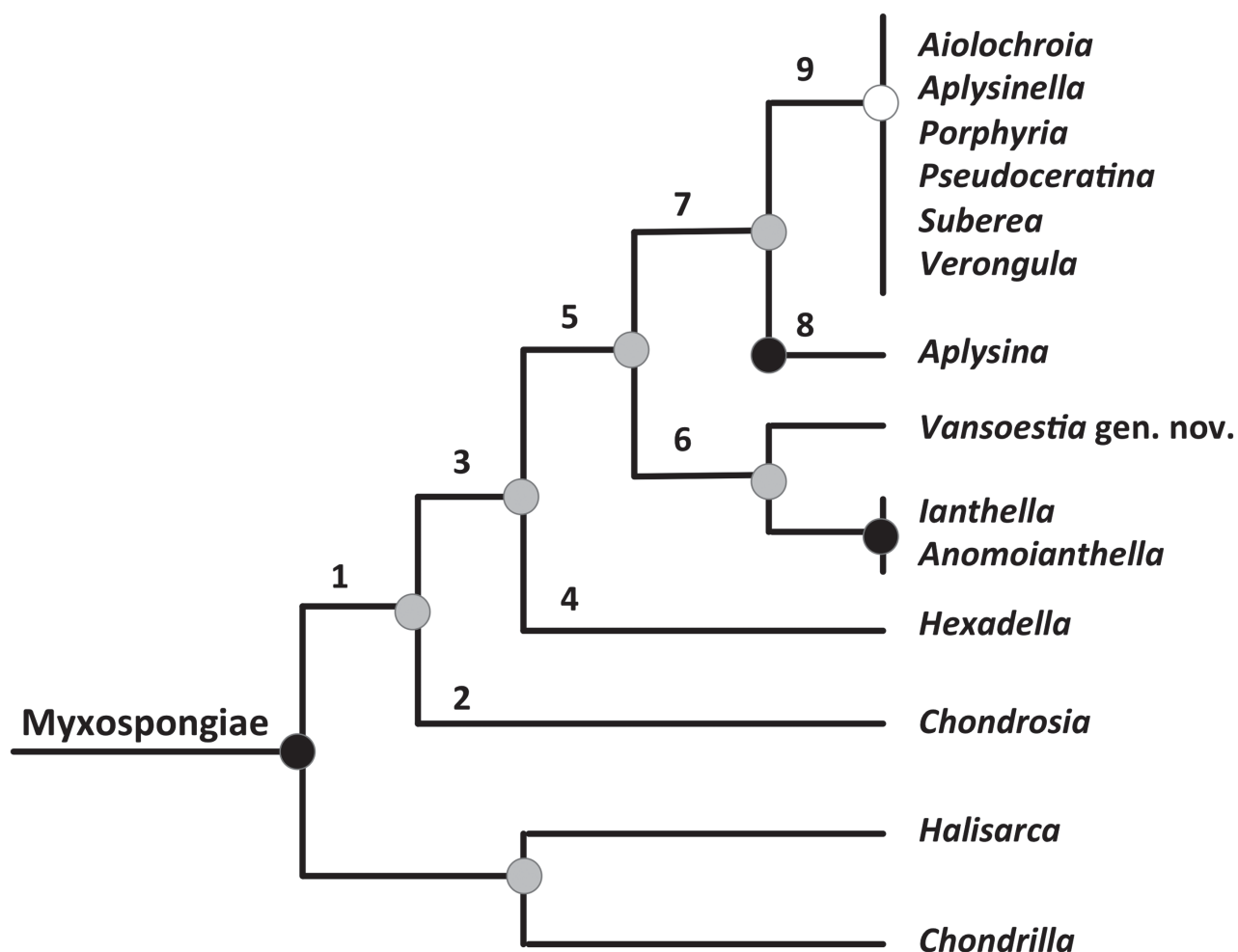


FIGURE 5. Schematic representation of the phylogenetic relationships of the genera of Verongida, summarizing four previously published phylogenies (Erwin & Thacker 2007 [ITS2+28S]; Díaz *et al.*, 2013 [cox1]; Redmond *et al.*, 2013 [18S]; Thacker *et al.*, 2013 [28S];). Black circles indicate nodes with 100% maximum likelihood bootstrap support in at least 2 studies; gray circles indicate nodes with 100% maximum likelihood bootstrap support in 1 study, and none under 85%; white circles indicate poorly resolved nodes, or phylogenies incongruent between studies. Proposed common characters are indicated with numbers: 1. Verongida with bundles of interstitial collagen fibrils either in the cortex, mesohyl, or within fibers; 2. Family Chondrosiidae (*sensu* Redmond *et al.*, 2013) with a thick, acellular collagenous cortex; 3. Clade represented by the rest of the Verongida, all containing spherulous cells and brominated secondary metabolites; 4. Clade represented by *Hexadella*, with eurypylous choanocyte chambers, a thin cuticle, and lacking fibers; 5. Poorly supported clade (62%) containing all the non-*Hexadella* classical genera of Verongida; 6. Moderately supported clade (85%) containing all eurypylous verongids with a cellularized collagenous cortex. 7. Verongids with diplodal choanocyte chambers; 8. Verongids with an isotropic, well-developed fiber reticle, with oval to hexagonal meshes, and fibers with a distinct organic pith and a bark (concentrically layered) throughout the body. 9. Verongids with a variably developed reticulation of fibers, sometimes absent, with thick fibers with or without apparent bark; a morphological synapomorphy is yet to be discovered.

Phylogenetic remarks. 18S and 28S sequences demonstrate that this fiber-less member of Ianthellidae is a sister group to the clade that includes *Ianthella* and *Anomoianthella*. (Redmond *et al.*, 2013; Thacker *et al.*, 2013). Figure 5 summarizes the current phylogenetic interpretation of the relationships among verongid genera based on the latest molecular, and morphologic studies of the group (Erwin and Thacker, 2007; Erpenbeck *et al.*, 2012; Díaz *et al.*, 2013; Redmond *et al.*, 2013; Thacker *et al.*, 2013). The two sister clades make up the subclass Myxospongiae, one containing the amended Verongida (after Redmond *et al.*, 2013) and the other containing *Chondrilla* and *Halisarca* (Order Chondrillida *sensu* Redmond *et al.*, 2013). All verongids are grouped in a strongly supported monophyletic clade (Figure 5, clade 1), which shares the presence of collagen fibrils forming bundles either in the cortex, in the mesohyl, or within fibers. *Chondrosia* (family Chondrosiidae) forms a well-supported sister clade to all other verongids (Figure 5, clade 2), and is represented by sponges with extremely high

collagen content, a thick (> 1 mm thick) “collagenous cortex”, and a fiber-less body. The rest of the verongids form a highly supported clade (Figure 5, clade 3), containing all taxa that produce brominated secondary metabolites and have abundant spherulous cells. Basal within this group, a highly supported clade (Figure 5, clade 4) contains all *Hexadella* species which share eurypylous choanocyte chambers, a thin cuticle (1–2 µm) and a very thin ectosome. The next clade (Figure 5, clade 5) is a moderately supported clade containing all non-*Hexadella* verongids. Within clade 5, two clades are distinguished: a moderately (85%) supported clade (Figure 5, clade 6) containing *Vansoestia* gen. nov. (skeleton less) and the fiber bearing Pacific taxa of genera *Ianthella* and *Anamoianthella*, and a moderately to highly supported clade (Figure 5, clade 7) including all the taxa possessing diplodal choanocyte chambers. Within clade 7 (Figure 5), a clearly monophyletic group of sponges (clade 8) contains all *Aplysina* species, whereas a poorly supported clade (clade 9) contains at least six genera (*Aiolochoira*, *Aplysinella*, *Porphyria*, *Pseudoceratina*, *Suberea*, *Verongula*) and an undescribed genus from Moorea (Díaz *et al.*, 2013).

The Verongida taxa with eurypylous, sac-shaped choanocyte chambers are placed in two distinct clades (Figure 5, clades 4 and 6), demonstrating that this feature is paraphyletic within Verongida. Current studies suggest the classification of Verongida comprises four main clades: (1) a clear monophyletic group containing all *Aplysina* species studied, and representatives of all Aplysinellidae, and Pseudoceratiniidae genera; (2) a clade that contains *Ianthella*, *Anomoianthella*, and *Vansoestia* gen. nov., but excludes *Hexadella*, which should be defined by an amended family Ianthellidae; (3) a clade that presently contains only *Hexadella* and that should be erected as a new family; and (4) a clade containing the family Chondrosiidae *sensu* Redmond *et al.* (2013).

We demonstrate here that the suprageneric classification of Verongida must be further revised in order to reflect our current knowledge of phylogenetic relationships among the genera of Myxospongiae. Considering the diagnostic characters that we have in hand, a thorough comparative review of the histological and ultrastructural features of representatives of each genus is definitely needed to improve the taxonomic diagnoses of these taxa.

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