

Two new haplosclerid sponges from Caribbean Panama with symbiotic filamentous cyanobacteria, and an overview of sponge-cyanobacteria associations

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Abstract: Two new species of the order Haplosclerida from open reef and mangrove habitats in the Bocas del Toro region (Panama) have an encrusting growth form (a few mm thick), grow copiously on shallow reef environments, and are of dark purple color from dense populations of the cyanobacterial symbiont *Oscillatoria spongelliae*. *Haliclona* (*Soestella*) *walentiniae* sp. nov. (Chalinidae) is dark purple outside and tan inside, and can be distinguished by its small oscules with radial, transparent canals. The interior is tan, while the consistency is soft and elastic. The species thrives on some shallow reefs, profusely overgrowing fire corals (*Millepora* spp.), soft corals, scleractinians, and coral rubble. *Xestospongia bocatorensis* sp. nov. (Petrosiidae) is dark purple, inside and outside, and its oscules are on top of small, volcano-shaped mounds and lack radial canals. The sponge is crumbly and brittle. It is found on live coral and coral rubble on reefs, and occasionally on mangrove roots. The two species have three characteristics that make them unique among the families Chalinidae and Petrosiidae: filamentous, multicellular cyanobacterial symbionts rather than unicellular species; high propensity to overgrow other reef organisms and, because of their symbionts, high rate of photosynthetic production. These are the first descriptions of West Atlantic haplosclerid species associated with an *Oscillatoria*-type symbiont; all previous records of haplosclerid-cyanobacteria associations were of symbioses with unicellular cyanobacteria. High rates of photosynthetic production of *Oscillatoria spongelliae* could explain the abundance and overgrowth capability of the two host sponges in the region's reef environments. An overview of associations between sponges and cyanobacteria is presented.

Keywords: Haplosclerida, new species, cyanobacteria, Panama

Introduction

The marine subtidal habitats of the Bocas del Toro region (coral reef, mangrove, and sea grasses) are abundantly colonized by marine sponges. A recent survey of sponges from non-cryptic habitats in this region reports 120 described species (Diaz 2005). The Haplosclerida Topsent, 1928 represent the most diverse sponge order at Bocas del Toro, with thirty five species spread across five sponge families: Chalinidae (12 spp.), Petrosiidae (8 spp.), Niphatidae (7 spp.), Callyspongiidae (4 spp.), and Phloeodictyidae (4 spp.). Two undescribed species were encountered during this survey, one belonging to *Haliclona* Grant 1835, sub-genus *Soestella* de Weerdt, 2000, family Chalinidae Gray, 1867, and the second one to *Xestospongia* de Laubenfels, 1932, family Petrosiidae van Soest, 1980. Both are thin to thickly encrusting species copiously packed with filamentous cyanobacteria identified as *Oscillatoria spongelliae* (Thacker *et al.* 2007). The presence of filamentous cyanobacteria as symbionts in these sponges

constitutes a unique occurrence, both phylogenetically and geographically. To date, 100 sponge species in 29 families are known to harbor cyanobacteria (Table 1). The order Haplosclerida contains the highest number of species with this type of association (25, in 11 genera). Of these, 24 species support unicellular cyanobacteria, while only one undescribed Caribbean species in the family Niphatiidae van Soest, 1980 is reported to have filamentous symbionts (Diaz 1996). This unique association seems to have two striking ecological consequences: a competitive advantage over other reef organisms through overgrowth, including even aggressive reef species such as *Millepora* (Hydrozoa, Cnidaria) and *Neofibularia* Hechtel, 1965 (Demospongeae, Porifera), and high photosynthetic rates which characterize these two species as phototrophic sponges (Thacker *et al.* 2007). The present paper describes the morphology and ecological features of both new species and discusses their systematic affinities with close relatives in the Caribbean.

Table 1: Sponge species with cyanobacterial symbionts, modified from Diaz (1996). Families assigned to orders: 1. Homoclerophorida; 2. Astrophorida; 3. Halichondrida (*sensu van Soest et al.*, 1989); 4. Poecilosclerida; 5. 'Lithistida'; 6. Hadromerida; 7. Haplosclerida (*sensu de Weerdt*, 1985); 8. Dictyoceratida; 9. Dendroceratida; 10. Verongida; 11. Clathrinida; 12. Leucettida; 13. Sycettida; 14. Spirophorida. Symbionts (SYM) include the unicellular *Aphanocapsa feldmanni*-like (Af), *A. raspigella*-like (Ar), *Prochloron* spp. (Pro), *Synechococcus spongiarum* (S.spo), *Synechocystis trididemni*-like (St), *Synechocystis* spp.-like (Sy), the filamentous *Oscillatoria* spp.-like (O.sp), *Oscillatoria spongeliae*-like (O.spo), ? = uncertain status and * = only cyanobacterial pigments detected with thin layer chromatography. Some species have more than one described symbiont; others may contain synonymous *Aphanocapsa* and *Synechococcus* symbionts. The regions surveyed: Australia (AUS), Bahamas (BAH), Belize (BEL), Great Barrier Reef (GBR), Guam (GU), Japan (JP) Mediterranean (MED), North and South Baja California (NBC, SBC), Palau (PAL), Papua New Guinea (PNG), Puerto Rico (PR), Red Sea (RS), Sulawesi (SUL) and Zanzibar (ZZ).

Family	Taxa	Sym	Region	Source
Plakinidae ¹	<i>Oscarella</i> sp.	Ar	MED	Wilkinson 1980
Plakinidae ¹	<i>Placinolopha mirabilis</i>	O.spo	SUL	Diaz 1996
Ancorinidae ²	<i>Penares</i> aff. <i>schulzei</i>	Af	SUL	Diaz 1996
Ancorinidae ²	<i>Jaspis stellifera</i>	Af	GBR	Wilkinson 1979
Ancorinidae ²	<i>Stelletta clavosa</i>	Af	PNG	Diaz 1996
Ancorinidae ²	<i>Stelletta kallitetilla</i>	S.spo	BAH	Steindler <i>et al.</i> 2005
Ancorinidae ²	<i>Stelletta pudica</i>	S.spo	BAH	Steindler <i>et al.</i> 2005
Geodiidae ²	<i>Geodia papyracea</i>	Af	BEL	Rützler 1990
Geodiidae ²	<i>Geodia neptuni</i>	Af	BEL	Rützler 1990
Geodiidae ²	<i>Geodia</i> sp. 1	Af	BEL	Rützler 1990
Axinellidae ³	<i>Cymbastela</i> sp.	?	PNG	Diaz 1996
Axinellidae ³	<i>Pseudaxinella tubulosa</i>	S.spo	BAH	Steindler <i>et al.</i> 2005
Halichondriidae ³	<i>Axinyssa aphysinoides</i>	?	PNG	Diaz 1996
Halichondriidae ³	<i>Halichondria</i> sp.	Ar	MED	Wilkinson 1980
Halichondriidae ³	<i>Pseudaxinyssa</i> sp.	Sy	GBR	Larkum <i>et al.</i> 1988
Dictyonellidae ³	<i>Dictyonella funicularis</i>	Ar	BEL	Rützler 1981
Dictyonellidae ³	<i>Svenzea zeai</i>	S.spo	BAH	Steindler <i>et al.</i> 2005
Desmacellidae ⁴	<i>Neofibularia irata</i>	Af	GBR	Wilkinson 1980
Desmacellidae ⁴	<i>Neofibularia notilangere</i>	Af	BEL	Rützler 1990
Chondropsidae ⁴	<i>Batzella melanos</i>	St	GBR	Larkum <i>et al.</i> 1988
Crambeidae ⁴	<i>Crambe</i> sp.	Af	MED	Wilkinson 1980
Hymedesmiidae ⁴	<i>Phorbas</i> sp.	Af, Ar	MED	Wilkinson 1980
Isodictyidae ⁴	<i>Coelocarteria singaporense</i>	?	PNG	Diaz 1996
Microcionidae ⁴	<i>Clathria</i> sp.	Af	MED	Wilkinson 1980
Mycalidae ⁴	<i>Mycale hentscheli</i>	Sy	NZ	Webb and Maas 2002
Rhabderemidae ⁴	<i>Rhabderemia sorokinae</i>	*	PNG	Diaz 1996
Rhabderemidae ⁴	<i>Rhabderemia</i> sp.	Af	SUL	Diaz 1996
Theonellidae ⁵	<i>Discodermia dissoluta</i>	Af	BEL	Diaz 1996
Theonellidae ⁵	<i>Theonella conica</i>	Af, O.sp, S.spo	SUL ZZ	Diaz 1996 Steindler <i>et al.</i> 2005
Theonellidae ⁵	<i>Theonella swinhoei</i>	Pro	JP	Hentschel <i>et al.</i> 2002
Theonellidae ⁵	<i>Theonella swinhoei</i>	Af S.spo	RS	Wilkinson 1978 Steindler <i>et al.</i> 2005
Theonellidae ⁵	<i>Theonella</i> sp. 1	Af	SUL	Diaz 1996
Theonellidae ⁵	<i>Theonella</i> sp. 2	Af	SUL	Diaz 1996
Theonellidae ⁵	<i>Theonella</i> sp. 3	O.sp	SUL	Diaz 1996
Siphonidiidae ⁵	<i>Leiodermatium</i> sp.	*	PNG	Diaz 1996
Alectonidae ⁶	<i>Neamphius huxleyi</i>	Af	PNG, SUL	Diaz 1996
Chondrosiidae ⁶	<i>Chondrilla australiensis</i>	S.spo	AUS	Usher <i>et al.</i> 2004a, 2004b
Chondrosiidae ⁶	<i>Chondrilla nucula</i>	Af, S.spo	MED	Sarà 1966
Clionaidae ⁶	<i>Sphaciospongia florida</i>	S.spo	ZZ	Steindler <i>et al.</i> 2005
Clionaidae ⁶	<i>Sphaciospongia</i> sp.	Af	BEL	Rützler 1990
Clionaidae ⁶	<i>Cliona</i> sp.	Af	MED	Sarà 1966
Tethyidae ⁶	<i>Tethya</i> sp.	O.sp	MED	Sarà 1966
Spirastrellidae ⁶	<i>Spirastrella</i> sp.	St	GBR	Cox <i>et al.</i> 1985
Latrunculiidae ⁶	<i>Latrunculia</i> sp.	Af	SUL	Diaz 1996
Callyspongiidae ⁷	<i>Callyspongia</i> sp.	Af	GBR	Wilkinson 1980
Callyspongiidae ⁷	<i>Siphonochalina</i> sp.	Af	RS	Wilkinson 1978

Table 1 (cont.)

Chalinidae ⁷	<i>Haliclona</i> sp.	*	RS	Wilkinson 1978
Chalinidae ⁷	<i>Haliclona (Reniera)</i> sp.	Ar	MED	Wilkinson 1978
Niphatidae ⁷	<i>Amphimedon</i> sp. 1	Ar	SUL	Díaz 1996
Niphatidae ⁷	<i>Amphimedon</i> sp. 2	Af	SUL	Díaz 1996
Niphatidae ⁷	<i>Cribrochalina dura</i>	Af	BEL	Rützler 1990
Niphatidae ⁷	<i>Cribrochalina vasculum</i>	Af	BEL	Rützler 1990
Niphatidae ⁷	<i>Niphates</i> sp.	O.sp	BAH, BEL	Díaz 1996
Petrosiidae ⁷	<i>Neopetrosia exigua</i>	Af, S.spo	PNG, SUL, PAL	Díaz 1996 Thacker 2005
Petrosiidae ⁷	<i>Neopetrosia subtriangularis</i>	Af, S.spo	BEL	Rützler 1990
Petrosiidae ⁷	<i>Petrosia ficiformis</i>	Af	MED	Sarà 1966
Petrosiidae ⁷	<i>Petrosia pellasarca</i>	Af	PR	Vicente 1990
Petrosiidae ⁷	<i>Petrosia</i> sp.	S.spo	ZZ	Steindler <i>et al.</i> 2005
Petrosiidae ⁷	<i>Xestospongia muta</i>	Af, S.spo	BEL	Rützler 1990 Steindler <i>et al.</i> 2005
Petrosiidae ⁷	<i>Xestospongia proxima</i>	S.spo	BAH	Steindler <i>et al.</i> 2005
Petrosiidae ⁷	<i>Xestospongia rosariensis</i>	Af	PR	Vicente 1990
Petrosiidae ⁷	<i>Xestospongia</i> sp.	Af	SUL	Díaz 1996
Petrosiidae ⁷	<i>Xestospongia testudinaria</i>	Af	PNG, SUL	Díaz 1996
Petrosiidae ⁷	<i>Xestospongia wiedenmayeri</i>	Af	BEL	Rützler 1990
Phloeodictyidae ⁷	<i>Calyx podatypa</i>	Af	BEL	Rützler 1990
Phloeodictyidae ⁷	<i>Oceanapia</i> sp.	*	PNG, SUL	Díaz 1996
Phloeodictyidae ⁷	<i>Oceanapia ambionensis</i>	Ar	SUL	Díaz 1996
Phloeodictyidae ⁷	<i>Pellina semitubulosa</i>	Af	MED	Sarà 1966
Dysideidae ⁸	<i>Dysidea granulosa</i>	O.spo	GU	Thacker and Starnes 2003
Dysideidae ⁸	<i>Dysidea</i> sp.	O.spo	GBR	Larkum <i>et al.</i> 1987
Dysideidae ⁸	<i>Dysidea</i> sp. 1	O.spo	PNG, SUL	Díaz 1996
Dysideidae ⁸	<i>Dysidea</i> sp. 2	O.spo	PNG, SUL	Díaz 1996
Dysideidae ⁸	<i>Dysidea</i> sp. 3	O.sp	PNG, SUL	Díaz 1996
Dysideidae ⁸	<i>Lamellodysidea chlorea</i>	O.spo	PNG, SUL	Díaz 1996
Dysideidae ⁸	<i>Lamellodysidea herbacea</i>	O.spo	GBR	Larkum <i>et al.</i> 1987
Irciniidae ⁸	<i>Ircinia campana</i>	Af, S.spo	BEL	Rützler 1990 Steindler <i>et al.</i> 2005
Irciniidae ⁸	<i>Ircinia felix</i>	Af, S.spo	BEL	Rützler 1990 Steindler <i>et al.</i> 2005
Irciniidae ⁸	<i>Ircinia ramosa</i>	*	GBR	Wilkinson 1983
Irciniidae ⁸	<i>Ircinia variabilis</i>	Af, Ar, S.spo	MED	Sarà 1971 Steindler <i>et al.</i> 2005
Irciniidae ⁸	<i>Psammocinia</i> sp.	*	PNG	Díaz 1996
Spongiidae ⁸	<i>Coscinoderma</i> sp.	Af	GBR	Wilkinson 1980
Spongiidae ⁸	<i>Phyllospongia alcicornis</i>	Af	GBR	Wilkinson 1992
Spongiidae ⁸	<i>Phyllospongia foliacens</i>	Af	GBR	Wilkinson 1978
Spongiidae ⁸	<i>Phyllospongia papyracea</i>	Af	GBR	Wilkinson 1992
Spongiidae ⁸	<i>Spongia</i> sp.	?	MED	Wilkinson 1980
Thorectidae ⁸	<i>Carteriospongia foliascens</i>	S.spo	ZZ	Steindler <i>et al.</i> 2005
Thorectidae ⁸	<i>Carteriospongia</i> sp.	Af	SUL, PNG	Díaz 1996
Thorectidae ⁸	<i>Carteriospongia</i> sp.	Af	GBR	Wilkinson 1992
Thorectidae ⁸	<i>Dactylospongia elegans</i>	*	PNG, SUL	Díaz 1996
Thorectidae ⁸	<i>Hyrtilos violaceus</i>	O.spo	BEL	Rützler 1990
Thorectidae ⁸	<i>Lendenfeldia frondosa</i>	Ar	SUL, PNG	Díaz 1996
Thorectidae ⁸	<i>Lendenfeldia dendyi</i>	Pro, O.spo	ZZ	Steindler <i>et al.</i> 2005
Aplysillidae ⁹	<i>Aplysilla</i> sp.	Ar	MED	Wilkinson 1980
Darwinellidae ⁹	<i>Darwinella</i> sp. 1	Af	SUL	Díaz 1996
Aplysinellidae ¹⁰	<i>Suberea azteca</i>	Af	SBC	Díaz 1996
Aplysinellidae ¹⁰	<i>Suberea mollis</i>	O.sp	RS	Wilkinson 1978
Aplysinidae ¹⁰	<i>Aplysina aerophoba</i>	Af, S.spo	MED	Sarà 1966 Hentschel <i>et al.</i> 2002
Aplysinidae ¹⁰	<i>Aplysina archeri</i>	Af, S.spo	BEL	Rützler 1990 Steindler <i>et al.</i> 2005

Table 1 (cont.)

Aplysinidae ¹⁰	<i>Aplysina cauliformis</i>	Af, S.spo	BEL	Rützler 1990 Steindler <i>et al.</i> 2005
Aplysinidae ¹⁰	<i>Aplysina fistularis</i>	Af, S.spo	BEL	Rützler 1990 Steindler <i>et al.</i> 2005
Aplysinidae ¹⁰	<i>Aplysina fulva</i>	Af, S.spo	BEL	Rützler 1990 Steindler <i>et al.</i> 2005
Aplysinidae ¹⁰	<i>Aplysina gerardogreeni</i>	Af, S.spo	SBC	Díaz 1996 Steindler <i>et al.</i> 2005
Aplysinidae ¹⁰	<i>Aplysina lacunosa</i>	Af, S.spo	BEL	Rützler 1990 Steindler <i>et al.</i> 2005
Aplysinidae ¹⁰	<i>Aplysina</i> sp.	Af	BEL	Díaz 1996
Aplysinidae ¹⁰	<i>Verongula rigida</i>	Af	BEL	Rützler 1990
Aplysinidae ¹⁰	<i>Verongula gigantea</i>	Af	BEL	Rützler 1990
Aplysinidae ¹⁰	<i>Verongula reiswigi</i>	Af	BEL	Rützler 1990
Clathrinidae ¹¹	<i>Clathrina</i> sp.	Ar	MED	Wilkinson 1980
Leucettidae ¹²	<i>Pericharax heteroraphis</i>	Af	GBR	Wilkinson 1979
Leucettidae ¹²	<i>Leucetta</i> sp.	?	PNG	Díaz 1996
Sycettidae ¹³	<i>Sycon</i> sp.	Ar	MED	Feldmann 1933
Tetillidae ¹⁴	<i>Cinachyrella australiensis</i>	*	PNG	Díaz 1996
Tetillidae ¹⁴	<i>Tetilla arb</i>	Af	BCN	Díaz 1996

Materials and methods

Specimens were collected during field work in 2003 and 2005, using snorkel and SCUBA equipment while exploring two reefs (Swan Cay and Crawl Cay Canal) between 0-15 m deep in the Bocas del Toro region. Sponges were fixed in 10% formalin in seawater and preserved in 70% ethanol. Skeletal and histological preparations for light microscopy and scanning electron microscopy (SEM) followed standard methodology (Rützler 1978). The skeletal arrangement was described, and the length and width of each spicule type were measured in each specimen. Type material is deposited in the Porifera collection of the Smithsonian Institution's National Museum of Natural History, Washington, DC (USNH), and in the Smithsonian Tropical Research Institute (STRI) laboratory at Bocas del Toro, Panama (BT).

Results

Systematic descriptions

Class Demospongiae Sollas, 1885.
Order Haplosclerida Topsent, 1928
Family Chalinidae Gray, 1867
Genus *Haliclona* Grant, 1835
Sub-Genus *Soestella* de Weerd, 2000

***Haliclona (Soestella) walentinae* sp. nov.**
(Figs. 1-3; Table 2)

Material examined. Holotype: USNM 1106220, Crawl Cay Canal (9°15'050"N, 82°07'631"W), 5-10 m deep, covering top and sides of *Acropora cervicornis* on a shallow reef where *Millepora*, and *Porites* were the dominant coral species, collectors M.C. Díaz and R. Thacker, 21-06-05.

Paratypes: USNM 1106221, Crawl Cay Canal (9°15'050"N, 82°07'631"W), 5 m, on top and along sides of *Acropora cervicornis*, collectors M.C. Díaz and R. Thacker, 21-06-05. BT-045, Swan Cay (9°27'198"N, 82°18'024"W), 5 m deep, between fire coral (*Millepora* sp), and lettuce coral (*Agaricia* sp.) on a shallow reef with strong surge and currents, collector M.C. Díaz, 08-2003.

Description

Shape and size: Thin encrusting sheets (1-2 mm thick) covering patches ranging from five to a few hundred cm² (Fig. 1A, B).

Surface: Smooth to irregularly rugose to the naked eye, porous under a microscope. Small oscules (1-2 mm in diameter) with transparent membranes, regularly distributed over the sponge surface. Radial canals converging toward oscules. Spicule tracts piercing through the skin (ectosome) create a microhispid appearance, only visible under a microscope (Fig. 1B).

Colour: In live, deep dark- brown to purple outside, tan inside. Cream to white in alcohol. External color due to the photosynthetic cyanobacteria.

Fig. 1: *In situ* morphology and skeleton arrangement of the new species: **A.** *Haliclona walentinae* sp. nov. habit (scale: 6 cm); **B.** detail showing bumpy surface, radial canals, and oscules (1-2 mm) with white oscular membranes (scale: 5 mm); **C.** cross section through the choanosome with *Soestella*-type arrangement of sub-anisotropic choanosomal skeleton of ill defined paucispicular primary lines connected by paucispicular secondary ones (scale: 100 µm); **D.** *Xestospongia bocatorensis* sp. nov. habit (scale: 2 cm); **F.** isotropic unispicular to paucispicular reticulation (2-3 spicules across) forming polygonal-shaped meshes (scale: 120 µm).

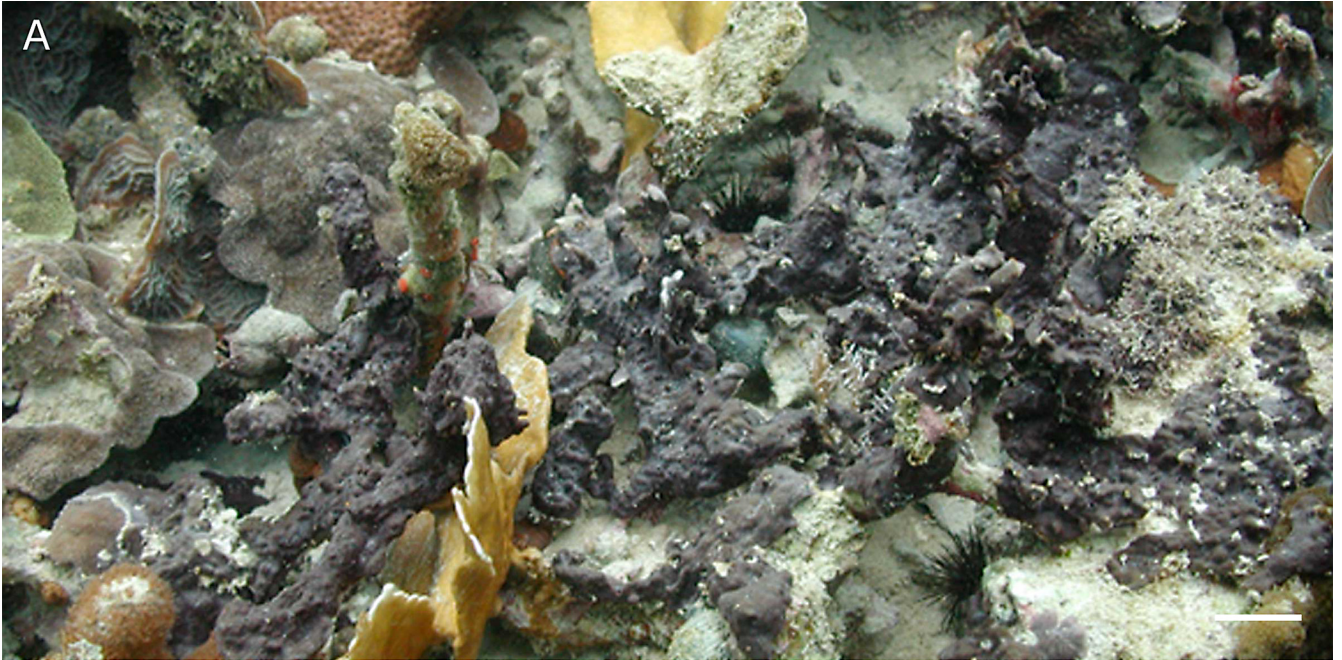


Table 2: Spicule measurements of specimens of *Haliclona walentinae* sp. nov. [max.-min. length (mean±SD) x max.-min. width (mean±SD)] in µm.

Material studied	Oxea
USNM 1106220	130–161 (140±9.3) x 6–9 (7.6±0.9)
USNM 1106221	130–160 (140±9.2) x 3–9 (4.8±1.6)
BT-045	100–180 (132±19) x 3–8 (5±1)

Consistency: soft, compressible, and resilient, easy to peel off the substrate.

Ectosomal skeleton: Poorly developed, some paucispicular spicule tracts and loosely strewn spicules (Fig. 1C). Ectosome not peelable. The ectosome on the underside of the sponge accumulates sand.

Choanosomal skeleton: Paucispicular, loosely organized primary skeleton tracts (20–40 µm in diameter), and mostly unispicular tracts or single spicules connecting them. Spicule tracts densely enveloped by filamentous cyanobacteria (Fig. 3A, B). Spongin scarce, barely discernable.

Spicules: Hastate to fusiform oxea, straight or slightly curved (100–180 x 3–9 µm). (Table 2, Fig. 2A).

Ecology: The species was found thriving on a shallow reef, profusely overgrowing fire corals (*Millepora* spp.), soft corals, scleractinians, and other sponges, such a *Neofibularia nolitangere* (Duchassaing and Michelotti, 1864). It appeared to be a rather aggressive species, dominating all neighboring sessile invertebrates.

Remarks: This species is here assigned to the subgenus *Soestella*, following the definition by de Weerd (2000) where “ill defined paucispicular primary lines, irregularly connected by unispicular secondary lines” characterize the skeletal architecture.

Eight additional species in this subgenus occur in the Caribbean: *H. (Soestella) caerulea* (Hechtel, 1965), *H. (S.) lehnerti* de Weerd (2000), *H. (S.) luciencis* de Weerd (2000), *H. (S.) melana* Muricy and Ribeiro (1999), *H. (S.) piscaderaensis* (van Soest, 1980), *H. (S.) smithsae* de Weerd (2000), *H. (S.) twincayensis* de Weerd *et al.* (1991), and *H. (S.) vermeuleni* de Weerd (2000). Four of these, *H. (S.) caerulea*, *H. (S.) piscaderaensis*, *H. (S.) twincayensis*, and *H. (S.) vermeuleni* are among common species in the region of Bocas del Toro (Diaz 2005). None of these, nor any other species of Chalinidae, are known to be associated with cyanobacteria (Table 1). Two species in *Soestella* (*melana*, and *luciencis*) are black to dark brown color, but only darkly pigmented cells are reported, at least for the former (de Weerd 2000). Distinct morphological and ecological differences separate *H. (S.) walentinae* from the other *Haliclona (Soestella)* Caribbean species. Among them a thinly encrusting growth habit, soft but resilient consistency, characteristic oscule morphology, and possession of cyanobacterial symbionts. The filamentous cyanobacteria turn out to be a branch of *Oscillatoria spongelliae*, with genetic affinities to certain Pacific sponge symbionts (Thacker *et al.* 2007), making

Haliclona walentinae a very interesting subject for both ecological and evolutionary studies.

Etymology: The species is named after Dr. Walentina de Weerd (University of Amsterdam) whose work with the Haplosclerida has been essential in our understanding of the group.

Family Petrosiidae van Soest, 1980
Genus *Xestospongia* de Laubenfels, 1932

***Xestospongia bocatorensis* sp. nov.**
(Figs. 1-3; Table 3)

Material examined. Holotype: USNM 1106222, Crawl Cay Canal (9°15'050"N, 82°07'631"W), 12 m, top of *Acropora cervicornis* on a shallow reef where *Millepora* and *Porites* were the dominant coral species, collectors M.C. Diaz and R. Thacker, 21-06-05. Paratypes: BT-019, Crawl Cay Canal (9°15'050"N, 82°07'631"W), 6 m, between fire coral, and *Agaricia* spp. colonies, on a shallow reef, collector: M.C. Diaz, 08-2003; BT-163, same data as holotype.

Description

Shape and size: Thinly encrusting species (2–5 mm thick), in patches from five to a few hundred cm².

Surface: Smooth. Oscules (1–2 mm diameter) on top of low volcano-shaped mounds (1–2 mm of height).

Consistency: Crumbly and brittle.

Colour: In live, dark purple, inside and out (Fig. 1D). Cream to white in alcohol.

Ectosomal skeleton: No organization, spicules strewn tangentially (Fig. 1E).

Choanosomal skeleton: Isotropic unispicular to paucispicular reticulation forming polygonal meshes (100–320 µm in diameter), and paucispicular primaries (2–3 spicules across) 200–300 µm apart. Filamentous cyanobacteria densely packed around the skeleton (Fig. 3C, D).

Spicules: Fusiform to slightly hastate stout oxeas in one size class (230–320 x 8–15 µm) (Table 3), with pointed ends. Sigmas, c-shaped (10–26 x <1 µm) (Fig. 2B).

Ecology: The species was found growing in small patches on mangrove roots, empty shells, or coral rubble, and occasionally profusely overgrowing live corals. Also found on shallow reefs (0–15 m deep) growing over coral and bare rock substrates.

Remarks: The predominance of unispicular over paucispicular reticulation, and the relatively light spicule density, compared to other *Xestospongia*, makes this species slightly atypical for the genus. However, two other Caribbean congeners, *X. arenosa* van Soest and de Weerd, 2001, and *X. wiedenmayeri* van Soest, 1980 are precedents for similar skeleton structure. The assignment to *Xestospongia* is based on spicule size, skeleton structure (more petrosiid than chalinid), and petrosiid consistency (brittle and crumbly); it was first suggested by Dr. Walentina de Weerd who examined our

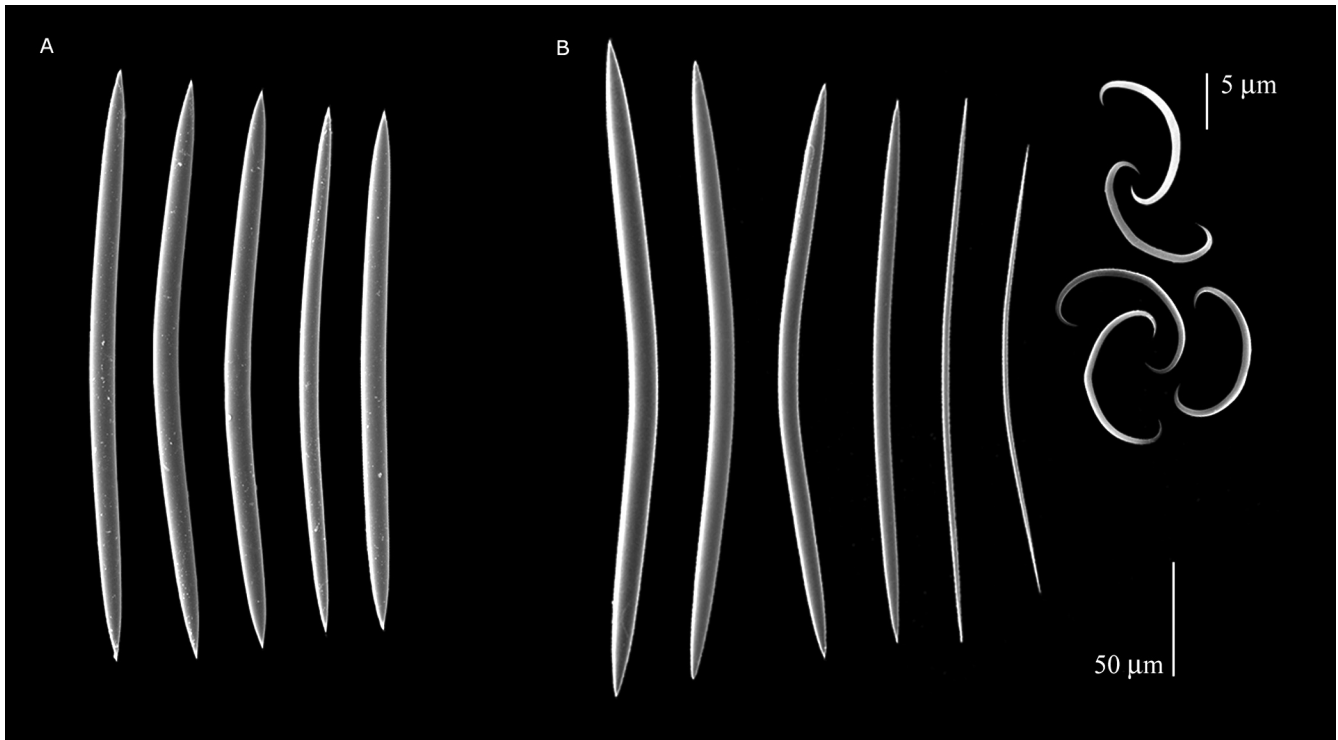


Fig. 2: SEM photomicrographs of spicules: **A.** *Haliclona walentinae* sp. nov. (USNM 1106220) oxeas; **B.** *Xestospongia bocatorensis* sp. nov. (USNM 1106222), oxeas and sigmas.

Table 3: Spicule measurements of specimens of *Xestospongia bocatorensis* sp. nov. [max-min. length (mean \pm SD-) x max.- min. width (mean \pm SD)] in μ m.

Material studied	Oxea	Sigma (length in μ m)
USNM 1106222	280–320 (302 \pm 11.5) x 12–15 (13 \pm 0.9)	20–25 (22 \pm 1.6)
BT-019	230–260 (248 \pm 11.2) x 8–12 (11.8 \pm 0.7)	10–12 (11.8 \pm 0.7)
BT-163	270–305 (293 \pm 12.4) x 8–12 (10.6 \pm 1.2)	10–26 (19 \pm 1.22)

material. Seven other *Xestospongia* species are recognized in the Caribbean: *X. arenosa* van Soest and de Weerdt (2001), *X. caminata* Pulitzer-Finali (1986), *X. deweerdtiae* Lehnert and van Soest (1999), *X. muta* (Schmidt, 1870), *X. portoricensis* van Soest (1980), *X. proxima* (Duchassaing and Michelotti, 1864), *X. rosariensis* Zea and Rützler (1983), none of these has the thinly encrusting morphology of *X. bocatorensis* sp. nov. Three are very common inhabitants of Bocas del Toro reefs: *X. proxima*, *X. muta*, *X. rosariensis*. Even though all of these species harbor symbiotic cyanobacteria, *Xestospongia bocatorensis* sp. nov. is unique for its possession of a host-specific clade of filamentous *Oscillatoria spongelliae*, rather than the more typical unicellular symbionts, *Candidatus Synechococcus spongiarum* (Usher *et al.* 2004a, 2004b, Thacker *et al.* 2007).

Etymology: The species is named after the Bocas del Toro region, an extensive system of islands with well developed

mangrove communities and patchy reefs in northeastern Panama where the new species was found.

Discussion and conclusions

To evaluate the relative frequency of associations between cyanobacterial symbionts and marine sponges, we compiled data from morphological and phylogenetic studies of sponges and their symbionts (Table 1, Diaz 1996, Steindler *et al.* 2005). Prior to genetic studies, many unicellular cyanobacterial symbionts were classified as *Aphanocapsa feldmanni* Frey, 1933; some of these have subsequently been recognized as members of the genus *Synechococcus* (Usher *et al.* 2006), including a proposed species of sponge-specific unicellular cyanobacteria, *Candidatus Synechococcus spongiarum* Usher, 2004. Here, we present symbiont names as given by the authors of each study, and recognize that some of

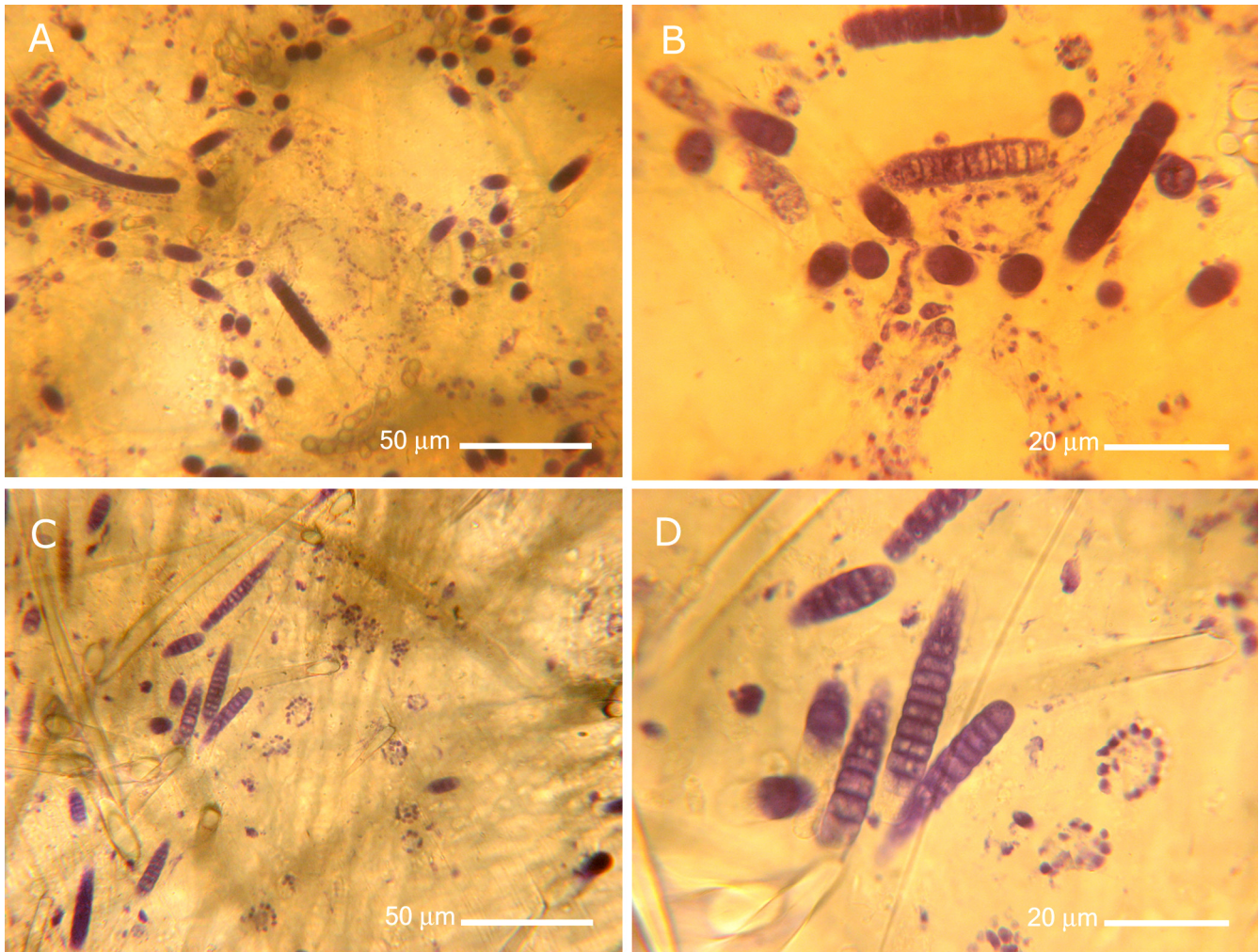


Fig. 3: Filamentous cyanobacteria (*Oscillatoria spongeliae*) and choanocyte chambers shown in sections of the new species: **A, B.** *Haliclona walentinae* sp. nov.; **C, D.** *Xestospongia bocatorensis* sp. nov.

these names may be synonyms (Table 1). Clearly, combined morphological and genetic studies are needed to resolve some of these issues.

Symbiosis of sponges and filamentous (*Oscillatoria*-type) cyanobacteria is a common occurrence in the Indo-Pacific region where at least 10 common species are known for this association. The families concerned are Plakinidae (Homosclerophorida), Theonellidae (“Lithistida”), Dysideidae and Spongiidae (Dictyoceratida), and Aplysinidae (Verongida). In the much better studied Mediterranean Sea, only one *Tethya* (Tethyidae, Hadromerida) is known with this kind of symbiont. Until our discovery of *Haliclona walentinae* sp. nov. and *Xestospongia bocatorensis* sp. nov., only two records of sponges with *Oscillatoria*-type symbionts existed in the tropical western Atlantic. One is the common “bleeder sponge” *Hyrtios violaceus* (Duchassaing and Michelotti, 1864) (Thorectidae, Dictyoceratida), of which the symbiont fine-structure was studied (Rützler 1990). The other is an undescribed species of *Niphates* (Niphatidae, Haplosclerida),

which was recorded from the Bahamas and Belize (Diaz 1996). The phototrophic properties of the new species, the nature of the cyanobacterial symbionts, and the phylogenetic affinities of the symbionts to those hosted by Pacific sponges (Thacker *et al.* 2007) lends these biological assemblages a unique ecological and evolutionary significance. An unsolved issue remains about the origin of the two new species: are they systematic and ecological oddities among Caribbean sponges, or are they invasive species that originated in the tropical Pacific?

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