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REEVALUATION OF STALKED APLYSINID SPONGES, WITH DESCRIPTION OF A NEW SPECIES FROM THE UPPER BAHAMIAN SLOPE

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ABSTRACT

A new aplysinid sponge, *Aplysina bathyphila* n. sp., is described from the upper Bahamian slope, where its populations show a stenobathic distribution limited to the range between 60 and 150 m deep. The species is characterized morphologically by a stalked, goblet-shaped body and a large oscular diaphragm. The sponge body is hollow, having a spacious atrial cavity that becomes a narrow canal extending the whole length of the stalk. The skeleton is a highly regular network of hexagonal meshes built with a single type of laminated, pithed fibers, as is typically in the genus *Aplysina*. Choanocyte chambers are spherical. Apart from *A. bathyphila*, two other stalk bearing species had previously been described in the genus, *Aplysina pedunculata* and *Aplysina aztecus*. However, on the basis of skeletal traits, we conclude that *A. bathyphila* is the only stalked sponge belonging to the genus *Aplysina*. *Aplysina pedunculata* and *A. aztecus*, characterized by a nearly dendritic pattern of fibers with a highly developed pith, are transferred to the genus *Suberea* in the Family Aplysinellidae.

The shallow-water sponge fauna of the Caribbean is one of the best known in the world, but little attention has been devoted to the diverse deep-water sponge fauna of the continental slope (see Van Soest and Stentoft, 1988; Maldonado and Young, 1996). Current research using submersibles has revealed that many poriferans living below SCUBA depths still remain undescribed (authors, current research; Pomponi, pers. comm.). In this paper, we describe large populations of a new species of *Aplysina* on the upper slope of The Bahamas, and reevaluate the two stalked aplysinids previously described, transferring them both to the family Aplysinellidae.

MATERIAL AND METHODS

Sponges were collected and observed by three manned submersibles: (*1*) JOHNSON-SEA-LINK-I submersible, off the southern side of Golding Cay (24°58′N, 77°34′W), near New Providence Island, Bahamas, (*2*) a Gamma-II submersible and (*3*) CLELIA, off the South eastern side of Lee Stocking Island (LSI; 23°46′N, 76°05′W), in Exuma Sound, Bahamas. Sponges were fixed in 10% seawater-formalin and preserved in 70% ethanol. Skeletal and histological slides for light microscopy were prepared according to standard methodology (Rützler, 1978). Material of the stalked keratose sponges *Aplysina aztecus* Gómez and Bakus, 1992 (paratype PG.ATLAS 2B-03, Instituto de Ciencias del Mar y Limnología of the Universidad Nacional Autónoma de México) and *Aplysina pedunculata* (Lévi, 1969) (two paratypes stored in the Muséum National d'Histoire Naturelle, Paris) was reexamined for comparative purposes.

Type material was deposited in the Porifera collection of the National Museum of Natural History in Washington D.C. (USNM). Halves of a voucher were deposited in the Porifera collections of Harbor Branch Oceanographic Institution (HBOI) and Museo Nacional de Ciencias Naturales (MNCN), respectively.

SYSTEMATIC STUDY

Order Verongida Bergquist, 1978
Family Aplysinidae Carter, 1875
Genus *Aplysina* Nardo, 1834

Aplysinidae characterized by a regular network with polygonal meshes made of a single type of fibers. Fibers are translucent, amber-colored and have a laminated bark and an opaque pith. Both bark and pith lack inclusions of foreign material. Most species display an oxidative color change, in which their original colors change into black, deep green or brown upon exposure to air (after Wiedenmayer, 1977).

Aplysina bathyphila new species

Studied material.—Holotype (USNM 40-754), paratypes (USNM 40-756), (MNCN 1-01/181) (Figs. 1A–F).

Type locality.—Eastern side of Lee Stocking Island (23°46.81'N, 76°04.97'W), Exuma, The Bahamas, 114 m depth.

Etymology.—The name refers to the fact that this species is found relatively deeper than most other species of the genus.

Description.—Stalked, goblet-shaped sponge (Figs. 1A–F). Individuals between 10 and 16 cm in total height, with stalk comprising between about 30 and 50 % of total height. Inflated portion of body between 4.8 and 6.5 cm in maximal diameter. Stalk measuring between 0.8 and 1.5 cm in maximal diameter, depending upon individuals. Individuals always isolated; never united basally in clusters. Ectosome whitish, with a pinkish tinge at the body parts exposed to light in those individuals living at the shallowest depths. Upon exposure to air, the color changes progressively to dark brown or greenish black. The consistency in life is firmly spongy, tough; harder at the basis of the stalk.

The sponge body is hollow, with a spacious atrial cavity (1–2 cm in maximal diameter) that becomes a narrow canal (2–3 mm in diameter) extending the whole length of the stalk. The external sponge surface is finely conulose, bearing short conules (<0.5 mm high) spaced 3 to 4 mm apart. Ostioles (pores) are located in the depressed areas resulting between conules. Ostioles measure between 40 and 70 µm in diameter, and they are spaced 42 to 142 µm apart. The atrium is lined by a translucent, non-conulose epithelium, and it is connected with the exterior trough a single circular or ellipsoidal osculum located at the top part of the goblet (Fig. 1B,G–H). This oscule is between 0.5 and 2 cm in maximal diameter, and is surrounded by a diaphragm-like membrane 0.7–0.8 mm thick, that lacks skeletal fibers (Fig. 1G–H). There are exhalant orifices (preoscules) irregularly scattered on the epithelium of the main atrial cavity, but they do not occur in the portion of the atrial canal found within the stalk. Preoscules are ellipsoidal in shape, ranging from 40 to 575 µm in diameter, and being spaced 100 to 1000 µm apart. In most individuals, some additional small subcircular oscules between 185 and 290 µm in diameter are also present on the external surface of the sponge.

The body wall is between 1 and 2 cm thick at the inflated end, and between 0.3 and 0.5 cm thick at the stalk. The ectosome, both at the external and atrial side, is a 40–55 µm

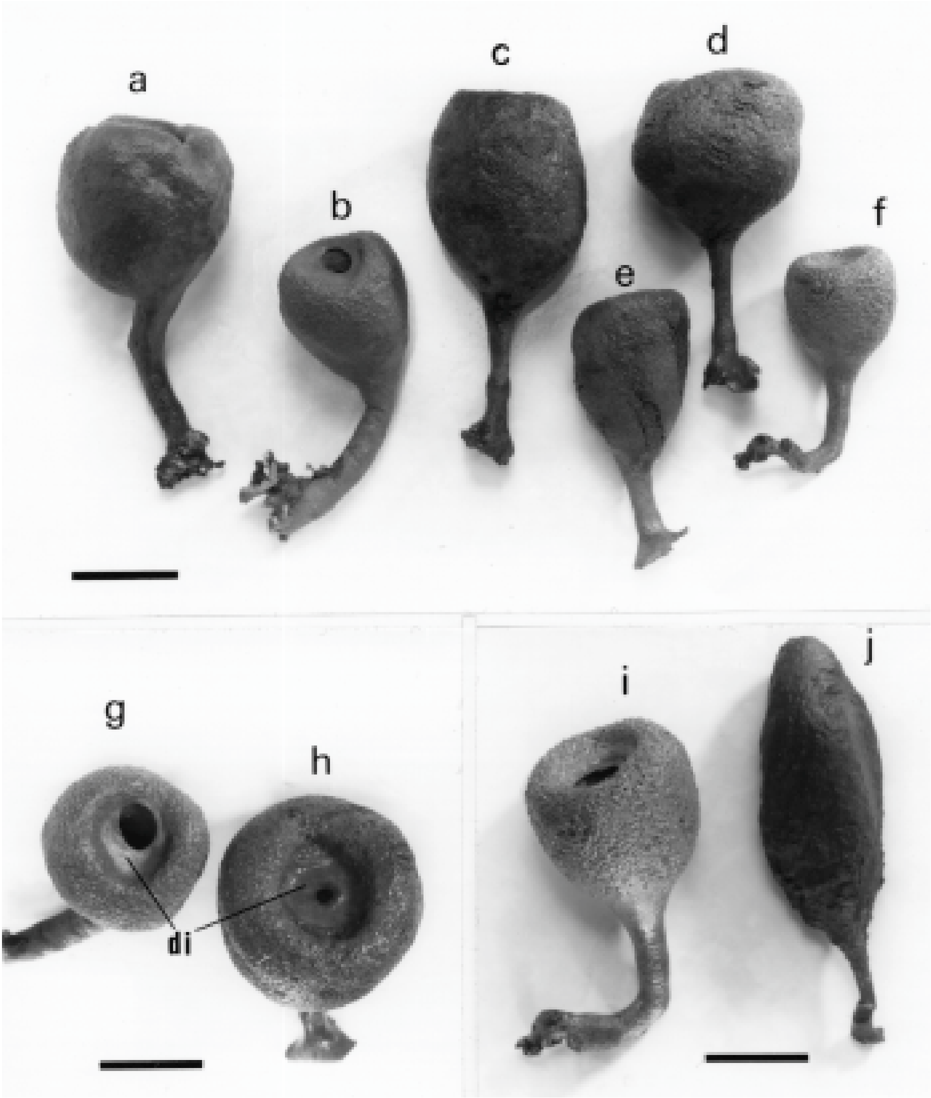

Figure 1. Collected material of *Aplysina bathyphila* n. sp.: (a) Specimen collected at LSI, 60 m deep. (b) Specimen collected at Golding Cay, 148 m deep. (c) Specimen collected at LSI, 106 m deep. (d) Specimen USNM 10-754 (holotype), collected at LSI, 143 m. (e) Specimen cataloged as additional material (MNCN 1-01/181), collected at LSI, 121 m deep. (f) Specimen USNM 10-756 (paratype), collected at LSI, 143 m deep. (g–h) The holotype (left) and a paratype (right) shown from the top to illustrate the diaphragm (di) surrounding the osculum. (i–j) Comparative view of a paratype of *A.bathyphila*, on the left (i), and a paratype of *Suberea aztecus* (= *Aplysina aztecus*), on the right (j). Scale bars represent 4 cm in Figures 1a–f and 3 cm in Figures. 1g–j.

thick membrane. Beneath the ectosome, there is a darker layer that can be up to 1 mm thick. The pigmented subectosomal layer is somewhat thicker in individuals collected at greater depths. The body wall is supported by a skeletal network made of spongin fibers

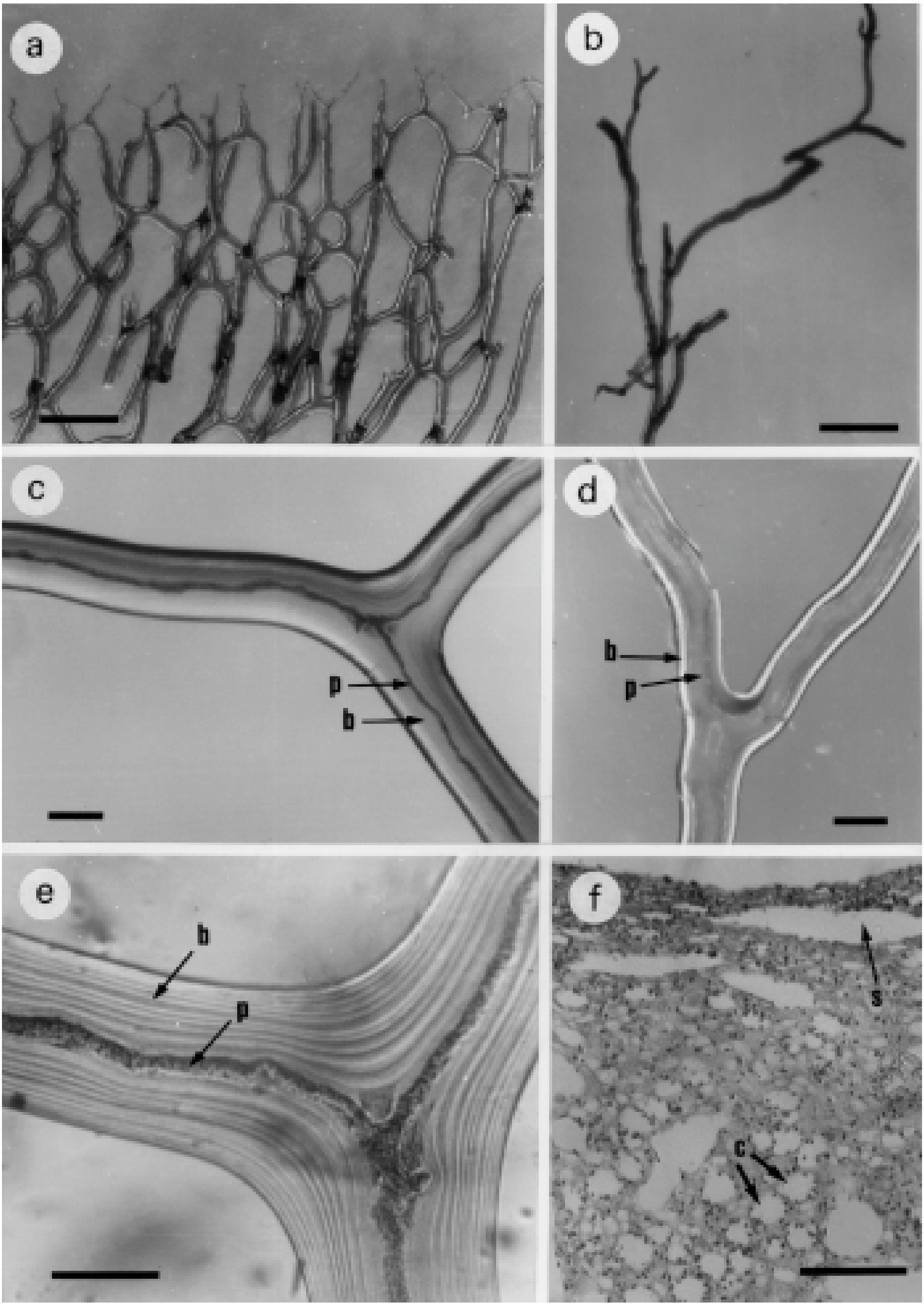

Figure 2. (a) General view of the regular fiber network of *Aplysina bathyphila* n. sp. (b) General view of the irregular, pseudodendritic fiber skeleton of *Suberea aztecus* (= *Aplysina aztecus*). (c) Fiber of *A. bathyphila*, showing a narrow pith (p) with respect to the bark (b). (d) Fiber of *S. aztecus* with a pith (p) enormously developed with respect to the bark (b). The bark remains as just a narrow, bright band at the fiber periphery. (e) Detail of a fiber of *A. bathyphila* showing the laminated bark (b) and the granulate pith (p). (f) Histological semithin section of *A.bathyphila* showing large subectosomal aquiferous spaces (s) and numerous spherical choanocyte chambers (c). Scale bars represent 1500 μm in Figures 2a-b, 100 μm in Figures 2c, 200 μm in Figure 2d, 75 μm in Figure 2e, and 25 μm in Figure 2f.

arranged in polygonal meshes (Fig. 2A). At the inner part of the body wall, meshes are lengthened polygons with the largest axis oriented tangential to the wall surfaces. Mesh orientation and shape shifts progressively towards the periphery of the body wall, where the holes become nearly hexagonal in shape and the largest axis is arranged perpendicular to the body wall. Mesh size is larger at the inner parts of the body wall (571–800 × 900–1850 µm), becoming somewhat smaller near the periphery (500–700 × 900–1300 µm). The body wall at the inflated end contains a skeleton consisting of between 11 and 15 polygonal meshes. Just under the ectosome, spongin fibers are not reticulated, but dichotomous, protruding through the ectosome to form conules (Fig. 2A).

Fibers are amber-colored, laminated and pithed (Figs. 2C,E). Although there is a single fiber type, those fibers at the inner parts of the body wall are somewhat thicker than the ones at the periphery, measuring 171–242 and 114–140 µm, respectively. The pith is bright white and extremely thin, measuring 20–23 µm in the internal fibers and about 15 µm in the peripheral fibers. The pith represents between 9 and 12 % of the fiber thickness (Figs. 2C,E).

The endosome is dense, with minute aquiferous canals (<1 mm in diameter), and is commonly parasited by the polychaete *Haplosyllis spongicola.* Choanocyte chambers are spherical, 10–20 µm in diameter and very abundant throughout the endosome (Fig. 2F).

Distribution and habitat.—Observations from submersibles reveal that this species is common in deep-reef habitats along the continental slope in many parts of the Bahamas. Most specimens grew on vertical rocky walls and overhangs, rarely on horizontal surfaces. Individuals were scattered, in densities ranging from 0 to 2 individuals m^{-2}, depending upon sites. The species appears to be stenobathic, with most of the population confined to depths between 60 and 150 m. The upper limit of this distribution seems to be marked by the lower limit of the macrophyte-dominated communities, whereas the lower limit is roughly at the winter level of the permanent thermocline (Maldonado and Young, 1996).

Discussion

The genus *Aplysina* is well represented in many Caribbean littoral communities, from sand flats to deep fore-reefs (e.g., Wiedenmayer, 1977; Van Soest, 1978; Zea, 1987). To date, there were six species known from this area: *Aplysina fistularis* (Pallas), *Aplysina fulva* (Pallas), *Aplysina hirsuta* Hyatt, *Aplysina cauliformis* (Carter), *Aplysina archeri* (Higgin), *Aplysina lacunosa* (Pallas) and *Aplysina ocracea* Alcolado. The species *Aplysina bathyphila* n. sp. is clearly distinct from the remaining Caribbean members of the genus, as they all others are non-stalked sponges.

The presence of a stalk is rather an uncommon feature in the genus *Aplysina*. Although two other stalked species have been described in this genus to date, a reexamination of this material suggests that they may not be actual aplysinids, but aplysinellids. One of these species, *Aplysina aztecus* Gómez and Bakus, 1992 from the Pacific coast of Mexico, appears somewhat closer morphologically to *A. bathyphila* (Figs. 1I–J). However, a reexamination of the paratype of *A. aztecus* (PG.ATLAS 2B-O3) revealed significant morphological and skeletal differences between the two species. Unlike *A. bathyphila*, the Pacific species lacks a diaphragm surrounding the oscule. Moreover, the skeleton is not a regular network with polygonal meshes, as characterizes the genus *Aplysina*. It rather has an overall dendritic pattern with occasional anastomosing between converging branches of the dendritic fibers (Fig. 2B). The fibers have an extremely thick pith occupying between 30 and 95 % of the fiber width (Fig. 2D). These fibers are much different from those of *A. bathyphila* where the pith represents less than 15 % of the fiber thickness (Fig. 2C). According to recent taxonomic criteria proposed by Bergquist (1995), the dendritic skeletal pattern and the more substantial pith occurring in the Pacific species suggest that it should be transferred to the genus *Suberea* Bergquist, 1995 in the family Aplysinellidae. The genus *Suberea*, as currently defined, includes massive, stalked or branching Verongida with coarse irregular dendritic fibers having a well-developed pith and a thin, strongly laminated bark.

The other stalked species is a black, cup-like sponge from South Africa described by Lévi (1969) as *Verongia penduculata*. The skeleton supporting the walls of the cup has a dendritic pattern originated by sparse, branching fibers that only anastomose each other occasionally (Fig. 3A). These fibers are dark (reddish brown), relatively thick (270–600 µm), and with a well-developed pith that in most cases represents between 55 and 75% of the total width (Fig. 3b). The pith component may be somewhat reduced at some fibers bifurcations, where it may represent just between 25 and 40% of the total width (Fig. 3C). The short anastomosing “fibers” connecting two ascending branches usually lack pith (Fig. 3b). We assume that they are not true fibers, but structures resulting from bark fusion between fibers coming in contact. The stalk contains two types of fibers. There is a central axis made by an ascending tract of well-pithed fibers, as those described in the globet. These axial fibers are surrounded by an extra-axial network made by fibers that are comparatively lighter in color (yellowish brown), much thinner (30–170 µm), and with a narrower pith (8–20 µm). They form a relatively dense network with nearly polygonal meshes (130–550 µm in mesh diameter). Lévi (1969) formerly described these fibers as primary and secondary fibers, respectively. However, if we accepted that real primary and secondary fibers occur, this species would have to be definitely excluded not only from the genus *Aplysina*, but also from the order. In Verongida, by definition, there is no difference between primary ascending and secondary connecting elements (Bergquist, 1980, 1995). Indeed, most of the morphological and skeletal traits of this sponge clearly indicate that it belongs to the order Verongida. Therefore, we interpret that a single fiber type occurs, and that the alteration of both the bark/pith ratio and the anastomosing pattern of the fibers in the stalk is a result of a particular adaptation to provide both flexibility and strength to this structure. The overall dendritic skeletal pattern within the walls of the cup, as well as the sparse fibers with a substantial pith suggest that this species should also be transferred to the genus *Suberea* Bergquist, 1995 in the family Aplysinellidae. Because of the stalked cup-like body and the dendritic pattern of the main-body skeleton, this species could also be regarded as belonging to *Porphyria* Bergquist, 1995. However, the dendritic fibers of this monotypic genus are not sparse and thick, but abundant and relatively thin, having short, often flexuous branches and reduced pith component.

After the above taxonomic re-interpretations, the new species *Aplysina bathyphila* remains as the only stalked member of the genus *Aplysina*. This species appears perfectly suited to exploit the energy in ambient currents. Because the osculum is far away from the substratum and its diameter is regulated by a diaphragm, water should be drawn unidirectionally from the ostia to the osculum by Bernoulli’s principle and by dynamic pressure (Vogel, 1974, 1978). The globose form of the main body should facilitate these processes, as flow direction should make no difference. Virtually all individuals we have

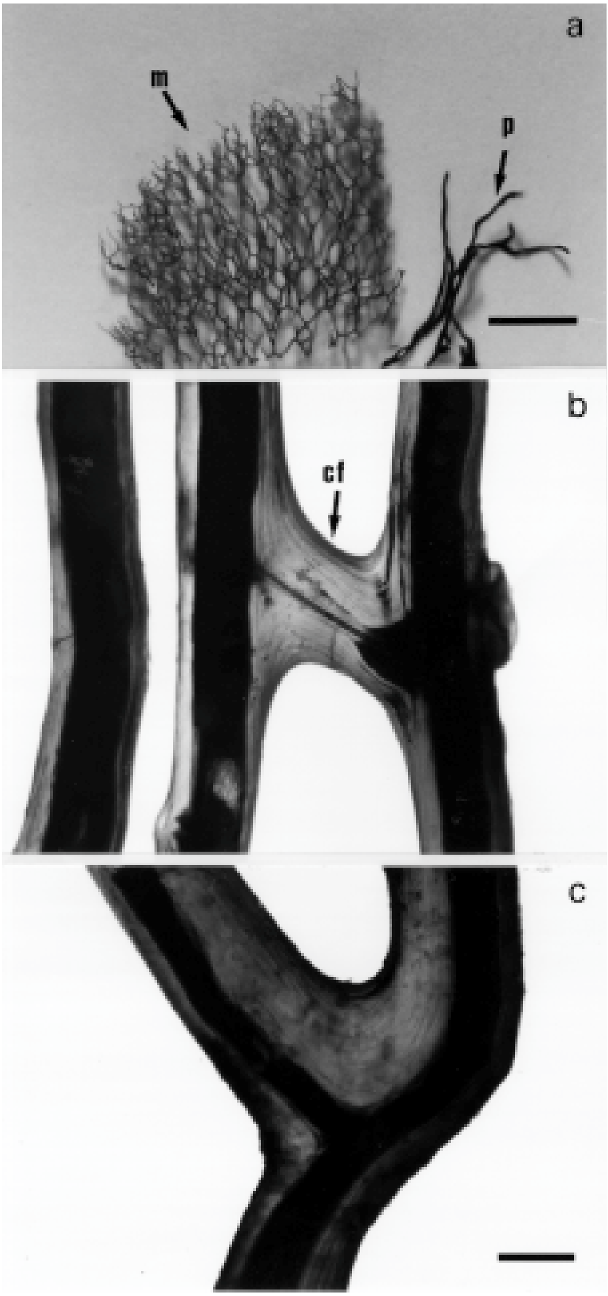

Figure 3. (a) Comparative view of pieces of the skeleton supporting the body wall in *Aplysina bathyphila* (m) and S*uberea pedunculata* (p) (= *Aplysina pedunculata*). (b) Ascending fibers with a transversal connection (cf) obtained from the body wall of *S. pedunculata*. Ascending fibers have a narrow bark and a thick pith, whereas pith is virtually absent in the transversal connection. (c) Bifurcation of a fiber of *S. pedunculata*, where the pith is usually thinner than in other parts of the fiber. The bark is always strongly laminated. Scale bars represent 3 mm in Figure 3A, and 350 µm in Figures 3b-c.

observed have been attached to vertical walls. In Exuma Sound, tidal currents in slightly shallower water (22 m deep) average 2.3 cm s^{-1} (Pitt and Smith, 1994), with a maximum velocity of 3.6 cm s^{-1}. We have measured maximum spring tide flows of up 18 cm s^{-1} slightly deeper than these sponges live in the Tongue of the Ocean (Young et al., 1993). At these flow rates, the sponges may find stalk flexibility to be useful, as they flex with the current.

The occurrence of stalked species in different families of Verongida supports that this body shape is not a homologous character in the order, but probably a convergent ecological adaptation.

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