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A new genus of Atlantic octocorals (Octocorallia: Gorgoniidae): systematics of gorgoniids with asymmetric sclerites

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Abstract

Gorgonian corals from the families Gorgoniidae and Plexauridae are among the most abundant and diverse shallow-water cnidarians found along tropical and temperate Atlantic coasts and reefs. Some morphological traits in the Gorgoniidae comprise a taxonomic challenge due to their morphological plasticity as well as a lack of discrete character states among most genera. Some gorgoniids have asymmetrical sclerites in the surface coenenchyme, a character trait that consists of a continuum among several genera and can cause confusion with members of the family Plexauridae. The collection of a unique gorgoniid in Tobago (Trinidad and Tobago), which contains this trait but also maintains affinities to many different genera, stimulated a wider morphological comparison of gorgoniids using scanning electron microscopy (SEM). Using the morphology of asymmetrical sclerites, gorgoniids could be grouped in four monophyletic clades that were compatible with recent molecular phylogenies and provide a provisional subfamilial classification: (1) a derived clade including gorgoniids with scaphoid sclerites, comprising the reef fauna from the western Atlantic (e.g. *Gorgonia*, *Pseudopterogorgia* [= *Antillogorgia*], *Pterogorgia*, and *Phyllogorgia*); (2) a related group with taxa containing capstan sclerites including genera with short capstans and/or disk-spindles sclerites such as *Pacifogorgia* and *Leptogorgia* (= *Lophogorgia*); (3) a clade of gorgoniids with asymmetrical spiny sclerites including the Atlantic genus *Muriceopsis* and the Indopacific *Pinnigorgia* together with the distant single species from the new genus and species *Tobagogorgia hardyi* (it is worth noting that *Muriceopsis* was previously classified in the Plexauridae, but there is overwhelming molecular support that groups it with the Gorgoniidae and morphological evidence that suggests affinity with *Pinnigorgia*); and finally (4) a basal clade with long and spiny spindles, which includes some African species such as *Filigorgia angolana* and *F. schoutedeni* as well as other new combinations (all species previously classified as *Leptogorgia* but not phylogenetically related). The combined set of sclerites of *Tobagogorgia* (e.g. both asymmetrical and irregularly bent spindles) separates it from the diagnostic characters of related genera such as *Muriceopsis* and *Pinnigorgia*. The latter two genera are also profusely branched, including pinnate patterns, whereas *T. hardyi* has only one or two branches. Externally, *T. hardyi* looks like some *Leptogorgia* colonies that branch minimally but it is clear that the sclerites are very different and thus also their phylogenetic divergence.

Keywords: *Gorgonian corals*, *Atlantic octocorals*, *Gorgoniidae*, *Tobagogorgia*, *Octocorallia*

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Introduction

Gorgonian coral systematics relies on a combination of characters such as axial skeleton (if any), colonial form, polyp arrangement, and sclerite (microscopic magnesium calcite formations) morphology (Bayer 1961). Excluding sclerite morphology, comparisons of these traits against molecular phylogenies have shown a great deal of homoplasy (Bayer 1961; Sánchez et al. 2003a, 2003b; Sánchez 2004). In addition, there are no landmarks in any of these traits (Sánchez and Lasker 2003). Unwieldy ancient literature with no or neglected illustrations and lost or badly preserved type material have played a major role concerning the current taxonomic confusion in octocoral systematics. Critical examinations of octocoral taxonomy have not been frequently used due to the absence of independent sources of characters. Opportunely, however, there has been a rebirth in invertebrate systematics due to the ever-increasing availability of DNA sequence characters, which can turn taxonomic observations into testable hypotheses (Mallet and Willmott 2003).

The Gorgoniidae is comprised of important genera of shallow-water octocorals distributed worldwide, and is characterized by having a thin coenenchyme and reduced sclerites that are regularly sculpted or ornate (Bayer 1961; Grasshoff and Alderslade 1997). However, some taxa include diagnostic characters that are not well defined at the generic level, and based on the family diagnosis some species could be classified in either the Gorgoniidae or Plexauridae. For instance, the axis of plexaurids can have a “cortex commonly (but not always) loculated” and in gorgoniids it can be “loculated little or not at all” (Bayer 1961, p 91, 192) and both can have a cross-chambered core. Axial characters were considered the key character for family-level distinction within the Holaxonia, but it is clear that there is no discrete differentiation in these two families and molecular results have strongly suggested multiple origins of gorgonian axes (McFadden et al. 2006). Some generic descriptions include traits such as tubercles arranged in whorls, but irregular in some species (Grasshoff and Alderslade 1997), but this irregular trait may correspond to some plexaurids. The thickness of the coenenchyme and sclerite size is also quite confusing between these two families. *Muriceopsis* spp. (Plexauridae), for example, has sclerites of intermediate size among the two families and a thin coenenchyme as in gorgoniids (Sánchez et al. 2003b). The genus *Plexaurella*, also Plexauridae, has reduced (<0.5 mm), regularly ornate sclerites yet has the thickest coenenchyme in the family. Both *Plexaurella* spp. and *Muriceopsis* spp. have sclerite types different from those of other plexaurid species. Interestingly, the molecular phylogeny of the Plexauridae and Gorgoniidae, according to three coding genes from mitochondrial DNA (ND2, ND6, and MSH1), clearly show how *Muriceopsis* and *Plexaurella* group with the Gorgoniidae (Sánchez et al. 2003b) suggesting that suprageneric taxa can be classified within precise morphological limits (e.g. sclerites <0.5 mm length) with a combination of molecular and morphological data. Similarly, the Plexauridae is a complex family, including multiple lineages and remarkably derived morphologies (Sánchez et al. 2003b; Sánchez 2005; Wirshing et al. 2005). Some gorgoniids have asymmetrical sclerites in the surface coenenchyme, which comprises a continuum among several genera and generates confusion with the family Plexauridae. The collection of a unique gorgoniid in Tobago (Trinidad and Tobago), which contains this trait but also maintains affinities with many different genera, stimulated a wider morphological comparison within the Gorgoniidae using scanning electron microscopy (SEM).

Aguilar and Sánchez (2007a) present several new phylogenetic hypotheses of most gorgoniid genera using ITS2 sequences and their predicted RNA secondary structures. Although there are several competing hypotheses for the relationships of basal nodes depending on the type of analysis of whether the source of characters were sequence- or

structure-based, support for many genera and some intrafamilial clades differ from the current taxonomy. This study describes a new octocoral, and compares its sclerite morphology, in the light of the recent molecular phylogenies, against a number of gorgoniids with an emphasis on species with asymmetrically spiny sclerites. Four reciprocally monophyletic clades were observed.

Methods

The subject specimens collected in Tobago (Trinidad and Tobago) and representative species from the Gorgoniidae, with and without asymmetrical spiny sclerites in the surface coenenchyme, as well as a few members of the Plexauridae as outgroups, were examined. Asymmetrical spiny spindles are defined as those structures with spines or different ornaments along only one side of the sclerite independent of whether the sclerite is bent. SEM analyses were done following the methods of Sánchez et al. (2003b) and Sánchez (2005) at the National Museum of Natural History (SEM-Leica Stereoscan, Laboratories of Analytical Biology, Smithsonian Institution, Washington, DC, USA). Specimen museum sources and catalogue numbers from species used for comparisons are presented in the figure legends.

The affinities of the questioned specimens with respect to other gorgoniids were based on the congruency of surface layer sclerites, considered one of the most phylogenetically informative characters in gorgonian corals (Sánchez et al. 2003b; Sánchez 2005; Wirshing et al. 2005), compared against the best supported molecular phylogenetic hypotheses obtained by Aguilar and Sánchez (2007a, see also 2007b).

Results and discussion

Figure 1 shows the best supported phylogenetic hypothesis from sequence alignments corrected with the RNA secondary structures according to maximum likelihood including common nodes and support values from maximum parsimony and Bayesian inference of phylogeny. Surface sclerite characters were mapped on this phylogenetic hypothesis (Figure 1). Gorgoniids could be grouped in four reciprocally monophyletic clades and provide a provisional subfamilial classification.

Systematic account

Class ANTHOZOA Ehrenberg, 1834
Subclass OCTOCORALLIA Haeckel, 1866
Order ALCYONACEA Lamouroux, 1816
Suborder HOLAXONIA Studer, 1887
Family GORGONIIDAE Lamouroux, 1812

Gorgonian octocorals (Holaxonia, see Bayer 1961; Sánchez et al. 2003a) with spindle-derived sclerites in the colony surface, <0.5 mm length, ornamented with complex (many internal geometrical/fractal subwarts) warts (or tubercles) disposed in transverse girdles, usually <20 µm wide (Sánchez et al. 2003b). Bayer and McIntyre (2001) proposed that calcite hydroxyapatite (CHAp) is only present in this family although it has not been found in all subfamilies and genera. Circumtropically distributed in shallow water (some

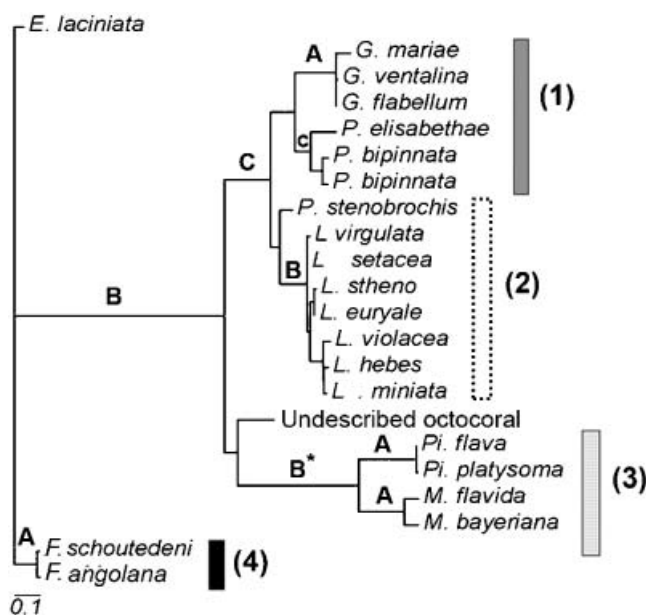


Figure 1. Phylogenetic hypothesis (maximum likelihood estimated phylogram) of Atlantic gorgoniids, modified from Aguilar and Sánchez (2007a, Figure 4A). The “Undescribed octocoral” refers to the new genus and species described below. Above node letters: A, support corresponding to values >90 in 100 bootstrap maximum likelihood replicates, 1000 bootstrap values in maximum parsimony together with values over 0.9 posterior probabilities of Bayesian inference; B, support corresponding to values >90 in 100 bootstrap maximum likelihood replicates but lesser values for maximum parsimony or Bayesian inference (<70 or 0.70, respectively); C, support corresponding to values <70 in 100 bootstrap maximum likelihood replicates but higher values for maximum parsimony or Bayesian inference (<90 or 0.90, respectively). Character mapping: grey bars, gorgoniids with scaphoid sclerites (Clade 1); open bars-dotted, gorgoniids with capstan-derived sclerites (Clade 2); grid bars, gorgoniids with asymmetrical spiny sclerites (Clade 3); black bars, gorgoniids with long and spiny spindles (Clade 4). Scale in substitutions per site. **Pinnigorgia* and *Muriceopsis* are also supported by a complete compensatory base change in their RNA secondary structure, a rare evolutionary event (see Aguilar and Sánchez 2007a).

symbiotic with zooxanthellae) with a few deep-water and sub-tropical species (e.g. Figure 2).

Clade 1. Gorgoniids with scaphoid sclerites

Gorgoniidae with scaphoid sclerites in the colony surface (Figure 3), 4–10 rows of warts, presence of CHAP in their axes and/or bases, and flattened branches with polyps in series at the edges. Five genera: *Gorgonia*, Caribbean *Pseudopterogorgia* spp. (= *Antillogorgia*) (probably some Indopacific *Pseudopterogorgia*: Williams and Vennam 2001), *Pterogorgia*, *Phyllogorgia*, and *Olindogorgia macgravi* (see Bayer 1961, 1981; and phylogenetic relationships in Sánchez et al. 2003b). Distributed only in the western Atlantic from Bermuda to Brazil, mostly symbiotic (zooxanthellate).

Clade 2. Gorgoniids with capstan sclerites

Gorgoniidae with capstan-derived (short stout spindles: Figure 4) sclerites with symmetrical whorls or girdles (< six rows) of warts and derived forms (e.g. *Leptogorgia* spp. disk

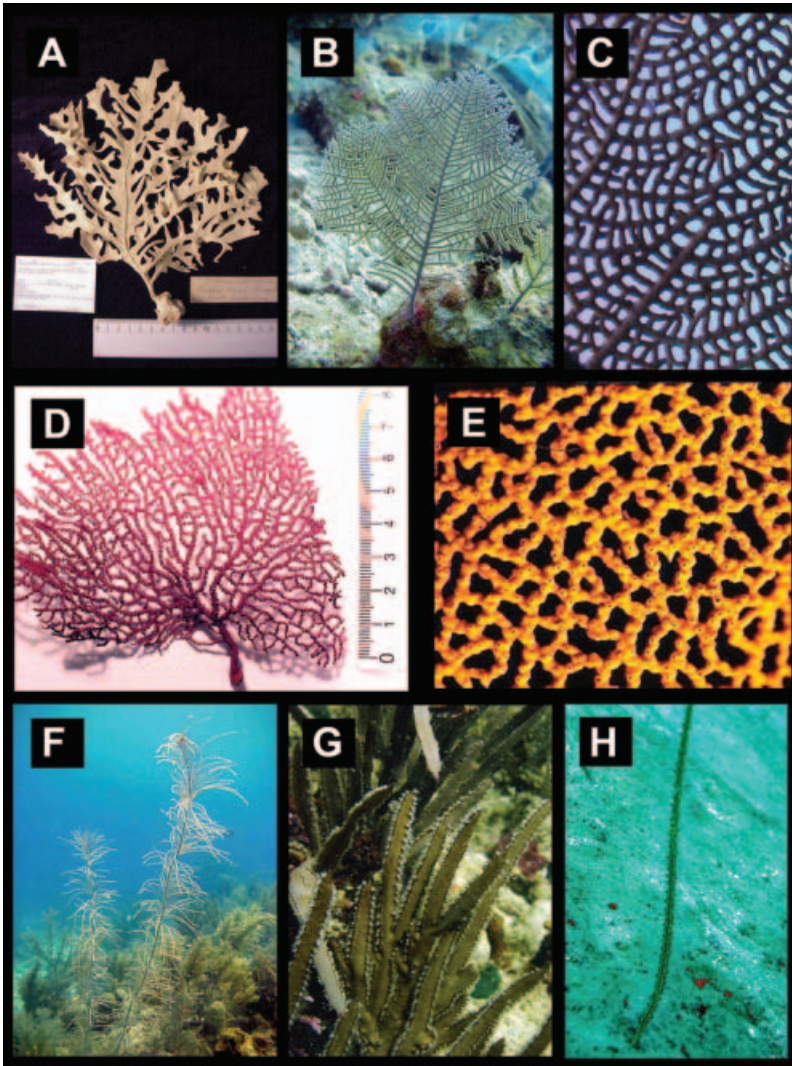


Figure 2. Diverse species of gorgoniids. (A) *Phyllogorgia dillatata* (Brazil, USNM 5252); (B) *Gorgonia mariae* (Carrie Bow Cay, Belize); (C) *G. ventalina* (San Salvador, Bahamas); (D) *Pacifigorgia elegans* (Brazil, USNM 50953); (E) *P. agassizi* (Colombia, Invemar collection); (F) *Pseudopterogorgia* sp. (Carrie Bow Cay, Belize); (G) *Pterogorgia anceps*; (H) *Leptogorgia stheno* (Bocas del Toro, Panamá).

spindles: Figure 4D–F) in the colony surface (Figure 3); polyps placed in series along the branches. Presence of CHAp in their axes and/or bases. *Leptogorgia* (= *Lophogorgia*, see Bayer 1961; and in part Grasshoff 1988; Williams and Lindo 1997), *Eugorgia* (Verrill 1868), *Pacifigorgia* (e.g. Breedy and Guzman 2003), *Phycogorgia* (Bayer 1956), and *Guaigorgia* (Grasshoff and Alderslade 1997). Circumtropically distributed with a few deep-water and subtropical species (Williams and Vennam 2001), mostly not symbiotic with zooxanthellae.

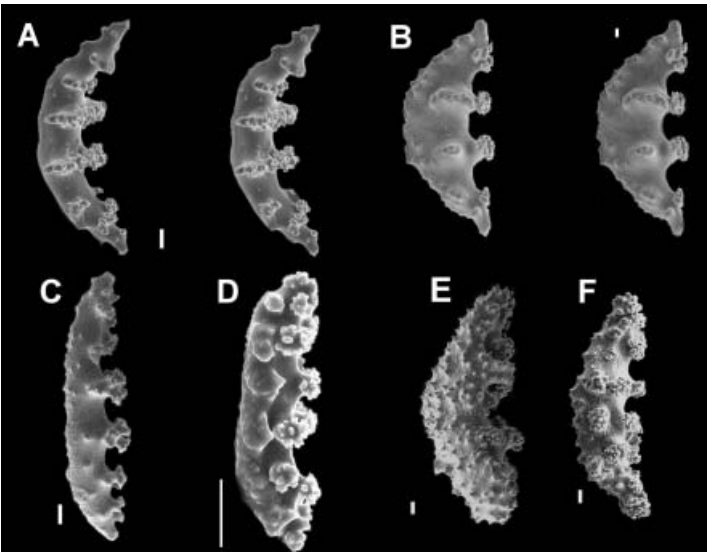


Figure 3. SEM stereopairs and/or images of sclerites from the surface coenenchyme layer of species of gorgoniids with scaphoids sclerites (Clade 1). (A) *Pseudopterogorgia acerosa* (Tobago), stereopair; (B) *Gorgia mariae* Bayer, stereopair (USNM 1007505); (C) *Olindogorgia macgravi* (Bayer); (D) *Pterogorgia anceps* (personal collection); (E, F) *Pterogorgia citrina* (USNM 1007406). Scale bars: 0.01 mm (A, C, E, F); 0.003 mm (B); 0.04 mm (D).

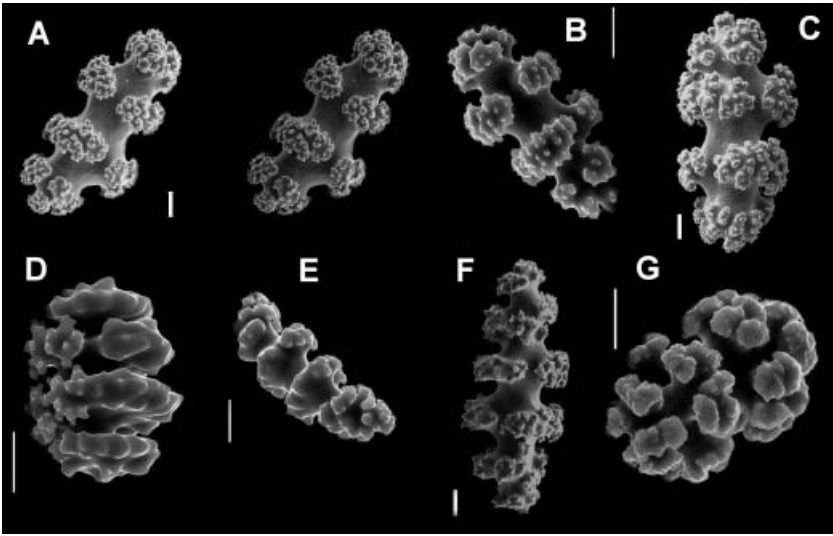


Figure 4. SEM stereopairs and/or images of sclerites from the surface coenenchyme layer of species of gorgoniids with capstan-derived sclerites (Clade 2). (A) *Lophogorgia hebes* Verrill, stereopair (USNM); (B) *Lophogorgia alba* Duchassaing and Michelotti (USNM 57091); (C) *Phycogorgia fucata* (Valenciennes) (USNM 56885); (D) *Eugorgia rubens* Verrill (USNM 50180); (E) *Pseudopterogorgia australiensis* (Ridley) (USNM 80952); (F) *Leptogorgia virgulata* (Lamarck) (USNM 1007414); (G) *Pacifigorgia stenobrochis* (Horn) (Eastern Pacific, personal collection). Scale bars: 0.01 mm (A, C, F, G); 0.02 mm (B, D, E).

Clade 3. *Gorgoniids with asymmetrical spiny sclerites*

Gorgoniidae with long asymmetrical spiny sclerites in the colony surface. Sclerite spines long and robust.

Genus *Muriceopsis* Aurivillius, 1931

Colonies with cylindrical branches and polyps placed irregularly all over the branches (Figure 5A, B). Slightly bent spindles with robust wart ornamentation with conic spindles (Figure 6). Type species *Muriceopsis tuberculata* Aurivillius. Tropical western Atlantic Ocean: *Muriceopsis flavida*, *M. petila*, *M. sulphurea*, and *M. bayeriana* (Sánchez 2001); tropical eastern Atlantic (Africa): *M. tuberculata* (Grasshoff 1992).

***Muriceopsis bayeriana* Sánchez, 2001, nom. nov.**

(Figure 5B)

Muriceopsis bayeri Sánchez 2001, p 167.

Muriceopsis sulphurea: Guzmán and Cortés 1985, p 132.

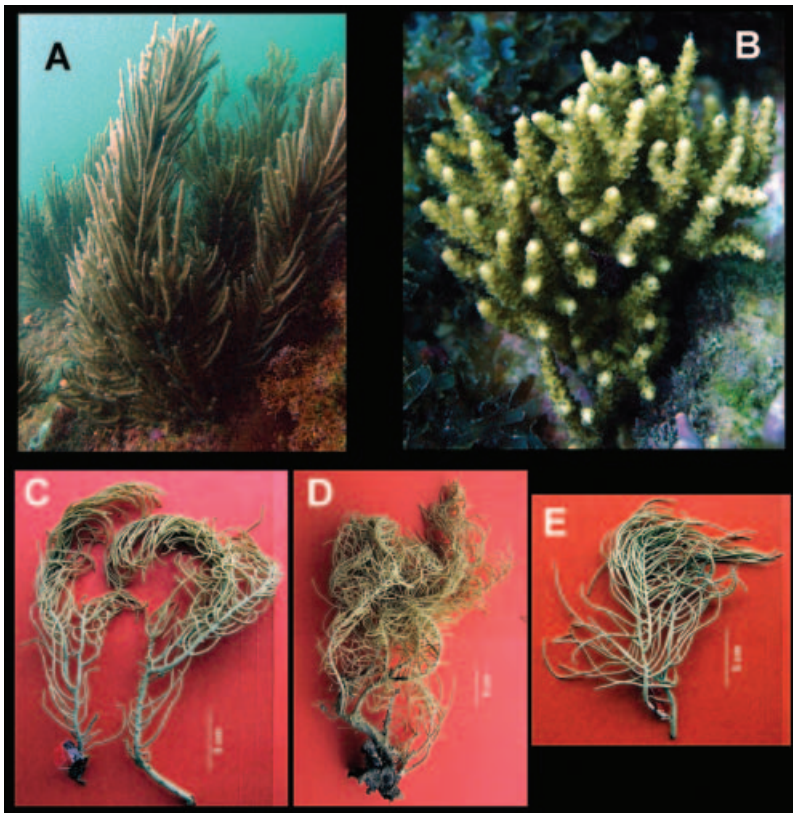


Figure 5. Photographs of gorgonian corals from gorgoniids with asymmetrical spiny sclerites (Clade 3) in their natural environment or dry preserved. (A) *Muriceopsis flavida* (Lamarck) (Caribbean Sea, Bocas del Toro, Panamá; 15 m); (B) *M. bayeriana* Sánchez (Caribbean Sea, Bocas del Toro, Panamá; 2 m); (C, D) *Pinnigorgia platysoma* (Nutting) (Northern Territory Museum, Darwin, Australia; C11674; C12123); (E) *P. flava* (Nutting) (C11661). (C–E) Courtesy: Phil Alderslade.

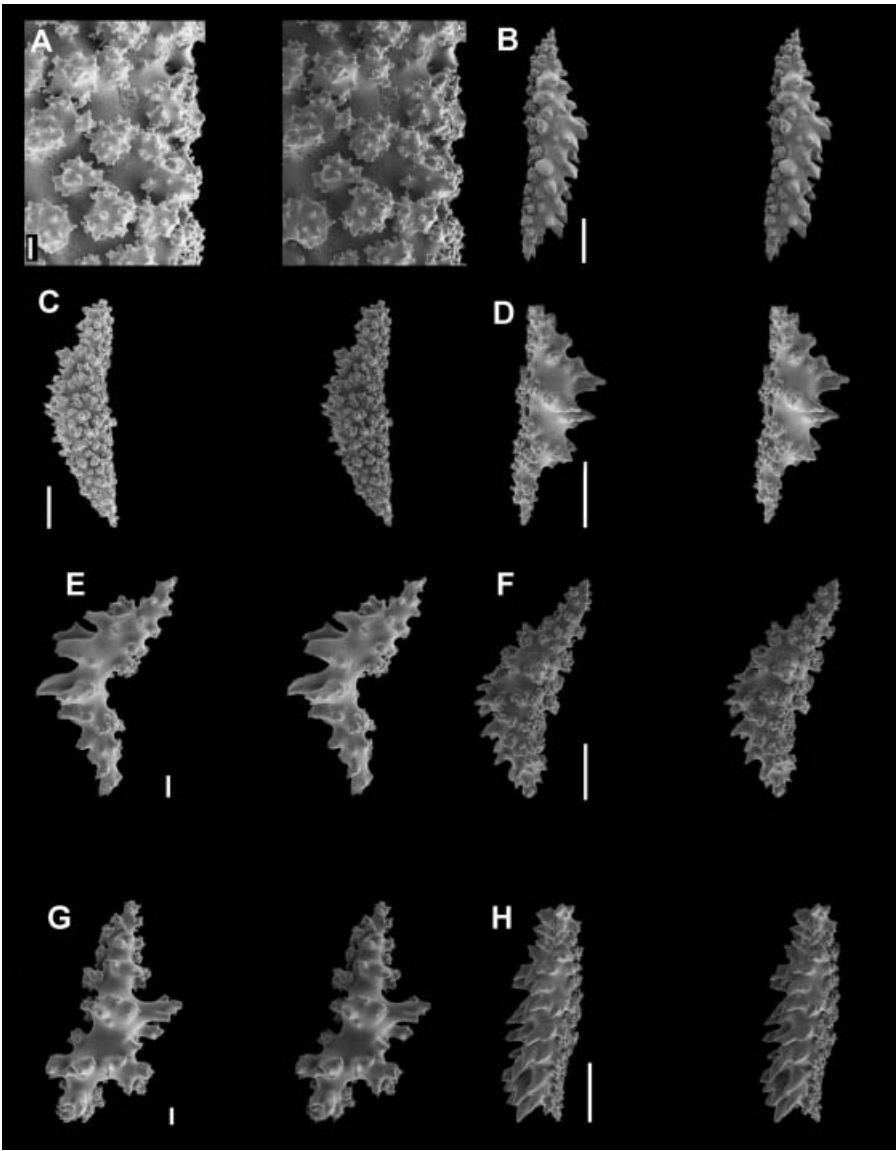


Figure 6. SEM stereopairs of *Muriceopsis sulphurea* Donovan (USNM 5298), Brazil. (A) Detail from (C) of the warts from sclerites of the surface coenenchyme; (B–H) different forms from the sclerites of the surface. Scale bars: 0.01 mm (A); 0.1 mm (B–D, F, H); 0.02 mm (E, G).

Not *Muriceopsis bayeri* (= *Muriceides sceptrum* [Studer, 1890]: Grasshoff 1977, p 49 = *Muriceopsis bayeri* Tixier-Durivault and d'Hondt 1974, p 1404).

The new name *M. bayeriana* is assigned because of the pre-existence of *M. bayeri* Tixier-Durivault and d'Hondt, 1974. Since the names correspond to different species and designations it is important to propose a new name for *M. bayeri* Sánchez (2001), due to the nomenclature rule of priority. It is important to note that *M. bayeri* by Tixier-Durivault

and d'Hondt (1974) was incorrectly described as new as the type specimen belongs to *Muriceides sceptrum* (Studer, 1890) as correctly stated by Grasshoff (1977).

Genus *Pinnigorgia* Grasshoff and Alderslade, 1997
(Figure 7)

Pinnate colonies (Figure 5C–E). Similar diagnostic characters to *Muriceopsis* (Figures 5A, B, 6). Spiny spindles from the surface always bent; spines flattened (Figures 7, 8). Type species *Plexaura flava* Nutting. Indo-Pacific reefs (*Pinnigorgia flava* [Nutting], *P. platysoma* [Nutting], and *P. perroteti* [Stiasny]), Indonesia, Timor Sea, Great Barrier Reef, Micronesia, and the Philippines (Fabricius and Alderslade 2001).

Tobagogorgia hardyi gen. et sp. nov.
(Figures 9, 10)

Holotype: USNM 1093840 (ethanol preserved). Paratypes: USNM 1093841 and 1093842 (dry preserved). All specimens from sand and rubble basin of Man-of-War Bay (off Booby Island coral reef), Charlotteville, Tobago (Trinidad and Tobago), western Atlantic, at 27 m (collected using scuba diving), 16 August 2002.

Diagnostic characters. The genus and species can be distinguished by the presence of both enlarged ornamentation with multiple spines on the convex side of the asymmetrical sclerites from the surface layer (Figure 9B), and irregularly bent spindles in the inner layer (Figure 9D). Cylindrical branches and polyps placed throughout the branch (no rows or

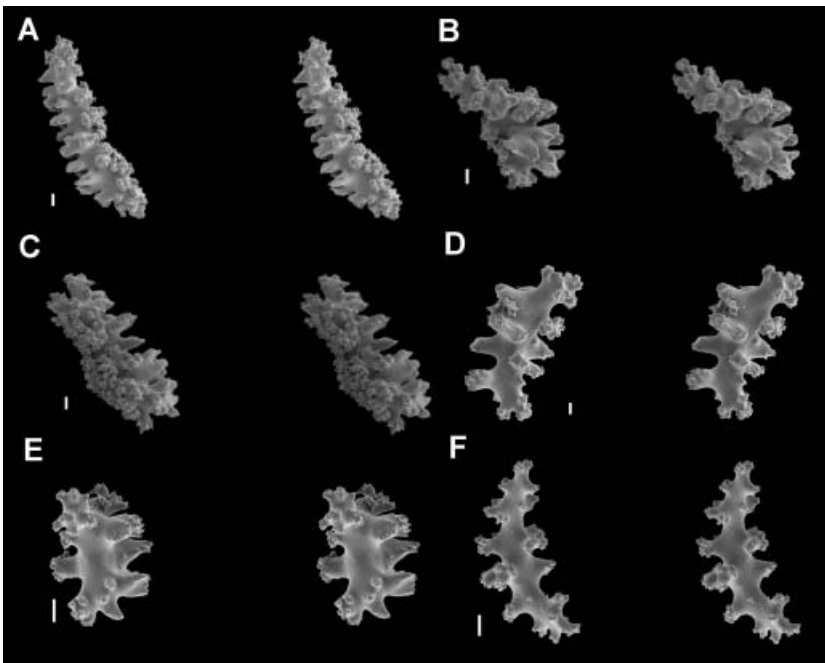


Figure 7. SEM stereopairs of *Pinnigorgia flava* (Nutting). (A–C) C11661, scales; (D–F) *P. USNM 92320*. Scale bars: 0.02 mm (A–C, E, F); 0.01 mm (D).

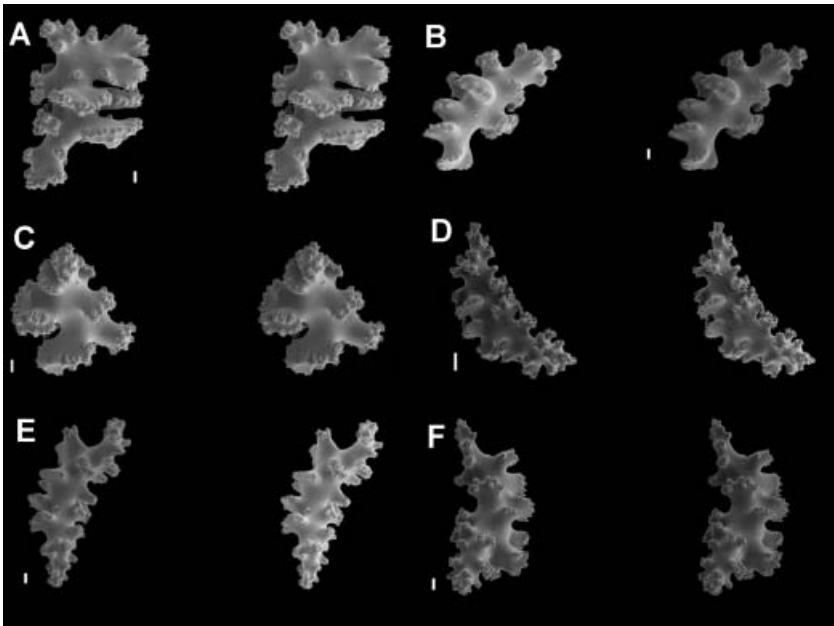


Figure 8. SEM stereopairs of *Pinnigorgia platysoma* (Nutting). (A–C) C12123; (D–F) C11674. Scale bars: 0.01 mm (A–C, E, F); 0.02 mm (D).

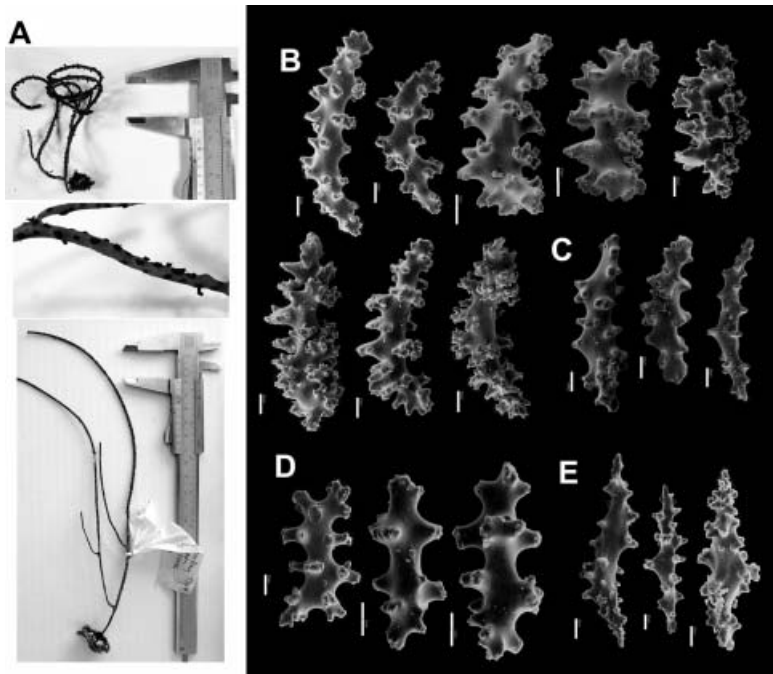


Figure 9. Holotype of *Tobagogorgia hardyi*, gen. et sp. nov. (A) Preserved alcohol colony, detail and a dry colony paratype; (B) spiny bent spindles from the surface layer; (C) polyp sclerites; (D) capstans from the inner layer; (E) spindles from the inner layer. Scale bars: 0.02 mm (B–E).

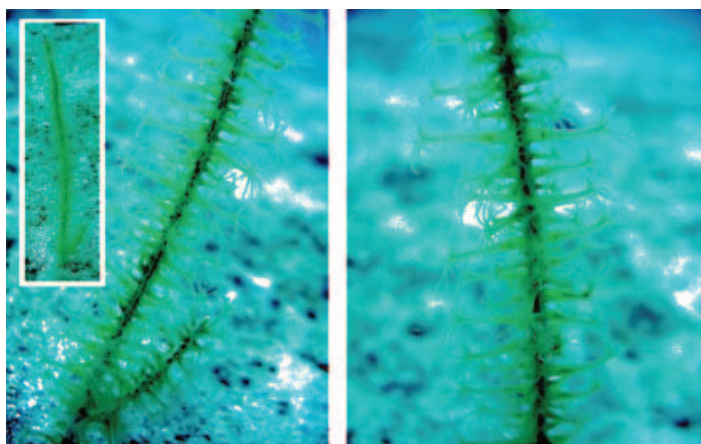


Figure 10. Colony of *Tobagogorgia hardyi*, gen. et sp. nov. off Bobby Island, 30 m, Tobago, Trinidad and Tobago, March 2006. Inset: complete colony.

grooves) can distinguish this genus from *Leptogorgia*, which have analogous sclerite forms. Type species: *Tobagogorgia hardyi* spec. nov.; by monotypy and original designation.

Description. *Tobagogorgia hardyi* has overall morphological features as other gorgoniid octocorals, which include spindles <0.3 mm and complex (many internal geometrical/fractal subwarts) warts (or tubercles) disposed in transverse girdles, usually <0.02 mm wide (Sánchez et al. 2003b). The holotype has slimy, whip-like, and sparsely branched colonies (one main branch and two to three daughter branches) up to 300 mm in length (Figure 9A). Its branches are thin and cylindrical (2–4 mm width). Living colonies are yellow (Figure 10) with even brighter polyps (grey when dry, black in alcohol). The polyps are placed throughout the branches and have robustly ornamented rods 0.12–0.16 mm long (Figure 9C) but do not form any particular structure. No rows or series of polyps are observable. Sclerites are colourless. Surface layer sclerites are composed of bent (asymmetrical) and ornamented spindles 0.1–0.17 mm long (Figures 2A–D, 9B). The inner sclerite layer harbours two different forms: small radiate capstans (0.05–0.16 mm: Figure 9D) and acute irregularly bent ornamented spindles (up to 0.2 mm long: Figure 9E).

Etymology. The new genus is named for the island Tobago and the suffix *gorgia* commonly used for gorgoniid genera (feminine gender). The species is named in honour of Jerry D. “Dave” Hardy, Jr who has dedicated his career to the study of biodiversity in Tobago.

Species comparisons. The molecular results by Aguilar and Sánchez (2007a), which showed that *Tobagogorgia* did not group close to any gorgoniid genera or species, validated a separation of this species as a new genus in spite of its colonies and sclerites resembling those of a number of other valid genera. *Tobagogorgia hardyi* is a gorgoniid species that does not have symmetrically sculptured spindles (e.g. Figure 12). The combined set of sclerites of *Tobagogorgia* (e.g. both asymmetrical and irregularly bent spindles) makes it different from the diagnostic characters of homologous genera such as *Muriceopsis* and *Pinnigorgia* (Figures 5–9). The latter two genera are also profusely branched, including pinnate patterns, whereas *T. hardyi* has one or two branches only. Externally, *T. hardyi* looks similar

to some *Leptogorgia* colonies that also barely branches but it is clear that the sclerites are very different and thus their phylogenetic divergence.

Clade 4. Gorgoniids with long and spiny spindles

Surface coenenchyme with long spindles with multiple (regular or irregular) rows of ornaments, occasionally spiny towards one side. This clade includes the *Leptogorgia ridouri* and *L. sanguinolenta* groups proposed by Grasshoff (1988).

Genus *Filigorgia* Stiasny, 1937

Profusely branched pinnate colonies. Long, slim, and mostly straight asymmetrically spiny sclerites in the colony surface (Figure 11). Surface coenenchyme with straight to slightly bent slim or robust spindles ornate with warts irregularly to zoned around the spindle (Figures 11, 12E, F).

***Filigorgia angolana* (Grasshoff, 1992) com. nov.**

Stenogorgia africana: Kükenthal 1919, p 644.

Filigorgia africana: Stiasny 1939, p 301.

Leptogorgia africana: Grasshoff 1988, p 117.

Leptogorgia angolana Grasshoff 1992, p 76.

***Filigorgia guineensis* (Grasshoff, 1988) comb. nov.**

Leptogorgia guineensis Grasshoff 1988, p 116.

***Filigorgia ridouri* Stiasny, 1937**

Filigorgia ridouri Stiasny 1937, p 307.

Leptogorgia ridouri: Grasshoff 1988, p 116.

***Filigorgia sanguinolenta* (Pallas, 1766) com. nov.**

Gorgonia sanguinolenta Pallas 1766, p 175.

Leptogorgia sanguinolenta: Grasshoff 1988, p 113.

***Filigorgia schoutedeni* (Stiasny, 1939) com. nov.**

Leptogorgia schoutedeni Stiasny 1939, p 106.

Leptogorgia schoutedeni: Grasshoff 1988, p 115.

Why are surface layer sclerites so important?

Since surface sclerites modify colony flexion by preventing compressibility of the outer cortex when they contact each other and help the colony to resist drag forces and flow (Lewis and Von Wallis 1991), a characteristic on which natural selection can act. Their interaction with the environment has produced a great array of forms and these structures are more variable than polyp or axial sheath sclerites (Sánchez et al. 2003b; Sánchez 2005). It is important to note, however, that the function of surface sclerites can be homoplasious and similar trends exist in many genera (e.g. Figure 12E, G). Nonetheless, surface sclerites can be helpful for supra familial classification and provide a better understanding of octocoral phylogeny in general.

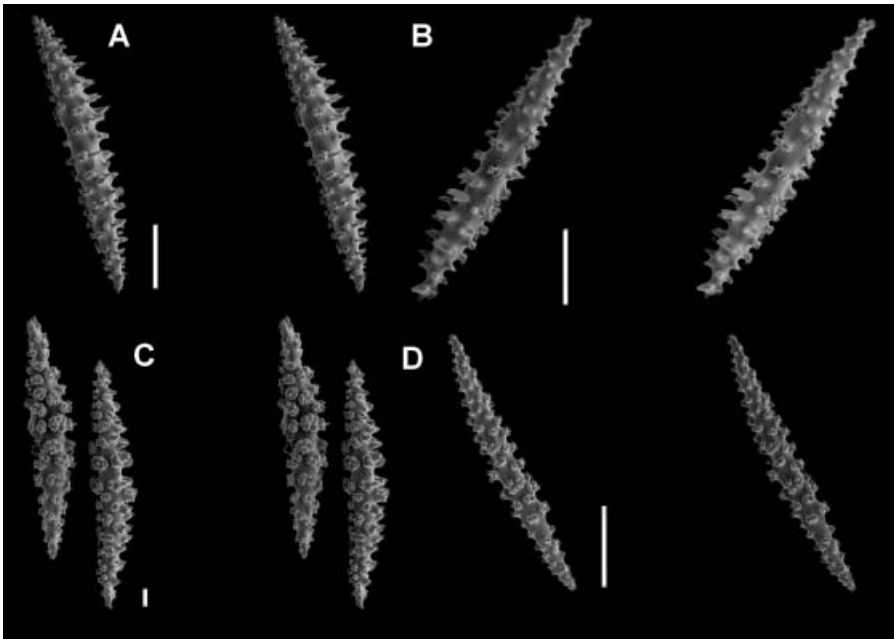


Figure 11. SEM stereopairs of gorgoniids with long and spiny spindles (Clade 4). (A, B) *Filigorgia angolana* (Senckenberg Museum Frankfurt, SMF 3865); (C, D) *F. ridouri* (SMF 5712). Scale bars: 0.1 mm (A, B, D); 0.02 (C).

It has been demonstrated that colonial characters such as branching and overall colony form are highly homoplasious, providing multiple analogous forms within the family Gorgoniidae, which should not be considered as characters for classification (e.g. whip like, sea fan, pinnate, etc.). For example, Bayer (1953) first proposed convergent evolution for gorgonian colony architectures such as sea fans (*Pacifigorgia* spp. and *Gorgonia* spp., Figure 2) and sea leaves (*Phycogorgia* spp. and *Phyllogorgia* spp., Figure 2). Bayer's hypothesis for sea fans has been corroborated with mitochondrial (Sánchez et al. 2003b; Sánchez 2004) and nuclear DNA sequences (Aguilar and Sánchez 2007a, 2007b). Pinnate morphologies such as *Pseudopterogorgia* spp. and *Pinnigorgia* spp. seemed to have evolved their branching morphologies separately (e.g. Figure 1). Surface layer sclerites under the resolution of SEM provided a good character to differentiate gorgoniid clades with very similar external characters.

The molecular contribution

The corroboration of *Filigorgia* as a genus apart from *Leptogorgia* is another example where recent molecular results have improved our understanding of some morphological characters (Fukami et al. 2004). The validation of the genus *Filigorgia* is also supported with previous molecular studies. Mitochondrial DNA sequences from the *mt-S* homolog gene (MSH1) show additional classification problems within the Gorgoniidae (A. LePard and S. France, personal communication). Although focusing on *Leptogorgia*, they found that supposed *Leptogorgia* “outgroups” such as *Pseudopterogorgia*, *Pacifigorgia*, and *Eugorgia* were intermingled with various clades of *Leptogorgia*, which clearly show that some of the African fauna from *Leptogorgia sensu lato* are not reciprocally monophyletic. Williams and

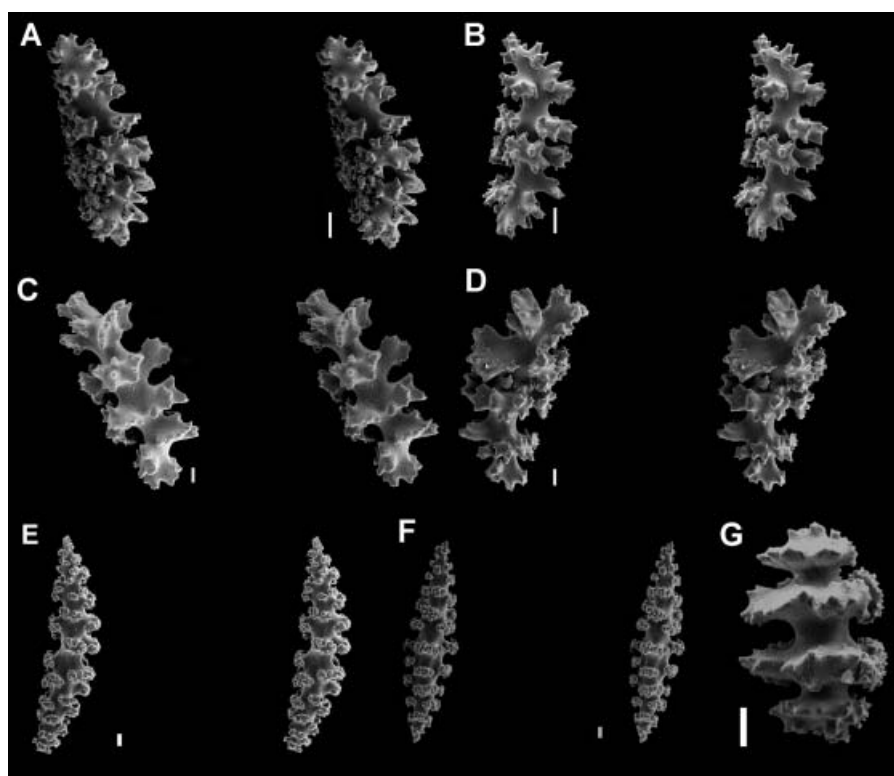


Figure 12. Surface sclerites of several gorgonian corals. (A–D) *Tobagorgia hardyi* new species; (E, F) *Filigorgia schoutedeni* (Stiasny); (G) *Leptogorgia virgulata* Linnaeus. (A–F) SEM stereopairs. Scale bars: 0.02 mm.

Lindo (1997) provided a detailed comparison of spindles of *Leptogorgia* spp. with several gorgoniid genera showing that scaphoid sclerites are not the best character to differentiate gorgoniid genera due to their high similarity, particularly with Indo-Pacific species of *Pseudopterogorgia*. Although it was not a goal of this paper, it was clearly noticed that Pacific and Atlantic *Pseudopterogorgia* spp. surface sclerites were not homologous (e.g. Figures 3A versus 4E), and deserve further study.

Finally, it is important to note that some genera assigned to the Gorgoniidae need careful revision (hopefully both taxonomical and molecular) in order to be unambiguously assigned to this family, such as in the case of *Hicksonella* and *Rumphella* (Grasshoff and Alderslade 1997), as well as *Adelogorgia* and *Eunicella*, whose sclerites are not likely homologous to the species presented here. In addition, there are a number of plexaurid genera such as *Swiftia* (Goldberg 2001) and *Plexaurella* that, with recent molecular analyses (Sánchez et al. 2003b; Wirshing et al. 2005; McFadden et al. 2006), have been found to resemble some gorgoniids.

Conclusions

Four monophyletic clades based on morphological synapomorphies from surface sclerites, that were compatible with at least one of the recent molecular phylogenies using ITS2 sequences and their predicted RNA secondary structures, were distinguished based on surface sclerites: (1) a derived clade, containing gorgoniids with scaphoid sclerites,

including the reef fauna from the western Atlantic (*Gorgonia*, *Pseudopterogorgia* [= *Antillogorgia*], *Pterogorgia*, *Phyllogorgia*, *Olindogorgia*, etc.); (2) a related group, with capstan-derived sclerites, including genera with small capstan, simple or disk-spindle, sclerites such as *Pacifigorgia*, *Phycogorgia*, *Eugorgia*, *Guaiaigorgia*, and *Leptogorgia* (= *Lophogorgia*); (3) a clade, with asymmetrical spiny sclerites, including the Atlantic genus *Muriceopsis*, the Indopacific *Pinnigorgia* together with the distant single species from the new genus and species *Tobagogorgia hardyi*; finally (4) a likely basal clade, gorgoniids with long and spiny spindles, including some African genera such as *Filigorgia angolana*, *F. rodouri*, *F. guineensis*, *F. schoutedeni*, and *F. sanguinolenta* (all species previously classified as *Leptogorgia* spp.).

The results presented here are not by any means definitive. Additional taxa and further tests of relatedness and monophyly can easily be done using the approach used here. Octocorals are often difficult to identify or classify because of a lack of reliable sets of diagnostic characters. The inclusion of molecular characters coupled with SEM provides a replicable approach.

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