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Resurrection of the octocorallian genus *Antilloorgia* for Caribbean species previously assigned to *Pseudopterogorgia*, and a taxonomic assessment of the relationship of these genera with *Leptogorgia* (Cnidaria, Anthozoa, Gorgoniidae)

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Abstract

The genus *Antilloorgia* Bayer, 1951 is resurrected for species of zooxanthellate, pinnately-branched gorgonians with sclerite complements that include well-developed scaphoids, and inhabit coral reefs of the western Atlantic, particularly from the Bahamas through the Caribbean. These species were previously assigned to the Indo-Pacific genus *Pseudopterogorgia* Kükenthal, 1919 by Bayer, 1958 (thus making *Antilloorgia* a junior synonym of *Pseudopterogorgia*), but are shown here to warrant generic separation. Both morphological as well as molecular evidence is provided to justify distinguishing the two genera. Taxonomic relationships to a third gorgoniid genus, *Leptogorgia*, are also discussed.

Key words: Gorgoniid octocorals, tropical western Atlantic, Indo-West Pacific, taxonomic assessment

Introduction

The gorgonian genus *Pseudopterogorgia* Kükenthal, 1919 as presently recognized, comprises two geographically distinct groups of species (Williams & Vennam, 2001: 71), and is comprised of at least twenty shallow-water species in tropical latitudes of the Indo-West Pacific and western Atlantic Oceans.

The genus was originally described by Kükenthal (1919: 854) and applied to four Indo-West Pacific gorgoniid species (from Sri Lanka, Indonesia, the Torres Straits, and the Philippines), with loosely-pinnate to irregular, non-anastomosing branches and with some sclerites that are curved, scaphoid-like spindles.

Since 1958, the name *Pseudopterogorgia* has frequently been used for a group of coral reef-inhabiting species of the tropical western Atlantic that have pinnate/plumose non-anastomosing branches, with some scaphoid sclerites (Bayer, 1961: 224), that show some superficial similarities to the Indo-Pacific species. This period of name application can be found in widespread and commonly used published works regarding octocoral systematics, marine ecology, and natural products biochemistry (among other fields in biology), as well as in field guides and popular publications. Examples include Bayer, 1958; Cadena and Sánchez, 2010; Human and DeLoach, 2002; and Rodríguez et al., 2009. In addition, the three genera (*Antilloorgia* Bayer, 1951, *Leptogorgia* Milne Edwards & Haime, 1857, and *Pseudopterogorgia* Kükenthal, 1919) have provided the sources of important chemical compounds regarding natural products biochemistry. Examples of such relevant research include Fenical, 1987 (*Antilloorgia*), Gerhart and Coll, 1993 (*Leptogorgia*), and Vanisree et al., 2001 (*Pseudopterogorgia*).

It is here considered that the Indo-Pacific and Western Atlantic species formerly allocated to *Pseudopterogorgia* actually represent two distinct genera, *Pseudopterogorgia* for azooxanthellate forms, invariably with colored sclerites, and with curved spindles having differentiated tuberculation on the convex vs. concave sides, which often represent more-or-less distinct scaphoids; and *Antilloorgia* for zooxanthellate species, mostly with colorless sclerites, but infrequently with some that are colored pale yellow or violet, and with conspicuous or well-developed scaphoids. Therefore, the genus *Antilloorgia* is here resurrected to encompass eleven presently-recognized species of the tropical western Atlantic, while *Pseudopterogorgia* is restricted to nine presently-recognized species of the Indo-West Pacific (Williams & Vennam, 2001: 87).

The genus *Olindagorgia* was erected by Bayer (1981: 922) to accommodate the Brazilian *Pseudopterogorgia marcgravi* Bayer, 1961, which was distinguished from other western Atlantic gorgoniid species by having small colonies (< 10 cm high), sparse and loosely pinnate branching, a sclerite complement that includes scaphoids, and with polyps retractile into conspicuous hemispherical calyces. In the absence of a detailed comparison of relevant material, we choose here to retain *Olindagorgia* and *Antillogorgia* as separate genera.

Affinities of *Antillogorgia* and *Pseudopterogorgia* with the widespread gorgonian genus *Leptogorgia* are covered in the Results and Discussion section.

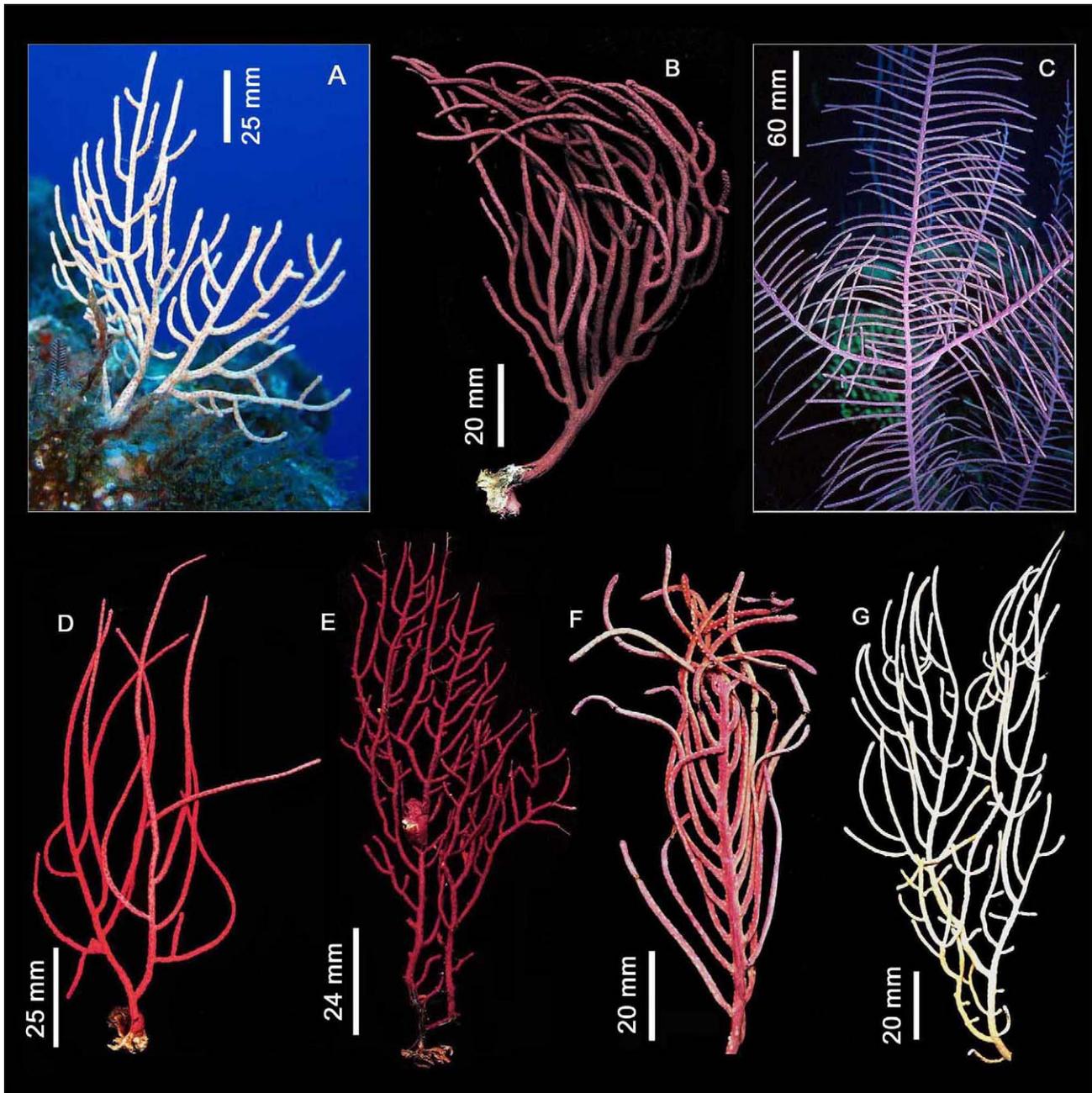


FIGURE 1. Photographs of gorgonian colonies: A. Underwater photograph of *Leptogorgia alba*, Cocos Island, Costa Rica; B. *Leptogorgia rigida* (CAS 097129), Gulf of California, Mexico; C. Underwater photograph of *Antillogorgia bipinnata*, Hunting Cay, Belize; D. *Pseudopterogorgia fredericki* (CAS 118507), Arabian Sea, India; E. *Pseudopterogorgia rubrotincta* (CAS 155043), Bay of Bengal, India; F. *Antillogorgia acerosa* (CAS 164615), Cancun, Mexico; G. *Leptogorgia alba* (CAS 107712), Cocos Island, Costa Rica.

Materials and methods

The material examined in this study is housed in the Department of Invertebrate Zoology and Geology at the California Academy of Sciences, San Francisco. Underwater photographs were taken during field operations by the first author (Cocos Island, Costa Rica, February 2007; Belize, February 1998), and Charles Delbeek, California Academy of Sciences (Curacao, Netherlands Antilles). Sclerites were isolated and examined using the protocol of Williams and Mattison (2006). Type specimens of *Pseudopterogorgia fredericki* Williams & Vennam, 2001, *P. australiensis* (Ridley, 1884), and *P. torresia* (Wright & Studer, 1889) were previously examined, described, and illustrated by Williams and Vennam (2001: 73–88).

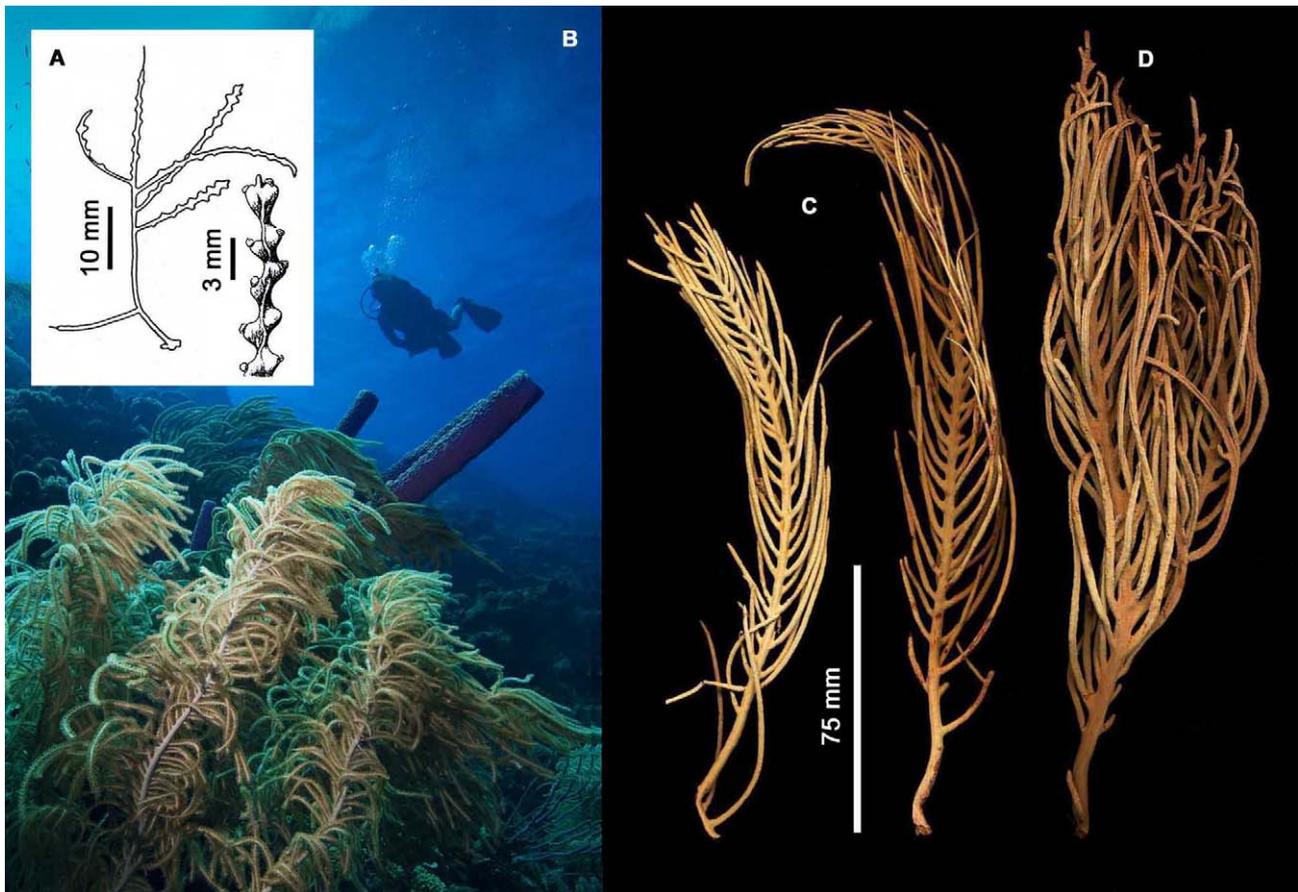


FIGURE 2. A. Tropical western Atlantic gorgoniids: A. *Olindagorgia marcgravii*; after Bayer, 1961 (256, FIGURE 82 a–b) as *Pseudopterogorgia marcgravii*; B. *Antillogorgia* sp., *in situ*, Sea Aquarium Reef, Curacao, Netherlands Antilles, August 2011, approximately 15 m depth, scale not given. Photo courtesy J. Charles Delbeek, Steinhart Aquarium, California Academy of Sciences; C. *Antillogorgia elisabethae* (CAS 098183, two specimens); D. *Antillogorgia acerosa* (CAS 078026).

Material examined. *Antillogorgia acerosa* (Pallas, 1766), CAS 078026, Caribbean Sea, West Indies, Puerto Rico SW coast, San Cristobal off La Parguera, 1 m depth, 6 June 1991, coll. G.C. Williams, one whole colony dry-preserved. *Antillogorgia acerosa*, CAS 164615, Mexico, Yucatan Peninsula, Cancun, 10.6 m depth, 14 January 2002, coll. C. Sánchez, one partial specimen wet-preserved 75% ethanol. *Antillogorgia acerosa*, CAS 097785, Florida, depth not recorded, date not recorded, collector not recorded, two specimens dry-preserved. *Antillogorgia elisabethae* Bayer, 1961, CAS 098183, Caribbean Sea, U.S. Virgin Islands, St. John, Lameshur Bay area, washed up on beach after Hurricane Hugo, September/October 1989, coll. G.C. Williams, two partial colonies dry-preserved. *Antillogorgia* sp. 1, CAS 100661, Puerto Rico, reefs off the southwest, <30 m depth, 1967–1969, coll. John T. Rees, one specimen dry-preserved. *Antillogorgia* sp. 2, CAS 164598, Mexico, Yucatan Peninsula, Cancun, Isla Mujeres, 10.6 m depth, 14 January 2002, coll. C. Sánchez, 3 specimens wet-preserved 75% ethanol. *Eunicea mammosa* Lamouroux, 1816, CAS 164596, Mexico, Yucatan Peninsula, Cancun, Isla Mujeres, 10.6 m depth, 14 January 2002, coll. C. Sánchez, 3 specimens wet-preserved 75% ethanol. *Leptogorgia alba*

(Duchassaing & Michelotti, 1864), CAS 107712, Costa Rica, Cocos Island, 6-24 m depth, 12 December 1995, coll. C. Arneson, one partial colony wet-preserved 75% ethanol. *Leptogorgia rigida* Verrill, 1864, CAS 097129, Mexico, Gulf of California, Bahia de Las Palmas, 4.6 m depth, 19 November 1972, coll. AJ Ferreira, one whole colony wet-preserved 75% ethanol. *Pseudopterogorgia fredericki*, CAS 118507, India, Arabian Sea, Karnatak, Saint Mary Isles, 6-8 m depth, 31 October 2001, coll. S.Y Kanat, two whole colonies wet-preserved 75% ethanol. *Pseudopterogorgia rubrotincta* (Thompson & Henderson, 1905), CAS 155043, India, Bay of Bengal, between Pondicherry and Cape Comerin, 15 July 2001, coll. S.A. Fernando, one whole colony wet-preserved 75% ethanol. Molecular analysis. All of the molecular bench work and data analysis were carried out in the Genomics Sequencing Lab, the Computer Lab, and the PhyloCluster of the Center for Comparative Genomics at the California Academy of Sciences, San Francisco.

DNA Extraction. The total genomic DNA was extracted from the following specimens: CAS 097785, CAS 100661, CAS 118507, CAS 155043, CAS 164596, CAS 164598 (Table 1). The DNeasy Blood & Tissue Kit (QIAGEN) was used and the manufacturer's Animal Tissues Spin-Column Protocol (QIAGEN) was applied. Roughly 1.5–2 cm of gorgonian fragment was obtained and chopped into small pieces to facilitate the tissue digestion. The concentration of the extracted DNA was then estimated using a micro-volume spectrophotometer NanoDrop 2000c (Thermo Scientific) and visually checked via gel electrophoresis.

TABLE 1. Specimens used for sequencing analysis and the GenBank accession numbers.

Taxa	Voucher no.	Collection Locality	Collection Date	GenBank Accession Number	
				16S-ND2	ND4L-mtMutS
ORDER ALCYONACEA					
[HOLAXONIA]					
Plexauridae					
<i>Eunicea mammosa</i>	CAS 164596	Yucatan Peninsula, MEXICO	14 Jan 2002	JX152774	JX152767
Gorgoniidae					
<i>Antillogorgia acerosa</i>	CAS 097785	Florida, USA	n/a	JX152769	JX152763
<i>Antillogorgia</i> sp. 1	CAS 100661	reefs of the SW, PUERTO RICO	1969	JX152770	JX152764
<i>Antillogorgia</i> sp. 2	CAS164598	Yucatan Peninsula, MEXICO	14 Jan 2002	JX152771	JX152765
<i>Pseudopterogorgia fredericki</i>	CAS 118507	Arabian Sea, INDIA	n/a	JX152772	JX152766
<i>Pseudopterogorgia rubrotincta</i>	CAS 155043	Bay of Bengal, INDIA	20 Jan 2001	JX152773	JX152768

PCR Amplification. Invitrogen™ 5U/ìl Recombinant *Taq* DNA Polymerase was used (0.25 ìl) in a 25 ìl PCR (polymerase chain reaction) with 2 ìl of DNA extraction template, where 15.25 ìl of Millipore water (Direct-Q® 3 Water Purification system), 2.5 ìl of 10X Invitrogen™ PCR Buffer, 1 ìl of 50 mM MgCl₂, 0.5 ìl of 10 mM dNTPs, 1.5 ìl of 10 mg/ml BSA (Bovine Serum Albumin), and 1 ìl of 10 ìM primer for each direction were added to the reaction. The DNA fragments of mitochondrial gene NADH-dehydrogenase subunit 2 (*ND2*) were amplified using the primers from McFadden *et al.* 2004—16S647F: 5'-ACACAGCTCGGTTTCTATCTACCA-3', ND21418R: 5'-ACATCGGGAGCCACATA-3' and the DNA fragments of octocoral-specific mitochondrial *mtMutS* homolog (*mtMutS*) were amplified using the primers from France and Hoover 2002—42599F: 5'-GCCATTATGGTTAACTA TTAC-3' and from Sánchez *et al.* 2003—Mut-3458R: 5'-TSGAGCAAAGCCACTCC-3'. A Bio-Rad C1000™ thermal cycler was used following the PCR protocols: 94°C for 2 min, 94°C for 30 s, 50°C–51°C for 30 s, 72°C for 45 s, 30 cycles, followed by 10 min extension at 72°C.

For specimens that weren't amplified by 16S647F & ND21418R (*ND2*) and ND42599F & Mut-3458R (*mtMutS*), new internal and external primers were designed from the complete genome of *Pseudopteroorgia bipinnata* mitochondrion (GenBank accession No. NC_008157, Medina, M. *et al.* 2006). The new designed internal primers are as follows, for *mtMutS*—MSH3010F-Pb (modified from McFadden *et al.* 2011): 5'-GGACAAAGGTTGGACTGTTATAAT-3', MSH3010R-Pb: 5'-ATTATAACAGTCCAACCTTTGTCC-3'; for *ND2*—16S846F: 5'-GCGGATAGCCCCTGGYATAC-3', 16S124F-Pb: 5'-CTACTATGTTGGACACAGGC-3', 16S124R-Pb: 5'-GCCTGTGTCCAACATAGTAG-3', ND2407R-Pb-new: 5'-CGCAACCAAACAGGAACAAYC-3'. The new external primers for *ND2* are as follows, 16S588F: 5'-ACCTGAGGTTGGTCTGTTCG-3', ND21457R: 5'-CGATAGATAATAGCGCAGCTACC-3'. Different PCR protocols were used when different primer combinations were chosen (Table 2).

TABLE 2. Primers used for amplifying and sequencing *ND2* and *mtMutS* fragment, the symbols by the primer names and PCR protocols indicate different primer pairs that were used in this study. Primer names printed in bold indicate the original primer pairs used in the referenced papers; the PCR protocols used in this study are also shown in bold.

Primer	Sequence	PCR protocol	Source
External			
16S647F	5'-ACACAGCTCGGTTTCTATCTACCA-3'	51°C, 30:30:45, 30×	McFadden <i>et al.</i> 2004
ND21418R	5'-ACATCGGGAGCCCACATA-3'		McFadden <i>et al.</i> 2004
16S588F*	5'-ACCTGAGGTTGGTCTGTTCG-3'	50°C, 30:30:45, 30x*	This study
ND21457R*	5'-CGATAGATAATAGCGCAGCTACC-3'	54°C, 30:30:45, 30x*	This study
ND42599F ^o	5'-GCCATTATGGTTAACTATTAC-3'	52°C, 30:30:45, 35× 51°C, 30:60:60, 30x ^o	France and Hoover 2002
Mut-3458R [▲]	5'-TSGAGCAAAAGCCACTCC-3'	51°C, 30:60:45, 30x [▲]	Sánchez <i>et al.</i> 2003
Internal			
16S846F*	5'-GCGGATAGCCCCTGGYATAC-3'	55°C, 30:30:45, 30x*	This study
16S124F-Pb*	5'-CTACTATGTTGGACACAGGC-3'	54°C, 30:30:45, 30x*	This study
16S124R-Pb*	5'-GCCTGTGTCCAACATAGTAG-3'	50°C, 30:30:45, 30x*	This study
ND2407R-Pb-new*	5'-CGCAACCAAACAGGAACAAYC-3'	55°C, 30:30:45, 30x*	This study
MSH3010F-Pb [▲]	5'-GGACAAAGGTTGGACTGTTATAAT-3'	51°C, 30:60:45, 30x [▲]	Modified from McFadden <i>et al.</i> 2011
MSH3010R-Pb ^o	5'-ATTATAACAGTCCAACCTTTGTCC-3'	51°C, 30:60:60, 30x ^o	Modified from McFadden <i>et al.</i> 2011

PCR Purification. When ideal DNA fragments were amplified, the PCR products were then purified to obtain clean sequences using USB[®] ExoSAP-IT[®] (Exonuclease I and Shrimp Alkaline Phosphatase), according to the USB[®] ExoSAP-IT[®] PCR Product Cleanup protocol. A Bio-Rad C1000[™] thermal cycler was used for incubation at 37°C for 30 min to degrade any remaining primers or nucleotides, and at 80°C for 15 min to inactivate the ExoSAP-IT reagent.

Cycle Sequencing. After the PCR products were purified, the cycle sequencing was carried out using the BigDye[®] Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). The 10 μ l reaction contained 0.75 μ l of BigDye v3.1 (contained fluorescent dye labeled ddNTPs which acts as a sequence terminator), 1.5 μ l of 5X BigDye Sequencing Buffer, 2 μ l of purified PCR products, 0.3 μ l of 10 μ M primer and Millipore water. A Bio-Rad MyCycler[™] Thermal Cycler was used, and the stepped elongation time (STeP) cycle sequencing protocol from Platt *et al.* 2007 was programmed: an initial 60 s incubation at 96°C; followed by a total of 25 cycles of reaction—15 cycles of 96°C for 10 s, 50°C for 5 s, 60°C for 75 s; and 5 cycles of 96°C for 10 s, 50°C for 5 s, 60°C for 90 s; and 5 cycles of 96°C for 10 s, 50°C for 5 s, 60°C for 2 min.

Ethanol Precipitation and Sequencing. To prepare for DNA sequencing, ethanol precipitation was performed following the Ethanol/EDTA Precipitation protocol by Applied Biosystems. In order to eliminate the surplus dye terminators and concentrate and recover the nucleic acid from the aqueous solution, salt 125 mM di-Na EDTA (pH 8.0) was added to the post-cycle sequencing products to neutralize the negative charge of the nucleic acids, and 100% EtOH was added to precipitate both salt and DNA; after centrifugation with an Eppendorf 5810R centrifuge, 70% EtOH was added to wash away the salt yet precipitate only the DNA pellets. After additional centrifugation,

the pellets were left to dry, and 10 μ l of Hi-Di™ Formamide (Applied Biosystems) was added for resuspension purposes then heated for 2 min at 95°C and placed on ice for 5 min. Finally, the samples were loaded on Applied Biosystems 16-capillary 3130xl Genetic Analyzers for sequencing reaction. All sequences are deposited in GenBank (Table 1).

Sequence Alignment. The raw sequence data were first viewed using Sequencing Analysis Software v5.2 (Applied Biosystems) to determine the quality of the sequence signals; then sequences of both directions with high signal strength and high resolution were assembled into contigs and trimmed using Sequencher™ 4.10.1 (Gene Codes Corporation). The contigs were then aligned using ClustalX 2.1 (Larkin *et al.*, 2007).

Phylogenetic Analysis. By using Geneious Pro 5.3.3 (Biomatters Ltd.) to assemble the sequences with the complete mitochondrial genome of *Pseudopterogorgia bipinnata* mitochondrion (GenBank accession No. NC_008157, Medina, M. *et al.* 2006) and *Acanella eburnea* (GenBank accession No. NC_011016, van der Ham *et al.* 2009), the alignments were partitioned into 10 blocks: three codon positions of *ND4L*, three codon positions of *mtMutS*, *16S* and three codon positions of *ND2*. The best-fit models of nucleotide substitution for all partitions were estimated under Akaike Information Criterion (AIC) by MrModeltest 2.3 (Nylander 2004). The best-fit models selected for the three codon positions of *ND4L* are as follows—codon position 1: HKY model, proportion of invariable sites (I) = 0; codon position 2: F81 model (I = 0) and codon position 3: K80 model (I = 0). For the three codon positions of *mtMutS*—codon position 1: K80 model (I = 0); codon position 2 and 3: HKY model (I = 0). For *16S*: K80 model (I = 0). For the three codon positions of *ND2*—codon position 1 and 3: GTR model (I = 0); codon position 2: F81 model (I = 0). Based on the models chosen above, the Bayesian inference was made by using MrBayes-3.1.2 (Ronquist & Huelsenbeck 2003) with 5×10^7 generations (burnin = 12500 generations) of Markov chain Monte Carlo (MCMC) analysis, and one consensus tree was constructed. The data partitions of *ND4L*, *mtMutS*, *16S* and *ND2* were implemented in RAxML v7.2.8 (Stamatakis *et al.* 2008), and the GTR+G+I model with 50000 bootstrap replications were applied to construct the maximum likelihood tree. The maximum parsimony tree with 50000 bootstrap replications was generated using PAUP version 4.0 beta (Swofford, 2003).

Results and Discussion

Taxonomic History. Ehrenberg (1834: 368–369) established the new genus *Pterogorgia* and allocated to it the western Atlantic species *Gorgonia acerosa* Pallas, 1766 and *G. anceps*. Pallas, 1766

Kükenthal (1919: 854, 920) described a new genus *Pseudopterogorgia* for four gorgoniid species from the tropical eastern Indian and western Pacific Oceans with C-shaped or scaphoid-like sclerites as well as other spindles, and designated *P. australiensis* as the type species. On the same page he allocated *Pterogorgia anceps* to the genus *Xiphigorgia*, as *X. anceps*, which he later reiterated (1924: 351–358). In that same work (pages 355–357), he also provided a key to and brief descriptions of the four *Pseudopterogorgia* species—*P. australiensis*, *P. luzonica* Kükenthal, 1919, *P. oppositipinna* (Ridley, 1888), and *P. pinnata* (Nutting, 1910).

Bayer (1951: 97) introduced the generic name *Antillogorgia* as a separate genus from *Pterogorgia* Ehrenberg, 1834, and designated *Gorgonia acerosa* as the type species. At that time, two of the species separated from *Pterogorgia* and placed in *Antillogorgia* were *A. acerosa* and *A. americana* (Gmelin, 1791). *Antillogorgia* was reserved for zooxanthellate species of the Caribbean region with pinnate to plumose branches and terminal branches (“twigs”) round in cross-section. Species of *Pterogorgia*, on the other hand, although also zooxanthellate and from the same region, differ by having mostly lateral branching with branches strongly flattened or triangular to square in cross-section. Included here by Bayer (1951: 96–97) were *P. anceps* and *P. citrina* (Esper, 1792). This was reiterated by Bayer (1953: 105), in which *Antillogorgia* was viewed as an exclusively West Indian genus of five species with pinnate to plumose branching in one plane, and sclerites of scaphoids and spindles. Bayer (1956: 212) retained recognition of the genus *Antillogorgia*, for species restricted to the West Indies with slender scaphoids and closely pinnate branches that do not anastomose, but subsequently (1958: 394) considered *Antillogorgia* inseparable from *Pseudopterogorgia*, and relegated *Antillogorgia* to a junior synonym. This was later reiterated by Bayer (1961: 224), and included twelve tropical western Atlantic species of *Pseudopterogorgia*.

Bayer (1981: 922) erected the genus *Olindagorgia* for the previously-described *Pseudopterogorgia marcgravi*. The generic separation was justified by the small, loosely-pinnate to unbranched colonies with polyps retractile into distinct calices in *Olindagorgia*, in contrast to the pinnate/plumose branching, without distinct polyp calices, in *Pseudopterogorgia* (Fig. 2A).

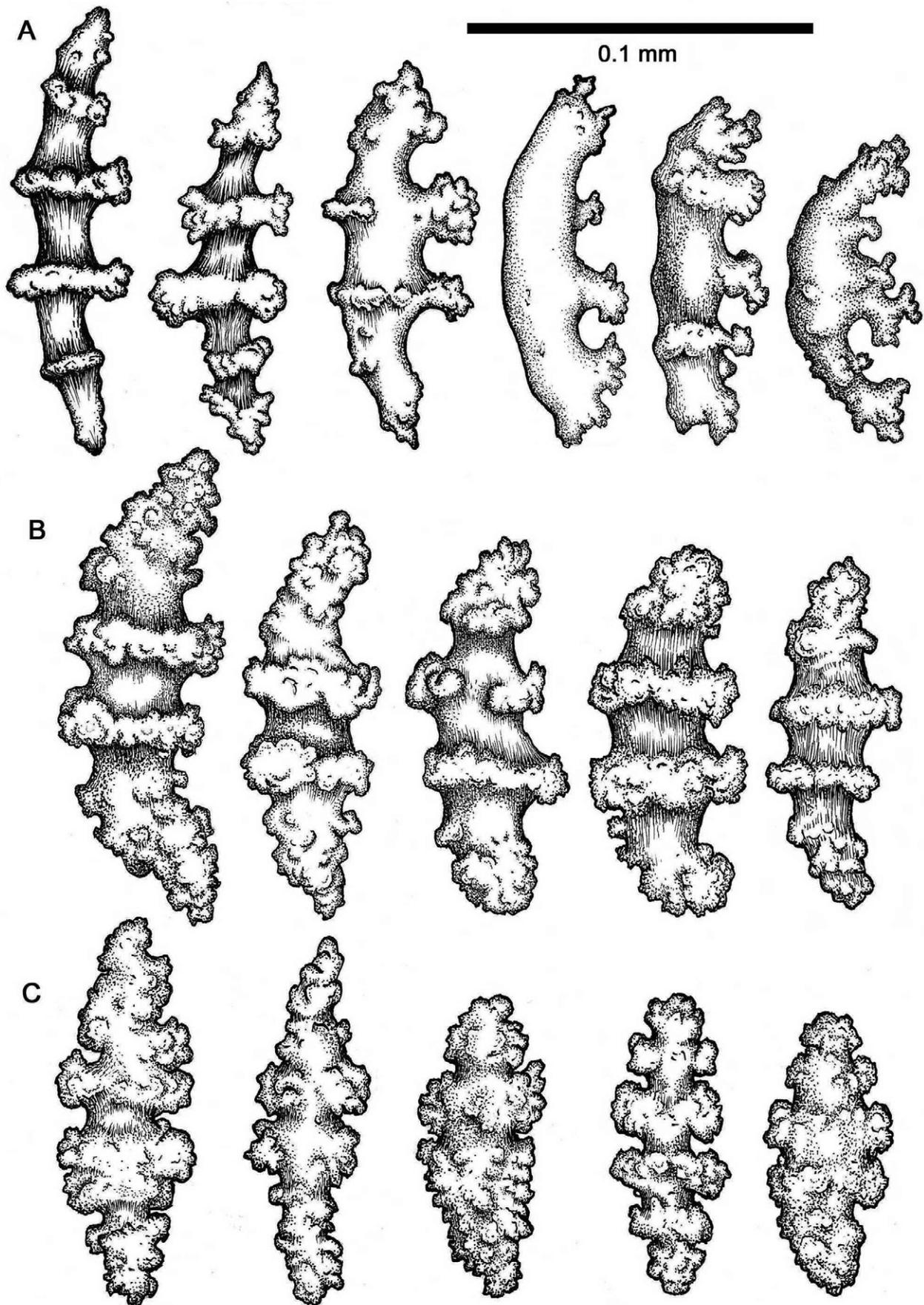


FIGURE 3. Curved coenenchymal sclerites, scaphoids and spindles: A. *Antillogorgia acerosa* (CAS 164615); B. *Pseudopterogorgia rubrotincta* (CAS 155043); C. *Leptogorgia alba* (CAS 107712).

Fabricius and Alderslade (2001: 220) stated, "...most Caribbean species of *Pseudopterogorgia* seem to be zooxanthellate and may represent a different genus." Grasshoff and Alderslade (1997: 23) list five genera of gorgoniid octocorals from Indo-Pacific reefs: *Guaiagorgia* Grasshoff & Alderslade, 1997, *Hicksonella* Nutting, 1910, *Pinnigorgia* Grasshoff & Alderslade, 1997, *Rumphella* Bayer, 1955, and *Pseudopterogorgia*. Regarding the latter genus they state, "*Pseudopterogorgia* is represented in the Indo-Pacific by several species which were, however, rarely found; the genus is well-known from the Caribbean region, where about ten species are among the most frequent shallow water gorgonians In the Indo-Pacific (gorgoniid) genera sclerites are colourless, except in *Pseudopterogorgia* where they are yellow or red.

Recent molecular studies show a divergence between Indo-Pacific and western Atlantic species, thus the two geographically disparate species groups represent two genera (present study and K Samimi-Namin & LP van Ofwegen, pers. comm.).

Nine species are currently recognized as valid for *Pseudopterogorgia* and eleven for *Antillogorgia*.

Two lines of evidence (both morphological and molecular) are here presented as justification for the resurrection of *Antillogorgia* and the recognition of two distinct and disparate genera—*Pseudopterogorgia* in the Indo-West Pacific, and *Antillogorgia* in the tropical western Atlantic.

Comparative Morphology (Figs. 1–3). Descriptions. *Antillogorgia acerosa*, CAS 078026, total specimen length 270 mm. Branching dense, pinnate, more-or-less planar. Terminal branches long, sinuous, ascending, mostly 50–120 mm long, somewhat flattened, 2.0 mm wide by 1.5 mm thick. Sclerites are spindles and scaphoids mostly with acute ends, 0.08–0.14 mm in length; mostly colorless, a few light yellow to pale violet. Convex surfaces of some scaphoids that are not tuberculated are finely echinulate instead. Color of dry-preserved colony light tan-white (Fig. 2D). *Antillogorgia elisabethae*, CAS 098183, total length of specimens 200 mm and 250 mm. Branching plumose, planar. Terminal branches cylindrical, mostly alternately arranged, 20–30 in number on each side of colony, strongly curved upwards, 15–70 mm long, 1.5–2.0 mm in diameter. Sclerites are spindles and scaphoids, 0.07–0.13 mm long, with varying development of tuberculation on convex surfaces, or smooth to finely echinulate; mostly colorless, a few violet. Color of dry-preserved colonies pale yellow-white (Fig. 2C). *Antillogorgia acerosa*, CAS 164615, total specimen length 310 mm. Branching pinnate to plumose, planar. Lower part of main stem more-or-less cylindrical, upper part of main stem flattened: 1.5 mm thick by 3.0 mm wide. Lateral branches vary in length from 20–80 mm, approximately 22 in number per side, opposite to sub-alternate, slightly flattened to somewhat quadrilateral in cross-section. Sclerites are spindles and scaphoids, 0.07–0.14 mm long, scaphoids with varying development of tuberculation on the convex surfaces, from conspicuous to absent (Fig. 3A). Sclerites mostly colorless, a few light yellow to pale violet. Color of wet-preserved colony dull violet with cream-white retracted polyps (Fig. 1F). *Leptogorgia alba*, CAS 107712, total specimen length 160 mm. Branching lateral. Branches planar, cylindrical to slightly flattened. Terminal branches 10–50 mm long, 1.0–1.5 mm in diameter, curving upwards. Sclerites mostly colorless spindles with two girdles and elongated spindles, 0.03–0.11 mm in length (Fig. 3C). Color of wet-preserved colony white (Figs. 1A, G). *Leptogorgia rigida*, CAS 097129, total specimen length 170 mm. Branching lateral, more-or-less in one plane. Branches cylindrical, 1.5–3.0 mm in diameter, 15–45 mm in length, curving upwards. Sclerites are predominantly red, robust eight radiates and elongated spindles, 0.03–0.11 mm long. Color of wet-preserved colony dark red-purple throughout (Fig. 1B). *Pseudopterogorgia fredericki*, CAS 118507; total specimen length 125 mm. Branching lateral, relatively sparsely branched. Terminal branches cylindrical, ascending, somewhat sinuous, 12–85 mm long, 1.0–1.5 mm in diameter, terminal tips acute. Sclerites pale red, elongated spindles and scaphoids, 0.06–0.20 mm in length. The scaphoids have tuberculation on both the convex and concave sides. Color of the colonies rose red (Fig. 1D). *Pseudopterogorgia rubrotincta*, CAS 155043, total specimen length 135 mm. Branching lateral and copious. Terminal branches relatively short, 6–26 mm long, 1.0–1.5 mm in diameter, terminal tips acute. Sclerites deep red, elongated spindles and scaphoids, 0.08–0.15 mm long. The scaphoids have tuberculation on both the convex and concave sides (Fig. 3B). Color of colony dark red (Fig. 1E).

Molecular Results (Fig. 5). The total alignment length for *ND2* mtDNA sequences was 758 bp and for *mtMutS* mtDNA sequences was 831 bp from the 6 gorgonian taxa examined herein, which generated a concatenated matrix of 1589 bp in length. Of the 1589 characters, 1443 (91%) characters are constant, 87 (5%) variable characters are parsimony-uninformative and 59 (4%) characters are parsimony-informative. Base frequencies were A = 0.283, C = 0.179, G = 0.210, T = 0.328.

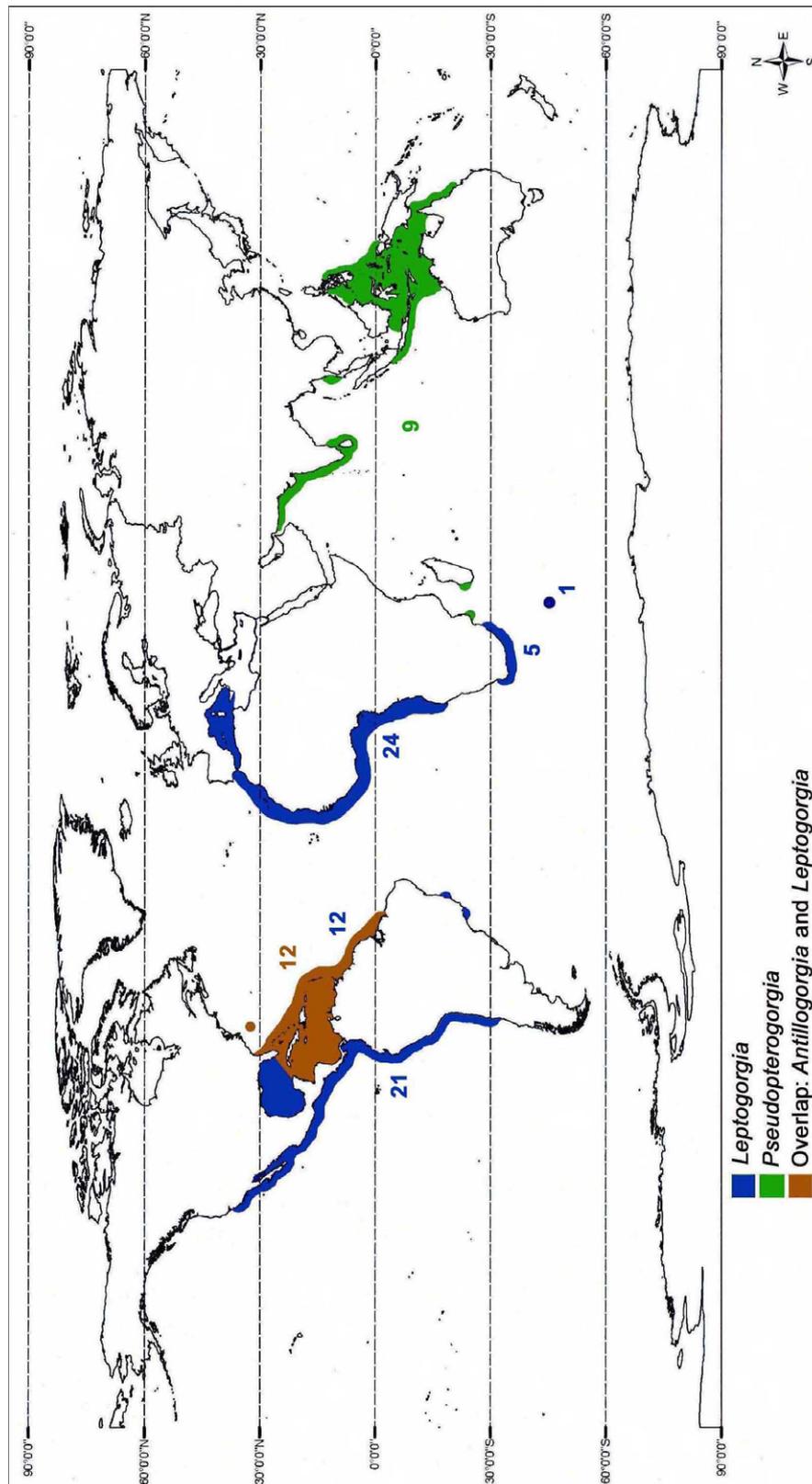


FIGURE 4. World map showing distributions of the genera *Antillogorgia*, *Leptogorgia*, and *Pseudopterogorgia*. Numbers represent numbers of species per region: *Antillogorgia* of the western Atlantic (12); *Leptogorgia* of the eastern Pacific (21); *Leptogorgia* of the western Atlantic and Gulf of Mexico (12); *Leptogorgia* of the eastern Atlantic and Mediterranean (24); *Leptogorgia* of southern Africa (5); *Leptogorgia* of the subantarctic (1); and *Pseudopterogorgia* of the Indo-West Pacific (9). References: Bayer (1961), Breedy & Guzman (2007, 2008), Breedy & Cortés (2011), Devictor & Morton (2010), Grasshoff (1988, 1992), Guzman & Breedy (2008), Samimi-Namin & Ofwegen (pers. comm.), Williams (1992a, 1992b), Williams & Lindo (1997), Williams & Vennam (2001).

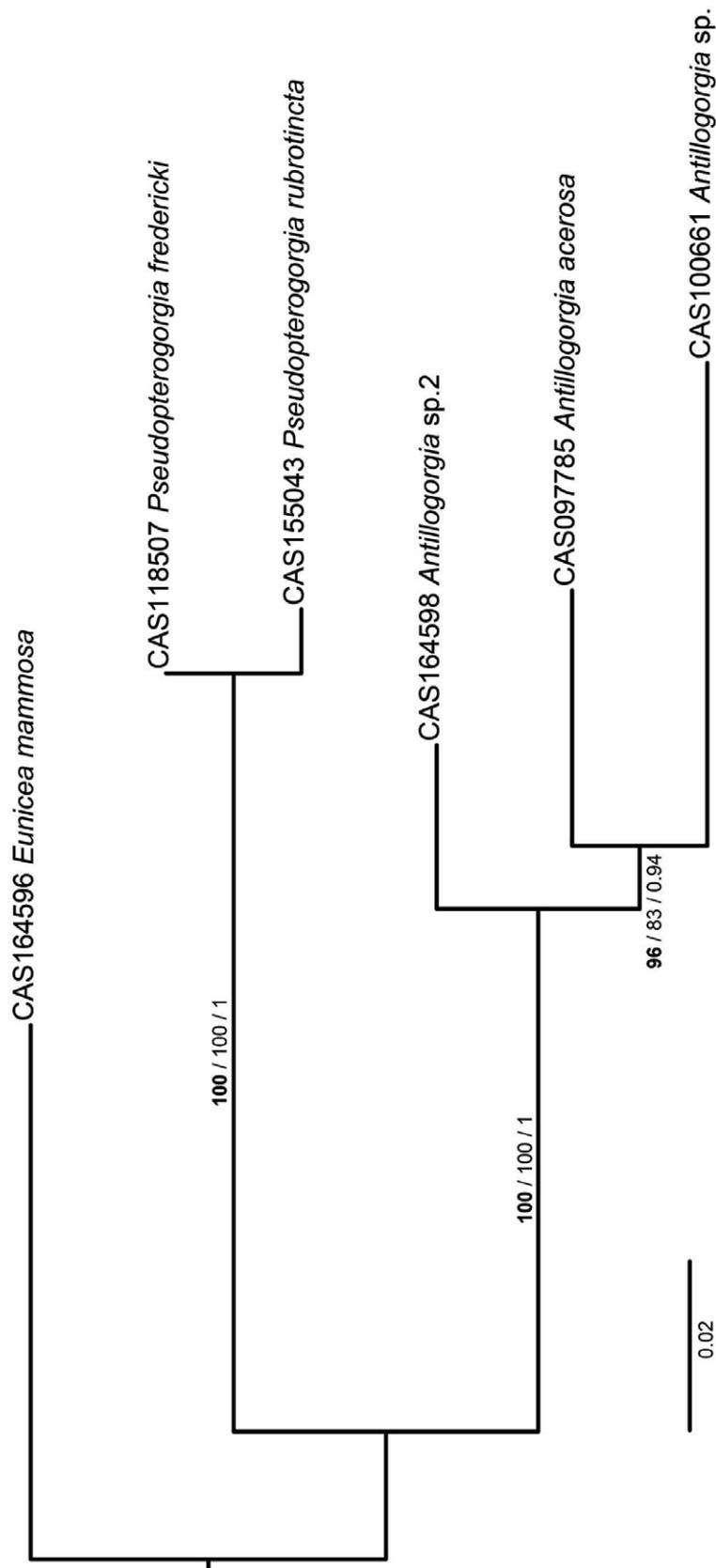


FIGURE 5. Maximum likelihood analysis inferred from concatenated sequences of *ND2* and *mtMutS* genes (1589 bp) with combined bootstrap support values from maximum likelihood (bold type), maximum parsimony and Bayesian posterior probabilities, respectively, for *Pseudopterogorgia* from the Indo-West Pacific and *Antillogorgia* from the tropical western Atlantic. Outgroup is the plexaurid gorgonian *Eunicea mammosa*. Scale bar = 0.02 substitutions/site.

The phylogenetic analysis was made using the concatenated matrix of *ND2* and *mtMutS* with maximum likelihood (final ML optimization likelihood: -2984.62), maximum parsimony (consistency index = 0.9739, homoplasy index = 0.0261, retention index = 0.9481) and Bayesian inference approaches. All trees from the three analyses revealed essentially identical topologies, the maximum likelihood tree (Fig. 5) shows two distinct clades representing *Pseudopterogorgia* from the Indo-West Pacific and *Antillogorgia* from the tropical western Atlantic. Both of these clades have robust bootstrap support values of 100% regarding maximum likelihood and parsimony analyses, as well as Bayesian posterior probabilities of 1, to demonstrate the distant relationship of these two different genera, given the results that are in concordance with the morphological evidences.

The taxonomic problem. The idea that the genus *Pseudopterogorgia* may in fact represent two separate genera is not a new one. Several authors have recognized the problematic taxonomic status of Indo-Pacific vs. tropical western Atlantic species of *Pseudopterogorgia* (in varying degrees of detail) for at least the past fifteen years. Included here are Williams and Lindo (1997: 517–518), Williams and Vennam (2001: 90–93), Fabricius and Alderslade (2002: 220), and Sánchez (2007: 496). The latter reference considers the Caribbean *Pseudopterogorgia* spp. as synonymous with *Antillogorgia*, as well as being phylogenetically sister to *Gorgonia* spp.

Williams and Lindo (1997: 517) first considered the situation of taxonomic uncertainty regarding the three genera *Antillogorgia*, *Leptogorgia*, and *Pseudopterogorgia* (see distribution map, Fig. 4). Williams and Vennam (2001: 91, 93) added five species to the Indo-Pacific *Pseudopterogorgia*, including four new combinations and one new species, thus recognizing a total of nine. In addition, due to the superficial similarity of *Pseudopterogorgia* to the Atlantic and eastern Pacific genus *Leptogorgia*, they proposed four possible taxonomic scenarios to be considered for future investigation as follows—(1) to maintain the two genera as presently recognized (*Leptogorgia* and two geographically disparate groups of taxa of *Pseudopterogorgia*); (2) to consider the two genera as congeneric (*Leptogorgia* by priority); (3) to consider *Leptogorgia* and the Indo-Pacific *Pseudopterogorgia* taxa as congeneric (*Leptogorgia* would have priority), while *Antillogorgia* would apply to the zooxanthellate West Indian taxa with well-developed scaphoids, or (4) to recognize three separate genera (*Leptogorgia*, *Pseudopterogorgia* for Indo-Pacific azooxanthellate taxa with scaphoids, and *Antillogorgia* for the zooxanthellate West Indian taxa with scaphoids).

Of the four possible scenarios regarding the taxonomic status of the three gorgoniid genera *Antillogorgia*, *Leptogorgia*, and *Pseudopterogorgia* provided by Williams and Vennam (2001: 93), it is here proposed that the last scenario represents the present situation best. This is to recognize three separate genera—*Leptogorgia* for Atlantic and eastern Pacific species, *Pseudopterogorgia* for Indo-West Pacific taxa, and *Antillogorgia* for the western Atlantic zooxanthellate species.

Further research to more clearly ascertain the relationship between the two genera *Leptogorgia* and *Pseudopterogorgia* will determine if they represent valid separate genera or if they are in fact congeners.

Resurrection of *Antillogorgia* Bayer, 1951. It is here considered that sufficient differences between the Indo-West Pacific and western Atlantic species of the presently-recognized genus *Pseudopterogorgia* warrant generic separation. The generic name *Antillogorgia* is therefore resurrected and hereby considered a valid taxon based on the following differentiation of three gorgoniid genera (Table 3).

Antillogorgia (Figs. 1C, F; 2B–D; 3A; 4, 5)—Zooxanthellate; branching pinnate to plumose; sclerites mostly colorless; spindles and scaphoids; coral reefs; western Atlantic; anti-inflammatory terpenoids (Fenical, 1987). Species included: *A. acerosa* (*Gorgonia acerosa* Pallas, 1766 = type species), *A. albatrossae* Bayer, 1961, *A. americana* (Gmelin, 1791), *A. bipinnata* (Verrill, 1864), *A. blanquillensis* (Stiasny, 1941), *A. elisabethae* Bayer, 1961, *A. hummelincki* Bayer, 1961, *A. hystrix* Bayer, 1961, *A. kallos* (Bielschowsky, 1918), *A. navia* Bayer, 1961, *A. rigida* (Bielschowsky, 1929).

Leptogorgia (Figs. 1A, B, G; 3C; 4)—Azooxanthellate; branching variable-filiform, dichotomous, lateral, or pinnate; sclerites mostly colored; spindles; non-coral reef environments; primarily Atlantic and eastern Pacific; terpenoids (Gerhart & Coll 1993). Approximately 63 species: 12 western Atlantic (Bayer 1961; Devictor & Morton 2010); 24 eastern Atlantic and Mediterranean (Grasshoff 1988, 1992); 6 southern Africa and subantarctic (Williams 1992a & b, Williams & Lindo 1997); and 21 eastern Pacific (Breedy & Cortés 2011; Breedy & Guzman 2007, 2008, Guzman & Breedy 2008).

Pseudopterogorgia (Figs. 1D, E; 3B; 4, 5)—Azooxanthellate; branching lateral to loosely pinnate; sclerites mostly colored; spindles and scaphoids; non-coral reef environments; Indo-West Pacific; anti-bacterial ceramides (Vanisree et al., 2001). Species included: *P. australiensis* (*Leptogorgia australiensis* Ridley, 1884 = type species),

P. formosa (Nutting, 1910), *P. fredericki* Williams & Vennam, 2001, *P. luzonica* Kükenthal, 1919, *P. oppositipinna* (Ridley, 1888), *P. pinnata* (Nutting, 1910), *P. thomassini* (Tixier-Durivault, 1972), *P. torresia* (Wright & Studer, 1889), *P. rubrotincta* (Thomson & Henderson, 1905).

TABLE 3. Comparative characters for three gorgoniid genera (modified from Williams & Lindo, 1997: 517).

	<i>Antilloorgia</i>	<i>Leptorgia</i>	<i>Pseudopterorgia</i>
Type of branching	pinnate/plumose	variable: filiform, lateral, dichotomous, pinnate	lateral or pinnate
Amount of branching	abundant	variable	sparse to abundant
Anastomosis	absent	absent to	absent
occasional			
Scaphoids	well-developed	absent	weakly-developed to well-developed
Largest tubercles on C-shaped sclerites	concave side	convex side	concave side
Distribution	Tropical western Atlantic	Panamic/Atlantic/ southern Africa	Indo-West Pacific
Zooxanthellae	zooxanthellate	azooxanthellate	azooxanthellate

The character comparison of zooxanthellate (with zooxanthellae) vs. azooxanthellate (without zooxanthellae) has been used as one of various characters to unify a particular group of species into a single genus of octocorals. Alderslade (2000: 242) states, “The presence and absence of zooxanthellae in soft corals represents a major point (or points) of evolutionary divergence, and is certainly a character that must be considered of generic level significance.” The approximately forty-eight shallow-water Indo-Pacific gorgonian genera treated in Fabricius and Alderslade (2001) are described as either zooxanthellate or azooxanthellate. However, a few genera of octocorals are now known to include both zooxanthellate and azooxanthellate species. Included here are only one gorgonian genus—*Junceella* (Williams, et al., 2010), and two pennatulacean genera—*Virgularia*, and *Cavernularia* (original observation).

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