

## New records of the genera *Leptogorgia*, *Pacifigorgia* and *Eugorgia* (Octocorallia: Gorgoniidae) from Ecuador, with a description of a new species

María del Mar Soler-Hurtado<sup>1,2</sup>, Annie Machordom<sup>1</sup>, Jesús Muñoz<sup>3,4</sup>,  
Pablo J. López-González<sup>2</sup>

<sup>1</sup>Dpto. Biodiversidad y Biología Evolutiva. Museo Nacional de Ciencias Naturales (MNCN-CSIC), 28006 Madrid, Spain. E-mail: [mar.s.hurtado@gmail.es](mailto:mar.s.hurtado@gmail.es); [annie@mncn.csic.es](mailto:annie@mncn.csic.es)

<sup>2</sup>Biodiversidad y Ecología de Invertebrados Marinos, Facultad de Biología, Universidad de Sevilla, 41012, Sevilla, Spain. E-mail: [pjlopez@us.es](mailto:pjlopez@us.es)

<sup>3</sup>Real Jardín Botánico (CSIC), Plaza de Murillo 2, 28014 Madrid, Spain. E-mail: [jmunoz@rjb.csic.es](mailto:jmunoz@rjb.csic.es)

<sup>4</sup>Centro de Biodiversidad y Cambio Climático, Universidad Tecnológica Indoamérica, Quito, Ecuador.

**Summary:** New records of the genera *Leptogorgia*, *Pacifigorgia* and *Eugorgia* (Octocorallia: Gorgoniidae) on the coast of Ecuador are reported. These new records redefine the current known limit of distribution of these species on the eastern Pacific coast (from southern California to Chile). Some of these species are reported for the first time since their original description. The newly collected specimens allow for the measurement of the variability of several morphological characters, from colonial to sclerite levels. Additionally, *Pacifigorgia machalilla* n. sp. is described and compared with its closest relatives. Morphological differentiation among related species is supported by genetic divergence estimated from an extended barcode of MutS + Igr + COI.

**Keywords:** Gorgoniidae; eastern Pacific; distribution; mtMutS; COI; barcode; Igr.

**Nuevos registros de los géneros *Leptogorgia*, *Pacifigorgia* y *Eugorgia* (Octocorallia: Gorgoniidae) en Ecuador, con la descripción de una especie nueva**

**Resumen:** Se han obtenido nuevos registros para los géneros *Leptogorgia*, *Pacifigorgia* y *Eugorgia* (Octocorallia: Gorgoniidae) en la costa de Ecuador. Estos nuevos registros redefinen el límite actual conocido en la distribución de estas especies en la costa del Pacífico Oriental (desde el sur de California hasta Chile). Algunas de estas especies han sido registradas por primera vez desde su descripción original. Las nuevas muestras recogidas permiten medir la variabilidad de los caracteres morfológicos, desde el nivel de colonia hasta el de esclerito. Además, se describe la especie *Pacifigorgia machalilla* n. sp., y se compara con sus congéneres más relacionados. Las diferenciaciones morfológicas encontradas entre estas especies, están apoyadas por la divergencia genética estimada a partir del “código de barras” ampliado, formado por los genes MutS + Igr + COI.

**Palabras clave:** Gorgoniidae; este del Pacífico; distribución; mtMutS; COI; “código de barras”; Igr.

**Citation/Como citar este artículo:** Soler-Hurtado M.M., Machordom A., Muñoz J., López-González P.J. 2016. New records of the genera *Leptogorgia*, *Pacifigorgia* and *Eugorgia* (Octocorallia: Gorgoniidae) from Ecuador, with a description of a new species. *Sci. Mar.* 80(3): 369-394. doi: <http://dx.doi.org/10.3989/scimar.04392.14A>

**LSID:** [urn:lsid:zoobank.org:pub:A6373513-5FFE-4D2E-B130-98C239C0EDF3](http://urn:lsid:zoobank.org:pub:A6373513-5FFE-4D2E-B130-98C239C0EDF3)

**Editor:** X. Turon.

**Received:** December 18, 2015. **Accepted:** June 1, 2016. **Published:** September 25, 2016.

**Copyright:** © 2016 CSIC. This is an open-access article distributed under the terms of the Creative Commons Attribution (CC-by) Spain 3.0 License.

### INTRODUCTION

The octocorals are found in marine habitats ranging from intertidal to abyssal waters and are distributed from the Arctic to the Antarctic (Bayer 1961). The

gorgonian octocorals are one of the best-represented taxonomic groups in sublittoral marine ecosystems, are ecologically important and are the dominant macrofaunal group on many tropical reefs (Sánchez et al. 2003, Williams and Breedy 2004). The study of the

eastern Pacific gorgonian octocorals, specifically in Ecuador, has not matched the intensity and number of publications dedicated to Caribbean species (see Bayer 1981). Despite important contributions by authors such as Breedy and Guzmán (2002, 2007), Williams and Breedy (2004) and Breedy et al. (2009) in the eastern Pacific, the knowledge on the gorgonian fauna of Ecuador is far from complete (but see Bielschowsky 1929 and Soler-Hurtado and López-González 2012). Four gorgoniid genera (Gorgoniidae) were previously reported in the eastern Pacific, *Phycogorgia* Milne-Edwards and Haime, 1850, *Leptogorgia* Milne-Edwards and Haime, 1857, *Eugorgia* Verrill, 1868 and *Pacifigorgia* Bayer, 1951. The genus *Leptogorgia*, with about 60 valid species (27 species in the eastern Pacific) is one of the most frequent genera in the shallow water communities of the eastern Pacific (Breedy and Guzmán 2007), with a wide distribution from southern California to Chile. This genus is also present in the Caribbean, western and eastern South African coasts, the eastern Atlantic and the Mediterranean Sea, and one species is known from the sub-Antarctic (Williams and Lindo 1997). The genus *Pacifigorgia* is geographically confined to the Pacific coast of tropical America, with the exception of *Pacifigorgia elegans* (Milne-Edwards and Haime, 1857) from the tropical western Atlantic. *Pacifigorgia* includes about 36 recognized species distributed throughout the eastern tropical Pacific region (Breedy and Guzmán 2002, 2003, 2004, Williams and Breedy 2004, Guzmán and Breedy 2011). The genus *Eugorgia*, which includes 16 species, is considered exclusive to the eastern Pacific (from southern California to Peru) (Breedy and Guzmán 2013). Finally, the genus *Phycogorgia*, with only one species, *Phycogorgia fucata* (Valenciennes, 1846), is distributed along the west coast of Central and South America (Bayer 1953).

The aim of this report is to present new information derived from material of the genera *Eugorgia*, *Leptogorgia* and *Pacifigorgia* collected in Ecuador. We expand the known distribution of some species in the eastern Pacific and describe new morphological variability for several taxa. Finally, using morphological and genetic data, we describe one new species of *Pacifigorgia*, emphasizing the set of morphological characters considered to be of taxonomic importance for this genus (Breedy and Guzmán 2002, 2003, 2004, Williams and Breedy 2004, Guzmán and Breedy 2011). We include the sequence analysis of the barcode of mtMutS plus COI with a short, adjacent intergenic region (Igr1) proposed by McFadden et al. (2011), with its closest congeners and available sequences in GenBank.

## MATERIALS AND METHODS

### Study area and sampling methodology

Eleven stations in Ecuadorian waters were sampled from February 2010 to June 2014 (Fig. 1). Gorgonians were collected by SCUBA diving in a depth range of between 5 and 30 m. Substrata in these habitats mainly include sand and rocky bottoms. During sampling, we

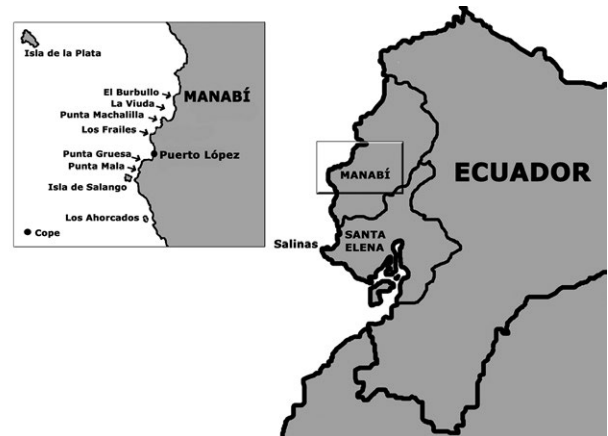


Fig. 1. – Station map in Ecuadorian waters where gorgonians octocorals were sampled from February 2010 to June 2014.

took colour photographs of the living specimens in their environment; specimens were also photographed outside the water, just after collection to ensure the accuracy of our colour descriptions. Subsamples were fixed in either absolute ethanol for further molecular analyses, or in 4% buffered formalin (after previous relaxation with menthol crystals for a few hours) for the morphological study; the rest of the colonies were allowed to air dry. Buffered formalin-fixed subsamples were subsequently transferred to 70% ethanol (Soler-Hurtado and López-González 2012).

### External morphology and SEM study

Fragments from different parts of the colony were prepared for study by SEM according to standard methods (Bayer and Stefani 1989, Alderslade 1998). Additionally, permanent mounts were made for light microscopy observation. The colonies are described and illustrated according to standard terminology (Bayer et al. 1983, Breedy and Guzmán 2003, 2007).

For either morphological and molecular comparisons, we studied types and additional materials deposited in the Museum of Comparative Zoology, Harvard University (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); the Natural History Museum, London (NHM); the Yale Peabody Museum of Natural History, New Haven (YPM); and the National Museum of Natural History, Smithsonian, Washington (NMNH).

Museum specimens were revised for morphological comparative purposes and, in some cases, for molecular analysis. These samples are listed in the text after the newly collected material of each species. Additional museum specimens of species revised but not found in Ecuador were the following:

*Eugorgia ampla* (Verrill, 1864): NHM 69.4.15.53, Baja California (Mexico), no further data. YPM 399, Baja California, 11-15 m depth, 1865. MCZ 65167, Mexico, no depth given, date unknown.

*Eugorgia aurantica* (Horn, 1860): YPM (4051), Baja California (Mexico), no depth given, 1867-1870. NHM 40.8.22.8, Baja California (Mexico), no depth given, date unknown. MCZ 36185, Baja California (Mexico), no depth given, date unknown.

Table 1. – *Pacifigorgia* species involved in the molecular comparisons carried out in this paper. Materials in bold are species sequenced for this study. Note that all GenBank sequences are considered here with the names as they appear in GenBank and their original publications (including numbers or letters). For sequences with duplicate complete names, we have included (1), (2), (3), etc., for the purpose of correctly identifying the sequence in Table 5.

Species	Catalog. Nos	Igr + COI	mtMutS
<i>Pacifigorgia bayeri</i>	voucher HGM77	HG917061	HG917044
<i>Pacifigorgia catedralensis</i> (1)	voucher HGM109	HG917065	HG917019
<i>Pacifigorgia catedralensis</i> (2)	voucher HMG112	HG917066	HG917020
<b><i>Pacifigorgia exilis</i></b>	YPM 4059	KX351878	KX351871
<b><i>Pacifigorgia firma</i></b>	MCZ 51918	KX351879	KX351872
<i>Pacifigorgia irene</i>	voucher HMG10	HG917070	HG917024
<b><i>Pacifigorgia irene</i></b>	MNCN 2.04/1174	KX351880	KX351873
<b><i>Pacifigorgia machalilla</i> n. sp. (1)</b>	MECN Ant0058	KX351881	KX351874
<b><i>Pacifigorgia machalilla</i> n. sp. (2)</b>	MECN Ant0059	KX351882	KX351875
<b><i>Pacifigorgia machalilla</i> n. sp. (3)</b>	MECN Ant0061	KX351883	KX351876
<i>Pacifigorgia media</i>	Parrin et al. 2009	GQ342421	GQ342497
<b><i>Pacifigorgia sculpta</i></b>	MCZ 57053	KX351884	KX351877
<i>Pacifigorgia smithsoniana</i>	voucher HMG59	HG917076	HG917023
<i>Pacifigorgia stenobrochis</i>	voucher HMG100	HG917078	HG917026
<i>Pacifigorgia rubicunda</i> (1)	voucher HMG01	HG917073	HG917032
<i>Pacifigorgia rubicunda</i> (2)	voucher HMG29	HG917074	HG917033

*Eugorgia nobilis* Verrill, 1868: YPM 1552a-e, type material, Las Perlas (Panama), 11-15 m depth, 1866. YPM 401, type material, Baja California (Mexico), no further data. MCZ 36316, Baja California (Mexico), no further data. USNM 49371, Gulf of Nicoya (Costa Rica), no depth given, 15 Jan. 1930. USNM 49372, Baja California (Mexico), no depth given, 16 Mar. 1911.

*Eugorgia multifida* Verrill, 1870: YPM 4605, type material, Mazatlan (Mexico), no depth given, date unknown. USNM 49368, Baja California (Mexico), 11-15 m depth, date unknown.

*Pacifigorgia adamsii* (Verrill, 1868): MCZ 391, type material, Panama, no depth given, 1863. MCZ 36079, type material, Panama, no depth given, 1866-1867. NHM 1930.6.173.9, South Pacific, no depth given, date unknown. YPM 1173g, type material, Panama, no depth given, 1866-1867. USNM 49688, Las Perlas (Panama), 33 m depth, 5 Mar 1888. USNM 49586, Mexico, no depth given, date unknown.

*Pacifigorgia agassizii* (Verrill, 1864): MCZ 374, type material, Panama, no depth given, 1863. MCZ 4035, Acapulco (Mexico), no depth given, 1859-1860. MCZ 36266, Baja California (Mexico), no depth given, date unknown. NHM 1885.5.18.2, type material, Mexico, no depth given, 1859-1860. YPM 956, type material, Baja California (Mexico), no depth given, 1860. MNHN-IK 1589, no depth given, date unknown. USNM 49369, Baja California (Mexico), no depth given, date unknown.

*Pacifigorgia arenata* (Valenciennes, 1846): MNHN-IK 1411, type material, New Zealand, no depth given, 1839.

*Pacifigorgia firma* Breedy and Guzmán, 2003: MCZ 51918, type material, Culebra Bay (Costa Rica), 20 m depth, 21 Sept. 1997.

*Pacifigorgia pulchra* var. *exilis* (Verrill, 1870): YPM 4059, type material, Baja California (Mexico), no depth given, 1867-1870. USNM 75076, Baja California (Mexico), no depth given, date unknown.

*Pacifigorgia rutila* (Verrill, 1868): MCZ 184, type material, Acapulco (Mexico), no depth given, date unknown. YPM 2266, type material, Acapulco (Mexico), no depth given, 1869-1870.

The newly collected specimens are deposited in the Museo Ecuatoriano de Ciencias Naturales (MECN), the octocoral reference collection of the research group “Biodiversidad y Ecología de Invertebrados Marinos” at the University of Seville (BEIM), the Museo Nacional de Ciencias Naturales in Madrid (MNCN-CSIC), the Museo de Zoología de la Universidad Tecnológica Indoamérica in Quito (UTI), and the Museu de Ciências Naturals in Barcelona (BCN).

#### DNA extraction, PCR amplification and sequencing

DNA was extracted from 20-30 mg of tissue using the DNeasy extraction kit (Qiagen, Inc.) according to the manufacturer’s protocol. Partial COII-COI (including Igr1 region) and MutS sequences were amplified by PCR using the following primers: COII8068F (McFadden et al. 2004), COIOCTR (France and Hoover 2002), the newly developed COI-Gorg1-R3 (5'-AGA-GAAGGTGGTAATAACCAGAAA-3') and COI-Gorg2-F2 (5'-GATTTCGAAATTGGTTTGTG-3') for COI + Igr1; ND42599F (France and Hoover 2002) and MUT3458R (Sánchez et al. 2003) for MutS. Amplifications were carried out in a final volume of 50 µL containing 5 µL of 10x buffer (containing 10x2 mM MgCl<sub>2</sub>), 1 µL dNTPs mix (10 mM), 0.8 µL of each primer (10 µM), 0.5 µL of Taq DNA polymerase (5U/µL) (Biotools) and 2 µL of genomic DNA. Thermocycling for the COI fragment included an initial 4-min denaturation step at 94°C, followed by 40 cycles of 45 s at 94°C, 1 min at 58°C and 1 min at 72°C. The cycle ended with 10 min of sequence extension at 72°C. For MutS, we used an initial 4-min denaturation step at 94°C, followed by 35 cycles of 90 s at 94°C, 90 s at 58°C and 1 min at 72°C. The cycle ended with 5 min of sequence extension at 72°C. The amplification products were purified by ethanol precipitation. The amplicons were sequenced for both strands using Big-Dye Terminator in an ABI 3730 genetic analyser (Applied Biosystems). The sequences obtained were edited using the Sequencher v.4.6 program (Gene Code Corporation, Ann Arbor, MI, USA). The resulting alignments were inspected by eye and manually checked

and adjusted with Se-AI v2.0a11 (Rambaut 2002). The distance matrix was obtained using PAUP\*v4.0b10 (Swofford 2001) with a neighbour joining clustering algorithm (Saitou and Nei 1987). A molecular data matrix was created with the morphologically closest species, together with other published sequences for Gorgoniidae in GenBank (see Table 1).

## RESULTS

Order ALCYONACEA Verrill, 1866  
Suborder Holaxonia Studer, 1887  
Family Gorgoniidae Lamouroux, 1812

Genus *Leptogorgia* Milne-Edwards and Haime, 1857

*Leptogorgia alba* (Duchassaing and Michelotti, 1864)  
(Figs 2, 3)

Synonymy. See Breedy and Guzmán (2007: 12).

*Newly collected examined material:* MECN (Ant0001), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 15 m depth, 27 Feb. 2010, three whole colonies. MECN (Ant0019), Isla de Salango, Manabí (Ecuador), 1°35'55.13"S 80°52'0.01"W, 7 m depth, 20 Nov. 2011, two whole colonies. MECN (Ant0020), Salinas, Santa Elena (Ecuador), 2°12'50.01"S 80°56'5.93"W, 15 m depth, 18 Dec. 2011, one whole colony. MECN (Ant0027), Los Frailes, Manabí (Ecuador), 1°30'14"S 80°48'33"W, 10 m depth, Dec. 2011, three whole colonies. MECN (Ant0030), Los Frailes, Manabí (Ecuador), 1°30'14"S 80°48'33"W, 15 m depth, 19 March. 2012. BEIM (0071), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 15 m depth, 27 Feb. 2010, one whole colony. BEIM (0074), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 5 m depth, 27 Feb. 2010, one whole colony. MNCN (2.04/482), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 10 m depth, Feb. 2010, one whole colony. MNCN (2.04/483), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 15 m depth, 28 Feb. 2010, one whole colony. MZB (2016-2989), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 15 m depth, 27 Feb. 2010, one whole colony. UTI (MZUTI-Inv02), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 15 m depth, 28 Feb. 2010, one whole colony. MECN (Ant0040), Punta Mala, Manabí (Ecuador), 1°33'41.37"S 80°50'8.79"W, 16 m depth, 02 Feb. 2013, one whole colony. MECN (Ant0041), Islote La Viuda, Manabí (Ecuador), 1°26'5.95"S 80°46'7.30"W, 15 m depth, 23 Nov. 2013, one whole colony. MECN (Ant0050) Punta Machalilla, Manabí (Ecuador), 1°28'33.53"S 80°47'38.04"W, 13 m depth, 24 Nov. 2013, one whole colony.

*Additional examined materials:* *Litigorgia laevis*, MCZ 5416, type material, Las Perlas (Panama), no depth given, date unknown; MCZ 7008, type material, Golfo de Nicoya, (Costa Rica), no depth given, May 1868. *Leptogorgia laevis*, YPM IZ 001639, type material, Las Perlas, (Panama), no depth given, 1868. *Leptogorgia alba*, NHM 1946.1.14.52, Toboga (Panama), no depth given, date unknown; NHM 30.6.17.13, Toboga (Panama), no depth given, date unknown. *Leptogorgia alba*, USNM 59078, Ecuador, 8-9 m depth, 8 May 1966; USNM 1016223, Ecuador, no depth given, Dec. 1937.

**Description.** The colonies measure up to 350 mm in length and 105 mm wide, irregularly pinnate; branches slender, mostly in a plane (Fig. 2A). Unbranched distal twigs up to 100 mm in length and 20 mm in diameter, compressed proximally, more cylindrical and slightly tapered distally (Fig. 2A, B). The holdfast circular, up to 5 mm in diameter. Slightly marked longitudinal grooves along the thick basal branches and near the base. The polyps retract within slightly raised polypmounds, sparsely distributed all around the branches with oblong apertures (Fig. 2B). The colour of the

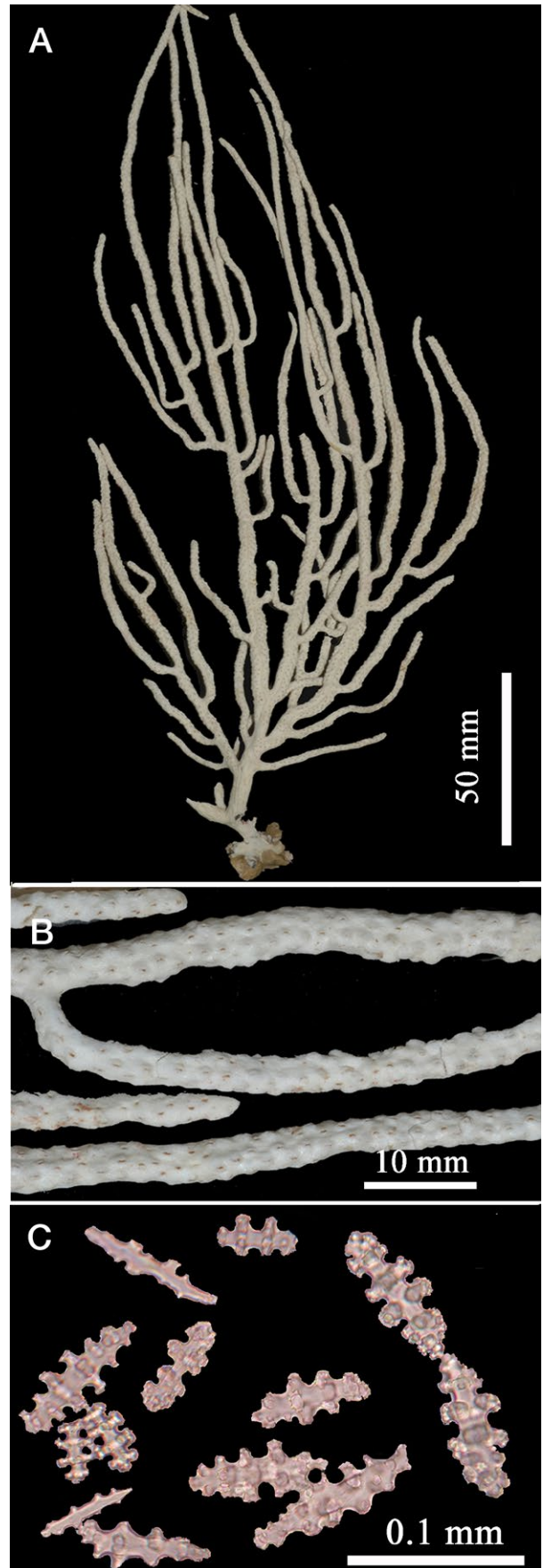


Fig. 2. – *Leptogorgia alba* (MNCN 2.04/482). A, colony; B, detail of a branch; C, light micrograph of sclerites.

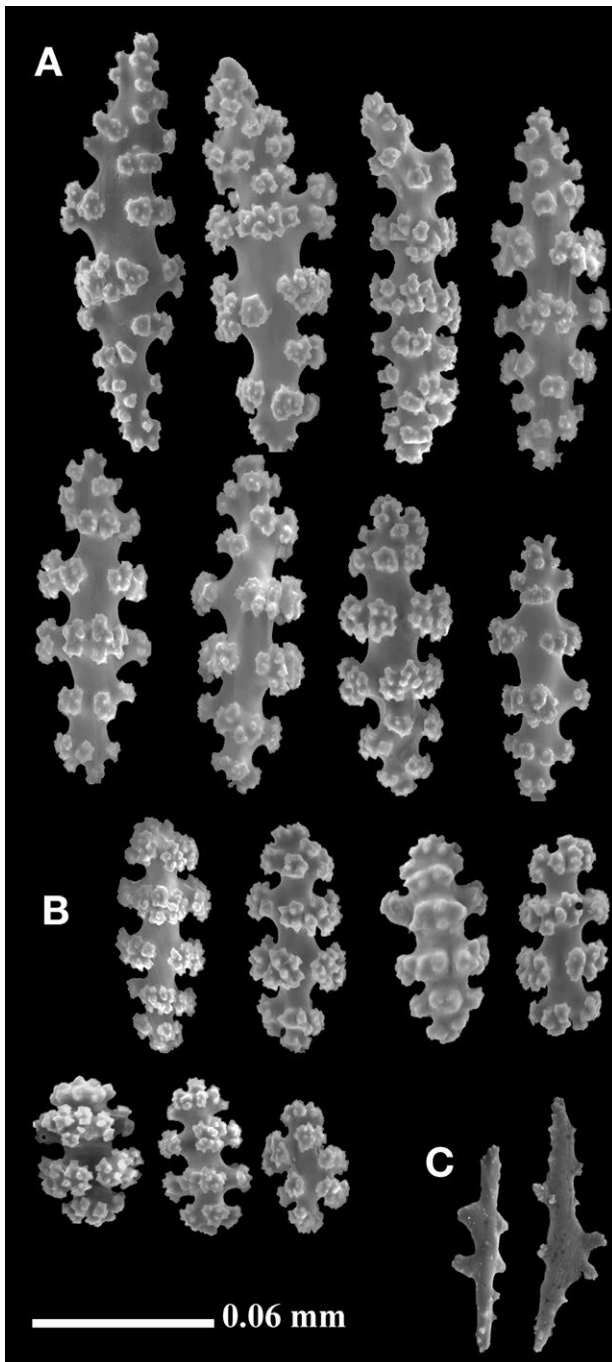


Fig. 3. – *Leptogorgia alba* (MNCN 2.04/482) SEM photographs. Coenenchymal sclerites, A, spindles; B, captans; C, anthocodial sclerites, rods.

colony is white. The coenenchymal sclerites hyaline (Fig. 2C). The dominant sclerite type spindles up to 0.14 mm in length and 0.03 mm wide, with 4-6 whorls of tubercles; straight or bent, some with a marked waist (Figs 2C, 3A). The captans up to 0.07 mm in length and 0.03 mm wide (Fig. 3B). Crosses not found. The anthocodial sclerites hyaline rods up to 0.08 mm in length and 0.02 mm wide, with some marginal projections (Figs 2C, 3C).

*Geographic and bathymetric distribution.* *Leptogorgia alba* has been reported in Mexico, El Salvador,

Costa Rica, Panama, Colombia, and the Galápagos Islands (Ecuador) (Duchassaing and Michelotti 1864, Bielschowsky 1929, Breedy and Guzmán 2007), at 3-30 m depth (Fig. 25A).

Although *Leptogorgia alba* has already been collected in Ecuador (Galápagos Islands) (Breedy and Guzmán 2007); this is the first time that it has been found on the continental coast since the paper of Bielschowsky (1929).

*Remarks.* Our material is in agreement with the original description (Duchassaing and Michelotti 1864:19) and its later re-description (Breedy and Guzmán 2007:12-19). Due to its white colour, it is easily recognizable underwater. Breedy and Guzmán (2007) considered that its morphological variability, especially the type of branching, could perhaps be a response to several environmental factors. In our samples we observe a more pinnate pattern, although there is a tendency towards a dichotomous branching in some specimens. In the type material, the spindles are long, up to 0.17-0.18 mm in length and 0.04-0.06 mm in width, with marked and complex tubercles. However, our material shows smaller spindles (up to 0.14×0.03 mm, Table 2) with a less marked ornamentation. In the same way, the anthocodial rods are considered very consistent in size and shape (long and conspicuous) in this species (up to 0.15 mm in length) (Breedy and Guzmán 2007). However, the examined Ecuadorian material shows a smaller maximum length (up to 0.08 mm).

*Leptogorgia diffusa* (Verrill, 1868)  
(Figs 4, 5)

Synonymy. See Breedy and Guzmán (2007: 32).

*Newly collected examined material:* MECN (Ant0032), Punta Mala, Manabí (Ecuador), 1°33'41.37"S 80°50'8.79"W, 13 m depth, 3 Abr. 2012, one whole colony. MECN (Ant0005), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 30 m depth, 28 Feb. 2010, two whole colonies. BEIM (0080), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 10 m depth, Feb. 2010, one whole colony. BEIM (0078), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 20 m depth, 28 Feb. 2010, one whole colony. MNCN (2.04/484), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 15 m depth, 27 March 2012, one whole colony. MNCN (2.04/485), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 30 m depth, 27 Feb. 2010, one whole colony. MZB (2016-2990), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 30 m depth, 27 Feb. 2010, one whole colony. MZB (2016-2991), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 25 m depth, 27 Feb. 2010, one whole colony. UTI (MZUTI-Inv09), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 30 m depth, 28 Feb. 2010, one whole colony. UTI (MZUTI-Inv01), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 10 m depth, 27 Feb. 2010, one whole colony. MECN (Ant0042), El Burbullón, Manabí (Ecuador), 1°28'23.59"S 80°51'23.04"W, 25 m depth, 23 Nov. 2013, one whole colony.

*Additional examined materials:* *Leptogorgia diffusa* MCZ 7081, type material, Golfo de Nicoya (Costa Rica), no depth given, May 1868. *Litigorgia diffusa* YPM 1659A, type material, Las Perlas (Panama), no depth given, 1866-1867. *Leptogorgia diffusa* MCZ 4972, Mexico, no depth given, date unknown. MNHN-IK 2233, no further data.

*Description.* The colonies are up to 670 mm in length by 950 mm in width. The branching pattern

Table 2. – Comparative general features of the species of the genera *Leptogorgia* and *Eugorgia* collected in this study, on the coast of Ecuador.

Characters	<i>Leptogorgia alba</i>	<i>Leptogorgia diffusa</i>	<i>Leptogorgia flexilis</i>	<i>Leptogorgia obscura</i>	<i>Eugorgia danitana</i>
Colour of colony	white	red	brown	purple	dark orange
Type of branching	irregularly pinnate	flat, lax, pinnate	irregularly pinnate	dichotomous	pinnate
Polyp-mounds	slightly raised	prominent	flat	prominent	double disc
Dominant sclerite type	spindles	spindles	capstans	spindles	red, yellow
Colour of sclerites	colourless	red	red, pink and yellow	red	yes
Bicolour sclerites	no	no	yes	no	yes
Acute spindles max. size (mm)	0.14×0.03	0.11×0.03	0.1×0.03	0.13×0.04	0.15×0.05
Capstan max. size (mm)	0.07×0.03	0.07×0.04	0.07×0.03	0.08×0.04	0.08×0.05
Crosses (mm)	no	0.04×0.05	0.03×0.03	0.06×0.04	0.14×0.06
Size and colour of anthocodial rods (mm)	colourless / 0.08×0.02	orange / 0.13×0.02	pink / 0.16×0.08	orange / 0.07×0.02	not obtained
Complete double disc	-	-	-	-	yes
Double disc max. size (mm)	-	-	-	-	0.07×0.06
Disc-spindles	-	-	-	-	yes

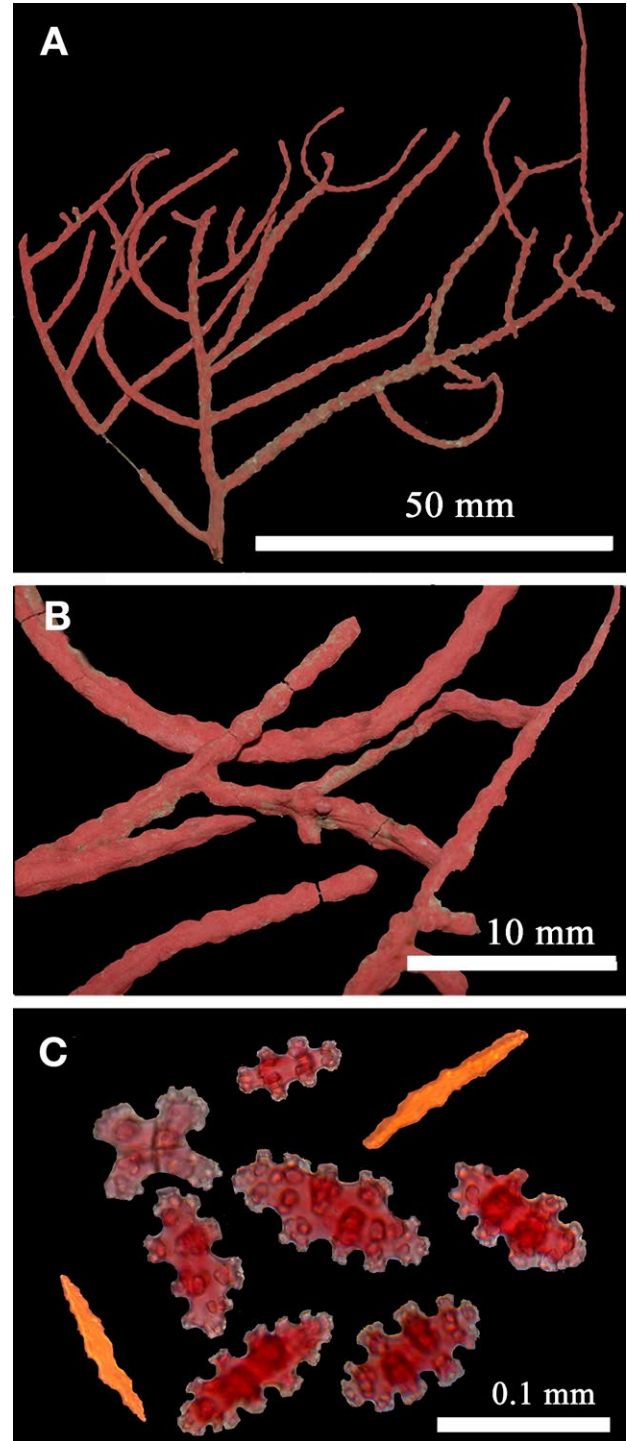


Fig. 4. – *Leptogorgia diffusa* (MNCN 2.04/1172). A, colony; B, detail of a branch; C, light micrograph of sclerites.

is irregularly pinnate; branches are flat, lax, pinnate, slender and on a plane (Fig. 4A). The unbranched distal twigs can reach up to 22 mm in length and 17 mm in diameter (Fig. 4A, B). The holdfast is slightly flat, up to 15 mm in diameter. The polyps retract within prominent polyp-mounds, sparsely distributed all around the branches with slit-like apertures (Fig. 4B). The colour of the colony and of the coenenchymal sclerites is red (Fig. 4A-C). The spindles are the dominant sclerite type, up to 0.11 mm in length and 0.03 mm in width,

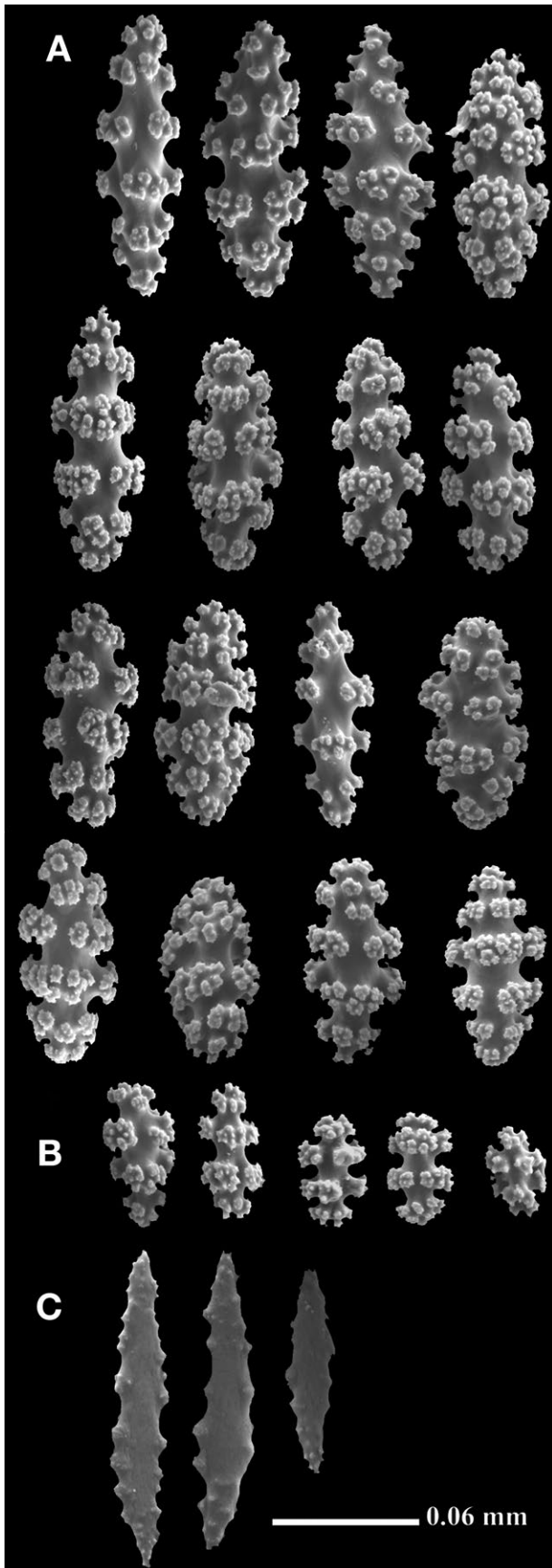


Fig. 5. – *Leptogorgia diffusa* (MNCN 2.04/1172) SEM photographs. Coenenchymal sclerites, A, spindles; B, capstans; C, anthocodial sclerites, flattened rods.

with 4–6 whorls of tubercles, they are straight or bent, some with a marked waist (Figs 4C, 5A). The capstans reach up to 0.07 mm in length and 0.04 mm in width (Figs 4C, 5B). Some small, scattered crosses are found (0.04×0.05 mm) (Fig. 4C). The anthocodial sclerites are orange flattened rods, up to 0.13 mm in length and 0.02 mm in width, with lobe-like marginal projections (Figs 4C, 5C).

**Geographic and bathymetric distribution.** *Leptogorgia diffusa* has been previously reported in California, El Salvador, Costa Rica, Panama, Colombia, and Chile at 5–30 m depth (see Verrill 1868, Bielschowsky 1929, Prahel et al. 1986, Breedy and Guzmán, 2007) (Fig. 25B). This new record fills the gap between the northern and southern records of the species. *Leptogorgia diffusa* probably has a wider distribution, especially in offshore areas of Mexico and Peru, but it may have been previously overlooked. Although this species is quite frequent in Ecuador, it is usually observed isolated within multispecies assemblages and does not form large gorgonian gardens.

**Remarks.** The morphology of this species is very constant in all examined samples. It is easily differentiable from other *Leptogorgia* species by the lax, pinnate style of branching, with prominent polyp-mounds. Breedy and Guzmán (2007: 34–35) noted anthocodial sclerites that were light orange, dark pink, or both; however, our materials are only orange. The coenenchymal sclerites are a bit smaller (up to 0.11×0.03 mm; Table 2) than previously described (up to 0.14–0.15×0.05 mm) (Verrill 1868: 398, Breedy and Guzmán 2007: 34). In addition, the Ecuadorian material has scattered small crosses not reported in this species before.

***Leptogorgia flexilis* (Verrill, 1868)**  
(Figs 6, 7)

Synonymy. See Breedy and Guzmán (2007: 40).

**Newly collected examined material:** MECN (Ant0034), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 10 m depth, 27 Feb. 2010, one whole colony. BEIM (0085), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 10 m depth, 27 Feb. 2010, one whole colony. MNCN (2.04/1171), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 5 m depth, 27 Feb. 2010, one whole colony.

**Additional examined materials:** *Litigorgia flexilis* (*Eugorgia flexilis*) MCZ 722 (4123), type material, Las Perlas (Panama), 6 to 8 m depth, 1860's. *Litigorgia flexilis* NHM 69.4.15.15 (1946.1.14.74), type material, Toboguilla (Panama), 5 m depth, 1915. *Leptogorgia flexilis* YPM 569, Panama, no depth given, 1867–1868.

**Description.** The colonies measure up to 200 mm in length by 40 mm in width. The branching pattern is irregularly pinnate, mostly on a plane; branches are lank and bushy with long, slender, and flexible branches, drooping slightly at the ends (Fig. 6A). The unbranched distal twigs can reach up to 50 mm in length and 18 mm in diameter (Fig. 6A, B). The holdfast is circular, up to 10 mm in diameter. The polyps retract within nearly flat polyp-mounds, closely distributed all around the branches, with oblong apertures (Fig. 6B). The colour

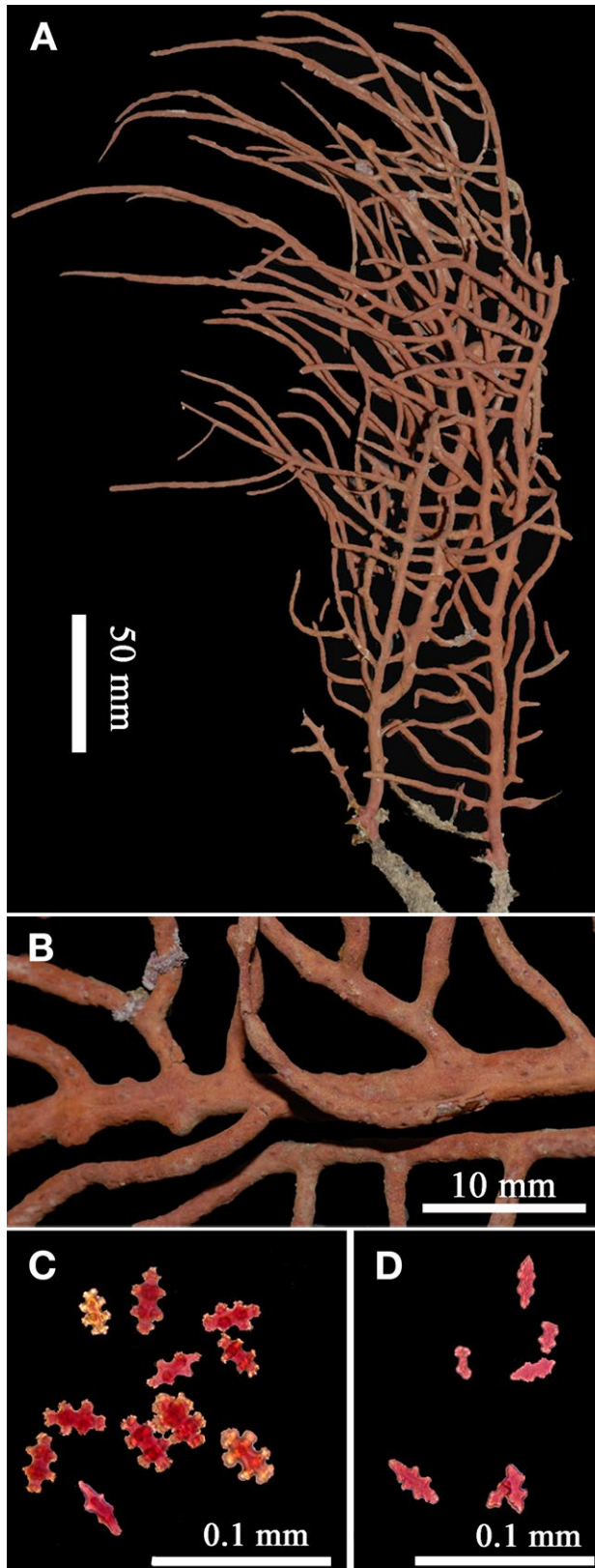


Fig. 6. – *Leptogorgia flexilis* (MNCN 2.04/1171). A, colony; B, detail of a branch; C, light micrograph of coenenchymal sclerites; D, light micrograph of anthocodial sclerites.

of the colony is brown (Fig. 6A, B). The coenenchymal sclerites are red, pink and yellow; some of them are bicoloured (Fig. 6C). The capstans are the dominant

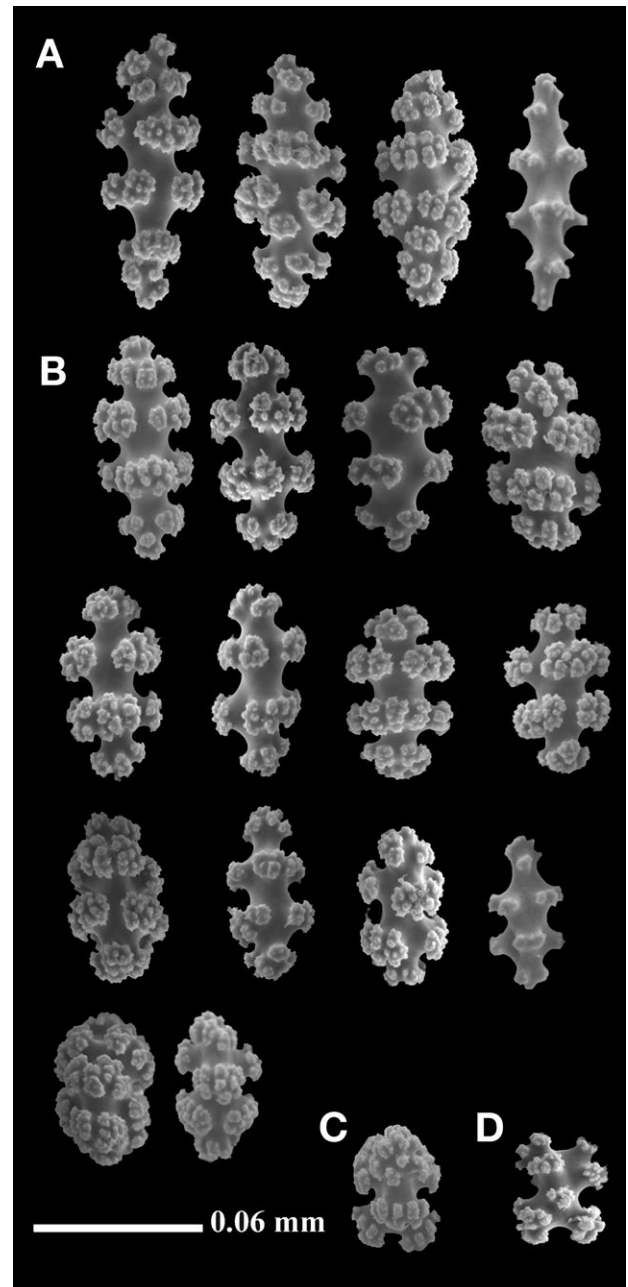


Fig. 7. – *Leptogorgia flexilis* (MNCN 2.04/1171) SEM photographs. Coenenchymal sclerites, A, spindles; B, captans; C, six-radiate; D, four-radiate.

sclerite type, up to 0.07 mm in length and 0.03 mm in width (Figs 6C, 7B). The spindles reach up to 0.1 mm in length and 0.03 mm in width, with 4-6 whorls of tubercles; they are straight or bent, some with a marked waist (Fig. 7A). Some crosses or four-radiates (up to 0.03×0.03 mm) (Fig. 7D) and six-radiates (up to 0.03×0.02 mm) are also found. The anthocodial sclerites are pink flattened rods up to 0.16 mm in length and 0.08 mm in width, with short lobe-like marginal projections (Fig. 6D).

*Geographic and bathymetric distribution.* This species has been previously reported in California, El Salvador and Panama at 5-30 m depth (Verrill 1868,



Breedy and Guzmán 2007) (Fig. 25C), and thus our specimens represent a sizeable expansion to the south.

*Remarks.* Under water, the species is characterized by its decumbent or drooping branching pattern and its brown colonies. However, in small colonies the drooping habit is not as evident, and sometimes the holdfast and basal branches are an intense yellow. Crosses or four-radiate sclerites were not mentioned by Breedy and Guzmán (2007) in their revision of different type materials (e.g. deposited at MZC and YPM). However, they are evident in our collections and in the type specimens at NHM. This type of sclerite had been noted by Verrill (1868) as well, and it should be considered diagnostic for the species.

*Leptogorgia obscura* Bielschowsky, 1929  
(Figs 8, 9)

Synonymy. See Breedy and Guzmán (2007: 57).

*Newly collected examined material:* MECN (Ant0011), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 10 m depth, 27 Feb. 2010, three whole colonies. MECN (Ant0028), Los Frailes, Manabí (Ecuador), 1°30'14"S 80°48'33"W, 10 m depth, 17 Feb. 2012, one whole colony. BEIM (CRO-0068), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 10 m depth, 27 Feb. 2010, one whole colony. BEIM (CRO-0069), Isla de Salango, Manabí (Ecuador), 1°35'55.13"S 80°52'0.01"W, 7 m depth, 19 Nov. 2011, one whole colony. MNCN (2.04/486), Isla de Salango, Manabí (Ecuador), 1°35'55.13"S 80°52'0.01"W, 7 m depth, 19 Nov. 2011, one whole colony. MNCN (2.04/487), Los Frailes, Manabí (Ecuador), 1°30'14"S 80°48'33"W, 10 m depth, 17 Feb. 2012, one whole colony. UTI (MZUTI-Inv03), Isla de Salango, Manabí (Ecuador), 1°35'55.13"S 80°52'0.01"W, 7 m depth, 19 Nov. 2011, one whole colony. UTI (MZUTI-Inv05), Isla de Salango, Manabí (Ecuador), 1°35'55.13"S 80°52'0.01"W, 13 m depth, 17 Feb. 2012, one whole colony. MZB (2016-2992), Isla de Salango, Manabí (Ecuador), 1°35'55.13"S 80°52'0.01"W, 13 m depth, 19 Feb. 2012, one whole colony. MZB (2016-2993), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 10 m depth, 27 Feb. 2010, one whole colony. MECN (Ant0043), Los Frailes, Manabí (Ecuador), 1°30'14"S 80°48'33"W, 15 m depth, 23 May. 2013, one whole colony. MECN (Ant0044), Isote La Viuda, Manabí (Ecuador), 1°26'5.95"S 80°46'7.30"W, 15 m depth, 23 Nov. 2013, one whole colony. MECN (Ant0049), Punta Machalilla, Manabí (Ecuador), 1°28'33.53"S 80°47'38.04"W, 13 m depth, 24 Nov. 2013, one whole colony.

*Description.* The colonies are up to 164 mm in length by 75 mm in width. The branching pattern is irregularly dichotomous; branches are bushy, closely ramified and rigid (Fig. 8A). The unbranched distal twigs can reach up to 5 mm in length and 2.3 mm in diameter, are compressed proximally, being more cylindrical and slightly tapered at the ends (Fig. 8A, B). The holdfast is circular, up to 14 mm in diameter. The polyps retract within prominent polyp-mounds leaving oblong apertures, and are closely distributed all around the branches (Fig. 8B). The colour of the colony is purple (Fig. 8A, B). The coenenchymal sclerites are red (Fig. 8C, D). The spindles are the dominant sclerite type, up to 0.13 mm in length and 0.04 mm in width, with 4-5 whorls of tubercles; they are straight or bent, some with a marked waist (Figs 8C, 9A). The capstans reach up to 0.08 mm in length and 0.04 mm in width (Figs 8C, 9B). Some crosses up to 0.06 by 0.04 mm are found (Fig. 9C). The anthocodial

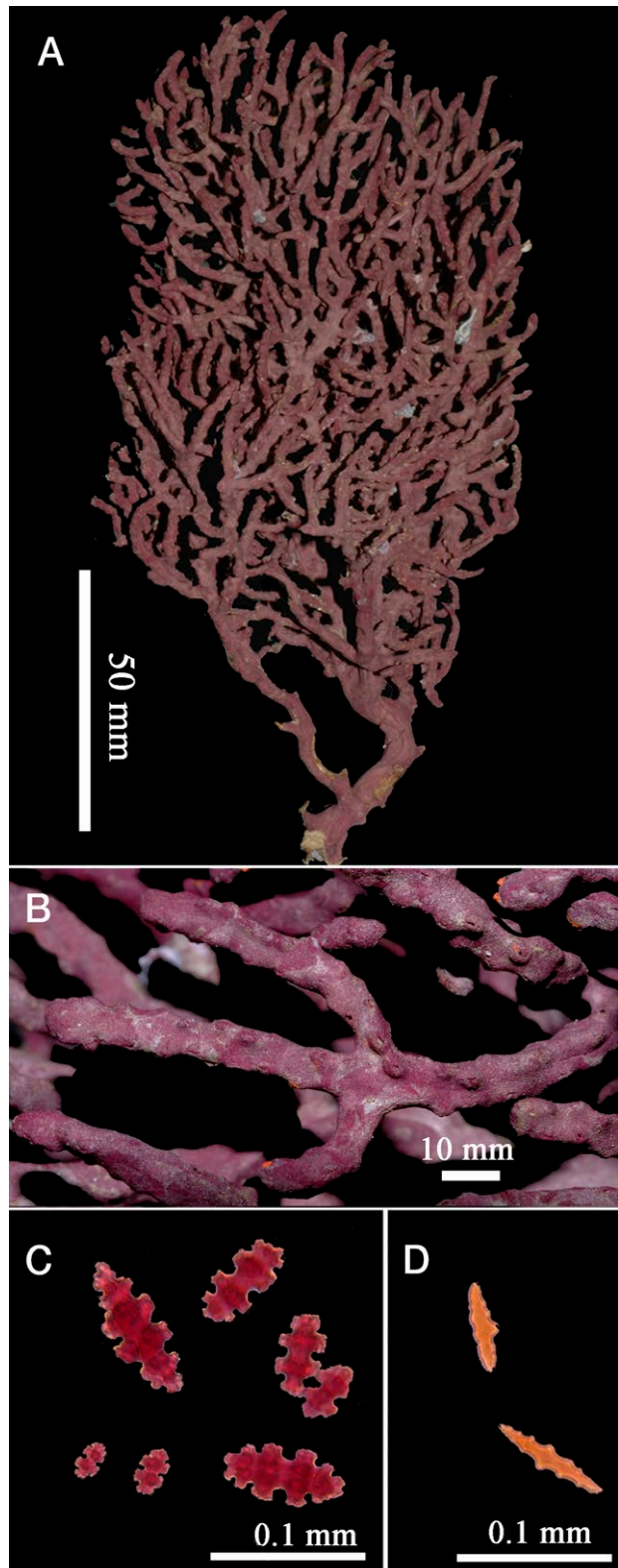


Fig. 8. – *Leptogorgia obscura* (MECN Ant0011). A, colony; B, detail of a branch; C, light micrograph of coenenchymal sclerites; D, light micrograph of anthocodial sclerites.

sclerites are orange flattened rods, up to 0.07 mm in length and 0.02 mm in width, with lobe-like marginal projections (Figs 8D, 9D).

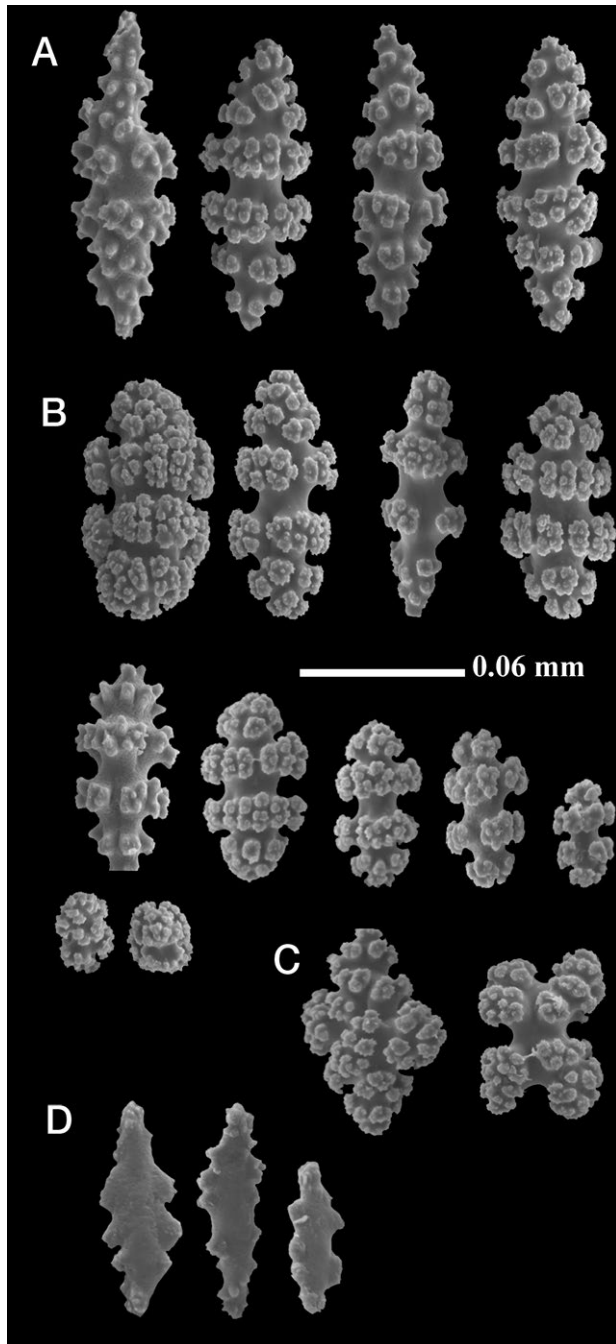


Fig. 9. – *Leptogorgia obscura* (MECN Ant0011) SEM photographs. Coenenchymal sclerites, A, spindles; B, captans; C, four-radiates; D, anthocodial sclerites, flattened rods.

**Geographic and bathymetric distribution.** *Leptogorgia obscura* was known previously only from the type locality (Bahía de Caráquez, Ecuador) (Bielschowsky 1929; Fig. 25D). There is an unpublished record from Baja California (Harden 1979), although Breedy and Guzmán (2007) note that this record should be verified. The only reliable previously known depth range for the species was 4–5 m (Bielschowsky 1929), which we now expand to 15 m.

This species is quite abundant in the study area on rocky bottom areas and usually grows along with *Leptogorgia alba*.

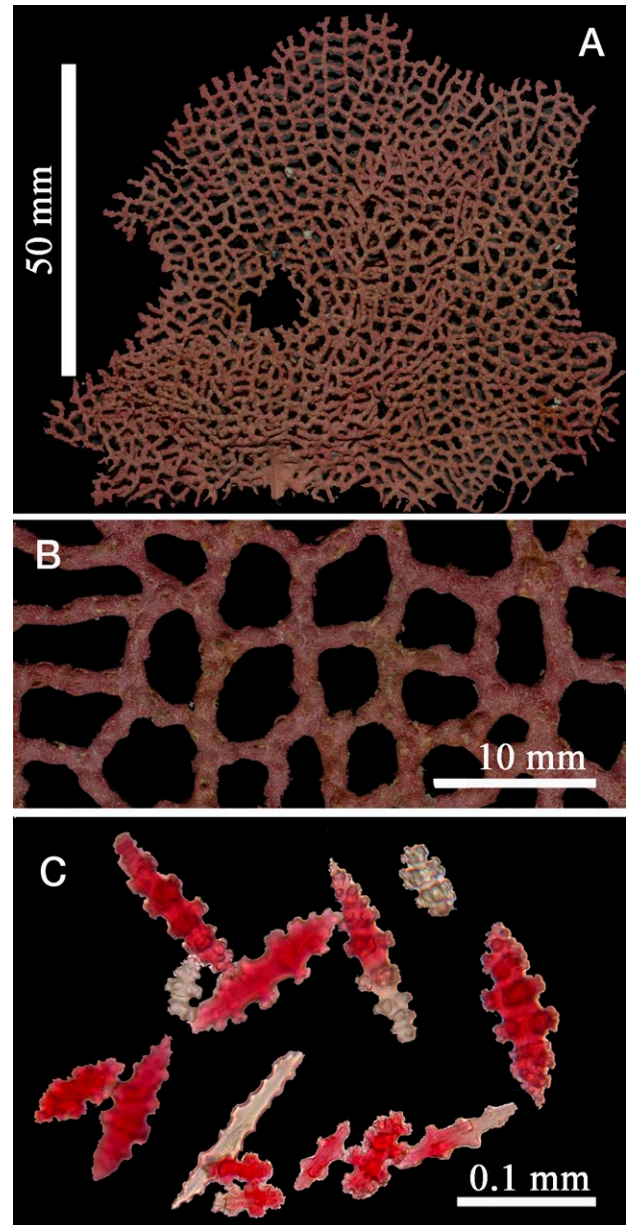


Fig. 10. – *Pacifigorgia cribrum* (MNCN 2.04/1170). A, colony; B, detail of a branch; C, light micrograph of sclerites.

**Remarks.** According to Bielschowsky (1929) and Breedy and Guzmán (2007: 57), captans are the dominant sclerites in the type material. However, spindles are the most common sclerites in our specimens. Crosses or four-radiates also occur, a type of sclerite not reported in this species before.

Genus *Pacifigorgia* Bayer, 1951

Synonymy. See Breedy and Guzmán (2002: 791).

*Pacifigorgia cribrum* (Valenciennes, 1846)  
(Figs 10, 11)

Synonymy. See Breedy and Guzmán (2002: 804).

**Newly collected examined material:** MECN (Ant0035), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 15 m depth,

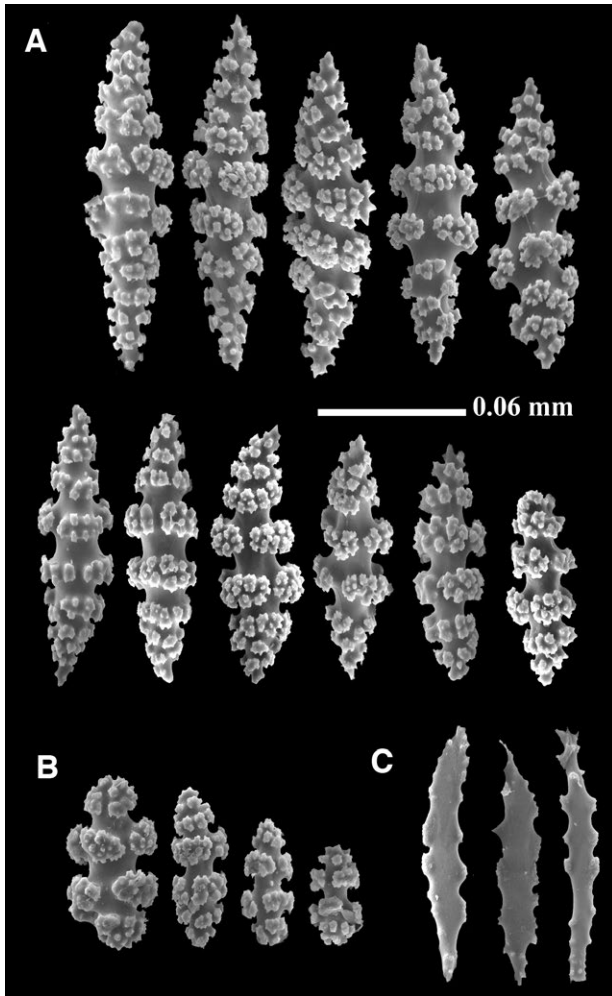


Fig. 11. – *Pacifigorgia cribrum* (MNCN 2.04/1170). SEM photographs. Coenenchymal sclerites, A, spindles; B, captans; C, anthocodial sclerites, flattened rods.

27 Feb. 2010, one whole colony. MECN (Ant0036), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 20 m depth, 28 Feb 2010, one whole colony. MECN (Ant0037), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 15 m depth, 27 Feb. 2010, one whole colony. BEIM (0088), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 25 m depth, 28 Feb. 2010, one whole colony. BEIM (0089), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 20 m depth, 28 Feb. 2010, one whole colony. MECN (Ant0046), El Burbullón, Manabí (Ecuador), 1°28'23.59"S 80°51'23.04"W, 25 m depth, 23 Nov. 2013, one whole colony.

*Additional examined materials:* *Rhipidigorgia cribrum* MNHN-1K 1661, type material, (New Zealand), no depth given, 1839. *Pacifigorgia cribrum* MZC 261 (4014), Cape St. Lucas, Baja California, (Mexico), no depth given, 1859-1861. MCZ 36264, Marcial Point (Mexico), no depth given, data unknown. *Pacifigorgia cribrum* USNM 49382 (Costa Rica), no depth given, Mar. 1927, F.M. Bayer (Id.). *Gorgonia cribrum* NMH 58.5.15.237 (Australia), no depth given, data unknown.

**Description.** The colonies are up to 50 mm in length by 73 mm in width, and are formed by two fans: the first fan is the largest and the second one radiates from the holdfast and extends in parallel together with the first fan, until a certain point where both may fused (Fig. 10A). The holdfast is very small, up to 4 mm in diameter. The branches are squarish, ranging from 0.6

Table 3. – Comparative general features of the species of the genus *Pacifigorgia* collected in this study, on the coast of Ecuador.

Characters	<i>Pacifigorgia rubicunda</i>	<i>Pacifigorgia cribrum</i>	<i>Pacifigorgia flavimaculata</i>	<i>Pacifigorgia stenobrochis</i>	<i>Pacifigorgia irene</i>
Colour of colony	brownish-orange	reddish (with yellow)	yellow with light brown	brown or yellow	reddish with yellow
Number of fans	several	two	two	one or more	one or more
Number of meshes cm <sup>-2</sup>	6-9	25	1-3	2	35
Mesh shape and maximum mesh size (mm)	square or oblong/ 10x3, 5.5x3	square / 2x2.8, 2.5x3	rounded-square, oblong 19x5, 9x4	oblong/ 55x6, 10x5	squarish/ 2x0.9
Polyp-mounts	slightly raised	slightly raised	prominent	flat	slightly raised
Colour of sclerites	pink, orange and lemon yellow	red and light yellow	pink and light yellow	light yellow	red, lemon yellow and orange
Bicolour sclerites	yes	yes	yes	not	yes
Acute spindles max. size (mm)	0.1x0.03	0.13x0.04	-	0.16x0.04	0.17x0.05
Blunt spindles max. size (mm)	0.1x0.04	0.08x0.03	0.14x0.04	0.12x0.04	-
Capstan max. size (mm)	0.07x0.03	0.07x0.04	0.09x0.04	0.09x0.04	0.08x0.04
Crosses	no	no	no	0.08 by 0.06	0.06x0.05
Size and colour of anthocodial (mm)	yellow 0.12x0.02	light yellow 0.10x0.02	orange 0.14x0.02	orange 0.09x0.02	pink and yellow 0.11x0.02

to 0.8 mm in diameter (25 meshes  $\text{cm}^{-2}$ ), and the end-branchlets are short, up to 2 mm long. The network is fine and regular; it is formed mostly by square meshes ( $2 \times 2.8$  mm by  $2.5 \times 3$  mm) (Fig. 10B). There are no midribs; nevertheless, adult specimens have large, slightly compressed principal branches, which arise from near the base, and diverge through the fan, but often for no more than a quarter of the height. The polyps retract within slightly raised polyp-mounds with asterisk-like apertures, placed in multiple rows all around the branches. The colour of the colony is reddish intermingled with yellow. The coenenchymal sclerites are red, light yellow, and bicoloured (Fig. 10C). They are spindles ( $0.13 \times 0.04$  mm) having acute ends and 4-6 whorls of tubercles; blunt spindles ( $0.08 \times 0.03$  mm) with 4 whorls of tubercles (Figs 10C, 11A); and capstans ( $0.07 \times 0.04$  mm) with tuberculate ends (Figs 10C, 11B). The dominant sclerite types are acute, straight or bent spindles, some with a marked waist. The anthocodial sclerites are light yellow flattened rods, up to 0.10 mm in length and 0.02 mm in width, with smooth or slightly lobed borders (Figs 10C, 11C).

**Geographic and bathymetric distribution.** *Pacifigorgia cribrum* has been previously reported in Mexico (Breedy and Guzmán 2002) (Fig. 25E), with additional questionable records from New Zealand (MNHN-IK 1661), Australia (NMH 58.5.15.237), and Costa Rica (e.g. USNM 49382, collected in 1927 and identified by M.F. Bayer). In this study we observed this species at 15-30 m depth. A depth range was lacking for it in the literature.

**Remarks.** According to Bayer and Macintyre (2001) and Breedy and Guzmán (2002), *Pacifigorgia cribrum*, *P. adamsii*, *P. agassizii* and *P. rutila* may represent a group sharing a set of morphological features, consisting of fine, regular and closely anastomosed networks.

In addition, *Pacifigorgia cribrum* is morphologically close to *P. arenata*, both species having a similar colony colour and sclerome characteristics (red, yellow, bicoloured coenenchymal sclerites, and yellow anthocodial sclerites up to 0.10-0.13 mm in length; Table 3). However, the two species differ in mesh features (presence of midrib and higher meshes in *P. arenata*, see Breedy and Guzmán 2002). In fact, one of the principal problems in recording the possible morphological and chromatic variability of *P. arenata* is that the only known specimen is the holotype, which is deposited in Paris (MNHN), and there are some fragments in the Smithsonian (USNM 49567).

***Pacifigorgia flavimaculata***  
Breedy and Guzmán, 2003  
(Figs 12, 13)

**Newly collected examined material:** MECN (Ant0021), Salinas, Santa Elena (Ecuador),  $2^{\circ}12'50.01''\text{S}$   $80^{\circ}56'5.93''\text{W}$ , 15 m depth, 10 Dec. 2011, one whole colony. MECN (Ant0022), Salinas, Santa Elena (Ecuador),  $2^{\circ}12'50.01''\text{S}$   $80^{\circ}56'5.93''\text{W}$ , 18 m depth, 11 Dec. 2011, one whole colony. BEIM (0075), Salinas, Santa Elena (Ecuador),  $2^{\circ}12'50.01''\text{S}$   $80^{\circ}56'5.93''\text{W}$ , 17 m depth, 10 Dec. 2011, one whole colony. BEIM (0070), Los Ahorcados, Manabí (Ecuador),  $1^{\circ}40'44''\text{S}$   $80^{\circ}50'08''\text{W}$ , 10 m depth, 27 Feb.

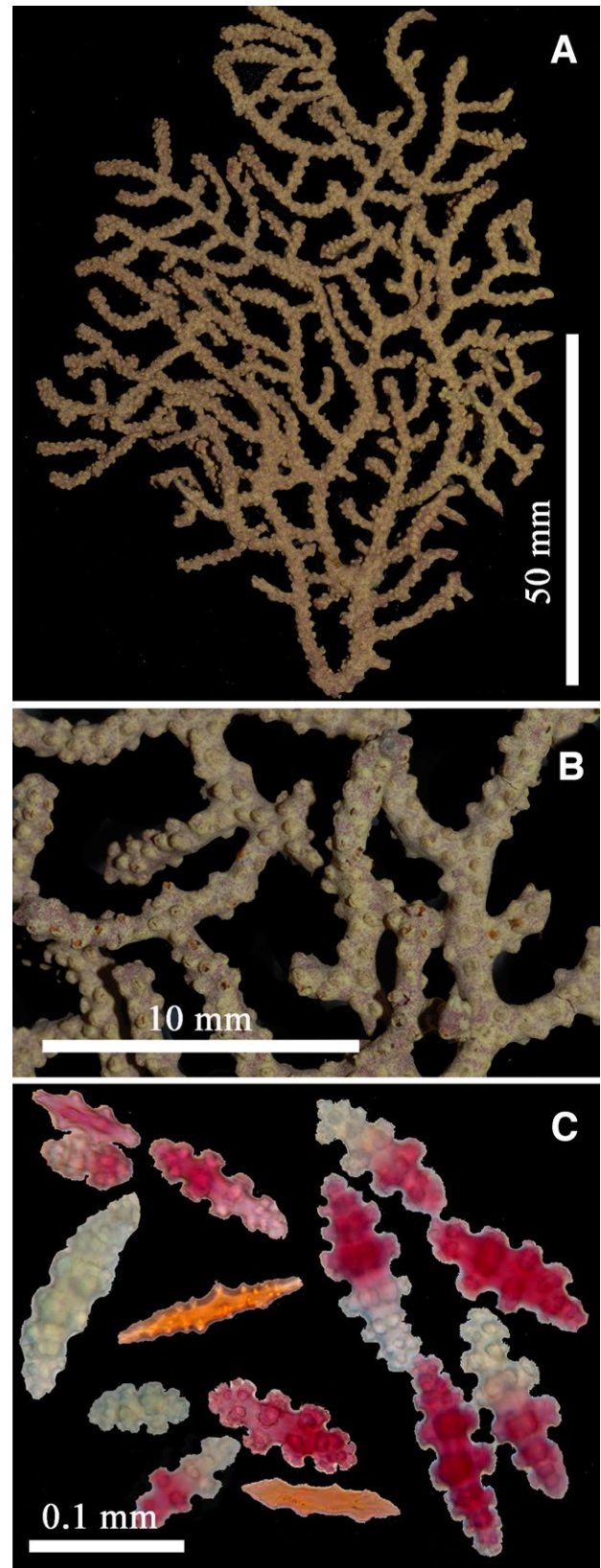


Fig. 12. – *Pacifigorgia flavimaculata* (MNCN 2.04/1178). A, colony; B, detail of a branch; C, light micrograph of sclerites.

2010, one whole colony. MNCN (2.04/490), Los Frailes, Manabí (Ecuador),  $1^{\circ}30'14''\text{S}$   $80^{\circ}48'33''\text{W}$ , 10 m depth, 13 March 2012, one whole colony. MNCN (2.04/491), Salinas, Santa Elena (Ecuador),  $2^{\circ}12'50.01''\text{S}$   $80^{\circ}56'5.93''\text{W}$ , 17 m depth, 10 Dec.

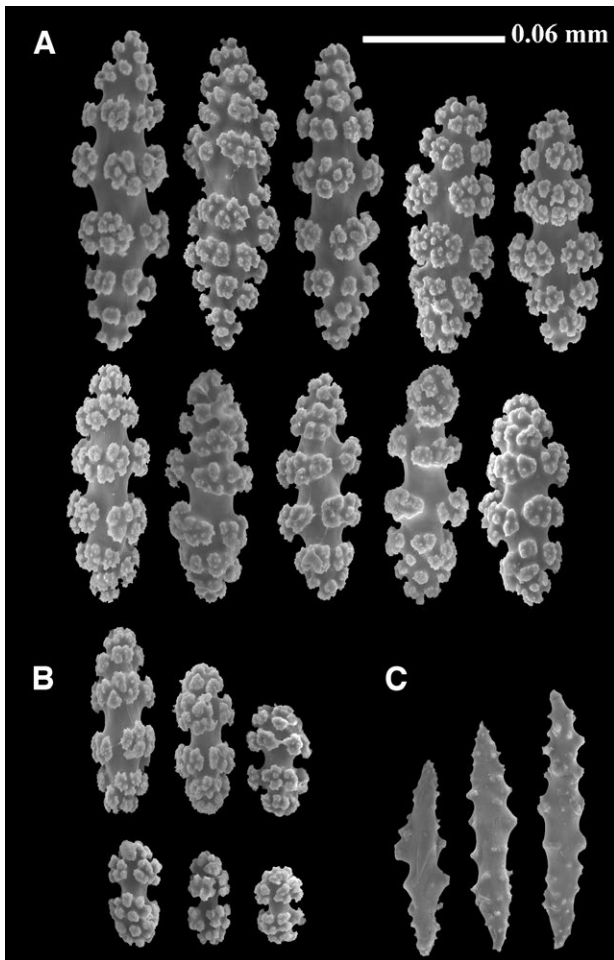


Fig. 13 – *Pacifigorgia flavimaculata* (MNCN 2.04/1178) SEM photographs. Coenenchymal sclerites, A, acute spindles; B, capstans; C, anthocodial sclerites, flattened rods.

2011, one whole colony. MZB (2016-2994), Los Frailes, Manabí (Ecuador), 1°30'14"S 80°48'33"W, 10 m depth, 20 Feb. 2012, one whole colony. UTI (MZUTI-Inv07), Los Frailes, Manabí (Ecuador), 1°30'14"S 80°48'33"W, 10 m depth, 20 Feb. 2012, one whole colony. UTI (MZUTI-Inv08), Los Frailes, Manabí (Ecuador), 1°30'14"S 80°48'33"W, 15 m depth, 10 March 2012, one whole colony. MECN (Ant0047), El Chichó, Manabí (Ecuador), 1°31'15.39"S 80°49'21.37"W, 20 m depth, 24 Nov. 2013, one whole colony. MECN (Ant0048), Punta Machalilla, Manabí (Ecuador), 1°28'33.53"S 80°47'38.04"W, 13 m depth, 24 Nov. 2013, one whole colony.

*Additional examined materials:* *Pacifigorgia flavimaculata* MCZ 51922, type material, Punta Salsipuedes (Costa Rica), 3 m depth, 22 Jan 1994.

**Description.** The colonies reach up to 105 mm in length by 70 mm in width and are formed by two parallel fans. The holdfast was not observed (Fig. 12A). The branches are cylindrical, ranging from 1.5-2.2 mm in diameter (1-3 meshes cm<sup>-2</sup>). The branches arise directly from the base and have incomplete anastomoses that form a loose, open and irregular network. The meshes are rounded-square, oblong or triangular (19×5 mm, 9×4 mm) (Fig. 12B). There are no distinct mid-ribs. There are long end-branchlets (up to 11 mm). The polyps retract within prominent polyp-mounds having rounded apertures, placed all around the branches in multiple rows. The colour of the colony is light brown

when alive and yellow intermingled with light brown and light purple when dry. The coenenchymal sclerites are pink and light yellow, some of them bicoloured (Fig. 12C). They are spindles (0.14×0.04 mm) having acute ends and 4-5 whorls of tubercles; blunt spindles (0.11×0.04 mm) with 4 whorls of tubercles (Figs 12C, 13A, B), and capstans (0.09×0.04 mm) with tuberculate ends, warty or smooth (Figs 12C, 13B). The dominant sclerite types are straight or bent spindles, some of them with a marked waist. The anthocodial sclerites are orange flattened rods, up to 0.13-0.14 mm in length and 0.02 mm in width, with pointed projections, and acute and warty ends (Figs 12C, 13C).

**Geographic and bathymetric distribution.** *Pacifigorgia flavimaculata* has only been reported from the type locality in Costa Rica at 3 m depth (Breedy and Guzmán 2003) (Fig. 25F). In the present study, it was observed at a 3-20 m depth.

Breedy and Guzmán (2003) pointed out that this species was only observed in the type locality (Punta Salsipuedes, Costa Rica), despite a significant sampling effort in the neighbouring areas. Therefore, our record from Ecuador is important in defining the geographic (and bathymetric) distribution of this species.

**Remarks.** Colonies of this species mainly form loose and irregular networks, sometimes almost pseudoanastomosed, yellow or brown in colour but with purplish or yellowish spots around a prominent polyp-mound, making the species easily recognizable.

The Ecuadorian specimens have a quite constant set of features in comparison with the type specimens examined (Breedy and Guzmán 2003, pers. observ.), except for the size of the anthocodial sclerites, which are longer (up to 0.13-0.14 mm, instead of up to 0.08-0.09 mm) (see Breedy and Guzmán 2003: 23, Table 3).

### *Pacifigorgia irene* Bayer, 1951 (Figs 14, 15)

**Synonymy.** See Breedy and Guzmán (2002: 825).

**Newly collected examined material:** BEIM (0091), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 10 m depth, 8 Dic. 2011, one whole colony. MNCN (2.04/1174), Punta Mala, Manabí (Ecuador), 1°33'41.37"S 80°50'8.79"W, 12 m depth, 16 Feb. 2012, one whole colony. MZB (2016-2995), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 15 m depth, 15 April 2012, one whole colony. MECN (Ant0062), Los Frailes, Manabí (Ecuador), 1°30'14"S 80°48'33"W, 15 m depth, 10 March 2012, one whole colony. MECN (Ant0054), El Chichó, Manabí (Ecuador), 1°31'15.39"S 80°49'21.37"W, 20 m depth, 24 Nov. 2013, one whole colony. MECN (Ant0055), Islote La Viuda, Manabí (Ecuador), 1°26'5.95"S 80°46'7.30"W, 15 m depth, 23 Nov. 2013, one whole colony.

**Additional examined materials:** *Pacifigorgia irene* USNM 49379, type material, Nicoya (Costa Rica), no depth given, Mar 1927; USNM 33611, type material, Costa Rica, no depth given, data unknown. *Pacifigorgia irene* MZC 36232, Gulf of Fonseca (Costa Rica), no depth given, data unknown.

**Description.** The colonies reach up to 600 mm in length by 500 mm in width, and are formed by one to several fans (Fig. 14A). The holdfast was not observed. The branches are slender, ranging from 0.3

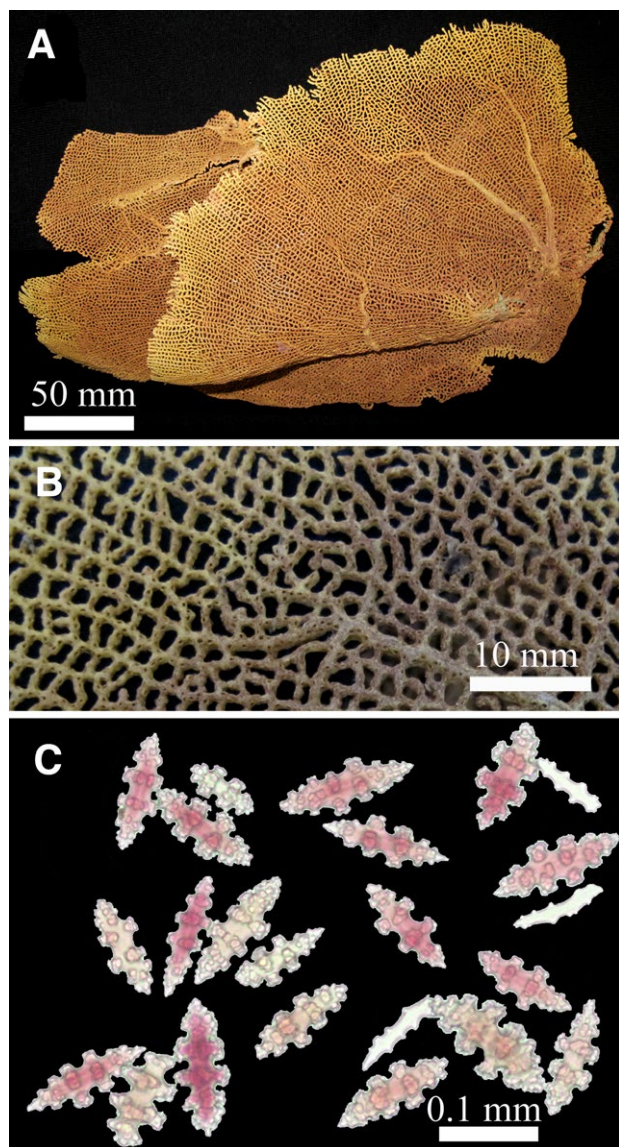


Fig. 14. – *Pacifigorgia irene* (MNCN 2.04/1174). A, colony; B, detail of a branch; C, light micrograph of sclerites.

to 0.7 mm in diameter (about 35 meshes  $\text{cm}^{-2}$ ). The branches form a fine and regular network. The network consists of small and squarish meshes (usually up to 1.2 by 0.9 mm) (Fig. 14B). The fans have several stout, rounded midribs. There are short end-branchlets (<1 mm long). The polyps retract within slightly raised and crowded polyp-mounds, placed all around the branches. The colour of the colony is reddish intermingled with yellow both when alive and dry, with a slight discoloration at the edges of the colony. The coenenchymal sclerites are red, lemon yellow and orange, some of them bicoloured (Fig. 14C). They consist of long spindles (0.17×0.05 mm) having acute ends and 5-6 whorls of tubercles (Figs 14A, 15A), and capstans (0.08×0.04 mm) with tuberculated ends (Fig. 15 B). In our specimens the dominant sclerite type are acute straight or bent spindles, some with a marked waist. Some crosses up to 0.06 by 0.05 mm occur as well (Fig. 15C). The anthocodial sclerites are light yellow and light pink flattened rods, up to 0.11 mm in

length and 0.02 mm in width, with smooth or slightly lobed borders (Fig. 14C).

**Geographic and bathymetric distribution.** *Pacifigorgia irene* has been previously reported in Panama and Costa Rica at 12-33 m depth (Bayer 1951, Breedy and Guzmán 2002, 2003) (Fig. 25G). Our finding represents a considerable southerly extension of its known distribution.

**Remarks.** This species is easily recognized by its characteristic morphology, showing a wide fan or fans, marked and thick midribs and small meshes. Some coenenchymal sclerites have been considered here as elongated capstans instead of blunt spindles, as commonly described. The morphology of some sclerites are not always easy to define in this taxon, and they can also be considered transitional forms of blunt spindles, depending on the development of the two opposite distal processes on the longitudinal axis with respect to

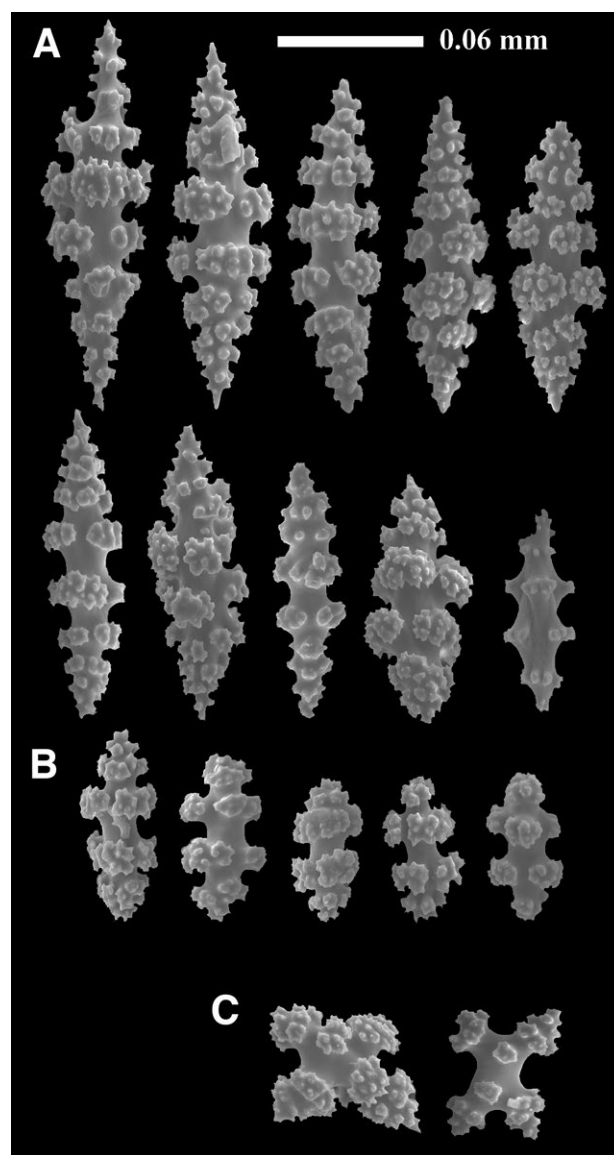


Fig. 15. – *Pacifigorgia irene* (MNCN 2.04/1174) SEM photographs. Coenenchymal sclerites, A, spindles; B, capstans; C, four-radiates.

the two central whorls with alternate tubercles (Vargas et al. 2010a). In any case, if these sclerites are considered blunt spindles, they would have equivalent forms with respect to the original description of this species. In situ specimens seen during this study show a more intense reddish and yellow colour than Costa Rican specimens. Bayer (1951) described the colour of the colony as dark purple with greenish borders, but this is not the case in the Ecuadorian material, where colour only fades slightly at the edges of the fans.

*Pacifigorgia machalilla* n. sp.  
(Figs 16-18)

*Examined material:* Holotype: MECN (Ant0061), Cope, Manabí (Ecuador), 1°43'34"S 80°59'85"W, 23 m depth, 8 Dic. 2012, one whole colony without holdfast. Paratypes: MBZ (2016-2996), Los Ahorcados, Manabí (Ecuador), 1°40'44"N 80°50'08"W, 10 m depth, 1 Dic. 2011, one whole colony. MNCN (2.04/1181), Cope, Manabí (Ecuador), 1°43'34"S 80°59'85"W, 23 m depth, 8 Dic. 2012, a fragment of the colony. Other material: UTI (Inv262), Cope, Manabí (Ecuador), 1°43'34"S 80°59'85"W, 23 m depth, 8 Dic. 2012, one whole colony. BEIM (0095), Isla de la Plata, Manabí (Ecuador), 1°16'25.84"S 81°4'11.70"W, 22 m depth, 22 Feb. 2012, two whole colonies. MECN (Ant0058), Los Ahorcados, Manabí (Ecuador), 1°40'44"N 80°50'08"W, 10 m depth, 27 Feb. 2010, one whole colony. MECN (Ant0059), Los Ahorcados, Manabí (Ecuador), 1°40'44"N 80°50'08"W, 10 m depth, 1 Dic. 2011, one whole colony.

*Description of the holotype.* The colony is formed by a single fan 250 mm in length by 290 mm in width (Fig. 16A). The holdfast is circular, up to 15 mm in diameter. The branches are cylindrical, ranging from 1.5–2 mm in diameter (7–9 meshes cm<sup>-2</sup>) and the end-branchlets reach up to 9 mm in length, and have blunt tips. The network is regular and complete, and is formed of mostly square and rectangular meshes (4×5 mm, 10×3 mm); in some cases, meshes are oblong (Fig. 16B). There are five or six prominent, long and strong midribs, which divide into others that progressively fuse among the anastomosed structure of the mesh (Fig. 16A). The polyps retract within slightly raised or flat polyp-mounds with slit-like apertures, placed in multiple rows all around the branches. The colour of the colony is intense red-brown when dry and bluish-grey when alive. The coenenchymal sclerites are pink, light yellow and orange, some of them bicoloured (Fig. 16C). They are spindles (up to 0.20×0.04 mm) having acute ends and 5–6 whorls of tubercles (Figs 16A, 17A); blunt spindles are absent, and there are capstans (up to 0.7×0.03 mm) with tuberculate ends (Figs 16C, 17B). The dominant sclerites are spindles, straight or bent, some of them with a distinct waist. There are irregular crosses with different branch lengths (up to 0.11×0.05 mm) (Fig. 17C). The anthocodial sclerites are pink, light orange and light yellow in colour, most of them bicoloured; flattened rods (0.11×0.02 mm) with short pointed or lobe-like marginal projections and acute or rounded ends also occur. There are also platelets (0.06×0.02 mm) (Figs 16C, 17D).

*Variability.* This new species is fairly constant with regard to colonial and sclerome characters. However, in some specimens there are small secondary fans grow-

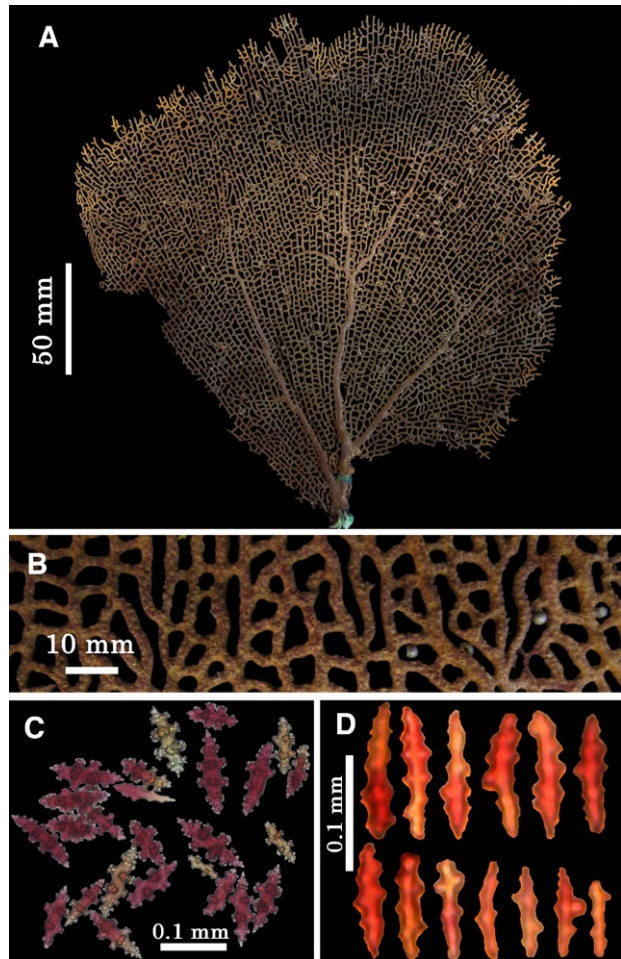


Fig. 16. – *Pacifigorgia machalilla* n. sp. Holotype MECN (Ant0053). A, colony; B, detail of anastomosed branches; C, light micrograph of sclerites; D, light micrograph of anthocodial sclerites.

ing parallel to the primary fan. In addition, in some small colonies (about 100 mm in length) the midrib is not very obvious or even absent, or is only formed by two short basal branches.

*Geographic and bathymetric distribution.* *Pacifigorgia machalilla* is only known from the type locality in Cope, Los Ahorcados, and Isla de la Plata (continental coast of Ecuador), living on rocky bottoms in shallow waters at a depth of 10–23 m.

*Etymology.* The new species is dedicated to the National Park of Machalilla (Ecuador) and its staff for their constant support and help during field work. Name considered as a noun in apposition.

*Comparison with other Pacifigorgia species.* *Pacifigorgia machalilla* is morphologically close to *P. exilis* and *P. firma*, having similar networks with the presence of a midrib, and similar mesh size (9–11.5 meshes cm<sup>-2</sup>) and anastomosis. The network in *P. machalilla* is formed by almost square or rectangular meshes, 10×3 mm, 4×5 mm, and 12×3 mm, 6×2 mm in *P. firma* (Table 4). *Pacifigorgia exilis* also has a similar type of network (open or closed and regular); however, it

Table 4. – Comparative morphological features of *Pacifigorgia machalilla* n. sp. with its closest congeners.

Characters	<i>Pacifigorgia machalilla</i>	<i>Pacifigorgia exilis</i>	<i>Pacifigorgia firma</i>
Colour of colony	intense red-brown	red-orange	light brown/ dark purple
Number of fans	one or two small	several	one (or two)
Number of meshes cm <sup>-2</sup>	7-9	7 - 9	11.5
Mesh shape and maximum	square -rectangular/ regular	square - oblong / irregular	rectangular /
Mesh size (mm)	10×3 - 4×5	3×0.5	regular 12×3 - 6×2
Presence of midrib	present	present	present
Polyp-mounds	slightly raised or flat	slightly raised	slightly raised
Colour of sclerites	pink /yellow/orange	red / yellow	red/pale yellow/orange
Acute spindles max. size (mm)	0.20 length 0.04 width	0.11 length 0.05 width	0.11 length 0.05 width
Blunt spindles max. size (mm)	absent	0.09 length 0.04 width	absent
Capstan max. size (mm)	0.07 length 0.03 width	0.07 length 0.04 width	0.09 length 0.05 width
Crosses or radiates	present	absent	absent
Anthocodial max. size (mm)	0.11 length 0.02 width	0.12 length 0.02 width	0.10 length 0.03 width
Shape and colour of anthocodial rods; Bicolour sclerites	flattened rods; pink/ orange / light yellow present; coenenchyme and anthocodial	flattened rods; yellow present; coenenchyme	flattened rods; light orange present; coenenchyme
References	This paper	Breedy and Guzmán 2002	Breedy and Guzmán 2003

has smaller square or oblong meshes (0.5×3 mm). Additionally, *P. machalilla* has blunt spindles while they are absent in both *P. exilis* and *P. firma*, and the acute spindles are larger in *P. machalilla* (up to 0.20×0.04 mm) than in *P. exilis* (up to 0.11×0.05 mm) and *P.*

*firma* (up to 0.11×0.05 mm). Finally, *P. machalilla* has crosses or radiate forms, which are lacking in the other two species.

The molecular distance matrix (COII + Igr + COI + MutS) shows that, within the genus *Pacifigorgia*,

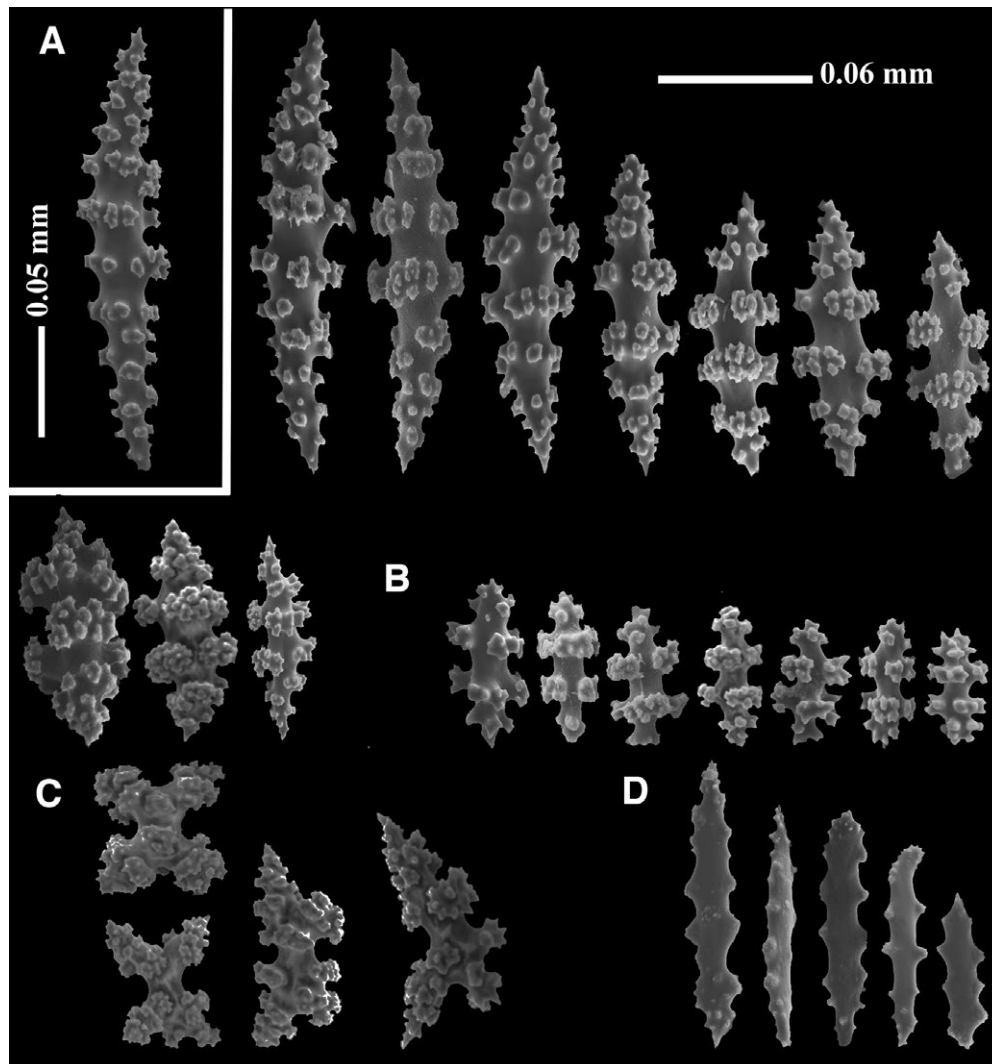


Fig. 17. – *Pacifigorgia machalilla* n. sp. Holotype MECN (Ant0053). SEM photographs. Coenenchymal sclerites, A, acute spindles; B, capstans; C, irregular crosses or four-radiates and butterfly; D, anthocodial sclerites, flattened rods.



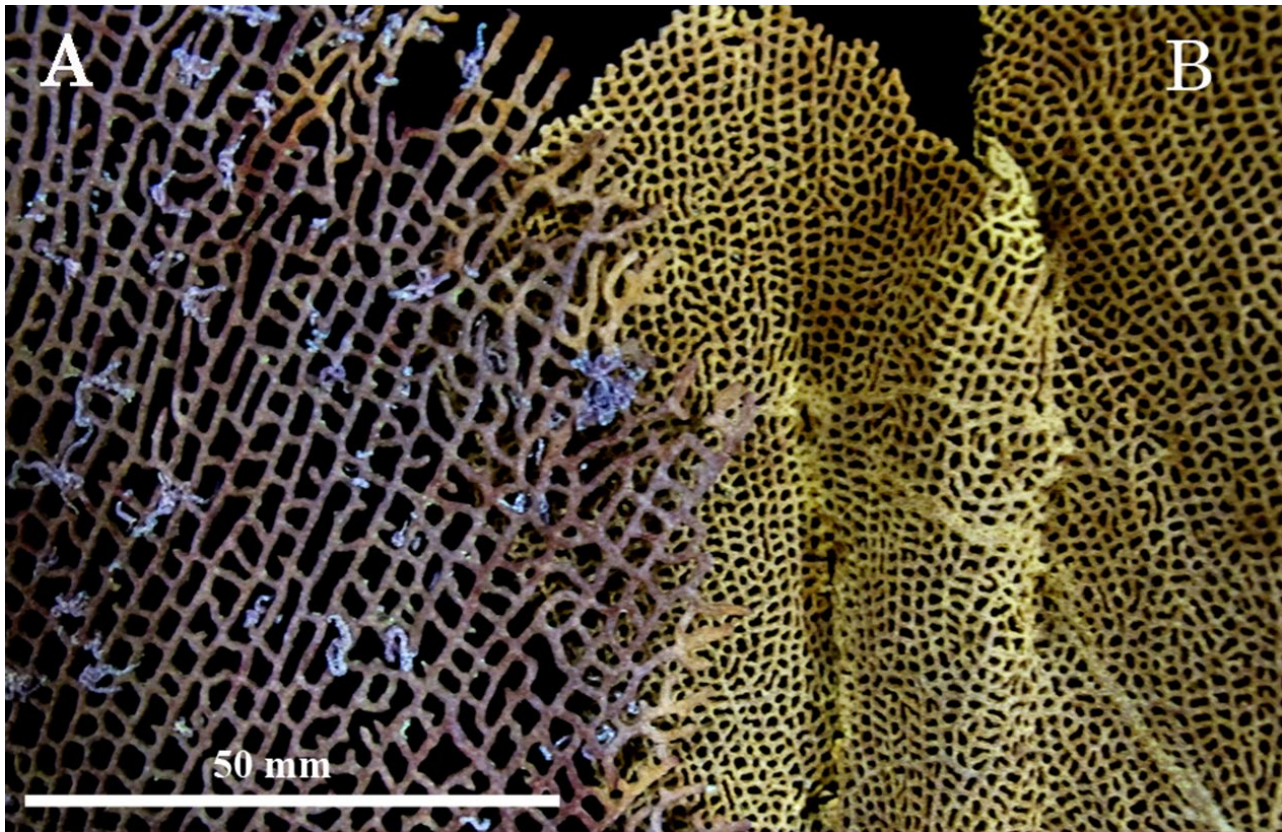


Fig. 18. – Comparison of the anastomosed branches in *Pacifigorgia machalilla* n. sp., holotype (A) and *Pacifigorgia irene* (B).

Table 5. – Genetic divergence matrix for the species examined based on the COII + Igr + COI and MutS-1 gene sequence.

	1	2	3	4	5	6	7	9	9	10	11	12	13	14
<i>P. firma</i>	1													
<i>P. rubicunda</i> (1)	2	0.0127												
<i>P. rubicunda</i> (2)	3	0.0128	0.0000											
<i>P. smithsoniana</i>	4	0.0024	0.0114	0.0114										
<i>P. stenobrochis</i>	5	0.0055	0.0108	0.0108	0.0042									
<i>P. catedralensis</i> (1)	6	0.0006	0.0115	0.0115	0.0024	0.0042								
<i>P. catedralensis</i> (2)	7	0.0006	0.0116	0.0116	0.0024	0.0043	0.0000							
<i>P. sculpta</i>	8	0.0060	0.0114	0.0114	0.0048	0.0018	0.0048	0.0049						
<i>P. exilis</i>	9	0.0133	0.0006	0.0006	0.0119	0.0118	0.0121	0.0122	0.0116					
<i>P. machalilla</i> n. sp. (1)	10	0.0030	0.0108	0.0108	0.0006	0.0036	0.0018	0.0018	0.0039	0.0110				
<i>P. machalilla</i> n. sp. (2)	11	0.0030	0.0108	0.0108	0.0006	0.0036	0.0018	0.0018	0.0039	0.0110	0.0000			
<i>P. machalilla</i> n. sp. (3)	12	0.0030	0.0108	0.0108	0.0006	0.0036	0.0018	0.0018	0.0039	0.0110	0.0000	0.0000		
<i>P. bayeri</i>	13	0.0012	0.0114	0.0114	0.0024	0.0042	0.0000	0.0000	0.0048	0.0120	0.0018	0.0018	0.0018	
<i>P. media</i>	14	0.0139	0.0006	0.0006	0.0125	0.0112	0.0126	0.0128	0.0118	0.0000	0.0118	0.0118	0.0118	0.0125
<i>P. irene</i>	15	0.0036	0.0114	0.0108	0.0012	0.0042	0.0018	0.0018	0.0048	0.0120	0.0006	0.0006	0.0006	0.0024 0.0125

the genetic divergence among species was close to 1% or lower in most cases. The new species showed no intraspecific variation (Table 5). Despite the fact that *P. machalilla* is closely related morphologically to *P. firma* and *P. exilis*, as stated previously, the three species are clearly separated molecularly. The maximum genetic divergence is 0.3% between *P. machalilla* and *P. firma*, and is 1% between *P. machalilla* and *P. exilis* (Table 5). However, *Pacifigorgia machalilla* is closely related molecularly to *P. irene* and *P. smithsoniana* (Breedy and Guzmán, 2004). The maximum genetic divergence between *P. machalilla* and *P. smithsoniana* or *P. irene* is 0.06%. However, in a thorough analysis of the sequences for these three species, we observed the following differences: 1) there is a silent mutation in COI for *P. machalilla* and *P. smithsoniana*; and 2)

there is a mutation in the first base of one triplet which changes Lys to Val, in COII for *P. machalilla* and *P. irene*. It may be interesting to extend the sequencing based on COII in the search of additional variable segments in the mtDNA of this group of species.

Despite its molecular similarities, there are clear morphological differences among these three species. *Pacifigorgia machalilla* differs from *P. smithsoniana* in having a midrib, and larger acute spindles (0.20×0.04 vs 0.14×0.05 mm). *Pacifigorgia machalilla* differs from *P. irene* in that its anastomosis forms a network of almost square or rectangular meshes 10×3 mm, 4×5 mm (only 2×0.9 mm in *P. irene*), its branches are larger, ranging from 1.5–2 mm in diameter (7–9 meshes cm<sup>-2</sup>), while the branches in *P. irene* are 0.5–0.7 mm in diameter (35 meshes cm<sup>-2</sup>), with longer end-branchlets (up

to 9 mm long), while these are very short in *P. irene*, less than 1 mm (Fig. 18). Finally, bicolour anthocodial sclerites are a unique feature for *P. machalilla*.

***Pacifigorgia rubicunda* Breedy and Guzmán, 2003**  
(Figs 19, 20)

*Newly collected examined material:* MECN (Ant0023), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 10 m depth, 27 Feb. 2010, two whole colonies. MECN (Ant0025), Punta Mala, Manabí (Ecuador), 1°33'41.37"S 80°50'8.79"W, 15 m depth, 15 Feb. 2012, three whole colonies. BEIM (0083), Isla de la Plata, Manabí (Ecuador), 1°16'25.84"S 81°4'11.70"W, 22 m depth, 19 Feb. 2012, one whole colony. BEIM (0082), Los Frailes, Manabí (Ecuador), 1°30'14"S 80°48'33"W, 10 m depth, 10 March 2012, one whole colony. BEIM (0081), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 5 m depth, 27 Feb. 2010, one whole colony. MNCN (2.04/488), Isla de la Plata, Manabí (Ecuador), 1°16'25.84"S 81°4'11.70"W, 20 m depth, 19 Feb. 2012, one whole colony. MNCN (2.04/489), Punta Mala, Manabí (Ecuador), 1°33'41.37"S 80°50'8.79"W, 12 m depth, 27 Feb. 2012, one whole colony. UTI (MZUTI-Inv04) Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 10 m depth, 27 Feb. 2010, one whole colony. MZB (2016-2997), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 5 m depth, 27 Feb. 2010, one whole colony. MZB (2016-2998) Isla de la Plata, Manabí (Ecuador), 1°16'25.84"S 81°4'11.70"W, 20 m depth, 19 Feb. 2012, one whole colony.

*Additional examined materials:* *Pacifigorgia rubicunda* MCZ 51917, type material, Gulf of Chiriquí (Panama), 14 m, Dec. 2001.

*Description.* The colonies reach up to 40 mm in length by 160 mm in width, and are formed by several fans. The secondary fans sprout from the main fan at a right angle and spread perpendicularly to form new fans. Several fans may reunite, adhering together and producing square arrangements like beehives. A short stem divides close to the holdfast (Fig. 19A), which is up to 12 mm in diameter. The branches are cylindrical, ranging from 0.8-1 mm in diameter (9-11 meshes cm<sup>-2</sup>). The end-branchlets are short. The network is closed and regular; it is formed of mostly square or oblong meshes (10×3 mm, 5.5×3 mm) (Fig. 19B). The polyps retract within slightly raised polyp-mounds with slit-like apertures, placed in multiple rows all around branches. The colour of the colony is brownish-orange when alive or preserved and a conspicuous burnt sienna colour speckled with yellow when dry. The coenenchymal sclerites are pink, orange and lemon yellow, bicoloured and multicoloured (Fig. 19C). They are spindles (0.1×0.03 mm) having acute ends and 10-12 whorls of tubercles (Figs 19C, 20A); blunt spindles (0.1×0.04 mm) with 4-5 whorls of tubercles (Figs 19C, 20B); and capstans (0.07×0.03 mm) with tuberculate ends (Figs 19C, 20C). The dominant sclerite types are blunt spindles straight or bent, some with a marked waist. Crosses are lacking.

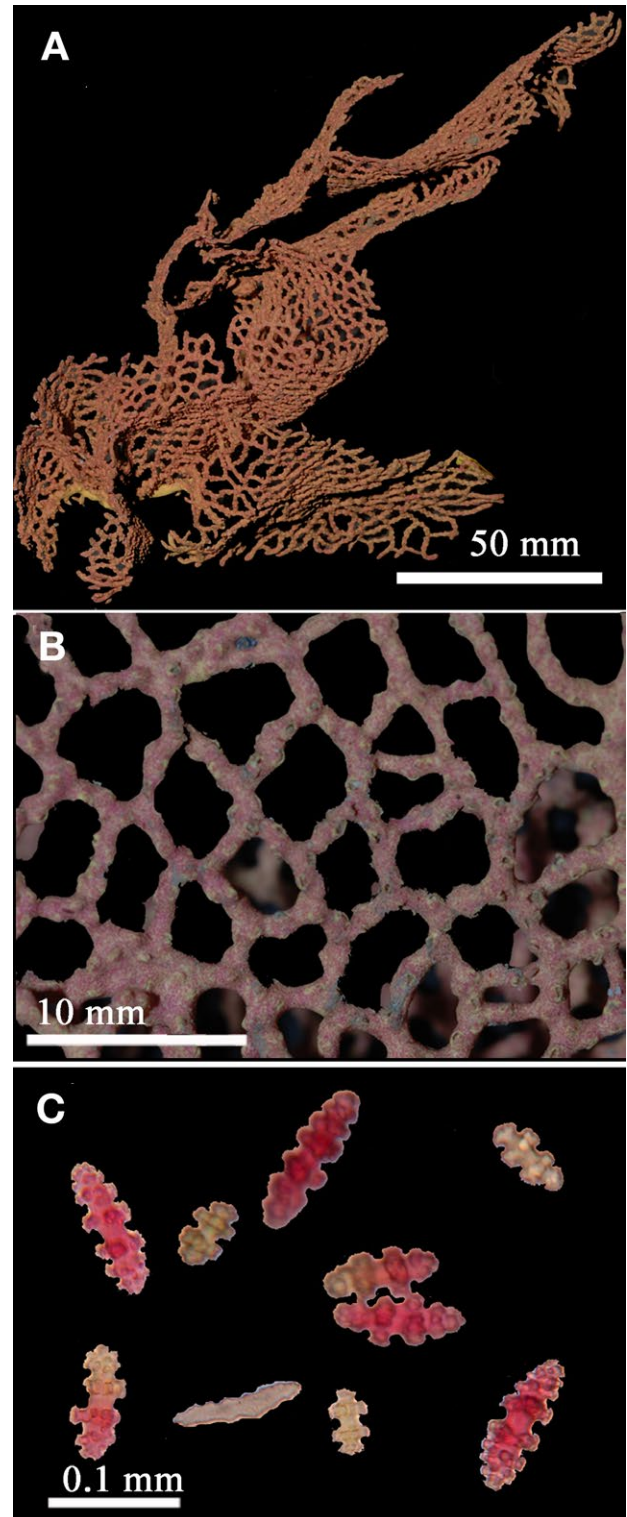


Fig. 19. – *Pacifigorgia rubicunda* (MZB 2016-2997). A, colony; B, detail of a branch; C, light micrograph of sclerites.

The anthocodial sclerites are yellow flattened rods up to 0.12 mm in length and 0.02 mm in width, with short lobe-like marginal projections, and acute and warty or smooth ends (Figs 19C, 20C).

*Geographic and bathymetric distribution.* *Pacifigorgia rubicunda* was originally described by Breedy

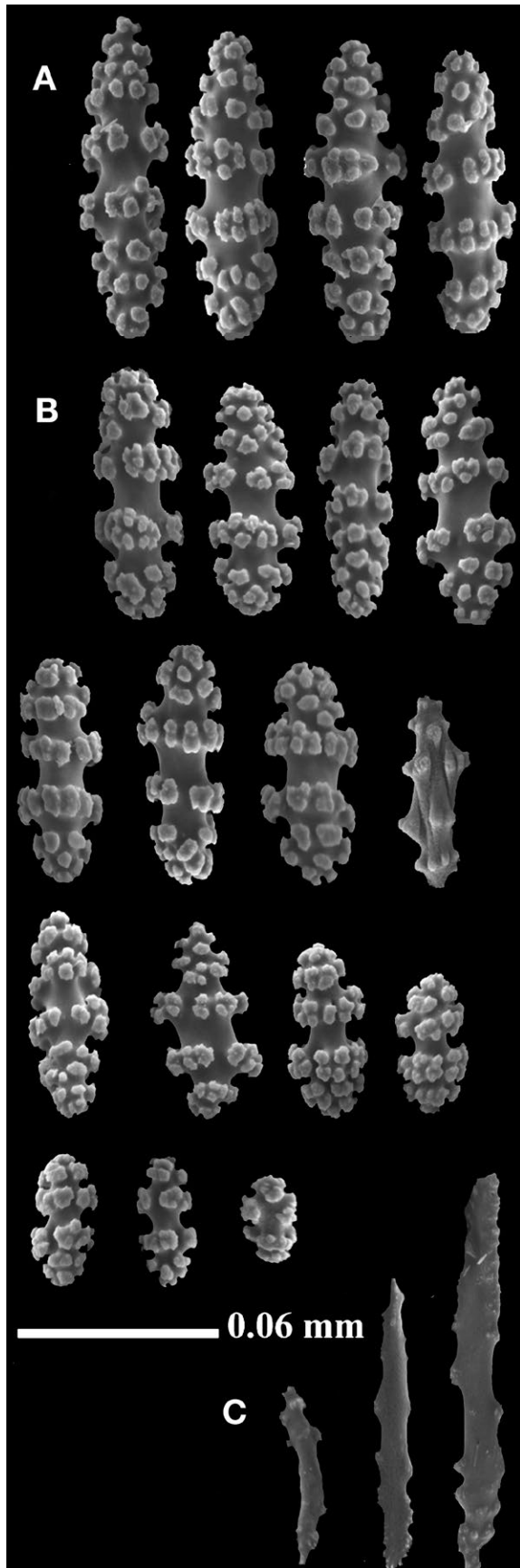


Fig. 20. – *Pacifigorgia rubicunda* SEM photographs. Coenenchymal sclerites, A, spindles; B, captans; C, anthocodial sclerites, flattened rods.

and Guzmán (2003) from Costa Rica (Fig. 25I). The geographic range of the species is here extended to Ecuador (Manabí). Its bathymetric distribution ranges from 5 to 30 m depth (Breedy and Guzmán 2003).

*Remarks.* There are some morphological differences between the specimens of *P. rubicunda* found in Ecuador and the original description of this species by Breedy and Guzmán (2003). The colour of sclerites is very similar (orange and yellow); however, in Ecuadorian material most of the sclerites are pink (bicoloured or multicoloured) and colourless sclerites are lacking. If compared with the type material (6–9 meshes  $\text{cm}^{-2}$ , 5–1.2×2.5–0.9 mm) (Breedy and Guzmán 2003), in our colonies the network is less compact, usually more elongate and larger, and there are no crosses.

Finally, the size of sclerites and anthocodial rods seem to be somewhat larger in the type material (spindles 0.09–0.12×0.03–0.04 mm, capstans 0.04–0.09×0.02–0.04 mm; anthocodial rods 0.14×0.05 mm) than in the Ecuadorian material (spindles 0.1×0.03 mm, capstans 0.07×0.03 mm; anthocodial rods 0.12×0.02 mm). In most cases, *P. rubicunda* was found forming colonies similar to beehives, irregularly stretching across the rocks. The midrib extends from the holdfast in parallel to the substrate, but the unique point of union is the holdfast, which is diagnostic for this species (Breedy and Guzmán 2003: 43).

Newly collected material of *P. rubicunda* from Ecuador permits the description of variability of some characters. The species is reported herein for the first time since its original description in Costa Rica.

*Pacifigorgia stenobrochis* (Valenciennes, 1846)  
(Figs 21, 22)

Synonymy. See Breedy and Guzmán (2002: 833).

*Newly collected examined material:* BEIM (0090), Salinas, Santa Elena (Ecuador), 2°12'50.01"S 80°56'5.93"W, 15m depth, 9 Dic. 2011, a fragment of colony. MNCN (2.04/1176), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 10 m depth, 12 Dic. 2011, a fragment of colony. MNCN (2.04/1177), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 13 m depth, 7 Dic. 2012, a fragment of colony. MZB (2016-2999), Punta Mala, Manabí (Ecuador), 1°33'41.37"S 80°50'8.79"W, 15 m depth, 12 Dic. 2012, a fragment of colony. MNCN (2.04/1175), Salinas, Santa Elena (Ecuador), 2°12'50.01"S 80°56'5.93"W, 15m depth, 11 Dic. 2011, a fragment of colony. MECN (Ant0065), Los Ahorcados, Manabí (Ecuador), 1°40'44"S 80°50'08"W, 10 m depth, 15 Mar. 2012, a fragment of colony. MECN (Ant0064), Punta Mala, Manabí (Ecuador), 1°33'41.37"S 80°50'8.79"W, 15 m depth, 15 Dic. 2011, a fragment of colony. MECN (Ant0063), Punta Mala, Manabí (Ecuador), 1°33'41.37"S 80°50'8.79"W, 13 m depth, 6 April 2012, a fragment of colony. MECN (Ant0051), El Chichó, Manabí (Ecuador), 1°31'15.39"S 80°49'21.37"W, 20 m depth, 24 Nov. 2013, a fragment of colony. MECN (Ant0052), El Burbullón, Manabí (Ecuador), 1°28'23.59"S 80°51'23.04"W, 25 m depth, 23 Nov. 2013, a fragment of colony. MECN (Ant0053), Islote La Viuda, Manabí (Ecuador), 1°26'5.95"S 80°46'7.30"W, 15 m depth, 23 Nov. 2013, a fragment of colony.

*Additional examined materials:* *Rhipidigorgia stenobrochis* MNHN-IK 1719, type material, New Zealand, no depth given, 1839. *Pacifigorgia stenobrochis* var. *engelmanni* (Horn 1860) MCZ 4042, Acapulco (Mexico), no depth given, 1856–1860; *Pacifigorgia stenobrochis* MCZ 28753, Mexico, no depth given, data unknown; *Gorgonia stenobrochis* NHM 1930.6.17.12 St. George (Mexico), no depth given, data unknown. *Pacifigorgia stenobrochis* USNM 49378, Gulf of Nicoya (Costa Rica), no depth given, March 1927.

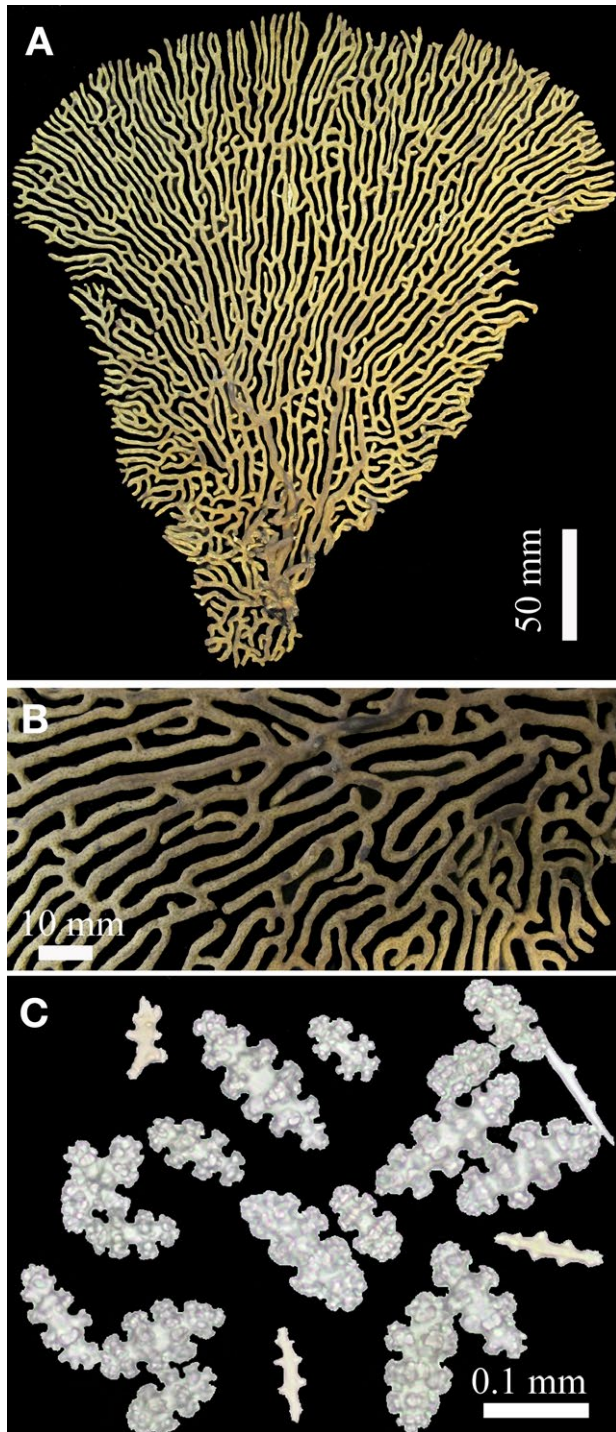


Fig. 21. – *Pacifigorgia stenobrochis* (MNCN 2.04/1175). A, colony; B, detail of a branch; C, light micrograph of sclerites.

*Pacifigorgia stenobrochis* USNM 8847, Baja California (Mexico), no depth given, 1911.

**Description.** The colonies are up to 280 mm in length by 270 mm in width and are formed by a single fan that may divide into smaller fans. The holdfast was not observed (Fig. 21A). The branches are rounded, ranging from 1.1-2.3 mm in diameter (2 meshes cm<sup>-2</sup>). The branches arise directly from the base and have an open and irregular network. The meshes are rectangu-

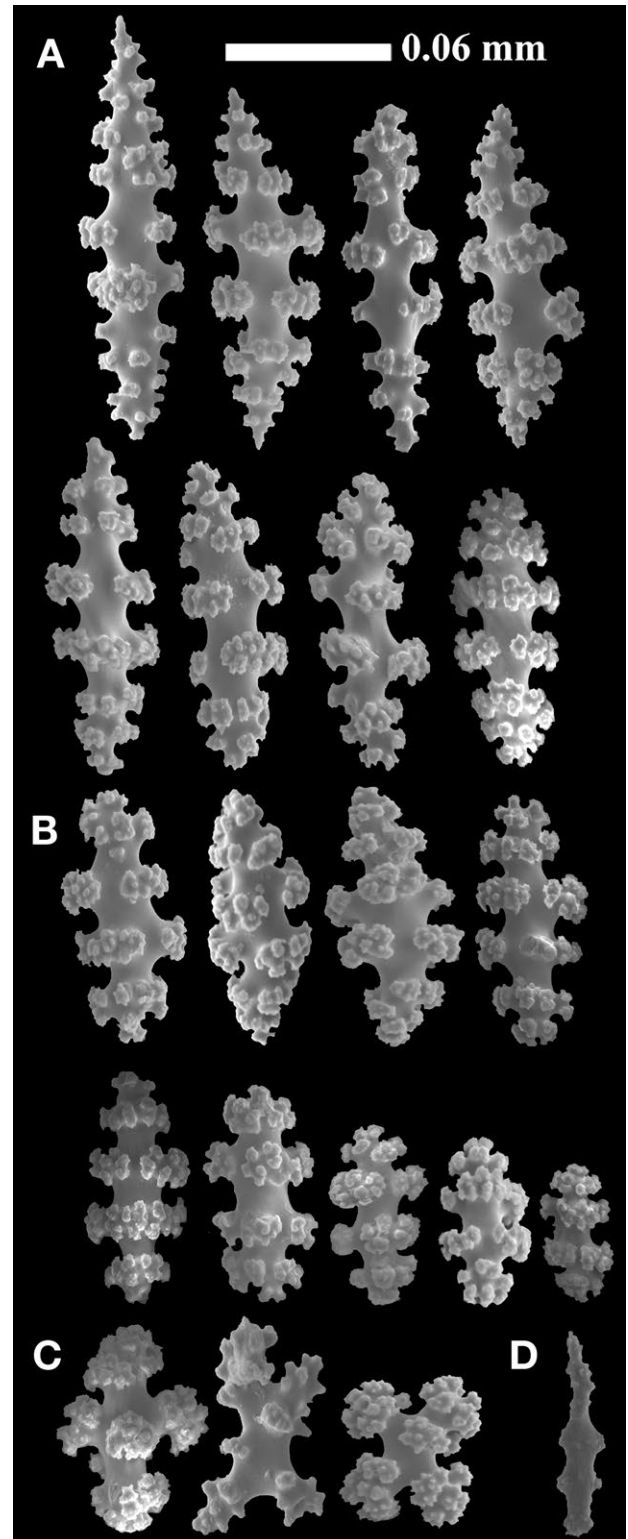


Fig. 22. – *Pacifigorgia stenobrochis* (MNCN 2.04/1175). SEM photographs. Coenenchymal sclerites, A, spindles; B, captans; C, crosses; D, anthocodial sclerites, flattened rods.

lar or oblong (55×6 mm, 10×5 mm) (Fig. 21B). There are no distinct midribs. There are long end-branchlets (up to 26 mm). The polyps retract within flat polypmounds, placed throughout the branches, on both sides. The colour of the colony is light brown or dark yellow when alive and yellow intermingled with brown. The

coenenchymal sclerites are light yellow (Fig. 21C). There are long acute spindles (0.16×0.04 mm), straight or bent, some with a marked waist, having 8 whorls of tubercles, and they are the dominant sclerite types. In addition, there are blunt spindles (0.12×0.04 mm) with 6 whorls of tubercles (Figs 21C, 22A), and capstans (0.09×0.04 mm) with tuberculate ends (Figs 21A, 22B). Some crosses up to 0.08 by 0.06 mm are also found (Fig. 22C). The anthocodial sclerites are light orange in colour, with flattened rods up to 0.09 mm in length and 0.02 mm in width, with smooth or slightly lobed borders (Figs 21A, 22D).

*Geographic and bathymetric distribution.* *Pacificorgia stenobrochis* has been reported in Mexico, El Salvador, Nicaragua, Costa Rica, Panama, Peru (Verrill 1868, Breedy and Guzmán 2003) and Ecuador (current study) at 3–30 m depth. In the original description, New Zealand is indicated as the type locality, which appears to be an error (see Valenciennes 1846, Breedy and Guzmán 2002, 2003) (Fig. 25J).

Generally, colonies of this species occur both solitary and mixed with other species in the same environment. The Ecuador records nicely connect the previously known localities from Mexico and Peru.

*Remarks.* The chromatic variability of the colonies and sclerites of this species has been known for a long time (Hickson 1928, Breedy and Guzmán 2002, 2003). In the Ecuadorian material studied here, all the coenenchymal sclerites are yellow. Pink and grey sclerites noted by other authors are lacking. The colour of Ecuadorian colonies varies between yellow and orange hues, while it is said to be reddish purple and brown in previous descriptions.

The presence of thick and robust branches, shape of the mesh and absence of the midrib are diagnostic for *P. stenobrochis*, and readily separate it from similar species, such as *P. firma*.

#### Genus *Eugorgia* Verrill, 1868

Synonymy. See Breedy et al. (2009: 8).

#### *Eugorgia daniana* Verrill, 1868 (Figs 23, 24)

Synonymy. See Breedy et al. (2009: 17).

*Newly collected examined material:* MECN (Ant0033), Salinas, Santa Elena (Ecuador), 2°12'50.01"S 80°56'5.93"W, 15 m depth, 9 Dic. 2011, one whole colony. MNCN (2.04/1173), Salinas, Santa Elena (Ecuador), 2°12'50.01"S 80°56'5.93"W, 15 m depth, 10 Dic. 2011, one whole colony. MECN (Ant0060), Punta Gruesa, Manabí (Ecuador), 1°33'38.15"S 80°50'5.28"W, 18 m depth, 20 Feb. 2013, one whole colony. MECN (Ant0056), El Chichó, Manabí (Ecuador), 1°31'15.39"S 80°49'21.37"W, 20 m depth, 24 Nov. 2013, one whole colony. MNCN (2.04/1179), El Burbullón, Manabí (Ecuador), 1°28'23.59"S 80°51'23.04"W, 25 m depth, 23 Nov. 2013, one whole colony.

*Additional examined materials:* *Eugorgia daniana* MCZ 7080, type material, Gulf of Nicoya (Costa Rica), no depth given, May 1868; MCZ 723, type material, Las Perlas (Panama), no depth given, 1866–1867; NHM 69.4.15.55, type material, Panama, no depth given, data unknown. *Eugorgia daniana* MCZ 02138, Cali (Colombia),

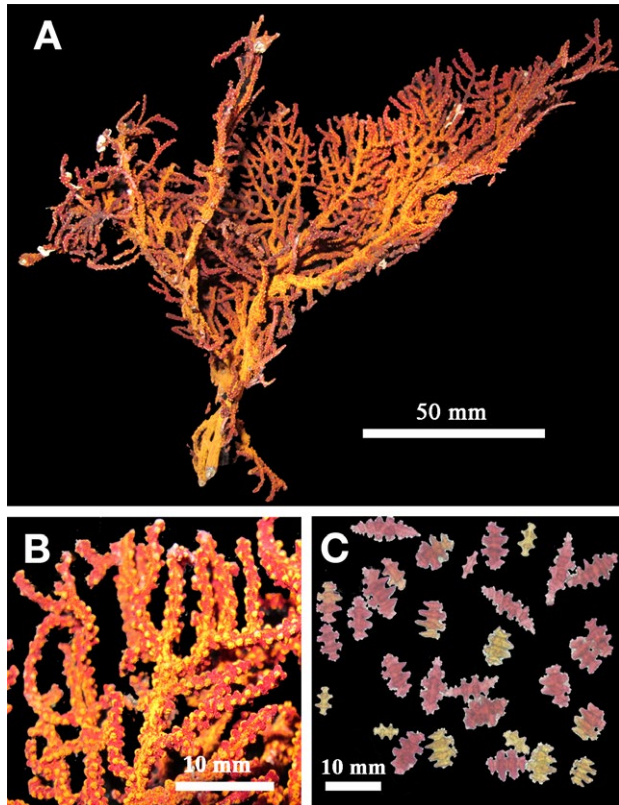


Fig. 23. – *Eugorgia daniana* (MNCN 2.04/1179). A, colony; B, detail of a branch; C, light micrograph of sclerites.

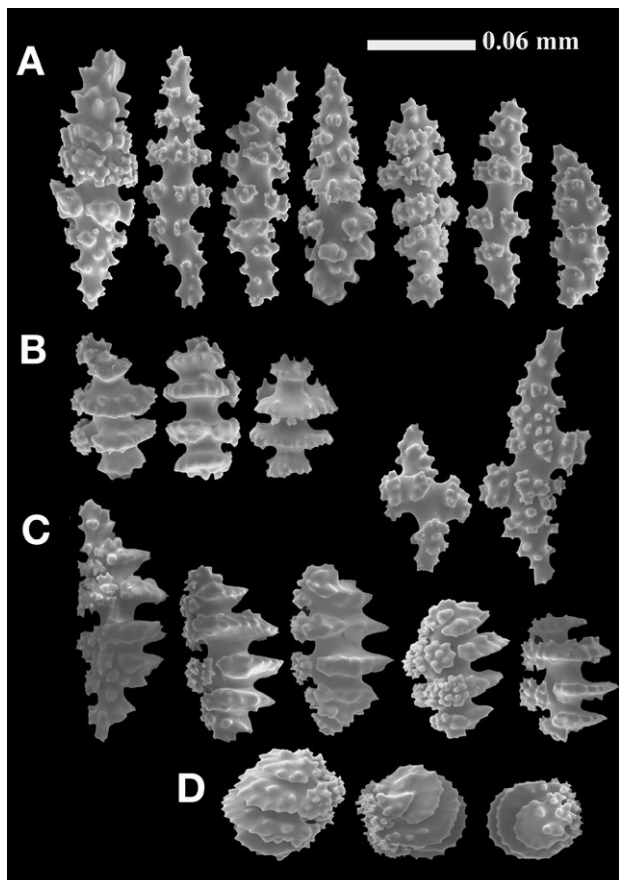


Fig. 24. – *Eugorgia daniana* (MNCN 2.04/1179) SEM photographs. A, coenenchymal sclerites, spindles; B, double disc; C, crosses; D, disc-spindles; E, complete double disc.

3 m depth, Dec. 1979; USNM 59084 Gulf of Guayaquil (Ecuador), 20 m depth, Sept. 1966.

**Description.** The colonies are up to 110 mm in length by 190 mm in width and arise from a circular holdfast, 0.5 mm in diameter. They are profusely and pinnately branched in multiple planes. Main stems are 3–5 mm in diameter, compressed, and very short (up to 10 mm long) or absent (Fig. 23A). The branches arise directly from the base, and are cylindrical, ranging from 0.8 to 1.2 mm in diameter. Some of the branches are pseudoanastomosed (anastomosis to the coenenchyme level, but not including the axes). The unbranched distal twigs can reach up to 15 mm in length and are blunt at the ends (Fig. 23A, B). In some branches, there are numerous and evident yellow, longitudinal grooves. The polyps retract within prominent polyp-mounds, leaving a small bilabiate aperture; they occur in multiple rows on all sides of the branches, sometimes having yellow spots. Colonies are dark orange or bright red streaked with bright yellow on the branches or on the polyp-mounds (Fig. 23B). The coenenchymal sclerites are red, yellow or bicoloured (Fig. 23C). They are double discs reaching up to 0.07 mm in length, 0.06 mm in width (Figs 23C, 24B). The capstans reach up to 0.08 mm in length, 0.05 mm in width (Fig. 23C). The dominant sclerite types are spindles (up to 0.15 mm in length, 0.05 mm in width); disc-spindles (up to 0.14 mm in length, 0.05 mm in width) are also abundant, with 4–6 whorls of warty tubercles; they are straight or bent, some with a marked waist (Fig. 24A, D). The crosses are up to 0.14 mm in length, 0.06 mm in width (Figs 23C, 24C). No anthocodial sclerites were obtained.

**Geographic and bathymetric distribution.** This species has a wide distribution along the eastern Pacific. It has been recorded in USA, Mexico, El Salvador, Nicaragua, Costa Rica, Panama, Colombia, Ecuador (Galapagos and the Gulf of Guayaquil) and Peru (Fig. 25K), at 3–30 m depth (Verrill 1868, Breedy et al. 2009, present record).

The only specimen of *Eugorgia daniana* previously found in continental Ecuadorian waters was collected in the Gulf of Guayaquil (identified by Bayer in 1966, and published by Breedy et al. 2009). Our record from Manabí and Santa Elena is the second finding of this species in continental Ecuador, providing information about the possible existence of widespread populations of this species in this area. Currently, *Eugorgia daniana* and *E. ahorcadensis* Soler-Hurtado and López-González, 2012 are the only species of this genus found in Ecuadorian waters.

**Remarks.** Differentiation between *E. daniana* and *E. aurantica* is difficult at first sight due to a similar branching pattern and colour of their colonies.

However, *E. aurantica* has polyp-mounds with characteristic yellow rings and lacks disc-spindles. *Eugorgia daniana*, *E. aurantica* and *E. multifida* Verrill, 1870 form the “*daniana*-group” (Breedy et al. 2009, 2013), which includes species with irregular pinnate branching, prominent polyp-mounds and a similar colour of colonies and sclerites.

## DISCUSSION

Seven of the species identified are new records for the octocoral fauna of Ecuador (Table 1, 2): *Leptogorgia diffusa*, *L. flexilis*, *Pacifigorgia cribrum*, *P. flavimaculata*, *P. irene*, *P. rubicunda* and *P. stenobrochis*. Another three species, *Leptogorgia alba*, *L. obscura* and *Eugorgia daniana*, had already been reported in Ecuador by other authors (Bielschowsky 1929, Breedy and Guzmán 2007). The new species described here, *Pacifigorgia machalilla*, requires additional records to better establish its geographical and bathymetric distribution.

These species, together with *Leptogorgia maria-rosae* Soler-Hurtado and López-González, 2012, *Eugorgia ahorcadensis* and *L. aequatorialis* (Bielschowsky, 1929), constitute the current list of gorgoniid species from the continental coast of Ecuador. Despite the recent contribution of Breedy et al. (2013) suggesting the synonymization of *E. ahorcadensis* with *E. nobilis* based on the consideration of an enlargement of morphology and chromatic variability of the latter, recent molecular analyses based on the study of both type materials demonstrated that they should be considered separate taxa (Soler-Hurtado et al. unpublished). In addition, to complete the species list for Ecuadorian waters, the species described above for the Galapagos Islands, *Pacifigorgia darwini* (Hickson, 1928), *P. dampieri* Williams and Breedy, 2004, *P. symbiotica* Williams and Breedy, 2004 and *P. rubripunctata* Williams and Breedy, 2004, should be added.

According to Bayer (1961), gorgonian corals systematics relies on a combination of characters such as axial skeleton (if any), colonial form, polyp arrangement and sclerite morphology. However, the often unwieldy older literature with no or neglected illustrations and lost or badly preserved type material have played a major role in the taxonomic confusion around octocoral systematics (Sánchez 2004, Soler-Hurtado and López-González 2012). Currently, variation in sclerite size, sculpture, and coloration and the relative proportion of the different sclerite types are the main criteria for species delimitation in Gorgoniidae (Williams and Lindo 1997, Breedy 2001, Sánchez et al. 2007, Vargas et al. 2010a). These characters vary widely and the ranges of variation have not been established for all gorgoniid taxa, hindering a robust taxonomy for the group.

The description of sclerite type can sometimes be difficult, because of continuous variation in size and ornamentation within and between species (Williams and Lindo 1997, Sánchez et al. 2003, Vargas et al. 2010a). This continuum represents a major obstacle to the assignment of size intervals or ranges that could be used to define and separate possible species. Vargas et al. (2010b) proposed for *Pacifigorgia* the combined use of continuous and discrete morphological characters, in order to define the relationships between species at different resolution level, in an integrative approach with molecular data.

Despite the rebirth of invertebrate systematics due to the ever-increasing availability of DNA sequence characters (Mallet and Willmott 2003, Sánchez 2004, Due-

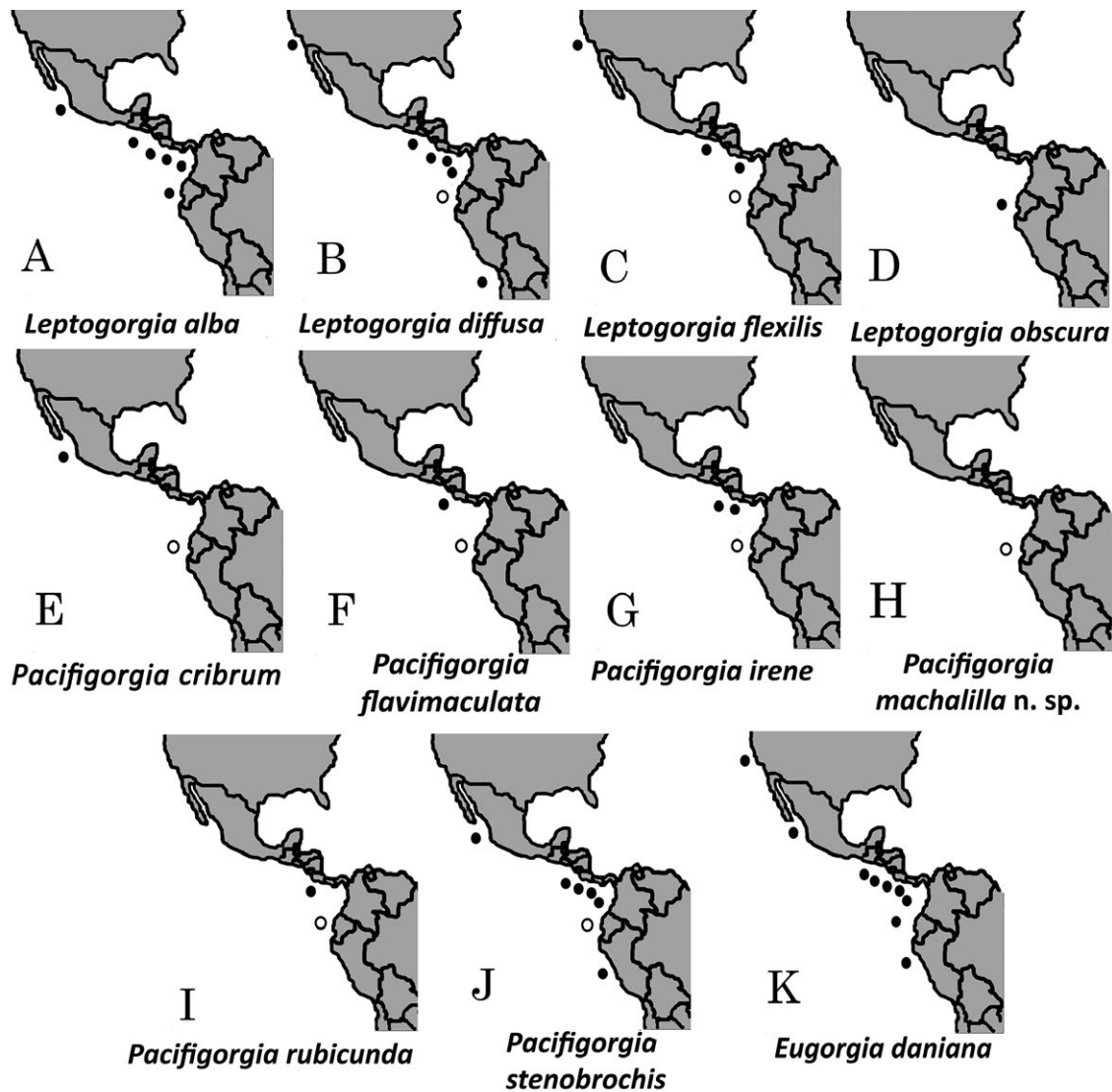


Fig. 25. – Geographical distribution of the *Leptogorgia*, *Pacifigorgia* and *Eugorgia* species mentioned in the paper. The solid circle shows the relative position of the species in the countries where they have been recorded. The empty circles indicate the first record for the species in Ecuador.

ñas and Sánchez 2009), evaluation of the effectiveness of molecular barcodes in octocorals is largely hindered by lack of knowledge regarding species boundaries in these organisms. One reason for this is that the rate of octocoral mitochondrial gene evolution is very slow. It is estimated to be 10–100× slower than in other metazoans (Chen et al. 2009, Brockman and McFadden 2012), resulting in insufficient resolution to discriminate species within many genera (Sánchez et al. 2003, Lepard 2003 in Cairns and Bayer 2005). Specimens identified as different morphospecies can share the same barcode, which should motivate additional taxonomic work to test species boundaries and quantify intraspecific morphological and molecular variation (McFadden et al. 2010). For instance, Sánchez et al. (2003), exploring mitochondrial genes ND2, ND6 and MutS, observed that in *Eunicea* spp. and *Plexaura* spp. the number of substitutions supporting nodes was low (less than 0.005 substitutions/site), and the clade formed by these two genera could be considered unresolved from a molecular point of view. In addition, McFadden et al.

(2011) showed that congeners of the genera *Isidella*, *Keratoisis* and *Lepidisis* were identical at COI and Igr1 sequences, and only varied 0%–2% for MutS.

In this study, we found that pairs of morphologically different species, *Pacifigorgia exilis* and *P. media* (Verrill, 1864), and *P. bayeri* Breedy, 2001 and *P. cathedralensis* Breedy and Guzmán, 2004, showed no interspecific variation (0%, in COII+Igr+COI+MutS, cf. Table 4); while others, *P. firma* and *P. cathedralensis*, *P. rubicunda* and *P. exilis*, and *P. rubicunda* and *P. media*, showed a very low genetic divergence (0.006%). In fact, the maximum genetic divergence observed in this study is 1.3%, between *P. media* and *P. firma*, and between *P. exilis* and *P. firma*, confirming the reduced variability in the genetic regions examined.

The analysis combining MutS and Igr1-COI for DNA barcoding indicates that these markers are not always suitable and conclusive for species-level identification of eastern Pacific octocorals (Vargas et al. 2014). However, we can say that these regions can at least define different species groups. This may serve

as a supporting tool for morphological findings among species within and between groups.

According to our results, based on strong morphological data and molecular tests with sufficient resolution for this set of octocoral species, we propose *Pacificorgia machalilla* as a new species.

In conclusion, we recommend the use of molecular tools as a necessary complement to morphological identification for future descriptions of new species. Although mitochondrial markers are known to evolve at much lower rates than in other zoological groups, they still provide information that should not be neglected. These mitochondrial markers can be complemented with nuclear regions (e.g. 28S, ITS and SRP54, among others) that have been demonstrated to be especially useful for some octocoral families and genera (Sánchez et al. 2007, McFadden et al. 2014, Wirshing and Baker 2015).

Although much more work is needed to fully understand the morphological diversification of octocorals, a combination of molecular and morphological data is a very promising approach to disentangling phylogenetic relationships among species (Breedy et al. 2013, McFadden and Van Ofwegen 2013, López-González et al. 2015) and intraspecific population ecology (Calderón et al. 2006, Prada et al. 2008, Prada and Hellber 2013). Molecular and morphological analytic tools will be essential to quantify the variety of evolutionary pathways within these groups (Sánchez et al. 2003, McFadden et al. 2006, Concepción et al. 2010).

However, even when combined, the two approaches do not seem to fully solve the taxonomic problems in this group, and more informative characters in both disciplines must be identified to distinguish closely related morphological species (e.g. McFadden and Van Ofwegen 2013 on stoloniferous octocorals), as well as to obtain more natural classifications, reducing the number of taxonomic synonyms (e.g. Grajales and Rodríguez 2016, on sea anemones). This will help to clarify the evolution of a zoological group that is very important in the structural functioning of benthic marine communities (Conell 1978, Fabricius and Alderslade 2001, Fabricius 2005).

Finally, the presence and abundance of these and other species of octocorals in shallow waters could be used as an environmental indicator, suggesting potential areas for protection. Intensive sampling on the coast of Ecuador in biotopes such as submarine ridges and coralligenous bottoms, rich in gorgonian species, could reveal unrecorded gorgonian species in this area. Therefore, much work remains to elucidate Gorgoniidae taxonomy on the coast of Ecuador. The octocorals are an important structural component of the rocky reef fauna of these waters. The present survey contributes towards resolving issues concerning the distribution and taxonomy of this fauna in this region.

#### ACKNOWLEDGEMENTS

This research was funded by the grant “Biología de la conservación de las comunidades de gorgonias tropicales en el Pacífico oriental (Ecuador)” of the

Universidad Tecnológica Indoamérica to JM. This research received support from the SYNTHESYS Project (<http://www.synthesys.info/>), financed by the European Community Research Infrastructure Action under the FP7 Capacities Programme, and “Ernst Mayr Travel Grants In Animal Systematics” for visiting MCZ at Harvard University. This research was partially supported by a grant from the Spanish Ministry of Economy and Competitiveness (CTM2014-57949-R). Our special thanks to Gonzalo Giribet and Adam J. Baldinger (MCZ) and Aude Andouche (MNHN), Andrew Cabrinovic and Miranda Lowe (NHM), Eric Lazo-Wasem and Lourdes Rojas (YPM), and Stephen Cairns and Herman H. Wirshing (Smithsonian, MNH) for helping in our museum work. We thank Santiago Villamarín (MECN), Machalilla National Park and Ministerio del Ambiente of Ecuador (Manabí) for collection permits; and Michel Guerrero and his team (Exploramar Diving) for his special interest and collaboration since we began our research. Special thanks to Micaela Peña for her unconditional help, and to Alicia Maraver, Valeria García and Damián Ramírez for their help on the collection expeditions, their friendship and their hard work. Thanks also to Eva Andrés Marruedo and Mónica Flores for their help during the subsequent fieldwork. Finally, we thank one anonymous referee for his/her suggestions for improving our manuscript.

#### REFERENCES

- Alderslade P. 1998. Revisionary systematics in the gorgonian family Isididae, with description of numerous new taxa (Coelenterata, Octocorallia). *Rec. West. Aust. Mus.* 55: 1-359.
- Bayer F.M. 1951. A revision of the nomenclature of the Gorgoniidae (Coelenterata: Octocorallia) with an illustrated key to the genera. *J. Wash. Acad. Sci.* 41: 91-102.
- Bayer F.M. 1953. Zoogeography and evolution in the octocorallian family Gorgoniidae. *Bull. Mar. Sci. Gulf Caribb.* 2: 100-119.
- Bayer F.M. 1961. The shallow water Octocorallia of the West Indian Region. A manual for marine biologists. Martinus Nijhoff, The Hague, 400 pp.
- Bayer F.M. 1981. Status of knowledge of octocorals of world seas. *Seminários de Biologia Marinha. Academia Brasileira de Ciências, Rio de Janeiro*, pp 1-17.
- Bayer F.M., Stefani J. 1989. Primnoidae (Gorgonacea) de Nouvelle-Calédonie. *Bull. Mus. Nat. His. Nat. Paris.* 4, 10(A) 3: 449-476.
- Bayer F.M., Grasshoff M., Verseveldt J. 1983. Illustrated trilingual glossary of morphological terms applied to Octocorallia. E.J. Brill, Leiden, 74 pp.
- Bayer F.M., Macintyre I.G. 2001. The mineral component of the axis and holdfast of some gorgonacean octocorals (Coelenterata: Anthozoa), with special reference to the family Gorgoniidae. *Proc. Biol. Soc. Wash.* 1: 309-345.
- Bielschowsky E. 1929. Die Gorgonarien Westindiens. 6. Die Familie Gorgoniidae, zugleich eine Revision. *Zool. Jahrb. Supplement* 16: 63-234.
- Breedy O. 2001. A new species of *Pacificorgia* from the eastern Pacific (Coelenterata: Octocorallia: Gorgoniidae). *Proc. Biol. Soc. Wash.* 10: 181-187.
- Breedy O., Guzmán H.M. 2002. A revision of the genus *Pacificorgia* (Coelenterata: Octocorallia: Gorgoniidae). *Proc. Biol. Soc. Wash.* 115: 787-844.
- Breedy O., Guzmán H.M. 2003. Octocorals from Costa Rica. The genus *Pacificorgia* (Coelenterata: Octocorallia: Gorgoniidae). *Zootaxa* 281: 1-60.
- Breedy O., Guzmán H.M. 2004. New species of the gorgonian genus *Pacificorgia* (Coelenterata: Octocorallia: Gorgoniidae) from the Pacific of Panama. *Zootaxa* 15: 1-15.
- Breedy O., Guzmán H.M. 2007. A revision of the genus *Leptogorgia* Milne-Edwards and Haime, 1857 (Coelenterata: Octocorallia: Gorgoniidae) in the Eastern Pacific. *Zootaxa* 1419: 1-90.



- Breedy O., Guzmán H.M. 2013. A new species of the genus *Eugorgia* (Cnidaria: Octocorallia: Gorgoniidae) from Mesophotic reefs in the Eastern Pacific. *Bull. Mar. Sci.* 3: 735-743. <http://dx.doi.org/10.5343/bms.2013.1014>
- Breedy O., Guzmán H.M., Vargas S. 2009. A revision of the genus *Eugorgia* Verrill 1868 (Coelenterata: Octocorallia: Gorgoniidae). *Zootaxa* 2151: 1-46.
- Breedy O., Williams G.C., Guzman H.M. 2013. Two new species of gorgonian octocorals from the Tropical Eastern Pacific Biogeographic Region (Cnidaria, Anthozoa, Gorgoniidae). *Zookeys* 350: 75-90. <http://dx.doi.org/10.3897/zookeys.350.6117>
- Brockman S.A., McFadden C.S. 2012. The mitochondrial genome of *Paraminabea aldersladei* (Cnidaria: Anthozoa: Octocorallia) supports intramolecular recombination as the primary mechanism of gene rearrangement in octocoral mitochondrial genomes. *Genome Biol. Evol.* 4: 994-1006. <http://dx.doi.org/10.1093/gbe/evs074>
- Cairns S.D., Bayer F.M. 2005. A review of the genus *Primnoa* (Octocorallia: Gorgonacea: Primnoidae), with the description of two new species. *Bull. Mar. Sci.* 77: 225-256.
- Calderón I., Garrabou J., Aurelle D. 2006. Evaluation of the utility of COI and ITS markers as tools for population genetic studies of temperate gorgonians. *J. Exp. Mar. Biol. Ecol.* 336: 184-197. <http://dx.doi.org/10.1016/j.jembe.2006.05.006>
- Chen I.P., Tang, C.Y., Chiou C.Y., et al. 2009. Comparative analyses of coding and non-coding DNA regions indicate that *Acropora* (Anthozoa: Scleractinia) possesses a similar evolutionary tempo of nuclear vs. mitochondrial genomes as in plants. *Mar. Biotech.* 11: 141-152. <http://dx.doi.org/10.1007/s10126-008-9129-2>
- Concepción G.T., Kahng S.E., Crepeau M.W., et al. 2010. Resolving natural ranges and marine invasions in a globally distributed octocoral (genus *Carijoa*). *Mar. Ecol. Prog. Ser.* 401: 113-127. <http://dx.doi.org/10.3354/meps08364>
- Conell J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 4335: 1302-1310. <http://dx.doi.org/10.1126/science.199.4335.1302>
- Duchassaing P., Michelotti J. 1864. Supplément au mémoire sur les coralliaires des Antilles. Extrait des mémoires de l'Académie des Sciences de Turin, 23: 1-112.
- Dueñas L., Sánchez J.A. 2009. Character lability in deep-sea bamboo corals (Octocorallia, Isidiidae, Keratoisidinae). *Mar. Ecol. Prog. Ser.* 397: 11-27. <http://dx.doi.org/10.3354/meps08307>
- Fabricius K. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar. Poll. Bull.* 2: 125-146. <http://dx.doi.org/10.1016/j.marpolbul.2004.11.028>
- Fabricius K., Alderslade P. 2001. Soft Corals and Sea Fans: a Comprehensive Guide to the Tropical Shallow-water Genera of the Central-West Pacific, the Indian Ocean and the Red Sea. *Aust. Inst. Mar. Sci., Townsville* 264 pp.
- France S.C., Hoover L.L. 2002. DNA sequences of the mitochondrial COI gene have low levels of divergence among deep-sea octocorals (Cnidaria: Anthozoa). *Hydrobiologia* 471: 149-155. <http://dx.doi.org/10.1023/A:1016517724749>
- Grajales A., Rodríguez E. 2016. Elucidating the evolutionary relationships of the Aiptasiidae, a widespread cnidarian-dinoflagellate model system (Cnidaria: Anthozoa: Actiniaria: Metridioidae). *Mol. Phyl. Evol.* 94: 252-263. <http://dx.doi.org/10.1016/j.ympev.2015.09.004>
- Guzmán H.M., Breedy O. 2011. *Pacifigorgia marviva* (Anthozoa: Octocorallia) a new species from Coiba National Park, Pacific Panama. *J. Mar. Biol. Assoc. UK* 92: 693-698. <http://dx.doi.org/10.1017/S0025315411000373>
- Hickson S.J. 1928. The Gorgonacea of Panama Bay together with a description of one species from the Galapagos Islands and one of Trinidad. *Vidensk. Medd. naturhistoriske Foren. Kovenhavn* 85: 325-422.
- Horn G.H. 1860. Descriptions of three new species of Gorgoniidae, in the collection of the Academy. *J. Acad. Nat. Sci. Phila.* 12: 233.
- Lamouroux J.V.F. 1812. Extrait d'une mémoire sur la classification des Polypiers coralligènes non entièrement pierreux. *Nou. Bull. Sci. Soc. Philom. Paris* 63: 181-188.
- Lepard A. 2003. Analysis of variation in the mitochondrial encoded *msh1* in the genus *Leptogorgia* (Cnidaria: Octocorallia) and implications for population and systematics studies. MS thesis, College of Charleston.
- López-González P.J., Grinyó J., Gili J.M. 2015. *Chironephthya mediterranea* n. sp. (Octocorallia, Alcyonacea, Nidaliidae), the first species of the genus discovered in the Mediterranean Sea. *Mar. Biodiv.* 45: 667-688. <http://dx.doi.org/10.1007/s12526-014-0269-5>
- Mallet J., Willmott K. 2003. Taxonomy: renaissance or Tower of Babel? *Trends Ecol. Evol.* 18: 57-59. [http://dx.doi.org/10.1016/S0169-5347\(02\)00061-7](http://dx.doi.org/10.1016/S0169-5347(02)00061-7)
- McFadden C.S., Van Ofwegen L.P. 2013. A second, cryptic species of the soft coral genus *Incrustatus* (Anthozoa: Octocorallia: Clavulariidae) from Tierra del Fuego, Argentina, revealed by DNA barcoding. *Helgol. Mar. Res.* 67: 137-147. <http://dx.doi.org/10.1007/s10152-012-0310-7>
- McFadden C.S., Tullis I.D., Hutchinson M.B., et al. 2004. Variation in coding (NADH dehydrogenase subunits 2, 3, and 6) and noncoding intergenic spacer regions of the mitochondrial genome in Octocorallia (Cnidaria: Anthozoa). *Mar. Biotechnol.* 6: 516-526. <http://dx.doi.org/10.1007/s10126-002-0102-1>
- McFadden C.S., France S.C., Sánchez J.S., et al. 2006. A molecular phylogenetic analysis of the Octocorallia (Cnidaria: Anthozoa) based on mitochondrial protein-coding sequences. *Mol. Phylogenet. Evol.* 41: 513-527. <http://dx.doi.org/10.1016/j.ympev.2006.06.010>
- McFadden C.S., Sánchez J.A., France S.C. 2010. Molecular Phylogenetic Insights into the Evolution of Octocorallia: A Review. *Integr. Comp. Biol.* 3: 389-410. <http://dx.doi.org/10.1093/icb/iccq056>
- McFadden C.S., Benayahu Y., Pante E., et al. 2011. Limitations of Mitochondrial Gene Barcoding in Octocorallia. *Mol. Ecol. Res.* 11: 19-31. <http://dx.doi.org/10.1111/j.1755-0998.2010.02875.x>
- McFadden C.S., Brown A.S., Brayton C., et al. 2014. Application of DNA barcoding in biodiversity studies of shallow-water octocorals: Molecular proxies agree with morphological estimates of species richness in Palau. *Coral Reefs* 33: 275-286. <http://dx.doi.org/10.1007/s00338-013-1123-0>
- Milne-Edwards H., Haime J. 1850. A monograph of the British fossil corals. Part I. Introduction; corals from the Tertiary and Cretaceous formations, London, pp 1-71.
- Milne-Edwards H., Haime J. 1857. Histoire naturelle des coralliaires ou polypes proprement dits. Vol. 1 pp. 1-xxxiv + 1-326, 8 plates, numbered A1-6, B1-2. Paris, à la Librairie Encyclopédique de Roret.
- Prada C., Hellberg M.E. 2013. Long pre-reproductive selection and divergence by depth in a Caribbean candelabrum coral. *Proc. Natl. Acad. Sci. USA* 119: 53-60.
- Prada C., Schizas N.V., Yoshioka P.M. 2008. Phenotypic plasticity or speciation? A case from a clonal marine organism. *BMC. Evol. Biol.* 8: 47. <http://dx.doi.org/10.1186/1471-2148-8-47>
- Prahl H., Escobar D., Molina G. 1986. Octocorales (Octocorallia: Gorgoniidae y Plexauridae) de aguas someras del Pacífico Colombiano. *Rev. Biol. Trop.* 34: 13-33.
- Rambaut A. 2002. Se-AL alignment editor. Version 2.0 all, University of Oxford, Oxford, UK. Available: <http://tree.bio.ed.ac.uk/software/seal/>
- Saitou N., Nei M. 1987. The neighbor-joining method: A new method for reconstructing phylogenetic trees. *Molec. Bio. Evol.* 4: 406-425.
- Sánchez J.A. 2004. Evolution and dynamics of branching colonial form in marine modular cnidarians: gorgonian octocorals. *Hydrobiologia* 1: 283-290. <http://dx.doi.org/10.1007/s10750-004-2684-2>
- Sánchez J.A., McFadden C.S., France S.C., et al. 2003. Molecular Phylogenetic analyses of shallow-water Caribbean octocorals. *Mar. Biol.* 142: 975-987.
- Sánchez J.A., Aguilar C, Dorado D., et al. 2007. Phenotypic plasticity and morphological integration in a marine modular invertebrate. *BMC Evol. Biol.* 1: 12. <http://dx.doi.org/10.1186/1471-2148-7-122>
- Soler-Hurtado M.M., López-González P.J. 2012. Two new gorgonian species (Anthozoa: Octocorallia: Gorgoniidae) from Ecuador (Eastern Pacific). *Mar. Biol. Res.* 8: 380-387. <http://dx.doi.org/10.1080/17451000.2011.634814>
- Studer T. 1887. Versuch eines Systemes der Alcyonaria. *Arch. Naturgesch.* 53: 1-74.
- Swofford D.L. 2001. PAUP\*. Phylogenetic Analysis Using Parsimony (\* and Other Methods), version 4. Sinauer Associates, Sunderland, Massachusetts.

- Valenciennes A. 1846. Zoophytes. In: Dupetit-Thouars A. (ed) Voyage autour du monde sur la frégate la Vénus, pendant les années 1836-1839. Atlas de Zoologie. Publié par ordre Du Roi, Paris, pp 1-15.
- Vargas S., Breedy O., Siles F., et al. 2010a. How many kinds of sclerite? Towards a morphometric classification of gorgoniid microskeletal components. *Micron* 41: 158-164. <http://dx.doi.org/10.1016/j.micron.2009.08.009>
- Vargas S., Breedy O., Guzmán H.M. 2010b. The phylogeny of *Pacifigorgia*: a case study of the use of continuous characters in the systematic of the Octocorallia. *Zoosystema* 1: 5-18. <http://dx.doi.org/10.5252/z2010n1a1>
- Vargas S., Guzmán H.M., Breedy O., et al. 2014. Molecular phylogeny and DNA barcoding of tropical Eastern Pacific shallow water gorgonian octocorals. *Mar. Biol.* 161: 1027-1038. <http://dx.doi.org/10.1007/s00227-014-2396-8>
- Verrill A.E. 1864. List of the polyps and corals sent by the Museum of Comparative Zoology to other institutions in exchange, with annotations. *Bull. Mus. Comp. Zool. at Harvard College*, 1: 29-60.
- Verrill A.E. 1866. On the polyps and corals from Panamá with descriptions of new species. *Proc. Boston Soc. Nat. Hist.* 10: 323-357.
- Verrill A.E. 1868. Notes on Radiata in the Museum of Yale College, Number 6: Review of the corals and polyps of the West Coast of America. *Trans. Conn. Acad. Arts Sci. (Second Edition)*, pp. 377-422.
- Verrill A.E. 1870. Notes on Radiata in the Museum of Yale College, Number 6: Review of the corals and polyps of the West Coast of America. *Trans. Conn. Acad. Arts Sci. (Second Edition)*, 1: 519-558.
- Williams G.C., Lindo K.G. 1997. A review of the octocorallian genus *Leptogorgia* (Anthozoa: Gorgoniidae) in the Indian Ocean and Subantarctic, with description of a new species and comparisons with related taxa. *Proc. Calif. Acad. Sci.* 49: 499-521.
- Williams G., Breedy O. 2004. The Panamic Genus *Pacifigorgia* (Octocorallia: Gorgoniidae) in the Galápagos Archipelago. *Proc. Calif. Acad. Sci.* 55: 54-87.
- Wirshing H.H., Baker A.C. 2015. Molecular and Morphological Species Boundaries in the Gorgonian Octocoral Genus *Pterogorgia* (Octocorallia: Gorgoniidae). *PLoS One* 10. <http://dx.doi.org/10.1371/journal.pone.0133517>