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Two new endemic species of Gorgoniidae (Cnidaria, Anthozoa, Octocorallia) from Revillagigedo Archipelago, Mexico

URSULA OLVERA[1], OSVALDO HERNÁNDEZ[1], CARLOS SÁNCHEZ[1,*] & JAIME GÓMEZ-GUTIÉRREZ[2]

[1]*Universidad Autónoma de Baja California Sur, Departamento de Ciencias Marinas y Costeras, Laboratorio de Fauna Arrecifal, Carretera al Sur km 4.5, CP 23080, La Paz, Baja California Sur, Mexico.*
E-mails: csanchez@uabcs.mx, eugorgia@gmail.com, ohernandez@uabcs.mx
[2]*Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, Departamento de Plancton y Ecología Marina, Av. IPN s/n, CP 23096, La Paz, Baja California Sur, Mexico. E-mail: jagomezg@ipn.mx*
**Corresponding author*

Abstract

Two new species of the genera *Eugorgia* and *Leptogorgia* were discovered while underwater collecting at the Revillagigedo Archipelago, Mexico. Sea fan species diversity and density population in these four volcanic islands is low (<12 spp.), and the possibility of endemism is high given their isolation from the mainland (403 km southwest of Cabo San Lucas, Baja California peninsula). Morphological features suggest *Eugorgia wilkiei* **sp. nov.** has a close relationship to species of the *daniana* group, particularly with *Eugorgia multifida* Verrill, 1870. However, *E. wilkiei* **sp. nov.** has densely branched irregular-pinnate colonies that grow in several simple planes or multiplanar flabelliform, and shows two distinct chromotypes (yellow or red). *Leptogorgia waltonae* **sp. nov.** is added here to the *ena* group because its similar in size and sclerites to *Leptogorgia ena* Breedy *et al.* 2012. However, the wart-like terminal twigs representing an enlargement of the axis (but not the coenenchyme which has the same thickness throughout the colony), 90°-angled lateral branching, and the red, purple, orange, or yellow coloration range of the colonies are the main taxonomic characters to distinguish *L. waltonae* **sp. nov.** from *L. ena.* Scuba diving observations in about 200 sampling locations done since 1995 to 2016 along the mexican Pacific coast, including the Gulf of California, indicate both new octocoral species are distributed only at Revillagigedo islands. Revillagigedo Archipelago is surrounded by oligotrophic oceanic waters, strong seawater currents, and relatively frequent hurricane perturbations that favor small or robust, and hard and resistant sea fan colonies, low-species diversity, and low-population density. These factors may enhance speciation processes supporting the comparatively high endemism of the islands benthic fauna as well.

Key words: *Eugorgia*, *Leptogorgia*, endemism, oceanic islands, Revillagigedo Archipelago, Mexico

Introduction

The Revillagigedo Archipelago includes four oceanic volcanic islands of varying surfaces (San Benedicto, 5.9 km^2; Socorro, 132 km^2; Roca Partida, 0.014 km^2; and Clarion, 19.8 km^2) and it is located 403–706 km southwest of Cabo San Lucas, Baja California peninsula, and 547–970 km west of Cabo Corrientes, Jalisco, Colima, Mexico.

Records of octocoral sea fans from the eastern Pacific oceanic islands are scant (Williams & Breedy 2004; Breedy & Guzman 2005; Breedy & Cortés 2008, 2011; Hickman 2008; Breedy *et al.* 2009b). Oceanic islands, like Revillagigedo, provide unique marine tropical oligotrophic conditions to a low-diverse but highly endemic benthic fauna (Ketchum & Reyes-Bonilla 2001; Mille-Pagaza *et al.* 2002; Cruz-Barraza *et al.* 2011). Octocorals are amongst the most abundant and diverse components of the coastal benthic habitat along the tropical eastern Pacific rocky reefs (Ulate *et al.* 2016). In oceanic islands, however, few taxonomic or ecological studies of this fauna have been carried out favoring the possibility to discover new species (Williams & Breedy 2004; Bedolla 2007). Indeed, Bedolla (2007) reported that octocoral richness at Revillagigedo Archipelago (<40 m seafloor depth) comprised four genera with ten species: *Muricea plantaginea* (Valenciennes, 1864), *Muricea austera* Verrill, 1869, *Muricea* sp. 1, *Muricea* sp. 2, *Muricea* sp. 3, *Muricea* sp. 4, *Pacifigorgia* sp. 1, *Pacifigorgia* sp. 2, *Eugorgia* sp., and

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Leptogorgia sp. Eight of these ten species are currently considered endemic with distinct morphology as compared to sea fans observed along coastal rocky reefs of Mexico's mainland. These observations suggest that they could be new species to be formally described. A remarkable finding, however, is that the genera *Eugorgia* and *Leptogorgia* in Revillagigedo Archipelago include only one non-described species each, which are reported here as two new species.

The external morphology of species of *Eugorgia* and *Leptogorgia* is quite similar as both show variable branching structures (lateral, partial dichotomous or pinnate) that grow flabellated, bushy, or arborescent (Breedy & Guzman 2007; Breedy *et al.* 2009a) (Table 1). Additionally, coloration of colonies and shape of the sclerites are highly variable among species (Verrill 1868; Breedy *et al.* 2009). A horny axis supports the colonies, which has a narrow cross-chambered central core filled with organic filaments frequently mineralized with carbonate-hydroxylapatite (CHAp) (Bayer 2000; Macintyre *et al.* 2000; Breedy *et al.* 2009). Polyps are fully retractile into the coenenchyme that could be prominent, or slightly raised. The main morphological character to distinguish species of both genera is the presence of sclerites with double discs in *Eugorgia* and its absence in *Leptogorgia* (Verrill 1868; Breedy *et al.* 2009) (Table 1).

All species currently known of genus *Eugorgia* are endemic of the eastern Pacific, with species distributing from California to Peru. The genus *Eugorgia* includes 15 nominal species grouped into five morphological groups: *ampla* (8 spp.), *daniana* (4 spp.), *rubens* (1 sp.), *siedenburgae* (1 sp.), and *beebei* (1 sp.) (Breedy & Guzman 2013; Breedy *et al.* 2009, 2013). However, for simplicity we propose that the three last monospecific groups must be considered as species with anomalous morphology in the genus *Eugorgia* rather than groups, that eventually could form groups upon the discovery of additional species matching their morphology (a group must be >2 species). Ten of the 15 species of *Eugorgia* (from all the morphological groups) have been reported along the mexican Pacific coast (Breedy & Guzman 2013; Breedy *et al.* 2009, 2013). In contrast, species of *Leptogorgia* have a widespread circum-tropical and subtropical distribution including approximately 58 extant species worldwide (Verrill 1868; Bayer 2000; Breedy & Guzman 2007, 2013; Breedy *et al.* 2009b, 2012; Breedy & Cortés 2011; Horvath 2011). Thirteen nominal *Leptogorgia* species have been recorded during the period of 1857–2013 along the mexican Pacific coast (Milne Edwards & Haime 1857; Horn 1860; Duchassaing & Michelotti 1864; Verrill 1864, 1865, 1868, 1869, 1870; Hickson 1928; Horvath 2011; Breedy *et al.* 2012, 2013). Two studies showed that three species [*Leptogorgia chilensis* Verrill, 1868, *Leptogorgia diffusa* (Verrill, 1868), and *Leptogorgia regis* Hickson, 1928] extended northward its distribution range into the mexican Pacific coast and discovered at least eight, so far, undescribed species (Sánchez 2010; Hernández 2014). Two recent studies of molecular phylogenetic relationships of *Pacifigorgia*, *Eugorgia*, and *Leptogorgia*, carried out in Ecuador (Soler-Hurtado *et al.* 2017) and the Eastern Pacific, the Atlantic Ocean, and Mediterranean Sea (Poliseno *et al.* 2017) show that species of *Eugorgia* must be included in *Leptogorgia* due to polygenetic origin and current lack of consistency between morphological features and genetic markers (nuclear and mitogenomics). However, they also argue that it is necessary to do a review of the world "*Leptogorgia*" to clarify the systematics of these species and provide a phylogenetically sound taxonomic system for these sea fan genera, particularly in species in the Eastern Pacific. Taxonomy of sea fans on the mexican Pacific coast and Gulf of California requires precise species identification and comprehensive and systematic ecological studies to provide an integrative perspective of species assemblages and ecological function of each sea fan species in the benthic ecosystem. Oceanic islands are places where species diversity is expected to be distinct because of their long-term isolation from the mainland; so, usually it is interesting from a taxonomic perspective, to explore such remote places to learn about species diversity of octocorals in insular habitats.

Material and methods

During four expeditions (Jan 16–20, 2000; Feb 9–24, 2006; Feb 15–26, 2013, Apr 2–20, 2016) carried out to the Revillagigedo Archipelago (18°20' to 19°20' N, -110°46' to -114°45' W), 113 monitoring dives were performed along transects, where multiple non-quantitatively collections of octocorals was also done. Fourteen colonies of *Eugorgia wilkiei* **sp. nov.** were collected: eight colonies with scuba diving between 10–55 m depth, and six colonies in five dives using a mechanical arm from the submersible DEEPSEE (Undersea Hunter Group) between 50–75 m depth (April 2016), and also several specimens were observed and photographed. Forty-five colonies of *Leptogorgia waltonae* **sp. nov.** were collected between 10–25 m depth. All specimens were dried and/or preserved

in 96% ethanol. The external morphology of the colonies and sclerites were analyzed. A portion of the colony was macerated in sodium hypochlorite (NaClO) for 15 min for sclerites extraction, washed with distilled water and preserved in ethanol 96%. Additionally, coenechyme from ten *Leptogorgia waltonae* **sp. nov.** colonies were macerated for axis morphology analysis. Sclerites were dried and attached to aluminum stubs with double adhesive bands. They were coated with gold and observed through scanning electron microscope (SEM, Hitachi S-3000N). Their morphological traits and coloration were compared against those of several nominal species of *Eugorgia* and *Leptogorgia* using taxonomic descriptions and revisions from holotypes, lectotypes, and other octocoral specimens from our own institutional collection (Universidad Autónoma de Baja California Sur, Proyecto Fauna Arrecifal: UABCS-PFA, N>2,500 specimens). Species identification and morphological comparisons among species and genera were assessed following techniques proposed by Verrill (1868), Breedy & Guzman (2007, 2013), Breedy *et al*. (2009a, 2012) and Horvath (2011) (Table 1). We used standard taxonomic terminology and criteria to identify nominal species and describe the new species according to Bayer *et al*. (1983), Calvo & Breedy (2002), Breedy *et al*. (2009a, 2013), and Breedy & Guzman (2007, 2013).

Taxonomy

Class Anthozoa Ehrenberg, 1834

Subclass Octocorallia Haeckel, 1866

Order Alcyonacea Lamouroux, 1812

Suborder Holaxonia Studer, 1887

Family Gorgoniidae Lamouroux, 1812

Genus *Eugorgia* Verrill, 1868

***Eugorgia wilkiei* sp. nov.**
(Figs. 1–3)

Holotype: USNM-1422107, dried specimen, El Cañón (19°17'52.0980" N, -110°48'16.9158" W), San Benedicto, Revillagigedo Archipelago, 55 m depth, January 20, 2000.

Paratypes: USNM-1422110 dried specimen, El Boiler (19°19'48.5898" N, -110°48'50.1474" W), San Benedicto, Revillagigedo Archipelago, 38 m depth, January 20, 2000; USNM-1422108, El Cañón, San Benedicto, Revillagigedo Archipelago, 55 m depth, January 20, 2000; USNM-1422109, dried specimen, El Cañón, San Benedicto, Revillagigedo Archipelago, 55 m depth, January 20, 2000.

Holotype colony: Yellow colony 35.3 cm tall, and 32.4 cm wide, profusely branched, growing in several planes (miltiplanar flabelliform) (Fig. 1A,D, Table 1). Main branches are compressed, branching irregularly pinnate. Main stem 1.9 cm diameter, 3.7 cm long, and slightly compressed. Morphology of the holdfast is unknown because it was removed during collection. The main stem is subdivided in two branches of 1.3 cm in diameter, emerging at angles of 44°–47° and producing three secondary branches resulting in thin (1–2 mm), short (1–9 mm) and closer (0.6–2.5 mm) branchlets showing a densely branched colony (Fig. 1A). Branching up to 13 times. The polyps are white and fully retractable in bilabiate mounds reaching up to 0.4 mm. These are arranged in multiple irregular bands at the branchlets (Fig. 1C) and more sparsely over the thick branches where they are observed in parallel rows on either side of the longitudinal grooves.

Holotype sclerites: The color of the sclerites is yellow (Fig. 1B). All types of sclerites found in *Eugorgia wilkiei* **sp. nov.** are shown in Fig. 2A–G, Table 1. The most abundant coenenchymal sclerites are incomplete double discs, followed by capstans and spindles. However, the complete double disc, spindly capstans, bent spindles, and crosses are present too. The biometry of sclerites for each type are: complete double disc (0.057 mm–0.040 mm), incomplete double disc (0.077 mm–0.047 mm), capstans (0.084 mm–0.056 mm), spindly capstans (0.054 mm–0.032 mm), crosses (0.092 mm–0.057 mm), spindles (0.151 mm–0.072 mm), and bent spindles (0.136 mm–0.076 mm), with 3–5 whorls of warty tubercles (Table 1). No anthocodial sclerites were found.

TABLE 1. Comparative features of ***Eugorgia wilkiei* sp. nov.** and ***Leptogorgia waltonae* sp. nov**., with selected nominal species based on taxonomic criteria from the original descriptions (regular font) (Verrill 1868; Breedy & Guzman 2007, 2013; Breedy *et al.* 2009, 2012, 2013; Horvath 2011) and collected samples (novel information, unclear information from the original description, or updated terminology is shown in **bold font**). Maximum sclerite length is shown. Type of branching: irregularly pinnate (irr-pin), laterally branched (lb), sparce-lateral branched (s-lb), branches/strands (bra-str), pseudo-anastomosis (p-ana); Polyp mounds: prominent (pro), slightly raised (s-rai); Polyp distribution row: regular (reg), irregular (irr); Color (colony or sclerite): brownish (b), cream (c), dark violet (dv), mauve (m), orange (o), pale orange (po), dark orange (do), pink (pi), purple (pu), red-purple (rp), red (r), transparent (t), white (w), yellow (y); Numerically dominant sclerites type: capstan (cap), incomplete double disc (idd), spindles (spi); absent or not found (-). Colony color in parentheses denotes multiple tones of a single solid chromotype.

	Colony				Branching				Polyp		Sclerite										
	Colony growth	Color of colony	Bicolor colony	Solid chromotypes	Type of branching	Max. number of branching	Branchlet length (mm)	Branchlet diameter (mm)	Polyp mounds	Polyp distribution	Complete double disc (mm)	Incomplete double disc (mm)	Capstan (mm)	Disc-spindles (mm)	Spindles (mm)	Crosses (mm)	Anthocodial sclerites	Dominant sclerites type	Coenenchymal sclerites color	Bicolor sclerites	Tentacular sclerites	Color of anthocodial sclerites
Eugorgia																						
E. aurantiaca	planar flabelliform	(do/y, r/y)	-	1	irr-pin	**7**	6-30	1-2.5	pro	reg	0.07	**0.07×0.05**	0.09	-	0.11×0.045	0.06×0.06	-	**idd**	r, y	yes	-	-
E. daniana	planar flabelliform	r, r/y	-	2	irr-pin	**9**	**1-15**	1-1.5	pro	irr	0.08	**0.08×0.065**	0.08	0.13×0.05	0.13×0.05	0.075×0.065	-	**idd**	r, y	yes	-	-
E. multifida	planar/**multiplanar flabelliform**	do/r	-	1	irr-pin	**9**	1-10	1-1.5	pro	irr	**-**	**0.07×0.05**	0.08	0.13×0.05	0.13	0.06×0.06	flat rod	**idd**	r, y	yes	-	o
E. rubens	sparse	pi	-	1	lb	5	2-30	1.5-2	pro	reg	**-**	0.07×0.06	-	0.1×0.05	0.10	-	-	**idd**	pi	-	-	-
E. siedenburgae	bushy	pi/o, pi/y	yes	2	irr-pin p-ana	10	2-30	1-1.5	pro	irr	0.067	0.08×0.05	0.07	0.11	0.11	0.078×0.071	-	idd	pi, y	yes	-	-
E. mutabilis	planar flabelliform	w/pi	-	1	irr-pin	7	1-10	1-2	pro	irr	0.075	0.075×0.045	-	0.15	0.15	-	-	idd	w, y	-	-	-
E. beebei	sparse/**multiplanar flabelliform**	w	-	1	irr-pin p-ana	10	2-50	1-2.5	pro	irr	0.07	0.07×0.06	-	0.14×0.05	0.14×0.05	0.08×0.06	-	**idd**	w	-	-	-
***E. wilkiei* sp. nov.**	**planar/multiplanar flabelliform**	**y, r**	**-**	**2**	**irr-pin**	**13**	**1-9**	**1-2**	**pro**	**irr**	**0.057x0.04**	**0.077×0.047**	**0.084**	**-**	**0.151×0.072**	**0.092×0.057**	**-**	**idd**	**y/r**	**-**	**-**	**-**
Leptogorgia																						
L. californica	**bushy,** flabelliform	(rp/y, **pu/y**)	-	1	lb	**5**	**5-15**	**2-3**	flat, **pro**	**reg**	-	-	**0.06**	-	-	-	rod	cap	r, pi, y	yes	-	po, **y, w, pu**
L. cuspidata	bushy**, arborescent**	pi/y, y/pu	-	2	lb	**5**	90	**2**-4	flat**, s-rai**	reg	-	-	0.09	-	0.13	**0.05×0.05**	rod	cap	pu, y	yes	-	y, pi
L. diffusa	planar, bushy, **flabelliform**	(r, **pi)**	-	1	s-lb	**5**	70-80	2-3	pro	**reg**	-	-	0.09	-	**0.08**	**0.06×0.06**	rod	cap	pi, r	-	-	po, pi
L. ena	cluster	dv, dv/y, **y**	yes	**3**	lb	6	**5**-10	2-3	pro, **s-rai**	irr	-	-	0.09	-	0.11	0.05×0.07	flat rod	cap	**pu, y, pi**	yes	yes	**pu, y**
L. filicrispa	multiple fine strands	c, m, pi, w	-	**4**	bra-str	2	200-300	0.5-1	**pro**	reg	-	-	-	-	0.10	-	?	spi	t, pi	-	yes	t, pi
L. exigua	bushy, **arborescent**	b-r/y, b-r/do	-	1	lb	**5**	14	3-4	s-rai	irr	-	-	0.10	-	0.13	-	-	cap	o, pi, r, y	yes	-	-
L. rigida	**bushy, arborescent**	pu	-	1	lb	**7**	30	2-3	s-rai	reg	-	-	0.08	-	0.12	0.04×0.04	rod	cap	pu	-	-	pi, y
***L. waltonae* sp. nov.**	**cluster, bushy**	**y, o, r, pu, pi**	**-**	**5**	**lb**	**4**	**5-15**	**2-4**	**s-rai/pro**	**irr**	**-**	**-**	**0.11**	**-**	**0.13×0.06**	**0.05×0.05**	**rod**	**cap**	**y, o, pi, r, pu**	**-**	**-**	**y, o, pi, r, pu**

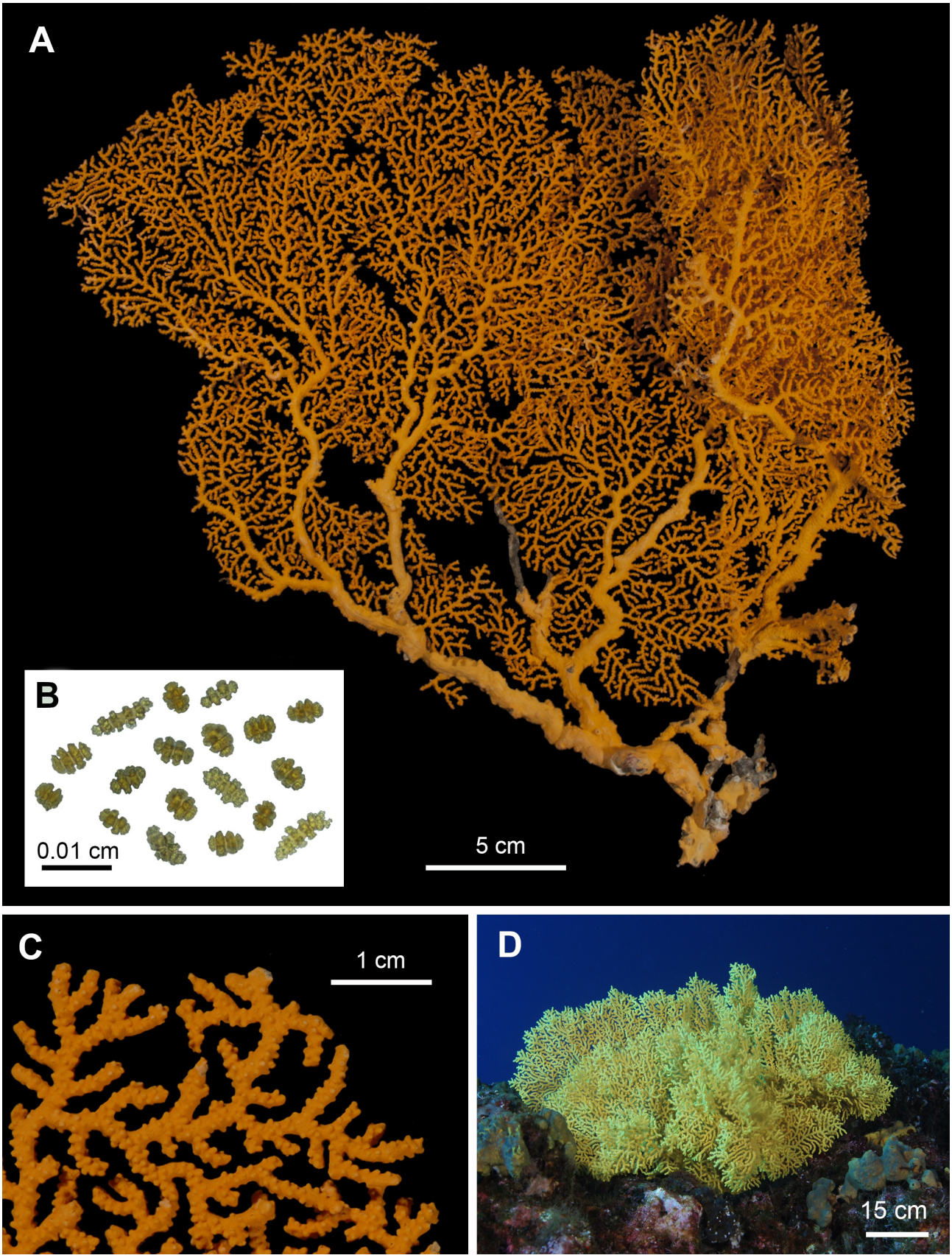

FIGURE 1. *Eugorgia wilkiei* **sp. nov.,** holotype USNM-1422107: A, entire yellow colony; B, yellow sclerites; C, detail of the branches and calyces; D, *in situ* alive multiplanar colony.

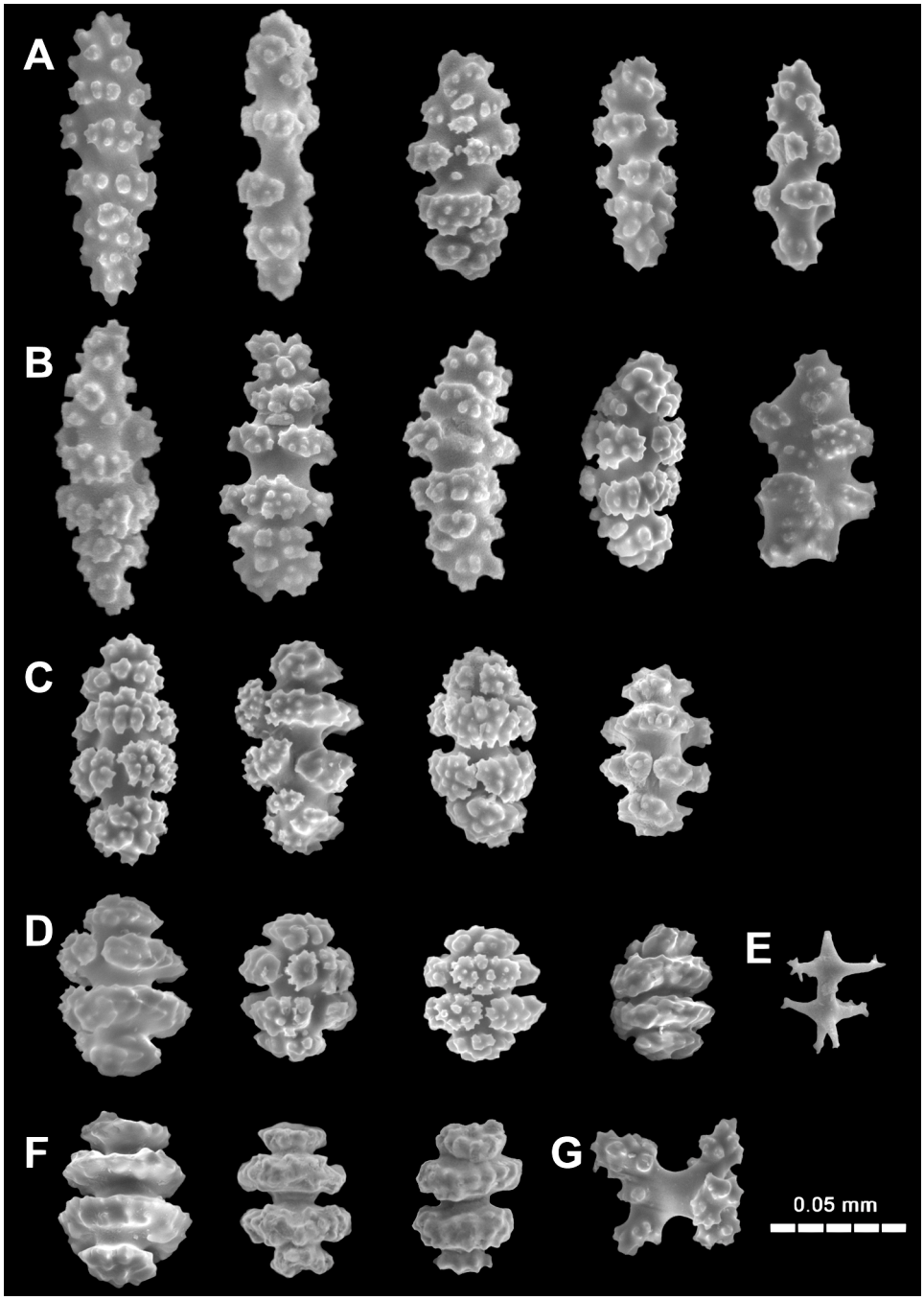

FIGURE 2. *Eugorgia wilkiei* **sp. nov.,** holotype USNM-1422107, MEB coenenchymal sclerites: A, spindles; B, spindles bent; C, capstans; D, incomplete double disc; E, spindly capstan; F, complete double disc; G, cross.

Variability. The paratypes of *Eugorgia wilkiei* **sp. nov.** deposited in the United States Natural Museum include three complete colonies from 21–35 cm tall to 9–32 cm wide. They have the same general morphology described for the holotype. However, in some cases, the growth occurs only in multiples planes (Fig. 3A, D). Samples have short branches (Fig. 3C) and densely branched up to 10 to 13 times within complete colonies. Colony and sclerite color is uniform, bright yellow or dark red (Fig. 3A–B).

Remarks. *Eugorgia wilkiei* **sp. nov.** and the species *Eugorgia rubens* Verrill, 1868, *Eugorgia siedenburgae* Breedy and Guzman, 2013, *Eugorgia beebei* Breedy, Williams and Guzman, 2013 (previously proposed as monospecific groups) and *daniana* group (including 4 species) have branching irregularly pinnate, prominent polyp-mounds and the incomplete double discs as the more abundant type of coenenchymal sclerites (Table 1). However, *E. wilkiei* **sp. nov.** is included in the *daniana* group because it branches between 10 and 13 times, has

flabellate growth, and polyps are arranged in irregular rows (Table 1). The four species included for *daniana* group are *Eugorgia aurantiaca* (Horn, 1860), *Eugorgia daniana* Verrill, 1868, *Eugorgia mutabilis* Breedy, Williams and Guzman, 2013 and *Eugorgia multifida* Verrill, 1870.

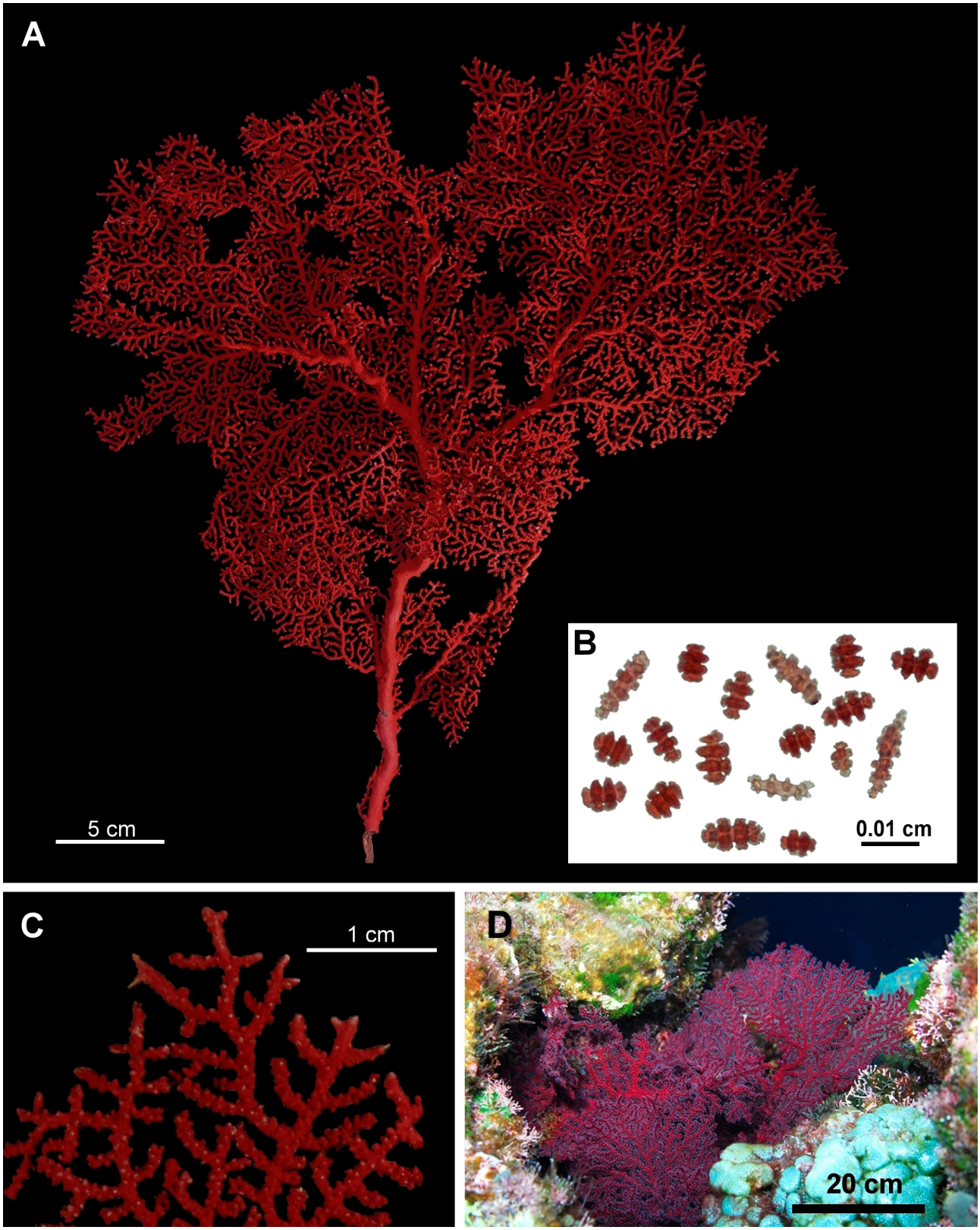

FIGURE 3. *Eugorgia wilkiei* **sp. nov.,** paratype USNM-1422108: A, entire red colony; B, red sclerites; C, detail of the branches and calyces; D, *in situ* alive simple planar colony.

The branching division in the *daniana* group are up to 7 times (except *E. aurantiaca* with branching up to 6 times), and the length of the terminal twigs between 0.8–1.5 cm; nevertheless, *E. wilkiei* **sp. nov.** branches up to 13 times and the terminal twigs to 0.1–0.3 cm in length makes the colonies look densely branching.

The color of the colonies in the *daniana* group is specific for each of the four species: *E. aurantiaca* have dark orange or red colonies with a contrasting yellow longitudinal groove, *E. daniana* possess bright red colonies with polyp-mounds amidst for yellow spots (Breedy *et al.* 2009a). *Eugorgia mutabilis* has white-pink colonies, and *E. multifida* have dark orange to bright red colonies with polyp-mound surrounded by bright yellow sclerites (Table 1). In contrast, *Eugorgia wilkiei* **sp. nov.** has two chromotypes with a solid color (yellow or red), the sclerites have the same color than the colonies, and never with a ring or spots in the polyp-mouth.

Eugorgia wilkiei **sp. nov.** is distinguished by its considerably dense flabellate growth, maximum branching up to 13 times, branches arise closer, the colony growth at several multiple planes and the yellow coloration of the colonies and their sclerites (the red chromotype is similar to *E. aurantica* and *E. multifida*). Its taxonomic features described here, suggest *E. wilkiei* **sp. nov.** is closely related to *E. multifida* with similar branch diameters and colony growth pattern. However, *E. multifida* has anthocodial rods that are absent in *E. wilkiei* **sp. nov.** (Table 1).

Habitat. Colonies were collected from 10–65 m depth attached to volcanic rocks (but more frequently observed between 50–100 m depth from the submersible DEEPSEE) on surfaces exposed or into crevices and holes. The yellow chromotype of *Eugorgia wilkiei* **sp. nov.** is common at 10–30 m depth, and the red chromotype (which is relatively more abundant in the population) is common at 20–100 m depth. Qualitative observations indicate that *E. wilkiei* **sp. nov.** colonies are present in low density (0.2 colonies/100 m^2) at shallow water between 10–30 m, and in high density (25 colonies/100 m^2) at deep water between 50–70 m.

Distribution. *Eugorgia wilkiei* **sp. nov.** is only known from Revillagigedo Archipelago (Socorro and San Benedicto Islands). Type locality: San Benedicto.

Etymology. *Eugorgia wilkiei* **sp. nov.** is named in memoriam of Donald Walter Wilkie (1931–2015), a Canadian-born who came to La Jolla in 1964 to begin his 35-years career as Director of the Scripps Aquarium and Founding Director of the Stephen Birch Aquarium. His life-long goal was to educate the public about marine life and ecology. A preeminent expert in his unique field as aquarium curator, educator, and ichthyologist, he cherished the collaborative scholarship program, the "Sea of Cortez Fellowship" along with the Universidad Autónoma de Baja California Sur in La Paz, Mexico to support brilliant marine biology students in the 1980's and 1990's. This Sea of Cortez Fellowship program promoted the formation of a new research group named Reef Fauna Project ("Proyecto Fauna Arrecifal" in Spanish) at UABCS since the 1990's.

Genus *Leptogorgia* Milne Edwards & Haime, 1857

Leptogorgia waltonae sp. nov.

(Fig. 4–6)

Holotype: USNM-1422111, dried specimen, Las Cuevas (19°17'54.026" N, -110°48'16.030" W), San Benedicto, Revillagigedo Archipelago, 20 m depth, January 20, 2000.

Paratypes: USNM-1422112 dried specimen, San Benedicto, Revillagigedo Archipelago, 18 m depth, 2006. USNM-1422113, dried specimen, San Benedicto, Revillagigedo Archipelago, 18 m depth, 2006. USNM-1422114, dried specimen, Las Cuevas, San Benedicto, Revillagigedo Archipelago, 20 m depth, January 20, 2000.

Holotype colony: A yellow colony considerably small (cluster growth), 1.7 cm in height and 1.3 cm in width (Fig. 4C). Holdfast rectangular (3–5 mm) from which arises a main stem 7 mm in width and 2 mm in diameter; which is divided by laterally growing into secondary branches <13 mm in length and 3 mm in diameter. The first and second branches branch off in ~45° angles, and the third in angles of ~90°, laterally. All terminal twigs show characteristic warty-like ends of 4–6 mm in diameter. Polyps arranged irregularly all along the colony except in the main steam where they are absent. Polyps are fully retractile into the coenenchyme forming slightly raised polyp mounds 0.5 mm with oblong apertures (1 mm in length). The first lateral branch is missing showing the nude dark brown axis of about 1 mm in diameter (Fig. 4C) (Table 1).

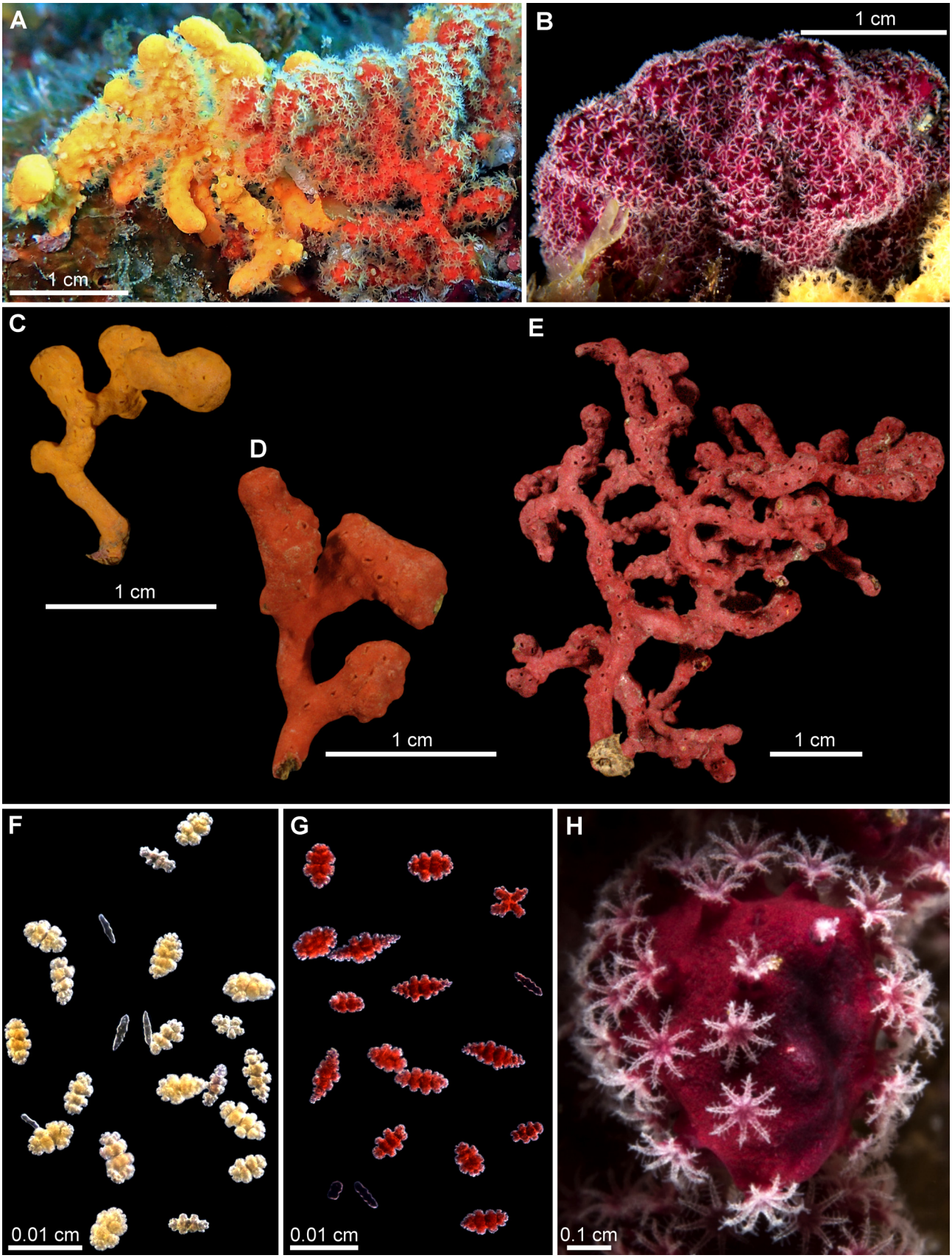

FIGURE 4. *Leptogorgia waltonae* **sp. nov.,** A, *in situ* alive yellow and orange colonies; B, *in situ* alive purple colony; C, Holotype USNM-1422111 yellow colony; D, dried orange colony; E, dried purple colony; F, Holotype yellow sclerites; G, red sclerites; H, spherical shaped tip. *In situ* photographs by Enric Ballesteros (A) and Octavio Aburto (B, H).

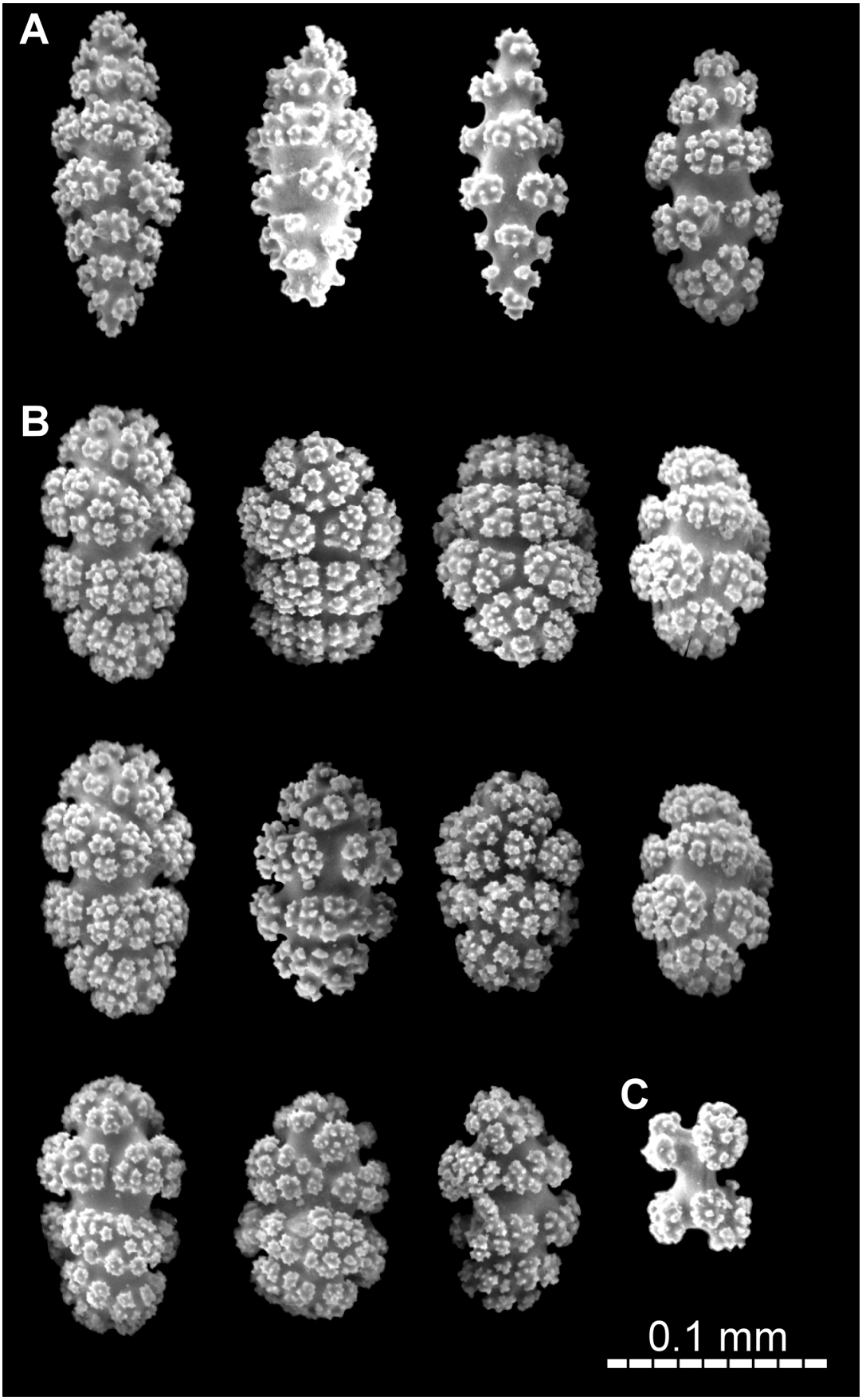

FIGURE 5. *Leptogorgia waltonae* **sp. nov.**, holotype USNM-1422111, coenenchymal sclerites: A, spindles; B, capstans; C, cross.

Holotype sclerites: The dominant type of sclerites is compact capstans (0.11 mm–0.065 mm) (Fig. 5C). Spindles are scarce (0.13 mm–0.06 mm) with 4–5 whorls of warty tubercles and acute ends (Fig. 5A,C, Table 1). Coenenchymal crosses are small up to 0.05 mm on each side (Fig. 5B). Coenenchymal and anthocodial sclerites are pale yellow (Fig. 4F, Table 1), the anthocodial sclerites are blunt rods with lobed margins (0.06 mm–0.03 mm) observed with an optical microscope (Fig. 4F) but not observed with SEM.

Variability. Colonies of *Leptogorgia waltonae* **sp. nov.** commonly have a highly varying coloration with polychromatic range of yellow, orange, pink, red, and purple in live and dried colonies and their sclerites (coenenchymal and anthocodial) (Fig. 4A–G). Larger but relatively uncommon colonies are bushy small (4.5 cm in height and 3.9 cm in width) with reddish-purple or pink coloration (Fig. 4B,D,E). All branches grow irregularly in several directions including some directed towards the substrate. Main branches of 5 to 15 mm in length and 2–4 mm in diameter arise from a holdfast up to 5 mm in length and 4 mm in width with a long main steam of 11 mm in length and 3 mm in diameter showing polyp mounds in the half top. Terminal twigs with conspicuous wart-like tips up to 6 mm in diameter are always present. Polyp mounds are slightly raised or prominent (about 2 mm) showing small circular or oval openings (Fig. 4H). The brownish nude axis (free of coenechyme) from ten colonies always shows several thin branches (1 mm diameter) at the base, but with conspicuously swollen, wart-like ends up to 3 mm in diameter (Fig. 6B). The main distinctive morphological character between small colonies and large colonies is that polyp mounds are slightly raised in small colonies and prominent in large colonies, so this attribute gives the colony a crumpled appearance.

Remarks. Breedy & Guzman (2011) divided all the species of the genus *Leptogorgia* from the American Pacific within three morphological groups according to internal and external morphological traits: *alba* (5 spp.), *rigida* (8 spp.), and *pumila* (11 spp.). *Leptogorgia waltonae* **sp. nov.** is different because colonies are cluster-shaped with few short branches that grow downward in angles between 90° and 180° with unequal thicknesses, tipped with sphere-shaped warts. We compared morphology of *L. waltonae* **sp. nov.** with *Leptogorgia ena* (Breedy *et al.* 2012) because it is the species of the genus with more morphological similarities (Table 1). *Leptogorgia ena* resembles *L. waltonae* **sp. nov.** because both species are small (<5 cm) and both have an uneven thickening along their branches. *Leptogorgia ena* has branches divided into two types of ramifications: (1) line with greater thickness in the intermediate zone but thinner in both the base and the tip, which can be sharpened and (2) thin branches at the base, but thick in both the intermediate portion and the tip; which are blunt. In contrast, *L. waltonae* **sp. nov.** has tips with sphere-shaped warts. We removed the coenenchyme from 10 colonies of *L. ena* collected at Oaxaca and 10 colonies of *L. waltonae* **sp. nov.** from Revillagigedo Archipelago, only the axis of *L. waltonae* **sp. nov.** always shows the tips with sphere-shaped warts (Fig. 6B) while *L. ena* shows the typical thin and homogeneous axis (Fig. 6A). Therefore, the thickness and shape of the branches in *L. ena* is due to thickening of the coenenchyme, while the thickness and shape of the branches in *L. waltonae* **sp. nov.** is due to the thickening of the axis. In fact, there is no other known *Leptogorgia* species in the American Pacific with the presence of this morphological character. Additionally, unlike *L. ena,* no tentacular sclerites were observed in *L. waltonae* **sp. nov.** These two distinctive morphological traits provide strong evidence that this is a new species (Table 1).

For practical purposes *Leptogorgia ena* was tentatively classified within the *pumila* group, however, Breedy *et al*. (2012) emphasized that for its particular traits (the small colony, the dominance of wide capstans, barrels and double heads, the low occurrence of spindles, the maximum length of spindles 0.10 mm, and lastly, the presence of tentacular sclerites) it should be segregated from their mutual resemblance (Table 1). We propose to group the species *L. ena* and *Leptogorgia waltonae* **sp. nov.** into a new group called *ena* group, because both species grow as small-grouping cluster-shaped colonies, their branching is asymmetric in thickness, and have wide capstans, barrels, double heads (Table 1).

Habitat. The colonies of *Leptogorgia waltonae* **sp. nov.** were collected attached to volcanic rocks up to 25 m depth and the highest density was observed at 10 m depth. Observations with the submersible DEEPSEE up to 200 m depth done in April 2016 confirmed this species has a shallow distribution pattern (<25 m depth). *Leptogorgia waltonae* **sp. nov.** shares its benthic habitat with a dominant sponge (*Aplysina revillagigedi* Cruz-Barraza, Carballo, Rocha-Olivares, Ehrlich & Hog, 2012), which has a high percentage of covered area on the volcanic rocks.

Distribution. *Leptogorgia waltonae* **sp. nov.** is only known from Revillagigedo Archipelago (Socorro and San Benedicto Islands). Type locality: San Benedicto.

Etymology. *Leptogorgia waltonae* **sp. nov.** is named *in honor* of Christy Ruth Walton (USA) underwater adventurer and photographer. A passionate woman that supports multiple research programs and expeditions in the

tropical eastern Pacific providing enthusiasm, funding, equipment, and travel support to scientists who are involved in research and conservation efforts of biota in the Gulf of California and the Mexican Pacific Ocean.

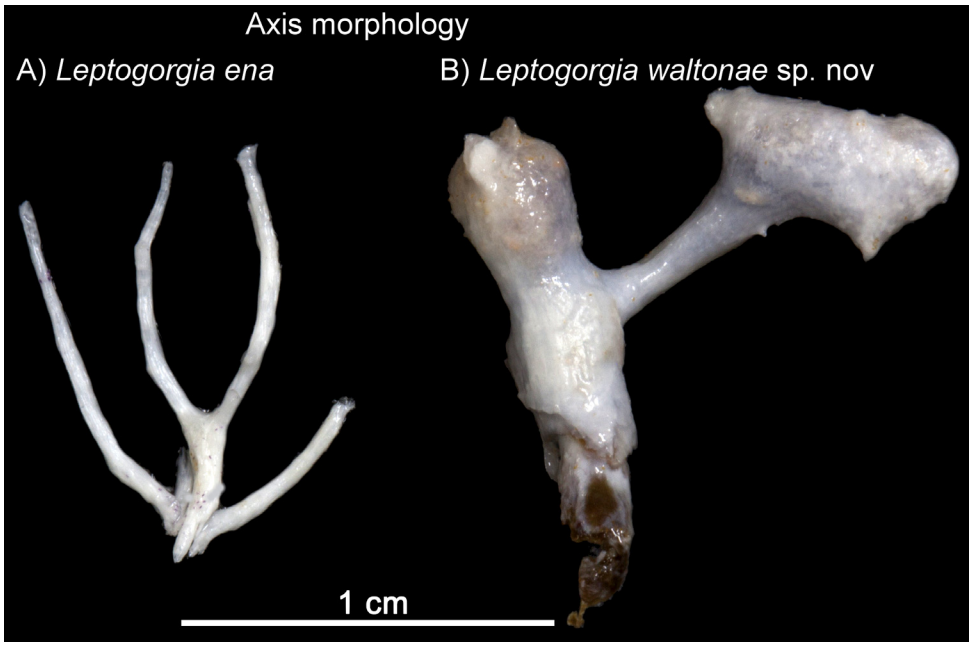

FIGURE 6. Comparison of axis morphology; A, *Leptogorgia ena* axis (Huatulco Bay, Oaxaca, Mexico); B, *Leptogorgia waltonae* **sp. nov.** axis (San Benedicto, Revillagigedo Archipelago).

Discussion

We propose the hypothesis that *Eugorgia wilkiei* **sp. nov.** and *Leptogorgia waltonae* **sp. nov.** are endemic species of the Revillagigedo Archipelago because they have never been seen or collected at any other sampling location during our 21 years monitoring efforts carried out by our research group (UABCS-PFA). This extensive monitoring and comprehensive research program have obtained sea fan collections at approximately 200 locations throughout the mexican Pacific and the Gulf of California between 1995 and 2016 (Fig. 7). Our collection currently has >2,500 sea fan colonies including 90 colonies of ten species from the Revillagigedo Archipelago. *Eugorgia wilkiei* **sp. nov.**, *L. waltonae* **sp. nov.** (this study), and other two nominal species identified as *Muricea appressa* Verrill, 1864 and *Muricea austera* Verrill, 1869 (Bedolla 2007) are the most recent check-list additions at Revillagigedo Archipelago. The relatively recent geological formation of the archipelago (i.e. Socorro Island, ~3.5 Ma; volcano at Isla Roca Partida, Late Pleistocene 126 kya; Volcán Bárcena at San Benedicto island formed in 1952), emerged from the Clarion ridge and the northern boundary of the Mathematicians oceanic mountains (Richard 1959, 1964; Harrison & Lee 1996), possibly explain its considerably high proportion of endemism and a relatively low diversity of its sea fan community (Bedolla 2007), besides of its isolation from the Mexican mainland. In fact, the Revillagigedo Archipelago have only 10 species of gorgonians representing one-third of the sea fan diversity observed along the west coast of the Baja California peninsula where 35 species have been reported, or within the Gulf of California with 30 species (14 nominal and 16 not described) (Carlos Sánchez pers. comm.; Hernández 2014, Gamero 2014). In comparison, only 14 gorgonians species occur at the Galapagos islands in Ecuador (Breedy *et al*. 2009b), and three shallow water gorgonian species have been reported at the oceanic Cocos Island, in Costa Rica: *Pacifigorgia curta* Breedy & Guzman, 2003, *Leptogorgia alba* (Duchassaing & Michelotti, 1864), and *Leptogorgia tricorata* Breedy & Cortés, 2011. Like at Revillagigedo Archipelago, Cocos island's communities have low population density and *L. tricorata* has only been observed there (Breedy & Cortés 2011) suggesting at Cocos also exist a relatively high proportion of endemic sea fans species. These observations show how oceanic islands can promote speciation processes in gorgonian sea fans.

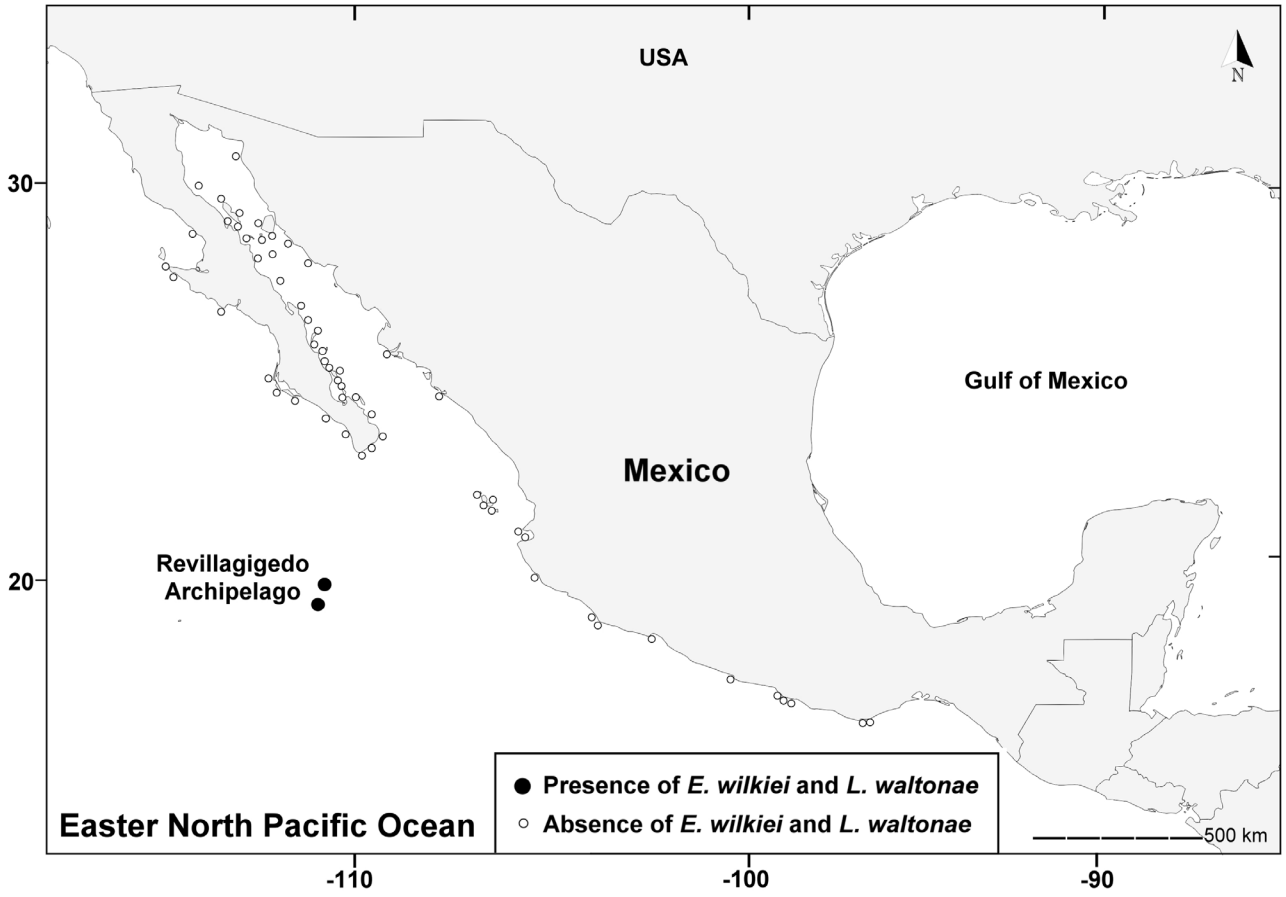

FIGURE 7. Map of octocoral sampling sites on rocky reefs along the Pacific coast of Mexico and Gulf of California carried out between 1995–2016, showing the sampling location of *E. wilkiei* **sp. nov.** and *L. waltonae* **sp. nov**.

Every year the Revillagigedo Archipelago are hit out along the path of several eastern Pacific hurricanes (May–Nov) originating from the Southern oceanic region of Mexico. These hurricanes disturb and modify the Archipelago coastal habitat, particularly the epibenthic fauna along the coast (<40 m depth). Historical analysis (1990–2016) reveals a mean occurrence of 6.9 hurricanes per year (Sánchez, C. unpublish. data) causing seasonal and frequent perturbations on benthic communities where only sea fans with robust and hard morphologies can survive being naturally selected. At Cocos island, *Leptgorgia tricorata* took its species name from its capacity to appear and disappear from the type locality, and its periodical detachment given its small holdfast -just as *Leptogorgia waltonae* **sp. nov.** seems to explain its low abundance and perhaps its main cause of mortality (Breedy & Cortés 2011). On the other hand, *Eugorgia wilkiei* **sp. nov.** can attain relatively larger colony sizes because it has a strong and robust holdfast and compacted sclerites in the coenenchyme. These morphological features provide a strong resistance to strong currents and seasonal climatic perturbations. Indeed, these powerful winds and hurricanes that enact strong wave action certainly represent an equally strong selection pressure in favor of morphologically small sea fans with sturdy attachments holdfast allowing them to affix themselves to rocky surfaces and shallow crevasse and holes, as observed in the small (<4 cm) endemic species *L. tricorata* at Cocos island (Breedy & Cortés 2011).

Hypothetically, these rough environmental conditions and presumably the low range of larval dispersion produce sea fans with unique morphologies, like those observed in *Eugorgia wilkiei* **sp. nov.** and *Leptogorgia waltonae* **sp. nov.** Isolation may explain the speciation processes taking place in such offshore islands. Unfortunately, sea fan knowledge at Revillagigedo Archipelago is scarce and more taxonomic studies are required to support future studies about their biology, ecology, biogeography and evolution of sea fans. Recent genetic studies demonstrated that *Leptogorgia* and *Eugorgia* are monophyletic and together form a highly supported clade sister to *Pacifigorgia* (Vargas *et al*. 2014). These three genera are highly endemic of oceanic islands like Revillagigedo, Cocos, or Galapagos, and *E. wilkiei* **sp. nov.** increases the number of *Eugorgia* extant species to 16

and *L. waltonae* **sp. nov.** is the 26th species of the genus *Leptogorgia* described in the eastern Pacific (Hernández 2014). Systematic monitoring programs will help to discover new species of sea fans and update their distribution ranges in Mexico.

Recent molecular phylogenetic evidence (nuclear and mitochondrial markers) of sea fans from the Eastern Tropical Pacific indicates that several species of *Eugorgia* and *Leptogorgia* from Ecuador are within a single genetic clade, and neither was recovered as monophyletic (Soler-Hurtado *et al.* 2017). In addition, a world review of the genus *Leptogorgia*, based on mitogenomics, demonstrate that this genus is a polyphyletic group with at least four clades distributed in the Eastern Atlantic-Mediterranean Sea, South Africa, Western Atlantic, and Eastern Pacific (Poliseno *et al.* 2017). They reveal a deep divergence among morphologically similar but geographically restricted octocoral lineages, currently included in the genus *Leptogorgia*. The Atlantic–Mediterranean species of "*Leptogorgia*" represent an old lineage, not closely related to the Western Atlantic-eastern Pacific "*Leptogorgia*" (which diverged and diversified recently). Poliseno *et al.* (2017) argued it is evident that a revision of the world "*Leptogorgia*" is necessary to clarify the systematics of these organisms and provide a phylogenetically sound taxonomic system for the fauna. Because the oldest described species of *Leptogorgia* is not from the Eastern Pacific, the taxonomic status of the genus "*Leptogorgia*" from this region is still unclear. Our current designation of the two new species proposed here was designated exclusively using the traditional morphological taxonomy of *Eugorgia* and *Leptogorgia* until the formal review of the "*Leptogorgia"* and *"Eugorgia"* from the Eastern Pacific is fully clarified.

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