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Diana Carolina Vergara-Florez, Rubén Abad, Karla. B Jaramillo, Jenny Rodríguez, Adriana Sarmiento & Juan Armando Sánchez

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New octocoral records for the Ecuadorian Tropical Eastern Pacific

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ABSTRACT

The genus Muricea, a highly speciose gorgonian coral group in the Tropical Eastern Pacific (TEP), is commonly found on shallow rocky reefs including Machalilla National Park (MNP), El Pelado Marine Reserve (REMAPE) and Galápagos Marine Reserve (GMR). Here, we report the presence of *M. hebes*, *M. echinata* and *M.* robusta, which have been not previously reported at the REMAPE area and along the Ecuadorian region. These new records for Muricea hebes (Verril, 1864) in Ecuador broaden the known geographical distribution of these species across the tempered waters of California and Mexico, and the Tropical Eastern Pacific, belonging to Panama and Ecuador. Muricea robusta (Verril, 1864) was previously recorded in Mexico and Colombia, whereas M. echinata (Verril, 1866) was only found in Panama. This report contributes to increasing the knowledge of marine diversity in Ecuador, and broadens the previously recorded geographic distribution of the genus Muricea throughout the TEP.

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Muricea; Octocorallia; Alcyonacea; Plexauridae; REMAPE; Tropical Eastern Pacific (TEP); Ecuador

Introduction

The only amphi-American and aposymbiotic group of octocorals is *Muricea* (Cnidaria: Plexauridae) (Sánchez 2016). This genus is usually abundant in shallow waters of the Tropical Eastern Pacific (TEP), in areas exposed to moderate water motion, commonly inhabiting rocky reefs or rocky caves and less commonly found on sandy bottoms (Breedy and Guzman 2016; Steiner et al. 2018). This group has a broad depth distribution, where most of the species thrive in euphotic shallow waters between 5 and 30 m, and two species inhabit the mesophotic zone between 30 and 220 m, one in the Caribbean Sea and the other in the Gulf of Mexico (Sánchez et al. 2019). Furthermore, the wide geographic distribution of the genus encompasses the TEP

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(Breedy and Guzman 2016) and the Atlantic Ocean, specifically the Caribbean Sea, the Gulf of Mexico, and part of the South Atlantic Ocean of Brazil (Marques and Castro 1995).

This wide distribution is feasible for Muricea and octocorals because they are considered mixotrophic organisms. Octocorals acquire energy through autotrophic means, via symbiont photosynthesis, and through additional heterotrophic behaviour, allowing them to successfully settle in different habitats. For instance, it is well known that octocorals are efficient filter feeders (Fabricius et al. 1995; Fabricius and Klumpp 1995; Oppen et al. 2005) by maximising nutrient acquisition where the concentration of light and plankton can be often limiting (Lewis 1982; Sánchez 2016). As an aposymbiotic genus, some species possess common symbiotic dinoflagellate algae, and some do not have that symbiont. This aposymbiotic status represents an interesting ecological issue that requires further research. The mutualistic relationship is mainly with photosynthetic dinoflagellates belonging to the Symbiodinaceae genus Breviolum (Oppen et al. 2005; LaJeunesse et al. 2018; Lau et al. 2019), as in M. echinata, M. laxa, M. muricata and M. atlantica. On the other hand, the mesophotic species *M. pendula* in the Gulf of Mexico and all the species in the Pacific Ocean, including M. echinata, M. crassa, M. plantaginea, M. purpurea, M. squarrosa, M. austera and Muricea sp., as well as endemic species of Ecuador such as M. galapagensis (Breedy and Guzman, 2016; Steiner et al. 2018), are azooxanthellate (Sánchez et al. 2019).

Along the TEP (Breedy and Guzman 2016) and specifically in the Equatorial Front, *Muricea* species are abundant and widely distributed in shallow rocky reefs. The El Pelado Marine Reserve (REMAPE), declared a Marine Protected Area (MPA) under the Marine Reserve category in 2012, is one of the richest localities for *Muricea* species. *Muricea* corals prefer the surrounding rocky reefs and can significantly shape the boundary layer in coral reef and rocky reef habitats, sharing an ecological setting living in sympatry, and exposed to fluctuations in salinity and temperature (Fiedler and Lavín 2017; Steiner et al. 2018) due to the mix of currents including the northern end of the Humboldt current. To assess the octocoral biodiversity of this zone, in 2018 we explored these rocky reef formations at El Pelado Islet and collected several octocoral species from multiple genera, including *Muricea* sp., *Pacifigorgia* sp., *Leptogorgia* sp. and *Carijoa* sp. Here, we report the first records of *M. hebes, M. robusta* and *M. echinata* for the Ecuadorian coast and update a checklist with all the octocoral samples collected in the study area.

Materials and methods

Study area

During 2018, we collected colonies from all the gorgonian coral species that we found by scuba diving at four stations around El Pelado Islet at the REMAPE area in the province of Santa Elena. The collecting stations were Laberinto, La Pared, Bajo 40 and Acuario. During the collection, all species were labelled and photographed (Figure 1 and Table 1).

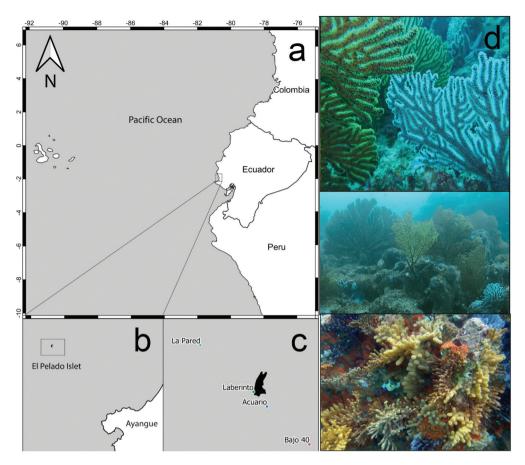


Figure 1. (a–c) Map of the sampling stations. (CENAIM-ESPOL, Bajo 40, Laberinto, Acuario, La Pared). Map credits: Divar Castro – CENAIM. (d) *In situ* rocky reefs of El Pelado which these species inhabit in sympatry. Exsitu Photos by D.C. Vergara and Juan A. Sánchez. Insitu Photos by Rubén Abad and Karla. B. Jaramillo.

Sampling description

The field and laboratory methodology used followed that described by Breedy and Guzmán (2003), with minor modifications. At the laboratory, the species identification and morphological descriptions (Supplementary material, Table S1) were achieved using voucher subsamples at the National Center of Aquaculture and Marine Investigations (CENAIM-ESPOL) repository.

Description

After their collection in October 2018, the soft coral samples were stored. During the data management process, the names of the specimens were checked with the World Register of Marine Species (WoRMS), the data set was prepared according to the Darwin Core standard at

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the CENAIM-ESPOL repository, and finally, the data were compared with previous reports and publications of octocoral species, focusing on standardised morphological feature guides to the relevant genera.

Geographic coverage

Description

El Pelado Islet is located 6950.11 m from the shore, near the San Pedro and Ayangue localities in the El Pelado Marine Reserve (REMAPE) on the Ecuadorian coastline in the province of Santa Elena, Ecuador. Samples were collected from four rocky reefs – Bajo 40, Laberinto, La Pared and Acuario (Figure 1) – with a mean temperature of 22–24°C and a salinity of 33.5–34 Practical Salinity Units (PSU).

Coordinates

Bajo 40: -1.919°S, -80.804°W Laberinto: -1.901°S, -80.835°W La Pared: -1.899°S, -80.840°W Acuario: -1.904°S, -80.820°W

Results

Description

The taxonomic coverage of the data set is limited to the soft coral assemblages of the study area. A list of the species included in the data set, also indicating the field code, museum code, locality and collection date, is given in Table 1.

Taxa included

We present a quantitative assessment of Alcyonaceae communities from the southern TEP. A total of 25 species were collected: 11 species of *Muricea* (*M. austera, M. crassa, M. echinata, M. fruticosa, M. plantaginea, M. purpurea, M. robusta, M. squarrosa, Muricea* sp., *M. californica* and *M. hebes*); five species of *Pacifigorgia* (*P. adamsii, P. irene, P. firma, P. rubicunda* and *Pacifigorgia* sp.); five species of *Leptogorgia* (*L. alba, L. cuspidata, L. pumila, L. obscura* and *L. taboquilla*); two species of *Heterogorgia* (*H. hickmani* and *Heterogorgia* sp.); *Psammogorgia arbuscula*; and *Carijoa riisei*. Moreover, we describe the features of the three species newly reported in this study (Table S1 and Figures 2–5).

Muricea hebes (Verrill, 1864)

The newly recorded specimens of *M. hebes* (Figures 2–3) were collected at 15 m depth inside a small crevice in the Bajo 40 mound. The *in situ* colony was dark reddish-orange with white polyps while the *ex situ* colony presented a yellowish-brown colour with a finger-like colony shape. The colony is 16 cm tall and 20 cm wide with an irregularly dichotomous branching pattern. Branches are flattened and 5–9 mm in diameter, and the

Table 1. Data set of the octocorals collected from the El Pelado Equatorial Front (October 2018).

Field code	Museum code	Collected from the El Pelado Species	Locality	Date
ECU003	181017EP07-03	Leptogorgia alba	Bajo 40	17 October 2018
ECU005	181017EP07-05	Muricea californica	Bajo 40	17 October 2018
ECU006	181017EP07-06	Heterogorgia hickmani	Bajo 40	17 October 2018
ECU007	181017EP07-07	Muricea purpurea	Bajo 40	17 October 2018
ECU008	181017EP07-08	Leptogorgia obscura	Bajo 40	17 October 2018
ECU009	181017EP07-09	Heterogorgia hickmani	Bajo 40	17 October 2018
ECU011	181017EP07-11	Leptogorgia obscura	Bajo 40	17 October 2018
ECU012	181017EP07-12	Heterogorgia hickmani	Bajo 40	17 October 2018
ECU013	181017EP07-13	Muricea fruticosa	Bajo 40	17 October 2018
ECU014	181017EP07-14	Heterogorgia sp.	Bajo 40	17 October 2018
ECU016	181017EP07-16	Muricea purpurea	Bajo 40	17 October 2018
ECU017	181017EP07-17	Leptogorgia cuspidata	Bajo 40	17 October 2018
ECU018	181017EP07-18	Muricea purpurea	Bajo 40	17 October 2018
ECU019	181017EP07-19	Muricea austera	Bajo 40	17 October 2018
ECU020	181017EP07-20	Leptogorgia pumila	Bajo 40	17 October 2018
ECU021	181017EP07-21	Muricea purpurea	Bajo 40	17 October 2018
ECU022	181017EP07-22	Muricea hebes*	Bajo 40	17 October 2018
ECU024	181017EP07-24 181017EP07-25	Leptogorgia cuspidata Muricea fruticosa	Bajo 40 Baia 40	17 October 2018 17 October 2018
ECU025 ECU026	181017EP07-25	Muricea austera	Bajo 40 Baio 40	17 October 2018
ECU028	181017EP07-28	Leptogorgia alba	Bajo 40 Bajo 40	17/ October 2018
ECU028 ECU029	181017EP07-28	Muricea purpurea	Bajo 40 Bajo 40	17 October 2018
ECU030	181017EP07-30	Muricea fruticosa	Bajo 40	17 October 2018
ECU031	181017EP07-31	Muricea fruticosa	Bajo 40	17 October 2018
ECU032	181017EP07-32	Carijoa riisei	Bajo 40	17 October 2018
ECU033	181017EP04-01	Psammogorgia arbuscula	Laberinto	17 October 2018
ECU034	181017EP04-02	Muricea austera	Laberinto	17 October 2018
ECU035	181017EP04-03	Muricea californica	Laberinto	17 October 2018
ECU036	181017EP04-04	Pacifigorgia rubicunda	Laberinto	17 October 2018
ECU037	181017EP04-05	Leptogorgia pumila	Laberinto	17 October 2018
ECU038	181017EP04-06	Pacifigorgia rubicunda	Laberinto	17 October 2018
ECU039	181017EP04-07	Psammogorgia arbuscula	Laberinto	17 October 2018
ECU040	181017EP04-08	Muricea squarrosa	Laberinto	17 October 2018
ECU041	181017EP04-09	Muricea squarrosa	Laberinto	17 October 2018
ECU042	181017EP04-10	Leptogorgia pumila	Laberinto	17 October 2018
ECU043	181017EP04-11	Psammogorgia arbuscula	Laberinto	17 October 2018
ECU044	181017EP04-12	Muricea squarrosa	Laberinto	17 October 2018
ECU045	181017EP04-13	Psammogorgia arbuscula	Laberinto	17 October 2018
ECU046	181017EP04-14	Muricea squarrosa	Laberinto	17 October 2018
ECU047	181017EP04-15	Pacifigorgia sp.	Laberinto	17 October 2018
ECU048	181017EP04-16	Muricea squarrosa	Laberinto	17 October 2018
ECU049	181017EP04-17	Muricea californica	Laberinto	17 October 2018
ECU050	181017EP04-18	Muricea californica	Laberinto	17 October 2018
ECU051	181017EP04-19	Heterogorgia hickmani	Laberinto	17 October 2018
ECU052	181017EP04-20	Muricea purpurea	Laberinto	17 October 2018
ECU053	181017EP04-21	Heterogorgia hickmani	Laberinto	17 October 2018
ECU054	181017EP04-22	Muricea squarrosa	Laberinto	17 October 2018
ECU055	181017EP04-23	Muricea fruticosa	Laberinto	17 October 2018
ECU056 ECU057	181017EP04-24 181017EP04-25	Muricea fruticosa Psammogorgia arbuscula	Laberinto Laberinto	17 October 2018 17 October 2018
ECU057 ECU058	181017EP04-25	Muricea fruticosa	Laberinto	17 October 2018
		Heterogorgia hickmani		17 October 2018
ECU059 ECU060	181017EP04-27 181017EP04-28	Pacifigorgia sp.	Laberinto Laberinto	17 October 2018
ECU061	181017EP04-29	Muricea squarrosa	Laberinto	17 October 2018
ECU062	181017EP04-30	Psammogorgia arbuscula	Laberinto	17 October 2018
ECU063	181017EP04-30	Muricea squarrosa	Laberinto	17 October 2018
ECU064	181017EP04-32	Pacifigorgia irene	Laberinto	17 October 2018
ECU065	181017EP04-33	Muricea fruticosa	Laberinto	17 October 2018
ECU066	181017EP04-34	Leptogorgia taboguilla	Laberinto	17 October 2018
ECU067	181017EP04-35	Pacifigorgia sp.	Laberinto	17 October 2018
ECU068	181017EP04-36	Leptogorgia pumila	Laberinto	17 October 2018
				(Continued)

(Continued)

Tab	ble	1. ((Continued)	١.

Field code	Museum code	Species	Locality	Date
ECU070	181017EP04-38	Muricea squarrosa	Laberinto	17 October 2018
ECU071	181017EP04-39	Pacifigorgia irene	Laberinto	17 October 2018
ECU073	181018EP01-02	Muricea echinata*	La Pared	18 October 2018
ECU075	181018EP01-04	Pacifigorgia sp.	La Pared	18 October 2018
ECU076	181018EP01-05	Muricea echinata*	La Pared	18 October 2018
ECU077	181018EP01-06	Muricea sp.	La Pared	18 October 2018
ECU078	181018EP01-07	Muricea sp.	La Pared	18 October 2018
ECU079	181018EP01-08	Muricea echinata*	La Pared	18 October 2018
ECU080	181018EP01-09	Muricea echinata*	La Pared	18 October 2018
ECU082	181018EP01-11	Muricea echinata*	La Pared	18 October 2018
ECU083	181018EP01-12	Muricea echinata*	La Pared	18 October 2018
ECU084	181018EP01-13	Carijoa riisei	La Pared	18 October 2018
ECU085	181018EP01-14	Muricea echinata*	La Pared	18 October 2018
ECU086	181018EP01-15	Muricea plantaginea	La Pared	18 October 2018
ECU087	181018EP01-16	Carijoa riisei	La Pared	18 October 2018
ECU089	181018EP01-18	Muricea echinata*	La Pared	18 October 2018
ECU090	181018EP01-19	Pacifigorgia irene	La Pared	18 October 2018
ECU091	181018EP02-01	Pacifigorgia rubicunda	Acuario	18 October 2018
ECU093	181018EP02-03	Pacifigorgia rubicunda	Acuario	18 October 2018
ECU096	181018EP02-06	Pacifigorgia adamsii	Acuario	18 October 2018
ECU097	181018EP02-07	Pacifigorgia rubicunda	Acuario	18 October 2018
ECU098	181018EP02-08	Pacifigorgia rubicunda	Acuario	18 October 2018
ECU099	181018EP02-09	Muricea austera	Acuario	18 October 2018
ECU113	181018EP02-12	Pacifigorgia irene	Acuario	18 October 2018
ECU114	181018EP02-13	Muricea purpurea	Acuario	18 October 2018
ECU116	181018EP02-15	Muricea crassa	Acuario	18 October 2018
ECU117	181018EP02-16	Muricea crassa	Acuario	18 October 2018
ECU118	181018EP02-17	Muricea crassa	Acuario	18 October 2018
ECU119	181018EP02-18	Muricea crassa	Acuario	18 October 2018
ECU100	181019EP07-01	Leptogorgia obscura	Bajo 40	19 October 2018
ECU107	181019EP07-02	Leptogorgia pumila	Bajo 40	19 October 2018
ECU108	181019EP07-03	Muricea robusta*	Bajo 40	19 October 2018
ECU109	181019EP07-04	Muricea robusta*	Bajo 40	19 October 2018
ECU120	181019EP07-05	Pacifigorgia firma	Bajo 40	19 October 2018
ECU124	181019EP07-06	Pacifigorgia firma	Bajo 40	19 October 2018
ECU121	181019EP07-07	Pacifigorgia firma	Roca	19 October 2018
ECU122	181019EP07-08	Pacifigorgia firma	Roca	19 October 2018
ECU123	181019EP07-09	Muricea hebes*	Bajo 40	19 October 2018

*New area reports

Note: The significance is explained at the bottom of the table. The asterisks and bolding indicate sample collected belonging to the species of interest of the study.

unbranched terminal ends measure up to 4 cm. The coenenchyma tissue is thick and brownish in colour. Calyxes are arranged closely at branchlets and they are located all around the branches, up to 1.2 mm long and 1 mm wide. This species was previously described by Breedy as a yellowish-brown colony with a finger-like colony shape and an irregularly dichotomous branching pattern of 3.2 cm length of the unbranched terminal branchlet. The coenenchyma tissue is thick, 1–1.8 calyx height at branches, and there is a close and slightly imbricate calyx arrangement at branchlets. The calycular sclerites are white, whereas the coenenchymal sclerites are pale yellow calycular and coenenchymal (Table S1). Colour: pale yellow. Previously described as unilateral spinose spindles (uss) (Breedy and Guzman 2016). *Muricea hebes* was previously reported in Mexico, at Pájaros Island, Mazatlan Bay, Sinaloa; in Cabo Pulmo, Gulf of California; and in the Pearl Islands, Panamá (Breedy and Guzman 2016).

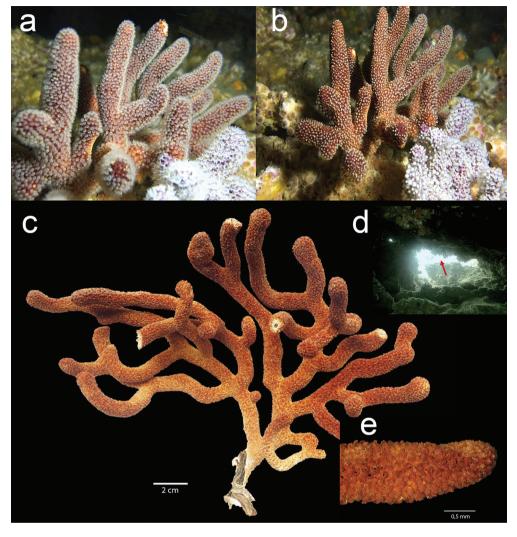


Figure 2. Underwater *in situ* record of *Muricea hebes* colony with (a) the white extended polyps, and (b) *M. hebes* with the polyps contracted. (c) *Ex situ* dry colony of *M. hebes*. (d) Location of colonies inside a cavern at the Bajo 40 site. (e) Close-up of the small tubular calyxes in a branch. Exsitu Photos by D.C. Vergara and Juan A. Sánchez. Insitu Photos by Rubén Abad and Karla. B. Jaramillo.

Muricea echinata (Verril, 1866)

The new record of *M. echinata* was collected (Figure 3) from La Pared at 15 m depth, embedded in coralline algae, on rocky substrates. The *in situ* colony was dark reddish to dark brown with white polyps (Figure 3(a)), while the *ex situ* colony (Figure 3(b)) presented a reddish-brown colour with a bushy colony shape. The colony is 10 cm tall and 8 cm wide, with an irregular lateral branching pattern extended in one plane. Branches are flattened, 4–6 mm in diameter, and the unbranched terminal ends measure up to 3 cm. The coenenchyma tissue is thin and reddish in colour. Calyxes are located all around the branches and they are

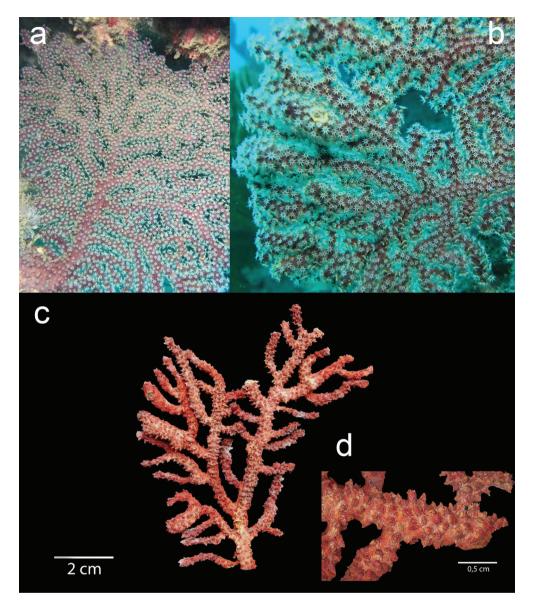


Figure 3. Underwater *in situ* record of *Muricea echinata*: (a) full colony with extended white polyps and close-up of the polyps at La Pared site. (b) *Ex situ* dry colony of *M. echinata*. (c) Close-up of the calyxes in a bifurcated branch. Exsitu Photos by D.C. Vergara and Juan A. Sánchez. Insitu Photos by Rubén Abad and Karla. B. Jaramillo.

prominent, up to 1.5 mm long and 1 mm wide (Figure 3(c)). The arrangement at bracelets is close. The colonies were previously described by Breedy and Guzman (2016) as having a colour that varies to a deeper orange hue and with an irregular branching pattern spreading in a single plane. Unbranched terminal ends reach up to 30 mm long. The colonies measure 8.5–10 cm tall and 7–14 cm wide. The branches are thinner at the base and a little ticker at the tips (Table S1). Calyxes

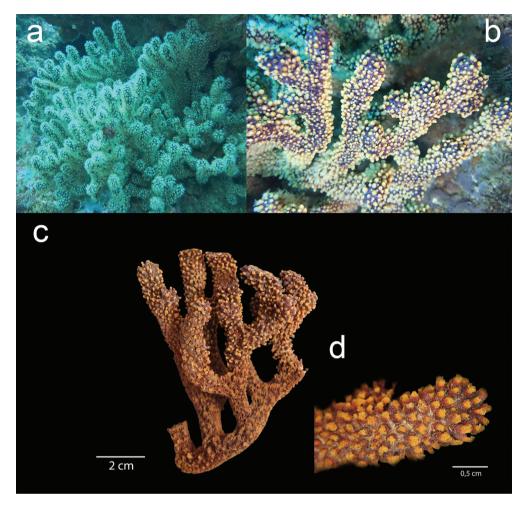


Figure 4. Underwater *in situ* record of *Muricea robusta*: (a) full colony with extended yellow polyps and close-up of the polyps in Bajo 40 site; and (b) with the polyps inside the colony. (c) *Ex situ* dry colony of *M. robusta*. (d) Close-up of the large orange calyxes in a branch. Exsitu Photos by D.C. Vergara and Juan A. Sánchez. Insitu Photos by Rubén Abad and Karla. B. Jaramillo.

are located all around the branches and they are prominent, up to 3 mm long and covered with large spindles with sharp ends. Coenenchyma is thin and composed basically of the calyx sclerites; they are orange and light brown, and the larger ones are darker (Figure 5). This species was previously reported in Pájaros Island in Panamá.

Muricea robusta (Verril, 1864)

The *M. robusta* colonies were collected at Bajo 40 at 15 m depth. Colonies have yellow polyps with purple soft tissue around them (Figure 4(a,b)), while the *ex situ* colony presented a brownish-orange colour and a bushy colony shape (Figure 4(c)). The colony measures 11 cm tall and 5 cm wide with an irregular dichotomous branching pattern.

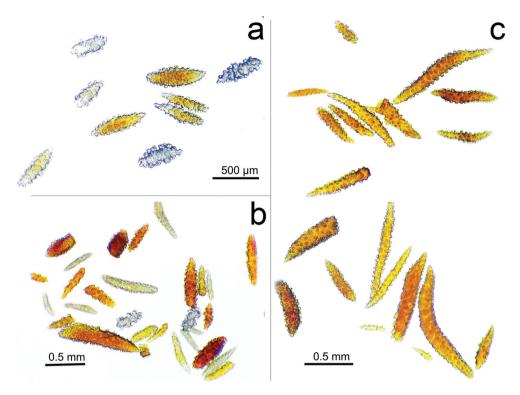


Figure 5. Sclerites of the three species (a) *Muricea hebes*, (b) *Muricea robusta* and (c) *Muricea echinata* collected at El Pelado Islet (REMAPE area). Sclerite Photos by Rubén Abad and Karla. B. Jaramillo.

Stems are slightly flattened, 11 mm in diameter and the unbranched terminal ends measure up to 7 cm. The coenenchyma tissue is thick and reddish-brown in colour. Calyxes are closely arranged at branchlets and are located all around the branches, up to 1 mm long and 0.8 mm wide. The calycular and coenenchymal sclerites are light orange and of a light type, with a mean size of 0.64×0.26 mm for calycular spindles and 0.15×0.05 mm for anthocodial sclerites (Figure 5).

Discussion

This report contributes to increasing the knowledge of marine diversity in Ecuador, and broadens the previously recorded geographic distribution of the genus *Muricea* throughout the TEP (Breedy and Guzman 2016). Previously, the REMAPE area included eight reported *Muricea* species (Steiner et al. 2018), whereas we were able to collect 11 *Muricea* species, with different morphotypes of some species (i.e., orange *Muricea planta-ginea*), as well as other gorgonian species (i.e. *Pacifigorgia* sp., *Leptogorgia* sp. and *Heterogorgia* sp.) with more than one morphotype per species (i.e., orange and white *Leptogorgia*). In the TEP three *Muricea* species were sampled, in The Gulf of California, Mexico, and Panama (*M. hebes*); in Mexico, Costa Rica and Panama (*M. echinata*); and in

Mexico and Colombia (*M. robusta*) (Breedy and Guzman 2016), expanding *Muricea's* tropical southern distribution to Ecuador (El Pelado Islet). Thus, our study has increased the known geographic distribution of the genus.

Furthermore, we contribute recent morphological descriptions of the newly recorded species. We present descriptions and photographs of *in situ* and *ex situ* colonies, facilitating future *Muricea* identification *in situ* for researchers performing scuba diving, and identification *ex situ* when researchers evaluate morphological differences using museum specimens. Moreover, sclerite descriptions were registered due to their phenotypic relevance; sclerites and spicules are known to be important morphological traits for octocoral identification.

Finally, we recommend an ongoing census of rocky coastal ecosystems, together with deeper explorations in mesophotic environments, to continue identifying and registering new gorgonian records, as well as recurrent invasive species such as the octocoral *Carijoa riisei*. We highlight the remarkable importance of tracking and recording the gorgonian marine diversity of shallow and mesophotic environments in tropical regions.

Temporal coverage

Notes

The field trips were conducted from 17 to 19 October 2018. The data set was created in October 2018. Some specimens could not be identified to the species level, and these samples will be analysed in the future for further genetic publications.

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Data resources

Data package title

List of 25 species collected, 11 species belonging to *Muricea*, five species of *Pacifigorgia*, five species of *Leptogorgia*, two species of *Heterogorgia*, *Psammogorgia arbuscula* and the invasive species *Carijoa riisei*, collected at El Pelado Islet (REMAPE area).

Number of data sets

One.

Data set name

Checklist of octocorals in the Equatorial Front. doi:10.6084/m9.figshare.15183828.

Data format version

1.0.

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Description

The data presented here correspond to the occurrences of deep-sea octocorals from the Equatorial Front and are based on identifying the collected specimens to the species level where possible.

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Disclosure statement

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Authors' contribution

DCV-F and JAS contributed to the conceptualisation of the study. DCV-F, RA and ASS contributed to the methodology and sampling. DCV-F, RA and KJ conducted morphological analyses. DCV-F and RA wrote the original draft. KJ and ASS contributed to writing, editing and reviewing the

manuscript. JAS, JR and DCV-F helped in the acquisition of funding. JAS and JR supervised the study. All authors read and approved the final manuscript.

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