Zootaxa 2151: 1–46 (2009)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

A revision of the genus *Eugorgia* Verrill, 1868 (Coelenterata: Octocorallia: Gorgoniidae)

ODALISCA BREEDY[1,2,3], HECTOR M. GUZMAN[3] & SERGIO VARGAS[1,2]

[1]Centro de Investigación en Ciencias del Mar y Limnología, Universidad de Costa Rica. [2]Museo de Zoología, Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica. E-mail: odalisca.breedy@ucr.ac.cr [3]Smithsonian Tropical Research Institute, MRC 0580-08, Box 0843-03092, Panama, Republic of Panama

Table of contents

Accepted by P. Alderslade: 4 Jun. 2009; published: 7 Jul 2009

Abstract

The species of the gorgoniid genus *Eugorgia* that occur along the eastern Pacific are taxonomically revised based on original type material of all species described until now, and reference specimens from recent surveys and expeditions. The genus *Eugorgia* is characterised by having a dominance of double disc sclerites in the coenenchyme which separate this taxon from the other gorgonians with similar external morphology such as *Leptogorgia*. In this revision, 12 species are recognized as valid and one is synonymised, *E. forreri*. Lectotypes were assigned for two species in order to establish their taxonomic status, and three varieties were established as species, *E. alba*, *E. excelsa* and *E. purpurascens*. All the species are described and illustrated. Based on the morphology of colonies and sclerites and supported by a phylogenetic analysis, we recognised three species groups within the genus *Eugorgia*: the "*ampla*-group" consisting of eight species, with slightly raised polyp-mounds and dichotomous branching or irregular variations of it; the "*daniana* group", consisting of three species, with prominent polyp-mounds and pinnate-like branching; and the "*rubens*-group" consisting of a single species, *E. rubens*, which is closely related to species within the second group. The fauna herein reported does not represent the diversity or geographical range of the species because more surveys are needed and more material stored in museums needs attention to complete the regional assessment.

Key words: Cnidaria, Coelenterata, octocorals, eastern Pacific, Mexico, Costa Rica, Panama, Ecuador, *Eugorgia*, phylogenetic analysis

Introduction

Gorgonians are widely distributed along the eastern Pacific, from Baja California to Peru including the oceanic islands, and the families Gorgoniidae and Plexauridae are the most abundant in shallow waters (<50 m in depth). Genera of these families have representatives in both the Pacific and Atlantic ocean, like *Muricea* Lamouroux, 1812, *Leptogorgia* Milne Edwards & Haime, 1857, and *Pacifigorgia* Bayer, 1951. However, the genus *Eugorgia* Verrill, 1868 has fewer species and is restricted to the eastern Pacific. Ten nominal species and three varieties were established (Horn 1860; Duchassaing & Michelotti 1864; Verrill 1864, 1868, 1868a, 1870; Studer 1883; Bielschowsky 1918, 1929), but not without problems. As pointed out for other genera, authors have failed to provide detailed illustrations in species descriptions, delineations were not clear, and in most cases, holotypes were not designated or are missing (Breedy & Guzman 2002, 2007). For some species, the type material is represented by one specimen, in some cases deteriorated, or by small fragments.

This revision is based on original type material of all species described until now, as well as reference specimens from recent surveys and expeditions along the eastern Pacific coast. The species are described or redescribed, and illustrated. In addition, a phylogenetic analysis is conducted using morphological characters to determine the relationships among species of *Eugorgia*. The species treated in this paper, in general, do not occur frequently and do not have a wide geographical distribution; several are known just from the type locality (Table 4), and some were collected deeper than 50 m by dredging.

This research represents the third contribution in a series proposed to evaluate the genera of gorgonians reported for the shallow eastern Pacific waters. The previous two deal with *Pacifigorgia* and *Leptogorgia*. Herein, we revise the genus *Eugorgia*.

Abbreviations

CASIZ: California Academy of Science, Invertebrate Zoology, San Francisco, USA; CDRS: Charles Darwin Research Station, Galapagos, Ecuador; MCZ: Museum of Comparative Zoology, Harvard University, Boston, USA; MNHN: Museum National d´Histoire Naturelle, France; MZUF: Museo Zoologico dell'Università di Firenze, Italy; SEM: Scanning Electron Microscopy; STRI: Smithsonian Tropical Research Institute, Panamá; RMNH: National Museum of Natural History Naturalis, Leiden, The Netherlands; UCR: Museo de Zoología, Escuela de Biología, Universidad de Costa Rica, Costa Rica; USNM: National Museum of Natural History, Smithsonian Institution, Washington, USA; YPM: Yale Peabody Museum of Natural History, New Haven, USA; and ZMHC: Hamburg Museum, Hamburg, Germany.

Materials and methods

Type specimens and comparative reference material used in this study were analyzed during visits to museums or acquired on loan from the CASIZ, MCZ, MZUF, USNM, YPM and ZMHC. In addition, specimens recently collected from along the Pacific coast of Mexico, Costa Rica, Panama, and Ecuador deposited in the UCR and STRI were studied. This material was collected by scuba diving, down to 40 m in depth, and some specimens were obtained by dredging to 60 m.

Morphological study

Morphological characters of colonies and sclerites are presented in Tables 1–2. For microscopic study, specimens were prepared for SEM following the protocol described in Breedy and Guzman (2002). For light microscopy, sclerites were mounted in water or glycerine and photographed with an Olympus LX 51 inverted stereoscope. Abundance of sclerites, forms and colours are given in terms of occurrences in unsorted sclerite samples observed under the light microscope. Double disc sclerites with different grades of fusion to form complete discs are the dominant type of sclerite in the genus. Occurrence of complete double discs, capstans or crosses is recorded when these specific types of sclerites appeared in the examined sample, but if the sclerites are not reported in a description this do not mean that they are absent, it rather means that its occurrence is low in the species. Measurements of the sclerites were obtained from pictures and directly from a light microscope using an optical micrometer. Length of the sclerites was measured from one tip to the other and the width was taken from the most distant points across the sclerites, reporting the largest sizes found in the samples and in some cases, a range of variation. Because of the importance of disc-like sclerites in the genus, illustrations are presented in different planes to provide a better idea of their architecture. Variation is expected on the diameter of stems and branches either in preserved or dry specimens, due to the preservation history of specimens. Most of the type material is dry and old. The drying or preservation process can affect some characteristics especially polyp-mounds, longitudinal grooves and colour. We have observed that the tendency of the polyp-mound (slightly raised, prominent) is kept after retraction during the drying, and that longitudinal grooves are also marked in living specimens by longitudinal lines on the coenenchyme. Colours mostly fade, and for this reason, when possible we mention the colour of the colonies alive, preserved and dry. Data on geographical distribution are from our personal collections, museum catalogues, and published monographs (Table 4). In general, former descriptions are poor and mostly lack illustrations. Although Addison Verrill (who described the majority of species in this genus) made fairly accurate text descriptions, he provided so few illustrations, and did not designate holotypes, this his descriptions could often fit several species. Therefore, we designated two lectotypes to establish the identity of the poorly defined species and to avoid future confusion.

Phylogenetic analysis

The phylogenetic relationships within *Eugorgia* were assessed using the program NONA (Goloboff 1999). A matrix consisting of 23 morphological characters (21 discrete and 2 continuous; Tables 2, 3) covering all recognized *Eugorgia* species was used to deduce a maximum parsimony phylogenetic hypothesis of the genus. Continuous characters, namely spindle length and maximum number of branches, were coded using Gap-Weighting (Thiele 1993) and treated as ordered transformation series. Sclerite colour mixture observed in a species was coded using non-additive binary coding (Wiley et al. 1991; Vargas 2008). All characters were scaled prior to the phylogenetic analysis in order to avoid undesired overweighting of transformation series with more character states (e.g. spindle length, colony colour), and to balance the influence of non-additive binary coded characters (i.e. sclerite colour mixture) in the analysis. In this respect, it must be noticed that sclerite colour mixture refers to a single character even though it was represented using six component binary vectors. Because of this, the weight of each component binary vector was corrected to 1/6 the weight of a binary (0–1) character preventing the analysis to be bias towards colour defined clades.

The final weight for each transformation series in the matrix can be found in Table 3; we chose a base value of 90 for binary (0, 1) transformation series in order to avoid fractional weights (not allowed by NONA) for other characters in the matrix after scaling. The final weight of a character can be easily calculated dividing the base value (i.e. 90) by the number of transformations in the character or, in the case of non-additive binary coded characters, by the number of component vectors of the character.

We set NONA to perform 1000 independent replicates using the tree bisection-reconnection algorithm (tbr; option mult*), and to save all the best trees (i.e. minimum length) found during the heuristic search. We found a single most parsimonious phylogenetic tree (L=2940; CI=0.56; RI=0.67) for the genus *Eugorgia*. In order to assess branch support using the Decay Index (DI; Bremmer 1988, 1994), we saved 25000 suboptimal trees up to 900 steps larger than the most parsimonious tree. Due to the weighting scheme used for the phylogenetic analysis of *Eugorgia*, we interpreted the DI values obtained using three different step costs, namely, maximum step cost (i.e. 90), median step cost (45) and minimum step cost (i.e. 10), and report branch support values both in absolute and in relative (i.e. corrected using step cost) steps (Fig. 16B). Finally, the tree was rooted using *Leptogorgia euryale* (Bayer, 1952) and *Leptogorgia virgulata* (Lamarck, 1815) as outgroups (Nixon & Carpenter1993). *Leptogorgia euryale* and *L. virgulata* were selected as outgroups because these two species have disc spindles in the coenenchyme as *Eugorgia* does, but never has the double disc sclerites invariably present in *Eugorgia*. Both species thus present a mixture of character features resembling *Leptogorgia* (*ex Lophogorgia* Milne Edwards & Haime, 1857) species and character features found in *Eugorgia*. This character mixture allowed us to polarize the character matrix of *Eugorgia*.

Terminology

Descriptions mostly follow the terminology proposed by Bayer *et al.* (1983), and Breedy and Guzman (2002, 2007). We list below the terminology applied to the characteristics of the colony and sclerites of the genus *Eugorgia*, based on definitions from Bayer (1961), Bayer *et al.* (1983), and Breedy and Guzman (2002, 2007).

Characteristics of the colony

Longitudinal grooves. Narrow, sinuous furrows extending along two sides of the main stems which corresponds to the primary stem canals. In dry specimens they are conspicuous grooves, and in wet specimens they are like a bare longitudinal row, which in some species is slightly raised, as in a quill. This character is influenced by the history of the specimen subsequent to collection; however, it is consistent in living animals (Breedy & Guzman 2007).

Main branches. Thick branches resulting from division of the stem, or individual branches that sprout close together directly from the holdfast.

Points. A chevron or inverted "V" arrangement of the anthocodial sclerites below each of the polyp tentacles.

Polyp-mounds. Protuberances resulting from polyps retracting into the coenenchyme. These are accentuated during the preservation process, but the general characteristic (slightly raised, moderately raised or prominently raised) proved to be consistent through specimens of the same species preserved or dry.

Stem. Basal part of the colony attached to the holdfast, from which branches subdivide.

Unbranched final twigs. Final portion of the branches that do not ramify; free ends, or terminal twigs (Grasshoff 1988).

Sclerites:

Capstan. Rod with two whorls of tubercles, or warts that do not fuse into discs, separated by a clear median space. Tubercles and warts may be present at the ends of these sclerites and fuse at different levels to form terminal tufts (Fig. 1A, B).

Disc-spindle. A spindle with whorls of tubercles more or less fused completely into discs (Fig. 1G).

TABLE 1. Comparative features of *Eugorgia* species.

Species	Polyp arrangement	Polyp distribution	Polyp mounds	Branching-tendency	Branches	Type of branching	Max no. branching	Dominant type sclerite	Complete double disc	Capstans	Disc-spindle	*Spindles >0.1 mm	Bent spindles	Crosses	Anth. rods	Colour of colony	Coenenchymal sclerite colour	Colour rings
E. alba	sp	two	sr	sb	st	irr-dich	3	dd	no	no	X	0.13 (3)	X		not found	w	cl	no
E. ampla	cpl	multi	sr	bu	st	irr-dich	6	dd	X	X	no	0.15 (5)	no	X	not found	o	o	no
E. aurantiaca	spl	four	p	bu	st	pi	6	dd	X	X	no	0.11 (1)	X	X	not found	do, r	r, y	y
E. bradleyi	cpl	two-four	sr	bu	st	irr-dich	5	dd	X	no	X	0.15 (5)	X	X	not found	pr, o	o, y	no
E. daniana	spl	multi	p	bu	st	pi	7	dd	X	X	X	0.13 (3)	X	X	not found	r	r, y	no
E. excelsa	cpl	multi	sr	bu	st	irr-dich	5	dd	X	X	X	0.10 (0)	no	no	not found	br	o	no
E. multifida	spl	multi	p	bu	st	pi	7	dd	no	X	X	0.13 (3)	X	X	0.08 mm	do, r	r, y	no
E. nobilis	cpl	multi	sr	bu	st	irr-dich	5	dd	X	X	no	0.15 (5)	no	?	not found	br	p, cl, ly	no
E. panamensis	cpl	multi	sr	?	st?	irr-dich	5?	dd	no	X	no	0.14 (4)	no	X	not found	lpu	p, cl	no
E. purpurascens	cpl	multi	sr	bu?	st	irr-dich	6	dd	no	X	no	0.13 (3)	no	X	not found	lpu	r, p, w	no
E. querciformis	cpl	multi	sr	sb	st	irr-dich	4	dd	X	no	X	0.13 (3)	X	X	not found	rpu	pu	no
E. rubens	spl	one	p	sb	st	pi	5	dd	no	no	X	0.10 (0)	no	no	not found	p	p	no
L. virgulata	spl	two	mr	sb	w	dich	4	sp	no	X	X	0.16 (6)	no	X	0.075	pu		no
L. euryale	spl	one	p	fi	w	unb	0	sp	no	X	X	0.18 (9)	X	X	0.14	p		

Polyp arrangement: cpl, closely placed, spl, sparsely placed
Polyp distribution: one, single lateral rows, two, two rows; four, four rows; multi, multiple rows
Polyp mounds: sr, slightly raised, mr, moderately raised, p, prominent
Branching tendency: bu, bushy; sb, sparse branches; fi, filiforme
Branches: st, stout; w, weak, loose
Type of branching: dich, dichotomous; irr-dich, irregular-dichotomous; pi, pinnate-like, unb, unbranched, occasional branching
Dominant type of sclerites: dd, double disc, sp, spindle
*Spindles, between parentheses the assigned character state (0-9) used for phylogenetic inference.
Colours: brown (br); colourless (cl); dark orange (do), light purple (lpu), light yellow (ly), orange (o), pink (p), purple (pu), purplish red (pr), red (r), reddish purple (rpu), yellow (y), white (w).

TABLE 2. Characters and character states used in the phylogenetic analysis of *Eugorgia.*

Character	Character states	Character code
Polyp arrangement	0. Sparsely placed 1. Closely placed	0
Polyp Mounds	0. Prominent 1. Moderately raised 2. Slightly raised	1
Branching tendency	0. Sparsely branched 1. Bushy	2
Branching aspect	0. Weak, loose 1. Stout	3
Type of branching	0. Unbranched 1. Dichotomous 2. Irregularly dichotomous 3. Pinnate	4
Max. branching (meristic char.)	0. No branching 3. Up to 3 branching 5. Up to 5 branching 6. Up to 6 branching 7. Up to 7 branching 9. Up to 9 branching	5
Dominant sclerite type	0. Spindles 1. Double-discs	6
Complete double-discs	0. Absent 1. Present	7
Disc-spindles	0. Absent 1. Present	9
Spindle size (continuous char.)	0. 0.10mm (min) 9. 0.18mm (max)	10
Bent-spindles	0. Absent 1. Present	11
Crosses	0. Absent 1. Present	12
Anthocodial rods	0. Present 1. Absent	13
Colony Color	0. White 1. Pink 2. Red 3. Light Purple 4. Purple 5. Orange 6. Brown	14
Colourless sclerites	0. Absent 1. Present	15
Pink sclerites	0. Absent 1. Present	16
Red sclerites	0. Absent 1. Present	17

continued next page.

TABLE 2. (continued)

Character	Character states	Character code
Purple sclerites	0. Absent 1. Present	18
Orange sclerites	0. Absent 1. Present	19
Yellow sclerites	0. Absent 1. Present	20
Polyp distribution	0. One row 1. Two rows 2. Four rows 3. Multiple rows	22
Contrastingly coloured polyp mound	0. Absent 1. Present	23

TABLE 3. Character matrix used for the phylogenetic analysis of the genus *Eugorgia*, as defined by Table 2. Step cost for each transformation series and additivity is given in the last two rows. Components of the character sclerite color combination appear gray highlighted.

	Character code																					
Species	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**22**	**23**
Leptogorgia euryale	0	0	-	0	0	0	0	0	0	6	1	1	0	0	1	0	1	0	0	0	0	0
Leptogorgia virgulata	0	1	0	0	1	5	0	0	0	9	0	1	0	4	0	0	1	0	0	0	1	0
Eugorgia alba	0	2	0	1	2	3	1	0	0	3	1	?	1	0	1	0	0	0	0	0	1	0
Eugorgia ampla	1	2	1	1	2	7	1	1	1	5	0	1	1	5	0	0	0	0	1	0	3	0
Eugorgia aurantiaca	0	0	1	1	3	7	1	1	1	1	1	1	1	2	0	0	1	0	0	1	2	1
Eugorgia bradleyi	1	2	1	1	2	6	1	1	0	5	1	1	1	5	0	0	0	0	1	1	[12]	0
Eugorgia daniana	0	0	1	1	3	9	1	1	0	3	1	1	1	2	0	0	1	0	0	1	3	0
Eugorgia excelsa	1	2	1	1	2	6	1	1	0	0	0	0	1	6	0	0	0	0	1	0	3	0
Eugorgia multifida	0	0	1	1	3	9	1	0	0	3	1	1	0	2	0	0	1	0	0	1	3	0
Eugorgia nobilis	1	2	1	1	2	6	1	1	1	5	0	?	1	6	1	1	0	0	0	1	3	0
Eugorgia panamensis	1	2	?	?	2	?	1	0	1	4	0	1	1	3	1	1	0	0	0	0	3	0
Eugorgia purpurascens	1	2	0	1	2	7	1	0	1	3	0	1	1	3	1	1	1	0	0	0	3	0
Eugorgia querciformis	1	2	0	1	2	5	1	1	0	3	1	1	1	4	0	0	0	1	0	0	3	0
Eugorgia rubens	0	0	0	1	3	?	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0
Step Weight	**90**	**45**	**90**	**90**	**30**	**10**	**90**	**90**	**90**	**10**	**90**	**90**	**90**	**15**	**15**	**15**	**15**	**15**	**15**	**15**	**90**	**90**
Character Additivity	-	-	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-

Double disc. (Double wheel, birotulate) Capstan with tubercles of the two whorls fused into discs or wheels, sometimes with radial crests. Tubercles of double discs present different degrees of fusion from just a few warts blended together (incomplete discs) (Fig. 1C–D), to complete circles like flying saucers (complete discs) (Fig. 1E).

Spindle. Sclerite with a straight or a slightly curved axis, with more than two whorls of tubercles or just sculptured with scattered, prominent warts, and with acute or blunt ends, or a combination of both (Fig. 1F).

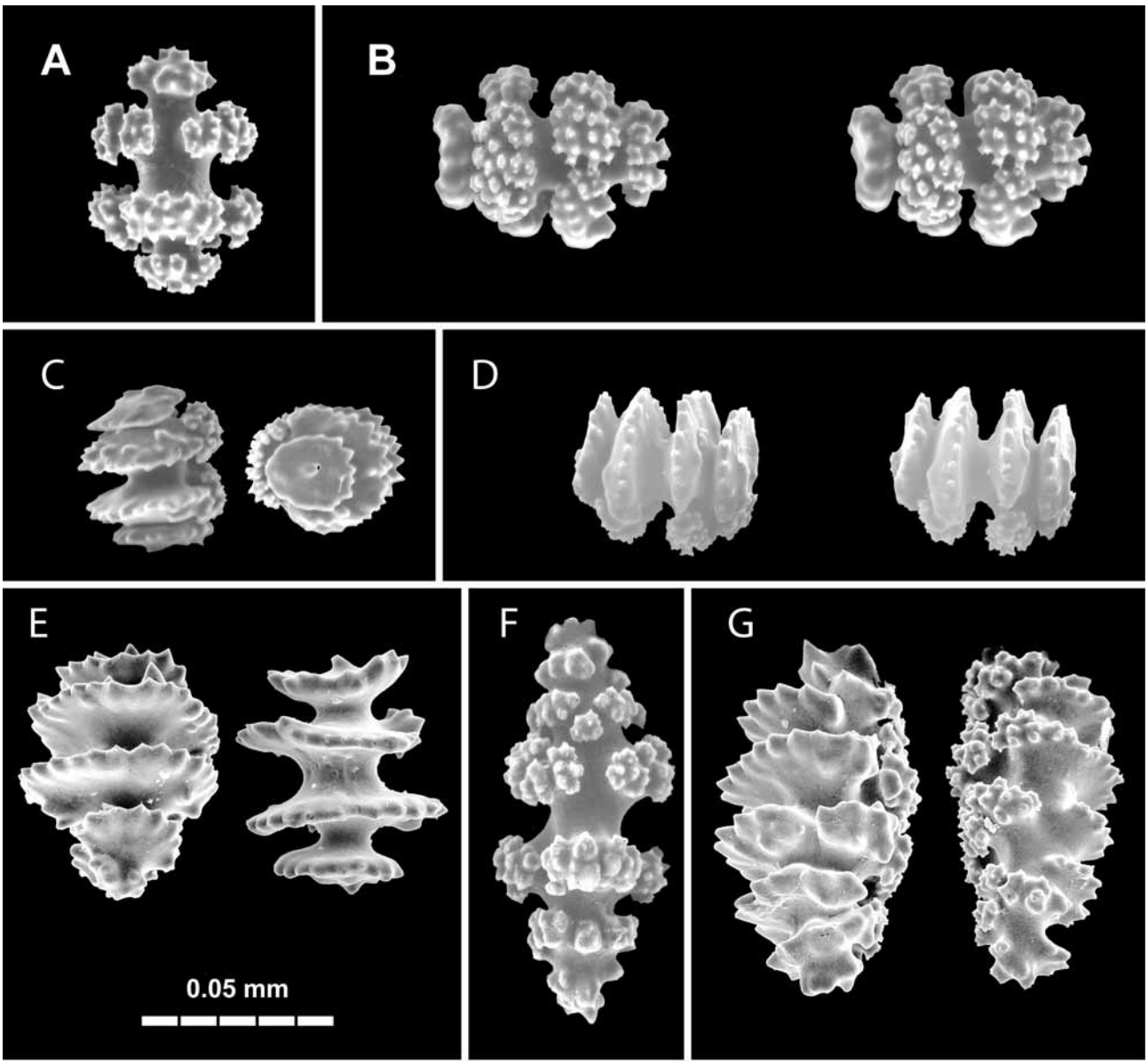

FIGURE 1. A, a capstan, *Eugorgia ampla* (MCZ 193a); **B**, a capstan, *E. aurantiaca* (YPM 389, stereoview); **C,** incomplete double disc, left, a lateral view, right, an end point view; **D**, incomplete double disc, *E. bradleyi* (MCZ 7005, stereoview); **E,** complete double disc, *E. alba* (ZMHC 2243); **F,** spindle, *E. ampla* (YPM 402); **G,** disc-spindle *E. alba* (ZMHC 2243). Scale 0.05 mm for A–G.

Family Gorgoniidae Lamouroux, 1812

Genus *Eugorgia* Verrill, 1868

Lophogorgia (pars) Horn 1860: 233.
Gorgonia (pars) Verrill 1864: 33; 1866: 327.
Leptogorgia Verrill 1864: 32.
Eugorgia (pars) Verrill, 1868a: 414.
Eugorgia Verrill, 1868: 406–407; Studer 1887: 64–65; Bielschowsky 1918: 39; 1929: 170; Kükenthal 1924: 343; Stiasny 1951:63, Bayer 1951: 99; 1981: 921.

Type species. *Leptogorgia ampla* Verrill, 1864, by subsequent designation: Verrill 1868: 386.

Diagnosis. Gorgoniids branching mainly in multiple planes, lateral, partially dichotomous, or pinnate-like, often bushy. True neat dichotomy or pinnate branching rarely occur in this genus, but some species show close patterns: simple lateral branching and even dichotomous or pinnate sections, thus irregular branching, so these terms are used herein accordingly. Branch anastomosis absent. Axis horny, with a cross-chambered central core with a network of organic filaments frequently mineralized. (Fig. 2A–B). Holdfast attached to hard substrates or extending on muddy sediments. Polyps fully retractile into the coenenchyme, in slightly raised to prominent mounds arranged in series of longitudinal rows, or evenly distributed on the branches. Coenenchymal sclerites of various type: spindle, disc-spindle, capstan, and the most dominant form that defines the genus is the characteristic double disc. Anthocodial sclerites rarely found, usually flat rods and platelets with lobed margins, forming a weak points-like arrangements at base of the polyp tentacles. Colour of colonies and sclerites variable: colourless, yellow, orange, red, violet, brownish, or combinations of these.

Distribution. The genus is considered exclusively eastern Pacific (from southern California to Peru).

TABLE 4. Geographic distribution of *Eugorgia* based on literature, museum catalogues, and personal observation.

Species	Costa Rica	Colombia	Panama	Nicaragua	Peru	Mexico	Ecuador	El Salvador	USA
E. alba								Acajutla	
E. ampla			Azuero Peninsula		Paita	Margarita Bay, Baja California, California Gulf, Sonora			
E. aurantiaca			West coast of Panama			La Paz, Mazatlán, Acapulco, Cabo Pulmo, Baja California			
E. bradleyi	Gulf of Nicoya		Pearl Islands						
E. daniana	Gulf of Nicoya, Samara Bay, Ballena Island	Isla Gorgona	Pearl Islands, Gulf of Panama, Chiriqui, Azuero		Piura	Guaymas, Baja California, Acapulco, Oaxaca	Galapagos, Gulf of Guayaquil	El Salvador	San Diego
E. excelsa						La Paz, Acapulco, Gyamas			
E. multifida						Mazatlán, Baja California, Acapulco			
E. nobilis	Gulf of Nicoya		Pearl Islands	Corinto	Paita	Acapulco			
E. panamensis			Isla Flamenco						
E. purpurascens			Pearl Islands	Corinto	Zorritos				
E. quercifomis								Acajutla	
E. rubens	Murciélago Islands				Paita	Puerto Angel, Oaxaca			Santa Cruz Island, Monterrey, La Jolla Canyon

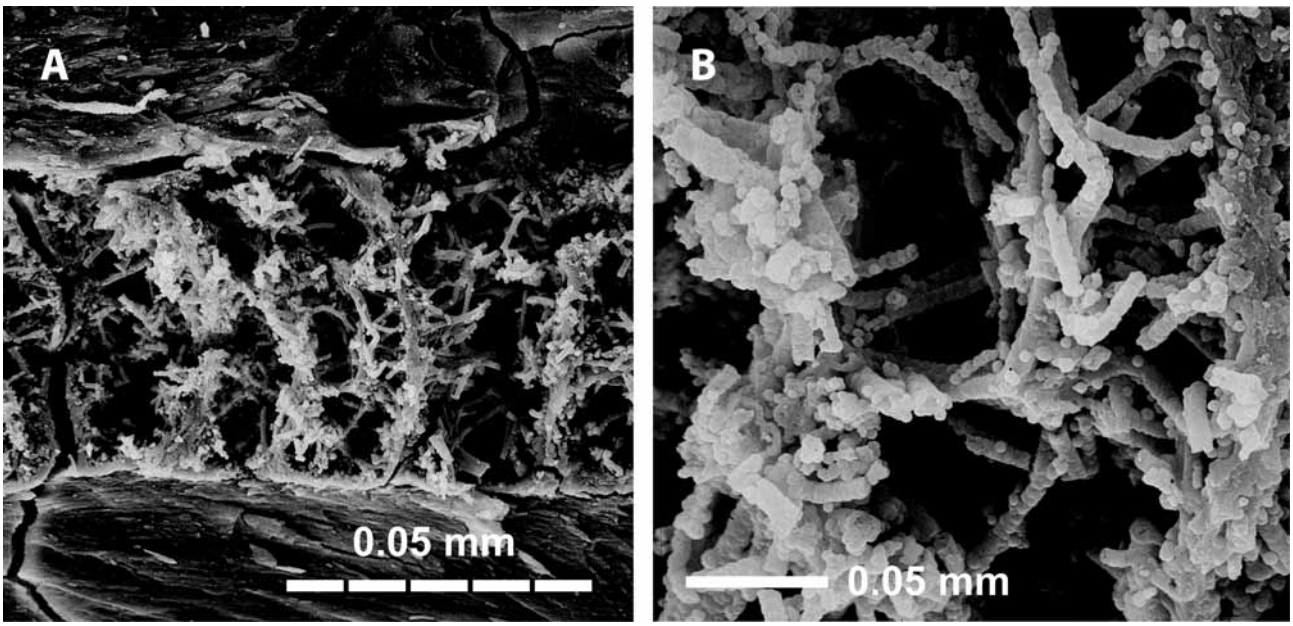

FIGURE 2. Axis mineralization, SEM-micrograph of a longitudinal section of a terminal branch of *Eugorgia multifida* Verrill, 1868 (YPM 2257b) after maceration in sodium hypochlorite; **A,** chambered core with mineralised filaments of CHAp; **B,** detail of CHAp microspheres coating organic filaments.

Remarks. Verrill (1868a) divided the Panamic species of gorgoniids known at that time, into two groups: one included species having only warty "double-spindles" (obsolete term for spindle), and the other included species having "double-spindles", and "double-wheels". In his first group he included species of the genera *Leptogorgia* Milne Edwards and Haime, 1857 and what later became *Pacifigorgia* Bayer, 1951; and in the second, he included a mixture of species of *Leptogorgia,* and others later placed in *Eugorgia* and *Pacifigorgia*. Later on, Verrill (1868) established the genus *Eugorgia* for species in his second group that, besides having the double-wheel sclerites, are "with a distinctly granulose surface, owing to the large number of small naked spicula, the cells are mostly in two lateral bands". However, the species of *Leptogorgia* and *Pacifigorgia* that he firstly included in the genus do not have double-wheel sclerites, and do not have a granulose surface. In 1868, Verrill redefined the genus *Eugorgia* including only the species with double-wheel (double discs) sclerites, and designated *Leptogorgia ampla* Verrill, 1864 as the type species. *Eugorgia* is presently considered an eastern Pacific genus; however, some Atlantic species of *Leptogorgia* are apparently related to it (Bayer 1951, 1952). Bayer (1952) transferred *Leptogorgia virgulata* (Lamarck, 1815) and three new species from the western Atlantic to *Eugorgia* based on the occurrence of disc-spindles and double discs in the coenenchyme. Since the external morphology of *Leptogorgia* and *Eugorgia* is very similar and the presence of disc-spindles and double discs is basically what made both genera different, it was a sensible decision. However, Bayer (1956, 1961) redefined the genus *Leptogorgia* to separate it from the monospecific genus *Lophogorgia* Milne Edwards & Haime,1857 on the basis of occurrence of symmetrical sclerites in the latter, and symmetrical and asymmetrical sclerites, "with flat tubercles fused into discs" in *Leptogorgia*. Thus, he transferred the four western Atlantic species to *Leptogorgia* again. Grasshoff (1988) in his revision of West African gorgoniid fauna found transitional forms between the two genera (*Lophogorgia* and *Leptogorgia*) and decided to synonymise both genera, so the four western Atlantic species with double discs remained in *Leptogorgia*. The southern African species *Leptogorgia gilchristi* (Hickson, 1904) was described as *Eugorgia* by Hickson (1904) and as *Eugorgia lineata* by Thomson (1917), but since *lineata* and *gilchristi* are the same species, and sclerites are consistent with the *Leptogorgia* type (Williams & Lindo 1997) instead of *Eugorgia*, Grasshoff (1992) established the new combination, *Leptogorgia gilchristi*, and synonymised both species.

***Eugorgia alba* Bielschowsky, 1929 comb. nov.**
Figures 3A–C, 4

Eugorgia bradleyi var. *alba* Bielschowsky, 1929: 177–178; Kükenthal 1924: 345.

Material examined. **Holotype:** ZMHC 2243, ethanol preserved, Acajutla, El Salvador, no further data.

Description. The holotype is a small colony, 5 cm in height and 3 cm in width. Branching is irregularly dichotomous (Fig. 3A). Two main branches arise from a short stem, 1.2 cm long, and subdivide up to three times. The holdfast is missing from the holotype, but from Bielschowsky's illustration (1929: plate 3, fig.15) it seems incrusting. Branches are slightly compressed in cross section, 3 mm in diameter at the base and tapered, more rounded at the branchlets. Branchlets are up to 2 mm in diameter. Unbranched final twigs reach up to 3 cm with pointed tips, about 1 mm in diameter. Polyps retract within slightly raised polyp-mounds with oval apertures (Fig. 3B). Polyp-mounds are distributed in 2–4 longitudinal rows on the branches, and sparsely placed. Colour of the colony is white. Sclerites of the coenenchyme are mostly colourless, some with a pale pink hue. They are mostly double discs reaching up to 0.075 mm in length, and 0.06 mm in width (Fig. 3C, 4). Spindles reach up to 0.13 mm in length, and 0.05 mm in width, with 4–6 whorls of tubercles, with ends mostly acute. No anthocodial rods were found in the samples.

Distribution. Known only from the type locality (Table 4).

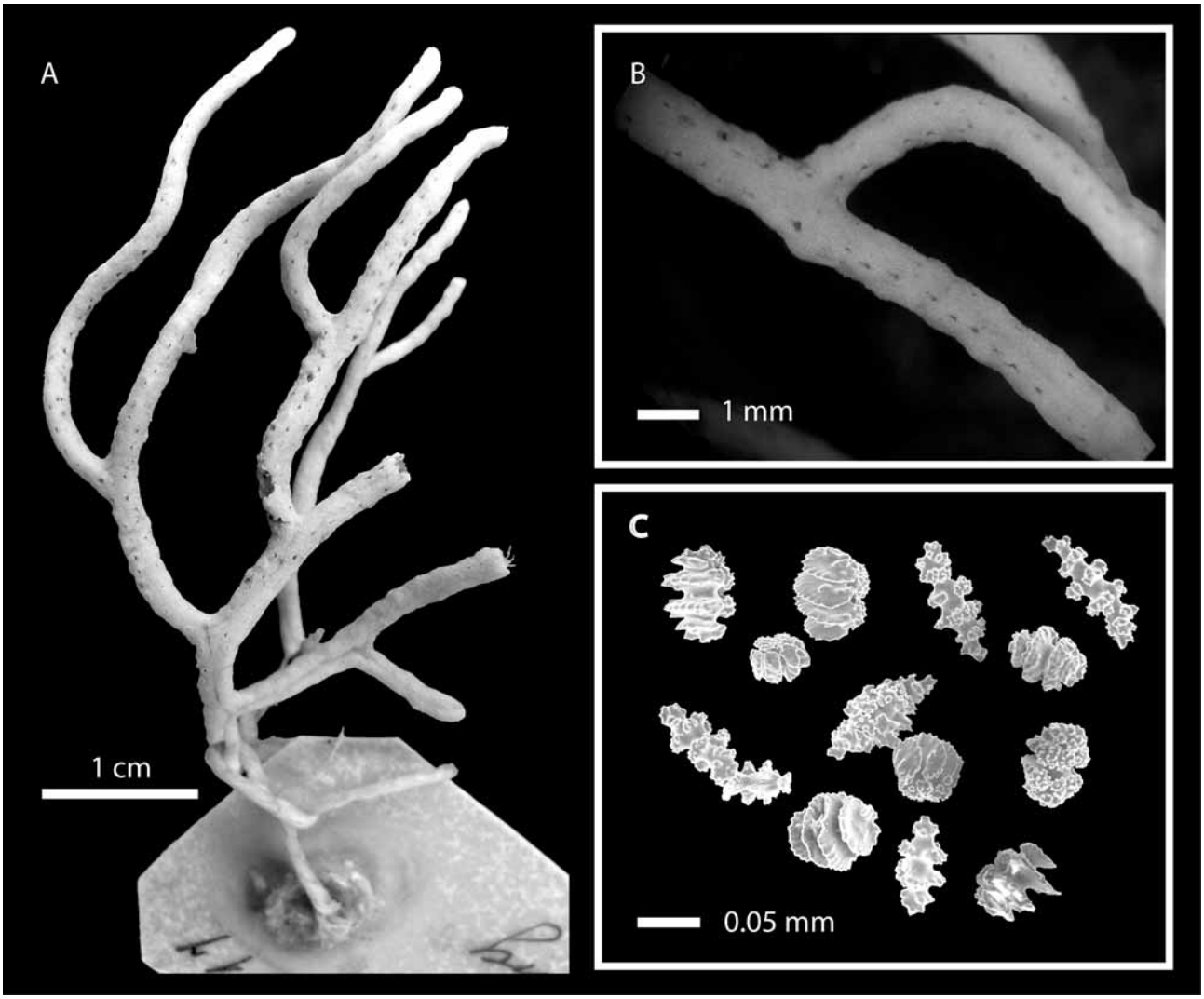

FIGURE 3. *Eugorgia alba*, holotype: A, colony; B, detail of branches; C, coenenchymal sclerites.

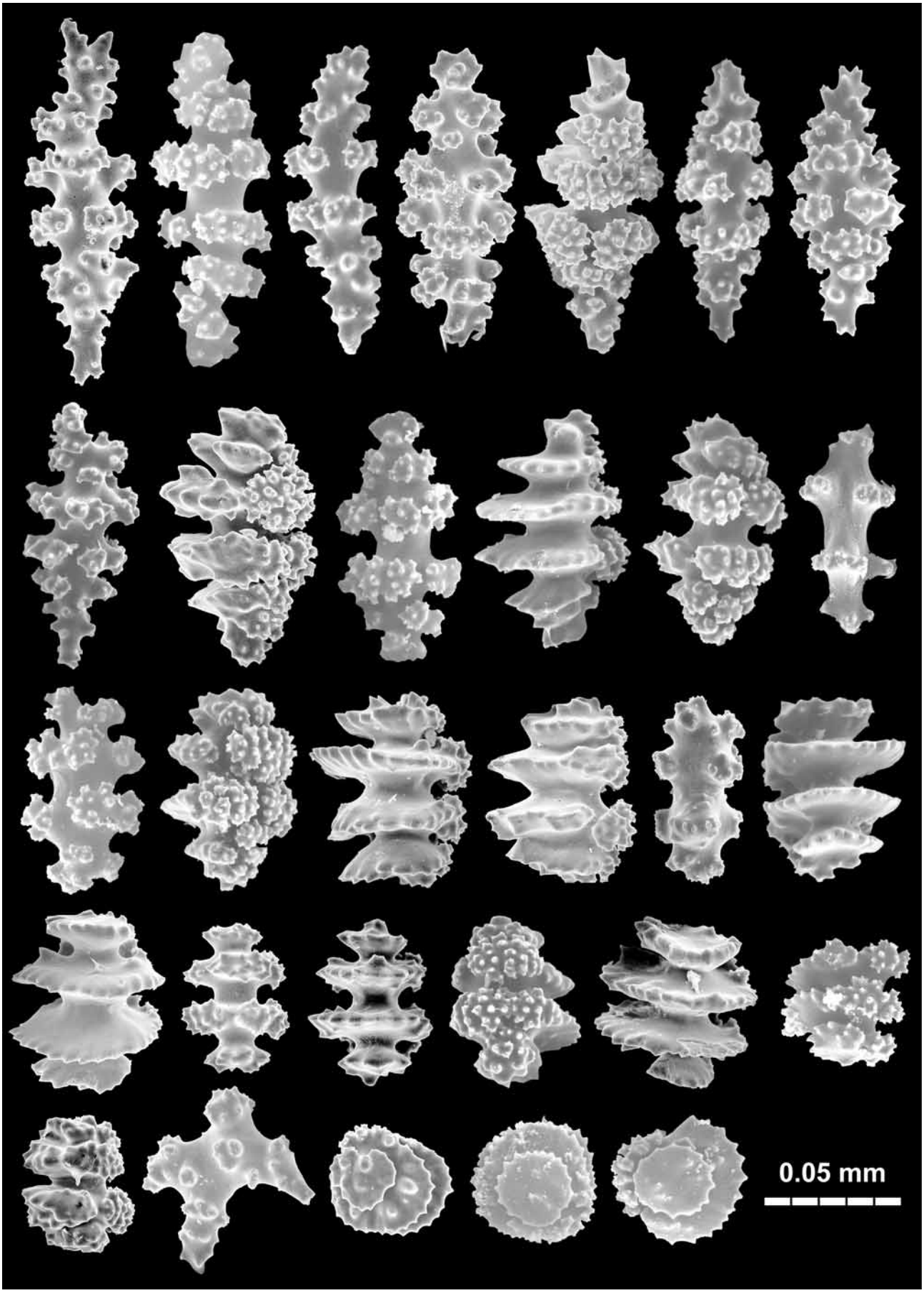

FIGURE 4. *Eugorgia alba* holotype, coenenchymal sclerites.

Remarks. Bielschowsky (1929) described this species with a specimen from the coast of El Salvador and assumed it to be a variety of *E. bradleyi*. Although the holotype is the sole specimen of this species and thus we cannot consider intera-specific variability; we consider that the differences between *E. bradleyi* and *E. bradleyi* var. *alba* are sufficient to regard them as different species. Moreover, there are no records of *E. bradleyi* from the coast of El Salvador at present, but exploration there has been minimal. External morphology and colour of *E. alba* are very consistent with *Leptogorgia alba* Duchassaing & Michelotti, 1864; however, the sclerites, and especially the presence of double discs in of the former, places it in this different genus.

***Eugorgia ampla* (Verrill, 1864)**
Figure 5, Plate 1A–C

Leptogorgia ampla Verrill, 1864: 32.
Eugorgia (*Gorgonia*) *ampla* Verrill 1868a: 415
Eugorgia ampla Verrill 1868: 407–408; Bielschowsky 1918: 44; Kükenthal 1924: 343; Stiasny 1951: 74 (dubious).

Material examined. Syntype series: MCZ 193a, dry, Margarita Bay, Baja California Sur, Mexico, no depth given, A. Garret, 1860. MCZ 193b, MCZ 36037, YPM 402 (fragment) dry, Margarita Bay, no depth given, A. Garret, 1860. MCZ 65167, dry, California Gulf, Sonora, Mexico, 9 April 1940, no further data. YPM 399, 400, dry, La Paz, Baja California Sur, 11–15 m, W.B. Rich, no date.

Other material: MEXICO: USNM 43012, dry, Magdalena Bay, Baja California, H.N. Lowe, no further data; USNM 8967, dry, Baja California, no further data. PANAMA: UCR 1129 (STRI 97), dry, Islote Frailes, Azuero Peninsula, 5–30 m, H.M. Guzman, 12 December 2001. PERU: USNM 1007028A-B, Paita, Piura, W.L. Schmitt, no depth given, 8 October 1926.

Description. Colonies studied measure up to 56 cm in height, and 40.7 cm in width. Branching is irregularly dichotomous. Unbranched distal twigs can reach up to 8 cm in length, and 1 mm in diameter. Colour of the colonies is mostly orange, but lighter or darker hues are found. Polyps are distributed all around the branches, and crowd the surface. Polyp-mounds are slightly raised, almost flat, with round apertures 0.2–0.3 mm in diameter when preserved, larger when dried.

The illustrated syntype MCZ 193a is a colony (Plate 1) 35.3 cm in height and the same in width, with a circular holdfast, flabelliform, and growing upright. Three main branches arise from a short stem, about 10 mm in diameter. Unbranched twigs compressed proximally, 5–8 mm in diameter, more cylindrical, and slightly tapered at the ends, with rounded tips, and about 2–3 mm in diameter. They reach up to 5 cm in length. Colony is orange throughout. Several slightly marked longitudinal grooves occur along the thick branches, and near the base. The polyps are evenly distributed all around the branches (Plate 1B). Polyp-apertures are small, up to 0.5 mm in diameter, and crowd the surface (Plate 1B). Coenenchymal sclerites are all orange (Plate 1C). They are mostly double discs reaching up to 0.06 mm in length and 0.06 mm in width, several with complete discs which are mostly as long as broad and with flat disc-ends 0.015–0.025 mm in diameter; capstans reach up to 0.09 mm in length and 0.06 mm in width. Spindles are less abundant, up to 0.13 mm in length, and 0.05 mm in width, with 4–5 whorls of warty tubercles (Fig. 5). In general, sclerites of the coenenchyme are mainly as in the illustrated specimen (MCZ 193a), with variation in the dominance of sclerite-types found in the samples. For example, in YPM 402, spindles with acute ends are more abundant than in MCZ 193a; in MCZ 36037, the double discs are more abundant than in MCZ 193a, both colonies (YPM 402 and MCZ 36037) were collected at the same locality during the same collection. Length of spindles can reach up to 0.15 mm in some samples. No anthocodial sclerites were obtained in the samples for study.

Distribution. Margarita Bay, La Paz, Baja California Sur; Gulf of California, Sonora, (type localities); Paita, Peru; and Azuero Peninsula, Panama. Bonin Islands (Ogasawara Islands), Japan is mentioned by Verrill (1864), but it is probably a mistaken locality. Stiasny (1951) reported a specimen of this species from the Sandwich Islands, but he remarked that the bad condition of the specimen made the identification uncertain.

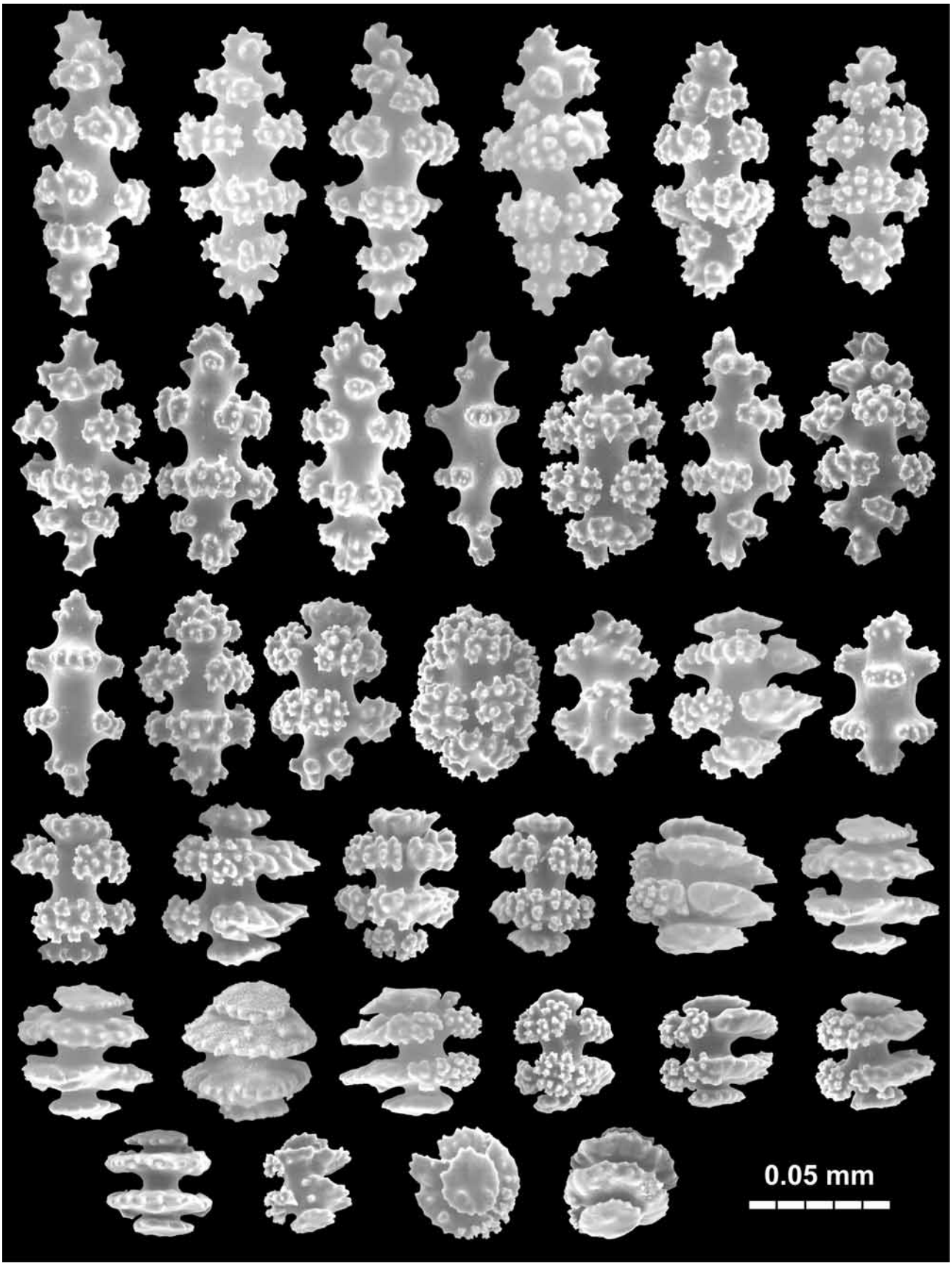

FIGURE 5. *Eugorgia ampla* (MCZ 193), coenenchymal sclerites.

Remarks. The species was originally described in 1864 in the genus *Leptogorgia* Milne Edwards & Haime, 1857 with doubts about the type locality, and without holotype designation. Nevertheless, the type series is consistent enough, to define the species.

***Eugorgia aurantiaca* (Horn, 1860)**
Figure 6, Plate 2A–D

Lophogorgia aurantiaca Horn, 1860: 233.
Gorgonia aurantiaca Verrill, 1864: 33 (non *Gorgonia aurantiaca*, Milne Edwards & Haime, 1857); Verrill 1866: 327.
Gorgonia (*Eugorgia*) *mexicana* Verrill, 1869: 415.
Eugorgia aurantiaca Verrill, 1868: 410–411; Bielschowsky 1918: 45; 1929: 182–183; Kükenthal 1924: 346; Stiasny 1951: 63–65; Sinsel-Duarte 1991: 30; Harden 1979: 122.
Eugorgia forreri ? Studer, 1883: 6, syn. nov.
Eugorgia forreri Bielschowsky 1918: 44; 1929: 178–179; Kükenthal 1924: 345; Harden 1979: 125.

Material examined. Lectotype, here designated: YPM 2269, dry fragment, Sinaloa, Mazatlán, G.H. Horn, (probably the type series collected before 1860 by Horn), no further data.

Paralectotype: YPM 389, same data as the lectotype.

Other material: MEXICO: MCZ 61014, 36185; YPM 8715, dry, La Paz, no depth given, J. Pedersen, 1867–70; YPM 397, dry, La Paz, 11–15 m, W.B. Rich, 1863; YPM 1707, dry, Acapulco, no depth given, A. Agassiz, 1859–1860; MNHN oct.0000-0549, dry, Baja California, no depth given, M.L. Diguet, 1897; MNHN oct.0000-0554, oct.0000-0559, dry, Mazatlan, no depth given, M. le Général Rollin, 1864. PANAMA: USNM 1016591, dry, west coast of Panama, E. Deichmann, no further data; USNM 33603, dry, no further data. Without data: MNHN oct.0000-0552, dry, original label from RMNH; MNHN oct.0000-0551, dry, original label from RMNH.

Description. The examined specimens reach up to 32 cm in height and 38 cm in width. The lectotype is a fragment 8 cm in height and 3 cm in width, and the paralectotype is a smaller fragment 3 cm in height and 1.5 cm in width (Plate 2A, branch and detail). Colonies form densely branched fans (Plate 2B, C). Main stems are 4–6 mm in diameter, compressed, and up to 2 cm long or absent, so the branches emerge directly from spreading holdfasts. Main branches are compressed and divergent, 2–3 mm in diameter, branching irregularly pinnate, the pinnae 1–2 mm in diameter and they are irregularly arranged and not close together (Plate 2C). Several of the pinnae rebranch giving off secondary pinnae, some are pseudoanastomosed (anastomosis of the coenenchyme, not of the axes). Unbranched terminal twigs are blunt, and reach up to 3 cm in length. Polyp-mounds are prominent, with bilabiate apertures, and reach up to 1 mm in diameter. The polyp-mounds are placed in irregular longitudinal rows along the branches, and do not crowd the surface (Plate 2C). Colonies are dark orange, streaked with bright yellow on the branches and with yellow rings on polyp-mounds. The main branches have numerous yellow, longitudinal grooves that are more evident on thick branches. Sclerites of the coenenchyme are red and yellow (Plate 2D). In the lectotype, they are mostly double discs reaching up to 0.07 mm in length, and 0.05 mm in width (Fig. 6). Capstans are about the same size with complex tubercles at the ends. Spindles reach up to 0.11 mm in length and 0.045 mm in width, with 3–5 whorls of warty tubercles, with mostly acute ends; and crosses about 0.06 by 0.06 mm (Fig. 6). No anthocodial sclerites were obtained in the samples examined. Size and shapes of the sclerites in the examined specimens are as in the lectotype.

Distribution. Sinaloa, type locality; La Paz, Acapulco, Cabo Pulmo (Sinsel-Duarte 1991) and Panama (Table 4).

Remarks. This species was described by Horn (1860) probably based on large specimens, but all that seems to have remained are the two fragments, YPM 2269 and 389, which were given to Verrill (YPM) by Horn from the Academy of Natural Sciences of Philadelphia. The original specimens collected by Horn were supposedly deposited in the Academy of Natural Sciences of Philadelphia, but we could not locate them. Horn reported an unknown locality of collection, but Verrill (1868) indicated that it was Mazatlan, as is the case for

Leptogorgia clavata (Horn, 1860) (Breedy & Guzman 2007), and *Pacifigorgia englemanni* (Horn, 1860) (Breedy & Guzman 2002).

Two specimens of *E. aurantiaca* from Mazatlan found in the MNHN (oct.0000-0554, oct.0000-0559) were identified by Valenciennes in 1864 as *Gorgonia bicolor* , however this species name was never published.

Studer (1883) identified a collection from the Gulf of California, La Paz and Mazatlan given to him by Alfonse Forrer. He reported 15 gorgonian species, among them three species of *Eugorgia*: *E. aurantiaca, E. bradleyi*, and the newly described *E. forreri*, with a question mark, with neither illustrations, nor holotype designation. We could not locate any syntypes of this species for examination, but Studer's description matches *E. aurantiaca*. For these reasons we herein synonymise *E. forreri*. Some specimens in the California Academy of Sciences identified as *E. forreri* do not match Studer´s description. They probably constitute new species but were found too late for inclusion in this work.

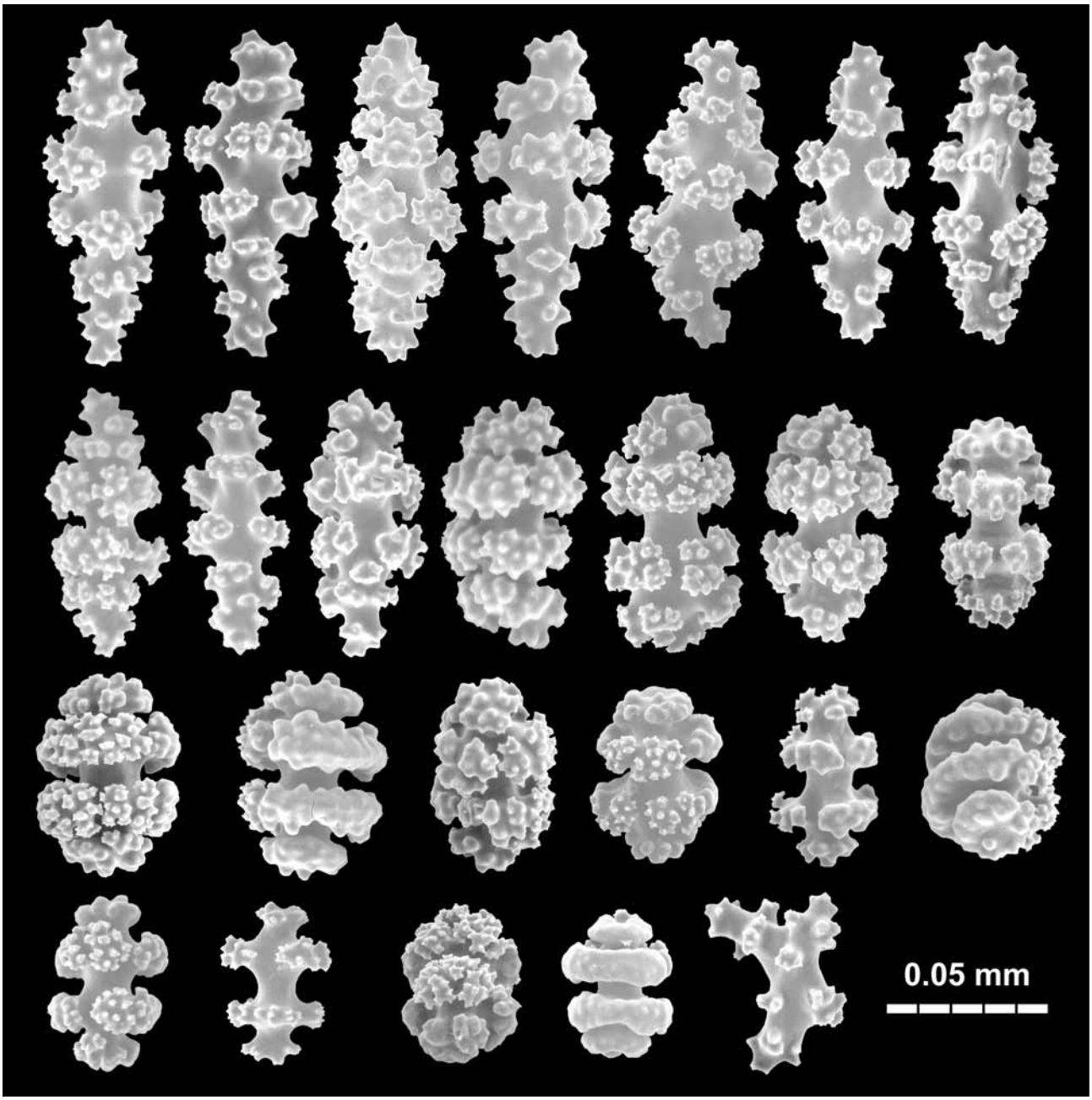

FIGURE 6. *Eugorgia aurantiaca* (YPM 2269), coenenchymal sclerites.

***Eugorgia bradleyi* Verrill, 1868**
Figure 7, Plate 3A–C

Eugorgia bradleyi Verrill, 1868: 411–412; Studer 1883: 7; Bielschowsky 1918: 44; 1929: 176–177; Kükenthal 1924: 344–345; Harden 1979: 123.

Material examined. Syntype series: MCZ 36033, 725, dry, Pearl Islands, Panama, no further data, F.H. Bradley, 1866–1867; MCZ 7005, 7006A–B, dry, Nicoya Gulf, Costa Rica, J.A. McNeil, no further data; MCZ 1575; YPM 568, 568A–C, YPM 787A–B, dry, Panama, F.H. Bradley, 1866, no further data; YPM 5147-5150, 5150A–B, dry, Nicoya Gulf, J.A. McNeil, no further data; YPM 1788, dry, Pearl Islands, no depth given, F.H. Bradley, 1866–1867.

Other material: COSTA RICA: USNM 44206, dry, Gulf of Nicoya, no depth given, M. Valerio, 20 February 1931.

Description. Colonies examined range from 7–20 cm in height and 2–16 cm in width. They arise from spreading holdfasts producing short stems, up to 4 cm in length, or subdivide very close to the base. Branches are slightly compressed, around 3 mm in diameter at the base and tapered. Thick branches are marked with longitudinal grooves. Branching is irregularly dichotomous, producing branchlets 1–2 mm in diameter, rounded in cross section, that rebranch up to 4 times in a more irregular manner. Unbranched final twigs reach up to 5 cm in length with pointed tips. The polyps are retracted within slightly raised polyp-mounds with oval slit-like apertures (Plate 3B). Polyp-mounds are distributed in 2–4 longitudinal rows, on the branches and close together. They are scarce on the stem, and absent on the holdfast (Plate 3A). Colour of the colonies varies from purplish red to orange or light brown. Sclerites of the coenenchyme are orange, yellow, and some bicoloured (Plate 3C). They are mostly double discs reaching up to 0.05 mm in length, and 0.045 mm in width (Fig. 7), some are larger reaching up to 0.08 mm in length, and 0.06 mm in width; they have warty tubercles with a minimal fusion in discs. Spindles are long, reaching up to 0.15 mm in length, and 0.05 mm in width, with 4–9 whorls of warty tubercles. Spindles are straight or bent, some with a marked waist (Plate 3C, Fig. 7). No anthocodial sclerites were found in the samples.

The illustrated specimen is 17 cm in height, and 19 cm in width (MCZ 7006B1), and of a bright orange colour (Plate 3A).

Distribution. Gulf of Nicoya, Pearl Islands, type localities (Table 4).

Remarks. In the branching pattern and the colour, this species is very similar to species in the *Leptogorgia alba* group, especially resembling *Leptogorgia ignita* Breedy & Guzman, 2008, however, the sclerites are very different. Despite our extensive exploration in Costa Rica and Panama, we have not yet found specimens of this species.

***Eugorgia daniana* Verrill, 1868**
Figure 8, Plate 4A–D

Eugorgia daniana Verrill, 1868: 409–410; Bielschowsky 1918: 45; 1929: 181; Kükenthal 1924: 346; Stiasny 1951: 65; Harden 1979: 123–125; Prahl et al. 1986: 17.

Material examined. Syntype series: MCZ 723, dry, Pearl Islands, 11–15 m, F.H. Bradley, 1866-67; MCZ 7080, dry, Gulf of Nicoya, Costa Rica, J.A. McNeil, no further data; YPM 1551a–d; 1629, 1629a–b, dry, Pearl Islands; 11–15 m, F.H. Bradley, 1866-67; YPM 5146, dry fragment, Gulf of Nicoya, J.A. McNeil, no further data.

Other material: COSTA RICA: UCR 1743, dry, Chora Island, Samara Bay, 18–19 m, O. Breedy, 29 March 1998; UCR 1744, dry, Ballena Island, Ballena Marine National Park, 26 m, O. Breedy, 27 April 2002; USNM 49387, dry, Isla San Lucas, Gulf of Nicoya, no depth given, M. Valerio, 15 January 1930. PANAMA: STRI 208 (UCR 1288), dry, Jicarita, Chiriqui Gulf, 10–30 m, H.M. Guzman, 19 April 2002; STRI 407, dry,

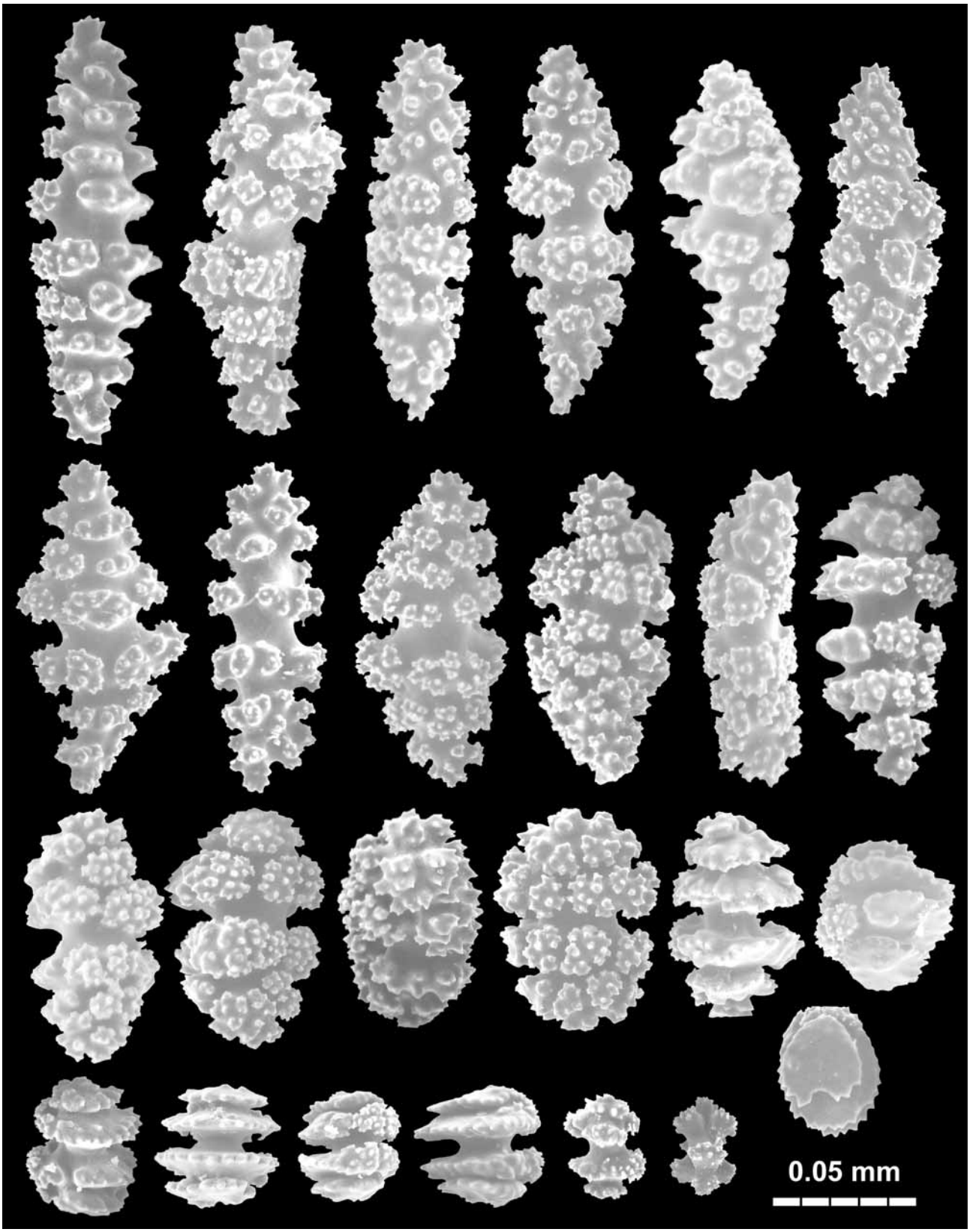

FIGURE 7. *Eugorgia bradleyi* (MCZ 7006B1), coenenchymal sclerites.

Isla Seca Grande, Chiriqui Gulf, 20 m, H.M. Guzman & O. Breedy, 26 August 2002; STRI 408, dry, Isla Seca Grande, Chiriqui Gulf, 20 m, H.M. Guzman, 26 August 2002; STRI 440, dry, Jicarita, 10–25 m, H.M. Guzman & O. Breedy, 29 August 2002; STRI 444, dry, Jicarita Island, Chiriqui Gulf, 10–25 m, H.M.

Guzman, 29 August 2002; STRI 460, dry, Bajo Foul, Peninsula de Azuero, 5–20 m, H.M. Guzman, 11 April 2003; STRI 511, dry, Ladrones Island, Chiriqui Gulf, 3–15 m, H.M. Guzman, 14 April 2003; STRI 551,

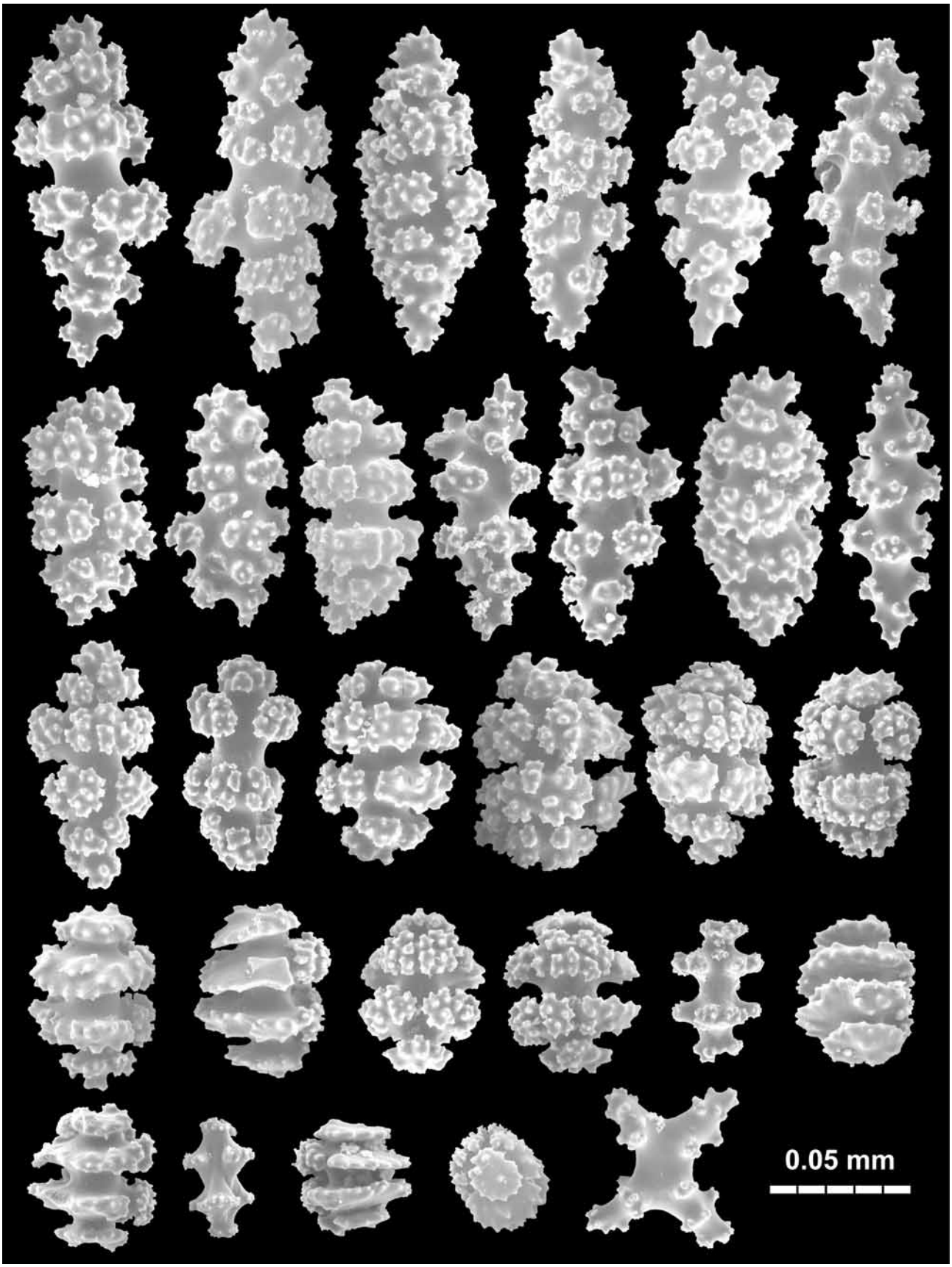

FIGURE 8. *Eugorgia daniana* (MCZ 7080), coenenchymal sclerites.

preserved, Isla Bolanito, Chiriqui Gulf, 6 m, H.M. Guzman, 16 April 2003; STRI 871, dry, Achotines, Chiriqui Gulf, 3–10 m, H.M. Guzman, 5 May 2004; STRI 978, dry, Roca Niagara, Pearl Islands, 3–20 m, H.M. Guzman, 23 September 2004; STRI 984, dry, Bajo Poligono 51, Pearl Islands, 12 m, H.M. Guzman, 15 June 2006; STRI 987, dry, Pacheca, Pearl Islands, 11 m, H.E. Guzman, 11 June 2006; STRI 997, dry, NW Pedro Gonzalez Island, Pearl Islands, 5–10 m, H.M. Guzman, 5 June 2006; STRI 1010, dry, Piedra Hacha, Chiriqui Gulf, H.M. Guzman, 11 October 2006; UCR 1325 (STRI 245), dry, Islote, Chiriqui Gulf, 25 m, H.M. Guzman, 20 April 2002; USNM 34058, dry, Gulf of Panama, no further data; USNM 49367, dry, Gulf of Panama, no depth given, P.S. Galtsoff, 1948. PERU: USNM 49347, dry, Piura, Cabo Blanco, no depth given, M. Lobell, 12 May 1941. ECUADOR: CDRS 05-197, 05-198, Darwin Bay, Isla Genovesa, Islas Galápagos, 25–29 m, A. Chiriboga, 25 March 2005; USNM 59084, 59084, ethanol preserved, Gulf of Guayaquil, 20 m, Anton Brunn R/V, 11 September 1966. MEXICO: CASIZ 73822, ethanol preserved, Isla Danzante, Baja California Sur, 6–21 m, G.C. Williams, 21 July 1990; M564, dry, Islas Gringas, Guaymas, 10–15 m, J.L. Carballo, 27 November 2002; Geof2, dry, Baja California Sur, 8–15 m, G. Shester, July 2006; MNHN Oct.000-0553, dry, Acapulco, no depth given, A. Agassiz, 1889; STRI 1123, dry, Salche, Puerto Angel, Oaxaca, fishing net, 40–70 m, R. Abeytia, 13 June 2008; USNM 52484, dry, Tortolo Bay, Turtle Bay, Baja California, 6 m, Turner, 14 March 1961. USA: USNM 57302, ethanol preserved, Escondida Bay, San Diego, California, no collector, 14 November 1968.

Description. The examined specimens reach up to 25 cm in height and 36 cm in width. Colonies grow in multiple planes, profusely branched. They are flabelliform, broad, and branched pinnately. Main stems are 2–4 mm in diameter, compressed, and very short (up to 1 cm long) or absent, so the branches emerge directly from the holdfasts. Main branches are compressed and divergent, about 1.5 mm in diameter, and the pinnae are around 1.0 mm in diameter, irregularly arranged and closely spaced (Plate 4A). Several of the pinnae rebranch giving off secondary pinnae. Unbranched terminal twigs are blunt, and reach up to 1.5 cm in length. Polyps are colourless, distributed in irregular lateral bands along the branches and do not crowd the surface. Polyp-mounds are prominent with small bilabiate apertures and sometimes yellow spots (Plate 4B). Colonies are bright red uniformly or streaked with bright yellow on the branches or on the polyp-mounds (Plate 4C). They keep the same colour regardless being alive, stored dry, or preserved in alcohol (Plate 4A, D). Some of the main branches have numerous yellow, thin longitudinal grooves that are more evident on dry specimens. Sclerites of the coenenchyme are red and yellow. They are mostly double discs reaching up to 0.08 mm in length, and 0.06 mm in width (Plate 4C, Fig. 8). Spindles and disc-spindles are abundant, reaching up to 0.13 mm in length and 0.05 mm in width, with 4–6 whorls of warty tubercles (Plate 4C, Fig. 8). Crosses are up to 0.075 by 0.065 mm. No anthocodial sclerites were obtained in the samples for study.

Distribution. Pearl Islands, Gulf of Nicoya, Corinto, El Salvador (Verrill 1868a), Isla Gorgona (Prahl *et al.* 1986), and other localities (see Table 4).

Remarks. The specimens in the syntype series are very consistent in all characteristics, they agree in most all aspects with the illustrated specimen (MCZ 7080). A variation in colour can be found in some specimens, as in CDRS 05-197, where the colony is bright red and a few sclerites are yellow (Plate 4D). A white variety has been observed in shoals in Costa Rica and Mexico occurring together with the red form.

Eugorgia excelsa Verrill, 1868

Figure 9, Plate 5A–C

Eugorgia nobilis var. *excelsa* Verrill, 1868: 409; 1870: 553–554; Bielschowsky 1929: 176; Kükenthal 1924: 344; Stiasny 1951: 65; Harden 1979:127–128.

Material examined. Syntype series: YPM 401, dry, La Paz, 11–15 m, W.B. Rich, no date; YPM 1710, dry, Acapulco, no depth given, A. Agassiz, 1859–1860; YPM 4052, a–d, 8716, a–b, 8717, a–b, 8718, a–f, 8719, a–c, 8720, a–f, 8721, 8722, 8723, 8724, 8725, 8902, MCZ 36316 (donor YPM), USNM 44148, USNM 33601

(fragment of YPM 4052, donor A.E. Verrill), dry, La Paz, 11–15 m, J. Pedersen, no date.

Other material: MEXICO: Gorgonia-6, dry, Islas Gringas, Guaymas, 10–15 m, J.L. Carballo, 27 November 2002; MNHN oct.0000-0550, dry fragments, La Paz, no depth given, M. Diguet, 1913.

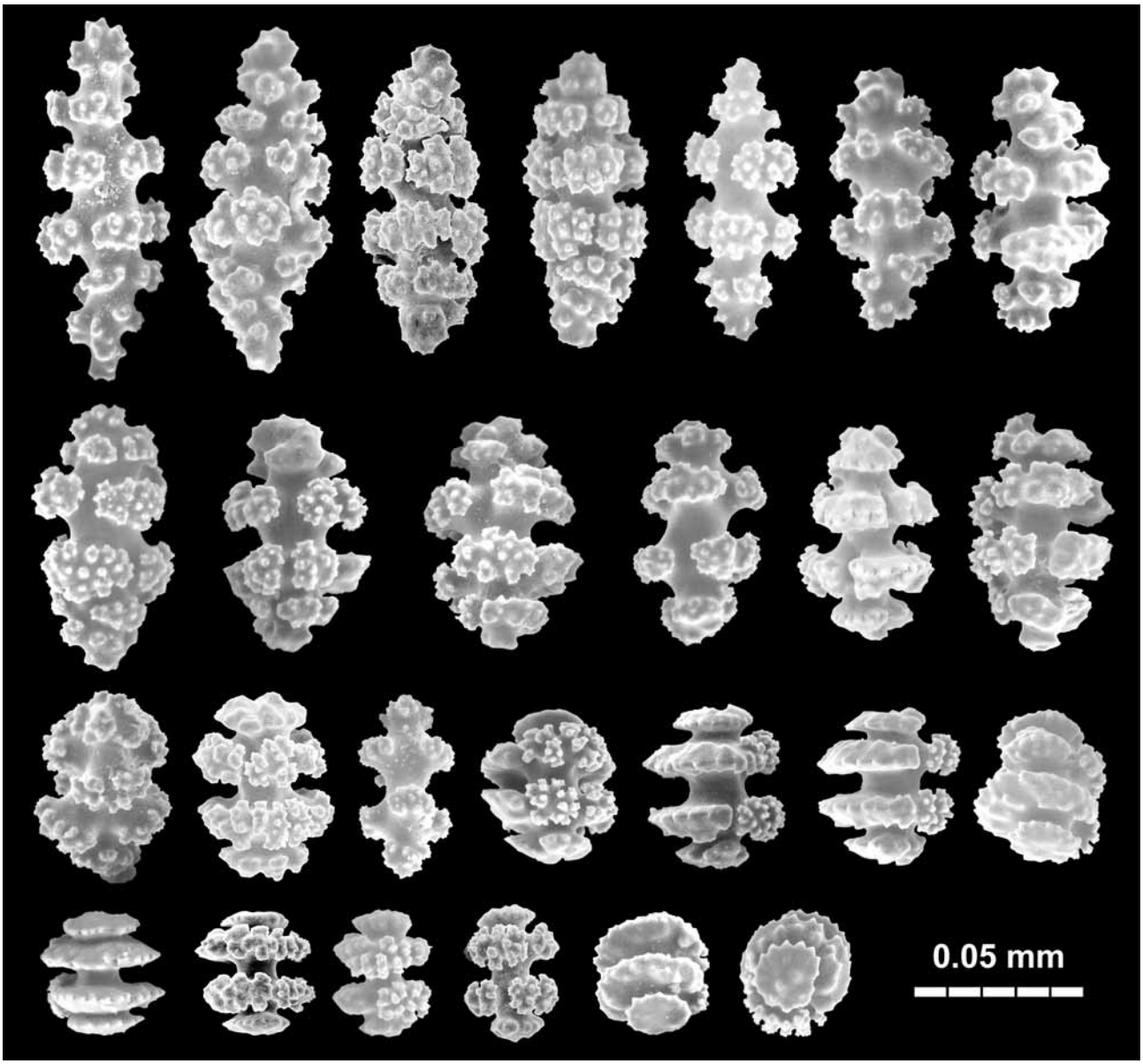

FIGURE 9. *Eugorgia excelsa* (MCZ 36316), coenenchymal sclerites.

Description. Colonies are large and flabelliform, mostly wider than high. Examined specimens measure up to 65 cm in height, and 85 cm in width. Branching is profuse, irregular and dichotomous (Plate 5A). Holdfasts are large, spreading and thick, in some colonies having a 1 cm thick layer of gorgonin deposited on the substrate. Holdfasts cover rocks and shells. In some colonies a thick stem, up to 3 cm in diameter, and 20–22 cm long arises from the holdfast and then branches, but generally several thick stems arise directly from the holdfast branching close to the base. Branches compressed at the base, 5–8 mm in diameter, more cylindrical, and tapered at the ends, 2–3 mm in diameter, with blunt or rounded tips, about 1–2 mm in diameter. Unbranched final twigs reach up to 10 cm in length. Some colonies present tumour-like growths on the branches that are covered by coenenchyme producing lumpy branches (Plate 5B). Full grown colonies have thicker branches and thinner branchlets, and the branching is more irregular and profuse. Colonies are dark reddish brown, varying somewhat in hue in different specimens, only YPM 1710 shows a purplish colour

(Plate 5A–B). Marked longitudinal grooves occur along the thick branches, and near the base. The polyps are evenly distributed all around the branches, crowding the surface, and the polyp-apertures are small, up to 0.5 mm in diameter (Plate 5B). Coenenchymal sclerites are orange and they are mostly double discs reaching up to 0.07 mm in length and 0.05 mm in width (Plate 5C, Fig. 9). Spindles are less abundant, up to 0.10 mm in length, and 0.043 mm in width, with 4–5 whorls of warty tubercles (Plate 5C, Fig. 9). No anthocodial sclerites were obtained in the samples for study.

The illustrated colony (MCZ 36316) measures 45 cm in height, and 63 cm in width (Plate 5A).

Distribution. Baja California Sur, Acapulco, type localities; Mazatlán (Table 4).

Remarks. This species was firstly described by Verrill (1868) as a variety of *E. nobilis* to separate the large flabelliform colonies of La Paz, Baja California, collected by Captain Pedersen from the short branched, more compact colonies of Panama and Nicaragua, *E. nobilis*. As a matter of fact the largest *Eugorgia* specimens examined in all collections belong to *E. excelsa*. In 1870 Verrill provided a fuller description of *E. nobilis var excelsa*, and included the locality of La Paz, collected by Major Rich, and Acapulco, collected by Professor Agassiz. Although it lacked of illustration and holotype designation, Verrill's description (1870) of this species is complete and consistent with the syntype series. We consider that this variety is different enough from *E. nobilis* to be treated as another species.

Eugorgia excelsa and *E. ampla* are the species that reach the largest sizes found in the collection, they both are bushy and very similar in their morphology. However, *E. ampla* has thicker and flatter branches, but thinner stems, polyp mounds closer together, and colonies are stouter than in *E. excelsa*. Sclerites of *E. ampla* and *E. excelsa* are similar in colour and morphology, but they differ in size and composition. Spindles reach up to 0.15 mm in *E. ampla*, and 0.10 mm in *E. excelsa*. Spindles are more abundant in samples of *E. ampla* than in *E. excelsa* (Table 1).

Eugorgia multifida **Verrill, 1870**

Figure 10, Plate 6A–D

Eugorgia multifida Verrill, 1870: 554–555; Bielschowsky 1918: 45; 1929: 179–180; Kükenthal 1924: 345; Harden 1979: 126–127.

Material examined. Syntype series: YPM 2257, dry, Acapulco, A. Agassiz, no further data; YPM 2257a–b, 4605, dry, Mazatlan, J. Dickinson, no further data; USNM 49368; YPM 4069, 8715, dry, La Paz, 11–15m, J. Pedersen, 1867-70. Other material: CASIZ 073819, ethanol preserved, NW Islote Blanco, SW Isla Danzante, Baja California, 4.5–12m, G.C. Williams, 22 July 1990; CASIZ 100846, ethanol preserved, Isla Cerralvo, Rock Islet Carpenteria, Baja California, 15 m, Ray (Chubb) Keys, 2 May 1976; CASIZ 103207, ethanol preserved, S Isla Danzante, off Candeleros, 24 m, Ray (Chubb) Keys, 1st May 1975; CASIZ 103393, ethanol preserved, 2 Km N off Boca del Tule to Arena Blanca, Baja California, 30 m, no collector, 26–27 April 1976.

Description. The examined specimens reach up to 35 cm in height and 35 cm in width. Colonies are flabelliform and densely branched. The main stem is up to 5 mm in diameter, compressed, and up to 2 cm long. It divides at the base into several, large, irregularly divergent branches or the branches arise directly from the holdfasts. Main branches are compressed, up to 4 mm in diameter, branching irregularly pinnate; the pinnae are 1–1.5 mm in diameter, short, and closely arranged (Plate 6A). They commonly rebranch giving off secondary and tertiary pinnae. Unbranched terminal twigs are blunt, and reach up to 1 cm in length. Polyps are distributed in irregular lateral bands along the branches, not very close and more distant on the thick branches, and separated by marked longitudinal grooves. Polyp-mounds are prominent, and reach up to 0.5 mm in diameter, with small apertures bordered by bright yellow sclerites (Plate 6B). Polyps have weak points-like arrangement, a few anthocodial sclerites at the base of the tentacles. Colonies are dark orange to bright red uniformly or streaked with bright yellow sclerites that blend with the red sclerites on the surface of the branches. Sclerites of the coenenchyme are red, yellow, and bicoloured (Plate 6C). They are mostly double

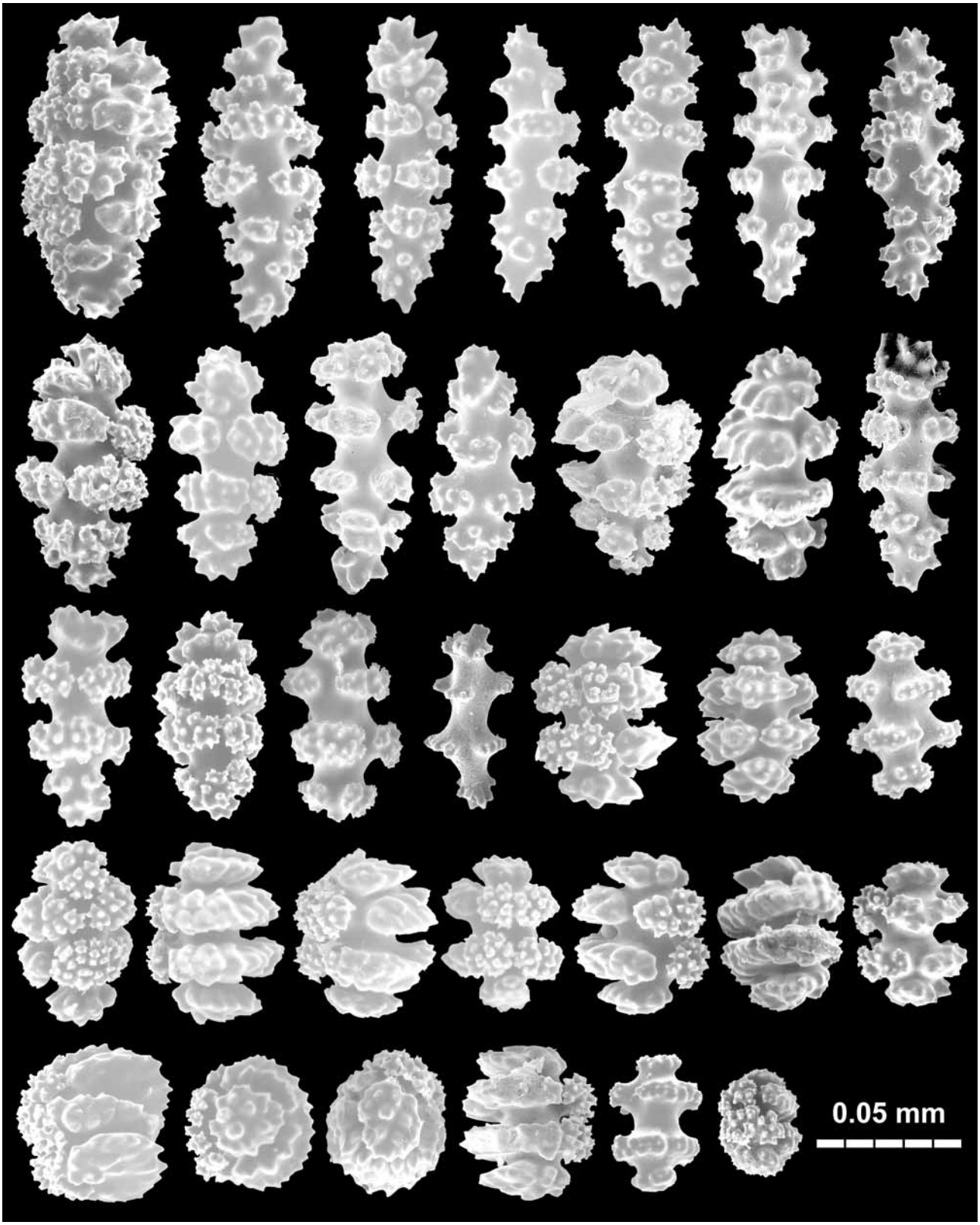

FIGURE 10. *Eugorgia multifida* (YPM 4605), coenenchymal sclerites.

discs reaching up to 0.07 mm in length, and 0.05 mm in width (Plate 6C, Fig. 10). There are also a few capstans about the same size with complex tubercles at the ends, and spindles reaching up to 0.13 mm in length, and 0.05 mm in width, with 3–6 whorls of warty tubercles (Plate 6C, Fig. 10). Furthermore, crosses are present about 0.06 by 0.06 mm. Anthocodial sclerites were only found in preserved specimens, they are

orange, flat rods, up to 0.08 mm in length, and 0.027 mm in width, lobed with serrated margins (Plate 6D). Other colonies examined agree in all aspects with the syntypes. In preserved specimens polyps are colourless, and the colour of the colonies does not change after preservation. The illustrated specimen, syntype YPM 4605, measures 14.5 cm in height and 29 cm in width, with the small remains of a conic holdfast (Plate 6A–B).

Distribution. La Paz, Baja California, Mazatlán, Acapulco (Table 4).

Remarks. *Eugorgia daniana*, *E. aurantiaca*, and *E. multifida* are very similar in their type of branching and their prominent polyp mounds. However, *E. multifida* is separated from this group by the compact, thick and short branchlets of the colony. *Eugorgia aurantiaca* is very similar to *E. daniana*, but the latter has the branches and branchlets more closely placed, thinner and less compressed with smaller polyp mounds. *Eugorgia aurantiaca* differs from the other two species in the presence of yellow rings on the polyp mounds, and in the distribution of the polyps that is more organised in two to four rows than in *E. daniana* or *E. multifida*, where the distribution is in multiple rows. Additionally, the double discs in *E. daniana* are sharper than in the other two species, and smaller spindles were found in *E. aurantiaca* (Table 1).

Eugorgia nobilis Verrill, 1868

Figure 11, Plate 7A–C

Eugorgia nobilis Verrill, 1868: 408–409; Bielschowsky 1918: 44, 1929: 175–176; Kükenthal 1924: 343; not Stiasny 1951: 65 (=*E. excelsa*); Harden 1979: 127.

Material examined. Lectotype (here designated): YPM 1552a, dry, Pearl Islands, 11–15 m, F.H. Bradley, 1866.

Paralectotypes: YPM 1552b–e, YPM 1658, data as the lectotype.

Other material: MEXICO: USNM 33599, dry, Acapulco, no further data. COSTA RICA: USNM 44207, dry, Golfo de Nicoya, no depth given, M. Valerio, 20 February 1931. PANAMA: STRI 783, dry, Isla San Telmo, Pearl Islands, 2 m, H.M: Guzman, 13 August 2003. PERU: USNM 50154, ethanol preserved, Paita, Piura, W.L. Schmitt, no depth given, 8 October 1926.

Lectotype description. Fan shaped colony, 24 cm in height, and 20 cm in width. Colony composed of two thick and compressed stems, 4–5 mm in diameter, these arise from a spreading holdfast and diverge laterally in sinuous branches, 3–4 mm in diameter. They subdivide irregularly giving off short and thick branchlets placed at short distances, 2–3 mm in diameter, several of them have enlarged tips, up to 3 mm in diameter. Unbranched twigs reach up to 3 cm in length (Plate 7A). Coenenchyme is thick and compact. Colony is brownish red (Plate 7A). The polyps were evenly distributed all around the branches (Plate 7B). Polyp-apertures are small, up to 0.2 mm in diameter, and closely placed on the branch' surface (Plate 7B). Coenenchymal sclerites mostly double discs, which are light purple, colourless and bicoloured (Plate 7C). Capstans reach up to 0.08 mm in length and 0.05 mm in width, double discs and incomplete double discs are small reaching up to 0.045 mm in length and around the same in width (Fig. 11). Spindles reach up to 0.15 mm in length and 0.05 mm in width, with 4–7 whorls of warty tubercles (Plate 7C, Fig. 11). No anthocodial sclerites were obtained in the samples for study.

Description. Examined colonies reach up to 25 cm in height, and 22 cm in width, the largest specimen is composed of three fans spreading laterally, in the same plane, arising from thick, compressed stems up to 0.5 cm in diameter. They subdivide irregularly, branching as in the lectotype. Small specimens have a very irregular branching pattern that looks more like a maze than like a fan. In some specimens branching is profuse and the branches are thinner and longer. Colonies are brownish red and darker hues (Plate 7A, B). Polyp mounds are slightly raised and evenly distributed all around the branches, arranged close together and with small apertures. Sclerites are as in the lectotype.

Distribution. Pearl Islands and Corinto (Verrill 1868a), type localities; Golfo de Nicoya, Acapulco and

Paita (Table 4).

Remarks. Verrill (1868) described this species with specimens from Pearl Islands, Corinto and La Paz. He introduced the variety "*excelsa*" with minimal description in a footnote, but designate La Paz as the type locality, thus he excluded all specimens from La Paz from *E. nobilis*, leaving Pearl Islands and Corinto as the type localities. However, the only material found in the type collections is from Pearl Islands. Later, Verrill (1870) more thoroughly described the variety *excelsa* restricted to the Mexican localities, La Paz and Acapulco. Although Verrill's description of *E. nobilis* (1870) is accurate, he neither designated a holotype nor illustrated the species, additionally, we could not find the specimens from Corinto, and for these reasons we herein designate YPM 1552a as the lectotype of *E. nobilis* to avoid future confusion.

This species is similar to *E. ampla*, and *E. excelsa*, but the short compact branchlets, and the sclerite colours and forms, especially the occurrence of colourless spindles, separates this species from the other two.

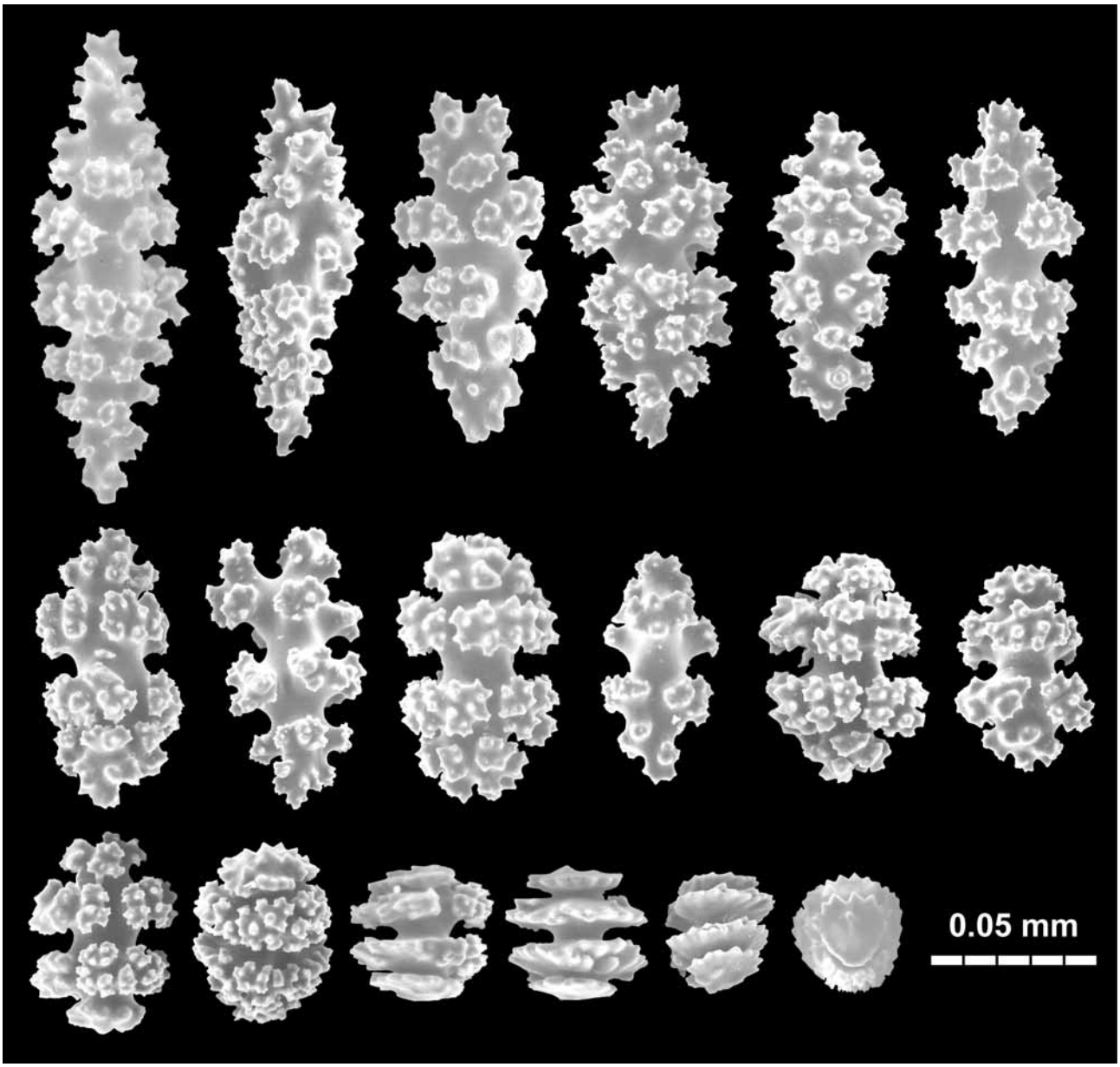

FIGURE 11. *Eugorgia nobilis*, lectotype, coenenchymal sclerites.

***Eugorgia panamensis* (Duchassaing and Michelotti, 1864)**
Figure 12, Plate 8A–C

Lophogorgia panamensis Duchassaing and Michelotti, 1864: 19; Harden 1979: 77–79; Volpi & Benvenuti 2003: 58.
Eugorgia panamensis Breedy and Guzman 2007: 17

Material examined. Holotype: MZUF 159 (figured specimen Duchassaing & Michelotti 1864), dry fragment, Isla Flamenco, Gulf of Panama, no further data.

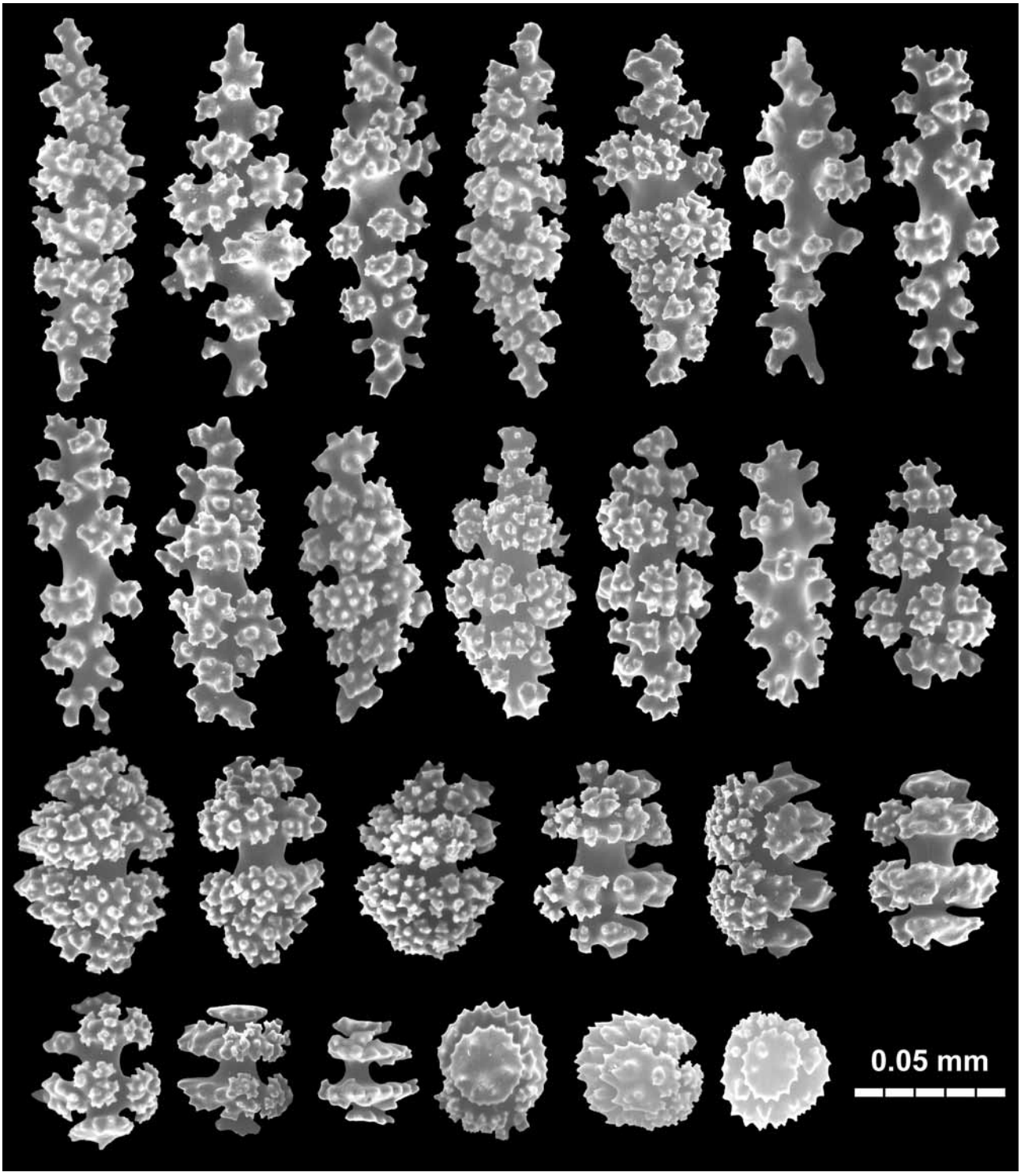

FIGURE 12. *Eugorgia panamensis*, holotype, coenenchymal sclerites.

Holotype description. Fragment of a colony 14.7 cm in height, and 5.5 cm in width. Branching seems to be irregularly dichotomous. Branches compressed at the lower part, reach up to 4 mm in diameter; they subdivide into more cylindrical branchlets 2–3 mm in diameter and tapered at the ends, with pointed tips of 0.5–1 mm in diameter. Unbranched final twigs reach up to 6 cm in length. Colony is light purple (Plate 8A). Marked longitudinal grooves occur along the thicker branches, and polyps are evenly distributed all around (Plate 8B). Polyp-apertures are small, up to 0.3 mm in diameter, and closely placed on the branch surface (Plate 8A–B). Coenenchymal sclerites are colourless, pink, and some bicoloured (Plate 8C); mostly double discs reach up to 0.06 mm in length and 0.05 mm in width (Fig. 12). Capstans reach up to 0.07 mm in length and 0.05 mm in width (Fig. 12). Spindles reach up to 0.14 mm in length, and 0.05 mm in width, with 4–6 whorls of warty tubercles (Fig. 12). No anthocodial sclerites were obtained in the samples for study.

Distribution. Only known from the type locality in the Gulf of Panama (Table 4).

Remarks. *Eugorgia panamensis* was described by Duchassaing and Michelotti (1864) in the genus *Lophogorgia*. They gave a brief diagnosis, but accurately illustrated the fragment of a colony that constitutes the holotype. This fragment could fit in *E. excelsa* or *E. purpurascens*, but some differences in the sclerites and uncertainty in other characters (as in the branching pattern) lead us to keep the specific status for the time being.

Eugorgia purpurascens Verrill, 1868

Figure 13, Plate 9A–C

Eugorgia ampla var *purpurascens* Verrill, 1868: 408; Bielschowsky 1929: 175.
Eugorgia ampla purpurascens Kükenthal 1924: 345.

Material examined. Syntypes: YPM 1630, dry, Pearl Islands, Panama, no depth given, F.H. Bradley, 1866-67; YPM1613, dry, Zorritos, Peru, no depth given, F.H. Bradley, 1866-67; YPM 4623, Corinto, Nicaragua, no depth given, J.A. McNiel, no date.

Description. Colonies measure up to 48 cm in height, and up to 37 cm in width; they are deprived of a holdfast. Branching is irregularly dichotomous. Branches compressed at their base, reaching 13–25 mm in diameter; unbranched terminal twigs are 3–8 mm in diameter, more cylindrical, and slightly tapered at the ends, with rounded tips about 1–2 mm in diameter. Branches and branchlets can be sinuous; some branchlets divide at obtuse angles. Unbranched final twigs reach up to 10 cm in length. Colonies are light purple to pinkish (Plate 9A). Slightly marked longitudinal grooves occur along the branches, and near the base and the polyps were evenly distributed all around (Plate 9B). Polyp mounds are slightly raised and placed close together on the branch surface (Plate 9A–B). Polyp-apertures are small, up to 0.5 mm in diameter. Coenenchymal sclerites are colourless, pink, and some bicoloured, or they are mostly colourless with some pinkish (Plate 9C). In specimen YPM 1613, sclerites are colourless, pink and purple, and mostly double discs. In specimen YPM 1630 sclerites are colourless and pale pinkish with an even occurrence of double discs and spindles in the slide-samples. Shapes and sizes of sclerites are consistent among the type series. Double discs reach up to 0.07 mm in length and 0.05 mm in width (Plate 9C, Fig. 13); capstans are about the same size. Spindles are up to 0.13 mm in length, and 0.05 mm in width, with 4–6 whorls of warty tubercles (Plate 9C, Fig. 13). Furthermore, some crosses are present, up to 0.08 by 0.07 mm (Fig. 13). No anthocodial sclerites were found in the samples for study.

The illustrated specimen (YPM 1630) is a large portion of a fan, 45cm in height, 37 cm in width, and 2.5 cm in diameter at the base (Plate 9A).

Distribution. Pearl Islands, Corinto, Zorritos, type localities (Verrill 1868) (Table 4).

Remarks. Verrill described this species as a variety of *E. ampla* but they differ in many aspects: colonies are not bushy as in *E. ampla*, they are more flexible, and the colour of the colonies and sclerites in this species is never orange, as is the case in *E. ampla*; spindles are smaller than in *E. ampla*, and also less abundant; no complete double discs were found in *E. purpurascens* (Tables 1–2). These species differ not only in the

morphology but also in geographic distribution; *E. purpurascens* has not been reported for any site in Baja California, type locality of *E. ampla*. Therefore, we consider *E. purpurascens* as a separate species (Table 4).

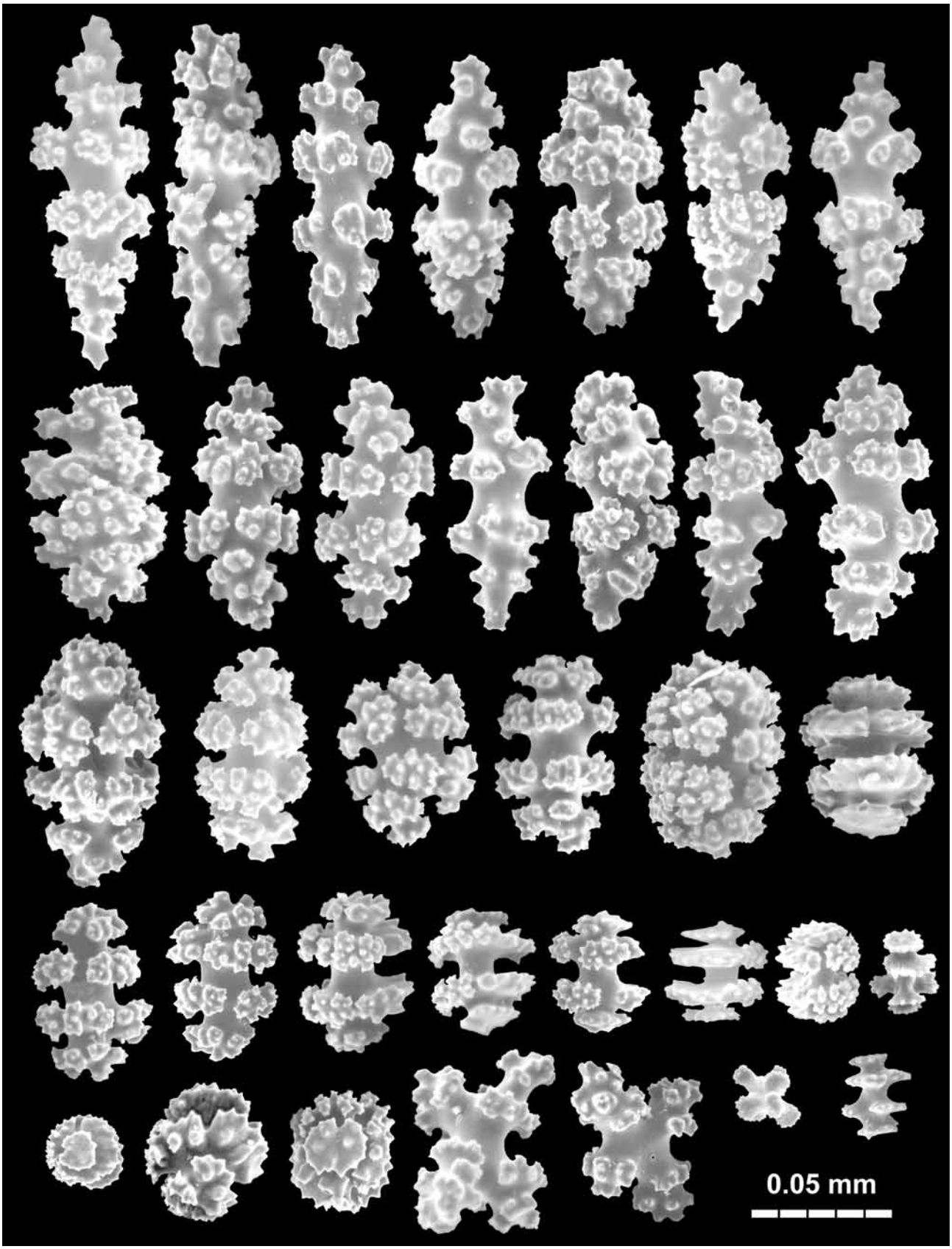

FIGURE 13. *Eugorgia purpurascens* (YPM 1630), coenenchymal sclerites.

***Eugorgia querciformis* Bielschowsky, 1929**
Figure 14, Plate 10A–C

Eugorgia querciformis Bielschowsky, 1918: 45 (nomen nudum); Bielschowsky 1929: 183–184; Kükenthal 1919: 916; Kükenthal 1924: 346–347.

Material examined. Holotype: ZMHC 4873, ethanol preserved, Acajutla, El Salvador, no further data.

Description. According to Bielschowsky the holotype was a colony, 11 cm in height, and 33 cm in width; it was composed of two main branches, compressed, about 7 mm in diameter, that subdivide from a 3.2 cm long stem, producing a flabellate colony, that was attached to the substratum by an incrusting holdfast. We examined a fragment 10 cm in height, and 6 cm in width (Plate 10A). Branching is lateral and irregular; branches subdivide up to 4 times in an irregular dichotomous manner. Branches are slightly compressed, 2.5–3 mm in diameter, branchlets are 2 mm in diameter, unbranched final twigs reach up to 3 cm long. Polyps are evenly distributed all around the branches, closely placed. They retract within slightly raised polyp-mounds leaving small oval apertures (Plate 10B). Colony is reddish purple (Plate 10A, B). Coenenchymal sclerites are all red; they are mostly double discs reaching up to 0.08 mm in length, and 0.05 mm in width (Plate 10C, Fig. 14). Spindles reach up to 0.13 mm in length, and 0.05 mm in width, with 3–5 whorls of tubercles. Some spindles have slightly bent ends (Fig. 14). Crosses and barrel-like sclerites occur in the sclerite samples. No anthocodial sclerites were found in the samples.

Distribution. Known only from the type locality, Acajutla, El Salvador (Table 4).

***Eugorgia rubens* Verrill, 1868**
Figure 15, Plate 11A–D

Eugorgia rubens Verrill, 1868: 411; Studer 1894: 69; Bielschowsky 1918: 45; 1929: 183; Kükenthal 1924: 346; Harden 1979: 128–129.

Material examined. Holotype: YPM 1779, dry fragment, Piura, Peru, no depth given, F.M. Bradley from G. Petrie, 1866–1867; MCZ 36047 (slide of the holotype).

Other material: COSTA RICA: UCR 1745, dry fragment, Islas Murciélago, Santa Elena Bay, 30 m, C. Jimenez, October 1997. MEXICO: STRI 1120, dry, Salche, fishing net, 40–70 m, R. Abeytia, 13 June 2008. USA: CASIZ 96606, ethanol preserved, Santa Cruz Island, Channel Islands, California, dredge, 15 March 1950; Cathy, dry, Point Lobos, Carmel, Monterey, California, 64 m, collected by a sport diver and given to L. Austin, August 2007; USNM 50180, dry, La Jolla Canyon, dredge 46–52 m, C. Limbaugh, 8 October 1955.

Description. The holotype consists of a dry small fragment, 7.5 cm in height, and 3.5 cm in width, almost devoid of sclerites (Plate 11A–B). Other examined specimens reach up 40 cm in height and 30 cm in width, they are mostly fragments and holdfasts are missing. Branches are slightly flattened in cross section, up to 2 mm in diameter, branchlets more rounded. Branching is irregularly pinnate; the branchlets are sparsely placed, separated by 0.5–2 cm, and are 1–1.5 mm in diameter and up to 4 cm long. They rebranch giving off secondary branchlets. Unbranched terminal twigs are blunt, and reach up to 5 cm in length. Polyp-mounds are prominent arranged in a single row along each edge of the branchlets, and distributed more irregularly along the thick branches (Plate 11B). Colonies are pink. Sclerites of the coenenchyme are pink and pale hues (Plate 11C). They are mostly double discs reaching up to 0.07 mm in length, and 0.05 mm in width (Fig. 15). Spindles reach up to 0.10 mm in length, and 0.05 mm in width, with 3–5 whorls of warty tubercles (Fig. 15). No anthocodial sclerites were found in the samples.

The illustrated specimen is a 20 cm fragment from Santa Cruz Island (CASIZ 96606) that matches the characteristics of this taxon (Plate 11D).

Distribution. Paita (Verrill 1868), type locality; Santa Cruz Island, Point Lobos, Monterey, California, Murciélago Islands, Puerto Angel, Oaxaca (Table 4).

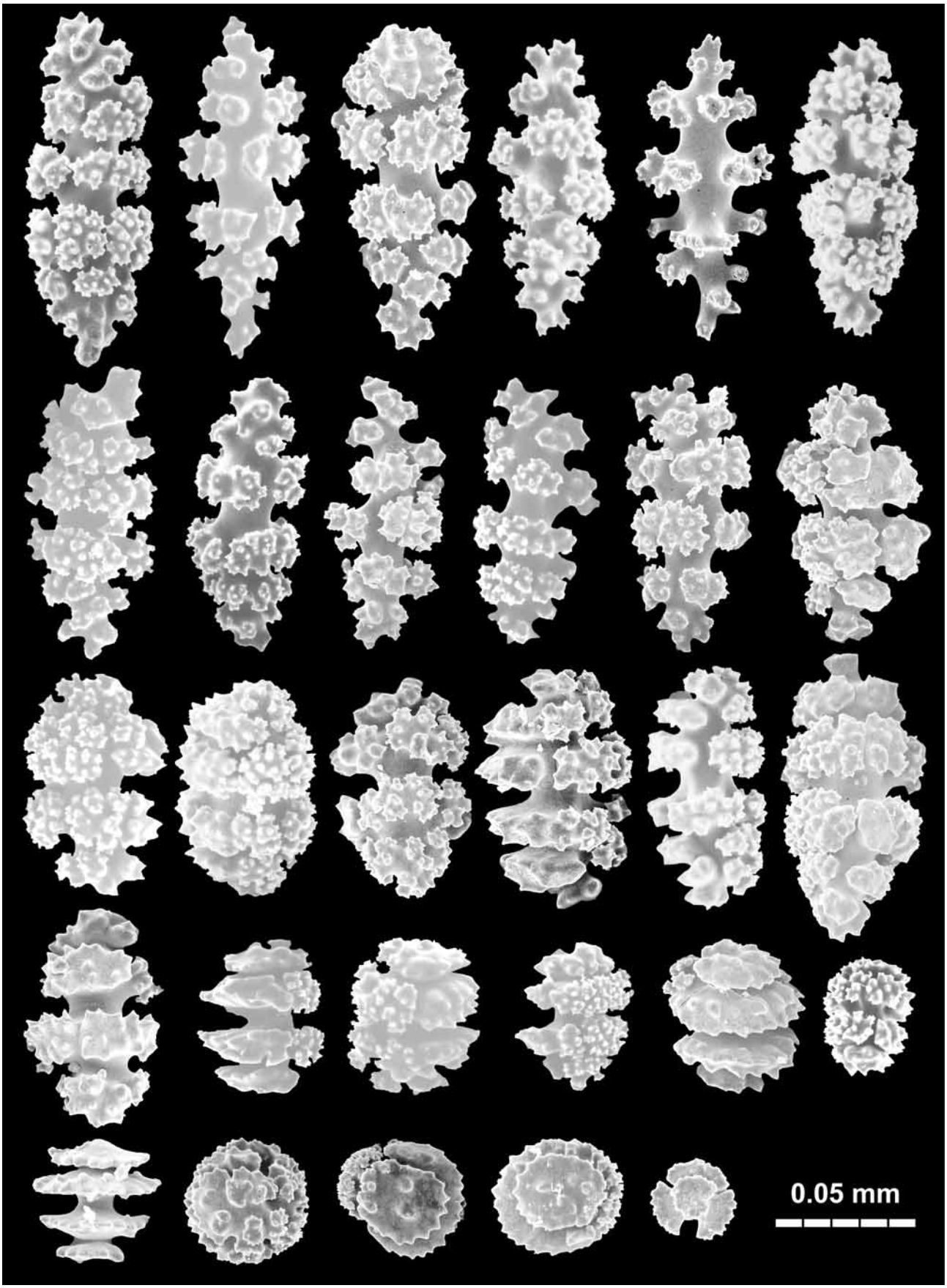

FIGURE 14. *Eugorgia querciformis*, holotype, coenenchymal sclerites.

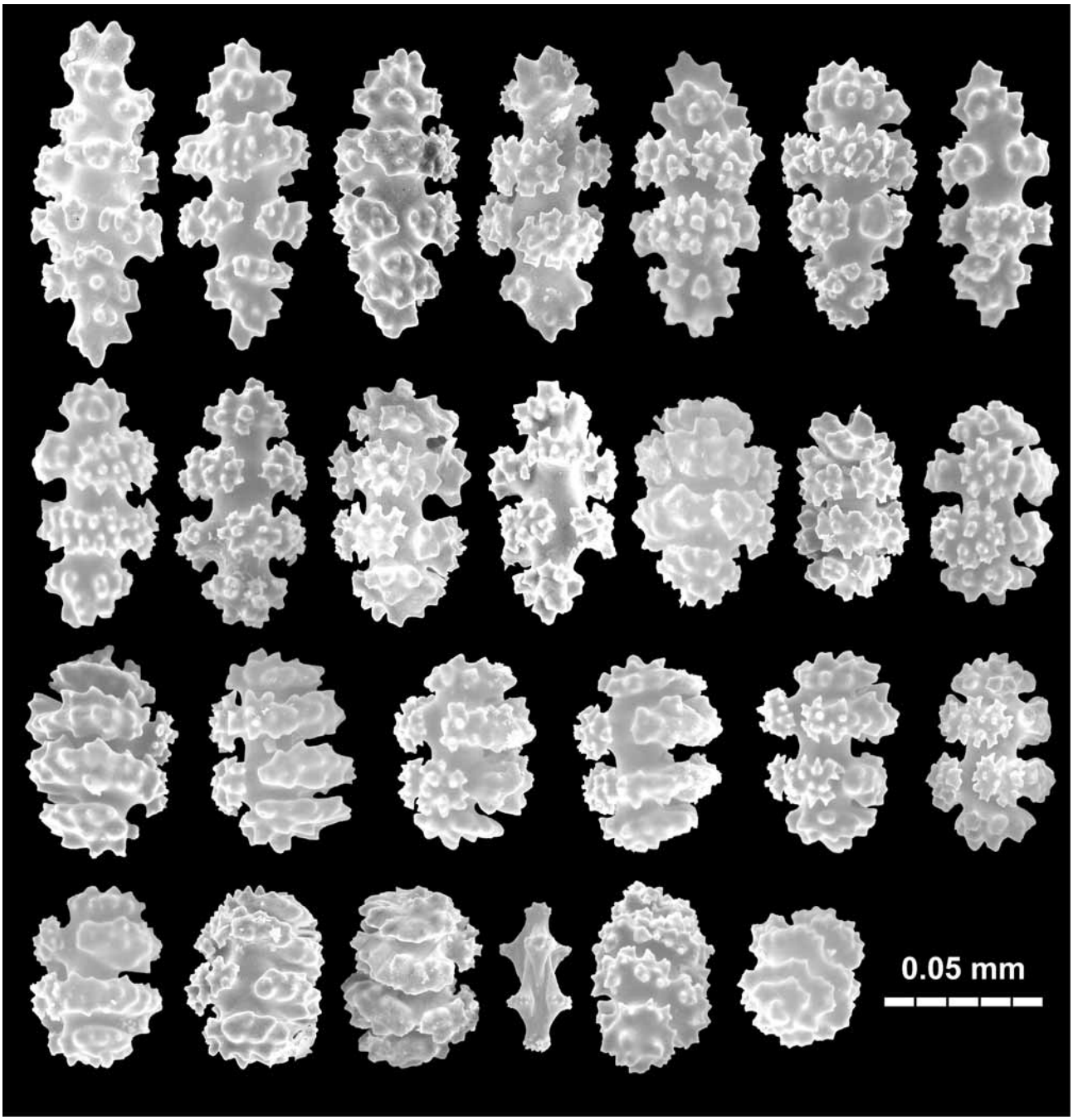

FIGURE 15. *Eugorgia rubens* (YPM 1779), coenenchymal sclerites.

Remarks. Verrill (1868) described this species from a specimen 60–90 cm across without illustration. What remains of the large specimen is the small fragment (YPM 1779) that agrees with the collection data given by Verrill, as well as the MCZ slide that apparently came from the same specimen, for this reason we consider it the holotype. This species is similar to *E. aurantiaca*, *E. daniana*, and *E. multifida* in the branching pattern, but differs from them in many other aspects, especially in the polyp distribution, and in the sclerites (Table 1).

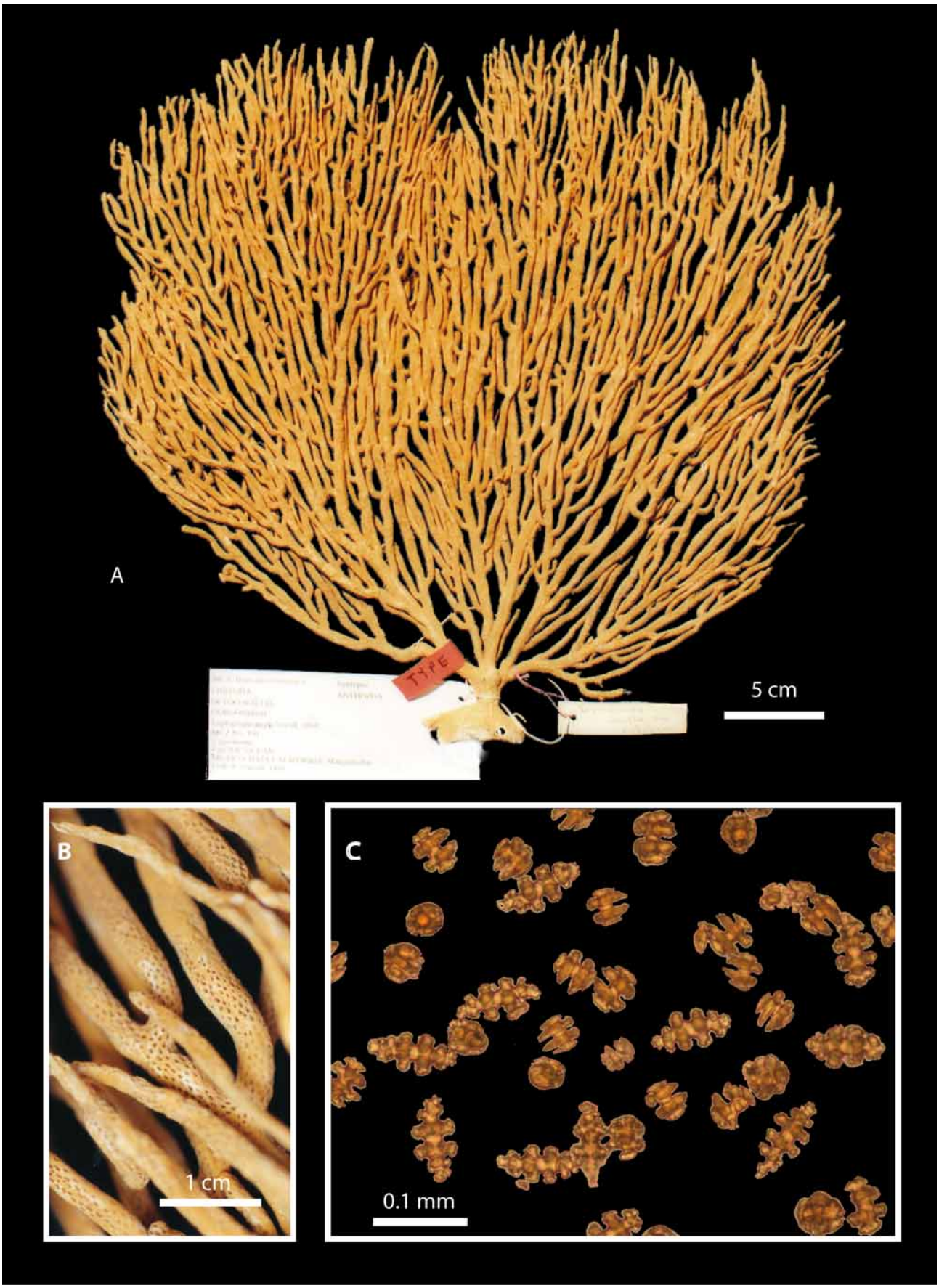

PLATE 1. *Eugorgia ampla* (MCZ 193): **A,** colony; **B,** detail of branches; **C,** light micrograph coenenchymal sclerites.

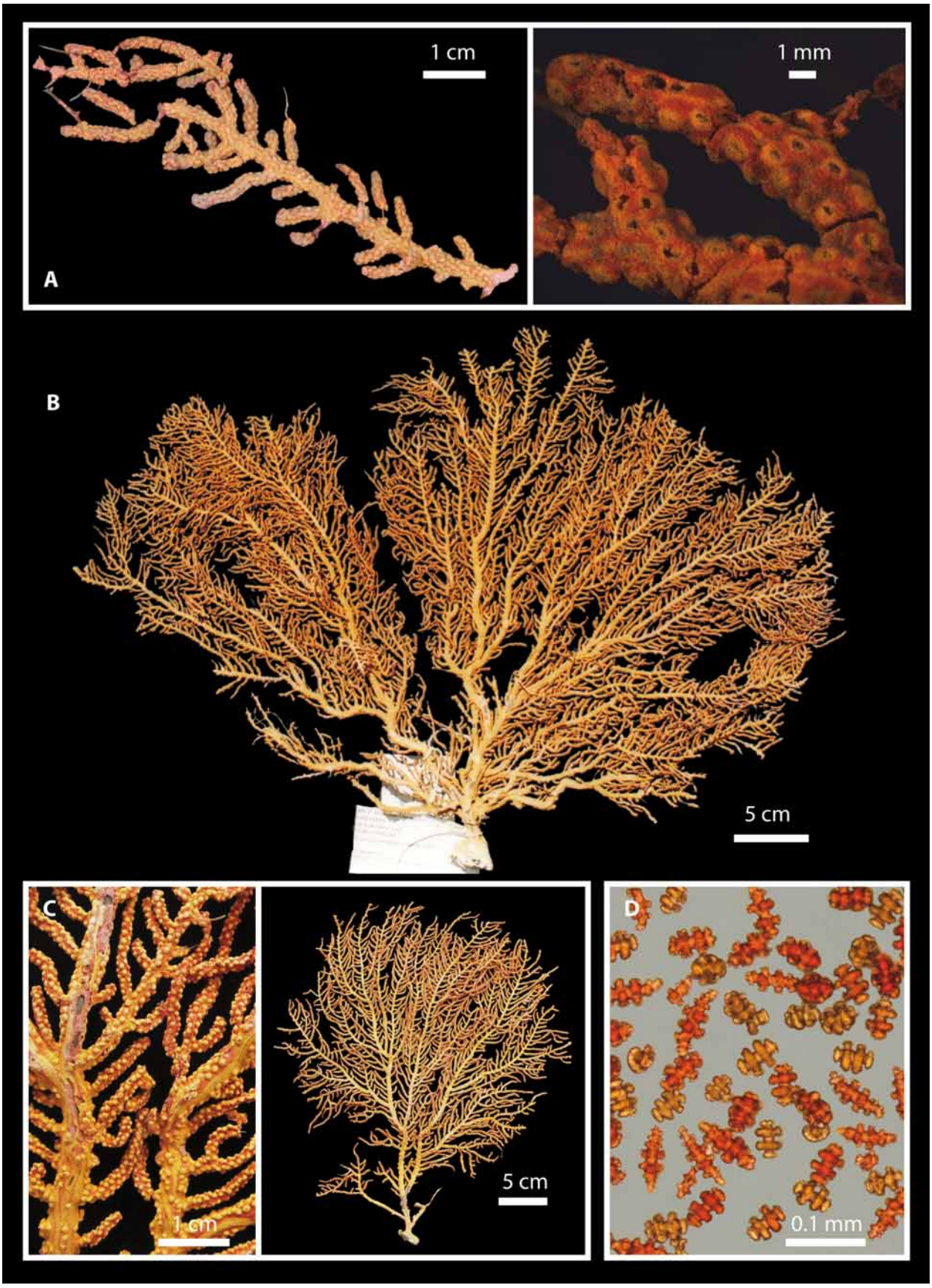

PLATE 2. *Eugorgia aurantiaca*: **A,** fragment of the lectotype and detail of the branch; **B,** complete colony (MCZ 61014); **C,** detail of branches and complete colony (USNM 1016591); **D,** light micrograph coenenchymal sclerites (YPM 2269).

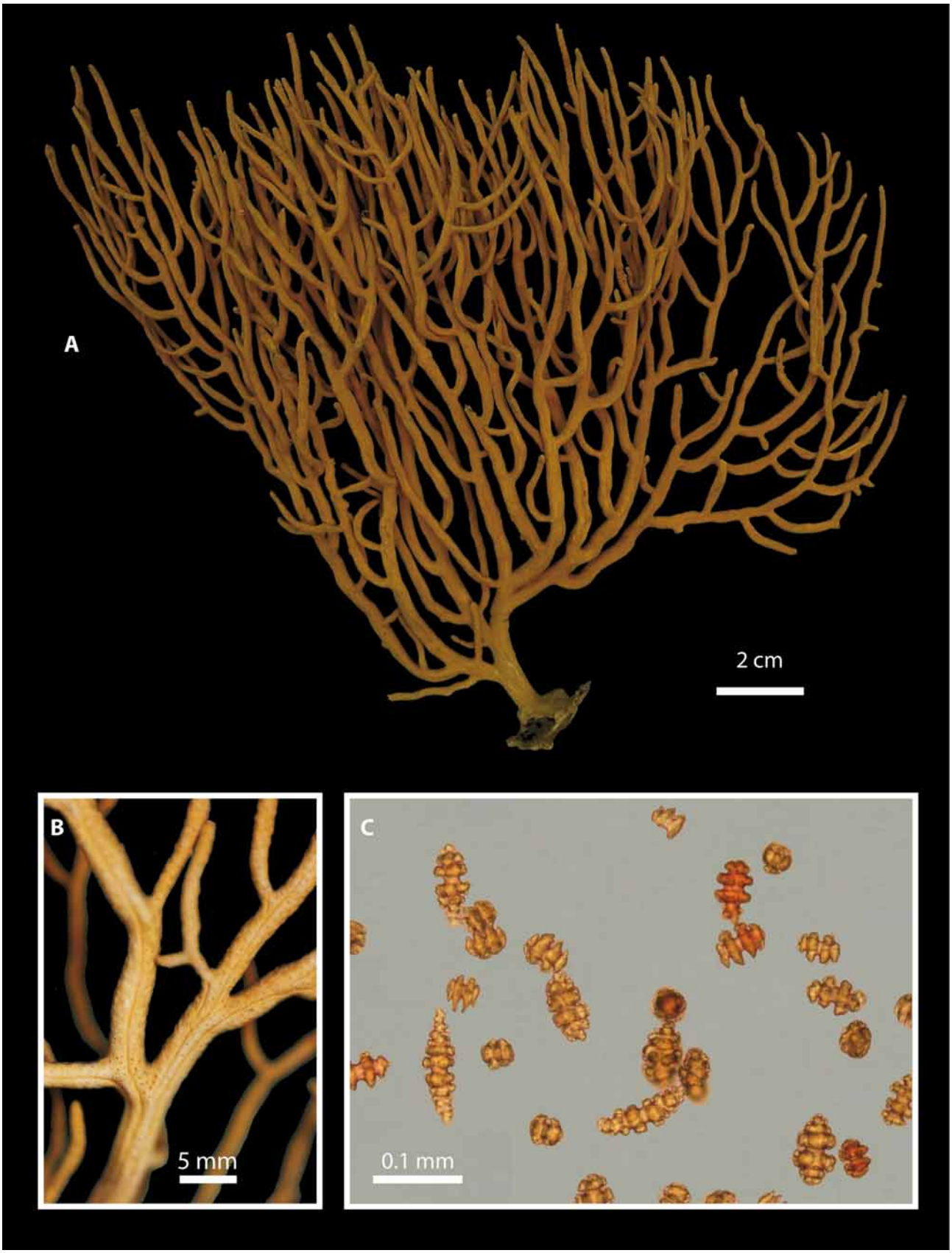

PLATE 3. *Eugorgia bradleyi* (MCZ 7006B1): **A,** colony; **B**, detail of branches; **C,** light micrograph coenenchymal sclerites.

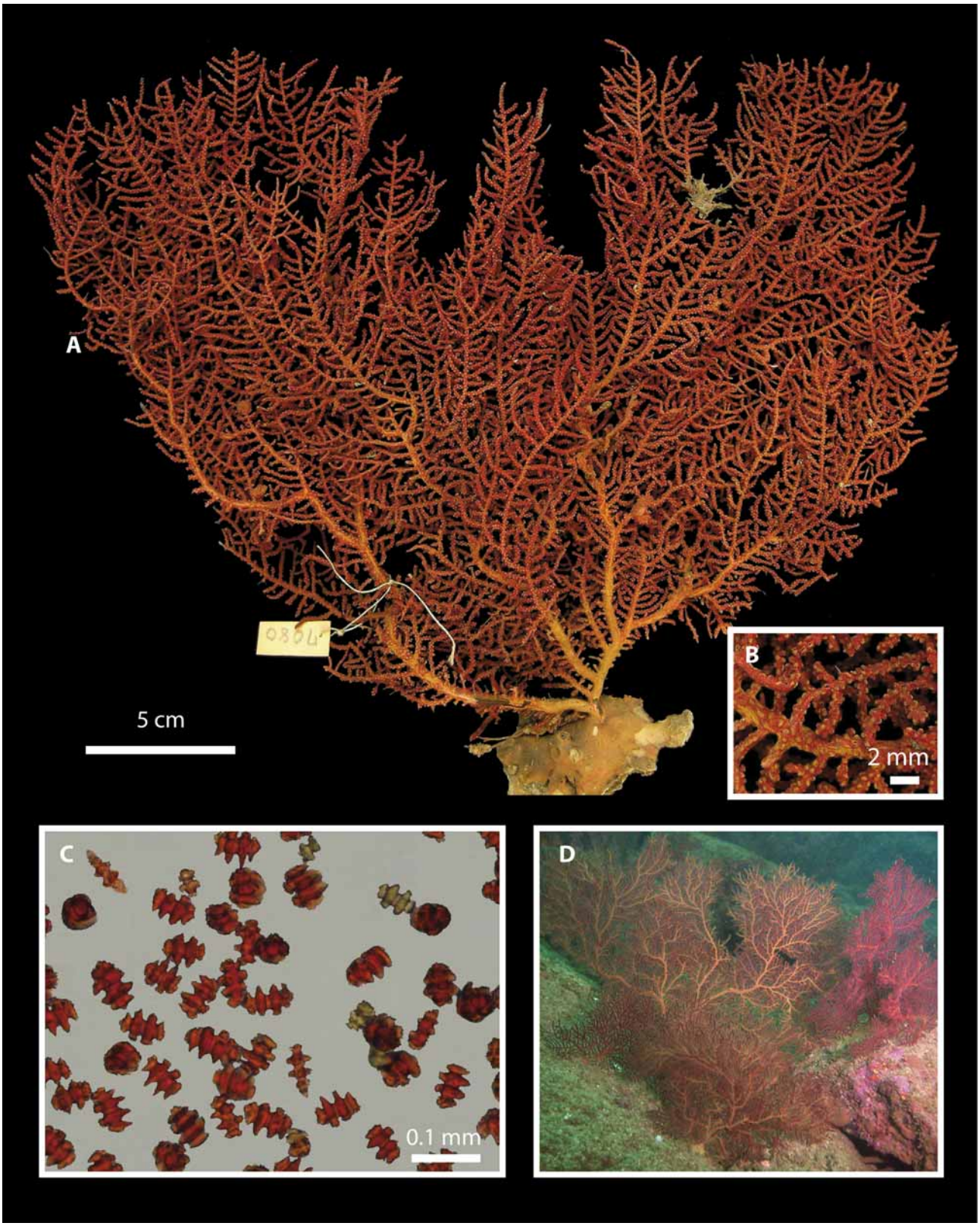

PLATE 4. *Eugorgia daniana* (MCZ 7080): **A,** colony; **B**, detail of branches; **C,** light micrograph coenenchymal sclerites; **D,** living colonies, red variety (right), and typical (left), 29 m deep, Isla Genovesa, Islas Galapagos, Ecuador (photograph: Angel Chiriboga).

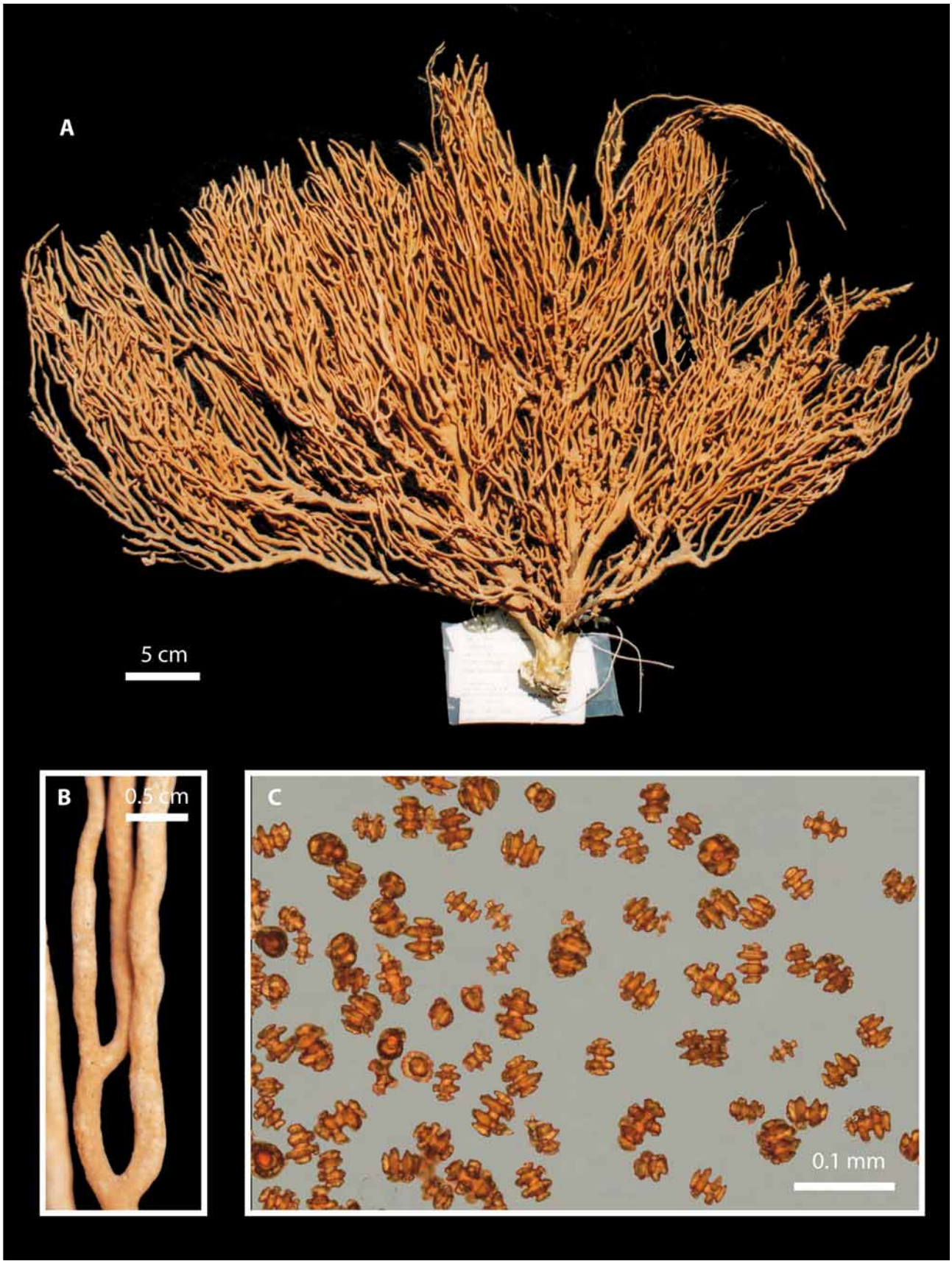

PLATE 5. *Eugorgia excelsa* (MCZ 36316): **A,** colony; **B**, detail of branches; **C**, light micrograph coenenchymal sclerites.

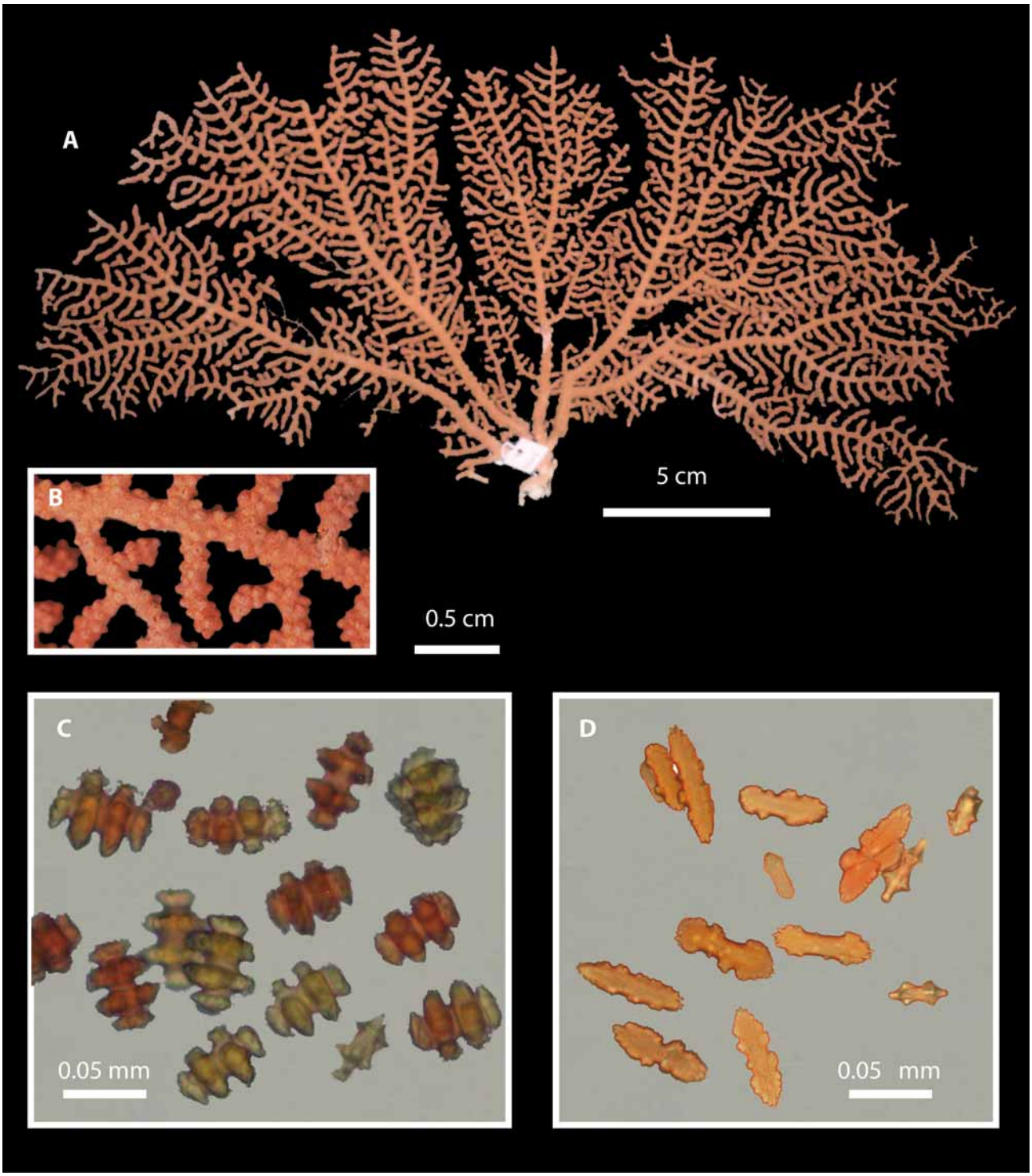

PLATE 6. *Eugorgia multifida* (YPM 4605): **A,** complete colony; **B,** detail of branches; **C,** light micrograph coenenchymal sclerites; **D,** anthocodial sclerites (CASIZ 103207).

Final Remarks

Distinction among species of *Eugorgia*, as in most gorgoniids (e.g. *Leptogorgia*, *Pacifigorgia*) is based on the combination of morphological characters: colony growth form, colour, and sclerites (Grasshoff 1992, Breedy & Guzman 2007, Guzman & Breedy 2008). The growth form in *Eugorgia* shows a range of variation of the general dichotomous or pinnate patterns. Most of the colonies are erect with stout branches, and very similar

in the external appearance, especially the bushy species (e.g. *E. daniana* and *E. aurantiaca*, or *E. ampla* and *E. excelsa*).

The general aspect of the colonies of the genus *Eugorgia* is similar to that of colonies of *Leptogorgia* with the remarkable abundance of double-discs in *Eugorgia* being the most conspicuous character differentiating these two genera. We have acknowledged the taxonomic value of anthocodial sclerites (Breedy & Guzman 2007) in genera as *Leptogorgia* and *Pacifigorgia*, but in the case of *Eugorgia*, we could find the anthocodials in only one species (*E. multifida*) in which they are arranged in a weak points-like ring.

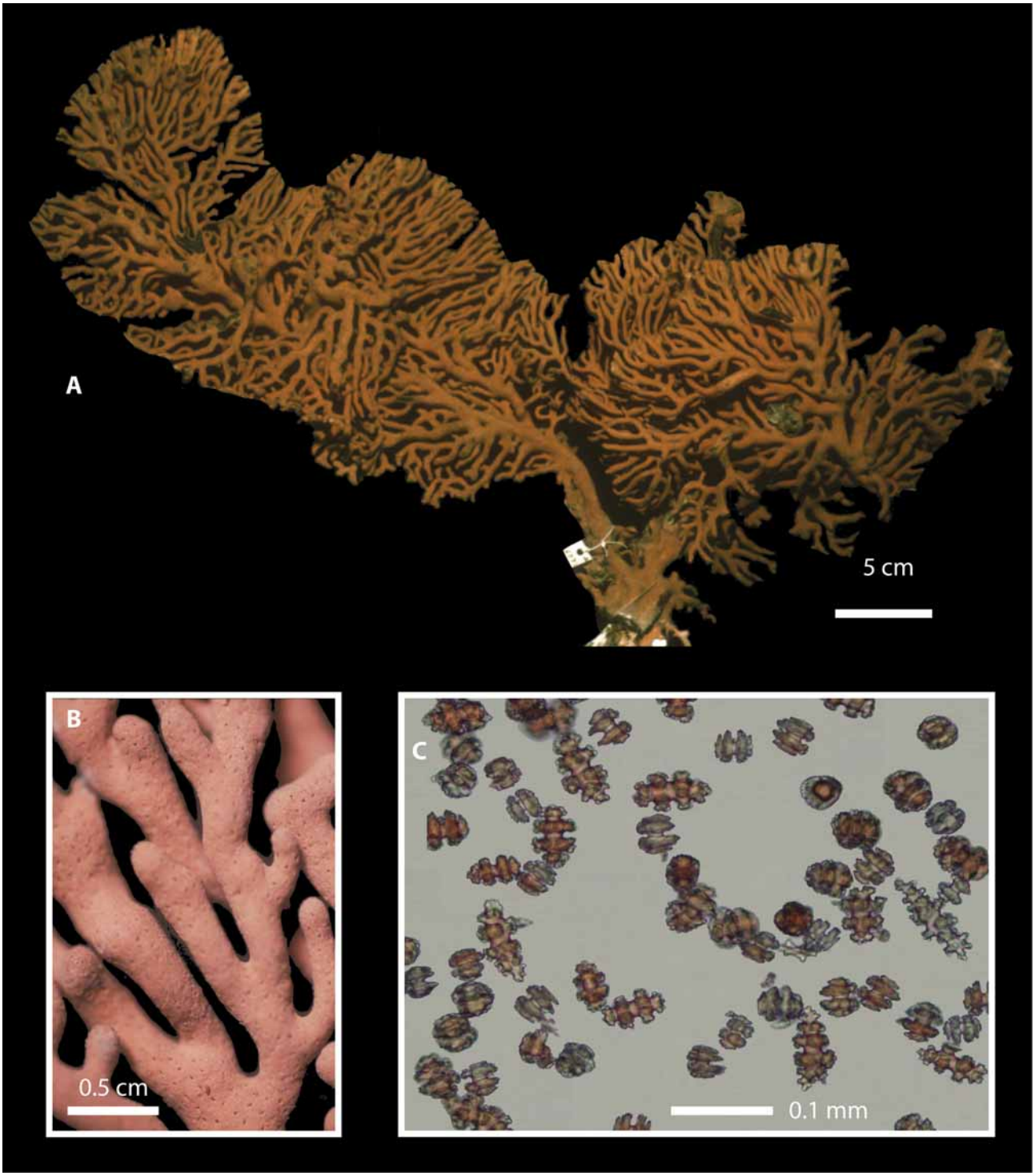

PLATE 7. *Eugorgia nobilis*, lectotype: **A,** colony; **B**, detail of branches; **C**, light micrograph coenenchymal sclerites.

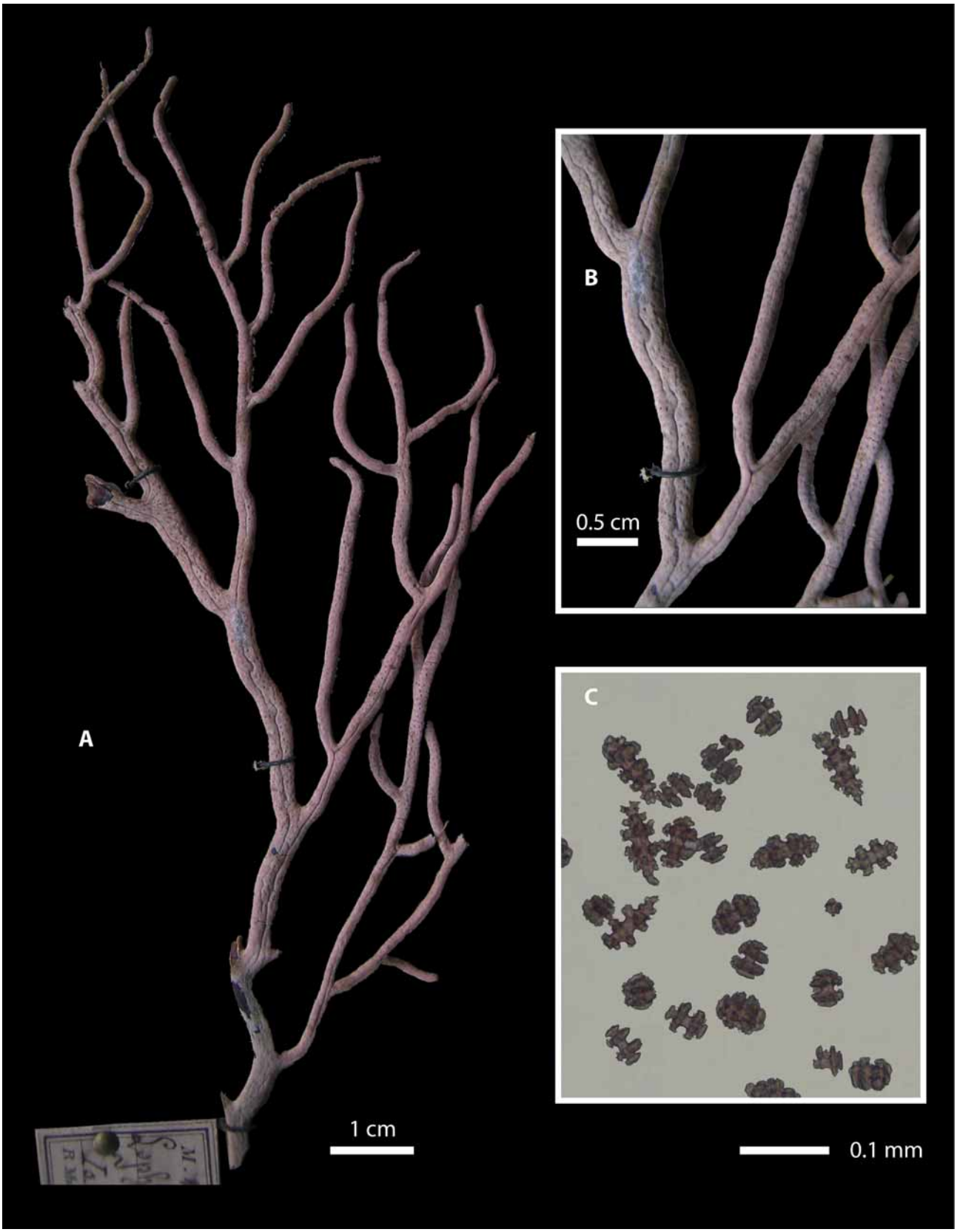

PLATE 8. *Eugorgia panamensis* , holotype: **A,** colony; **B**, detail of branches; **C**, light micrograph coenenchymal sclerites.

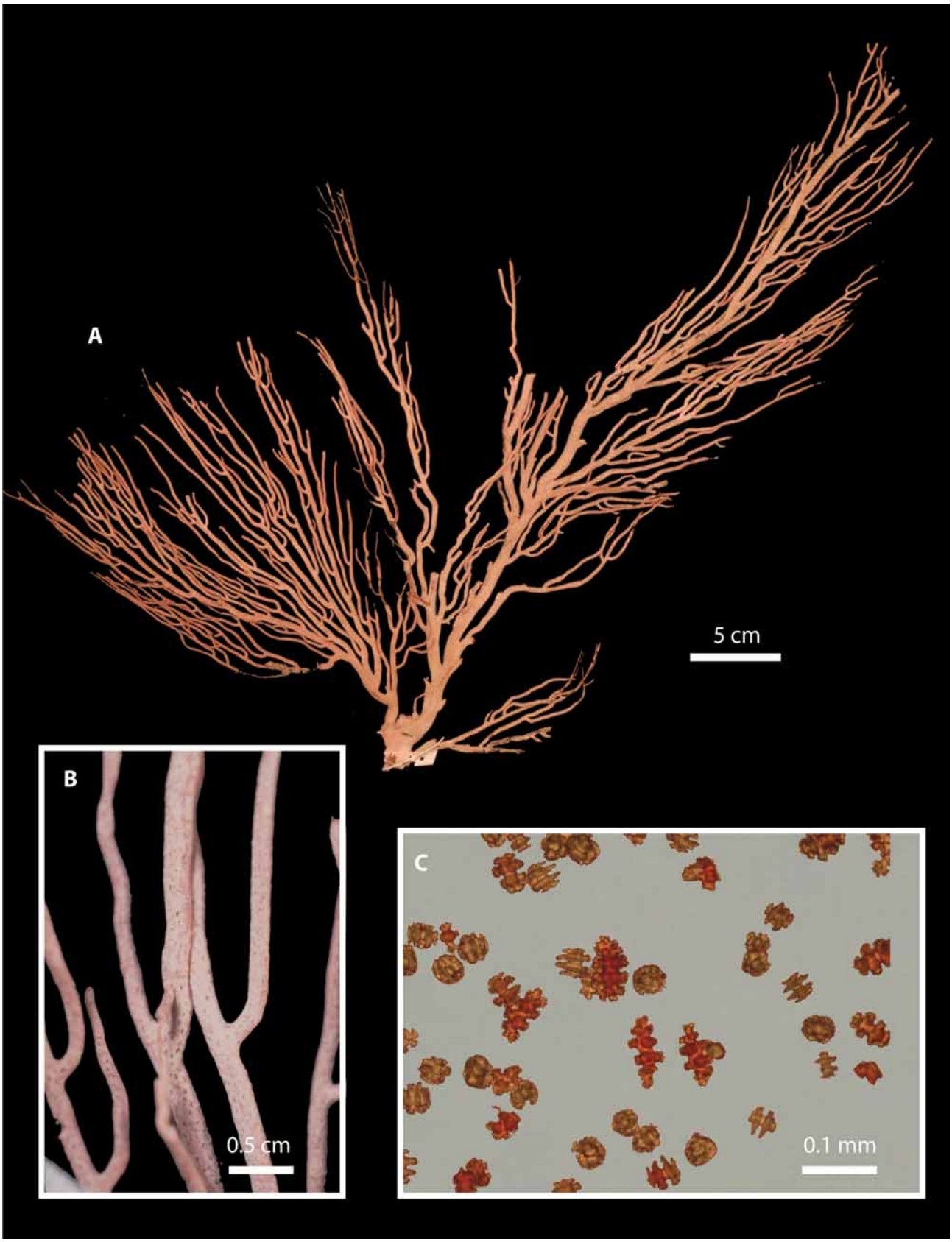

PLATE 9. *Eugorgia purpurascens* (YPM 1630): **A**, colony, photo E. Lazo-Wasem; **B**, detail of branches; **C**, light micrograph coenenchymal sclerites.

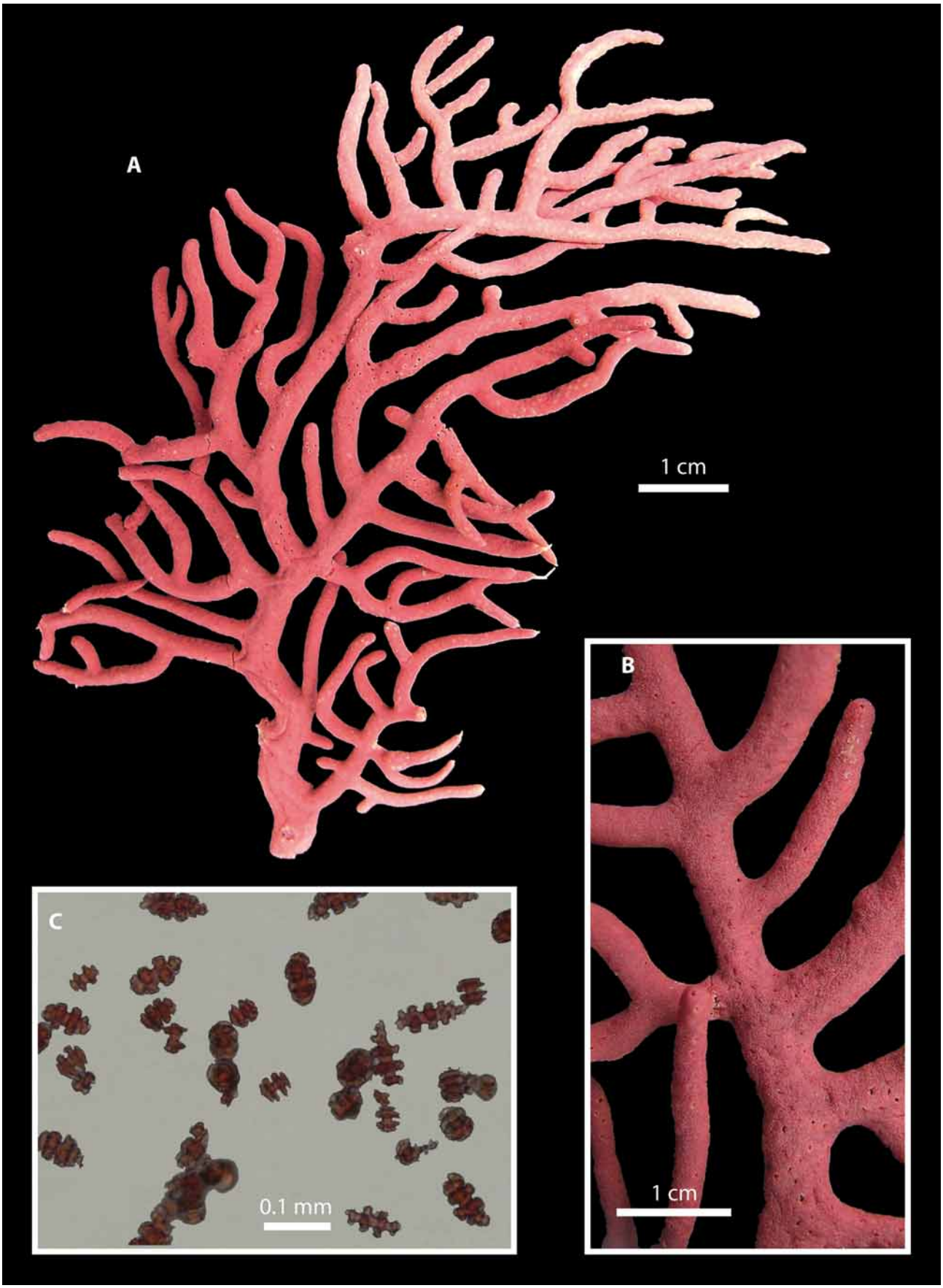

PLATE 10. *Eugorgia querciformis*, holotype: **A,** colony; **B**, detail of branches; **C**, light micrograph coenenchymal sclerites.

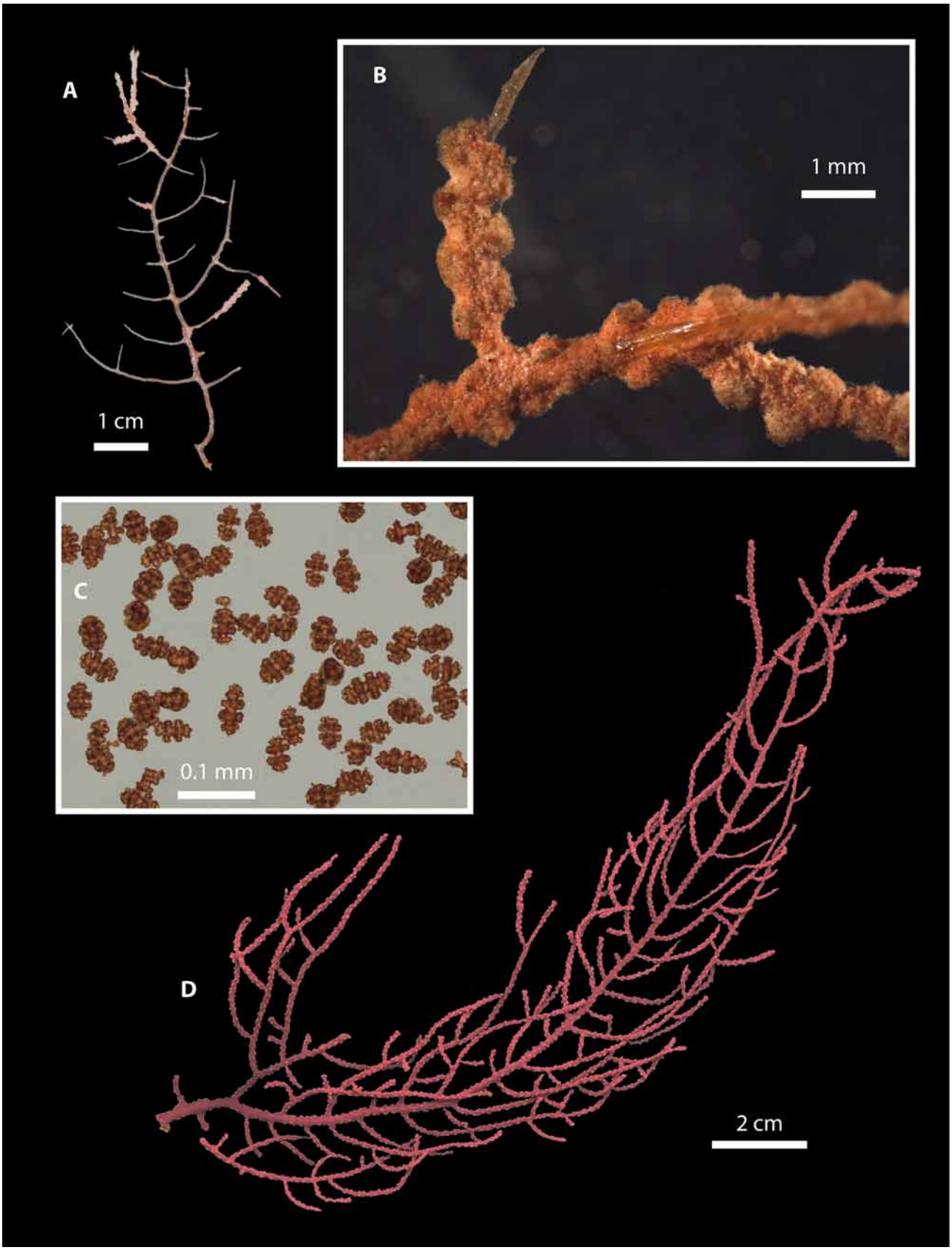

PLATE 11. *Eugorgia rubens,* holotype: **A,** colony; **B,** detail of branches, photos E. Lazo-Wasem; **C,** light micrograph coenenchymal sclerites; **D,** colony (CASIZ 96606), photo G. Williams.

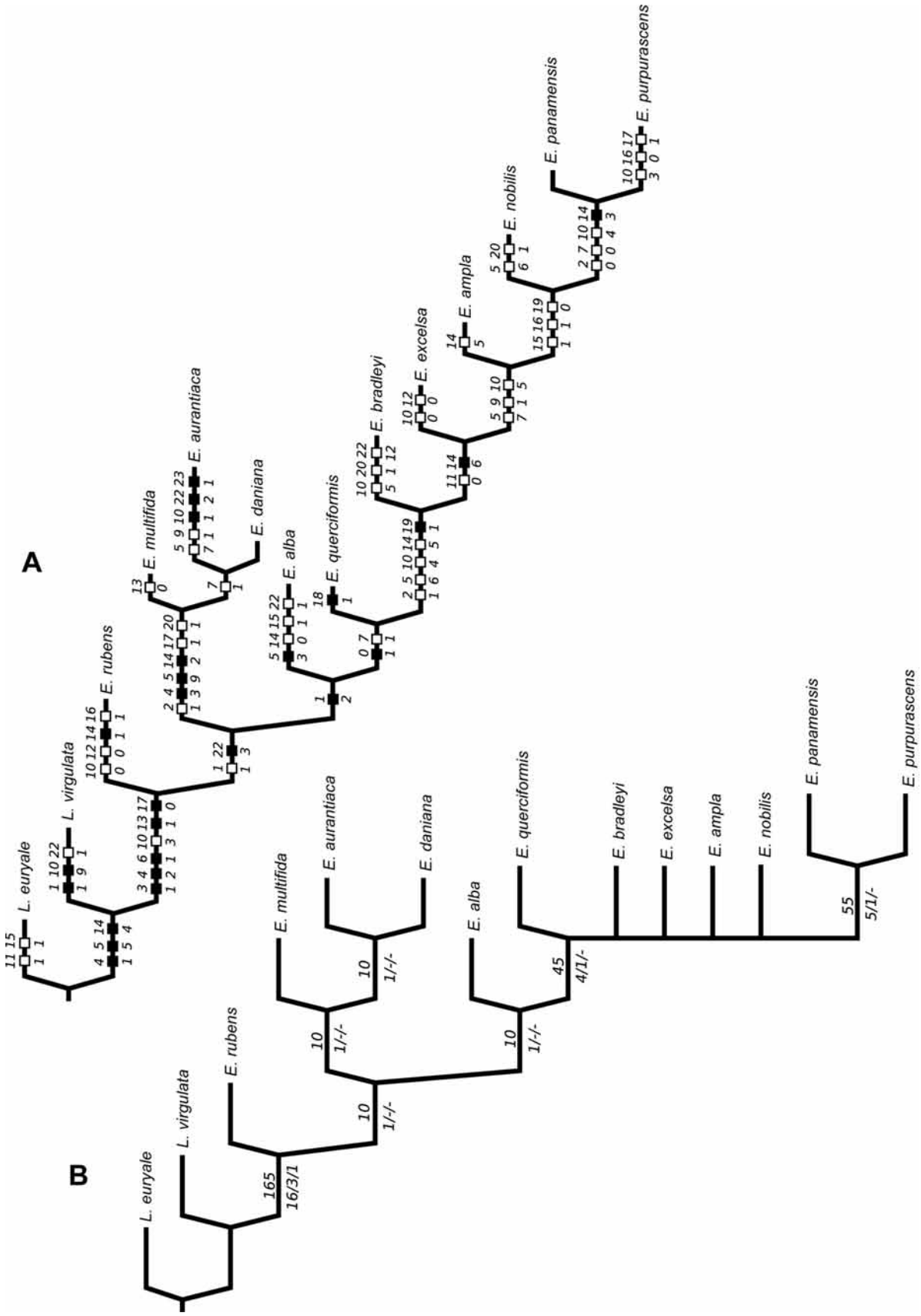

FIGURE 16. Phylogeny of the genus *Eugorgia* Verrill, 1868 from the eastern Pacific. A, most parsimonious phylogenetic tree showing character reconstruction, black squares represent the homologous characters; white squares represent the homoplasic characters. B, decay index (DI) values for each node in the tree, values placed above branches are absolute number of steps; values placed below branches are relative number of steps.

Phylogenetic Analysis

A single most parsimonious phylogenetic tree (L=2940; CI=0.56; RI=0.67) for the genus *Eugorgia* was found (Fig. 16A). The tree shows two major clades of *Eugorgia* species consisting of: 1. *Eugorgia* species showing pinnate-like branching, and 2. *Eugorgia* species showing irregularly dichotomous branching. The species in the first group, *E. aurantiaca*, *E. daniana* and *E. multifida*, hereafter collectively called the *daniana*-group, are similarly coloured, pinnately branching up to nine times, with prominent polyp mounds and share the presence of yellow and red sclerites in the coenenchyme. Species in the second group, *E. alba*, *E. ampla*, *E. bradleyi*, *E. excelsa*, *E. nobilis*, *E. panamensis*, *E. purpurascens* and *E. querciformis*, hereafter called the ampla-group, show irregular dichotomous branching patterns. They are more variable morphologically but share the absence of red coloured sclerites (with the exception of *E. purpurascens* in which some sclerites could be red), and the presence of slightly raised polyp mounds. The phylogenetic analysis clearly separates these two groups as different clades but expounds a third clade of only one species, *E. rubens*. *Eugorgia rubens* represents a close relative of the *daniana*-group because of the type of branching and the prominent polyp mounds, however the distinctive arrangement of the polyps in single lateral longitudinal rows, and the presence of only pink sclerites segregates *E. rubens* from the *daniana*-group and suggest another species group, the *rubens*-group.

Branch support was low for all branches of the phylogeny with the exception of the basal split between *Eugorgia* and *Leptogorgia;* nothing surprising for the Octocorallia where only a reduced number of characters are available for cladistic inference. Interestingly the phylogenetic hypothesis found for the genus supports the grouping of species with similar colony morphology and ecological habits. For instance, *E. rubens* has been so far reported from waters generally deeper than 40 meters. Moreover, low support values obtained for the species within the *ampla*-group (Fig. 16B) reflect some of the uncertainty faced when classifying species of this group. Members of the *ampla*-group generally show a mixture of characters that makes species delimitations difficult, and a rather confusing taxonomic history. It is likely that a more intensive exploration of the eastern Pacific waters will provide further reasons to join or to keep segregated *Eugorgia* species belonging to the *ampla*-group, and provide a complete overview of the diversity and distribution of this genus.

Geographic distribution is shown in Table 4, but the fauna herein reported does not represent the diversity or geographical range of the species because more surveys are needed and more material stored in museum needs attention to complete the regional assessment.

Acknowledgements

Our sincere gratitude to Phil Alderslade (Museum and Art Gallery of the Northern Territory), Stephen Cairns (USNM), Leen van Ofwegen (RMNH), Gary Williams (CAS), and Jorge Cortes (CIMAR) for their advice, critical review, and suggestions. We acknowledge the following people and institutions for their generosity in making available the specimens and information used in this study: BM: Andrew Cabrinovic and Sheila Halsey; CAS: Gary Williams and Bob Vansyoc; CDRS: Cleve Hickmann; Harvey Mudd College, California: Catherine McFadden; MZUF: Cecilia Volpi; MCZ: Ardis Johnston and Van Wallace; MNHN: Aude Andouche; Stanford University, Hopkins Marine Station, California: Geoffrey Shester; Universidad Autonoma de Mexico, Instituto de Ciencias del Mar y Limnologia: Jose Luis Carballo; Universidad de Guadalajara, Mexico: Ernesto López Uriarte; Universidad de Oaxaca, Mexico: Rosalinda Abeytia Sánchez; YPM: Eric Lazo-Wasem; ZMHC: Peter Stiewe. Our appreciation to: Alberto Alape (Centro de Investigación en Estructuras Microscópicas, CIEMIC); Eleazar Ruiz (CIMAR); Carlos Guevara and crew members from R/V Urraca (STRI); Rita Vargas and Cristian Trejos (UCR), and Percy Denyer (Escuela de Geologia, UCR) for their invaluable contribution to make this project possible. Thanks to the governments of Costa Rica and Panama for allowing visits and collections in their National Parks and reserves. This project was partially sponsored by the Smithsonian Institution's Marine Science Network, Smithsonian Tropical Research Institute,

the Vicerrectoría de Investigación, Universidad de Costa Rica, the USNM through its Short Term Visitors Program, and the MCZ Ernst Mayr Grant. Finally, we would like to express our appreciation to Ardis Johnston (MCZ) for her interest and collaboration since we began our research in the octocorals many years ago; we wish Ardis the very best in her retirement.

References

Bayer, F.M. (1951) A revision of the nomenclature of the Gorgoniidae (Coelenterata: Octocorallia) with an illustrated key to the genera. *Journal of the Washington Academy of Sciences*, 41, 91–102.

Bayer, F.M. (1952) New western Atlantic records of octocorals (Coelenterata: Anthozoa), with descriptions of three new species. *Journal of the Washington Academy of Science*, 42, 183–189.

Bayer, F.M. (1956) Octocorallia. *In*: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology, part F, Coelenterata*. University of Kansas Press, Lawrence, Kansas, pp. 167–231.

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) Key to the genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa), with diagnoses of new taxa. *Proceedings of the Biological Society of Washington*, 94, 902–947.

Bayer, F.M., Grasshoff, M. & Verseveldt, J. (1983) *Illustrated trilingual glossary of morphological terms applied to Octocorallia*. E.J. Brill, Leiden, 74 pp.

Bielschowsky, E. (1918) *Eine Revision der Familie Gorgoniidae*. Inaugural-Dissertation zur Erlangung der Doktorwürde der Hohen Philisophischen Facultät der Schlesischen Friedrich-Wilhelms-Universität zu Breslau. Buchdruckerei H. Fleischmann, Breslau, 66 pp.

Bielschowsky, E. (1929) Die Gorgonarien Westindien. 6. Die Familie Gorgoniidae, zugleich eine Revision. *Zoologische Jahrbücher*, Supplement 16, 63–234.

Breedy, O. & Guzman, H.M. (2002) A Revision of the genus *Pacifigorgia* (Coelenterata: Octocorallia: Gorgoniidae). *Proceedings of the Biological Society of Washington*, 115, 787–844.

Breedy, O & Guzman, H.M. (2007) A revision of the genus *Leptogorgia* Milne Edwards & Haime, 1857 (Coelenterata: Octocorallia: Gorgoniidae) in the eastern Pacific. *Zootaxa*, 1419, 1–90.

Breedy, O. & Guzman, H.M. (2008) *Leptogorgia ignita*, a new shallow-water coral species (Octocorallia: Gorgoniidae) from the tropical eastern Pacific. *Journal of the Marine Biological Association, U.K.* 88, 893–899.

Bremmer, K. (1988) The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution*, 42, 795–803.

Bremmer, K. (1994) Branch support and tree stability. *Cladistics*, 10, 295–304.

Duchassaing, P. & Michelotti, J. (1864) Supplément au mémoire sur les coralliaires des Antilles. *Extrait des mémoires de l'Académie des Sciences de Turin*, Series 2, 23, 1–112.

Goloboff, P. (1999) *NONA (NO NAME) Ver. 2 [Computer software]*. Tucuman, Argentina: Published by the author.

Grasshoff, M. (1988) The genus *Leptogorgia* (Octocorallia: Gorgoniidae) in West Africa. *Atlantide Report*, 14, 91–147.

Grasshoff, M. (1992) Die Flachwasser-Gorgonarien von Europa und Westafrika (Cnidaria, Anthozoa). *Courier Forschungsinstitut Senckenberg* 149, 1–135.

Guzman, H.M. & Breedy, O. (2008) *Leptogorgia christiae* (Octocorallia: Gorgoniidae) a new shallow water gorgonian from Pacific Panama. *Journal of Marine Biology Association, U.K.*, 88, 719–722.

Harden, D.G. (1979) *Intuitive and Numerical classification of east Pacific Gorgonacea (Octocorallia)*. Ph.D. Thesis, Illinois State University, USA, 214 pp.

Hickson, S. J. (1904) The Alcyonaria of the Cape of Good Hope. Part II. *Marine Investigations in South Africa*, 3, 211–239.

Horn, G.H. (1860) Descriptions of three new species of Gorgonidae, in the collection of the Academy. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 12, 233.

Kükenthal, W. (1919) Gorgonaria. *Wissensschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia"*, 1898–1899, 13(2), 1–946.

Kükenthal, W. (1924) Gorgonaria. *Das Tierreich, 47*. Walter de Gruyter and Co., Berlin und Leipzig, 478 pp.

Lamarck, J.B.P (1815) Sur les polypiers corticifères. *Mémoires du Muséum d'Histoire Naturelle, Paris*, 1, 401–416, 467–476.

Lamouroux, J.V.F. (1812) Extrait d'un mémoire sur la classification des Polypiers coralligènes non entièrement pierreux. *Nouveau Bulletin des Sciences, par la Société Philomatique, Paris*, 63, 181–188.

Milne Edwards, H. & Haime, J. (1857) *Histoire naturelle des coralliaires ou polypes proprement dits*, Vol. 1 pp. I–xxxiv + 1–326, 8 plates, numbered A1-6, B1-2. Paris, à la Libraire Encyclopédique de Roret.

Nixon, K.C. & Carpenter, J.M. (1993) On outgroups. *Cladistics*, 9, 413–426.
Prahl, H. von, Escobar, D. & Molina, G. (1986) Octocorales (Octocorallia: Gorgoniidae y Plexauridae) de aguas someras del Pacífico Colombiano. *Revista de Biología Tropical*, 34, 13–33.
Sinsel-Duarte, F. (1991) *Taxonomía, distribución, abundancia y diversidad de los gorgónidos (Octocorallia: Gorgonacea) del arrecife de Cabo Pulmo, Baja California Sur, México.* B.Sc. Thesis, Departamento de Biología Marina, Universidad Autónoma de Baja California Sur, La Paz, 95 pp.
Stiasny, G. (1951) Alcyonides et Gorgonides des collections du Muséum National d'Histoire naturelle. (II). *Mémoires du Muséum d'Histoire Naturelle (Nouvelle Série), Zoologie* A, 3, 1–80.
Studer, T. (1883) Mittheilungen aus dem Museum für Naturgeschichte. 1. Kalifornische Korallen. *Mittheilungen der Naturforschenden Gesellschaft in Bern*, 1 Heft, Abhandlungen, 3–8.
Studer, T. (1887) Versuch eines Systemes der Alcyonaria. *Archiv Naturgeschichte*, 53, 1–74.
Studer, T. (1894) Note préliminaire sur les alcyonaires. Reports on the dredging operations carried on by the U.S. Fish Commission steamer "Albatros", during 1891. *Bulletin of the Museum of Comparative Zoology, Harvard*, 25, 53–69.
Thiele, K. (1993) The holy grail of the perfect character: The cladistic treatment of morphometric data. *Cladistics*, 9, 275–304
Thomson, J. S. (1917) South African Gorgonacea. *Memoirs and Proceedings of Literary and Philosophical Society of Manchester*, 61, 1–56.
Vargas, S. (2008) *Sistemática y Biogeografía histórica del género Pacifigorgia Bayer, 1951 (Octocorallia: Gorgoniidae*). M.Sc. Thesis, Universidad de Costa Rica, Costa Rica, 125 pp.
Verrill, A.E. (1864) List of the polyps and corals sent by the Museum of Comparative Zoology to other institutions in exchange, with annotations. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 1, 29–60.
Verrill, A.E. (1866) On the polyps and corals from Panamá with descriptions of new species. *Proceedings of the Boston Society of Natural History*, 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. *Transactions of the Connecticut Academy of Arts and Sciences*, (Second Edition), 1, 377–422.
Verrill, A.E. (1868a) Critical remarks on the halcyonoid polyps in the Museum of Yale College, with descriptions of new genera. *The American Journal of Science and Arts*, 45, 411–415.
Verrill, A.E. (1869) Critical remarks on the halcyonoid polyps with description of new species in the Museum of Yale College. *The American Journal of Science and Arts, Series 2*, 48, 419–429.
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. *Transactions of the Connecticut Academy of Arts and Sciences*, (Second Edition), 1, 519–558.
Wiley, E.O., Siegel-Causey, D.R., Brooks, D.R. & Funk, V.A. (1991) The compleat cladist: A primer of phylogenetic procedures. *The University of Kansas Museum of Natural History Special Publication* No. 19, 158 pp.
Volpi, C.& Benvenuti, D. (2003) The Duchassaing & Michelotti collection of Caribbean corals: status of types and location of the specimens. *Atti Società italiana Scienze naturali Museo civico di Storia naturale di Milano*, 144, 51–74.
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. *Proceedings of the California Academy of Sciences*, 49, 499–521.