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Revision of the genus *Adelogorgia* Bayer, 1958 (Cnidaria: Anthozoa: Octocorallia) with the description of three new species

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Abstract

The genus *Adelogorgia* is distinguished from other holaxonians in having conspicuously ornamented double-disc sclerites and leaf clubs in the coenenchyme, and non-mineralised axis cores. The two eastern Pacific species currently recognised as *Adelogorgia* are diagnosed and illustrated. Three new species for the genus are described from new localities and depth ranges. Analysis of external and internal characters, especially sclerite colours and sizes, and colony colour, shape and branching, allows separating the species. An identification key to the five species is provided, as well as a character table for comparisons. This study was based on newly collected specimens from 50 to 200 m deep, and re-examination of all historical material. We conclude that the genus comprises five valid species with a wider distribution than previously reported. This research is a contribution to the octocoral systematics and biodiversity from mesophotic and deep waters.

Key words: *Adelogorgia*, Alcyonacea, biodiversity, eastern Pacific, plexaurid, soft corals, taxonomy

Introduction

The genus *Adelogorgia* was established for a plexaurid found near La Jolla, California, *Adelogorgia phyllosclera* Bayer, 1958, collected by dredging and trawling from 30 to 73 m depth. Later another species was included, *Adelogorgia telones* Bayer, 1978, found in the Galápagos Islands from 23 m in depth. The latter was collected by SCUBA diving in 1973. According to Bayer (1978) the genus does not occur in collections from Baja California, the Gulf of California and along the coast of Central America and South America. However, Harden (1979) mentioned the genus in Baja California, and there is an erroneous report of the genus (C. Castro, (http://sealifebase.org)) for the northwestern Atlantic. Apart from these records the genus has not been reported for any other locality and was considered rare, until now.

We found three new species of *Adelogorgia* during recent expeditions to evaluate the biodiversity from mesophotic and deep habitats in Costa Rica and Panamá. These habitats have been historically impacted especially by destructive fishing practices with an associated lost in biodiversity (Roberts 2002; Watling *et al*. 2011; Pham *et al*. 2014). The discovery of new species when exploring new habitats makes evident the scant knowledge of this fauna in the region and hence their potential functional role in the ecosystems. Octocorals are long-lived and resistant animals (Sanchez 2016), consequently, species richness estimation is an important parameter to evaluate and model the potential natural and human induced impacts affecting these communities in the future.

This research follows other contributions (Breedy & Guzman 2013, 2016; Breedy *et al.* 2013) to the octocoral systematics and biodiversity that provide insights into the structure and composition of the mesophotic and deep-water habitats in the eastern Pacific region.

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Materials and methods

The type material of *Adelogorgia* was obtained by loans from NMNH and by visits to the NMNH collection. The new species were collected from entangled fishing lines, from bottom trawling surveys by the R/V *Urracá*, July 2005 and from box core by the R/V *Victor Hensen*, July 1993, along the Pacific coast of Costa Rica. Samples from Panamá were obtained during two expeditions to Hannibal Bank by the M/V *SeaHunter* using the submersible *DeepSee*; and M/V *Alucia* using the submersibles *Nadir* and R2D2.

Morphological Study. Specimens were fixed in 70 or 95% ethanol or air dried. For the microscopic study, specimens were prepared according to the protocol described by Breedy and Guzman (2002), and observed using optic microscopy, Olympus LX 51 inverted microscope, and scanning electron microscopy, Hitachi 3700, at the Research Center of Microscopic Structures (CIEMIC) of the University of Costa Rica (UCR), and a Zeiss EVO 40 at the Electron Microscopy Laboratory (Tupper Research and Conference Centre).

The taxonomic approach was by the evaluation of relevant characters for the genus following Bayer (1958, 1978). Morphological characters of colonies and sclerites were assessed and presented in synoptic character tables for comparison among species in the genus. Measurements of branches are given taking into account the length of the polyp mounds whether preserved in ethanol or dry. Polyp mounds are considered flat, slightly raised and prominent for the genus (*sensu* Bayer 1958, 1978), not in comparison to other genera. When the polyp-mound is described as flat, it means that after retraction, the polyp hides within the coenenchyme leaving an inconspicuous protuberance or, none at all. Although some change happens after fixation, this characteristic is still preserved in all specimens. Length of clubs was taken from one tip to the other, and width was taken from the most distant points of the head. Width of double discs was taken from the most distant points of the discs. The holotype and paratypes from Costa Rica are deposited in the Zoology Museum, UCR (MZUCR), and the holotype and paratypes from Panamá are deposited in the Smithsonian Tropical Research Institute (STRI). Terminology used in descriptions mostly follows Bayer (1958; 1978); and Bayer et al. (1983).

Molecular procedures. DNA was purified from tissue of ethanol preserved samples using the NucleoSpin Tissue kit (Macherey-Nagel Duren, Germany), following manufacturer's protocols. The mitochondrial mismatch repair gene (i.e., mtMutS), was amplified using the primers ND42599F (5'-GCCATTATGGTTAACTATTAC-3') and Mut-3458R (5'-TSGAGCAAAAGCCACTCC-3') McFadden et al. 2011. PCR reactions were set up for 50 µL reactions using 50 ng DNA, 1X Dream Taq Buffer (Thermo Scientific, MA), 0.2 mM dNTPs, 0.3 µM of each primer, 2.5 units Taq DNA polymerase (Thermo Scientific), 0.05 mg BSA and sterile water to complete a total of 50 µl per reaction. The PCR reactions were done on a Applied Biosystems 2720 thermocycler under the following conditions: 2 min at 94 °C; 35 cycles of 0:30 min at 94 °C, 1:30 min at 45 °C, and 0.5 min at 72 °C; and then a final extension of 5 min at 72 °C. PCR products were purified and sequenced at the Macrogen facility, Korea, using the same primers used for PCR. Sequences were edited and assembled using DNA Baser (Heracle BioSoft) and taxonomic affiliation was determined using NCBI's BLAST (Johnson et al. 2008).

All sequences were deposited in the National Center for Biotechnology Information under accessions MF579538–MF579542 (mtMutS).

Molecular results. The sequences obtained grouped together in BLAST, in *Adelogorgia phyllosclera* (unpublished), *Swiftia pacifica*, and *Swiftia simplex* in the family Plexauridae. Phylogenetic analyses could be possible when more sequences of identified samples of sister groups were available.

Museum abbreviations

MZUCR, Museo de Zoología, Universidad de Costa Rica, Costa Rica, known also as UCR.
NMNH, National Museum of Natural History, Smithsonian, Washington DC, USA (specimens prefaced with USNM)
STRI, Smithsonian Tropical Research Institute, Panamá.
USNM, United States National Museum, Smithsonian Institution, Washington DC, USA.

Results

Class Anthozoa Ehrenberg, 1834

Subclass Octocorallia Haeckel, 1866

Order Alcyonacea Lamouroux, 1816

Family Plexauridae Gray, 1859

Genus *Adelogorgia* Bayer, 1958

Adelogorgia Bayer, 1958: 46; Bayer 1978: 1026–1027; Harden 1979: 137.

Type species. *Adelogorgia phyllosclera* Bayer, 1958 by original designation **Type locality.** La Jolla, California.

Diagnosis (modified from Bayer, 1958; 1978). Colonies bushy, fan-shaped or sparsely branched. Branching lateral, irregular, or dichotomous; with moderately thick coenenchyme; polyps fully retractile, communicating directly with the longitudinal canal system (gastrodermal canals, solenia); anthocodia with eight subtentacular points consisting of spinous rods, not forming a distinct collaret. Polyp mounds prominent, slightly raised or flat, without specific types of sclerites, but leaf clubs concentrated around polyp apertures. Outer coenenchyme with conspicuous double discs with expansions on one side having various degrees of ornamentation; tuberculate spindles and leaf clubs. Axial sheath containing less developed spindles, radiates and capstans. Axis with wide cross-chambered central core. Loculi between lamellae and central core without mineralised filaments.

Colony colours white, lemon-yellow, pink, orange and various hues of red. Sclerites of the same colours and colourless.

Distribution. The species has been reported from La Jolla, California, USA; Galápagos Islands, Ecuador (Bayer 1958, 1978); Baja California, Mexico (Harden 1979); and recently found along Pacific coast of Costa Rica and off Pacific coast of Panamá. Reported from 30 to 300 m deep (Cairns *et al.* 2002).

Remarks. The genus was originally placed in Plexauridae by Bayer (1958). Later, he transferred it to Gorgoniidae (Bayer 1985, in key) without explanation. Plexauridae is a morphologically and taxonomically diverse family with approximately 39 genera (Williams & López-González 2005). The main differences between the holaxonian families, Plexauridae and Gorgoniidae are related to the composition of the axes and the sclerites. In Gorgoniidae the core of the axis is filled with organic fibres mineralised with carbonate hydroxylapatite; in Plexauridae the organic fibres are either mineralised or not, depending on the genus (Bayer, 2001). The coenenchymal sclerites in Gorgoniidae are mostly spindles with warty tubercles in whorls, capstans and radiates that are mostly symmetric and no longer than 0.3 mm. The anthocodial sclerites are basically flat rods with serrated, lobed or smooth borders. In Plexauridae the coenenchymal and anthocodial sclerites are of many kinds, unilateral spinose spindles, irregular spindles, branched spindles, torches, clubs, and variations of them; and can reach up to 0.5 mm long. The anthocodial sclerites are warty rods, spines, and arranged in a well-developed collaret and points, or in weaker structures. Thus, from the morphological point of view, for the time being, the genus *Adelogorgia* is included in Plexauridae.

Key to the species of the genus *Adelogorgia* Bayer, 1958

1. Colony colour white or lemon-yellow; coenenchymal sclerites colourless or yellow; polyp mounds almost flat; anthocodial rods up to 0.3 mm long . . . . . *A. telones*
1´. Colony colour in red tones (pink, orange, red); coenenchymal sclerites red, orange, pink, whitish or colourless; polyp-mounds flat, slightly raised or prominent; anthocodial rods less than 0.3 mm long 2
2. Colony orange, sparsely branched, flexible; branching scarce, dichotomous; end branches up to 7 cm long; polyp-mounds prominent . . . . . *A. hannibalis*
2´. Colony red brighter or darker, flabellate or bushy; branching abundant, lateral, dichotomous or irregular; end branches up to 4 cm; polyp mounds almost flat, or slightly raised 3
3. Polyp-mounds prominent, with a distinct coral red colour, contrasting with the colony colour . . . . . *A. osculabunda*
3´. Polyp-mounds almost flat or slightly raised, without a distinct colour, blending with the colony colour 4

4. Colony red, flabellate, in one plane; polyp mounds almost flat; sclerites red and colourless; anthocodial sclerites up to 0.17 mm long . . . . . *A. phyllosclera*

4′. Colonies dark red, bushy, in several planes; polyp mounds slightly raised; sclerites red, dark orange and colourless; anthocodial sclerites up to 0.23 mm long . . . . . *A. adusta*

Adelogorgia phyllosclera **Bayer, 1958**

Figs. 1–2, 3A-B

Adelogorgia phyllosclera Bayer, 1958: 46–48; Harden 1979: 137–138.

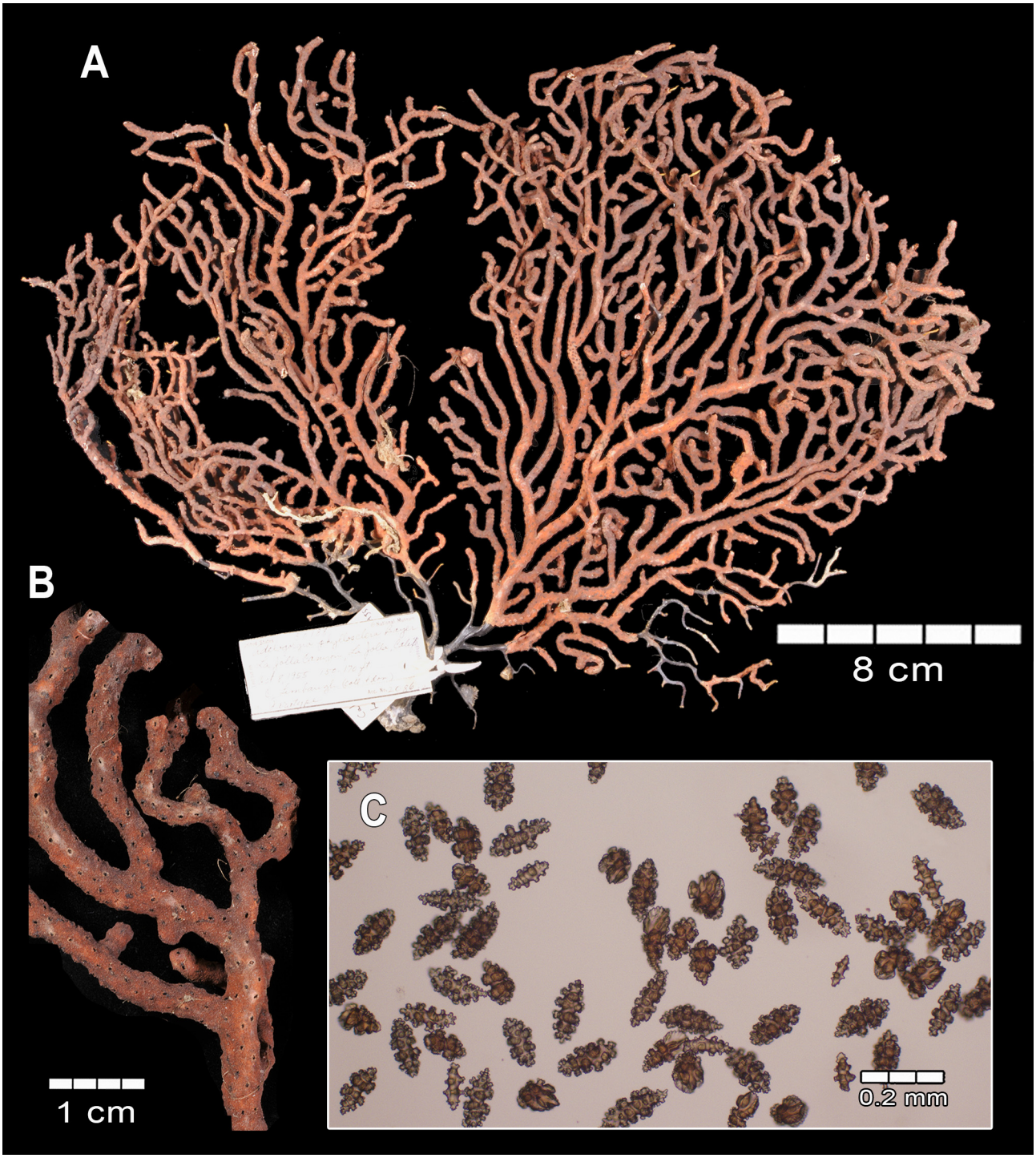

FIGURE 1. *Adelogorgia phyllosclera*, USNM 50188 (paratype) (A) colony; (B) detail of the branches; (C) sclerites. A and B photographs by Robert Ford.

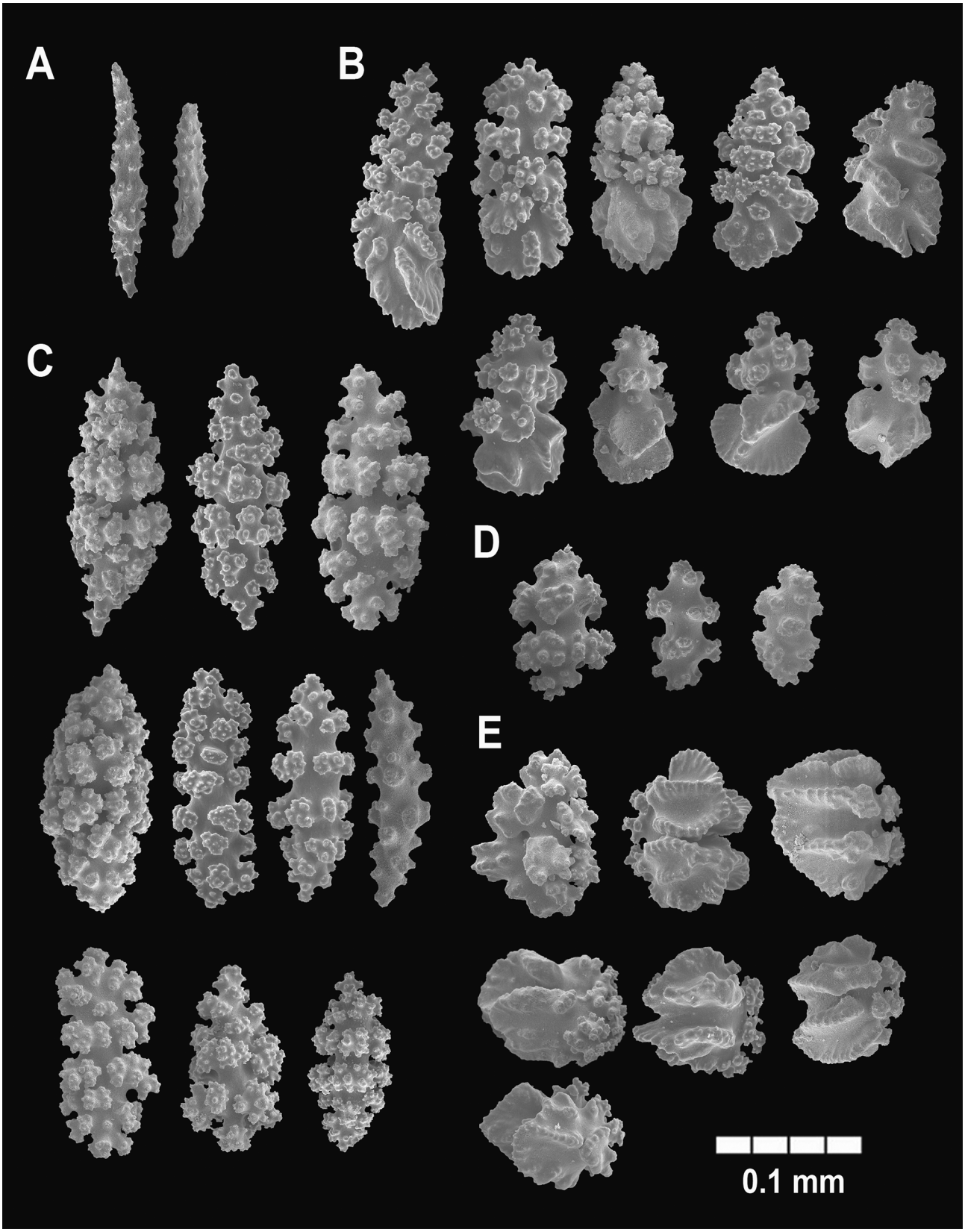

FIGURE 2. *Adelogorgia phyllosclera*, USNM 50188 (paratype) SEM micrographs. (A) anthocodial rods; (B) leaf clubs; (C) spindles; (D) radiates from inner coenenchyme; (E) double-discs.

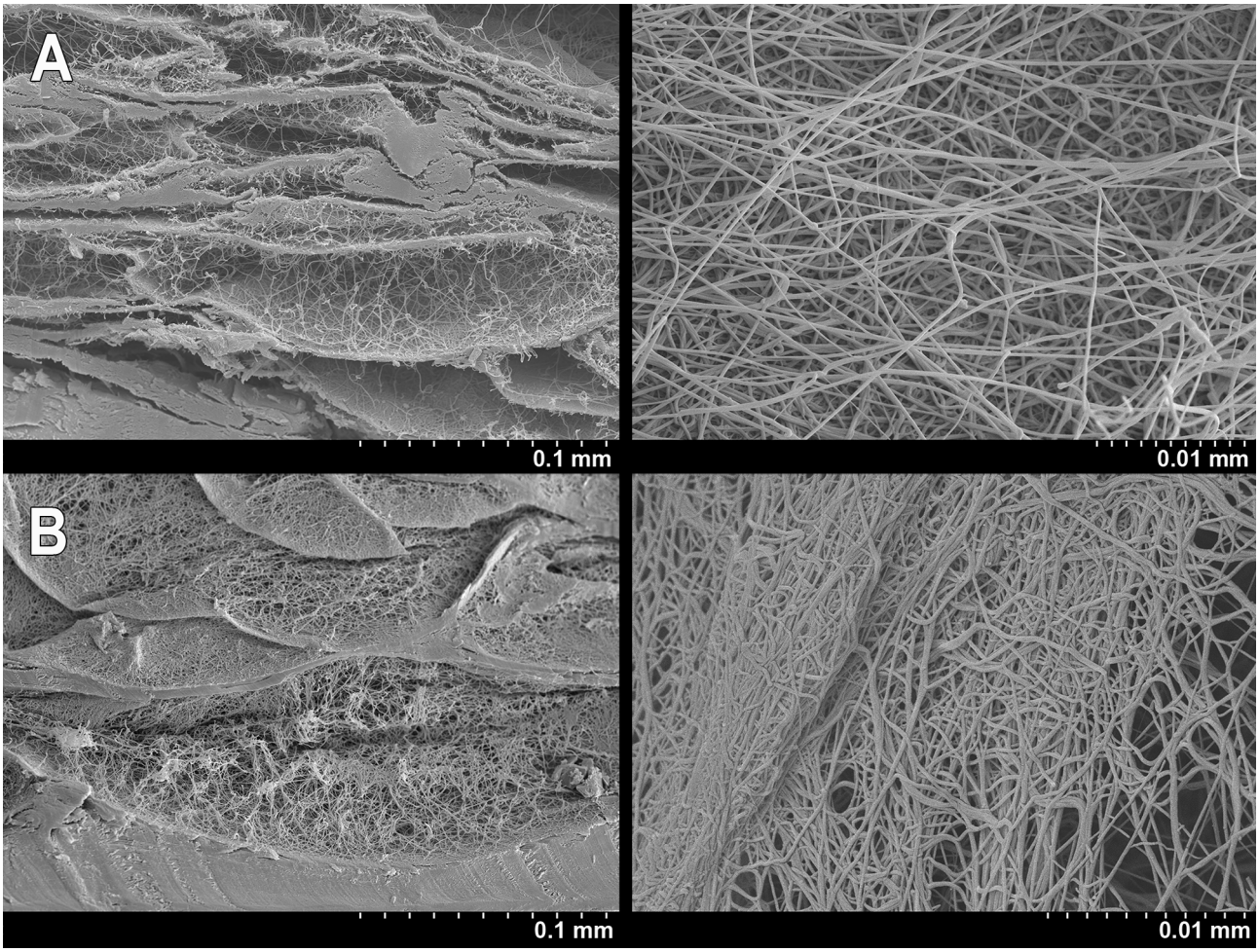

FIGURE 3. Structure of non-mineralised axes: Longitudinal section of axial core showing chambers with fibres (left); detail of fibres (right). (A) *Adelogorgia phyllosclera*; (B) *Adelogorgia telones*.

Material examined.

Holotype: USNM 50186, dry preserved, La Jolla Canyon, California, 30–33m, L. Limbaugh, 19 March 1954.

Paratypes: USNM 50187, 2 specimens, dry preserved, La Jolla Canyon, 20–23m, L. Limbaugh, 8 October 1955. USNM 50188, 6 specimens, dry preserved, La Jolla Canyon, 50–57m, L. Limbaugh, 8 October 1955.

Diagnosis. Colony flabelliform, branching lateral, dichotomous and irregular, mostly in one plane, without anastomoses. Branches 2–4.5 mm in diameter, sinuous, with clavate tips; terminal branches 3-4 cm long; main stem up to 6 mm diameter (Figs. 1A-B). Axes of gorgonin layers, loculi between lamellae and central core with complex meshes of not mineralised filaments (Fig. 3A). Axes dark brown, lighter at branchlets. Polyps distributed all around branches, 2-2.5 mm apart. Anthocodia with 2–4 slightly curved spinous rods 0.1–0.17 mm long and 0.02–0.045 mm wide, at each side of points (Fig. 2A), without collaret. Polyp mounds almost flat, blending with adjacent coenenchyme or forming low rims around polyps, without a special type of sclerites but mostly containing leaf clubs and spindles. Coenenchyme contain double discs with serrate edges or foliate crests, 0.089–0.12 mm long and 0.075–0.09 mm wide (Fig. 2E), tuberculate spindles, 0.13–0.2 mm long and 0.05–0.095 mm wide (Fig. 2C), and leaf clubs 0.1–0.19 mm long and 0.06–0.085 mm wide (Fig. 2B). Axial sheath containing less developed spindles, radiates and capstans 0.08–0.1 mm long and 0.05–0.07 mm wide (Fig. 2D).

Colony colour red (Figs. 2A-B) and sclerites red and colourless (Fig. 2C).

Distribution. La Jolla, California (type locality), 20-57 m. Harden (1979) reports samples for outer coast of Baja California, Mexico from 91.4 m.

Variability. The species has some variation in branch diameter; some paratypes have branches a few millimeters thinner, 2–3.5 mm in diameter. The red colour of the colonies varies from darker to lighter hues.

Remarks. Bayer (1958) pointed out the similarity in external appearance of this species and *Psammogorgia arbuscula* Verrill, 1868, but the different sclerite composition and types justified the new taxon. Colonies of *Adelogorgia* are similar those of *Psammogorgia*, not only in external morphology but also in habitat preference. Both genera occur in shallow waters, and are also found in mesophotic and deep habitats on similar substrates (pers. obs.). In any case, as in many other gorgonians, the sclerites are the key elements to separate genera. The species of *Adelogorgia* share the presence of double-disc sclerites conforming to the outer coenenchyme, in contrast to *Psammogorgia*, which lacks double-discs. The composition of outer coenenchyme sclerites varies in *Adelogorgia* species. In this sense, *A. phyllosclera* and the new species *A. osculabunda* (see description below), contain a similar amount of wide warty spindles and double-discs. For this reason, in unsorted samples of sclerites of these species, the occurrence of double-discs is not as abundant as in the other three species (*A. telones*, *A. hannibalis* sp. nov. and *A. adusta* sp. nov.). In *A. osculabunda* the double-discs are less ornamented than in *A. phyllosclera*. The differences between this species and the others are shown in Tables 1 and 2.

TABLE 1. Comparative gross morphological features of the species of *Adelogorgia* Bayer, 1956.

Species	Colony shape	Colour of colony	Branching type	Branches thickness (mm)	End branches length (cm)	Distinct polyp mounds colour	Polyp mounds
A. phyllosclera	fla	red	lat, dic, irr	2-4.5	3-4	no	flat
A. telones	fla	yellow, white	lat	2.5-3.5	0.4-4	no	flat
A. osculabunda	fla	reddish pink	dic, irr	3-5	0.3-3.5	coral red	prominent
A. hannibalis	spa	orange	dic	1.5-2	3-7	little darker tone	prominent
A. adusta	bu	bright red	lat	3-4	1.5–3.5	no	slightly raised

Colony shape: bu, bushy; fla, flabellate, fan shape; spa, sparse, flexible, with few branches
Branching type: dic, dichotomous-like; irr, irregular, not a specific type of branching; lat, lateral

TABLE 2. Comparative sclerites features of species of *Adelogorgia* Bayer, 1956.

Species	Colour of sclerites	Colour of anthocodials	Points structure	Length of spindles	Length of leaf clubs	Length and width of double-discs	Length and width of radiates	Length of anthocodial sclerites
A. phyllosclera	red, colourless	red, colourless	4–8	0.13–0.20	0.1–0.19	0.09–0.12x0.075–0.09	0.08–0.1x0.05–0.07	0.1–0.17
A. telones	white/lemon yellow	whitish, colourless/ yellow	15–20	0.11–0.16	0.13–0.17	0.06–0.1x0.06–0.08	0.06–0.09x0.05–0.07	0.16–0.31
A. osculabunda	pink, clolourless	whitish, colourless, pale pink	8–10	0.15–0.21	0.13–0.24	0.10–0.13x0.07–0.09	0.075–0.11x0.06–0.085	0.17–0.26
A. hannibalis	orange, yellowish	orange, colourless	6–8	0.11–0.17	0.11–0.2	0.05–0.09x0.02–0.05	0.06–0.09x0.08–0.11	0.14–0.2
A. adusta	red, dark orange, colourless	red, colourless	6–8	0.15–0.20	0.11–0.18	0.06–0.09x0.07–0.01	0.08–0.12 x 0.06–0.098	0.10–0.23

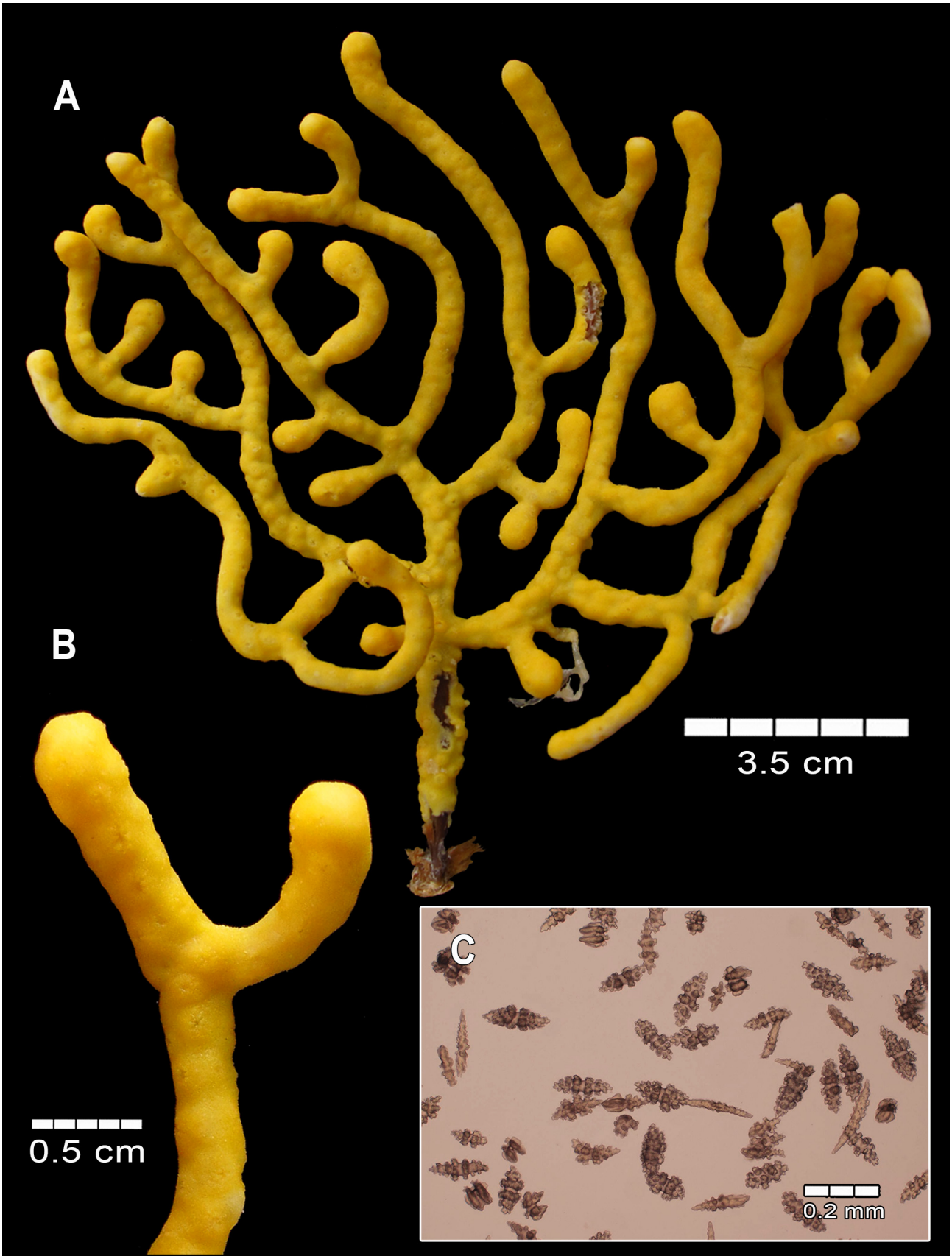

FIGURE 4. *Adelogorgia telones*, USNM 57455 (lemon-yellow paratype) (A) colony; (B) detail of the branches; (C) sclerites.

***Adelogorgia telones* Bayer, 1978**
Figs. 4-6, 3B

Adelogorgia telones Bayer, 1978: 1027–1033; Breedy *et al.* 2009: 28.

Material examined.

Holotype: USNM 57453, ethanol preserved, Kicker Rock, Galápagos Islands, Ecuador, 23m deep, D. Hope, 19 February 1978.

Paratypes: USNM 57454, 57455 data as the holotype.

Diagnosis. Colonies flabellate, branching mostly lateral, without anastomoses. Branches of nearly uniform thickness 2.5–3.5 mm in diameter with clavate tips about 1 mm greater, up to 4.6 mm in diameter. End branches 0.4–4 cm long (Fig. 4A-B, 6A-B). Axes of gorgonin layers, loculi between lamellae and central core with complex meshes of not mineralised filaments (Fig. 3B). Polyps distributed all around the branches, 1.5-2.2 mm apart (Fig. 4B, 6B). Anthocodia with approximately 15–20 slightly curved spinous rods in points, 0.16–0.31 mm long and small curved rods from oral disk (Fig. 5A-B). Polyp mounds flat, blending with the adjacent coenenchyme (Fig. 4B, 6B), without a special type of sclerites but mostly containing leaf clubs and spindles. Coenenchyme with double discs with serrate edges or foliate crests, 0.06–0.1 mm long and 0.06–0.08 mm wide (Fig. 5G); tuberculate spindles, 0.11–0.16 mm long and 0.06–0.085 mm wide (Fig. 5D-E), and leaf clubs 0.13–0.17 mm long and 0.032–0.06 mm wide (Fig. 5C). Axial sheath containing less developed spindles, radiates and capstans 0.06–0.09 mm long and 0.05–0.07 mm wide (Fig. 5F).

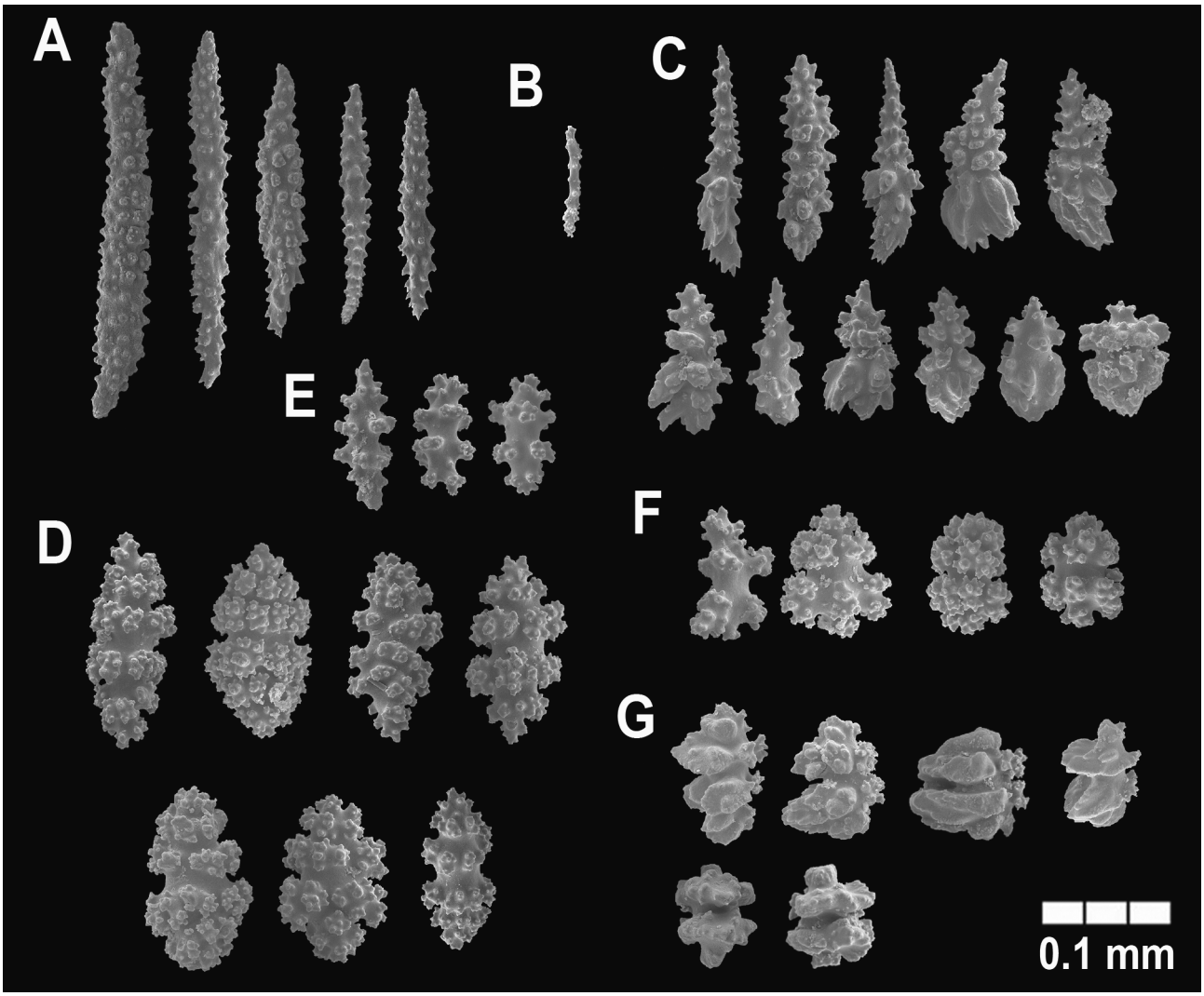

FIGURE 5. *Adelogorgia telones*, USNM 57455 (lemon-yellow paratype) SEM micrographs. (A) anthocodial rods; (B) oral disc rod; (C) leaf clubs; (D) spindles; (E) immature spindles from inner coenenchyme; (F) radiates; (G) double-discs.

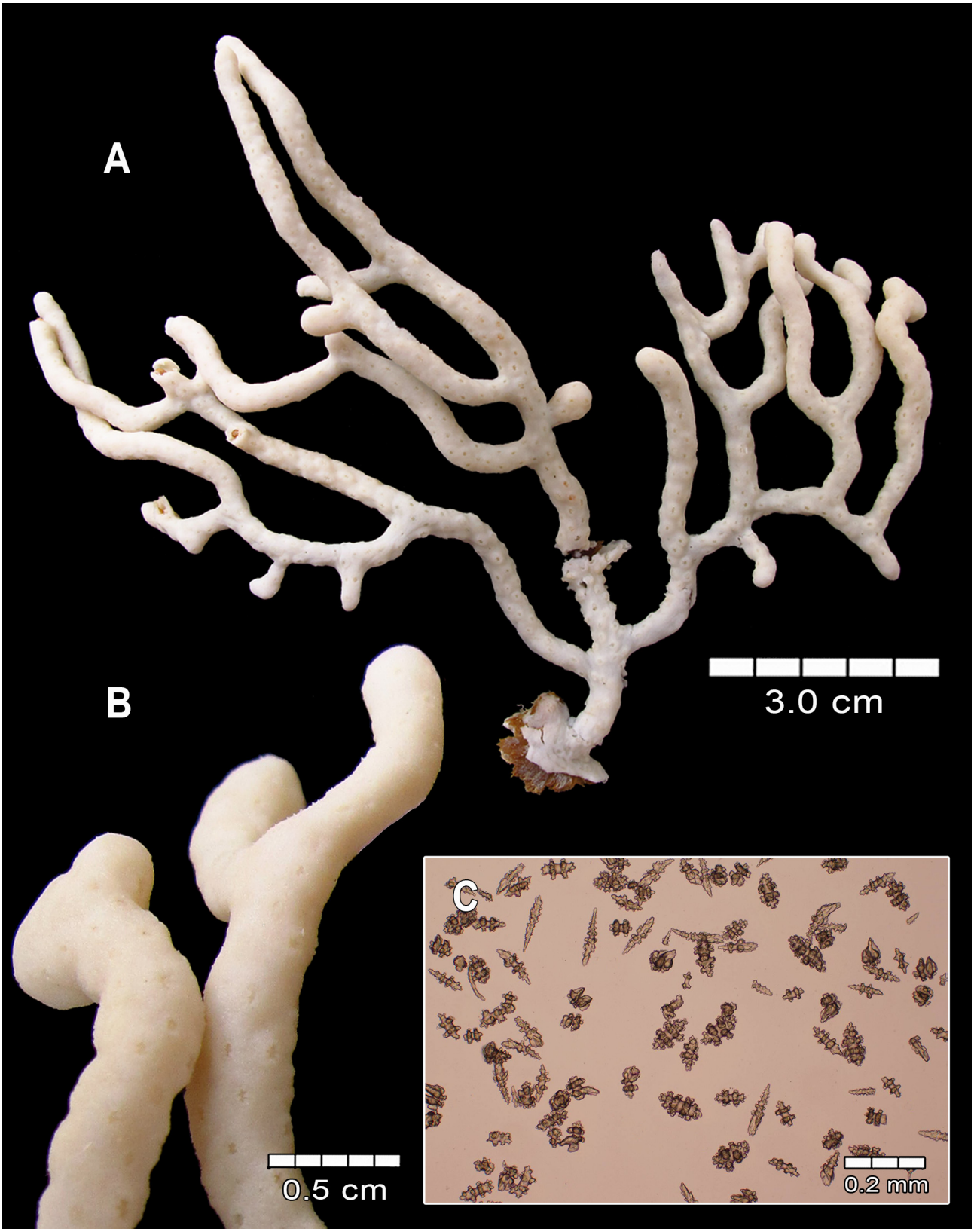

FIGURE 6. *Adelogorgia telones*, USNM 57454 (white paratype) (A) colony; (B) detail of the branches; (C) sclerites.

Colony colours, white, or lemon–yellow (Figs. 4A–B, 6A–B). Sclerite colours, whitish and transparent, or yellow or (Figs. 4C, 6C).

Distribution. Known only from the type locality, Kicker Rock, the Galápagos Islands. No specimens of this species have been recovered since the initial description of the species (Breedy et al. 2009).

Variability. The species was described from three specimens (two white and one lemon-yellow) (Figs. 4, 6), measuring 7.5–10 cm long and 9–11 cm wide. The only difference despite the colour is that in the lemon-yellow variety, the anthocodial sclerites are larger than in the two white specimens, reaching up to 0.31 mm long.

Remarks. This species is separated from the others by its thick branches and especially the colours of colonies and sclerites, because none of the other four species have white or lemon-yellow colonies. The polyp-mounds are almost flat in *A. phyllosclera*. This means that when polyps retract, they are completely flush with the surrounding coenenchymal surface or form a low coenenchymal rim (Bayer 1979). Differences between this species and the others are shown in Tables 1 and 2.

Adelogorgia osculabunda sp. nov.
(Figs. 8–9, 7A)

Material examined.

Holotype: MZUCR 2494 (OCT 0083), ethanol preserved, off Punta Mala, Puntarenas, 09°22.085N − 084°32.206W, 09°22.280N – 084°32.037W, 44.2–44 m, R/V *Urracá*, Trawl 44, R. Vargas, 17 July 2005.

Paratypes: COSTA RICA: MZUCR 750, ethanol preserved, Ballena Bay, Nicoya Gulf, 65 m, R/V *Víctor Hensen*, 3 July 1993. MZUCR 2495 (OCT 0087) (15 specimens), MZUCR 2496 (OCT 0088) (13 specimens), MZUCR 2496A, ethanol preserved, Santa Elena Gulf, Guanacaste, 10°58.10N − 085° 46.09W, 10°59.41N – 085°45.68W, 50.7-51.7 m, Y. Camacho, Trawl 4, R/V *Urracá*, 9 July 2005. MZUCR 2497 (OCT 0089), ethanol preserved, off Punta Mala, Puntarenas, 44–44.2 m, R. Vargas, Trawl 44, R/V *Urracá*, 17 July 2005. MZUCR 2498 (OCT 0091), ethanol preserved, Santa Elena Gulf, 10°57.82N − 085°46.76W, 10°57.82N – 085°46.42W, 50.7–51.7 m, 54.2–51.5 m, Y. Camacho, Trawl 3, R/V Urracá, 9 July 2005. MZUCR 2499 (OCT 0092) (2 specimens), MZUCR 2500 (OCT 0094) (2 specimens), as the holotype. MZUCR 2501 (OCT 0093), dry, Santa Elena Bay, Guanacaste, 50 m, E. Ruiz, June 2012. MZUCR 2506-2508, 2511, dry preserved, Santa Elena Gulf, Guanacaste, 10°57.82N − 085°46.76W, 10°57.82N –085°46.42W, 50.7-51.7 m, Y. Camacho, Trawl 4, R/V *Urracá*, 9 July 2005. MZUCR 2502, 2507, dry, Santa Elena Gulf, 10° 57.82N – 085° 46.76W, 10° 57.82N – 085° 46.42W, 50.7–51.7 m, 54.2–51.5 m, Y. Camacho, Trawl 3, R/V *Urracá*, 9 July 2005. MZUCR 2505, dry preserved, Naranjo Bay, Papagallo Gulf, 10° 45.565N–085° 40.757W, 30 m, R. Vargas, R/V *Urracá*, dredging, 15 July 2005. PANAMÁ: STRI 895, 3 specimens, ethanol preserved, Station 0, Pearl Islands, Panamá Gulf, 80 m, H. Guzman, dredging, R/V *Urracá*, 18 August 2004.

GenBank accession numbers MF579538 and MF579541.

Diagnosis. Colonies mostly flabellate, branching mostly dichotomous, with some pseudo-anastomoses. Branches of nearly uniform thickness 3-5 mm in diameter with tapered tips. Branching up to 10 times. End branches up to 35 mm long. Polyps distributed all around the branches. Polyp mounds closely placed and prominent. Anthocodia with 8–10 slightly curved spinous rods in each point, up to 0.26 mm long, and 2–3 rods arranged horizontally in a weak collaret. Coenenchyme with tuberculate spindles, up to 0.21 mm long, double discs with serrate edges up to 0.13 mm long and 0.09 mm wide; and leaf clubs up to 0.25 mm long. Outermost coenenchyme with a predominance of wide warty spindles over double discs. Axial sheath containing radiates and capstans up to 0.11 mm long and 0.09 mm wide, and less developed spindles. Colony colour, pink and coral red polyp mounds. Sclerites pink and whitish, transparent.

Description. The holotype is a flabellate, 10.5 cm long and 13 cm wide colony; branching is mostly dichotomous (Fig. 8A). Two branches partially joined rise from a holdfast of 2 cm diameter. They form the main stem measuring about 3.5 mm diameter each, and 3 mm long (Fig. 8A-B). The main branches subdivide producing several secondary branches of uniform thickness, 4–5 mm diameter, with tapered tips, about 3 mm diameter. The branches emerge at angles of 30–90°, spreading irregularly in one plane like a fan. Some branches stick one to another growing longitudinally at certain points in the colony, and some others with coenenchyme-anastomosis that form triangles or squares. The colony branches up to 10 times. Unbranched terminal ends are 3–35 mm long (Fig. 8A-B). The axes are composed of longitudinal gorgonin layers with a loculated central cord filled with organic fibres without mineralization (Fig. 7A). The coenenchyme is moderately thick and granular. The polyps are distributed all around the branches, closely placed at the branch-tips, about 0.5–1 mm apart and more separated at the middle and the base of the branches, 1.5–2.5 mm apart. The polyps are translucent, but look like orange due to the light orange anthocodial sclerites. The polyps are fully retractile into prominent polyp mounds, 1–1.5 mm tall,

with spiny rims around the circular polyp apertures (Fig. 8B). The polyp mounds do not present a special type of sclerites, but a concentration of thorny, irregular spindles and some leaf clubs appear, around the oral aperture. The anthocodiae are composed of eight subtentacular points consisting of about 8-9 straight to slightly bent spiny rods, 0.17–0.26 mm long and 0.029–0.036 mm wide, 2–3 horizontally arranged forming a weak collaret (Fig. 9A). The coenenchyme is composed of a superficial layer of wide warty spindles, 0.15–0.21 mm long and 0.04–0.08 mm wide (Fig. 9C) and double discs with serrate crests, 0.10–0.13 mm long and 0.07–0.09 mm wide (Fig. 9D), and leaf-clubs 0.13–0.24 mm long and 0.04–0.1 mm wide (Fig. 9B). Beneath this layer, the coenenchyme contains radiates 0.075–0.11 mm long and 0.06–0.085 mm wide (Fig. 9E); and also, immature forms are present. Anthocodial sclerites are whitish and pale pink. Coenenchymal sclerites are mostly pink and of some lighter hues and whitish to transparent (Fig. 8C).

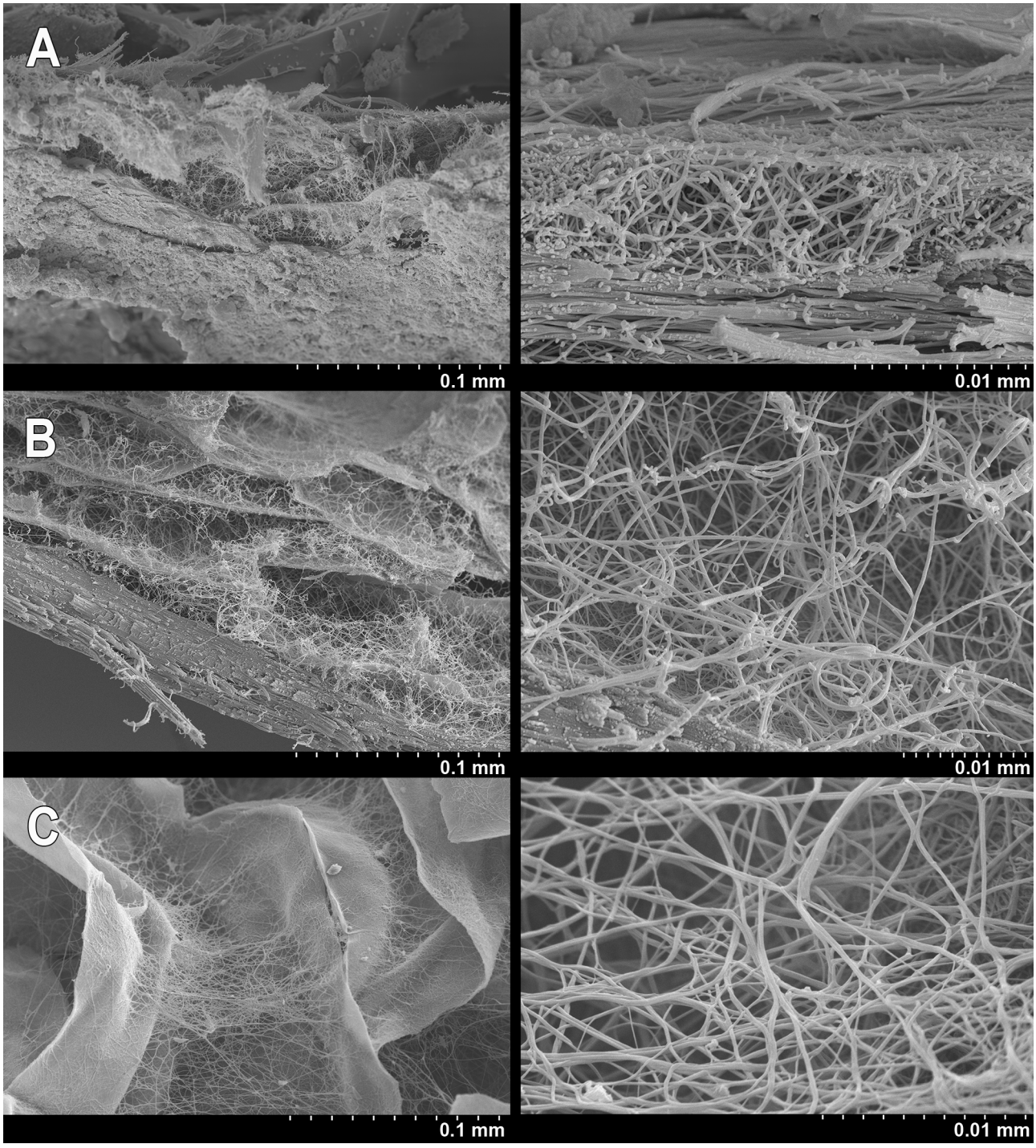

FIGURE 7. Structure of non-mineralised axes: Longitudinal section of axial core showing chambers with fibres (left); detail of fibres (right). (A) *Adelogorgia osculabunda*; (B) *Adelogorgia hannibalis*; (C) *Adelogorgia adusta*.

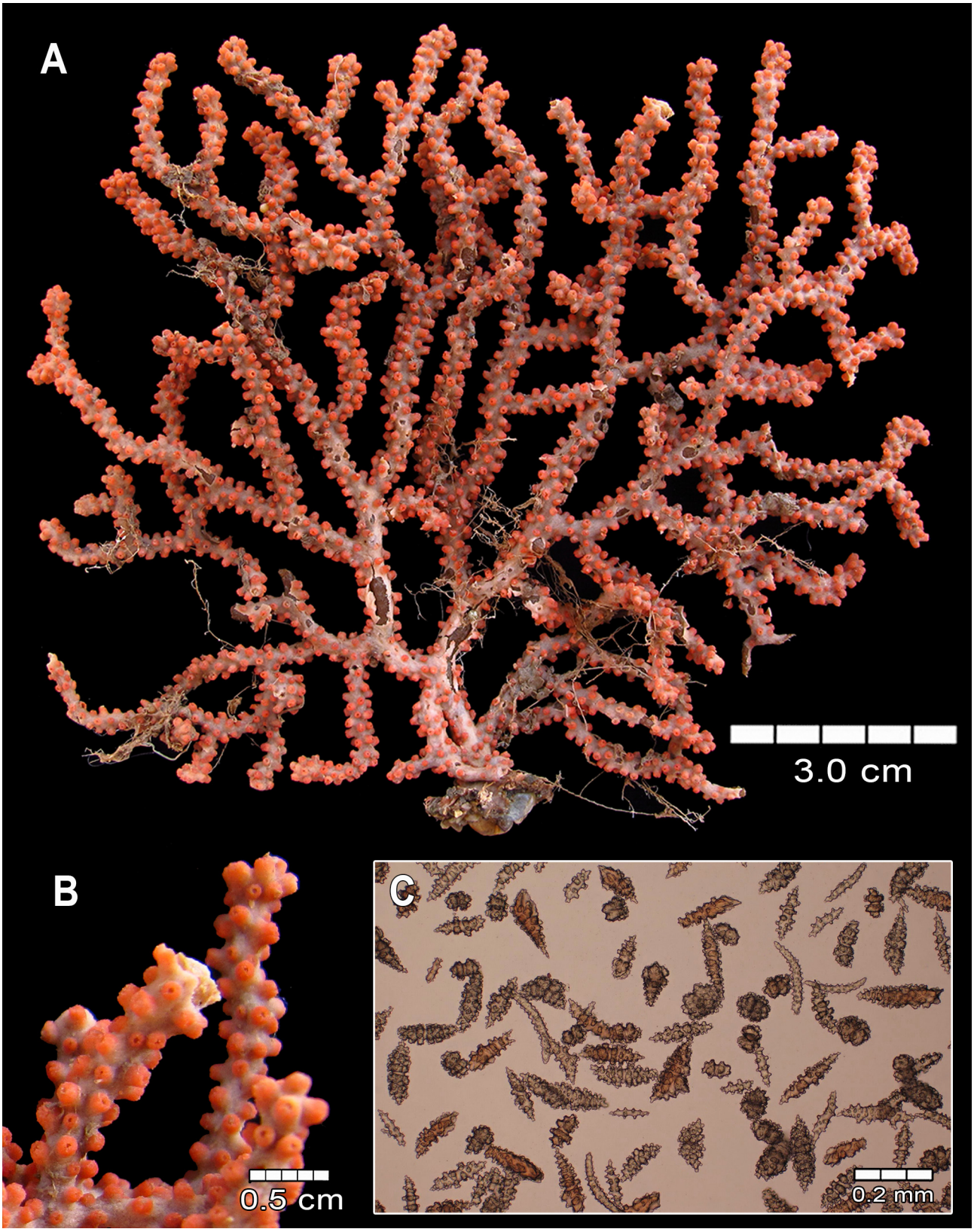

FIGURE 8. *Adelogorgia osculabunda* sp. nov., MZUCR 2494 (OCT-0083) (holotype) (A) colony; (B) detail of the branches; (C) sclerites.

The colony is pink with a conspicuous coral red colour polyp mound (Fig. 8C). The colonies keep the colours either in ethanol or dry preserved, the polyps are translucent. The gastric cavities of the polyps are full of whitish eggs in this specimen.

Variability. The examined colonies reach up to 15 cm tall and about the same width. The branches are thinner, 2–3 mm in diameter in some small colonies. The colony shape varies from a few branches to fan-like colonies. The coenenchyme and sclerites colour are very consistent in the paratype series. The coral-red polyp mounds are always present, and is a distinctive feature for the species that is observed in dry or preserved colonies. However, in some cases in ethanol preserved animals the polyp-mounds are darker as a consequence of alcohol soluble pigments.

Habitat and Distribution. The species has been collected by bottom trawls from sandy or muddy-sand substrata. It was also obtained from fishing lines and nets from rocky shoals, where the colonies were ripped as by-catch or were entangled in the lines from 40 to 60 m deep. *Adelogorgia osculabunda* was commonly collected together with *Leptogorgia regis* Hickson, 1928, *Muricea fruticosa* Verrill, 1868, *Muricea subtilis* Breedy and Guzman, 2016 and two *Psammogorgia* species. The species was found at various localities in Costa Rica, from: off Salinas Bay and Santa Elena Bay to Cape Santa Elena, Guanacaste (northern Pacific); and Punta Mala, Puntarenas (central Pacific) that suggests a wide distribution of the species along the Pacific. In Panamá, Pearl Islands, the colonies were obtained by dredging at 80 m deep, which presently represents the deepest record.

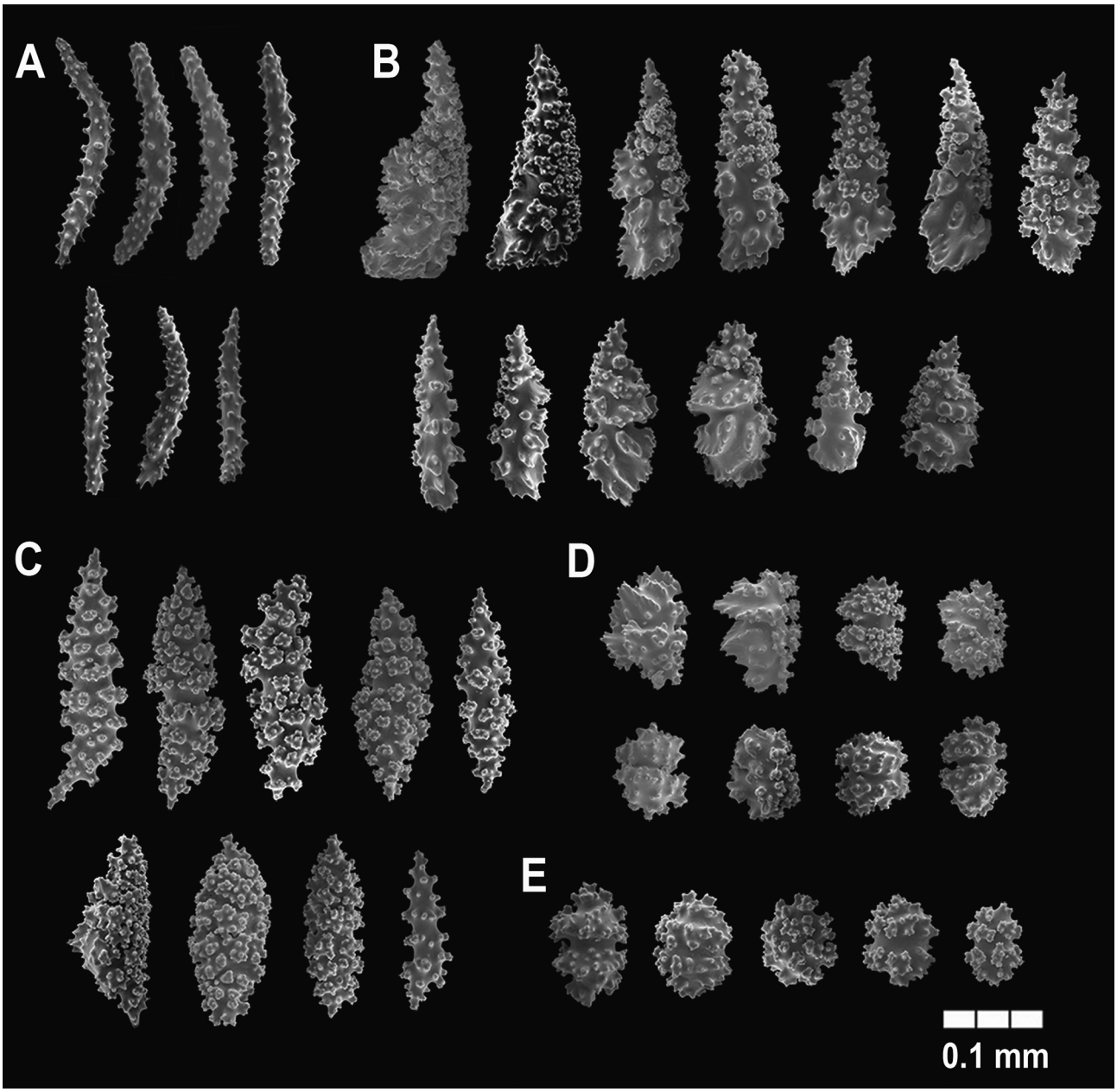

FIGURE 9. *Adelogorgia osculabunda* sp. nov., MZUCR 2494 (OCT-0083) (holotype) SEM micrographs. (A) anthocodial rods; (B) leaf clubs; (C) spindles; (D) double-discs; (E) radiates from inner coenenchyme.

Etymology. Named *osculabunda*, Latin adjective derived from *osculum*: little mouth, kiss. In Latin context, *osculabunda* is the one that covers with kisses, in allusion to the red prominent polyp-mounds that cover the branches.

Remarks. This species is similar to *A. hannibalis* in the prominent polyp-mounds showing a little darker orange contrasting with the colony colour, but is not as evident as in *A. osculabunda*. Thinner colonies of *A. osculabunda* look similar to *A. hannibalis*, but in *A. osculabunda*, the polyp-mounds are closer and stiffer than in *A. hannibalis*. Additionally, sclerite analysis shows clear differences between the two species. Comparisons with the other species are shown in Tables 1 and 2.

***Adelogorgia hannibalis* sp. nov.**
(Figs. 10–11, 7B)

Material examined.

Holotype: STRI 1206A, ethanol preserved, Hannibal Bank, Panamá, 184 m deep, Dive 1552, submersible *DeepSee*, M/V *SeaHunter*, 9 March 2012.

Paratypes: STRI 1205, 1206B, 1207-1212, data as the holotype. STRI 1243, ethanol preserved, Hannibal Bank, Panamá, 200 m deep, Dive 1552, submersible *DeepSee*, M/V *SeaHunter*, 9 March 2012. STRI-HH 1047, ethanol preserved, Hannibal Bank, 181 m deep, Dive 288, submersible *Nadir*, M/V *Alucia*, 2 April 2015. HH 1088, ethanol preserved, Hannibal Bank, 182 m deep, Dive 290, submersible *Nadir*, M/V *Alucia*, 5 April 2015. STRI-HH 1090, ethanol preserved, Hannibal Bank, 203 m deep, Dive 290, submersible *Nadir*, M/V *Alucia*, 5 April 2015. STRI-HH 1142, ethanol preserved, Hannibal Bank, 188 m deep, DR 310, submersible *Nadir*, M/V *Alucia*, 5 April 2015.

GenBank accession numbers MF579539 and MF579542.

Diagnosis. Colonies flexible with few branches, branching dichotomous, without anastomoses. Branches thin, of uniform thickness 1.5–2 mm in diameter. Branching up to 12 times, mostly 3–6 times. End branches up to 70 mm long. Polyps distributed all around branches. Polyp mounds prominent, sparsely placed, closer at branch tips. Anthocodiae with about 8 slightly curved spinous rods in points up to 0.2 mm long. Coenenchyme with tuberculate spindles, up to 0.15 mm long, double discs with serrate edges up to 0.11 mm long and 0.09 mm wide; and leaf clubs up to 0.19 mm long. Outermost coenenchyme with predominance of double discs. Axial sheath with less complex spindles and smaller radiates. Colony orange. Sclerites orange, red, whitish to transparent.

Description. The holotype is a sparse, flexible colony, 18 cm long and 16 cm wide colony. The branching is mostly dichotomous (Fig. 10A). The stem, 2 mm diameter and 3 mm long, rises from a 1 cm diameter holdfast. The stem subdivides producing branches of uniform thickness, 1.5–2 mm diameter. They bifurcate mostly 0.5–2.5 cm apart at angles of 30–90°. Some branches extend and curl inwards in larger angles (180°). The colony branches up to 12 times. Unbranched terminal ends are 3–7 cm long (Fig. 10A-B). The polyps are distributed all around the branches, up to 2 mm apart, closer at the tips (Fig. 10B). The axes are composed of longitudinal gorgonin layers with a loculated central cord filled with organic fibres without mineralization (Fig. 7B). The polyps are fully retractile into raised polyp mounds, 0.5-0.75 mm height, with circular apertures (Fig. 10B). The polyp mounds do not have a special type of sclerites but they mostly contain leaf clubs and spindles. The anthocodiae are composed of eight points consisting of a few vertically arranged spiny rods each one, without a collaret. The anthocodial rods are 0.148–0.2 mm long and 0.029–0.06 mm wide (Fig. 11A). The coenenchyme is thin. The superficial layer with a dominance of double discs. Beneath this layer, warty spindles, radiates, and immature forms. The leaf clubs are 0.11–0.196 mm long and 0.04–0.08 mm wide (at the head) with warty handlers and from elongated warts to foliate heads (Fig. 11B). The spindles are 0.11–0.17 mm long and 0.06–0.078 mm wide (Fig. 11C), immature forms 0.09–0.10 mm long and 0.05–0.08 mm wide; radiates are 0.05–0.09 mm long and 0.02–0.05 mm wide (Fig. 11D). The double discs are 0.06–0.088 mm long and 0.08–0.11 mm wide (along the disc's crests) (Fig. 11E). Coenenchymal sclerites are orange, red and whitish to transparent (Fig. 10C). Colour of the colony is orange, with reddish polyp mounds (Fig. 10A-B).

The colony has some nude branches colonised by polychaete tubes and cirripedia.

Variability. The colony colour varies to lighter hues of orange in some paratypes (STRI 1209, 1212) and the branch thickness reaches up to 3 mm in the paratype STRI 1212. The polyp mounds extend up to 1 mm in STRI 1212. The paratype series are 7-16.5 cm long. All of them with scant branching, less than the holotype, which is the most copious colony. The paratype sclerites are consistent with the holotype.

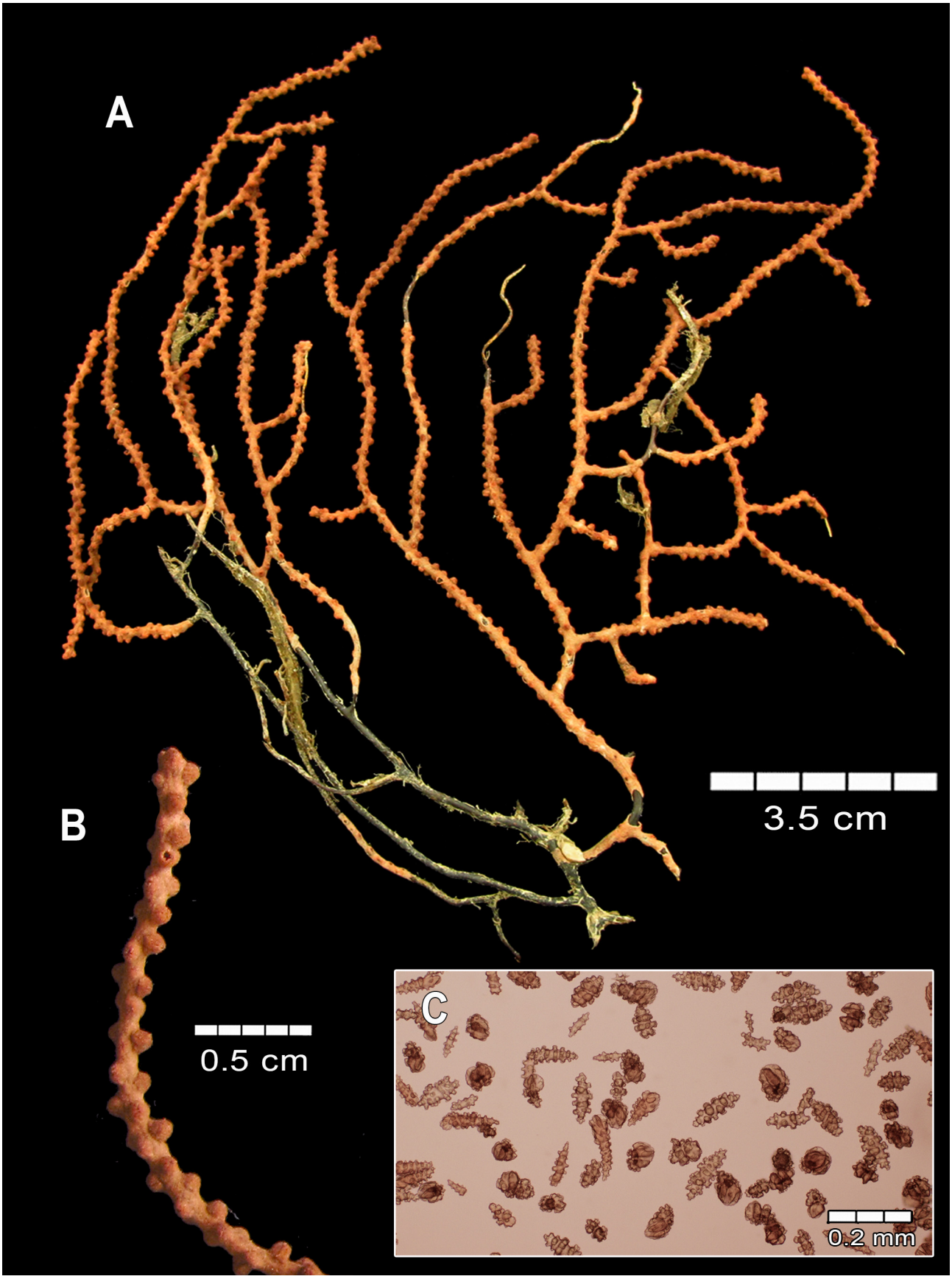

FIGURE 10. *Adelogorgia hannibalis* sp. nov., STRI 1206 (holotype) (A) colony; (B) detail of the branches; (C) sclerites.

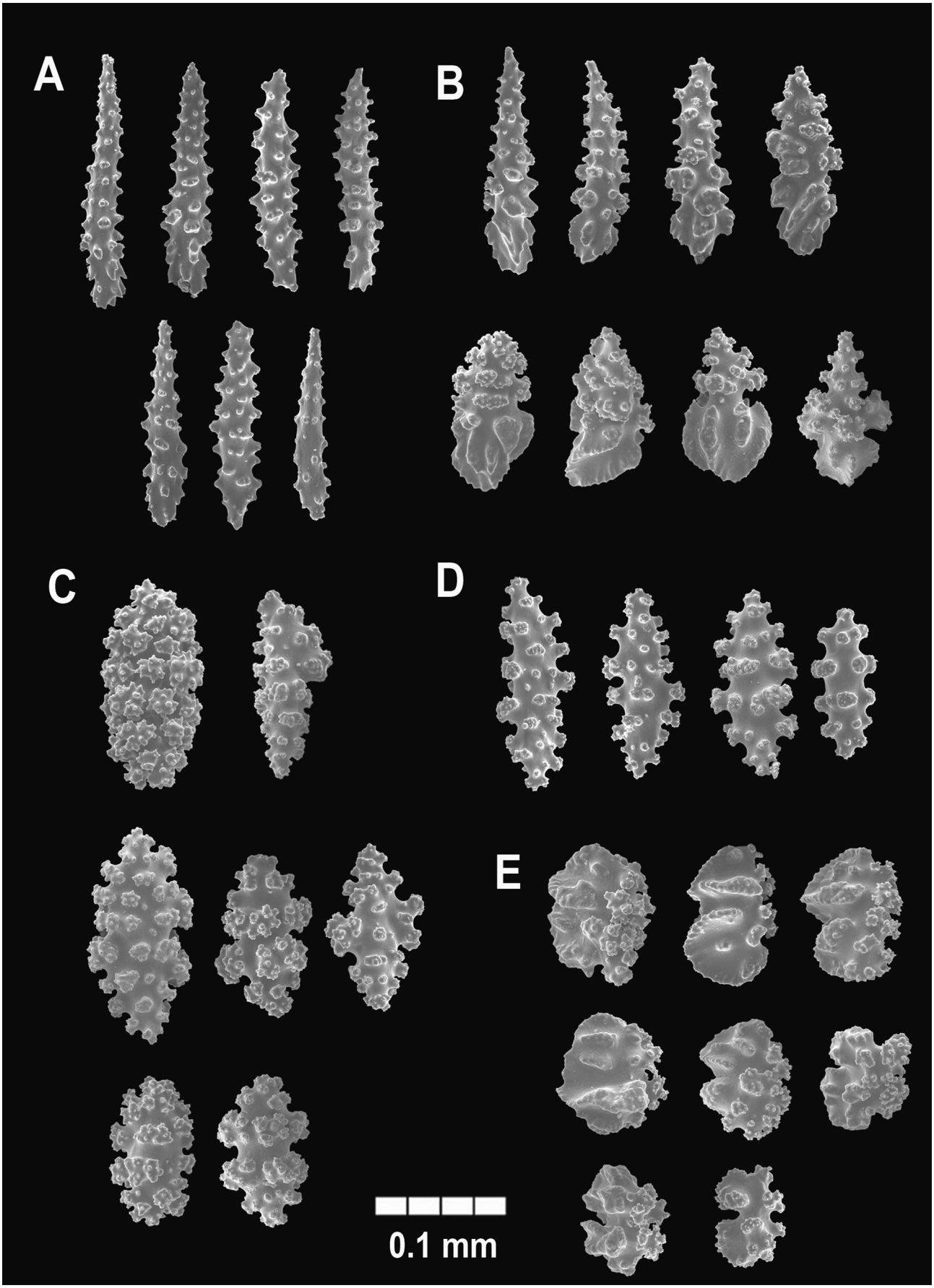

FIGURE 11. *Adelogorgia hannibalis* sp. nov., STRI 1206 (holotype) SEM micrographs. (A) anthocodial rods; (B) leaf clubs; (C) spindles; (D) spindles from inner coenenchyme; (E) double discs.

Habitat and Distribution. The species was found on the Hannibal Bank, a coastal guyot-type seamount that rises from approximately 500 m to 45 m, located 50 km from the mainland (Cunningham et al. 2013). The seamount is relatively protected as part of the Coiba National Park and World Heritage. The species was found on rocky substrate with strong currents. It is only known from the type locality, Hannibal Bank, from 180 to 200 m deep.

Etymology. Named after the Hannibal Bank and the surveyor USS *Hannibal* that discovered and charted the bank for the first time, presumably in 1934. The name Hannibal evokes the Carthaginian general, considered one of the greatest military commanders in ancient history. In genitive: *hannibalis* (L) meaning ¨of Hannibal¨.

Remarks. This species is the only one that has colonies with elongated branches and free branches up to 7 cm long. Furthermore, it has a characteristic orange colony. The closest species is *A. osculabunda* (as discussed above). However, the flabellate branching pattern in *A. osculabunda*, the prominent polyp-mounds and the coenenchymal sclerites, make clear distinction among these two species. The comparative characteristics are in Tables 1 and 2.

Adelogorgia adusta sp. nov.

(Figs. 12–13, 7C)

Material examined.

Holotype: STRI-HH 1220, ethanol preserved, Hannibal Bank, Panamá, 73 m deep, Dive 293, submersible *Nadir*, M/V *Alucia*, 9 April 2015.

Paratypes: STRI-HH 1289 (3 fragments), ethanol preserved, Hannibal Bank, 91 m deep, Dive 297, submersible *Nadir*, M/V *Alucia*, 13 April 2015. STRI-HH 1307 (complete colony), ethanol preserved, Hannibal Bank, 94 m deep, Dive 297, submersible *Nadir*, M/V *Alucia*, 13 April 2015.

GenBank accession number MF579540.

Diagnosis. Colonies bushy, branching lateral, without anastomoses. Branches of nearly uniform thickness 3-4 mm in diameter with wide tips up to 4.5 mm in diameter. Branching up to 10 times. End branches up to 3.5 cm long. Polyps distributed all around the branches. Polyp mounds closely placed, and slightly raised. Anthocodiae with 8 slightly curved spinous rods in points up to 0.23 mm long. Coenenchyme with tuberculate spindles, up to 0.20 mm long, double discs with serrate edges up to 0.09 mm long and 0.10 mm wide; and leaf clubs up to 0.18 mm long. Outermost coenenchyme with predominance of double discs. Axial sheath containing radiates up to 0.12 mm long and 0.10 mm wide. Colony bright red. Sclerites red, orange, whitish to transparent, and bicoloured.

Description. The holotype is a bushy, 11 cm long and 12 cm wide colony, branching is mostly lateral and in several planes, up to four (Fig. 12A). The stem, 3 mm in diameter, rises a few millimetres from a 1.5 cm diameter holdfast. It subdivides producing several secondary branches of uniform thickness, about 3 mm diameter, with wider tips, 3–4.8 mm diameter. Some branchlets are thinner about 2–2.5 mm in diameter. The branches mostly bifurcate 0.5–1.0 cm apart, at angles of 45–90°. The colony branches up to 10 times. Unbranched terminal ends are 1.5–3.5 cm long (Fig. 12A-B). The axes are composed of longitudinal gorgonin layers with a loculated central cord filled with organic fibres without mineralization (Fig. 7C). The polyps are distributed evenly all around the branches, closely placed about 1 mm apart. The polyps are fully retractile into slightly raised polyp mounds, with circular polyp apertures (Fig. 12B). The polyp mounds do not have a special type of sclerites but they mostly contain leaf clubs and spindles. The anthocodiae are composed of eight points consisting of about 8 almost straight and slightly bent spiny rods, without a collaret. The anthocodial rods are 0.10-0.23 mm long and 0.02–0.03 mm wide (Fig. 13A). The coenenchyme is moderately thick. The superficial layer with a dominance of red and orange double discs, and wide globose spindles, white, orange, red and bicoloured (Fig. 13C). Beneath this layer are the warty spindles, radiates, and immature forms (Fig. 13D-E) The leaf clubs are 0.11–0.18 mm long and 0.045–0.06 mm wide with warty handles and elongated or foliate heads (Fig. 13B). The spindles are 0.15–0.20 mm long and 0.06–0.08 mm wide (Fig. 13C); smaller immature forms are 0.11–0.12 mm long and 0.04–0.07 mm wide (Fig. 13D); and globose radiates are 0.08–0.12 mm long and 0.06–0.10 mm wide (Fig. 13E). The double discs are 0.06–0.09 mm long and 0.07–0.10 mm wide (Fig. 13F). Coenenchymal sclerites are red, orange, whitish to transparent and bicoloured with the inner part red and the periphery transparent (Fig. 12C). The colour of the colony is bright red when recently collected (Fig. 12A on deck photograph), it gets darker after ethanol preservation or dry to a brownish orange, looks like burnt (Fig. 12B).

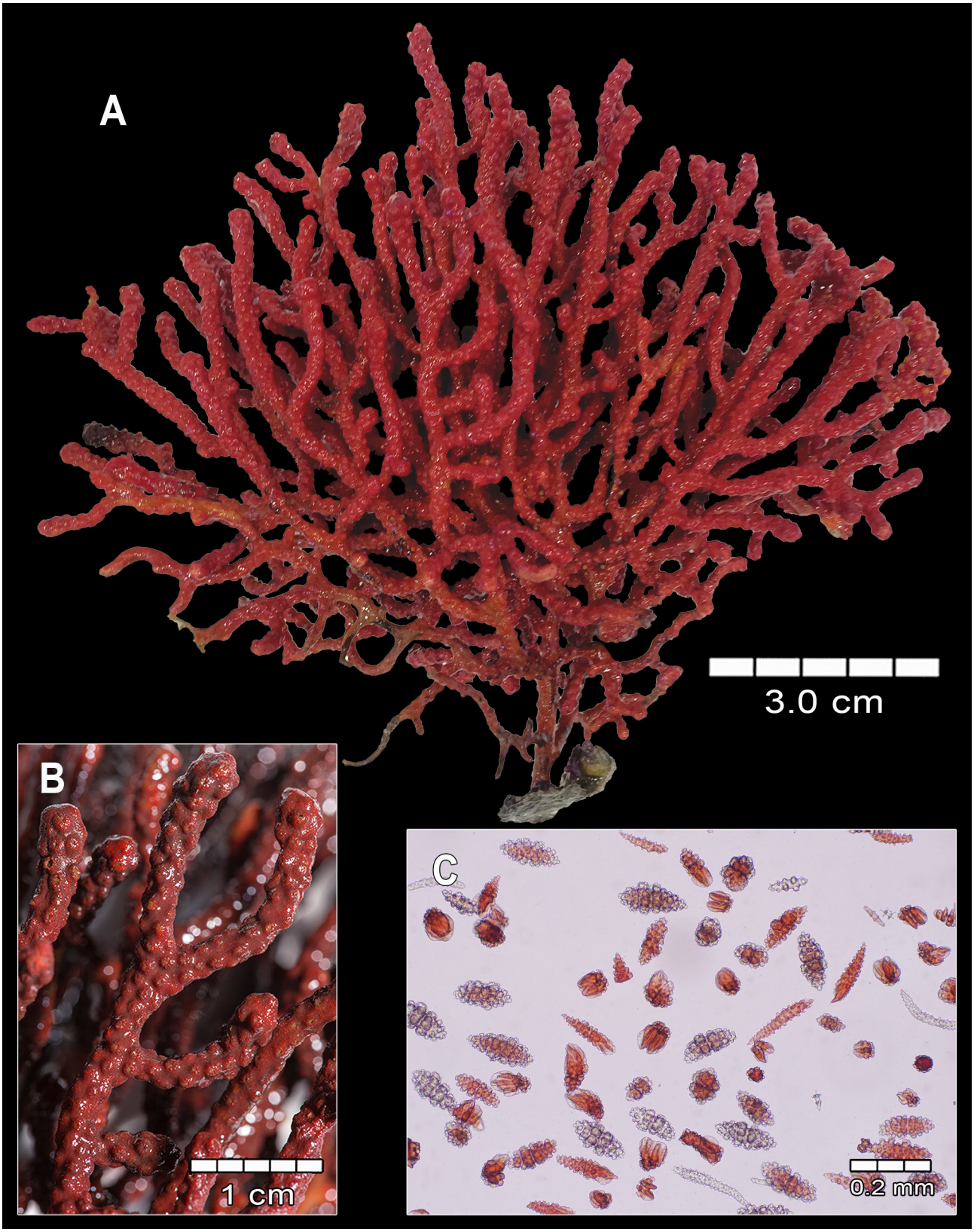

FIGURE 12. *Adelogorgia adusta* sp. nov., STRI-HH 1220 (holotype). (A) colony; (B) detail of the branches; (C) sclerites. B, photograph by Sean Mattson.

Variability. The paratype STRI-HH 1307 is a 10 by 10 cm colony, more openly branched than the holotype, and mostly branching in two planes. It has a small black coral attached at the base. Cirripedia tumours were found in some branches of the holotype and the paratype STRI-HH 1307.

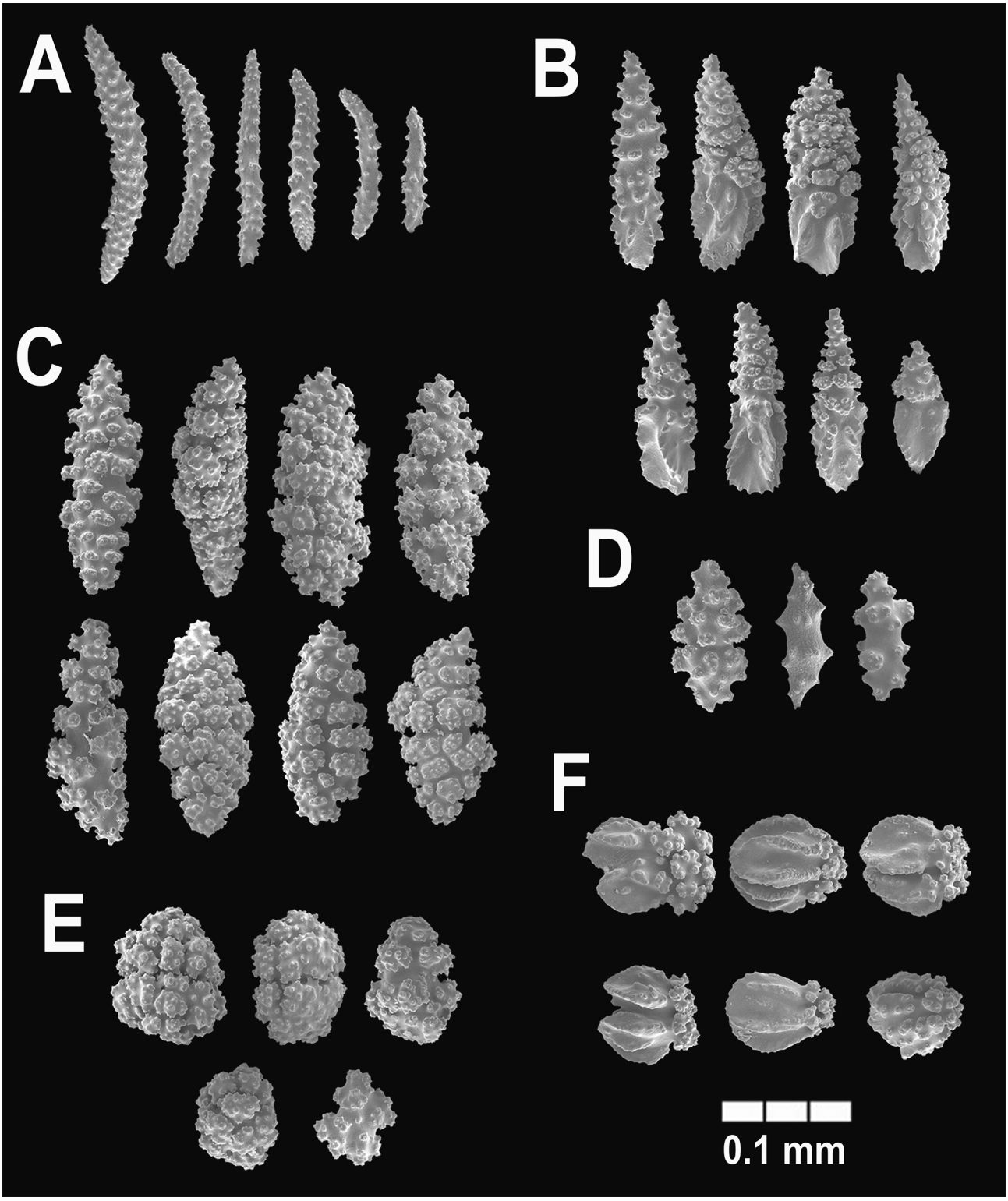

FIGURE 13. *Adelogorgia adusta* sp. nov., STRI-HH 1220 (holotype) SEM micrographs. (A) anthocodial rods; (B) leaf clubs; (C) spindles; (D) spindles from inner coenenchyme; (E) globose radiates; (F) double discs.

The other paratypes are two 2 cm fragments. The paratypes' characteristics are according with those of the holotype.

Habitat and Distribution. The species was found in the Hannibal Bank, on rocky substrates impacted by currents. *Adelogorgia adusta* is only known from the type locality Hannibal Bank, from 73 to 94 m deep.

Etymology. Named *adusta*, Latin adjective meaning burnt, scorched, charred, in allusion to the burnt

appearance that the colony takes after fixation. The word *adustus,* in Castellan language, *adusto*, was evoked in verse 62 of *The Fable of Polifemo and Galatea* (Spanish poet Luis de Góngora) referring to the son of the Pirineo (giant mount) who supposedly was put in flames.

Remarks. The colony colour and the shape of *A. adusta* are clearly different from the other four species. The closest species could be *A. phyllosclera* which is similar in the lateral branching style, thickness of branches and end-branches length, especially in the paratype STRI-HH 1307. But the sclerites composition and size of anthocodial sclerites definitely separate these species. Differences between the species are shown in Tables 1 and 2.

Discussion

In this review, distinction among species of *Adelogorgia*, as in most gorgonians, is based on the combination of morphological characters: colony growth form, colour, and sclerite kinds and structure. The growth form and colour are the most evident characteristics in distinguishing *Adelogorgia* species. For example, in *A. telones* the white and the yellow-lemon colour varieties separate the species from the rest; *Adelogorgia hannibalis* differs from the other species in the sparse, flexible colony having the thinnest branches; the polyp mounds in *A. osculabunda* are prominent and of a conspicuous coral red colour that is a distinctive feature for the species. Although interspecific variation is observed in the species of *Adelogorgia*, the analysis of morphological characters in the genus proved to be appropriate to separate species. However, given the difficult access and availability of this material, we included DNA sequence data into the new species descriptions (the commonly used mitochondrial marker for octocorals), to be used in a future comprehensive study.

We conclude that the genus *Adelogorgia* is composed of five valid species and its habitat and geographic distributions are wider than previously reported.

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