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A revision of the genus *Muricea* Lamouroux, 1821 (Anthozoa, Octocorallia) in the eastern Pacific. Part II

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Abstract

The species of the genus *Muricea* were mainly described from 1846 to 1870. After that very few contributions were published. Although the highest richness of *Muricea* species is in the eastern Pacific shallow waters, a comprehensive systematic study of the genus does not exist. Recently we started a taxonomic review of the genus in order to validate the status of four species previously included in the genus *Eumuricea*. Herein we present the second part of the *Muricea* revision dealing with the species-group characterised by shelf-like calyces instead of tubular-like calyces (the *M. squarrosa*-group). Original type material was morphologically analysed and illustrated using optical and scanning electron microscopy. Comparative character tables are provided for the genus. The taxonomic status of the species was analysed and established by designating lectotypes, alternatively by recognising a holotype by monotypy. We conclude that the genus *Muricea* comprises 20 valid species, including the previous four in the *M. squarrosa*-group. We propose 10 lectotypes, a new combination and three more species groups for the genus based on morphology: the *M. fruticosa*-group, *M. plantaginea*-group and *M. austera*-group.

Keywords

Alcyonacea, Cnidaria, eastern Pacific, *Muricea*, plexaurid gorgonian, soft corals, taxonomy

Introduction

The genus *Muricea* Lamouroux, 1821 is widely distributed along the eastern Pacific shallow waters (less than 40 m deep), and although it has representatives in the western Atlantic, the highest species richness is attained in the eastern Pacific. We deal with the eastern Pacific *Muricea* species in the present taxonomic review. The first record appeared as *Gorgonia plantaginea* Valenciennes, 1846 (Plate 15, Fig. 14A, herein) from Mazatlan, México, collected during the French expedition, "Voyage autour du monde sur la frégate la Vénus" (Valenciennes 1846). The major contribution to the knowledge of this taxon was made by Verrill (1868–1870) in his paper "Notes on Radiata", where he described 16 new species and revised the former records. Other contributions were made in the XX century: Kükenthal (1919, 1924) published a key and a short review of the described species; Hickson (1928) described two *Muricea* species from the Pacific coast of Panamá; Aurivillius (1931) described three more species, pointing out that he did not have access to the type material of the former described species so his new species were uncertain to some extent; Stiasny (1941, 1943) also wrote about the octocorals of Panamá and reviewed the species previously described by Hickson (1928); and finally Deichmann (1941) described a new species from the Galápagos Islands, Ecuador. After this, no taxonomic research was conducted dealing with the genus. Hardee and Wicksten (1996) re-described and compared three *Muricea* species from California, USA. The status of most species is uncertain because previous authors did not designate holotypes and the specimen and sclerite illustrations are poor in most cases. Some species have been described from a few specimens or from fragments, and type material was lost or misplaced. Therefore, a comprehensive review of this genus is inexorable for the advancement of ecological and evolutionary research in soft corals.

Recently, we published the first part of the review of *Muricea* (Breedy and Guzman 2015) dealing with the species assigned by Verrill (1869, p. 449) to the genus *Eumuricea* Verrill, 1869 and concluded that there is not enough support to keep these genera apart. Therefore *Eumuricea* is treated as a synonym of *Muricea*, comprised of four valid and one dubious species: *Muricea acervata* Verrill, 1866; *Muricea hispida* Verrill, 1866; *Muricea squarrosa* Verrill, 1869; *Muricea tubigera* Verrill, 1869; and *Muricea horrida* Möbius, 1861 (sp. dubia).

The present research represents the second part of the fifth review, in a series of six proposed, aiming to evaluate the genera of gorgonians historically reported for the shallow eastern Pacific waters. Previous reviews dealt with *Pacifigorgia* Bayer, 1951 (Breedy and Guzman 2002), *Leptogorgia* Milne, Edwards & Haime, 1857 (Breedy and Guzman 2007) and *Eugorgia* Verrill, 1868a (Breedy et al. 2009), in the family Gorgoniidae; *Heterogorgia* Verrill, 1868b (Breedy and Guzman 2011) and *Muricea* Lamouroux, 1821 (Breedy and Guzman 2015), in the family Plexauridae.

Material and methods

Acronyms

CASIZ	California Academy of Science, Invertebrate Zoology, San Francisco, USA
CDRS	Charles Darwin Research Station, Galápagos, Ecuador
CIMAR	Centro de Investigación en Ciencias del Mar y Limnología, Universidad de Costa Rica, San José, Costa Rica
CIEMIC	Centro de Investigación en Estructuras Microscópicas, Universidad de Costa Rica
CRBMco	Colección de referencia de Biología Marina Universidad Del Valle, Cali, Colombia
ICZN	International Code of Zoological Nomenclature
IMARPE	Instituto del Mar de Perú, Lima, Perú
INN	NAZCA Instituto de Investigaciones Marinas, Salinas, Ecuador
MCZ	Museum of Comparative Zoology, Harvard University, Boston, USA
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MNHUK	Museum of Natural History (former BM, British Museum), London, UK
MZUF	Museo Zoologico dell'Università di Firenze, Firenze, Italia
MZUT	Museo Regionale di Scienze Naturali, Torino, Italia
RMNH	Netherlands Centre for Biodiversity Naturalis, Leiden, (former National Museum of Natural History Naturalis)
SEM	Scanning Electron Microscopy
SMNH	Swedish Museum of Natural History, Stockholm, Sweden
STRI	Smithsonian Tropical Research Institute, Panamá
UCR / MZUCR	Museo de Zoología, Universidad de Costa Rica, Costa Rica
UNAM	Universidad Nacional Autónoma de México, México
UNIANDES-BIOMMAR	Universidad de Los Andes, Laboratorio de Biología Molecular Marina, Bogotá, Colombia
UPCH	Colecciones Biológicas, Universidad Peruana Cayetano Heredia, Lima, Perú
NMNM	National Museum of Natural History, Smithsonian Institution, Washington, USA
YPM	Yale Peabody Museum of Natural History, New Haven, USA
ZMHC	Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Germany
ZMUC	Zoologisk Museum Kobenhavn, Danmark
ZSM	Zoologische Staatssammlung München, Deutschland

The type specimens and comparative reference material used in this study were analysed during visits to museums or acquired on loan from the CASIZ, MCZ, MNHN, MNHUK, NMNM and YPM. Other collections that house type material MZUF, MZUT, ZSM were revised. In addition, specimens recently collected along the Pacific coast of Costa Rica, Ecuador, Mexico, Panamá and Perú deposited in the UCR, STRI and other institutions (CDRS, CRBMco, IMARPE, INN, UNAM, UNIANDES-BIOMMAR, UPCH) were studied. The material was collected by scuba diving, down to 45 m in depth, and some specimens were obtained by dredging down to 60 m.

Morphological study

The microscopic study was done at the CIEMIC, the specimens were prepared for SEM following the protocol described in Breedy and Guzman (2002) and the pictures were obtained using Hitachi SEMs: S-570, N-S2370 and S-3700N. For optic microscopy, sclerites were mounted in water or glycerin and photographed with an Olympus LX 51 inverted microscope. Sclerites of the coenenchyme and calyces are very varied in size and form; the prevailing types are illustrated and described here. Measurements of the sclerites were obtained from pictures and directly from the microscope using an optical micrometer. The 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, in some cases including the length of the longest spine, reporting the largest sizes found in the samples and in some cases, a range of variation. In case of curved sclerites, the length reported was without taking in account the curvature. The sclerites were illustrated by SEM micrographs. We also present optic microscope micrographs for colour details and sclerite composition. The diameter of the branches, branchlets, and stems are given taking in account the length of the calyces. Most of the analysed type material is dry and old. The drying or preservation process can affect the diameter of branches in general, and especially the calyces, however, we have observed that the tendency of the calyces (slightly raised, prominent) is kept after preservation and is consistent with living colonies (Breedy and Guzman 2015). In general, the colours of the colonies and sclerites are stable, and persist after fixation. Some species tint the alcohol when preserved, but keep their colours. Some fading is observed in dry specimens. 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. Verrill and the other authors who described *Muricea* species (Aurivillius, Hickson Deichmann and Valenciennes) did not designate holotypes and in cases, the descriptions could often fit several species. In some cases, only one specimen in the collection was under a species name that automatically constitutes the holotype by monotypy. When the status was unclear we designated lectotypes to establish the identity of the poorly defined species and to avoid future confusion.

Table 1. Sclerite comparison for the eastern Pacific *Muricea* species. Measurements given are from the holotypes and paratypes, in mm.

Species	Sclerite colours	Anthocodial sclerite colours	Dominant type of coenenchymal and calycular sclerites	Coenenchymal and calycular spindles maximum size	Anthocodial maximum size
M. fruticosa	w, rb, py	yellow, w	uss	2.0×0.5	0.64×0.1
M. formosa	w	w	uss	1.5×0.25	0.175×0.075
M. aspera	pb, w	w	uss	1.35×0.35	0.25×0.04
M. echinata	o, lb	lo, w	uss	2.4×0.34	0.25×0.05
M. galapagensis	amb, lo	lo, w	uss	4.1×0.75	0.25×0.06
M. plantaginea	rb, amb/w	lo, lb/w	ls	1×0.2	0.25×0.08
M. californica	ro,ly,amb	lo	ls	0.54×0.2	0.23×0.06
M. mortensenii	w	w	s	0.7×0.12	0.21×0.08
M. austera	rb,o,ly	w	uss	1.5×0.5	0.36×0.06
M. albida	w	w	uss	1.4×0.05	0.25×0.03
M. crassa	rb	lb, w	uss	2.5×0.7	0.22×0.04
M. retusa	rp, p,o	o, ly	uss	1.2×0.6	0.4×0.1
M. purpurea	dr, ro	ro	ls	0.7×0.3	0.3×0.055
M. hebes	py	py	uss	0.83×0.20	0.45×0.1
M. nariformis	bo,lb	o	ls	0.52×0.28	0.17×0.035
M. robusta	o, bo, lb	o	ls	0.64×0.26	0.15×0.05

Colours: amb, amber; bo, brownish orange; lb, light brown; lo, light orange; ly, light yellow; o, orange; p, purple; pb, pale brown; py, pale yellow; rb, reddish brown; ro, reddish orange; rp, reddish purple; w, white, colourless

Type of coenenchymal and calycular sclerites: ls, leaf-like spindle; s, warty spindles; uss, unilateral spinose spindles

"-" no data; "?" uncertain

The terminology is according to Bayer et al. (1983), modifications made by Breedy and Guzman (2015) and others defined herein.

Comparative character tables are provided for the *Muricea* species (Tables 1–2).

Terminology

unilateral spinous spindles: spindle often massive, sculptured on inner surface by crowded complex tubercles and on outer surface by simple spines or prickles, and in some species with a few more or less prominent coarse, prickly projections.

prickly spindle: warty, irregular spindle with prickly, pointed processes at one tip.

leaf-like spindle: warty spindles with flat, leaf-like processes, terminal or laterally placed.

spinous club-like spindle: club shaped sclerite, with head ornamented by thorny or leafy, sometimes unilaterally placed processes and with warty, thin handle.

Table 2. Comparative features of the eastern Pacific *Muricea* species. Measurements given are from the holotypes and paratypes, in mm.

Species	Colony colour	Colony shape	Branching pattern	Length of unbranched terminal branchlets	Diameter of end branchlets (mm)	Coenenchyme	Calyx height at branchlets	Calyx arrangement at branchlets
M. fruticosa	rb, w, bi	bu	irr	15–40	3–6	t	1–1.2	c
M. formosa	w	bu	irr lat, dich	28	6–9	t	2.8–3	c
M. aspera	lb	fla ?	irr, lat	6–30	4–5	t	1–2	c, slightly imbr
M. echinata	rb	bu	irr, lat	6–30	5–8	t	2.8–3	c
M. galapagensis	lo	fall	lat	80	1.6–3	t	0.6–1	s
M. plantaginea	db/w	fla	irr, lat	10–50	2–3	t	0.7–1.2	c, imbr
M. californica	ro	bu	irr, lat	0.5–2.8	3–3.2	mt	1.1–1.9	c, slightly imbr
M. mortensenii	py	fla	irr	2–4	2–3	t	0.7–1	c
M. austera	rb	bu	dich, lat	50	7–8	T	1.7–2	c
M. albida	w	cand	dich	11	5–7	T	0.8–1.8	c, slightly imbr
M. crassa	db	bu	dich, lat	70	7–10	T	2.7–3	c
M. retusa	rp	-	dich	50	7–8	T	1–1.5	c
M. purpurea	rp	bu	dich	50–80	9–11	T	1.5–1.8	c, slightly imbr
M. hebes	yb	fing	dich	32	6–9	T	1–1.8	c, slightly imbr
M. nariformis	bo	fing	dich	24	57	T	0.8–1.2	c
M. robusta	bo	bu	dich	70	7–8.5	T	0.7–1.2	c

Colours: bi, bicoloured; bo, brownish orange; db, deep brown; lo, light orange; lb, light brown; py, pale yellow; rb, reddish brown; ro, reddish orange; rp, reddish purple; yb, yellowish brown; w, white, colourless.
Colony shape: bu, bushy; cand, candelabrum; fall, falling branches; fla, flabelliform; fing, finger-like
Branching pattern: dich, irregularly dichotomous; irr, irregular; lat, lateral
Coenenchyme: t, thin, mt, medium thickness; T, thick
Calyx arrangement at branchlets: c, close, not imbricate; imbr, imbricate; s, sparse
“-” no data; “?” uncertain

Notes on morphological characters

The most informative characters for the genus are the branch diameter, the colours (colonies and sclerites) and the type, size and combination of sclerites. The colours, although some variation exist, are very constant and a reliable characteristic (Breedy and Guzman 2015). Branch diameter and colony form could vary according to the age of the colony and the exposure to the currents, but in general it is possible to have a primary approximation for identification purposes. Calyx size and spacing vary from the larger branches to the thinner in most of the species, being larger, acuter and closer set at the branchlets and shorter, blunter, and more distantly arranged at the main branches. The sclerites, which are the most informative characters, show a continuum in shapes. It is difficult to find limits to the variety of forms; for example, a prickly spindle is basically a modified leaf spindle, or a leaf-like spindle - as defined here is as described in the octocoral glossary (see Bayer et al. 1983). There are many intermediate sclerite forms and it is not sensible to name each and every one. In most cases it is not one type of sclerite that defines a species, it is rather the combination of forms, colours, and sizes. We made approximate descriptions of the sclerite types, but the illustrations that we present for each species are the best reference, and intra-specific variation could be deduced from those. The polyp sclerites were basically warty rods and spindles arranged in points at the base of the tentacles or longitudinally set along the polyp neck zone. In some cases, small leaf-like spindles are also part of the anthocodiae. Undeveloped sclerites were found by dissecting polyps, in some cases the same types are found in the axial sheath. In species with thin and deteriorated coenenchyme it was not possible to determine different sclerite layers. But it seems that the axial sheath contains the undeveloped sclerites, capstans, radiates and spindles, while the external coenenchyme, is constituted by unilateral spinous, leaf-like, warty or prickly spindles, either a specific type or a combination of them. These are the same sclerites that constitute the external calyx wall. There is also a combination of sclerites that make the internal calyx wall, especially the leaf-like, warty, or prickly spindles, and various types of clubs. The spiny tips of some of these sclerites project beyond the calyx border in many species, giving a prickly appearance to the colonies; because of that, some *Muricea* species are commonly known as spiny sea fans.

Presently, the boundaries among octocorals species are based on common characters, basically colony and sclerite shapes and colours that could be influenced, at certain point, by the environment. For that, in determining an octocoral morpho-species the combination of these morphological characteristics results in a more accurate assessment. Furthermore, analysis of several specimens aid in identifying intraspecific variation. Field observation and evaluation of habitat in terms of oceanographic conditions could provide information in the decision making process.

Systematics

Class Anthozoa Ehrenberg, 1834
Subclass Octocorallia Haeckel, 1866
Order Alcyonacea Lamouroux, 1812
Family Plexauridae Gray, 1859

Genus *Muricea* Lamouroux, 1821

Muricea Lamouroux, (pars.) 1821: 36; Blainville (pars.) 1834: 509; Ehrenberg (pars.) 1834: 134; Dana 1846: 673; Milne Edwards and Haime 1857: 142; Kölliker 1865: 135; Verrill 1868b: 411; Verrill 1869: 418–419, 450; Studer 1887: 58; Wright and Studer 1889: 93; Gorzawsky 1908: 8; Nutting 1910: 9; Kükenthal 1919: 835;

1924: 141; Riess 1929: 383–384; Aurivillius 1931: 102–104; Deichmann 1936: 99; Bayer 1956: F210; 1959: 12; 1961: 179–180; 1981: 930 (in key); 1994: 23–24; Tixier-Durivault 1970: 154; Harden 1979: 140; Hardee and Wicksten 1996: 127–128; Marques and Castro 1995: 162; Castro et al. 2010: 779.

Eumuricea (pars.) Verrill, 1869: 449; Riess 1929: 397.

Type species. *Muricea spicifera* Lamouroux, 1821, by subsequent designation: Milne Edwards and Haime 1857. [*M. spicifera* was later synonymised with *Muricea muricata* (Pallas, 1766) after Bayer 1961: 179–180].

Diagnosis (based on Breedy and Guzman 2015). Colonies planar or multiplanar, bushy, arborescent, laterally branched, pinnately branched, dichotomous or with long flexible branches, with some occasional branch anastomosis. Branches and branchlets upward bending almost parallel, and with about the same thickness all along, frequently with slightly enlarged tips. Coenenchyme moderately to very thick (compared to other plexaurids) with a circle of longitudinal canals surrounding the axis and dividing the coenenchyme into a thin inner layer or axial sheath, and a thicker outer layer. Polyps fully retractile within prominent calyces longitudinally and closely placed all around the branches and branchlets, or spaced in loose spirals around the branches and branchlets. Calyces prominent, shelf-like or tubular, with prickly projecting spindles, longitudinally arranged. Base of the anthocodia without sclerites or with flat rods arranged in weakly differentiated collaret and points below the tentacles, or just transversely set along the neck zone of the polyp. Sclerites of the outer coenenchyme and of the calyx mostly long, unilateral spinous spindles, often massive, sculptured on inner surface by crowded complex tubercles and on outer surface by simple spines or prickles, and in some species with a few more or less prominent coarse, prickly projections. Spindles with laterally placed spinous or leaf-like processes are the dominant type in some species. Axial sheath composed of capstans, spindles, or oval forms, and undeveloped sclerites. Sclerite colours are white, various hues of yellow, amber, orange, purple and red. Anthocodials with lower hues.

Distribution. From Cape Hatteras, North Carolina to Brazil, including Bahamas, Greater and Lesser Antilles, Gulf of México, and Caribbean islands (Bayer 1961); in the eastern Pacific from southern California to Perú and presumably in Chile. The genus occurs at depths down to 200 m, but normally found less than 100 m. *Muricea midas* Bayer, 1959 is the deepest record for the genus in the western Atlantic (Bayer 1959); and *Muricea galapagensis* Deichmann, 1941 in the eastern Pacific.

Remarks. Based on calyx morphology, Verrill (1869) subdivided *Muricea* from the eastern Pacific in two main groups, one with tubular calyces (former *Eumuricea*, see Breedy and Guzman 2015) and the other with shelf-like calyces. As Breedy and Guzman (2015) noted, there are many intermediate forms referring to calyx structure and two extreme structures: tubular and shelf-like. For this reason the more sensible alternative was the division of the genus in two groups: the first, having tubular calyces (already revised by Breedy and Guzman 2015) and the second, having shelf-like calyces (in this work). The second group might be subdivided according to the branch thickness and the dominant type of sclerites of the outer coenenchyme and the calyx. The shelf-like structure of the calyx could vary from prickly prominent to slightly raised borders, and from raised adaxial borders to minute abaxial rims blending with the coenenchyme. Species groups based on the former characters are proposed herein.

Muricea fruticosa **group**

Figures 1–4

Muricea fruticosa Verrill, 1869.

Muricea fruticosa Verrill, 1869: 428; Kükenthal 1919: 752; Kükenthal 1924: 142; Harden 1979: 147; Hardee and Wicksten 1996: 129.
Muricea fruticosa typica Kükenthal 1924: 142; Harden 1979: 147.
Muricea fruticosa var. *miser* Verrill, 1869: 430; Kükenthal 1919: 752; Kükenthal 1924: 143; Harden 1979: 149 (syn. n.).
Thesea crosslandi Hickson, 1928: 354–356 (syn. n.).
Pseudothesea crosslandi (Hickson, 1928); Stiasny 1943: 64–66 (syn. n.).

Material. Lectotype (here designated). YPM 1574c, dry, Pearl Islands, Panamá, 11–14 m, F.H. Bradley, 1866. (YPM 1792, fragment from lectotype, Verrill's 1868 figured specimen). Paralectotypes. PANAMÁ: MCZ 706 (fragment from YPM 1574); MCZ 7020; USNM 33588; YPM 1566 (as *M. fruticosa* var. *miser*), dry, Pearl Islands, F.H. Bradley, 1866, no more data; YPM 1660; YPM 1574a-b, d-e, same data as the lectotype; YPM 3067, dry, with the holotype of *M. retusa* at the base, Pearl Islands, 11–14 m, F.H. Bradley, 1866.

MCZ 5002; YPM 1566a-d; ZMUC-ANT 193 (as *M. fruticosa* var. *miser*), dry, Pearl Islands, F.H. Bradley, 1866. MCZ 4126 (*Parisis fruticosa*), ZMUC-ANT 169 (as *Thesea crosslandi*), ethanol preserved, San Jose Island, Pearl Islands, 49.3 m, T. Mortensen, 27 January 1916.

Description. The lectotype is a large, bushy colony 35 cm tall, and about 45 cm wide. Four main branches, 25–35 mm in diameter, somewhat flattened, arise from an irregular, 52 mm diameter holdfast. The holdfast is spreading and raised about 30 mm above substrate, the specimen is attached to a plaster base for a past years museum display (Fig. 1A). The main branches subdivide very close to the base in secondary branches that immediately divide and subdivide in an irregular manner producing branches and branchlets closely placed, no more than 20 mm apart, at angles 45°–90°. Secondary branches and branchlets are 3–5 mm in diameter, mostly crooked and curved upwards or downwards. Some anastomosis occurs at the ends of branchlets. Unbranched terminal ends are 3–5 mm in diameter and 15–40 mm long. The axis is clear amber at the tips and darker at the base. The calyces are close together, or few millimetres apart, not imbricate, spreading outward and upward. They have large, strong, sharp sclerites forming the shelf-like projecting platform, 1–1.2 mm long, on the lower side (Fig. 1B). Polyps are on the upper side of the prominent calyces. The calyx sclerites give a prickly appearance to the

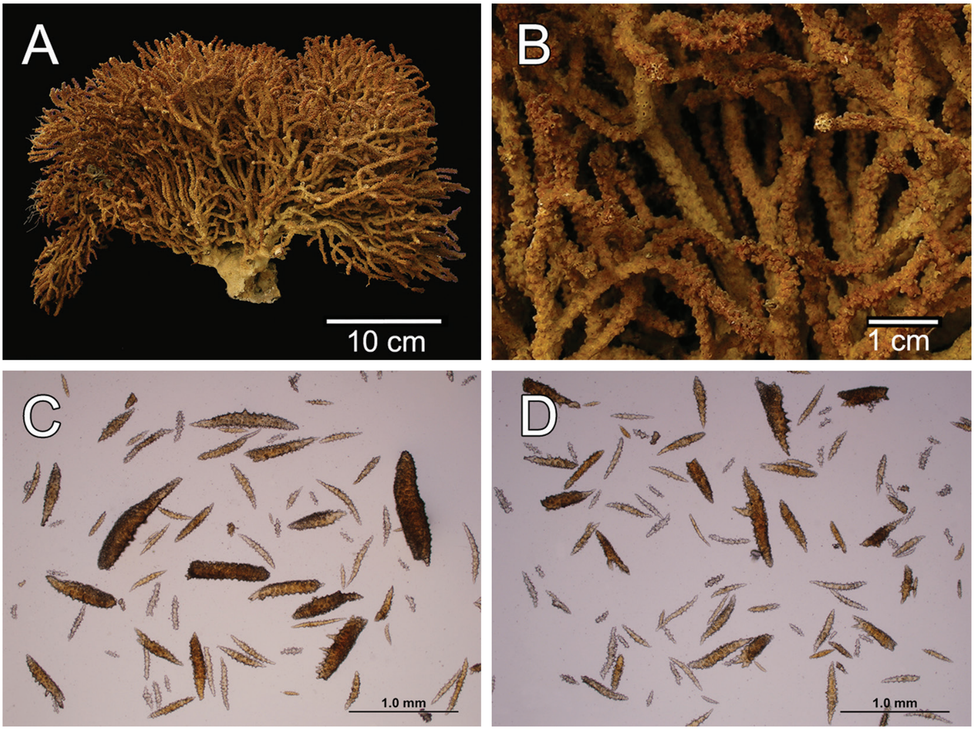

Figure 1. *Muricea fruticosa* Verrill, 1869 YPM 1574c. **A** Colony **B** Detail of branches **C–D** Sclerites, light micrograph.

colony (Fig. 1A–B). The calyx size and spacing vary from the larger branches to the thinner, being larger and acute, and closer placed at the branchlets and shorter, blunt, and distant at the main branches. The polyp apertures are covered by anthocodial sclerites. The coenenchyme is thin, composed of reddish-brown, amber, pale yellow to whitish sclerites (Fig. 1C–D). The outer coenenchyme and the calycular sclerites are composed of large, conspicuous unilateral spinous spindles visible to the naked eye (Fig. 2A–B). These spindles are of diverse shapes, with blunt or acute ends, or irregular with one acute end and the other blunt, with bifurcated ends or with spiny tips. The unilateral spinous spindles are basically spinulose on the outer surface and tuberculate on the inner surface in this species, some tubercles are large, sharp and spiny. The spindles are deep reddish brown, brownish yellow to pale yellow, and combinations of them (Fig. 1C). These spindles are 0.53–2.1 mm long, and 0.11–0.55 mm wide (Fig. 2A–B); they are forming the calyces and lying between them. The spindles bordering the calyx are long with stout, terminal spikes, 0.32–1 mm long and 0.07–0.2 mm wide, some with bifurcated warty ends (Fig. 2B). The axial sheath is composed of small, pale yellow to colourless spindles, 0.30–1 mm long and 0.05–0.12 mm wide, with whorls of small warts, and long spindles (Fig. 2C–D). Anthocodial sclerites are of a yellow to a very pale yellow colour, arranged in irregular points, mostly composed of warty spindles, 0.40–0.64 mm long,

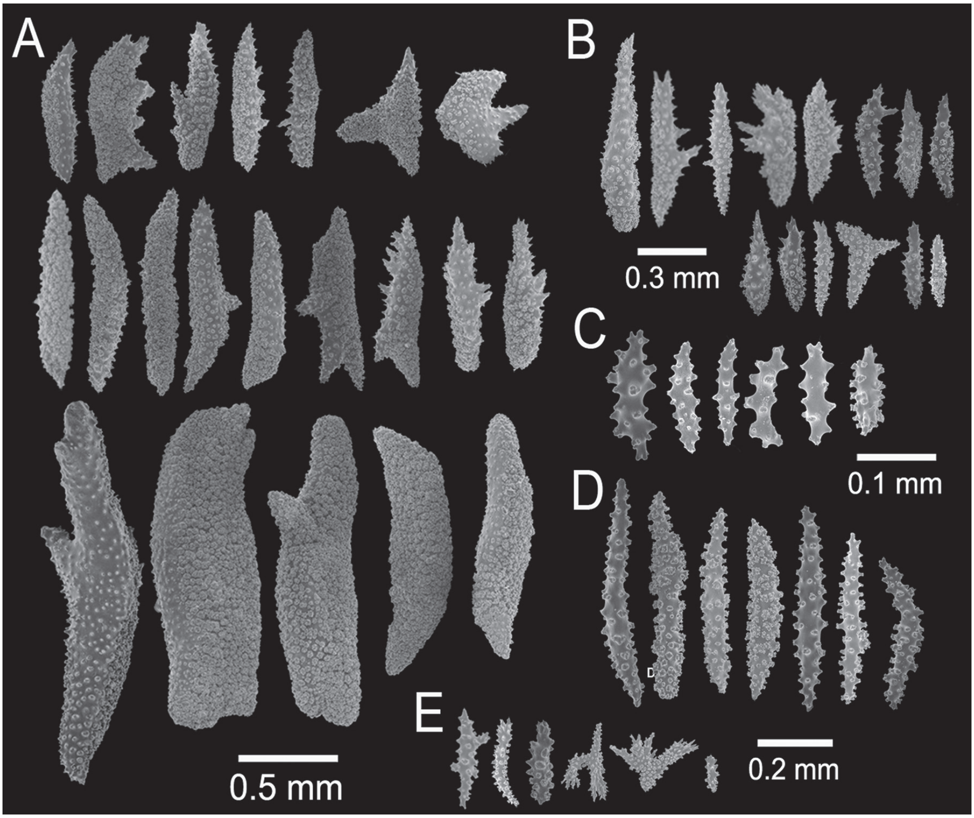

Figure 2. *Muricea fruticosa* Verrill, 1869 YPM 1574c. **A–B** Calycular and coenenchymal sclerites **C–D** Axial sheath **E** Anthocodial sclerites.

and 0.07–0.1 mm wide, small warty rods 0.2–0.38 mm long and 0.5–0.1 mm wide, and small branched spindles around 0.20 mm long, and 0.15 mm wide (Fig. 2E).

The colony is bicoloured, reddish brown at the tips, fading to a light yellow towards the base (Fig. 1A–B).

Habitat and variability. There are two colour patterns in the syntype series, a marked bicoloured pattern, with dark reddish tips and whitish to pale yellow stems (Fig. 3C–D), and intermediate patterns less differentiated (Fig. 3B). The bicoloured pattern is more evident in small specimens than in large colonies (Figs 1A, 3A), and in some case there is a dominance of white colour in the branches. In large colonies, we have observed both patterns in different branches in the same colony (Fig. 3A, arrows). The lectotype (YPM 1574c) is the largest specimen and with the most profuse branching, some other colonies in the syntypes are formed by just a few branches. Our recent collected material shows the bicolour pattern and the colonies can reach up to 25 mm long and 30 mm wide. They are mostly bushy, openly ramified colonies with white polyps. Some specimens change colour after drying, the white part becomes a rusty reddish. When preserved in alcohol they keep the colours unaltered and do not

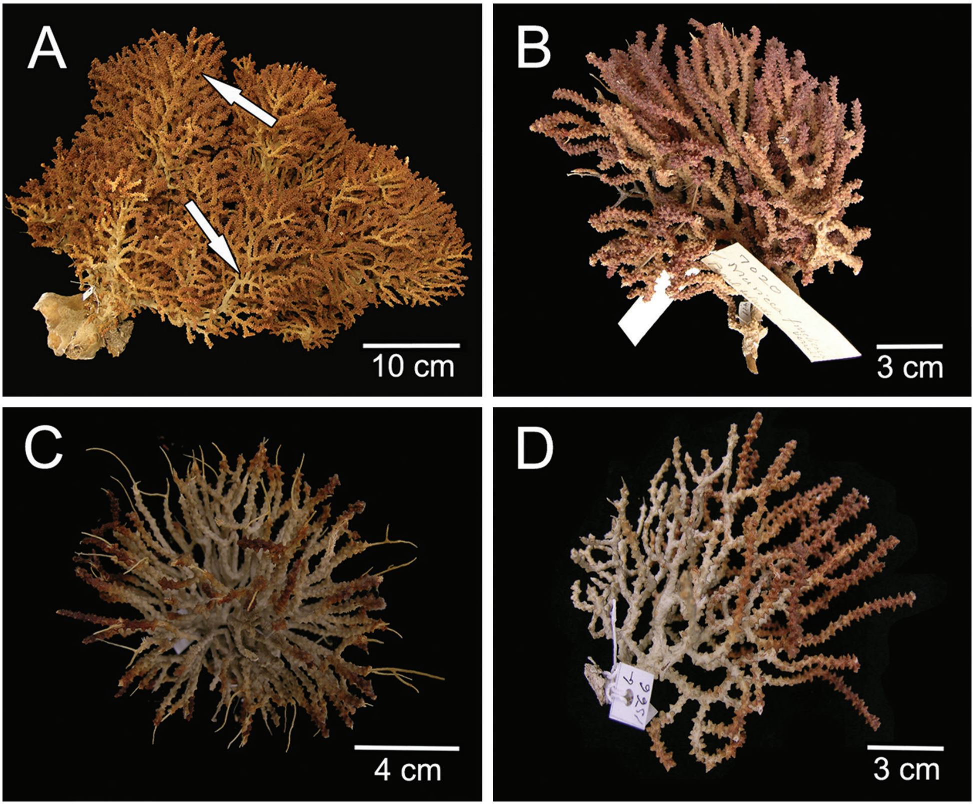

Figure 3. *Muricea fruticosa* Verrill, 1869 Morphological variation. **A** YPM 1574a, arrow showing two branch variations in the same colony **B** MCZ 7020 **C** YPM 1566d **D** YPM 1566b.

tint the spirit. The sclerites of the paralectotypes and the other material analysed are in the variation range of the species. The calyces can be more sparsely set and shorter in some colonies. The species is found on rocky substrata in clusters or solitary, attached to small debris or shells, especially when sparsely distributed. The colonies are in caves or exposed to the currents. They are found in clear or turbid waters. *Muricea fruticosa* is found at various localities in the Galápagos Islands, exposed to moderate currents and in caves, reaching no more than 15 cm wide (Fig. 4A) (Hickman 2008, Breedy et al. 2009). The deepest record for the species is down to 102 m at Cocos Island seamounts (Fig. 4B), but it is found shallower in other places from 8 to 25 m deep.

Distribution. From México to Perú. Type locality, Pearl Islands, Panamá.

Remarks. Verrill (1869) described *M. fruticosa* with a collection of specimens from Panamá, and *M. fruticosa* var. *miser* based on some small specimens from the same locality but from shallower waters. He pointed out that the differences between the species and the variety are the small size of the colonies and the marked bicolour pattern. He also noticed that the calyces at the base of the branches were shorter, and that the sclerites were similar to the typical form but smaller. However, the reduction

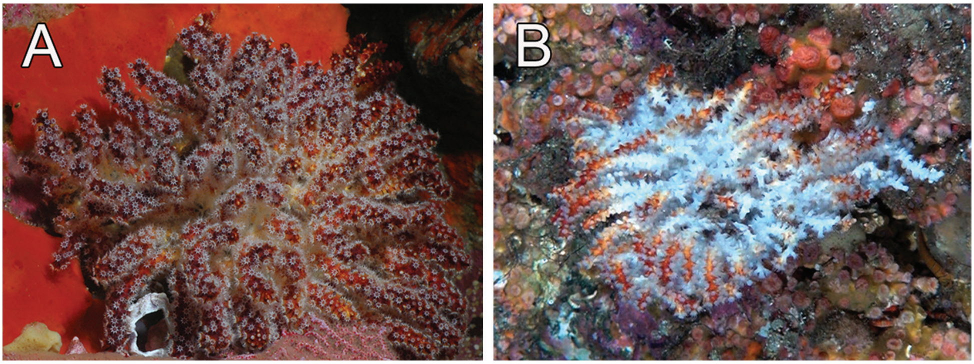

Figure 4. *Muricea fruticosa* Verrill, 1869. **A** *In situ* colonies, with expanded polyps, Nameless Islet, Galápagos Islands National Park, Ecuador. Photograph: Graham Edgar **B** *In situ* colonies, Everest mount, Isla del Coco National Park, 95 m deep. Photograph: *DeepSee* submersible.

of the calyx size at the base of the branches occurs in most species of the genus, and the size of sclerites is in the range of variation found in the examined specimens. Hickson (1928) described *Thesea crosslandi* with specimens from Taboga Island, and San José Island (Pearl Islands), Panamá. Later, Stiasny (1943) re-examined Hickson specimens acknowledging the differences with the genus *Thesea* Duchassaing & Michelotti, 1864, and assigned the genus *Pseudothesea* Kükenthal, 1919 to the specimen. However, the description and the sclerite illustrations given by Hickson (1928), and Stiasny (1943) clearly refer to *M. fruticosa*, and we corroborated this after examination of Hickson's specimens in the BM. For this reason, *T. crosslandi* and *P. crosslandi* are herein treated as synonyms of *M. fruticosa*.

In order to establish the identity of this species, the YPM 1574c specimen is herein designated as the lectotype of *M. fruticosa*.

Other material revised. COSTA RICA: UCR 482, 486, dry, Punta Conejo, Herradura, Puntarenas, 10 m, J. Cortés, 21 September 1996; UCR 520 (3), dry, Nicoya Gulf, CJ Kalb, 2 March 1967; UCR 576, dry, San Juanillo, Guanacaste, 12.5 m, J. Cortés, 14 June 1991; UCR 588, dry, Pitahaya Beach, Guanacaste, 20–23 m, J. Cortés, 15 June 1991; UCR 837-839, dry, Ballena Bay, Nicoya Gulf, 40 m, R/V Victor Hensen, 2 December 1993. ECUADOR: CASIZ 105032, ethanol preserved, Santa Cruz Island, Nameless Islet, Galápagos Islands, 20 m, P. Humann, no collection date. CDRS 03-76, ethanol preserved, Los Hermanos, Galápagos Islands, 9 m, C. Hickman, 17 January 2003. CDRS 06-33, ethanol preserved, Nameless Island, Galápagos Islands, 9–10 m, C. Hickman, 25 May 2006. IIN 7, 9, dry, Tambip, Salinas, 12–14 m, F. Rivera, P. Martínez, 20 July 2010; IIN 21, dry, Bajo Lunes, Salinas, 18 m, F. Rivera, P. Martínez, 21 July 2010; IIN 34, 69, Gigima, Salinas, 12–14 m, F. Rivera, P. Martínez, 22 July 2010; IIN 88, 89, 123, dry, Los Ahorcados, Machalilla National Park, 10–12 m, F. Rivera, P. Martínez, 25 July 2010. EL SALVADOR: UCR 1938, ethanol preserved, Departamento la Libertad, Playa Mizata, J. Segovia, 27 February 2010. MÉXICO: CASIZ 097734, ethanol preserved, Roca Partida, South side, Revillagigedo Islands, 36 m, R.J.

Van Syoc, M/V "Royal Star, Clipperton Island Expedition 1994, 2 May 1994. CASIZ 103387, ethanol preserved, Boca del Tule to Arena Blanca, Baja California Sur, 30 m, W. Lee, J. Moran, J. McCosker, 26–27 April 1976; CASIZ 100843, ethanol preserved, Roca Alejos, Baja California Sur, 18–33, Robert Van Syoc, Cordell Expeditions, 5 November 1990. STRI 1124, 1130B, 1151, ethanol preserved, La Blanca, Oaxaca, 46–48 m, R. Abeytia, 23 August 2004. PANAMÁ: STRI 405, Seca Grande Island, 20 m, H. Guzman, 26 August 2002; STRI 534, Bajo Bolano, 25 m, H. Guzman, 16 April 2003; STRI 572, ethanol preserved, Viudas Island, 10–20 m, H. Guzman, 18 April 2003; STRI 836, San Telmo Island, 27 m, H. Guzman, 7 April 2004; STRI 848, Sur Pacheca, 2 m, H. Guzman, 20 April 2004; STRI 865, Achotines, 3–10 m, H. Guzman, 5 May 2004; STRI 879, Pearl Island, H. Guzman; STRI 888, Pearl Island, 25 m, H. Guzman, 15 August 2004; STRI 892, Pearl Island, H. Guzman, 15 August 2004; STRI 942, Pearl Island, 3–20 m, H. Guzman, 23 September 2004. USNM 34063, dry, Gulf of Panamá, L.C. Cash, no more data. PERÚ: CZA 230, dry, Foca Island, 12–15m, Y. Hooker, 14 June 2009; CZA 255; 293, dry, Punta Sal, 12–15m, Y. Hooker, 2 July 2011.

Muricea formosa Verrill, 1869

Figures 5–7

Muricea formosa Verrill, 1869: 434–436; Kükenthal 1919: 752; Kükenthal 1924: 143; Harden 1979: 146.

Material. Holotype. YPM 1621a, ethanol preserved, Zorritos, Tumbes Department, Perú, 5 m, F.H. Bradley, 1866–1867. Schyzotypes. PERÚ: MCZ 35945, 3 dry fragments, YPM 1621b, ethanol preserved fragment, Zorritos, 5 m, F.H. Bradley, 1866–1867.

Description. The holotype is a 10 cm long and 6 cm wide colony, branching lateral, in one plane and irregularly dichotomous (Fig. 5A). It arises from a conical holdfast about 100 mm tall and about the same in diameter. Two main branches bifurcate from a short stem, 7.5 mm in diameter, producing secondary branches that subdivide again at distances of 5–50 mm apart. The branches split at angles of 45° to 90°. The branches are 6–9 mm in diameter and little tapered toward the tips. The unbranched terminal ends are up to 28 mm long. The calyces are all around the branches, close together, not imbricate (Fig. 5B). They are elongated, sub-conical, projecting perpendicular to the branches, and directed upwards at smaller angles at the upper branches. The calyces reach up to 3 mm long with projecting spiny borders. The sclerites are all whitish to colourless (Fig. 5C). The outer coenenchyme and calycular sclerites are elongated with both ends sharp or with one end sharp and the other truncated or forked. They are unilateral spinous spindles, 0.33–1.5 mm long and 0.14–0.25 mm wide (Fig. 6A), the inner side with numerous small warts and the outer side with short spines. The spindles bordering the calyx are prickly spindles and modified leaf spindles, 0.3–0.475 mm long and 0.04–0.1 mm wide, with lateral or terminal spiny processes (Fig. 6B) that project beyond the calyx border, and elongated warty spindles, 0.41–0.7 mm long and

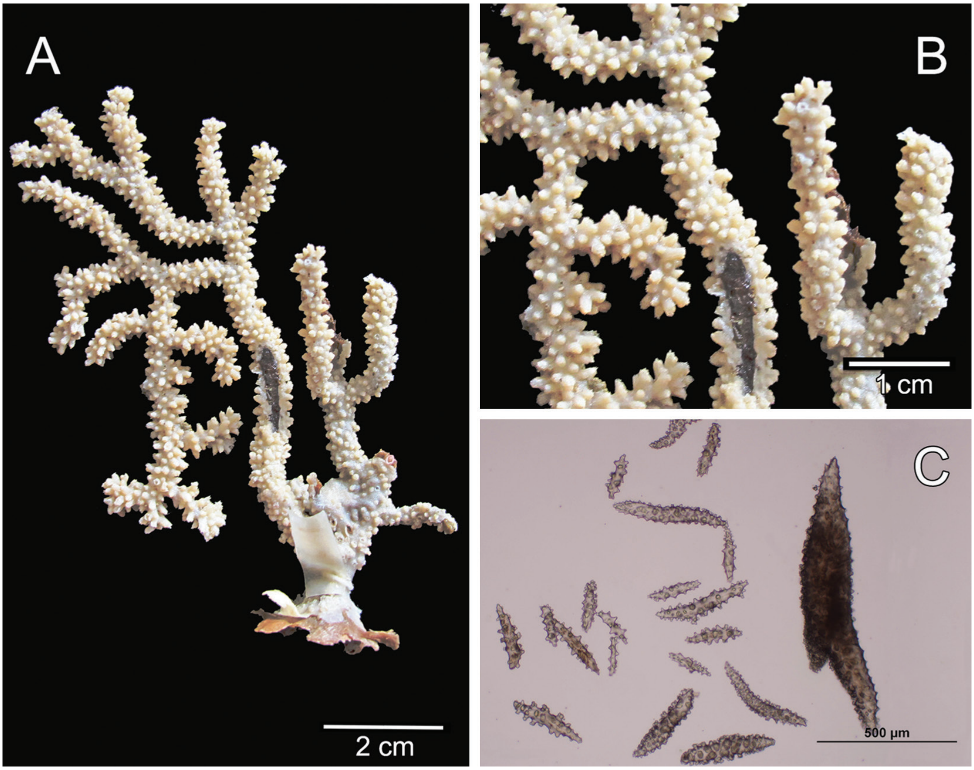

Figure 5. *Muricea formosa* Verrill, 1869 YPM 1574c. **A** Colony **B** Detail of branches **C** Sclerites, light micrographs.

0.075–0.1 mm wide (Fig. 6C). The axial sheath is mostly composed of tuberculate, irregular spindles, 0.195–0.25 mm long and 0.084–0.13 mm wide (Fig. 6D). Anthocodial sclerites 0.086–0.175 mm long and 0.034–0.075 mm wide (Fig. 6E).

Colour of the colony is white.

Habitat and variability. The species has been found living on rocky bottoms, caves and outcrops at 10–13 m in depth. The colonies are mostly growing in one plane, but in some cases they extend in two or three planes (Y. Hooker pers. comm.) (Fig. 7A). The examined colonies are bushy, mostly with lateral and irregular branching subdividing up to 10 times. Some branch anastomosis occurs. Colonies reach up to 25 cm long by 21 cm wide and bifurcate up to 10 times, diameter of branches reaches up to 10 mm. Sclerites are as in the holotype. The colonies are infested with a polychaete species that perforates the axes, and are also colonised in some branches by small cirripedia.

Distribution. Reported from Las Ánimas Islet, Gulf of California by Harden (1979) and Canoas de Punta Sal, Perú (Y. Hooker pers. comm.), and Mazatlán, México (J.L. Carballo pers. comm.). Type locality, Zorritos, Perú.

Remarks. Verrill (1869) described this species with a single specimen that was infested by a parasitic worm; this is consistent with the YPM 1621a specimen (Fig. 7A). All the recently collected material from Perú by Y. Hooker (2011–2012) is also hosting

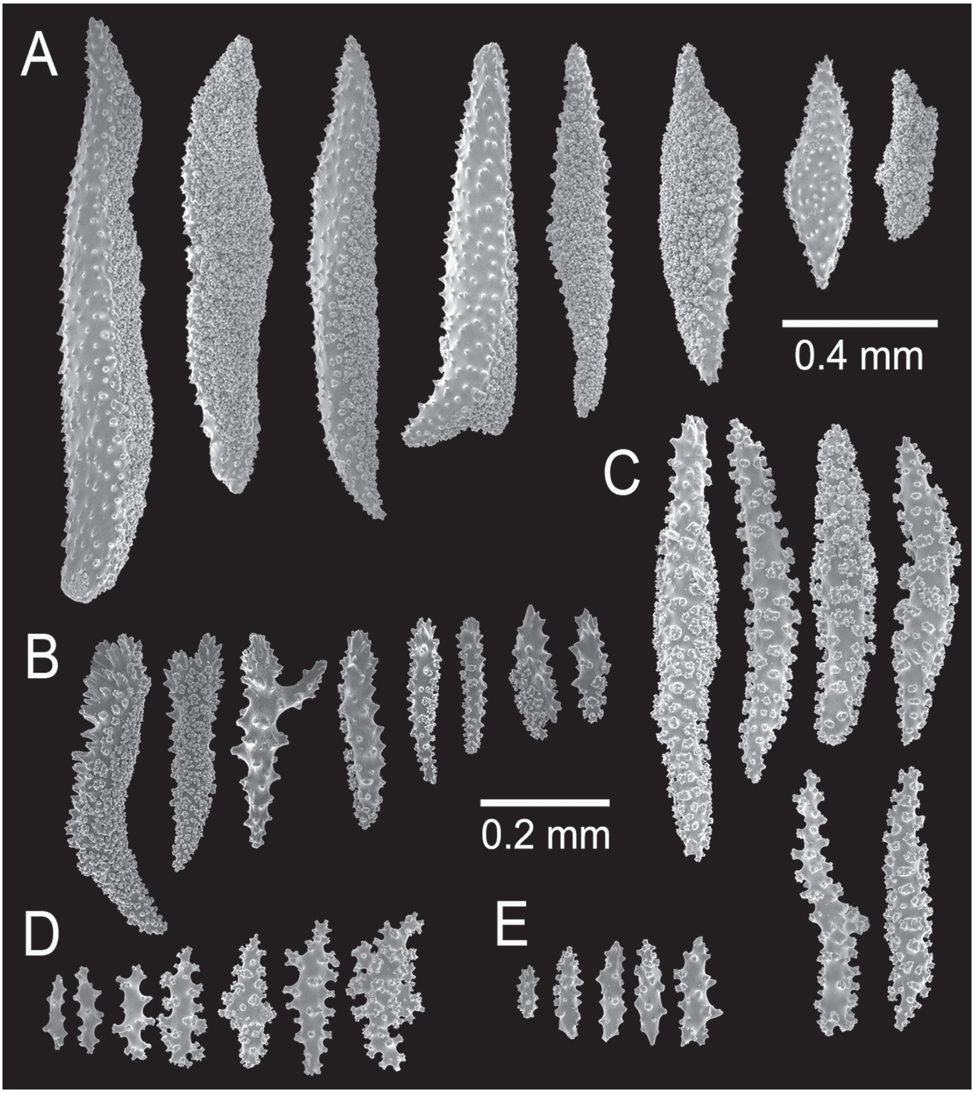

Figure 6. *Muricea formosa* Verrill, 1869 YPM 1574c. **A–C** Calycular and coenenchymal sclerites **D** Axial sheath sclerites **E** Anthocodial sclerites.

the same polychaete (Fig. 7A–B). We examined two small specimens from México that also show the tunnels and axial projections made by the worm.

Other material revised. MÉXICO. M 18, dry, Punta Tiburón, Kino Bay, Sonora, 5.5 m, J.L. Carballo, 11 October 1999. PERÚ. CZA 286, dry, Canoas de Punta Sal, 12 m, Y. Hooker, 2 July 2011. CZA 412–416, 419, 424, dry, Canoas de Punta Sal, 13 m, Y. Hooker, 13 August 2012. CZA 286, Canoas de Punta Sal, 13 m, Y. Hooker, 2 July 2011. CZA 417–418, 420–423, Cabo Blanco, Piura, Y. Hooker, 13 August 2012. CZA 425, dry, El Ñuro, Piura, 10 m, Y. Hooker, 8 August 2012.

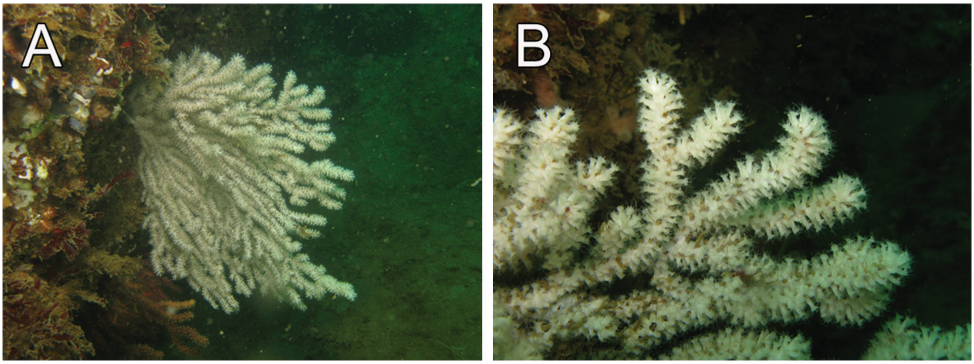

Figure 7. *Muricea formosa* Verrill, 1869. *In situ* colonies, Canoas de Punta Sal, Perú. Photograph: Yuri Hooker.

Muricea aspera Verrill, 1869

Figures 8–9

Muricea aspera Verrill, 1869: 448–449; Kükenthal 1919: 752; Kükenthal 1924: 144–145; ?Harden 1979: 143.

Material. Lectotype. YPM 1663A, dry fragment, Panamá, F.H. Bradley, 1866.

Paralectotypes. PANAMÁ: MCZ 35970; YPM 1663B-C, dry fragments, F.H. Bradley, 1866. YPM 1657, ethanol preserved, Pearl Islands, F.H. Bradley, 1866.

Description. Type series is comprised of fragments, the larger ones are 12 cm tall and 9 cm wide, and 8.5 cm tall and 4.5 cm wide, probably fragments of a larger specimen (Verrill 1869).

The lectotype is 12 cm tall and 9 cm wide (Fig. 8A), the branching is lateral and irregular; branches subdivide up to 5 times. Branches are 4 mm in diameter, they subdivide producing branchlets, 4–5 mm in diameter, closely placed, about 6–12 mm apart, mostly at angles of 45°, but some stick out at 90° angles. Unbranched terminal ends are 6–30 mm long. Calyces are prominent, 1–2 mm long from the base to the tip, with lower borders elongated, with straight tips or slightly curved inwards (Fig. 8B). Calyces are close together and slightly imbricate. Coenenchyme is thin, covered with long spindles. All sclerites are of a pale brown to whitish colour (Fig. 8C). The coenenchymal and calycular sclerites are mostly unilateral spinous spindles with one warty side and the other with sparse short spines. These spindles are 0.60–1.35mm long and 0.10–0.35 mm wide (Fig. 9A). Furthermore, elongated thin spindles are present, 0.80–1.15 mm long and 0.10–0.13 mm wide (Fig. 9B). The axial sheath is composed by irregular radiates and spindles, 0.14–0.40 mm long and 0.055–0.085 mm wide (Fig. 9C). Anthocodial sclerites are mostly flat warty rods, 0.15–0.25 mm long and 0.02–0.04 mm wide (Fig. 9D).

Colour of the colony is light brown.

Distribution. Only reported for the type locality at extreme low waters (according to Verrill 1869). Type locality, Panamá.

Figure 8. *Muricea aspera* Verrill, 1869 YPM 1663a. **A** Colony **B** Detail of branches **C** Sclerites, light micrograph.

Remarks. Verrill (1869) described this species from two colony fragments that constitute the type series of *M. aspera*.

Other material revised. PANAMÁ: STRI 559, ethanol preserved, Palito afuera Island, 5–8 m, H.M. Guzman, 17 April 2003.

Muricea echinata Verrill, 1866

Figures 10–11

Muricea echinata Verrill, 1866: 328 (pars.); Verrill 1869: 426–427; Kükenthal 1919: 752; Kükenthal 1924: 143; Hickson 1928: 361–363.

Muricea echinata var. *flabellum* Verrill, 1869: 427–428; Kükenthal 1919: 752; Kükenthal 1924: 143.

not *Eunicea echinata* Valenciennes, 1855: 13 (nom. nud.); Kükenthal 1924: 123.

not *Muricea echinata* Milne Edwards & Haime, 1857: 143

Material. Lectotype: YPM1565d, dry, Pearl Islands, Panamá, F.H. Bradley, 1866.

Paralectotypes: PANAMÁ: MCZ 67511, YPM 560 a-f, YPM 1565a,c-h, dry, Pearl Islands, F.H. Bradley, 1866.

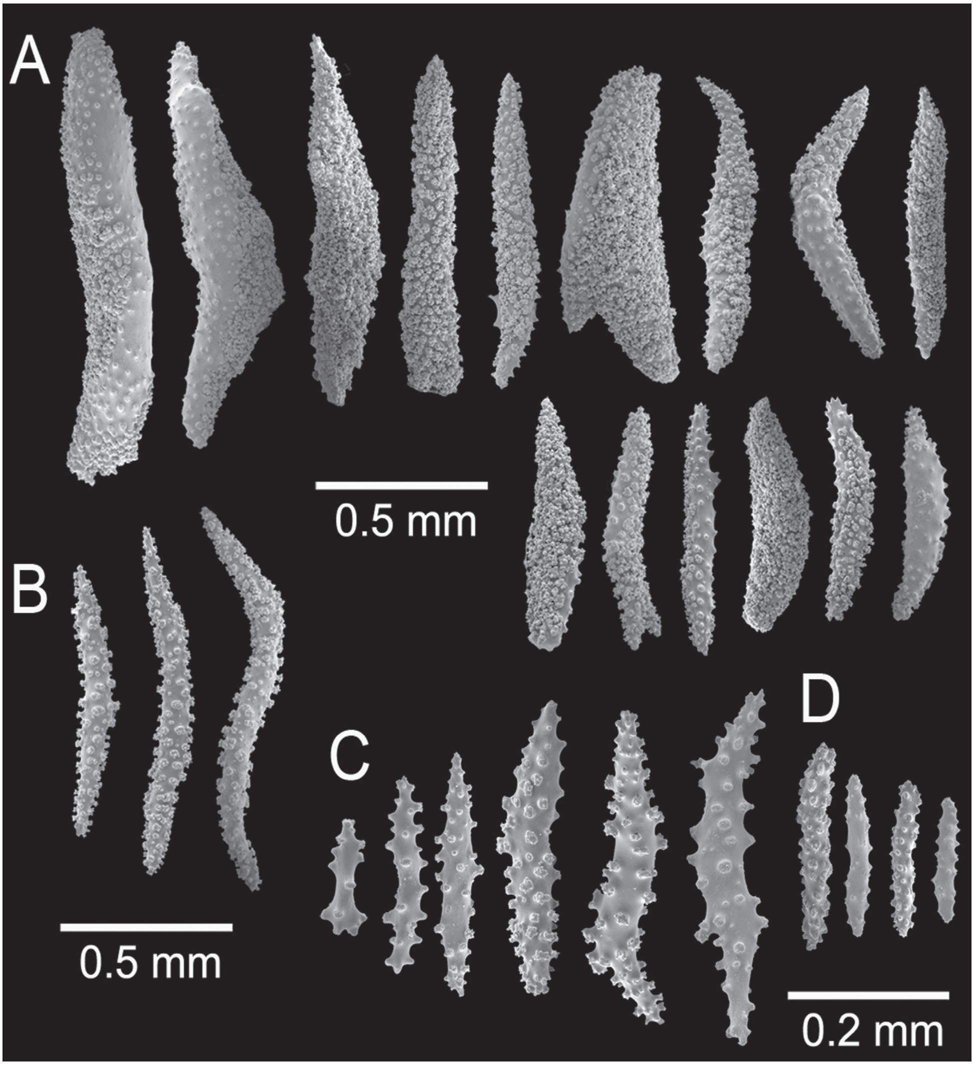

Figure 9. *Muricea aspera* Verrill, 1869 YPM 1663a. **A–B** Calycular and coenenchymal sclerites **C** Axial sheath **D** Anthocodial sclerites.

Description. The lectotype is a colony 8.5 cm long and 7 cm wide, branching lateral and irregular and spreading in almost one plane (Fig. 10A). The main stem is 15 mm tall and 8 mm in diameter, it subdivides in three secondary branches, 5–7 mm in diameter, and then subdivides up to 6 times in an irregular manner producing subordinate branches, no more than 15 mm apart, at angles 35°–90°. These branches are of the same diameter, or thinner at the base and little thicker toward the tips, which are wide and clavate. The secondary branches are mostly crooked and curved upwards. About 1 cm oval portion of the holdfast remains. No anastomosis occurs. Unbranched terminal ends are 5–7 mm in diameter and 6–30 mm long. Axes are amber at the tips and darker at the base. Calyces are all around the branches, around 0.5 mm apart, not

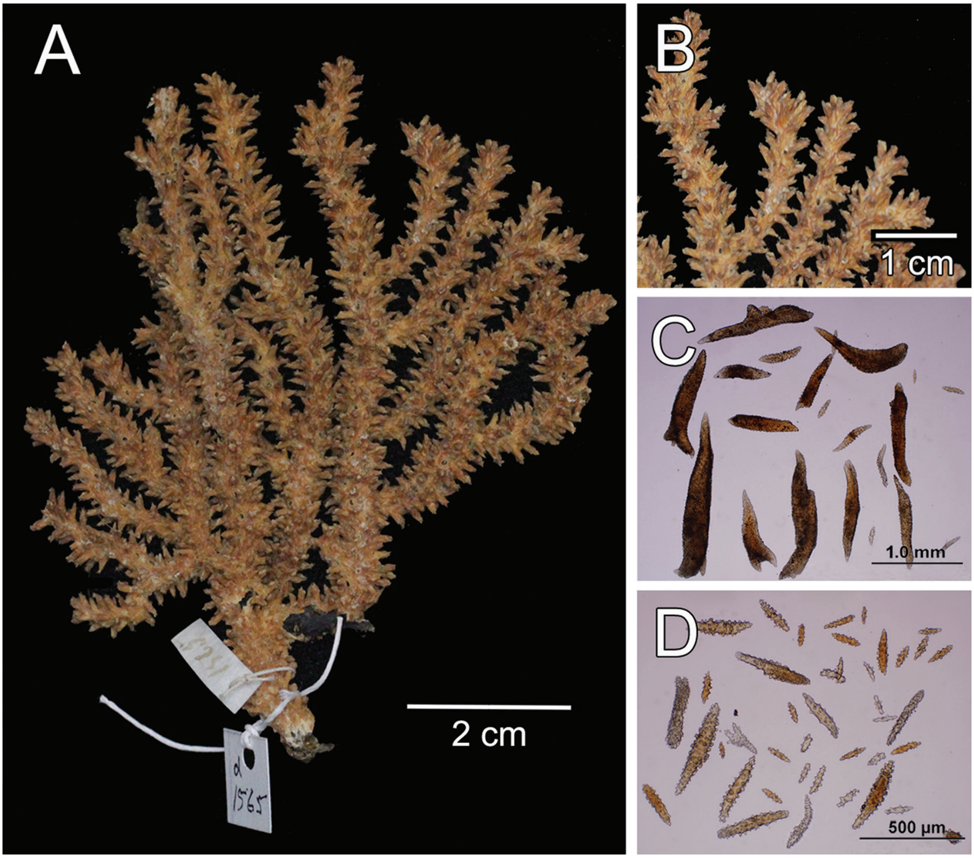

Figure 10. *Muricea echinata* Verrill, 1866. YPM 1565d. **A** Colony **B** Detail of branches **C–D** Sclerites, light micrographs.

imbricate (Fig. 10B). They are prominent, up to 3 mm long, and 1–2 mm wide at the base, covered with large spindles with sharp ends, some of them project from the outer side (abaxial) elongating the lower border. The calyx size and spacing vary from the larger branches to the thinner, being larger and acute, and closer arranged at the upper branches and shorter and more distant at the lower or main branches. Polyps are small, on the upper (adaxial) side of the calyces. Coenenchyme is thin, outer coenenchyme is composed basically by the calyx sclerites, they are orange and light brown, the larger are darker (Fig. 10C–D). The outer coenenchymal and calycular spindles are of diverse shapes, unilateral spinous, spinulose on the outer surface and tuberculate on the inner, with conspicuous forms with bifurcated ends or cuspidate prolongations. These spindles are 1.55–2.4 mm long and 0.20–0.32 mm wide (Fig. 11A). Furthermore modified prickly-spindles are present, 0.35–0.6 mm long and 0.1–0.22 mm wide, with lateral thorny processes (Fig. 11B) and some with bifurcated ends. The axial sheath is composed of small, light brown warty spindles, 0.3–0.53 mm long and 0.09–0.13 mm wide (Figs 10D, 11C). Anthocodial sclerites are light brown rods and whitish-

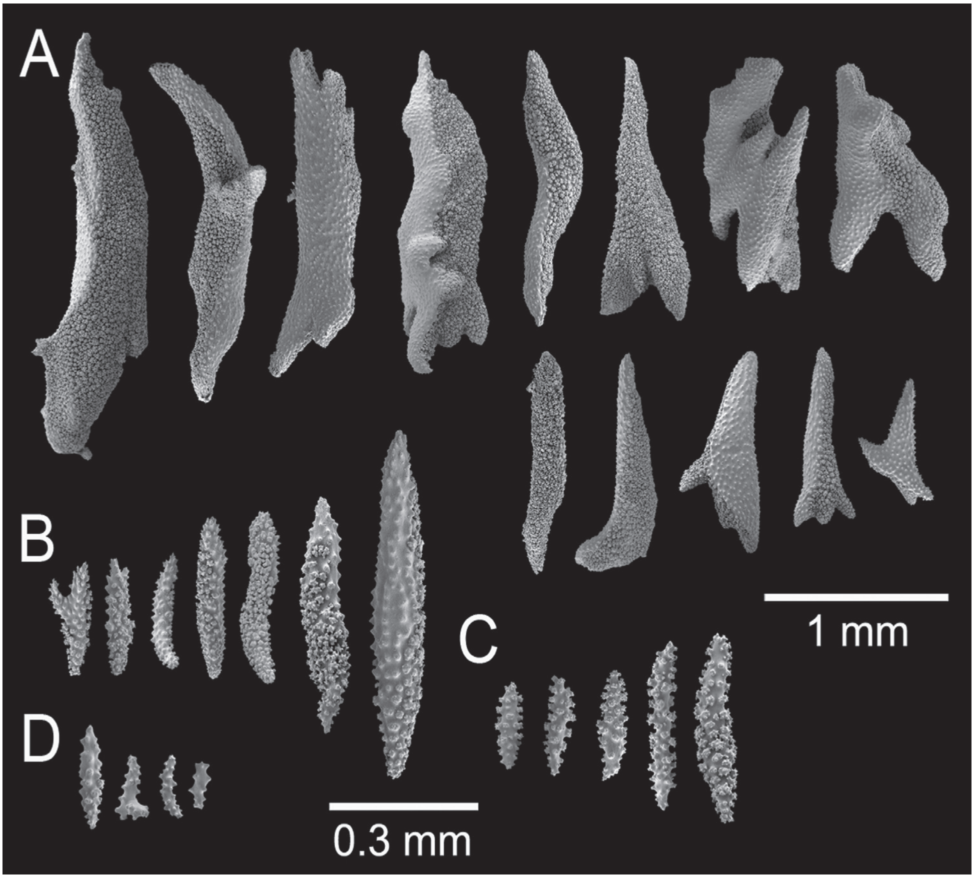

Figure 11. *Muricea echinata* Verrill, 1866. YPM 1565d. **A–B** Calycular and coenenchymal sclerites **C** Axial sheath sclerites **D** Anthocodial sclerites.

branched spindles (Fig. 11D), 0.07–0.2 mm long and 0.025–0.05 mm wide. They are longitudinally arranged at the base of the tentacles.

Colour of the colony is reddish brown.

Variability. The examined colonies are up to 10 cm tall and up to 14 cm wide, branching irregular, spreading in almost one plane. Calyces can be up to 3.5 mm long. Colour of the colonies varies to a deeper orange hue.

Remarks. *Muricea echinata* was erroneously mentioned by Verrill (1866) as *M. echinata* Valenciennes, 1855 (which was originally *Eunicea echinata*), with a minimal description. Later Verrill (1869) re-described the species with specimens from Pearl Islands, Panamá. We searched for the *M. echinata* type in the MNHN where Valenciennes' specimens are kept, and found two specimens labeled as *M. echinata*: one, in the dry collection collected by Duchassaing in 1851 (that is the only information available), but only the wooden base of the specimen is left (S. Cairns pers. comm.); and the other collected by Agassiz in 1863, in the wet collection. None of these specimens could have been Valenciennes species because Duchassaing collections of *Eunicea* and *Muricea* species were from the Atlantic. Moreover, the wet specimen was collected after the species was named. Besides, there is no reference that could corroborate that Verrill analysed any of Valenciennes' specimens. We conclude that *Eunicea* (*Muricea*) *echinata* Valenciennes was a *nomen nudum* or an inexistent species. Consequently, Verrill was the author of the species, producing the first description. Many different specimens have been assigned to this species in museum collections because its status was not clearly defined. We designate the specimen YPM 1565d as the lectotype to establish the taxonomic status of *M. echinata*. Verrill (1869) described *M. echinata* var. *flabellum* based on colonies with more branches, but in any other aspect this variety was consistent with the typical form. Therefore we consider it a synonym.

Other material revised. COSTA RICA: USNM 44213, dry, Golfo de Nicoya, M Valerio, 20 February 1931. MÉXICO: USNM 42132, dry, Baja California, La Paz Bay, AL Herrera, 27 November 1919; USNM 57094, dry, Nayarit, West of Tepic, CR Orcutt, 30 August 1922. PANAMÁ: BM 1946.1.14.47; BM 1946.14.46; BM 30.6.17.17, dry, rock pools, low water mark, off Balboa, C. Crossland, 1914–1916. MNHN no catalogue number, ethanol preserved, M. Agassiz, 1863.

Muricea galapagensis Deichmann, 1941

Figures 12–13

Muricea (?) *galapagensis* Deichmann, 1941: 6–9; Harden 1979: 150–151.

Material. Holotype. USNM 43449, a colony and a fragment, Elizabeth Bay, Albemarle Island, Galapágos Islands, Ecuador, 91.4 m, W.L. Schmitt, Presidential Cruise, 26 July 1938.

Description. The holotype is a 10 cm tall and about 5 mm wide colony, it has one broken branch and according to Deichmann's illustration (1941: 7, Fig. 2) the colony was wider and openly branched. The stem, 1 cm long and 0.3 cm in diameter, is attached to a black coral fragment by a conical holdfast about 1 cm in diameter. The stem subdivides (the lower branches are stumps) producing few long secondary branches sparsely placed, 3.7–29 mm apart, diverging at angles 30°–90° and curved upwards. Branches are 1.6–3 mm in diameter all along their length, and bifurcate up to 4 times (Fig. 12A). Unbranched terminal ends reach up to 80 mm long. The axis is clear amber at the tips and darker at the base. The calyces are low shelf-like, spreading outward and at right angles, no more than 1 mm long, not close or imbricate (Fig. 12B–C). The lower border is composed of 3-6 projecting spindles and the adaxial border, when present, of smaller spindles in an indistinct rim. The coenenchyme is thin, composed of amber to light orange sclerites (Fig. 12D–E). The outer coenenchyme and the calyces are composed of large, usually curved, unilateral spinous spindles that project beyond

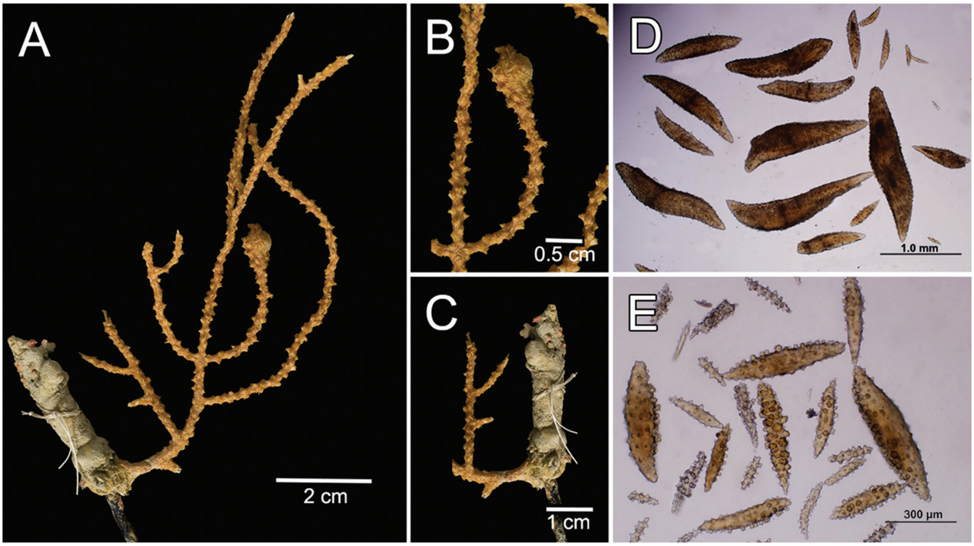

Figure 12. *Muricea galapagensis* Deichmann, 1941. USNM 43449. **A** Colony **B–C** Detail of branches, photographs: Walter Larrimore **D–E** Sclerites, light micrographs.

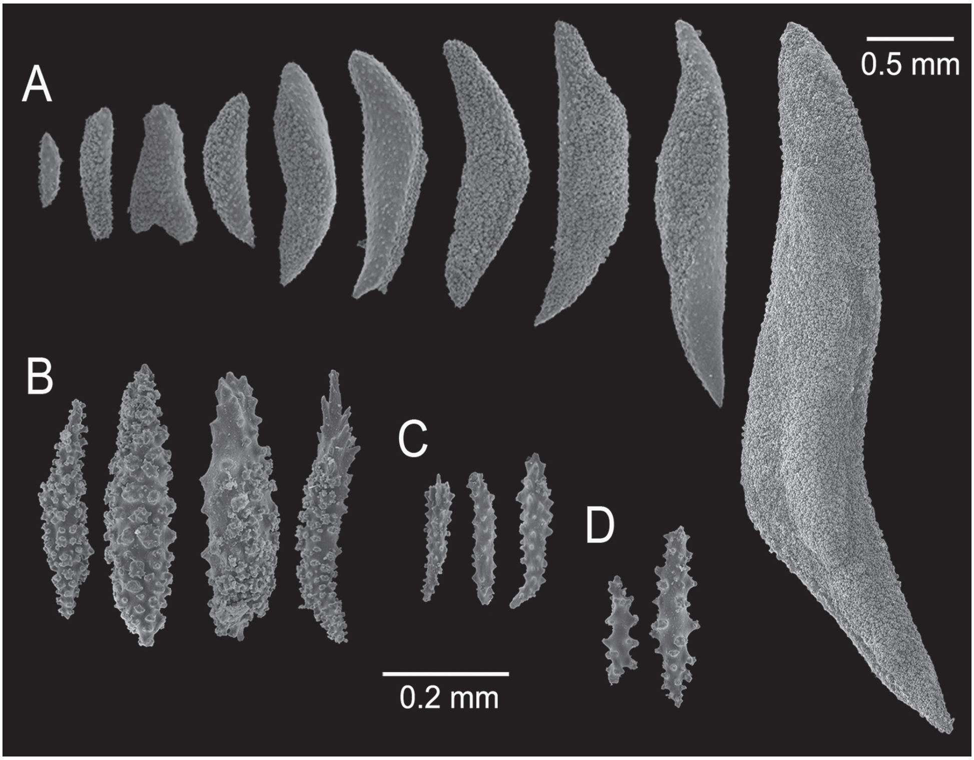

Figure 13. *Muricea galapagensis* Deichmann, 1941. USNM 43449. **A–B** Calycular and coenenchymal sclerites **C** Anthocodial sclerites **D** Axial sheath sclerites.

the calyx borders (Fig. 13A–B). They are visible to the naked eye. The largest size of sclerites in the genus is found in this species. These spindles are of diverse shapes, with blunt, acute or bifurcated ends, 0.43–4.1 mm long and 0.12–0.75 mm wide (Fig. 13A). Furthermore, warty spindles and prickly spindles are present, 0.35–0.45 mm long and 0.075–0.11 mm wide (Fig. 13B). The axial sheath is composed of warty spindles, 0.17–0.30 mm long and 0.04–0.08 mm wide (Fig. 13D). The polyp apertures are covered by pale orange and whitish anthocodial rods and small prickly spindles that were probably transversely placed at the base of the tentacles (Deichmann 1941). These rods and spindles are 0.2–0.25 mm long and 0.04–0.06 mm wide (Fig. 13C).

The colony is light orange (Fig. 12A–B).

Distribution. Reported only from the type locality, Elizabeth Bay, Albemarle Island, Galapágos Islands, Ecuador.

Remarks. Deichmann (1941) described this species with a specimen attached to a colony of *Antipathes galapagensis* Deichmann, 1941 that was pulled up with an anchor chain at the type locality. She reported another smaller and paler specimen in the MCZ (96.6 m, *Albatross* Sta. 3405). The specimen USNM 43449 represents the holotype.

Species-group comparison summary

The *Muricea fruticosa* group comprises five species: *M. fruticosa*, *M. formosa*, *M. aspera*, *M. echinata* and *M. galapagensis*. This species-group is characterised by thin branches, long, prickly calyces and outer coenenchyme and calyces with unilateral spinous spindles (Tables 1–2). *Muricea fruticosa*, *M. echinata* and *M. galapagensis* have the largest spindles in the group, in the first they reach up to 2 mm long, the second 2.4 mm and the third 4 mm [Deichmann (1941) reported 2 mm long]. However, they are different in several characteristics; *M. fruticosa* has a profuse branching, mostly bicolored colony that separates it from the rest of the group. *Muricea galapagensis* differs from the others in having the thinnest branches and orange colonies. *Muricea formosa* differs from the others in that the colony and sclerites are white coloured and together with *M. echinata* have the most prominent calyces in the group (Table 2). It is comparable with *M. albida* (see *M. austera* group) which is also white with a similar colony form, but with thicker branches, shorter calyces, up to 2 mm long, which are more numerous and slightly imbricate. The outer coenenchymal sclerites in *M. albida* are wider (up to 0.40 mm) than those in *M. formosa* which are thinner (less than 0.05 mm) with acute ends (Table 1). The leaf-like spindles in *M. formosa* are not present in *M. albida*. In *M. albida* instead, there are modified warty spindles, shorter than in *M. formosa*, with a spiny end and a wider base (Figs 6, 30 below). *M. echinata* is similar to *M. aspera* and *M. fruticosa* by the prickly calyces but the longest are present in *M. echinata*, and the colour of the latter is reddish brown, darker than the light brown of *M. aspera* and different from the bicolour pattern of *M. fruticosa* (Tables 1–2).

***Muricea plantaginea* group**

***Muricea plantaginea* (Valenciennes, 1846), comb. n.**

Figures 14–19

Gorgonia plantaginea Valenciennes, 1846: pl 15.
not *Gorgonia plantaginea* Lamarck, 1815: 163 (Antilles).
not *Eunicea plantaginea* Valenciennes, 1855: 13; Milne Edwards and Haime 1857: 151
Eunicea tabogensis Duchassaing & Michelotti, 1864: 17.
Muricea appressa Verrill, 1864: 37; Verrill 1866: 329; 1868: 412; 1869: 444–446; Kükenthal 1919: 752; Kükenthal 1924: 145; Riess 1929: 390–391; Hardee and Wicksten 1996: 132–136 (syn. n.).
Muricea appressa var. *flavescens* Verrill, 1869: 446; Kükenthal 1919: 752; Kükenthal 1924: 145 (syn. n.).
Muricea tenella Verrill, 1869: 446–448; Kükenthal 1919: 752; Kükenthal 1924: 145; Hickson 1928: 371–372; Riess 1929: 389–390; Stiasny 1943: 72–74; Harden 1979: 160 (syn. n.).

Material. Holotype. MNHN oct 0541, dry, Mazatlán, Mexico, Voyage sur la Frégate La Vénus, M.A. Du Petit Thouars, 1836–1839.

Other type material. *Muricea appressa*: MCZ 381–384, 3950 (380), 3950A-B, ethanol preserved, Panamá, P.H. Sternberg, July 1863. USNM 33585, 33587, 44162, dry, Panamá, J.H. Sternberg, no more data found. *Muricea appressa var. flabescens*: YPM 1616A, Zorritos, Perú, 5–9 m, F.H. Bradley, 1866–1867. MCZ 705; YPM 1179A-D, USNM1130760 (YPM 1616), dry, Pearl Islands, Gulf of Panamá, F.H. Bradley, 1866–1867. *Muricea tenella*: YPM 1617A-B MCZ4978 (708), dry, Zorritos, Perú, F.H. Bradley, 1867. YPM 1180B, dry, Pearl Islands, Panamá, F.H. Bradley, 1866. YPM 1657, ethanol preserved, Pearl Islands, F.H. Bradley, 1866.

Description. The holotype is a large, flabelliform colony 40 cm tall and 18 cm wide. The colony is in bad shape, the main branches are almost nude and branchlets are bent to the sides (Fig. 14B). However, from Valenciennes′ illustration (Fig. 14A) it is possible to tell the flabelliform original aspect. A thick, 4.32 cm main branch arises from an irregular holdfast 5.29 cm in diameter, then bifurcates 6 cm above the base, producing two secondary branches 10–12 mm in diameter. One secondary branch is broken and the other subdivides many times into 4–3 mm wide branches which subdivide in an irregular manner producing branchlets 2–3 mm in diameter. Branchlets closely placed, about 10–15 mm apart, mostly at angles of 30°–45°. Unbranched terminal ends are 10–20 mm long. Calyces are small, 0.7–1 mm long from the base to the tip, with elongated lower borders curved inwards. Calyces are numerous, very close together and imbricate, 10–20/cm around the branchlets and more crowded and smaller at the branches. Coenenchyme is thin. Calycular and coenenchymal sclerites are reddish-brown and amber (Fig. 14D–E). Coenenchymal and calycular sclerites are

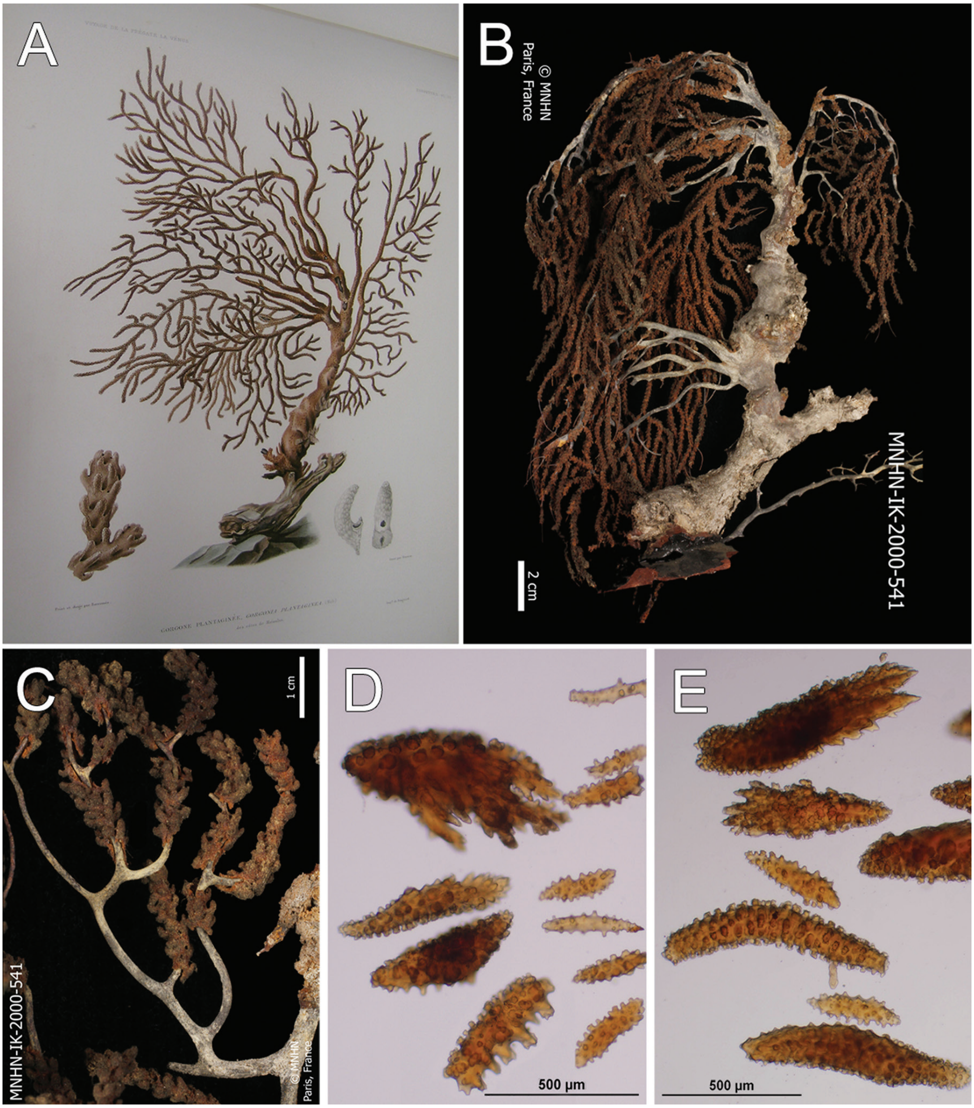

Figure 14. *Muricea plantaginea* (Valenciennes, 1846). MNHN oct 0541. **A** Original figure of the holotype, Valenciennes 1846: plate15 **B** Colony **C** Detail of branches, **B** and **C** photographs: Aude Andouche **D–E** Sclerites, light micrographs.

mostly reddish-brown leaf-like spindles, 0.22–1.0 mm long and 0.09–0.20 mm wide (Fig. 15A), and amber elongated warty spindles 0.24–0.53 mm long and 0.06–0.10 mm wide (Fig. 15B). The axial sheath is composed of spindles, with single or bifurcated ends and radiates, 0.10–0.3 mm long and 0.05–0.09 mm wide (Fig. 15C). Anthocodial sclerites are lobed and warty rods, 0.06–0.23 mm long and 0.02–0.05 mm wide (Fig. 15D).

Colour of the colony is deep brown.

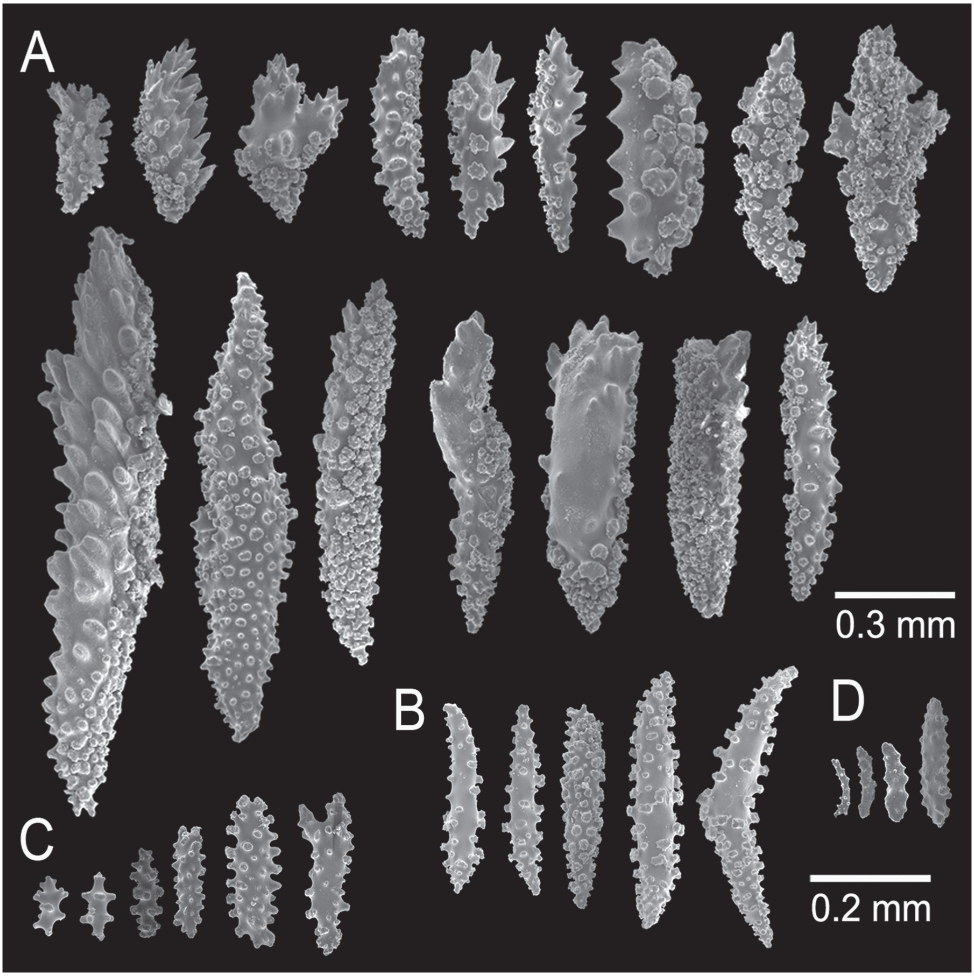

Figure 15. *Muricea plantaginea* (Valenciennes, 1846). MNHN oct 0541. **A–B** Calycular and coenenchymal sclerites **C** Axial sheath sclerites **D** Anthocodial sclerites.

Habitat and variability. Verrill´s type series is very consistent in all characters with respect to the Valenciennes' holotype. For example, the specimen MCZ 3950 (Fig. 16A–C) shows the flabellate colony with imbricate calyces, and the types and colours of the sclerites (Fig. 16C) matching the holotype. Some colour variation was found in the syntypes of *M. appressa* var. *flavescens* and *M. tenella* that are herein considered synonyms of *M. plantaginea*. The colony colour varies from lighter hues of brown to yellowish or whitish as in the former *M. apressa* var. *flavescens* and *M. tenella* (Figs 17A–B, 18 A–B), and also sclerites colour is whitish in these varieties (Figs 17C, 18C). Variation in sclerite's size was observed in some specimens respect to the holotype, the leaf-spindles could be shorter (about 0.50 mm) and the warty spindles longer (about 0.70 mm). In living colonies, the polyps can be white or yellow (Fig. 19B–D). Branches reach up to 15 mm in diameter and branchlets up to 5 mm. Colonies could

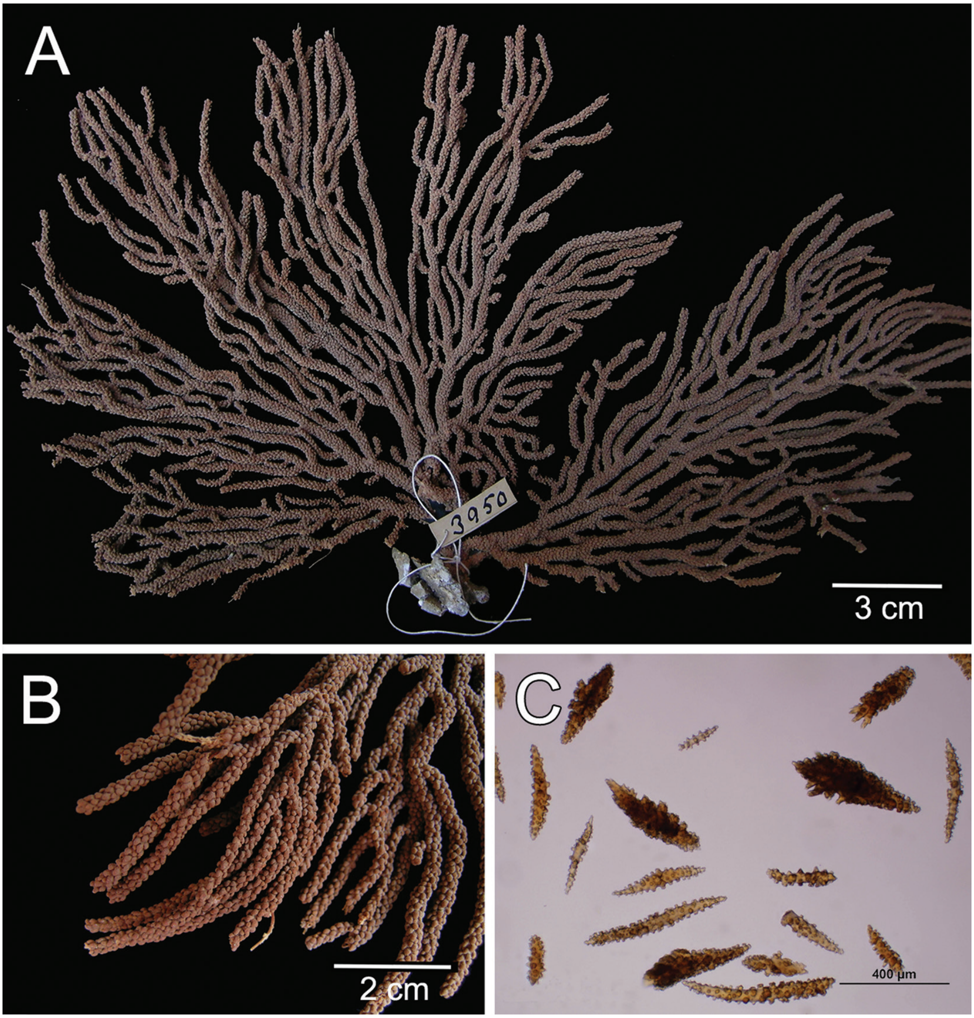

Figure 16. *Muricea plantaginea* (Valenciennes, 1846), MCZ 3950. **A** Colony **B** Detail of branches **C** Sclerites, light micrographs.

have thinner branchlets (less than 2.5 mm diameter) and longer unbranched terminal ends up to 15 cm long (Fig. 18A). Calyces could reach up to 1.2 mm long, density around branches and branchlets could vary 8–22 calyces/cm. Calyces are imbricate especially at the branchlets, more scarcely imbricate at thick branches or stems.

The species is widespread throughout the central archipelago of the Galápagos (Breedy et al. 2009, Hickman 2008), and along the coast of Ecuador (Rivera and Martínez 2011). The species is abundant in Bajo Lunes (coast of Ecuador, 18–20 m deep) where they grow on a flat rocky bottom covered by sand and thin grain sediment. The thin grain sediment suspends in the water column producing high turbidity. In this locality we have found the largest colony sizes, up to 1.20–1.30 m tall and 1.5 m wide

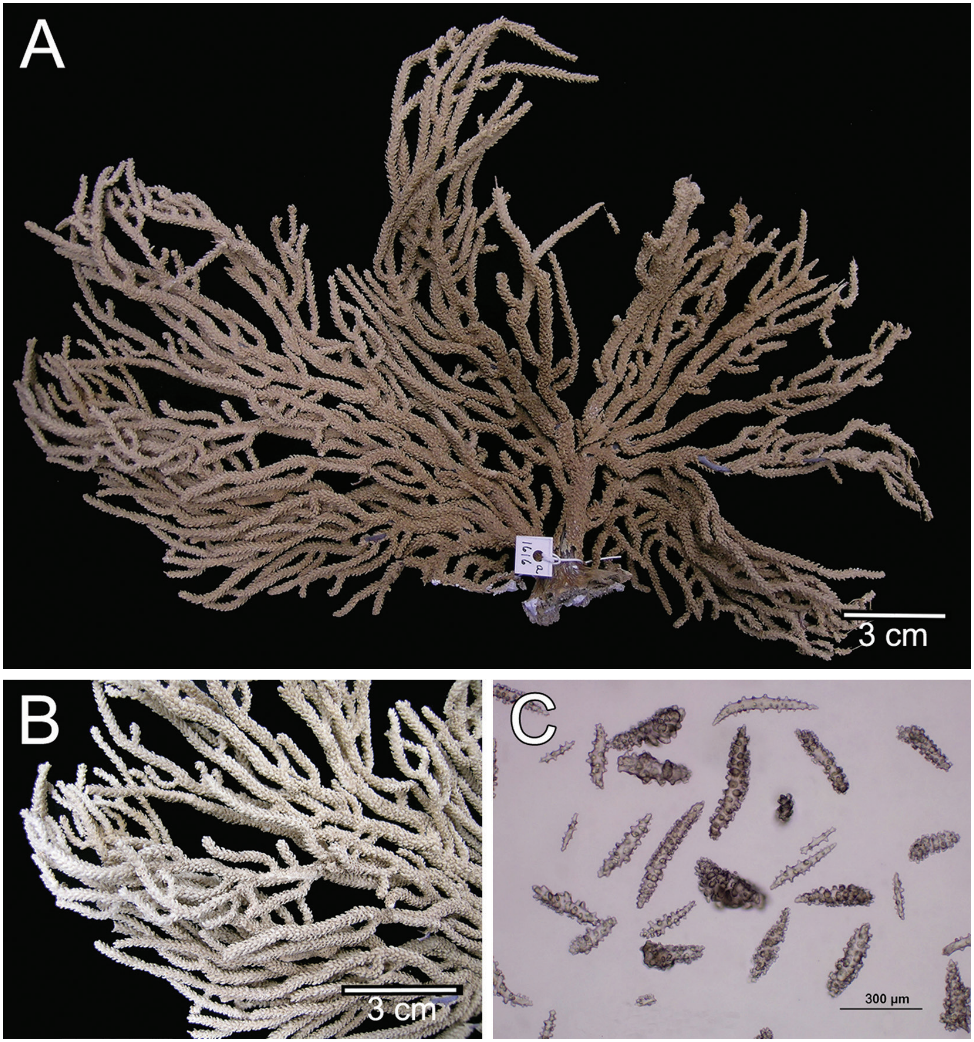

Figure 17. *Muricea plantaginea* (Valenciennes, 1846). YPM 1616A, Verrill syntype of *M. appressa* var. *flavescens*. **A** Colony **B** Detail of branches **C** Sclerites, light micrograph.

(Fig. 19A–B). In the Galápagos the colonies are of smaller size, around 0.5–0.6 by 0.5–0.70 m, and they are found deeper, down to 30 m on rocky bottoms and in clear water (Fig. 19C). Along the coast of Panamá the colonies do not reach more than a half-meter in size. The species reaches its deepest record, down to 65 m, at Hannibal Bank, off Panamá coast.

Distribution. A widespread distribution, it has been reported from México to Perú, at a depth range from 10–65 m including the oceanic islands, Galápagos (Ecuador) and Revillagigedos (México). Type locality: Mazatlán, México.

Remarks. The species appears for the first time in Valenciennes' book (1846) *as Gorgonia plantaginea*, apart from the illustration (Plate XV) of this species there is no

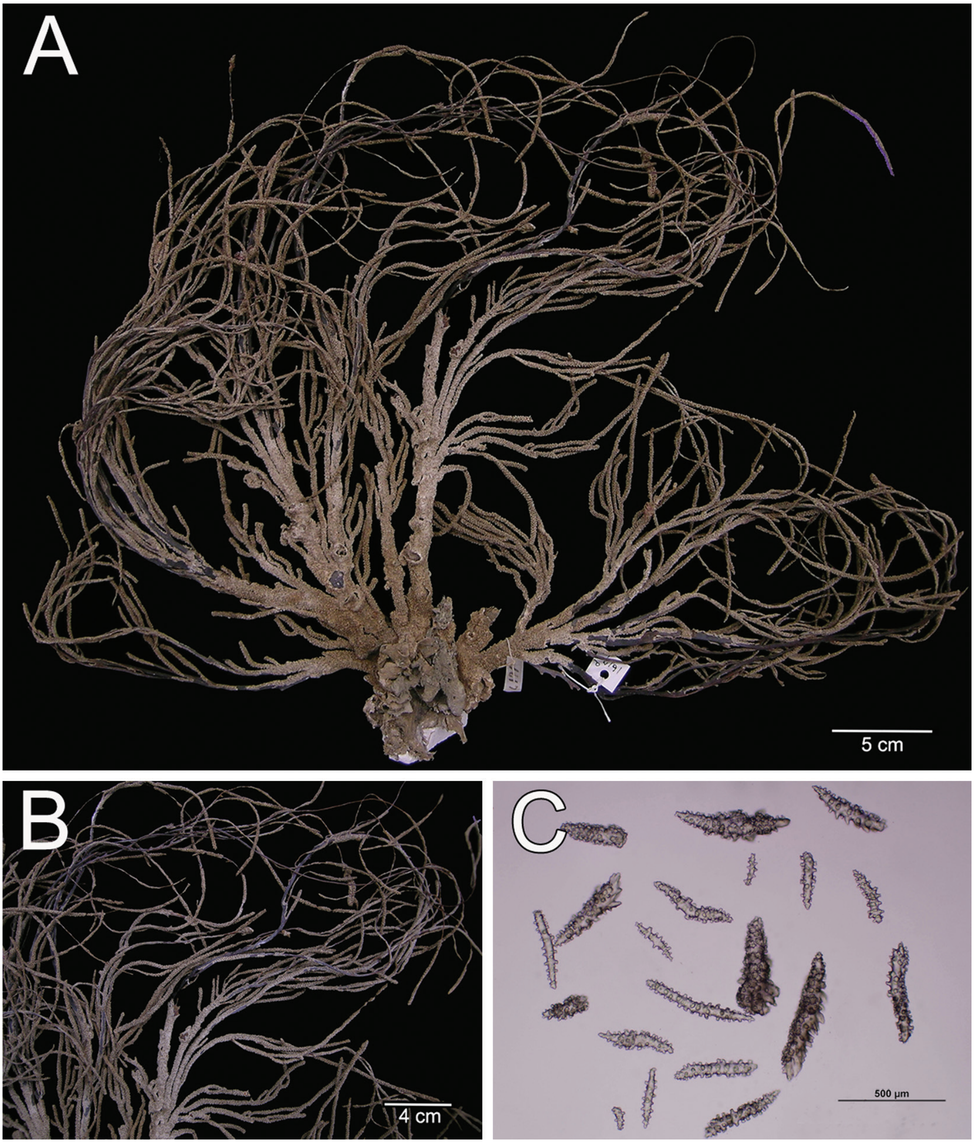

Figure 18. *Muricea plantaginea* (Valenciennes, 1846). YPM 1617A, Verrill syntype of *M. tenella*. **A** Colony **B** Detail of branch **C** Sclerites, light micrographs.

description. The specimen MNHN oct 0541 matches Valenciennes´ drawing (Fig. 14A–B). Verrill (1864) proposed the genus *Muricea* for this species, describing it as *Muricea appressa*, and properly described it in 1868, but overlooked the previous name that according to the ICZN has priority. Verrill (1869) also mentioned a variety of this species *M. appressa* var. *flavescens* based on some difference in colour and size of sclerites (Fig. 17). He also described *M. tenella* based on the slender branches, acute calyces and slender and sharp spindles (Verrill 1869). However, he made these observations

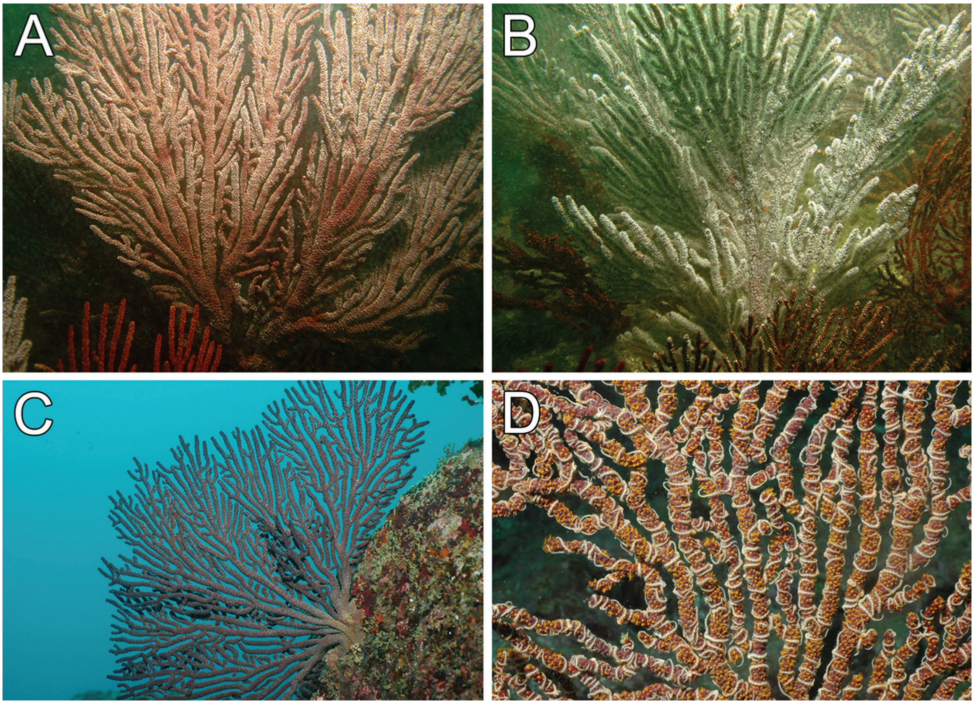

Figure 19. *Muricea plantaginea* (Valenciennes, 1846), colonies *in situ*, submarine pictures. **A–B** Bajo Lunes, Ecuador, photograph: Fernando Rivera **C–D** Albermarle, Galápagos Islands, Ecuador, photograph: Graham Edgar.

from one specimen (YPM 1617A) that out of the long untidy branches, do not present significant difference to be considered another species.

Other material revised. COSTA RICA: UCR 591, dry, Pitahaya Beach, Guanacaste, 23 m, J. Cortés, 15 June 1991; UCR 634, dry, Las Cocineras, Santa Elena Bay, Guanacaste, at the beach, O. Piedra B., 20 February 1965; UCR 945, dry, Caño Island, 22 m, H. Guzman, 11 February 1984. USNM 49389, dry, San Lucas, Gulf of Nicoya, Puntarenas, M. Valerio, January 1st 1930. ECUADOR: CDRS 04-302-304, ethanol preserved, Punta Albemarle, Galápagos Islands, 20–22 m, C. Hickman, 29 November 2004; CDRS 06-32, ethanol preserved, Nameless Island, Galápagos Islands, C. Hickman, 25 May 2006. IIN 23,24, 27a, 27, 28, dry, Bajo Lunes, Salinas, 18 m, F. Rivera, P. Martínez, 21 July 2010; IIN 30, 31, 40, 63-65, 72, dry, Gigima, Salinas, 12–14 m, F. Rivera, P. Martínez, 22 July 2010; IIN 92, 124, dry, Los Ahorcados, Machalilla National Park, 10–12 m, F. Rivera, P. Martínez, 25 July 2010.

MÉXICO: CASIZ 099631, 097735, ethanol preserved, Roca Partida, Revillagigedo Islands, 36 m, R.J. Van Syoc, M/V "Royal Star, Clipperton Island Expedition 1994, 2 May 1994. MNHN oct, dry, Baja California, M.L. Piquet, 1898, no more data. M-Gorgonia7, dry, Islas Gringas, San Carlos Bay, Sonora, 5–25 m, J.L. Carballo, 27 November 2002. PANAMÁ: STRI 557, etanol preserved, Palito Afuera Island, 5–8 m, H. Guzman, 17 April 2003; STRI 778, Pedro Gonzales Island, 3 m, H. Guzman, 11 August 2003; STRI 829, 831, 833, San Telmo Island, 27 m, H. Guzman, 7 April 2004; STRI 902, 903, 906, Pedro Gonzales Island, 10 m, H. Guzman, 23 September 2004. USNM 34065, dry, Gulf of Panamá, Panamá Bay, no more data found.

Muricea californica Aurivillius, 1931

Figures 20–21

Muricea californica Aurivillius, 1931: 111–114; Harden 1979: 144–145; Hardee and Wicksten 1996: 130–132.

Material. Lectotype. USA: SMNH 1122, ethanol preserved, Santa Catalina, California, 18–27.4 m, Leg. G. Eisen, 1874.

Description. The lectotype is a bushy colony 5.6 cm tall and 7.8 cm wide. Two main branches, diameter 4.6–5 mm, arise from an oval holdfast, 1.38 cm in diameter (Fig. 20A). Branches are cylindrical, mostly in one plane, subdividing, and curving upwards parallel to the main branches. They are about 3–3.2 mm in diameter, of even thickness at the ends. Branching is lateral and irregularly dichotomous, dividing up to 8 times. Unbranched terminal ends are 0.5–2.8 mm long. The axis is amber at the base and lighter at tips. Calyces are closely set all around the branches, more distantly placed at the base of the colony and the holdfast. The calyces are elongate, 1.1–1.9 long and about 0.9–1.0 mm wide (up to 1.4 wide after Aurivillius 1931), extending upwards and slightly imbricate (Fig. 20B). The outer side of the calyces (abaxial) with numerous imbricate sclerites, and the adaxial with very few. Polyps are white (Fig. 20B). The coenenchyme is thin, composed of reddish-orange and light yellow to amber sclerites (Fig. 20C–D). Coenenchymal and calycular sclerites are mostly reddish-orange and amber leaf-like spindles, 0.19–0.54 mm long and 0.08–0.2 mm wide (Fig. 21A), and elongated spindles, 0.24–0.34 mm long and 0.07–0.09 mm wide (Fig. 21B). Aurivillius (1931) reported larger sclerite sizes in other specimens, up to 0.66 mm long and 0.3 mm wide, but we did not find this size either in the lectotype or in the other samples. The axial sheath is composed of spindles, with single or composed tubercles, and star-like radiates, 0.12–0.34 mm long and 0.07–0.13 mm wide (Fig. 21C), and small radiates and spindles 0.10–0.16 mm long and 0.05–0.07 mm wide (Fig. 21D). Anthocodial sclerites are lobed and warty rods, 0.08–0.23 mm long and 0.017–0.06 mm wide, light orange.

Colour of the colony is reddish orange.

Habitat and variability. Hardee and Wicksten (1996) found colonies of *M. californica* with white polyps on one set of branches and yellow polyps on the other branches. They reported that most of the colonies in Catalina Island area have orange and yellow polyps instead of white. Most of the colonies were fan-shaped but they found some shrubby ones. Grigg (1972) observed that the branch diameter of *M. californica* could vary according to exposure to current flow.

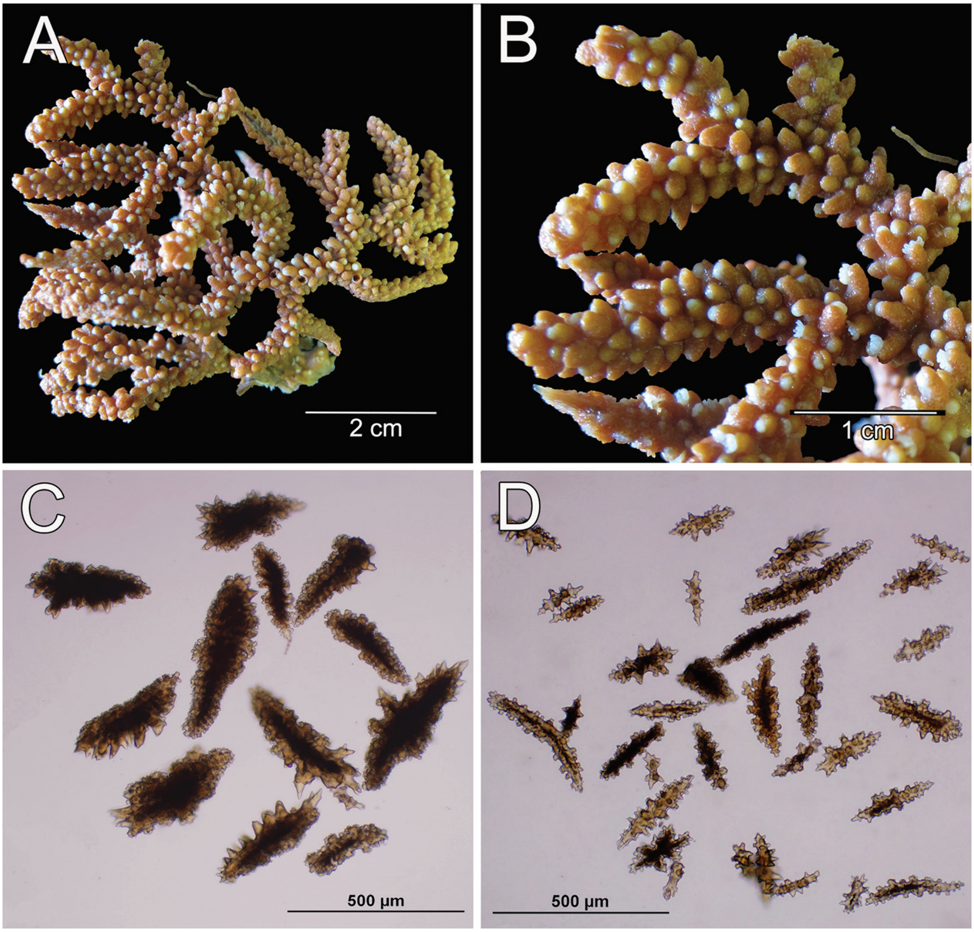

Figure 20. *Muricea californica* Aurivillius, 1931. SMNH 1122. **A** Colony **B** Detail of branches **C–D** Sclerites, light micrograph.

According to Hardee and Wicksten (1996) colonies of *M. californica* were found living at the lowest intertidal level on the Los Angeles Harbor Breakwater at San Pedro reaching down to 30 m along Santa Catalina Island. The colonies were found on granite and other hard rocks, shale reefs, pilings or attached to shells. Grigg (1972, 1977) reported the coexistence of *M. fruticosa* and *M. californica* off La Jolla, California. He reported that *M. californica* grew exposed on outer surfaces on rocks and hole borders while *M. fruticosa* was in the interior of holes or growing on the lower surface of overhangs. We have observed the same type of habitat for *M. fruticosa* in the Galápagos Islands, Panamá and Costa Rica, but we have not observed *M. californica* in these southern areas.

Distribution. South of point Conception, California to Santa María, Baja California, Mexico (Grigg 1977); Santa Catalina, California (Aurivillius 1931, Hardee and Wicksten 1996); Isla Tiburón, Kino Bay, Sonora, Mexico (J.L. Carballo, pers. comm.).

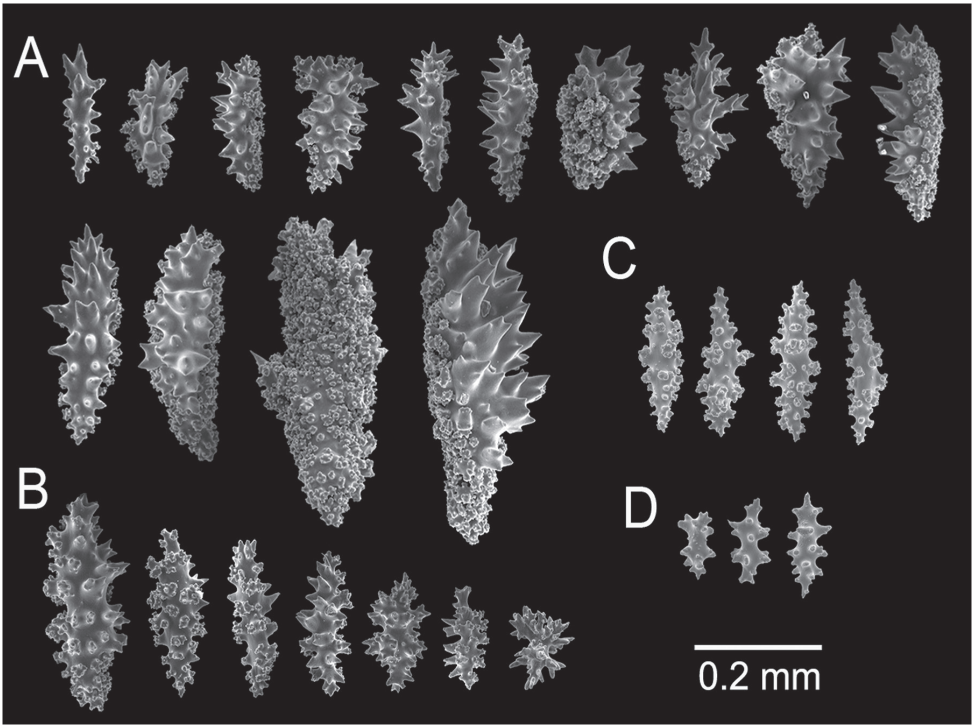

Figure 21. *Muricea californica* Aurivillius, 1931. SMNH 1122. **A–B** Calycular and coenenchymal sclerites **C–D** Axial sheath sclerites.

Remarks. The species was originally described by Aurivillius (1931) with two specimens from Santa Catalina, California. He made reference to other analysed material and provided a general diagnosis but he did not designate a holotype. The specimen SMNH 1122 is herein designated as the lectotype of *M. californica* in order to clearly establish the taxonomic status of the species.

Other material revised. MÉXICO: Geoff1, dry, Baja California, Geoff Shester, 2007. Gorgonia 11, dry, Isla Tiburón, San Carlos Bay, Sonora, 5–25 m, J.L. Carballo, 27 April 2001. PANAMÁ: BM 30.6.17.18 (fragment), (erroneously identified as M. hebes), ethanol preserved, off Panamá, low tide, St. George, Scientific Expedition, Pacific Cruise, C. Crossland, 1923–1924.

Muricea mortensenii Hickson, 1928

Figures 22–23

Muricea mortensenii Hickson, 1928: 369–371; Stiasny 1943: 69–72.

Material. Holotype. MZUC ANT 106, ethanol preserved, Rey Island, Pearl Islands, Panamá, T. Mortensen, 27.4 m, 26 January 1916. Schizotype RMNH Coel 6553.

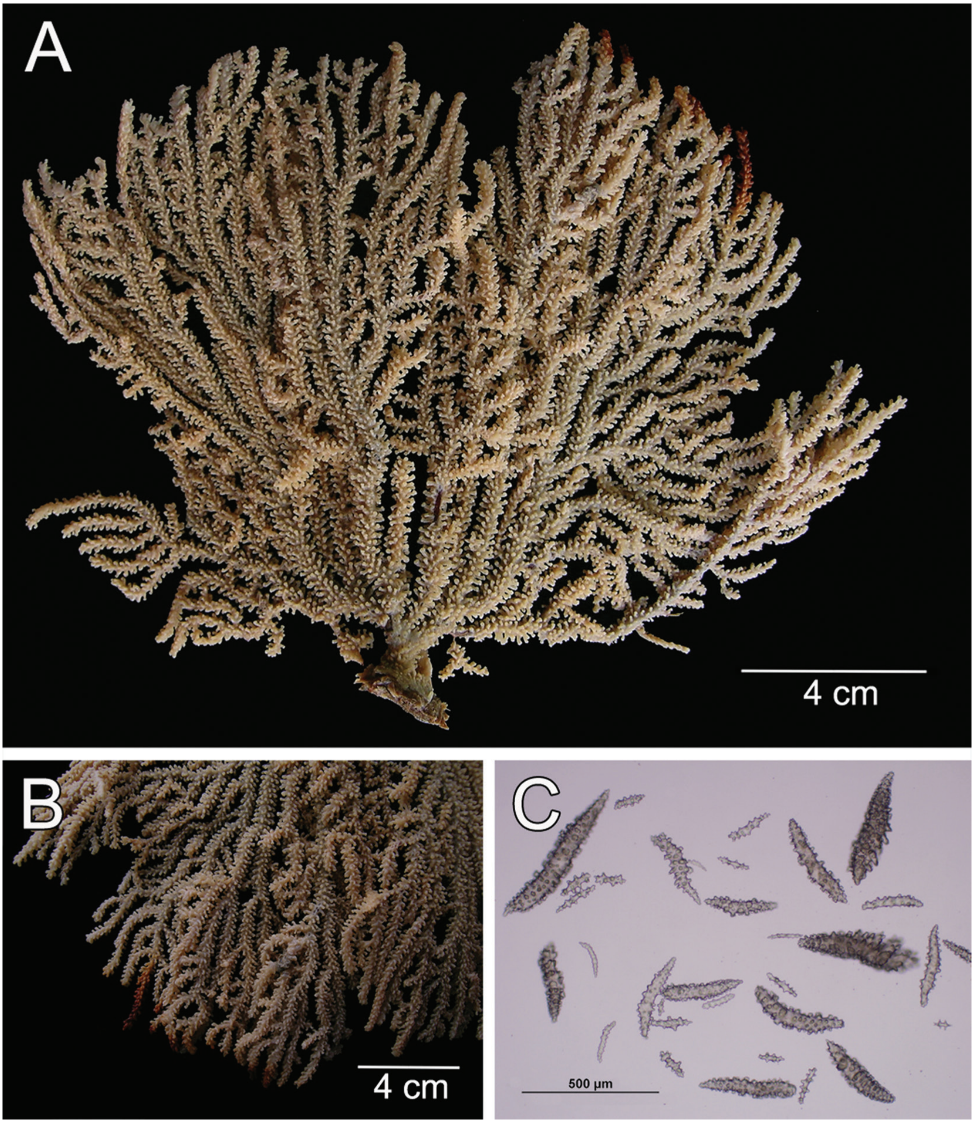

Figure 22. *Muricea mortensenii* Hickson, 1928. MZUC ANT 106. **A** Colony **B** Detail of branches **C** Sclerites, light micrograph.

Description (see also Hickson 1928). The holotype is a flabelliform colony 15 cm tall and 18 cm wide (Fig. 22A). A short stem, 6 mm in diameter, arises from an irregular holdfast, 22 mm in diameter, which bears a few scattered polyps. The stem divides into numerous branches, each about 3 mm in diameter; they subdivide in an irregular manner producing branchlets, 2–3 mm in diameter, closely placed, mostly 1–2 mm apart, and at angles 30–45°. Branchlets are very numerous and overlap on the surface of the fan, but do not anastomose. Branches subdivide up to

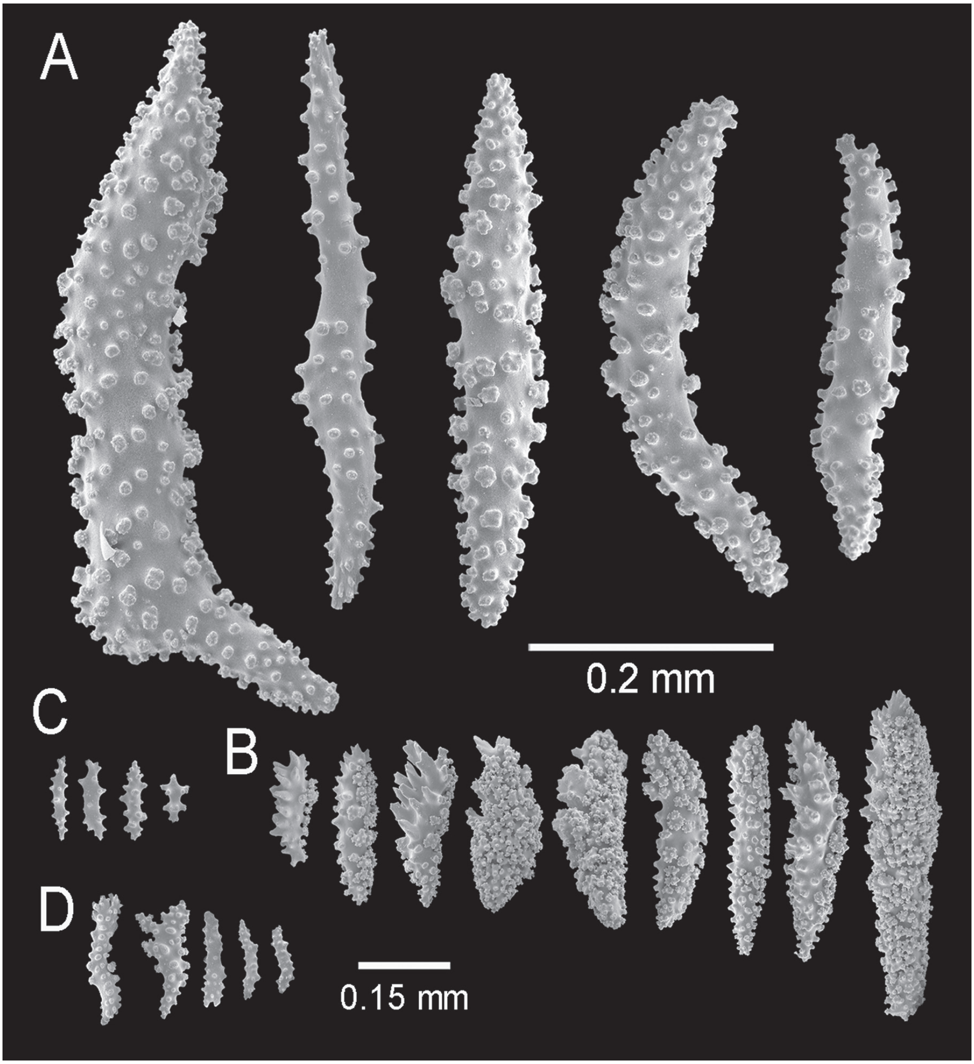

Figure 23. *Muricea mortensenii* Hickson, 1928. MZUC ANT 106. **A–B** Calycular and coenenchymal sclerites **C** Axial sheath sclerites **D** Anthocodial sclerites.

four times. Unbranched terminal ends are mostly 2–4 mm long. Calyces are elongated, 0.7–1.0 mm long from the base to the tip, with lower borders slightly curved inwards. Calyces are numerous, not imbricate, placed all around the branches, very close together, about 18–20 calyces/cm around the branches, 10–15/cm around the branchlets, (Fig. 22B). Polyps are whitish preserved in ethanol. All sclerites are whitish to colourless (Fig. 22C). Coenenchyme is very thin, composed of warty spindles, 0.35–0.7 mm long and 0.07–0.12 mm wide, of diverse shapes, straight, curved or irregular with one side curved and the other straight (Fig. 23A). Leaf spindles and modified forms 0.18–0.53 mm long and 0.068–0.13 mm wide, with long lateral sharp spines, are also present (Fig. 23B). The axial sheath is composed of immature forms, spindles and capstans, 0.08–0.13 mm long and 0.03–0.05 mm wide (Fig. 23C). Anthocodial sclerites are warty rods, 0.11–0.21 mm long and 0.02–0.08 mm wide, some with bifurcated ends (Fig. 23D).

Colour of the colony is pale yellow.

Distribution. Reported for the type locality, Rey Island, Pearl Islands, Panamá.

Remarks. Hickson (1928) described this species with one colony from Panamá. He indicated that the colour of the colony was pale umber brown, darker than the holotype which is pale yellow; we assumed that the colony was decoloured when preserved. The species is different from the others found in the area and we have not collected this species in any of our recent surveys in Panamá. According to Hickson 1928 this species is closely related to *Muricea hispida* Verrill, 1866 and *Muricea horrida* Möbius, 1861; however, the characteristic tubular calyces of these species separate *M. mortensenii*, which has shelf-like calyces. The species can be placed in the same group together with *M. californica* and *M. plantaginea* based on the lack of unilateral spinous spindles as structural part of coenenchyme and calyces, the thin branches, and the fan-shaped colony that have one or more planes. The holotype is the only colony presently found of *M. mortensenii*.

Species-group comparison summary

The *Muricea plantaginea* group comprises three species: *M. plantaginea*, *M. mortensenii* and *M. californica*. The group is characterised by thin coenenchyme, thin branches and the lack of unilateral spinous spindles (as defined for the genus). The main components of the calyces and outer coenenchyme are leaf-like spindles with prominent spines and elongated warty spindles. *Muricea mortensenii* is conspicuously different from the others in the profuse branching, very crowded upwards-curved calyces and soft texture of the colony. *Muricea californica* and *M. plantaginea* (typical) have similar colony and sclerites colours. Respect to the colony morphology, *M. californica* is not as fan-shaped as *M. plantaginea*. Colonies could develop in various planes. *Muricea californica* differs also from *M. plantaginea* in having shorter spindles, no more than 0.55 mm long, and longer, not imbricate calyces (Tables 1–2).

Muricea austera group

Muricea austera Verrill, 1869
Figures 24–26

Muricea austera Verrill, 1869: 430–432; Kükenthal 1919: 752; Kükenthal 1924: 142; Harden 1979: 143–1 44; Hickson 1928: 367–369.

Material. Lectotype: YPM 1569a, dry, Pearl Islands, Panamá, 11–14 m, F.H. Bradley, 1866. Paralectotypes: MÉXICO: MCZ 4974; USNM 3094; dry, Cape San Lucas, Baja California, J. Xantus, April 1859-August 1861. USNM 52291; USNM 1130762 (part

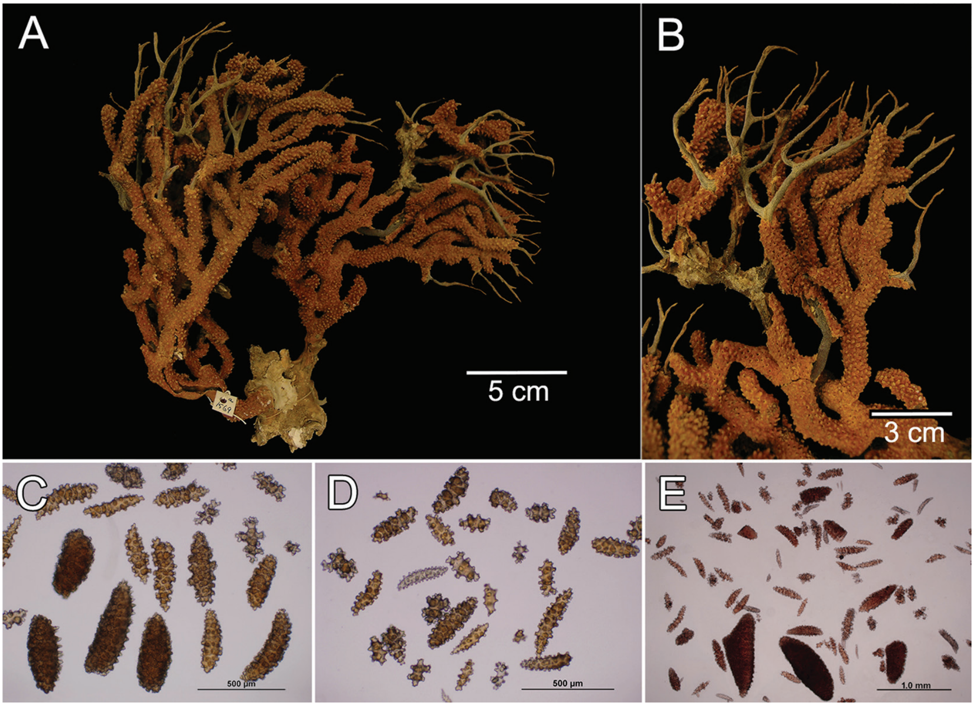

Figure 24. *Muricea austera* Verrill, 1869. YPM 1569a. **A** Colony **B** Detail of branches **C–E** Sclerites, light micrographs.

of YPM 8660); YPM 8660, dry, La Paz, Baja California, J. Pedersen, no date. PANAMÁ: USNM 1130761 (part of YPM 1569a); YPM809a-c; YPM 1569b; ZMUC-ANT 191 (part of YPM 809), dry, Pearl Islands, 11–14 m, F.H. Bradley, 1866.

Description. The lectotype is a bushy colony, 20 cm long and 23 cm wide, with brittle coenenchyme that is partially lost on some branches and with mostly naked terminal ends (Fig. 24A). Two slightly flattened stems, each 7–10 mm in diameter, arise from a large holdfast, about 6 cm long, devoid of coenenchyme and with a small white sponge attached (Fig. 24A). The branching is mostly dichotomous and mostly in one plane (Fig. 24A). The stems extend up to 15 mm long and subdivide into secondary branches, that bifurcate up to 6 times producing subordinate branches, no more than 25 mm apart. Some branches are wider at the lower part of the colony, up to 10 mm in diameter, but they are mostly of even thickness up to the tips, 7–8 mm in diameter. The branches bifurcate at close angles 30°–45°, and curved upwards. Some occasional branch anastomosis occurs, especially at the base. Unbranched terminal ends are up to 5 cm long, with rounded tips, and 6–9 mm in diameter. Axes are brownish and lighter at the tips. The calyces are all around the branches, bent upwards and close together, not imbricate but a little overlapped (Fig. 24B). They are raised, up to 2 mm long. The coenenchyme is thick and rough, composed of reddish–brown, orange and light yellow sclerites (Fig. 24C–E). The

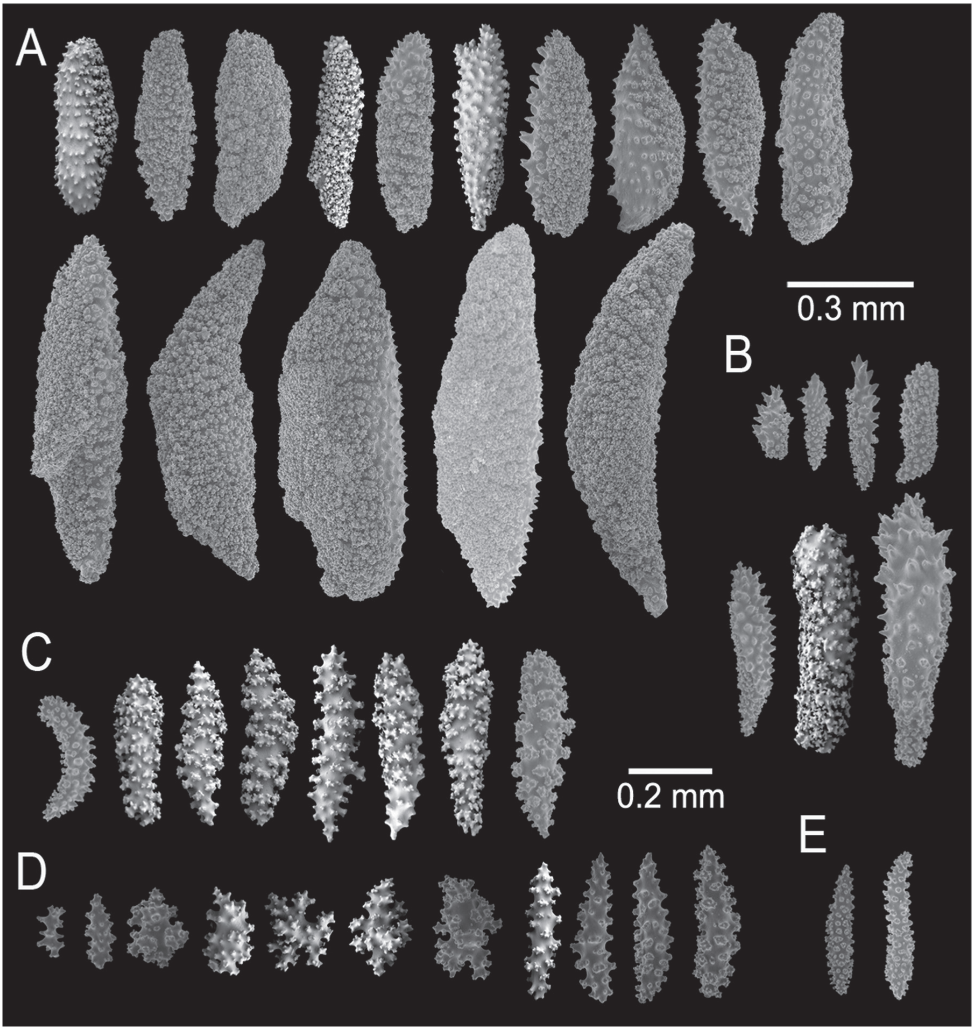

Figure 25. *Muricea austera* Verrill, 1869. YPM 1569a. **A–C** Calycular and coenenchymal sclerites **D** Axial sheath sclerites **E** Anthocodial sclerites.

outer coenenchymal and calycular spindles are of various types: mostly unilateral spinous with the inner side heavily warty, and the outer side with short spines. They are elongated, with round ends, or with one end tapered and the other wide and blunt, or with one end acute or bifurcated, or tapered at both ends, 0.55–1.5 mm long and 0.20–0.50 mm wide (Fig. 25A). The largest sclerites are of a darker colour in the central part with lighter hues around the borders. Furthermore, leaf-like spindles are present, 0.22–0.65 mm long and 0.06–0.20 mm wide (Fig. 25B), with a spiny end that projects beyond the calyx border, and warty spindles, 0.35–0.48 mm long and 0.11–0.14 mm wide (Fig. 25C). The axial sheath is composed of warty radiates, 0.12–0.36 mm long and 0.12–0.2 mm wide, and spindles (Fig. 25D). Anthocodial sclerites are pale yellow to whitish, 0.14–0.36 mm long and 0.02–0.06 mm wide (Figs 24E, 25E).

Colour of the colony is reddish brown.

Habitat and variability. The colonies ramify producing a bouquet-like structure (Fig. 26A) or mostly grow in one plane (Fig. 26B–C), in some cases, the holdfast extends for some distance along the substrate producing many more branches in a fringing-like colony that in some cases is growing upside down. The polyps are orange to yellow (Fig. 26A–B). In the examined specimens the larger sclerites reach up to 0.2 mm long. The branches vary in diameter from 6–10 mm, in some cases few bifurcations occur forming candelabrum-like colonies or single finger-like short branches joint by extending holdfast.

Distribution. It has a widespread distribution, from México to Perú. Type locality: Pearl Islands, Panamá.

Remarks. Verrill (1868) described this species with specimens from Pearl Islands, Cape San Lucas and La Paz, Baja California. Later, Hickson (1928) revised a specimen from Taboguilla Island, Gulf of Panama and added some details about variation in calyx length (little larger) and found larger sclerites, up to 2 mm long. Verrill (1868) and Hickson (1928) considered the species as rare in Panamá, but we found it common at various localities around Pearl Islands and Gulf of Chiriquí.

Verrill did not designate a holotype for the species. The specimen YPM 1569a is the largest of the syntype series and closely matches Verrill's description of the species, therefore, we designate this specimen as the lectotype of *M. austera* with the purpose of clearly establishing its taxonomic status.

Other material revised. COSTA RICA: UCR 623–624, 633a, dry, Bajo Isla Chora, Sámara Bay, Guanacaste, 10 m, H. Guzman, 18 March 1984; UCR 779, dry, Peñón de la Bruja, Santa Rosa National Park, 10 m, J. Cortés, 5 March 1994; UCR 836, dry, Cabo Blanco Islet, SW from Cabo Blanco National Reserve, Puntarenas, 12 m, L. Mena, 26 April 1994. ECUADOR: IIN 4b, 5, 6, dry, Tambip, Salinas, 12–14 m, F. Rivera, P. Martínez, 20 July 2010; IIN 23, dry, Bajo Lunes, Salinas, 18 m, F. Rivera, P. Martínez, 21 July 2010; IIN 62, dry, Gigima, Salinas, 12–14 m, F. Rivera, P. Martínez, 22 July 2010; IIN 104, 118, dry, Los Ahorcados, Machalilla National Park, 10–12 m, F. Rivera, P. Martínez, 25 July 2010. EL SALVADOR: UCR 1936, ethanol preserved, Departamento la Libertad, Playa Mizata, J. Segovia, 26 February 2010. MÉXICO: M 11, dry, León echado Island, San Carlos Bay, Sonora, 5–25 m, J.L. Carballo, 6 December 2000; M 29, dry, Lobos Island, Mazatlan Bay, Sinaloa, 5–25 m, J.L. Carballo, 17 November 1998. STRI 1128, ethanol preserved, El Faro, Oaxaca, 8 m, R. Abeytia, 2 September 2004; STRI 1139, ethanol preserved, El Faro, Oaxaca, 8 m, R. Abeytia, 13 August 2004. PANAMÁ: STRI 25, 27, dry, Santa Cruz Island, Chiriquí Gulf, 5–10 m, H. Guzman, 10 December 2001; STRI 143, 204, Jicarita Island, Chiriquí Gulf, 10–20, H. Guzman, 9 May 2002; STRI 145, dry, Jicarita Island, Chiriquí Gulf, 10–30 m, H. Guzman, 19 April 2002; STRI 290, Piedra Hacha, Chiriquí Gulf, 20–30m, H. Guzman, 22 April 2002; STRI 319, dry, Chiriquí Gulf, 5–10 m, H. Guzman, 24 April 2002; STRI 406, Seca Grande Islande Chiriquí Gulf, 20 m, H. Guzman, 26 August 2002; STRI 417, Chiriquí Gulf, 20 m, H. Guzman, 26 August 2002; STRI

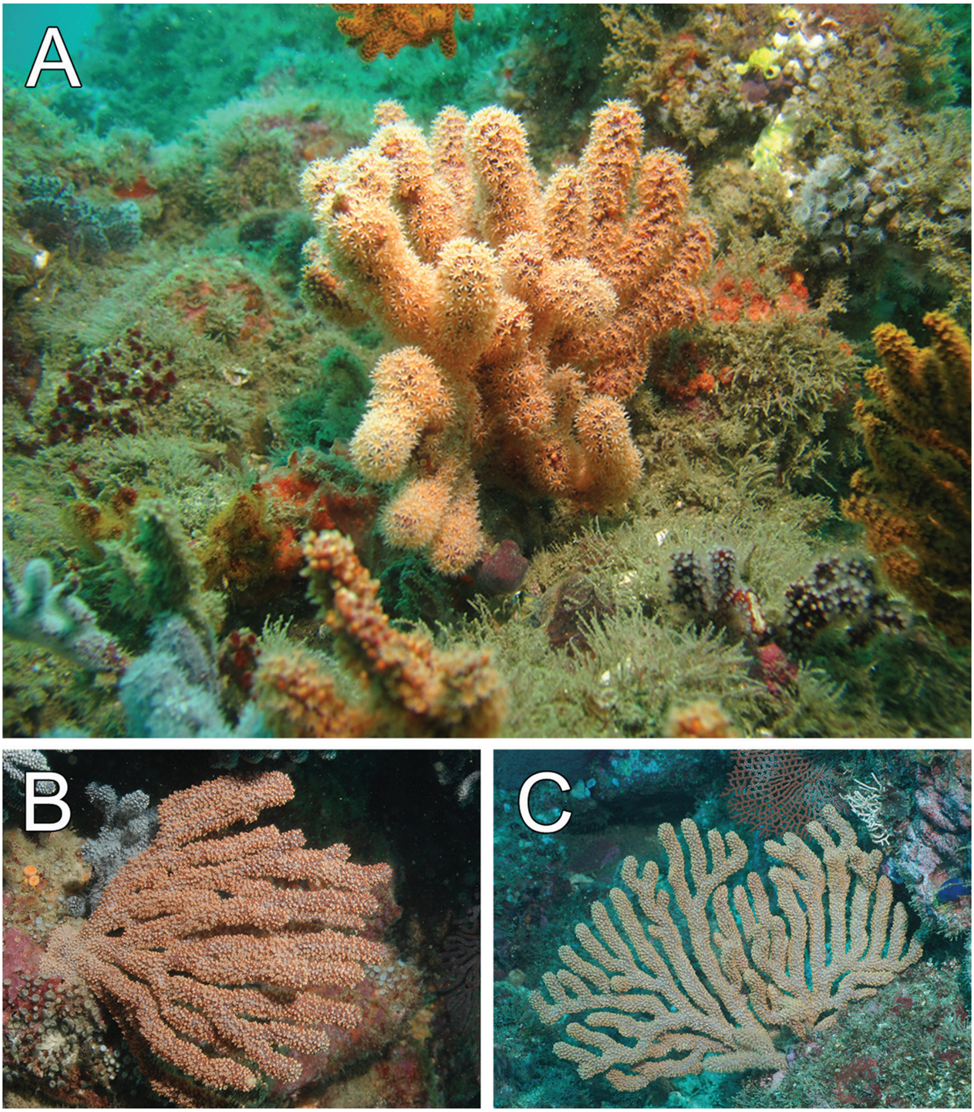

Figure 26. *Muricea austera* Verrill, 1869, colonies *in situ*, submarine pictures. **A** Gigima, AMP Puntilla de Santa Elena, Ecuador, photograph: Fernando Rivera **B** Salango, Machalilla National Park, Ecuador, photograph: Fernando Rivera **C** Coiba National Park, Panamá, photograph: Graham Edgar,.

445, Jacarita Island, 10–25 m, H. Guzman, 29 August 2002; STRI 525, Bajo Bolano, Chiriquí Gulf, 25 m, H. Guzman, 16 April 2003; STRI 751, Roca Trollope, 10–20 m, H. Guzman, 6 August 2003; STRI 777, Pearl Islands, 3 m, H. Guzman, 11 August 2003; STRI 791, San José Island, 3 m, H. Guzman, 11 October 2003; STRI 810, Pearl Islands, 2 m, H. Guzman, 6 April 2004; SRTI 821, 822, Pearl Islands, 3 m, H. Guzman, 6 April 2004; STRI 834, Pearl Islands, 27 m, H. Guzman, 7 April 2004; STRI 838, Pearl Islands, 2 m, H. Guzman, 8 April 2004; STRI 845, Pearl Islands, 3 m, H.

Guzman, 20 April 2004; STRI 866, Achotines, Chiriquí Gulf, 3–10 m, H. Guzman, 5 May 2004; STRI 900, 901, 930, Pearl Islands, 10 m, H. Guzman, 23 September 2004; STRI 943, Pearl Islands, 3–20 m, H. Guzman, 23 September 2004; ethanol preserved, STRI 137B,145B, 1213, Saboga Island,1–5 m, H. Guzman, 14 December 2001; STRI C5, Coiba Island, Chiriquí Gulf, H. Guzman, 3 August 2002.

Muricea albida Verrill, 1868

Figures 27–28

Muricea robusta (pars.) Verrill, 1866: 329.

Muricea albida Verrill, 1868b: 412; Verrill 1869: 437–439; Kükenthal 1919: 752; Kükenthal 1924: 146; Hickson 1928: 363–364; Riess 1929: 393–394; Harden 1979: 142–143.

Material. Lectotype. YPM 1559a, dry, Pearl Islands, Panamá, 11–14 m, F.H. Bradley, 1866. Paralectotypes. PANAMÁ: MCZ 712; MCZ 4976; MCZ 7016; dry; YPM 563, 3 specimens; YPM 563h; YPM 1559b-d, ZMUC-ANT 190, 2 specimens (part of YPM 1559); dry; YPM 1633, 2 fragments, ethanol preserved, data as in the lectotype.

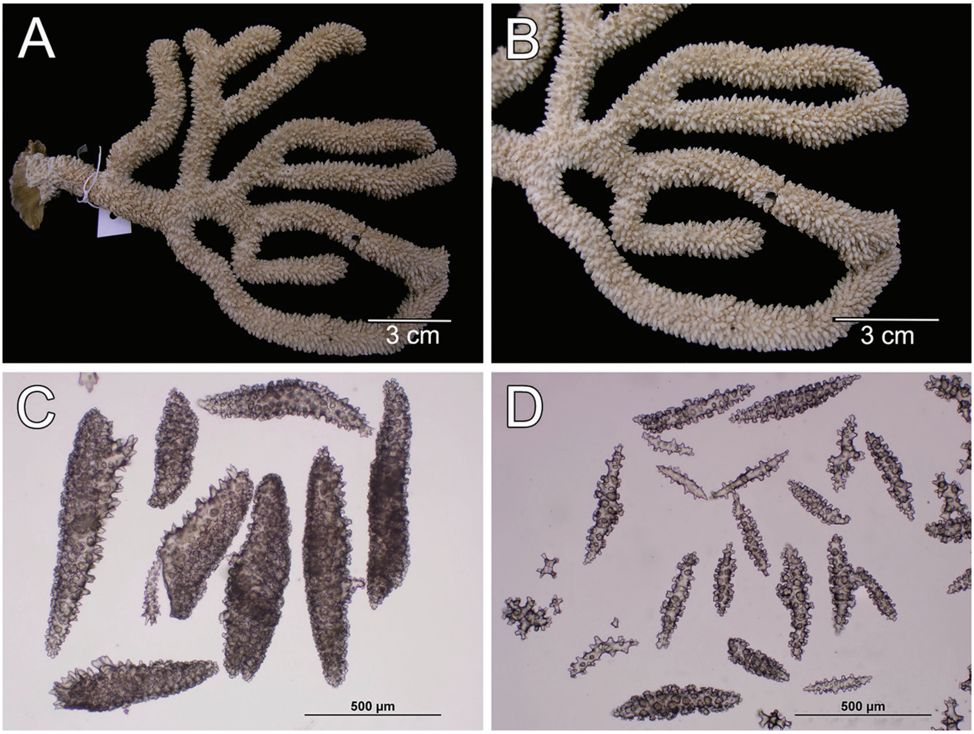

Figure 27. *Muricea albida* Verrill, 1868b. YPM 1559a. **A** Colony **B** Detail of branches **C–D** Sclerites, light micrographs.

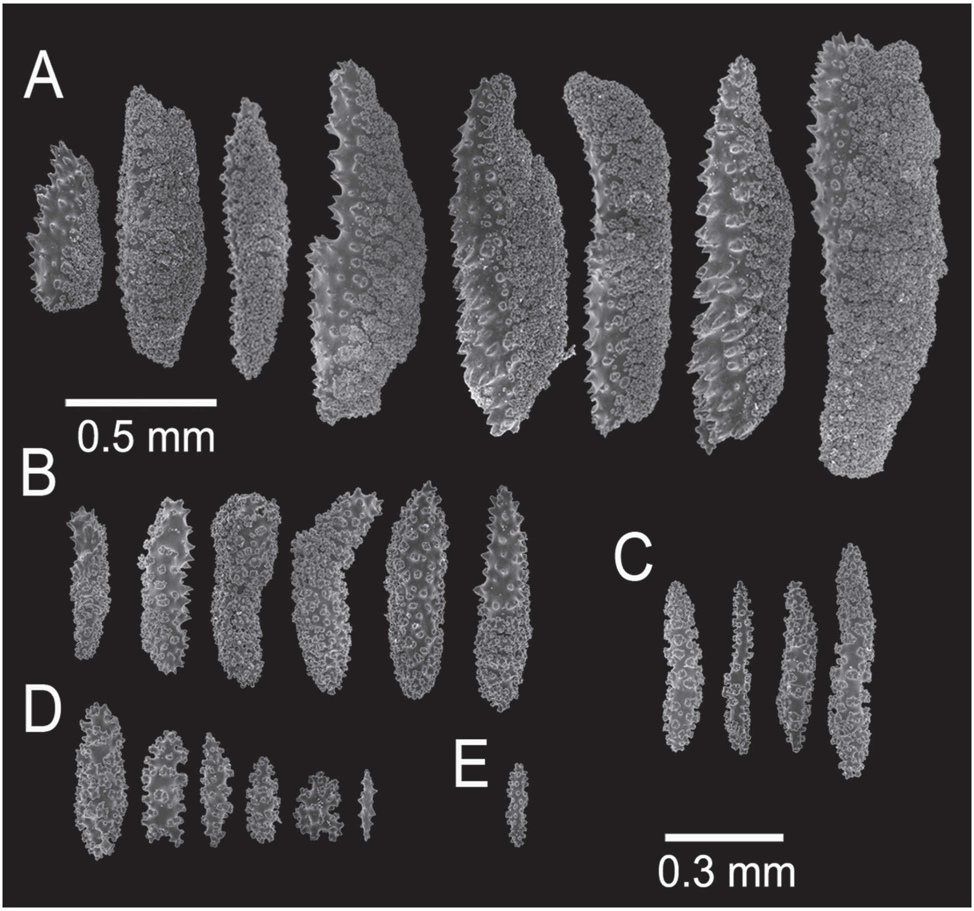

Figure 28. *Muricea albida* Verrill, 1868b. YPM 1559a. **A–C**. Calycular and coenenchymal sclerites **D** Axial sheath sclerites. **E** Anthocodial sclerites.

Description. The lectotype is a 15 cm long and 12 cm wide, candelabrum-like colony, branching in one plane and mostly dichotomous (Fig. 27A). The colony arises from a conical holdfast, about 24 mm in diameter, partially devoid of coenenchyme. The stem is 10 mm in diameter slightly flattened, and 23 mm long, it bifurcates producing secondary branches that subdivide again at distances up to 1.5 cm apart, two of them remain as long simple branchlets. The branches and branchlets are stout, 7–10 mm in diameter and are tapered toward the tips, reaching 5–7 mm in diameter. The branches split at close angles, about 45°, and some branchlets project at acute or wider angles. The unbranched terminal ends are up to 11 mm long. The calyces are all around the branches, close together, slightly imbricate at the upper part of the branches (Fig. 27B). They are elongated, sub-conical, about 2 mm long, and mostly project at right angles to the branches. The coenenchyme is thick and compact. The sclerites are white, and greyish (Fig. 27C–D). The outer coenenchyme and calycular sclerites are of various types. The larger ones are unilateral spinous spindles with the inner side with small numerous warts and the outer side with short spines, they are elongated, with blunt ends, or with one end tapered and the other wide and blunt, 0.60–1.41 mm long and 0.25–0.05 mm wide, (Fig. 28A). Furthermore, spiny spindles with one spiny end and a warty body are present, 0.29–0.6 mm long and 0.09–0.14 mm wide (Fig. 28B), the sharp or spiny ends project beyond the calyx border; and warty, elongated spindles 0.44–0.60 mm long and 0.07–0.11 mm wide (Fig. 28C). The axial sheath is composed of warty, irregular spindles, and radiates 0.18–0.30 mm long and 0.05–0.14 mm wide with acute or bifurcated ends, and radiates (Fig. 28D). Anthocodial sclerites are flat warty rods, some with one bifurcated end, 0.11–0.25 mm long and 0.01–0.03 mm wide (Fig. 28E).

Colour of the colony is white.

Distribution. It is known from the type locality, Pearl Islands, and reported from Taboguilla Island. However, *M. albida* has not been found during our recent extensive surveys along Pacific Panamá.

Remarks. The species was described by Verrill (1869) with specimens from Panamá, Hickson (1928) added some not relevant details to the description. Verrill did not designate a holotype for the species, thus we chose specimen YPM 1559a, that is probably the figured specimen (Verrill 1869 Pl. 7, Fig. 9), as the lectotype of *M. albida* to clearly establish its taxonomic status.

Other material revised. PANAMÁ: BM 1946.1.14.43, off Taboguilla, 9 m, C. Crossland, 22 November 1915.

***Muricea crassa* Verrill, 1869**

Figures 29–30

Muricea crassa Verrill, 1869: 425–426; Kükenthal 1919: 752; Kükenthal 1924: 144; Riess 1929: 392–393.

Material. Lectotype: YPM 1798 (figured specimen), dry, Pearl Islands, Panamá, F.H. Bradley, 1866, no further data. Paralectotypes: PANAMÁ: MCZ 702; MCZ 7015; YPM 1558; ZMUC-ANT 19, same data as the lectotype.

Description. The lectotype is a large bushy colony, 40 cm long and 50 cm wide. The holdfast is irregular, and swollen, about 7 cm wide and 4 cm high covering one side of the rock remains to which is attached. The branching is irregularly dichotomous, mostly lateral, in one plane (Fig. 29A). There is not a common stem, but 4 main branches arise directly from the holdfast. They are up to 15 mm in diameter, extending up to 7.5 cm and subdivide in secondary branches, that bifurcate up to 6 times producing subordinate branches, no more than 25 mm apart. They project at angles 45°–90°, and curve upwards. They are of the same diameter, and thicker toward the tips, which are wide and clavate. Some branch anastomoses occur, especially at the base. Unbranched terminal ends are up to 7 cm long, with expanded tips 7–10

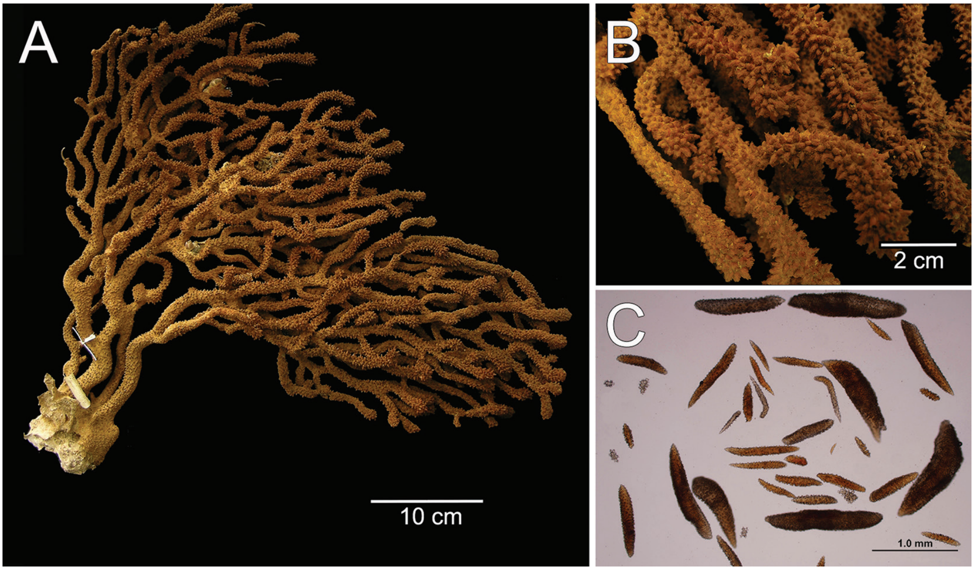

Figure 29. *Muricea crassa* Verrill, 1869, YPM 1798. **A** Colony **B** Detail of branches **C** Sclerites, light micrograph.

mm in diameter, some short branchlets 1–2 cm long, are up to 12 mm in diameter. Axes are of a dark brown at the base, lighter at the tips. The calyces are all around the branches, close together, not imbricate (Fig. 29B). They are prominent, up to 3 mm long, covered with large spindles with echinulate ends. The calyces on the lower branches are more conical and blunter that the ones on the upper branches, also more distantly spaced and smaller. The coenenchyme is coarse, composed of large and irregular spindles, they are reddish-brown and of lighter and darker hues (Fig. 29C). Outer coenenchymal and calycular sclerites are large and strong. They are mostly unilateral spinous spindles with an inner surface of crowded complex small warts and an outer surface with short sparsely placed spines or prickles. They are of diverse shapes, unequal with one side truncate and the other acute, bifurcated at one side, others are triangular or with almost rectangular forms, 0.56–2.5 mm long and 0.40–0.70 mm wide (Fig. 30A). The calycular wall is composed of elongated spindles with acute ends and spindles with prickly terminal spikes or bifurcated, 0.92–0.32 mm long and 0.8–0.1 mm wide (Fig. 30B). These types of sclerites give the calyces a stout, rough appearance characteristic of this species. The axial sheath is composed of small, colourless radiates, and small spindles, 0.08–0.38 mm long and 0.07–0.09 mm wide (Fig. 30D). Anthocodial sclerites are light orange to yellowish spindles. They have long and sharp terminal spines or with spiny shafts, 0.3–0.65 mm long and 0.04–0.12 mm wide (Fig. 30C) that are at the base of the polyps. Furthermore, some irregular branched forms, 0.15–0.2 mm long and 0.03–0.06 mm wide, and small rods 0.09–0.3 mm long and 0.01–0.04 mm wide.

Colour of the colony is dark brown.

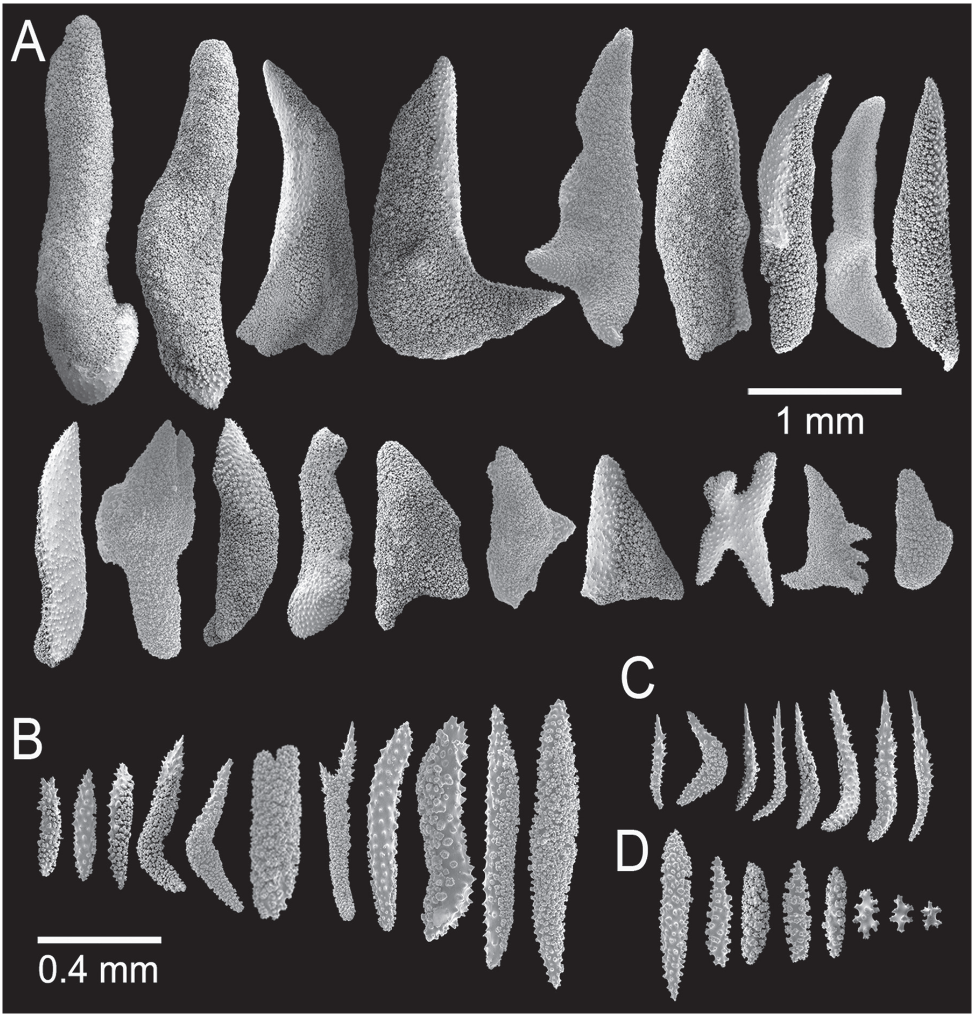

Figure 30. *Muricea crassa* Verrill, 1869. YPM 1798. **A–B** Calycular and coenenchymal sclerites **C** Anthocodial sclerites **D** Axial sheath sclerites.

Habitat and variability. The examined colonies are up to 50 cm tall and up to 40 cm wide, but smaller specimens, around 30 cm tall are the majority. The branch tips could reach up to 15 mm in diameter, and the unbranched terminal ends up to 13 cm long. This species is very conspicuous because of the dark colour and strong and prickly branches with wide terminal tips. We have observed *M. crassa* at various localities in Panamá, from 3–12 m deep around Pearl Islands, Gulf of Panamá and the deepest records are around Coiba Island in the Gulf of Chiriquí, 20–30 m deep. It is not abundant and is sparsely distributed in patches dominated by other species.

Distribution. It has a widespread distribution from México to Perú. Type locality, Pearl Islands, Panamá.

Remarks. Verrill (1868b) described this species with specimens from Pearl Islands, Panamá; he registered larger sizes of sclerites, up to 3.2 mm long and 0.875 mm wide, however the other characteristics are very consistent with the examined specimens. Verrill did not designate a holotype for the species. We chose the specimen YPM 1798 as the lectotype of the species with the purpose of clearly establishing the taxonomic status of *M. crassa*. On the label of specimen YPM 1798 it was written down this as Verrill's (1868b) figured specimen.

Other material revised. ECUADOR: IIN 94, 121, dry, Los Ahorcados, Machalilla National Park, 10–12 m, F. Rivera, P. Martínez, 25 July 2010. PANAMÁ: STRI 28, dry, Santa Cruz Island, Chiriquí Gulf, 5–10 m, H. Guzman, 10 December 2001; STRI 104, dry, Isla Barca, 5–10 m, H. Guzman, 18 April 2002; STRI 292, dry, Piedra Hacha, 5–10 m, H. Guzman, 22 April 2002; STRI 354, dry, Almohada Island, 5–15 m, H. Guzman, 29 April 2002; STRI 374, 375, 376, dry, Toboguilla Island, 5–10 m, H. Guzman, 9 May 2002; STRI 553, etanol preserved, Bolanito Island, 6 m, H. Guzman, 16 April 2003; STRI 768, San Telmo Island, 3–8 m, H. Guzman, 7 August 2003; STRI 779, 781, 782, Pedro Gonzales Island, 3 m, H. Guzman, 11 August 2003; STRI 787, San Jose Island, 4 m, H. Guzman, 10 October 2003; STRI 907, 908, Pedro Gonzales Island, 10 m, H. Guzman, 23 September 2004.

Muricea retusa **Verrill, 1869**

Figures 31–32

Muricea retusa Verrill, 1869: 432–434; Kükenthal 1919: 752; Kükenthal 1924: 148; Harden 1979: 158.

Material. Holotype. YPM 3068, dry, attached to a colony of *M. fruticosa*, Pearl Islands, Panamá, 11–14 m, F.H. Bradley, 1866–1867. Schizotype. USNM 1013283, same data as in the holotype.

Description. The holotype is a 7 cm long and about 6 cm wide colony. It is attached to the holdfast of a large *M. fruticosa* colony (Fig. 31A). The holotype has a conical holdfast about 14 mm diameter. The branching is dichotomous, in one plane (Fig. 31A). Two main branches arise from a short stem, and bifurcate producing secondary branches, that subdivide again at a distance 25–50 mm apart. The branches split at angles of about 45°, and the only one that is complete is slightly curved, and clavate at the end. The branches are 7–8 mm in diameter and are of the same diameter along their length, and little enlarged toward the tips. Unbranched terminal ends are up to 50 mm long, but most are stumps. The calyces are all around the branches, close together, not imbricated but little overlapped and composed of two horizontal rows of sclerites. They are sub-conical, as wide as long, 1–1.5 mm in height, directed upwards at angles

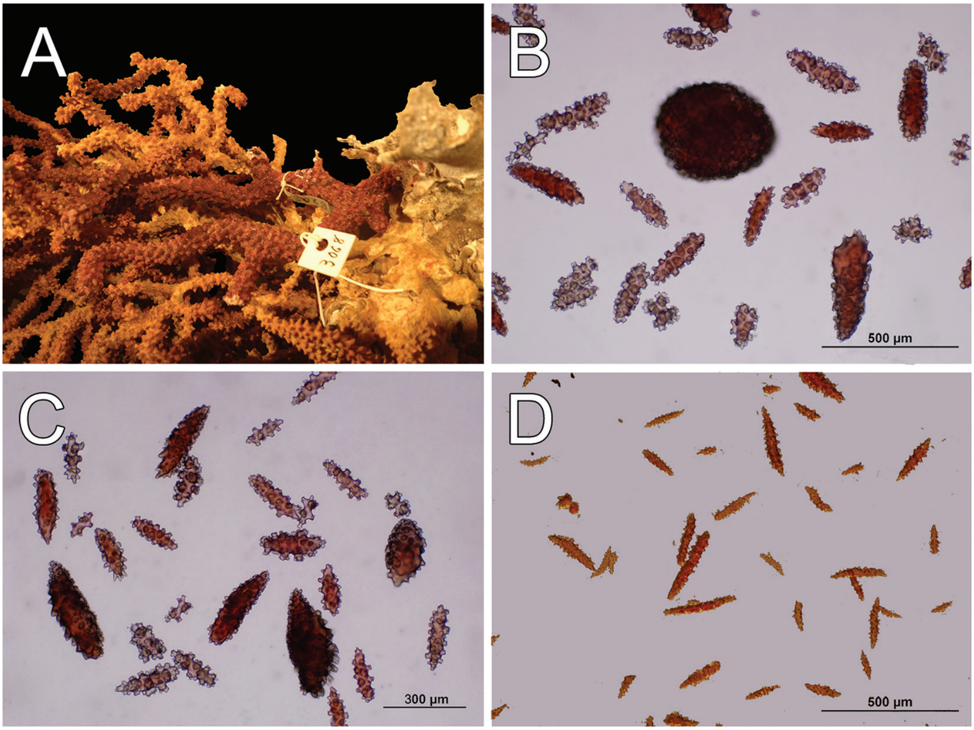

Figure 31. *Muricea retusa* Verrill, 1869, YPM 3068. **A** Colony **B–D** Sclerites, light micrographs.

of 30°–45° at the upper branches and at greater angles at the lower branches, also more distantly spaced and smaller (Fig. 31A). The coenenchyme is coarse, composed of large and irregular-shaped spindles giving a granulose aspect to the colony. The sclerites are reddish purple, purple varying to light orange (Fig. 31B–D). The outer coenenchymal and calycular sclerites are mostly unilateral spinous spindles, 0.35–1.2 mm long and 0.15–0.6 mm wide, one side crowded by small warts and the other spinulate, with short or large spines. They are of diverse shapes, unequal with one side truncate and the other acute, with triangular or with almost rectangular forms (Fig. 32A), and warty cylindrical spindles 0.30–0.45 mm long and 0.12–0.20 mm wide (Fig. 32B). The axial sheath is composed of light orange irregular spindles and radiates, 0.10–0.30 mm long and 0.06–0.14 mm wide (Fig. 32C). Anthocodial sclerites are orange and light yellow irregular spindles and warty rods 0.06–0.40 mm long and 0.02–0.10 mm wide (Figs 31D, 32D).

Colour of the colony is reddish purple.

Distribution. It is only known from the type locality, Pearl Islands, Panamá.

Remarks. Verrill (1869) described this species from just one specimen on the holdfast of a 36 cm by 29 cm *M. fruticosa* colony. Except for Harden (1979), who mentioned this species, no other author has referred to it, and no other specimens are identified as *M. retusa* in the museums visited.

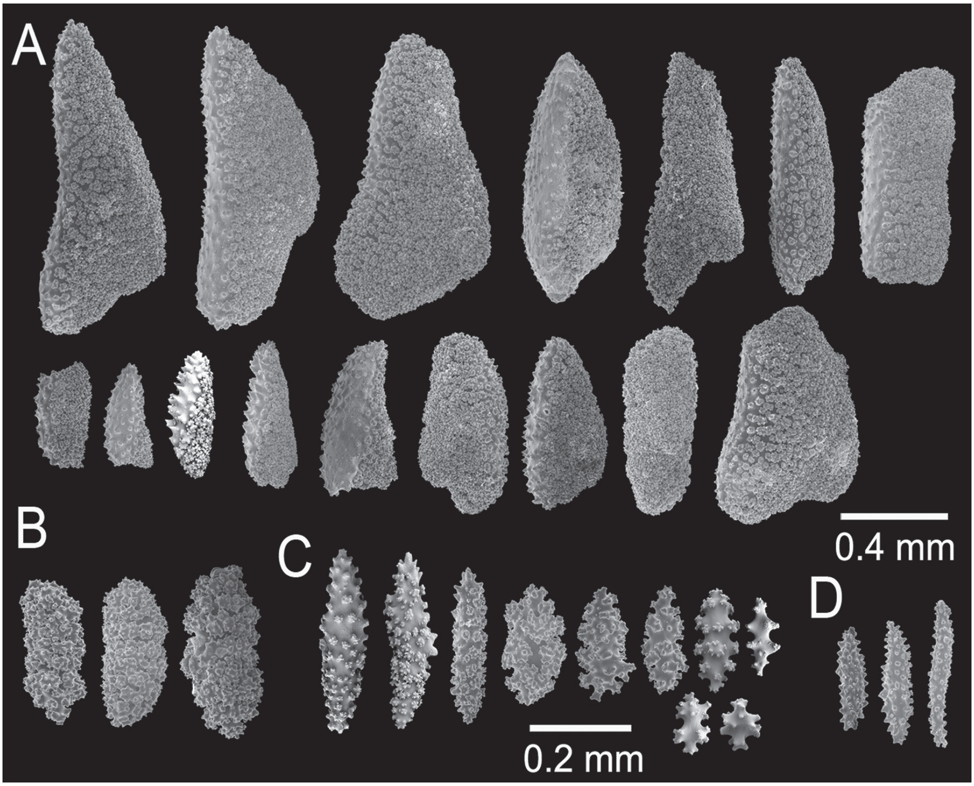

Figure 32. *Muricea retusa* Verrill, 1869, YPM 3068. **A–B** Calycular and coenenchymal sclerites **C** Axial sheath sclerites **D** Anthocodial sclerites.

Muricea purpurea Verrill, 1864

Figures 33–38

Muricea hebes (pars.) Verrill, 1864: 36.

Muricea purpurea Verrill 1868b: 412; Verrill 1869: 441–444; Kükenthal 1919: 752; Kükenthal 1924: 146; Hickson 1928: 366–367; Riess 1929: 394–395; Stiasny 1943: 66–68; Harden 1979: 157–158.

Muricea purpurea var. *nigra* Hickson, 1928: 367 syn. n.

Muricea rubra Aurivillius, 1931: 108–109 syn. n.

Material. Lectotype. YPM 1795A, dry, Pearl Islands, Panamá, F.H. Bradley, 1866–1867, no more data. Paralectotypes. PANAMÁ: MCZ 7018 (707, fragment); YPM 808; YPM 1560A-G; YPM 1795B; ZMUC ANT-194 (YPM 1560), dry, Pearl Islands, F.H. Bradley, 1866–1867, no more data. YPM 1637 (fragment), alcohol preserved; Pearl Islands, F.H. Bradley, 1866–1867, no more. MÉXICO: MCZ 55, ethanol preserved; Acapulco, A. Agassiz, 1859–1860, no more data. MCZ 4066 (188); MCZ 4067 (188); YPM 391, dry, Acapulco, A. Agassiz, 1859–1860, no more data.

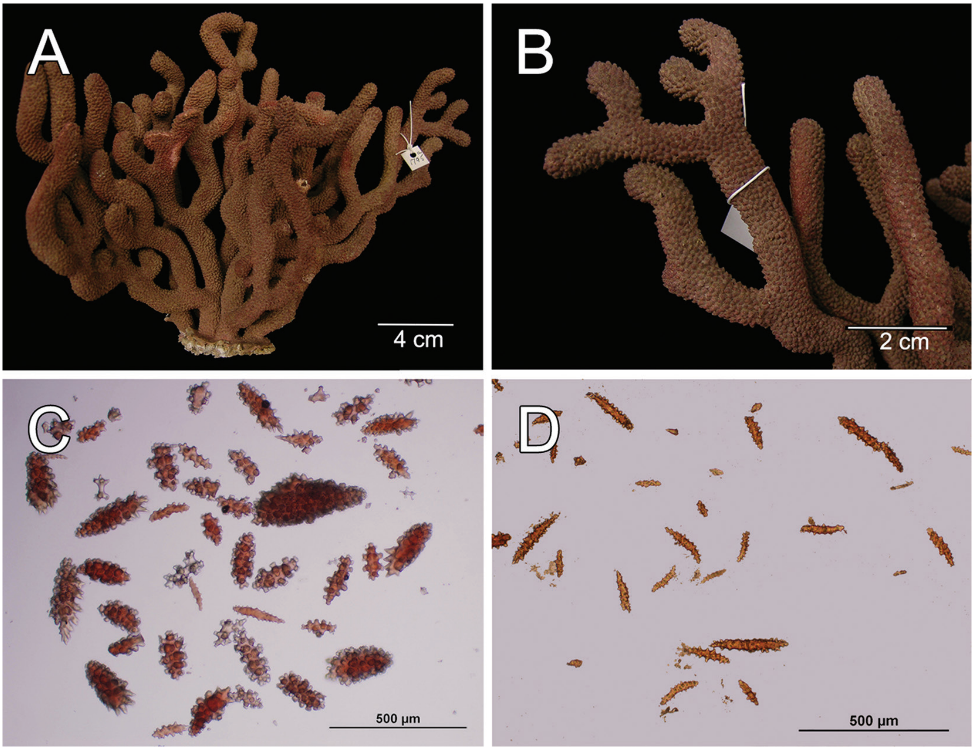

Figure 33. *Muricea purpurea* Verrill, 1864, YPM 1795a. **A** Colony **B** Detail of branches **C–D** Sclerites, light micrographs.

Other type material. PANAMÁ: BM 1946.1.14.44, dry, off Taboguilla Island, 9 m, T. Mortensen, 27 November 1915. USNM 34062, dry, Gulf of Panamá, Panamá, no more data. ZMUC ANT-142 (Hickson's holotype of *M. purpurea* var. *nigra*, ethanol preserved, Taboga Island, Panamá, 9 m, T. Mortensen, 25 November 1915. NICARAGUA: SMNH 1693 (Aurivillius's holotype of *M. rubra*); USNM 44190 (fragment of SMNH 1693), dry, off Realejo, Leg. Palme, no more data.

Description. The lectotype is a 22 cm long and 21 cm wide colony with branching in one plane and mostly dichotomous (Fig. 33A). The colony is composed of four stems that arise from a spreading holdfast about 5 mm in diameter and devoid of coenenchyme at the base. The four stems, 6–11 mm in diameter, are slightly flattened, and 12–45 mm long. They bifurcate producing secondary branches, that subdivide again at distances of 12–75 mm apart, 2–3 branches do not subdivide, reaching up to 12 cm long, but most of them do, some of them up to 5 times. The branches are stout, 12–14 mm in diameter and are little tapered toward the tips, 9–11 mm in diameter. The branches are wider and flattened at the branching points, 12–14 mm in diameter. They are mostly crooked, split at close angles 45°–60° at the upper branches, and at wider angles close to the base; these branches curve and some of them bend upwards (Fig. 33A). The unbranched terminal ends are 50–80 mm long. Axes are

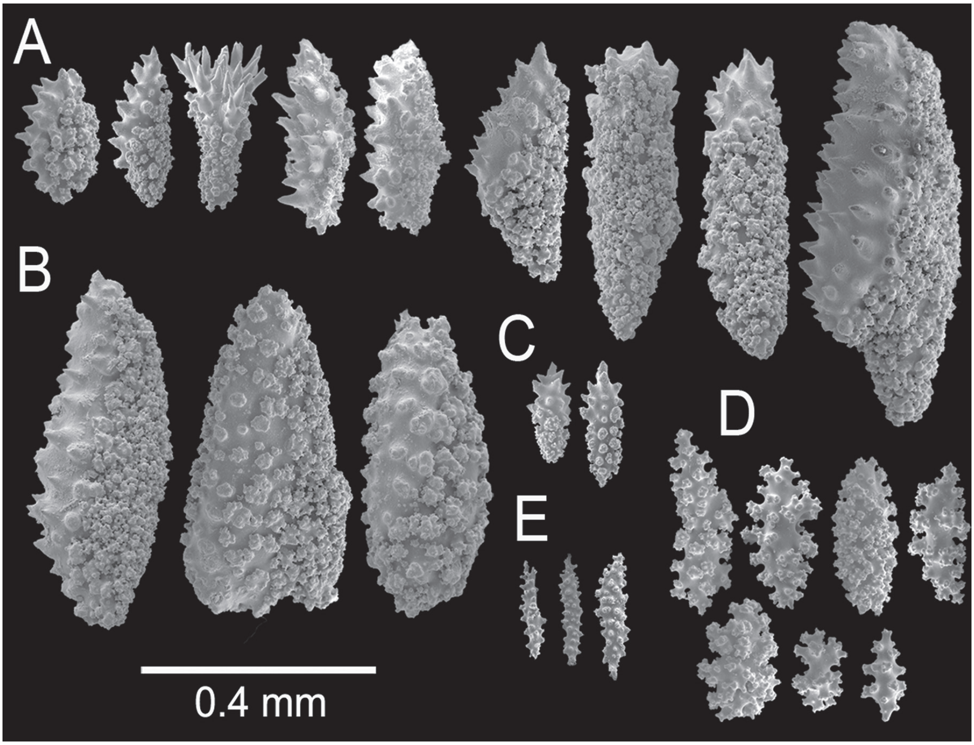

Figure 34. *Muricea purpurea* Verrill, 1864, YPM 1795a. **A–C** Calycular and coenenchymal sclerites **D** Axial sheath sclerites **E** Anthocodial sclerites.

brownish and with darker hues at the thicker branches. The calyces are all around the branches, close together and slightly imbricate (Fig. 33B). They are small, up to 1.8 mm long, sub-conical, with a granulose appearance. The calyces extend upwards with the tips pointed and often incurved; they are smaller and truncated at the lower parts of the branches. The coenenchyme is thick, sclerites are dark red and reddish orange (Fig. 33C–D), and those from the axial sheath are pink. The calycular and the outer coenenchymal sclerites are leaf-like spindles, 0.3–0.70 mm long and 0.10–0.30 mm wide, with spiny lateral process and a warty surface (Fig. 34A). Spinous club-like spindles are abundant especially toward the calyces and slightly project beyond the calyx border. They are stout and rough, 0.15–0.20 mm long and 0.07–0.08 mm wide, with a warty base, and a thorny head (Fig. 34C). Unilateral spinous spindles are smaller, 0.23–0.62 mm long and 0.13–0.30 mm wide, with one side warty and the other spinulose (Fig. 34B). The axial sheath is composed of irregular spindles up to 0.24–0.40 mm long and 0.10–0.14 mm wide with acute or bifurcated ends and tuberculate radiates 0.13–0.21 mm long and 0.09–0.14 mm wide (Fig. 34D). Anthocodial sclerites are reddish orange, composed of warty rods, 0.09–0.30 mm long and 0.03–0.055 mm wide, (Fig. 34E).

Colour of the colony is reddish purple.

Habitat and variability. Verrill's type collection is composed of specimens from Panamá and Acapulco, México. The description of *M. purpurea* was mostly based on the Panamá specimens (Verrill 1869), YPM 1795 was the figured specimen (Verrill 1869 plate VII, 6). However we found that there are two different morphologies among the specimens. The ones from Mexico are finger-like colonies, composed of one or more single branches, with a more intense red colour (reddish purple) and with larger calyces (Fig. 35A) than the specimens from Panamá. The largest sclerites in the Mexican specimens reach up to 1.0 mm long (Fig. 36A), larger than 0.625 mm as stated by Verrill for *M. purpurea*. The larger sclerite sizes were not found in the typical series from Panamá, where the maximum size was 0.70 mm. The sizes and types of the rest of sclerites are mostly consistent with the typical specimens (Fig. 36B–C). The sclerites of the specimens from México in the YPM type series are morphologically consistent among them, but in the Panamá specimens we found both sclerite morphologies (e.g., YPM 7018 from Panamá matches the sclerites of the Mexican morphotype). There is a series of intermediate types of sclerites among the examined specimens and the lectotypes (Figs 35B–C; 37B, D). In some specimens there is a dominance of spindles with terminal spiny processes, others with lateral spiny processes. In some cases the spines of the leaf-like spindles are shorter than in others, e.g., paralectotype MCZ 4066 (Fig. 35A–C) and MCZ 4067. The sclerite colours are mostly as in the lectotype, but some variation toward darker hues was observed. The colour of the colonies is from reddish purple to dark purple (Figs 35A; 37A, C; 38A–B). The extremes can be observed in the former *M. rubra* and *M. purpurea* var. *nigra* (syns. n. in this paper). The lighter colours are in the former and the darker hues in the latter (Fig. 37A, C). We have found all these morphologies in our recent collections from Costa Rica, Panamá, Ecuador, Nicaragua and México. Perhaps population biology research of these communities could reveal affinities among the morphotypes that could justify further species separation.

The colonies are found on rocky substrates, mostly vertically placed or upside down in caves. They also occur in crevices at rocky bottoms and grow straight up. The colonies can extend along the substrate by spreading holdfast up to 30 cm long producing separate branches forming large colonies. When alive, polyps look, or greenish yellow (Fig. 38A), or whitish on a dark purple colony (Fig. 38B). When polyps retract colonies look darker, more blackish (Fig. 38A).

Distribution. It is a widespread species distributed from México to Perú. The species has been reported for Acapulco, México; Corinto, Nicaragua; Ecuador (Kükenthal 1924), from Santa Clara Island to Esmeraldas (Rivera and Martínez 2011) and Panamá. We have observed it at several sites along the Pacific coast from México to Perú. The depth range is from 3 to 25 m, but mostly it occurs at 8 to 15 m.

Type locality, Pearl Islands, Panamá.

Remarks. The species was first mentioned by Verrill (1864) together with other species that he separated and properly described later (1869). *Muricea purpurea* was described with specimens from Panamá and México, Verrill did not designate a holotype. The specimen YPM 1795A is herein designated as the lectotype of this species in order to clearly establish its taxonomic status.

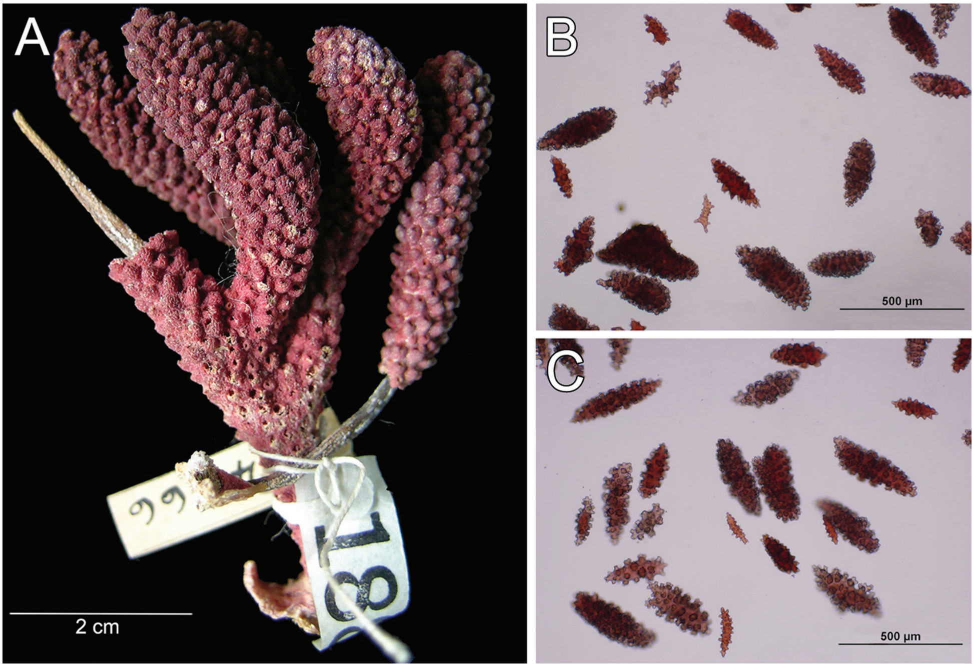

Figure 35. *Muricea purpurea* Verrill, 1864, MCZ 4066. **A** Colony **B–C** Sclerites, light micrographs.

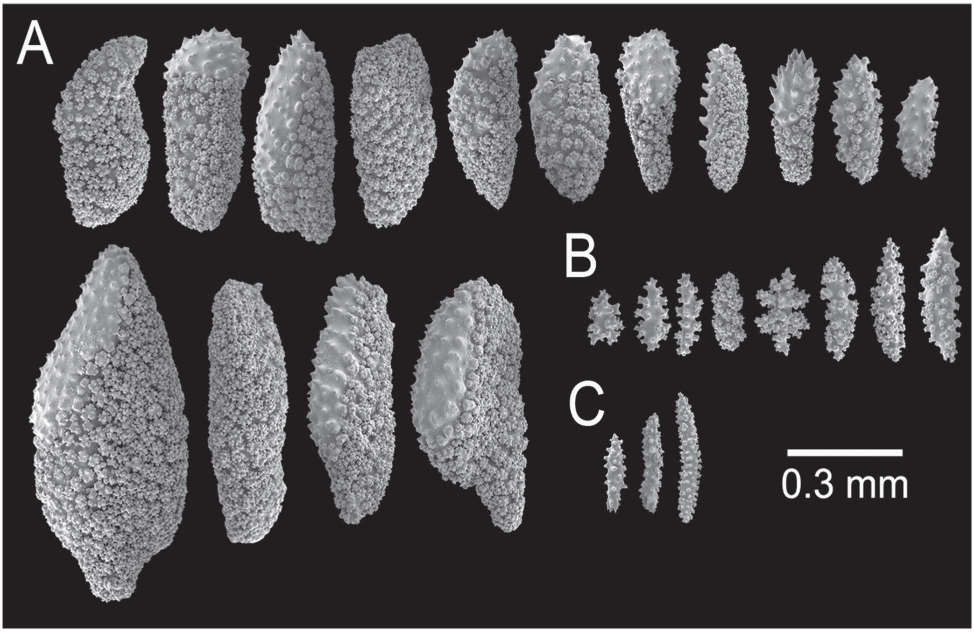

Figure 36. *Muricea purpurea* Verrill, 1864, MCZ 4066. **A** Calycular and coenenchymal sclerites **B** Axial sheath sclerites **C** Anthocodial sclerites.

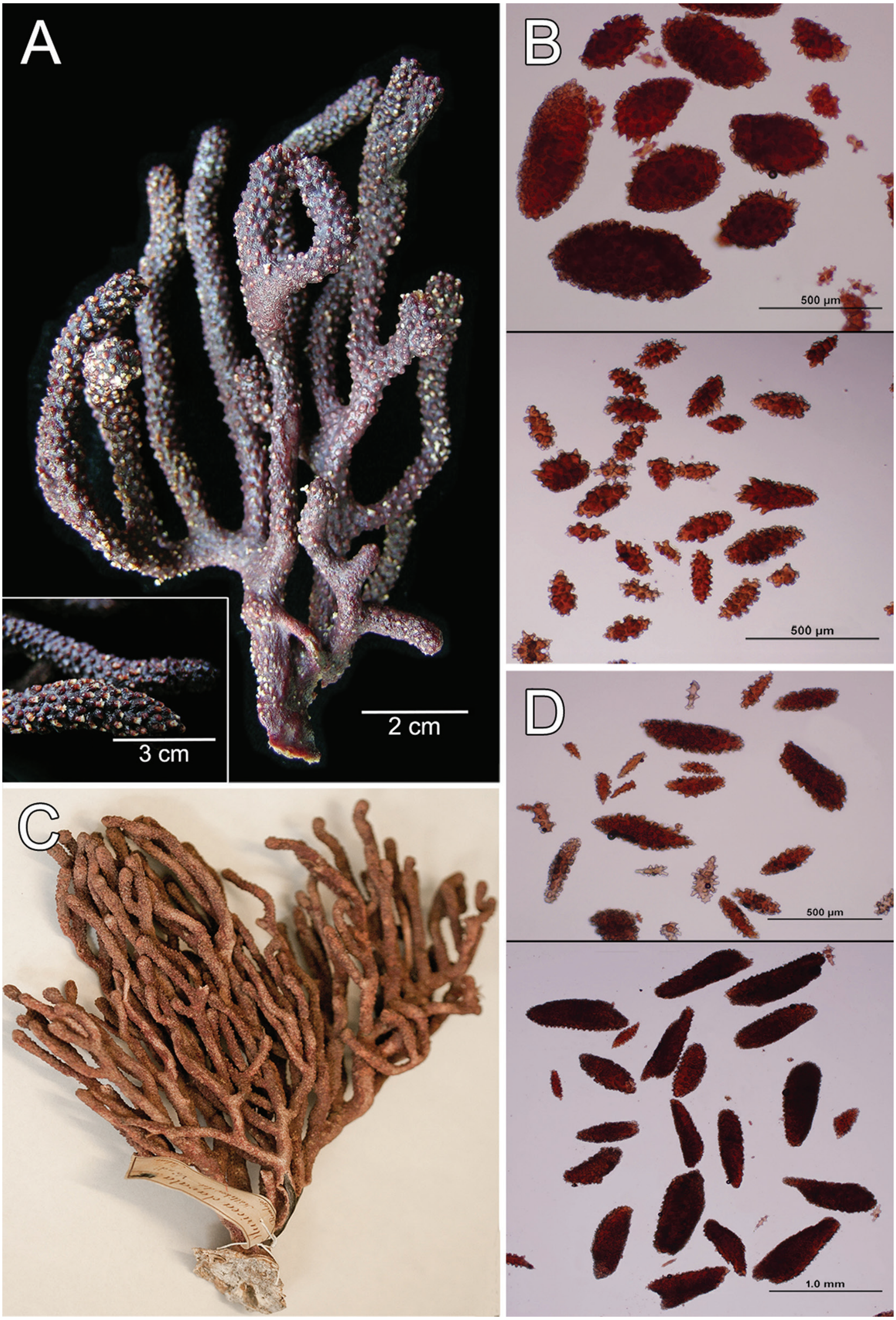

Figure 37. *Muricea purpurea* Verrill, 1864. **A** ZMUC ANT-142 (*M. purpurea* var. *nigra* Hickson, 1928, syn. n.) colony **B** Sclerites, light micrographs **C** SMNH 1693 (*M. rubra* Aurivillius, 1931, syn. n.) colony, photograph: Elin Sigvaldadottir **D** Sclerites, light micrographs.

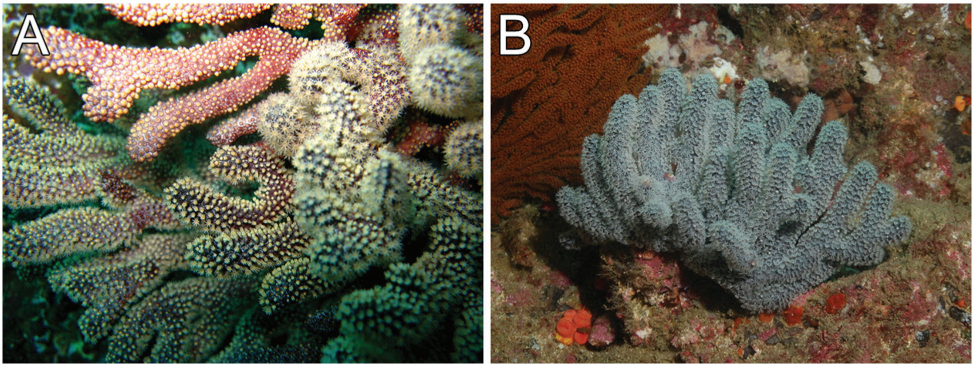

Figure 38. *Muricea purpurea* Verrill, 1864, colonies *in situ*, submarine pictures. **A** Oxaca, México, photograph: Rosalinda Abeytia **B** Ahorcados Islet, Machalilla National Park, photograph: Graham Edgar.

There are two other related species *M. rubra* and *M. purpurea* var. *nigra.* Hickson (1928) proposed a variety of *M. purpurea* (var. *nigra*) based on the colour (very dark purple) and the ramification (bushier). However, according to Hickson the sclerites of this species were that close to *M. purpurea* that he could not consider them as separate species. We conclude that Hickson´s ZMUC ANT-142 specimen is in the variation range of *M. purpurea*, for this reason it is considered herein as a synonym. *Muricea rubra* was described by Aurivillius (1931) with a specimen from Nicaragua. The author stated that he never had the opportunity to revise any material previously established and that he could not identify the species from the existing descriptions at that time (Aurivillius 1931, pag.104). We analysed Aurivillius' holotype (SMNH 1693) and, as in the case of *M. purpurea* var. *nigra*, we did not find *M. rubra* out of the variation range of *M. purpurea*. Herein it is also considered as a synonym of *M. purpurea*.

Other material revised. COSTA RICA. UCR 479a, dry, Herradura Beach, 10 m, J Cortés, 2 September 1983; UCR 510, 632a, dry, Sámara Beach, Guanacaste, 12 m, H. Guzman, 18 March 1984; UCR 800, dry, Olocuita Islet, Manuel Antonio National Park, Puntarenas, 8 m, J Cortés, 2 July 1995; UCR 1620, ethanol preserved, Carrillo Beach, Guanacaste, 10 m, J Cortés, 2006; UCR 1693, ethanol preserved, Salinas Bay, Guanacaste, O Breedy, 7 December 2006. ECUADOR: IIN 20, dry, Tambip, Salinas, 12–14 m, F. Rivera, P. Martínez, 20 July 2010; IIN 43, 48, dry, Gigima, Salinas, 12–14 m, F. Rivera, P. Martínez, 22 July 2010; IIN 99, 117, 119, 120, dry, Los Ahorcados, Machalilla National Park, 10–12 m, F. Rivera, P. Martínez, 25 July 2010; IIN 129, dry, Salango Island, Machalilla National Park, 12–25 m, F. Rivera, P. Martínez, 25 July 2010. PANAMÁ: STRI 360, dry, Otoque Island, Chiriquí Gulf, 5–10 m, H. Guzman, 9 May 2002; STRI 361, dry, Otoque Island, 5–10 m, H. Guzman, 9 May 2002; STRI 378, dry, Taboguilla Island Chiriquí Gulf, 5–10 m, H. Guzman, 9 May 2002; STRI 716, H Station, 45 m, H. Guzman, 6 August 2003; STRI 766, 767, San Telmo Island, 3–8 m, H. Guzman, 7 August 2003; STRI 784, San Telmo Island, 3 m, H. Guzman, 10 October 2003; STRI 809, 813, Del Rey SE Island, 4 m, 6 April 2004 ; STRI 823, Puerco Island, 3 m, H. Guzman, 6 April 2004; STRI 827, Elefante Island, 4 m, H.

Guzman, 7 April 2004 ; STRI 847, Sur Pacheca, 2 m, H. Guzman, 20 April 2004 ; STRI 854, Pearl Island, 3 m, H. Guzman, 21 April 2004 ; STRI 855, Pearl Island, 4 m, H. Guzman, 21 April 2004 ; STRI 860, 861, Pearl Island, 2–4 m, H. Guzman, 23 April 2004 ; STRI 894, San Telmo Island, 3–8 m, H. Guzman, 18 August 2004 ; STRI 905, Pedro Gonzales Island, 10 m, H. Guzman, 23 September 2004; STRI 931, 932, 933, Pedro Gonzales Island, 10 m, H. Guzman, 23 September 2004.

Muricea hebes Verrill, 1864

Figures 39–40

Muricea hebes (pars.) Verrill, 1864: 36.

Muricea hebes Verrill 1866: 328; Verrill 1868b: 411–412; Verrill 1869: 439–441; Kükenthal 1919: 752; Kükenthal 1924: 146; Hickson 1928: 365–366; Riess 1929: 395–396; Harden 1979: 151.

Material. Lectotype. YPM 564a, dry, Pearl Islands, Panamá, F.H. Bradley, 1866. Paralectotypes. YPM 564 b-f, dry, Pearl Islands, Panamá, F.H. Bradley, 1866.

Description. The lectotype is 6 cm long and 9 cm wide (Fig. 39A); it has a worm tube in one of the lower lateral branches. Two slightly flattened stems, 5–6 mm in diameter, arise from an oval holdfast, about 1 cm diameter, almost devoid of coenenchyme (Fig. 39A). The branching is irregularly dichotomous and multiplanar (Fig. 39A). The stems extend 12–15 mm and subdivide in secondary branches that bifurcate up to 4 times at close angles 30°–40°, and curve upwards. Branches are 10–12 mm apart. They are flattened, 5–8 mm in diameter, little wider at the tips, 6–9 mm in diameter. Unbranched terminal ends are up to 3.2 cm long. Axes are brownish. Calyces are all around the branches, curved upwards and close together, slightly imbricate (Fig. 39A), up to 1.8 mm long, and around 1 mm wide. Polyps are on the upper and inner part of the calyces, nearly covered by the incurved outer border of the calyces. The

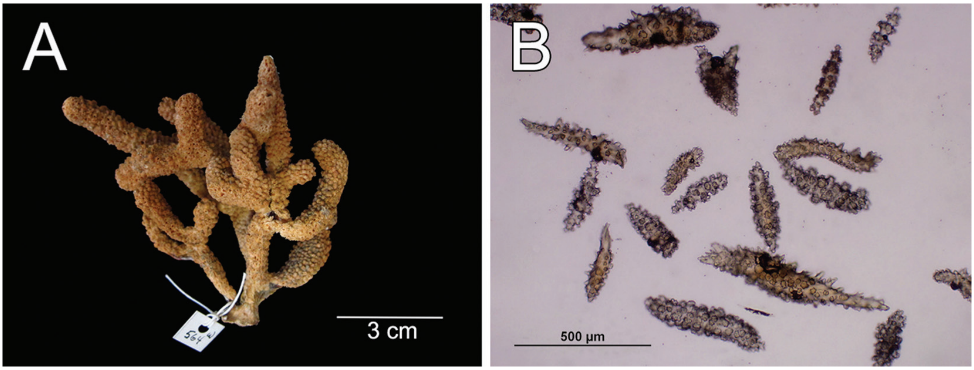

Figure 39. *Muricea hebes* Verrill, 1864. YPM 564a. **A** Colony **B** Sclerites, light micrographs.

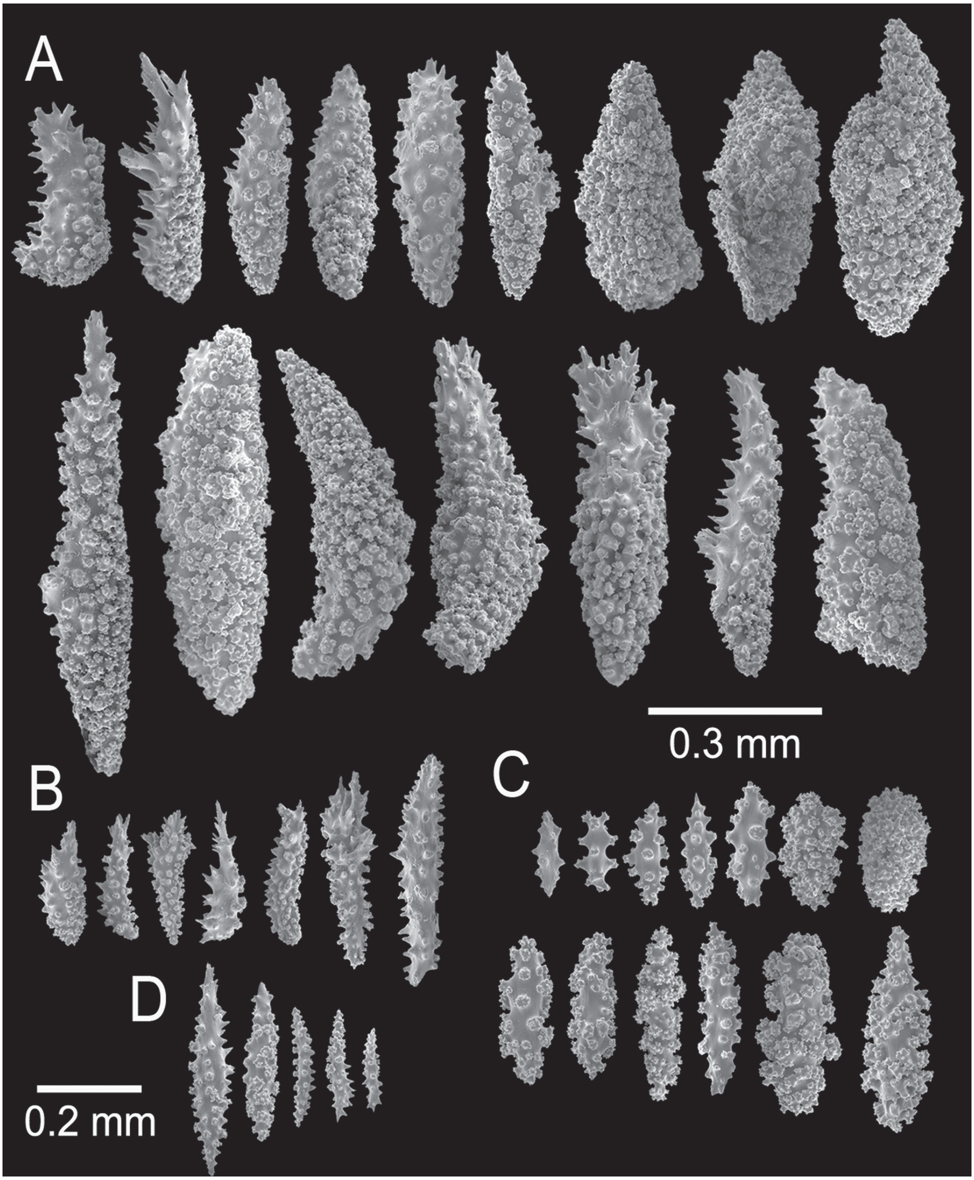

Figure 40. *Muricea hebes* Verrill, 1864. YPM 564a. **A–B** Calycular and coenenchymal sclerites **C** Axial sheath sclerites **D** Anthocodial sclerites.

adaxial border of the calyx is imperceptible. The coenenchyme is thick, composed of pale yellow and yellowish sclerites (Fig. 39B). The outer coenenchymal and calycular spindles are of various types (Fig. 40A–B), unilateral spinous with a warty inner side and a small outer portion with projecting spines, and with the inner side warty, and the outer side with large sharp spines, prickly spindles and spinous club-like spindles. These sclerites are 0.32–0.83 mm long and 0.14–0.2 mm wide. They vary from elongated to shorter forms, with round ends, or with one end tapered and the other wide and blunt, or with one end acute or bifurcated, or tapered at both ends (Fig. 40A). Furthermore, smaller forms are present, 0.24–0.28 mm long and 0.07–0.1 mm wide (Fig. 40B), that concentrate around the calyx border (Fig. 40B). The axial sheath is composed of warty radiates and spindles, 0.15–0.40 mm long and 0.053–0.15 mm wide (Fig. 40C). Anthocodial sclerites are warty rods, 0.054–0.45 mm long and 0.015–0.1 mm wide, some with distal spines (Fig. 40D).

Colour of the colony is yellowish brown.

Distribution. Found in México in Pájaros Island and reported for Cabo Pulmo, Gulf of California (according to Covarrubias et al. 1996). Type locality, Pearl Islands, Panamá.

Remarks. The species was created by Verrill in 1864 with specimens from Acapulco, México collected by Agassiz. Later Verrill (1869) made a more detailed description and included specimens from Nicaragua and Panamá. However, the type series in the YPM only includes specimens from Panamá collected by Bradley. The specimens from México were included in *M. purpurea*. However *M. hebes* was found in Mexican islands by J.L. Carballo. The specimen YPM 564a is herein designated as the lectotype of *M. hebes* to clearly establish its taxonomic status.

Other material revised. MÉXICO: M 61, dry, Pájaros Island, Mazatlan Bay, Sinaloa, 5–25 m, J.L., 3 February 1999.

Muricea nariformis Aurivillius, 1931

Figures 41–42

Muricea nariformis Aurivillius, 1931: 109–111.

Material. Holotype. SMNH 1121, alcohol preserved, locality unknown, Leg. Salmin 1873, Rijksmuseum, No. 64.

Description. The holotype consists of two branches, about 6 cm long and 3 cm wide each (Fig. 41A). The branching is dichotomous and bifurcate up to 3 times. The branches bifurcate at angles 45°–50°, 7.5–10 mm apart. Branches and branchlets are all of similar thickness, 56 mm in diameter, with rounded tips slightly expanded. Unbranched terminal ends are up to 24 mm long. Axes are brownish. The calyces are all around the branches and close together. They are mostly low cones with a slightly elevated margin around the polyps, 0.8–1.2 mm in height (Fig. 41B), and the abaxial border slightly more prominent and curved upwards (Fig. 41B). The coenenchyme is thick, composed of brownish orange and light brown to whitish sclerites (Fig. 41C–D). As in many other species in this genus, a division of sclerite layers is not clear and the coenenchyme is formed of a combination of several types of sclerites intermingled. The coenenchymal and calycular sclerites are mostly of the

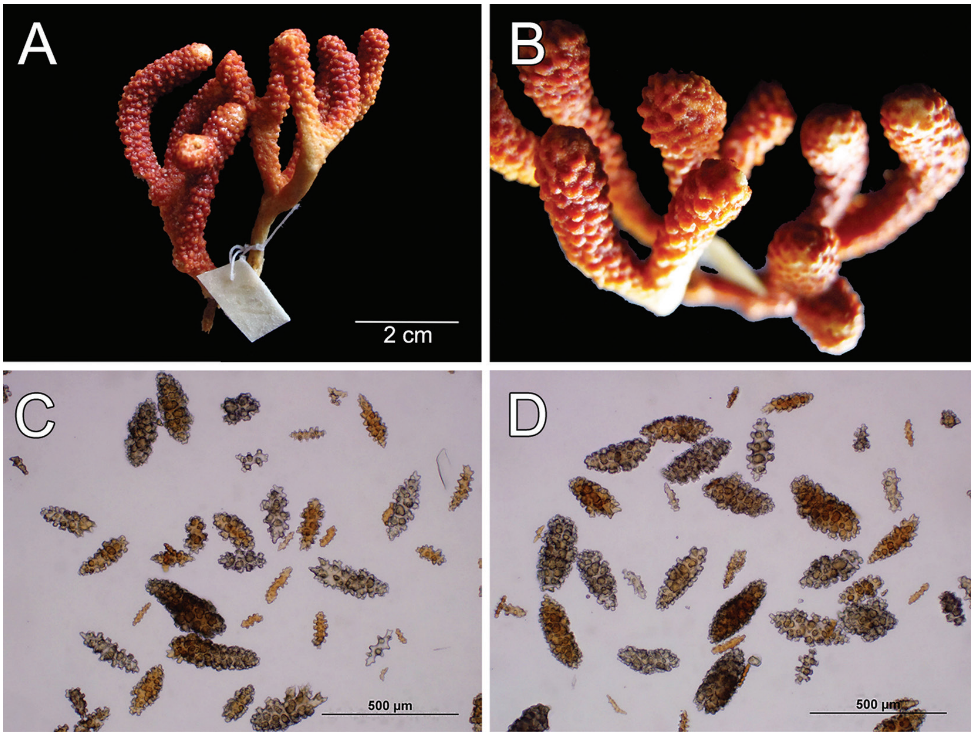

Figure 41. *Muricea nariformis* Aurivillius, 1931. SMNH 1121. **A** Colony **B** Detail of branches **C–D** Sclerites, light micrographs.

same type. Few unilateral spinous spindles are present; the larger ones are rather leaf-like spindles with a thorny lateral quill and wide cylindrical forms (Fig. 42A). The larger ones are covered with warts almost up to the thorny end, and the others have a pronounced upper or lateral ridge of large spines. The spindles are 0.2–0.52 mm long and 0.04–0.28 mm wide (Fig. 42A). Warty spindles and some cylinder-like, 0.25–0.32 mm long and 0.06–0.15 mm wide (Fig. 42B), compose the axial sheath and the inner coenenchyme. Anthocodial sclerites are orange warty rods and irregular forms, 0.05–0.17 mm long and 0.01–0.035 mm wide (Figs 41C, small orange sclerites, 42C). Colour of the colony is brownish orange; the lower part of the branches is of a lighter hue.

Distribution. Unknown.

Remarks. The species was described by Aurivillius (1931) based on specimens from an unknown locality in the southern Pacific. He described the species as new without comparing with any type material and remarked that the new species was similar to *M. robusta* (Aurivillius 1931). The two species indeed have some similarity discussed below. Presently we do not have specimens matching this species.

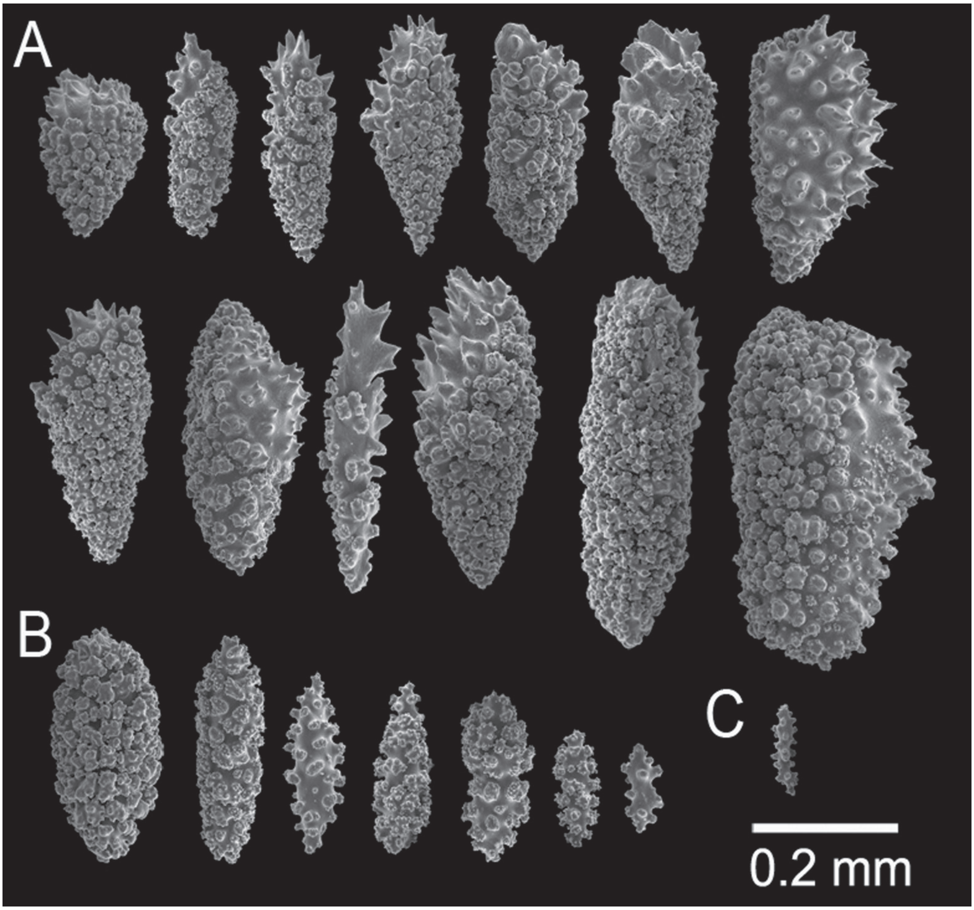

Figure 42. *Muricea nariformis* Aurivillius, 1931. SMNH 1121. **A** Calycular and coenenchymal sclerites **B** Axial sheath sclerites **C** Anthocodial sclerite.

Muricea robusta Verrill, 1864

Figures 43–44

Muricea robusta Verrill, 1864: 36; Verrill 1869: 436–437; Kükenthal 1919: 752; Kükenthal 1924: 144; Riess 1929: 396–397; Harden 1979: 159.
Muricea robusta (pars.) Verrill 1866: 329.

Material. Lectotype. YPM 1189a, dry, Acapulco, Mexico, A.E. Agassiz, 1859–1860, no more data. Paralectotypes. MÉXICO: MCZ 189; MZUC-ANT 195 (part of MCZ 189); YPM 1712 (figured fragment, Verrill 1869); YPM 1189b, dry, Acapulco, A.E. Agassiz, 1859–1860, no more data.

Description. The lectotype is a 20 cm long and 10 cm wide colony with partially broken coenenchyme on some branches and with three naked distal axes (Fig. 43A).

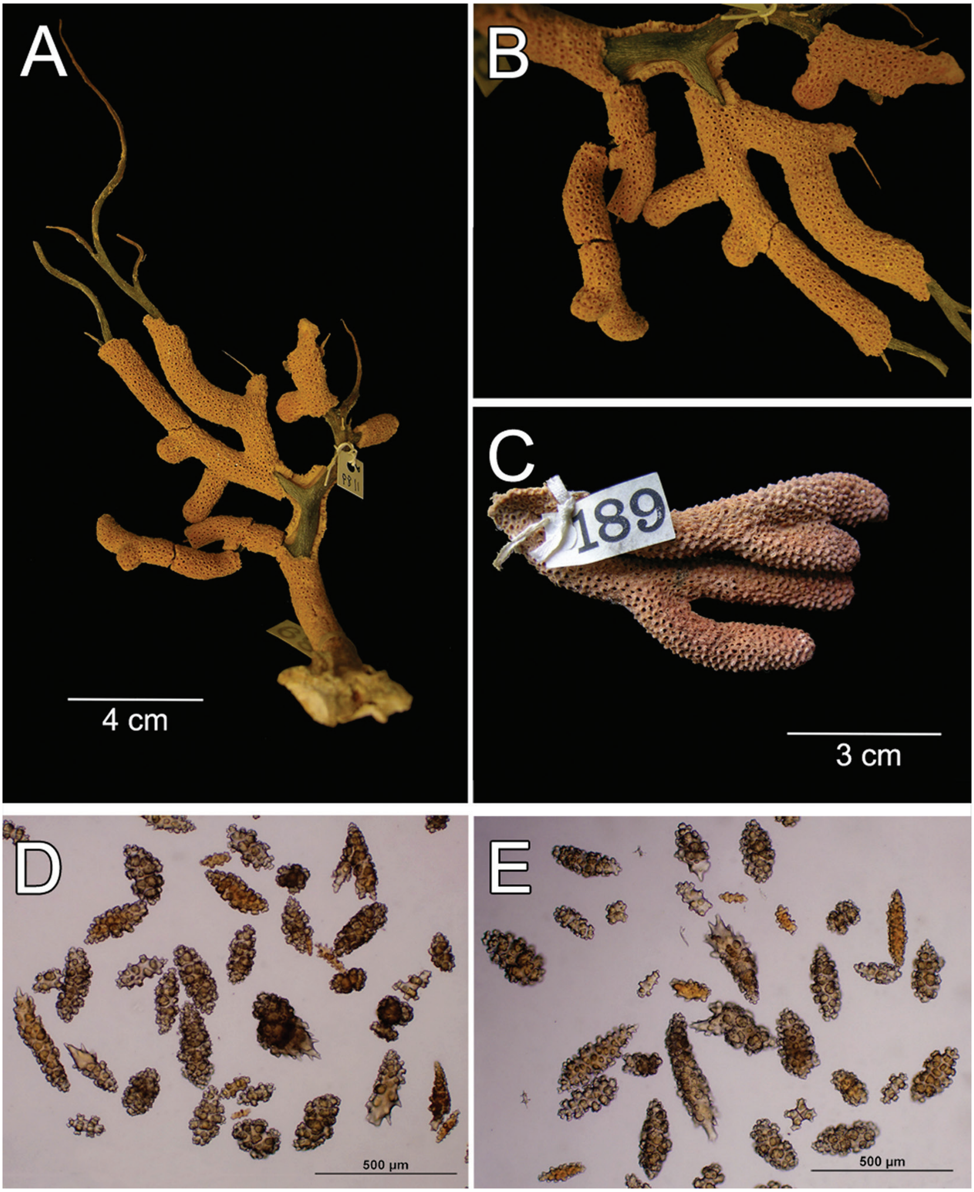

Figure 43. *Muricea robusta* Verrill, 1864. **A** Colony, YPM 1189a **B** Detail of branches, YPM 1189a **C** Detail of calyces, ZMUC ANT 195 (YPM 1189a. (189) fragment) **D–E** Sclerites, light micrographs, YPM 1189a.

A slightly flattened stem, 11 mm in diameter, arises from an oval holdfast, about 4 cm in diameter (Fig. 43A). The branching is mostly dichotomous in one plane (Fig. 43A). The stem extends up to 36 mm and subdivides in two main branches, which bifurcate up to 5 times producing secondary branches and branchlets of less than 10

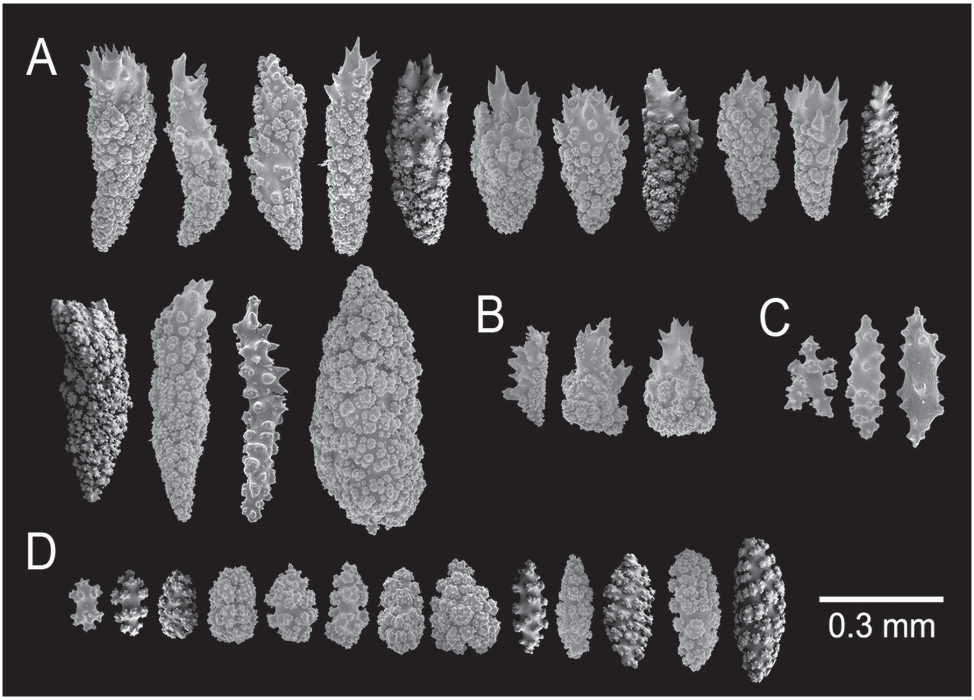

Figure 44. *Muricea robusta* Verrill, 1864. YPM 1189a. **A–B** Calycular and coenenchymal sclerites **C** Anthocodial sclerites **D** Axial sheath sclerites.

mm in diameter, all of similar diameter. The branches bifurcate at angles 45°–60°, 3.5–5 mm apart; the branchlets, that are short, are almost at right angles. The upper branches are curved inferring from the naked axes (Fig. 43A). Unbranched terminal ends are up to 16 mm long, with rounded tips, up to 8.5 mm in diameter. The naked unbranched terminal ends reach up to 70 mm long. No anastomosing branches are present. Axes are black and brownish at the tips. The calyces are all around the branches and close together. They are mostly low cones, 0.7–1.2 mm in height, with a slightly elevated margin around the polyps (Fig. 43B) that are more prominent towards the end of the branches (Fig. 43C). At the upper branches, the lower margin of the calyx curves upwards. The polyp apertures are large, and conspicuous. The coenenchyme is thick and granulose, composed of orange, brownish orange and light brown to whitish sclerites (Fig. 43D–E). As in many other species in this genus, a division of sclerite layers is not clear and the coenenchyme is formed of a combination of several types of sclerite types intermingled. The coenenchymal and calycular sclerites are mostly the same type of spindles. The unilateral spinous spindles were rare in the samples, the larger sclerites are rather irregular spindles, bent or almost straight; the larger ones are covered with warts, almost up to the thorny end, and the others have a pronounced upper ridge of large spines (prickly spindles). The term cristate, suggested by Hickson (1928), could be applied to these sclerites (Fig. 44A–B). They are 0.24–0.64 mm long and 0.08–0.26 mm wide. There are some small leaf-like spindles and irregular cristate forms (Fig. 44B). The axial sheath and the inner coenenchyme have some conspicuous sub-spheroidal sclerites densely covered with warty tubercles, warty spindles, and some cylinder-like sclerites, 0.30–0.40 mm long and 0.13–0.19 mm wide, and tuberculate capstans, 0.16–0.25 mm long and 0.08–0.12 mm wide (Fig. 44D). Anthocodial sclerites are orange warty rods and irregular forms, 0.043–0.15 mm long and 0.04–0.05 mm wide (Fig. 44C). Colour of the colony is brownish orange.

Variability. The revised specimens are consistent with the lectotype.

Distribution. Found in México in Venado Island by J.L. Carballo and reported for Cape San Lucas (Harden 1979). Also found in Isla del Gallo, Colombia by Prahl et al. (1986) Type locality Acapulco, México.

Remarks. The species was first mentioned by Verrill in 1864 and formerly described in 1869 with a specimen from Acapulco. We believe that Verrill's type series are all fragments of the same colony; however, because this is not clear, herein we designated the specimen YPM 1189a as the lectotype of the species with the purpose of clearly establishing its taxonomic status.

Other material revised. COLOMBIA: USNM 79466, dry, Isla del Gallo, near Tumacao, 0.5 m, H. von Prahl, 4 February 1982. MÉXICO: M12, dry, Venados Island, Mazatlan Bay, Sinaloa, 5–25 m, J.L. Carballo, 2 February 1999.

Species-group comparison summary

The *Muricea austera*-group comprises eight species: *M. austera*, *M. albida*, *M. crassa*, *M. retusa*, *M. purpurea*, *M. nariformis*, *M. hebes* and *M. robusta*. The group is characterised by thick coenenchyme, thick branches and stout colonies that can be bushy, finger-like or candelabrum-like. Species comparisons are in Tables 1–2. The colour of the colony in this genus is remarkably constant (Verrill 1869, Hickson 1928). Therefore, it could be used as a primary character to separate species in the *M. austera*-group. First, colonies from deep brown to yellowish brown including *M. crassa*, *M. robusta*, *M. nariformis*, *M. austera* and *M. hebes* (ordered from darker to lighter colour). *Muricea crassa* is different from all others, especially in the larger size, thickness of the branches and the large rough calyces. The larger sizes of the sclerites are also found in *M. fruticosa* and *M. echinata* (in the *M. fruticosa* group), up to 2.4 mm long, but the species are different in many aspects, as discussed under the *M. fruticosa* group. *Muricea nariformis* and *M. robusta* differ from the others in the group by the leaf-like spindle as the dominant type of sclerites and the lowest calyces (Tables 1–2). Aurivillius (1931) noticed that *M. nariformis* was similar to *M. robusta*, with respect to the calyx shape and height, the colours of the colony and sclerites. Considering that Aurivillius never saw a specimen of *M. robusta*, he was rather correct. It is likely that

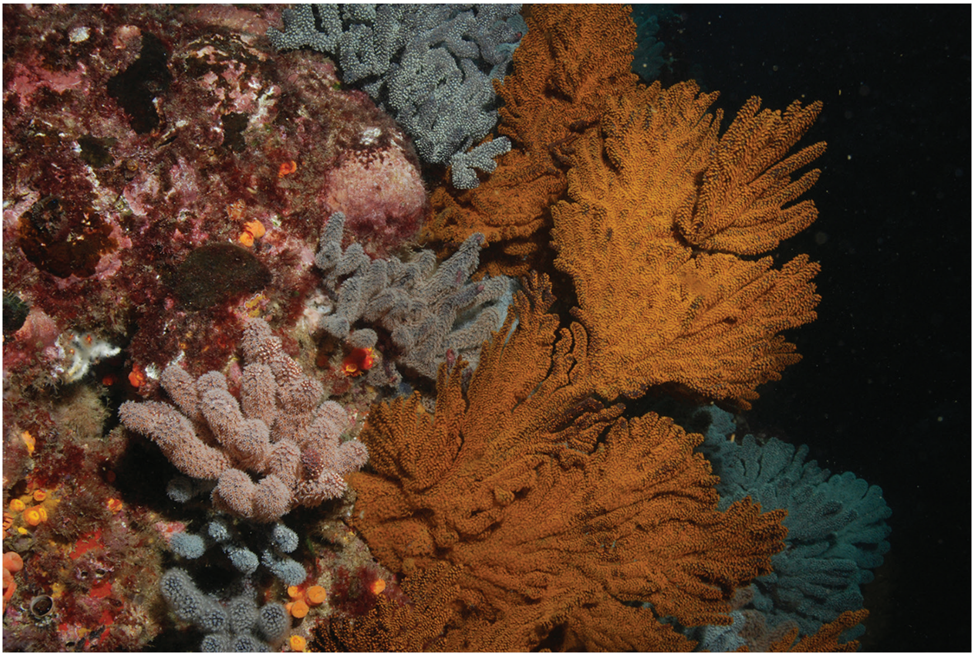

Figure 45. *Muricea* species, *M. purpurea* (left side) and *M. plantaginea* (right side). Ahorcados Islet, Machalilla National Park, Ecuador. Photograph: Graham Edgar.

M. nariformis is just a morphotype of *M. robusta*, showing just a different growing pattern and a lighter colour, but more specimens and field observation will be needed to synonymise them in the future. *Muricea austera* and *M. hebes* are similar in the colour of colony and sclerites, but differ in other characteristics (Table 2), especially in the sclerite sizes that are much smaller in *M. hebes*. According to Verrill *M. austera* is comparable with *M. echinata* (in the *M. fruticosa* group), especially in the colour of the colony and external appearance. However, *M. austera* differs from *M. echinata* in the thicker coenenchyme, smaller sclerites and shorter, broader and conical calyces (Tables 1–2).

The second group contains white colonies, including only *M. albida*. In this group (Table 2), the sclerites are similar in shapes and sizes to *M. austera* but they are not white or colourless as in *M. albida*. It could be compared with *M. formosa* but differs in many other aspects as discussed under *M. fruticosa* group.

The third group contains reddish purple colonies, including *M. retusa* and *M. purpurea*. These species are similar also in the dichotomous branching, the arrangement of the calyces and the calyx sclerites (in rows) (Tables 1–2). The main difference is the lack of large unilateral spinous spindles in *M. purpurea*. *Muricea purpurea* as established here differs from most of the other species in the *M. austera*-group in the relatively small size of the sclerites and the abundant and characteristic leaf-like spindles.

Conclusion

We conclude that the genus *Muricea* in the eastern Pacific comprises 20 valid species that could be separated by their morphological characters into four groups: the *M. squarrosa*-group represented by four species with tubular calyces (Breedy and Guzman 2015), and 16 species with shelf-like calyces, *M. fruticosa*-group, *M. plantaginea*-group and *M. austera*-group herein presented. There is a range of variation among group-species, but a larger number of specimens might be examined in order to decide about close species relationships. Some species are abundant while others are known only from type material. Presently, the most common species found were *M. austera*, *M. purpurea*, *M. plantaginea* (see Fig. 45) and *M. fruticosa*. They were found in clusters scattered over rocky outcrops, platforms or on muddy and sandy bottoms attached to debris, shells or any solid object. The deepest record is *M. fruticosa*, down to 100 m deep at Cocos Island seamounts (Fig. 4B) and Hannibal Bank seamount, Panamá. Future exploration could render more species with a wide distribution range.

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Sinularia polydactyla (Ehrenberg, 1834) (Cnidaria, Octocorallia) re-examined, with the description of a new species

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Abstract

Sinularia polydactyla (Ehrenberg, 1834) is re-described and a lectotype assigned. This led to examination of related material from various Indo-Pacific regions. Consequently, *Sinularia levi* **sp. n.** is described from Eilat, Israel (Gulf of Aqaba, northern Red Sea) and *S. compressa* Tixier-Durivault, 1945 and *S. candidula* Verseveldt & Benayahu, 1983 are synonymized with *S. polydactyla*. Additional specimens identified in the literature as *S. polydactyla* are provisionally reassigned to other taxa.

Keywords

Alcyonacea, re-description, new species, Indo-Pacific, Red Sea, taxonomy, phylogeny, coral reefs, COI, mtMutS

Introduction

The Indo-Pacific genus *Sinularia*, with an estimated number of ~190 nominal species, is the most speciose of the zooxanthellate, reef-dwelling octocoral genera (Ofwegen 2002). *Sinularia* species exhibit diverse growth forms and colony sizes, and occupy a wide range of depths from shallow water just below the tideline to deep reef habitats (Fabricius and Alderslade 2001). Occasionally, *Sinularia* colonies form large aggregations, dominating extensive areas on cross-equatorial reefs, including some at the margins of their geographical distribution range (e.g., Benayahu et al. 2012). Some species even deposit large amounts of sclerites in the form of spiculite, and are thus considered to be reef-builders (Jeng et al. 2011). In recent years, along with taxonomic descriptions of new *Sinularia* species, molecular systematic approaches have been applied to resolve species boundaries in the genus (e.g., McFadden et al. 2009). In conjunction with such studies, original type material has also been re-examined, some of which was previously considered lost (e.g., Ofwegen et al. 2013).

During his revision of the soft coral genus *Sinularia*, Verseveldt (1980) could not find the type specimens of several species, and as a result he re-described those species erroneously based on material from specimens of other, but similar-looking species. This became especially obvious with the first molecular phylogenetic study of the genus *Sinularia* (McFadden et al. 2009), in which colonies identified as *S. leptoclados* and *S. polydactyla* showed up in several different clades. As discussed by Ofwegen et al. (2013), *S. leptoclados* (Ehrenberg, 1834) appeared in different sub-clades of Clade 5C presented by McFadden et al. (2009). Likewise, *S. polydactyla* (Ehrenberg, 1834) appeared in several different clades, with specimens from the Red Sea in Clade 4B (characterized by polyps with point sclerites; clubs with central wart distinct, or clubs absent), while Indo-Pacific specimens belonged to Clade 4D (polyps without sclerites; clubs with central wart distinct). Recently we discovered three syntype specimens of *S. polydactyla* in the Zoological Museum of Berlin (ZMB), which were probably overlooked by Verseveldt because they were originally labeled as *Lobularia*. Examination of their sclerites proved two of these syntypes (ZMB 298, 299) to belong to genus *Sinularia* Clade 4D and one of them (ZMB 300) to the genus *Cladiella*. Therefore, we consider the Red Sea specimens previously identified as *S. polydactyla* but belonging to Clade 4B (McFadden et al. 2009) to belong to a yet unknown species, which is described and depicted below. Re-examination of additional material misidentified as *S. polydactyla* revealed another seven specimens belonging to this new species, giving it a distribution from the Red Sea to East Africa (West Indian Ocean).

We also managed to find the material used by Verseveldt (1980) to re-describe *S. polydactyla*, RMNH Coel. 15950. It was also re-examined and found to belong to Clade 4B rather than 4D, and therefore it cannot be *S. polydactyla*.

While examining the syntypes of *S. polydactyla*, it became obvious that *S. compressa* Tixier-Durivault, 1945 and *S. candidula* Verseveldt and Benayahu, 1983 are very similar to S. *polydactyla*. As *S. compressa* was also included in the molecular study and also occurred in two different parts of the phylogenetic tree (McFadden et al.

2009), specimens of these species were also re-examined. Neither these specimens nor the syntypes of *S. compressa* (Verseveldt, 1980: 30) differ much from *S. polydactyla*, and therefore we synonymize *S. compressa* with *S. polydactyla*. The type of *S. candidula* RMNH Coel. 11837, whose original description was accompanied by drawings of sclerites (Verseveldt and Benayahu 1983), was also re-examined in the present study. SEM images of its sclerites are presented below. No distinct differences could be found between specimens of *S. candidula* and specimens previously identified as *S. compressa* or *S. polydactyla* and therefore *S. candidula* is also synonymized with *S. polydactyla*. Other specimens identified as *S. polydactyla* and those with DNA sequences similar to material identified as *S. polydactyla* are also re-examined and discussed.

Material and methods

Morphological examination

In order to identify the material, sclerites from different parts of each specimen were obtained by dissolving tissue in 10% sodium hypochlorite, followed by rinsing in fresh water. When appropriate, they were prepared for scanning electron microscopy as follows: the sclerites were carefully rinsed with double-distilled water, dried at room temperature, coated with gold and examined with a Jeol 6480LV electron microscope, operated at 10 kV.

Abbreviations of museum collections

Material studied is deposited in the Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (ZMB), Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie, Leiden, the Netherlands (RMNH)) and the Zoological Museum, Department of Zoology, Tel Aviv University, Israel (ZMTAU).

Molecular phylogenetic analyses

Published methods (McFadden et al. 2011) were used to obtain new *mtMutS* and *COI* sequences for specimens ZMTAU Co 36607 and Co 36585, collected in 2014 from Eilat, Israel (Gulf of Aqaba, Red Sea), and material from Guam used by Hoover et al. (2008) (GenBank accession numbers KU230366-KU230389). All other sequences were obtained from GenBank, and have been included in previous phylogenetic analyses (McFadden et al. 2009, 2011, 2014; Haverkort-Yeh et al. 2013) (Suppl. material 2). Sequences were aligned using the L-INS-i method in MAFFT (Katoh et al. 2005), and evolution models were selected for each gene separately using jModeltest (Guindon and Gascuel 2003, Darriba et al. 2012). Maximum likelihood analyses were run using Garli 2.0 (Zwickl 2006) for *mtMutS* alone and in a combined analysis of *mtMutS* plus *COI* with different models of evolution applied to each data partition (*mtMutS*: HKY+G; *COI*: HKY+I). Bayesian analyses of the separate (*mtMutS*) and combined (*mtMutS* + *COI*) data sets were run using MrBayes v. 3.2.1 (Ronquist et al. 2012) with the same evolution models applied to separate data partitions. Bayesian analyses were run for 2 million generations (until standard deviation of split partitions < 0.01) with a burn-in of 25% and default Metropolis coupling parameters. MEGA v.5 (Tamura et al. 2011) was used to calculate pairwise measures of genetic distance (Kimura 2-parameter) among sequences.

Molecular phylogenetic results

Phylogenetic analyses of *mtMutS* included sequences for 76 specimens identified as 44 morphospecies belonging to *Sinularia* Clade 4 (McFadden et al. 2009); an additional six specimens representing four morphospecies belonging to Clade 2 served as the outgroup. A total of 20 specimens had previously been identified as either *S. polydactyla* or *S. compressa*. Those specimens fell into five separate clades within the *mtMutS* gene tree (Figure 1). Four specimens from Eilat, Israel, previously identified as *S. polydactyla*, belonged to a well-supported, genetically distinct sub-clade within Clade 4B. Mean genetic distances (Kimura 2-parameter) between this clade and other clades containing specimens of *S. polydactyla* or *S. compressa* ranged 3.0–3.8% (Table 1). Four additional specimens from the Red Sea, all previously identified as *S. compressa*, belonged to a moderately well-supported clade within Clade 4D. Mean genetic distances between this clade and others ranged 0.7–3.0%. Another nine specimens, all from the western Pacific, belonged to a different well-supported clade within Clade 4D. These included seven specimens identified previously as *S. polydactyla*, one *S. compressa*, and a specimen of *S. gibberosa*. Mean genetic distances between this clade and other clades of *S. polydactyla* and *S. compressa* ranged 1.1–3.8%. Three specimens from Guam, however, fell outside of this western Pacific clade and grouped instead with specimens identified as *S. scabra* and *S. nanolobata*. Finally, a single specimen of *S. polydactyla* from Eilat, Israel (ZMTAU Co 34181) belonged to none of these clades, differing from these by >0.7%. The phylogenetic position of ZMTAU Co 34181 within the *mtMutS* tree was poorly resolved, but genetically it was closer to species in Clade 4C than to those in Clade 4D.

COI sequences were available for only 42 of the 76 Clade 4 specimens, representing 24 morphospecies and 15 of 20 individuals of *S. polydactyla* and *S. compressa*. Results of the combined analysis of *mtMutS* and *COI* for this more limited dataset were congruent with and provided stronger ML bootstrap support for the same clades of *S. polydactyla* / *S. compressa* identified in the *mtMutS* tree (Suppl. material 1).

Genetic distances among specimens in each of the two Red Sea clades ranged from 0–0.1%, suggesting that each of those clades represents a single species (Table 1). Within the clade of western Pacific specimens, however, genetic distances ranged

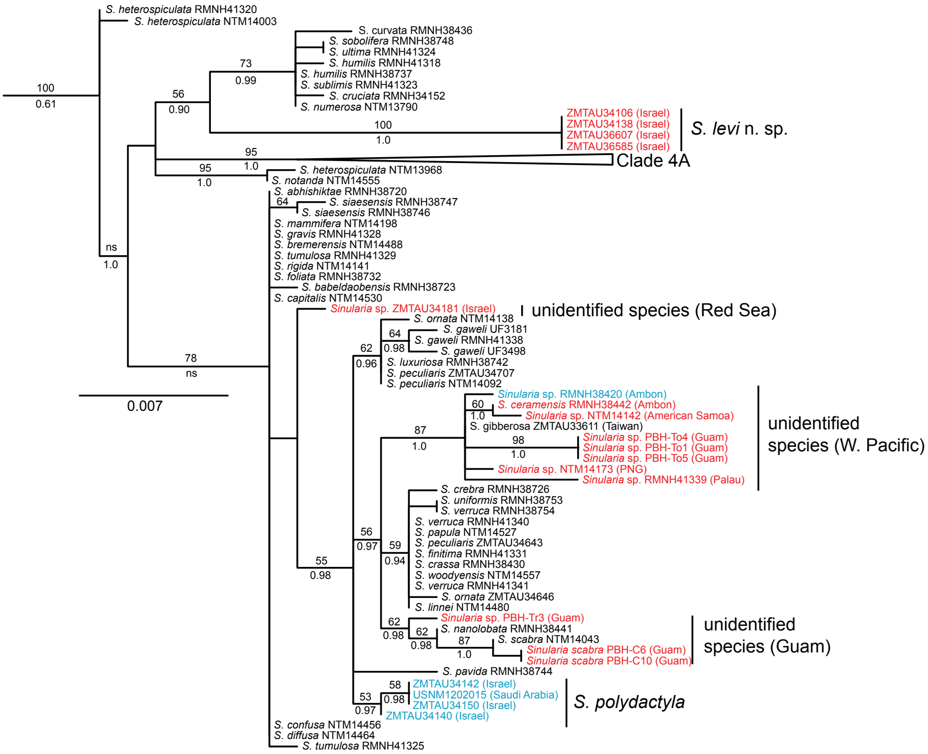

Figure 1. Maximum likelihood tree of *Sinularia* Clade 4 (McFadden et al. 2009) based on 735 bp of *mtMutS* sequence. Outgroup (*Sinularia* Clade 2) not shown. Numbers above branches are ML bootstrap percentages; numbers below branches are posterior probabilities from Bayesian Inference. Red: specimens identified in previous work as *S. polydactyla*; blue: specimens identified in previous work as *S. compressa*.

Table 1. Mean genetic distances (Kimura 2-parameter, ± s.d.) among *mtMutS* sequences within and between the clades of *Sinularia* highlighted in Fig 1.

	***S. levi* sp. n.**	***S. polydactyla***	**W. Pacific clade**	**Guam clade**
***S. levi* sp. n.**	0.000 ± 0.0000			
S. polydactyla	0.030 ± 0.0006	0.001 ± 0.0007		
W. Pacific clade	0.038 ± 0.0026	0.011 ± 0.0023	0.005 ± 0.0031	
Guam clade	0.035 ± 0.0007	0.009 ± 0.0021	0.013 ± 0.0028	0.005 ± 0.0040
ZMTAU 34181	0.031 ± 0.0000	0.007 ± 0.0007	0.013 ± 0.0023	0.011 ± 0.0024

0–1.1%. Intraspecific variation in *mtMutS* is rarely >0.5% (McFadden et al. 2011, 2014), which suggests that this clade may comprise more than one species. RMNH Coel. 41339 from Palau differed from all other specimens in the western Pacific clade by ≥0.5%, as also did three specimens from Guam. Among the three specimens from Guam that did not belong to the western Pacific clade, one (PBH-Tr3) differed from the other two by 0.7%, suggesting that it represents yet another different species.

Taxonomy

Sinularia polydactyla (Ehrenberg, 1834)

Figures 2A–C, F–G, 3–14

Lobularia polydactyla Ehrenberg, 1834: 58 (Red Sea).

? *Sinularia polydactyla*; Benayahu and Schleyer 1996: 6 (Mozambique); Benayahu et al. 2003: 56 (Mozambique); Dautova and Savinkin 2013: 220 (Vietnam).

Sinularia polydactyla (partly); Benayahu et al. 2002: 278 (Red Sea).

Sinularia compressa Tixier-Durivault, 1945: 150 (Red Sea); Verseveldt 1980: 30 (older literature); Benayahu et al. 2002: 278; 2003: 55 (Mozambique); Samimi Namin and Ofwegen 2009: 8 (Persian Gulf); Haverkort-Yeh et al. 2013: 286 (Red Sea).

Sinularia compressa (partly); McFadden et al. 2009: 318; 2011: 25; Benayahu et al. 2013: 1544.

Sinularia candidula Verseveldt & Benayahu, 1983: 11 (Red Sea).

NOT *Sinularia polydactyla*; Verseveldt 1971: 4 (Madagascar); Tixier-Durivault 1972: 677 (Reunion; = *S. shlagmani* Benayahu & Ofwegen, 2012); Verseveldt 1972: 457 (Eniwetok Atoll, Marshall Islands); 1974: 96 (New Caledonia): 1977: 3 (Fiji, Guam, Samoa); 1978: 50 (Guam, Palau); 1980: 108 (older literature); Ofwegen and Benayahu 1992: 140 (Tanzania); Ofwegen and Vennam 1994: 138 (Ambon); Benayahu 1995: 107 (Ryukyu Archipelago); Ofwegen 1996: 208 (Bismarck Sea); Benayahu 1997: 237 (Guam, *in situ* image); 2002: 20 (Ryukyu Archipelago); Benayahu et al. 2004: 551 (Taiwan; *in situ* image); Manuputty and Ofwegen 2007: 192 (Ambon; = *S. ceramensis*); McFadden et al. 2009: 321; 2011: 25; Benayahu and Ofwegen 2011: 118 (Singapore); Benayahu et al. 2013: 1544.

NOT *Sinularia compressa*; Benayahu 1997: 215 (Guam); 2002: 18 (Japan); Benayahu et al. 2004: 551 (Taiwan); Manuputty and Ofwegen 2007: 191 (Ambon); Benayahu and Chou 2010: 4 (Singapore).

Type material examined. ZMB 299, lectotype (herein designated), Red Sea, leg. Hemprich, Ehrenberg; ZMB 298, two paralectotypes, same data as holotype; ZMB 300, same data as holotype.

Other material examined. RMNH Coel. 8890, Gulf of Aqaba, Red Sea, 1.5 km N of Saudi Arabian border, 50–70 cm, 10–20 m from coast, 15 February 1972, coll. H. Schumacher, det. J. Verseveldt, one specimen and two microscope slides; RMNH Coel. 8891, Gulf of Aqaba, Red Sea, 1.5 km N of Saudi Arabian border, 80 cm, 18 February 1972, coll. H. Schumacher, det. J. Verseveldt, one specimen and two microscope slides; RMNH Coel. 8892, Marsa el Muqeibla (= Makbala), Gulf of Aqaba, Red Sea, from reef wall, 6 January 1968, coll. Hebrew University, Jerusalem - Smithsonian Red Sea project 63/SLR 1147, det. J. Verseveldt, one specimen and 3 microscope slides; RMNH Coel. 8944, Marsa abu Zabad, Gulf of Aqaba, Red Sea, 15 September 1967, coll. Hebrew University, Jerusalem - Smithsonian Red Sea project, det. J. Verseveldt, one specimen and

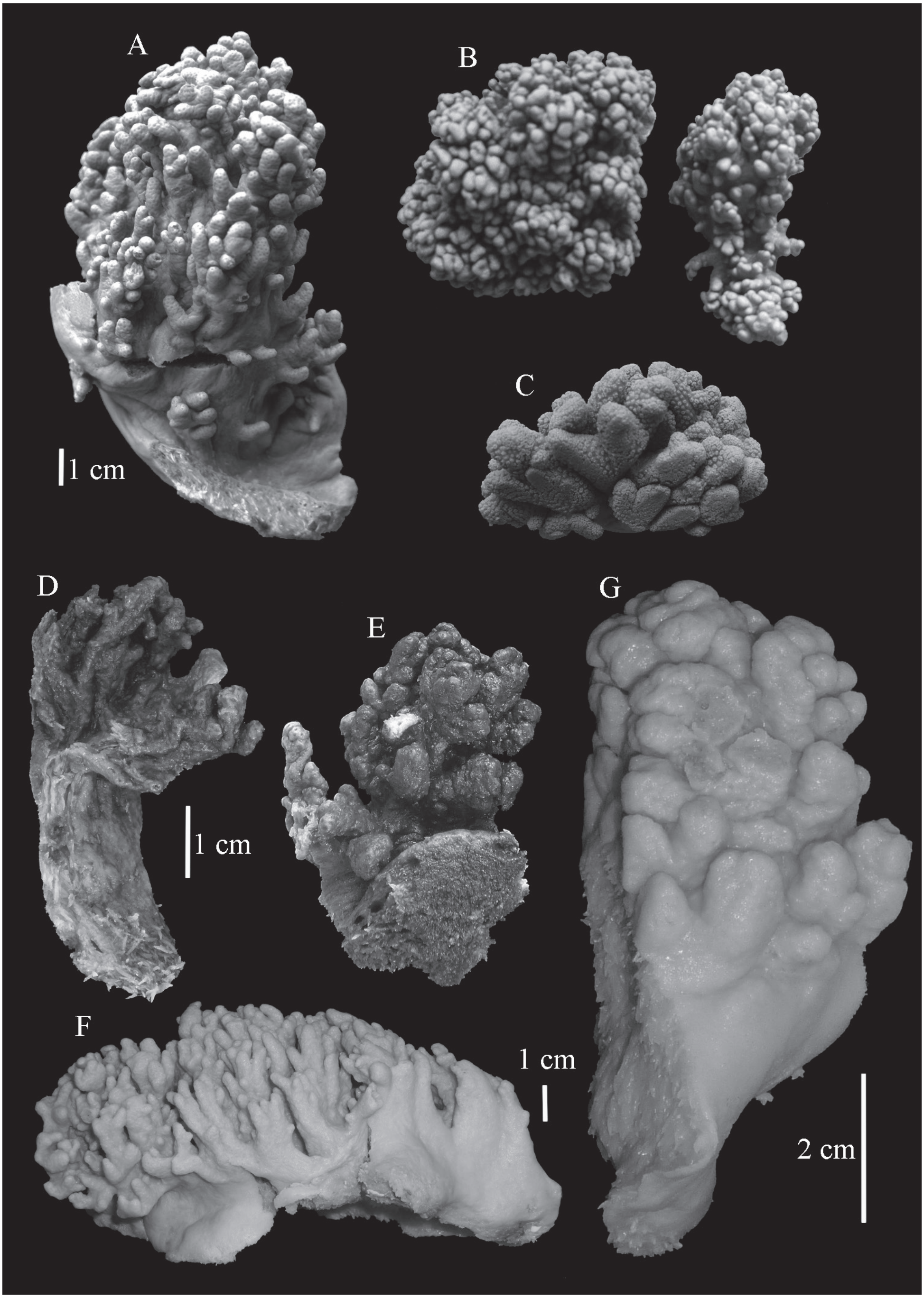

Figure 2. Colonies. **A** *Sinularia polydactyla* (Ehrenberg, 1834), lectotype ZMB 299 **B** paralectotype ZMB 298 **C** paralectotype ZMB 300 **D** *S. levi* sp. n. holotype ZMTAU Co 34106 **E** paratype ZMTAU Co 34138 **F** *S. compressa* Tixier-Durivault, 1945, ZMTAU 31610 **G** ZMTAU 34142.

five microscope slides; RMNH Coel. 8951, Marsa el Maqeilba, Gulf of Aqaba, Red Sea, 6 January 1968, coll. Hebrew University, Jerusalem - Smithsonian Red Sea project, det. J. Verseveldt, one specimen and four microscope slides; ZMTAU Co 25287, Red Sea, Gulf of Aqaba, Nakeb Shahin, 25 m, coll. Y. Benayahu, 29 November 1981; ZMTAU Co 25309, Red Sea, southern tip of Sinai Peninsula, Sharm El Sheikh, 25 m, coll. Y. Benayahu, 30 November 1981; ZMTAU Co 25378, Red Sea, Gulf of Aqaba, Nakeb Shahin, 18-24 m, coll. Y. Benayahu, 5 November 1981; ZMTAU Co 25419, Red Sea, Gulf of Aqaba, Taba, 1 m, coll. Y. Benayahu, 30 July 1984; ZMTAU Co 26119, Red Sea, North, Tawila Island, 6 m, coll. Y. Benayahu, 24 September 1989; ZMTAU Co 31609, Red Sea, Eritrea, Dahlak Archipelago, Dahlak Island, channel in front of Lul hotel, coll. M. Schleyer, 12 February 1998; ZMTAU Co 31610, Red Sea, Eritrea Dahlak Archipelago, Intere Island, 15°38.504'N, 39°53.580'E, 12.5 m, coll. M. Schleyer, 3 May 1997; ZMTAU Co 32947, Red Sea, Eritrea, Dahlak Archipelago, between Nocra Island and Dahlak Island, southern entrance to the channel, 15°41.60'N, 39°56.40'E, 2–3 m, coll. Y. Benayahu, 15 February 2005; ZMTAU Co 32961, Red Sea, Eritrea, Dahlak Archipelago, Shumma Island, 15°32.00'N, 40°00.00'E, 8–12 m, coll. Y. Benayahu, 16 February 2005; ZMTAU Co 33104, Israel, Gulf of Aqaba, Eilat, Marine laboratory, reef off the Inter University Institute for Marine Sciences, 50 m, coll. S. Einbinder, 8 June 2004; ZMTAU Co 35301, Israel, Gulf of Aqaba, Eilat, reef off the Inter University Institute for Marine Sciences, 14 m, coll. Y. Benayahu, 19 January 2011; *S. compressa* material: ZMTAU 34140, ZMTAU 34142, and ZMTAU 34150 used by McFadden et al. (2011).

Re-description. The lectotype is 14.5 cm high and 9 cm wide (Figure 2A). The primary lobes give off short finger-like lobules up to 1 cm long. The polyp openings are visible as small pits.

Sclerites. Polyps without sclerites. The surface layer of the lobules has clubs with a distinct central wart, the smallest are 0.07 mm long, most are around 0.10 mm, but some reach even a length of 0.15 mm (Figure 3A). Furthermore, the surface layer of the lobules has spindles, up to 0.25 mm long, with simple tubercles (Figure 3B). The sclerites of the surface layer of the base of the colony resemble those of the surface layer of the lobules, but the clubs are much shorter, only up to 0.10 mm long, with wider handles. The spindles are also wider and shorter than those of the top of the colony, up to 0.15 mm long (Figure 4). The interior of the colony has unbranched spindles. In the lobules the spindles are up to 2 mm long (Figure 5A), featuring simple or complex tubercles (Figure 5B). In the base of the colony they are up to 3 mm long (Figure 5C), many with more complex tubercles (Figure 5D).

Colour. The alcohol-preserved specimen is light brown.

Remarks. The two paralectotypes ZMB 298 are smaller than the lectotype (Figure 2B) but the sclerites are similar (Figure 6). Paralectotype ZMB 300 is not a *Sinularia*, but a *Cladiella* specimen, as proven by its colony shape and typical suite of figure-eight and dumbbell sclerites (Figures 2C, 7–8).

Notably the Red Sea *S. polydactyla* colonies can be much larger than the lectotypes and have longer lobules (Figure 2F, ZMTAU 31610).

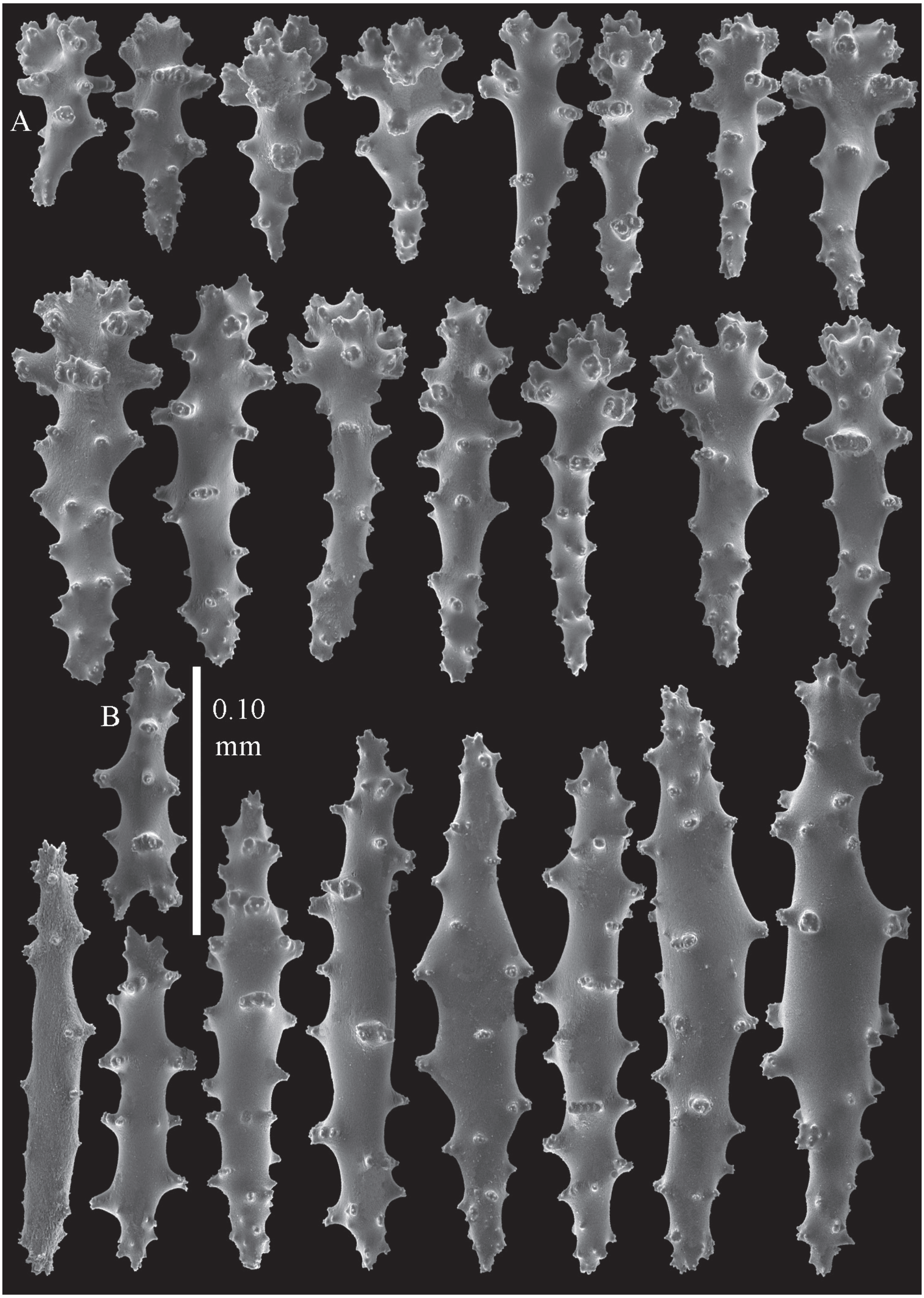

Figure 3. *Sinularia polydactyla* (Ehrenberg, 1834), lectotype ZMB 299. **A** clubs of surface layer top of colony **B** spindles.

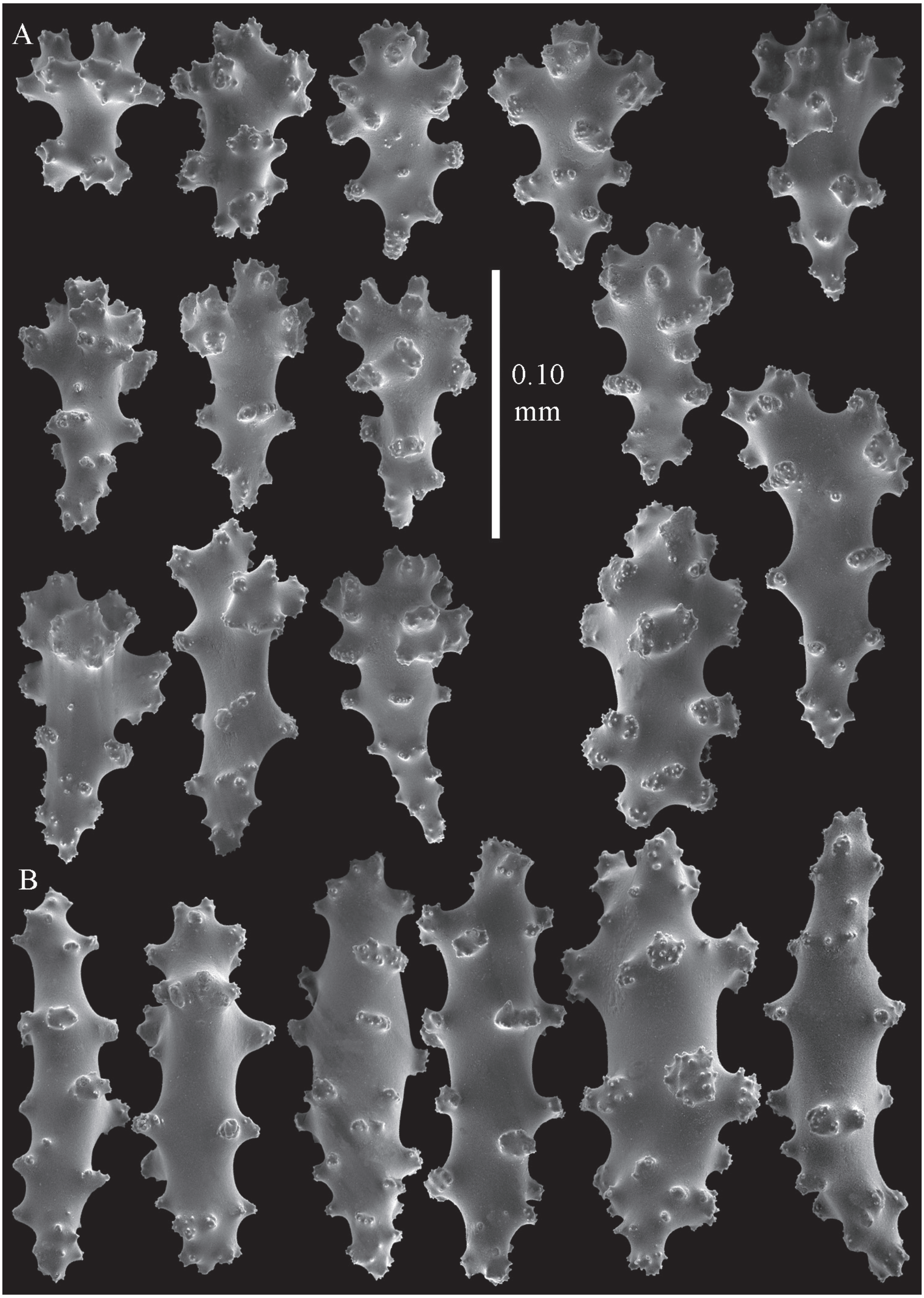

Figure 4. *Sinularia polydactyla* (Ehrenberg, 1834), lectotype ZMB 299. **A** clubs of surface layer base of colony **B** spindles.

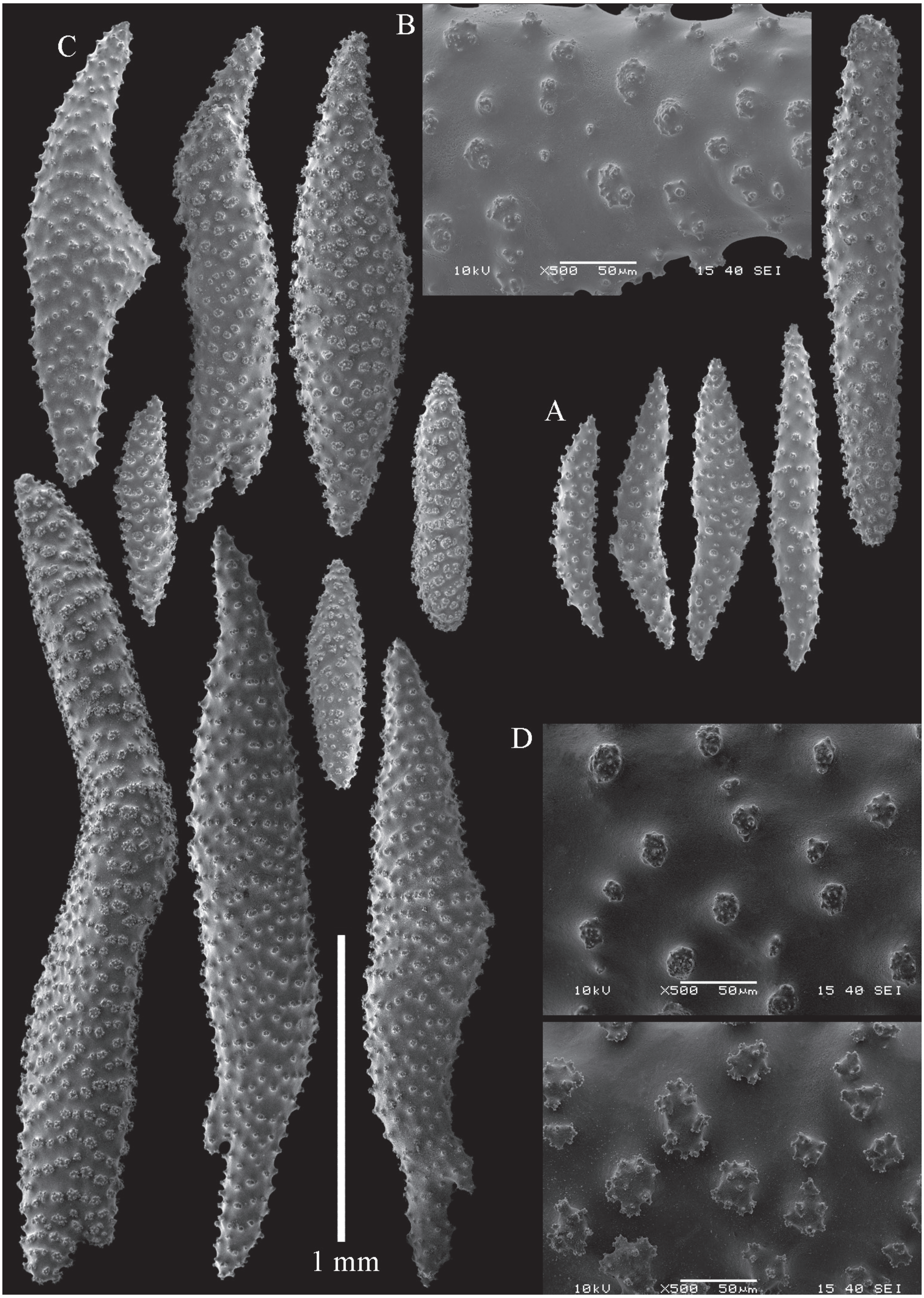

Figure 5. *Sinularia polydactyla* (Ehrenberg, 1834), lectotype ZMB 299. **A** spindles of interior of top of colony **B** tuberculation of one of the spindles **C** spindles of the interior of base of the colony **D** tuberculation of the spindles.

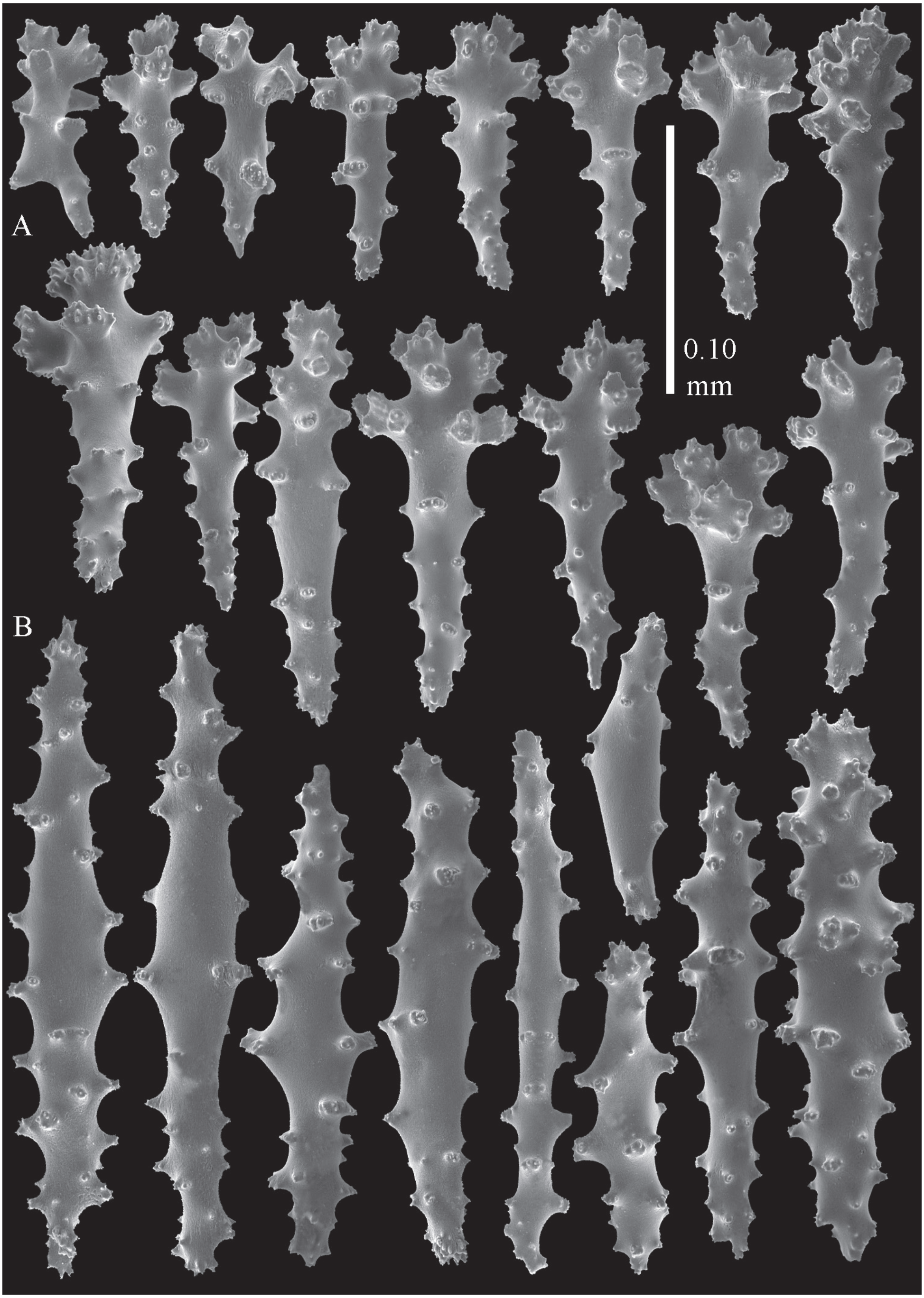

Figure 6. *Sinularia polydactyla* (Ehrenberg, 1834), paralectotype ZMB 298 (smallest colony). **A** clubs of surface layer top of colony **B** spindles.

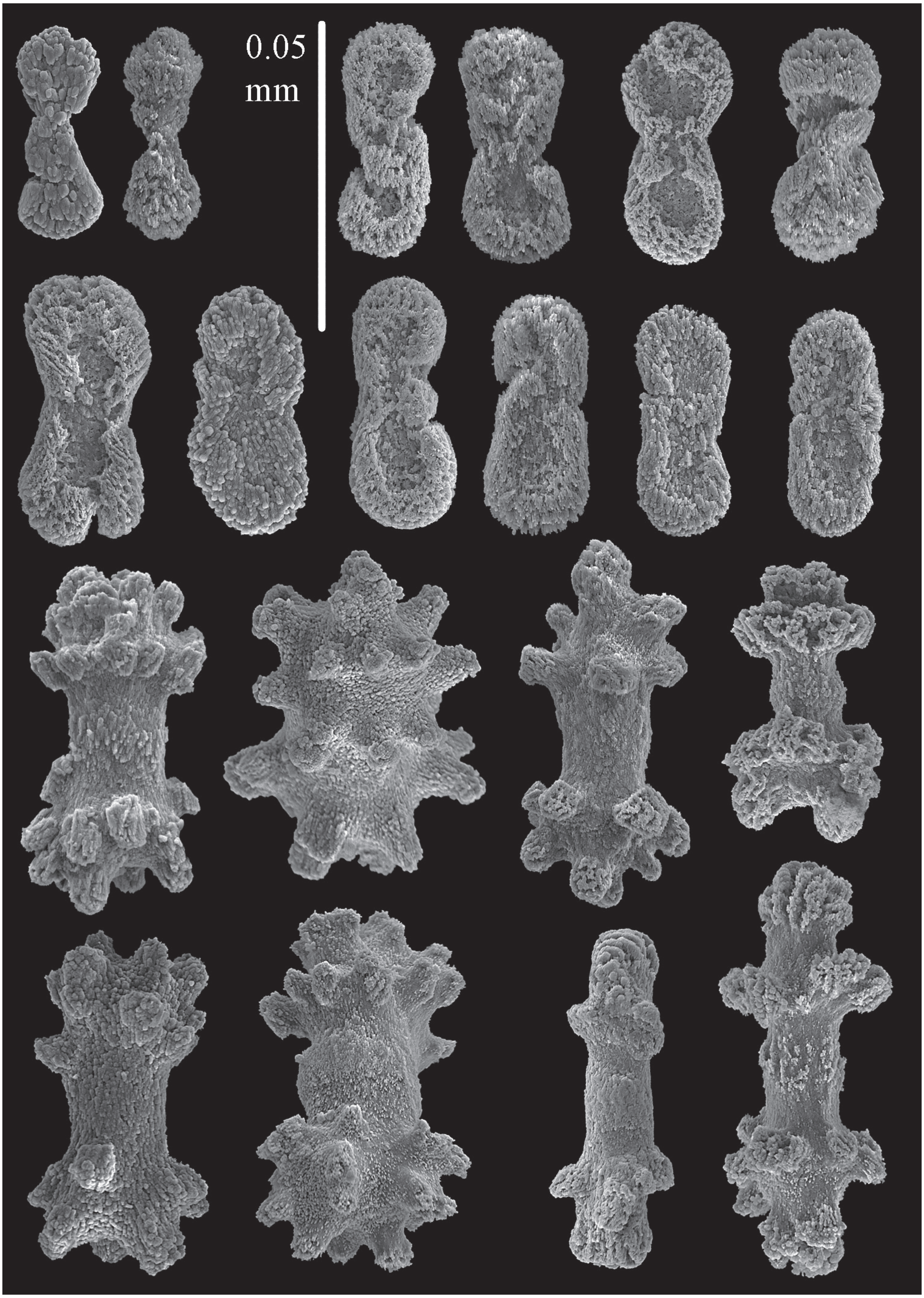

Figure 7. *Sinularia polydactyla* (Ehrenberg, 1834), paralectotype ZMB 300. Sclerites of top of colony.

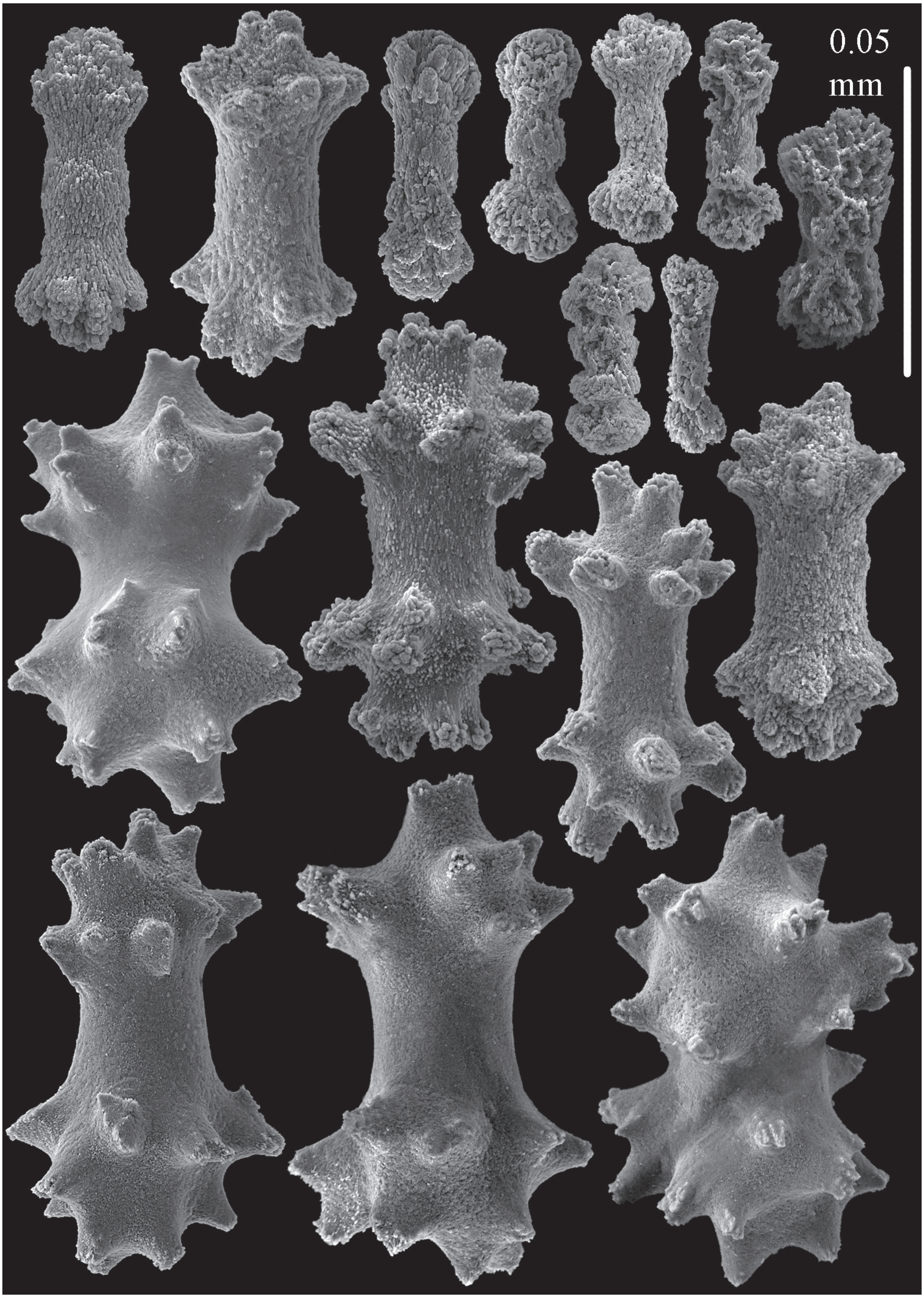

Figure 8. *Sinularia polydactyla* (Ehrenberg, 1834), paralectotype ZMB 300. Sclerites of base of colony.

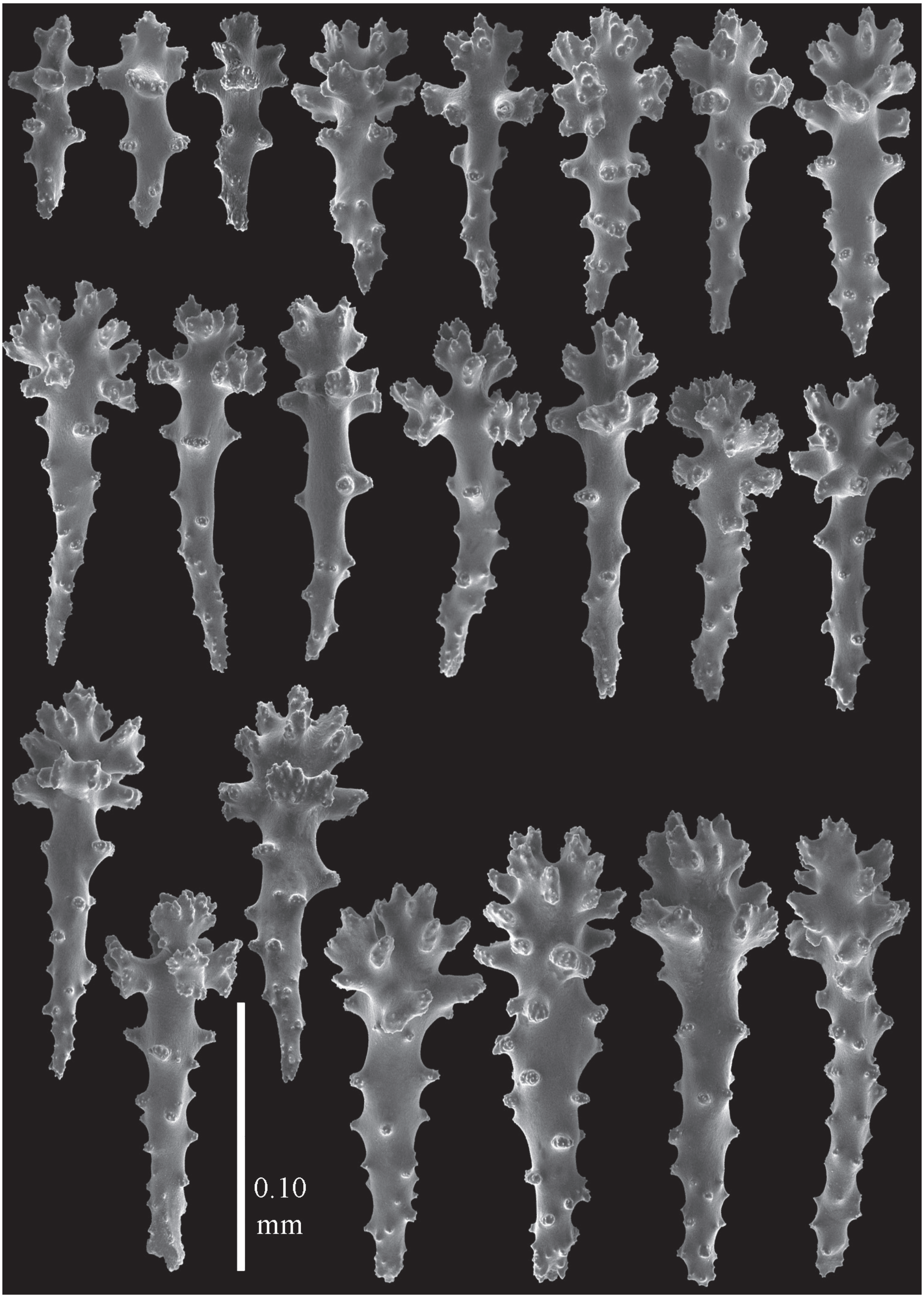

Figure 9. *Sinularia compressa* Tixier-Durivault, 1945, ZMTAU 34142. Clubs of surface layer of top of colony.

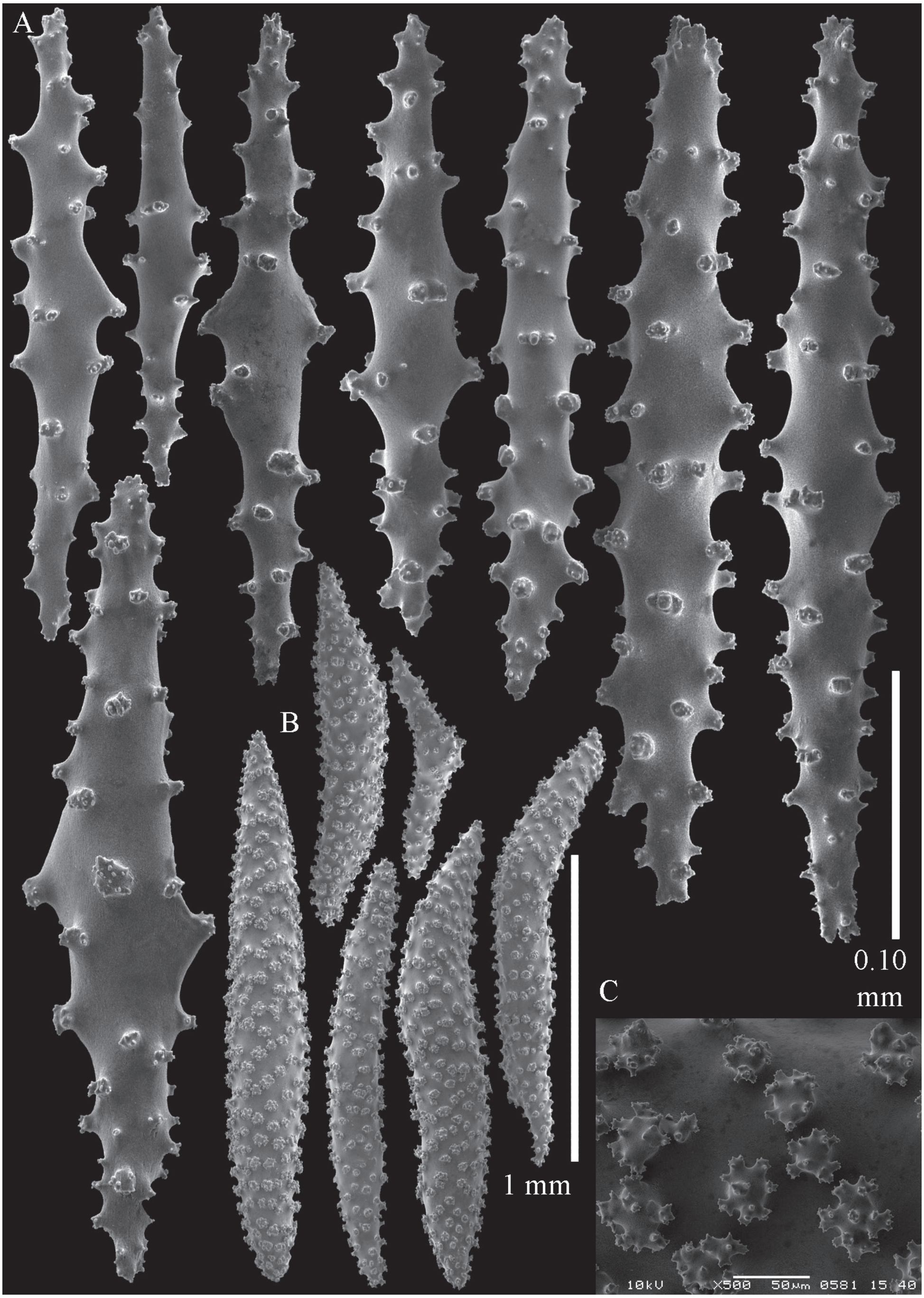

Figure 10. *Sinularia compressa* Tixier-Durivault, 1945, ZMTAU 34142. **A** spindles of surface layer of top of colony **B** spindles of interior of top of colony **C** tuberculation of a spindle.

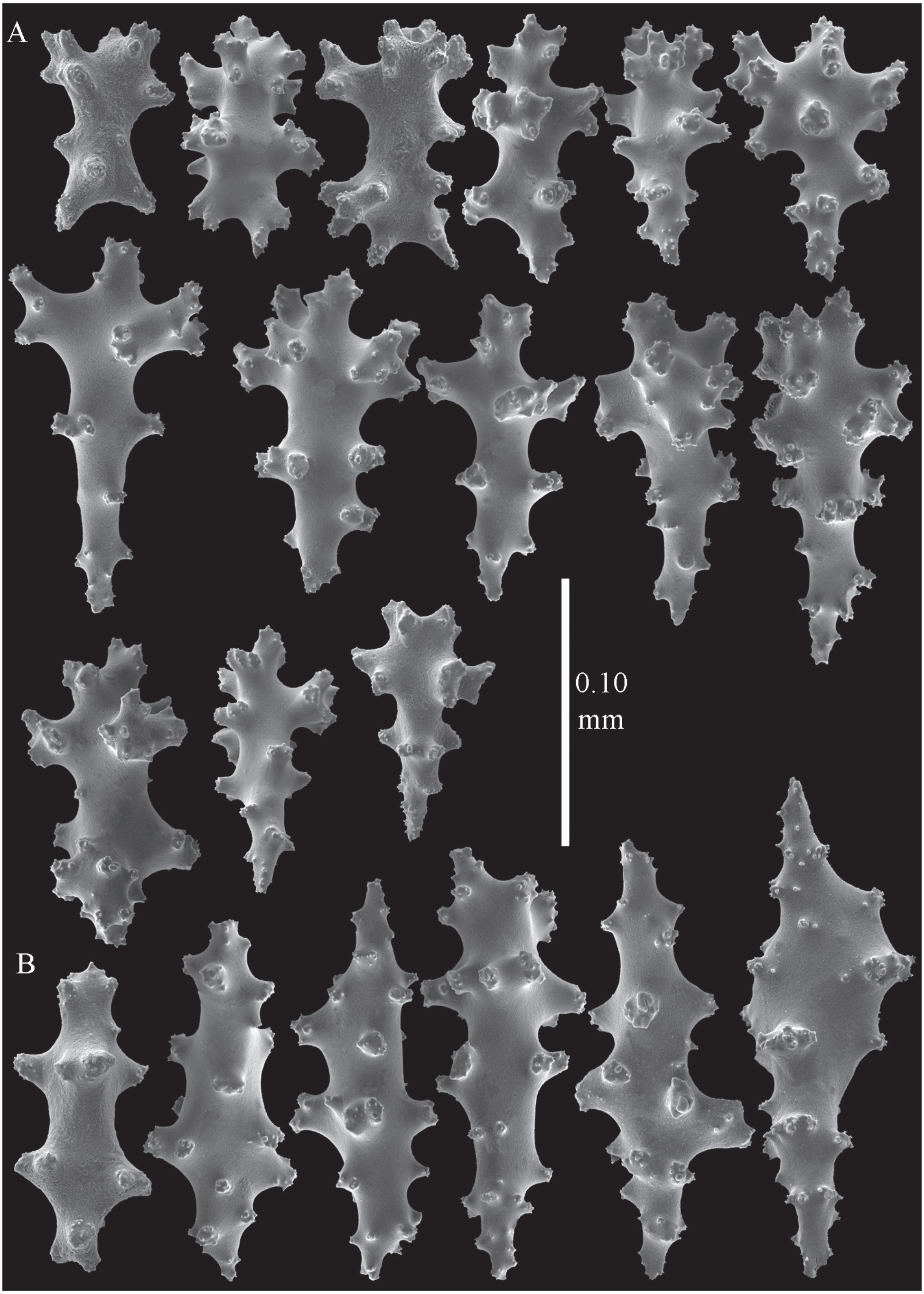

Figure 11. *Sinularia compressa* Tixier-Durivault, 1945, ZMTAU 34142. **A** clubs of surface layer base of colony **B** spindles.

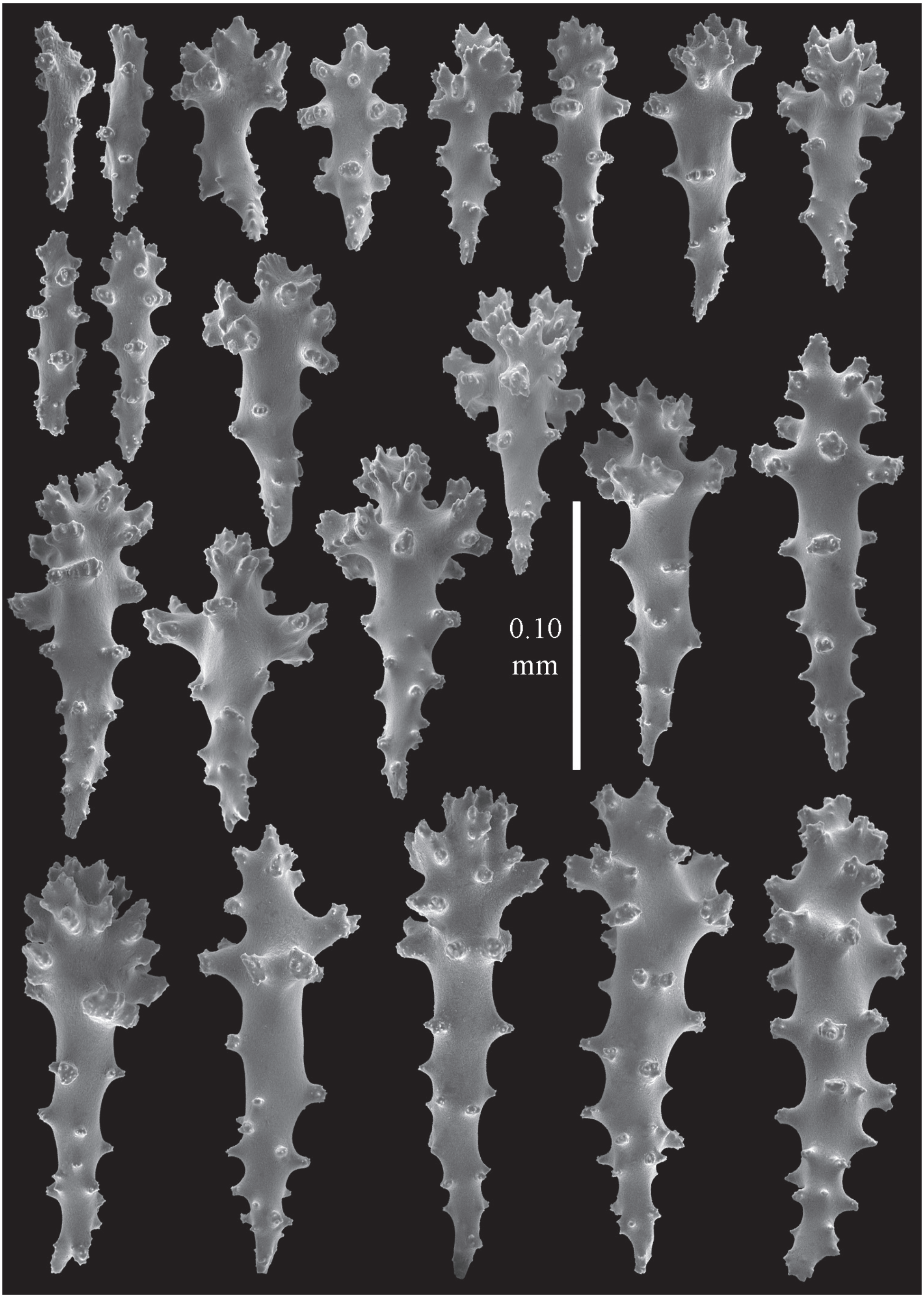

Figure 12 *Sinularia candidula* Verseveldt & Benayahu, 1983. Clubs of surface layer top of colony.

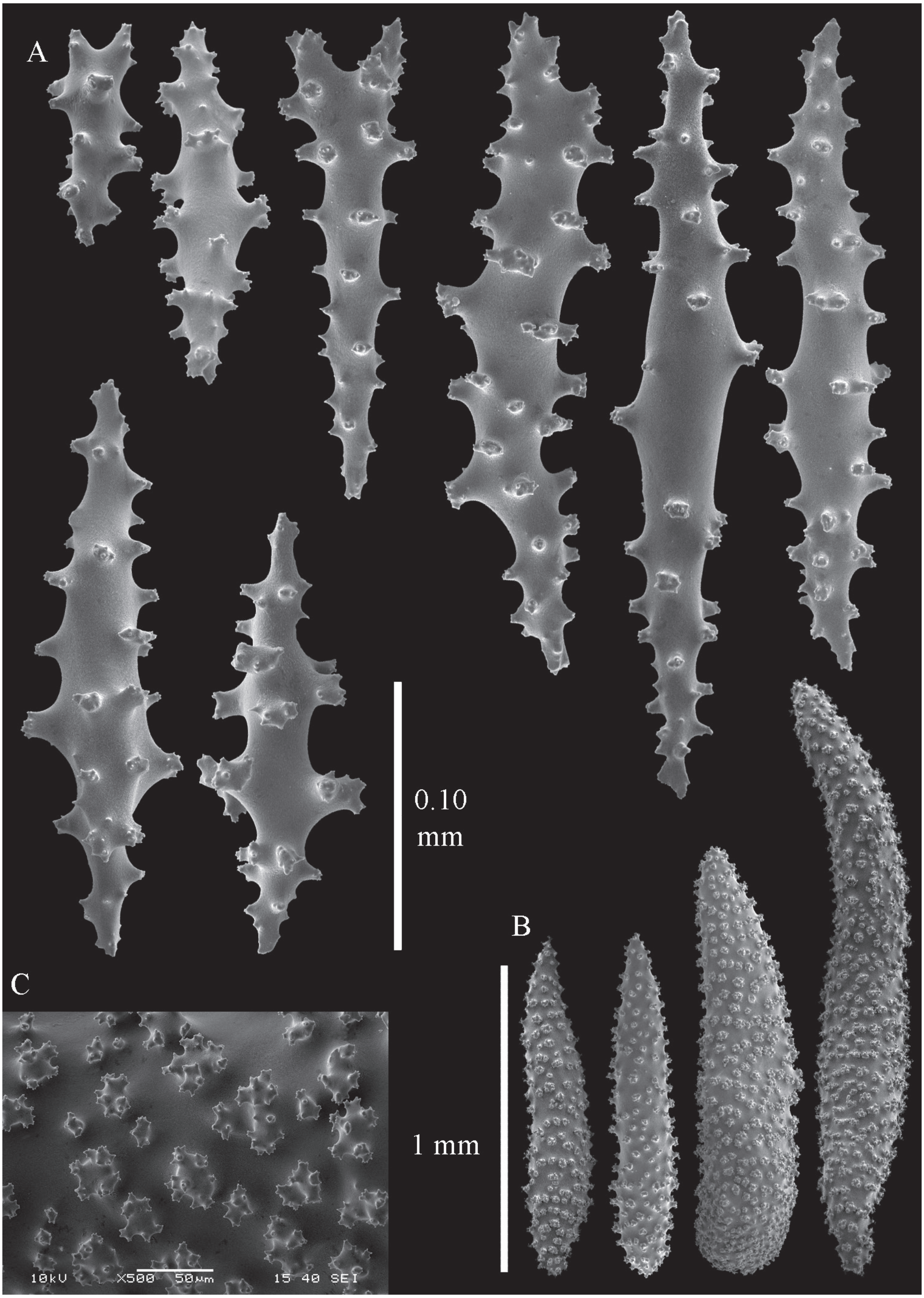

Figure 13 *Sinularia candidula* Verseveldt & Benayahu, 1983. **A** spindles of surface layer of top of colony **B** spindles of interior of top of colony **C** tuberculation of a spindle.

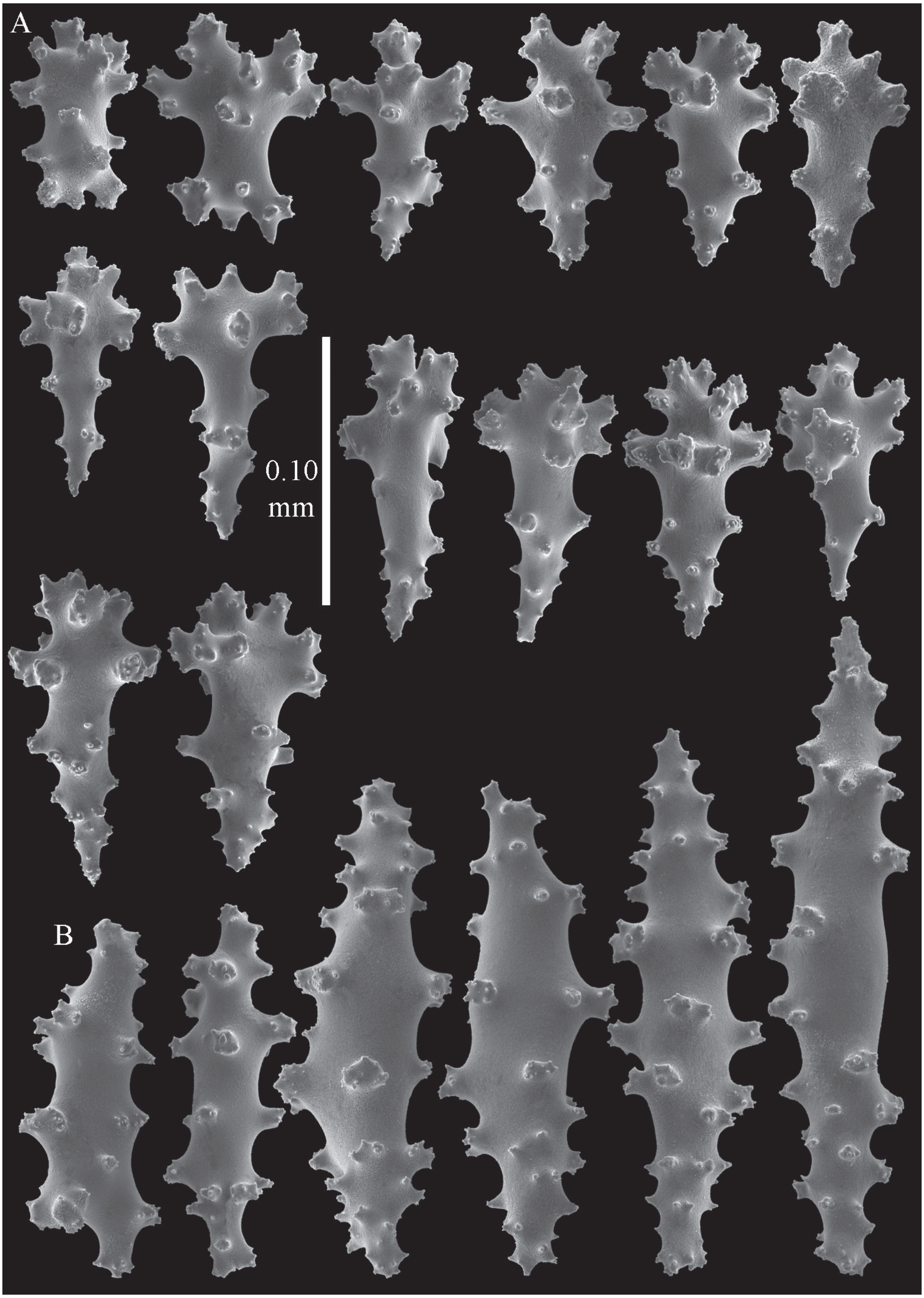

Figure 14 *Sinularia candidula* Verseveldt & Benayahu, 1983. **A** clubs of surface layer base of colony **B** spindles.

Sinularia compressa Tixier-Durivault, 1945 exhibits close similarity to *S. polydactyla*. It differs in having clubs in the surface layer of the lobes with more slender handle and spinier head. *S. compressa* specimens ZMTAU 34140, 34142, and 34150, all from the Red Sea (Figure 2G) feature similar sclerites (Figures 9–11) despite differences in their colony shape.

Finally, we re-examined the type of *S. candidula* Verseveldt & Benayahu, 1983, RMNH Coel. 11837, also depicting its sclerites (Figures 12–14). There were no noticeable differences between that species and specimens identified as *S. polydactyla*, and therefore we synonymized *S. candidula* also with *S. polydactyla*.

Sinularia levi **sp. n.**

http://zoobank.org/1EBC5A7A-629C-4A43-8A1D-C5A45B1B494B
Figures 2D–E, 15–18, 44

Sinularia polydactyla (partly); Verseveldt 1971: 4 (Madagascar).
Sinularia polydactyla; McFadden et al. 2009: 321 (Eilat, northern Red Sea); 2011: 25.

Type material examined. holotype: ZMTAU Co 34106, Eilat Nature Reserve, Gulf of Aqaba, northern Red Sea (Israel), 29°30.6'N, 34°55.35'E, depth 2.4-5.5 m, coll. Y. Benayahu, 24 July 2007; paratype: ZMTAU Co 34138, same data as holotype.

Other material examined. RMNH Coel. 6648, W of harbour, Hellville, Nosy Bé, Madagascar, 12 m, 26 July 1967, coll. A.G. Humes, 1205, det. J. Verseveldt, one specimen and six microscope slides; RMNH Coel. 6649, Ambariobe, near Nosy Bé, Madagascar, 2 m, 22 August 1967, coll. A.G. Humes, 1307, det. J. Verseveldt, one specimen and four microscope slides; RMNH Coel. 6650, Banc de Cinq Mètres, near Nosy Bé, Madagascar, 20 m, 6 August 1967, coll. A.G. Humes, det. J. Verseveldt, one specimen and four microscope slides; RMNH Coel. 6651, Banc de Cinq Mètres, near Nosy Bé, Madagascar, 20 m, 6 August 1967, coll. A.G. Humes, det. J. Verseveldt, one specimen and three microscope slides; ZMTAU 34108, Eilat, Gulf of Aqaba, northern Red Sea, Israel, 29°30.6'N, 34°55.35'E, 2.4–5.5 m, 24 July 2007, coll. Y Benayahu; ZMTAU 36585, Eilat, Gulf of Aqaba, northern Red Sea, Israel,1–2 m, June 2014, coll. E. Shoham and Y. Benayahu; ZMTAU 36607, Eilat, Gulf of Aqaba, northern Red Sea, Israel, 1–2 m, June 2014, coll. E. Shoham and Y. Benayahu.

Description. The holotype is 5.5 cm high and 3 cm wide (Figure 2D) with a stalk 3 cm long. The primary lobes give off short knob-like lobules up to 5 mm long. The polyp openings are visible as small pits.

Sclerites. Polyps without collaret, but with points featuring poorly developed clubs, up to 0.15 mm long (Figure 15A). Tentacles with rods that sometimes are ramified, up to 0.08 mm long (Figure 15B). The surface layer of the lobules has clubs with a central wart, the smallest are 0.08 mm long, most are around 0.10 mm, some reach a length of 0.25 mm (Figure 15C). Furthermore, the surface layer of the lobules has spindles, up to 0.35 mm long, with simple tubercles (Figure 16A). The sclerites of the

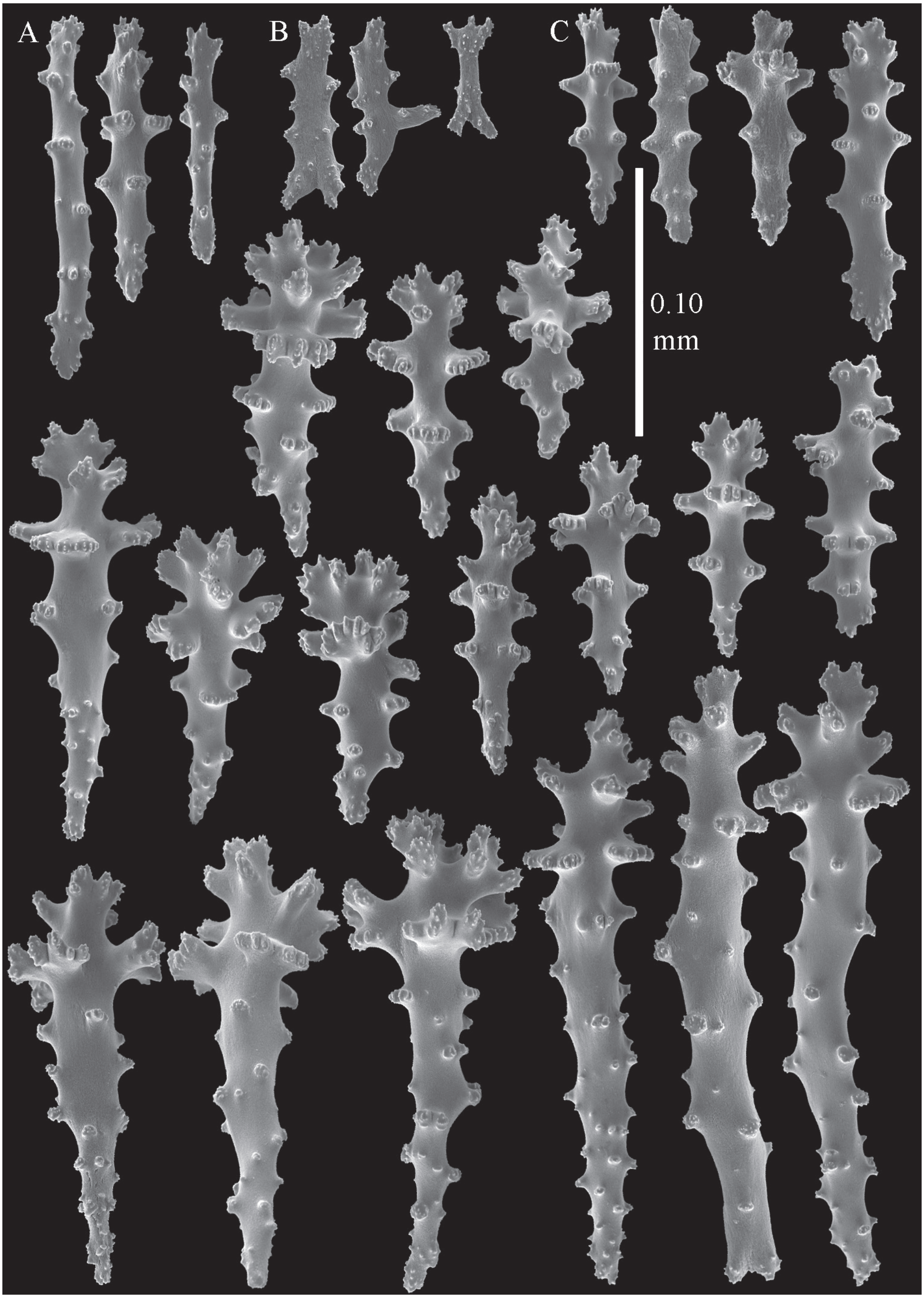

Figure 15. *Sinularia levi* sp. n. holotype, ZMTAU Co 34106. **A** point clubs **B** tentacle rods **C** clubs of surface layer top of colony.

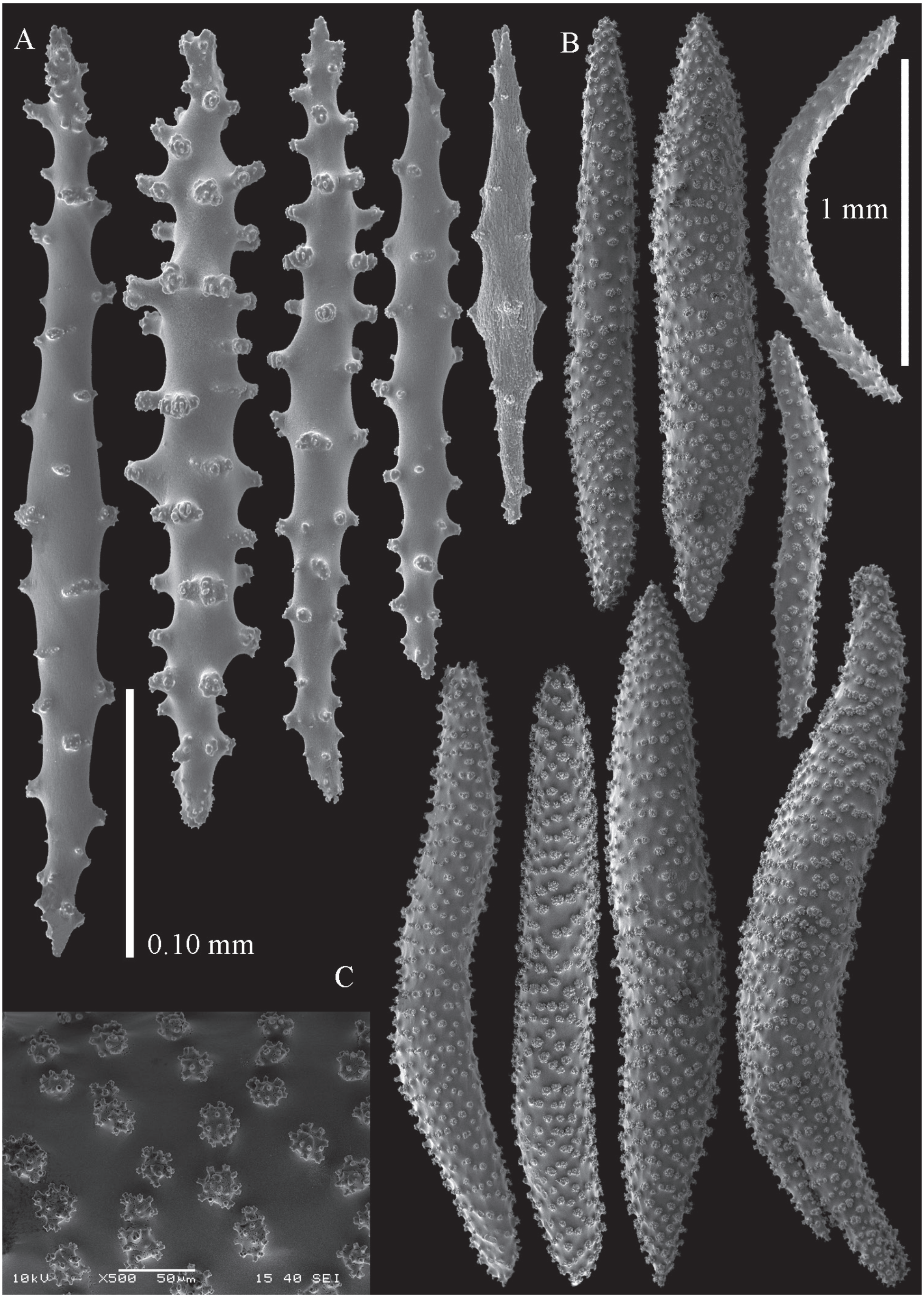

Figure 16. *Sinularia levi* sp. n. holotype, ZMTAU Co 34106. **A** spindles of surface layer top of colony **B** spindles of the interior of top of colony **C** tuberculation of a spindle.

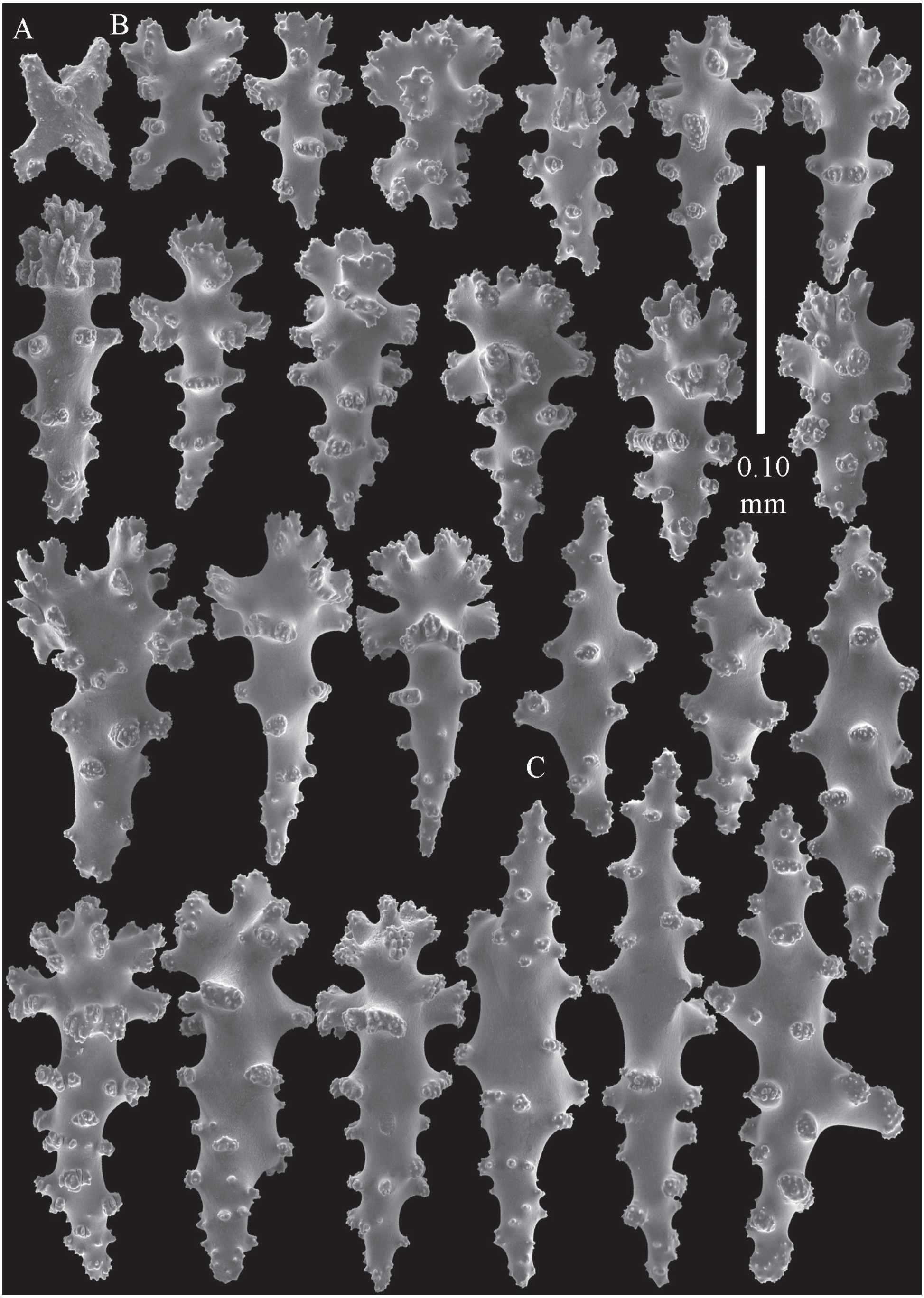

Figure 17. *Sinularia levi* sp. n. holotype, ZMTAU Co 34106. **A** cross of surface layer of the base of the colony **B** clubs **C** spindles.

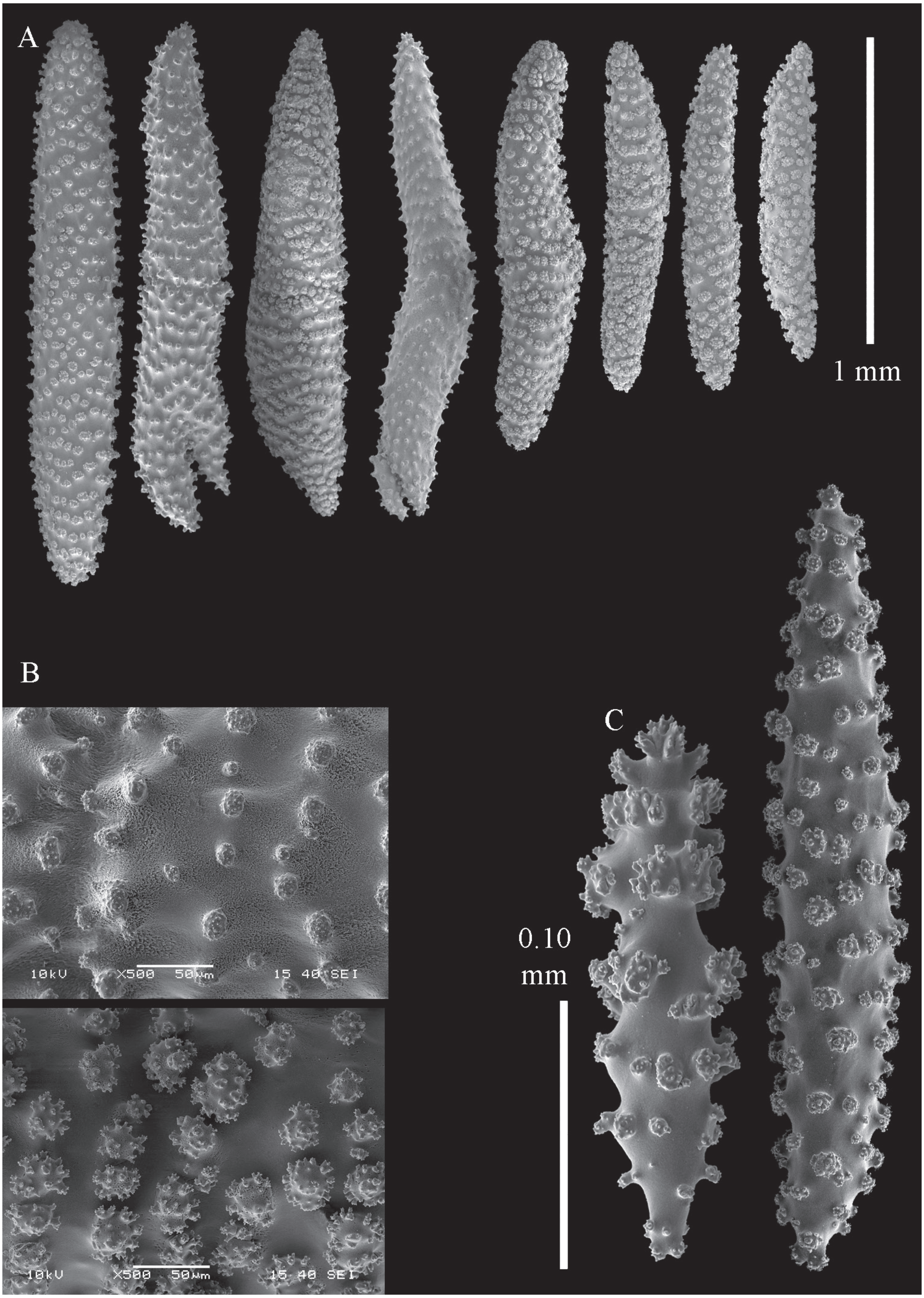

Figure 18. *Sinularia levi* sp. n. holotype, ZMTAU Co 34106. **A** spindles of interior of base of colony **B** tuberculation of two of the spindles **C** spindle and club intermediate between surface and interior sclerites.

surface layer of the base of the colony resemble those of the surface layer of the lobules, but clubs and spindles are shorter, up to 0.20 mm long, and the spindles and handles of the clubs are wider (Figure 17). A few sclerites intermediate between those of surface and interior are also present (Figure 18C). The interior of the colony has unbranched spindles. In the lobules the spindles are up to 2.5 mm long (Figure 16B), almost all having complex tubercles (Figure 16C). In the base of the colony they are up to 2 mm long (Figure 18A), many with complex tubercles (Figure 18B).

Colour. The alcohol-preserved specimen is brown.

Etymology. Named after the late Prof. Lev Fishelson, Tel Aviv University, pioneering and outstanding marine biologist, who investigated Red Sea coral reefs.

Intraspecific variation. The paratype ZMTAU Co 34138 (Figure 2E) has similar sclerites, colony shape and colour.

Remarks. Preserved specimens have a brown colony colour. In the RMNH, only four specimens from Madagascar identified by Verseveldt as *S. polydactyla* can be referred to this species. Live colonies are shown in Figure 44.

Discussion

Material used by Verseveldt (1980: 108, fig. 57) to describe what he considered to represent *S. polydactyla*, RMNH Coel. 15950 from Laing Island, Papua New Guinea was re-examined. Six specimens are present in the jar, but only one has clear signs of tissue sampling (Figure 19A) and therefore it must be the specimen studied by Verseveldt. The four microscope slides were claimed by Verseveldt to lack any polyp sclerites, but in the present study they proved to be clearly present (Figure 20A). These sclerites can be confused with the smallest clubs of the surface layer of the lobes (Figure 20B), but dissection of a single polyp of RMNH Coel. 15950 demonstrated that they are indeed derived from the polyps. Presence of polyp sclerites assigns the specimen to Clade 4B; in contrast, Ehrenberg's lectotype (ZMB 299) lacks polyp sclerites, a character that assigns it to Clade 4D. This discrepancy suggests that Verseveldt's identification of RMNH Coel. 15950 as *S. polydactyla* was a mistake. Within Clade 4B the species that most closely resembles RMNH Coel. 15950 is *S. sobolifera* Verseveldt & Tursch, 1979. Like Verseveldt's *S. polydactyla*, *S. sobolifera* also was described from the Bismarck Sea, but from Mililat Bay. *S. sobolifera* differs in having longer clubs, up to 0.27 mm long, with an almost smooth handle whereas the present material has clubs up to 0.18 mm long, with tuberculate handles. For completeness of the current study we depict the sclerites of the interior (Figure 21B–C) and base (Figure 22) of RMNH Coel. 15950.

Both molecular and morphological evidence suggest that other specimens identified in the recent literature as *S. polydactyla* or *S. compressa* belong to neither of the two species described here, but instead represent either misidentifications or as yet undescribed species. ZMTAU Co 34181 (Israel, Gulf of Aqaba, Eilat, south Oil Jetty, 29°31.05'N, 34°55.86'E, 1.5 m, coll. Y. Benayahu, 25 July 2007), previously identified as *S. polydactyla*, has a colony shape that differs from all other specimens examined, as it is not stalked but cup-shaped (Figure 19B). However, its sclerites do not differ much in shape from those of *S. polydactyla* (Figures 23–27). This specimen is unique genetically, however, and its *mtMutS* sequence is unlike that of *S. polydactyla* or any of the other reference species included in our analyses (Figure 1).

Three of the nine specimens from the western Pacific that belonged to a well-supported clade within Clade 4D were not re-examined in the current study: NTM C14142 (*S. polydactyla*, American Samoa), NTM C14173 (*S. polydactyla*, Papua New Guinea), and RMNH Coel. 41339 (*S. polydactyla*, Palau); the first two were not available and the third was a very small fragment. The other specimens belonging to this western Pacific sub-clade have been re-examined. ZMTAU Co 33611 (*S. gibberosa* Tixier-Durivault, 1970) was also re-examined as its *mtMutS* (*msh1*) sequence placed it among specimens of *S. polydactyla* in Benayahu et al. (2013: 1544). The colony of ZMTAU Co 33611, shown in Figure 19C, is somewhat different from the normal colony shape of *S. gibberosa* (Verseveldt, 1980: pls. 17-18). However, its sclerites (Figures 28–29) very much resemble those of *S. gibberosa* and therefore the original identification is maintained in the present study despite the fact that more recently obtained sequences from specimens identified as *S. gibberosa* do not match this one (unpublished data). RMNH Coel. 38420 (*S. compressa*, Ambon) has a much longer stalk (Figure 19D) than commonly found in *S. polydactyla* and *S. compressa* although no distinct differences among the sclerites of these species were shown (Figures 30–33). It is genetically different from the Red Sea *S. compressa* specimens under study, and therefore it is considered a misidentification and probably represents an as yet undescribed species. RMNH Coel. 19566 from Ambon (Figure 34A), identified by Ofwegen and Vennam (1994) as *S. polydactyla*, was also re-examined (Figure 35) and found to be close to RMNH Coel. 38420.

RMNH Coel. 38442 (*S. polydactyla*, Ambon) is now considered and assigned, with some doubts, to *S. ceramensis* Verseveldt, 1977. Verseveldt described that species with the following characters: lobes up to 4 cm high, flattened; surface layer of coenenchyme with clubs with a central wart, 0.06–0.09 mm long, some up to 0.14 mm; small spindles, 0.15–0.25 mm long, with simple tubercles. Stalk surface with wider clubs. Interior with pointed and blunt-ended spindles up to 3 mm long, with a median constriction and covered with medium sized warts. RMNH Coel. 38442 differs from this in having long tapering lobes (Figure 34B), and many of the clubs with a central wart are up to 0.15 mm long (Figure 36A). In addition, some intermediates (Fig. 36B) between small spindles (Figure 36C) and clubs, even up to 0.20 mm long are also found. The surface of the base shows shorter and wider sclerites, many with tubercles with acute ends (Figure 37), which were not reported for *S. ceramensis*. Because of these differences and the previously unknown colony shape of *S. polydactyla*, this specimen was originally identified as that species.

Material used by Hoover et al. (2008) (*S. polydactyla*, Guam) was also re-examined as their specimens identified as *S. polydactyla* appeared to belong to three different species in the phylogenetic tree (Figure 1). Their three "PBH-To" fragments did not contain any sclerites, probably because the material was preserved using a chemical

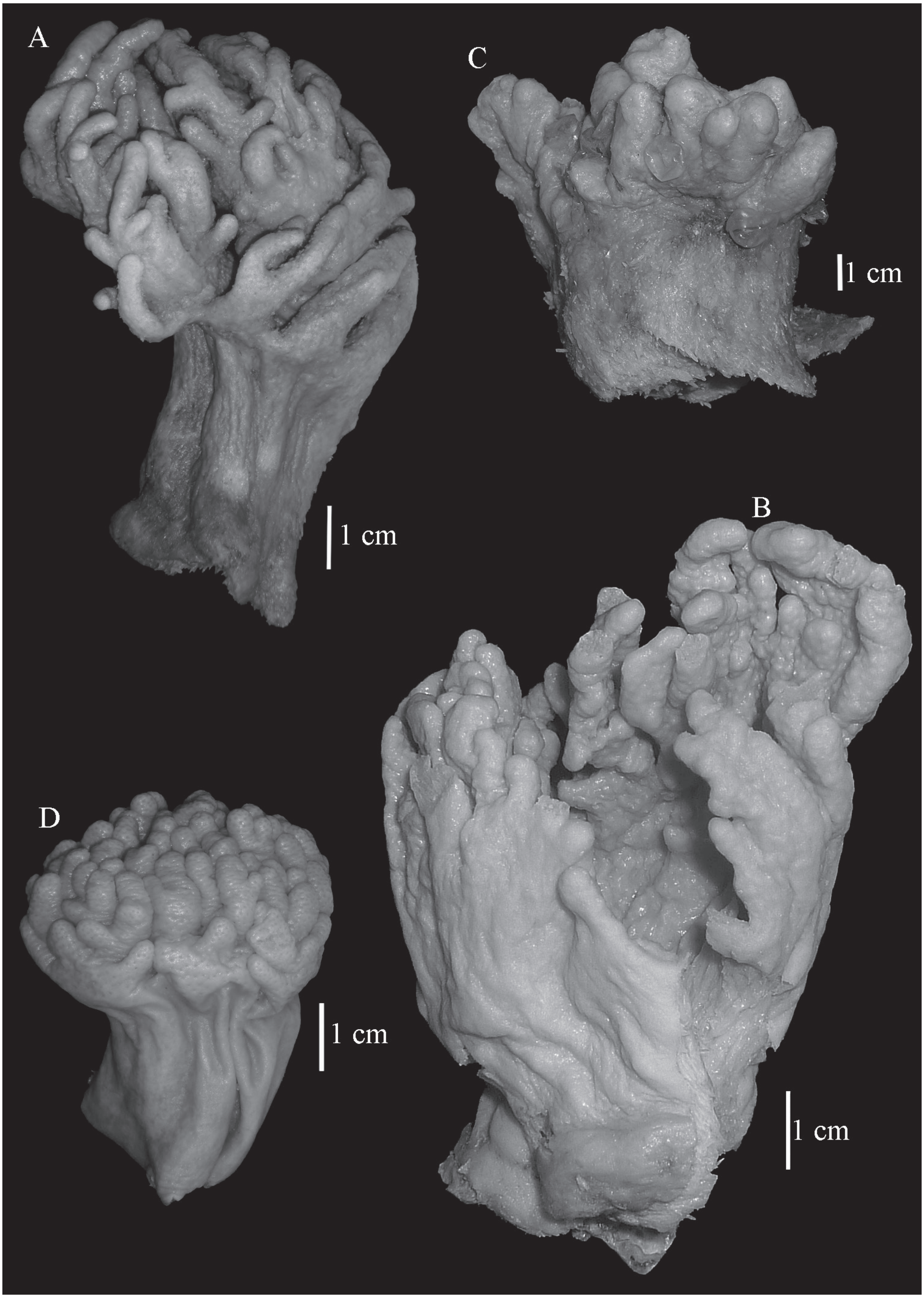

Figure 19. Colonies. **A** *Sinularia polydactyla*, RMNH 15950 **B** *S. polydactyla*, ZMTAU Co 34181 **C** *S. gibberosa*, ZMTAU 33611 **D** *S. compressa*, RMNH 38420.

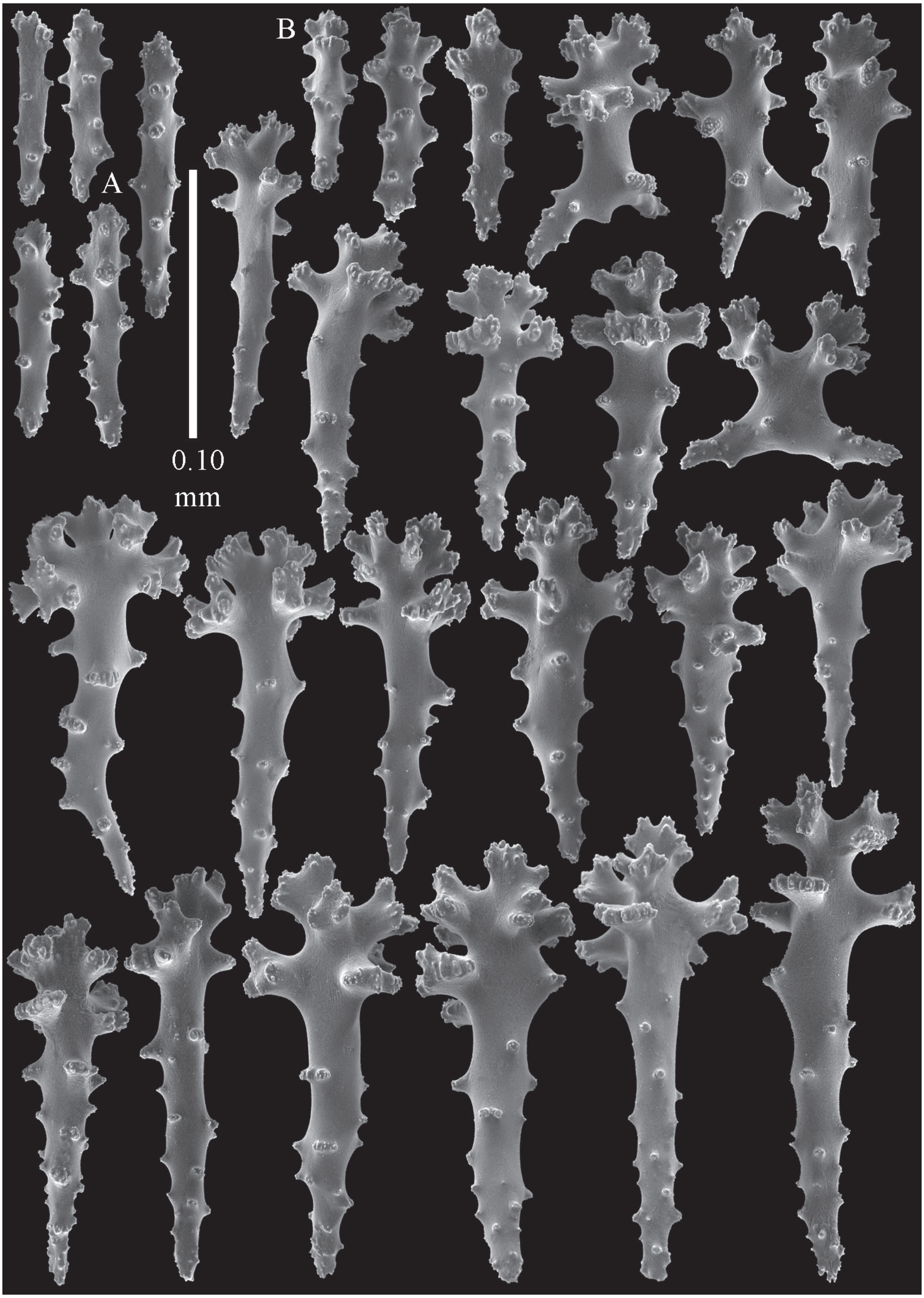

Figure 20. *Sinularia polydactyla* (Ehrenberg, 1834), RMNH 15950. **A** point clubs **B** clubs of surface layer top of colony.

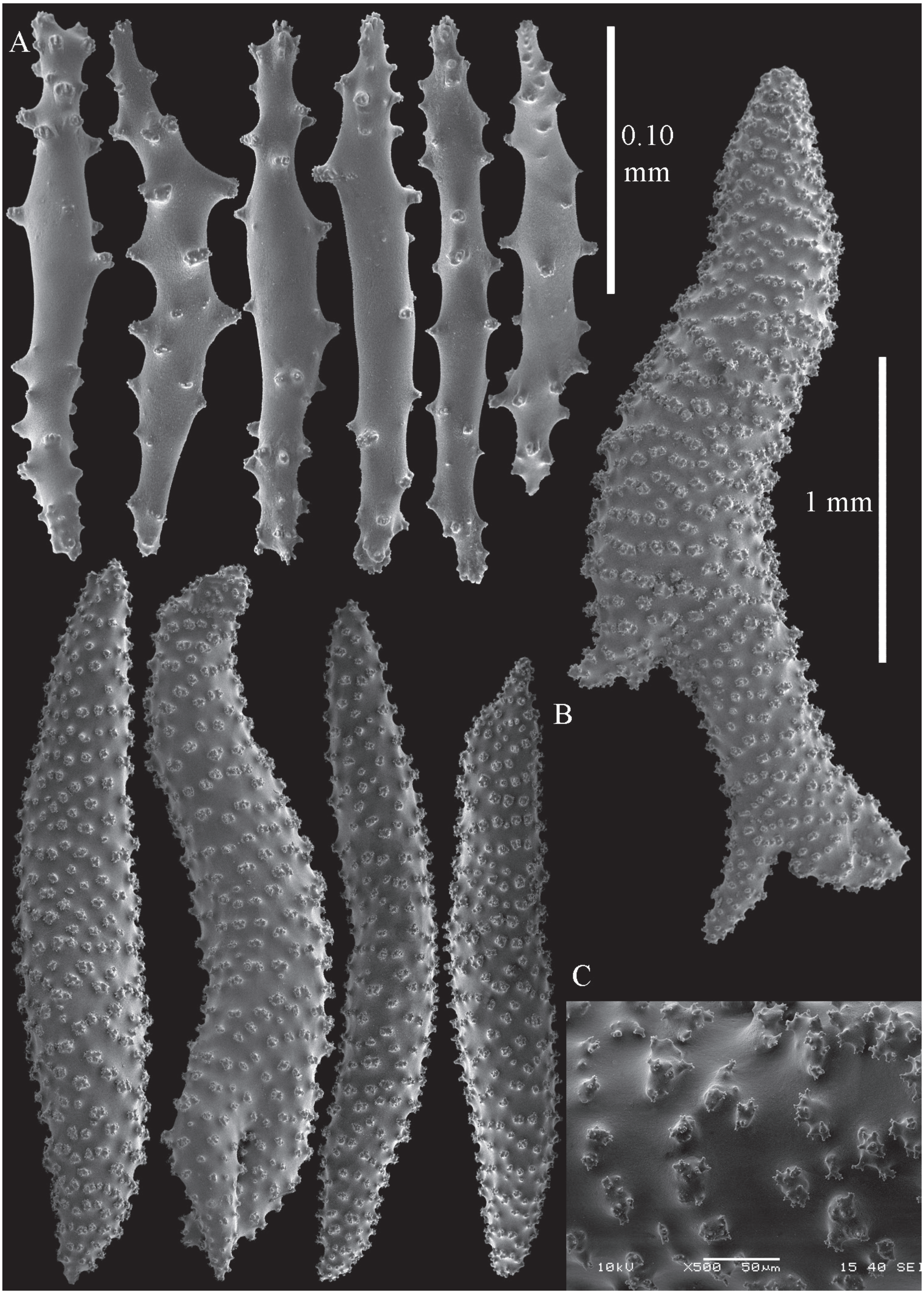

Figure 21. *Sinularia polydactyla* (Ehrenberg, 1834), RMNH 15950. **A** spindles of surface layer of top of colony **B** spindles of interior **C** tuberculation of a spindle.

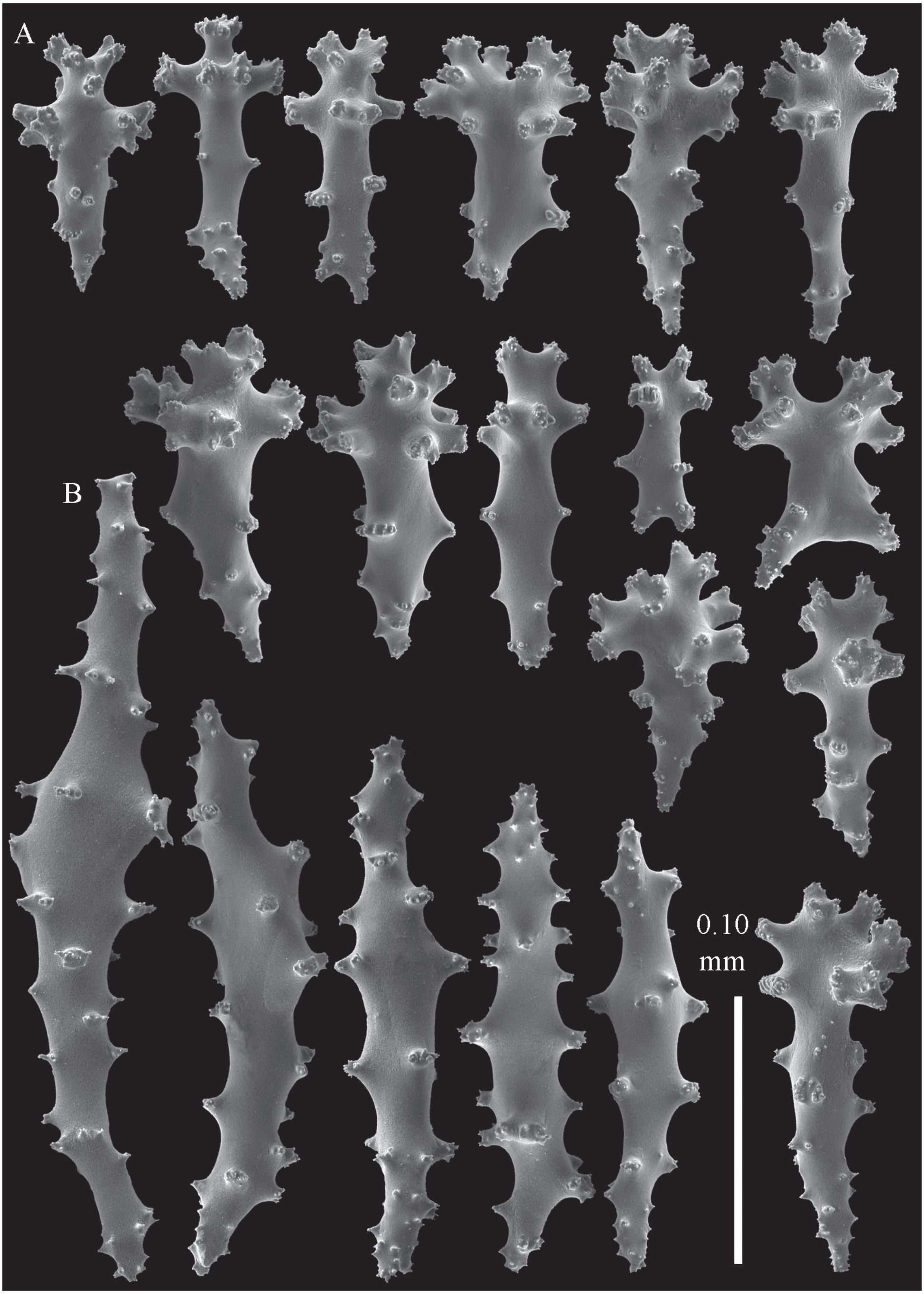

Figure 22. *Sinularia polydactyla* (Ehrenberg, 1834), RMNH 15950. **A** clubs of surface layer base of colony **B** spindles.

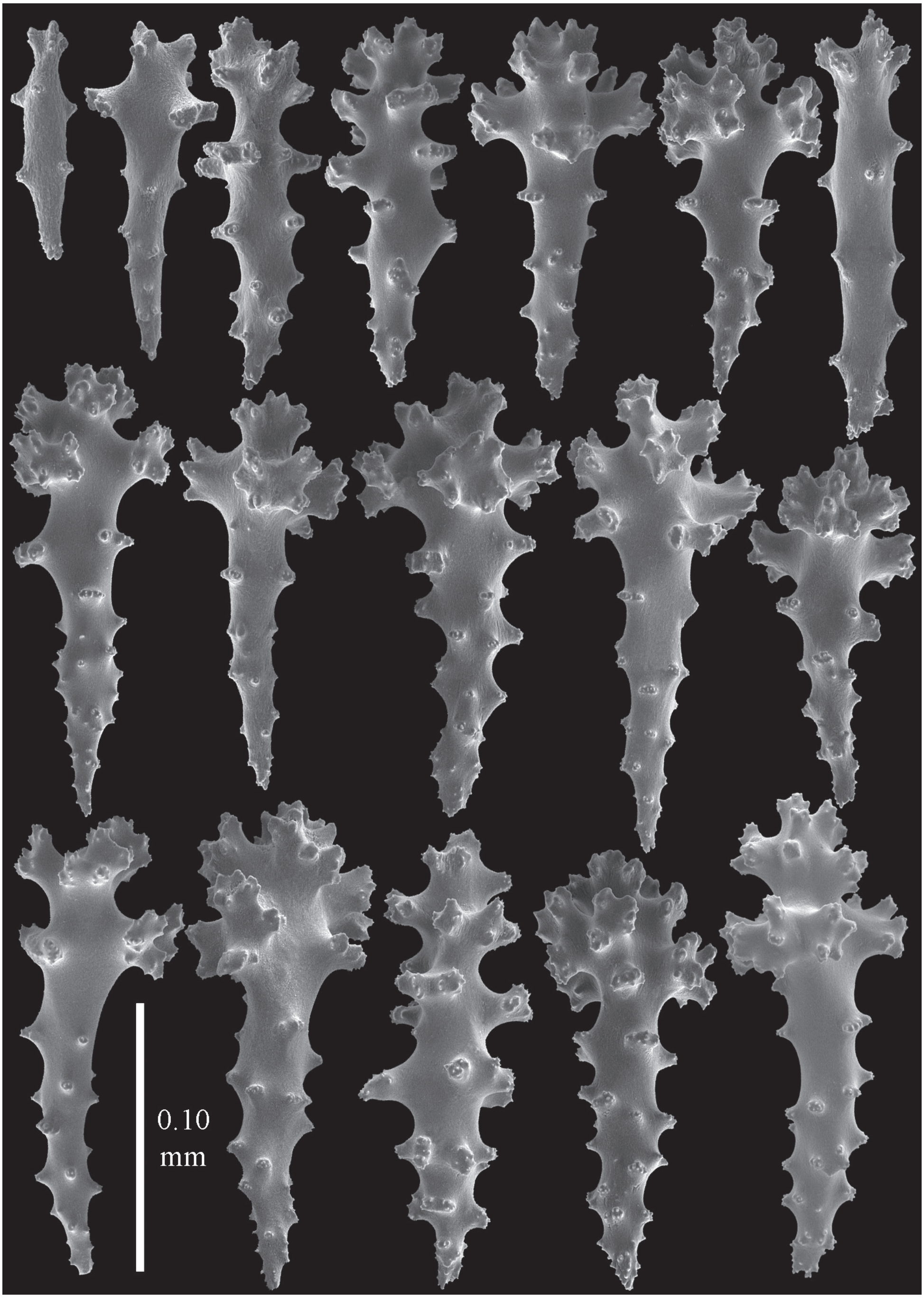

Figure 23. *Sinularia polydactyla* (Ehrenberg, 1834), ZMTAU Co 34181. Clubs of surface layer top of colony.

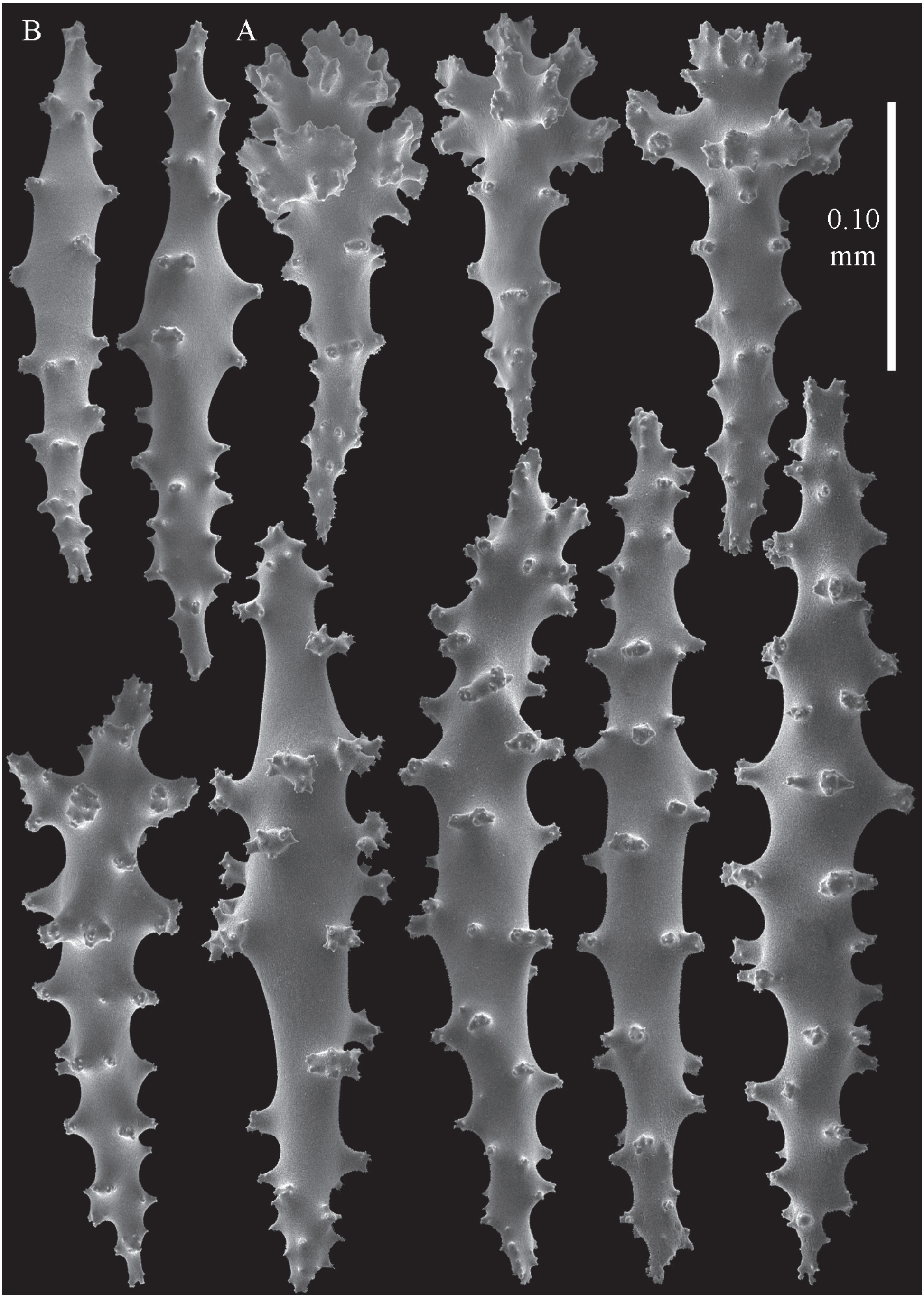

Figure 24. *Sinularia polydactyla* (Ehrenberg, 1834), ZMTAU Co 34181. **A** clubs of surface layer top of colony **B** spindles of surface layer top of colony.

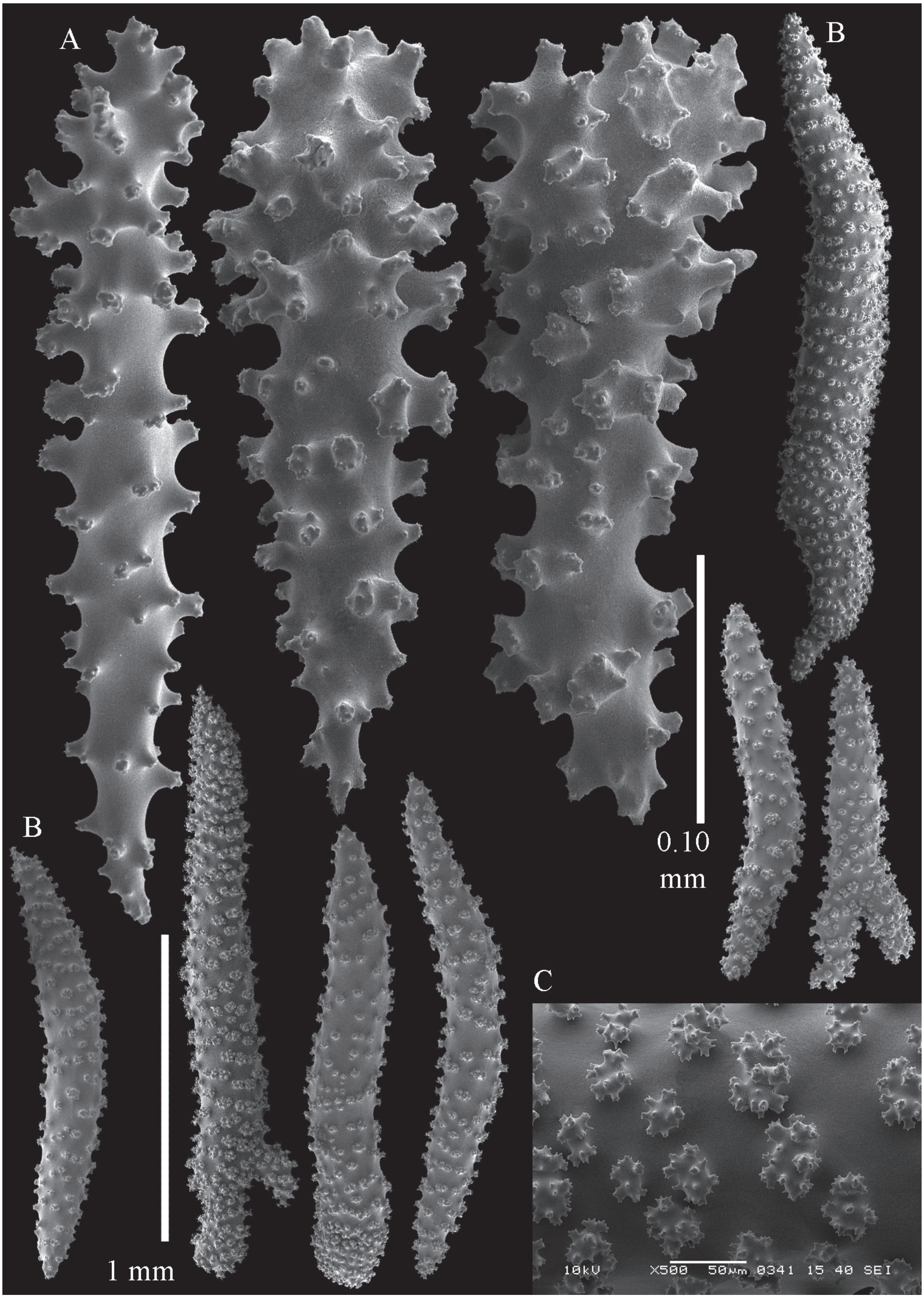

Figure 25. *Sinularia polydactyla* (Ehrenberg, 1834), ZMTAU Co 34181. **A** clubs of surface layer top of colony **B** spindles of interior of top of colony **C** tuberculation of a spindle.

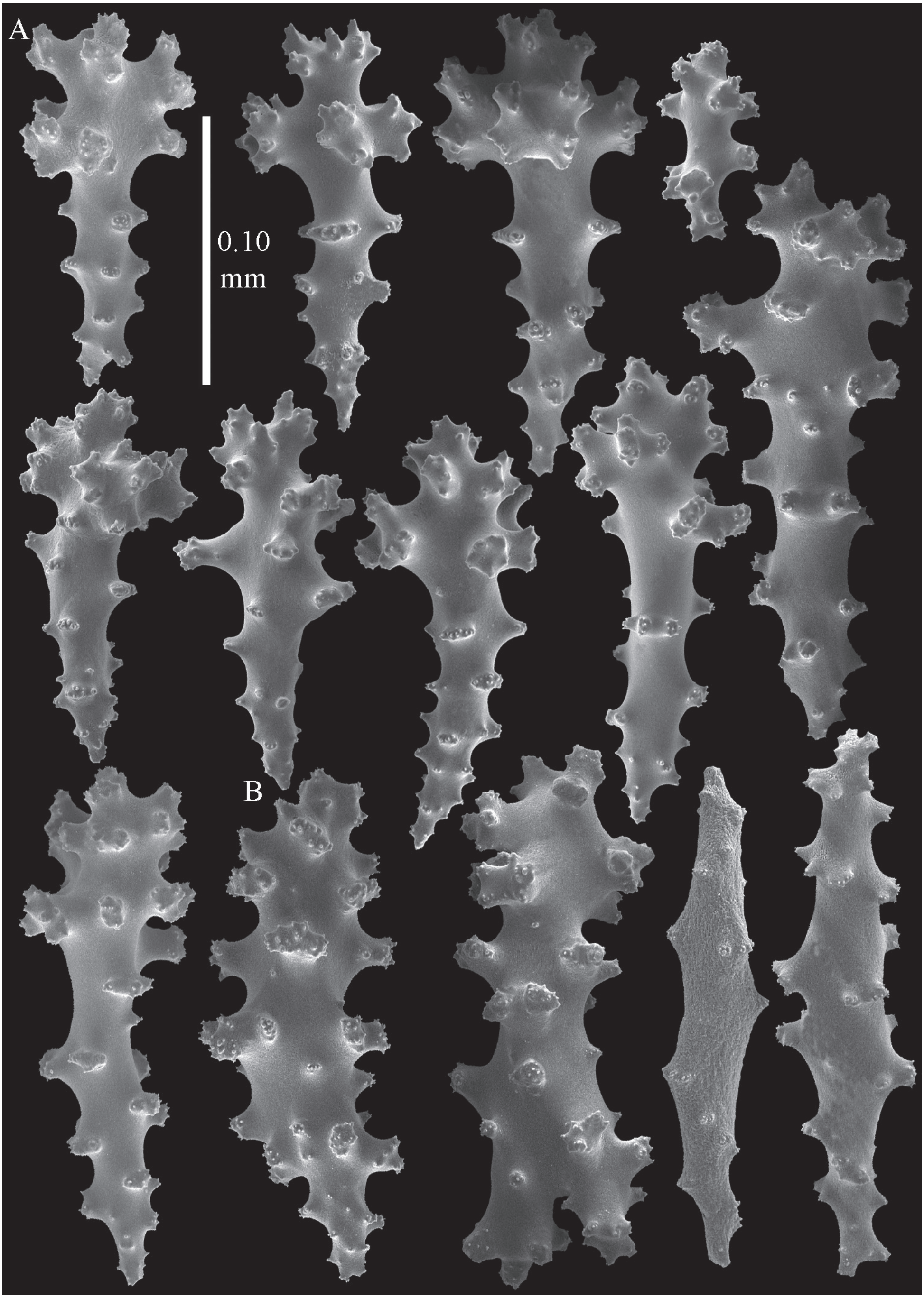

Figure 26. *Sinularia polydactyla* (Ehrenberg, 1834), ZMTAU Co 34181. **A** clubs of surface layer base of colony **B** spindles.

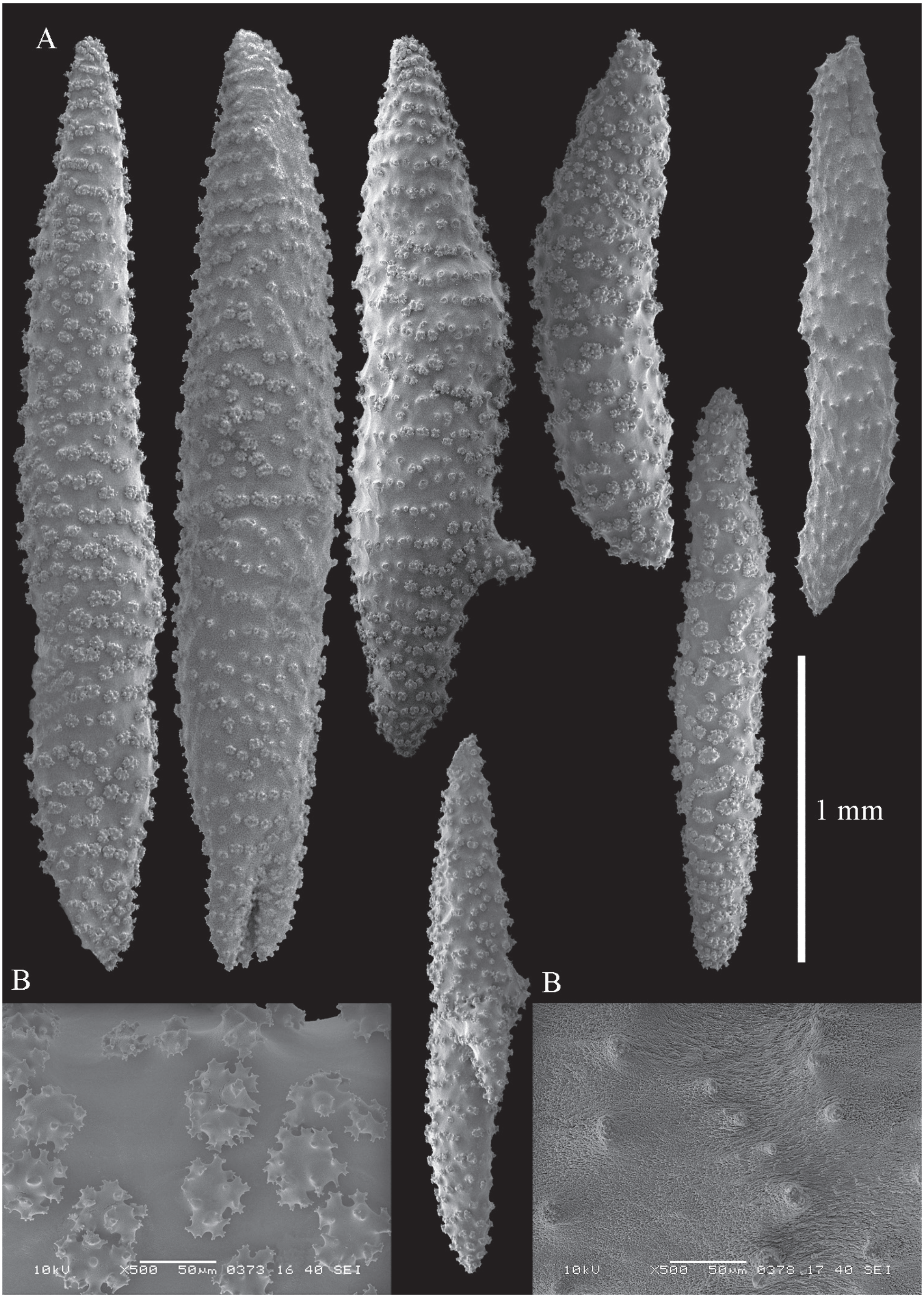

Figure 27. *Sinularia polydactyla* (Ehrenberg, 1834), ZMTAU Co 34181. **A** spindles of interior of base of colony **B** tuberculation of two of the spindles.

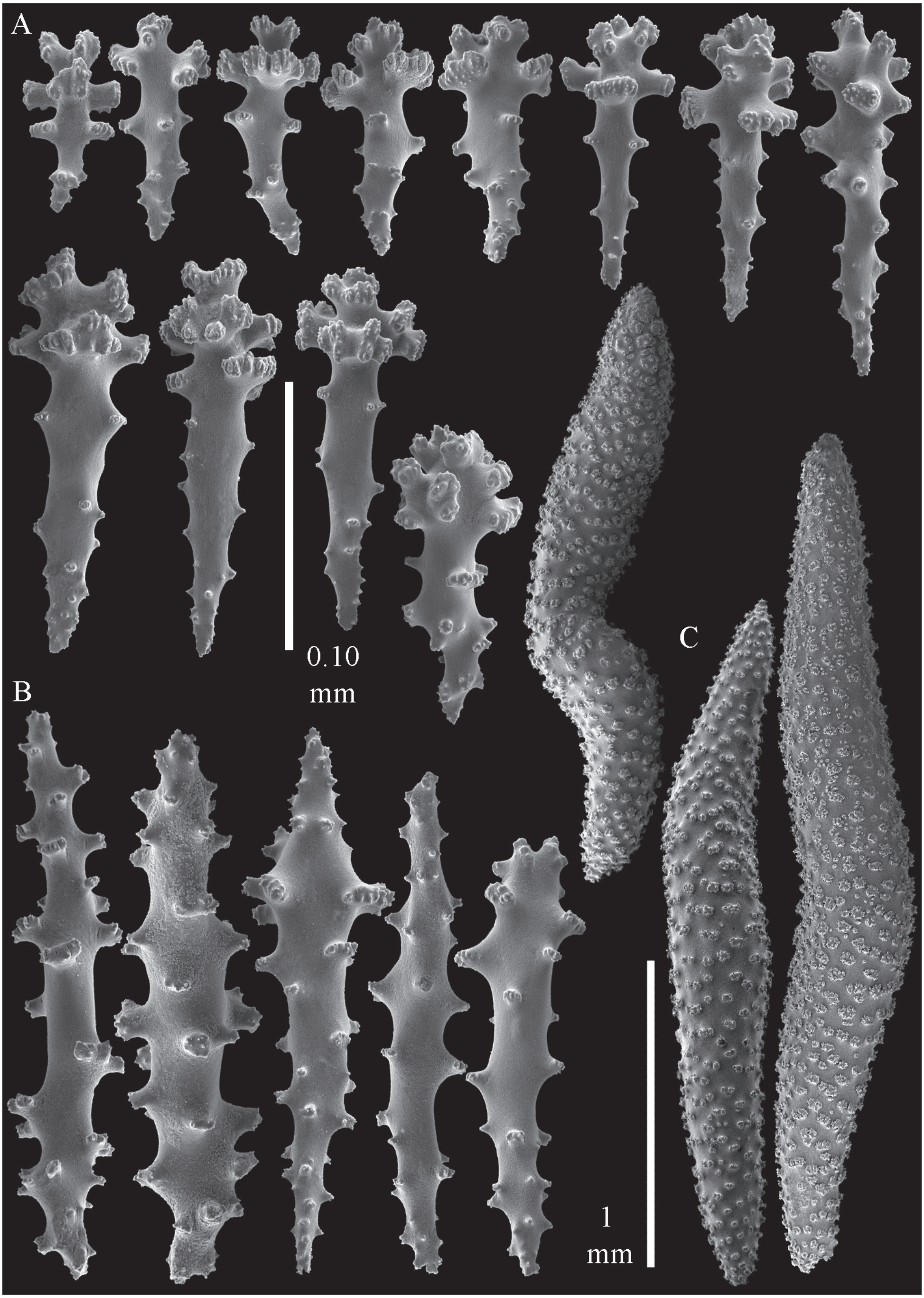

Figure 28. *Sinularia gibberosa* Tixier-Durivault, 1970, ZMTAU 33611. **A** clubs of surface layer base of colony **B** spindles **C** interior spindles.

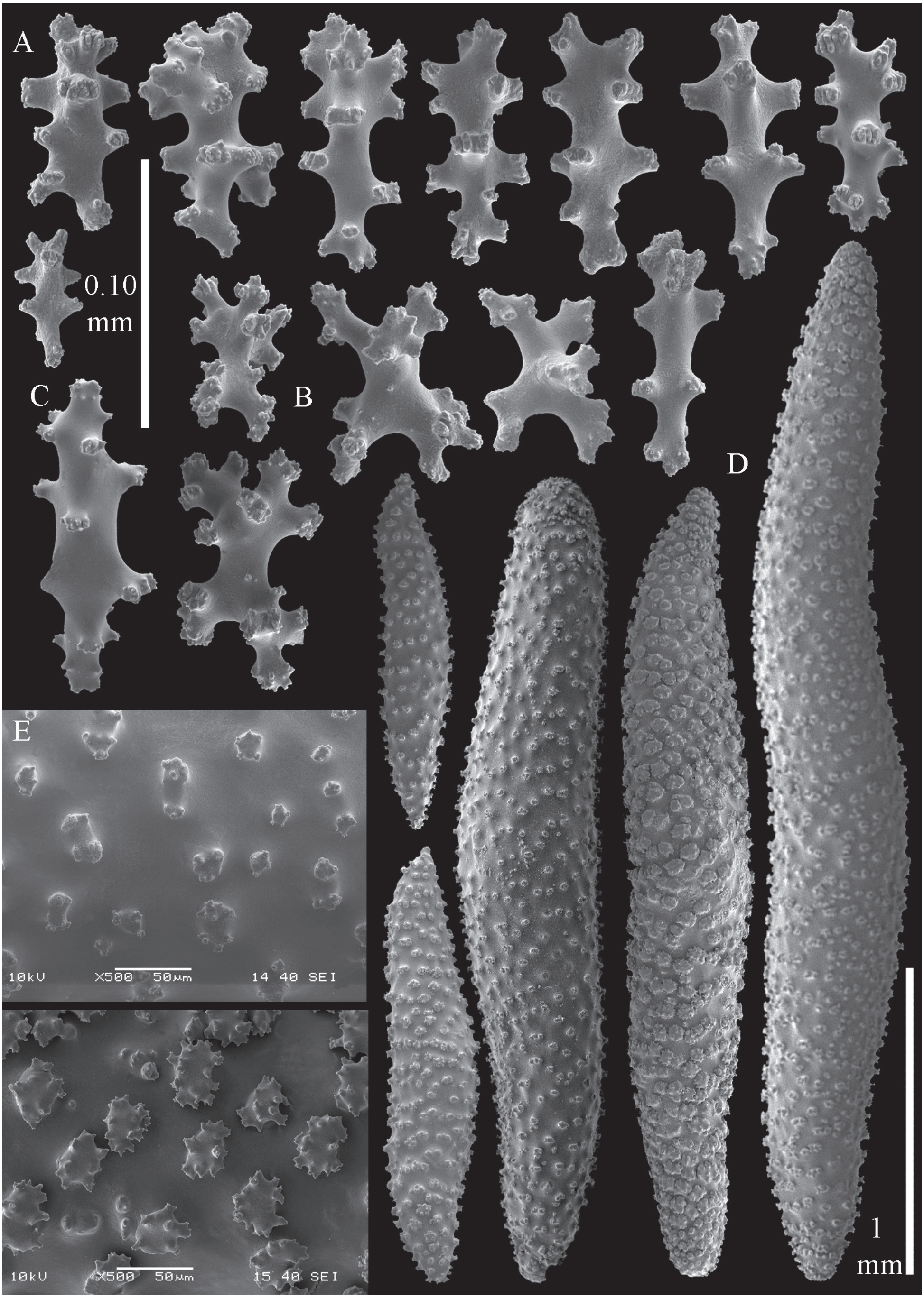

Figure 29. *Sinularia gibberosa* Tixier-Durivault, 1970, ZMTAU 33611. **A** clubs of surface layer base of colony **B** crosses **C** spindle **D** interior spindles **E** tuberculation of spindles.

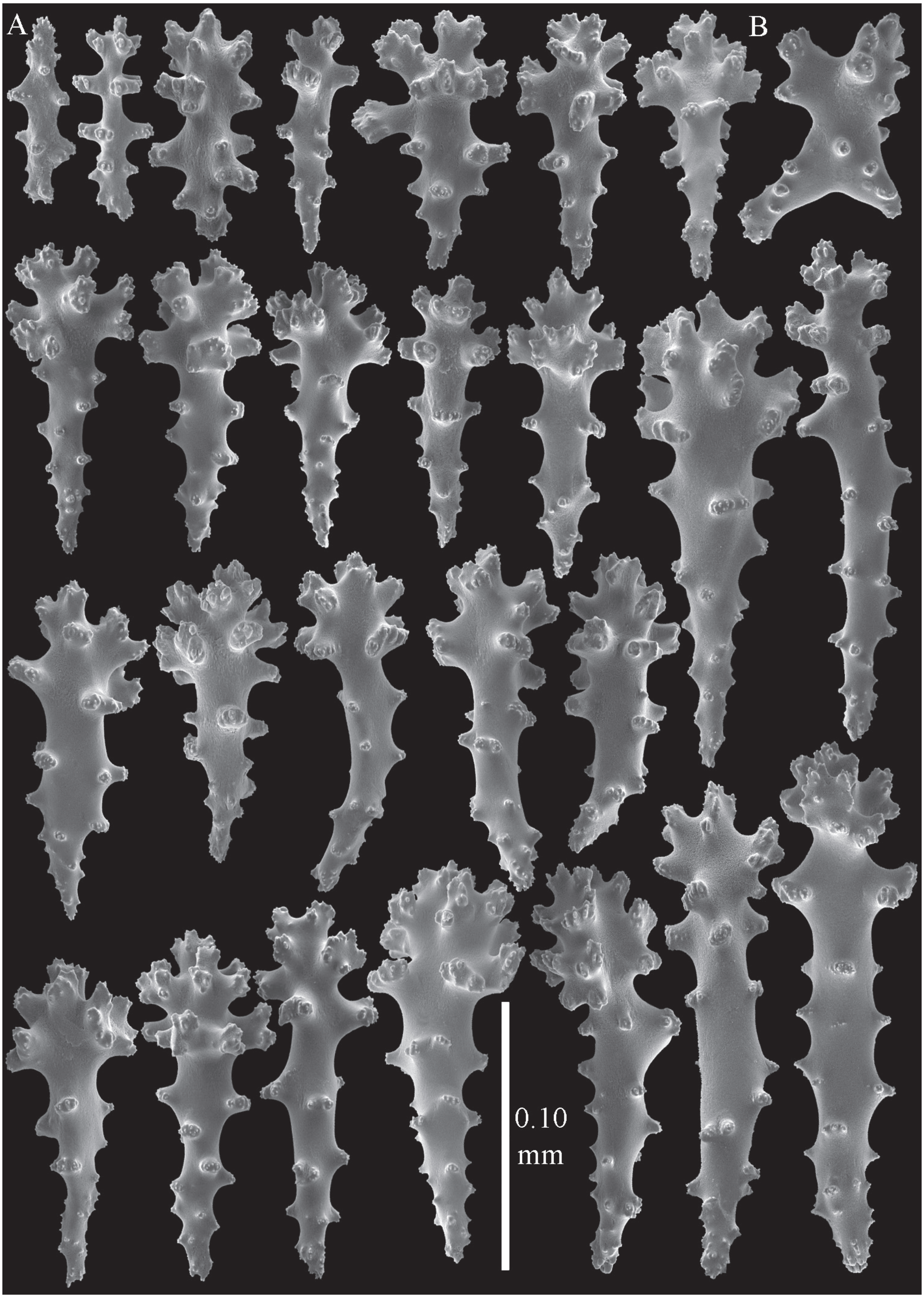

Figure 30. *Sinularia compressa* Tixier-Durivault, 1945, RMNH Coel. 38420. **A** clubs of surface layer top of colony **B** cross.

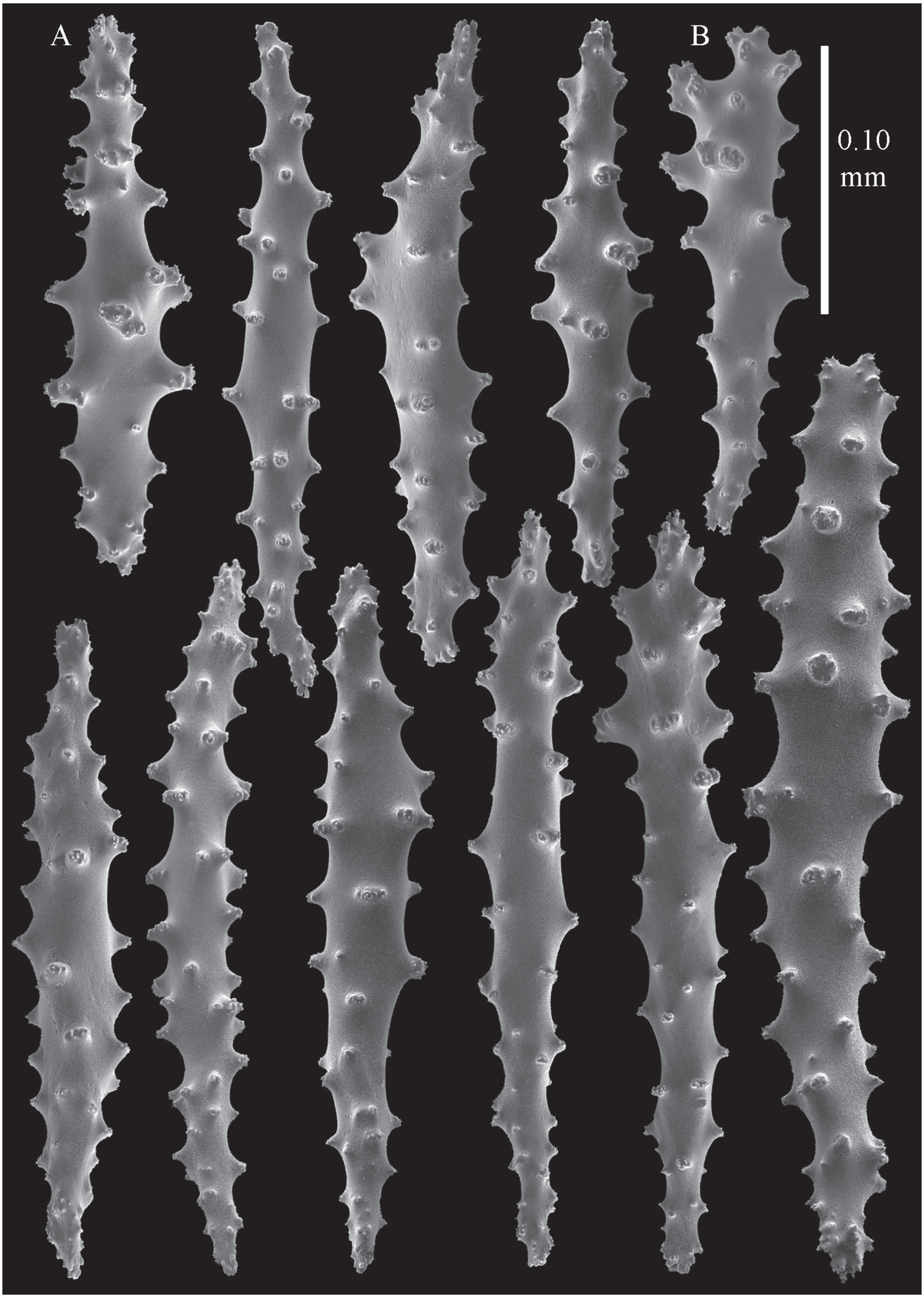

Figure 31. *Sinularia compressa* Tixier-Durivault, 1945, RMNH Coel. 38420. **A** spindles of surface layer of top of colony **B** club.

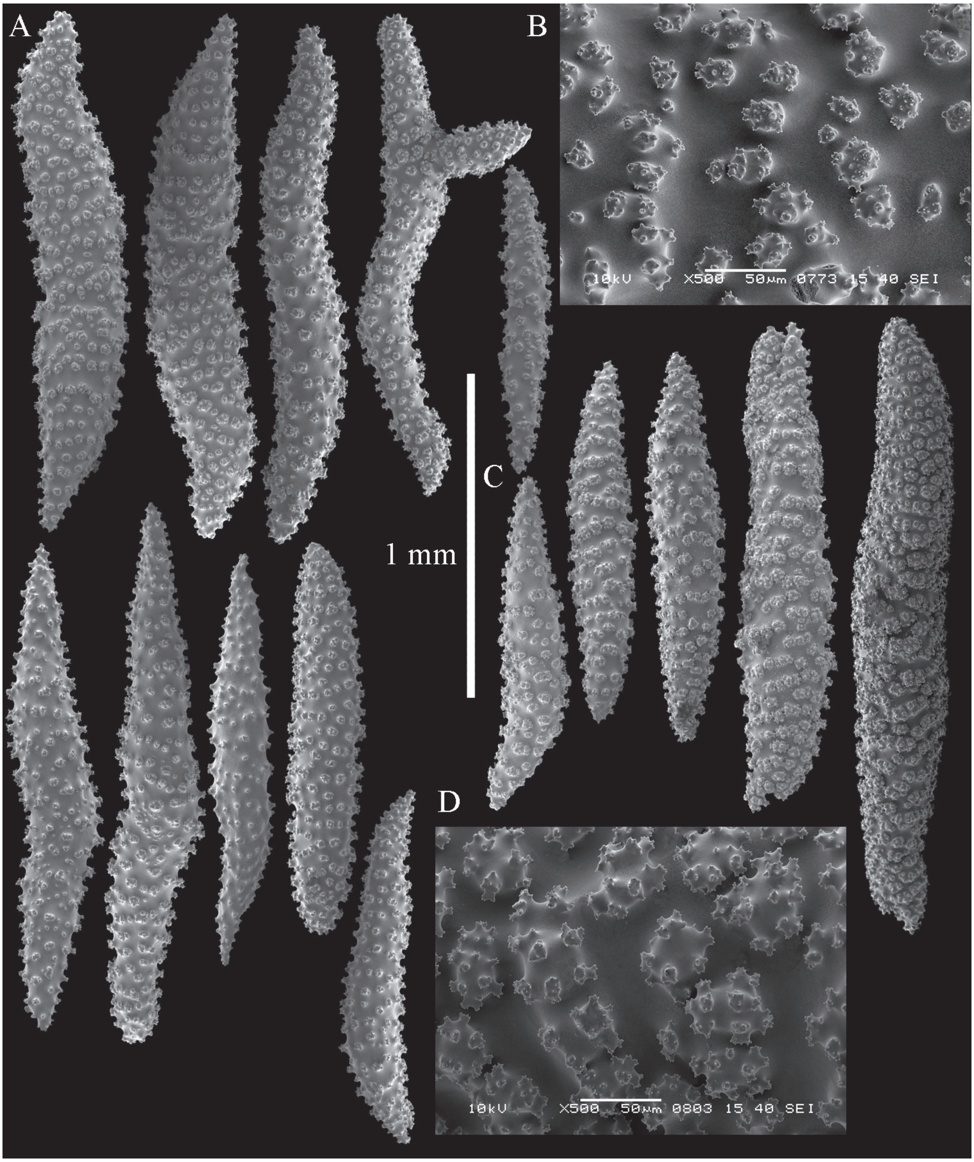

Figure 32. *Sinularia compressa* Tixier-Durivault, 1945, RMNH Coel. 38420. **A** spindles of interior of top of colony **B** tuberculation of one of the spindles **C** spindles of the interior of the base of the colony **D** tuberculation of one of the spindles.

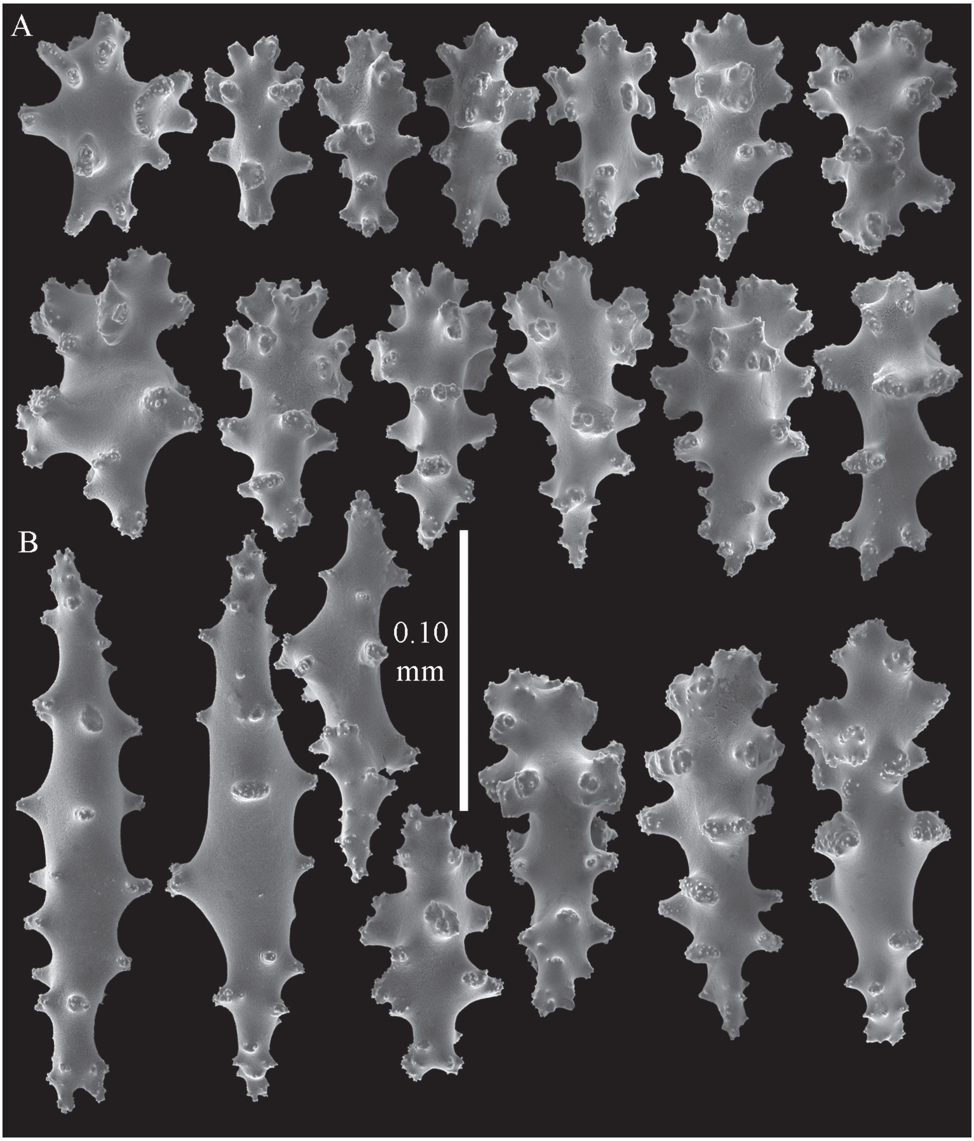

Figure 33. *Sinularia compressa* Tixier-Durivault, 1945, RMNH Coel. 38420. **A** clubs of surface layer base of colony **B** four spindles.

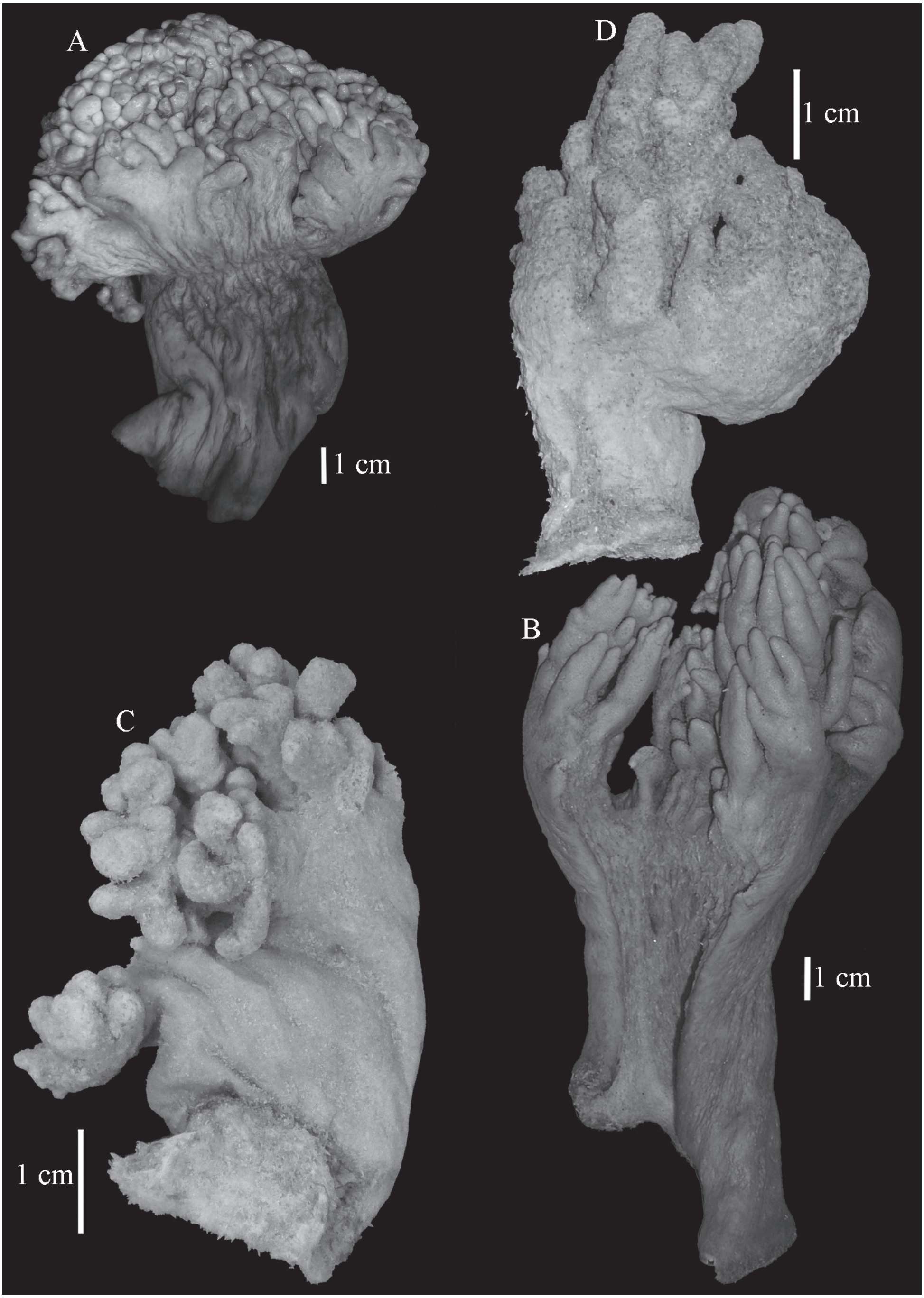

Figure 34. Colonies**.** A *Sinularia polydactyla*, RMNH 19566 **B** *S. ceramensis*, RMNH 38442 **C** *S. polydactyla*, "PBH-Tr3" **D** *S. polydactyla*, "PBH-C10".

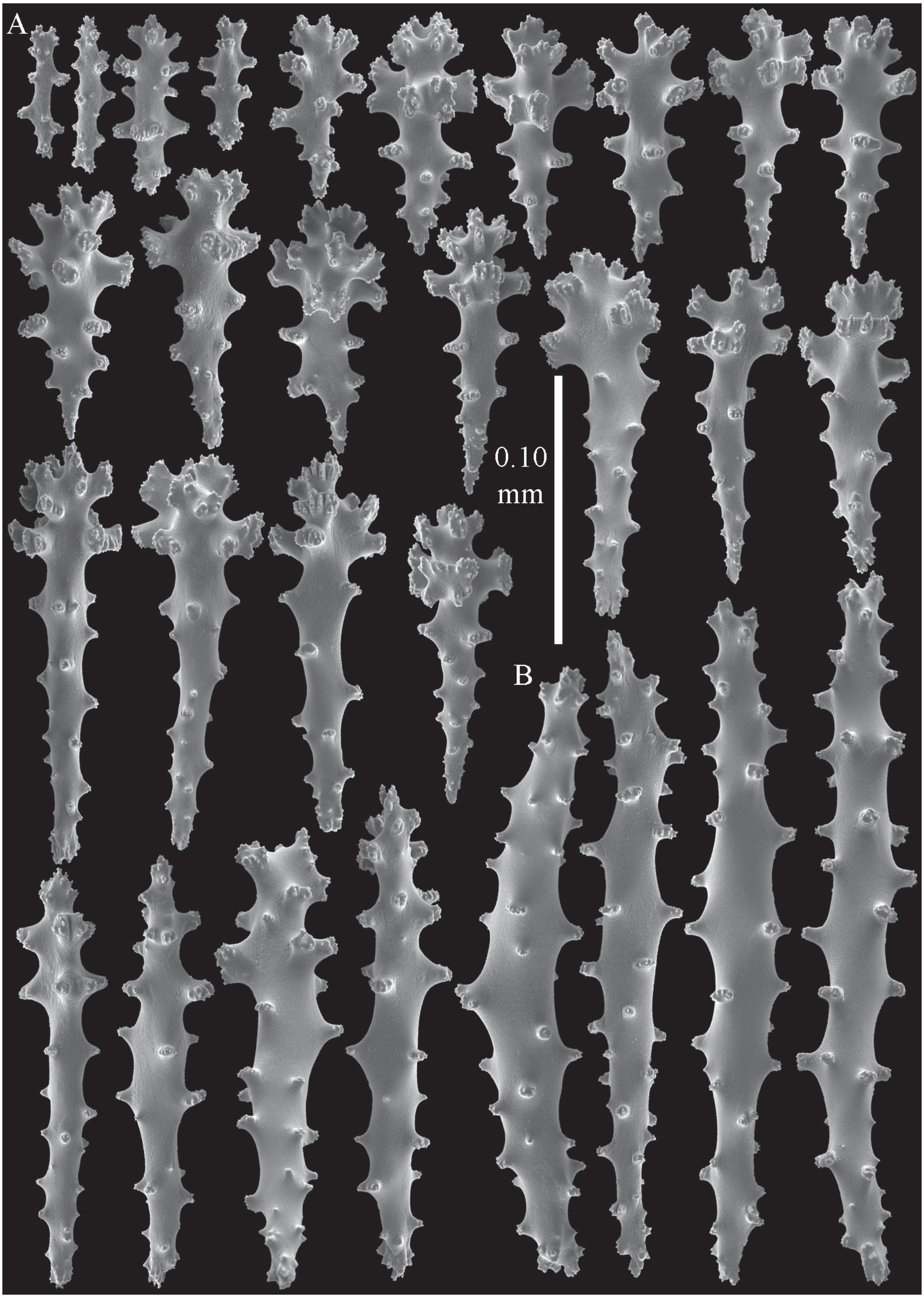

Figure 35. *Sinularia polydactyla* Tixier-Durivault, 1945, RMNH Coel. 19566. **A** clubs of surface layer top of colony **B** spindles.

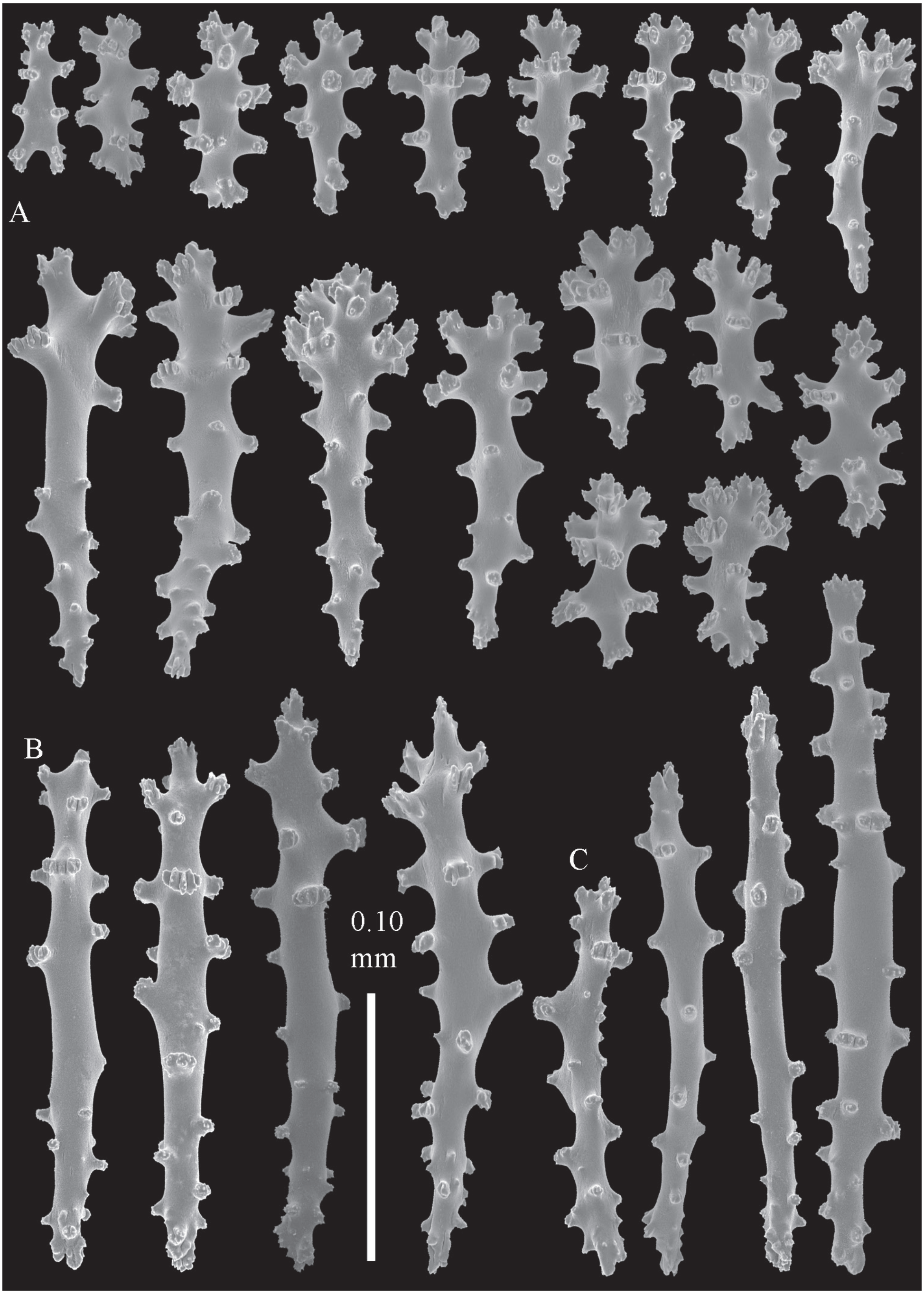

Figure 36. *Sinularia ceramensis* Verseveldt, 1977, RMNH 38442. **A** clubs of surface layer top of colony **B** intermediates between clubs and spindles **C** spindles.

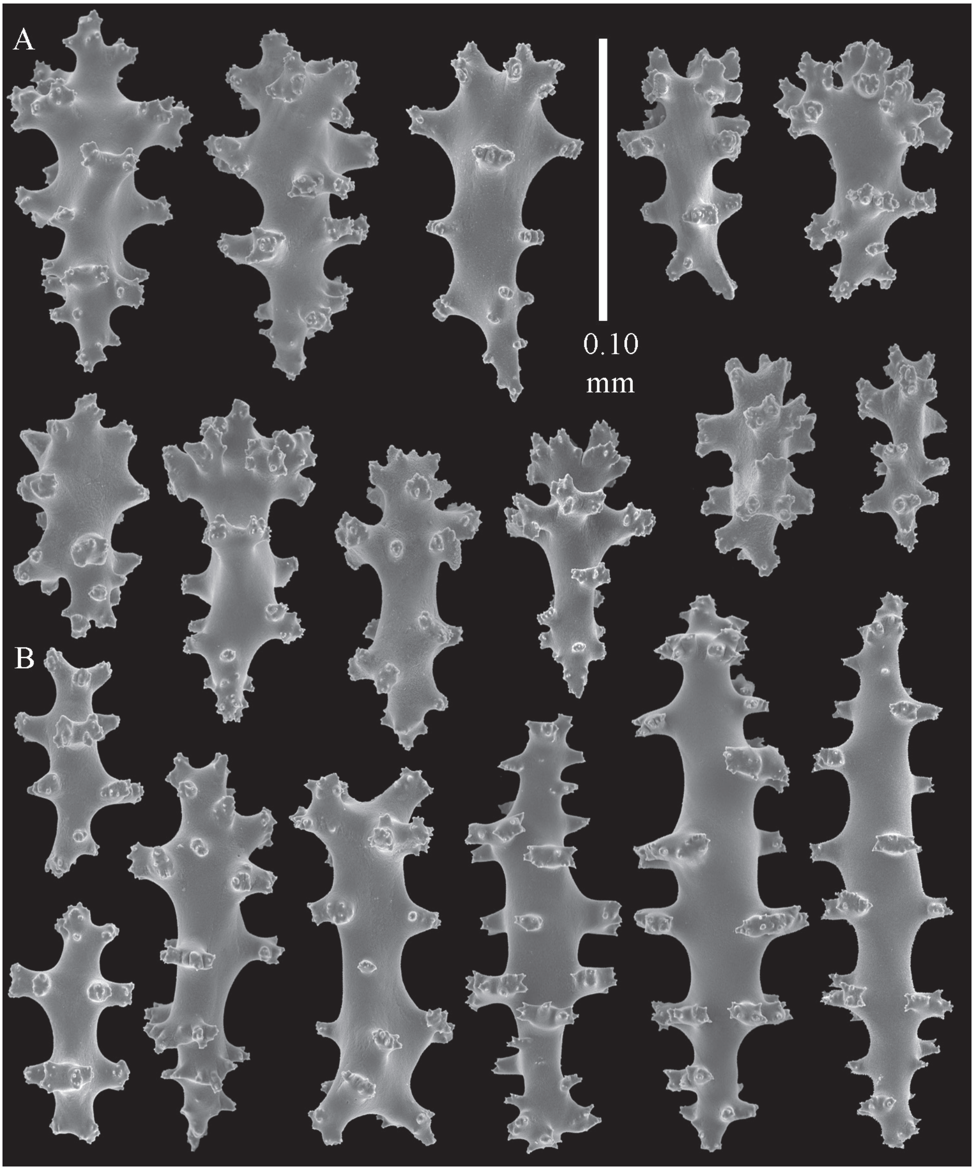

Figure 37. *Sinularia ceramensis* Verseveldt, 1977, RMNH 38442. **A** clubs of surface layer base of colony **B** spindles.

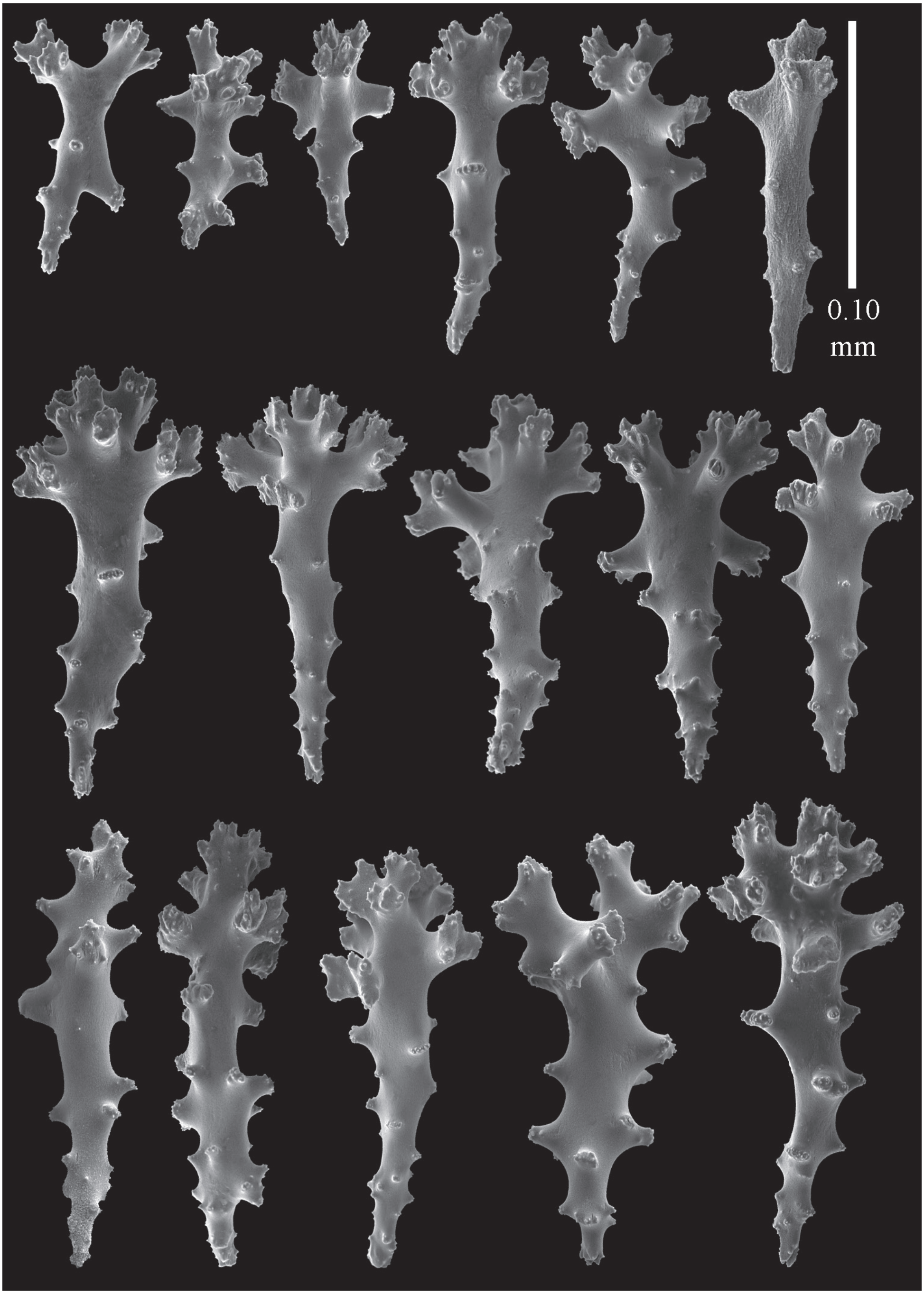

Figure 38. *Sinularia polydactyla*, “PBH-Tr3”. Clubs of surface layer top of colony.

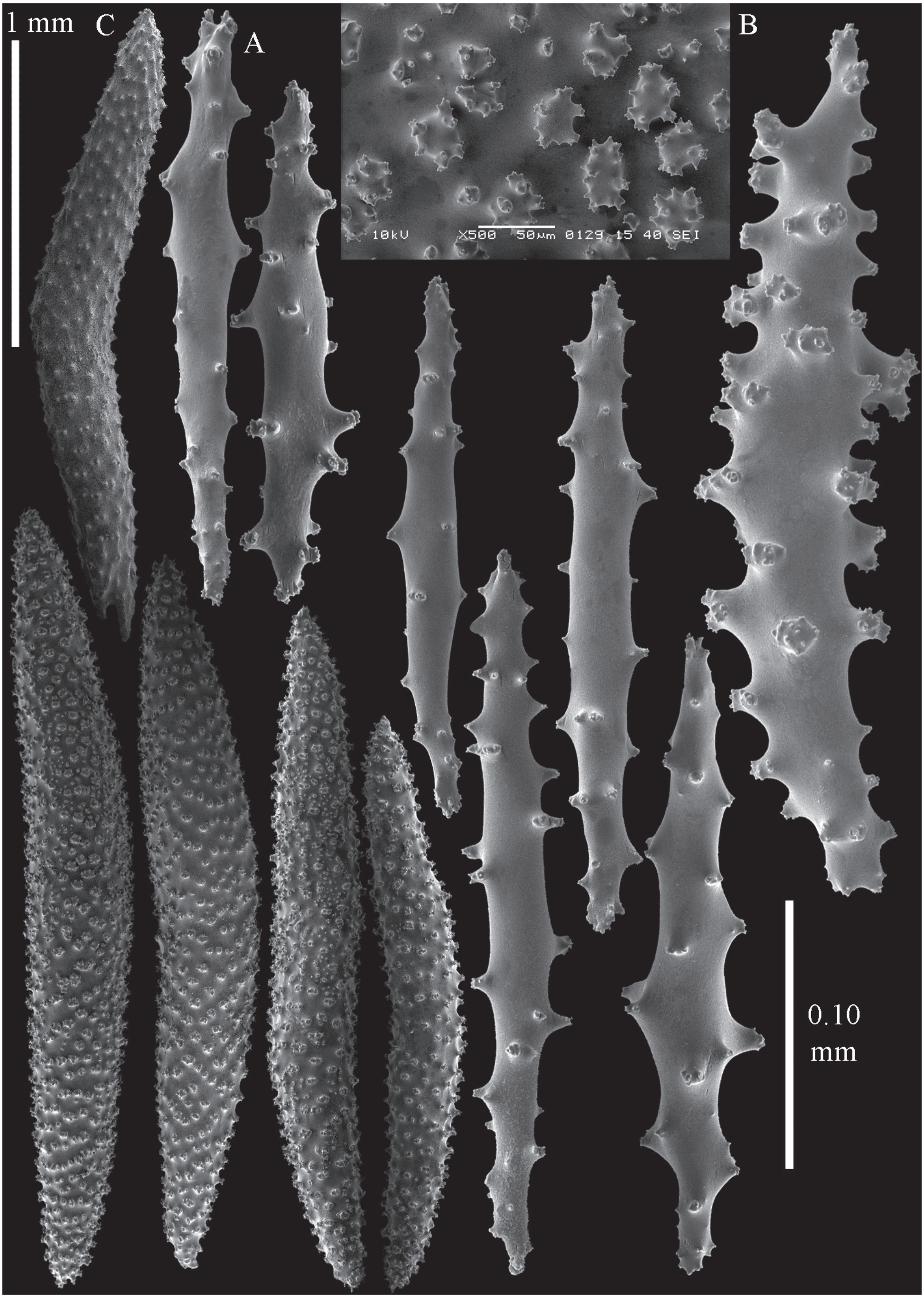

Figure 39. *Sinularia polydactyla*, "PBH-Tr3". **A** spindles of surface layer top of colony **B** tuberculation of one of the spindles **C** spindles of the interior of the top of the colony.

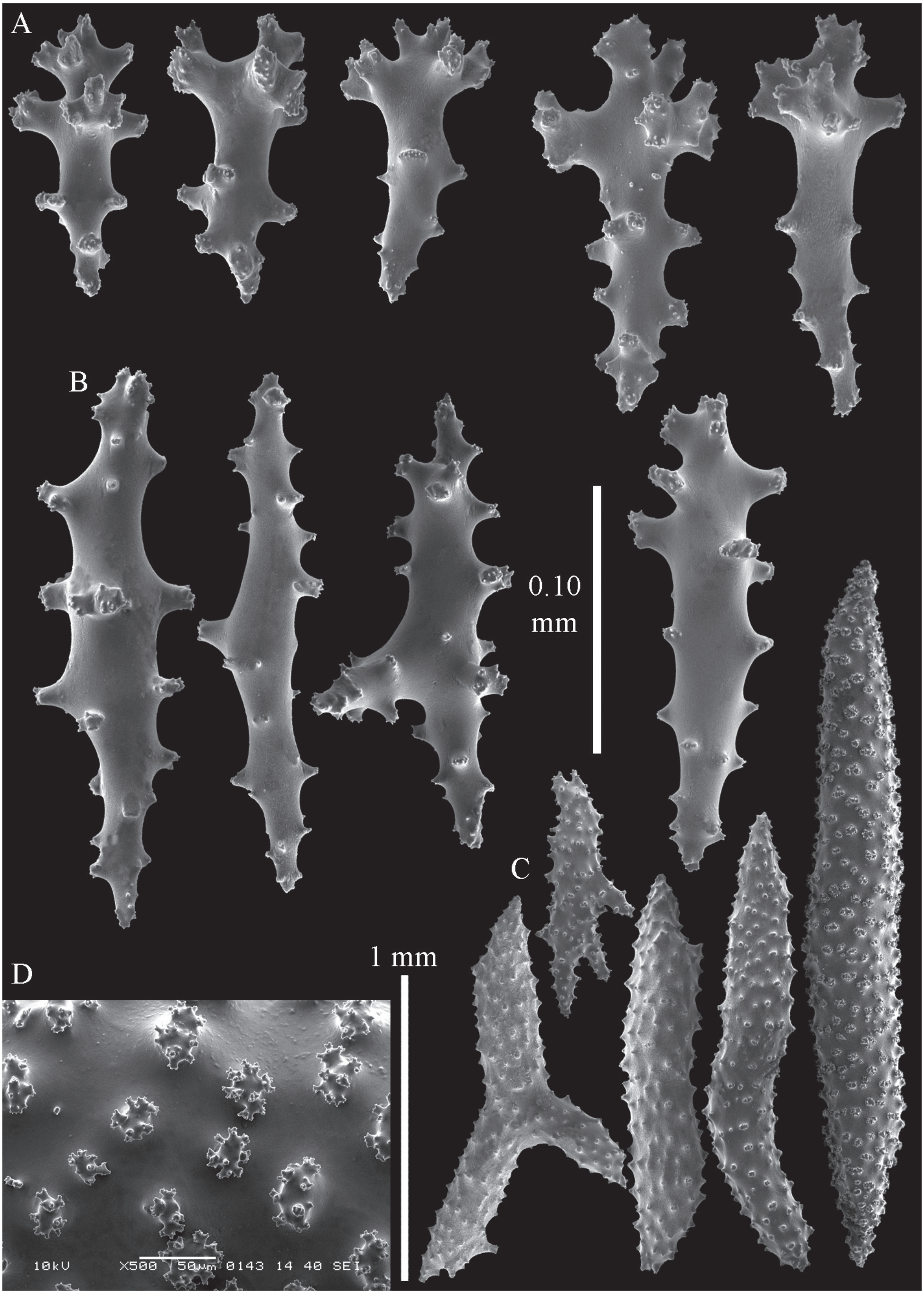

Figure 40. *Sinularia polydactyla*, "PBH-Tr3". **A** clubs of surface layer base of colony **B** spindles **C** spindles of the interior of the base of the colony **D** tuberculation of one of the spindles.

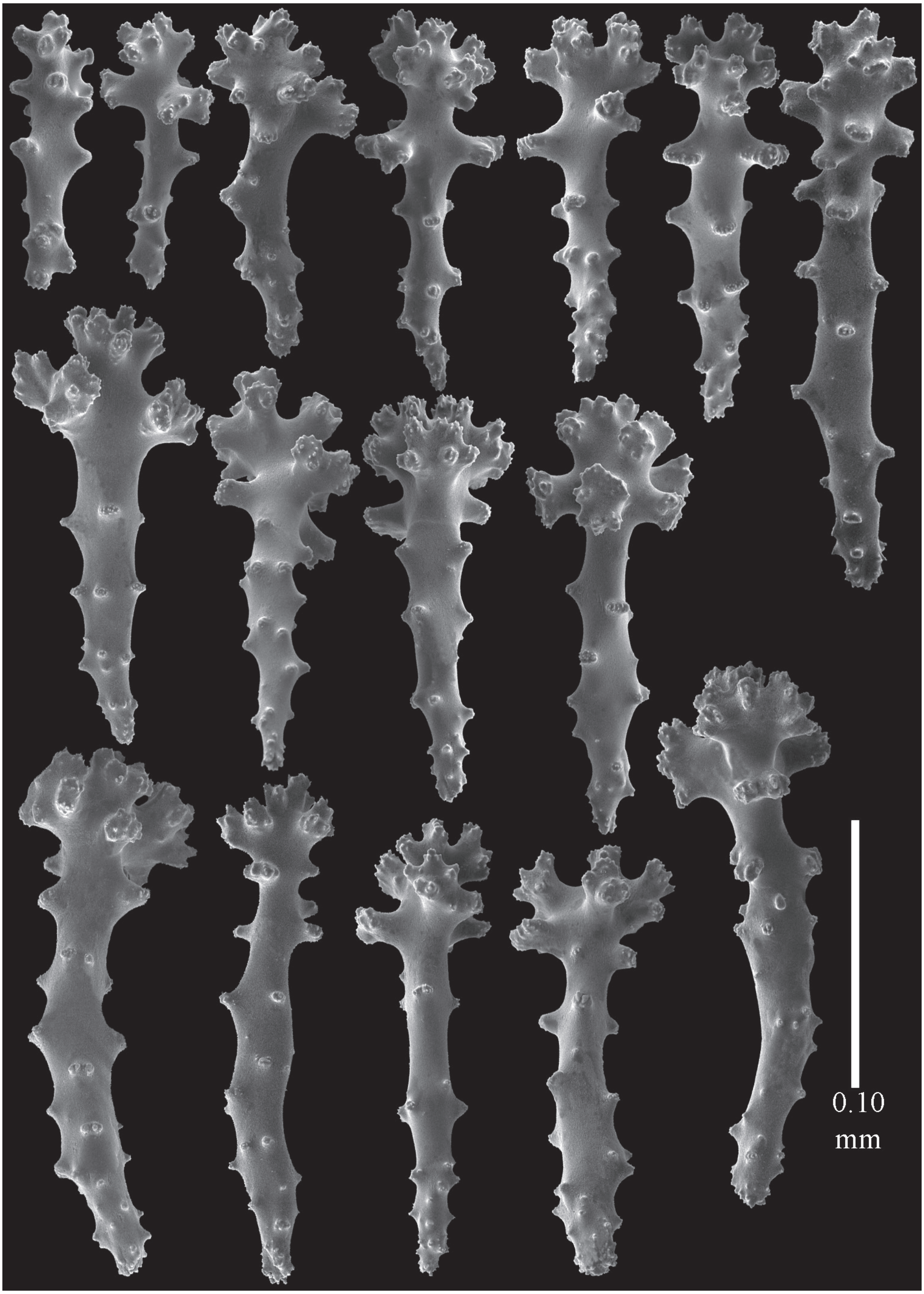

Figure 41. *Sinularia polydactyla*, “PBH-C10”. Clubs of surface layer top of colony.

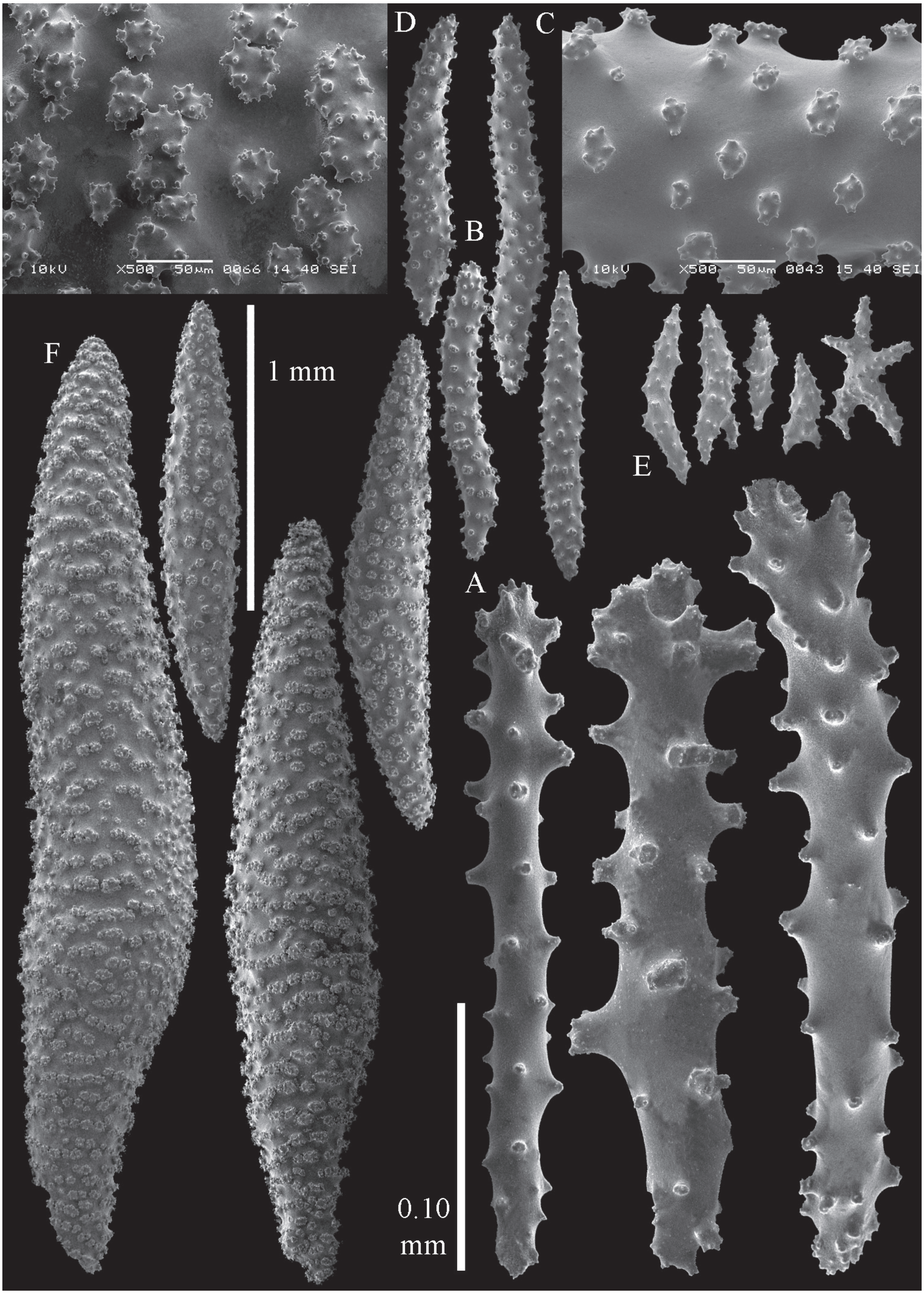

Figure 42. *Sinularia polydactyla*, "PBH-C10". **A** clubs of surface layer top of colony **B** spindles of the interior of the top of the colony **C** tuberculation of one of the spindles of the interior of the top of the colony **D** tuberculation of one of the spindles of the interior of the base of the colony **E-F** spindles of the interior of the base of the colony.

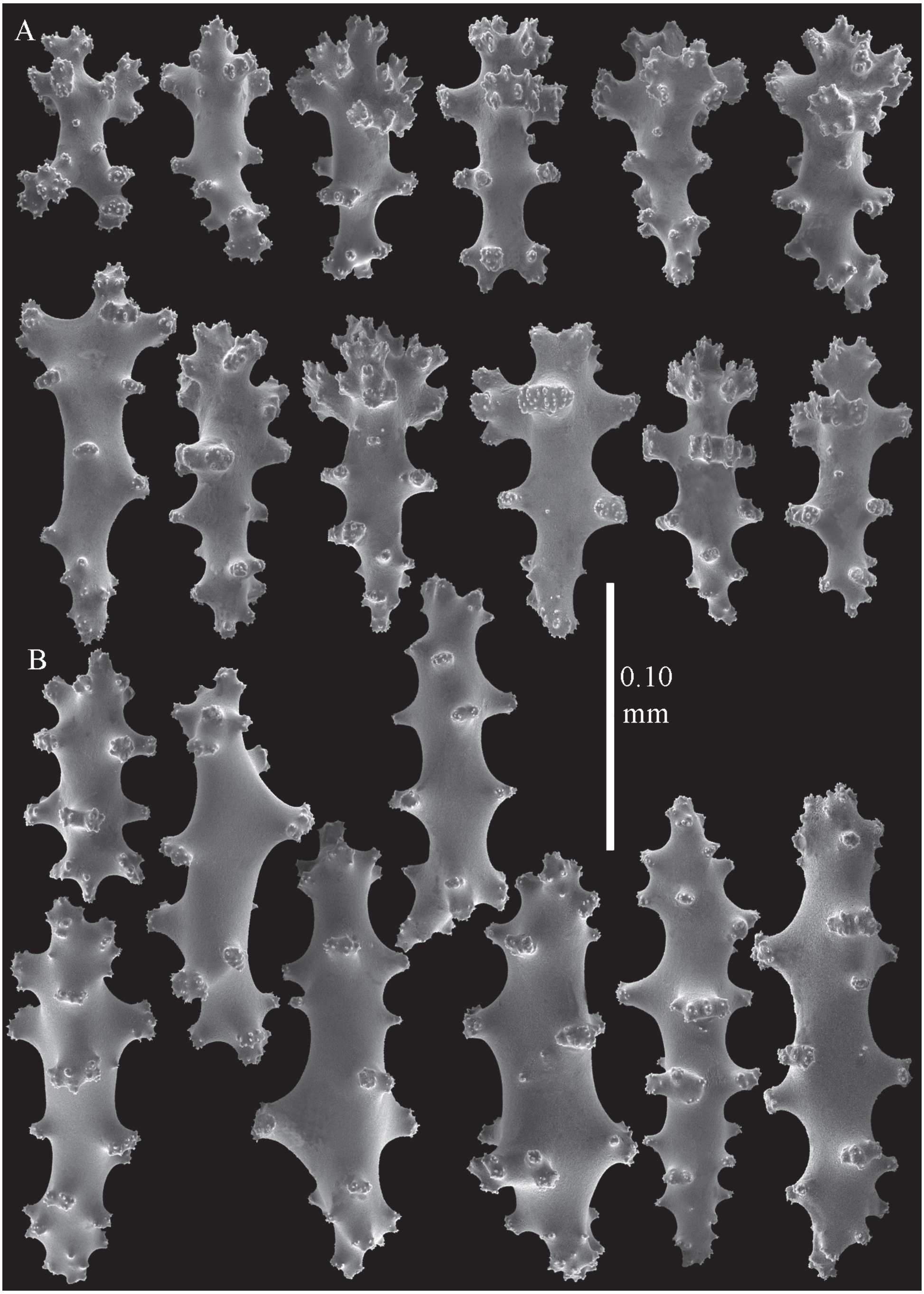

Figure 43. *Sinularia polydactyla*, "PBH-C10". **A** clubs of surface layer base of colony **B** spindles.

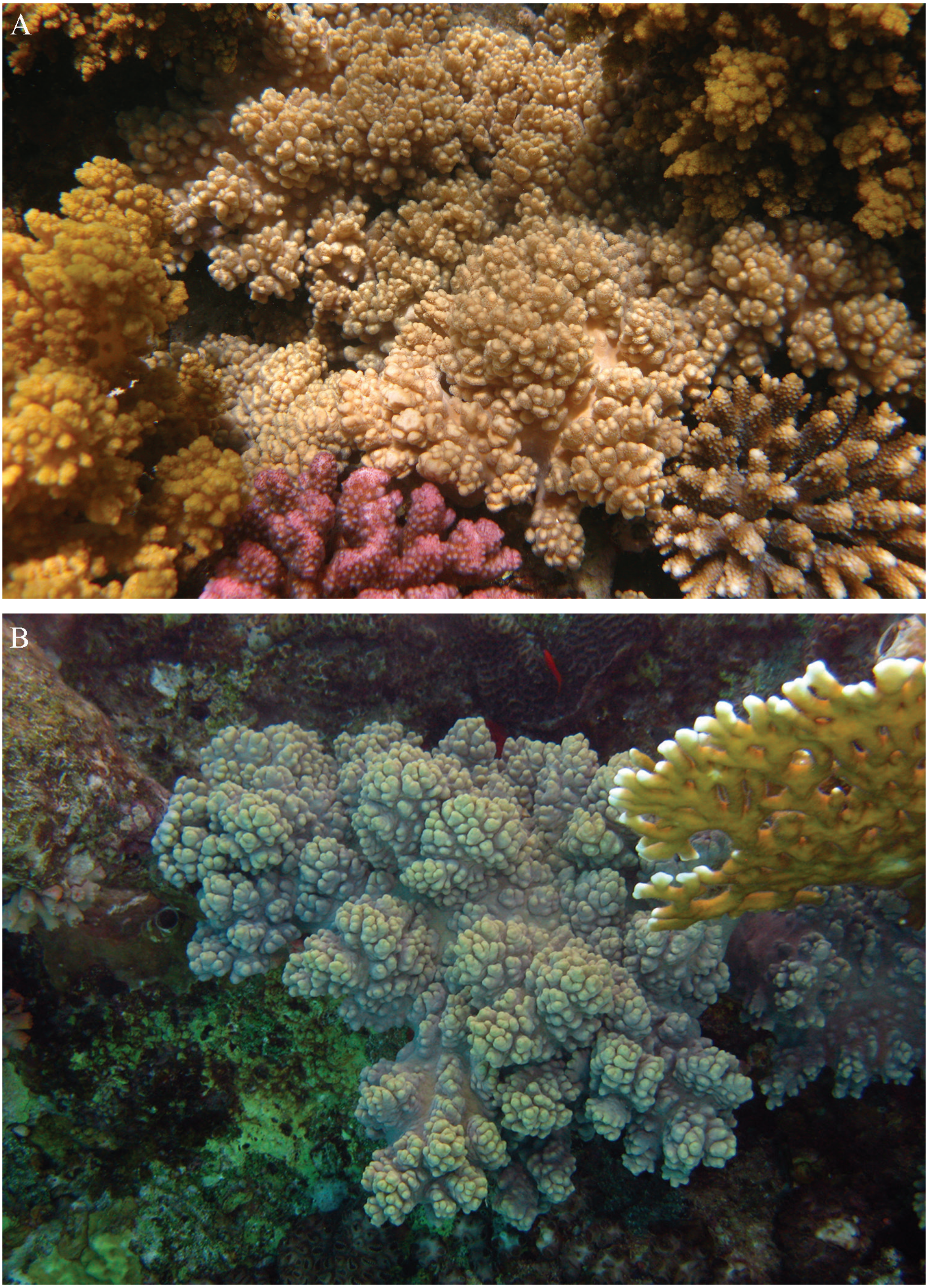

Figure 44. Live colonies *Sinularia levi* sp. n. **A** ZMTAU 36585 **B** ZMTAU 36607. Photographs by Erez Shoham.

(RNAlater, Ambion Inc.) that dissolves sclerites. Their *S. polydactyla* specimens "PBH-Tr3", and "PBH-C6" and "PBH-C10" formed a sub-clade with *S. nanolobata* Verseveldt, 1977 and *S. scabra* Tixier-Durivault, 1970 (Fig. 1). The "PBH-Tr3" specimen (Figure 34C) featured sclerites (Figures 38–40) that are quite different from *S. polydactyla* but did not match any other *Sinularia* species known at present. The club-shaped sclerites of "PBH-C10" (Figures 41, 42A, 43A) resemble those of *S. scabra*, the sister taxon in the phylogenetic tree, as does its colony shape (Figure 34D). The internal spindles (Figure 42B-F) are however quite different from those described by Verseveldt (1980). It showed much smaller spindles in the lobes (Figure 42B) and many small branched spindles in the colony base (Figure 42E) that were not reported by Verseveldt (1980). Despite these differences "PBH-C10" is presently considered to belong to *S. scabra*. Notably, "PBH-C6" did not differ much from "PBH-C10". The three dry specimens discussed above are in poor condition and not suitable for a formal taxonomic description.

Acknowledgements

For this research (Application DE-TAF-662) Y.B. received support from the SYNTHESYS Project http://www.synthesys.info/, which is financed by European Community Research Infrastructure Action under the FP7 "Capacities" Program. The study also was in part supported by The Israel Cohen Chair in Environmental Zoology to Y.B. We would like to thank Dr. Carsten Lüter, Museum für Naturkunde der Humboldt Universität, Berlin, Germany, for entrusting us with the syntypes of *S. polydactyla*. We wish to thank Alex Shlagman for curatorial skills, Michal Weis and Asaul Gonzalez for technical assistance, Erez Shoham for underwater photographs, and the Interuniversity Institute for Marine Sciences in Eilat (IUI) for facilities.

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Supplementary material 1

Maximum likelihood phylogeny

Authors: Leen P. van Ofwegen, Catherine S. McFadden, Yehuda Benayahu

Data type: Figure

Explanation note: Maximum likelihood phylogeny of *Sinularia* clade 4 based on a combined, partitioned analysis of mtMutS (735 bp) and COI + igr1 (815 bp). Numbers above branches are ML bootstrap percentages; numbers below branches are posterior probabilities from Bayesian Inference. Red: specimens identified in previous work as *S. polydactyla*; blue: specimens identified in previous work as *S. compressa.*

Supplementary material 2

GenBank accession numbers

Authors: Leen P. van Ofwegen, Catherine S. McFadden, Yehuda Benayahu

Data type: occurence

Explanation note: Specimens of *Sinularia* included in molecular phylogenetic analysis. NTM = Museum and Art Gallery of the Northern Territory; RMNH = Naturalis Biodiversity Center (Rijksmuseum, Leiden); ZMTAU = Zoological Museum, Tel Aviv University; UF = Florida Natural History Museum; USNM = Smithsonian Institution. NA = no sequence available.

ZooKeys 581: 127–140 (2016)
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RESEARCH ARTICLE

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A new species of *Bothriembryon* (Mollusca, Gastropoda, Bothriembryontidae) from south-eastern Western Australia

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Abstract

Bothriembryon sophiarum **sp. n.** is described, based on shell and anatomical morphology, from the coastal area of south-easternmost Western Australia. This is the first description of a new extant Australian bothriembryontid in 33 years. The shell of *B. sophiarum* is slender with a unique teleoconch sculpture. It is found in low coastal scrub on cliff edges and escarpments and because of its restricted distribution, qualifies as a short range endemic.

Keywords

Western Australia, Orthalicoidea, ecology, anatomy, micro-CT

Introduction

Along with the diverse and generally more northern and eastern Camaenidae, the endemic Australian genus *Bothriembryon* (Bothriembryontidae) forms a large and characteristic component of the Australian terrestrial molluscan fauna, particularly in Western Australia (Iredale 1939; Kershaw 1985; Solem 1998). Thirty five extant and seven fossil *Bothriembryon* species are currently known from Australia (Iredale 1939; Breure 1979;

Smith 1992; Richardson 1995; Smith et al. 2002; Breure and Whisson 2012) but many undescribed species have been proposed based on specimen identifications by former Western Australian Museum malacologists.

Recent taxonomic work on this group has been limited, with the last description of a new extant species being over thirty years ago (Hill et al. 1983). The majority of *Bothriembryon* species are limited to mesic south-western Western Australia with two species endemic to South Australia, one species to the lower Northern Territory and one species to south-eastern Tasmania. During the 1970's a somewhat slender shell from the Caiguna and Cocklebiddy areas was identified as a new species by Western Australian Museum malacologist Hillary Merrifield but was never named. This taxon is described herein.

Material and methods

A total of 22 lots comprising 242 specimens were examined from the malacological collection of the Western Australian Museum. Three relaxed formalin-fixed specimens were used for 3D visualisation (Walker et al. 2014) and stained in a solution of 1% iodine in 70% ethanol for four days. Due to the narrowly elongated shape of the shells the staining of the upper whorls is less strong than those of the animal extending outside the shell (Fig. 5A). Subsequently they were scanned using the Nikon Metrology HMX ST 225 micro-CT scanner at the Imaging and Analysis Centre at the Natural History Museum, London. This system is equipped with a detector panel (2000 × 2000 pixels) with a maximum resolution of 5 µm and a maximum energy of 225 kV. A tungsten reflection target was used with the following parameters: 180 kV, 180 µA, 500 ms exposure time and 3,142 projections were taken. Images acquired during the scanning process were subsequently reconstructed using CT Pro (Nikon Metrology, Tring, UK), which employs a modified version of the back-projection algorithm created by Feldkamp et al. (1984). Output files were analysed with ImageJ 2.0.0-rc-9 (2D), and Avizo 8.1 and Mimics 15.01 (3D).

Shell dimensions followed the methods figured by Breure (1974: fig. 2) and Kendrick and Wilson (1975: fig. 1) for whorl counts. Measurements were made through digital calipers to 0.1 mm for maximum shell height (H) and maximum shell diameter (D) and a Leica M80 Dissecting Microscope for number of shell whorls (W), number of protoconch whorls (P) and number of spiral lines on the penultimate whorl (SP). Finer measurements of height of aperture (HA), width of aperture (WA) and height of last whorl (LW) were taken from digital photographs using a Leica MZ16A microscope with Leica DFC500 camera. Photographs of live and preserved specimens were also taken with this equipment. Anatomical features are following the terminology of Tompa (1984), and—contrary to Breure (1978)—proximal and distal refer to organ (or parts of organ) positions relative to the direction of the gamete flow, i.e. from tip of flagellum (proximal) to genital pore (distal).

Abbreviations of depositories: AM, Australian Museum, Sydney, Australia; RMNH, Naturalis Biodiversity Center, Leiden, the Netherlands; WAM, Western Australian Museum, Perth, Australia. Data for material examined have been transcribed as per specimen labels and distributional maps were plotted using ArcGis 10.1 software.

Systematics

Superfamily Orthalicoidea Albers, 1860
Family Bothriembryontidae Iredale, 1937
Subfamily Bothriembryontinae Iredale, 1937
Genus *Bothriembryon* Pilsbry, 1894

Subgenus *Bothriembryon* Pilsbry, 1894

Type species. *Helix melo* Quoy & Gaimard, 1832 by original designation

Remarks. The use of subgenera within this genus is disputed. Breure (1978, 1979) recognized *Bothriembryon* (*Bothriembryon*) and *B.* (*Tasmanembryon*) while Kershaw (1986), after a detailed study of external and internal morphology, concluded that his evidence suggested only one generic unit. We follow the opinion of Breure (1978, 1979) supported in recent reviews (Smith 1992, Richardson 1995, Smith et al 2002) and recognise two subgenera. Support for subgenera within *Bothriembryon* will be examined in a near-comprehensive molecular systematic assessment of the genus (Kirkendale et al. in prep.).

Bothriembryon (*Bothriembryon*) *sophiarum* sp. n.

http://zoobank.org/2EE13185-B302-42DC-9E55-DAFAB0B44899
Figs 1 and 3–5, Table 1

Type material. Holotype. Western Australia, Nullabor Plain, Baxter Cliffs near Burnabbie Ruins, 32°07'30"S, 126°20'45"E, V. Kessner collector (ex J. Hemmen collection) 6 October 1989, dry, WAM S66478. **Paratypes** (from type locality) WAM S66479 (2 dry specimens) and RMNH.334653 (2 dry specimens); Western Australia, Nullabor Plain, Baxter Cliffs near Burnabbie Ruins, 32°07'30"S, 126°20'45"E, V. Kessner collector, 6 October 1989, WAM S30768 (6 dry specimens), AM C.477954 (3 dry specimens), RMNH.334654 (1 dry specimen).

Other material examined. Western Australia: Israelite Bay, W.G. Buick Collection No. 13096, Pre June 1992, WAM S7972 (2 dry specimens); Israelite Bay area, start of cliffs at E end, Point Culver area, A. Longbottom, 21 October 1983, WAM S7977 (46 dry specimens); Nuytsland Nature Reserve, Toolina Cove, A. Cummings, 31 August.2010, WAM S64829 (4 preserved specimens); Top of Toolina Cliff, J. Lowry, 07 November 1966, WAM S7978 (8 dry specimens); Nuytsland Nature Reserve,

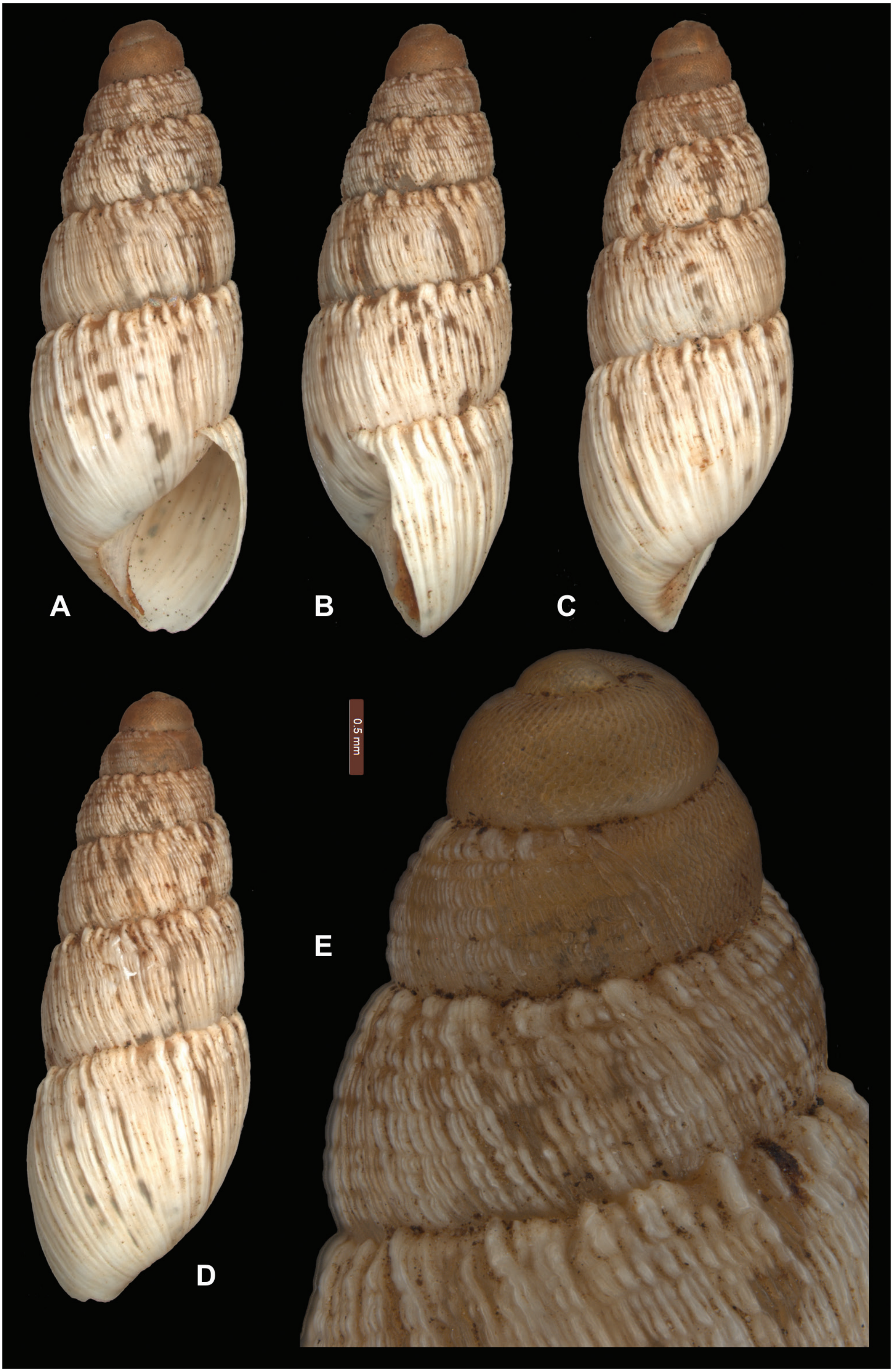

Figure 1. *Bothriembryon* (*B.*) *sophiarum* sp. n. **A–D** holotype WAM S66478 (H = 14.4 mm) **E** Protoconch and early teleoconch sculpture; scale line 0.5 mm.

Baxter Cliffs, near Baxter Memorial, A. Cummings, 30 August 2010, WAM S64824 (6 preserved specimens); South of Baxter Memorial, 50 feet from edge of cliff, P. Bridge and B. Robinson, 19 December 1966, WAM S7968 (6 dry, 24 preserved specimens); 38 km S of Caiguna, sea cliff top, K.A. Lance, 07 January 1976, WAM S7966 (25 dry specimens); S of Caiguna, between the Baxter Memorial and coast, P. Bridge and B. Robinson, 19 December 1966, WAM S7971 (8 dry specimens); S of Caiguna; near coast, B. Robinson, April 1966, WAM S8006 (2 dry specimens); 6 km SE of Baxter Memorial, top of Baxter Cliffs, A. Saar and K. Lance, 07 January 1976, WAM S7970 (10 dry, 4 preserved specimens); Twilight Cove, on cliff slope east of the cave, J. Lowry, 05 November 1966, WAM S7973 (33 dry specimens); 13 miles SE of Cocklebiddy, 7 miles N of Eyre, K. Thies, 21 May 1971, WAM S7974 (12 dry specimens); Eyre Homestead, escarpment face, W. Humphreys, March 1985, WAM S7969 (1 dry specimen); 14 miles ESE of Cocklebiddy, on face of Hampton Escarpment, A. Baynes and W. Youngsen, 04 September 1969, WAM S8031 (25 dry, 2 preserved specimens); Eyre, foot of escarpment, E. Sedgwick, August 1977, WAM S8053 (8 dry specimens); Baxter Cliffs 1.3 km E of Burnabbie Ruins, 32°07'6.54"S, 126°21'4.50"E, R. Phillips, 6 March 2015, WAM S67680 (1 wet specimen).

Diagnosis. A slender shell characterised by plicate teleoconch whorls, often with pillared sculpture formed from incised spiral lines which become less frequent on the body whorl, and a strongly crenulate suture.

Description. *Shell morphology*. Shell slender, mostly turriform, diameter 4.7–6.7 mm (mean 5.5 mm, sd 0.45), height 12.7–24.4 mm (mean 16.2 mm, sd 2.39) with 6.20–8.50 whorls (mean 7.05, sd 0.63) and a H/D ratio of 2.4–3.8 (mean 2.9, sd 0.26), rimate (Table 1, Suppl. material 1). Protoconch of 1.80–2.45 whorls (mean 2.18, sd 0.14) with very short, separate oblique wrinkles extending from suture before reticulating into a dense pattern of uniform punctated thimbles (honeycomb pattern). Teleoconch consisting of slightly convex, but regularly rounded plicate whorls, sculptured with narrow, crowded (often bifurcate) flattened or slightly raised axial ribs that are smooth and often translucent. The axial ribs become irregularly spaced on the last whorl, fading away towards the lower part of the whorl. Axial ribs usually crossed by only a few (mean 5.0, sd 1.0 on penultimate whorl) faint incised spiral lines creating a pillared sculpture that becomes less obvious on the body whorl. Suture irregularly

Table 1. Shell measurements of the type material of *Bothriembryon* (*B.*) *sophiarum* sp. n.

B.* (*B.*) *sophiarum **Registration number**	**n**	**Shell height mm (sd)**	**Shell diameter mm (sd)**	**H/D Ratio (sd)**	**No. Whorls (range)**
WAM S66478 (Holotype)	1	14.4	5.0	2.9	6.75
WAM S66479	2	12.7 (0)	4.7 (0)	2.7 (0)	6.28 (6.20–6.35)
RMNH.334653	2	13.7 (0.35)	5.0 (0)	2.7 (0.07)	6.48 (6.20–6.75)
WAM S30768	6	15.3 (1.07)	5.4 (0.30)	2.8 (0.07)	6.62 (6.25–7.00)
AM C.477954	3	15.2 (0.06)	5.4 (0.21)	2.8 (0.12)	6.57 (6.50–6.60)
RMNH.334654	1	16.2	5.7	2.8	6.85
Grand Mean	**15**	**14.7 (1.23)**	**5.2 (0.35)**	**2.8 (0.09)**	**6.56 (6.20–7.00)**

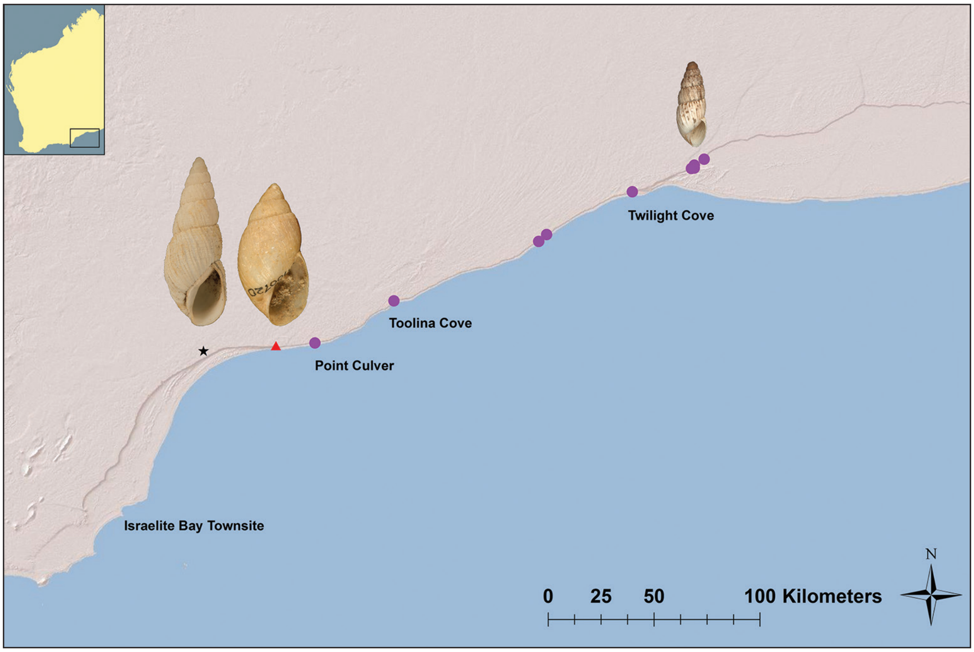

Figure 2. Distribution map of *Bothriembryon* (*B.*) *sophiarum* sp. n. (dot) including photo of holotype (WAM S66478, H = 14.4 mm) and type localities and photos of nearby coastal species *B.* (*B.*) *perditus* Iredale, 1939 (triangle, AM C100720, H = 23.2 mm) and *B.* (*B.*) *gratwicki* (Cox, 1899) (star, AM C127559, H = 29.5 mm); Inset: Western Australia highlighting enlarged area

but strongly crenulate formed from axial ribs terminating as large, rectangular nodules at the suture line, with a single nodule often forming from multiple axial ribs. Colour reddish-brown at the protoconch, the teleoconch cream with irregular blotches of reddish- to greyish-brown. Aperture relatively small, skewed elongate-ovate, lip thin, simple, basal margin slightly angular at the transition to the columellar margin, which is triangular dilated above; parietal callus thin and transparent.

Animal external morphology. Body and foot sculptured with regular honeycomb pattern. Upper body and tentacles dark brown to black with an olive to green foot base and sides, the latter relatively wide (Fig. 3A).

Genital morphology. (Based on micro-CT images, see Figs 4A–B, 5A–E) Phallus gradually becoming narrower, with the distal part of the epiphallus and the proximal part of the flagellum subcylindrical. Distal part of penis lumen star-shaped (five-legged), lined with a high epithelium and gradually changing into the epiphallus, of which the narrow lumen is also star-shaped. Near the transition to the flagellum the lumen becomes three-legged star-shaped with five very narrow side-branches; more proximally the lumen is rectangular with five very narrow side-branches. The vagina is externally swollen, internally the lumen is elongated and undivided in its distal part, becoming forked at the tail-ends near the split into the spermathecal duct and spermoviduct. The spermathecal duct is comparatively broad with a club-shaped bursa

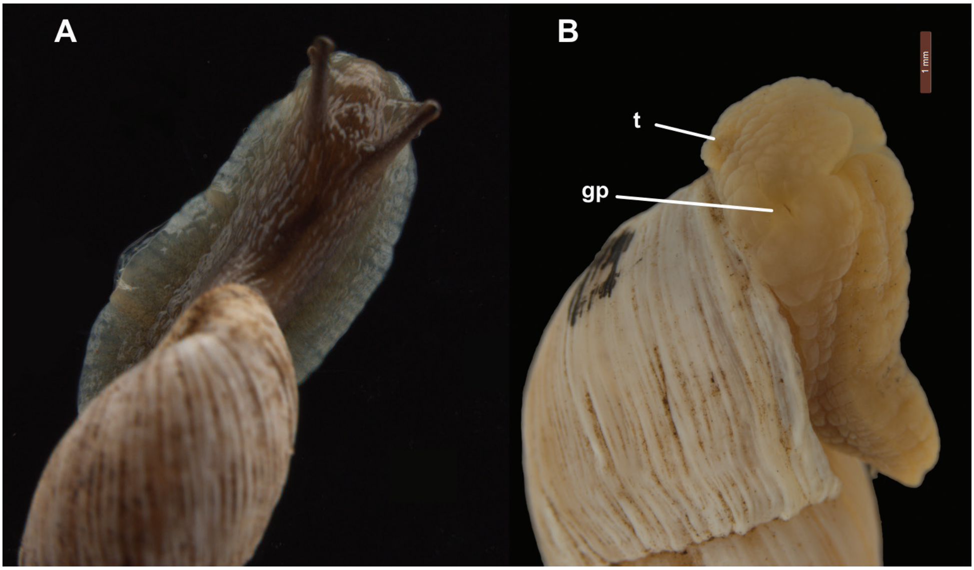

Figure 3. **A** *Bothriembryon* (*B.*) *sophiarum* sp. n., **A** living animal WAM S67680 **B** relaxed narcotized specimen showing the genital pore, WAM S7968. Scale lines 1.0 mm (B). Abbreviations: gp, genital pore; t, retracted tentacle.

copulatrix. The spermoviduct is slender (as far as traceable). In 3D (Fig. 4A) the genitalia are extruded outside the body of the animal; the female part cannot be traced towards its distal end, the phallus is heavily curled towards its distal end.

Distribution. Western Australia; along the escarpment and cliff tops of the Baxter Cliffs and Hampton Ranges from the Point Culver area eastward to the Burnabbie Ruins, a linear distance of about 180 kilometres (Fig. 2). Museum records (WAM S7972) suggest it might occur further westward to Israelite Bay (townsite) but the veracity of the location data is questionable.

Habitat. Very open, low coastal scrub on limestone cliff-edge or slope scattered (often densely) with low limestone rocks and stones. Dominant plant species were *Westringia dampieri*, *Correa backhouseana* var. *coriacea* and *Carpobrotus virens* and very occasionally *Melaleuca* and *Eucalyptus* trees. In dry conditions living specimens are commonly found in rock crevices or fissures; under stones or around tree roots, and occasionally in litter. When wet, crawling snails have been observed on soil and stones and on branches of scrub (Fig. 6).

Remarks. *Bothriembryon* (*Bothriembryon*) *sophiarum* can be distinguished from most other *Bothriembryon* species by its shell morphology, notably its slender turriform shape and a teleoconch sculpture of coarsely plicate whorls and strongly crenulate sutures. Most *Bothriembryon* species are ovate to elongate-conical in shape and have a teleoconch sculpture of faint or narrow axial growth lines. The nearby *Bothriembryon* (*B.*) *perditus* Iredale, 1939 has similar shell morphology but its shell is much broader being elongate-conical in shape and has sutures which are more finely crenulate. The

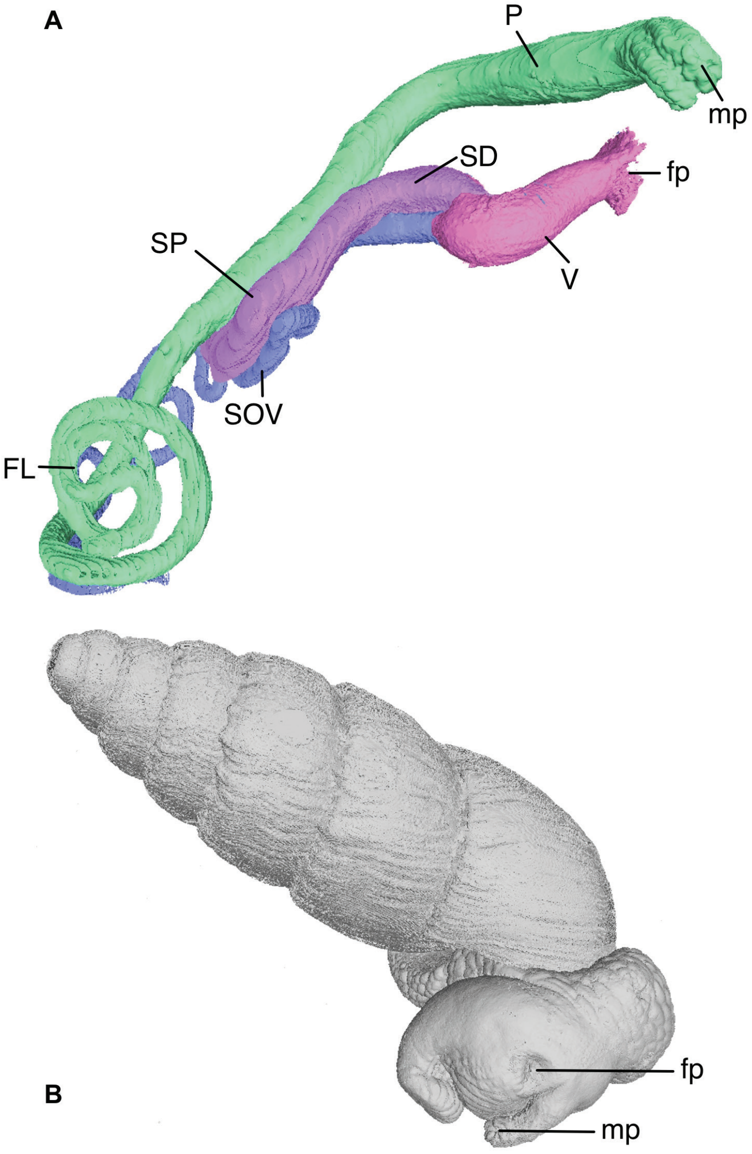

Figure 4. *Bothriembryon* (*B.*) *sophiarum* sp. n., WAM S7968, genitalia (extruded) **A** segmented in Mimics to show the different parts **B** *in situ*. Abbreviations: FL, flagellum; fp, female pore; mp, male pore; P, penis (or phallus); SD, spermathecal duct; SOV, spermoviduct; SP, spermatheca (or bursa copulatrix); V, vagina.

other nearby species *Bothriembryon* (*B.*) *gratwicki* (Cox, 1899) is similar in shape but its shell is broader and usually more elongated, with a coarse nodulose teleoconch sculpture (Fig. 2). Only one fossil species occurs nearby, *Bothriembryon kremnobates* Kendrick, 2005 which is found further east on the Roe Plain and is ovate-conical in

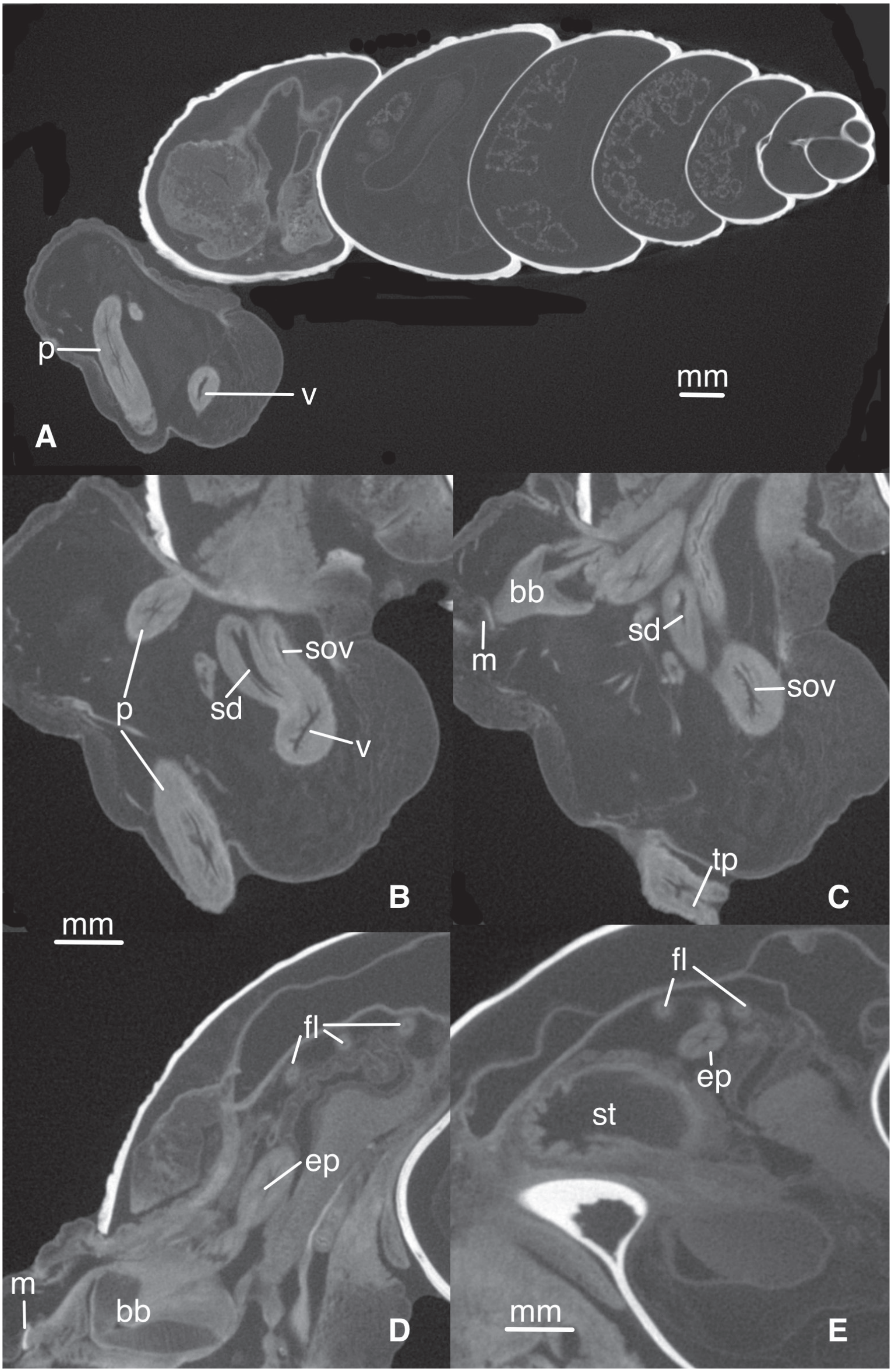

Figure 5. *Bothriembryon* (*B.*) *sophiarum* sp. n., WAM S7968, anatomy shown with micro-CT. **A** Longitudinal view of total snail **B–E** Details showing parts of genitalia at different cross-sections. Abbreviations: bb, buccal bulb; ep, epiphallus; fl, flagellum; m, mandibula; p, penis; sd, spermathecal duct; sov, spermoviduct; st, stomach; tp, tip of penis; v, vagina.

Figure 6. *Bothriembryon* (*B.*) *sophiarum* sp. n., habitat for WAM S64824 **A** Inland view **B** Detail showing host plants *Westringia dampieri*, *Carpobrotus virens* and *Correa backhouseana* var. *coriacea* among limestone (photos courtesy Andrew Cummings and Ben Schneider).

shape. Anatomically *B.* (*B.*) *sophiarum* differs only slightly from known *Bothriembryon* (*Bothriembryon*) species which have a long, narrow spermathecal duct and a short rounded bursa copulatrix. The short and broad spermathecal duct and relatively broad, elongate bursa copulatrix of *B.* (*B.*) *sophiarum* agrees more with *Bothriembryon* (*Tasmanembryon*) *tasmanicus* (Kershaw 1986, Breure 1978). However in this paper we have tentatively placed *Bothriembryon sophiarum* in the subgenus *Bothriembryon* on account of its shell morphology and its geographical proximity to other members of the same subgenus. The specimens examined have their genitalia somewhat extruded, hence the male and female genital pores seem to be separated; in other preserved, non-extruded specimens these pores are united inside the atrium (Fig. 4A). It is interesting to note that *B.* (*B.*) *sophiarum* specimens from Point Culver (WAM S7977) at the western edge of its range, are slightly taller (mean height 20.3 mm, sd 2.11) with a higher H/D ratio (mean 3.4). This collection is a large series (n = 46) and most likely represents population variation due to local environmental conditions, a common occurrence within *Bothriembryon* as suggested by Main and Carrigy (1953).

Etymology. Named in honour of Sophie Jade Whisson, first daughter of the senior author and Sophie J. Breure, spouse of the second author; noun in plural genitive case.

Discussion

Bothriembryon (*B.*) *sophiarum* appears to have a restricted range with a linear distribution of ca. 180 km and as it currently occupies an area less than 10000 km^2 qualifies as a Short Range Endemic (SRE) (Harvey 2002). Like many land snail species in arid environments (Slatyer et al. 2007) *B.* (*B.*) *sophiarum* has developed strategies to avoid desiccation, such as occupying a niche of rocky near coastal cliff-edges and escarpments, an environment that would support higher rainfall and lower temperatures as well as provide shelter and shade. Live *Bothriembryon* (*B.*) *sophiarum* collected in the hot dry months suggests they mostly aestivate within rocks fissures or loosely under rocks on the soil surface, being a free-sealer with a white calcareous epiphragm for long-term aestivation. Resting specimens that were recently active have been observed with a clear mucoid seal over the aperture. This observed aestivation pattern of *B.* (*B.*) *sophiarum* fits the definition of a rock-dweller provided by Heller (1987), where rock-dwelling land snails aestivate during summer in rock crevices, cliffs, among boulders or beneath stones. This pattern also contains those species that burrow in soil but will rest temporarily beneath stones or between crevices of boulders

B. (*B.*) *sophiarum* has a slender, high-spired shell shape which is intriguing and differs from almost all known members of *Bothriembryon* which are predominantly ovate to elongate-conical in shape. Breure and Whisson (2012) remarked that the nearby and similarly shaped *B. gratwicki* (Cox, 1899) was "aberrant within the genus *Bothriembryon*" (see Fig. 2). Heller (1987) found that there were differences in shell shape depending on what habitat a species occupied and that shell form was largely governed by the foot size requirements for each habitat and the ability to move easily within a habitat. The rocky limestone substrate in which *B.* (*B.*) *sophiarum* is found is often fractured with narrow cracks and fissures, and the slender shell shape would allow easy access into these cavities and/or under rocks. It would also aid climbing the vertical surface of the rocks. Additionally, the shell colour of *B.* (*B.*) *sophiarum* (cream with red/grey brown blotches) may provide camouflage from predators while in or on the similarly coloured limestone rocks.

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Supplementary material 1

Bothriembryon (_B._) _sophiarum_ measurements of all material examined.

Authors: Corey S. Whisson, Abraham S.H. Breure

Data type: specimens measurements

Explanation note: See main text for abbreviations and methods used.

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RESEARCH ARTICLE

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A new species of *Anomognathus* and new Canadian and provincial records of aleocharine rove beetles from Alberta, Canada (Coleoptera, Staphylinidae, Aleocharinae)

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Abstract

A new species, *Anomognathus athabascensis* Klimaszewski, Hammond & Langor, **sp. n.**, and nine new provincial records including one new country record of aleocharine beetles are presented for the province of Alberta. Diagnostics, images of habitus and genital structures, distribution, natural history information and new locality data are provided for the newly recorded species. A checklist for all recorded aleocharines from Alberta is updated.

Keywords

Coleoptera, rove beetles, Staphylinidae, Aleocharinae, new provincial records, new species, Canada, Alberta

Introduction

A survey of beetles from several localities, mainly in the Athabasca region of Alberta, was conducted in 1997 by J. Hammond and D. Langor of the Canadian Forest Service, Northern Forestry Centre. As a result, 33 species of rove beetles were identified. Of these, 29 belong to aleocharines and 5 to other families of Staphylinidae (*Anotylus* sp., *Carpelimus* sp., *Heterothops minor* Smetana, *Phloeonoma laesicollis* Mäklin and *Phloeostiba lapponica*

Zetterstedt). Among the aleocharines, we discovered one species new to science, *Anomognathus athabascensis*, the second known species of this genus from North America, as well as one new country and eight new provincial distribution records for species known in other parts of Canada (Table 1).

These findings are reported together with an updated checklist of all species from the province (Table 1). The previous lists were published by Bousquet et al. (2013), Gouix and Klimaszewski (2007), and Klimaszewski et al. (2015).

Materials and methods

All specimens in this study were dissected to examine the genital structures. Extracted genital structures were dehydrated in absolute alcohol, mounted in Canada balsam on celluloid micro-slides, and pinned with the specimens from where they originated. Images of the entire body and the genital structures were taken using an image processing system (Nikon SMZ 1500 stereoscopic microscope; Nikon Digital Camera DXM 1200F, and Adobe Photoshop software).

Morphological terminology mainly follows that used by Seevers (1978) and Klimaszewski et al. (2011). The ventral side of the median lobe of the aedeagus is considered to be the side of the bulbus containing the foramen mediale, the entrance of the ductus ejaculatorius, and the adjacent ventral side of the tubus of the median lobe with the internal sac and its structures (this part is referred to as the parameral side in some recent publications); the opposite side is referred to as the dorsal part. In the species descriptions, microsculpture refers to the surface of the upper forebody (head, pronotum and elytra).

Depository/institutional abbreviations

LFC	Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, R. Martineau Insectarium, Québec, Canada.
NoFC	Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Arthropod Museum, Edmonton, Alberta, Canada.

Abbreviations of Canadian provinces and territories

AB –	Alberta	NB –	New Brunswick	ON –	Ontario
NF –	Newfoundland	PE –	Prince Edward Island	QC –	Quebec
BC –	British Columbia	NS –	Nova Scotia	SK –	Saskatchewan
LB –	Labrador	NT –	Northwest Territories	YT –	Yukon Territory
MB –	Manitoba	NU –	Nunavut		

USA state abbreviations follow those of the US Postal Service.

Table 1. Species of Aleocharinae recorded from Alberta, and their provincial and territorial distribution within Canada. Provinces and territories in bold denote new records given in the present publication. Species marked with (†) indicate adventive species and species marked with (*) are Holarctic.

ALEOCHARINI	
Aleochara bilineata Gyllenhal†	AB, BC, MB, NB, NF, NS, ON, PE, QC, SK
Aleochara bimaculata Gravenhorst	AB, BC, LB, MB, NB, NF, NS, ON, QC, SK, NT
Aleochara castaneipennis Mannerheim	AB, BC, LB, NB, NF, NS, NT, ON, QC, YT; USA: AK
Aleochara fumata Mannerheim	AB, BC, LB, NB, NF, NS, NT, ON, QC, YT; USA: AK
Aleochara lacertina Sharp	AB, BC, MB, NB, NF, NS, ON, QC, SK
Aleochara lanuginosa Gravenhorst†	AB, BC, MB, NF, NB, NS, ON, QC, SK
Aleochara sekanai Klimaszewski	AB, LB, MB, NB, NT, ON, SK, YT; USA: AK
Aleochara speculicollis Bernhauer	AB, ON, QC
Aleochara suffusa (Casey)	AB, BC, MB, QC; USA: AK
Aleochara tahoensis Casey	AB, BC, MB, NB, NS, NT, ON, SK, YT
Aleochara verna Say	AB, BC, LB, MB, NB, NF, NS, ON, PE, QC, SK, YT; USA: AK
Aleochara villosa Mannerheim†	AB, BC, NB, QC
Tinotus morion (Gravenhorst)†	AB, BC, NB, NF, NS, ON, QC, SK; USA: CT, NV
ATHETINI	
***Atheta borealis* Klimaszewski & Langor**	**AB**, NF
Atheta dadopora C.G. Thomson*	AB, BC, LB, NB, NF, NS, ON, PE, SK, YT; USA: AK, NY, PA, RI
Atheta districta Casey	AB, BC, LB, NB, NF, NS, ON, QC
Atheta fanatica Casey	AB, BC, LB, NB, NS, QC, SK, YT; USA: AK, NV
Atheta graminicola (Gravenhorst)*	AB, BC, LB, MB, NB, NF, NT, ON, QC, SK, YT; USA: AK, OR
***Atheta hampshirensis* Bernhauer**	**AB**, BC, NB, NF, NS, ON, QC; USA: AK, CA, NC, NH, NY, OR, PA, RI, WA
Atheta klagesi Bernhauer	AB, NB; USA: ME, PA [all other previously published records of this species need to be revised]
Atheta modesta (Melsheimer)	AB, NB, NS, ON, QC; USA: CT, DC, MI, NY, PA, RI, VA, VT
Atheta platonoffi Brundin*	AB, BC, LB, NB, NF, NS, ON, SK, YT; USA: AK
***Atheta pseudoklagesi* Klimaszewski &Webster**	**AB**, NB [all published records of *A. klagesi* need to be revised because they may contain mixed series with *A. pseudoklagesi*]
Atheta pseudosubtilis Klimaszewski & Langor	AB, LB, NB, NF, QC
Atheta remulsa Casey	AB, BC, LB, NB, NF, NS, ON, QC, YT
Atheta ventricosa Bernhauer	AB, BC, LB, NB, NF, NS, ON, QC, SK, YT; USA: AK, DC, NC, NJ, NY, PA, VT
Boreophilia davidgei Klimaszewski & Godin	AB, YT
Boreophilia islandica (Kraatz)*	AB, NF, NT, NU, YT; USA: AK
Boreostiba parvipennis (Bernhauer)	AB, LB, NF, NT, QC, YT; USA: AK, NH
Dalotia coriaria (Kraatz)†	AB, BC, NB, NS, ON; USA: LA, NY
Dinaraea angustula (Gyllenhal)†	AB, LB, NB, NF, NS, ON, PE, QC, YT; USA: CA, NY
Dinaraea pacei Klimaszewski & Langor	AB, BC, LB, NB, QC, YT; USA: AK
Dinaraea worki Klimaszewski & Jacobs	AB, QC
Earota dentata (Bernhauer)	AB, BC, MB, NB, NF, NS, ON, QC, YT; USA: AK
Liogluta aloconoides Lohse	AB, LB, NF, NS, YT
Lypoglossa franclemonti Hoebeke	AB, MB, NB, NF, NS, NT, ON, QC, SK, YT; USA: NY, VT
Mocyta breviuscula (Mäklin)	AB, BC, LB, NB, NF, NS, ON, QC, YT; USA: AK, OR
Mocyta fungi (Gravenhorst)†	AB, BC, LB, NB, NF, NS, NU, ON, PE, QC, SK, YT: USA: AK

Paragoniusa myrmicae Maruyama & Klimaszewski	AB, BC, LB
Philhygra botanicarum (Muona)*	BC, LB, NB, NF, NS, ON, SK, YT
Philhygra satanas (Bernhauer)	AB; USA: CA
Philhygra sinuipennis Klimaszewski & Langor	NB, LB, NF, SK, YT
***Philhygra subpolaris* (Fenyes)**	**AB**; USA: AZ
Schistoglossa campbelli Klimaszewski	AB, BC
Schistoglossa hampshirensis Klimaszewski	AB, NB, QC; USA: NH
Seeversiella globicollis (Bernhauer)	AB, BC, NB, NF, NS, ON, QC, SK; USA: AZ, CO, ID, MN, MT, NH, SD, WI; Mexico; Guatemala
Strophogastra pencillata Fenyes	AB, MB, NB, NS, ON, QC
Trichiusa pilosa Casey	AB, BC, NS, ON; USA: ID, IN, KS, OH, RI
AUTALINI	
Autalia rivularis (Gravenhorst)†	AB, BC, LB, NB, NF, NS, ON, QC
FALAGRINI	
Falagria caesa Erichson†	AB, NB, ON, QC
Falagria dissecta Erichson	AB, BC, MB, NB, NS, ON, QC; across USA
GYMNUSINI	
Gymnusa atra Casey*	AB, BC, LB, MB, NB, NF, NS, NT, NU, ON, QC, YT; USA: AK
Gymnusa pseudovariegata Klimaszewski	AB, BC, LB, MB, NB, NF, NS, NT, ON, QC, YT; USA: AK
HOMALOTINI	
***Agaricomorpha vincenti* Klimaszewski & Webster**	**AB**, NB
***Anomognathus athabascensis* Klimaszewski, Hammond & Langor , sp. n.**	**AB**
Gyrophaena keeni Casey	AB, BC, LB, NB, NF, ON, QC, YT; USA: FL, MA, MT, NH, NY, TN, WA, WI
Gyrophaena modesta Casey	AB, NB, NF, NS, ON; USA: IL, IN, MI, MN, NH
Gyrophaena nana (Paykull)*	AB, BC, MB, NB, NF, NS, ON; USA: MA, ME, MT, WI, WY
***Gyrophaena sculptipennis* Casey**	**AB**, NB, NS, ON, QC; USA : MA, NH, NY, WI
Gyrophaena uteana Casey	AB, BC, NB, ON, QC, SK; USA: CA, CO, UT
Gyrophaena wisconsinica Seevers	AB, NB, QC; USA: WI
Homalota plana (Gyllenhal)†	AB, NB, NF, NS; USA: AK; Palaearctic: Europe, Asia
Leptusa gatineauensis Klimaszewski & Pelletier	AB, BC, NB, NF, NS, ON, QC
Neotobia albertae Ashe	AB, MB, NB, ON, QC
Phymatura blanchardi (Casey)	AB, NB, ON
Silusa californica Bernhauer	AB, BC, LB, NB, NF, NS, ON, PE, QC, YT; USA: AK, CA, MN
Silusa densa Fenyes	AB, LB, NB, NF; USA: CA
Silusa langori Klimaszewski	AB, NB
LOMECHUSINI	
Pella criddlei (Casey)	AB, MB, QC
Pella gesneri Klimaszewski	AB, MB, NB, ON
Xenodusa reflexa (Walker)	AB, BC, MB, NB, NS, QC, ON, SK
MYLLAENINI	
Myllaena arcana Casey	AB, LB, NB, NF, NS, ON, QC, SK; USA: AL, FL, IA, IL, MA, NH, NJ; Mexico

Myllaena insomnis Casey	AB, BC, LB, MB, NB, NF, NS, NT, ON, QC, SK, YT; USA: AK, ID, MA, MN, WI
OXYPODINI	
Devia prospera (Erichson)*	AB, BC, LB, MB, NB, NT, ON, SK, YT; USA: AK, CO, MI, MN, NM, OR, SD, UT, WA, WY
Gnathusa eva Fenyes	AB, BC, YT; USA: CA
Gnathusa tenuicornis Fenyes	AB, BC, NB, YT; USA: CA, OR
Gnypeta caerula (C.R. Sahlberg)*	AB, BC, LB, MB, NB, NF, NS, NT, ON, PE, QC, SK, YT; USA: AK
Gnypeta canadensis Klimaszewski	AB, ON
Gnypeta carbonaria (Mannerheim)	AB, MB, NB, NF, NT, ON, QC, SK; USA: AK
Gnypeta helenae Casey	AB, BC, ON
***Hylota cryptica* Klimaszewski & Webster**	**AB**, NB
Oxypoda canadensis Klimaszewski	AB, LB, MB, NF, NT, ON, QC, YT; USA: AK
Oxypoda convergens Casey	AB, LB, NB, NF, NS, ON, QC; USA: IA, MO, NY
Oxypoda frigida Bernhauer	AB, BC, LB, NF, NB, NS, NT, ON, QC, YT; USA: AK
Oxypoda grandipennis (Casey)	AB, BC, LB, NB, NF, NS, ON, QC, SK, YT; USA: AK, NH
Oxypoda hiemalis Casey	AB, LB, NB, NF, NS, NT, ON, QC; USA: AK
Oxypoda lacustris Casey	AB, BC, LB, MB, NB, NF, NS, NT, ON, QC, SK, YT; USA: AK
Oxypoda lucidula Casey	AB, LB, MB, NB, NF, NT, ON, QC, YT; USA: AK, IA, MO, NH, NY
Oxypoda operta Sjöberg†	AB, LB, NS, ON, QC, YT; USA: NH
Oxypoda orbicollis Casey	AB, LB, NB, NS, ON, QC, SK, YT; USA: WI
Oxypoda pseudolacustris Klimaszewski	AB, NB, NF, NS, ON, QC, SK
Tachyusa americanoides Casey	AB, BC, MB, NB, NF, NS, NT; USA : IL, MA, NH, NY
PLACUSINI	
Placusa incompleta Sjöberg†	AB, BC, NB, NF, NS, ON, QC; USA: WA
Placusa pseudosuecica Klimaszewski	AB, BC, ON, QC
Placusa tachyporoides (Waltl)†	AB, BC, NB, NS, ON, QC
Placusa tacomae Casey	AB, BC, NB, NF, NS, NT, ON, QC, YT; USA: AZ, MA, WA, WI
***Placusa vaga* Casey**	**AB**, BC, NB, NS, NT, ON, QC, YT; USA: CA
96 species, 9 new records including one new country record and one new species.	7 adventive and 4 Holarctic species

Discussion

A new study of aleocharine rove beetles from Alberta revealed one subcortical species new to science, and eight other species representing new provincial records, including one new to Canada. A checklist of aleocharine species from Alberta, including present data, indicates 96 species classified in nine tribes. Of these, 78 are considered to be native species, six Holarctic and 12 adventive (Table 1). The total number of 96 species is very low in comparison with the eastern provinces and reflects poor knowledge of this group in Alberta. The true number of aleocharines in Alberta remains unknown but it is anticipated to be comparable to or surpass that of Newfoundland and Labrador, currently estimated at 189 species (Klimaszewski et al. 2011, and unpublished data). New taxonomic inventories are badly needed to provide baseline taxonomic data by which to assess change due to anthropogenic and natural disturbances and climate change.

Taxonomic review

ATHETINI Casey

Atheta (s. str.) *borealis* Klimaszewski & Langor

Figs 1–4

Atheta (s. str.) *borealis* Klimaszewski & Langor, in Klimaszewski et al. 2011: 116.

Diagnosis. This species may be distinguished from other Nearctic *Atheta* (s. str.) by its uniformly black and glossy body, sparse pubescence of forebody, antennal articles elongate, and the shape of its genital structures (Figs 2–4). For a detailed description, see Klimaszewski et al. (2011).

Distribution.

Origin	Nearctic
Distribution	Canada: NF, **AB**
New records	New provincial record: **Canada, Alberta**: Slave Lake, 4 km SW Mitsue Lake, 55.2080°N, 114.6789°W, Hammond window-trap, H-68-3-6 (SL), 1997.08.11 (NoFC) 1 female
Reference	Klimaszewski et al. 2011

Natural history. Very little is known about the life history of this species. Adults in Newfoundland were captured in pitfall traps on a coastal limestone barren and in riparian forest (Klimaszewski et al. 2011). The Alberta specimen was captured in a window-trap attached to aspen snag in boread aspen forest harvested 29 years previously. Adults were collected in August in Alberta and Newfoundland.

Comments. This species is likely continuously distributed in northern boreal forest of Canada.

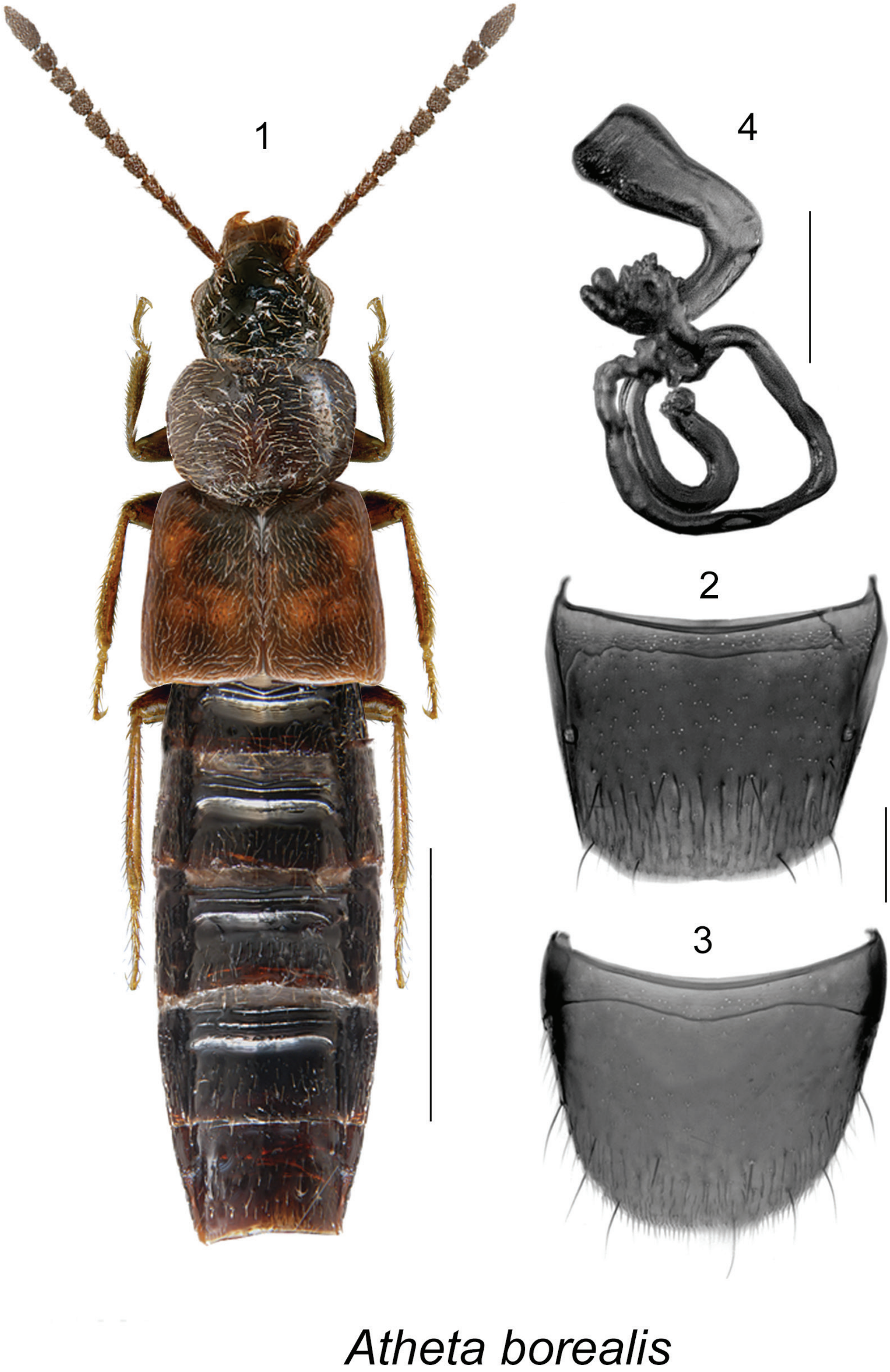
Atheta (*Dimetrota*) *hampshirensis* Bernhauer

Figs 5–12

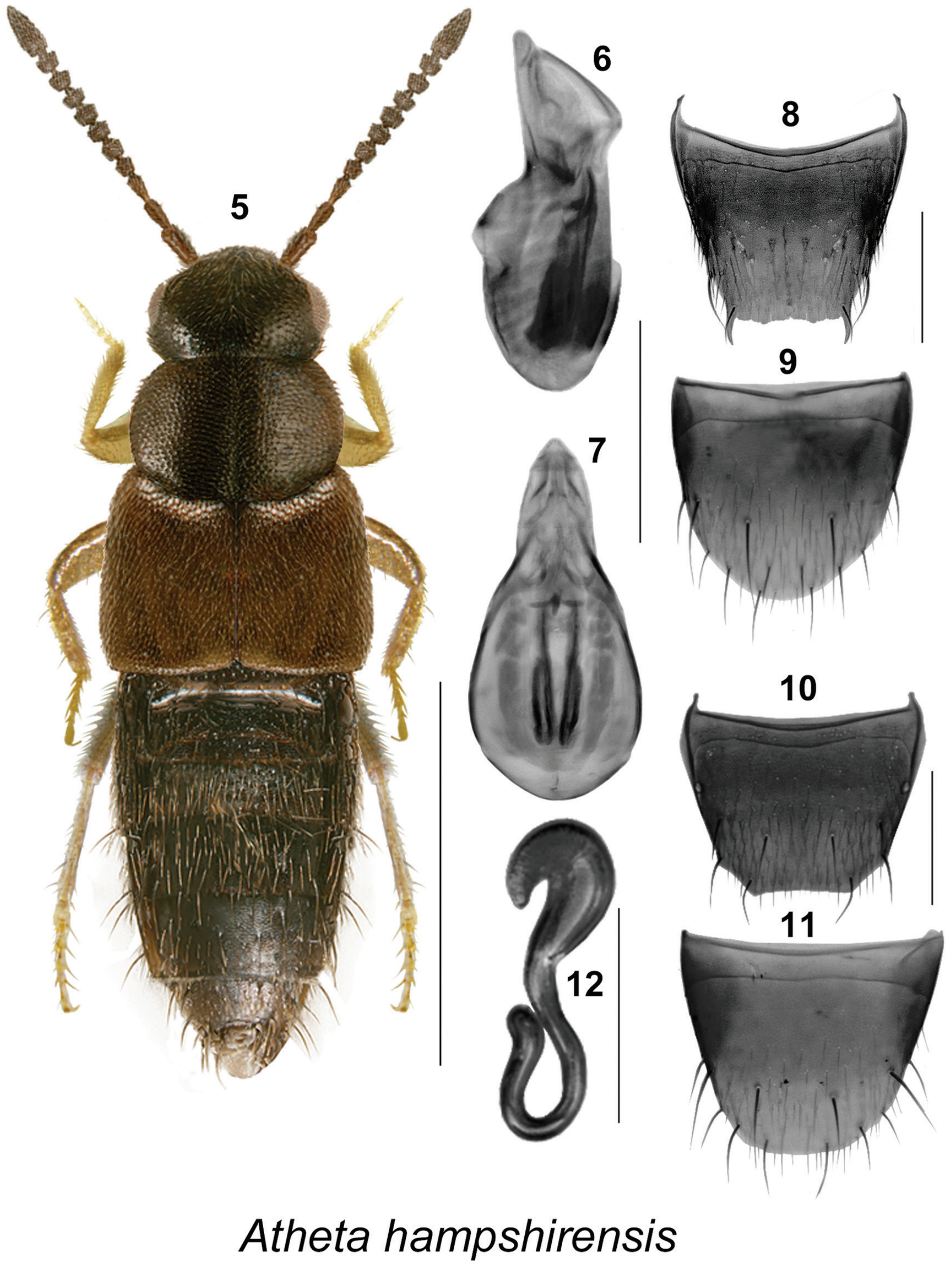
Atheta (*Dimetrota*) *hampshirensis* Bernhauer 1909: 525, Gusarov 2003: 43, Klimaszewski et al. 2011: 139.

Diagnosis. This species may be distinguished from other Nearctic *Atheta* (*Dimetrota*) by its small size (length 2.2–2.6 mm), uniformly black body, dense and asperate punctation of forebody, antennal articles slightly to strongly transverse (Fig. 5), and the shape of its genital structures (Figs 6–12). For a detailed description, see Klimaszewski et al. (2011).

This species may be confused with *A. dadopora* Thomson and *Strophogastra pencillata* Fenyes. *Strophogastra pencillata* differs from *A. hampshirensis* by having numerous



Figures 1–4. *Atheta* (s. str.) *borealis* Klimaszewski & Langor (female): **1** habitus in dorsal view **2** tergite VIII **3** sternite VIII **4** spermatheca. Scale bar of habitus = 1 mm; remaining scale bars = 0.2 mm.



Figures 5–12. *Atheta* (*Dimetrota*) *hampshirensis* Bernhauer: **5** habitus in dorsal view **6** median lobe of aedeagus in lateral view **7** median lobe of aedeagus in dorsal view **8** male tergite VIII **9** male sternite VIII **10** female tergite VIII **11** female sternite VIII **12** spermatheca. Scale bar of habitus = 1 mm; remaining scale bars = 0.2 mm.

strong ventral setae near the apical part of the abdomen and *A. dadopora* is more elongate and has different body proportions. All three species differ in the shape of male tergite VIII, median lobe of aedeagus and spermatheca.

Distribution.

Origin	Nearctic
Distribution	Canada: NF, NS, NB, QC, ON, **AB**, BC. USA: AK, CA, NC, NH, NY, OR, PA, RI, WA
New records	New provincial record: **Canada, Alberta**: Smith, 10 km N Lawrence Lake, 55.0432°N, 113.6650°W, Hammond window-trap, H-95-3-1 (LL), 1997.07.16 (NoFC) 1 female
References	Bernhauer 1909, Lohse and Smetana 1985, Klimaszewski and Winchester 2002, Gusarov 2003, Klimaszewski et al. 2005, Webster et al. 2009, Majka and Klimaszewski 2008, 2010, Klimaszewski et al. 2011

Natural history. In Newfoundland, adults were collected from June to August using carrion-baited pitfall traps and flight intercept traps in mixedwood and coniferous forest types and on coastal barrens (Klimaszewski et al. 2011). In British Columbia, adults were taken from Sitka spruce forest, June through September, with peak abundance in August/September (Klimaszewski and Winchester 2002). In New Brunswick, adults were found in red spruce forest from July to September (Klimaszewski et al. 2005), and in Nova Scotia in coniferous and deciduous forests, open habitats, on mushrooms, in compost and on carrion (Majka and Klimaszewski 2008).

The Alberta female was captured in July in a window-trap attached to the trunk of an aspen snag in a two-year-old harvested boreal aspen stand.

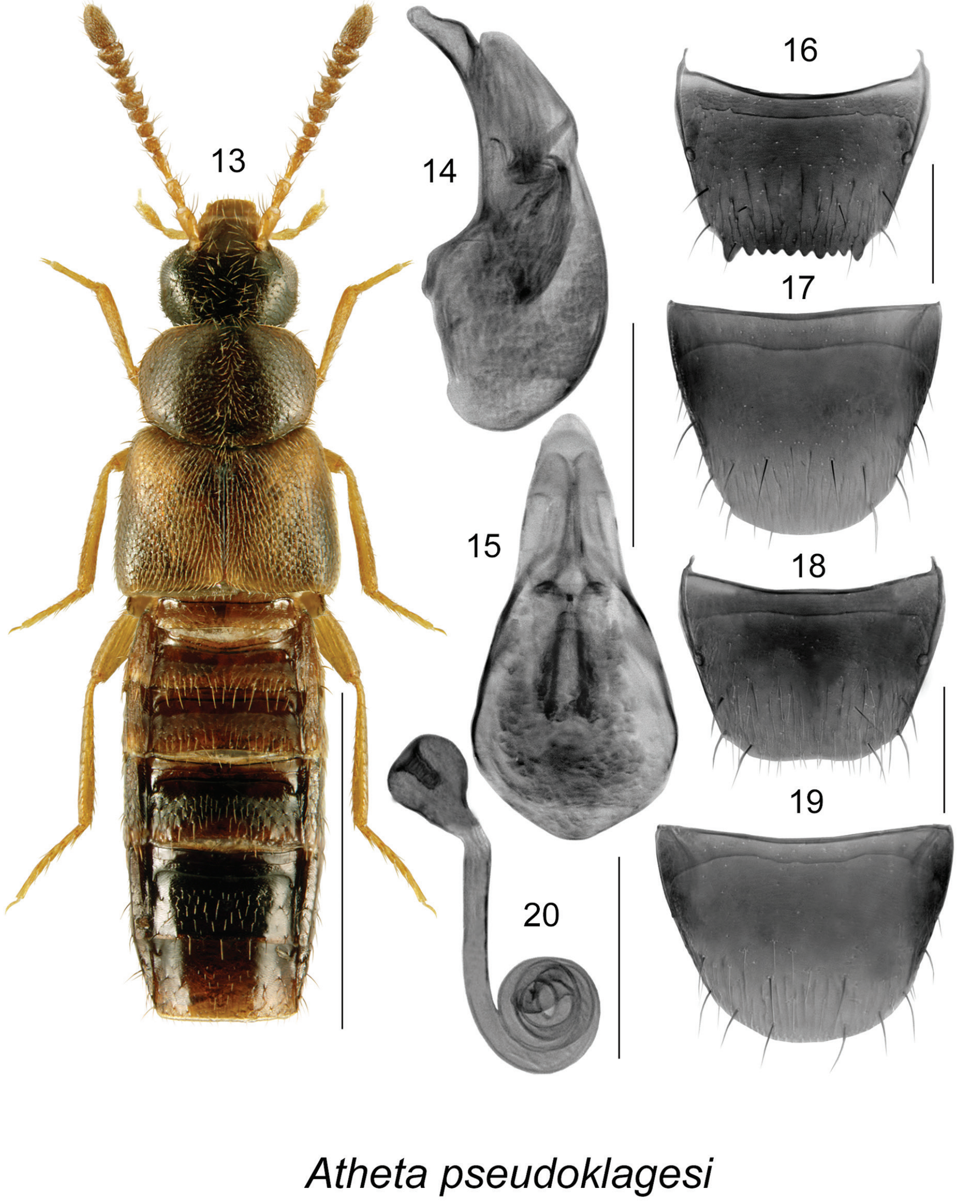
Comments. This species is broadly distributed in Canada and the USA.

***Atheta* (*Pseudota*) *pseudoklagesi* Klimaszewski & Webster**

Figs 13–20

Atheta (*Pseudota*) *pseudoklagesi* Klimaszewski & Webster (in Webster et al. 2016: 132)

Diagnosis. This is a sibling species of *A. klagesi* Bernhauer and was frequenly confused with the latter in collections. It may be distinguished from *A. klagesi* by its slightly larger size, less glossy body, less intense yellowish colouration of spots on elytra, less intense yellowish colouration of legs, bases of antennae and maxillary palps and overall less contrasting body colour (Fig. 13); median lobe of aedeagus has longer tubus and slightly different shape of apex in lateral view (Fig. 14); spermatheca is very similarly shaped in the two species (Fig. 20), and females may be difficult to identify without accompanying males.



Figures 13–20. *Atheta* (*Pseudota*) *pseudoklagesi* Klimaszewski & Webster: **13** habitus in dorsal view **14** median lobe of aedeagus in lateral view **15** median lobe of aedeagus in dorsal view **16** male tergite VIII **17** male sternite VIII **18** female tergite VIII **19** female sternite VIII **20** spermatheca. Scale bar of habitus = 1 mm; remaining scale bars = 0.2 mm.

Distribution.

Origin	Nearctic
Distribution	Canada: NB, **AB.** Currently known only from New Brunswick and Alberta, but because of confusion with *A. klagesi*. This species will undoubtedly prove to be more widespread.
New records	New provincial record: **Canada, Alberta**: Ft. McMurray, 15 km N Mariana Lake, 56.1848°N, 111.9513°W, Hammond window-trap, F-95-3-1 (FM), 1997.07.09 (NoFC) 1 female; Ft. McMurray, 15 km N Mariana Lake, 56.1848°N, 111.9513W, Hammond window-trap, F-95-3-3 (FM), 1996.08.01 (NoFC) 1 male; same data except – F-95-3-1 (FM), 1997.07.24 (NoFC) 1 male.
Reference	Webster et al. (2016)

Natural history. In New Brunswick, adults of this species were found in mature mixed forest, old-growth and old white spruce and balsam fir forests, a mature red spruce forest, and in a wet alder swamp (Webster et al. 2016). Specimens were collected from coral fungi on *Populus* log, fleshy polypore fungi at base of a dead standing *Populus*, in decaying gilled mushrooms, in gilled mushrooms, and under bark of red spruce (Webster et al. 2016). Adults were collected from May to September. The Alberta specimens were captured in July in a window-trap.

Comments. This species is very likely broadly distributed in Canada and the northern USA, but the existing records for *A. klagesi* (except for type series) need to be revised because they may contain mixed series of *A. klagesi* and *A. pseudoklagesi*.

Philhygra subpolaris (Fenyes)

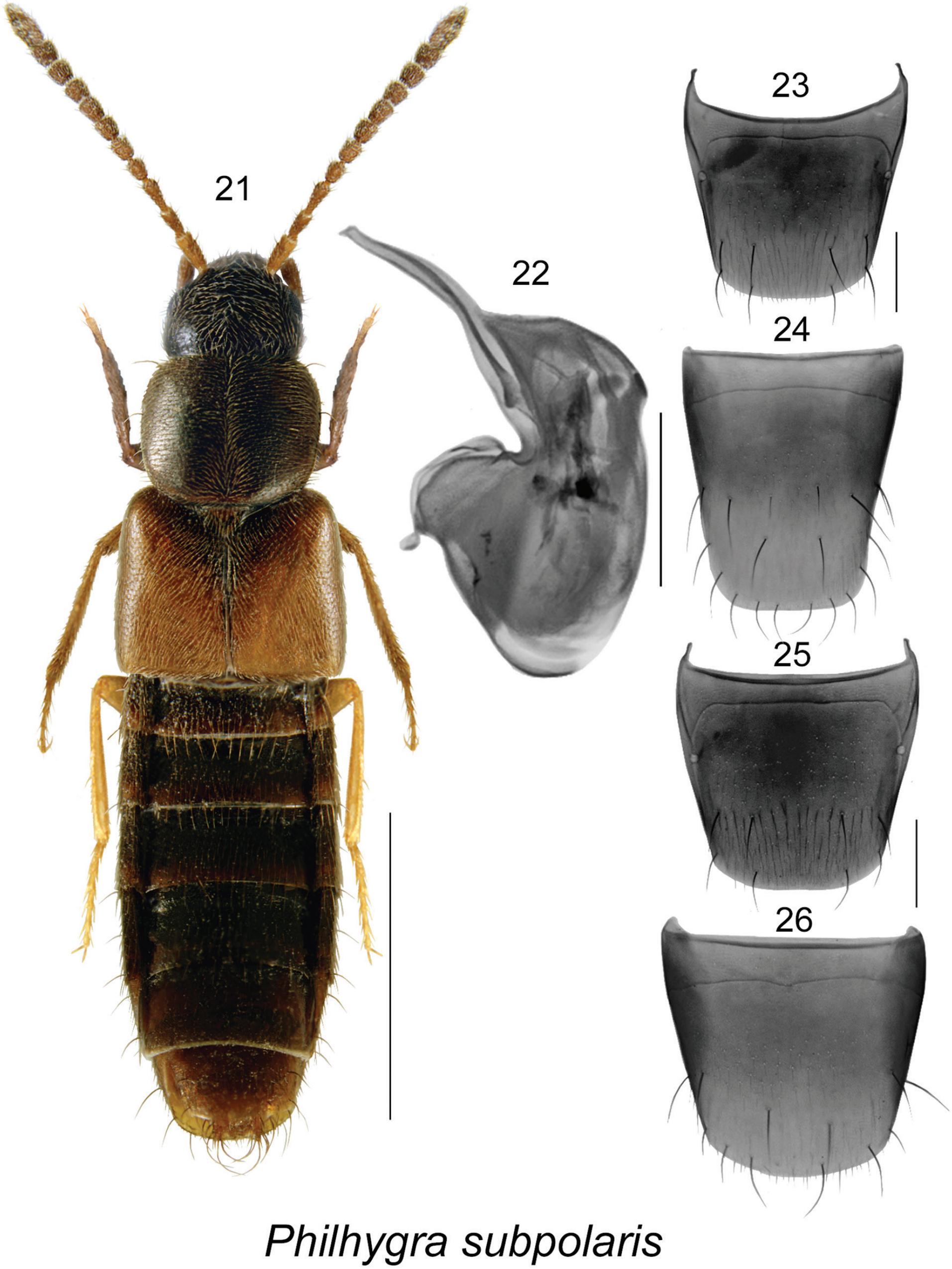
Figs 21–26

Brundinia subpolaris Fenyes 1909: 423.

Diagnosis. This species may be distinguished from other Canadian *Philhygra* by its small subparallel body (length 2.8-3.2 mm), colour dark brown with reddish or yellowish elytra and darker scutellar section, subquadrate pronotum, elytra slightly longer than pronotum, antennal articles V-X subquadrate to slightly elongate (Fig. 21), and distinctive genital structures and terminalia (Figs 22–26).

Distribution.

Origin	Nearctic
Distribution	Canada: **AB**. USA: AZ
New records	New country and provincial record: **Canada, Alberta**: Athabasca, 19 km N Calling Lake, 55.3046°N, 113.4848W, Hammond window-trap, H-95-2-2, 1997.07.24 (NoFC) 1 male; Lacombe, La17-2002 pitfall, 52.28°N, 113.44°W, 11–18.07.2003, plot#108 back (LFC) 1 male, same data except 27.06–4.07.2003, plot#306 front (LFC) 1 male; La52-2003 pitfall, 3-10.07.2003, plot#106 (LFC) 1 female; La17-2005, 7-14.07.2005, J. Broatch (LFC) 1 male, 1 sex undetermined.
Reference	Fenyes 1909



Figures 21–26. *Philhygra subpolaris* (Fenyes): **21** habitus in dorsal view **22** median lobe of aedeagus in lateral view **23** male tergite VIII **24** male sternite VIII **25** female tergite VIII **26** female sternite VIII. Scale bar of habitus = 1 mm; remaining scale bars = 0.2 mm.

Natural history. In Alberta, adults were caught in window traps attached to aspen snags in a boreal aspen stand harvested two years previously, and in pitfall traps deployed in canola fields. Adults were collected in July.

Comments. It is the first record of this species in Canada, and its broader distribution in Canada is unknown. It is probably continuously distributed in the Rocky Mountains, from Arizona in the south to Canada in the north.

HOMALOTINI Heer

Agaricomorpha vincenti Klimaszewski & Webster

Figs 27–33

Agaricomorpha vincenti Klimaszewski & Webster (2016).

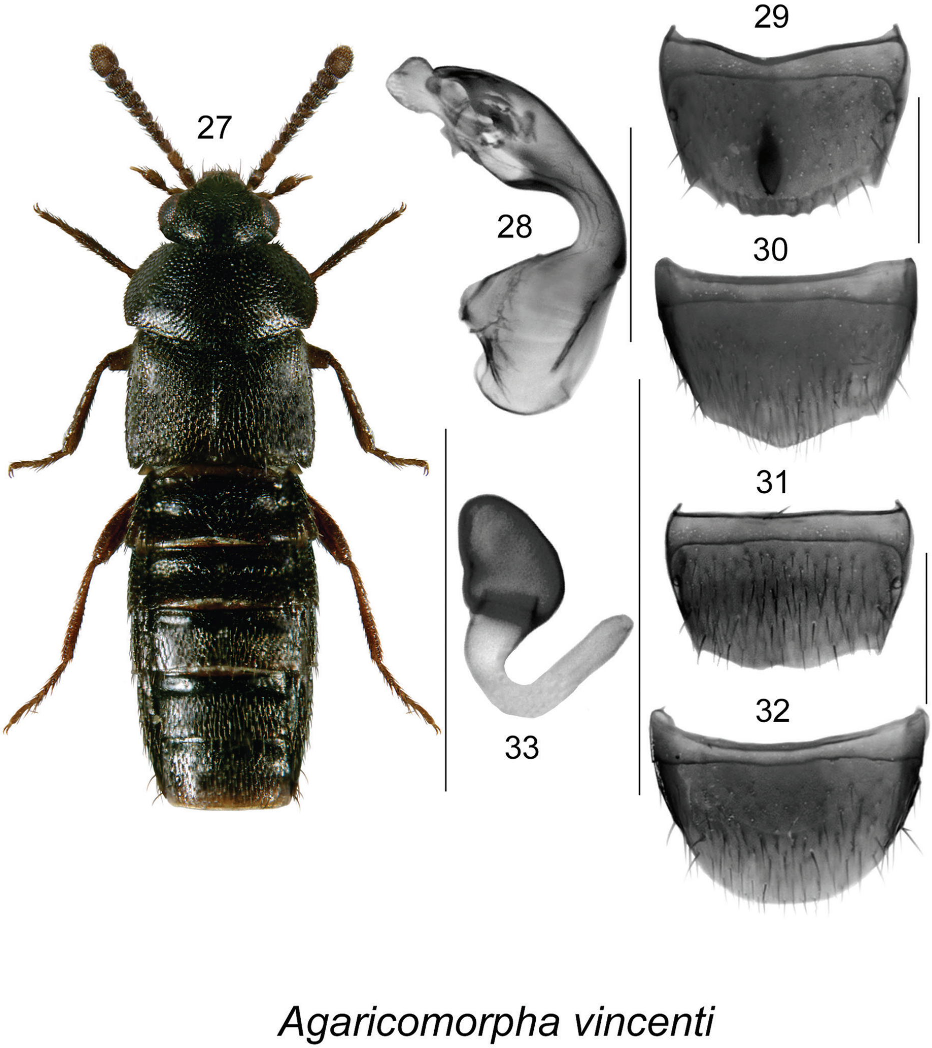
Diagnosis. This species is distinguishable by its small body that is compact and narrowly oval in outline (Fig. 27); length 1.7–1.9 mm; uniformly black; forebody with strong microsculpture, that on elytra and abdomen forming scale-like structures, punctation coarse, sparse and flatly impressed, pubescence sparse and approximately evenly distributed on forebody (Fig. 27).

Agaricomorpha vincenti may be readily distinguished from *A. websteri* Klimaszewski & Brunke by the differently shaped pronotum, which is much broader than the elytra (Fig. 27), by its uniformly black body, and by the shape of median lobe of aedeagus (Fig. 28), male tergite VIII (Fig. 29), and spermatheca (Fig. 33).

Distribution.

Origin	Nearctic
Distribution	Canada: NB, **AB**
New records	New provincial record: **Canada, Alberta**: Athabasca, 19 km N Calling Lake, 553046°N, 113.4848°W, Hammond window-trap, H-95-2-1, 1996.08.29, H-95-2-4, 1996.2.4, H-95-2-3, 1997.05.28 (NoFC) 1 male, 2 females; Smith, 10 km N Lawrence Lake, 55.0432°N, 113.6650°W, Hammond window-trap, H-95-3-1, 1997.08.11, H-95-3-6, 1996.09.24 (NoFC) 2 females.
Reference	Webster et al. (2016)

Natural history. In New Brunswick, specimens of *A. vincenti* were captured in Lindgren funnel traps in a rich Appalachian hardwood forest, a *Populus tremuloides* stand with a few conifers, an old-growth northern hardwood forest, and a hardwood forest on an island in a river. In Alberta, adults were captured in window traps attached to aspen snags in a boreal aspen stand harvested two years previously. Adults were



Figures 27–33. *Agaricomorpha vincenti* Klimaszewski & Webster: **27** habitus in dorsal view **28** median lobe of aedeagus in lateral view **29** male tergite VIII **30** male sternite VIII **31** female tergite VIII **32** female sternite VIII **33** spermatheca. Scale bar of habitus = 1 mm; remaining scale bars = 0.2 mm.

collected during May, June, and July in New Brunswick, and in May, August and September in Alberta.

Comments. This species is probably continuously distributed from New Brunswick to Alberta and likely extends further to Alaska.

Anomognathus athabascensis **Klimaszewski, Hammond & Langor, sp. n.**

http://zoobank.org/F7A228CE-1A0B-463F-A85E-79D846E8B3F9
Figs 34–40

Holotype (male). **Canada, Alberta**, Athabasca, 19 km N Calling Lake, 55.3046°N, 113.4848°W, Hammond window-trap, H-95-2-6 (CL), 1997.06.23 (NoFC). **Paratypes**. **Canada, Alberta**, Athabasca, 19 km N Calling Lake, 55.3046°N, 113.4848°W, Hammond window-trap, H-95-2-3 (CL), 1997.06.23 (LFC, NoFC) 1 female; **Canada, Alberta**, Athabasca, 19 km N Calling Lake, 55.3046°N, 113.4848°W, Hammond window-trap, H-95-2-3 (CL), 1997.07.09 (NoFC) 1 female.

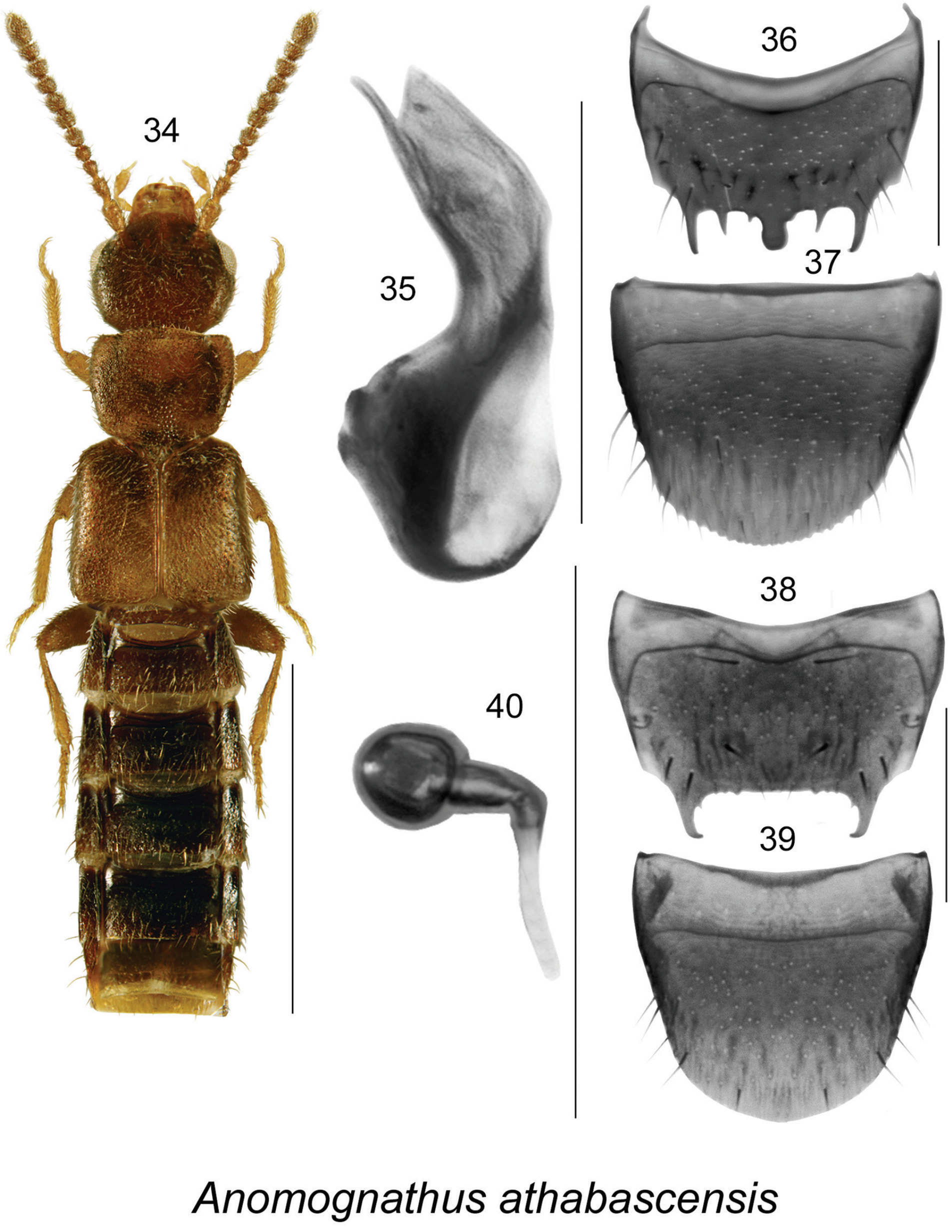
Etymology. *Athabascensis* is a Latin adjective derived from the name of the Athabasca region in Alberta, where the type series was discovered.

Diagnosis. Body length 2.5–2.7 mm; narrow and flat (Fig. 34); more or less uniformly dark brown or reddish-brown with darker head and abdomen, with legs reddish-brown, moderately densely punctate and pubescent, pubescence short and adhering to the body, integument with dense meshed microsculpture, denser on forebody, sculpticells hexagonal, and punctation asperate on forebody; head large, rounded posteriorly and with postocular area strongly converging basally (Fig. 34), slightly wider and longer than pronotum, with small eyes shorter than postocular area; antennae with articles I-III elongate and IV-X subquadrate to slightly transverse (Fig. 34); pronotum about trapezoidal in shape, narrowest at base, widening apically to about apical third and then narrowed apically, slightly transverse, much narrower at base than elytra (Fig. 34); elytra flattened, longer than pronotum, with strong angular shoulders (Fig. 34); abdomen narrow and subparallel, paratergites well developed (Fig. 34). MALE. Median lobe of aedeagus with tubus strongly produced ventrally in lateral view (Fig. 35); internal sac without distinct sclerites (Fig. 35); tergite VIII truncate apically with three pairs of dorsal teeth and narrow median lobe (Fig. 36); sternite VIII wide, broadly rounded apically (Fig. 37). FEMALE. Tergite VIII truncate apically, with two large and hooked apically lateral teeth and some crenulation on apical margin (Fig. 38); sternite VIII rounded apically and with broad space between base of the disc and antecostal suture (Fig. 39); spermatheca with small spherical capsule and narrow and short stem (Fig. 40).

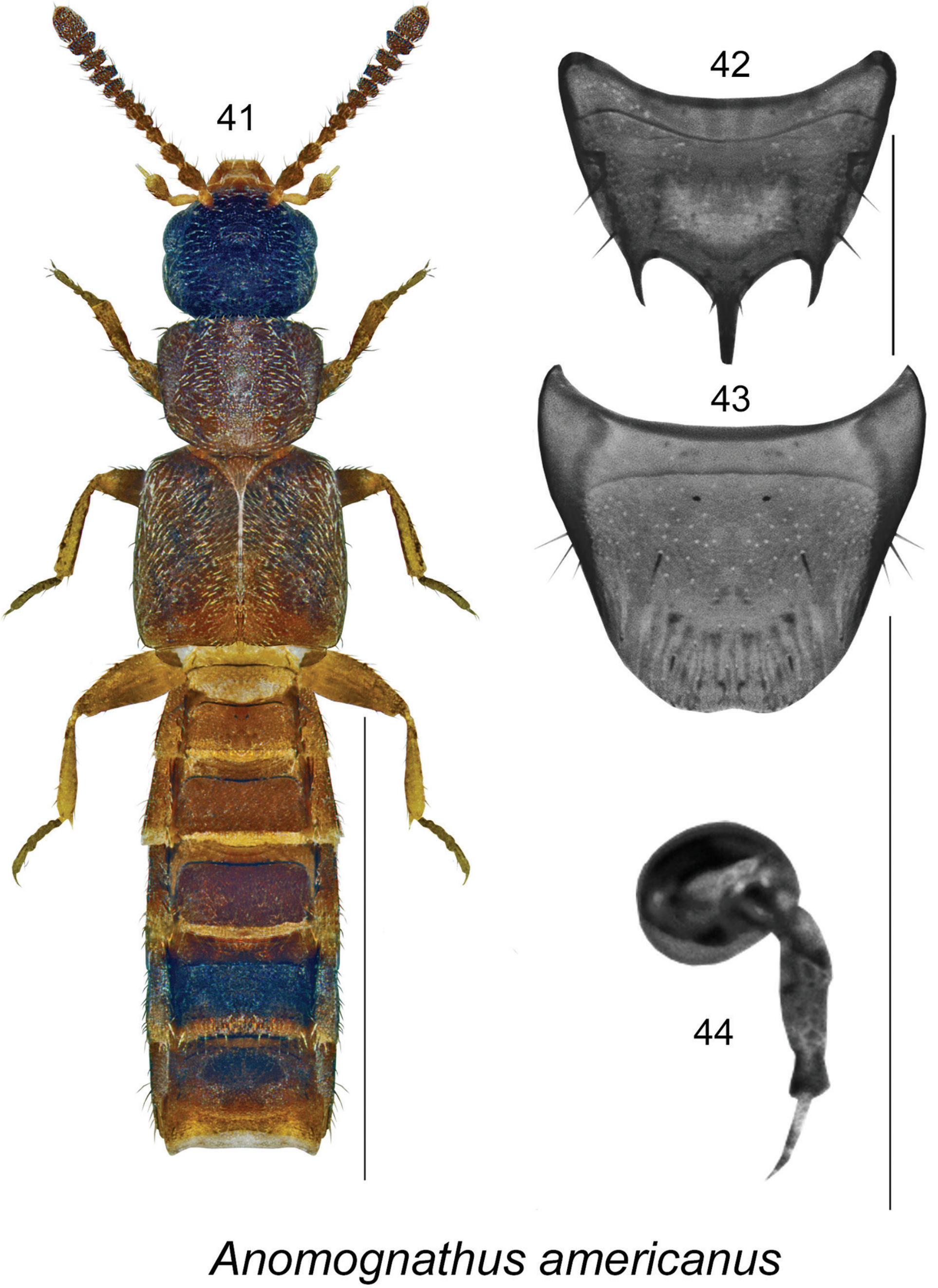
This species is readily distinguishable from *A. americanus* Casey, the only other representative of this genus in North America (Figs 41–44), by the different body proportions (Fig. 34), head large, longer and wider than pronotum (Fig. 34), and differently shaped tergite VIII of female (male of *A. americanus* is unknown), with two large and hooked apically lateral teeth (Fig. 38), while in *A. americanus* tergite VIII has two lateral teeth and one long median spine (Fig. 42).

Distribution. Known only from Alberta, Canada.

Natural history. This species was captured in June and July in Alberta. This is a subcortical species whose life history remains unknown. It is most likely associated with galleries of wood boring insects.



Figures 34–40. *Anomognathus athabascensis* Klimaszewski, Hammond & Langor: **34** habitus in dorsal view **35** median lobe of aedeagus in lateral view **36** male tergite VIII **37** male sternite VIII **38** female tergite VIII **39** female sternite VIII **40** spermatheca. Scale bar of habitus = 1 mm; remaining scale bars = 0.2 mm.



Figures 41–44. *Anomognathus americanus* (Casey): **41** habitus in dorsal view **42** female tergite VIII **43** female sternite VIII **44** spermatheca. Scale bar of habitus = 1 mm; remaining scale bars = 0.2 mm.

Gyrophaena sculptipennis Casey

Figs 45–51

Gyrophaena sculptipennis Casey 1906: 298; Seevers 1951: 689.

Diagnosis. This species is easily distinguishable from other *Gyrophaena* by body shape and colouration (Fig. 45), and the shape of the male and female genital structures (Figs 46-51). For a detailed description, see Seevers (1951).

Distribution.

Origin	Nearctic
Distribution	Canada: NB, NS, QC, ON, **AB**. USA: MA, NH, NY, WI
New records	New provincial record: **Canada, Alberta**: Ft. McMurray, 35 km N Mariana Lake, 56.2821°N, 111.8337°W, Hammond window-trap, F-82-3-5 (FM), 1996.08.29 (NoFC) 1 male.
References	Casey 1906, Seevers 1951, Bousquet et al. 2013

Natural history. Very little is known about the life history of this species. The Alberta specimen was captured in a window trap attached to aspen snag in a forest that burned 15 years previously. Adults were collected in Alberta in August and elsewhere in June and August (Seevers 1951).

Comments. This species is probably continuously distributed from Nova Scotia and New Brunswick to the eastern Rocky Mountains.

PLACUSINI Mulsant & Rey

Placusa vaga Casey

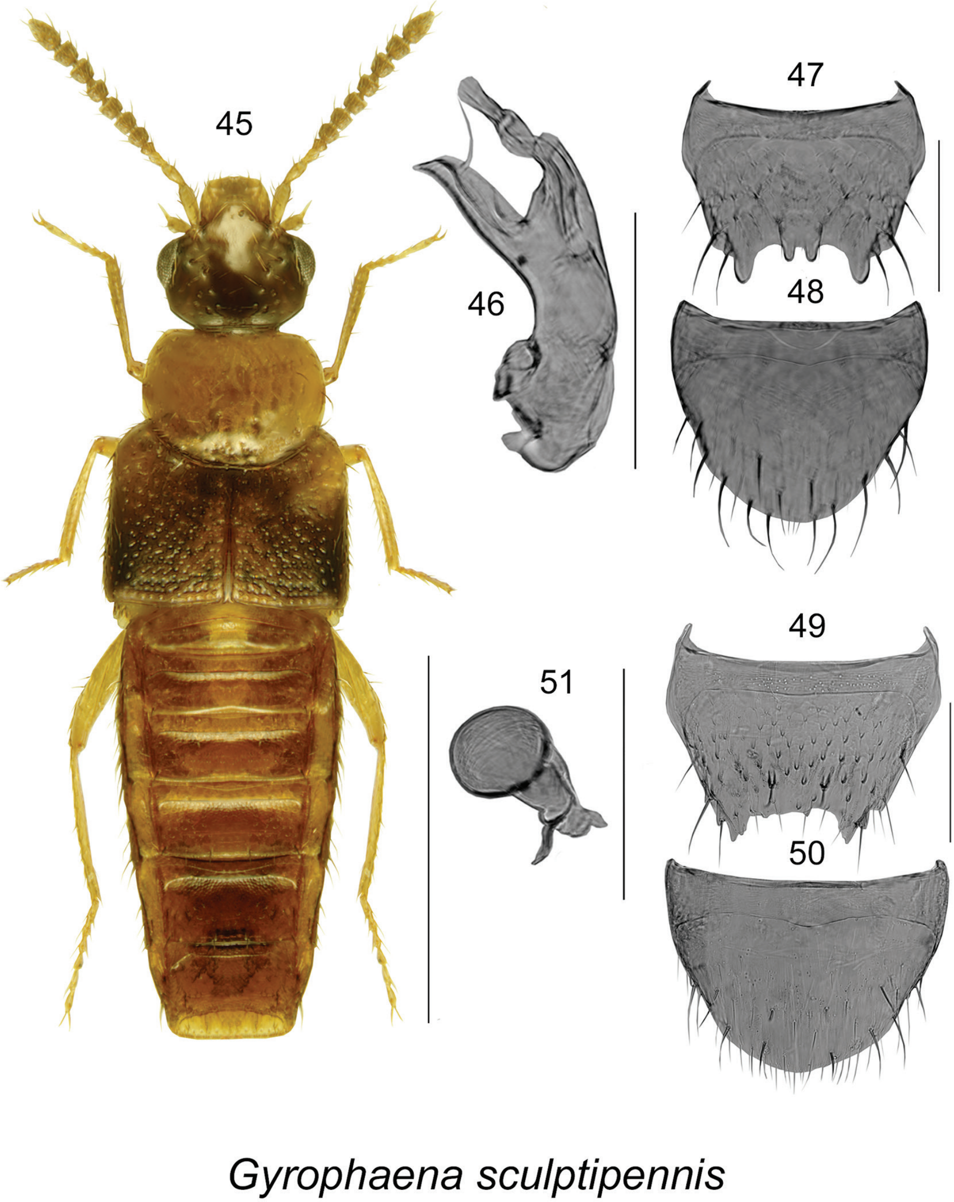
Figs 52–59

Placusa vaga Casey 1911: 189, Klimaszewski et al. 2001: 27; Bousquet et al. 2013: 123.

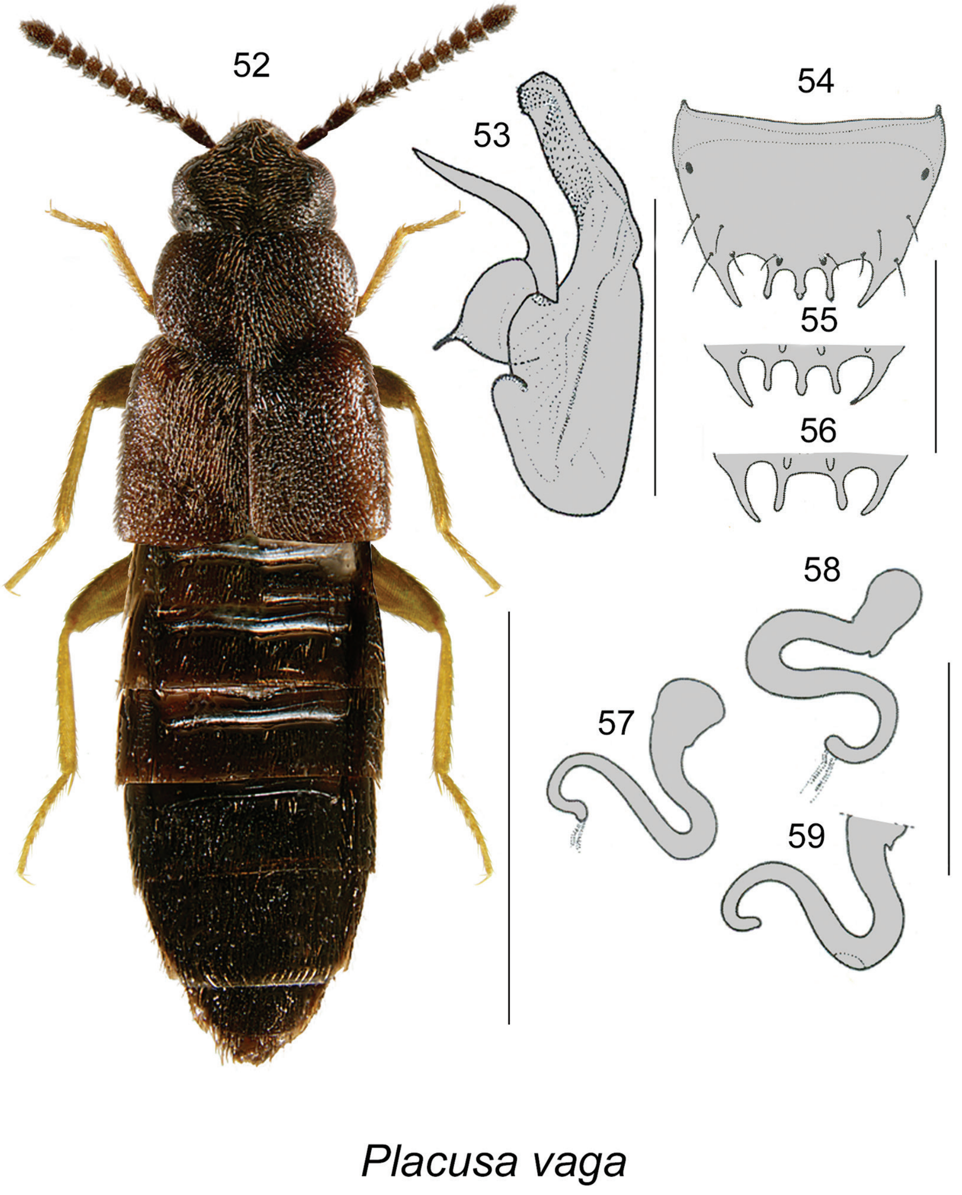
Diagnosis. This species is easily distinguishable from other Nearctic *Placusa* by its uniformly black to rarely dark brown body, long elytra (Fig. 52), and the shape of the genital structures (Figs 53–59). For a detailed description, see Klimaszewski et al. (2001).

Distribution.

Origin	Nearctic
Distribution	Canada: NS, NB, QC, ON, **AB**, YT, NT, BC. USA: CA
New records	New provincial record: **Canada, Alberta**: Ft. McMurray, 15 km N Mariana Lake, 56.1848°N, 111.9513°W, Hammond window-trap F-68-1-6 (SL), H-95-3-1 (LL) D.W. Langor (NoFC) 1 male, 2 females
References	Casey 1911, Klimaszewski et al. 2011, Bousquet et al. 2013



Figures 45–51. *Gyrophaena sculptipennis* Casey: **45** habitus in dorsal view **46** median lobe of aedeagus in lateral view **47** male tergite VIII **48** male sternite VIII **49** female tergite VIII **50** female sternite VIII **51** spermatheca. Scale bar of habitus = 1 mm; remaining scale bars = 0.2 mm.



Figures 52–59. *Placusa vaga* Casey: **52** habitus in dorsal view **53** median lobe of aedeagus in lateral view **54–56** male tergite VIII **57–59** spermatheca. Scale bar of habitus = 1 mm; remaining scale bars = 0.2 mm.

Natural history. Very little is known about the life history of this species. Adults in Quebec were captured in coniferous forests and mainly trapped in Lingren funnel traps (Klimaszewski et al. 2001). The Alberta specimens were captured in a window-traps attached to aspen snag in boreal aspen stands burned two years previously. Adults were collected in Alberta in August and elsewhere in June and August (Seevers 1951).

Comments. This species is likely continuously distributed from Nova Scotia to British Columbia in northern boreal forest.

OXYPODINI C.G. Thomson

Hylota cryptica Klimaszewski & Webster

Figs 60–66

Hylota cryptica Klimaszewski & Webster, in Webster et al. (2016)

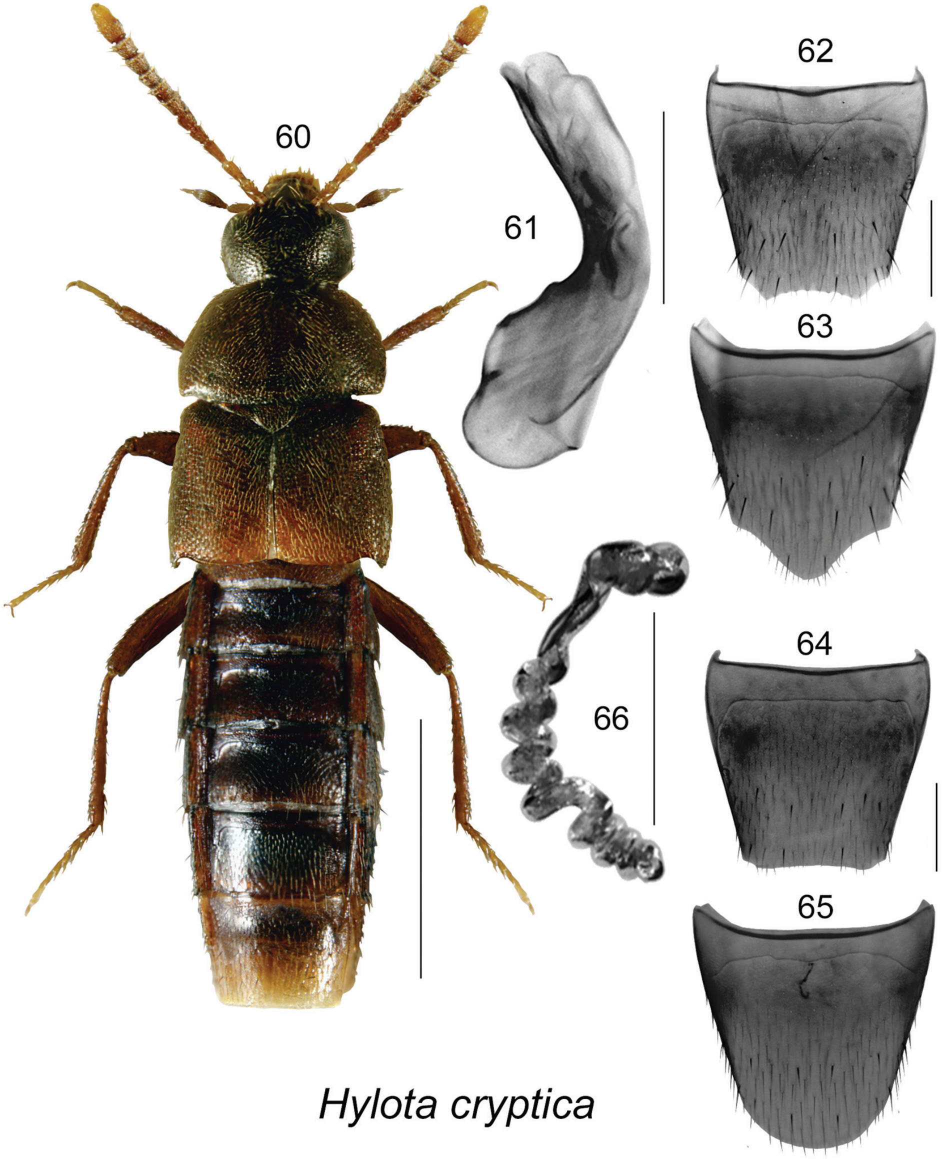
Diagnosis. This species is distinguishable by length 3.2–3.4 mm, body narrowly oval, dark brown except for paler antennae, tarsi, and posterior part of elytra near suture (Fig. 60); forebody densely punctate and pubescent; head about one-third of maximum pronotal width; antennal articles IV-X from slightly elongate to subquadrate (Fig. 60); pronotum broadest at basal third and strongly narrowed apically, at base as wide as elytra (Fig. 60). *Hylota cryptica* may be separated from *H. ochracea* by its larger, broader and darker body, pronotum at least as wide as elytra at base (slightly narrower in *H. ochracea*), elongate antennal articles V-X (transverse in *H. ochracea*), less bent tubus of median lobe laterally (Fig. 61), apical margin of male tergite VIII with minute crenulation (Fig. 62) (with teeth in *H. ochracea*), and spermatheca with fewer coils (Fig. 66) (8–9 in *H. cryptica* and about 15–17 in *H. ochracea*).

Distribution.

Origin	Nearctic
Distribution	Canada: NB, **AB**
New records	New provincial record: **Canada, Alberta**: Ft. McMurray, 15 km N Mariana Lake, 56.1848°N, 111.9513W, Hammond window-trap, F-82-3-4, 1997.06.23, F-82-3-2, 1997.06.10 (NoFC) 2 females; Slave Lake, 11 km N town Slave Lake, 55.4045°N, 114.6431°W, Hammond window-trap, H-82-3-3, 1997.06.18 (NoFC) 1 female.
References	Klimaszewski et al. 2006, Webster et al. (2016)

Natural history. All New Brunswick specimens of *H. cryptica* were captured in Lindgren funnel traps or flight intercept traps in various forest types (Webster et al. 2016). These included a red oak forest, an old mixed forest with red oak, mixed forests, a hardwood forest on an island in a river, an old-growth northern hardwood forest, an old-growth white spruce and balsam fir forest, an old jack pine forest, an old red pine forest, and an old white pine stand (Webster et al. 2016). The Alberta specimens were captured in June in window traps attached to aspen snag in boreal aspen stands harvested and burned 15 years previously.

Comments. This species is most likely continuously distributed from New Brunswick to Alberta.



Figures 60–66. *Hylota cryptica* Klimaszewski & Webster: **60** habitus in dorsal view **61** median lobe of aedeagus in lateral view **62** male tergite VIII **63** male sternite VIII **64** female tergite VIII **65** female sternite VIII **66** spermatheca. Scale bar of habitus = 1 mm; remaining scale bars = 0.2 mm.

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