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New shallow water species of Caribbean *Ircinia* Nardo, 1833 (Porifera: Irciniidae)

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Abstract

Seven *Ircinia* morphospecies were collected from three sites in the Caribbean (Bocas del Toro, Panama; the Mesoamerican Barrier Reef, Belize; and the Florida Keys, United States of America). Previous research used an integrative taxonomic framework (genome-wide SNP sampling and microbiome profiling) to delimit species boundaries among these *Ircinia*. Here, we present morphological descriptions for these species, six of which are new to science (*Ircinia lowi* **sp. nov.**, *Ircinia bocatorensis* **sp. nov.**, *Ircinia radix* **sp. nov.**, *Ircinia laeviconulosa* **sp. nov.**, *Ircinia vansoesti* **sp. nov.**, *Ircinia ruetzleri* **sp. nov.**) in addition to one species *conferre* (*Ircinia* cf. *reteplana* Topsent, 1923).

Key words: Integrative taxonomy, Porifera, benthos, sponges

Introduction

The genus *Ircinia* Nardo, 1833 is currently comprised of 88 recognized species, 14 of which are documented to occur off the Atlantic coast of the Americas (van Soest *et al.* 2021). Three of these species are common in coral reefs and seagrass beds in the Caribbean: *I. campana* Lamarck, 1814; *I. strobilina* Lamarck, 1816; and *I. felix* Duchassaing & Michelotti, 1864 (Rützler *et al.* 2000, Diaz 2005). Caribbean *Ircinia* are often among the most abundant species in sponge communities (Rützler *et al*. 2000, Diaz 2005, Wulff 2013) and possess microbial communities that are involved in processes at the base of the food web such as photosynthesis (Wilkinson & Cheshire 1990, Erwin & Thacker 2007) and biogeochemical cycling (Archer *et al.* 2017). Alongside these three species can be found several *Ircinia* growth forms that are recognizable in the field based on the overall shape of their bodies, the height and spacing of their conules, and the position and size of their oscula (van Soest 1978, Wulff 1994, Rützler *et al.* 2000, Diaz 2005, Erwin & Thacker 2007, Wulff 2013). The growth forms are also regarded as being ecologically distinct in that they contain different tissue densities of chlorophyll *a* (Erwin & Thacker 2007), can exhibit habitat preference, and have distinct microbiome compositions (Kelly *et al.* 2021). Despite the ecological importance of *Ircinia* in the Caribbean and the longstanding recognition of these growth forms as putative species, a new species of Caribbean *Ircinia* has not been described in over forty years, with the last being *I. hummelincki* van Soest, 1978. Given their importance to ecological processes and the biodiversity that they impart to Caribbean benthos, the clarification of their taxonomy is of utmost importance.

The study of *Ircinia* taxonomy has been historically problematic as the genus, like other members of the order Dictyoceratida Minchin, 1900, does not produce endogenous spicules and presents few anatomical features that can be used to infer relatedness and taxonomic boundaries among species (Erpenbeck *et al.* 2020). *Ircinia* species also display a considerable degree of intraspecific morphological plasticity that confounds the identification of features that are representative of a given species (Cook & Bergquist 1999). Single-locus genetic barcoding has likewise seen limited success, as the loci that are typically used to provide species- and population-level phylogenetic resolution in metazoans, which include the *cytochrome oxidase c subunit 1* (CO1) and the internal transcribed

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spacer set (ITS), can be either incompletely sorted or largely invariant among nominal species of *Ircinia* (Kelly & Thacker 2020 *in review*). The pitfalls that arise from the use of morphological data alone or by restricting genetic data to a single locus or a few loci, which is also a practice best avoided due to the high probability of gene tree and species tree discordance (Degnan & Rosenberg 2006), necessitate the implementation of integrative taxonomic research frameworks within *Ircinia* that include genome-wide evidence of species boundaries. Recently, genetic species boundaries were delimited among several of these growth forms using Bayesian species delimitation with genome-wide SNP data (BFD*) (Leaché *et al*. 2014, Kelly *et al.* 2021). On the basis that these growth forms are genetically and morphologically distinct and are likely ecologically divergent as evidenced by their possession of unique microbiomes (Kelly *et al.* 2021), we designate the morphospecies as new species to science and provide taxonomic descriptions.

Methods

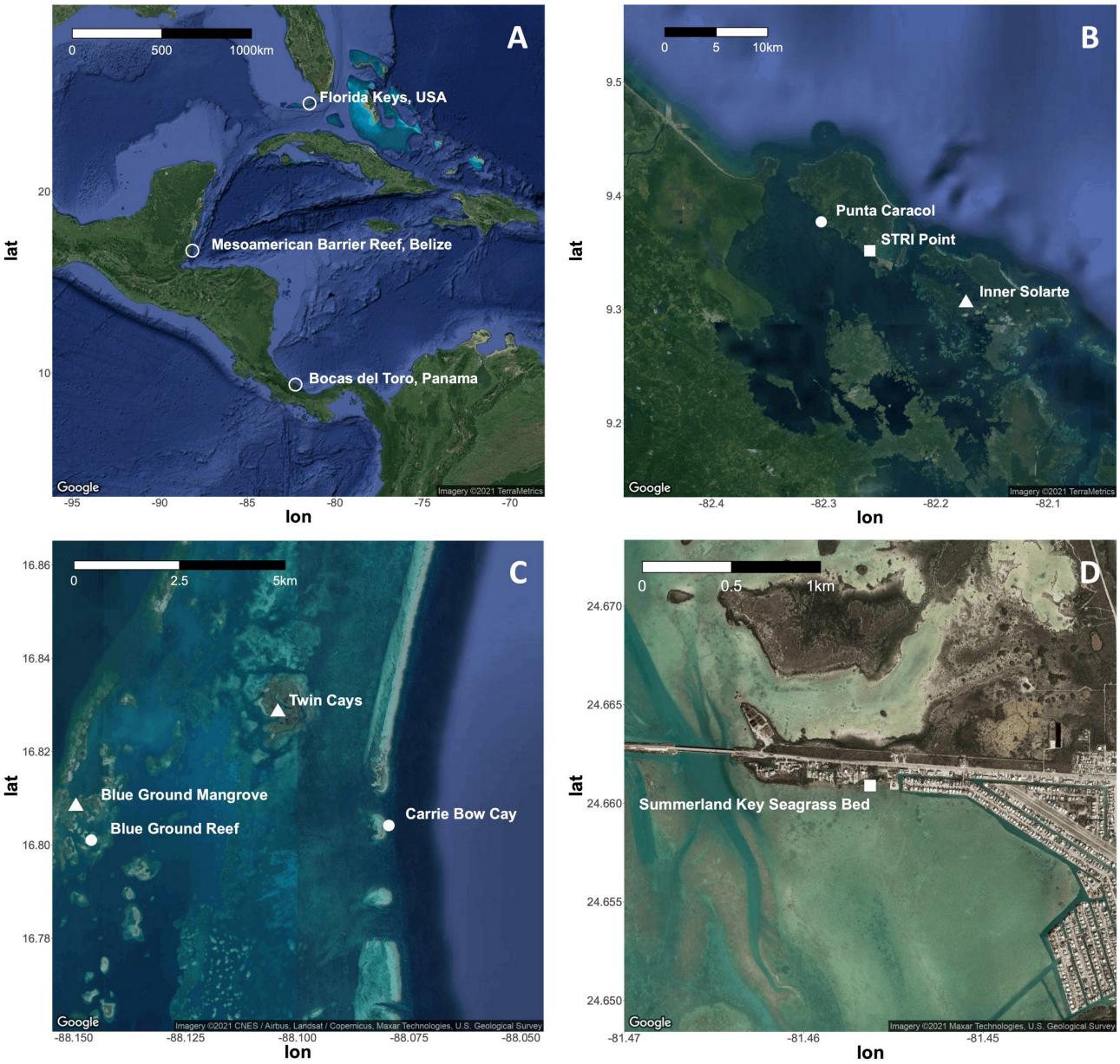

FIGURE 1. Maps of sampling locations. **A:** Overview of three sites; **B:** Bocas del Toro, Panama; **C:** Mesoamerican Barrier Reef, Belize; **D:** Summerland Key, United States of America. Open circles in A denote the location of field sites. In B-D, filled circles are coral reefs or coral patch reefs, squares are seagrass beds, and triangles are mangroves.

TABLE 1. Sampling locations of *Ircinia* spp.

	Site	Geographic coordinates	*I. felix*	*I. strobilina*	*I. campana*	*I. lowi* **sp. nov.**	*I. bocatorensis* **sp. nov.**	*I. radix* **sp. nov.**	*I. laeviconulosa* **sp. nov.**	*I. vansoesti* **sp. nov.**	*I. ruetzleri* **sp. nov.**	*I.* cf. *reteplana*
Panama	Punta Caracol (coral patch reef)	9.37767, -82.3032		X	X	X						
	STRI Point (seagrass bed)	9.35133, -82.2593		X	X		X		X			
	Inner Solarte (mangrove prop roots)	9.30583, -82.1732						X				
Belize	Carrie Bow Cay (forereef)	16.8042, -88.0796	X	X								
	Twin Cays (mangrove prop roots)	16.8285, -88.1044								X		
	Blue Ground (mangrove prop roots)	16.8083, -88.1496								X		
	Blue Ground (coral reef)	16.8010, -88.1461		X							X	
USA	Summerland Key (seagrass bed)	24.6609, -81.4563			X							X

Ircinia spp. specimens were collected from three sites in the Caribbean: four morphospecies were collected from Bocas del Toro, Panama; two from the Mesoamerican Barrier Reef, Belize; and one from the Florida Keys, United States of America (Figure 1, Table 1). Immediately after collection and prior to fixation, measurements of oscula diameters were made using a dissecting microscope and measurements of conule heights were made under compound light microscopy using hand-cut sections.

Tissue samples were fixed in 4% paraformaldehyde (PFA) that was prepared by diluting 32% PFA stock in filtered seawater. The 4% PFA solution was replaced at the 24- and 48-hour marks to ensure complete irrigation of the tissue. 50 and 75 micron-thick histological sections were made of fixed tissue samples embedded in paraffin. Measurements of skeletal fiber widths and observations of fiber coring were then made using compound light microscopy. Fibers were measured at the midpoint between their connections to other fibers since they thicken as they approach the intersection.

Results

Among the 34 of the specimens collected at the sites indicated were three currently recognized species and seven additional morphospecies (Figure 1, Table 1). The species are distinguished morphologically based on their bodies' growth shapes, oscula sizes and positions, conule heights, fiber widths, and coring. Only one species, *I. vansoesti*, was found in more than one site visited. Below we produce taxonomic descriptions that allow the distinction of the morphospecies encountered.

Systematics

Phylum Porifera Grant, 1836

Class Demospongiae Sollas, 1885

Subclass Keratosa Grant, 1861

Order Dictyoceratida Minchin, 1900

Family Irciniidae Gray, 1867

Genus *Ircinia* Nardo, 1833

Diagnosis. The proteinaceous skeleton of irciniids is composed of primary fibers that are meshed together in fascicles. A system of secondary fibers intersect, often perpendicularly, with the fascicles and can differ in the degree of coring and fiber widths relative to the primary fibers. The networks of interconnecting secondary and fascicular primary fibers are reinforced by nearly transparent, thin fibers (termed irciniid filaments) that can be tightly packed in pleat-like layers or arranged in tracts, making the bodies of many irciniids compressible though difficult to tear. *Ircinia* are distinguishable from *Psammocinia* Lendenfeld, 1889 by the former's absence of a thick outer layer of sediment that forms a cortical armor. The dermis of *Ircinia* is conulated and often clear of epibiont growth. *Ircinia* display a wide range of intraspecific variation in morphological characters at the macro- and microscopic level. Modified from Hooper & van Soest (2002); see Discussion for remarks on secondary fiber coring.

Ircinia lowi sp. nov.

Figures 2, 3; Tables 1, 2.
urn:lsid:zoobank.org:act:78177724-A5A5-4396-B78D-F6A8181ACB82

Holotype: USNM 1582268 (P16x42; 9.37767, -82.3032; appx. 0.5 m depth; coll. J.B.K.; 22 July 2016).

Paratypes: USNM 1582267 (P16x41; 9.37767, -82.3032; appx. 0.5 m depth; coll. J.B.K.; 22 July 2016), USNM 1582269 (P16x43; 9.37767, -82.3032; appx. 0.5 m depth; coll. J.B.K.; 22 July 2016), USNM 1582270 (P16x44; 9.37767, -82.3032; appx. 0.5 m depth; coll. J.B.K.; 22 July 2016), USNM 1582278 (P16x52; 9.37767, -82.3032; appx. 0.4 m depth; coll. J.B.K.; 23 July 2016).

Type locality: Bocas del Toro, Panama.

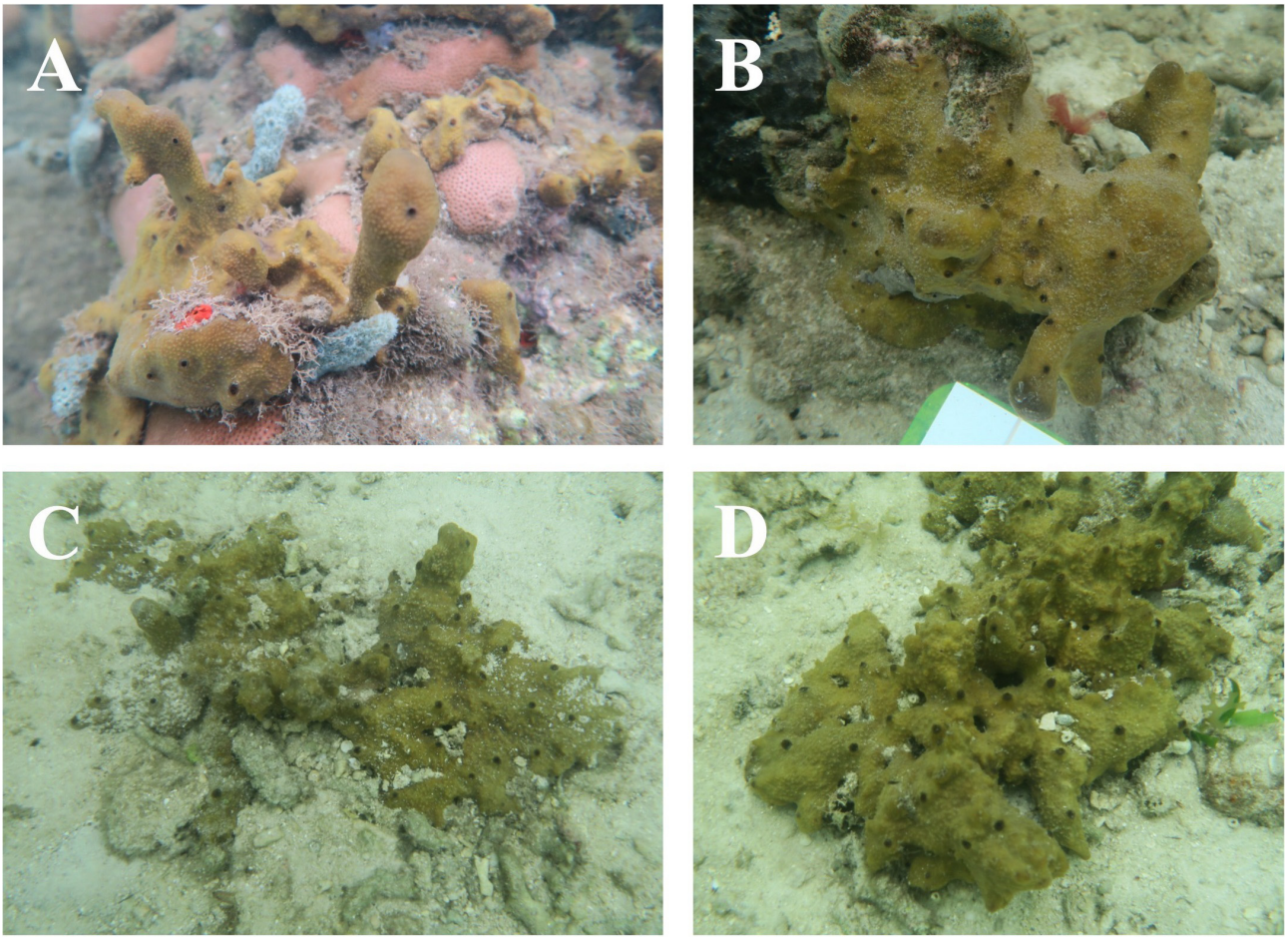

FIGURE 2. *Ircinia lowi* **sp. nov. A:** USNM 1582268 (holotype), **B:** USNM 1582267 (paratype), **C:** USNM 1582269 (paratype), **D:** USNM 1582270 (paratype). Note the wide points of attachment to hard substrate and coral rubble.

External morphology. *Ircinia* with a thickly encrusting growth habit and a forest green external surface color. Sometimes possesses lobate, short branches departing from base (Figure 2). Conules small (1.5–2 mm in height), sometimes of lighter color than the rest of the body. The body is dotted with black oscula that are uniform in size (0.4–0.5 cm diameter) and are either slightly elevated or flushed to the surface.

Interior morphology. Primary fascicular fibers 80–200 µm wide, cored. Interconnecting fibers 20–60 um wide, nearly uncored to completely uncored (Figure 3). Irciniid filaments 1–4 µm wide, terminating in spherical knobs 6–10 µm in diameter.

Ecology. All specimens were collected from shallow depths (0.4–0.5 m) on patch reefs that occur in association with small seagrass beds.

Etymology. This species is named for the immunologist Jun Siong Low for his methodological advances in identifying pan-coronavirus antibodies.

Remarks. Tissue takes on a slightly crisper consistency when preserved in ethanol for several days. Referred to as the 'Encrusting' growth form in Kelly *et al.* (2021).

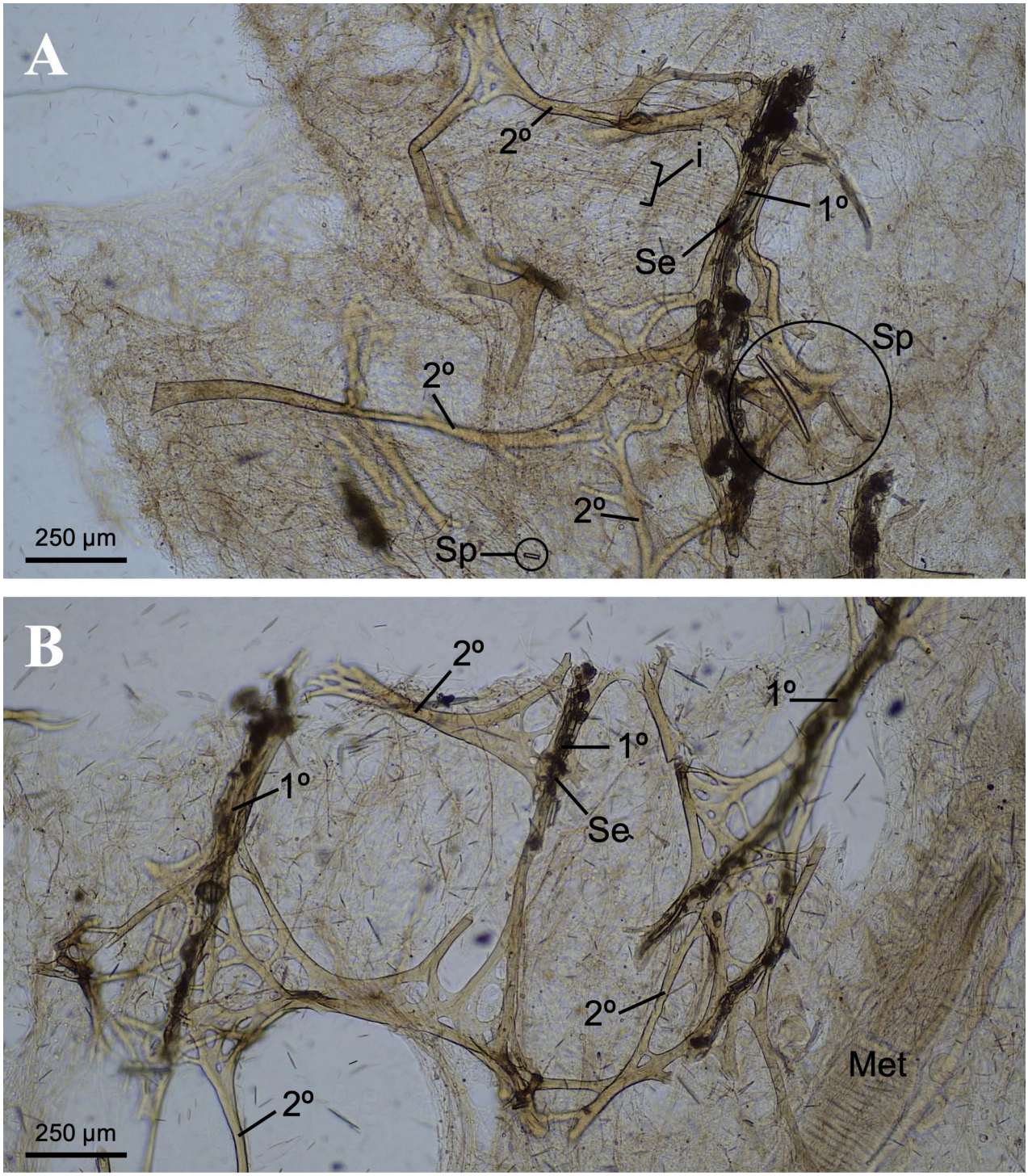

FIGURE 3. Histological sections of *Ircinia lowi* **sp. nov.**, specimen voucher USNM 1582268 (holotype). Abbreviations: 1°: primary fibers, 2°: fibers, Sp: spicules, Se: sediment grains, Met: symbiotic metazoan, i: irciniid filaments. **A:** Bands of parallel irciniid filaments are visible throughout the mesohyl, with one plane of bands annotated by the bracket in the upper right-hand quadrant. Large, foreign spicule fragments are highlighted in the bottom right quadrant and at center bottom-left. **B:** Three primary fibers are joined by secondary fibers. Note the sand grains and spicule fragments in the primary fibers and their near absence from secondary fibers.

***Ircinia bocatorensis* sp. nov.**
Figures 4, 5; Tables 1, 2.
urn:lsid:zoobank.org:act:D3F0FC15-2302-453D-BBAB-B3528E4D8D0A

Holotype: USNM 1582284 (P16x58; 9.35133, -82.2593; appx. 5 m depth; coll. J.B.K. and R.W.T.; 26 July 2016).

Paratypes: USNM 1582282 (P16x56; 9.35133, -82.2593; appx. 5 m depth; coll. J.B.K. and R.W.T.; 26 July 2016), USNM 1582287 (P16x61; 9.35133, -82.2593; appx. 5 m depth; coll. J.B.K. and R.W.T.; 26 July 2016), USNM 1582289 (P16x63; 9.35133, -82.2593; appx. 5 m depth; coll. J.B.K. and R.W.T.; 26 July 2016), USNM 1582291 (P16x65; 9.35133, -82.2593; appx. 5 m depth; coll. J.B.K. and R.W.T.; 26 July 2016), USNM 1582295 (P16x69; 9.35133, -82.2593; appx. 5 m depth; coll. J.B.K. and R.W.T.; 26 July 2016).

Type locality: Bocas del Toro, Panama.

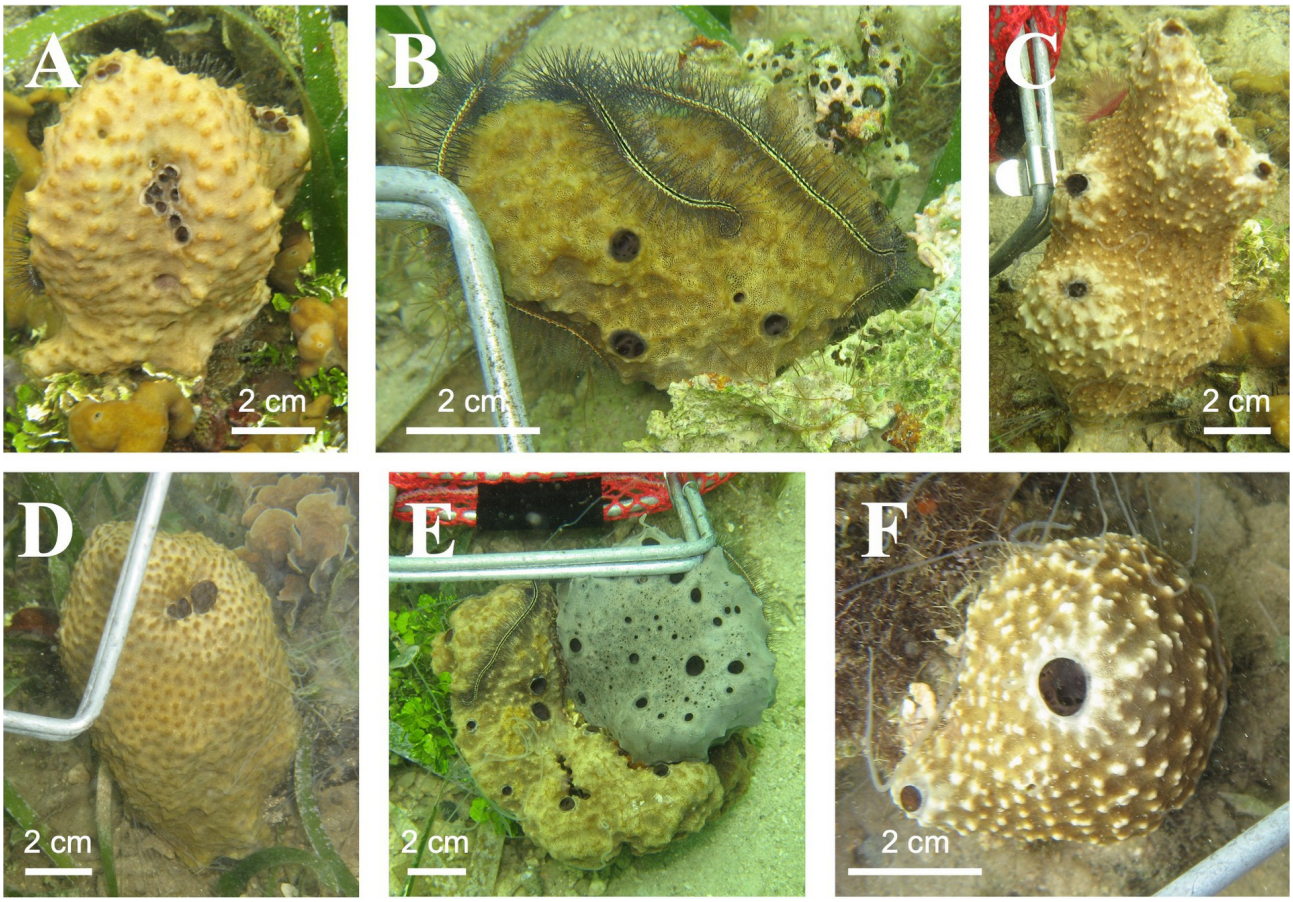

FIGURE 4. *Ircinia bocatorensis* **sp. nov. A:** USNM 1582284 (holotype), **B:** USNM 1582289 (paratype) with ophiuroid, **C:** USNM 1582287 (paratype), **D:** USNM 1582295 (paratype), **E:** USNM 1582291 (paratype, brownish) adjacent to *I. strobilina* (grayish), **F:** USNM 1582282 (paratype).

Exterior morphology. *Ircinia* with a massive, sometimes cone-like growth morphology and a tan exterior color (Figure 4). Conules 3–5 mm in height, dully sharp to knobby, typically darker or lighter in color than the rest of the sponge body. Oscula usually black, either flush or apical on cone-like outgrowths, sparsely distributed, sometimes clumped. Oscule diameter 0.5–1.5 cm.

Internal morphology. Primary fascicular fibers 200–520 µm wide, heavily cored. Interconnecting fibers 15–65 µm wide, moderately cored and sometimes becoming uncored further from the point of connection with the primary fibers (Figure 5). Irciniid filaments 1–4 µm wide, terminating in spherical to oval knobs 5–10 µm in diameter.

Ecology. All specimens were collected from a *Thalassia* bed interspersed with small coral colonies.

Etymology. The species is named for the Panamanian province Bocas del Toro.

Remarks. One specimen was observed growing in physical contact with *I. strobilina*. Referred to as the 'Massive B' growth form in Kelly *et al.* (2021).

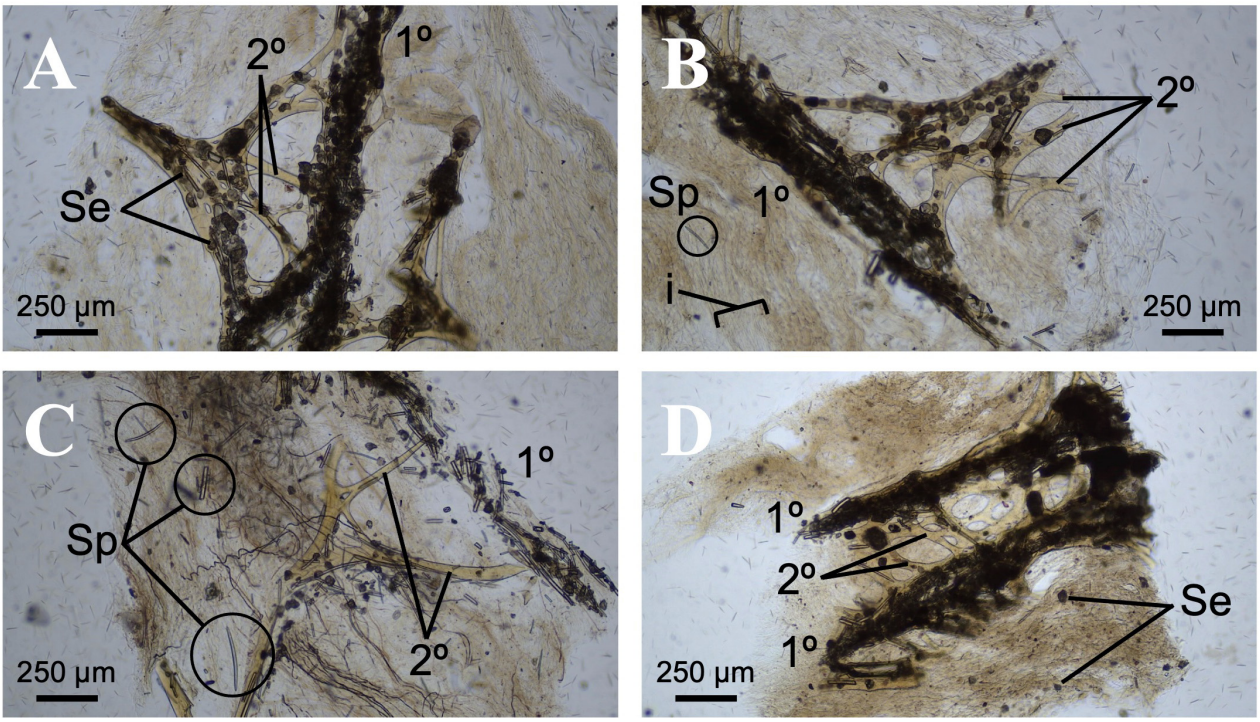

FIGURE 5. Histological sections of *Ircinia bocatorensis* **sp. nov.** Abbreviations follow Figure 3. **A, B:** USNM 1582284 (holotype). The holotype was chosen in part due to the success of the histology in demonstrating the variability in the degree of coring observed in the secondary fibers within a given individual of this species. A representative band of parallel irciniid filaments is annotated by the bracket in B. **C:** USNM 1582289 (paratype). Note the sparse coring of the secondary fibers. **D:** USNM 1582282 (paratype). This tissue fragment shows the often-parallel orientation of the primary fibers.

***Ircinia radix* sp. nov.**

Figures 6, 7; Tables 1, 2.

urn:lsid:zoobank.org:act:5E1E2B6C-0345-4449-B185-5E27D58DE4E2

Holotype: USNM 1582258 (P16x32; 9.30583, -82.1732; appx. 0.5 m depth; coll. J.B.K. and R.W.T.; 21 July 2016).

Paratypes: USNM 1582257 (P16x31; 9.30583, -82.1732; appx. 0.5 m depth; coll. J.B.K. and R.W.T.; 21 July 2016), USNM 1582259 (P16x33; 9.30583, -82.1732; appx. 0.5 m depth; coll. J.B.K. and R.W.T.; 21 July 2016), USNM 1582260 (P16x34; 9.30583, -82.1732; appx. 0.5 m depth; coll. J.B.K. and R.W.T.; 21 July 2016).

Type locality: Bocas del Toro, Panama.

External morphology. *Ircinia* with a massive growth form and light to bright pink pinacoderm (Figure 6). Growth morphology can range from a round ball (Figure 6A–C) to massive form with variously shaped upright elongations (Figure 6D). Surface with low, rounded conules (1.5–2 mm). Oscula, 0.2–1.2 cm in diameter, flushed to the surface or slightly recessed, with a lighter-colored oscular membrane, usually white. Secondary smaller apertures may be sparsely distributed, made by animals inhabiting the sponge interior.

Interior morphology. Fascicular fibers 110–250 µm wide, heavily cored. Interconnecting fibers 10–50 um wide, lightly cored with elongate foreign spicules oriented in parallel to the axis of the fiber and occasional sediment grains (Figure 7). Irciniid filaments 1–4 µm wide, terminating in knobs with highly variable shapes, ranging from spherical to oval to tear-drop, and measuring 4–12 µm in diameter.

Ecology. This species inhabits shaded entanglements of mangrove roots.

Etymology. The name refers to the mangrove roots that this species lives on.

Remarks. Referred to as the 'Massive A pink' growth form in Kelly *et al.* (2021).

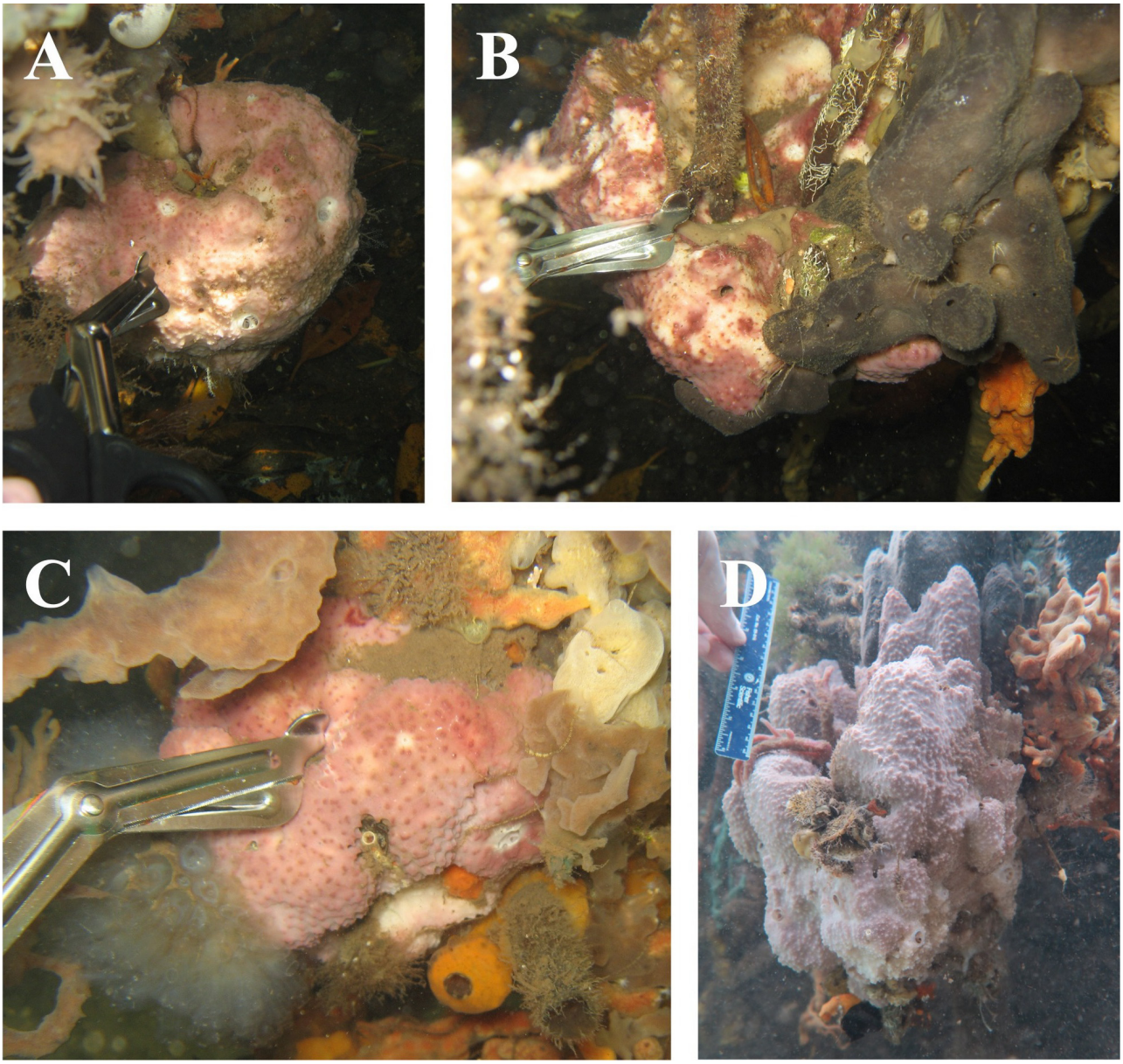

FIGURE 6. *Ircinia radix* **sp. nov. A:** USNM 1582258 (holotype), **B:** USNM 1582259 (paratype), **C:** USNM 1582260 (paratype), **D:** USNM 1582257 (paratype). All specimens were found growing on *Rhizophora* prop roots in shaded spots.

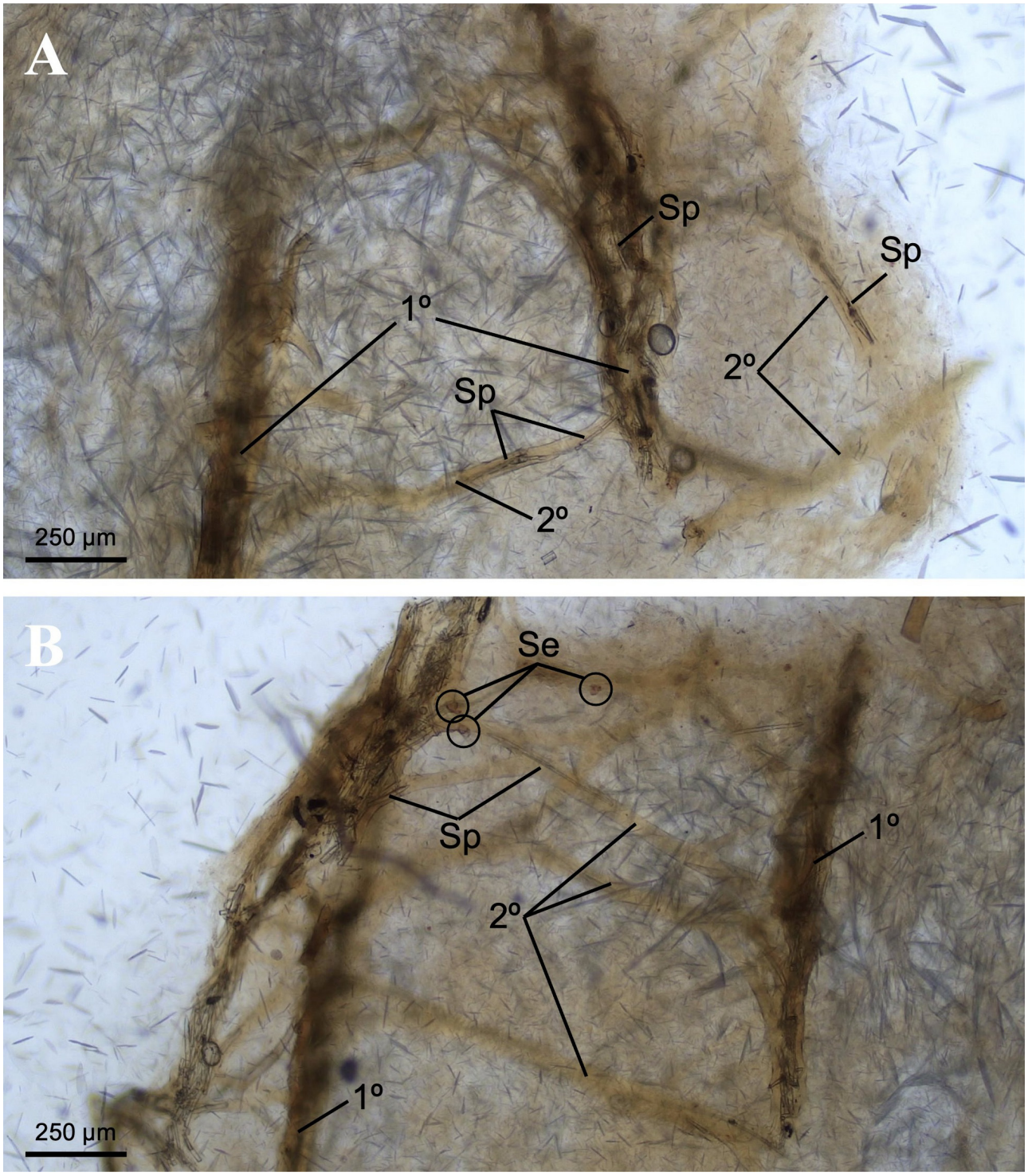

FIGURE 7. A, B: Histological sections of *Ircinia radix* **sp. nov.**, specimen voucher USNM 1582258 (holotype). Abbreviations follow Figure 3.

***Ircinia laeviconulosa* sp. nov.**
Figures 8, 9; Tables 1, 2.
urn:lsid:zoobank.org:act:2F579603-36E6-4D5A-9009-FBB43A99247C

Holotype: USNM 1582283 (P16x57; 9.35133, -82.2593; appx. 5 m depth; coll. J.B.K. and R.W.T.; 26 July 2016).
Paratypes: USNM 1582285 (P16x59; 9.35133, -82.2593; appx. 5 m depth; coll. J.B.K. and R.W.T.; 26 July

2016), USNM 1582286 (P16x60; 9.35133, -82.2593; appx. 5 m depth; coll. J.B.K. and R.W.T.; 26 July 2016), USNM 1582288 (P16x62; 9.35133, -82.2593; appx. 5 m depth; coll. J.B.K. and R.W.T.; 26 July 2016).

Type locality: Bocas del Toro, Panama.

External morphology. *Ircinia* with a massive growth form and dark green pinacoderm (Figure 8). Body diameter 10–15 cm. Possesses low conules (1.5–1.75 mm). Oscula flush, sometimes slightly darker than the exterior of the sponge, 0.4–1.2 cm in diameter, and with a thin dark green or gray membrane.

Interior morphology. Massive fascicular fibers 110–160 µm wide, heavily cored. Interconnecting fibers 20–50 um wide, sparsely cored (Figure 9). Irciniid filaments 1–5 µm wide, terminating in spherical to tear-drop knobs measuring 6–9 µm in diameter.

Ecology. This species is found among *Thalassia* spp. and coral patches in shallow depths.

Etymology. The name refers to the texture imparted by the species' low conules.

Remarks. All specimens collected had a globose growth morphology. Referred to as the 'Massive A green' growth form in Kelly *et al.* (2021).

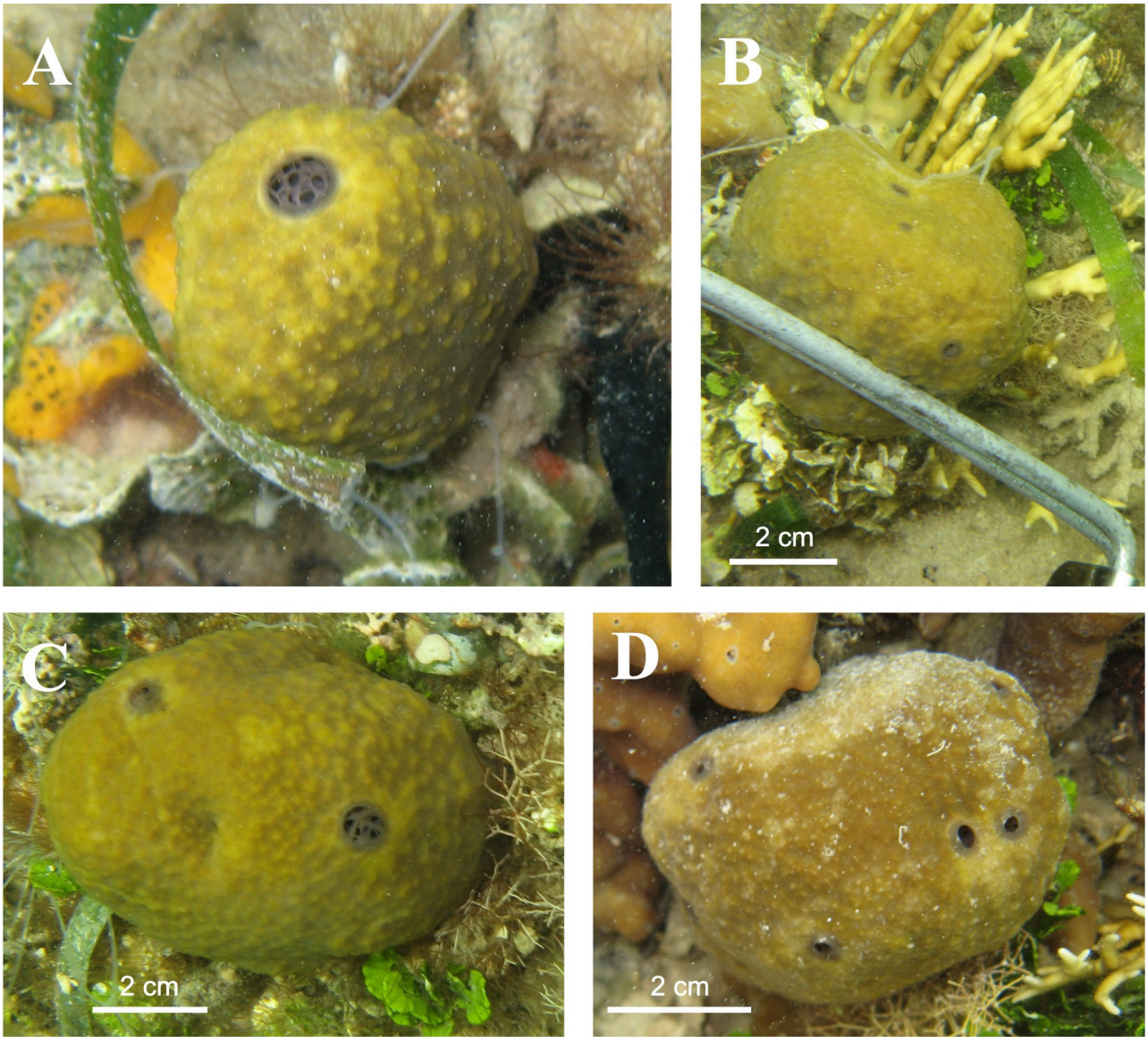

FIGURE 8. *Ircinia laeviconulosa* **sp. nov. A:** USNM 1582283 (holoype), **B:** USNM 1582285 (paratype), **C:** USNM 1582288 (paratype)**, D:** USNM 1582286 (paratype). Note the variation in oscular position, from a single large osculum (A) to multiple smaller oscula (B-D).

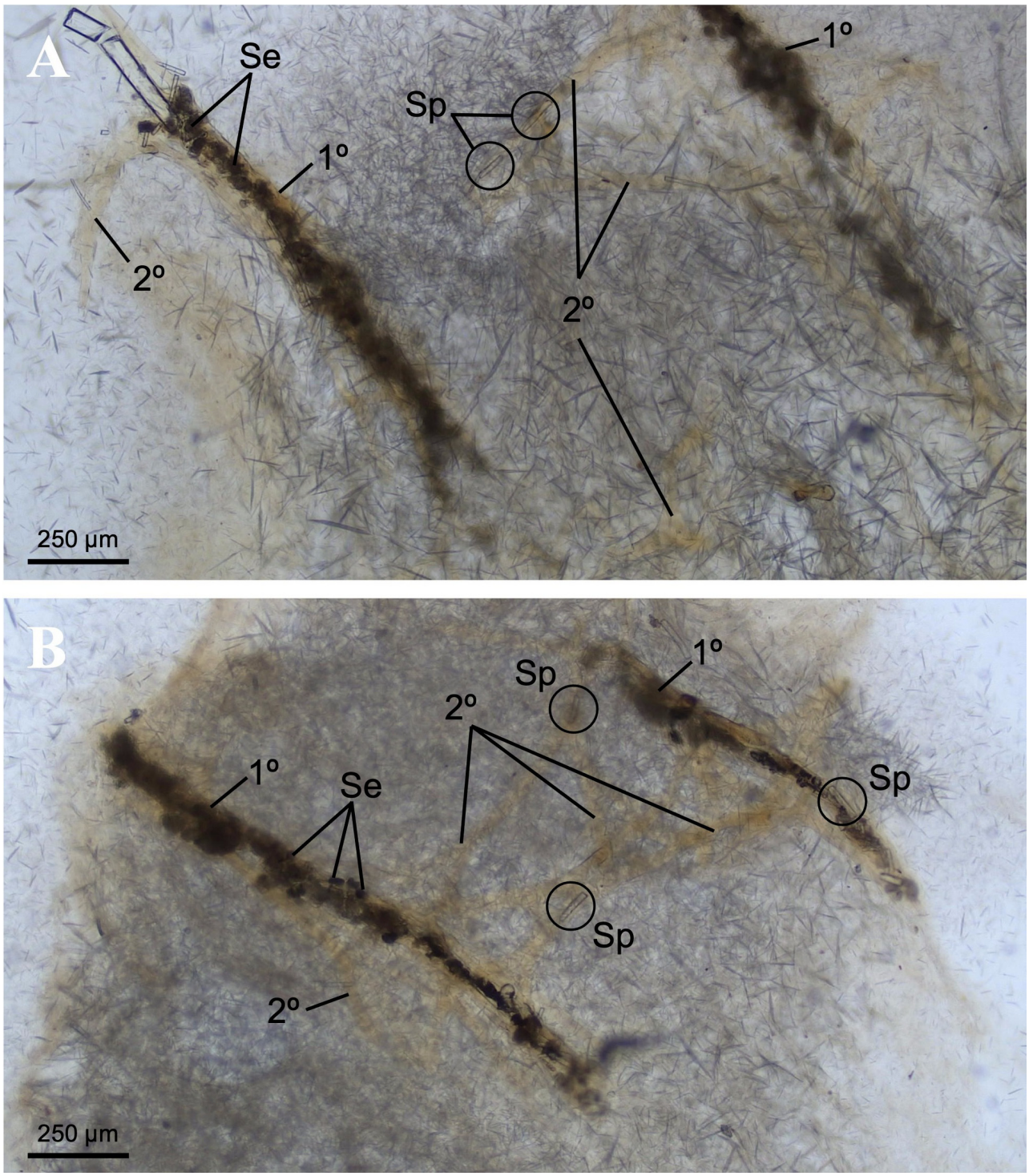

FIGURE 9. A,B: Histological sections of *Ircinia laeviconulosa* **sp. nov.**, specimen voucher USNM 1582285 (paratype). Abbreviations follow Figure 3.

***Ircinia vansoesti* sp. nov.**
Figures 10, 11; Tables 1, 2.
urn:lsid:zoobank.org:act:D3C1295B-95FC-4DDB-A3EF-35B0C2EAF3A8

Holotype: USNM 1641998 (JK18x20; 16.8285, -88.1044; appx. 0.6 m depth; coll. J.B.K.; 16 August 2018).

Paratypes: USNM 1641996 (JK18x18; 16.8285, -88.1044; appx. 0.6 m depth; coll. J.B.K.; 16 August 2018), USNM 1642006 (JK18x28; 16.8083, -88.1496; appx. 0.5 m depth; coll. J.B.K.; 18 August 2018), USNM 1642012

(JK18x34; 16.8083, -88.1496; appx. 0.5 m depth; coll. J.B.K.; 18 August 2018), USNM 1642013 (JK18x35; 16.8083, -88.1496; appx. 0.5 m depth; coll. J.B.K.; 18 August 2018).

Type locality: Mesoamerican Barrier Reef, Belize.

External morphology. *Ircinia* with a ramose growth form, although can be occasionally massive lobate in smaller individuals (Figure 10). This species is polymorphic with regard to pinacoderm coloration, and multiple color morphs (gray, dark red, dark green) can be found within a population. Possesses smaller conules (1–1.5 mm). Oscula typically 0.5–1.2 cm in diameter.

Interior morphology. Massive fascicular fibers 90–300 µm wide, sometimes cored, and always more heavily than interconnecting fibers. Interconnecting fibers 25–60 um wide, usually uncored (Figure 11). Irciniid filaments 2–6 µm wide terminating in spherical to tear-drop knobs measuring 4–11 µm in diameter. Foreign spicules and sediment are occasionally included in the cortex and are seldom found in the in mesohyl. Fascicles can be rare and difficult to discern from interconnecting secondary fibers (Figure 11).

Ecology. This species is found growing on *Rhizophora* prop roots.

Etymology. This species is named for the sponge researcher Rob van Soest.

Remarks. Interior morphology can vary somewhat depending on population, as the Twin Cays specimens contained less foreign inclusions relative to the Blue Ground specimens. Referred to as the 'Sp. 1' growth form in Kelly *et al.* (2021).

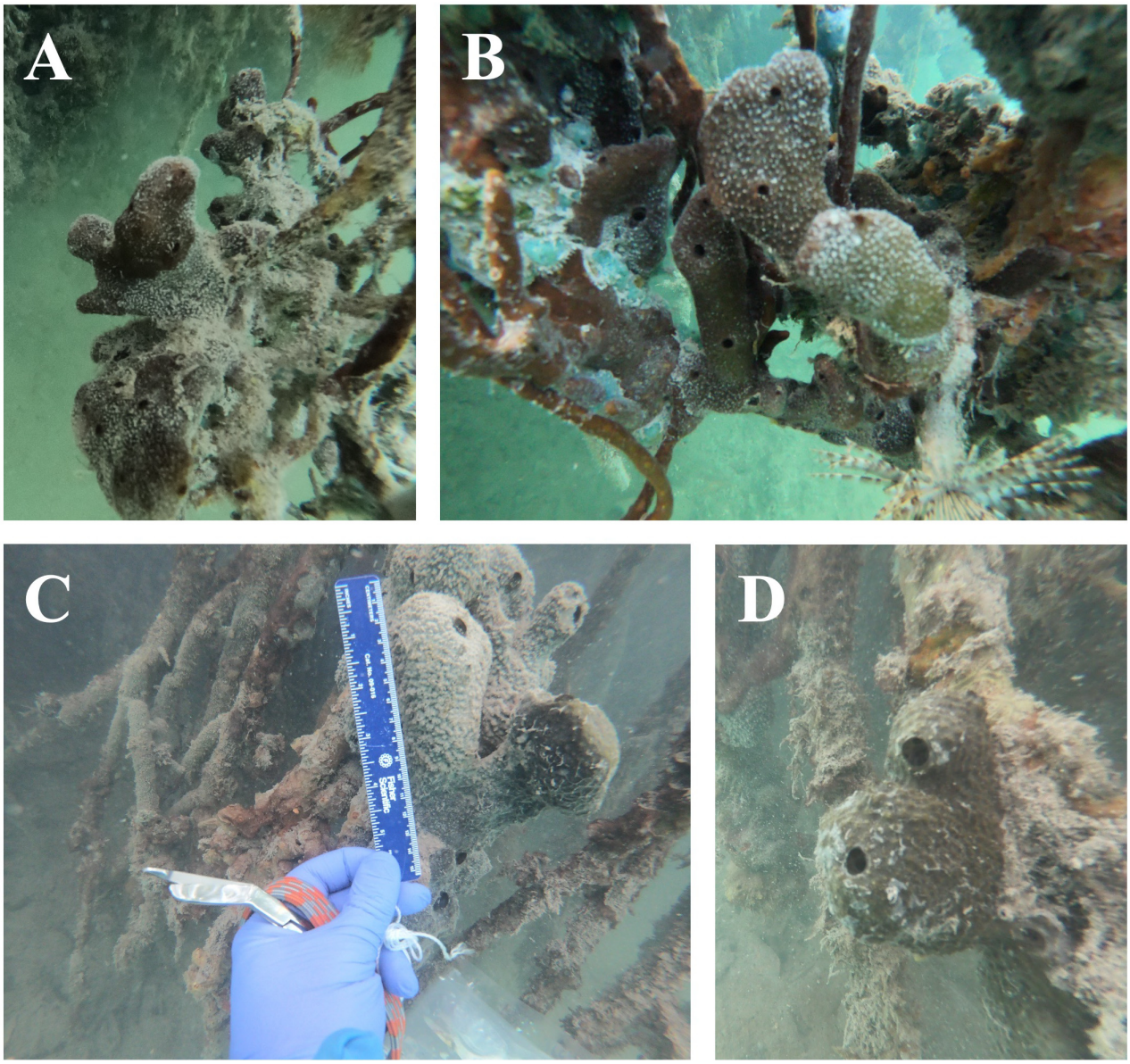

FIGURE 10. *Ircinia vansoesti* **sp. nov. A:** USNM 1641998 (holotype), **B**: USNM 1641996 (paratype), **C:** USNM 1642006 (paratype), **D**: USNM 1642013 (paratype).

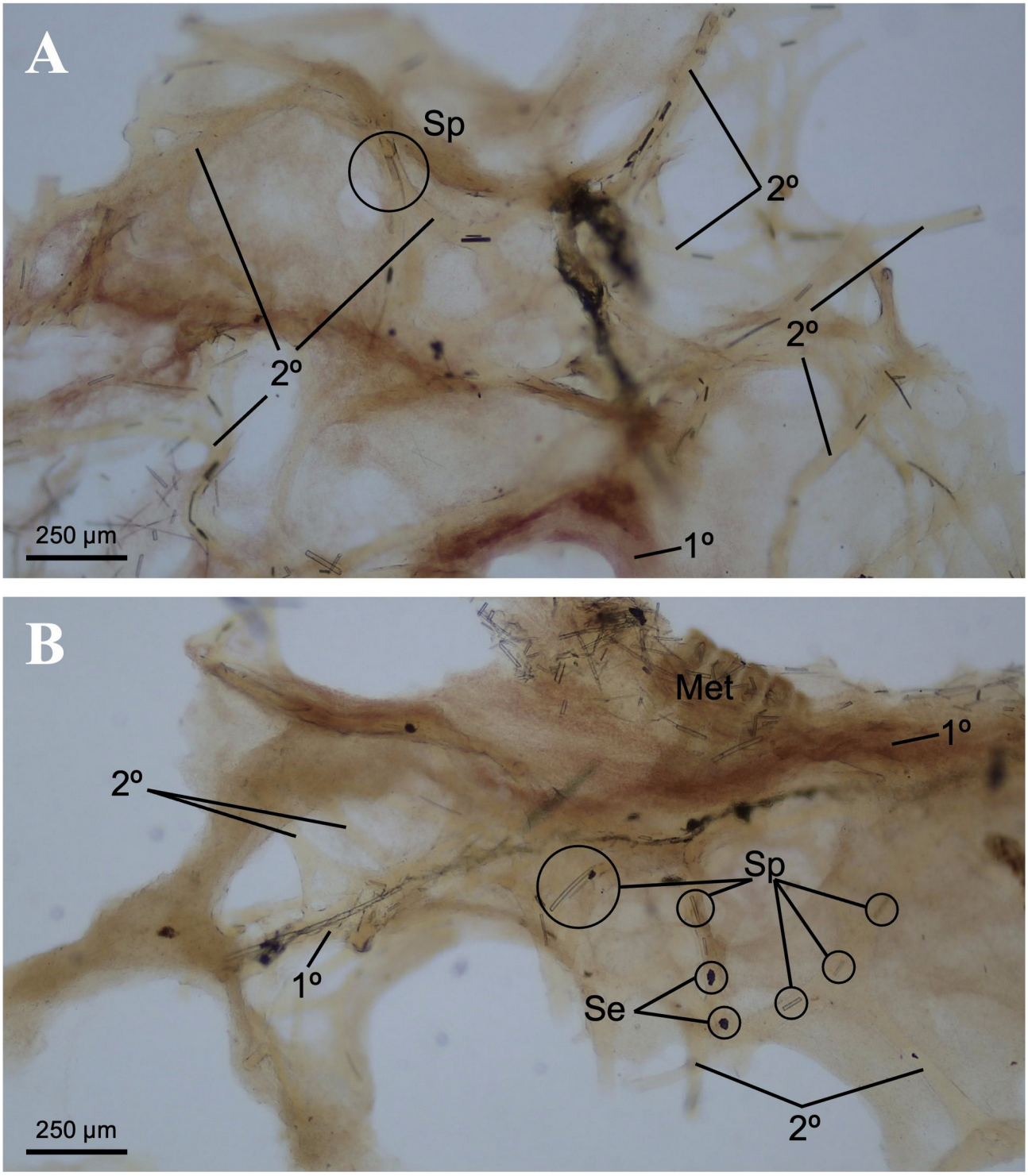

FIGURE 11. Histological sections of *Ircinia vansoesti* **sp. nov.** USNM 1641998 (holotype). Abbreviations follow Figure 3. **A:** Histological section demonstrating low degree of coring in secondary fibers. **B:** Section showing the higher degree of coring in primary fibers, most notably in the lower of the two primary fibers that runs horizontally across the image.

***Ircinia ruetzleri* sp. nov.**
Figures 12, 13; Tables 1, 2.
urn:lsid:zoobank.org:act:C789E5F2-0BAB-4D78-9EFB-FD01E5E57D87

Holotype: USNM 1642001 (JK18x23; 16.8010, -88.1461; appx. 0.8 m depth; coll. J.B.K.; 17 August 2018).

Paratypes: USNM 1641999 (JK18x21; 16.8010, -88.1461; appx. 0.8 m depth; coll. J.B.K.; 17 August 2018), USNM 1642000 (JK18x22; 16.8010, -88.1461; appx. 0.8 m depth; coll. J.B.K.; 17 August 2018), USNM 1642003 (JK18x25; 16.8010, -88.1461; appx. 0.8 m depth; coll. J.B.K.; 17 August 2018), USNM 1642004 (JK18x26; 16.8010, -88.1461; appx. 0.8 m depth; coll. J.B.K.; 17 August 2018).

Type locality: Mesoamerican Barrier Reef, Belize.

External morphology. *Ircinia* with an encrusting growth form, commonly with digitate projections, and dark gray pinacoderm (Figure 12). Conules 1–1.3 mm in height. Oscula flush or slightly raised, always black, 0.2–1 cm in diameter.

Interior morphology. Massive fascicular fibers 120–240 µm wide, heavily cored and tightly bound. Interconnecting fibers 30–50 um wide, lightly cored (Figure 13). Irciniid filaments 2–5 µm wide, terminating in spherical knobs, 5–10 µm in diameter. Cortex contains abundant inclusions of sand grains.

Ecology. This species is found on patch reefs co-inhabited by *I. strobilina* in shallow depths (0.5–1 m) adjacent to mangrove hammocks inhabited by *I. vansoesti* **sp. nov.** The surface is often covered with loose sand. The species commonly grows in close association with hydroids and multicellular algae.

Etymology. This species is named in honor of the sponge researcher Klaus Rützler.

Remarks. Referred to as the 'Sp. 2' growth form in Kelly *et al.* (2021).

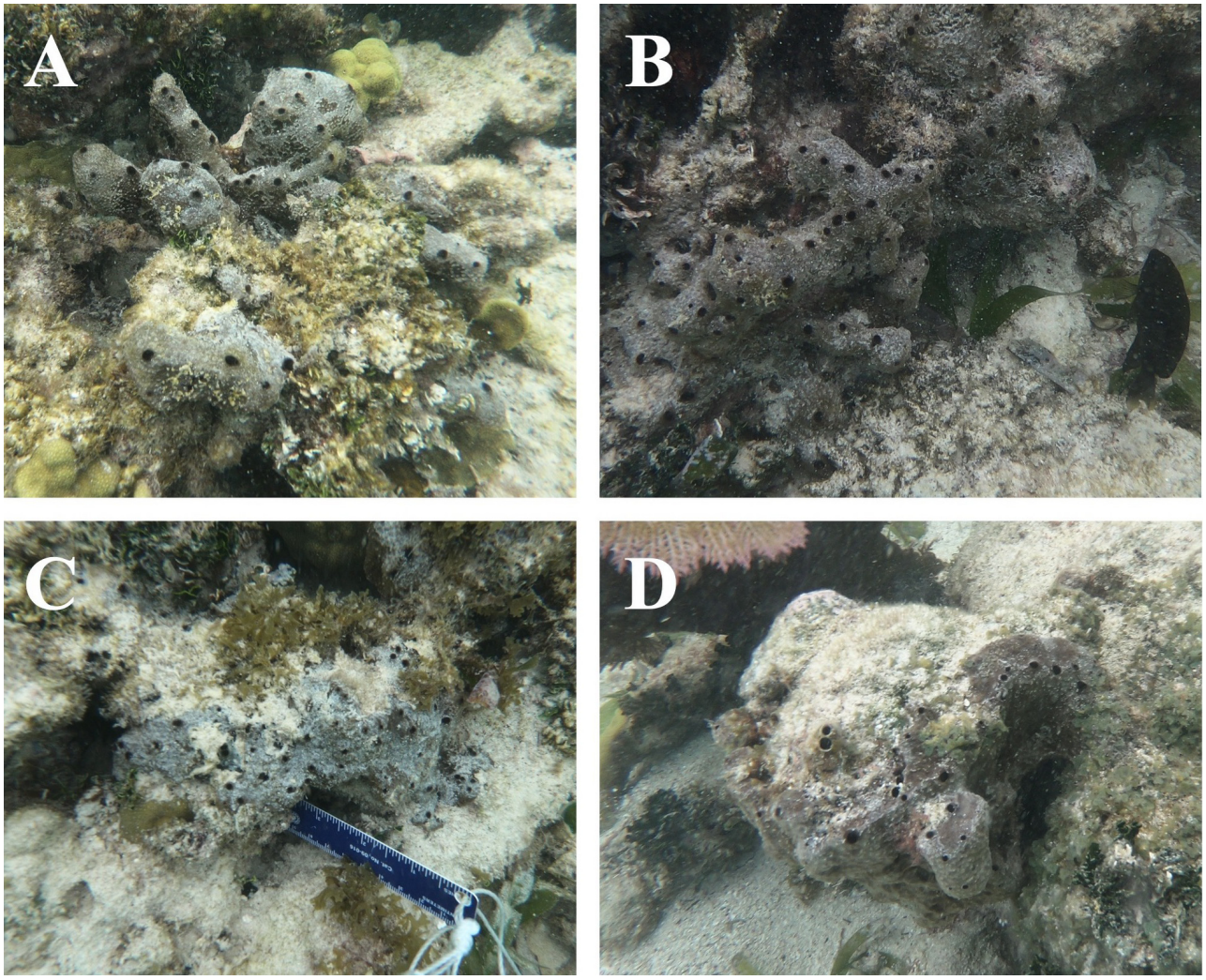

FIGURE 12. *Ircinia ruetzleri* **sp. nov. A:** USNM 1642001 (holotype), **B:** USNM 1642004 (paratype), **C:** USNM 1642000 (paratype), **D:** USNM 1642003 (paratype).

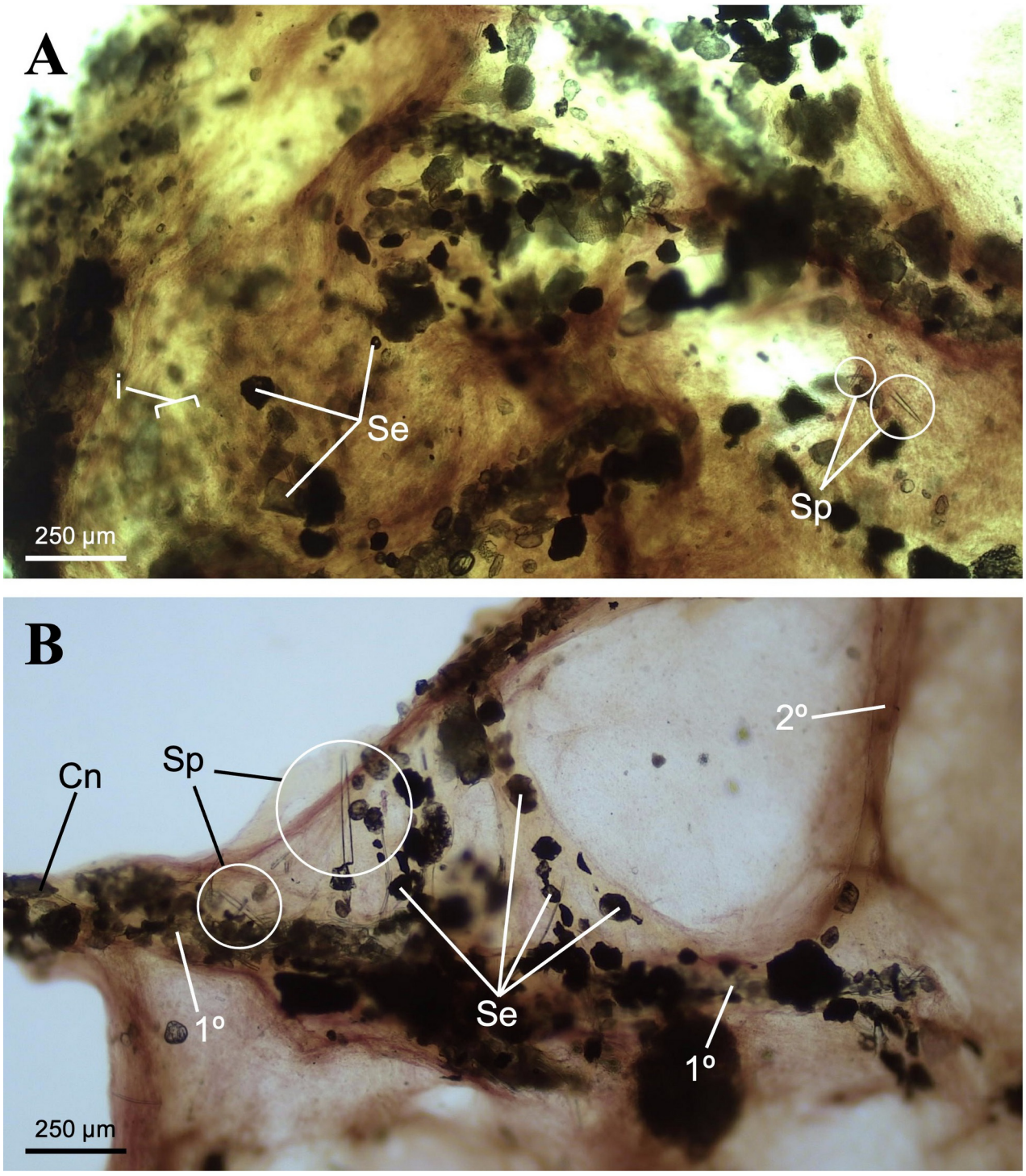

FIGURE 13. Histological sections of *Ircinia ruetzleri* **sp. nov.** USNM 1642001 (holotype). Abbreviations follow Figure 3. Cn denotes conule. **A:** Image showing sediment and spicules included in the mesohyl. A representative band of irciniid filaments is highlighted. **B:** Examples of sediment coring in a delta-like formation of secondary fibers. At the left of the image, a primary fiber terminates at the tip of a conule.

***Ircinia* cf. *reteplana* (Topsent, 1923)**
Figures 14, 15; Tables 1, 2.

Representative specimens: USNM 1641981 (JK18x6; 24.6609, -81.4563; appx. 1.2 m depth; coll. J.B.K.; 5 July 2018), USNM 1641982 (JK18x7; 24.6609, -81.4563; appx. 1.2 m depth; coll. J.B.K.; 5 July 2018), USNM 1641984

(JK18x9; 24.6609, -81.4563; appx. 1.2 m depth; coll. J.B.K.; 5 July 2018), USNM 1641985 (JK18x10; 24.6609, -81.4563; appx. 1.2 m depth; coll. J.B.K.; 5 July 2018), USNM 1641989 (JK18x14; 24.6609, -81.4563; appx. 1.2 m depth; coll. J.B.K.; 5 July 2018).

Collection locality: Summerland Key, Florida.

External morphology. *Ircinia* with a flattened, branching morphology. Branches are usually not interconnecting (Figure 14). Surface with 1–1.2 mm-high conules. Most oscula are around 0.5 cm in diameter and are found across the face of the branches, where they sit flush, as well as at the edges of the branches.

Interior morphology. Massive fascicular fibers are tightly bound, 90–250 µm wide, and heavily cored. Interconnecting fibers 20–80 um wide, moderately cored with spicules and sand (Figure 15). Irciniid filaments 2–6 µm wide, terminating in spherical knobs measuring 9–15 µm in diameter. Cortex routinely incorporates sand and foreign spicule fragments.

Ecology. Specimens were collected from a *Thalassia*-dominated seagrass bed and co-occurred next to *I. campana*, sometimes within a meter of each other. Symbiotic metazoans in the sponge are mostly crustaceans and polychaetes.

Remarks. The body shape of *I. reteplana* Topsent, 1923 is distinct from those of the aforementioned *Ircinia* in that it is composed of flattened, interconnecting branches. Because the Floridian *Ircinia* growth form, called 'Ramose' in Kelly *et al.* (2021), often displays a flattened branching morphology, we designate this growth form as *Ircinia* cf. *reteplana* Topsent, 1923, and maintain it as *conferre* due to the moderate degree of coring observed in secondary fibers, a characteristic that is absent from *I. reteplana* Topsent, 1923. Additionally, the branches of *I.* cf. *reteplana* seldom interconnect, as is reported for *I. reteplana* Topsent, 1923, and can also possess a rounded branching morphology. This growth form represents either a new species of *Ircinia* or it represents an extension of the documented range of *I. reteplana* to the Florida Keys. For reference, the range of *I. reteplana* encompasses the entirety of the Antilles and spans the Caribbean to the coast of Venezuela, and extends to the tip of the Yucutan Peninsula (van Soest *et al.* 2021). The collections of *I. strobilina*, *I. felix*, and *I. campana* were made within the documented ranges of these species (Table 1).

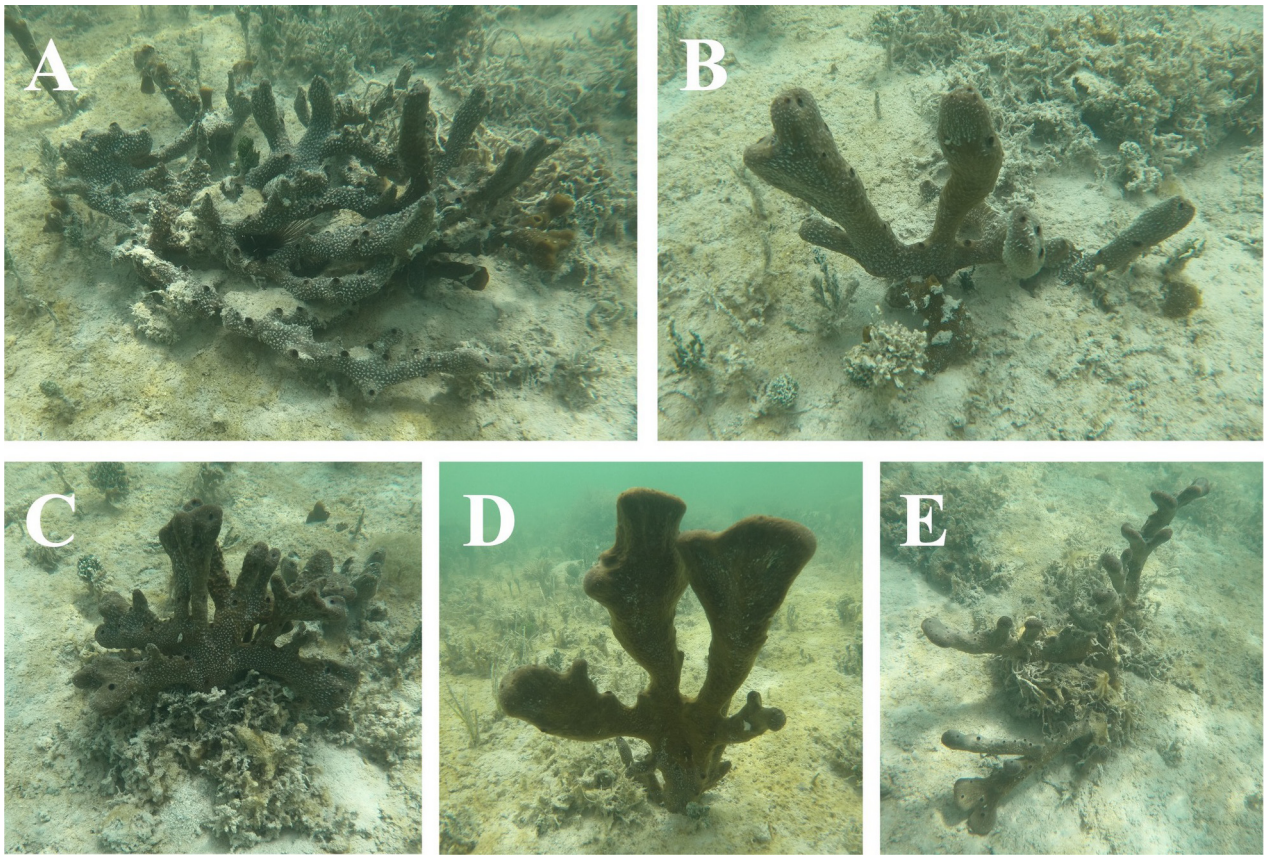

FIGURE 14. *Ircinia* cf. *reteplana* (Topsent, 1923). **A:** USNM 1641984, **B:** USNM 1641982, **C:** USNM 1641981, **D**: USNM 1641985, **E:** USNM 1641989.

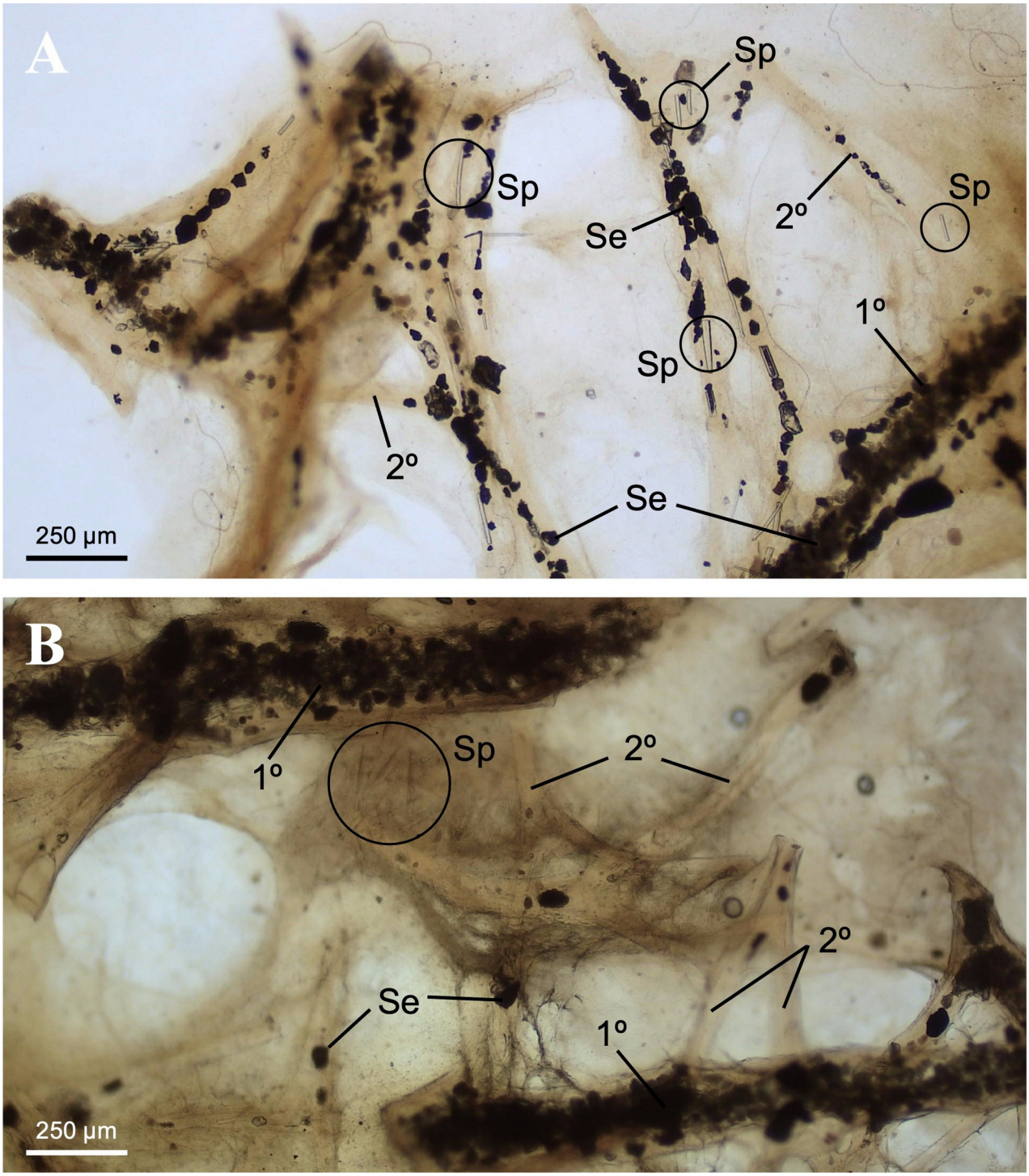

FIGURE 15. Histological sections of *Ircinia* cf. *reteplana* USNM 1641982. **A:** Image showing moderately cored secondary fibers. A primary fiber terminates in a conule on the left of the image. **B:** Two primary fibers running in parallel, connected by a mesh of secondary fibers. A group of spicules is circled below the topmost primary fiber. Note the difference in the degree of coring of secondary fibers between A and B. Annotations follow Figure 3.

Discussion

Inclusion within *Ircinia*

All *Ircinia* **spp. nov.** were difficult to tear when live and produced a sulfurous smell. The *Ircinia* **spp. nov.** of the current study all possess cored fascicular primary fibers, albeit lightly cored in *I. vansoesti* **sp. nov.**, thus separating

them from *Sarcotragus* (Hooper & van Soest 2002). The *Ircinia* **spp. nov.** are clearly distinguished morphologically from *Psammocinia* in that they do not possess an armoring, crustose layer of sediment on the cortex (Hooper & van Soest 2002), although note that several do contain foreign spicules and sand in the outer dermal layer. However, several of the *Ircinia* **spp. nov.** are less clearly distinguished morphologically from *Psammocinia* in the degree of coring in their secondary fibers; *I. bocatorensis* **sp. nov.** and *I.* cf. *reteplana* Topsent, 1923 possess cored secondary fibers and three others (*I. laeviconulosa* **sp. nov.**, *I. radix* **sp. nov.**, and *I. ruetzleri* **sp. nov.**) have lightly to intermittently cored secondary fibers. Among irciniids, cored secondary fibers are thought to only occur in *Psammocinia* (Hooper & van Soest 2002). Given that these five species neither form an outgroup nor are monophyletic in the ingroup of the species tree of Kelly *et al.* (2021), which was inferred using a multi-species coalescent model with genome-wide SNP data, they are unlikely to be *Psammocinia* mistakenly identified as *Ircinia*. However, complete phylogenetic resolution of Irciniidae will require an integrative taxonomic study, ideally employing genome-wide SNP data, that encompasses all genera in this family.

Distinctions among the *Ircinia* spp. nov.

The *Ircinia* **spp. nov.** generally fall into two categories in terms of gross body morphology: those with a massive mound or globular morphology and those with digitate projections. In the first category are *I. laeviconulosa* **sp. nov.**, *I. radix* **sp. nov.**, and *I. bocatorensis* **sp. nov.** The latter can be readily distinguished from the other two based on two characteristics of the skeletal network: first, the primary fascicular fibers are on average at least twice (200–520 μm) the width observed in *I. radix* **sp. nov.** (110–250 μm) and in *I. laeviconulosa* **sp. nov.** (110–160 μm) and, second, the interconnecting secondary fibers are cored to a heavier extent in *I. bocatorensis* **sp. nov.** (Table 2, Figures 5, 7, 9). Additionally, *I. bocatorensis* **sp. nov.** possesses higher conules (3–5 mm) relative to those of *I. laeviconulosa* **sp. nov.** and *I. radix* **sp. nov.** (less than 2 mm for both) (Table 2). The other two species, *I. radix* **sp. nov.** and *I. laeviconulosa* **sp. nov.** can be distinguished by the differences in the widths of their primary fibers, with *I. radix* **sp. nov.** having a larger maximum width (110–250 μm) relative to *I. laeviconulosa* **sp. nov.** (110–160 μm), and a larger degree of coring in its secondary fibers in contrast to those in *I. laeviconulosa* **sp. nov.** (Table 2, Figures 7, 9).

In the second category of body growth morphology, those with digitate projections, are *I. lowi* **sp. nov.**, *I. vansoesti* **sp. nov.**, and *I. ruetzleri* **sp. nov.** The characteristics that distinguish *I. ruetzleri* **sp. nov.** from the other two are the higher degree of coring in its secondary fibers relative to those of *I. lowi* **sp. nov.** and *I. vansoesti* **sp. nov.** In the latter two species, coring of secondary fibers is absent or nearly absent. A further sorting character is the larger minimum width of the primary fibers, 120–240 μm in *I. ruetzleri* **sp. nov.**, compared to 90–300 μm in *I. vansoesti* **sp. nov.** and 80–200 μm in *I. lowi* **sp. nov.** (Table 2, Figures 3, 11, 13). *I. lowi* **sp. nov.** can be separated from *I. vansoesti* **sp. nov.** as it possesses a higher degree of coring by sediment in the primary fibers (whereas coring in *I. vansoesti* **sp. nov.** is mostly spicule fragments), a more obvious demarcation between secondary and primary fibers, and a smaller maximum width of primary fibers (80–200 μm), in contrast to those in *I. vansoesti* **sp. nov.** (90–300 μm) (Table 2, Figures 3, 11). This summary of morphological characteristics (Table 2) can be used as a multiple-factor guide for taxonomic identification of Caribbean *Ircinia*.

Phenotypes, Genetics, and Restricted Host Ranges

The fact that each *Ircinia* **sp. nov.** was only found in one habitat type and was restricted to only one or two sites brings to question whether the phenotypes are simply growth forms of much fewer species (*i.e.* those of *I. campana* or *I. felix*) and whether the differences in the microbiomes, which are distinct within each morphospecies (Kelly *et al.* 2021), are simply the product of localized environmental regimes found at each site and habitat type. The first issue was addressed in Kelly *et al.* (2021), which evaluated genome-wide SNP data and compared several competing species-grouping models that lumped the morphospecies with *I. felix* and *I. campana* to represent the hypothesis that the morphospecies are phenotypes of these two species, and by evaluating support for hypotheses that represented various combinations of lumping growth forms together into a single species based on sympatry, shared habitat types, and morphological similarities. Again, the best-supported hypothesis of Kelly *et al* (2021) modeled each morphospecies as a genetically distinct species.

Multispecies-coalescent analyses, which include BFD*, have been criticized for over-splitting populations into individual species (Sukumaran & Knowles 2017). The authors of Kelly *et al.* (2021) encountered a similar pattern in that the best-supported hypothesis split two geographically distant *I. strobilina* populations (one from Belize and the other from Panama) into two different (though sister) species. Since sponges generally produce larvae that settle within hours to days (Maldonado & Riesgo 2008), the authors interpreted this as a benchmark for population-

level genetic differentiation and cautioned against splitting this species without further evidence. However, the hypothesis that received the highest support from BFD* also split the Floridian and Panamanian *I. campana* into two distinct species that fell into different clades that were separated by the maximum genetic distance on the tree. This finding of high genetic structure between the same two populations in Kelly *et al.* (2021) has been corroborated independently by another study that suggested cryptic speciation might be present within the nominal species *I. campana* (Griffiths *et al.* 2021). Given the similarities in the genetic results between the two studies, we advocate for further investigations into the possibility of splitting *I. campana* into multiple species.

Kelly *et al.* (2021) discovered that the *Ircinia* **spp. nov.** each possess compositionally unique and conserved microbiomes, a trend that held for the other Caribbean *Ircinia* species *I. felix, I. strobilina,* and *I. campana* (although with population-level differences), and that dissimilarities in microbiome compositions also scaled significantly with host genetic distances. Thus, two questions stand: first, is the environment or host identity a stronger force in shaping microbiome compositions and, second, can the microbiome composition be used as a taxonomic character? Based on the compositional distinctiveness of the microbiomes among Caribbean *Ircinia*, including those that share the same physical habitat, and the compositional differences between *Ircinia* microbiomes and the microbial communities of the surrounding seawater (Kelly *et al.* 2021), it is reasonable to postulate that the hosts are exerting some control over their microbiomes. Additionally, microbiome compositions of other *Ircinia* species are stable despite fluctuations in temperature and irradiance (Erwin *et al.* 2012) and salinity (Glasl *et al.* 2018). Despite these data, we do not have any direct evidence of whether Caribbean *Ircinia* can alter their microbiomes to better exploit the resources found in each environment, or whether they preferentially settle in locations that would best suit the specific microbiome composition that they have evolved to maintain. However, given that multiple studies have now found that microbiome dissimilarity scales positively with genetic distance at the level of the population (Griffiths *et al.* 2019, Easson *et al*. 2020), among congeneric species (Kelly *et al.* 2021), and among more distantly related species (Schöttner *et al.* 2013, Easson & Thacker 2014, Thomas *et al.* 2016), their use as taxonomic characters in the future remains a possibility. In order to disentangle the effects of environment and host genotype, and consequently identify if any aspects of the microbiome could be used as taxonomic identifiers of the hosts, reciprocal transplant experiments and long-term monitoring of Caribbean *Ircinia* microbiomes should be performed.

Additional Notes on the Use of Phenotype in Irciniid Taxonomy and Outlook

The three *Ircinia* **spp. nov.** in the second (branching) morphology category appear more morphologically similar than the three *Ircinia* **spp. nov.** in the massive mound or globular morphology category and might be difficult to distinguish in the field. These similarities hold in the overall impressions that the gross morphologies of the sponges give and in the overlap among the dimensions of their finer-scale characteristics (*e.g.* oscula diameters and fiber widths). However, none of the three *Ircinia* **spp. nov.** in the branching category are the next closest relatives to each other; in fact, each is included in one of the three major clades of the species tree of Kelly *et al.* (2021). Additionally, the genetic distances reported by Kelly *et al.* (2021) between *I. vansoesti* **sp. nov.** (as 'Sp. 1') and either *I. ruetzleri* **sp. nov.** (as 'Sp. 2') or *I. lowi* **sp. nov.** (as 'Encrusting') is the maximum genetic distance on the tree which, for reference, also includes two populations of each *I. strobilina* and *I. campana*, and one population of *I. felix*. Likewise, the genetic distance between *I. lowi* **sp. nov.** and *I. ruetzleri* **sp. nov.** is the second greatest on the tree. For additional context, *I. felix* appeared more closely related to *I. strobilina* than any of these three *Ircinia* **spp. nov.** are to each other. Thus, the use morphological dissimilarity in *Ircinia* is not a stand-alone indicator of species boundaries. As discussed above, the splitting of *I. campana* into multiple, genetically distinct species could be a further demonstration of this principle.

Phenotypic variability and the resultant difficulties that it presents to identifying boundaries among genera and species of irciniids is an obvious issue that must be resolved in the future. One problematic taxonomic character that can be addressed on the basis of the current study is the use of the absence of secondary primer coring as a diagnostic feature for *Ircinia* (Hooper & van Soest 2002). This assertion is corroborated by the results of Sandes & Pinheiro (2014), who also described *Ircinia* with coring of secondary fibers. To further resolve the appropriateness of morphological characters for use in irciniid taxonomy, we advocate for an expansion of integrative taxonomic approaches that include genome-wide and phenotypic data to delimit species boundaries, which could help guide the identification of morphological traits that set apart species and genera.

Understanding sponge biodiversity is imperative to the protection of tropical marine habitats given the multitude of core ecological functions sponges perform (Diaz & Rützler 2001, Wulff 2001, Bell 2008). *Ircinia* are among

TABLE 2. A morphological comparison of shallow water Caribbean *Ircinia*.

Species	Massive fascicular fiber width (µm)	Inter–connecting fiber width (µm)	Irciniid filament width (µm)	Filament head shape	Filament head dimensions (µm)	Conule height (mm)	Oscula diameter (cm)	Coring of secondary fibers	Source
Ircinia campana Lamark, 1816	300–700	30–150	3–6	round knob	9–10	2–8	0.4–1	light	van Soest (1978)
Ircinia strobilina Lamark, 1816	200–1000	8–60	1–6	knob	5–12	2–15	0.4–1	light	van Soest (1978)
Ircinia felix Duchassaing & Michelotti, 1864	200–550	15–100	2–6	round knob	5–12	0.5–4	0.1–0.8	light	van Soest (1978)
Ircinia reteplana Topsent, 1923	not reported	25–100	~6	slightly oval	10–16	not reported	0.6–0.8	absent to nearly absent	Topsent (1923)
Ircinia lowi **sp. nov.**	80–200	20–60	1–4	spherical	6–10	1.5–2	0.4–0.5	absent to nearly absent	Present study
Ircinia bocatorensis **sp. nov.**	200–520	15–65	1–4	spherical to oval	5–10	3–5	0.5–1.5	moderate	Present study
Ircinia radix **sp. nov.**	110–250	10–50	1–4	spherical to oval to tear-drop	4–12	1.5–2	0.2–1.2	light	Present study
Ircinia laeviconulosa **sp. nov.**	110–160	20–50	1–5	spherical to tear-drop	6–9	1.5–1.75	0.4–1.2	light	Present study
Ircinia vansoesti **sp. nov.**	90–300	25–60	2–6	spherical to tear-drop	4–11	1–1.5	0.5–1.2	nearly absent	Present study
Ircinia ruetzleri **sp. nov.**	120–240	30–50	2–5	spherical	5–10	1–1.3	0.2–1	light	Present study
Ircinia cf. *reteplana* Topsent, 1923	90–250	20–80	2–6	spherical	9–15	1–1.2	~ 0.5	moderate	Present study
Ircinia sergipana Sandes & Pinheiro, 2014	35–130	not reported separately	2.5–5	circular	5–7.5	10	< 0.1	present	Sandes & Pinheiro (2014)
Ircinia repens Sandes & Pinheiro, 2014	125–287.5	35–112.5	2.5–5	oval	5–6.3	< 1	0.2	present, although some secondary fibers uncored	Sandes & Pinheiro (2014)

the most abundant and ecologically influential sponges on Caribbean reefs although they are also, unfortunately, among the most susceptible to environmental perturbations (Wulff 2006, 2013). Here, we have demonstrated that disentangling species boundaries within *Ircinia*, arguably one of the most taxonomically challenging sponge genera, can be accomplished with high confidence using an integrative taxonomic framework that evaluates morphology, microbiome composition, and genome-wide SNP data (Kelly *et al.* 2021). The adoption of these data criteria in future species delimitation studies could help further describe species richness within this ecologically important genus and ultimately help science document and defend the hidden biodiversity in sponge fauna.

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