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Iotrochota revisited: a new sponge and review of species from the western tropical Atlantic (Poecilosclerida: Iotrochotidae)

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Abstract. The systematics of tropical and subtropical western Atlantic species of *Iotrochota* is re-examined in light of the discovery of an undescribed species. *Iotrochota birotulata* (Higgin), the type species, is found to have more characters than previously recognised and is redefined with emphasis on a skeleton of spongin fibres containing stout, curved styles and strongyles (category I) and an interstitial spiculation consisting mainly of longer, slender and straight styles (II). *Iotrochota bistylata* Boury-Esnault is confirmed as a synonym of the above. The new species, named *I. arenosa*, sp. nov., differs in external morphology, strong mucus development, incorporation of sand and interstitial spicules that are mainly long, straight strongyles. *Iotrochota atra* (Whitfield), thought to be a synonym of *I. birotulata*, is recognised as a separate species occurring exclusively in the Bahamas and is found to be a senior synonym of *I. imminuta* Pulitzer-Finali; it is morphologically very similar to *I. birotulata*, but lacks birotulae and has a strongly reduced skeleton of megascleres (mostly one category of delicate strongyles). *Iotrochota agglomerata* Lehnert & van Soest is recognised as the fourth distinct species for its unusual colour (orange), thinly encrusting habit and special spiculation (styles with tylostylote modifications).

Additional keywords: Caribbean coral reefs, distributional ecology, diversity, new species, Porifera, sympatric distribution, systematic revision.

Introduction

Discovery of an undescribed species of the genus *Iotrochota* in Belize prompted this review of all known taxa in the group. *Iotrochota* currently comprises ~12 species, most of which have been described from tropical seas; only one species is known from the Arctic. Various authors placed the genus in different families of Poecilosclerida, including Desmacididae, Desmacidonidae, Esperiopsidae, Myxillidae and Tedaniidae, but it has finally been assigned to Iotrochotidae Dendy, 1922 (van Soest 2002). The type species, *I. birotulata* (Higgin, 1877: as *Halichondria)* is Caribbean (first described from Venezuela and Jamaica); a senior synonym, *Hyrtios musciformis* Duchassaing & Michelotti, 1864, also from the West Indies (St Thomas), was suppressed as nomen oblitum (Wiedenmayer 1977) in favour of Higgin's well-established and often-cited name, *I. birotulata.* The Bahama population of *Iotrochota* differs from *I. birotulata* by having a strongly reduced spiculation (Wiedenmayer 1977) and was therefore described as a separate species, *I. imminuta* (Pulitzer-Finali, 1986). However, our study of type material at the Yale Peabody Museum of Natural History shows that *I. imminuta* is a junior synonym of *Hircinia atra* Whitfield, 1901 (from Nassau, Bahamas), which previous authors, who had not examined the skeleton, thought to be conspecific with *I. birotulata* (Wiedenmayer 1977; van Soest 2002).

Iotrochota birotulata is known as a very common and characteristic shallow-water species in Caribbean reef, mangrove and seagrass environments and has been pictured and described in several monographs and field guides (e.g. de Laubenfels 1932, 1936; Hechtel 1965; Wiedenmayer 1977; Colin 1978; Gómez López and Green 1984; van Soest 1984; Pulitzer-Finali 1986; Zea 1987; Humann 1992; Gómez 2002; van Soest 2002). Three other species from the tropical western Atlantic are *I. imminuta*, mentioned above, *I. bistylata* Boury-Esnault, 1973, off Brazil and *I. agglomerata* Lehnert & van Soest, 1999, from Jamaica.

During an ongoing study of the sponges of Belize, we found a species of *Iotrochota* that clearly differs from the others and will be described below. To determine the morphological and anatomical variability of taxonomic characters among western Atlantic populations of the genus, we examined a large number of specimens of the type species, *I. birotulata*, from the entire zoogeographic range, including various habitats in Belize. We then compared the results with data from other species provided by previous authors (Table 1) or from specimens examined by us.

Materials and methods

This paper is part of a project analysing the silicon cycle in the Belizean section of the Mesoamerican barrier reef ecosystem. The general setting of the Carrie Bow Cay research area

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Table 1. *Iotrochota* spicule types and dimensions reported in the literature for western Atlantic species
Measurements are ranges (length, or length × width) and means (where available); in μm. NR = not reported

Species	Styles I	Styles II	Strongyles I	Strongyles II	Oxeas	Birotulas	Author
I. birotulata							
Jamaica and Venezuela	[cf. strongyles I]	254 × 5.1	173 × 7.6	NR	NR	13.5	Higgin (1877)
Florida Keys	124 × 4	NR	153 × 3	NR	NR	14	de Laubenfels (1932)
Florida Keys	145 × 5	NR	110 × 5	NR	NR	14	de Laubenfels (1936)
Jamaica	129–253 × 5–10	NR	117–286 × 3–8	NR	152–188	10–18	Hechtel (1965)
Bahamas [=*I. atra*]	NR	NR	115–257 × 1–4 (177 × 2.5)	NR	NR	NR	Wiedenmayer (1977)
Curaçao	142–242 × 3–6 (184.7 × 3.8)	NR	146–230 × 3–5 (183.6 × 4.0)	NR	Rare	10–14 (12.8)	van Soest (1984
Puerto Rico, Dominican Republic, Jamaica [Type I]	<120–200 × 2.5–6.5 (curved) [modified strongyles]	220–250 × 2.5–4.5 (straight)	120–200 × 2.5–6.5 (curved)	NR	Rare	9.2–15	Pulitzer-Finali (1986)
Puerto Rico, Jamaica [Type II=*I. arenosa*?]	<120–200 × 2.5–6.5 (curved) [modified strongyles]	NR	120–200 × 2.5–6.5 (curved)	220–250 × 2.5–4.5 (straight)	Rare	9.2–15	Pulitzer-Finali (1986)
Colombia	133–185 × 3.8–8.1 (165.1 × 5.5) (curved)	228–266 × 1.4–4.7 (243.7 × 3.8) (straight)	123–214 × 0.9–5.2 (184.5 × 3.8)	NR	NR	13–15 (14.1)	Zea (1987)
Colombia	161–204 × 9.0–17.1 (180.5 × 14.7) (curved)	219–261 × 4.3–7.6 (248.0 × 5.7) (straight)	171–209 × 1.4–12.8 (194.3 × 9.0)	NR	NR	16–18 (17.1)	Zea (1987)
Jamaica	140–247 × 4–8	NR	150–220 × 4–7	NR	NR	10–15	Lehnert and van Soest (1999)
Jamaica [Lectotype]	140–240 × 3-6	NR	140–230 × 3–5	NR	NR	10–15	van Soest (2002)
I. bistylata							
Brazil [=*I. birotulata*]	153–234 × 3–8 (curved)	210–319 × 1.5–5 (straight)	160–221 × 3–6 (curved)	NR	NR	12–19	Boury-Esnault (1973)
I. imminuta							
Bahamas [=*I. atra*]	NR	NR	150–190 × 2.5	NR	NR	NR	Pulitzer-Finali (1986)
I. agglomerate							
Jamaica	256–390 × 3–6 (aff. tylostyles)	NR	NR	NR	NR	12–18	Lehnert and van Soest (1999)

(16°48.1′N, 88°04.9′W) has been described by Rützler and Macintyre (1982) and Rützler *et al*. (2000). Material was collected by free diving or SCUBA, fixed in formaldehyde–seawater (10%) or glutaraldehyde in sodium-cacodylate buffer with sucrose (1.5%), followed by preservation in 70% ethylene alcohol. Hand sections, ground epoxy sections and spicule preparations were made as previously described (Rützler 1978). Scanning electron microscope (SEM) preparations were made by the usual liquid-ashing of tissue in fuming nitric acid, followed by thorough rinsing in distilled water and multiple changes of ethylene alcohol; dried spicule mounts were gold coated and viewed on a Philips XL-30 ESEM (environmental SEM, Eindhoven, The Netherlands) at 500×, 600×, 800×, 2500× and 4000× primary magnification. Spicule measurements (25 for each type and dimension) were made by light microscopy and from SEM images. We distinguished between megascleres that were primarily part of the skeleton fibres (styles I, strongyles I) and interstitial megascleres that were mostly seen free (single or in strands) in the cellular tissue (category II).

Museum designations are: AMNH, American Museum of Natural History, New York; USNM, United States National Museum (National Museum of Natural History), Smithsonian Institution, Washington, DC; YPM, Yale Peabody Museum of Natural History, Yale University, New Haven, CT.

Family **IOTROCHOTIDAE** Dendy, 1922

Diagnosis

Poecilosclerida (Myxillina) with reticulate or hymedesmioid choanosomal skeleton of megascleres cemented by spongin; with birotulae as microscleres (Dendy 1922; see also van Soest 2002).

Genus ***Iotrochota*** Ridley, 1884

Hiattrochota de Laubenfels, 1950: 20.

Iotrochotyla de Laubenfels, 1954: 150.

Type species: *Halichondria birotulata* Higgin. Type localities: Bay of Kingston, Jamaica (Lectotype) (Ridley 1884; van Soest 2002); Puerto Cabello, off Caracas, Venezuela (Paralectotype).

Diagnosis

Iotrochotidae with principal skeleton of smooth megascleres (styles, strongyles) that are typically separable into two shape and size categories.

Iotrochota birotulata (Higgin)

(Figs 1–3; Tables 1, 2)

Halichondria birotulata Higgin, 1877: 296, pl. XIV, figs 11–15. (For further synonyms see Hechtel 1965: 24; Wiedenmayer 1977: 138; Zea 1987: 149; van Soest 2002: 598–599.)

Not *Iotrochota birotulata*: Bahamas specimens of Higgin 1877: 298; Wiedenmayer 1977: 138.

Material examined

Belize: Lighthouse Reef, SW Fore Reef, USNM 32306; Carrie Bow Cay lagoon, USNM 32962, USNM 33176, USNM 41358; Carrie Bow Cay, inner fore reef, USNM 47850 (dry); Carrie Bow Cay (1 km WSW), lagoon reef, USNM 47851 (dry); Blue Ground Range, west of Carrie Bow Cay, USNM 1091296; Manatee Cay, USNM 1091297; Carrie Bow Cay south, patch reef, USNM 1091298; Carrie Bow Cay south, inner barrier reef, USNM 1091299; Carrie Bow Cay south, patch reef, USNM 1091300; Carrie Bow Cay, lagoon due north-west; USNM 1091301. **Brazil:** USNM 1091302. **Colombia:** Rosario Islands, Pajarales, USNM 31970 (dry), USNM 31976 (dry); Santa Marta, Punta de Betin, USNM 31992. **Florida:** Gulf of Mexico, USNM 33965, USNM 33968; West Palm Beach, USNM 1091293; Dry Tortugas, USNM 22600, USNM 22601, USNM 22604 (dry); Dry Tortugas, Bird Key, USNM 22599; Dry Tortugas, NW Channel, Dry Rocks, USNM 31867; Looe Key, Middle Spur, USNM 30400; Florida Keys, USNM 1091294, USNM 1091295. **Panamá:** San Blas Islands, Cichime Cays, USNM 32912. **Puerto Rico:** La Parguera, SW of Island (near laboratory), USNM 31599, USNM 31603; Montalvo Bay, towards La Parguera, USNM 31849. **Virgin Islands:** St. John Island, Current Hole, USNM 31581; St. Croix Island, east slope of Salt River Canyon, USNM 32242.

Diagnosis

Purplish black to greenish, branching erect or repent, moderately mucous *Iotrochota*. Main skeleton composed of network of fibres containing tightly packed megascleres bound by spongin. Megascleres curved, stout styles (mean length × width: 167 × 6.5 μm) and strongyles (mean length × width: 181 × 5.0 μm); accessory spicules straight, thin styles – rarely strongyles – single or in strands (mean length × width: 241 × 4.5 μm) and birotulae (mean length 14.9 μm) (Table 2).

Morphology of type material

Lectotype, BMNH 1877.3.9.1 (dry, from Jamaica, not examined in this study), described as a branching, sharply conulose specimen supported by thick (35–100 μm) spicule tracts containing strongyles (140–230 × 3–5 μm) and styles (140–240 × 3–6 μm) and loosely scattered megascleres and microscleres (birotulae 10–15 μm); paralectotype, BMNH 1877.3.9.2 (2 slides, from Venezuela, not seen by authors) (van Soest 2002: 599, fig. 3*A–D*).

Fig. 1. Map of *Iotrochota* species distribution in the tropical western Atlantic (see also Tables 1, 2). (Symbols: circles, *Iotrochota agglomerata*; triangles, *I. arenosa*; squares, *I. atra*; diamonds, *I. birotulata*; ?, identification not confirmed.)

Description

External features

Colour purplish black, with an emerald green sheen over part of the surface. Specimens erect, branching to fan-shaped, or encrusting with sprawling branches. Branches 1–4 cm diameter, depressed, wider where anastomosing and 30–50 cm long, up to nearly 1 m in some calm-water habitats. Surface spiny conulose, particularly noticeable on specimens removed from the water. Conules 0.5–2 mm high, 1–4 mm apart, terminating in fine brushes of protruding fibres. Subectosomal, meandering aquiferous canals lined by clusters of emerald-green-pigmented cells. Oscula 1–3 mm in diameter, usually conspicuous but not elevated, randomly scattered, 4–5 cm apart. Pores (50–150 μm diameter) clustered in fields between the conules.

Consistency

Stiff and spiny, tough to tear, releasing purplish mucus when handled.

Anatomy

Ascending fibres 180–450 μm in diameter, connecting fibres 40–125 μm. Mesh diameter from 50 μm to more than 1 mm. Fibres composed of closely packed megascleres (curved or undulating, stout styles I and strongyles I) bound by varying

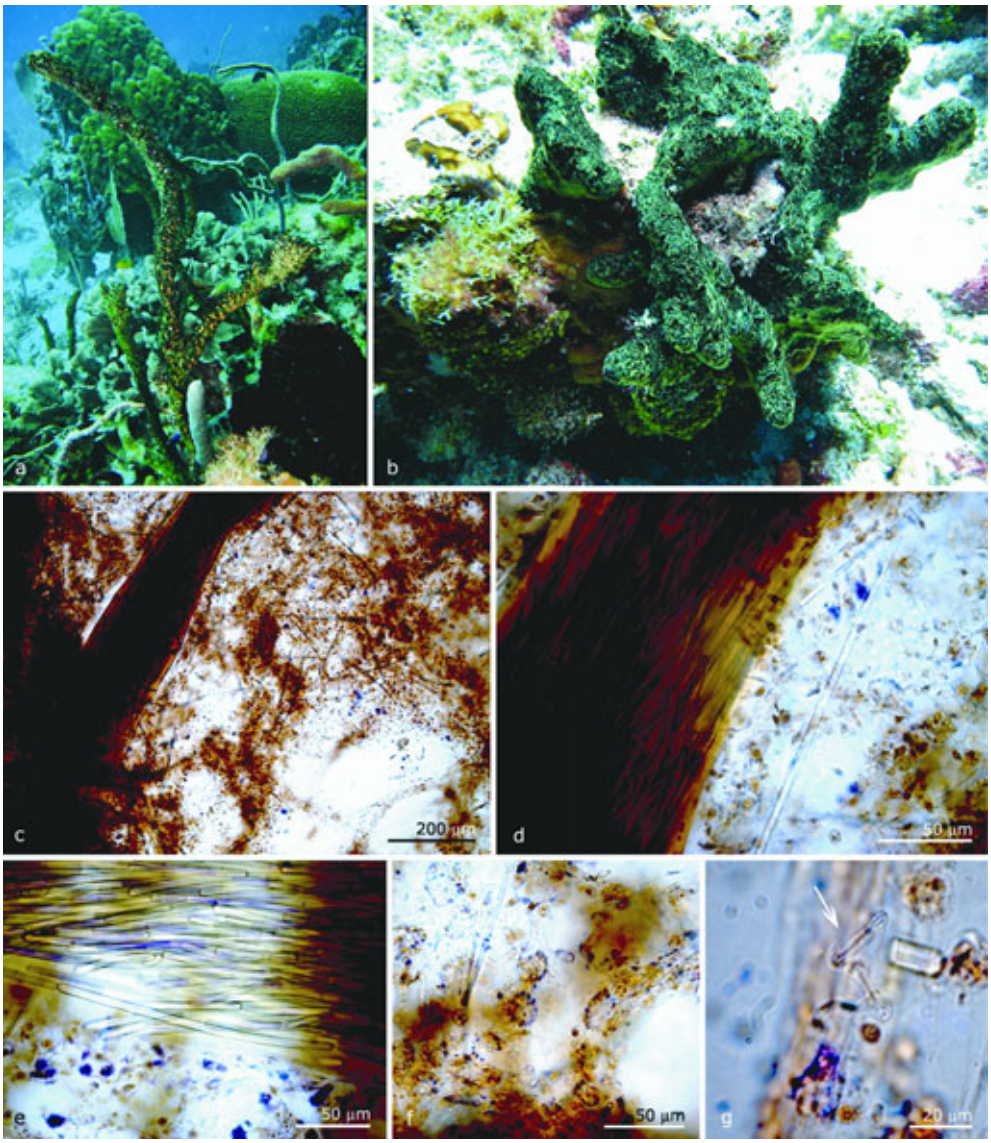

Fig. 2. *Iotrochota birotulata*, live specimens *in situ* (*a*, *b*) and microanatomy (*c*–*g*). (*a*) Branching erect specimen covered by *Parazoanthus swiftii* on a reef off Carrie Bow Cay, Belize, 8 m depth (picture width, 50 cm; photo, Mikel Becerro). (*b*) Specimen sprawling over coral rock, Florida Keys, 5 m depth (picture width, 20 cm; photo, M. Becerro). (*c*) Skeleton fibre and accessory megascleres. (*d*) Spicule-charged spongin fibre with accessory spicule (style II). (*e*) Detail of skeleton fibre showing tightly packed spicules (styles I, strongyles I). (*f*) Choanocyte chambers. (*g*) Cellular tissue with birotulas (arrow).

quantities of spongin. Interstitial megascleres (long, thin, straight styles II) common, sometimes occurring in strands. Microscleres are birotulae scattered throughout tissue. Spicule measurements summarised in Table 2. Choanocyte chambers average 20–30 μm in diameter; they have long thin prosopyles but lack apopyles and open directly into excurrent canals.

Ecology and distribution

Common among mangroves and in sea grass (*Thallassia*) beds, sand and dead coral in lagoons and on shallow reefs; typically 0.1–20-m depth, a few records to 65-m depth. Association with the bright yellow to orange epizoic zoanthid *Parazoanthus swiftii* (Duchassaing & Michelotti) is common and affects 10–25% of the population. This species is among the sponges most commonly eaten by fish and sea urchins (Randall and Hartman 1968; Santos *et al*. 2002).

Specimens were collected in the Gulf of Mexico (off Florida and Mexico), the Atlantic coast of Florida (West Palm Beach), Dry Tortugas and Florida Keys, Cuba, Dominican Republic, Puerto Rico, Virgin Islands, Belize, Colombia, Curaçao, Bonaire, Venezuela, Panama (Atlantic coast), and Brazil. Bahamas specimens are here referred to another species, *I. atra.*

Remarks

Our specimens of *Iotrochota birotulata* agree well with the original description of the type material from Jamaica and Venezuela (Higgin 1877; van Soest 2002), and several subsequent analyses, particularly of material from the Dry Tortugas (de Laubenfels 1932, 1936), Jamaica (Hechtel 1965), Curaçao, Bonaire, St Martin, Puerto Rico (van Soest 1984) and Caribbean Colombia (Zea 1987). Differences concern mainly variations in spicule type and size and many authors did not discriminate between megasclere categories. Higgin (1877) distinguished two spicule forms, a curved 'subcylindrical one' (our strongyle I), some found pointed at one end, and an associated 'long fine straight arcuate spicule' (style II) 'found also in considerable numbers in the dermal sarcode' (Higgin 1877, p. 298) (Table 2). He also mentioned similar looking specimens from Nassau with spicules of 'slender cylindrical form, but lacking altogether the flesh-spicules [birotulas]' (Higgin 1877, p. 298), but his plan to examine the relationship did not materialise.

A detailed discussion of systematics, histology, regeneration and ecology based on reaction of cell suspensions to environmental variables was provided by de Laubenfels (1932, 1936) as a result of a field-laboratory study in the Dry Tortugas (Florida). Complementary to our findings in the present study, de Laubenfels observed a flabellate shape in specimens exposed to oscillating currents. Colour in life was described as very dark purple, with a thin sheen of emerald green over much of surface caused by ectosomal archaeocytes containing emerald-green inclusions. He considered strongyles and styles to be mixed indiscriminately, mostly localised in spongin fibres and he found very few birotulae, with 12 or 16 clads.

Hechtel (1965) studied the species collected from the type locality, Jamaica. He found long, thin styles and relatively large birotulae (20–30 μm) scattered in the ectosome, styles also common interstitially elsewhere and birotulae abundant near canals. He also noted a reticulation of stout skeleton fibres ending in the conules and composed of curved strongyles or anisostrongyles, and less common curved styles, complementing to our findings in the present study.

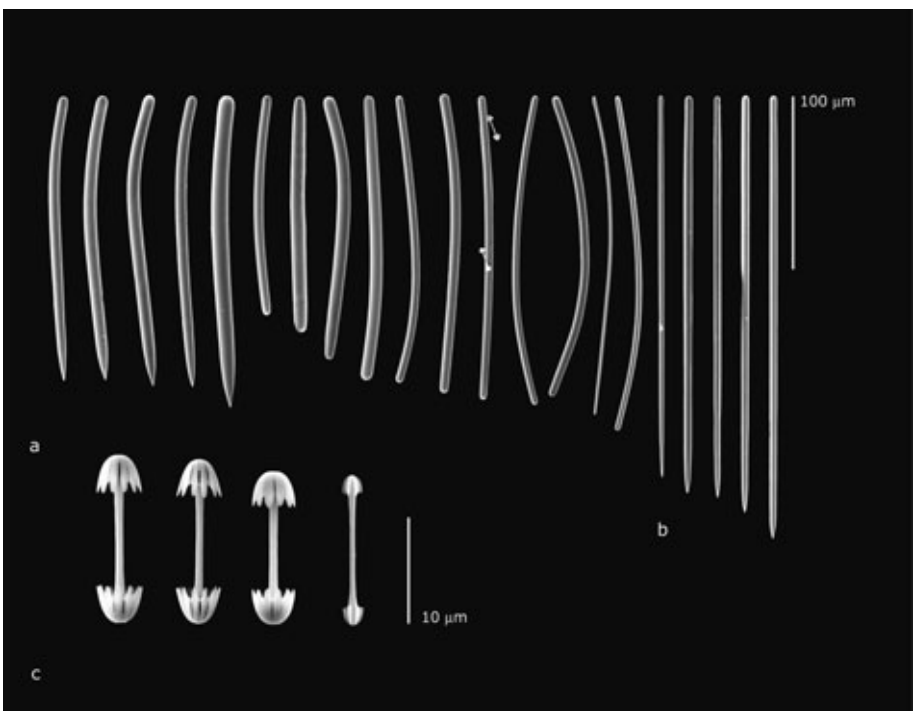

Fig. 3. Spicules (scanning electron micrographs) of *Iotrochota birotulata*. (*a*) Curved styles I and strongyles I. (*b*) Straight accessory spicules (styles II). (*c*) Birotulae.

Table 2. Spicule types and measurements for *Iotrochota* specimens examined

Measurements (means, in μm) apply to length, or length × width. NA = not applicable (spicule type not found, or very rare and thus suspected to be a foreign enclosure or malformation)

Specimen	Styles I	Styles II	Strongyles I	Strongyles II	Birotulas	Oxeas
Iotrochota birotulata						
USNM 33965, Florida (Gulf)	171.6 × 5.6	229.1 × 4.9	162.3 × 5.4	NA	16.6	NA
USNM 33968, Florida (Gulf)	176.1 × 4.8	244.4 × 4.0	176.8 × 4.5	NA	16.1	NA
USNM 1091293, East Florida	147.5 × 5.5	233.1 × 3.2	182.8 × 3.7	NA	15.2	161.6 × 3.8
USNM 22599, Florida Keys	139.4 × 4.2	230.6 × 2.9	151.3 × 3.5	NA	16.1	135.3 × 3.9
USNM 22600, Florida Keys	158.0 × 4.4	268.6 × 2.7	158.4 × 3.5	NA	14.5	167.6 × 4.7
USNM 22601, Florida Keys	145.4 × 3.9	218.9 × 3.3	167.9 × 3.4	NA	13.3	166.0 × 4.3
USNM 22604, Florida Keys	156.7 × 4.4	232.7 × 3.5	158.6 × 3.7	NA	14.8	NA
USNM 31867, Florida Keys	166.0 × 5.4	238.6 × 3.6	177.9 × 4.2	NA	14	NA
USNM 30400, Florida Keys	152.5 × 3.9	222.1 × 3.3	170.9 × 3.2	NA	14.6	NA
USNM 1091294, Florida Keys	178.9 × 5.3	239.2 × 3.6	165.6 × 3.8	NA	14.6	NA
USNM 1091295, Florida Keys	167.0 × 5.6	254.2 × 4.3	179.1 × 4.3	NA	15.4	131.4 × 4.0
USNM 31599, Puerto Rico	172.6 × 6.5	234.2 × 3.5	178.4 × 4.9	NA	14.2	NA
USNM 31603, Puerto Rico	138.2 × 5.3	220.0 × 3.5	175.1 × 3.9	NA	14.4	NA
USNM 31849, Puerto Rico	174.6 × 6.2	258.3 × 4.7	192.4 × 4.8	NA	14.5	NA
USNM 31581, Virgin Islands	167.9 × 5.0	236.7 × 3.2	189.1 × 3.7	NA	12.9	NA
USNM 32242, Virgin Islands	143.8 × 4.7	266.6 × 7.9	160.3 × 3.5	NA	11	NA
USNM 32306, Belize	162.7 × 7.4	233.9 × 4.4	178.3 × 5.2	NA	15.2	NA
USNM 32962, Belize	183.1 × 7.3	248.0 × 4.3	197.4 × 5.8	NA	14.8	NA
USNM 33176, Belize	168.5 × 5.0	252.1 × 4.9	188.9 × 5.3	NA	14.9	NA
USNM 41358, Belize	187.4 × 6.9	255.9 × 4.6	187.8 × 5.0	NA	15.4	NA
USNM 47850, Belize	171.9 × 7.4	233.8 × 5.2	189.5 × 5.5	NA	15	NA
USNM 47851, Belize	157.0 × 6.4	265.2 × 4.5	189.0 × 4.0	NA	15.4	NA
USNM 1091296, Belize	168.7 × 6.2	234.5 × 4.2	186.5 × 5.4	NA	14.9	NA
USNM 1091297, Belize	183.0 × 7.5	242.7 × 4.0	193.4 × 5.8	NA	15.7	NA
USNM 1091298, Belize	171.6 × 7.5	248.5 × 5.0	185.8 × 5.7	NA	15.4	NA
USNM 1091299, Belize	161.0 × 8.2	231.0 × 4.3	171.4 × 5.1	NA	15.9	NA
USNM 1091300, Belize	169.9 × 5.9	245.2 × 4.3	170.4 × 5.1	NA	15.4	NA
USNM 1091301, Belize	175.8 × 8.2	259.1 × 4.7	187.0 × 6.5	NA	15.1	NA
USNM 30475, Colombia	171.8 × 10.8	234.8 × 4.1	193.8 × 9.2	NA	16	NA
USNM 31970, Colombia	178.3 × 10.8	169.5 × 14	229.9 × 6.7	NA	16.4	NA
USNM 31976, Colombia	197.8 ×11.1	243.4 × 5.9	196.0 × 8.3	NA	16.8	NA
USNM 31992, Colombia	169.4 × 9.2	248.9 × 4.3	186.7 × 5.9	NA	15.2	NA
USNM 32912, Panama	185.7 × 10.4	250.7 × 5.8	192.8 × 6.9	NA	15.8	NA
USNM 1091302, Brazil	155.2 × 5.6	251.6 × 3.5	186.0 × 3.6	NA	12.5	154.7 × 5.0
Range of means	138.2–197.8 × 3.9–11.1	169.5–268.6 × 2.7–14.0	151.3–229.9 × 3.2–9.2	NA	11.0–16.8	131.4–167.6 × 3.8–5.0
Means of means	166.9 × 6.5	240.5 × 4.5	181.1 × 5.0	NA	14.9	152.7 × 4.3
Iotrochota arenosa						
USNM 60307, Belize	157.8 × 4.7	NA	150.4 × 4.2	216.9 × 4.1	11.4	NA
USNM 1091288, Belize	162.6 × 4.7	NA	145.0 × 4.9	230.0 × 3.9	11.2	NA
USNM 1091289, Belize	141.7 × 4.6	NA	144.5 × 4.7	211.1 × 3.7	11.3	NA
USNM 1091290, Belize	143.1 × 4.5	NA	150.6 × 4.2	205.2 × 4.2	10.9	NA
USNM 1091291, Belize	167.9 × 4.3	NA	151.6 × 4.7	225.2 × 4.0	11.2	NA
USNM 1091292, Belize	174.1 × 8.0	NA	155.9 × 6.7	214.9 × 3.7	12.4	NA
USNM 1092280, Belize	166.6 × 6.2	NA	158.1 × 6.8	217.9 × 4.8	12.1	NA
Range of means	141.7–174.1 × 4.3–8.0	NA	144.5–158.1 × 4.2–6.8	205.2–230.0 × 3.7–4.8	10.9–2.4	NA
Means of means	159.1× 5.3	NA	150.9 × 5.1	217.3 × 4.1	11.5	NA
I. atra						
AMNH 49, Bahamas, Nassau	NA	NA	164.9 × 2.5	NA	NA	NA
YPM 8530, Bahamas, Nassau	NA	NA	165.5 × 2.9	NA	NA	NA
USNM 30232, Bahamas, Bimini	NA	NA	188.1 × 2.7	NA	NA	NA
USNM 1091303, Bahamas, Bimini	NA	NA	170.8 × 3.6	NA	NA	NA
USNM 30233, Bahamas, Andros Island	NA	NA	184.6 × 2.9	NA	NA	NA
USNM 1091304, Bahamas, San Salvador	NA	NA	210.2 × 3.4	NA	NA	NA
Range of means	NA	NA	164.9–210.2 × 2.4–3.6	NA	NA	NA
Means of means	NA	NA	180.7 × 3.0	NA	NA	NA

Based on material of *Iotrochota birotula* from the Dominican Republic, Jamaica and Puerto Rico, Pulitzer-Finali (1986, fig. 61) described long, thin, straight accessory styles from specimens with strongly spiny surface. In contrast, softer, more mucous, not conspicuously aculeated specimens with smooth surfaces from Puerto Rico mangroves and Jamaica reefs and pilings contained accessory strongyles; these are here referred to *I. arenosa*, sp. nov.

Van Soest (1984, fig. 11) redescribed the holotype of *Hyrtios musciformis* Duchassaing & Michelotti, 1864, a synonym of *Iotrochota birotulata*. Although it is a thin incrustation on coral, the skeleton fibre reticulation and spicule complement (styles, strongyles, birotulae) are in full agreement with the latter species. Additional description of material from the Dutch West Indies mentions strongyles (some oxeote), styles and birotulae, but disputes any localisation of strongyles and styles as claimed by Bergquist (1965), also referring to material from Jamaica.

Iotrochota bistylata Boury-Esnault, 1973 (synonomised by Hechtel 1976) is based on two black, encrusting or erect claviform specimens collected off the central cost of Brazil (34 m, 57 m), which were characterised as having relatively large megascleres and two categories of styles. Both features are consistent with observations made on typical specimens of *I. birotulata* from Caribbean locations and are shared by another specimen from offshore Brazil examined by us (USNM 1091302: Collette and Rützler 1977).

A few (seven in all) fragments obtained by the South-west Florida Shelf Ecosystem Study (for Mineral Management Service) in the Florida Gulf of Mexico from 32 to 52 m and examined by us contained primarily accessory strongyles instead of styles. The taxonomic significance of this variation has yet to be determined. Other characteristics were typical for the species and different specimens from the same location had the typical spicule complement.

Iotrochota arenosa, sp. nov.

(Figs 1, 4, 5; Tables 1, 2)

Material examined

Holotype. USNM 60307, Belize, Carrie Bow Cay, lagoon due north-west; 16°48.506′N, 88°05.233′W, *Thalassia* seagrass and sand, 6 m, K. Ruetzler, 7.iii.2006.

Paratypes. USNM 1091288, Belize, Carrie Bow Cay, lagoon due north-west, 16°48.506′N, 88°05.233′W, K. Ruetzler, 7.iii.2006. USNM 1091289, USNM 1091290, USNM 1091291 (same data as above). USNM 1091292, Belize, Blue Ground Range, west of Carrie Bow Cay, 16°48.55′N, 88°08.89′W, 1–2 m, R.W.M. van Soest *et al*., 1.viii. 1997.

Diagnosis

Dark purple, cushion-shaped to massive, strongly mucuous *Iotrochota* incorporating large amounts of coarse sand. Main skeleton fibres charged with short, curved, stout styles (mean 159 × 5.3 μm) and strongyles (mean 151 × 5.1 μm) and with longer, straight, thin accessory strongyles (free, or in wispy strands; mean 217 × 4.1 μm). Birotulae common, 11.5 μm average length (Table 2).

Morphology of type material

Holotype, USNM 60307, purplish black, thickly encrusting, smooth surface, 17 cm long, by 2.2–5 cm wide, by 1.6–2.5 cm thick. Soft in life and strongly mucous when touched, incorporates abundant coarse carbonate sand and small coral fragments. Spicule tracts present among sediment grains in the choanosome (55–85 μm thick). Spicules, styles and strongyles contained in fibres, accessory strongyles and scattered birotulae (Table 2). Paratypes from same habitat with very similar morphology (5–10 cm diameter, with short branches, 0.6–2.5 cm thick); one (USNM 1091292), from mangrove lagoon 7 km south-west, more rounded and massive.

Description

External features

Colour uniform, very dark (near black) purplish brown. Shape lumpy encrusting or cushion-like repent, with few branches separating and anastomosing. Older specimens irregularly massive to 10-cm high, with irregular chimney-like protuberances. Average size (297 individuals) 13.9 cm^3. Upper surface leathery smooth, except for embedded coarse sediment grains (1–4 mm) and small clusters of conules. Sporadic conules less than 1 mm tall, lifted by converging brushes of spicule fibres. In fixed specimens, small oscula (0.5–1.5 mm) here and there, mostly inconspicuous in depressed areas. In life, oscula (2–4 mm diameter) with raised collars (5 mm height) resulting from extension of translucent, delicate exopinaderm. Outer membrane separates from underlaying choanosome, revealing wide subectosomal aquiferous spaces converging upon the oscules. Pinacoderm collapses almost instantaneously upon disturbance of pumping sponges, oscules close and retract. Ostia common and in sieve-like clusters. Lower sponge surface incorporates large sand grains (6 mm, and more), covered by thin layer of ectosome. Few large particles exposed, having served as attachment points for sponges that generally lay loose on the bottom, except where wrapped around seagrass (*Thalassia*) blades and algae. No signs of necrosis or colour fading where up to half of sponge grows buried in sediment, indicating adaptation to life in sand substrata rather than accidental burial.

Consistency

Smooth except for partially embedded sediment grains; easily broken or torn. When damaged, exuding large amounts of purple mucus (mucus not evident in preservation alcohol, only in water-based fixatives such as glutaraldehyde, formaldehyde–seawater).

Anatomy

Large quantity of embedded sand conspicuous when cutting specimens. Sand derived from habitat substratum, consisting of carbonate shells and skeletal remains of calcified algae (e.g. Corallinaceae, *Halimeda),* protozoans (foraminiferans) and invertebrates (corals, molluscs, echinoids). Spongin fibres packed with spicules (styles I, strongyles I) meandering among embedded sand grains, forming loose meshwork and ending in surface conules. Fibre diameter 100–330 μm. Loose megascleres (strongyles II) scattered throughout tissue, also in poorly

organised strands fanning out towards sponge surface. Rare oxeas present, but location in choanosome undetermined. Microscleres (birotulae) scattered, most located along canals and near ectosome. Spicule measurements in Table 2. Choanocyte chambers identical to those of type species.

Ecology and distribution

The species co-occurs with *Iotrochota birotulata* in both habitats where it has been collected, among *Thalassia* seagrass in the outer Belizean shelf lagoon, and in a mangrove pond inside one of the Blueground Range mangrove islands; 1–6 m depth. No association with a zooanthid was observed. Examination of 165 random quadrats (1 × 1 m) revealed a patchy distribution of this sponge in the *Thalassia* bed, with some localised areas of very high density (3.5 individuals per m^2 on average; 67 quadrats) and adjacent areas containing no individual (98 quadrats). Examination of similar numbers of quadrats at adjacent patch and fore reefs and mangroves did not reveal the presence of any individual of this species. The contiguous distribution may be indicative of species dispersal by means of short-lived larvae with phylopatric recruitment, asexual reproduction based on production of relatively large body fragments, or a combination of both processes. The species is known from the type locality in Belize and, possibly, from Puerto Rico and Jamaica (there from 0.1–45 m depth; see comments below).

Remarks

Iotrochota arenosa differs from all other Caribbean species of the genus by its evenly purplish brown colour, smooth surface, very strong mucus production when handled and a spicule complement of one category of styles (I, in fibres) and two categories of strongyles (I, in fibres, and II, free in the tissue). Moreover, according to our observations, strongyles in fibres are much rarer than the same type in *I. birotulata.*

Specimen USNM 1091292 is unusual because it is irregularly massive and rather porous in internal structure. The

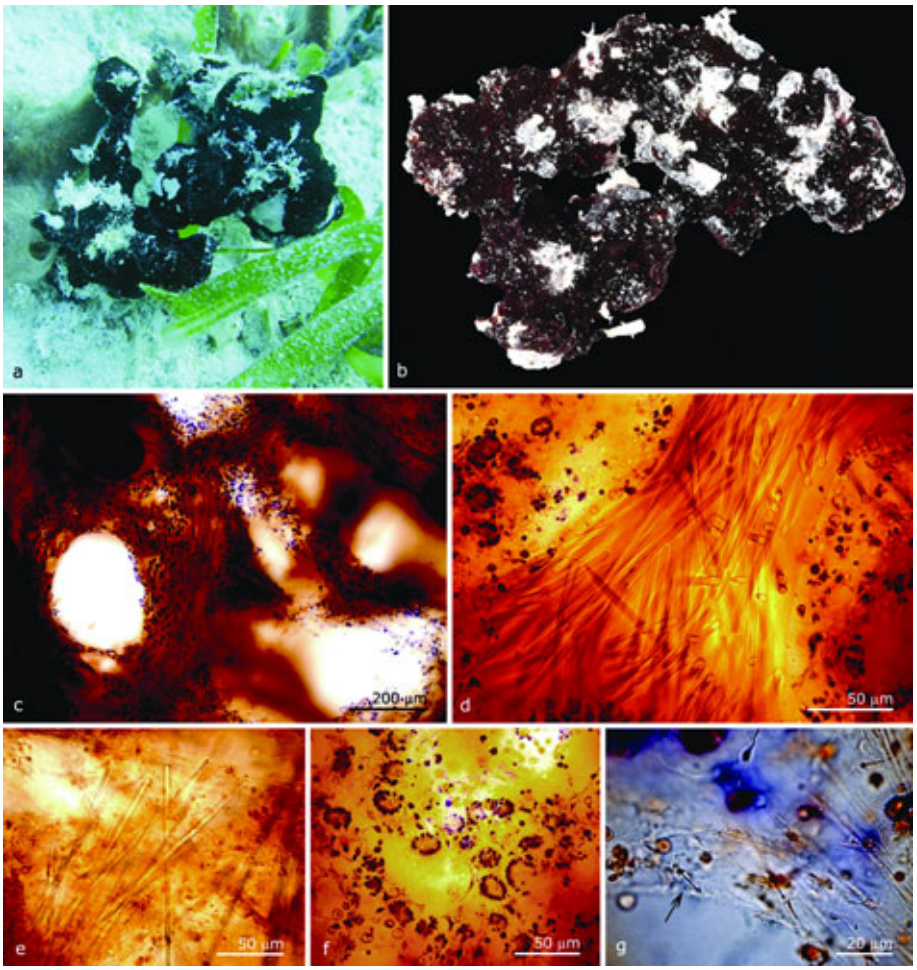

Fig. 4. *Iotrochota arenosa*, sp. nov. (*a*, *b*) Live specimens and (*c*–*g*) microanatomy. (*a*) Cushion-shaped sponge on sandy lagoon bottom with *Thalassia* seagrass, north-west of Carrie Bow Cay, 6 m depth (picture width, 20 cm;). (*b*) Specimen from same location in the laboratory, cleaned of loose sand (picture width, 20 cm). (*c*) Choanosome with embedded sand grains. (*d*) Spicule strand made up of tightly intertwined styles I and strongyles I. (*e*) Accessory spicules (strongyles II). (*f*) Choanocyte chambers. (*g*) Cellular tissue with birotula (arrow).

spicules, although identical in complement to that of the typical encrusting form, are considerably more robust (Table 2), a phenomenon that can be interpreted as the result of an environmental influence (the habitat was the bottom of a very calm mangrove pond), or an age condition. For the time being, we have no grounds to separate this single specimen from the *Iotrochota arenosa* population.

In his study of *Iotrochota birotulata,* Pulitzer-Finali (1986, fig. 61) described a few softer, more mucous, not conspicuously spined (conulose) specimens that had accessory strongyles. They occurred in a mangrove in Puerto Rico (his specimen LP.72), and on wharf pilings and reefs in Port Royal (KC.14; PR.20) and Duncans (NC.6), Jamaica, between 0.1 m and 45 m depth, and may well be representatives of the present species.

Another recently described species, *Iotrochota agglomerata* Lehnert and van Soest (1999) occurs on the deep fore reef (79 m) off Discovery Bay, Jamaica. It is encrusting and, like *I. arenosa*, agglutinates substrate particles (calcareous polychaete tubes, *Halimeda* chips), and sand is incorporated throughout the choanosome. The principal difference to *I. arenosa* is the orange colour and the spicules, which are exclusively styles with transitions to tylostyles, contained in and protruding from skeleton fibres and occurring free.

Etymology

Named for one of its distinctive properties: *arenosus* (Latin), full of sand.

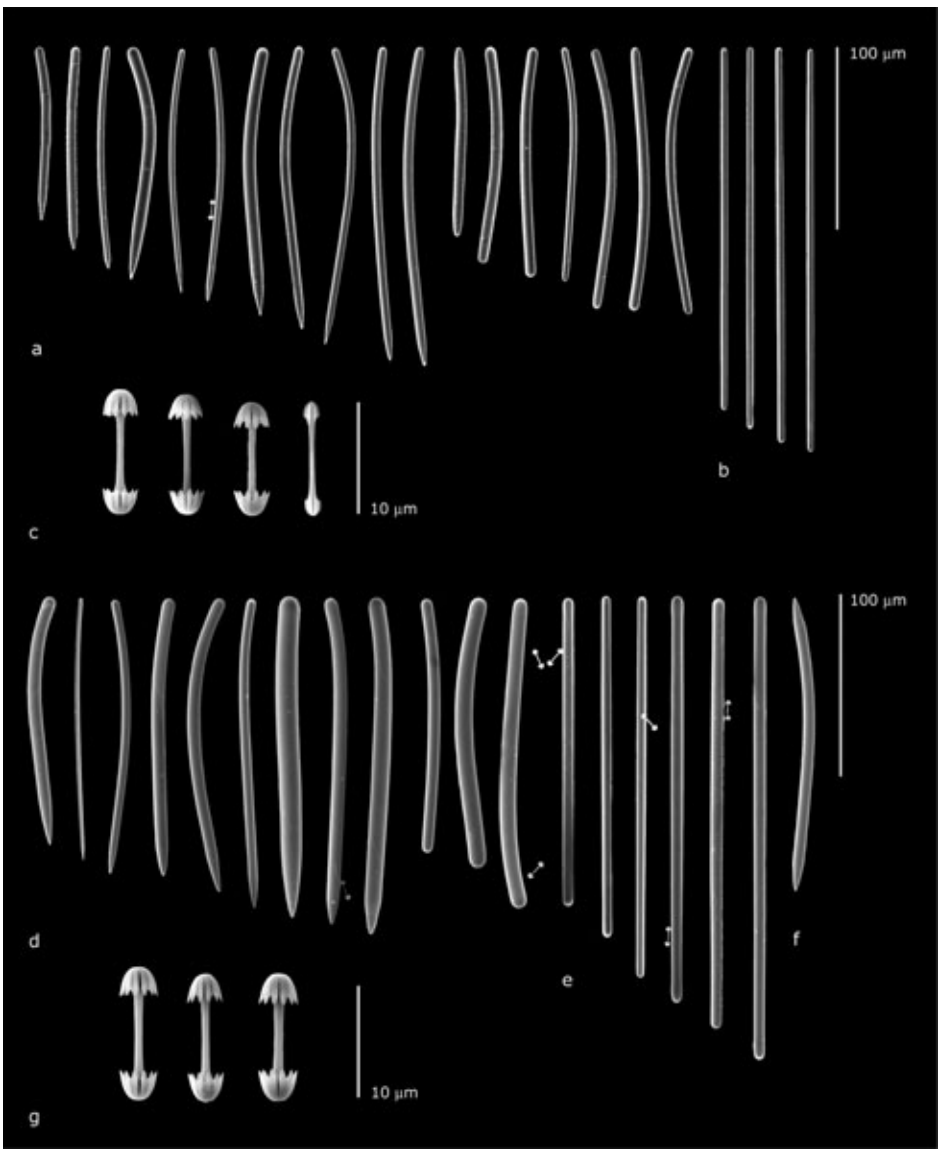

Fig. 5. Spicules (scanning electron micrographs) of *Iotrochota arenosa*, sp. nov. collected in Carrie Bow Cay lagoon (*a–c*) and Blueground Range (*d–h*). (*a*) Curved styles I and strongyles I. (*b*) Straight accessory spicules (strongyles II). (*c*) Birotulae. (*d*) Curved styles I and strongyles I. (*e*) Straight accessory spicules (styles II). (*f*) Oxea (location in skeleton undetermined). (*g*) Birotulae.

Iotrochota atra (Whitfield)

(Figs 1, 6, 7; Tables 1, 2)

Hircinia atra Whitfield, 1901: 49, plate V.

Halichondria birotulata Higgin, 1877: 298 (specimens in the 'Argo' collection from Nassau, Bahamas).

Iotrochota birotulata (Higgin): Wiedenmayer, 1977: 138, fig. 144, pl. 21–25.

Iotrochota imminuta Pulitzer-Finali, 1986: 141, figs 62, 63.

Material examined

Holotype. AMNH 49 (dry) (fragment at YPM; specimen at AMNH was unavailable); Bahamas, Nassau, New Providence, 25°04′N, 77°21′W; R.P. Whitfield, 1899.

Other material examined. **Bahamas:** Nassau, New Providence, YPM 8530 (dry); Bimini, W of S Turtle Rock, USNM 30232 (dry); Bimini, Turtle Rocks, coral-rock, USNM 1091303; Andros Island, SW of Long Rock, USNM 30233 (dry); San Salvador, USNM 1091304.

Diagnosis

Purplish black to greenish, branching erect (single branches, fans, bushes), somewhat mucous *Iotrochota*. Spiculation characteristic for megascleres reduced to one type (strongyles and modifications, 181 × 3.0 μm) and lack of microscleres.

Morphology of type material

According to original description (Whitfield 1901: pl. V), sponge was deep, shining black when alive (retained in dried state) and colour readily given off on being handled. Specimens rigid, bush-like, profusely branched and growing to 60 cm or more in height (type specimen 24-cm tall). Branches 2-cm diameter, broader at bases. Fragment (examined by us) revealed fibres (65–225 μm thick) composed exclusively of tightly packed, thin strongyles (some with tapering or pointed terminals). Spicules (measurements, Table 2) easily broken during preparation; similar megascleres also scattered throughout the remaining tissue.

Description

External features

Purplish black, with emerald-green or yellowish to pinkish tinges in places. Ramose to bushy, erect to sprawling, irregularly branching and anastomosing. Branch diameter 1–2 cm, up to 3 cm at base. Dark purplish, mucous exudate when handled. Externally, specimens not distinguishable from *Iotrochota birotulata.*

Consistency

Stiff, conulose; some specimens fairly smooth, with grooves between fibres running along the surface (possibly an effect of age, or fixation).

Anatomy

Irregular reticulation of spongin fibres (30–250-μm diameter) containing densely intertwined, slender strongyles as the

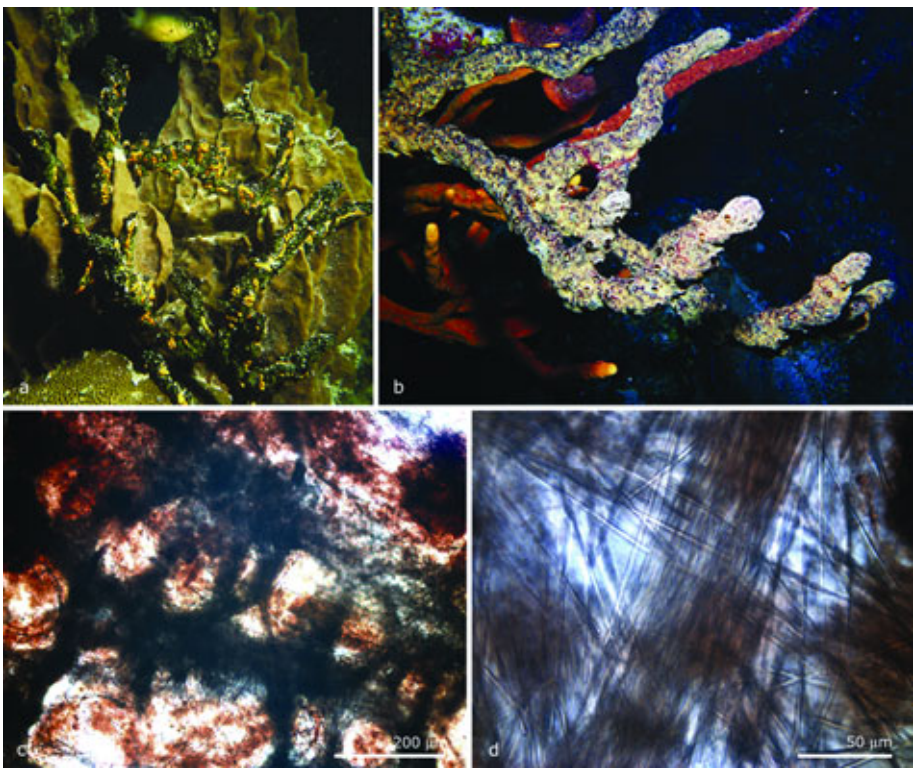

Fig. 6. *Iotrochota atra*. (*a*, *b*) Live specimens *in situ* and (*c*, *d*) microanatomy. (*a*) Branching erect purplish to black sponge covered by golden *Parazoanthus swiftii* on a reef near Bimini, 6 m depth (picture width, 50 cm). (*b*) Blackish-to-yellow specimen from a reef off San Salvador, 12 m depth (picture width, 16 cm; photo, R. Ritson-Williams). (*c*) Fibres charged with strongyles and randomly positioned interstitial spicules. (*d*) Detail of skeleton fibre and spicule arrangement.

only spicule type; strongyles of the same size category also scattered between fibres, without particular orientation (measurements, Table 2). Strongyles very thin and delicate, straight to bent, some tapering towards the ends approaching the shape of styles or oxeas, or anisostrongylote; a few are looped (cf. Wiedenmayer 1977). Choanocyte chambers not different from the other species.

Ecology and distribution

On reefs and rocky lagoon bottom, also cave habitats, 1–5 m depth. Association with zoanthids, *Parazoanthus swiftii*, is common.

Exclusive to the Bahamas, including Bimini, New Providence (off Nassau), San Salvador and Andros islands.

Remarks

Pulitzer-Finali (1986) established a new species from the Bahamas, *Iotrochota imminuta*, based on the absence of styles and birotulae. Higgin (1877) too considered his Bahamas specimens to be different despite the outer morphological resemblance, postponing judgment until further studies that were never done. He referred to a greater spongin content of the fibres, but mainly to the absence of birotulae. Whitfield (1901) was apparently unaware of Higgin's species and did not include spicule components in his description. Wiedenmayer (1977) stated, although hesitantly, that the uniform megascleres (stongyles only) and the absence of microscleres were acceptable variations within a species. He listed the syntypes of *I. birotulata* as having originated from Puerto Cabello, Venezuela (BMNH 1877.3.9.1) and Nassau, Bahamas (BMNH 1877.3.9.2), but neither he nor van Soest (2002) commented on the spicule composition of the latter (no specimen available, only two spicule slides).

Key to species of Atlantic *Iotrochota*

1. Sponge branching; greenish black 2
   Sponge encrusting or massive 3
2. Spicules include styles, strongyles and birotules. . . . . *I. birotulata* (Higgin)
   Spicules composed of strongyles, no microscleres . . . . . *I. atra* (Whitfield)

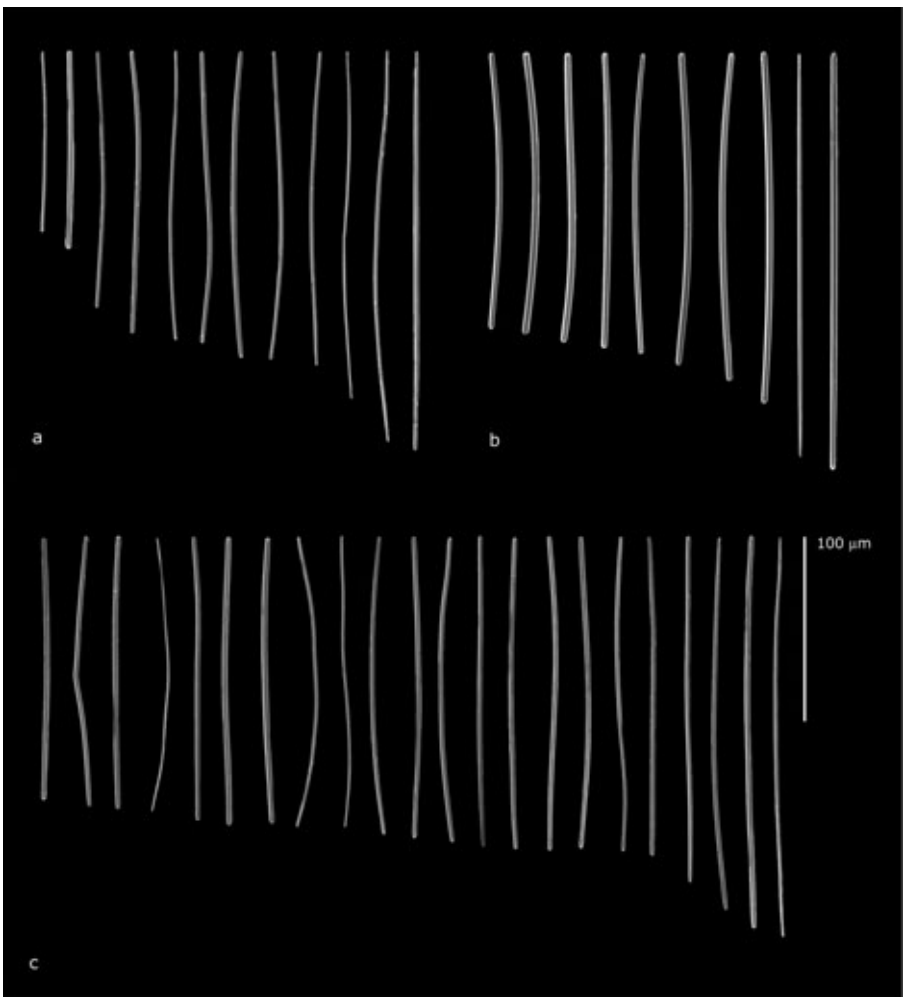

Fig. 7. Spicules (scanning electron micrographs) of *Iotrochota atra,* strongyles with few styloid and oxeote modifications. (*a*) Holotype, AMNH 49. (*b*) USNM 1091303. (*c*) YPM 8530.

3. Sponge encrusting; orange; with styles and birotules . . . . . *I. agglomerata* Lehnert & van Soest
Sponge massive; purplish black; with strongyles and birotules . . . . . *I. arenosa*, sp. nov.

Discussion and conclusion

The poecilosclerid *Iotrochota birotulata* is among the 10 most common siliceous sponges in a typical tropical western Atlantic coral-reef ecosystem and contributes significantly to the process of silicon cycling (Rützler and Macintyre 1978). It is not only the type species of the genus, but for more than 120 years it was considered the only species in the area, despite two described additions (Boury-Esnault 1973; Pulitzer-Finali 1986), which were generally dismissed as junior synonyms. Only recently, a different species of *Iotrochota* became known from a deep-reef habitat off Jamaica (Lehnert and van Soest 1999). This discovery and our own findings of distinctive congeneric specimens in Belize encouraged us to re-examine the morphological attributes on which species of *Iotrochota* have been or should be based.

In the present study we used all available ecological and zoogeographical information, and employed biometry and high resolution SEM; even though the latter technique does not necessarily reveal new features, it greatly clarifies structural details. The conclusion is that we can now distinguish, in the field and employing only basic microscopy, four species of *Iotrochota*: the type species *I. birotulata,* based on primarily erect branching growth, greenish to blackish colour, stiff consistency, a spicule complement of two categories styles, one category strongyles and birotulae, and occurrence on shallow reefs except those of the Bahama Bank; *I. agglomerata,* characterised by an orange colour, thinly encrusting, sediment-agglutinating habit, one category of styles (transitions to tylostyles) and birotulae, and known occurrence restricted to deep-reef habitat off Jamaica; *I. arenosa,* which is purplish black, cushion-shaped to massive, fairly soft and mucuous but incorporating coarse sediment grains, has spicules consisting of one category styles, two categories strongyles, and birotulae, and occurs in shallow lagoons near the barrier reef of Belize, possibly elsewhere (yet to be confirmed); and *I. atra,* which is nearly identical in all aspects to *I. birotulata,* but has a spiculation reduced to just one kind, thin strongyles and a distribution restricted to shallow reefs of the Bahamas. It is interesting to note that *I. atra* has an external morphology seemingly identical to the type species, but is the only species with a radically different (strongly reduced) spiculation and a distinctive geographical distribution. The other three species are sympatric but morphologically easily distinguishable.

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