

Lissodendoryx: rediscovered type and new tropical western Atlantic species (Porifera: Demospongiae: Poecilosclerida: Coelosphaeridae)

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Seven syntypes of *Halichondria isodictyalis*, type species of *Lissodendoryx*, were rediscovered and studied. By choosing a lectotype and studying it along with the paralectotypes, we find that *L. isodictyalis*, subgenus *Lissodendoryx*, is a Caribbean sponge characterized by smooth megascleres, ectosomal tylotes and choanosomal styles, and one size-class of microscleres comprising arcuate isochelae and sigmas. Having determined these characteristics, we re-erect *Lissodendoryx (Lissodendoryx) carolinensis* (previously synonymized with *L. isodictyalis*), with the same smooth megascleres but two distinct size categories of microscleres, isochelae and sigmas; and we add a new western Atlantic species, *Lissodendoryx (L.) spinosa* sp. nov., with coarse spines on the megasclere terminals and with two size-classes of isochelae and sigmas. Other species in the region are *Lissodendoryx (L.) colombiensis*, with smooth tylotes and robust strongyles, and two categories of microscleres (isochelae and sigmas) accompanied by conspicuous raphids arranged in trichodragmas; *Lissodendoryx (L.) strongylata*, with smooth tylotes and slim strongyles, one size-class each of isochelae and sigmas, rare and very thin raphids. *Lissodendoryx signata* is here assigned to the subgenus *Anomodoryx*, with smooth tylotes exclusively as megascleres, two size-classes of isochelae, and one or two sizes of sigmas; it may represent a species complex far more diverse than previously thought. To this subgenus we add another species, *Lissodendoryx (A.) amphispinulata* sp. nov., characterized by fine spines ornamenting both tyles of part of the tylotes. A third subgenus, *Ectyodoryx*, is represented by *Lissodendoryx (E.) acanthostylota* sp. nov., with smooth tylotes and finely spined acanthostyles in two size-classes, as well as two size-classes each of isochelae and sigmas as microscleres. All species studied alive occur in shallow lagoon habitats with mangroves and sea grass (*Thalassia*) but museum specimen records show that some may reach a depth of 60 m.

INTRODUCTION

The type material for *Halichondria isodictyalis* Carter, 1882 type species of the genus *Lissodendoryx* Topsent, 1892 (subgenus *Lissodendoryx* Topsent), has not been examined since the original species description (Carter, 1882). It was considered lost, at least in part, as a result of World War II bombing of Britain, but recently discovered in the collection of the National Museums Liverpool (LIVM). Seven of the eight syntypes are conspecific and considered representative of the species; all are from Puerto Cabello, Venezuela (one belongs to Haplosclerida, collected in the Bahamas, and is obviously mislabelled and not part of the series).

Over the past three decades we collected specimens of *Lissodendoryx* throughout the tropical western Atlantic, from Florida and the Bahamas to Venezuela, Panama and Belize. Members of the genus occur mainly in lagoon environments and are easily recognized by a spicule combination of ectosomal tylotes, choanosomal styles, subtylostyles, strongyles, or tylotes, and microscleres including arcuate isochelae and sigmas in various combinations and size-classes, and, in some species, trichodragmas.

Based on earlier descriptions (for instance, Hartman, 1958), we presumed that one of the common sponges was the type species *Lissodendoryx isodictyalis* Carter, characterized by smooth tylotes and styles, and two size categories of isochelae and sigmas. In addition, we discovered that there were very similar-looking specimens that had only one size-class of these microscleres, others that contained megascleres that were ornated by spines. In a monograph of the poecilosclerid fauna of the Netherlands Antilles (van Soest, 1984), followed by a revision of the genus (van Soest, 2002), one of the spined specimens was described erroneously as typical *L. isodictyalis*, apparently because it was a common sponge at a location close to where the types were obtained, and because the type material could not be located at the Natural History Museum, London, where it was presumed to be deposited (Wiedenmayer, 1977).

Rediscovery of the syntypes of *Lissodendoryx isodictyalis* allows us to characterize the 'real' type species and thus define seven other Caribbean species, four of them new, by studying specimens deposited in Washington's National Museum of Natural History.

MATERIALS AND METHODS

This contribution emerged as part of a long-term study of sponges in mangrove islands on the Mesoamerican barrier reef near Carrie Bow Cay, Belize (16°48.1'N 88°04.9'W) (Rützler et al., 2000, 2004; Díaz et al., 2004). New material was collected by snorkelling or free diving, fixed in formalin-seawater (10%) and preserved in 70% ethylene alcohol. Hand sections and spicule preparations, after gentle boiling in concentrated nitric acid, were made for the study of skeleton structure and spicule morphology. For scanning electron microscopy (SEM), spicules were cleaned by extra 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) at 500×, 600×, 800×, 2500× and 4000× primary magnification. Spicule measurements (20 for each type and dimension) were made of selected specimens (from diverse localities, if applicable) by both light microscopy and from SEM images.

Museum designations and abbreviations are: AMNH, American Museum of Natural History, New York City, New York; BMNH, the Natural History Museum, London; ICN-MHN(Po), Instituto de Ciencias Naturales, Museo de Historia Natural Porifera Collection, Bogotá D.E., Colombia; LIVM, National Museums Liverpool; MMS-BLM, Minerals Management Service-Bureau of Land Management; 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, Connecticut; ZMA, Zoological Museum, Amsterdam.

SYSTEMATICS

Order POECILOSLERIDA Topsent, 1928

Suborder MYXILLINA Hajdu, van Soest & Hooper, 1994

Family COELOSPHAERIDAE Dendy, 1922

Genus *Lissodendoryx* Topsent, 1892

Synonymy

Lissodendoryx Topsent, 1892: 97 (for more synonyms, see van Soest, 2002: 540).

Type species

Tedania leptoderma Topsent, 1889: 49 [= *Lissodendoryx isodictyalis* (Carter, 1882) fide Topsent, 1897: 456].

Diagnosis

Thickly encrusting, or irregularly massive to lobate, volcano-shaped, or digitate coelosphaerid sponges; large oscula usually on top of projections. Surface smooth to rugose. Tangential ectosomal skeleton of tylotes, or strongyles, in tracts. Choanosomal skeleton composed of smooth or acanthose styles, tylotes, or oxeas in isodictyal, renierid reticulation; some occurring in multispicular strands, loose in between the meshes, or echinating. Microscleres include arcuate isochelae, sigmas, and raphides (arranged in trichodragmas).

Remarks

Five subgenera are distinguished (van Soest, 2002). From the study of our material, three of these are represented in

the Caribbean: *Lissodendoryx*, with full spicule complement but lacking echinating megascleres; *Anomodoryx*, like the former subgenus but with a single type of megascleres (tylotes or strongyles); and *Ectydoryx*, possessing echinating acanthostyles.

Lissodendoryx (Lissodendoryx) isodictyalis (Carter, 1882)
(Figures 1A,B & 2; Table 1)

Halichondria isodictyalis Carter, 1882: 285; pl. XI (2a–e).

Tedania leptoderma Topsent, 1889: 49, figure 12.

Dendoryx (Lissodendoryx) leptoderma (Topsent): Topsent, 1892: 97.

Lissodendoryx isodictyalis (Carter): de Laubenfels, 1936: 93, pl. 11 (2); de Laubenfels, 1950: 73, figure 33; Hartman, 1958: 41, figure 11; Hechtel, 1965: 38 (with more synonyms); Wiedenmayer, 1977: 135, figures 141, 142, pl. 29 (2); Pulitzer-Finali (1986: 146; specimen BL, 32 only); Zea, 1987: 159, figure 53 (with more synonyms); Rützler, 1986: 120, figure 31, pl. 3.1 (7); Díaz, 2005: 472; Collin et al., 2005: 651 (+figure). [Non] van Soest, 1984: 4; figure 19; pl. V (2–3) = *L. spinulosa* sp. nov.

Esperiopsis fragilis Verrill, 1907: 333; pl. XXXV–C (1–3).

[Non] *Lissodendoryx isodictyalis sensu* Topsent, 1897: 456 (= *L. similis* Thiele, 1899, fide Hofman & van Soest, 1995: 90; *Lissodendoryx carolinensis* Wilson, 1911: 11; George & Wilson, 1919: 150, pl. LXI (26–28), LXVI (62a–e) (see redescription below).

Type material

Lectotype: Venezuela, Puerto Cabello (10°28'N 68°01'W; habitat and water depth: not given); coll. by Argo Expedition, 1876 (LIVM Sp. 64).

Paralectotypes: Venezuela, Puerto Cabello (coordinates, as above); coll. by Argo Expedition, 1876 (LIVM Sp. 57, 58, 62, 63, 66, 73).

Type locality

Venezuela. The original description (Carter, 1882) includes material from Acapulco (Pacific Mexico), none of the extant syntypes are from this location. Another Carter specimen (supposedly of this species) in the Liverpool collection, labelled Nassau [Bahamas] Sp. 113, is a chalinid sponge, order Haplosclerida (containing oxeas and sigmas).

Comparative material examined in detail

Bahamas: West Andros Island (24°26'N 77°57'W; 2 m); coll. by F. Wiedenmayer, 1965 [USNM 30226; described under field number O-747 in Wiedenmayer, 1977: 135].

Belize: Twin Cays (16°49.366'N 88°05.750'W; mangrove, Dock; water depth: 1 m); coll. by K.P. Smith and K. Ruetzler, 26 May 1986 [USNM 42984]. Twin Cays (16°49'43.3"N 88°6'17.1"W; mangrove, Sponge Haven; water depth: 0.5 m); coll. by S. Duran, 29 July 2004, date [USNM 1104598]. Blueground Range (16°48.531'N 88°08.927'W; mangrove pond; water depth: 1 m); coll. by R.W.M. van Soest et al., 1 August 1997 [USNM 1104599].

Bermuda: Harrington Sound (32°19'49.9"N 64°43'19.0"W; mangrove; water depth: 0.5 m); coll. by W. Bergmann, 1946 [USNM 31659]. Walsingham Pond (32°19'N 64°44'W; mangrove; water depth 0.6–2.5 m); coll. by J.H. Cardellina, August 1983 [USNM 32846].

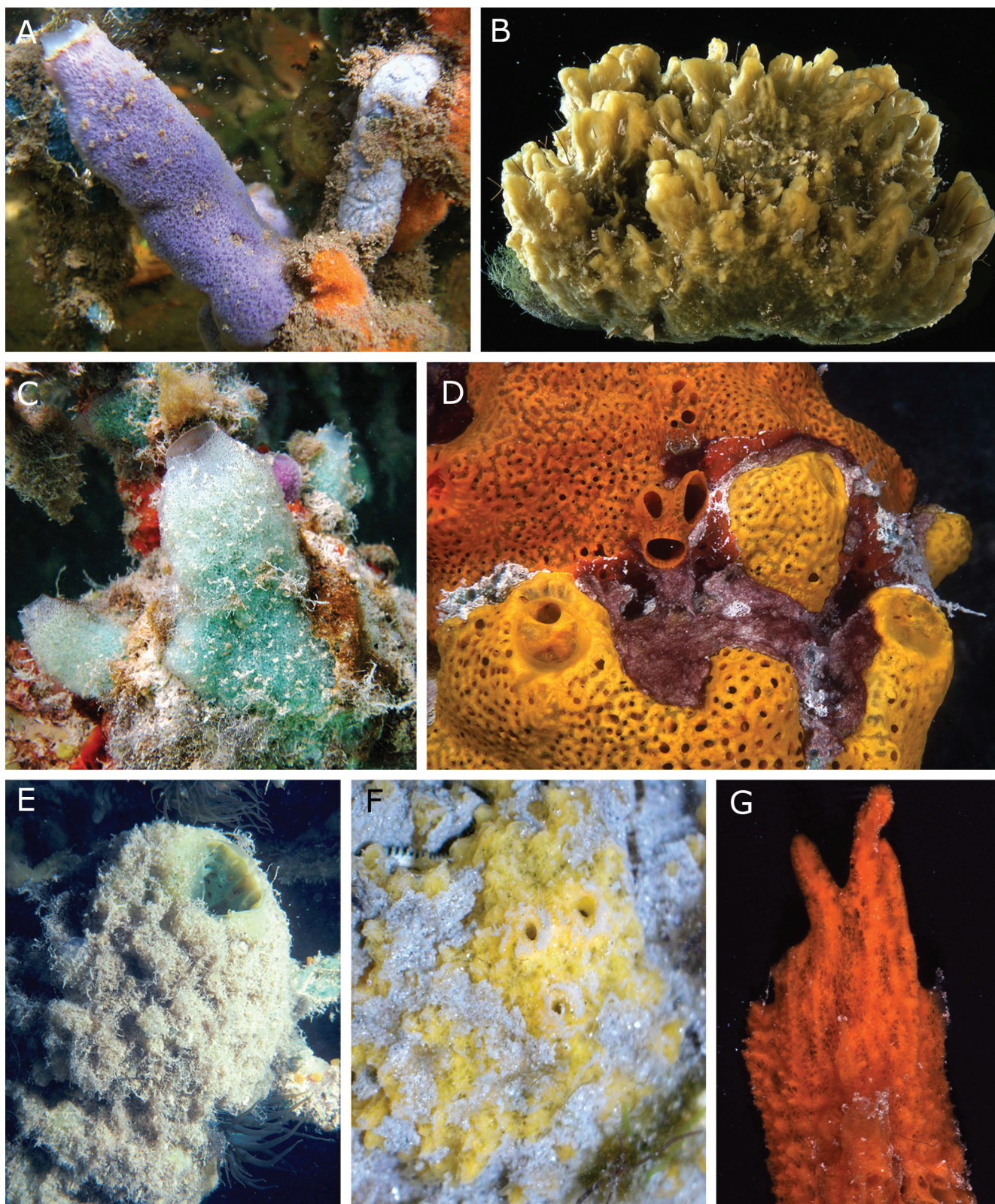


Figure 1. (A–G) Live specimens of *Lissodendoryx* species illustrating variations in shape and colour. (A) *Lissodendoryx isodictyalis* (Carter) *in situ*; Twin Cays, Belize, mangrove; (B) same species live in aquarium; Harrington Sound, Bermuda (photograph: G.K. Jensen & W.E. Sterrer); (C) *L. carolinensis* Wilson *in situ*; Twin Cays (photograph: S. Duran & M. Becerro); (D) *L. colombiensis* Zea & van Soest, two colour variants *in situ*; Twin Cays; (E) *L. spinosula* sp. nov. *in situ*; Twin Cays; (F) *L. signata* (de Laubenfels), var. nov.? *in situ*; Atlantic Florida; (G) *L. signata* (de Laubenfels), live in aquarium; Twin Cays.

Cayman Islands: Grand Cayman, North Sound (19°23'12.0"N 81°20'46.8"W; mangrove lagoon; water depth: 0.3 m); coll. by R. Schroeder, 1 July 1972 [USNM 32922].

Dominican Republic: Bahia las Calderas, Las Salinas (19°53'N 71°40'W; mangrove; water depth: 0.1 m); coll. by V. Vicente, 23 July 1978 (USNM 32254).

Table 1. *Spicule types and measurements for representative specimens of Lissodendoryx (L.) isodictyalis (Carter). Measurements are means (N=20, in µm) of maximum dimensions (length, or length×width) of spicules.*

| Specimen, location | Tylotes | Styles | Isochelae | Sigmas | Raphids |
|--|---------------------|---------------------|-----------|-----------|------------|
| LIVM Sp. 64, Venezuela (Lectotype) | 202.8×4.2 | 168.3×4.8 | 23.7 | 20.5 | n.a. |
| LIVM Sp. 57, Venezuela (Paralectotype) | 200×3.8 | 163.7×5 | 25.2 | 20.4 | n.a. |
| LIVM Sp. 73, Venezuela (Paralectotype) | 197.1×4 | 156.6×4.8 | 25.8 | 20.8 | 81.3 |
| USNM 42984, Belize | 207.9×4.2 | 175.2×4.8 | 41.4 | 22.1 | n.a. |
| USNM 32846, Bermuda | 177.9×3.1 | 148.6×3.8 | 19.6 | 18.3 | 125.7 |
| USNM 1104600, Florida Keys | 197.4×4.2 | 169×5.7 | 24.1 | 21.9 | n.a. |
| USNM 32254, Dominican Republic | 204.7×3.6 | 170.7×4.4 | 24.1 | 22.9 | n.a. |
| Range of means | 177.9–207.9×3.1–4.2 | 148.6–175.2×3.8–5.7 | 19.6–41.4 | 18.3–22.9 | 81.3–125.7 |
| Means of means | 198.3×3.9 | 164.6×4.8 | 26.3 | 21 | 103.5 |

n.a., not applicable.

Florida: Dry Tortugas (24°37'43"N 82°52'24"W; Fort Jefferson moat; water depth: 10 m); coll. by M.W. de Laubenfels, 28 June 1932 [USNM 22462; 22471]. Florida Keys (24°41'9.6"N 81°21'36"W; mangrove, Keys Marine Laboratory; water depth: 0.5 m); coll. by S. Duran, 30 May 2004 [USNM 1104600].

Additional material surveyed

The following microscope slides in USNM were checked and the spicules found in agreement with this species. Bahamas: USNM 30227 (described under field number B-933 in Wiedenmayer, 1977: 136). Belize (Twin Cays): USNM 34617, 34622, 34624, 41250, 41251, 41254, 41280, 41284, 41355, 42910, 42947, 42974, 42981, 42982, 43010, 43011, 1104601. Bermuda: 5 uncatalogued specimens, field numbers BE 5; BE 36B; 77.9.13-10; 77.9.19-3; 77.9.19-9. Mexico (Pacific coast): preparations made from three fragments coll. by J.L. Carballo (Universidad Autónoma de México, Mazatlán) in shallow coastal waters; USNM 1104602 (Mazatlán), USNM 1104603 (Isleta Los Cantaros), and USNM 1104604 (Estero El Zacate).

Diagnosis

Lissodendoryx with choanosomal styles, ectosomal tylotes, and microscleres consisting of one category each of arcuate isochelae and sigmas. This species is the type species.

Description of lectotype

The lectotype is a reddish tan, amorphous, coarsely porous dry specimen, ~4×4×5 cm. The paralectotypes are in similar condition and measure 9.5×4 cm (Sp. 57); 5×4 cm (Sp. 58); 6×4 cm (Sp. 62); 3×2 cm, 2.5×2.5 cm (Sp. 63, 2 fragments); 4×3 cm (Sp. 66); 2–3 cm (Sp. 73, numerous conspecific fragments). Dimensions were taken from scaled photographs. Spicules of lectotype consist of ectosomal smooth tylotes, 181.2–215.8 µm (202.8 ±8.9 µm, mean ±SD) × 2.8–5.5 µm (4.2 ±0.6 µm); choanosomal smooth styles, 150.1–174.6 µm (168.3 ±5.4 µm) × 3.4–5.7 µm (4.8 ±0.5 µm); isochelae, 21.3–26.9 µm (23.7 ±2.2 µm); and sigmas, 17.6–24.9 µm (20.5 ±2.1 µm).

Description

Colour: highly variable, from purple, blue, pale blue, bluish-grey, bluish green, turquoise, olive-grey, clear green,

yellow-green, clear yellow, golden yellow, to grey and almost white (Figure 1A,B). The interior is often just a bit lighter in hue as the surface, or drab to grey and whitish; the bleaching seems to be caused or enhanced by tissue damage during low-tide exposure to air. There is no correlation between colour and habitat or geographical distribution.

Shape, size, consistency: thickly encrusting to amorphous massive, 0.5–12.0 cm thick, up to 20 cm in diameter. Surface undulating but smooth, often formed by a colourless ectosomal membrane over subectosomal spaces that converge toward oscula. Oscula conspicuous (1–30 mm diameter), with membranaceous, translucent collars, raised on 2–15 cm high digitate processes or mounds. Choanosome bread-like, cavernous, lumina of oscular tubes may reach 1 cm diameter. Consistency soft but not slimy, compressible, limp, and easily torn; colour exudes when the sponge is squeezed under water. A strong specific smell is responsible for the common name garlic sponge.

Skeleton: ectosomal membrane with tylotes strewn about or forming tangential strands; some erect spicule columns are supporting this membrane. In choanosome, smooth styles arranged in more or less isodictyal reticulation.

Spicules (for measurements see Table 1): megascleres include straight or curved smooth skeletal styles (commonly bent near the tapering rounded end) and slim, smooth, straight or slightly bent or undulating ectosomal tylotes; microscleres consist of arcuate isochelae and contorted sigmas in one size category each (Figure 2).

Habitat observations

This species was shown to be highly resistant to environmental stress such as extended exposure to air and high temperature at extended, very low tides, and low salinity after heavy rain in shallow mangrove environments (Rützler, 1995). Even if large portions of the tissue die, as indicated by yellowish drab colour, the remaining skeleton structure becomes re-colonized by new cell growth after stress has ceased.

Several descriptions (for instance, de Laubenfels, 1950) emphasize—and our observations confirm—that these sponges grow around and incorporate substrate sand, rubble pieces, or other organisms, such as the calcified green alga *Halimeda*, *Thalassia* sea grass blades, or stony coral, *Porites*.

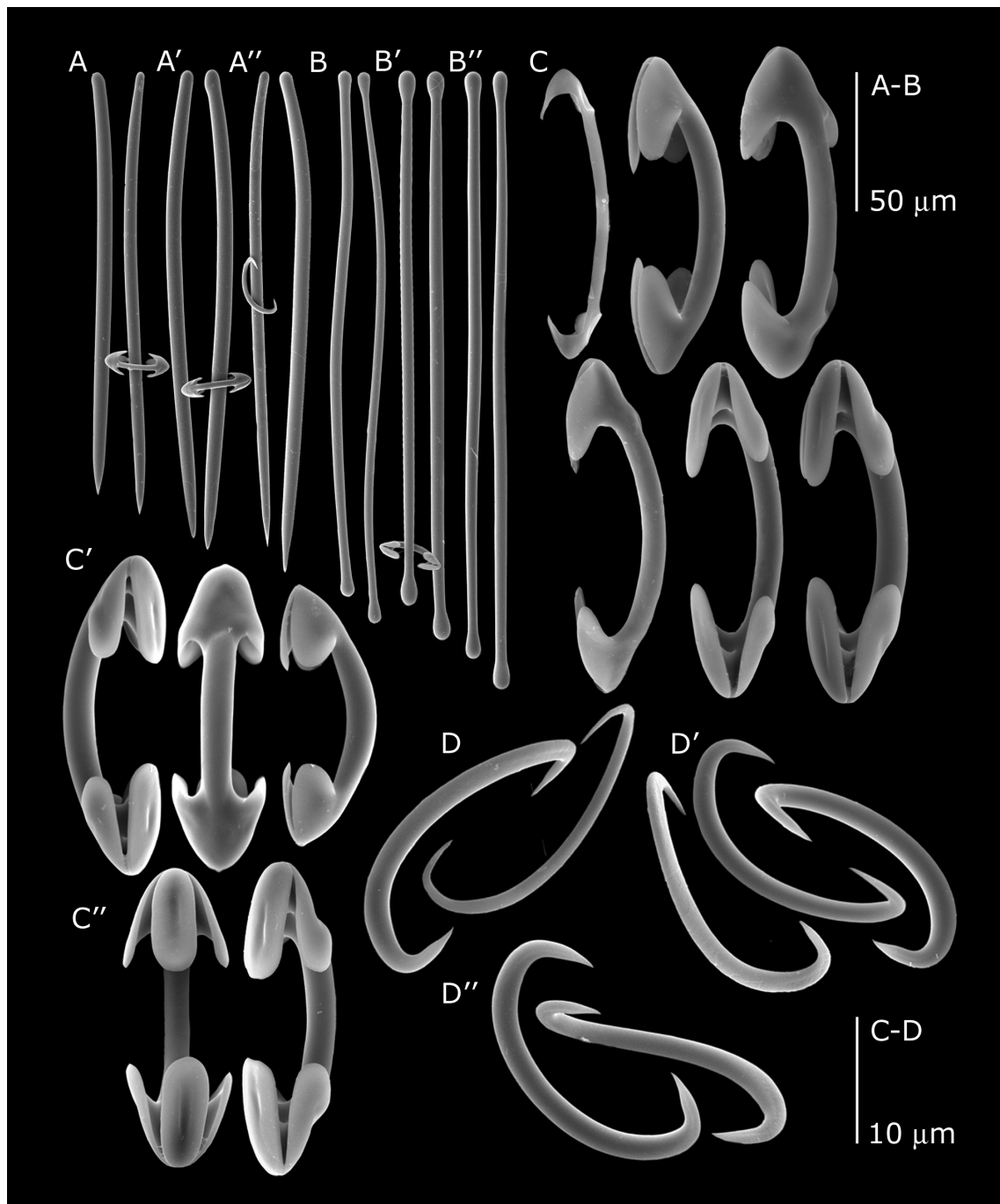


Figure 2. (A–D) *Lissodendoryx isodictyalis* (Carter). (A) Styles (lectotype, Venezuela); (A') styles (specimen from Florida Keys); (A'') styles (Twin Cays, Belize); (B) tylotes (lectotype); (B') tylotes (Florida Keys); (B'') tylotes (Twin Cays); (C) isochelae (lectotype); (C') isochelae (Florida Keys); (C'') isochelae (Twin Cays); (D) sigmas (lectotype); (D') sigmas (Florida Keys); (D'') sigmas (Twin Cays).

Common on sediment lagoon bottoms, fouling harbour structures, and enveloping red mangrove roots, from above mean low tide level to 2 m; rarely found to 10 m depth.

Distribution

Bermuda, Florida (Keys and Dry Tortugas), Bahamas, Venezuela, Colombia, Panama, Belize, Cuba, Gulf of Mexico (Zea, 1987; Díaz, 2005; Rützler et al., in press.) Reports of *Lissodendoryx isodictyalis* from New England, the Mediterranean, the Indo-Pacific, and East Pacific need to be reconfirmed (see remarks below).

Remarks

As seen in the type material and in other Caribbean specimens, the microscleres of *Lissodendoryx isodictyalis* are quite similar in size, isochelae on average slightly larger than sigmas. Material listed by the original author (Carter, 1882) from Acapulco (Pacific Mexico) seems to be lost. Three specimens from Pacific Mexico (near Acapulco) kindly provided by José Luiz Carballo turned out to possess microscleres in two size-classes, nearly indistinguishable from those of specimens belonging to *L. carolinensis* (see below); average measurements are: tylotes, 158×3.8 µm

Table 2. Spicule types and measurements for representative specimens of *Lissodendoryx* (L.) *carolinensis* Wilson. Measurements are means ($N=20$, in μm) of maximum dimensions (length, or length \times width) of spicules.

| Specimen, location | Tylotes | Styles | Isochelae I | Isochelae II | Sigmas I | Sigmas II |
|--------------------------------------|------------------------------|------------------------------|-------------|--------------|-----------|-----------|
| USNM 23630, North Carolina (neotype) | 182.3 \times 4.7 | 160.9 \times 5.5 | 23.8 | 14.6 | 35.1 | 22.2 |
| USNM 1104605, Bahamas | 186.7 \times 3.5 | 172.6 \times 3.5 | 22.3 | 12.1 | 23.2 | 19.3 |
| USNM 1104606, Belize | 196.8 \times 4.6 | 168.9 \times 5.1 | 25.5 | 21.3 | 24.4 | 21.9 |
| USNM 1104607, Florida | 199.9 \times 3.3 | 202.1 \times 5.4 | 18.1 | 13.3 | 40.9 | 21.4 |
| Range of means | 182.3–199.9 \times 3.3–4.7 | 160.9–202.1 \times 3.5–5.5 | 18.1–25.5 | 12.1–14.6 | 23.2–40.9 | 19.3–22.2 |
| Means of means | 191.4 \times 4 | 176.1 \times 4.9 | 22.4 | 15.3 | 30.9 | 21.2 |

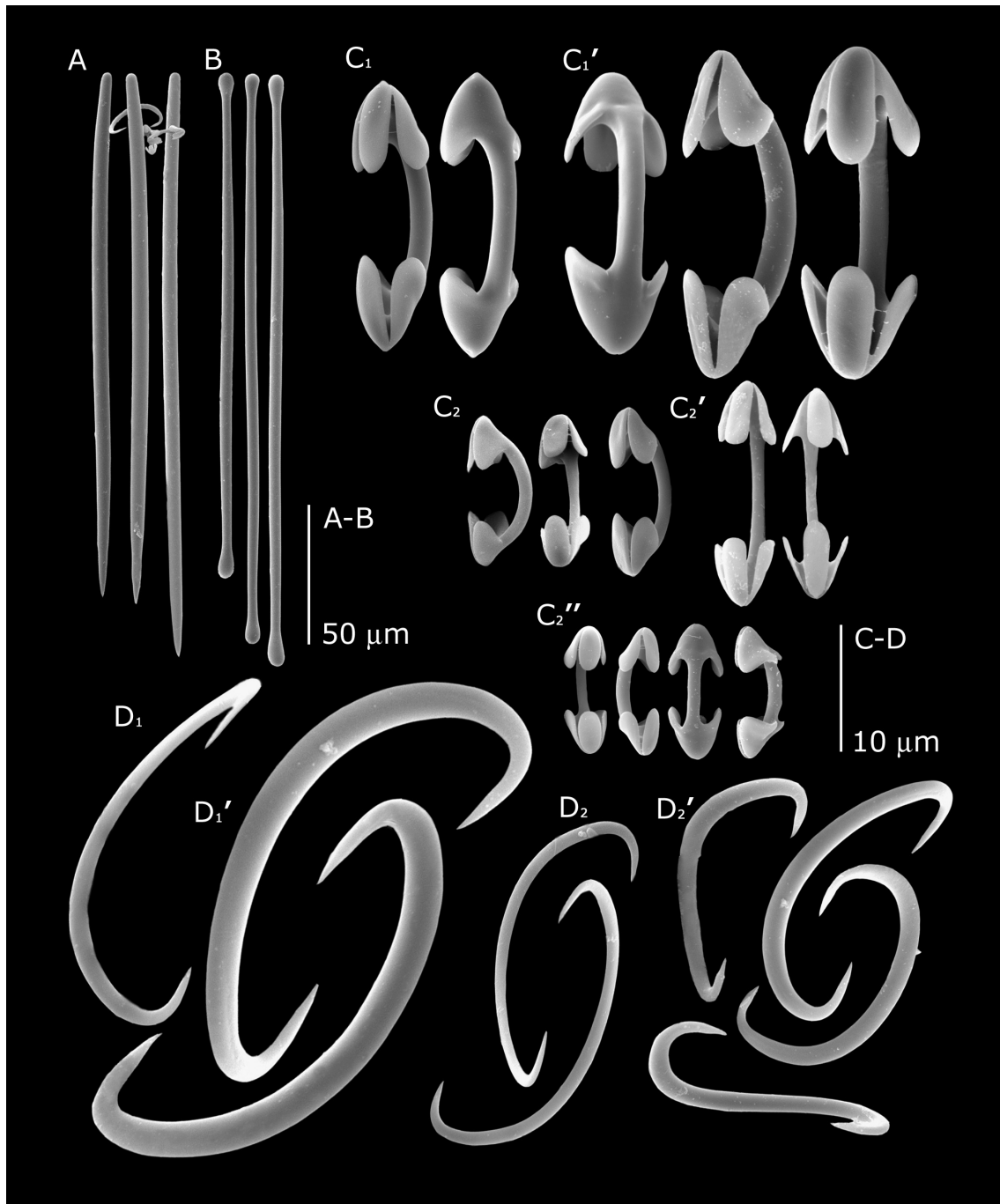


Figure 3. (A–D) *Lissodendoryx carolinensis* Wilson. (A) Styles (specimen from Florida Cays); (B) tylotes (Florida Keys); (C1) isochelae I (Bimini, Bahamas); (C1') isochelae I (Twin Cays, Belize); (C2) isochelae II (Bimini, Bahamas); (C2') isochelae II (Twin Cays); (C2'') isochelae II (Florida Keys); (D1) sigmas I (Bimini, Bahamas); (D1') sigmas I (Florida Keys); (D2) sigmas II (Bimini, Bahamas); (D2') sigmas II (Florida Keys).

(possibly in two size-classes); smooth styles, 168×3.8 µm; two size-classes isochelae, 15.6 and 28.4 µm; two classes sigmas, 19.8 and 36.3 µm.

Authors who considered this species to have two size categories of microscleres may have done so erroneously because Carter (1882, pl. XI 2c–e) illustrated some at lower and higher magnifications. Verrill (1907, pl. XXXV–C 2cd,c'd') too illustrated his *Esperiopsis fragilis* (= *Lissodendoryx isodictyalis*) microscleres in two magnifications.

Hartman (1958) observed that one could distinguish a northern (Atlantic coast of North America) population of *Lissodendoryx isodictyalis*, the 'carolinensis type', which extends from New England to North Carolina, by sigmas that are larger than the isochelae. It is contrasted with a subtropical population (*isodictyalis*-type) which occurs in Bermuda and Dry Tortugas, Florida. Material described by Little (1963) from the north-eastern Gulf of Mexico was also considered to be of the *carolinensis* type. It will take more analyses to decide how important and constant these differences are and, above all, which of the specimens under discussion belong indeed to *L. isodictyalis*. In our material we saw the trend to have sigmas larger than isochelae only in higher-latitude populations of *L. carolinensis* (north of Florida) where *L. isodictyalis* does not occur (see comments, below).

Verrill (1907, pl. XXXV–C 2e) illustrates raphids for a specimen from Bermuda, but these spicules were not found in any other specimens from the same location and may be part of incorporated foreign material.

The two size-classes of microscleres shown in van Soest (1984, figure 19e, f; 2002, figure 8A) belong to another species, *Lissodendoryx spinulosa* sp. nov. (described below), as indicated by the spiny heads of the styles.

Lissodendoryx (*Lissodendoryx*) *carolinensis* Wilson, 1911
(Figures 1C & 3; Table 2)

Lissodendoryx carolinensis Wilson, 1911: 11; George & Wilson, 1919: 150; pl. LXI (26–28), pl. LXVI (62a–e).

Lissodendoryx isodictyalis (Carter): de Laubenfels, 1947: 35; Hartman, 1958: 42, figure 11 (specimens YPM nos. 616, 931, 2037F-1&2, 2117 only); Wells & Wells, 1960, figure 29; Pulitzer-Finali, 1986: 146 (specimen BL. 34 only).

[Non] *Lissodendoryx isodictyalis* Carter, 1882 (see *L. isodictyalis* synonymy above).

Type material

No type was designated by the original author and an effort to find one during a visit by one of us (K.R., in 1972) to the University of North Carolina confirmed that none was in existence. We are therefore establishing a neotype from a location and habitat close to that of the original material (Beaufort Harbour, under the wharves); this is the specimen described and illustrated by Wells & Wells, 1960).

Neotype: Hatteras Harbour, North Carolina (35°13'10"N 75°41'25"W; on pilings; water depth: not given); coll. by H.W. Wells, 22 December 1959 [USNM 23630].

Type locality

Hatteras Harbour, North Carolina.

Comparative material examined

Bahamas: Bimini (25°44'N 79°15'W; central lagoon near Big Mangrove, water depth: 0.8 m); coll. by K. Rützler, 31 July 1967 [USNM 1104605].

Belize: Twin Cays (16°49'22.0"N 88°5'44.9"W; mangrove, Batfish Point; water depth: 0.1 m); coll. by K. Rützler, 13 June 1983 [USNM 41265]. Twin Cays (16°49'43.3"N 88°06'17.1"W; mangrove, Sponge Haven South; water depth: 0.5 m); coll. by S. Duran, 29 July 2004 [USNM 1104606].

Florida: Florida Keys (24°41'9.6"N 81°21'36"W; mangrove, Keys Marine Laboratory; water depth: 0.5 m); coll. by S. Duran, 30 May 2004 [USNM 1104607].

Georgia: Johnson Creek near Saint Catherine Island (34°1'44.14"N 84°11'54.88"W; water depth: not given); coll. by M. Gray, 28 February 1967 [USNM 33292; 33295].

Diagnosis

Lissodendoryx with choanosomal reticulation of smooth styles, tangential ectosomal tyloles, and a microsclere complement of two size-classes each of arcuate isochelae and sigmas.

Description of neotype

The massive sponge consists now of several fragments that amount to about 8 ml of volume; it is ethanol-preserved. The structure is porous, breadlike, most pores just under 1 mm in diameter. One obvious osculum is collapsed, 5 mm in diameter. The colour in ethanol is drab. Megascleres consist of smooth, straight and slender tyloles, 175.3–186.2 µm (182.3 ± 4.1 µm, mean ± SD) × 3.5–5.6 µm (4.7 ± 0.5 µm); smooth styles, slightly bent in the upper third where they start tapering toward the rounded end, 152.4–162.4 µm (160.9 ± 3.9 µm) × 3.9–5.7 µm (5.5 ± 0.6 µm). Microscleres are arcuate isochelae in two size-classes, 22–25.6 µm (23.8 ± 2 µm) and 14.1–15.3 µm (14.6 ± 0.5 µm); and contorted sigmas (very rarely S-shaped), also in two size categories, 32.7–38.6 µm (35.1 ± 3.1 µm) and 19.6–25.4 µm (22.2 ± 1.9 µm).

Description

Colour: blue, green and greenish-tan, to dirty orange (Figure 1C); one specimen from Bimini, Bahamas, believed to belong here, was reported as bright orange (Pulitzer-Finali, 1986; specimen no. 43).

Shape, size, consistency: thin crusts, to cushions, to amorphous massive reaching 20 cm diameter. Oscula of 2–5 mm diameter elevated on chimney-like lobes. Ectosomal membrane over meandering subsurface canals. Fragile, compressible and crumbly.

Skeleton: choanosome supported by reticulation of spicule bundles and strands, tangential tyloles in surface membrane; some tyloles scattered among the meshes. Microscleres abundant in all body regions.

Spicules (for measurements see Table 2): smooth styles and tyloles; isochelae and sigmas in two size-classes, as described for the neotype (Figure 3).

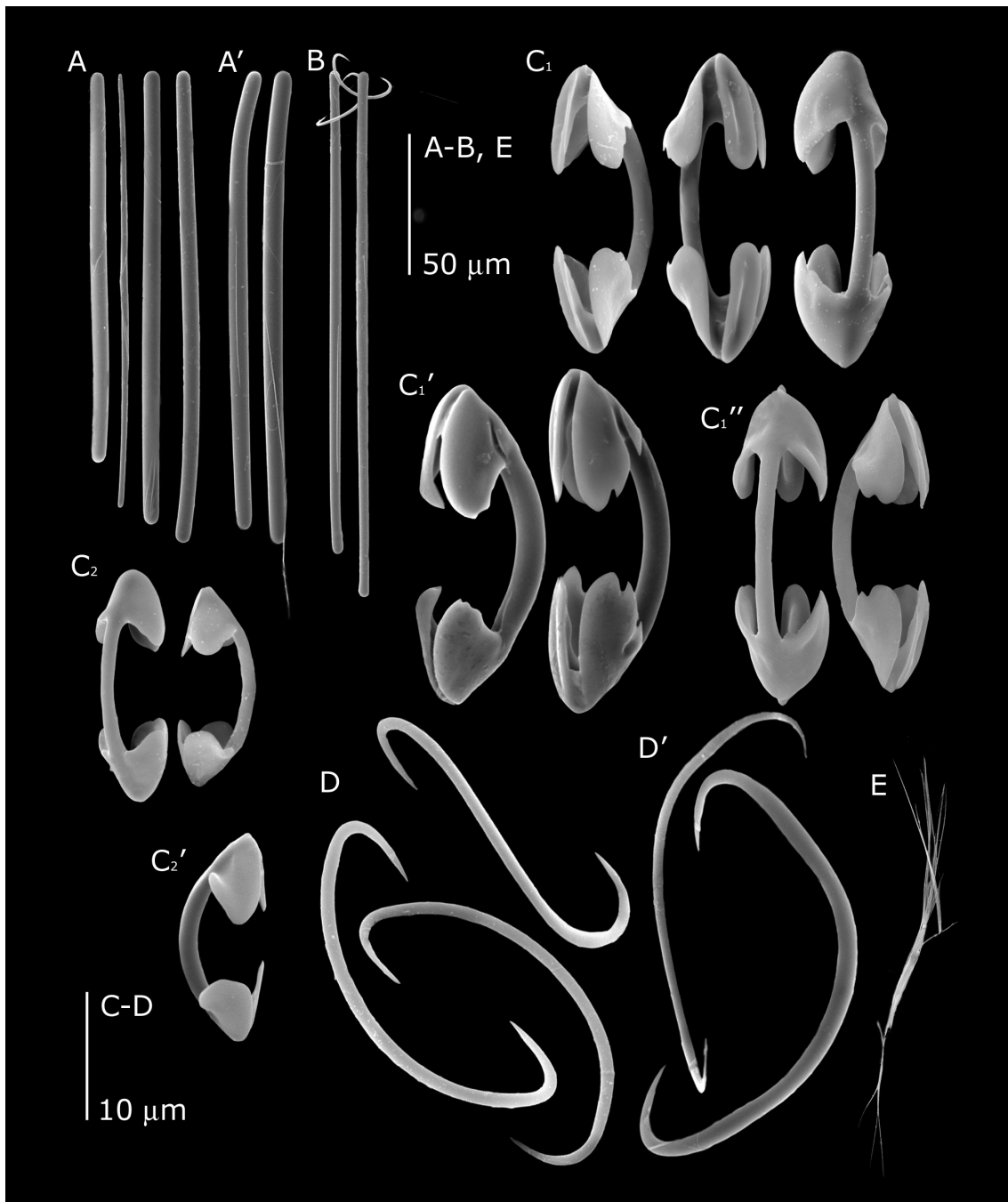
Habitat observations

The sponges are common on harbour piers and red mangrove roots, 0.5–1.0 m deep. It has a remarkable tolerance to a large temperature and salinity range and despite its strong odour houses a diverse endofauna of

Table 3. Spicule types and measurements for representative specimens of *Lissodendoryx* (L.) *colombiensis*. Measurements are means ($N=20$, in μm) of maximum dimensions (length, or length \times width) of spicules.

| Specimen, location | Tylotes | Strongyles | Isochelae I | Isochelae II | Sigmas | Raphids |
|---|------------------------------|----------------------------|-------------|--------------|-----------|-----------|
| USNM 31957, Colombia (paratype) | 182.9 \times 3.8 | 176.5 \times 6.4 | 24.5 | 14.9 | 24.4 | 66.5 |
| USNM 1104608, Belize | 179.9 \times 3.9 | 157.1 \times 5.9 | 23.6 | 16.9 | 35.8 | 76.3 |
| USNM 1104611, Belize | 187.5 \times 3.6 | 185 \times 4.2 | 25.1 | 16.6 | 26.3 | 86.7 |
| USNM 42012, Gulf of Mexico, off Florida | 243.2 \times 7.3 | 253.4 \times 8 | 45.1 | 15.5 | 11.5 | n.a. |
| USNM 32912, Panama | 188.1 \times 4.4 | 170.1 \times 6.4 | 30 | 22.4 | 27.9 | 97.7 |
| Range of means | 179.9–243.2 \times 3.6–4.4 | 157.1–253.4 \times 3.4–8 | 23.6–45.1 | 14.9–22.4 | 11.5–35.8 | 66.5–97.7 |
| Means of means | 196.2 \times 4.6 | 188.4 \times 5.6 | 29.7 | 17.3 | 25.2 | 81.5 |

n.a., not applicable.

**Figure 4.** (A–E) *Lissodendoryx colombiensis* Zea & van Soest; three specimens from Blueground Range, Belize. (A) Strongyles [USNM 1104608]; (A') strongyles [USNM 42660]; (B) tylotes [USNM 1104608]; (C1) isochelae I [USNM 1104608]; (C1') isochelae I [USNM 42660]; (C1'') isochelae I [USNM 1104611]; (C2) isochelae II [USNM 1104608]; (C2') isochelae II [USNM 42660]; (D) sigmas [USNM 1104608]; (D') sigmas [USNM 42660]; (E) raphids [USNM 1104608].

nematodes, annelids and amphipods (de Laubenfels, 1947; Hartman, 1958).

Distribution

From Cape Cod (Massachusetts) to coastal North and South Carolina, Georgia, Florida, Bahamas, and Belize. A close relative seems to occur along the coast of Pacific Mexico (see remarks for *L. isodictyalis*).

Remarks

Pulitzer-Finali (1986) pointed out that his specimen BL 34 was different (from typical *L. isodictyalis*) for its two size categories of microscleres. Many authors who described species of *Lissodendoryx* gave ranges of microsclere dimensions but failed to recognize separation into size-classes. We consider this feature important at the species level, but original material has to be examined in each case to determine whether there is great size variation or separation into classes. In our experience with members of this genus, a large size range given in a publication is a good indication that two classes are present (for instance, Hartman, 1958; table 12: specimens from north of Florida; figure 11 clearly illustrates two categories of microscleres).

Lissodendoryx (Lissodendoryx) colombiensis Zea & van Soest, 1986 (Figures 1D & 4; Table 3)

Lissodendoryx colombiensis Zea & van Soest, 1986: 362, figure 4.

Type material

Holotype (not examined): Colombia, Cartagena region (10°24'N 75°30'W; water depth: 4 m); coll. by S. Zea, 14 June 1979 [ICN-MHN(Po) 0103].

Paratypes (examined): Colombia, Pajarales, west of Islas de Rosario (10°10'1.2"N 75°46'1.2"W; water depth: 4–22 m); coll. by R. Kaufmann, 28 May 1968 (USNM 31957); Islas de Rosario (10°10'1.2"N 75°46'1.2"W; water depth: 2–3 m); coll. by A. Pabon, July 1970 [USNM 31959]. Panama: San Blas Islands (9°27'1"N 78°54'43"W; ship wreck; water depth: 4 m); coll. by P.W. Glynn, 11 December 1970 [USNM 32912]. (For additional paratypes, see Zea & van Soest, 1986.)

Type locality

Cartagena region, Colombia.

Comparative material examined

Belize: Blue Ground Range (16°48.531'N 88°08.927'W; mangrove pond; water depth: 0.2 m); coll. by B. Bingham, 23 June 1988 [USNM 42660]. Blue Ground Range (16°48.531'N 88°08.927'W; mangrove pond; water depth: 1 m); coll. by S. Duran, 5 August 2004 [USNM 1104608]. Twin Cays (16°49.367'22"N 88°5'44.9"W; South Channel entrance, sea grass *Thalassia*; water depth: 1 m); coll. by K.P. Smith and K. Ruetzler, 28 April 1985 [USNM 42931]. Twin Cays (16°49.367'N 88°05.750'W; sea grass *Thalassia*; south-east corner of island; water depth: 1 m); coll. by K. Rützler, 20 May 1979 [USNM 43046]. Twin Cays (16°49.367'N 88°05.750'W; 'Cuda Cut, red mangrove roots; water depth: 0.5 m); coll. by K. Rützler, 2 May 1994 [USNM 1104609]. Cat Cay, Pelican Cays (16°37'N 88°12'W; lagoon bottom;

water depth: 0.5 m); coll. by K. Rützler, 7 May 1994 [USNM 1104610]. Cat Cay, Pelican Cays (16°37'N 88°12'W; lagoon bottom; water depth: 0.5 m); coll. by R.W.M. van Soest, 3 August 1997 [USNM 1104611].

Florida: Sanibel Island, Gulf of Mexico (26°17.867'N 82°12.617'W; water depth: 13 m); coll. by Continental Shelf Associates for Mineral Management Service, 5 December 1982 [USNM 42012; 42013].

Diagnosis

Lissodendoryx with cavernous structure; megasclere complement of stout choanosomal strongyles and slim ectosomal tyloles; microscleres made up by two size categories of isochelae, one of sigmas, and very fine raphids.

Description

Colour: orange, to yellow-orange and yellow (Figure 1D).

Shape, size, consistency: tubular or massive sponges with lobes and chimneys, up to 30 cm diameter and 20 cm height; internal structure cavernous, with atrial spaces ending in pseudoscula (1–4 cm diameter); smooth surface with circular or elongate perforations; tough elastic but crumbles under pressure.

Skeleton: ectosomal tangential tyloles, often arranged in bundles and tracts, accompanied by raphids arranged as trichodragmas. Choanosome reticulate, with one or several strongyles forming triangular meshes; microscleres throughout.

Spicules (for measurements see Table 3): stout strongyles, straight or slightly bent, a few showing styloid modifications; tyloles straight, slender, with slightly inflated terminals (tyles); isochelae in two size-classes, the larger ones having alae with serrated edges; thin sigmas, one size; raphids (Figure 4.)

Habitat observations

Attached to rock and rubble among sea grass (*Thalassia*) in mangrove and protected lagoon environments; 0.2–13 m. Specimens tend to attach to and incorporate neighbouring algae, sea grass blades, sponges (*Haliclona*, *Dysidea*), stony corals (*Porites*, *Millepora*), and gorgonians, with which they coexist without harming each other.

Distribution

Colombia, Panama, Belize and Gulf of Mexico (off Florida).

Remarks

The cavernous structure of these sponges offers ample refuge space for associated invertebrates such as snapping (alpheid) shrimps, other crustaceans, and ophiuroid echinoderms (brittle stars).

Lissodendoryx (Lissodendoryx) spinulosa sp. nov.
(Figures 1E, 5 & 6; Table 4)

Lissodendoryx isodictyalis (Carter): van Soest, 1984; figure 19; pl. V (2–3); van Soest, 2002: 540; figure 8A.

Type material

Holotype: Belize, Twin Cays (16°49.367'N 88°05.750'W; Batfish Point mangrove; water depth: 1 m); coll. by K. Smith

Table 4. Spicule types and measurements for representative specimens of *Lissodendoryx* (L.) *spinulosa* sp. nov. Measurements are means ($N=20$, in μm) of maximum dimensions (length, or length \times width) of spicules.

| Specimen, location | Tylotes | Styles | Isochelae | | | Sigmas | |
|---|----------------------------|------------------------------|-----------|---------|---------|-----------|-----------|
| | | | I | II | III | I | II |
| USNM 42948, Belize (holotype) | 215.6 \times 4.1 | 194 \times 4.8 | 31.4 | 19.1 | 10.2 | 35.2 | 19.8 |
| USNM 34634, Belize (paratype) | 224.7 \times 3.6 | 189.6 \times 5.9 | 32.6 | 15.1 | 10.3 | 38.5 | 18.7 |
| USNM 1104612, Florida Atlantic (paratype) | 215.7 \times 5.6 | 182.1 \times 9 | 35.8 | n.a. | 9.8 | 40.3 | 12.5 |
| USNM 33978, Gulf of Mexico, off Florida | 216 \times 4 | 174.5 \times 6.8 | 37.5 | 29.6 | 10 | 33.2 | 11.9 |
| USNM 33364, North Carolina | 227.6 \times 4.7 | 213.4 \times 2.9 | 39.4 | 29.9 | 14.3 | 37.3 | 29.1 |
| ZMA POR 03992, Curaçao | 200 \times 3.1 | 162.1 \times 5.4 | 25.8 | 15 | 10 | 34.8 | 15.1 |
| Range of means | 200–227.6 \times 3.1–5.6 | 162.1–213.4 \times 2.9–6.8 | 25.8–39.4 | 15–29.9 | 10–14.3 | 33.2–40.3 | 11.9–29.1 |
| Means of means | 216.6–4.1 | 185.9–5.8 | 33.7 | 21.7 | 10.8 | 36.5 | 17.8 |

n.a., not applicable.

and K. Rützler, 19 April 1986, 1 August 1997 [USNM 42948].

Paratypes: Belize, Twin Cays (16°49.367'N 88°05.750'W; mangrove pond, red mangrove root; water depth: 0.5 m); coll. by I. Goodbody, May 1984 (USNM 34634). Belize, Twin Cays (16°49.367'N 88°06.575'W; Sponge Haven, red mangrove; water depth: 1 m); coll. by I. Goodbody, 22 February 1984 [USNM 32961]. Netherlands Antilles: Bonaire (12°15'N 68°45'W; Lac. Poejito, north-east, red mangrove (*Rhizophora*); water depth: 0–0.5 m); coll. by P. Wagenaar Hummerlinck, 19 September 1967 [ZMA POR.3992] (van Soest, 1984).

Type locality

Twin Cays, southern barrier reef complex, Belize.

Comparative material examined

North Carolina, (33°32.200'N 77°25.100'W; off-shore bottom; water depth: 29 m); coll. by Duke University for MMS/BLM, 4 September 1980 [USNM 33364].

Florida: Fort Pierce, County Boat Ramp (27°28'59"N 80°18'22"W; water depth: 0.5 m); coll. by S. Duran, 2 March 2004 [USNM 1104612]. Gulf of Mexico, off Florida (identified as *Erylus formosus* Sollas) (24°47'25.0"N 83°51'8.9"W; water depth: 76.1 m); coll. by Continental Shelf Associates for BLM/MMS, 21 November 1980 [USNM 33835]. Gulf of Mexico, off Florida (25°45'42.0"N 83°11'3.9"W; water depth: 53.7 m); coll. by Mote Marine Laboratory for BLM/MMS, 12 February 1982 [USNM 33975]. Gulf of Mexico, off Florida (24°47'45.9"N 83°8'0.9"W; water depth: 53.5 m); coll. by Continental Shelf Associates for BLM/MMS, 20 November 1980 [USNM 33979]. Gulf of Mexico, off Florida (25°16'54.0"N 83°43'10.9"W; water depth: 88.2 m); coll. by Mote Marine Laboratory for BLM/MMS, 1 August 1981 [USNM 33845].

Virgin Islands: Saint Thomas (18°20'N 64°55'W; mangrove lagoon; water depth 0–1 m); coll. by K. Rützler, 5 April 1967 [USNM 31556].

Diagnosis

Lissodendoryx with ectosomal tylotes and choanosomal subtylostyles bearing coarse, deforming spines on their

heads and, less commonly, near the points; two size-classes of isochelae and sigmas.

Description of holotype

A thickly encrusting green to yellow sponge overgrowing a subtidal red mangrove stilt root; dimensions about 17 cm length and 2 cm thickness; one large (12 mm diameter) osculum was located on top of a tapered process (chimney). The preserved specimen has turned drab. Accessory megascleres are smooth, straight, slender tylotes, 206.7–221.3 μm (215.6 \pm 4.1 μm , mean \pm SD) \times 2.9–4.9 μm (4.1 \pm 0.6 μm), with tyles barely wider than the centre of the shaft. Spicules of the main skeleton are subtylostyles or styles with smooth shaft and spiny head, bent near the top and tapering toward the head, 177.8–202.9 μm (194 \pm 7 μm) \times 1.6–6.8 μm (4.8 \pm 1.5 μm); the head is slightly inflated but, despite the spines, has a smaller diameter than the centre of the shaft; there are about 3–8 spines on each head, some near the terminal points. Microscleres are arcuate isochelae in three size-classes, 28.4–35 μm (31.4 \pm 2.4 μm), 18.1–19.6 μm (19.1 \pm 0.6 μm) and 9.3–11.1 μm (10.2 \pm 0.5 μm); and sigmas, two classes, 30.2–39.7 μm (35.1 \pm 3 μm) and 15.9–24.4 μm (19.8 \pm 3.5 μm).

Description

Colour: blue, bluish-grey, green to deep (mustard) yellow (Figure 1E); the cause of these diverse colour morphs is unknown.

Shape, size, consistency: massive amorphous or volcano-shaped with terminal oscula (7–mm diameter); smooth to warty surface; up to 10 cm diameter, 5 cm thick; soft, compressible, and crumbly.

Skeleton: ectosome includes tangential tylotes, criss-cross and in strands, and microscleres; choanosomal reticulation of meshes made up by single or a few bundled styles.

Spicules (for measurements see Table 4): slender smooth tylotes with elongate but distinct tyles. Stout, curved subtylostyles, mostly with a sharp bend in the basal quarter of their length; with heads small or missing (styles) and generally adorned by one or several (up to 12) small but coarse, crooked spines; spines, in rare cases, may also be present near or at the points of the spicules (Figures 5 & 6). A few subtylostyles have a bulbous inflation near the

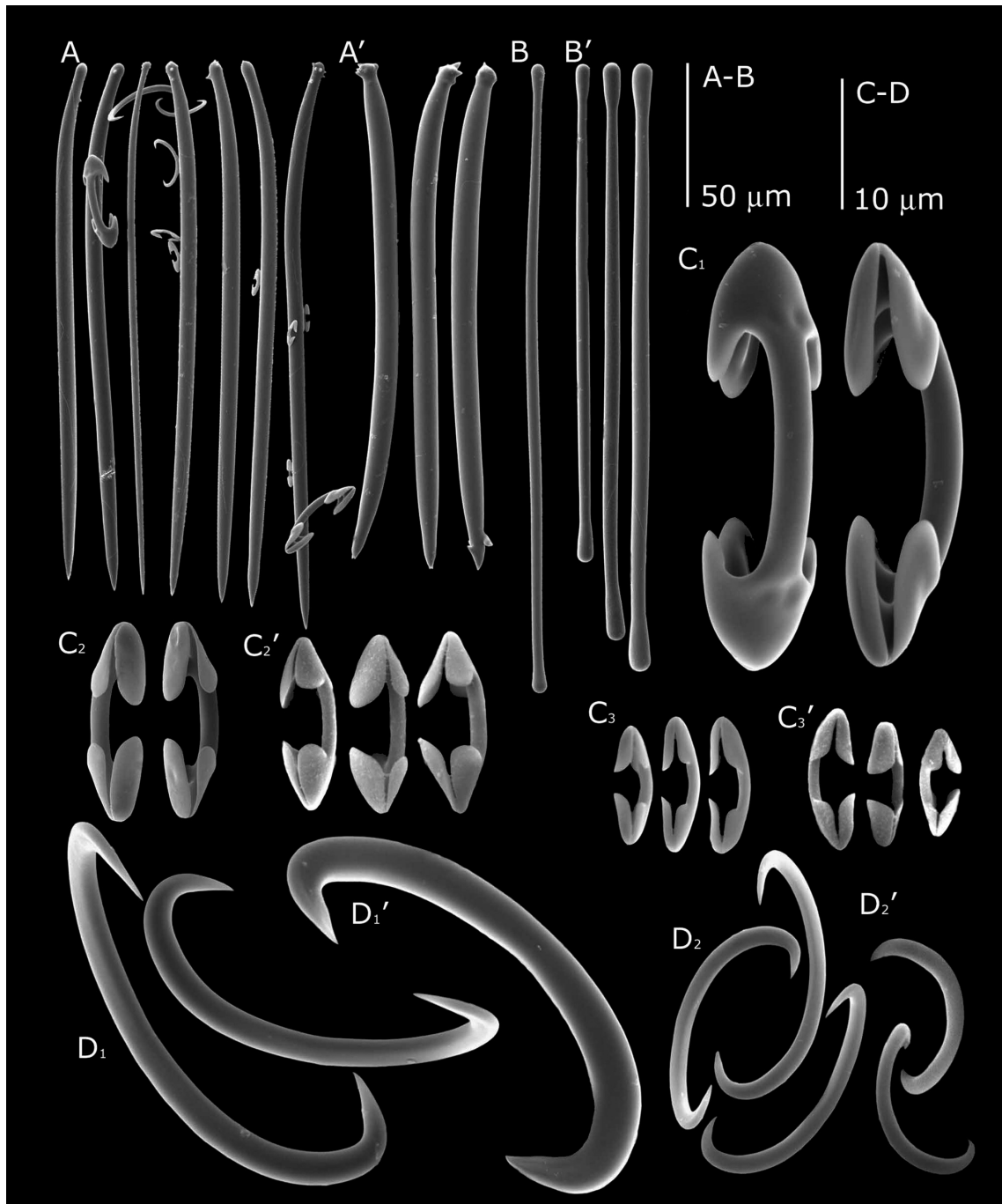


Figure 5. (A–D) *Lissodendoryx spinulosa* sp. nov. (A) Styles (holotype; Twin Cays, Belize); (A') styles (specimen from Atlantic Florida); (B) tylotes (holotype); (B') tylotes (paratype; Atlantic Florida); (C1) isochelae I (holotype); (C2) isochelae II (paratype; North Carolina); (C2') isochelae II (paratype; Bonaire); (C3) isochelae III (holotype); (C3') isochelae III (Bonaire); (D1,2) sigmas I and II (holotype); (D1,2') sigmas I and II (Atlantic Florida).

point. Microscleres (isochelae, sigmas) are present in two or three distinct size-classes (one or the other size-class may be missing in a specimen or processed sample).

Habitat observations

Mangrove lagoons, on *Rhizophora* roots, 0–1.5 m. An orange ascidian, *Distaplia bermudensis*, is commonly attached (Sponge Haven).

Distribution

North Carolina, Florida (Atlantic and Gulf of Mexico coasts), US Virgin Islands, Netherlands Antilles, and Belize.

Etymology

The name is derived from *spinulosus* (Latin), beset with small spines.

Remarks

Lissodendoryx species with one category of acanthostyles as choanosomal spicules belong to the subgenus *Acanthodoryx* but, according to the definition by van Soest (2002), that group is defined by a choanosomal skeleton of radiating bundles rather than a reticulated arrangement of acanthostyles. Furthermore, in the type and only species of *Acanthodoryx*, *L. (Acanthodoryx) fibrosa* (Lévi), acanthostyles are spined all over

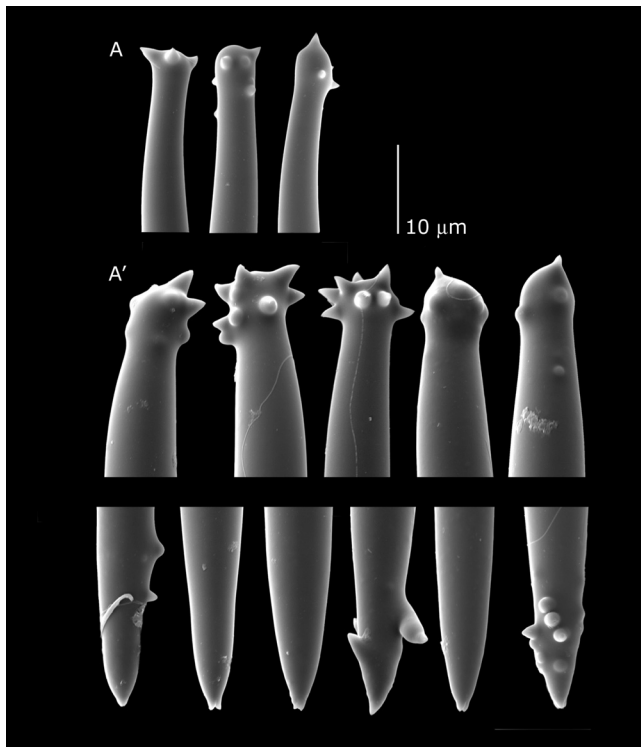


Figure 6. *Lissodendoryx spinulosa* sp. nov., magnified views of style spiny heads and points. (A) Holotype, Twin Cays, Belize; (A') specimen from Atlantic Florida.

and sigmas are lacking. Lastly, the new species presented above is distinguished by choanosomal spined subtylostyles rather than styles.

Topse (1928: 240) described a species with very similar choanosomal megascleres, *Lissodendoryx isodictyalis* var. *paucispina*, from 91 m depth off the Cape Verde Islands (eastern Atlantic), but this variety lacks the distinct separation of microsclere into two or three categories. Another species with spiny megascleres, *Lissodendoryx paucispina* (Ridley & Dendy), has scarce spines covering the styles entirely, accompanied by isochelae in two size-classes and sigmas in one, but with a large size range; the species distribution is Indo-Pacific (Hofman & van Soest, 1995).

Lissodendoryx (Lissodendoryx) strongylata van Soest, 1984
(Figure 7; Table 5)

Lissodendoryx strongylata van Soest, 1984: 58; figure 21; pl. V 4–5.

Type material

Holotype: Netherlands Antilles, Curaçao (12° 10'N 69° 0'W; Piscadera Baai; water depth: 2–3 m); coll. by J.H. Stock, 21 December 1973 [ZMA POR 3508] (examined).

Comparative material examined

Belize, Glovers Reef (16° 43'30.1"N 87° 51'44.9"W; southwest fore reef; water depth: not stated); coll. by J. Faulkner, July 1977 [USNM 32368].

Florida, Gulf of Mexico, off Florida (25° 45.583'N 83° 20.233'W; off-shore; water depth: 58.5 m); coll. by Continental Shelf Associates for MMS, 15 November 1980 [USNM 48384].

Diagnosis

Lissodendoryx with porous structure; megasclere complement of choanosomal strongyles and ectosomal tylotes; microscleres made up by one size category each of isochelae, sigmas and raphids.

Type locality

Piscadera Baai, Curaçao, Netherlands Antilles.

Description

Colour: brick-red or orange where known.

Shape, size, consistency: encrusting or amorphous masses with oscula in depressions, not elevated on lobes or cones; interior bread-like porous; specimens reach 10 cm in diameter; very soft and crumbly, easily broken up.

Skeleton: ectosome containing tangential, single tylotes and microscleres; choanosome supported by a reticulation and a few tracts of strongyles.

Spicules (for measurements see Table 5): slender, straight choanosomal strongyles and similarly shaped tylotes, the latter with small terminal tytes and a slight bend near one end; one size-class of skinny arcuate isochelae, two of thin sigmas. A fragment of the type examined by us, and the specimen from Belize, contained also raphids (50–70 µm long) (Figure 7).

Habitat observations

On lagoon bottoms among *Halimeda* algae, 2–5 m; deepest record, 59 m (Gulf of Mexico).

Distribution

Netherlands Antilles, Belize, Gulf of Mexico (Florida).

Table 5. Spicule types and measurements for representative specimens of *Lissodendoryx (L.) strongylata* van Soest. Measurements are means ($N=20$, in µm) of maximum dimensions (length, or length×width) of spicules.

| Specimen, location | Tylotes | Strongyles | Isochelae | Sigmas I | Sigmas II | Raphids |
|---|-------------------|---------------------|-----------|-----------|-----------|---------|
| USNM 48384, Gulf of Mexico, off Florida | 186×3.7 | 170.9×4.1 | 20 | 26.6 | 10.6 | n.a. |
| USNM 32368, Belize | 189.6×2.9 | 161.5×4.5 | 19.2 | 26.5 | 14.3 | 53.9 |
| Range of means | 186–189.6×2.9–3.7 | 161.5–170.9×4.1–4.5 | 15.7–20 | 26.5–26.6 | 10.6–4.3 | n.a. |
| Means of means | 187.8×3.3 | 166.2×4.3 | 19.6 | 26.6 | 12.4 | 53.9 |

n.a., not applicable.

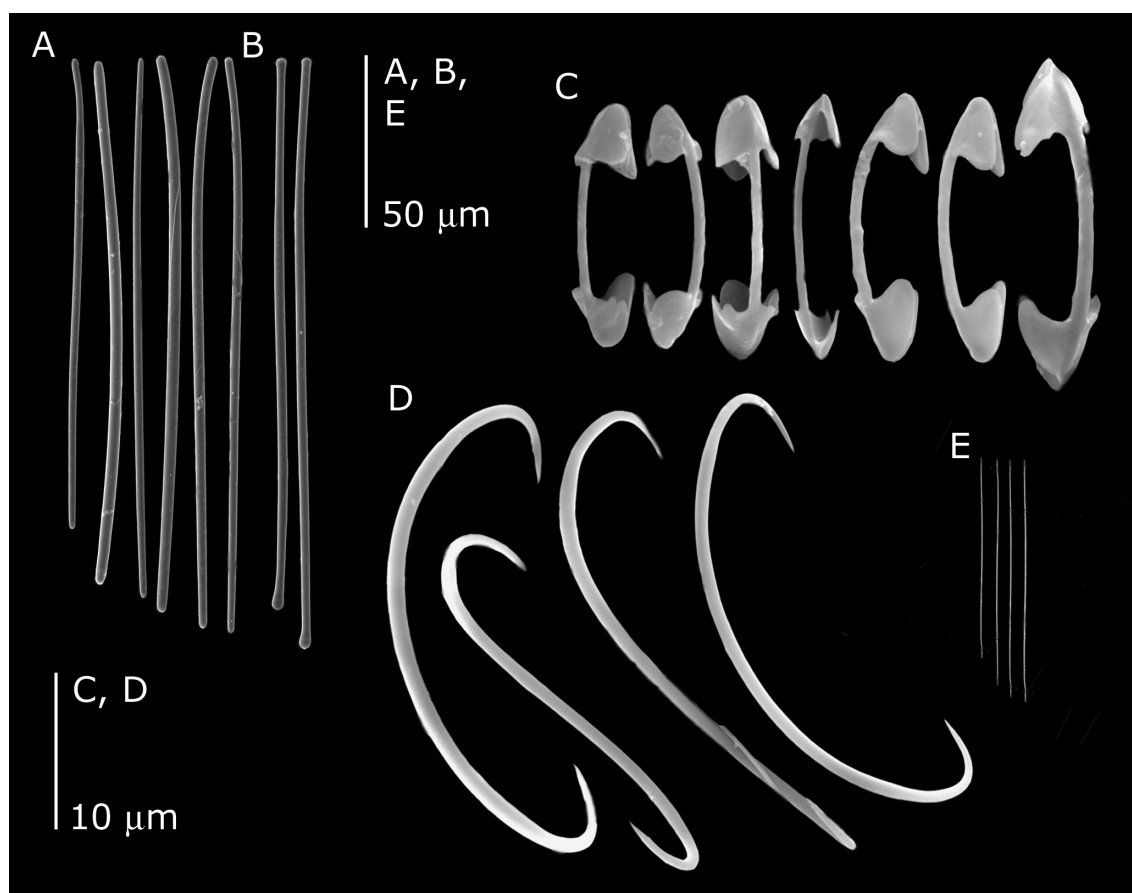


Figure 7. (A–E) *Lissodendoryx strongylata* van Soest; holotype, Curaçao. (A) Strongyles; (B) tylotes; (C) isochelae; (D) sigmas; (E) raphids.

Remarks

In the original description (van Soest, 1984) tylotes and strongyles are shorter and thinner than in our specimens (means for tylotes, $167.4 \times 2.6 \mu\text{m}$; for strongyles, $145.5 \times 3.1 \mu\text{m}$) and isochelae and sigmas were both considered to be in one size-class; these differences do not seem significant. Raphids were not observed by the original describer but found in preparations of a fragment of the holotype kindly provided by R.W.M. van Soest; however, we found them rare or absent in some other specimens.

Lissodendoryx (*Anomodoryx*) *amphispinulata* sp. nov. (Figure 8; Table 6)

Holotype: Gulf of Mexico, off Florida ($26^{\circ}16'44.0''\text{N}$ $83^{\circ}42'48.9''\text{W}$; lagoon, water depth: 71 m); coll. by Continental Shelf Associates for BLM/MMS, 3 November 1980 [USNM 48383].

Paratypes: Gulf of Mexico, off Florida ($25^{\circ}45'34.9''\text{N}$ $83^{\circ}20'13.9''\text{W}$; water depth: 59 m); coll. by Continental Shelf Associates for BLM/MMS, 15 November 1980 [USNM 33976]. Gulf of Mexico, off Florida ($24^{\circ}47'45.9''\text{N}$ $83^{\circ}8'0.9''\text{W}$; water depth: 54 m); coll. by Continental Shelf Associates for BLM/MMS, 20 November 1980 [USNM 33977, USNM 33979].

Diagnosis

Lissodendoryx with mainly choanosomal acanthotylotes, ectosomal tylotes, and microscleres in one size-class, arcuate isochelae and sigmas.

Description of holotype

No colour observations are available; the preserved sponge is grey. The specimen was a thick incrustation of an estimated $3 \times 2 \times 1 \text{ cm}$ but is broken up into fragments. Porous, bread-like, crumbly consistency. Spicules are smooth, straight tylotes, $259.2\text{--}273.1 \mu\text{m}$ ($267.4 \pm 3.5 \mu\text{m}$) \times $5\text{--}7.2 \mu\text{m}$ ($6.4 \pm 0.7 \mu\text{m}$) and straight, bent, or kinked tylotes with spiny tyles, $213.7\text{--}240.5 \mu\text{m}$ ($226.9 \pm 8.4 \mu\text{m}$, mean \pm SD) \times $5.9\text{--}7.4 \mu\text{m}$ ($6.6 \pm 0.5 \mu\text{m}$). Isochelae, $22.2\text{--}29.78 \mu\text{m}$ ($26.4 \pm 1.8 \mu\text{m}$), and sigmas $10.8\text{--}19.8 \mu\text{m}$ ($15.9 \pm 2.1 \mu\text{m}$) occur in one size-class only.

Description

Colour: live colour not known; the ethanol-preserved sponges are grey to drab.

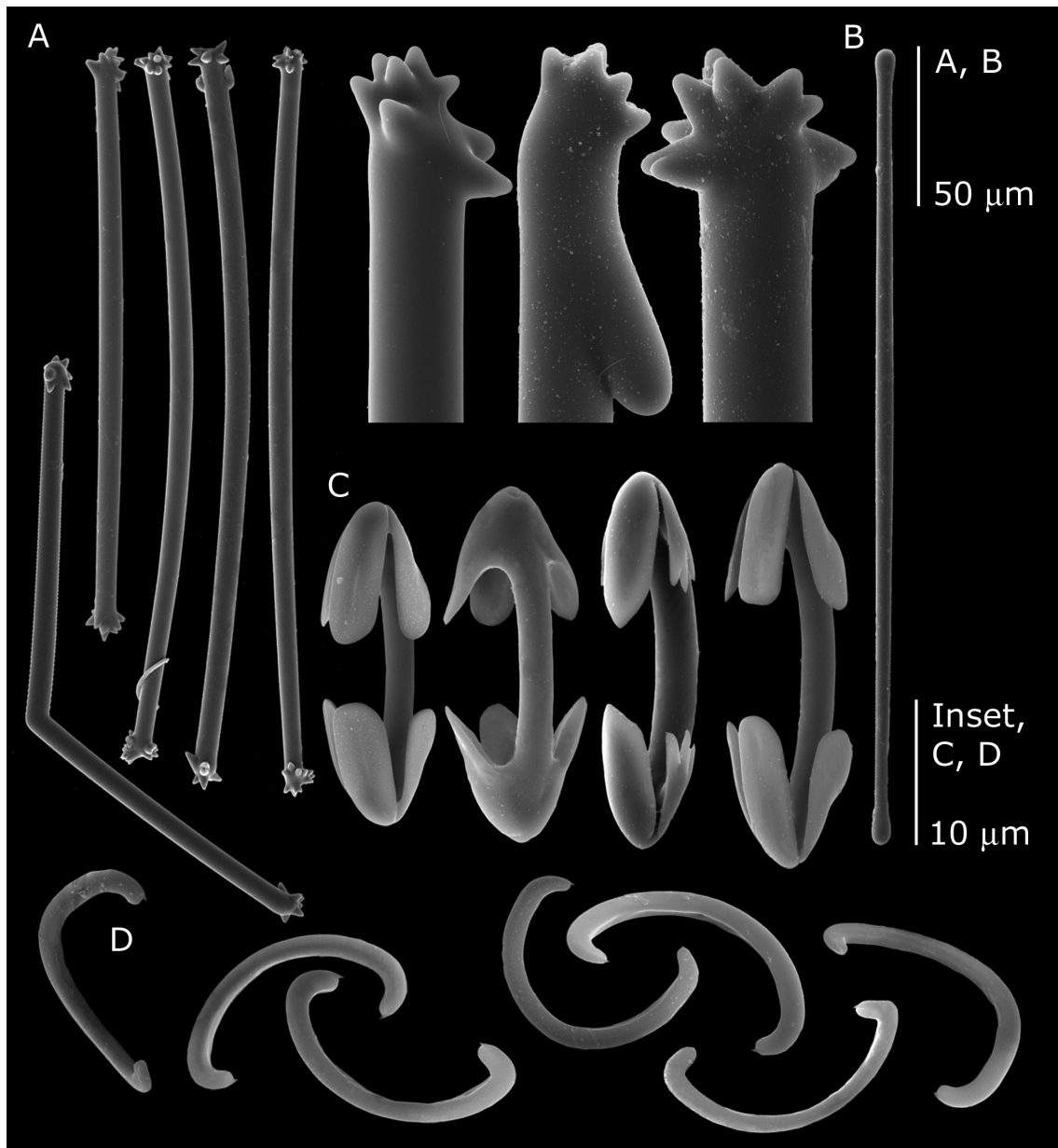
Shape, size, consistency: massive, amorphous (now mostly broken into chunks), with oscula (where discernible) elevated on conical, rounded elevations resembling chimneys; specimens covered between 6 and 50 cm^2 , and reached a thickness of 5 cm; oscula are 3–12 mm in diameter; soft and crumbly, easily torn; various quantities of sand are incorporated.

Skeleton: the ectosome contains smooth tylotes but is also supported by ascending acanthotylote tracts. The choanosome shows the acanthotylotes, which form a reticulation of multispicular meshes. Microscleres abound throughout the sponge body.

Spicules (for measurements see Table 6): straight, curved or kinked acanthotylotes, with tyles covered by several (7–15, approximately) coarse spines, similar to those ornamenting the subtylostyles of *Lissodendoryx*

Table 6. Spicule types and measurements for representative specimens of *Lissodendoryx* (A.) *amphispinulata* sp. nov. Measurements are means ($N=20$, in μm) of maximum dimensions (length, or length \times width) of spicules.

| Specimen, location | Acanthotyloles | Tyloles | Isochelae | Sigmas |
|--|------------------------------|------------------------------|-----------|-----------|
| USNM 48383, Gulf of Mexico, off Florida (Holotype) | 226.9 \times 6.6 | 267.4 \times 6.4 | 26.4 | 15.9 |
| USNM 33976, Gulf of Mexico, off Florida (Paratype) | 208 \times 6.4 | 245.6 \times 5.5 | 27.3 | 16.2 |
| USNM 33977, Gulf of Mexico, off Florida (Paratype) | 200.8 \times 5.5 | 236.3 \times 4.7 | 23.9 | 16.1 |
| USNM 33979, Gulf of Mexico, off Florida (Paratype) | 204.2 \times 5.9 | 244.6 \times 4.5 | 25.7 | 15.3 |
| Range of means | 226.9–204.2 \times 5.5–6.6 | 236.3–267.4 \times 4.5–6.4 | 23.9–27.3 | 15.3–16.2 |
| Means of means | 210 \times 6.1 | 248.5 \times 5.3 | 25.8 | 15.9 |

**Figure 8.** (A–D) *Lissodendoryx amphispinulata* sp. nov.; holotype, Gulf of Mexico. (A) Acanthotyloles; (inset) acanthotylole heads, magnified; (B) tyloles; (C) isochelae; (D) sigmas.

spinulosa, but greater in numbers; smooth straight tyloles with tyloles barely wider than the centre of the shaft, but set off by a narrower neck region. Arcuate isochelae, some

with serrations along the edges of the alae, as observed in *Lissodendoryx colombiensis* above; and blunt contorted sigmas (Figure 8).

Table 7. Spicule types and measurements for representative specimens of *Lissodendoryx* (A.) *sigmata* (de Laubenfels). Measurements are means ($N=20$, in μm) of maximum dimensions (length, or length \times width) of spicules.

| Specimen, location | Tylotes | Isochelae I | Isochelae II | Sigmas I | Sigmas II |
|---|------------------------------|-------------|--------------|-----------|-----------|
| USNM 30228, Bahamas | 243.3 \times 5.8 | 22.4 | 12 | 52.3 | 13.4 |
| USNM 1104613, Belize | 257.1 \times 5.8 | 20.6 | 12.7 | n.a. | 11.5 |
| USNM 1104614, Florida, Atlantic | 226.6 \times 6.7 | 43.7 | 16.1 | 52.4 | n.a. |
| USNM 34212, Gulf of Mexico, off Florida | 246.7 \times 5.3 | 43.7 | 15.1 | 47.2 | n.a. |
| USNM 48258, Georgia | 189.9 \times 3.7 | 36.2 | 14.6 | 43.8 | n.a. |
| Range of means | 189.9–257.1 \times 3.7–6.7 | 20.6–43.7 | 12–16.1 | 43.8–52.4 | 11.5–13.4 |
| Means of means | 232.7 \times 5.4 | 33.3 | 14.1 | 48.9 | 12.5 |

n.a., not applicable.

Habitat observations

All specimens were dredged from hard bottoms in 54–71 m depth, deeper than most members of *Lissodendoryx* in our material. No other habitat details are known. Many sand grains, foreign sponge spicules, and carbonate skeletons of other invertebrates (notably bryozoans) are incorporated in these sponges.

Distribution

Only encountered in the Gulf of Mexico, off-shore the west coast of Florida.

Etymology

The name refers to the small-spine arrangement (Latin, *spinulum* = small spine) on both (Greek, *amphi-*) tytes of the tylotes.

Remarks

The spined tylotes (acanthotylotes) are distinctive; they have not previously been described for a member of this genus or subgenus.

Lissodendoryx (*Anomodoryx*) *sigmata* (de Laubenfels, 1949)
(Figures 1F, G; 9 & 10; Table 7)

Xytopsene sigmatum de Laubenfels, 1949: 15; Little, 1963: 40.
Lissodendoryx sigmata Wiedenmayer, 1977: 136, figure 14; pl. 21 (7), 22 (1–2) (with more synonyms); van Soest, 1984: 57; figure 20; Pulitzer-Finali, 1986: 147; Gómez, 2002: 76 (+ figure).

Type material

Holotype: Bahamas, Bimini (25°44'N 79°15'W; lagoon; water depth: 0.5 m); coll. by M.W. de Laubenfels, 1 July 1948 [AMNH 469]. (Not examined.)

Paratype: Same data as above [AMNH 491]. (Not examined.)

Type locality

Bimini, Bahamas.

Comparative material examined in detail

Bahamas: Bimini (25°44'N 79°15'W; lagoon bottom; water depth 0.5 m); coll. by F. Wiedenmayer, ~1965 [USNM 30228].

Belize: Twin Cays (16°49'43.3"N 88°6'17.1"W; Sponge Haven mangrove cove; water depth: <1 m); coll. by J. Wulff, 2 August 1972 [USNM 1104613].

Florida, Atlantic: Spoil Islands, Indian River (Fort Pierce) (27°58.50'N 80°32.47'W; rock and oyster rubble; water depth: 0–0.5 m); coll. by Raphael Ritson-Williams et al., 2 March 2004 [USNM 1104614].

Florida: Gulf of Mexico, off Florida (24°47'45.9"N 83°8'0.9"W; water depth: 54 m); coll. by Continental Shelf Associates for BLM/MMS, 24 April 1981 [USNM 34212].

Georgia: off-shore (31°23'24"N 80°53'24"W; water depth: 17 m); coll. by RV 'Vessel Oregon', 4 March 1981 [USNM 48258].

Additional material surveyed

Spicule preparations in USNM examined and found in close agreement with or quite similar (indicated by 'cf.') to this species. Bahamas: USNM 30229; Belize: USNM 33179 (cf.); Florida, Gulf of Mexico: USNM 42014, 42015, 33974, 34213. Panama, Atlantic: USNM 32399 (cf.); North Carolina: USNM 32683; South Carolina: USNM 36572; Trinidad and Tobago: USNM 42750 (cf.).

Diagnosis

Lissodendoryx with megasclere skeleton entirely composed of tylotes; microscleres are arcuate isochelae and sigmas in one or two size categories.

Description

Colour: yolk yellow, pale to orange yellow, to orange-red, to red (Figure 1F,G).

Shape, size, consistency: a massive base, often covered by sediment, supporting conical or digital fistules with or without terminal oscula (2–6 mm diameter); up to 30 cm diameter, 8 cm thick; firm but compressible, easily torn.

Skeleton: ectosome with tangentially strewn tylotes and microscleres; choanosomal tylotes in strands and plumose tracts, without distinct reticulation.

Spicules (for measurements see Table 7): megascleres are exclusively tylotes with elongated tytes, a few may have the tyle drawn out into a terminal point. There are generally two size-classes of arcuate isochelae and sigmas, but in a few specimens, one size sigmas may be missing. The rims of the alae of most isochelae are toothed, particularly distinctively in the specimen from Atlantic Florida (Fort Pierce, Figure

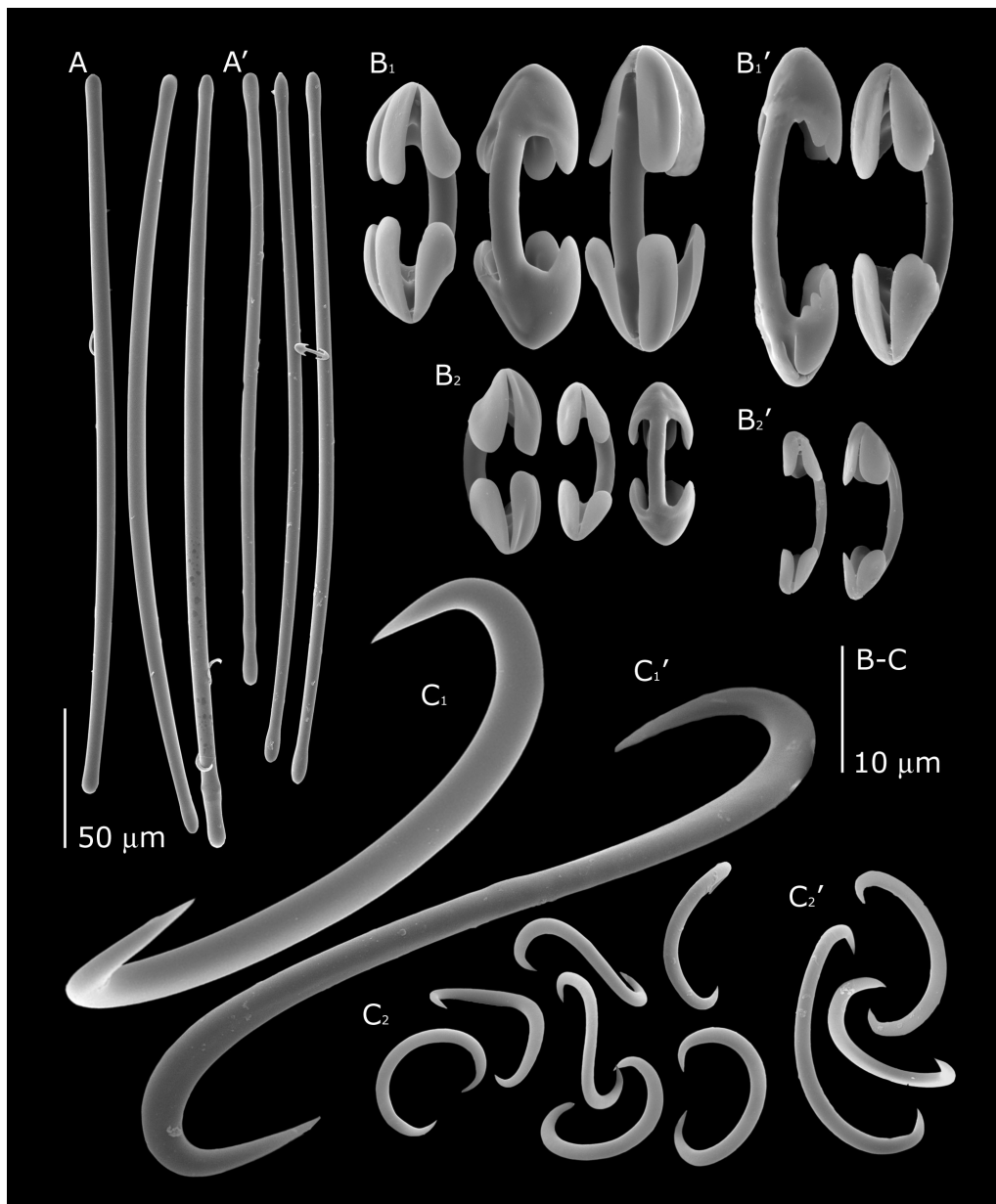


Figure 9. (A–C) *Lissodendoryx signata* (de Laubenfels). (A) Tylotes (specimen from Twin Cays, Belize); (A') tylotes (Bimini); (B1) isochelae I (Twin Cays); (B1') isochelae I (Bimini, Bahamas); (B2) isochelae II (Twin Cays); (B2') isochelae II (Bimini); (C1) sigmas I (Twin Cays); (C1') sigmas I (Bimini); (C2) sigmas II (Twin Cays); (C2') sigmas II (Bimini).

10); in the same sponge, the centres of some isochela shafts bear one perpendicular protuberance pointing in the direction of the central blade (possibly a malformation; Figure 10).

Habitat observations

The sponges are usually attached to lagoonal rock bottom with sea grass (*Thalassia*) and covered by a layer of sand, only the fistules protruding. Generally in shallow water, 0–1 m, but dredging off the Carolinas, Georgia, and Florida (Gulf of Mexico) produced specimens from 14–76 m.

Distribution

From North Carolina to Florida (Atlantic and Gulf of Mexico coasts); Bahamas; Trinidad and Tobago; Panama, and Belize.

Remarks

Based on the fact that megascleres are comprised by tylotes only, this species is here assigned to the subgenus *Anomodoryx*. It is similar in spiculation to the type species, *Lissodendoryx* (*Anomodoryx*) *deudyi* (Whitelegge, 1901); the latter, however, has only one category of microscleres and occurs in New South Wales, Australia.

De Laubenfels (1949) described two sizes of sigmas but only one category of isochelae; however, the second size-class could have been overlooked or, as we found in our survey, can be missing from some specimens. One specimen collected from the type locality in the Bahamas (USNM 30228) had indeed two sizes of isochelae (Figure 9).

Another specimen relating to this species is located in the Natural History Museum (London) under number 1934.11.26.22 (van Soest, 1984: 60). It is labelled as *Hamigera*

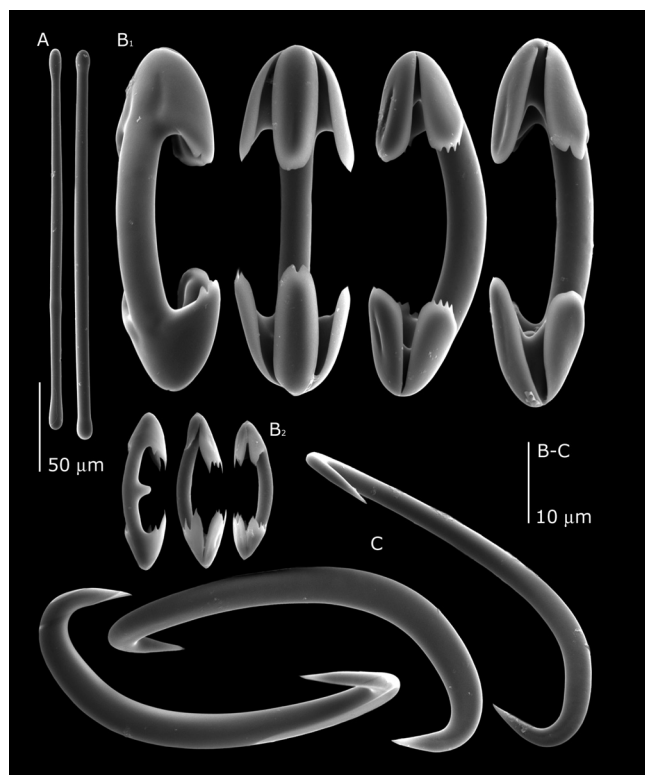


Figure 10. (A–C) *Lissodendoryx sigmata* (de Laubenfels), var. nov.? Fort Pierce, Atlantic Florida. (A) Tyloids; (B1) isochelae I; (B2) isochelae II; (C) sigmas.

and comes from a shallow sea grass field in shallow water, south-east Bight of Turneffe Island, Belize. The specimen is reported as having raphids in addition to isochelae and two size-classes of sigmas. We did not have the chance to examine the London specimen, but three of the ones listed above (USNM 33179, Twin Cays, Belize; USNM 32399, Atlantic, Panama; and USNM 42750, Trinidad and Tobago) show similar differences to typical *L. sigmata*; they are also distinguished by tyloids that are nearly double the typical length and width and are curved or undulating instead of straight.

There may indeed be two or more varieties (formae) or species present in the *Lissodendoryx sigmata* complex but more well-preserved material with good data will be required than is available to us at this time. Our (only) specimen from Fort Pierce (USNM 1104614; Figures 1F & 10) shows important spicule differences if compared to specimens from the type locality (Bimini, Bahamas; USNM 30228) and our study site in Belize (Twin Cays; USNM 1104613) (Figure 9), particularly, shorter tyloids with well pronounced tyles, very large isochelae I (Table 7), strong serration of both sizes of isochelae, and large sigmas in only one size-class.

Lissodendoryx (*Ectydoryx*) *acanthostylota* sp. nov.
(Figure 11; Table 8)

Type material

Holotype: Gulf of Mexico, off Florida (26°16'40.0"N 84°4'5.0"W; lagoon, water depth: 137 m); coll. by Continental Shelf Associates for BLM/MMS, 25 July 1981 [USNM 48382].

Paratype: Gulf of Mexico, off Florida (25°16'50.0"N 83°57'20.9"W; lagoon; water depth: 127 m); coll. by Continental Shelf Associates for BLM/MMS, 2 August 1981 [USNM 48380].

Diagnosis

Lissodendoryx with megasclere skeleton composed of acanthostyles and tyloids; microscleres are arcuate isochelae in three and sigmas in two size-classes.

Description of holotype

The specimen is light tan, massive but amorphous, measuring 3.5×5 cm, 2.5 cm in maximum thickness. It incorporates foreign objects from the sediment, serpulid worm tubes, and even parts of another sponge (a chalinid haplosclerid characterized by oxea and sigmas). The skeleton consists of smooth ectosomal tyloids, 233–278.5 µm (259.4 ±22.2 µm, mean ±SD) × 3.5–4.9 µm (4.1 ±0.3 µm); two size-classes of choanosomal acanthostyles, 237.1–348.9 µm (286.8 ±19 µm) × 6.7–12.18 µm (9.5 ±1.1 µm) and 116.9–168.8 µm (126.4 ±15.8 µm) × 4.4–6.5 µm (5.5 ±0.6 µm); two classes of isochelae, 47.5–55.6 µm (51.5 ±2 µm) and 8.3–13.8 µm (11.3 ±0.9 µm); and two of sigmas, 28.4–33.9 µm (30.7 ±2.7 µm) and 23.5–27.9 µm (25 ±0.9 µm).

Description

Colour: live colour was not recorded by the collectors; in ethanol the sponges are light tan.

Shape, size, consistency: only the type fragments were available for examination; the paratype looks like the holotype except for its smaller size, 3.5×1.5×1.5 cm; the interior is coarsely porous and full of incorporated foreign matter, such as sand and coral and bryozoan skeletons. The preserved specimens are firm, elastic, but easily torn.

Skeleton: the ectosome contains tyloids in disorganized fashion, many single, some in strands. The choanosome is mainly supported by a multispicular reticulation of acanthostyles, but smooth tyloids are seen among them. Microscleres are present throughout the body. The structure is difficult to make out in sections because the sponge, like most within the genus, is packed with sand and skeleton fragments from other organisms.

Spicules (for measurements see Table 8): acanthostyles in a large size range but with a separate small category clearly set off; small, thorn-like spines cover the shaft and are directed toward the rounded end of the spicule; spines covering the head are larger and recurved toward the spicule's tip. Tyloids, smooth and straight, without taper toward the small tyles. Isochelae and sigmas in two size-classes; some of the largest sigmas (which reach more than 200 µm) in our preparation are serrated and are most likely foreign (Figure 11).

Habitat observations

No data on the habitat were recorded; the relatively deep distribution (below 100 m) is unusual for members of the genus.

Distribution

Only known from the Gulf of Mexico, off Florida.

Table 8. Spicule types and measurements for representative specimens of *Lissodendoryx* (E.) *acanthostylota* sp. nov. Measurements are means ($N=20$, in μm) of maximum dimensions (length, or length \times width) of spicules.

| Specimen, location | Tylotes | Acanthostyles I | Acanthostyles II | Isochelae I | Isochelae II | Sigmas I | Sigmas II |
|---|--------------------------|------------------------------|------------------------------|-------------|--------------|-----------|-----------|
| USNM 48380, GOM, off Florida (Holotype) | 259.5 \times 4.1 | 286.9 \times 9.5 | 126.4 \times 5.5 | 51.5 | 11.3 | 30.7 | 25 |
| USNM 48382, GOM, off Florida (Paratype) | 269.2 \times 4.1 | 303.7 \times 8.2 | 157.2 \times 5.1 | 46.6 | 12 | 32.8 | 27.2 |
| Range of means | 269.2–259.5 \times 4.1 | 286.9–303.7 \times 8.2–9.5 | 126.4–157.2 \times 5.1–5.5 | 46.6–51.5 | 11.3–12 | 30.7–32.8 | 25–27.2 |
| Means of means | 264.4 \times 4.1 | 295.3 \times 8.8 | 141.8 \times 5.3 | 49.1 | 11.7 | 31.8 | 26.1 |

GOM, Gulf of Mexico.

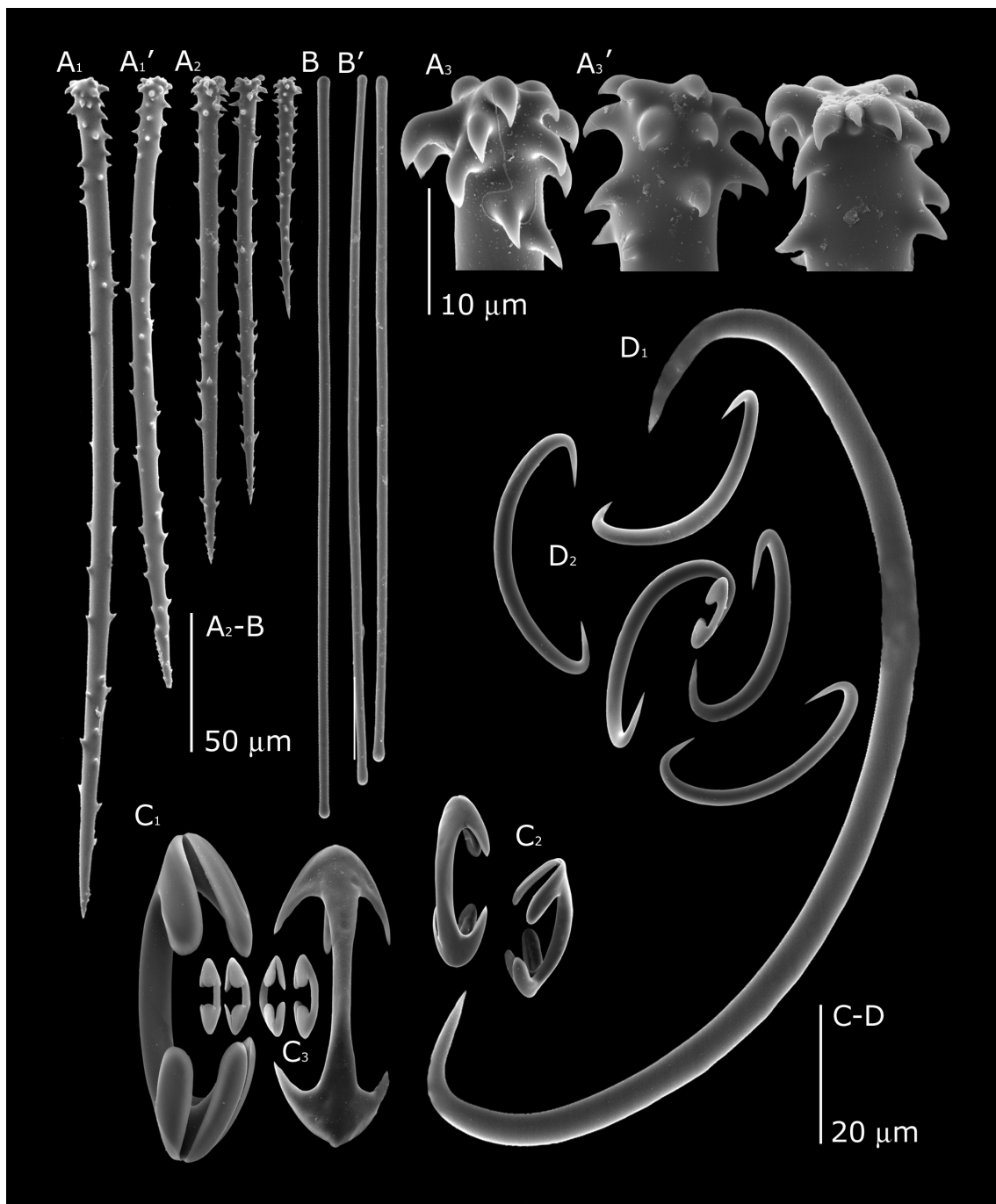


Figure 11. (A–D) *Lissodendoryx acanthostylota* sp. nov. (A1) Acanthostyle I (holotype, Gulf of Mexico); (A1') acanthostyle I (paratype, Gulf of Mexico); (A2) acanthostyles II (paratype); (inset) magnified acanthostyle heads; (B) tylote (holotype); (B') tylotes (paratype); (C1–3) isochelae I–III (holotype); (D1,2) sigmas I, II (holotype).

Etymology

Named for the spiny principal choanosomal spicules, acanthostyles.

Remarks

This is the first record of a species in the subgenus *Ectyodoryx* in the tropical western Atlantic. Other species in this group, including the type species, are poorly known but have very different growth forms (foliate, thinly encrusting) and were found only in the North Atlantic, off Greenland (van Soest, 2002).

Key for identification of Caribbean species of *Lissodendoryx*

1. Choanosomal skeleton made up by styles or subtylostyles2
— Choanosomal spiculation different5
2. Styles regular, smooth3
— Styles spiny4
3. One size-class of microscleres (isochelae, sigmas)
..... *L. (L.) isodictyalis*
— Two size-classes of microscleres (isochelae, sigmas)
..... *L. (L.) carolinensis*
4. Styles grading into subtylostyles, with coarse spines
deforming the head; two to three size categories of
microscleres (isochelae, sigmas) *L. (L.) spinulosa*
— Acanthostyles regular, covered by fine spines
..... *L. (E.) acanthostylota* sp. nov.
5. Choanosomal spicules strongyles6
— Choanosomal spicules tyloles7
6. Strongyles stout; 2 size categories isochelae, 1 size sigmas;
very fine, short raphids *L. (L.) colombiensis*
— Strongyles slender; 1 size isochelae, 1 size sigmas; robust
short raphids *L. (L.) strongylata*
7. Tyloles smooth, 2 sizes isochelae, 1 or 2 size classes
sigmas *L. (A.) signata*
— Tyloles with finely spiny heads, 1 size-class isochelae, 1
size sigmas *L. (A.) amphispinulata* sp. nov.

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REFERENCES

- Carter, H.J., 1882. Some sponges from the West Indies and Acapulco in the Liverpool Free Museum described, with general and classificatory remarks. *Annals and Magazine of Natural History*, **5**(9), 266–301, 346–368, pls 11–12.
- Collin, R., Díaz, M.C., Norenburg, J., Rocha, R.M., Sánchez, J. A., Schulze, A., Schwarz, M. & Valdés, A., 2005. Photographic identification guide to some common marine invertebrates of Bocas del Toro, Panama. *Caribbean Journal of Science*, **41**, 638–707.
- Díaz, M.C., 2005. Common sponges from shallow marine habitats from Bocas del Toro region, Panama. *Caribbean Journal of Science*, **41**, 465–475.
- Díaz, M.C., Smith, K.P. & Rützler, K., 2004. Sponge species richness and abundance as indicators of mangrove epibenthic community health. *Atoll Research Bulletin*, **518**, 1–17.
- George, W.C. & Wilson, H.V.P., 1919. Sponges of Beaufort (N.C.) Harbor and vicinity. *Bulletin of the Bureau of Fisheries*, **36**, 130–179, pls 56–61.
- Gómez, P., 2002. *Esponjas marinas del Golfo de México y el Caribe*. AGT Editor, S.A.: Mexico.
- Hartman, W.D., 1958. Natural history of marine sponges of southern New England. *Bulletin of the Peabody Museum of Natural History Yale*, **12**, i–xii, 1–155, fig. 1–46, pls 1–12.
- Hechtel, G.J., 1965. A systematic study of the Demospongiae of Port Royal, Jamaica. *Bulletin of the Peabody Museum of Natural History*, **20**, i–iv, 1–103, pls 1–8.
- Hofman, C.C. & Soest, R.W.M. van, 1995. *Lissodendoryx* species of the Indo-Malayan Archipelago (Demospongiae: Poecilosclerida). *Beaufortia*, **45**(6), 77–104.
- Laubenfels, M.W. de, 1936. A discussion of the sponge fauna of the Dry Tortugas in particular and the West Indies in general, with material for a revision of the families and orders of the Porifera. *Carnegie Institute of Washington (Tortugas Laboratory Paper No. 467)*, **30**, 1–225.
- Laubenfels, M.W. de, 1947. Ecology of the sponges of a brackish water environment, at Beaufort, N.C. *Ecological Monographs*, **17**, 31–46.
- Laubenfels, M.W. de, 1949. Sponges of the Western Bahamas. *American Museum Novitates*, **1431**, 1–25.
- Laubenfels, M.W. de, 1950. The Porifera of the Bermuda Archipelago. *Transactions of the Linnean Society of London*, **27**, 1–54, pls 1–2.
- Little, F.J., Jr, 1963. An experimental or tentative revision of the genus *Cliona* utilizing the principles of numerical taxonomy. *Tulane Studies in Zoology*, **11**(2), 31–71.
- Pulitzer-Finali, G., 1986. A collection of West Indian Demospongiae (Porifera) with, in appendix, a list of the Demospongiae hitherto recorded from the West Indies. *Estratto dagli Annali del Museo Civico di Storia Naturale di Genova*, **86**, 1–216. Institute of Zoology, University of Genoa, Genoa, Italy.
- Rützler, K., 1986. Porifera. In *Marine Fauna and Flora of Bermuda* (ed. W. Sterrer), pp. 111–128. New York: John Wiley & Sons, Inc.
- Rützler, K., 1995. Low-tide exposure of sponges in a Caribbean mangrove community. *PSZNI: Marine Ecology*, **16**, 165–179.
- Rützler, K., Díaz, M.C., Soest, R.W.M. van, Zea, S., Smith, K.P., Alvarez, B. & Wulff, J., 2000. Diversity of sponge fauna in mangrove ponds, Pelican Cays, Belize. *Atoll Research Bulletin*, **476**, 229–248.
- Rützler, K., Goodbody, I., Díaz, M.C., Feller, I.C. & Macintyre, I.G., 2004. The aquatic environment of Twin Cays, Belize. *Atoll Research Bulletin*, **512**, 1–49.
- Rützler, K., Soest R.W.M. van & Piantoni, C., in press. Sponges (Porifera) of the Gulf of Mexico. In *Gulf of Mexico—its origins, waters and biota* (ed. D.F. Felder and D.K. Camp). Texas: Texas A & M University Press.

- Soest, R.W.M. van, 1984. Marine sponges from Curaçao and other Caribbean localities. Part III. Poecilosclerida. In *Studies on the Fauna of Curaçao and other Caribbean Islands* (ed. P.W. Hummelinck and L.J. van der Steen), **66**(199), 1–167.
- Soest, R.W.M. van, 2002. Family Coelosphaeridae Dendy, 1922. In *Systema Porifera: a guide to the classification of sponges* (ed. J.N.A. Hooper and R.W.M. van Soest), pp. 528–546. New York: Kluger Academic/Plenum Publishers.
- Topsent, E., 1889. Quelques spongiaires du Banc de Campêche et de la Pointe-à-Pitre. *Extrait des Mémoires de la Société Zoologique de France*, **2**, 30–52.
- Topsent, E., 1892. Contribution à l'étude des spongiaires de l'Atlantique Nord. *Résultats des Campagne Scientifique accomplies sur son yacht par Albert I Prince Souverain de Monaco*, **2**, 1–165, pls 1–11.
- Topsent, E., 1897. Spongiaires de la baie d'Amboine. Voyage de M.M.M. Bedot et C. Pictet dans l'Archipel Malais. *Revue Suisse de Zoologie et Annales du Musée d'Histoire Naturelle de Geneve*, **4**(21), 421–487.
- Topsent, E., 1928. *Spongiaires de l'Atlantique et de la Méditerranée, provenant des croisières du Prince Albert Ier de Monaco*. Monaco: Imprimerie de Monaco.
- Verrill, A.E., 1907. The Bermuda Islands. Part IV. Geology and paleontology, and part V. An account of the coral reefs. *Transactions of the Connecticut Academy of Arts and Sciences*, **12**, 45–348, pls 16–40 [Porifera, pp. 330–344, fig. 176–181, pl. 35 C–D].
- Wells, H.W. & Wells, M.J., 1960. I. Systematic Treatment. In *Marine sponges of North Carolina* (ed. H.W. Wells et al.), pp. 200–245. *Journal of the Elisha Mitchell Scientific Society*, no. 76.
- Wiedenmayer, F., 1977. *Shallow-water sponges of the Western Bahamas*. Basel: Birkhäuser Verlag.
- Wilson, H.V.P., 1911. Development of sponges from dissociated tissue cells. *Bulletin of the Bureau of Fisheries*, **30**, 1–30, pls 1–5.
- Zea, S., 1987. *Esponjas del Caribe Colombiano*. Colombia: Editorial Catálogo Científico.
- Zea, S. & Soest, R.W.M. van, 1986. Three new species of sponges from the Colombian Caribbean. *Bulletin of Marine Science*, **38**(2), 355–365.

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