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A Tale of Three Oceans—Taxonomy of the *Holothuria* (*Thymiosycia*) *arenicola* Semper, 1868 complex (Echinodermata: Holoturoidea: Holothuriidae)

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Abstract

The ubiquitous sea cucumber *Holothuria* (*Thymiosycia*) *arenicola* Semper, 1868, externally characterized by a double row of dark blotches of various sizes on its dorsal body wall and a cryptic behaviour, is generally assumed to have a wide tropical distribution, although it has not been reported from the Eastern Atlantic. Careful morphological examination, with emphasis on the ossicle assemblage, of type and non-type *H. arenicola* specimens sampled in the Indian, Pacific and Atlantic Ocean, its subjective synonyms and species with a similar colouration and habit, revealed that *H. arenicola* is often confused with other species. This paper formally separates the different species in the *H. arenicola* complex, one of them being a species new to science: *Holothuria* (*Thymiosycia*) *kerriensis* **sp. nov.** Additionally, we describe two other species that are often confused with *H. arenicola*: *Holothuria* (*Lessonothuria*) *gracilis* Semper, 1868 and *H.* (*Thymiosycia*) *strigosa* Selenka, 1867. The *H. arenicola* complex *per se* is keyed-out, with the ossicle assemblage of the musculature being recognised as an important, previously largely neglected, guide. This contribution highlights the importance of building and curating well-maintaned natural history collections to understand biodiversity through time and space.

Key words: sea cucumbers, *Holothuria conusalba*, *Holothuria gracilis*, *Holothuria kerriensis* sp. nov**.**, *Holothuria milloti*, *Holothuria rathbuni*, *Holothuria strigosa*, *Holothuria unicolor*, *Holothuria zihuatanensis*, nomenclature.

Introduction

Taxonomy starts with the detection (through *de novo* sampling in the field, or through *post*-sampling examination of specimens deposited in natural history collections) and description of the components of biodiversity (alpha taxonomy), continues with the exploration and understanding of the classification of taxa according to evolutionary relationship (beta taxonomy), and culminates with conclusions on the origin and functioning of the investigated taxa and the ecosystems that contain them (gamma taxonomy). Current holothuroid taxonomy increasingly touches on these three levels simultaneously (*e.g.* O'Loughlin *et al.* 2007; Borrero-Perez & Vanegas-González 2019), although isolated alpha (*e.g.* Massin 1999; Martinez *et al*. 2019), beta (*e.g.* Kerr & Kim 2001; Mongiardino Koch *et al.* 2023) or gamma (*e.g.* Kerr *et al*. 2005) or combinations thereof continue to be produced (*e.g.* Samyn & Tallon 2005).

In the present study we used the alpha taxonomy approach to delineate the different species in the *Holothuria arenicola* complex, whereby we used comparative anatomical study, relying especially on the ossicle assemblage, to demarcate them.

Holothuria (Thymiosycia) arenicola Semper, 1868 is a cryptic species, living fully buried in the sand according to some (*e.g.* Cherbonnier 1988) or under rocks according to others (*e.g.* Samyn *et al*. 2006) and in a non-specified habitat according to most (*e.g.* Purcell *et al*. 2023). The reported colour pattern of *H. arenicola* ranges from light yellow to light brown whereby two more or less pronounced dorsal rows of brown blotches are mostly apparent. The size, colour intensity and connectivity (in some specimens sometimes forming longitudinal or transverse bands) of these markings is highly variable. So variable that Deichmann (1926: 14) opted that 'it will be natural to keep them separate, at least as varieties.'

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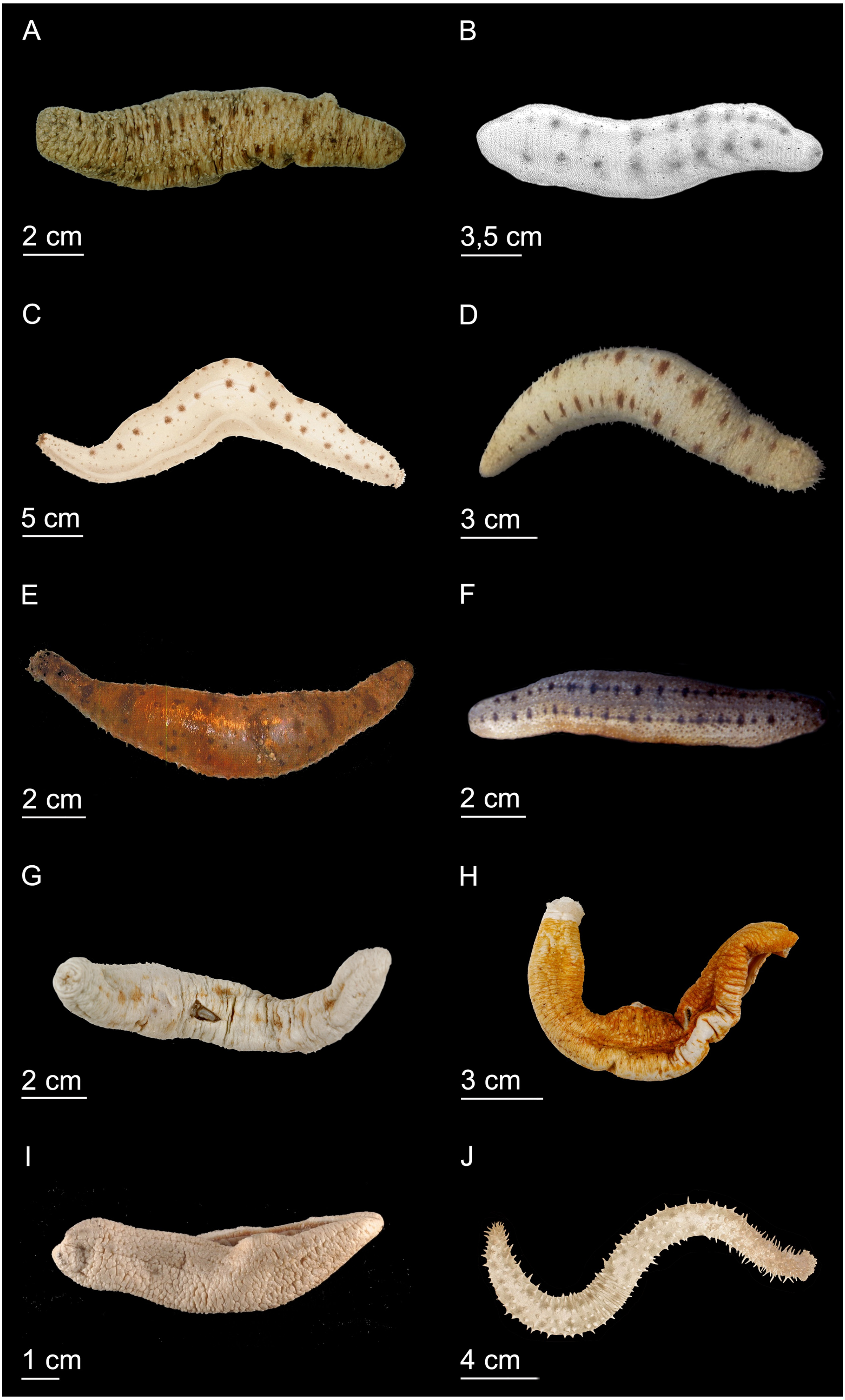
A
2 cm
B
3,5 cm
C
5 cm
D
3 cm
E
2 cm
F
2 cm
G
2 cm
H
3 cm
I
1 cm
J
4 cm

PLATE 1. Colour pattern of species in the *Holothuria* (*Thymiosycia*) *arenicola* complex: A, from the Caribbean, Barbados (= Holotype of *H. unicolor* Selenka, 1867); B, from the Caribbean, Panama (= Original drawing of *H. subditiva* Selenka, 1867); C. from the Central Pacific, Bohol, Philippines (= Original drawing of *H. arenicola* Semper, 1868); D, from the Central Pacific, Guam, USA (= *H. arenicola* Semper, 1868); E, from the Eastern Pacific, Mexico (= *H. zihuatanensis* Caso, 1965); F, West Indian Ocean, Kenya (= *H. kerriensis* sp. nov); G, South West Indian Ocean (= Holotype *H. milloti* Cherbonnier, 1988); H, Pacific Ocean, New Caledonia (= Holotype *H. conusalba* Cherbonnier & Féral, 1984); I, Central Pacific Ocean, Bohol, Philippines (Holotype of *H. strigosa* Selenka, 1867); J, from Central Pacific Ocean, Bohol, Philippines (Original drawing of *H. gracilis* Semper, 1868). Pictures by Y. Samyn (A, D, F), D. VandenSpiegel (G, H, I) and F. Solis-Marin (E).

Plate 1 gives an impression of the variety in pattern and coloration of species in the *Holothuria arenicola* complex.

Holothuria arenicola is believed to have a wide Indo-Pacific distribution from the Red Sea (Cherbonnier 1955) to the eastern Pacific (Cherbonnier 1988; Maluf 1988; Liao & Clark 1995; Hickman 1998). There has also been documented sightings in the Mediterranean (Abdel Razek *et al*. 2007), although this sighting may be a misidentification. However, it cannot be ruled out that this species, like *Holothuria (Theelothuria) hamata* Pearson, 1913, is another example of a Lessepsian migrant (Aydin *et al.* 2019). *H. arenicola* is also reported from the tropical western Atlantic, from the Caribbean (Hendler *et al.* 1995; Liao & Clark 1995) to Bermuda (Clark 1942) up to Rio de Janeiro (Tommasi 1969) and Ascension Island (Pawson 1978). To our knowledge *H. arenicola* has never been reported from the Eastern Atlantic Ocean.

Re-examination of type and non-type specimens identified as *Holothuria arenicola* from several museums showed that many were misidentified. These specimens correspond to: (1) consubgeneric species such as *Holothuria (Thymiosycia) conusalba* Cherbonnier & Féral, 1984, *H. (T.) gracilis* Semper, 1868, *H. (T.) strigosa* Selenka, 1867, *H. (T.) milloti* Cherbonnier, 1988, *H. (T.) zihuatanensis* Caso, 1965 and a species new to science: *H.* (*T.*) *kerriensis* **sp. nov.**, (2) species classified in other subgenera, but having a similar colour pattern, such as *H. (Lessonothuria) pardalis* Selenka, 1867 and (3) subjective synonyms of *H. (T.) arenicola*, such as *H. (T.) unicolor* Selenka, 1867 and perhaps *H. rathbuni* Lampert, 1885.

The aim of the present paper is threefold: (1) clarify the taxonomy of the different species in the *Holothuria arenicola* complex and (2) re-describe, preferentially based on available type material, the recognised species (including a species new to science) and (3) stabilize the names by typification where needed.

To facilitate identification, we have provided a dichotomous key to the recognized species in the *Holothuria arenicola* complex.

Often confused with species, *Holothuria* (*Thymiosycia*) *gracilis* Semper, 1868 and *H.* (*T.*) *strigosa* Selenka, 1867, are also described and illustrated.

Material and methods

We examined material from the collections of the Los Angeles County Museum, Los Angeles (LACM); the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); the Muséum National d'Histoire Naturelle de Paris, Paris (MNHNP); the Natural History Museum, London (NHM); the Royal Belgian Institute of Natural Sciences, Brussels (RBINS); the Royal Museum for Central Africa, Tervuren (RMCA); the United State National Museum, Washington DC (USNM); the Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin (ZMB); the Universidad Nacional Autonoma de Mexico (UNAM); the Zoologisches Museum zu Universität Hamburg, Hamburg (ZMH) and the Zoological Museum of Moscow State University, Moscow (ZMMSU).

Morphological observations and measurements were made following the conventional methods described by such workers as Rowe & Doty (1977), Massin (1999), Samyn (2003) and Samyn *et al.* (2006).

Other acronyms used include: GBR = Great Barrier Reef, Australia; IWP = Indo-West Pacific; Pac. = Pacific; QLD = Queensland, Australia; RSAKZN = Republic of South Africa Kwa-Zulu Natal; ULB = Université Libre de Bruxelles.

Ossicle types are defined as in conventional works such as Massin (1999), Samyn (2003) and Samyn *et al*. (2006), except for 6-holed buttons in which we distinguish three categories: (i) normal buttons (Figure 1A); plump buttons with open perforations (Figure 1B) and (iii) obliterated buttons (Figure 1C). In addition, closed buttons are also defined (Figure 1D).

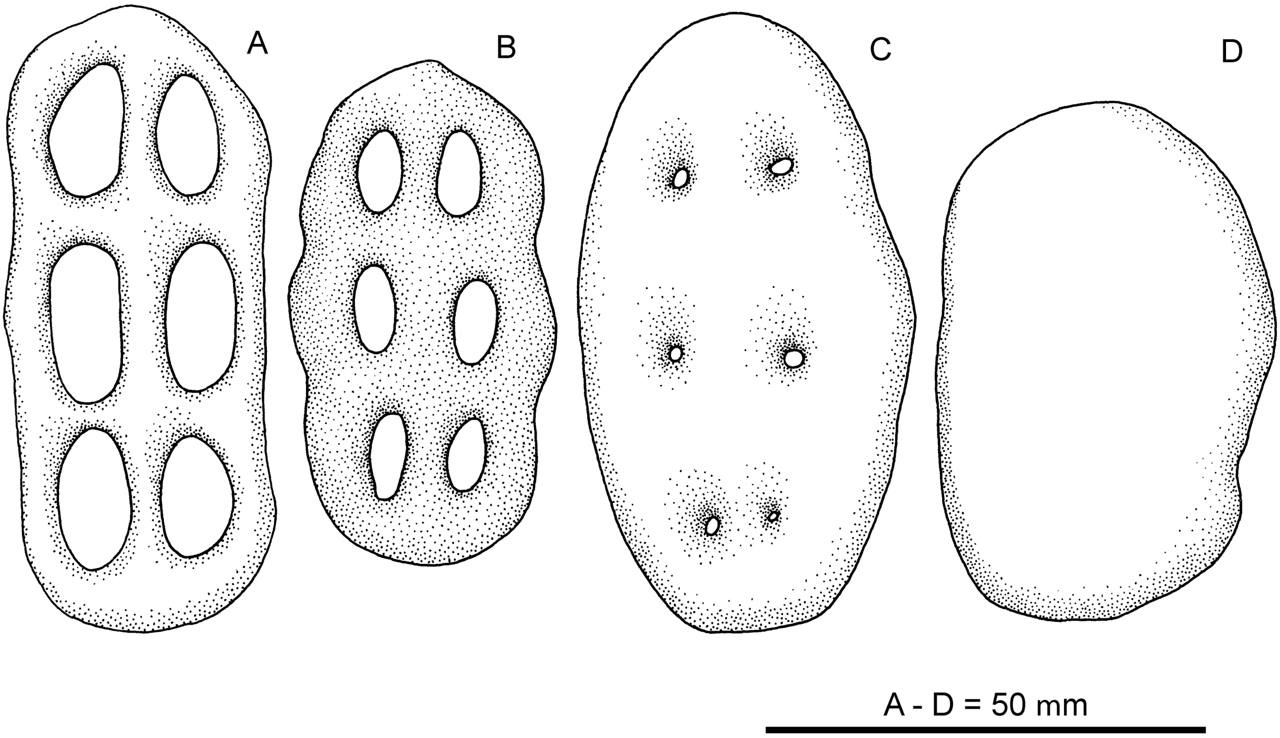

FIGURE 1. Button types in the *Holothuria arenicola* complex. A, normal (from *H. unicolor* Selenka, 1867): with margins only slightly undulating and with open elongated perforations; B, plump (from *H. milloti*): with margins swollen, distal side rounded and with open perforations; C, obliterated (from *H. kerriensis* **sp. nov.**): with perforations largely closed; D. closed (from *H. kerriensis* **sp. nov.**): with perforations completely absent.

Results

Systematics

Order Holothuriida Miller *et al.*, 2017

Family Holothuriidae Ludwig, 1894

Genus *Holothuria* Linnaeus, 1758

Subgenus *Thymiosycia* Pearson, 1914

The six species identified in *the Holothuria arenicola* complex are keyed hereunder. Annotated descriptions of the keyed-out species are provided below the key.

Key to the *Holothuria arenicola* complex

1 Ossicles present in the longitudinal and cloacal suspensor muscles **2**

- Ossicles absent in the longitudinal muscles, ossicles present or absent in the cloacal suspensor muscles **4**

2 Majority of buttons of ventral body wall regular, not plump; central Pacific distribution. . . . . ***Holothuria (Thymiosycia) arenicola* Semper, 1868**

\- Majority of buttons of ventral body wall plump, regular or irregular **3**

3	Ends of tentacle rods multi perforated and spiny; buttons regular; Western Indian Ocean distribution . . . . ***Holothuria (Thymiosycia) milloti*** **Cherbonnier, 1988**	
-	Tentacle rods small, few in number and non-or single perforated and smooth; buttons irregular; Indo-West Pacific distribution . . . . ***Holothuria (Thymiosycia) conusalba*** **Cherbonnier & Féral, 1984**	
4	Ossicles present in the cloacal suspensor muscles; Western Indian Ocean (Red Sea included) distribution. . . . . ***Holothuria (Thymiosycia) kerriensis*** **sp. nov.**	
-	Ossicles absent in the cloacal suspensor muscles.	**5**
5	Ventral buttons strongly obliterated; Atlantic Ocean distribution . . . . ***Holothuria (Thymiosycia) unicolor*** **Selenka, 1867**	
-	Ventral buttons not obliterated; East Pacific distribution. . . . . ***Holothuria (Thymiosycia) zihuatanensis*** **Caso, 1965**	

Holothuria (Thymiosycia) unicolor **Selenka, 1867**

Plate 1A, B, Figures 2A–J, 3A–B, 4A–P

Holothuria unicolor Selenka, 1867: 329–330, pl. 18, figures 63 & 64; Lampert, 1885: 78; Théel, 1886: 216; Panning, 1929: 119; Panning, 1934: 77, figure 59.

Holothuria densipedes H.L. Clark, 1901a: 257, pl. 17, figure 1; Deichmann, 1930: 68; Clark, 1933: 103.

Holothuria Rathbunii Lampert, 1885: 73.

Holothuria rathbunii; Théel, 1886: 68; Clark, 1901a: 259, pl. 17, figures 3–10; Clark, 1901b: 345; Verrill, 1902: 37, figures 6–7; Verrill, 1907: 145, figure 38; Sluiter, 1910: 332; Clark, 1919: 63, 73; Deichmann, 1926: 13.

Holothuria subditiva Selenka, 1867: 338, pl 19, figure 87; Semper, 1868: 248, 278; Lampert, 1885: 69; Théel, 1886: 225; Ludwig, 1889-92: 330; Bedford, 1898: 839 (= *H. pardalis*); Sluiter, 1887: 192 (= *H. pardalis*).

? *Brandtothuria arenicola*; Deichmann, 1958: 291, pl. 1, figures 10–13 (*partim*); Deichmann, 1963: 109; Tikasingh, 1963: 88; figs 34–38; Tommasi, 1969: 6, Figure 5; Martinez, 1973: 46, pl. 1, figures 3 & 4, pl. 4, figs 1–3; Suárez, 1974: 15; Martinez & Mago Hermison, 1975: 190.

Holothuria (Holothuria) arenicola; Panning, 1935: 88, figure 73 a–v (*partim*).

Holothuria arenicola; Semper, 1868: 81, 277 (*partim*); Deichmann, 1930: 66, pl. 4, figures 1-9; Caso, 1955: 513, pl.5, figures 1–21; Tommasi, 1969: 6, figure 5; Pawson, 1978: 27; Miller & Pawson, 1984: 10.

Holothuria grisae; Deichmann, 1930: 76.

? *Holothuria maculata*; Lampert 1885: 73.

Holothuria (Thymiosycia) arenicola; Hendler *et al*., 1995: 297, figure 168 (colour picture), figure 186A–E; Cutress, 1996: 84, figures 23B–C, 24, 25; Laguarda-Figueras *et al*., 2001: 20, figure 6A–E; Hasbun & Lawrence, 2002: 673, figure 2F; del Valle-Garcia *et al*., 2008: 24; *Alvarado et al*., 2008: 46.

Material examined. Type material. Holotype *Holothuria unicolor* Selenka, 1867: ZMB 1781, Barbados, collecting date unknown, coll. Wessel. Syntypes *Holothuria arenicola* Semper, 1868: ZMMSU H-13 (one specimen), Surinam, collecting date unknown, coll. C. Semper (non *H. arenicola*); NHM 84.3.86 (one specimen), Surinam, collecting date unknown, coll. C. Semper (non *H. arenicola*).

Non-type material. USNM E 43377 (one specimen): Puerto Rico (La Paguera, La Gata and Caracoles Reefs), 1966, coll. C.E. Cutress. USNM E 2776 (one specimen): Colombia (Caribbean Sea, Sabanilla), 16.iii.1884, coll. Albatross R.V. USNM E 2787 (one specimen): Colombia (Caribbean Sea, Sabanilla), iii.1884, coll. Albatross R.V. USNM E 2799 (one specimen): Bahamas (Little Bahama Bank, Abaco Island), 02.v.1886, coll. Albatross. USNM E 21376 (one specimen): R.V., Grenada (Tobago Cay, Baradal), 17.iii.1956, coll. Schmitt & Chase. USNM E 21377 (one specimen): Bahamas (Andros Island, Calabash Bay), 10.iii.1966, coll. M.C. Jones. USNM E 22316 (one specimen): Barbados (Pelican Island), 11.v.1918, shore, low tide, coll. W.K. Fisher. USNM E 27985 (one specimen): United States (Florida, Dry Tortugas, Long Key), 29.ix.1982, under rocks, 0.5-1 m depth, coll. J.E. Miller.USNM E 27986 (one specimen): United States (Florida, Dry Tortugas, Bush Key), 30.ix.1982, under rocks, 1 m depth, coll. J.E. Miller. USNM E 31671 (one specimen): Puerto Rico (Las Pelotas, 4-5 km W of La Parguera), 18.vii.1983, around mangrove islands in coarse sand with Porites rubble and Thalassa, unknown depth, coll. D. Pawson. IRSNB Hol/661 521 (six specimens): Venezuela (Chimano Grande Island), x.1997, under stones, 1 m depth, coll. unknown.

Type locality. Barbados.

Etymology. *Unicolor* means uniform in coloration. Selenka (1867: 330) described the coloration of the holotype as ‘Schwarz’. We, however, re-examined the holotype (no other types existent) and note that it has a beige body wall marked with darker blotches, especially dorsally (*cf.* Figure 1A).

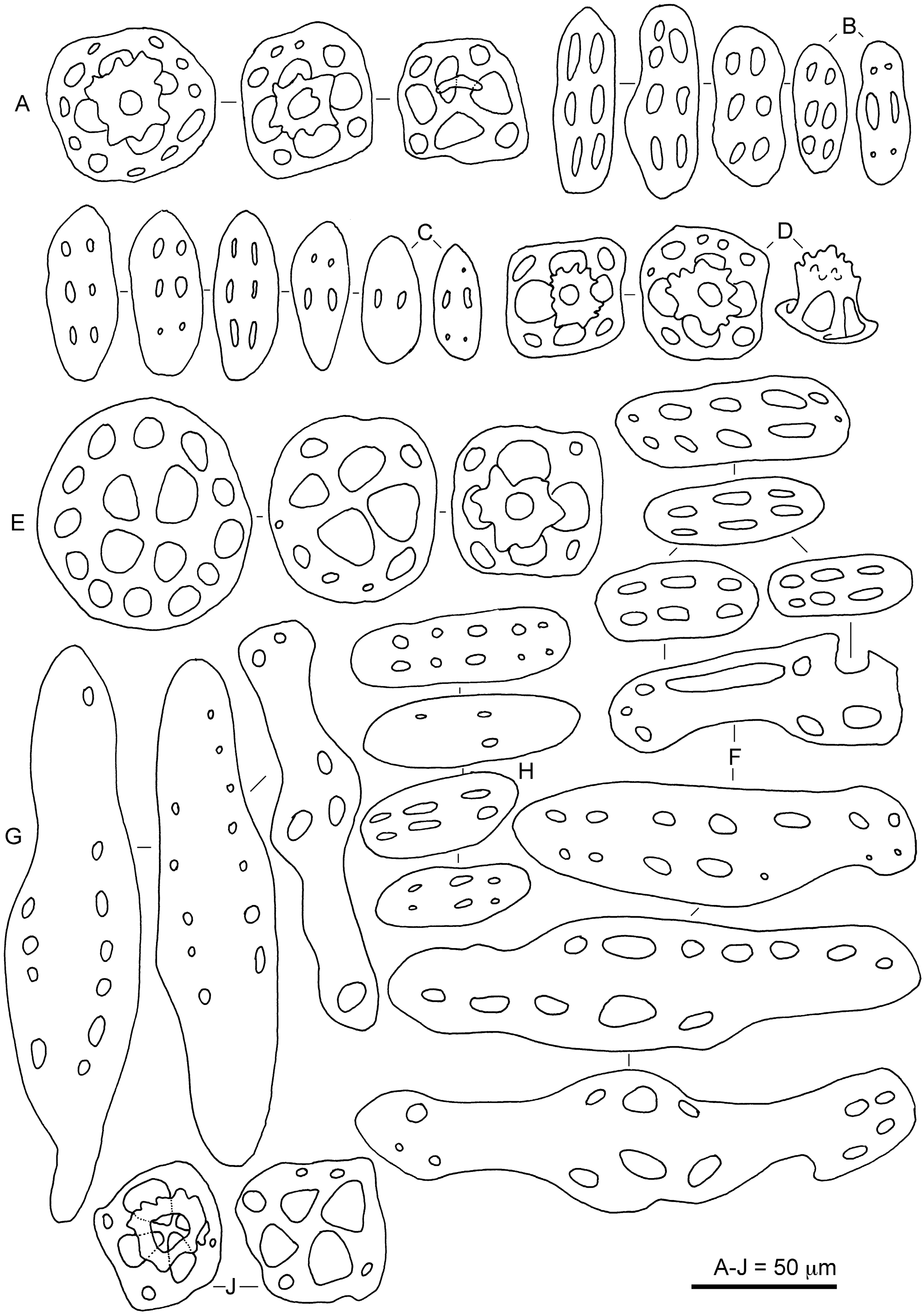

FIGURE 2. *Holothuria (Thymiosycia) unicolor* Selenka, 1867 (holotype, ZMB 1781). A, tables of dorsal body wall; B, buttons of dorsal body wall; C, buttons of ventral body wall; D, tables of ventral body wall; E, tables of dorsal tube feet; F, buttons and perforated rods of dorsal tube feet; G, perforated rods of ventral tube feet; H, buttons of ventral tube feet; J, tables of ventral tube feet.

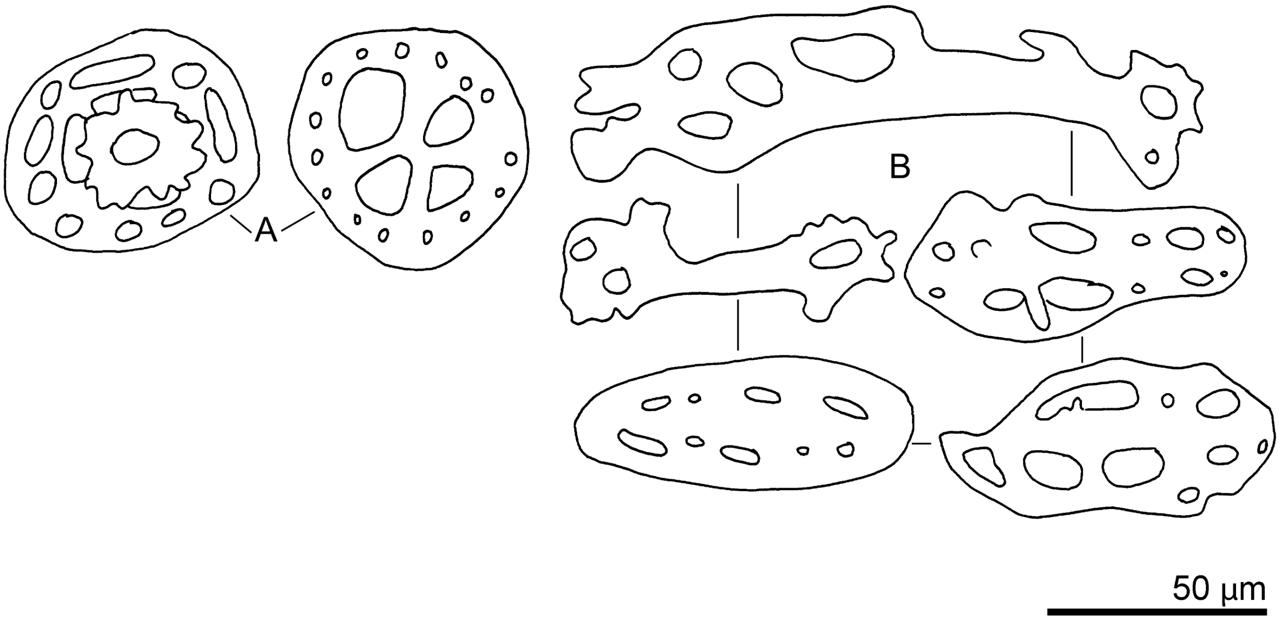

FIGURE 3. *Holothuria (Thymiosycia) unicolor* Selenka, 1867 (holotype, ZMB 1781). A, Tables of anal papillae; B, rods and buttons of anal papillae.

Known geographical distribution. According to verified vouchers, *Holothuria unicolor* occurs in the Caribbean Sea from Florida to Surinam. The records from the subtropical East coast of South America, Bahia, Brazil (Tommasi 1969), and those from the central Atlantic Island Ascension (Pawson 1978) are now being referred to as *H*. cf. *unicolor* (see also below; remarks with *H. unicolor*). We retrieved no museum or literature records of *H. unicolor* from the East Atlantic Ocean, unless Greeff's (1882) records of *Holothuria grisae* Selenka, 1867 from Sao Thomé (see also Deichmann, 1930: 77), would prove to be *H. unicolor.*

Taxonomic description. *External Anatomy (holotype):* Medium-sized holothurian, preserved holotype 115 mm long and 10–27 mm across; size of living adults unknown. Body cylindrical, gritty to the touch, with body wall 2 mm thick. Mouth ventral. Number, position and size of tentacles could not be determined without causing irreversible damage to the holotype. Anus terminal, surrounded by anal papillae. Colour beige dorsally and ventrally, with dorsally two rows of large blotches and widespread smaller dots and ventrally with scarcer and smaller, somewhat irregularly placed darker markings. Tube feet beige; ventrally all over surface, but mainly in ambulacral areas; dorsally in distinct rows along the ambulacrae.

External anatomy (non-type material): Medium-sized holothurian, preserved adult specimens 70–154 mm long and 13–22 mm across; size of living adults unknown. Body cylindrical, gritty to the touch, with body wall 2–3 mm thick. Mouth ventral, surrounded by 20 very small beige tentacles. Anus terminal, surrounded by five valves, each with 2–5 papillae. Colour beige dorsally and ventrally, with dorsally two rows of large blotches or widespread smaller blotches. Some dorsal blotches enlarged forming transverse bands. Some specimens uniform in colour. Tube feet beige, more numerous ventrally than dorsally, spread without alignment on bivium and on trivium.

Internal anatomy (holotype): Was not assessed to avoid damage.

Internal anatomy (non-type material): Calcareous ring with radial and interradial plates of equal width, radials quadrangular in shape. Tentacle ampullae very short, 1–5 mm long. 1–3 Polian vesicles. Single stone canal, orange to red, ending in an ovoid madreporic plate. Cuvierian tubules present, short, white to beige (when live, individuals expel them and appear ballon-like according to Kerr, pers. com). Cloaca large, 1/5 of body length.

Ossicles (holotype): Dorsal body wall with numerous buttons (Figure 2B), 45–65 µm long, with 3 pairs of non-obliterated holes; tables (Figure 2A) rare, with disc squarish to circular, 45–60 µm across, flat disc perforated by 4 large central holes and 6–12 small peripheral holes, pillar very short, ending in crown of spines. Ventral body wall with numerous buttons (Figure 2C), 40–60 µm long, perforated by 3 pairs of holes, some obliterated; tables as in dorsal body wall (Figure 2D), but more numerous. Dorsal tube feet with numerous tables (Figure 2E), disc 50–70 µm across, 4 central and 4–12 peripheral holes; buttons (Figure 2F) as in dorsal body wall, but occasionally with up to 7 pairs of holes; and few button-derived rods 100–200 µm long. Ventral tube feet with buttons with 3–5 pairs of

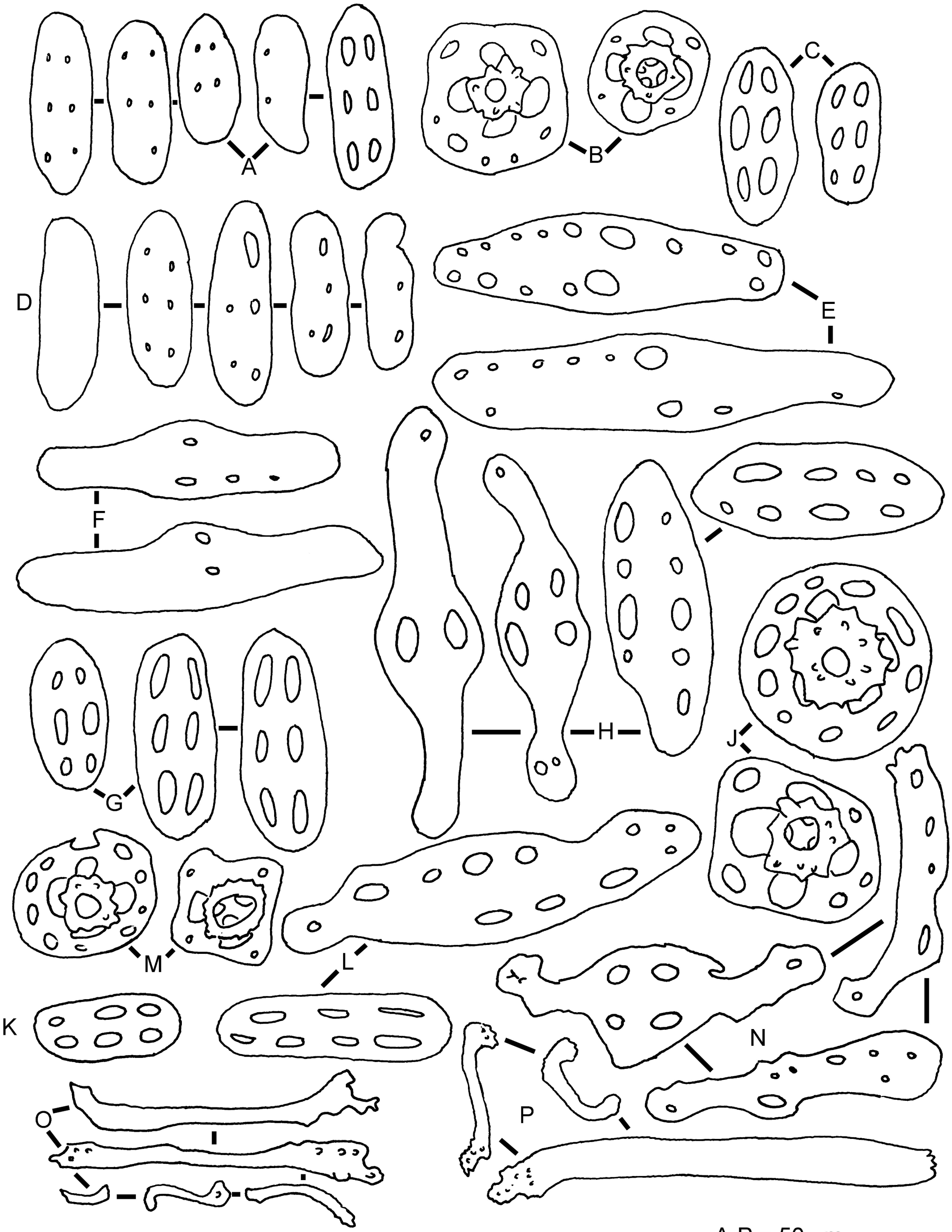

FIGURE 4. *Holothuria (Thymiosycia) unicolor* Selenka, 1867 (A–O: from USNM E43377, Puerto Rico; P, from specimen USNM E27985, Florida). A, buttons of ventral body wall; B, tables of ventral body wall; C, buttons of dorsal body wall; D, buttons of ventral tube feet; E, elongated buttons of ventral tube feet; F, perforated, rod-like elongated buttons of ventral tube feet; G, buttons of dorsal tube feet; H, rods of dorsal tube feet; J, tables of dorsal tube feet; K, buttons of anal papillae; L, elongated buttons of anal papillae; M, tables of anal papillae; N, rods of anal papillae; O & P, rods of tentacles.

obliterated holes (Figure 2H), tables as in ventral body wall (Figure 2J), button-derived rods (Figure 2G) with occasionally obliterated holes, around end-plate, up to 300 µm long. Anal papillae with numerous tables (Figure 3A) and rare buttons and rods (Figure 3B); tables with round disc, perforated by 4 central holes and up to 15 peripheral perforations some of these strongly obliterated, 55–60 µm across; buttons irregular with 3–5 pairs of holes, 70–80 µm long; and few irregular, 75–145 µm long rods. Respiratory trees, gonad, gut, longitudinal and cloacal suspensor muscles devoid of ossicles. Ossicle assemblage of tentacles not assessed to avoid damage.

Ossicles (from non-type material): Dorsal and ventral body wall with numerous buttons and few tables. Ventrally, buttons 40–65 µm long, with 3 pairs of holes, some partly obliterated (Figure 4A) and tables, 40–50 µm across, with flat disk perforated by 4 large central holes and 0–10 small peripheral holes with 4 very short pillars ending in a small crown of spines (Figure 4B). Dorsally, buttons 50–70 µm long, perforated by 3 pairs of elongated holes, never obliterated (Fig 4C) and tables as in ventral body wall but with disc somewhat larger, 50–65 µm across. Ventral tube feet with buttons, 50–60 µm long, with 3 pairs of holes, most partly obliterated, some without holes (Figure 4D); tables as in ventral body wall with disc 40–55 µm across, and elongated buttons, 80–150 µm long, perforated by up to 10 pairs of holes (Figure 4E), largest ones, 150–175 µm long, looking like perforated rods (Figure 4F), elongated buttons and rods located close to 375 µm wide single-pieced end-plate. Dorsal tube feet with same ossicle assemblage as that of ventral tube feet: buttons (Figure 4G), rods (Figure 4H), tables, 60–70 µm across, (Figure 4J) and single-pieced end-plate, 240–270 µm across. Anal papillae with buttons (Figure 4K), elongated buttons (Figure 4L), tables (Figure 4M) and rods (Figure 4N); buttons 50–80 µm long, with 3 pairs of elongated holes; tables and rods similar in shape and size as those of body wall. Tentacles with numerous rods, 15–150 µm long, straight or slightly curved, smooth with knobbed extremities (Fig 4O–P); apex of tentacles with some small C- or S-shaped rods (Figure 4O–P). Longitudinal and suspensor muscles of cloaca devoid of ossicles.

Remarks. It is remarkable that *Holothuria unicolor* Selenka, 1867 has sunk into oblivion since Deichmann (1930: 77) stated that 'it is very likely' that it is identical to *Holothuria grisae* Selenka, 1867, a hypothesis refuted by Panning (1929, 1934) who listed *H. unicolor* as a valid species. However, since Panning (1934) nobody acknowledged the name *H. unicolor*, and specimens in the *H. arenicola* complex collected in the West Indies and the central Atlantic have commonly been referred to *H. arenicola*. This comes as a surprise as several authors have noted (*e.g.* Deichmann 1926) or illustrated (*e.g.* Hendler *et al*. 1995) buttons of the (ventral) body wall with nearly obliterated perforations, a character-state absent in *H. arenicola*. Confusion probably originated with the type series of *H. arenicola* that contains both species, as became evident when we relocated two of the syntypes in the ZMMSU: one (H-81 = *H. arenicola*) collected in Bohol, Philippines, the other (H-13 = *H. unicolor)* collected in Surinam. With our observations on these syntypes at hand, we feel armed to comment on some of the historical subjective synonyms of *H. arenicola,* which we judge would best be allocated to the synonymy of *H. unicolor*. These are:

- *Holothuria densipedes* H.L. Clark, 1901; described based on a single specimen from Puerto Rico. Clark (1901a: 258) stressed that its ossicles are 'exactly those of *H. rathbuni* Lampert'; the latter species also considered a synonym of *H. arenicola* (see also below). Deichmann (1930: 68) stated that *H. densipedes* possibly is just 'an abnormal *H. arenicola'* that differs from it by having Cuvierian organs which are 'long and fine'. Such Cuvierian tubules are reported from Caribbean *H. arenicola* (=*H. unicolor*) specimens (Kerr, pers. comm.). Although we have not studied the holotype of *H. densipedes*, Clark's (1901a) description leaves little doubt that we are dealing with the Caribbean form in the *arenicola* complex, that is: *H. unicolor.* It's color is described as 'brown, with a few scattered dull purple or blackish blotches'. Unfortunately, H.L Clark's (1901a, pl. 17, Figure1) illustration is in black and white and is blurry, providing little information, and not showing the blotches. Clark's (1901a) description of the ossicle assemblage of *H. densipedes* matches remarkably well with that of *H. unicolor.* So, the main difference between both species seems to be limited to the presence of 'very numerous and crowded pedicels' (H.L. Clark 1901a). We think that this observation is most possibly a reflection of the fact that the description was based on a life, well-relaxed, specimen.
- *H. rathbuni* Lampert, 1885; described based on a single specimen from Bahia, Brazil. Despite the following differences: (i) allopatry between *H. rathbuni* (in the Province of Bahia, East coast of Brazil) and *H. unicolor* (in the Caribbean *s.l.*), (ii) ossicle morphology, with the Brazilian form showing tables with a more squarish disc (Tommasi 1969) and *H. unicolor* presenting tables with a more roundish disc, and (iii) coloration, with *H. rathbuni* described as: 'body brownish yellow with dorsally 2 rows of large brown-red areas and many smaller, irregularly-spread, dots; additionally, body covered with a meshwork of light-purplish lines' (translated in diagnostic style from Lampert 1885: 74), and *H. unicolor* here reported without a meshwork of lines, we have opted to treat *H. rathbuni* as putative junior subjective synonym of *H. unicolor* (referring to it as *H.* cf. *unicolor*) until we can study material from Brazil and the central Pacific (Ascension Island). With this decision, we fail Deichmann (1930) who treated *H. unicolor* merely as a potential synonym of *H. grisae* Selenka, 1867

and who suggested using the name *H. rathbuni* for the Atlantic forms of *arenicola*. Current populations of *H. rathbuni* are separated from Caribbean *H. unicolor* populations by at least two major distribution filters. First, the vast plumes of freshwater and amounts of sediment that two of South America's largest rivers, the Amazon and the Sao Francisco, push between the *H. unicolor* and *H. rathbuni* populations. Second, the Atlantic current system with the South Equatorial Current flowing westward across the Atlantic and splitting into the Northbound North Equatorial Current and the Southbound Brazil current upon arrival on the horn of Brazil, makes that the Caribbean and the Brazilian populations are unlikely to be presently connected. Given these two distribution filters, we are unable to explain the presence of *'H. arenicola'* in the central and West Atlantic. One putative explanation to this distribution would be that these populations have established themselves through 'founders' that were taken from the Indian Ocean by the Northbound Benguela current that flows along the western side of the African continent up to about the equator where it gives rise to the South Equatorial Current. To test that hypothesis, we would need to have access to the phylogeny of the complex to determine how the E African forms in the complex relate to the East and Southwest Atlantic forms. Also, one would have to re-investigate the Atlantic coasts of Africa to verify the absence of '*H. arenicola'* in that region.

- *Holothuria subditiva* Selenka, 1867, described on an undetermined number of specimens collected in Panama, is a mixed type series, with the one specimen restudied belonging to *Holothuria* (*Semperothuria) surinamensis* Ludwig, 1875. Even though we were not in the position to study all the syntypes deposited in the MCZ, we feel no hesitation to use our power as 'First reviser' to treat *H. subditiva* as junior subjective synonym of *H. unicolor* Selenka, 1867, given the original descriptions and illustrations (cf. Plate 1A&B). By giving *H. unicolor* precedence over *H. subditiva* we serve ICZN recommendation 24A because the original type series of *H. unicolor* only holds the holotype, whereas the type series of *H. subditiva* holds several species.

Holothuria unicolor can be recognised from *Holothuria arenicola* by:

(i) its geographic distribution: Atlantic (Caribbean, from Florida to Bermuda to Surinam and perhaps even to Bahia, Brazil, and Ascension Island) for *Holothuria unicolor*, and central to perhaps even Eastern Pacific (see also below, with remarks with *H. arenicola*) for *H. arenicola*;
(ii) the morphology and size of the buttons of the ventral body wall: some with holes partly obliterated, 40–65 µm long for *Holothuria unicolor*, and without obliterated holes, 40–50 µm long for *H. arenicola*, with those of *H. unicolor* also more slender;
(iii) the presence of ossicles in the longitudinal and cloacal suspensor muscles: absent in *H. unicolor*, while present as irregular buttons and rods in *H. arenicola*;
(iv) the number and type of ossicles in the tentacles: numerous and generally long (apart from those coming from the apex) in *H. unicolor* while very rare and small in *H. arenicola*;
(v) its ecology: 'always buried in a rubble-free expanse of coralline sand, perhaps associated with seagrass and underneath a small but characteristic mound of sand' for *H. unicolor*, versus 'on the reef flat, under large flat coralline rubble, on well-sorted, aerated coralline sand' for *H. arenicola* (Kerr pers. comm.);
(vi) the behaviour of the Cuvierian tubules: expellable for *H. unicolor*, while non-expellable for *H. arenicola* (Kerr pers. comm.).

Unfortunately, we were not able to examine live specimens from the Caribbean to document any, more subtle, differences in morphology, behaviour and ecology.

Holothuria (Thymiosycia) arenicola **Semper, 1868**

Plate 1C&D, Figures 5A–L, 6A–D

Holothuria arenicola Semper, 1868: 81, 277, pls. 20, 30, Figure 13, 35 Figure 4; Théel, 1886: 222.
Holothuria (Holothuria) arenicola; Panning, 1935: 88, Figure 73a–v (partim)
Holothuria (Thymiosycia) arenicola[1]; Rowe, 1969: 147; Rowe & Doty, 1977: 232; Paulay, 2003: 578.
Sporadipus (Acolpos) maculatus Brandt, 1835: 46–47.
Holothuria (Holothuria) maculata; Domantay, 1936: 399, pl. 6, Figure 62.
Holothuria maculata; Selenka, 1867: 331; Ludwig, 1883: 156; Lampert, 1885: 73; Bell, 1887: 140; Bell, 1888: 389; Ludwig, 1888: 807; Ludwig, 1889-92: 330; Mitsukuri, 1896: 407; Bedford, 1898: 842; Bedford, 1899: 146; Sluiter, 1901: 9; Koehler & Vaney, 1908: 11; Mitsukuri, 1912: 103; Pearson, 1913: 80, plate 11, Figure 8; Domantay, 1934: 110, plate 1, figure 1A–H; Daniel & Halder, 1974: 428.
Holothuria humilis Selenka, 1867: 339, plate 19, figure 89 (suppressed name; ICZN Opinion 1533).
? *Holothuria monsuni* Heding, 1939: 217, figures 18–26; Deichmann, 1958: 291 (cited as a synonym of *H. arenicola*).

1 It should be noted that we do not list all the citations of *Holothuria* (*Thymiosycia*) *arenicola* as the descriptions often do not allow to judge if they are true *H. arenicola* specimens or other species in the complex.

Material examined. Type material. Lectotype (here designated) - *Holothuria arenicola* Semper, 1868: Indonesia (Ambon), unknown collection date and depth, leg. Rosenberg, ZMB Ech.1576 (largest of two specimens in sample). Paralectotypes (here designated) - *Holothuria arenicola* Semper, 1868: Indonesia (Ambon), unknown collection date and depth, leg. Rosenberg, ZMB Ech.1576 (smallest of two specimens in sample); Philippines (Bohol), unknown collection date and depth, coll. C. Semper, ZMMSU H-81 (1 specimen).

Non-type material. NHM 89.6.15.4 (one specimen): Java Sea, collector and collecting date unknown. NHM 83.3.15.6 (one specimen); Timor, collector and collecting date unknown. USNM E16676 (one specimen): Philippines (Luzon Island, Maculabo Island, 14°25'N, 122°47'E), coll. Albatross R.V., 14.vi.1909. USNM E 40766 (one specimen): Philippines (Luzon Island, 13°37'36" N, 124°02'54" E), coll. Philexp-89, 5.iv.1989. USNM E 24600 (one specimen): Tonga, coll. Albatross R.V., 1889, shore. USNM E 35726 (one specimen): Cook Islands (Rarotonga), off Matavera, outer reef slope, 21°14'S, 159°46'W), coll. G. Paulay, 8.IX.1984, 4 m depth, under rock in sand. USNM E22621 (one specimen): Fiji (Luva reef), coll. New Zealand Expedition State University of Iowa. IRSNB IG 31 558 (one specimen): USA (Guam), coll. Samyn & VandenSpiegel, 06.vi.2010; 1–2 m depth.

Type locality. Indonesia, Ambon.

Known geographical distribution. Literature suggests an Indo-Pacific distribution (Panning, 1935), but verified vouchers restrict the area of *H. arenicola* to the west and central Pacific.

Taxonomic description. *External anatomy (lectotype, complemented with other vouchers)*: Medium to large-sized species, preserved adult specimens 48–215 mm long and 10–21 mm across; size of living adults possibly only slightly larger as little contraction occurs upon preservation. Body cylindrical, tapering at both sides, but more posteriorly (Semper, 1868). Body wall gritty to the touch. Mouth ventral, surrounded by 20 very small tentacles. Anus terminal, surrounded by five groups of papillae, each with 5 papillae. According to Semper (1868), colour of live individuals is dirty greyish yellow, with two rows of brownish blotches in radial areas and dark-brown dots over entire body. Dorsal and ventral tube feet beige; former spread all over bivium but with majority in ambulacral zones; latter restricted to ambulacral areas.

Internal anatomy (lectotype): not assessed to avoid damage to the type.

Internal anatomy (paralectotype): Calcareous ring with radial and interradial plates of equal width, radial ones ± 1.5 x longer than interradial ones, posterior side of interradial plates slightly indented, posterior side of radial plates mostly straight. Tentacle ampullae short, 8 mm. Single Polian vesicle, 7 mm long. Stone canal was not observed in the paralectotype, but very short according to Semper (1868). Cuvierian tubules were not observed. Cloaca less than 1/10 of body length.

Ossicles (lectotype): Dorsal and ventral body wall with buttons and tables of the same kind and size (Figure 5A-D). Buttons very regular, 40–50 µm long, nearly round (L/W= 1.3–1.5), with 3 pairs of holes, holes round or slightly elongated, never obliterated or closed (Figure 5A, C). Tables very small, 40–55 µm across, flat, often reduced to the smooth-edged quadrangular disc, perforated by 4 large central holes and 0–4 small peripheral holes, pillars very short, ending in a few spines or a small crown of spines (Figure 5B, D). Ventral tube feet with buttons, tables and rods (Figure 5E, F, G); buttons larger, 60–70 µm long, and more elongate (L/W = 2.5) than those of body wall, with three pairs of holes, elongated, never closed (Figure 5E), some buttons much longer, 80–110 µm long, irregular and with 4–7 pairs of holes (Figure 5G); tables, 55–65 µm across, very similar to those of body wall but with disc perforated by four large and 4–12 small peripheral holes, and with crown of spines nearly always present (Figure 5F); end-plate of tube feet in one piece, 280–290 µm across; rods, 155–180 µm long, perforated by 1–2 large central holes and 0–4 distal ones. Dorsal tube feet with tables, buttons and rods like those of ventral tube feet (Figure 5J–L), but large buttons, 50–225 µm long, with 3–10 pairs of holes, abundant (Figure 5J). Anal papillae with tables and perforated rods (Figure 6A,B); tables large, 65–100 µm across, with disc perforated by four large central and numerous (up to 25) small peripheral ones, spire with 4 pillars connected by 1–4 cross beams (Figure 6A); perforated rods, ± 165 µm long, with perforations predominantly in enlarged central part (Figure 6B). Longitudinal muscles with small, 20–65 µm long, irregular buttons and rods (Figure 6C). Cloacal suspensor muscles with few, 35–50 µm long, very irregular buttons (Figure 6D). Ossicle assemblage of tentacles not observed. Respiratory trees, cloaca and gut devoid of ossicles.

Remarks. When Semper (1868: 81) introduced the name *H. arenicola*, he had material from Bohol (the Philippines), Ambon (the Philippines), Fiji and Surinam before him, though only the material from Bohol was collected by him. The specimen from Bohol (ZMMSU H-81) he superbly illustrated (cf. Semper 1868, Figure 1C), and therefore it would have been just to designate this specimen as the lectotype of *H. arenicola*. However, because

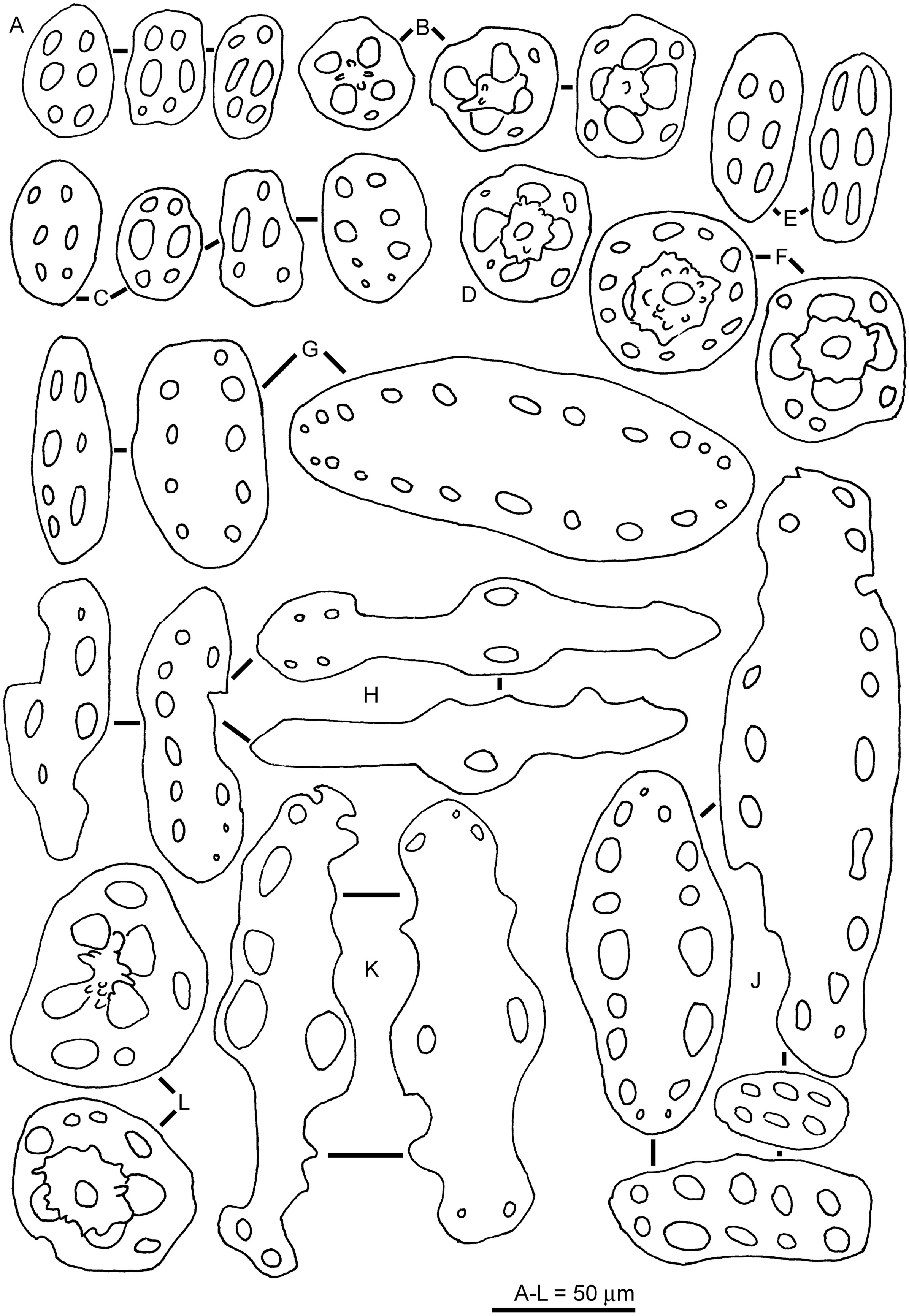

FIGURE 5. *Holothuria (Thymiosycia) arenicola* Semper, 1868 (lectotype, ZMB Ech. 1576). A, buttons of dorsal body wall; B, tables of dorsal body wall; C, buttons of ventral body wall; D, tables of ventral body wall; E, buttons of ventral tube feet; F, tables of ventral tube feet; G, elongated buttons of ventral tube feet; H, rods of ventral tube feet; J, buttons of dorsal tube feet; K, rods of dorsal tube feet; L, tables of dorsal tube feet.

the state of this voucher is so poor due to an accident in 1909 (a collapsing cupboard according to the included label), we opted to select one of the syntypes from Ambon (ZMB 1576, largest specimen of lot of 2) as the name-bearing type. Consequently, the type locality changes from Bohol (the Philippines) to Ambon (Indonesia). Specimen ZMMSU H-13 from Surinam (one of the syntypes of *H. arenicola*) proved to be *H. unicolor* Selenka, 1867. The syntype (ZMH E. 2508) from Fiji we refer to *H. conusalba*, although with doubt.

Semper (1868) noted that in his specimen from Ambon, he found a few small Cuvierian tubules; we failed to find these in the type-material, so this observation is to be treated with caution.

Holothuria monsuni Heding, 1939 we now keep as a subjective synonym of *H. arenicola*. However, given the high spire of some of the tables that Heding (1939) illustrated, we would not be surprised if we need to revisit that decision once the holotype can be studied.

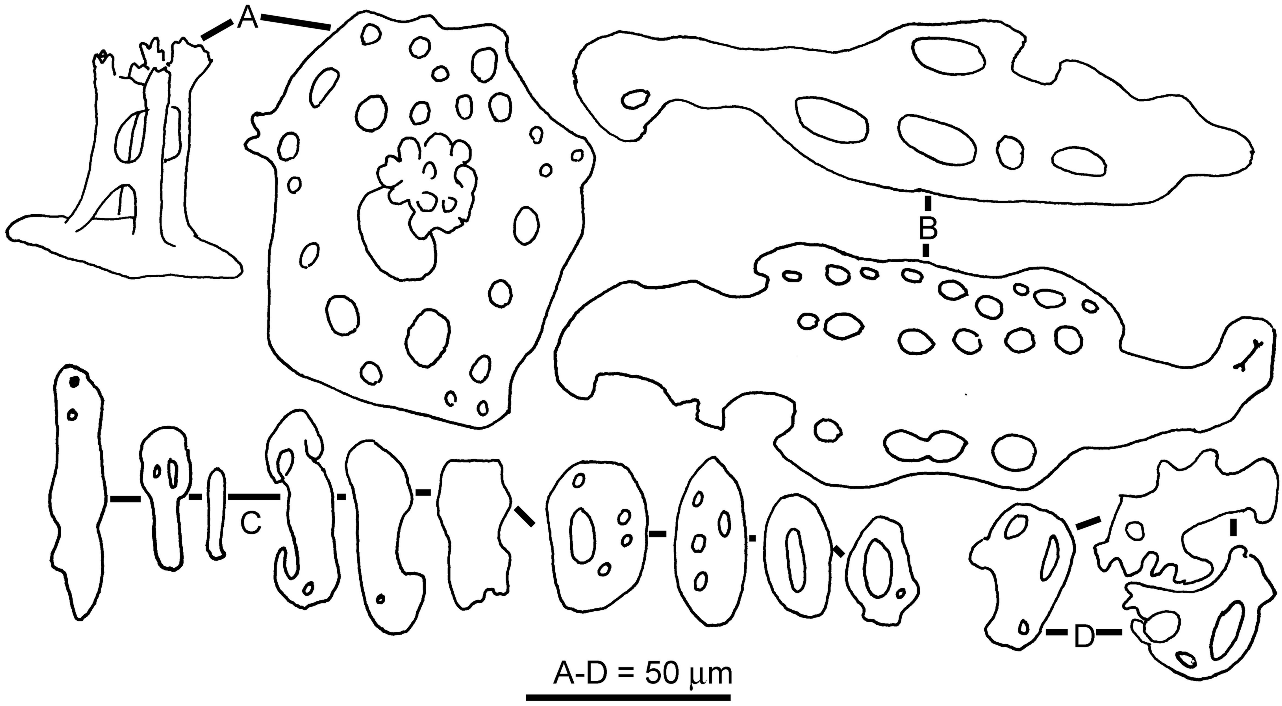

FIGURE 6. *Holothuria (Thymiosycia) arenicola* Semper, 1868 (lectotype, ZMB Ech. 1576). A, tables of anal papillae; B, perforated rods of anal papilale; C, rods and irregular buttons of longitudinal muscles; D, irregular deposits of cloacal suspensor muscles.

Holothuria (Thymiosycia) conusalba Cherbonnier & Féral, 1984

Plate 1H, Figures 7A–D

Holothuria (Thymiosycia) conusalba Cherbonnier & Féral, 1984: 685, figure 16A–J, plate 3B; Féral & Cherbonnier 1986: 94; Rowe & Gates, 1995: 302; Rowe & Richmond, 1997: 304, figure on p. 305.
? *Holothuria maculata*; Bell, 1887: 140; Bell, 1888: 389; Koehler & Vaney, 1908: 11; Daniel & Halder, 1974: 428.
Holothuria (Thymiosycia) arenicola; Gibbs *et al.,* 1976: 138, plate 1, figure 4.
Holothuria (Cystipus) inhabilis; Schoppe, 2000: 114.

Material examined. Type material. Holotype of *Holothuria (Thymiosycia) conusalba* Chebonnier & Féral, 1984: MNHNP Ech.3065, New Caledonia (Ricaudy Reef: 22°19'S-166°27'E), reef flat, 1 m depth, sandy bottom with sea grass, xi.1981, coll. J.L. Menou. Syntype of *H. arenicola* Semper, 1868: ZMH E. 2508 (1 specimen), Fiji, unknown collection date and depth, coll. Graeffe. (non *H. arenicola*).

Non-type material. MCZ 1097 (two specimens): Philippines (Mindoro, Port Galera), collecting date, depth and collector unknown; NHM 86.6.26.76 (one specimen): India (Andaman Islands), collecting date, depth and collector unknown; NHM 1955.10.14.37 (one specimen): Maldives (Manadi Reef), coll. S. Gardiner, collecting date and depth unknown; ZMH 2507 (one specimen; Museum Godeffroy Nr. 7318): Samoa; collector, coll. date and depth unknown.

Type locality. Reef flat of Ricaudy Reef (22°19'S-166°27'E), New Caledonia.

Known Geographical distribution. Suggested to be an Indo-West Pacific species by Rowe & Richmond (1997), but verified vouchers restrict the distribution to: New Caledonia, Australia (N.E. Coast, Great Barrier Reef, Queensland), Fiji, the Philippines (Mindoro, Palawan) and the West Indian Ocean (Maldives and Andaman Islands). The Maldives is a new location for *H. conusalba*. Previously, its presence in the Indian Ocean was mentioned only by Rowe & Richmond (1997) and not in compilations on Indian Ocean Holothuroidea (Samyn 2003; Sastry 2005; 2007).

Taxonomic description. *External and internal anatomy (holotype)*: Cherbonnier & Féral (1984: 695, 696) provide a very detailed description. However, we could not observe the bright green coloration of the internal body wall (most possibly this coloration faded due to preservation in alcohol). Also, we fail to confirm the presence of Cuvierian tubules, but this could again just be a preservation artefact.

Ossicles (holotype): Cherbonnier & Féral (1984: 697, figure 16) provide an excellent description. We confirm that the dorsal and ventral body wall contain very small, often reduced to the disc, tables (disc 30–40 µm across) and irregular buttons, 30–50 µm long (Figure 7C–E). We note in addition that the tables of the dorsal tube feet are somewhat larger, with disc diameters of 40–70 µm. Moreover, we complement Cherbonnier & Féral (1984) by noting the presence of irregular rods and buttons, 40–75 µm long, in the longitudinal and suspensor muscles of the cloaca (Figure 7A, B). Just as Cherbonnier & Féral (1984), we also report only very rare small, 20–30 µm long, rods from the tentacles.

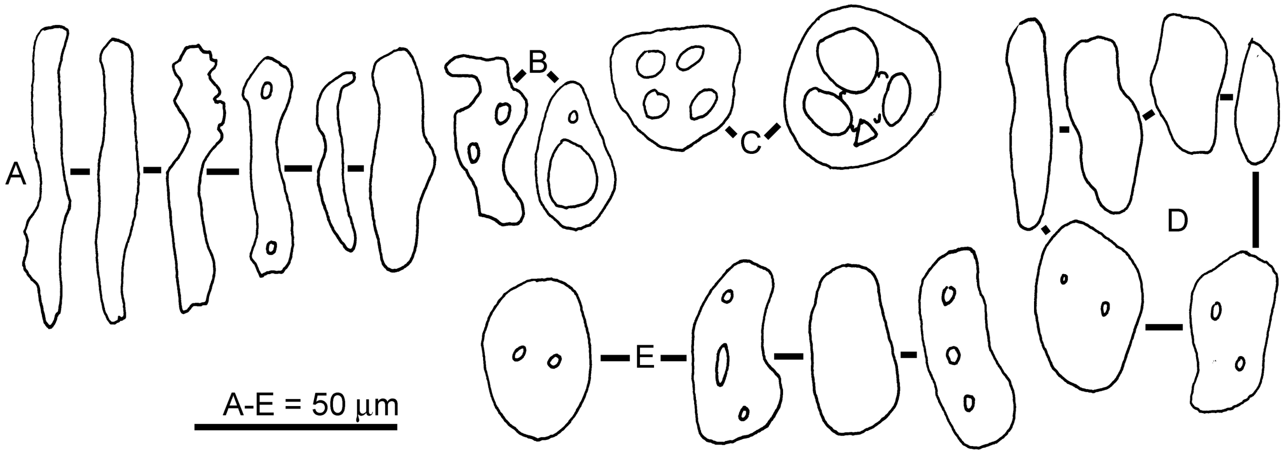

FIGURE 7. *Holothuria (Thymiosycia) conusalba* Cherbonnier & Féral, 1984, (holotype, MNHNP Ech.3065). A, rods of cloacal suspensor muscles; B, pseudobuttons of longitudinal muscles; C, tables of dorsal body wall; D, irregular, plump and obliterated button-like deposits of dorsal body wall; E, irregular, plump and obliterated button-like deposits of ventral body wall.

Remarks. Cherbonnier & Féral (1984) argued that the main difference between Semper's (1868) *Holothuria arenicola* and their *H. conusalba* lay in the coloration pattern between both species: *H. conusalba* being characterised by irregularly arranged dark spots and patches against a lighter background on the dorsal body wall and, most notably (and hence the name *conusalba*), distal sides whitish in colour (the anterior end with a narrow white ring, marked with papillae, and the posterior end with a much wider whitish ring), while *H. arenicola* has a double row of rather regularly darker spots and no distal whitening. We do not agree that these colour differences constitute the separation of species though, as we have found *H. arenicola* specimens with a white anal ring and *H. conusalba* specimens without such coloration pattern. *H. conusalba* can however be distinguished from its closest relatives (*H. arenicola* and *H. milloti*) by the more irregular and more pointed form of the buttons.

Holothuria (*Thymiosycia*) *milloti* Cherbonnier, 1988

Plate 1G, Figures 8A–F

Holothuria (*Thymiosicia*) *milloti* Cherbonnier, 1988: 84, figure 33A–M; Samyn, 2003: 81, 86.
Holothuria (*Thymiosycia*) *arenicola*; Conand *et al*., 2010: 148, figure 2 (fourth picture in first column).

Material examined. Type material. Holotype *Holothuria (Thymiosicia) milloti* Cherbonnier, 1988: MNHNP Ech.2722, Iles Glorieuses (North of Madagascar), ix.1958, coll. J. Millot.

Non-type material. RMCA.2694 (one specimen): South Africa (Natal, Sodwana Bay, 9-mile reef), 2.ii.2001, coll. Y. Samyn; RMCA 1240 (one specimen): Seychelles (Mahé), vii-ix. 1966, coll. Mission Zoologique MRAC-ULB; RMCA 1809 (four specimens): Comoros, Grande Comore (Mitsamiouli), 26.v.2005, coll. Y. Samyn & D. VandenSpiegel; RMCA 1810 (two specimens): Comoros, Grande Comore (Itsandra), 22.v.2005, coll. Y. Samyn & D. VandenSpiegel; RMCA 1814 (one specimen): Comoros, Grande Comore (Itsandra), 22.v.2005, coll. Y. Samyn & D. VandenSpiegel; RMCA.2695 (two specimens): Comoros, Grande Comore (Itsandra), 22.v.2005, coll. Y. Samyn & D. VandenSpiegel; MNHNP EcHh 2934 (three specimens): Madagascar (Tuléar, station 2/15), unknown coll. date, collecting by P. Galeron; MNHNP EcHh.2174 (ten specimens): Madagascar (Tuléar, station 2/15, 8/15, 14/15), 1972, coll. P. Galeron; NHM 1955.10.14.5 (one specimen): Maldives, coll. Gardiner, collecting date and depth unknown.

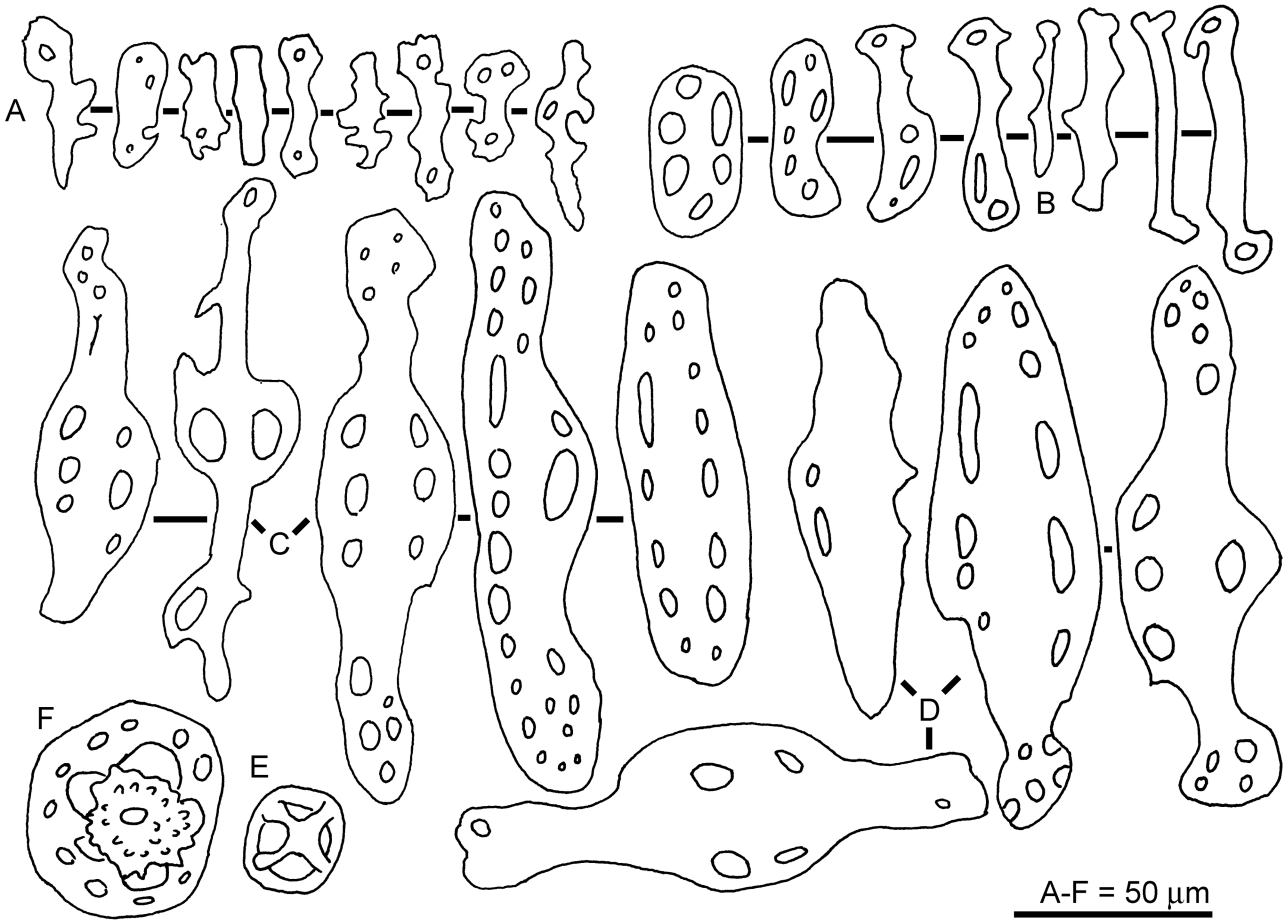

FIGURE 8. *Holothuria* (*Thymiosycia*) *milloti* Cherbonnier, 1988 (holotype, MNHNP Ech.2722). A, rods of longitudinal muscles; B, rods and pseudobuttons of cloacal suspensor muscles; C, perforated rods and plates of ventral tube feet; D, perforated plates and rods of dorsal tube feet; E, table of body wall; F, large table of body wall.

Type locality. Iles Glorieuses.

Known geographic distribution. Prior to this study, this species was only known from the type locality. Verified vouchers extend the area of distribution to the Comoros, Tuléar (Madagascar), KwaZulu-Natal (S. Africa), La Réunion, the Maldives and the Seychelles.

Taxonomic description. *External and internal anatomy*: see Cherbonnier (1988: 84).

Ossicles: see Cherbonnier (1988: figure 33), complemented with our observation that the longitudinal muscles contain small spiny rods, 25–50 µm long (Figure 8A), the suspensor muscles of the cloaca smooth rods and irregular buttons, 40–60 µm long (Figure 8B), the ventral tube feet rods and perforated plates (Figure 8C) and the dorsal tube feet tube rods and perforated plates 100–150 µm long (Figure 8D). The rods of the ventral tube feet are located mainly around the end-plate which measures 380–400 µm across and is made of several pieces. Large tables, 50 µm across, characterized by a highly developed crow of spines (Figure 8F), and small tables, 25 µm across (Figure 8E), are also present in the body wall.

Remarks. *H. milloti* is separated from the other species in the *H. arenicola* complex by the highly developed crown on spines of the tables. The irregular rods and buttons illustrated by Cherbonnier (1988; figure 33H), documented to be derived from the body wall, are instead deposits from the longitudinal muscles. This presence of ossicles in the longitudinal and cloacal suspensor muscles makes it possible to easily differentiate *H. milloti* from the sympatric *K. kerriensis* **sp. nov.** described below. The latter lacks ossicles in its longitudinal muscles.

Holothuria (Thymiosycia) kerriensis **Samyn sp. nov**
Plate 1F, Figures 9A–J, 10A–C

Holothuria (Thymiosycia) arenicola Semper, 1868; Samyn & VandenBerghe, 2000 (2002): 27 (non *H. arenicola*); Samyn, 2003: 81, figure 32A-E (non *H. arenicola*).
? *Holothuria arenicola*; Tortonese, 1977: 275.
? *Holothuria maculata*; Hérouard, 1893: 133, pl. 7, figure B; Lampert, 1896: 54; Ludwig, 1899: 561; Helfer, 1912: 327; Erwe, 1919: 182.

Material examined. Type material. Holotype *Holothuria (Thymiosicia) kerriensis* Samyn sp. nov; MRAC 1898: Malindi Marine National Park (Kenya), viii.1998, 1 m depth, coll. Y. Samyn. Paratypes *Holothuria (Thymiosycia) kerriensis* **sp. nov.**; MRAC 2009, MRAC 2119, MRAC 2068: Malindi Marine National Park (Kenya), iv.1998, 1 m depth, coll. Y. Samyn; MRAC 2697: Malindi Marine National Park (Kenya), viii.1998, 0–1 m depth, coll. Y. Samyn.

Non type material. MRAC 1872, MRAC 1901: Vanga (Kenya), viii.1997, 0-1 m depth, coll. Y. Samyn; MRAC 2696: Kiunga Marine National Reserve (Kenya), iv.1998, intertidal, coll. Y. Samyn; ZMH E5921 (one specimen): Egypt (Suez); ZMH E2521 (one specimen), Suez, Bannwarth leg., unknown collection date and depth.

Type locality. Malindi Marine National Park, Malindi, Kenya.

Etymology. This species is named after Dr Alexander Kerr (now at the University of Guam) for his merit to recognize some ecological differences between Caribbean and Pacific forms in the *H. arenicola* complex and for his tremendous contributions to holothuroid taxonomy and systematics in general.

Known geographical distribution. As of now, the species is known from the Kenyan coast (Kiunga, Malindi, Mombasa and Vanga) and from the Red Sea (Suez).

Taxonomic description. *External anatomy (holotype*): Medium-sized holothurian, preserved holotype 90 mm long and 10–15 mm across; size in life approximately the same. Body cylindrical, slightly curved (dorsal surface shorter). Colour in alcohol same as in life: ventral body wall from greyish yellow to brown with white tube feet, dorsal body wall brown with two longitudinal rows of blotches which fuse into longitudinal lines posteriorly; close to anus, colour paler. Skin gritty to the touch, with body wall 2,5 mm thick. Mouth ventral. 15 Short tentacles observed (additional ones most probably hidden by calcareous ring protruding through mouth). Anus terminal, surrounded by five groups of anal papillae. Ventral tube feet in three rows in each ambulacrum; interambulacral areas without tube feet. Dorsal tube feet in several rows along the ambulacrae, but less crowded than ventrally, and with some spreading into the interambulacral areas.

Internal anatomy (holotype): Calcareous ring and adjacent structures in poor condition because of partial expulsion through the mouth. Cuvierian tubules not observed. Longitudinal muscles very wide and flat. Gut filled with rough white sand.

Ossicles (holotype): Tentacles with few rods, 10–85 µm long, smooth, unperforated, nearly straight, with extremites sometimes enlarged (Figure 9A). Ventral body wall with few tables (Figure 9B) and buttons (Figure 9C); table disc 50–65 µm across, perforated by 4 large central holes and 4–10 peripheral holes; nearly all buttons with 3 pairs of holes and 40–65 µm long, perforations from open to completely obliterated, rarely plump. Dorsal body wall with few tables (Figure 9D) and many buttons (Figure 9E); tables and buttons like those of ventral body wall, except plump buttons more abundant. Dorsal tube feet with tables, buttons, and rods (Figure 9F, G); disc of the tables 65 µm across, perforated by up to 10 peripheral holes, buttons 50–70 µm long, from normal 3 pairs of holes to fully obliterated. Rods with few perforations centrally and distally, 80–145 µm long. End-plate 330–450 µm across, in one piece. Ventral tube feet with tables, buttons and rods (Figure 9H, J); tables similar to the ones of the ventral body wall;

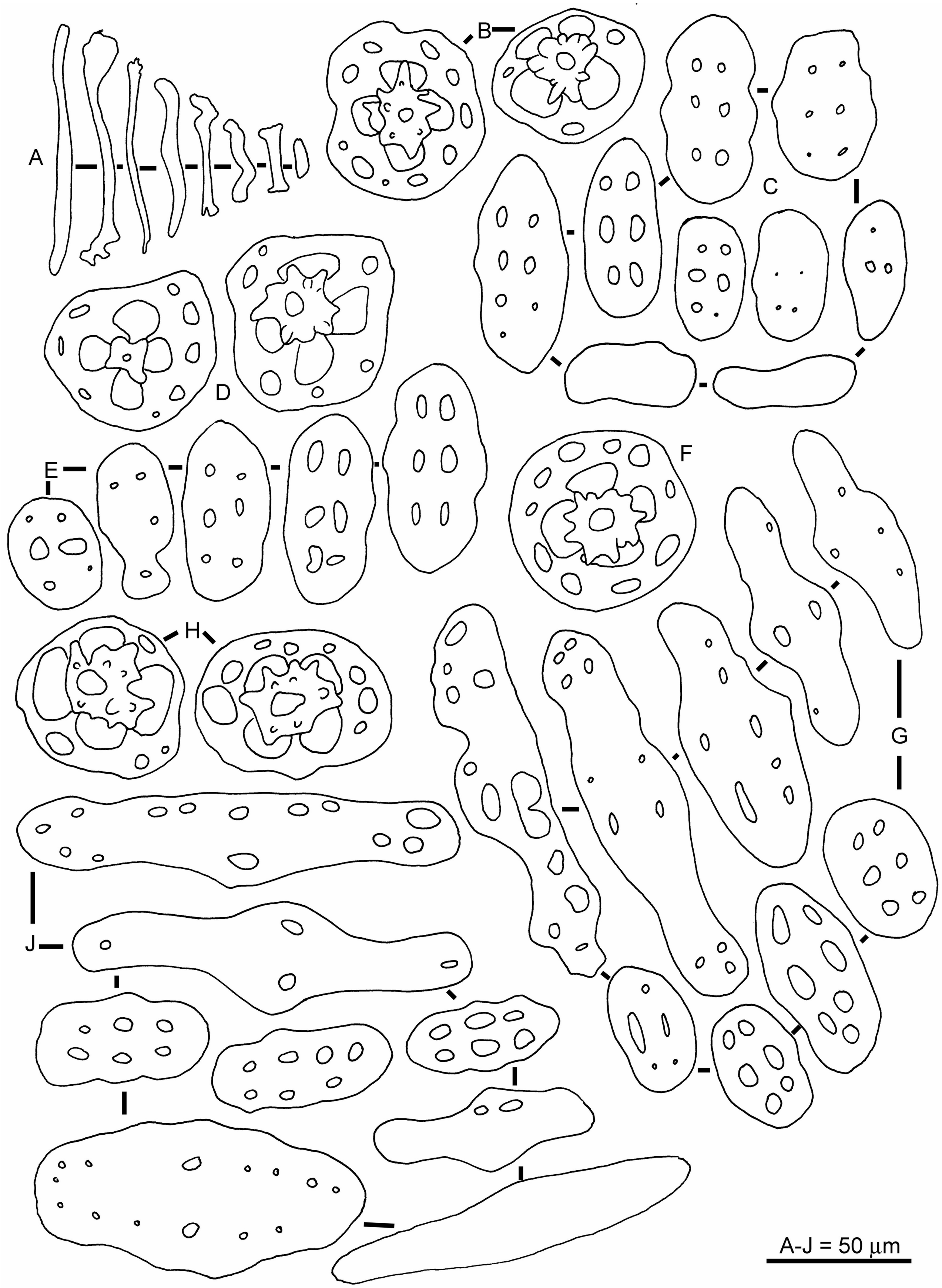

FIGURE 9. *Holothuria (Thymiosycia) kerriensis* **sp. nov.** (holotype, MRAC.1898). A, rods of tentacles; B, tables of ventral body wall; C, buttons of ventral body wall; D, tables of dorsal body wall; E, buttons of dorsal body wall; F, table of dorsal tube feet; G, buttons and perforated rods of dorsal tube feet; H, tables of ventral tube feet; J, buttons and perforated rods & plates of ventral tube feet.

buttons 50–65 µm long with 3 pairs of holes, normal or partly obliterated; majority of buttons plump; few very large buttons (up to 120µm long) with 6–7 pairs of holes also present; rods 80–160 µm long, smooth with a few perforations at mid length and at the extremities; few rods full obliterated. End-plate 300–400 µm across in one piece. Anal papillae with tables, rods, irregular plates and few buttons (Figure 10A, B, C); tables numerous, large, disc 50–80 µm across with 11–15 small peripheral holes; rim of disc irregular, spiny; buttons 50–100 µm long with 4–6 pairs of holes never obliterated; rods irregular, spiny, with or without perforations, 85–140 µm long. Longitudinal muscles devoid of ossicles. Suspensor muscles of the cloaca with small irregular, occasionally perforated rods, 30–80 µm long (Figure10C).

External and internal anatomy (paratypes + non-type material): see Samyn, 2003: 81.

Ossicles (paratypes + non-type material): see Samyn, 2003: 83, figure 83A–G.

Remarks. This species can easily be recognized from the sympatric *Holothuria* (*Thymiosycia*) *milloti* Cherbonnier, 1988 in that it lacks ossicles in its longitudinal muscles.

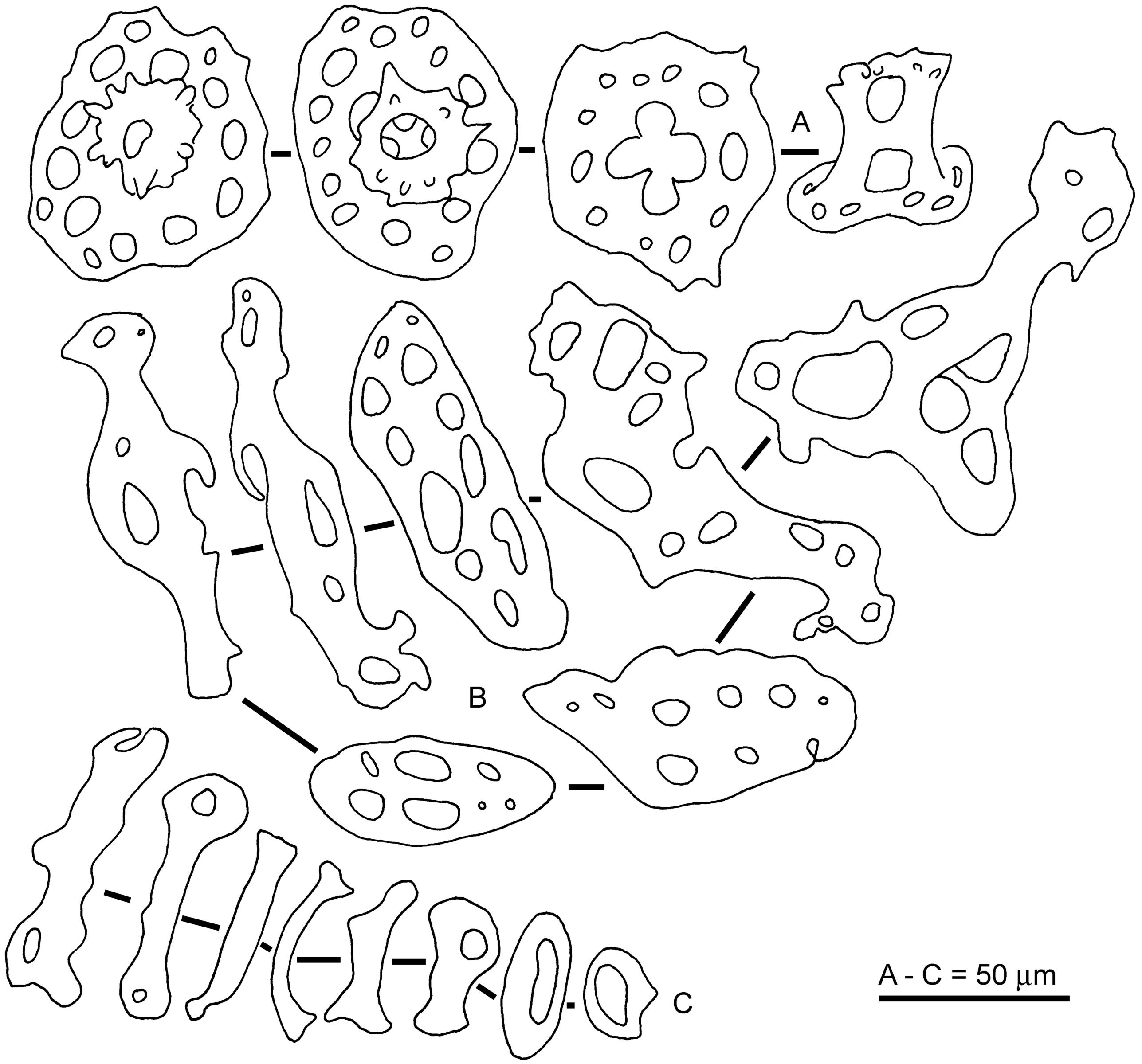

FIGURE 10. *Holothuria (Thymiosycia) kerriensis* **sp. nov.** (holotype, MRAC.1898). A, tables from anal papillae; B, buttons and irregular perforated rods from anal papillae; C, rods from cloacal suspensor muscles.

Holothuria (Thymiosycia) zihuatanensis **Caso, 1965**

Plate 1E, Figures 11A–L

Microthele (Paramicrothele) zihuatanensis Caso, 1965: 105-114, 3 plates + 2 text figures; Rowe, 1969: 147; Caso, 1976: plates. 45–47; Maluf, 1988: 158 (cited as a synonym of *H. (T.) gyrifer* (Selenka, 1867)).

? *Brandtothuria arenicola*; Deichmann, 1958: 291, plate 1, figures 10–13 (partim); Hertlein, 1963: 236.

? *Holothuria (Thymiosycia) arenicola*; Honey-Escandon, 2008: 68.

? *Holothuria maculata*; Ludwig, 1887: 2; Ludwig, 1894: 7.

Material examined. Type material. 1 Syntype of *Holothuria (Thymiosycia) zihuatanensis* Caso, 1965; ICML-UNAM 5.27.0, Ixtapa Island, 12 km west of Zihuatanejo (17°40`N and 101°40'W), Guerrero, Mexico, Eastern Pacific, coll. Date 6.i.1964, coll. M.E. Caso & E. Rioja.

Non type material. LACM 397.22 (three specimens): Ecuador (Galapagos Islands, Albemale Island, Cartago Bay), intertidal, coll. Allan Handcock Expedition, date coll. 22.12.1938; LACM 397.43 (one specimen): Ecuador (Galapagos Islands), intertidal, coll. Allan Handcock Expedition, 11.12.1934; MCZ 397-25 (one specimen): Panama (Honda Bay: Handcook station 816-38), 01.iii.1938; USNM 397.67 (one specimen): Ecuador (Galapagos Islands, Charles Island, South of Black Beach), intertidal, coll. 4.xii.1934.

Type locality. Ixtapa Island, 12 km west of Zihuatanejo (17° 40`N and 101° 40'W), Guerrero, Mexico, Eastern Pacific.

Known geographical distribution. Given that this species name has sunk into the synonymy of *H. (T.) arenicola* since Rowe (1969) proposed such action, it is difficult to delimit its distribution, especially since the character that allows easy identification (tentacles with numerous, distally widening and perforated, rods) is seldom scored by authors. Verified records however suggest that *H. zihuatanensis* is present from the Galapagos to Cocos Islands to the West Coast of America (Mexico, Panama, Peru).

Taxonomic description. External and internal anatomy: see Caso (1965).

Ossicles (syntype): Tentacles with rods, 30–300 µm long, larger ones with distal ends spiny, perforated and branching (Figure 11A). Ventral body wall with tables (Figure 11B) and buttons (Figure 11C); tables with smooth-rimmed disc perforated by four central holes and 4–8 peripheral ones, no to single cross beam and a narrow crown, disc 45–65 µm across; buttons never plump, with rim smooth and apexes occasionally pointed, 3–5 pairs of holes which can be partly obliterated, 45–80 µm long. Dorsal body wall with similar ossicle assemblage (Figure 11D, E) as ventral body wall, although tables slightly large, disc up to 75 µm across, and with buttons with more open perforations. Ventral tube feet with tables like those of body wall (Figure 11 F), buttons with 3–10 pairs of often obliterated holes (Figure 11G), perforated plates (Figure 11H) and perforated rods with central and distal parts swollen and with obliterated perforations (Figure 11J). Dorsal tube feet with tables (Figure 11K), buttons and perforated rods (Fig11L). Cloacal suspensor muscles and longitudinal muscles devoid of ossicles.

Remarks. According to the illustrations of Caso (1965 and 1976) *Holothuria zihuatanensis* is like *H. impatiens*, a species that is known to hold several different taxa (Michonneau 2015). Our comparative morphological and molecular analyses (Paulay & Michonneau pers. comm) however indicate that *H. zihuatanensis* belongs to the *H. arenicola* complex. *H. zihuatanensis* can easily be recognized from the other species in the *H. arenicola* complex by the presence of large, distally perforated and occasionally branched rods in the tentacles (Figure 11A). *H. milloti* Cherbonnier, 1988 also presents distally widened and perforated rods in the tentacle, but the species live allopatric (*H. milloti* in the Western Indian Ocean, *H. zihuatanensis* in the Eastern Pacific Ocean). Moreover, *H. milloti* has ossicles in its longitudinal muscles, while *H. zihuatanensis* does not. Caso (1965) didn't mention presence/absence of ossicles in the musculature of *H. zihuatanensis*, most possibly because she didn't check those tissues for ossicles, rather than observing their absence after examination.

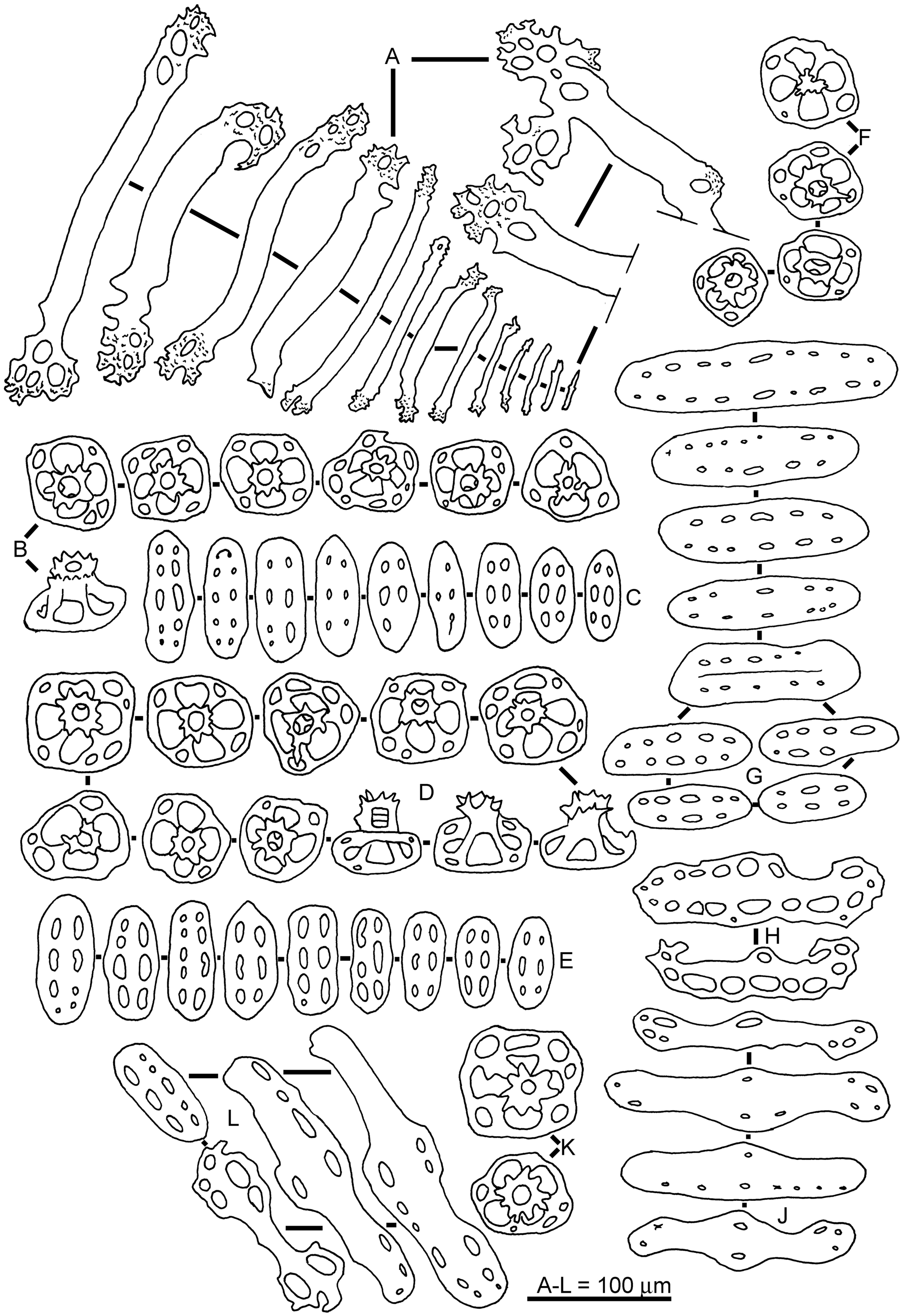

FIGURE 11. *Holothuria (Thymiosycia) zihuatanensis* Caso, 1965. (syntype, ICML-UNAM 5.27.0). A, rods of tentacles; B, tables of ventral body wall; C, buttons of ventral body wall; D, tables of dorsal body wall; E, buttons of dorsal body wall; F, tables of ventral tube feet, G, buttons of ventral tube feet; H, perforated plates of ventral tube feet; J, perforated rods of ventral tube feet; K, tables of dorsal tube feet; L, buttons and rods of dorsal tube feet.

Holothuria **(*Thymiosycia*) sp.**
Figures 12 A–J

? *Holothuria Boutani* Hérouard, 1893: 132, plate 7A, 1–22.
? *Holothuria arenicola* var. Boutani; Panning, 1935: 89, figure 74; Cherbonnier, 1955: 153.
Holothuria maculata; Hérouard, 1893: 133 plate 7B, 1–25.

Material examined. Non type material. NHM 83.3.15.6 (1 specimen): Timor, depth, collector and collecting date not recorded (*Holothuria maculata* (Brandt, 1835), *sensu* Hérouard, 1893).

Known geographical distribution. Only known from two localities: Suez and Timor.

Taxonomic description. *External and internal anatomy*: Single specimen under study 95 mm long and ± 15 mm wide, cylindrical, tapering at both extremities. Colour in alcohol brown to beige, without rows of blotches dorsally. Mouth and anus terminal; anus not guarded by papillae. Skin thin (1–1.5 mm), gritty to the touch. Tentacles fully retracted, not countable. Tube feet more densely crowded ventrally than dorsally, no distinct rows. Longitudinal muscles large, bifid, rounded (2.5 mm across). No Cuvierian tubules observed.

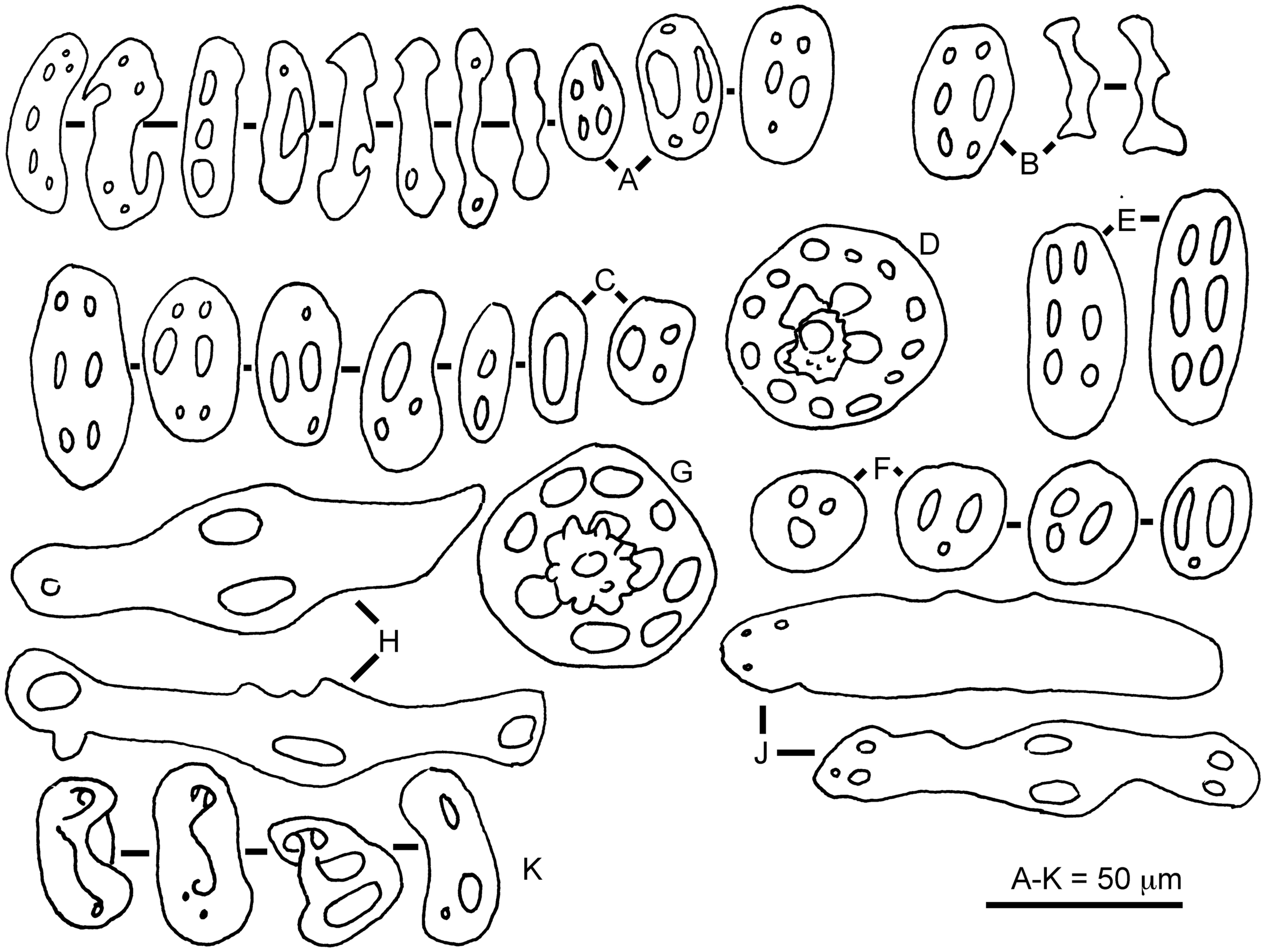

FIGURE 12. *Holothuria (Thymiosycia)* sp. (NHM 83.3.15.6). A, ossicles of the longitudinal muscles; B, ossicles of the cloacal suspensor muscles; C, buttons of the ventral body wall; D, table of the ventral body wall; E, elongated buttons of the dorsal body wall; F, round buttons of the dorsal body wall; G, table of the dorsal body wall; H, rods of dorsal tube feet; J, rods of the ventral tube feet; K, twisted buttons of ventral body wall.

Ossicles: Longitudinal muscles with irregular buttons and rods, 25–50 µm long (Figure 12A). Cloacal suspensor muscles with mainly irregular rods and few buttons (Figure 12B). Dorsal and ventral body wall with buttons and tables; buttons range from irregular with 1–3 pairs of holes (Figure 12C) to regular with 3 pairs of holes (Figure 12E) to rounded (especially in dorsal body wall) with few perforations (Figure 12F), to twisted (Figure 12K) with perforations somewhat obliterated; tables with round disc, 60–65 µm across, perforated by 4 large central holes and 8–12 small peripheral holes, with 4 short pillars ending in a small crown of spines (Figure 12D, G). Dorsal and ventral tube feet with tables and buttons like those of body wall, except that few buttons have up to 4 pairs of holes, and few rods around the end-plate, 120–140 µm long, with 1–3 perforations in the mid and at extremities (Figure 12H, J). Ventral tube feet also present few massive rods without perforations. Tentacles devoid of ossicles.

Remarks. This specimen from Timor, identified in the London collection as *Holothuria arenicola*, poses problems in assigning it to one of the known species in the *H. arenicola* complex. The closest matches we can find are with *Holothuria maculata* (Brandt, 1835) as identified by Hérouard in 1893, *Holothuria arenicola* var. *boutani* as identified by Cherbonnier in 1955 and *Holothuria boutani* Hérouard, 1893.

The round (Figure 12F) and twisted (Figure 12 K) buttons of the Timor specimen very much resemble those figured for *H. boutani* (Hérouard, 1893: pl. 7A, figures 2 &12 and 3&4) and for *H. maculata* (Hérouard, 1893: plate 7B, figures 2&3). The Timor specimen also is characterized by having ossicles in the longitudinal and cloacal suspensor muscles (Figure 12A&B); ossicles which largely resemble those illustrated by Hérouard (1893; plate 7B, figures 16–22) and Cherbonnier (1955; plate 37, figure y) and which we suspect also derive from the longitudinal muscles. The Timor specimen differs from all the species in the *H. arenicola* complex in having these round and twisted buttons and in presenting large tables (Figure 12D&G).

We refrain from identifying the Timor specimen as *H. boutani* because we were not able to compare it with the holotype of *H. boutani* of which the whereabouts are unknown. We refrained from establishing a neotype for *H. boutani*, because we lack material from the type locality (Suez).

Species confused with the *Holothuria arenicola* complex

While doing this work we found that two species are often erroneously identified as *Holothuria arenicola*: *H. strigosa* Selenka, 1867 and *H. gracilis* Semper, 1868. We here provide a re-description of these two species.

Holothuria (Thymiosycia) strigosa Selenka, 1867

Plate 1I, Figures 13A–L, Figure 14A–E

Holothuria strigosa Selenka, 1867: 334, pl. XIX, figure 77–79; Ludwig, 1880: 6; Lampert, 1885: 72; Théel, 1886: 220; Schmidt, 1930: 415, figures 73, 77, 96; Daniel & Halder, 1974: 427.
Holothuria (Holothuria) strigosa; Panning, 1934: 70, figure 48.
Holothuria (Thymiosycia) strigosa; Rowe, 1969: 147; Clark & Rowe, 1971: 178; Price, 1982: 11; Levin, 1979: 22; Tortonese, 1980: 107, 135.
Holothuria (Platyperona) strigosa; Cherbonnier, 1988: 95, figure 38A-0.
Holothuria arenicola; Cherbonnier, 1988: 82 (non *H. arenicola* Semper, 1868)

Material examined. Type material. MCZ 708 (holotype): Zanzibar, depth, collecting date and collector unknown.

Non-type material. RMCA 1324 (one specimen): Mozambique (Inhaca), vii–viii. 1969, collected by Mission zoologique ULB, unknown depth; ? MNHNP EcHh2301 (two specimens): Madagascar (Tuléar, Sangoritelo Reef), 02.ix.1969, coll. B. Thomassin, unknown depth.

Type locality. Zanzibar.

Known Geographic distribution. Based on verified vouchers and descriptions with sufficient illustrations we can indicate the presence of *H. strigosa* in: Zanzibar, the Red Sea, Madagascar (Tuléar), Somalia (Sar Uanle), Yemen (Socotra), the Arabian Sea and the S.W. Indian Ocean.

Taxonomic description. *External anatomy (holotype*): see Selenka (1867); Cherbonnier (1988) for non-type material.

Internal anatomy (holotype): see Selenka (1867); Cherbonnier (1988) for non-type material.

Ossicles (holotype): Tentacles devoid of ossicles. Dorsal body wall with numerous tables and buttons; tables with flat and smooth-rimmed disc, 50–70 µm across, quadrangular in outline for small tables, round for large tables, perforated by 4 large central holes and 4–12 small peripheral holes, 4 pillars ending is narrow spiny crown (Figure 13A); buttons regular, 40–65 µm long, with undulating rim, mostly smooth, perforated by 3 pairs of large holes (Figure 13B),

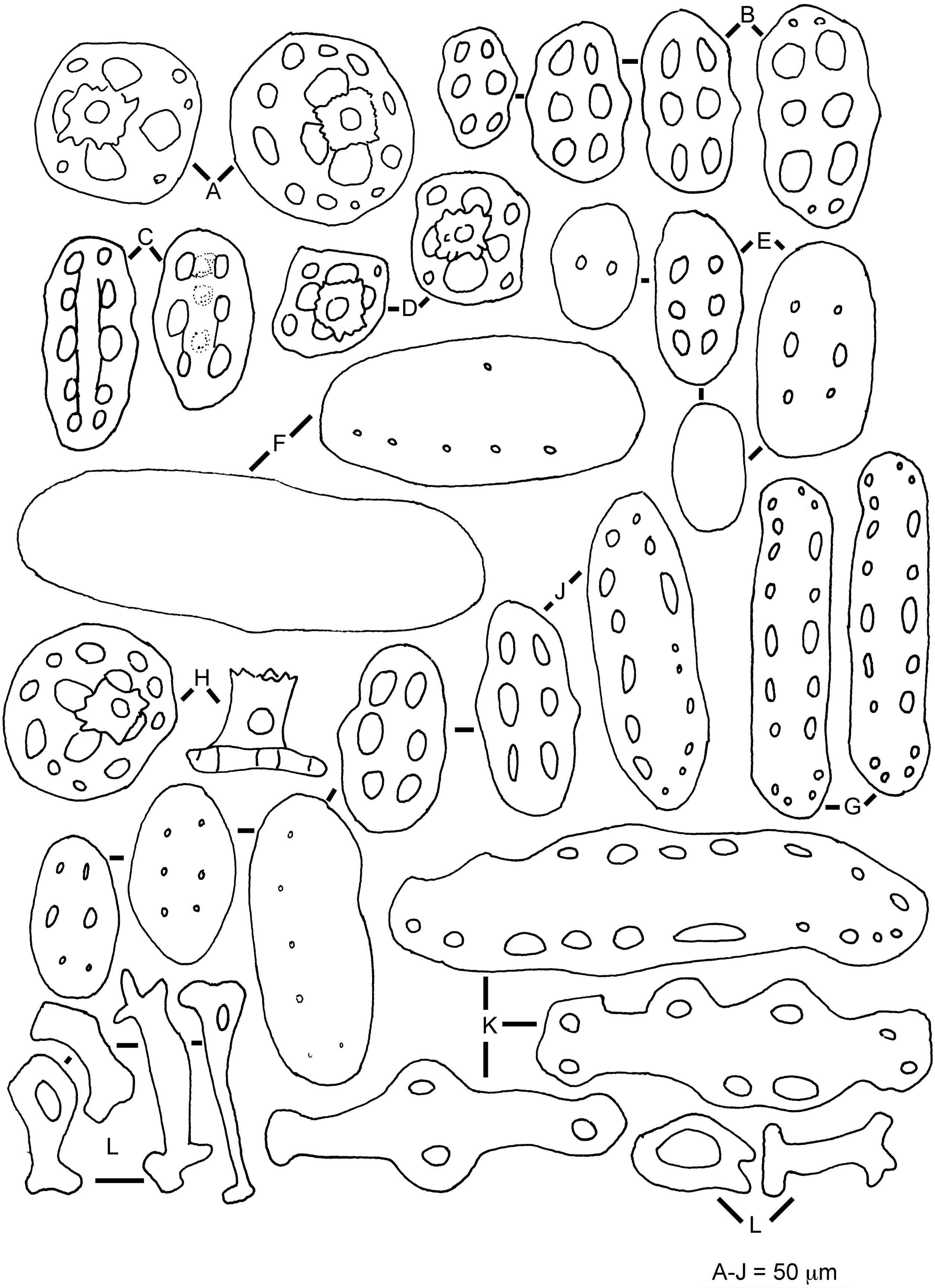

FIGURE 13. *Holothuria (Thymiosycia) strigosa* Selenka, 1867 (holotype, MCZ 708). A, tables of dorsal body wall; B, buttons of dorsal body wall; C, knobbed buttons of dorsal body wall; D, tables of ventral body wall; E, buttons of ventral body wall; F, rods of ventral tube feet; G, plates of ventral tube feet; H, tables of dorsal tube feet; J, buttons of dorsal tube feet; K, rods of dorsal tube feet; L, rods of cloacal suspensor muscles.

some buttons slightly larger, 75–80 µm long, with 4–5 pairs of holes (Figure 13B), few buttons also knobbed (Figure 13C). Ventral body wall with buttons and tables; tables as in dorsal body wall, but smaller with disc 30-50 µm across (Figure 13D); buttons 35–75 µm long, with rim not undulating, perforated by 1–4 pairs of holes, some with holes partly or completely obliterated (Figure 13E). Ventral tube feet with tables and buttons as in body wall, although buttons with up to 11 pairs of holes, 85–140 µm long, also present (Figure 13G), as well as massive rods without perforations, 50–210 µm long (Figure 13F). Dorsal tube feet with tables (Figure 13H) and buttons (Figure 13 J) as in body wall, although few buttons with reduced holes (Figure 13J) as well as perforated plates derived from buttons, 115–180 µm long with 7–11 pairs of holes (Figure13K), and rods, 120–130 µm long, perforated by few central and distal holes (Figure 13K). Cloacal suspensor muscles with smooth, irregular rods, occasionally perforated (Figure 13L). Longitudinal muscles devoid of ossicles

Remarks. *Holothuria* (*Thymiosycia) strigosa* can easily be recognized from the other species here treated by the presence of fully obliterated rods in the ventral tube feet (cf. Figure 13F).

***Holothuria* (*Lessonothuria*) *gracilis* Semper, 1868**

Plate 1J, Figures 14A–F, 15A–D

Holothuria gracilis Semper, 1868: 84, 248, 277, plate 23, pl. 30, figure 17, plate 31, figure 8, pl. 33, figure 1, plate 35, figure 6; Lampert, 1885: 68; Théel, 1886: 234; Ludwig, 1889–92: 329; Liao, 1998: 80.

Holothuria (Holothuria) gracilis; Panning, 1935: 71, figure 49a–c.

Holothuria (Thymiosycia) gracilis; Rowe, 1969: 147; Clark & Rowe, 1971: 178, plate 28, figure 6; Liao, 1980: 117; Liao, 1984: 231, figure 10; Cherbonnier, 1988: 91, figure 36A–K; Levin & Dao Tan Ho, 1989: 57; Liao & Clark, 1995: 462, figure 275a–d; Pawson, 1995: 189; Liao, 1997: 140, figure 82a–d; Rowe & Gates, 1995: 302; Lane *et al.,* 2000: 489; Samyn, 2003: 81, 86; Sastry, 2005: 110.

Material examined. Type material. ZMH E.2559: lectotype (here designated), Bohol, Philippines, collection date and depth unknown; ZMMSU H-63: paralectotype (here designated), Bohol, collection date and depth unknown.

Non-type material. ZMH E 2558 (considered a cotype in the ZMH catalogue. This cannot be as Semper (1868) only had material from Bohol before him): Palau, Coll. By Kubary, date and depth unknown.

Type locality. Bohol, Philippines.

Known Geographic distribution. Zanzibar, Madagascar (Nosy Bé), India (Andaman Islands, Port Blair), Philippines (Bohol, Cebu), Vietnam, China, Australia (NE coast, GBR, QLD), Palau Island.

Taxonomic description. *External anatomy (lectotype*): Preserved specimen 78 mm long and 28 mm wide. Color in alcohol: dorsal and ventral body uniform greyish beige, although ventrally somewhat lighter. Body cylindrical with rounded extremities. Mouth ventral surrounded by 20 small tentacles of which the whitish base of stalk is dotted with grey dots. Anus terminal, unguarded. Ventral and dorsal tube feet spread without order over entire surface, although rows of larger tube feet on ambulacrae.

Internal anatomy (lectotype): Calcareous ring, undulating with radial pieces 1,5 times as wide and 2 x as high as interradial plates. Two Polian vesicles, each ± 40 mm long. Stone canal and madreporite not observed. Longitudinal muscles wide and thick (touching each other), attached at edges.

Ossicles (lectotype): Tentacles devoid of ossicles. When present, each kind presents a patchy distribution. Dorsal and ventral body wall with buttons and tables. In ventral body wall, majority of buttons large, 50–75 µm long, with 3 pairs of large holes, smooth edged with non-undulating rim (Figure 14A); few irregular buttons with 4–5 pairs of holes and with longitudinal carina also present (Figure 14B). Tables large, disc 70–120 µm acrosss, with 4 short pillars ending in a narrow crown of spines; disc perforated by 4 central holes and 8 peripheral holes (up to 10 for largest tables) (Figure 14C). Dorsal body wall presents same ossicle assemblage as ventral body wall, with regular buttons, 60–85 µm long, with 3 pairs of holes (Figure 14D), and irregular buttons, 60–100 µm long and with 3–7 pairs of holes (Figure 14E), and tables with disc 60–110 µm across (Figure 14F). Ventral tube feet with huge number of ossicles: buttons with 3 pairs of holes, 60–90 µm long, buttons with 4 pairs of holes 90–100 µm long (Figure 14G); tables, with disc 80–90 µm across, like those of body wall; rods, 230–380 µm long, with perforations at extremities and, occassionaly, also centrally (Figure 14 H). Dorsal tube feet with tables, buttons and rods like those of ventral tube feet: majority of buttons with 3 pairs of holes, 80–100 µm long (Figure 15B), some with 6 pairs of holes, up to 150 µm long (Figure 15C); rods with enlarged perforated extremities straight (Figure 15D) or slightly

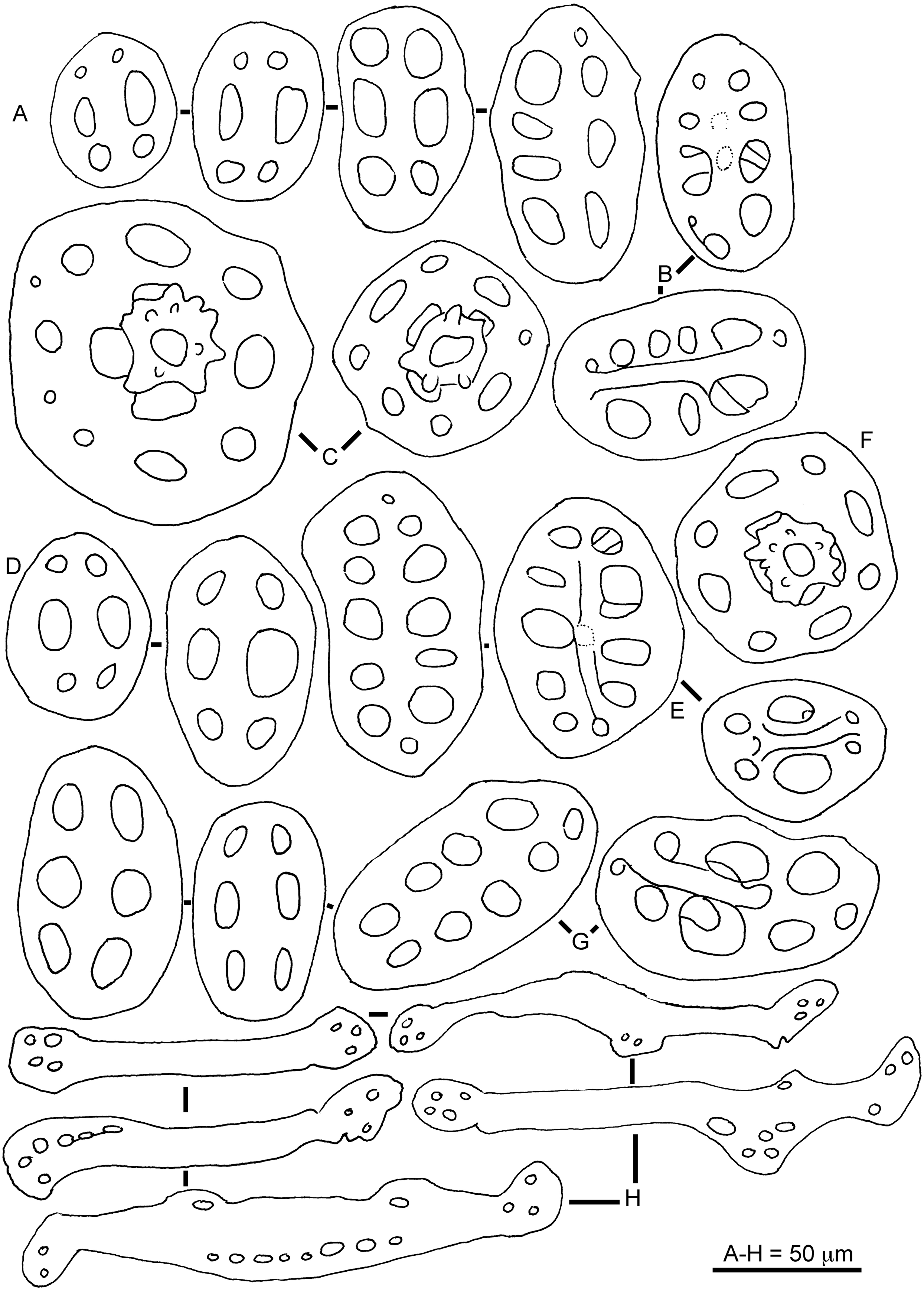

FIGURE 14. *Holothuria (Thymiosycia) gracilis* Semper, 1868. (lectotype, ZMH E.2559). A, regular buttons of ventral body wall; B, irregular buttons of ventral body wall; C, tables of ventral body wall; D, regular buttons of dorsal body wall; E, irregular buttons of dorsal body wall; F, table of dorsal body wall; G, buttons of ventral tube feet; H, perforated rods of ventral tube feet.

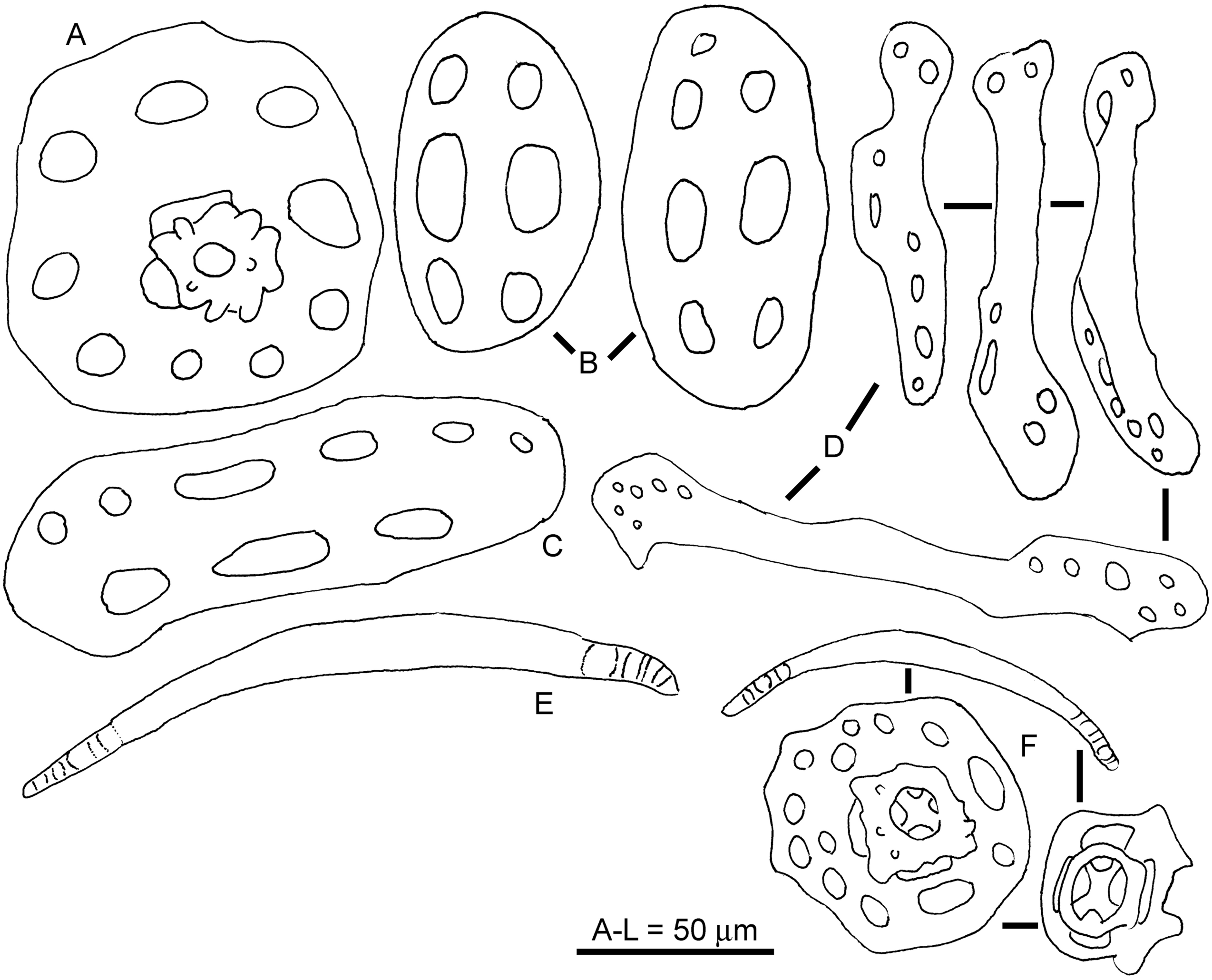

FIGURE 15. *Holothuria (Thymiosycia) gracilis* Semper, 1868. (lectotype, ZMH E.2559). A, table of dorsal tube feet; B, buttons of dorsal tube feet; C large buttons of dorsal tube feet; D, perforated rods of dorsal tube feet; E, curved rod of dorsal tube feet; F, curved rod and tables of anal papillae.

curved (Figure 15E), 190–380 µm long. Anal papillae with tables and rods (Figure 15F): rods, 210–260 µm long, as in tube feet; tables with disc 30–80 µm across, small ones irregular with only 4 central holes, large ones with up to 13 peripheral holes. Longitudinal and suspensor muscles of cloaca devoid of ossicles.

Remarks. *Holothuria gracilis* can easily be recognized from the other *Thymiosycia* species studied in the present paper by the size of the tables (twice as big as those in the other species) and by the size and shape of the buttons (presence of knobs and/or a central longitudinal hull). Cherbonnier (1988) observed rods in the tentacles (Figure 36c). But the rods he illustrated are, according to us and Liao &Clark (1995), rods from the tube feet, whereas the small rods (Figure 36d) belong to the tentacles. These rods are rare, very small and easily overlooked.

Discussion

On the value of Natural History collections

Well-maintained natural history collections, especially when built through coherent and systematic sampling efforts, are heavens for species discovery because, as demonstrated by a.o. Bebber *et al.* (2010) and Fontaine *et al.* (2012), such collections invariably lead to the discovery of new taxa (e.g. Massin *et al.* 2004; Samyn & Thandar 2010 for examples involving sea cucumbers). This is especially the case for cryptic taxa that are thought to be easily identifiable through superficial examination (here: tropical, burrowing, shallow-water holothurians with a double row of blotches = the *H. arenicola* complex). The presence of unidentified or misidentified taxa in natural history collections makes it difficult to compare these historical vouchers with modern survey data. As a result, a full causal understanding of the patterns of biodiversity cannot be fully achieved (Lister *et al*. 2011, Briggs & Bowen 2012). For taxa that provide important ecosystem services such as sea cucumbers that bring bioturbation and nutrient cycling in oligotrophic waters, having accurate identification is crucial as it will drive meaningful conservation and eventual restoration of damaged ecosystems (Purcell *et al.* 2023). We, therefore argue that effort, funding, and research-focus should be directed to collecting new material in the field, but also to the examination of extant natural history collections, which provides open windows to understanding, sustainably managing and protecting biodiversity (Suarez & Tsutsui 2004).

On the value of natural history observations

Experienced field workers have noted marked differences in the ecology of individuals identified as *H. arenicola* in different localities. In Guam, the Philippines and Kosrae, Kerr (pers comm.) invariantly found *H. arenicola* specimens on the reef flat, under large flat coralline rubble, on well-sorted, aerated coralline sand. Kerr (pers. comm.) also sampled *H. arenicola* in the Caribbean (British Virgin Islands, Florida Keys) and reports that these specimens were 'always buried in a rubble free expanse of coralline sand, perhaps associated with seagrass and underneath a small but characteristic mound of sand'. The latter behavior is like that observed for *H. kerriensis*, which was sampled in coralline sand next to stony boulders (Samyn pers. observ.). In the same way, Kerr (pers. comm.) reported that the Caribbean '*H. arenicola*' (=*H. unicolor*) specimens which he relaxed in $MgCl_2$ extruded long, blunt-tipped translucent Cuvierian tubules. On the other hand, Kerr (pers comm.) has let us know that he has never observed such behavior in Indo-Pacific *H. arenicola* specimens. Such, 'on the ground' natural history observations are as crucial as geo-spatial data on the specimens that are deposited in collections as they form an important part of the multisource approach to exploring biological diversity, called integrative taxonomy (Dayrat 2005; Schliek-Steiner *et al*. 2010; Padial *et al*. 2010)

On the value of distributional data

The distribution of marine taxa in time and space is limited by abiotic parameters such as past and present continental boundaries, water temperature and currents, biotic factors such as availability of suitable habitat, dispersal abilities, competition, predation, extinction and speciation (*e.g.* Briggs & Bowen 2013).

The taxa studied here appear in three of the five warm (tropical and warm temperate) provinces Briggs and Bowen (2012) recognised based on fish distribution, namely the Western Atlantic Province (*Holothuria unicolor*), the Tropical Indo-West Pacific Province (*H. arenicola, H. conusalba, H. milloti* & *H. kerriensis*) and the Eastern Pacific Province (*H. zihuatanensis*). The absence of this clade in the warm Eastern Atlantic is surprising, especially since *H. arenicola* has been recorded from Ascension Island (Pawson 1978). Moreover, Briggs & Bowen (2013) have shown, based upon data from fish, that invasions in the Atlantic via South Africa can occur despite the 'soft barrier' of the Benguela and that species can cross the open-water expanse of the mid-Atlantic. It is very probable that as Price *et al.* (1999) argue that the disparity in sampling efforts determines our understanding of geographic patterns. Indeed, the sea cucumber fauna of the tropical and subtropical East Atlantic remains relatively poorly known (*e.g.* Koehler & Vaney 1905; Hérouard 1929; Cherbonnier 1963, 1964; Panning 1940; Massin 1993; Thandar *et al.* 2010; Thandar & Mjobo 2014)

The distribution pattern of the species in the *H. arenicola* complex parallels that of other sea cucumbers. Uthicke *et al.* (2004) found three distinct clusters in the Indo-Pacific teatfish. The distribution of *H. unicolor* can be explained by vicariance that took place when the Isthmus of Panama closed.

We unfortunately did not have access to material from the Mediterranean Sea, so we cannot confirm its presence there. However, if it does occur there, it can be explained as another case of Lessepsian migration (Aydin *et al*. 2019). We believe these records are just misidentfications.

Conclusion

Our conclusion on the taxonomy of the *arenicola* complex is that six species can be recognized: (i) *Holothuria (Thymiosycia) arenicola* Semper, 1868, restricted to the large central Pacific, (ii*) H. (T.) conusalba* Cherbonnier & Féral, 1984 present in the Indo-Pacific, (iii) *H. (T.) kerriensis* sp. nov confined to the Indian Ocean and the Red Sea, (iv*) H. (T.) milloti* Cherbonnier, 1988 present only in the southern Indian Ocean, (v) *H. (T) unicolor* Selenka, 1867 found off the Caribbean coasts as far east as up to Bermuda and (vi) *H. (T.) zihuatanensis* Caso, 1965 living in the eastern Pacific from the Galapagos up to the East coast of America.

Only more (fresh) material will allow the comparative morphological and genetic characterization for recognizing additional taxa in the *H. arenicola* complex. Available names are: *Holothuria rathbuni* Lampert, 1885, of which the type locality is Bahia (Brazil) and *Holothuria monsuni* Heding, 1939, of which the type locality is the Red Sea.

Acknowledgments

A study of this scope is not possible without the help of many colleagues. We would like to thank the different collection curators who loaned us reference material and/or welcomed us at their museum: Dr Andreas Schmidt-Rhaesa and Mr. P. Stewie of the ZMH, Dr A. Martynov of the ZMMSU, Dr N. Cominardi of the MNHN, Dr D VandenSpiegel of the RMCA, Dr A Gabrinowicz of the NHM and Dr C. Lueter of the ZMB. We are further in debt to the referees of this paper and to the editor for their judged decisions.

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