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Taxonomy of the heavily exploited Indo-Pacific sandfish complex (Echinodermata: Holothuriidae)

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Two commercially valuable holothurians, the sandfish and golden sandfish, vary in colour and have a confused taxonomy, lending uncertainty to species identifications. A recent molecular study showed that the putative variety *Holothuria* (*Metriatyla*) *scabra* var. *versicolor* Conand, 1986 ('golden sandfish') is a distinct species from, but could hybridize with, *H.* (*Metriatyla*) *scabra* Jaeger, 1833 ('sandfish'). Examination of the skeletal elements and external morphology of these species corroborates these findings. The identity of *H.* (*M.*) *scabra* is unambiguously defined through the erection and description of a neotype, and several synonyms have been critically re-examined. The nomenclaturally rejected taxon *H.* (*Metriatyla*) *timama* Lesson, 1830 and *H.* (*M.*) *scabra* var. *versicolor* (a *nomen nudum*) are herein recognized as conspecific and are allocated to a new species, ***Holothuria lessoni* sp. nov.**, for which type specimens are described. The holotype and only known specimen of *H. aculeata* Semper, 1867, has been found and is redescribed. It is considered to be a valid species. Taxonomic clarification of this heavily exploited species complex should aid its conservation and permit species-specific management of their fisheries.

ADDITIONAL KEYWORDS: conservation biology – *Holothuria aculeata* – ***Holothuria lessoni* sp. nov.** – *Holothuria scabra* – *Holothuria scabra versicolor* – *Holothuria timama* – nomenclature.

INTRODUCTION

Some 20 large sea cucumber species in the order Aspidochirotida are fished commercially throughout the Indo-Pacific. We suspect, however, that this is an underestimate of the actual number of aspidochirotid species exploited because several species are poorly defined taxonomically. This absence of sound taxonomic research to provide unique, stable and universal scientific names (e.g. Mace, 2004) is a hindrance to successful conservation and management plans. Clarity over scientific nomenclature is of particular concern for the conservation and management of these species. For example, current moves to add some of these species to the CITES annexes are hampered by insufficient knowledge of their taxonomic status. Here, we clarify the taxonomy of the Indo-Pacific sandfish group, consisting of species so heavily exploited (for local examples see Lovatelli *et al.*, 2004; Uthicke & Conand, 2005) that they face local to global extinction if no conservation measures are taken.

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Sandfish are, next to the 'teatfish', the most commercially valuable of tropical sea cucumber species. Whereas the identity and scientific names of teatfish species have become increasingly clear thanks to taxonomic studies (Rowe & Gates, 1995), and biogeographical and genetic studies (Uthicke, O'Hara & Byrne, 2004), the sandfish group remains taxonomically chaotic. Irrespective of this scientific malaise, fishermen and traders from various places in the Indo-West Pacific commonly distinguish two kinds of sandfish: the 'sandfish' (*sensu stricto*) and the 'golden (or spotted) sandfish'. The scientific names that have been attributed to these two forms are unfortunately not unambiguous. In general, the 'sandfish' is denominated *Holothuria* (*Metriatyla*) *scabra* Jaeger, 1833, whereas the golden sandfish is referred to by a variety of scientific names such as *H. timama* Lesson, 1830, *H. aculeata* Semper, 1868 or (most commonly) *H. scabra* var. *versicolor* Conand, 1986. The availability and validity of the latter scientific names has not been dealt with in a conclusive, taxonomically and nomenclaturally sound study. This partly results from the fact that it was long thought that the Indo-Pacific golden sandfish was merely a variety (Conand, 1986) or at best a subspecies (Conand, 1989) of the common Indo-Pacific sandfish.

A recent genetic study, using both nuclear and mitochondrial markers, however, demonstrated that the Pacific golden sandfish warrants separate species status and that its three colour forms are conspecific (Uthicke, Purcell & Blockmans, 2005). In the present paper we review the taxonomy of the Indo-Pacific sandfish complex and assign correct scientific names to its different species. These unambiguous and stable names will allow for easy reference and thus engender better protection, for instance, by facilitating their addition to one of the CITES annexes or by installing species-specific fisheries regulations.

MATERIAL AND METHODS

The bulk of the study material originated from the shallow reef flat of Îlot Maître (22°20.4′S, 166°24.8′E), New Caledonia. On animals located at random, body length, papillae (dorsal) length and depth of dorsal body wrinkles were measured *in situ*, taking care not to disturb the animals. Some specimens were subsequently anaesthetized in 5% magnesium chloride for 4 h, transferred to 100% buffered alcohol for 1 day and transferred to 70% buffered alcohol for permanent storage. Type material of *H. lessoni* and *H. scabra* was fixed in 10% buffered formaldehyde for about 3 months, prior to permanent storage in 70% buffered alcohol. Original fixation of *H. aculeata* is unknown; at present it is stored in 70% buffered alcohol. Type material of *H. lessoni* and *H. scabra* was selected in agreement with Article 75.3.6 of the International Code of Zoological Nomenclature (ICZN), i.e. 'as nearly as practicable from the original type locality'.

For further comparative studies, we examined other material from the collections of the Royal Belgian Institute of Natural Sciences in Brussels (RBINS), the Zoological Museum of Moscow State University (ZMMSU), the Musée national d'Histoire naturelle in Paris (MNHN), Naturalis in Leiden (RMNH), the Museum and Art Gallery of the Northern Territory in Darwin (MAGNTD) and the Natural History Museum of London (NHM).

Morphological observations and measurements were made following the conventional methods described by such workers as Rowe & Doty (1977) and Massin (1999) and compared with results from recent genetic (Uthicke *et al.*, 2005) and ecological observations. Partial 16S mtDNA sequences from *H. scabra* specimens from New Caledonia and Australia have previously (Uthicke *et al.*, 2005) been deposited in GenBank (accession numbers AY509130–136). Partial mitochondrial 16S sequences of *H. lessoni* sp. nov. from New Caledonia and Australia were previously lodged in GenBank (Uthicke *et al.*, 2005) (accession numbers AY509142–146 as *H. scabra versicolor*, name on sequences to be changed to *H. lessoni*).

In the citation lists of each species, the sign 'ss' indicate that the species is mentioned on the indicated page and also on subsequent ones.

RESULTS

SYSTEMATIC ACCOUNTS

Ordo Aspidochirotida Grube, 1840
Familia Holothuriidae Ludwig, 1894
Genus *Holothuria* Linnaeus, 1767
Subgenus *Metriatyla* Rowe, 1969

HOLOTHURIA (*METRIATYLA*) *LESSONI* SP. NOV.

(FIGS 1A–D, 3A–G, 4A–H, 5A–C)

Holothuria timama Lesson, 1830: 118, pl. 43; Lampert, 1885: 94; Théel, 1886: 240; Clark, 1963: 383ss; Opinion 762, 1966: 15ss; Melville & Smith, 1987: 301.

Holothuria timana (*lapsus calami*); Panning 1931: 117; Cherbonnier, 1951b: 396; Cherbonnier, 1951a: 295, figs 1a–r, 2a–g.

Holothuria (*Metriatyla*) *timana*; Rowe & Gates, 1995: 295; Marsh & Morrison, 2004: 339.

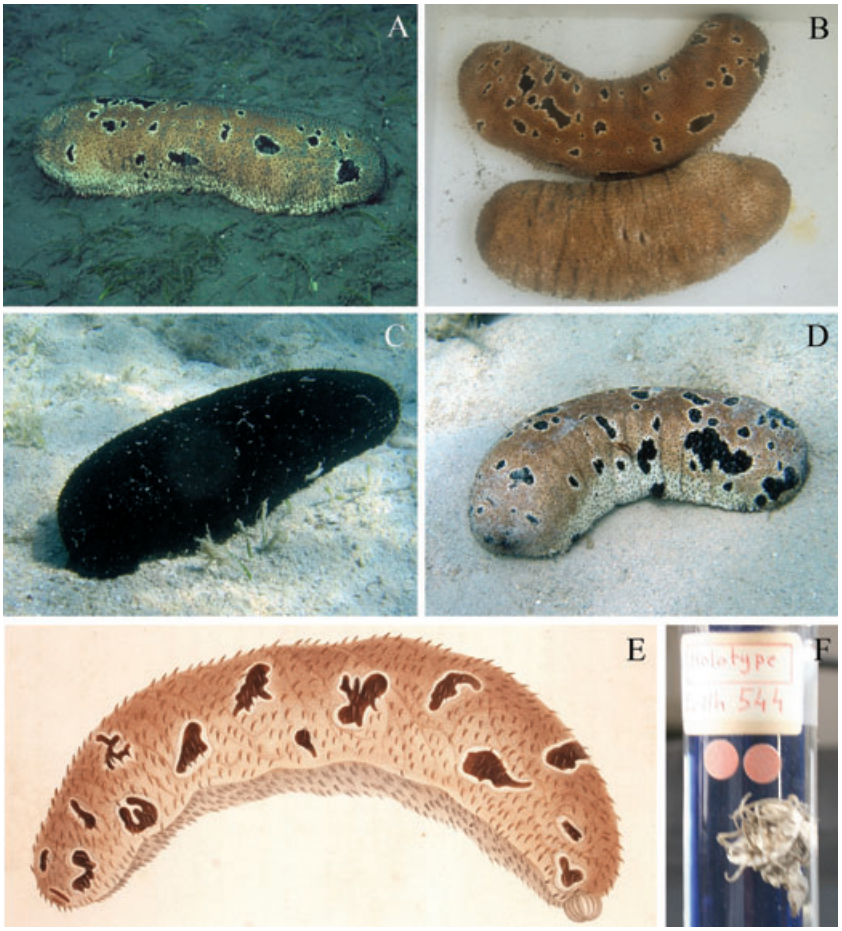

Figure 1. A–D, ***Holothuria* (*Metriatyla*) *lessoni* sp. nov.** A, holotype (the covering fine layer of sand was gently brushed away); B, holotype (top) and paratype (bottom); C, black form (IG 30768/5); D, mottled form (IG 30768/4). E, *H. timama* Lesson, 1830, original drawing; F, *H. timama* Lesson, 1830, remaining fragment of holotype. Photographs A & B by C. Massin, C & D by S. Purcell; E & F by Y. Samyn.

Holothuria (*Metriatyla*) *scabra*; VandenSpiegel, Ovaere & Massin, 1992: 168, figs 2, 3A–E, 4A–G (non *H.* (*M.*) *scabra* Jaeger, 1833).

Holothuria scabra var. *versicolor* Conand, 1986: 19; Conand, 1991: 170; Conand & Byrne, 1993: 3ss; Conand, 1998: 1180, text fig. + map; Conand, 1999: 10ss; Forbes *et al.*, 1999: 38 (colour plate); Hamel *et al.*, 2001: 146ss, fig. 4B; Conand, 2004: 14, fig. 1(4); Baine, 2004: 120; Rasolofonirina, Mara & Jangoux, 2004: 137; Tuwo, 2004: 51; Uthicke *et al.*, 2005: 261ss, fig. 1B–D; Purcell, 2005: 31, fig. 2b; Ivy & Giraspy, 2006: 28ss, figs 1–4.

? *Holothuria scabra* var. *versicolor*; Schoppe, 2000: 119 (colour plate); Pouget, 2005: 23.

Holothura aculeata; Cherbonnier, 1951a: 298 (non *H. aculeata* Semper, 1868); Catala, 1979: 245, fig. 91 (colour plate) (non *H. aculeata* Semper, 1868); Rowe & Gates, 1995: 295 (cited as a synonym of *H. timana* (sic) (= *H. lessoni* sp. nov.).

Holothuria (*Metriatyla*) *aculeata*; Rowe, 1969: 160 (*partim*, records from East Indies only); Clark & Rowe, 1971: 176 (*partim*, records from East Indies only); Marsh *et al.*, 1993: 64; Marsh, 1994: 11.

Material examined

Type material

Holotype H. lessoni sp. nov.: RBINS IG 27754/179, Hansa Bay (Madang Province, Papua New Guinea), muddy bottom with sparse seagrass bed, 6-m depth, coll. C. Massin 01.x.1990.

Paratype H. lessoni sp. nov: RBINS IG 27754/180, same data as holotype.

Holotype H. timama Lesson, 1830 (buccal apparatus only): MNHN EcHh 544, Waigeo Island, substrate and depth not given, coll. unknown.

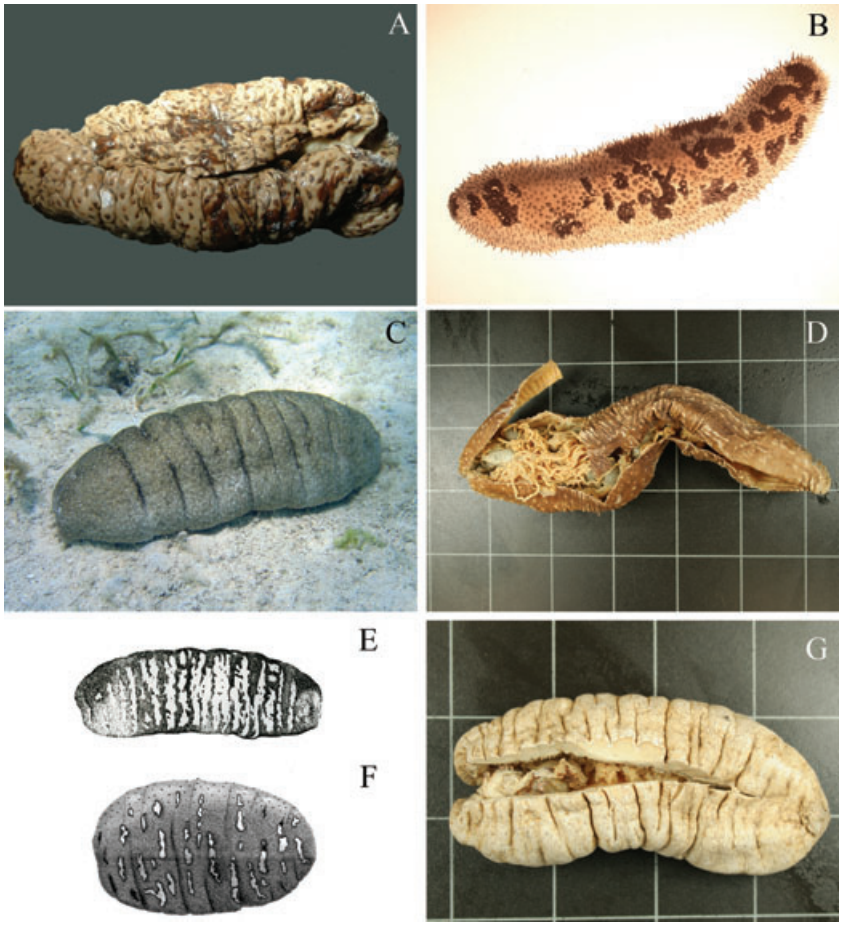

Figure 2. A, *Holothuria* (*Metriatyla*) *aculeata* Semper, 1868, holotype; B, *H. aculeata*, original drawing; C. *Holothuria* (*Metriatyla*) *scabra*, non-type material, New Caledonia (IG 30768/1); D, *Holothuria cadelli* Bell, 1887, lectotype; E, *Holothuria gallensis* Pearson, 1903, original drawing; E, *Holothuria* cf. *gallensis* Pearson, 1903, drawing by Selenka, 1867 as *H. tigris* Brandt, 1835; G, *Holothuria saecularis* Bell, 1887, paralectotype. Photograph A by A. Martynov; B, D–G by Y. Samyn; C. by S. Purcell.

Non-type material

RBINS IG 27598/133 (1 specimen): Hansa Bay (Madang Province, Papua New Guinea), muddy bottom with sparse seagrass bed, 11 m depth, coll. C. Massin 13.x.1989.

RBINS IG 27598/135 (1 specimen): Hansa Bay (Madang Province, Papua New Guinea), muddy bottom with sparse seagrass bed, 10 m depth, coll. C. Massin 13.x.1989.

RBINS IG 30768 (6 specimens; labelled RBINS IG 30768/2 to 30768/7): Îlot Maître (New Caledonia), sandy bottom with sparse seagrass bed, 0.5–2 m depth, coll. S. Purcell 23.ii.2007.

MAGNTD Q004089: Ashmore Reef Lagoon, 12°15′20″S, 122°59′30″E, stn. 935 (Australia), 1 m depth, coll. L. Vail 10.iv.1987.

Type locality

Hansa Bay, Madang Province, Papua New Guinea.

Etymology

The name *lessoni* is given in honour of Dr R. P. Lesson who, in 1830, was the first to recognize and describe the species under the name *Holothuria timama* (Fig. 1E). However, as the name *timama*, as published in the binomen *Holothuria timama*, is suppressed (ICZN Opinion 762, 1966), it can no longer be used to denominate this species.

Known geographical distribution

Indian and Pacific Ocean; for details see Table 1.

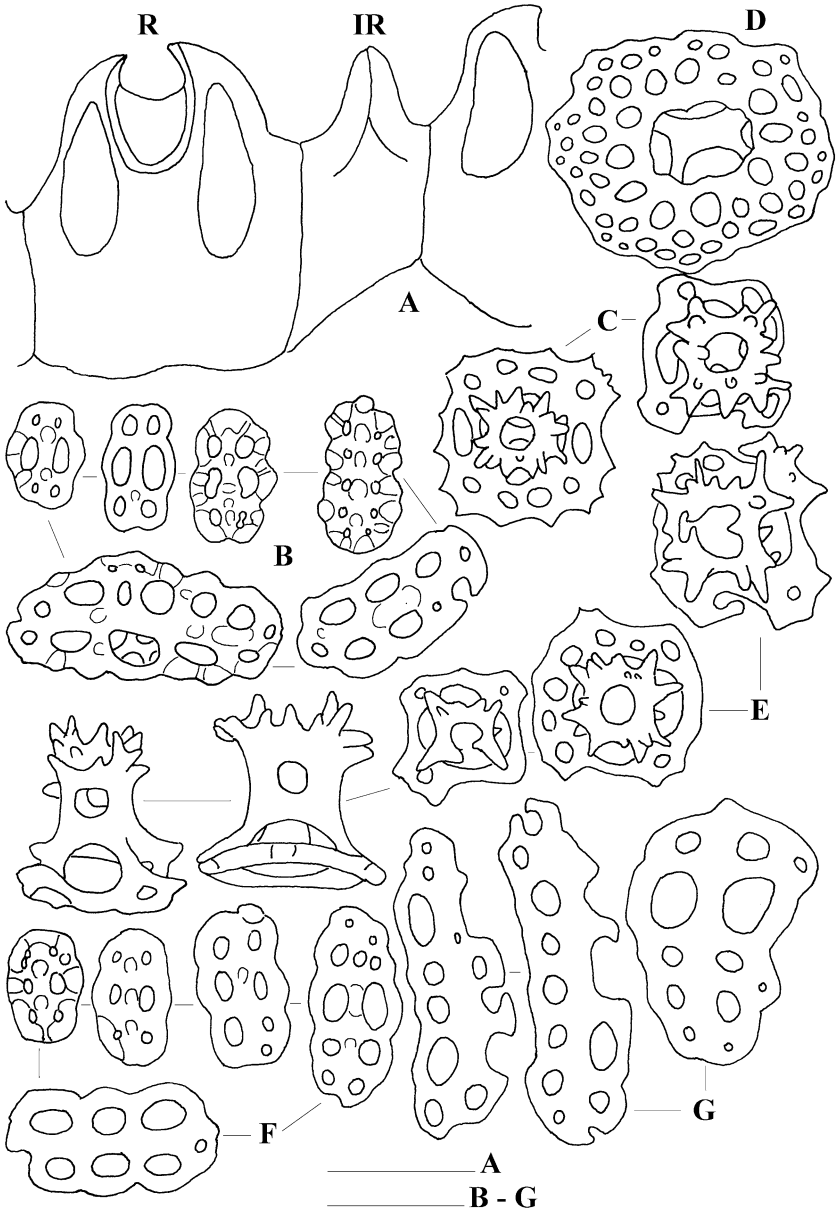

Figure 3. ***Holothuria* (*Metriatyla*) *lessoni* sp. nov.**, holotype. A, calcareous ring (R, radial plate; IR, interradial plate); B, buttons of dorsal body wall; C, tables of dorsal body wall; D, large table of dorsal body wall; E, tables of ventral tube feet; F, buttons of ventral tube feet; G, perforated plates of ventral tube feet. Scale bars: A = 5 mm; B–G = 50 μm.

Taxonomic description

Gross morphology: Large holothurian; preserved adult specimens 20–25 cm long, 8–10 cm wide; living adults commonly around 25–35 cm long, but occasionally up to 48 cm long. Body slightly flattened, with distinct ventral sole, rounded extremities. Mouth ventral, surrounded by 20 large tentacles (counted indirectly by number of tentacle ampullae). Papillae around mouth prominent in live specimens, but difficult to distinguish in contracted specimens as is the case with most of specimens at hand. Anus terminal, without anal teeth, five groups of anal papillae present. Dorsal surface brown-beige, with or without black patches which are sometimes surrounded by a white margin (Fig. 1A, B); some specimens completely black (Fig. 1C) or mottled with black and beige-brown (Fig. 1D). Tube feet as brown or black dots covering bivium. Contracted specimens with few transverse ridges. Ventral surface white to beige, or grey in the black colour variants, with deep longitudinal, median groove, darker than rest of surface. Tube feet brown or black, spread evenly over trivium. Blotchy variants

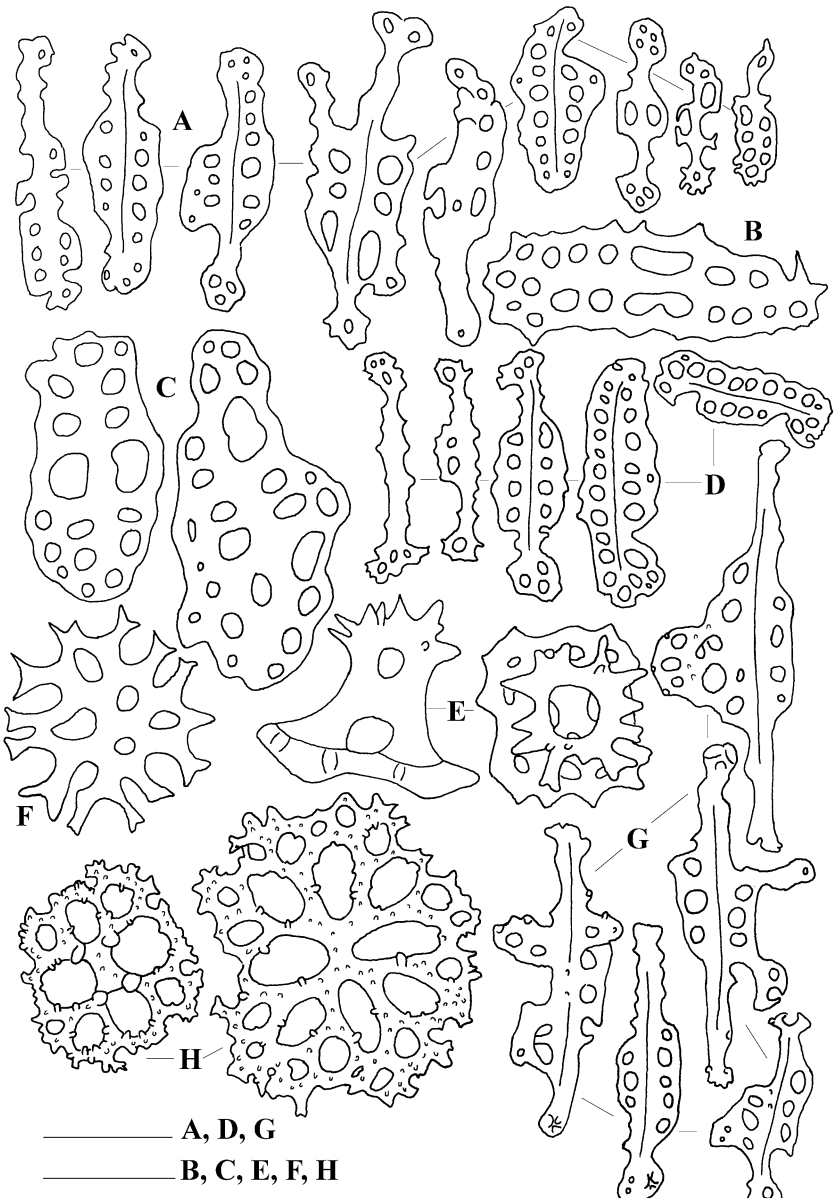

Figure 4. ***Holothuria* (*Metriatyla*) *lessoni* sp. nov.**, holotype. A, perforated rods of ventral tube feet; B, perforated plates of ventral tube feet; C, perforated plates of dorsal tube feet; D, perforated plates and rods of dorsal tube feet; E, tables of dorsal papillae; F, reduced end plate of a dorsal papilla; G, perforated plates of the anal papillae; H, perforated plates of cloacal wall. Scale bars: A, D & G = 100 μm; B, C, E, F & H = 50 μm.

occasionally have black patches ventrally. Undisturbed animals from Papua New Guinea covered dorsally by thin layer of sand. Body wall smooth to the touch, 10–15 mm thick in contracted specimens. Calcareous ring very stout (Fig. 3A), radials twice as wide as inter-radials, radials with deep anterior notch. Tentacle ampullae 20–50 mm long in preserved material. One Polian vesicle, 30–37 mm long in preserved material. Stone canal single, very long, 150–190 mm long in preserved material. Gonad well developed, with numerous, very long, non-branching tubules. Longitudinal muscles flat, wide, margins not attached to body wall, slightly curled upwards. Cuvierian tubules absent.

Ossicles: Dorsal and ventral body wall with tables and buttons: buttons 40–60 μm long, nodulous, with 3–4 pairs of small holes (Fig. 3B); tables generally 50–80 μm high, with spiny, quadrangular disc, 55–70 μm across, with one central hole and one circle of 4–10 peripheral holes, spire of four pillars with one cross-beam ending in large crown of acute spines

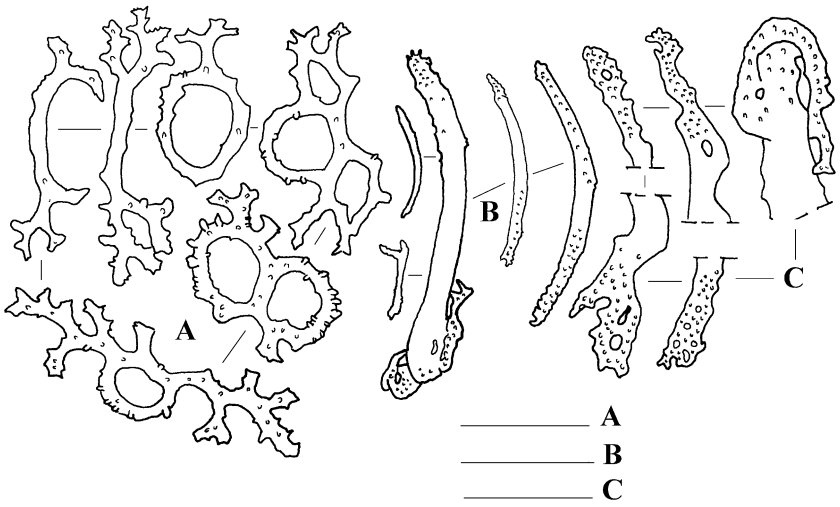

Figure 5. ***Holothuria* (*Metriatyla*) *lessoni* sp. nov.**, holotype. A, rods and small perforated rods of the cloacal wall; B, tentacle rods; C, detail of the extremities of large tentacle rods. Scale bars: A = 50 μm; B = 200 μm; C = 100 μm.

Table 1. Distribution of the golden sandfish, ***H.* (*M.*) *lessoni* sp. nov**., based on scientific literature and credible reports

Locality	Reference
New Caledonia	Conand 1986*, Catala, 1979§
Papua New Guinea	VandenSpiegel *et al.*, 1992‡
Torres Strait	SU, T. Skewess pers. comm.
Great Barrier Reef	Rowe & Gates 1995†
Moreton Bay	Uthicke *et al.*, 2005*
Western Australia	Marsh *et al.*, 1993§
Indonesia	Tuwo 2004*
East Indies	Clark & Rowe 1971§
Seychelles	Aumeeruddy & Payet, 2004*
Madagascar	Conand 1999*
East Africa (Kenya)	Samyn 2003†

*As *H. scabra* var. *versicolor*; †as *H. timana*; ‡as *H. scabra*; §as *H. aculeata*.

(Fig. 3C), crown of spines can be as wide as table disc. Dorsal body wall with additional, few, large tables, discs up to 110 μm across, with several circles of holes; spire reduced (Fig. 3D). Ventral body wall with few tables. Ventral tube feet with tables, buttons, perforated rods and perforated plates: tables as in body wall (Fig. 3E); buttons mostly nodulous (Fig. 3F), similar to those of body wall, but some smooth, large buttons, 60–80 μm long, with 3–4 pairs of large holes (Fig. 3G) also present; perforated rods, 115–265 μm long, with small central perforated process (Fig. 4A); perforated plates, 85–280 μm long, with smooth or spiny edge (Fig. 4B). End plate highly variable in size, 130–500 μm across, composed of several pieces perforated by irregular holes. Dorsal appendages with perforated plates (Fig. 4C), buttons, tables and rods; buttons smooth or nodulous with 3–4 pairs of holes; perforated plates with two rows of holes (Fig. 4D); tables as in body wall, 55–80 μm across (Fig. 4E). End plate 130–250 μm across, sometimes very reduced (85 μm across, Fig. 4F) or absent. Anal papillae with tables, buttons and perforated rods: buttons and tables as in body wall but tables slightly larger (70–85 μm across); rods, 150–310 μm long, with well-developed central perforated process (Fig. 4G) and median longitudinal line. Cloacal wall with large spiny perforated plates 60–130 μm across with 9 to more than 30 holes (Fig. 4H) and irregular spiny rods, 60–130 μm long (Fig. 5A). A few rods may be present at the base of the suspensor muscle close to the cloaca. Tentacles with rods, 60–650 μm long, slightly curved with spiny irregular extremities (Fig. 5B, C). Gonads, longitudinal muscles, intestine and respiratory tree devoid of ossicles.

REMARKS

It is usually possible to distinguish between the species *lessoni* and *scabra* in the field (no field data for *H. aculeata* are available) based on colour patterns, form and length of papillae/tube-feet and presence/absence of wrinkles in the body wall (see Table 2). As these characters are known to show some variation (see below), the identification of each species must rely on the study of the ossicle assemblage. The most striking differences are: (1) the edge of the disc of the tables in *H. lessoni* has a spiny rim, whereas *H. aculeata* and *H. scabra* have tables with a smooth rim, and (2) the cloacal wall of *H. lessoni* has irregular rods, while these are lacking in *H. aculeata* and *H. scabra*.

Coloration is highly variable in this species, and does not alone differentiate it from its close congeners *H. aculeata* and *H. scabra* (cf. descriptions below). The typical coloration pattern for *H. lessoni* varies from uniformly black (IG 30768/5) to brownish with distinct black patches surrounded (IG 30768/4) or not (IG 30768/2 and IG 30768/3) by white. Two of the six specimens in the lot from Îlot Maître (New Caledonia) were collected because they were of the phenotype (as identified by S.P., who also identified samples for the previous study) previously identified as hybrids between *H. scabra* and *H. scabra* var. *versicolor* (= *H. lessoni* sp. nov.) (Uthicke *et al.*, 2005). One of these specimens (IG 30768/7) is uniform beige with transverse darker bands and thus it is somewhat closer to the coloration of *H. scabra*; the other (IG 30768/6) is grey with black blotches and thus resembles somewhat the blotchy colour variant of *H. lessoni* (cf. also Uthicke *et al.*, 2005; Fig. 1E, F). Examination of the ossicle assemblage of these two specimens agrees with the results from the molecular study and we thus also consider these to be hybrids of *H. scabra* (HS) and *H. lessoni* (HL). The beige-coloured specimen (IG 30768/7) presents table discs that are predominantly smooth (= HS-like), but occasionally also spiny (= HL-like) and has its cloacal wall filled with perforated plates with few large holes (= HS-like) and rods (= HL-like). In the grey-coloured specimen (IG 30768/6), the edge of the table disc is smooth (= HS-like), and the cloacal wall has perforated plates with numerous small holes (= HL-like) but no rods (= HS-like). Colour pattern (transverse stripes) is more characteristic of *H. scabra* whereas dark blotches are more characteristic of *H. lessoni*.

Holothuria (*Metriatyla*) *aculeata* Semper, 1868 (Figs 2A, B, 6A–M, 7A–C)

Holothuria aculeata Semper, 1868: 84, 277, pl. 24, pl. 30, fig. 19a, b; Lampert, 1885: 78; Théel, 1886: 235; Lampert, 1896: 55; Mitsukuri, 1912: 140; Pearson, 1913: 52ss; Sérène, 1937: 26; Clark, 1963: 383ss.
Holothuria (*Holothuria*) *aculeata*; Panning, 1935: 80, fig. 65a–c.
Holothuria (*Metriatyla*) *aculeata*; Rowe, 1969: 160 (partim; only the record from the Philippines); Clark & Rowe, 1971: 176, pl. 28, fig. 1 (partim, only the record from the Philippines).

Material examined

Type material
Holotype (labelled 'Unicum' on the original label): ZMMSU H115.

Non-type material
None.

Type locality

Bohol, Philippines.

Known geographical distribution

Literature accounts (cf. synonymy above) suggest that this species is present in the Philippines (Bohol) and in Vietnam. However, the record from Vietnam has not been seen by us and thus remains uncertain.

Taxonomic description

Gross morphology: Medium-sized holothurian; preserved specimen 95 mm long and 35 mm across, cylindrical, with transverse ridges; dimensions in life 22 cm long and 6 cm wide at mid body (according to Semper, 1868: pl. 24). Mouth ventral, surrounded by (at least) 17 brown tentacles and a collar of well-developed papillae. Anus terminal, anal papillae not observed. Colour in alcohol: dorsal surface cream with irregular brown dots, ventral surface whitish, tube feet deep brown (Fig. 2A). Colour in life (according to Semper, 1868): ventral surface uniform whitish; dorsal surface darker, somewhat reddish with irregular dark brown patches; tube feet darker than background colour (Fig. 2B). Dorsal appendages not aligned in rows. Ventral tube feet sparse, spread evenly over trivium. Body wall gritty to the touch, 4–9 mm thick. Original dissection of holotype makes observation of calcareous ring detrimental to unique specimen. Tentacle ampullae short, 7–10 mm long. Polian vesicles, two, very large (19 and 20 mm long). Stone canal, single, large, 12 mm long. Gonad branched. Longitudinal muscles very large, thick, lateral sides not attached to body wall, margins heavily curled upwards, giving muscles U-shaped form. Respiratory trees present. Cuvierian tubules absent. Digestive tract missing except a small part of anterior dorsal lobe.

Ossicles: Dorsal body wall with tables and buttons: tables with disc quadrangular, smooth, perforated by four central holes and one circle of peripheral holes, pillar short, united by one cross-beam ending in crown of short blunt spines (Fig. 6A), majority of tables 50 μm across and 30 μm high, few large ones with two circles of peripheral holes and up to 80 μm across (Fig. 6B); buttons with 3–4 pairs of holes, very knobbed, 40–60 μm long (Fig. 6C). Dorsal tube feet with tables, few buttons, perforated plates and

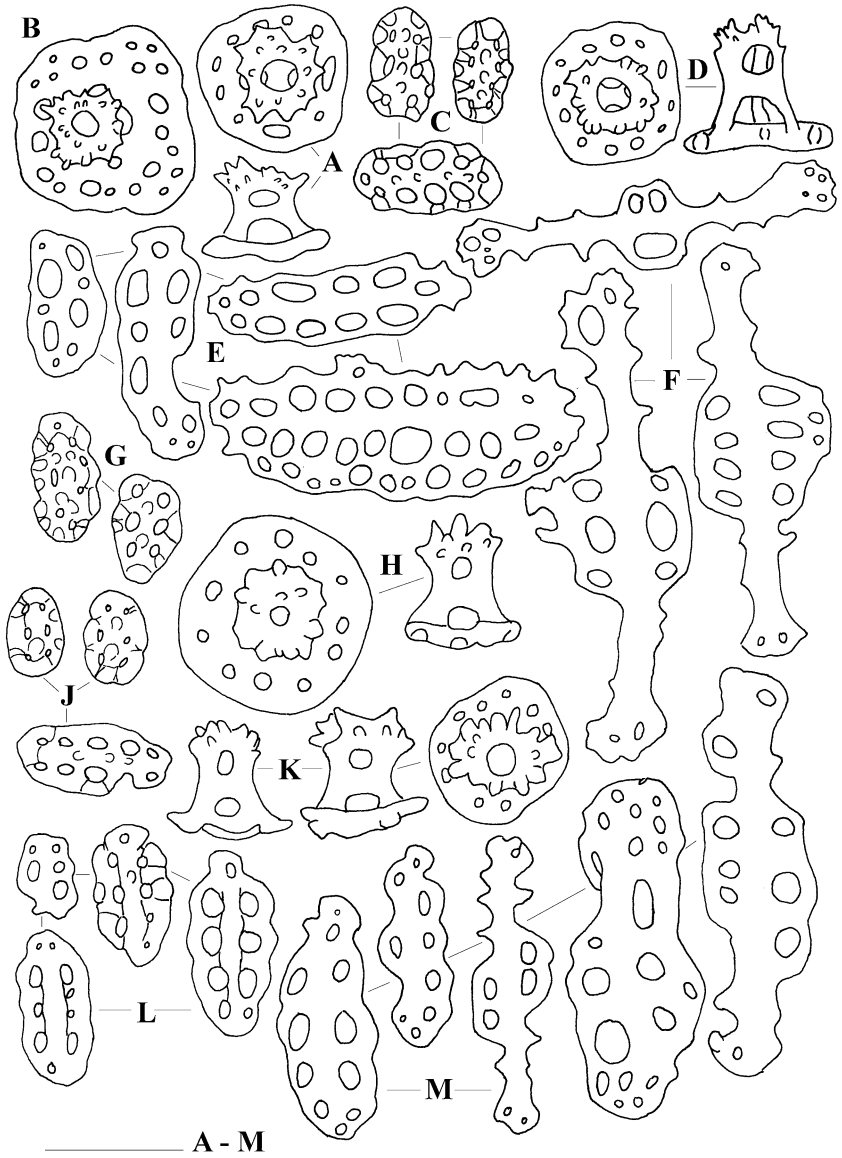

Figure 6. *Holothuria aculeata* Semper, 1868, holotype. A, tables of dorsal body wall; B, large table of dorsal body wall; C, buttons of dorsal body wall; D, table of dorsal papillae; E, perforated plates of dorsal papillae; F, rods of the dorsal papillae; G, buttons of dorsal papillae; H, table of ventral body wall; J, buttons of ventral body wall; K, table of ventral tube foot; L, buttons of ventral tube feet; M, perforated plates and rods of ventral tube feet. Scale bars: A–M = 50 μm.

rods: tables as high as wide (50–60 μm) (Fig. 6D); buttons very similar to those of body wall (Fig. 6G); perforated plates up to 150 μm long (Fig. 6E); rods, 100–190 μm long, with central perforated process (Fig. 6F). End plate made of several pieces and more or less 400 μm across. Ventral body wall with tables (Fig. 6H) and buttons (Fig. 6J); very similar to those of dorsal body wall but nearly all the buttons with three pairs of holes and smaller (30–40 μm long) than dorsally. Ventral tube feet with tables, 30–65 μm across (Fig. 6K); large, sparsely knobbed buttons, up to 70 μm long (Fig. 6L); and perforated plates (Fig. 6M); end plate, 300–350 μm across, in a single piece. Smooth large buttons intergrade with small-perforated plates. Cloacal wall with small perforated ossicles (40–65 μm long), with 2–4 very large perforations, very often spiny (Fig. 7C). Tentacles with rods, 40–470 μm long, strait with spiny, sometimes forked extremities (Fig. 7A, B). Longitudinal muscles and suspensors of cloaca lack ossicles. Gonads, intestine and respiratory tree not examined for ossicles.

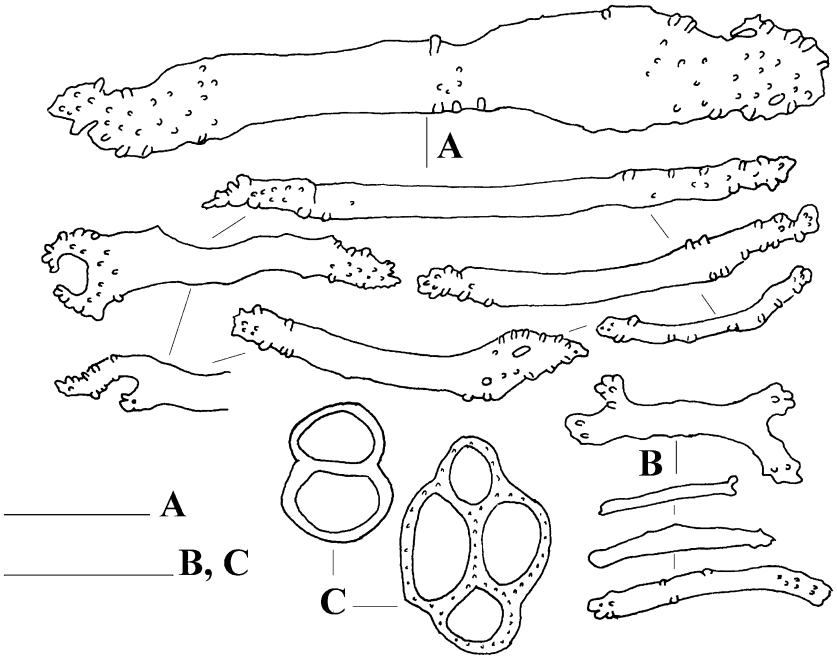

Figure 7. *Holothuria aculeata* Semper, 1868 holotype. A & B, tentacle rods; C, ossicles of cloacal wall. Scale bars: A = 100 μm; B & C = 50 μm.

Remarks

Despite several records in the literature (cf. synonymy list above), either as a valid species, as a misidentified species or as a synonym of *H. timama* Lesson, 1830 (= *H. lessoni* sp. nov.), virtually no information directly attributable to this form subsequent to the original description of *H. aculeata* exists. This is due, at least in part, to the fact that the type material of *H. aculeata* was considered lost (cf. Rowe & Gates, 1995) as it could not be located in any of the German museums that hold type material of Semper (C. Lüter, pers. comm.). However, through Drs A. Smirnov and A. Martynov, we were able to locate the material in the ZMMSU. To our knowledge, this specimen – the holotype as the label bears the denomination 'Unicum' – is the only available voucher. This implies that our knowledge of the intraspecific variety of this species is non-existent.

The holotype presents irregular dorsal black areas as do some specimens of *H. lessoni* sp. nov. In spite of this, the body wall ossicles of *H. aculeata* are closer to those of *H. scabra* than to those of *H. lessoni*. However, *H. aculeata* differs from *H. scabra* by the colour pattern (dorsal surface with dark irregular patches versus uniform grey green colour, respectively), by the large tables of the dorsal body wall (up to 80 μm across with normal pillars versus up to 120 μm across with reduced pillars, respectively) and by the ossicles of the cloacal wall (40–65 μm across with 2–4 holes, versus 80–140 μm across with 4–17 holes, respectively). Moreover, the longitudinal muscles of *H. aculeata* are much thicker than those of *H. scabra*, regardless of body size.

Holothuria aculeata differs from *H. lessoni* in the diameter of the table crown, which is always smaller than that of the table disc, and by the presence of short blunt spines on the table crown (long and acute for *H. lessoni*). The ossicles of the cloaca of *H. lessoni* are also much larger (60–130 μm long) than those of *H. aculeata*. Moreover, the ossicles of the cloaca of *H. lessoni* are perforated by numerous holes (9 to more than 30) and are very spiny.

The fact that *H. aculeata* has only been identified with certainty from the type, and that none of us has seen this species in the wild, suggests that it is either rare or endemic to the Philippines. The possibility that it is another form of hybrid between *H. scabra* and *H. lessoni* cannot be excluded until further vouchers allow better characterization of the variation in this taxon. Also, given that *H. scabra* and *H. lessoni* both have successfully been produced in aquaculture (James *et al.*, 1994; Lovatelli *et al.*, 2004; Ivy & Giraspy, 2006), it should be investigated whether hybridization between these species is possible. Morphology and genetics of such putative hybrids should then be critically compared with *H. aculeata*.

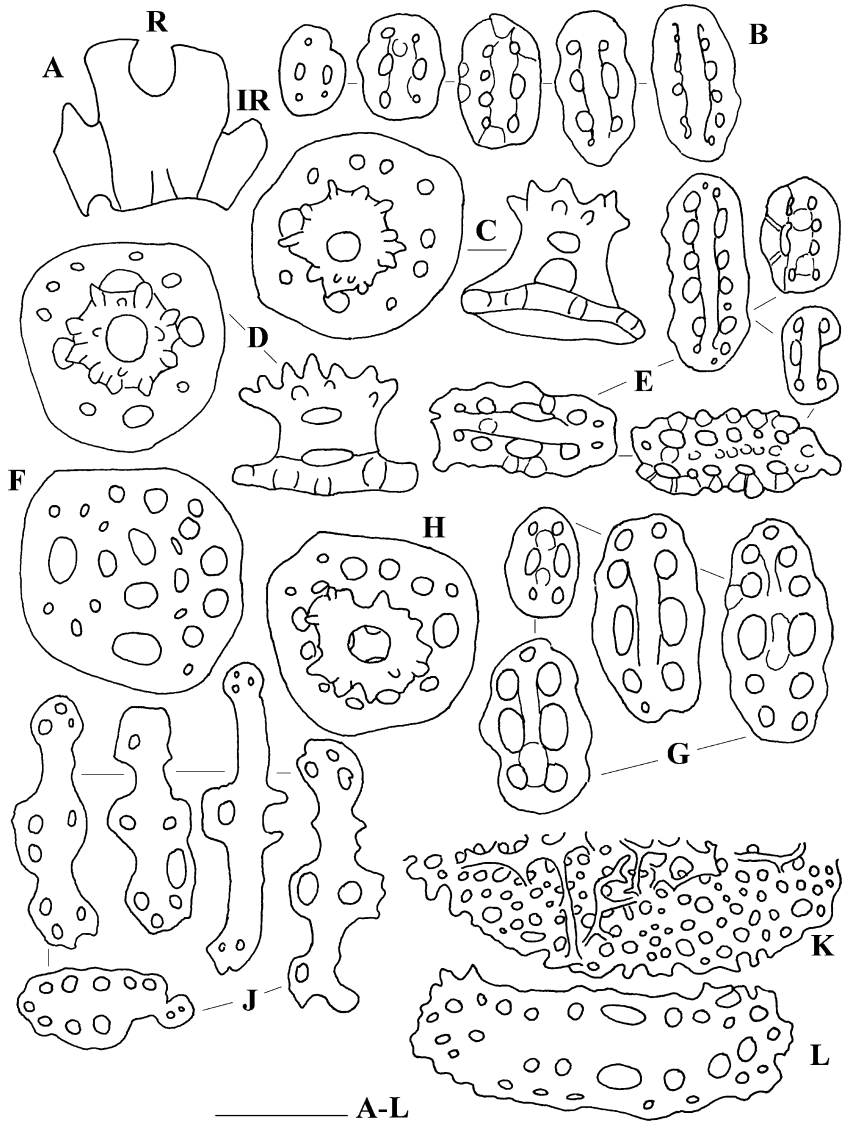

Figure 8. *Holothuria scabra* Jaeger, 1833, neotype. A, calcareous ring (R, radial plate; IR, interradial plate); B, buttons of ventral body wall; C, tables of ventral body wall; D, tables of dorsal body wall; E, buttons of dorsal body wall; F, large table of dorsal body wall; G, buttons of ventral tube feet; H, tables of ventral tube feet; J, perforated rods of ventral tube feet; K, end plate of ventral tube foot; L, perforated plates of ventral tube feet. Scale bars: A = 5 mm; B–H, L = 50 μm; J & K = 100 μm.

HOLOTHURIA (*METRIATYLA*) *SCABRA* JAEGER, 1833 (FIGS 2E, 8A–L, 9A–D, 10A, B)

Holothuria scabra Jaeger, 1833: 23; Semper, 1869: 120; Panning, 1935: 80, fig. 66a–f (list of references before 1935); Cherbonnier, 1980: 647, fig. 16A–L (list of references before 1980); Massin, 1999: 30, figs 22a–l, 23 (map), 110f (colour plate) (list of references before 1998); Hamel *et al.*, 2001: 129ss (list of references before 2000); Hamel, Battaglene, Mercier, 2001: 349; Marshall, Milledge & Afonso, 2001: 45ss; Mercier, Battaglene & Hamel, 2001: 357; Morgan, 2001: 6ss; Uthicke & Benzie, 2001: 109ss; Battaglene *et al.*, 2002: 31ss; Kinch, 2002: 5; Kithakeni & Ndaro, 2002: 163ss; Chen, 2003: 20; Dance, Lane & Bell, 2003: 495ss; Ramofafia, Byrne & Battaglene, 2003a: 658ss; Lane & VandenSpiegel, 2003: 148 (colour plate); Ramofafia *et al.*, 2003b: 281ss; Aumeeruddy & Payet, 2004: 241; James, 2004: 385ss, figs 1–7; Purcell & Kirby, 2006: 54ss; Uthicke & Purcell, 2004: 520ss; Eeckhaut *et al.*, 2004: 312ss; Hasan, 2005: 491ss; Purcell, 2005: 31, fig. 2a; Rasolofonirina *et al.*, 2005: 62ss; Shiell, 2005: 8; Mmbaga & Mgaya, 2006: 3ss;

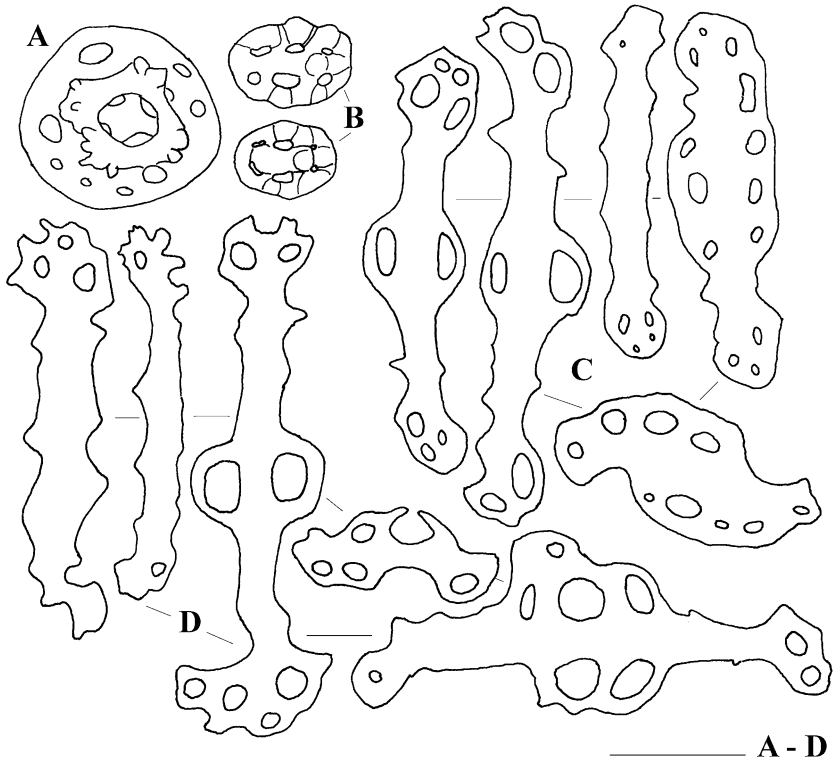

Figure 9. *Holothuria scabra* Jaeger, 1833, neotype. A, tables of dorsal papillae; B, buttons of dorsal papillae; C, perforated rods of dorsal papillae; D, perforated rods of anal papillae. Scale bars: A–D = 50 μm.

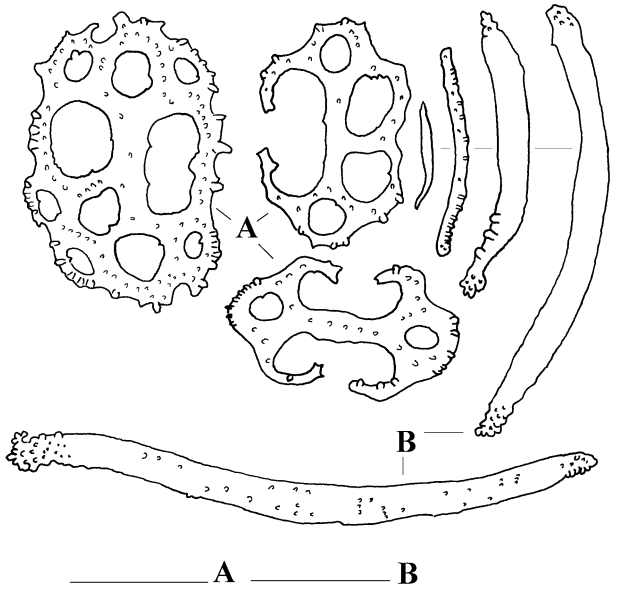

Figure 10. *Holothuria scabra* Jaeger, 1833, neotype. A, perforated plates of cloacal wall; B, tentacle rods. Scale bars: A = 50 μm; B = 100 μm.

Purcell, Blockmans & Agudon, 2006: 238ss; Purcell, Blockmans & Nash, 2006: 284ss.
Holothuria (*Holothuria*) *scabra*; Panning, 1935: 80, fig. 66a–f; Domantay, 1936: 399.
Holothuria (*Metriatyla*) *scabra*; Rowe, 1969: 160, fig. 20a–c; Clark & Rowe, 1971: 178, fig. 87H, pl. 28, fig. 15; Gibbs, Clark & Clark, 1976: 138; Cherbonnier, 1980: 647, fig. 16A–L; Cherbonnier, 1988: 135, fig. 55A–O; Massin, 1999: 30, figs 22a–l, 23 (map), 110f (colour plate); Bussarawit & Thongtham, 1999: 35; Samyn & Vanden Berghe, 2000: 24; Schoppe, 2000: 118 (colour plate); Lane *et al.*, 2000: 489; Samyn, 2003: 50, figs 19A–E, 53D (map), pl. 3A (colour plate); Hamel *et al.*, 2001: 129ss; Paulay, 2003: 578; Putchakarn & Sonchaeng, 2004: 425; Thandar & Samyn, 2004: 255; Marsh & Morrison, 2004: 303, 339; Samyn, VandenSpiegel & Massin, 2005: 15; Samyn, Appeltans & Kerr, 2005: 108ss.
Holothuria (*Halodeima*) *scabra*; Mortensen, 1934: 6.
Fossothuria scabra; Domantay & Conlu, 1968: 170.
Holothuria (*Mertensiothuria*) *scabra*; Kumara, Cumaranathunga & Linden, 2005: 25.
? Holothuria tigris; Selenka, 1867: 333, pl. 19, figs 70–72 (non *H. tigris* Brandt, 1835).
Holothuria saecularis Bell, 1887b: 534, pl. XLV, fig. 6.

? Holothuria gallensis Pearson, 1903: 203, pl. 3, figs 46–50 (I); Daniel & Halder, 1974: 419.
Holothuria (*Microthele*) *tigris* Brandt, 1835: 55.
Holothuria (*Metriatyla*) *ocellata*; Mukhopadhaya, 1988: 6 (non *H. ocellata* Jaeger, 1833).
Holothuria (*Cystipus*) *rigida*; Mukhopadhaya, 1988: 7 (non *H. rigida* Selenka, 1867).

Material examined

Type material
Neotype of *H. scabra* (designated here): RBINS IG 28251/36, Panikiang (Sulawesi, Indonesia), reef flat at low tide, coll. C. Massin 30.viii.1994.

Four syntypes of *Holothuria cadelli* Bell, 1887: NHM 1886.6.26.86–92, Andaman Islands, coll. Dr Anderson, date unknown; the largest specimen (180 mm long) is here designated as lectotype.

Two syntypes of *Holothuria saecularis* Bell, 1887: NHM 1866.4.13.5, Angola, coll Dr Welxitch, date unknown. the largest specimen (180 mm long) is here designated as lectotype.

Non type material
RMNH Ech 6081 (one specimen): Panikiang (Sulawesi, Indonesia), reef flat at low tide; coll. C. Massin 30.viii.1994.

RBINS IG 28767 (ten specimens from aquaculture): Vonavona lagoon (Kohinggo Island, Western Province, Solomon Islands), 2-m depth, coll: J. F. Hamel ii.1998.

RBINS IG 30768/1 (one specimen): Îlot Maître (New Caledonia), on a sandy bottom with sparse seagrass beds at 1-m depth; coll: S. Purcell 27.ii.2007.

Type locality

Panikiang, Sulawesi, Indonesia.

Known geographical distribution

According to the literature (HL. Clark, 1946; Rowe & Gates, 1995; Massin, 1999; Hamel *et al.*, 2001) this species has a wide Indo-West Pacific distribution: from the Red Sea and coast of East Africa to Raratonga (Cook Islands) but it is apparently absent from Hawaii, the East Pacific and along the Pacific American Coasts. Present comparative studies, however, indicate that the sandfish from the Indian Ocean (cf., among many others, James & James, 1994; Samyn, 2003; Rasolofonirina *et al.*, 2004; Conand, Dinhut & Roland, 2005; Pouget, 2005) are possibly not conspecific with those from the Pacific. Only further comparative study with more material from the Indian Ocean will determine whether this is the case.

Taxonomic description of neotype

Gross morphology: Medium-sized holothurian; preserved neotype 175 mm long and 40 mm wide. Body arched dorsally and more or less flat ventrally; one median longitudinal groove ventrally. Mouth ventral, surrounded by 20 short tentacles. Anus terminal with anal papillae. Dorsal surface grey-green with transverse greenish bands (Fig. 2C). Ventral surface grey-white, speckled with dark tiny dots corresponding to tube feet. Body wall gritty to the touch, thin (2–3 mm thick). Calcareous ring with radial plates twice as wide as interradial pieces. Radial pieces with deep anterior notch (Fig. 8A). Stone canal single, 20 mm long. One Polian vesicle, 32 mm long. Tentacle ampullae nearly as long as Polian vesicle. Longitudinal muscles thin, flat with free extremities. No Cuvierian tubules. Gonads not observed. Respiratory trees simple, reaching up to calcareous ring. Digestive tract with a long loop, filled with coarse sand.

Ossicles: Dorsal and ventral body wall with buttons and tables. Ventrally buttons very numerous, comparatively large, 40–75 μm long (Fig. 8B); tables rare, 40–55 μm high with disc 60–95 μm across, quadrangular, smooth, perforated by one central hole and one circle of 8–16 peripheral holes; spire of four short pillars united by one cross-beam, and ending in a crown of blunt spines (Fig. 8C); crown never as wide as table disc. Dorsally, tables very similar to ventral ones (Fig. 8D); buttons nodulous, 40–50 μm long, with 3–4 pairs of holes (Fig. 8E); a few large buttons with 5–7 pairs of holes (Fig. 8E). Dorsally, a few large tables (Fig. 8F), 80–90 μm across (up to 120 μm across in other specimens) with numerous holes and with reduced pillars. Ventral tube feet with nodulous buttons, 40–90 μm long (Fig. 8G); perforated rods, 110–175 μm long (Fig. 8J); and tables, 50–100 μm across (Fig. 8H), very similar to those of body wall; end plate 400–460 μm across with a second layer (Fig. 8K), and surrounded by spiny perforated plates (Fig. 8L). Dorsal papillae with few rods (Fig. 9C) and numerous buttons nearly all with three pairs of holes and similar to those of tube feet (Fig. 9B); tables rare (Fig. 9A) or absent; end plate more or less 270 μm across, comprising several pieces. Anal papillae with tables, buttons and rods; rods slightly curved, 130–200 μm long with few perforations at extremities and sometimes 1–2 central perforations (Fig. 9D). Tables 60–100 μm across with a quadrangular, spiny disc and often an irregular crown of spines. Cloacal wall with large spiny perforated plates 80–140 μm across with 4–17 holes (Fig. 10A); most of the plates with

4–6 large holes. Tentacles with spiny rods 80–440 μm long, slightly curved (Fig. 10B). Ossicles absent in longitudinal and suspensor muscles of cloaca, digestive tract and respiratory tree. Gonad of neotype missing; non-type specimen (RBINS IG 30768/1) with gonad that is devoid of ossicles.

Remarks

The neotype of *H. scabra* has a particularly thin body wall in comparison with larger specimens of the species. This body wall thickness is in agreement with the length–weight relationship of *H. scabra.* Specimens grow generally to 150–170 mm in length; larger specimens become heavier by an increase of body-wall thickness (Pitt & Nguyen, 2004). Colour in live specimens can be quite variable. Entirely black morphs have been observed on Australia's east coast; these were genetically indistinguishable from the green to grey morphs (Uthicke & Benzie, 1999). We also observed specimens with chocolate brown dorsal sides from Bali (Indonesia; S. Uthicke unpubl. data). Black morphs of *H. scabra* are also quite common in New Caledonia (S. W. Purcell, pers. observ.).

The species *Holothuria cadelli* Bell, 1887, *H. gallensis* Pearson, 1903 and *H. tigris* Brandt, 1835 have been included in the synonymy at least since Panning's (1935) report. Considering the confusion surrounding the true concept of the species *scabra*, as demonstrated above, the type series of *cadelli* was re-examined. Type specimens of both *gallensis* and *tigris* have not been located, although the original descriptions have served well in understanding their external morphology. The type specimen of a fourth species, *H. saecularis* Bell, 1887, listed by Panning as a valid species (but poorly described) has also been examined and we herein are able to commit it to the synonymy of *H. scabra.*

To clarify the relationship between each of these species and *H. scabra* we briefly discuss them, in alphabetical order, below.

Holothuria cadelli Bell, 1887

Decision for synonymy: Panning (1935).

Type data: Four syntypes, NHM 1866.6.26.86–92 with type locality Andaman Islands; largest specimen (180 mm long, NHM 1886.6.26.86a) here designated as lectotype; paralectotypes with collection numbers NHM 1886.6.26.86b–d.

Taxonomic description *(see also Bell, 1887a):* Type material well preserved, well relaxed. Largest specimen 180 mm long and 40 mm wide at mid body. Body cylindrical with rather fusiform extremities, especially posteriorly. Ventral side flattened, dorsal side somewhat arched. Mouth ventral; number of tentacles could not be determined. Anus terminal, surrounded by anal papillae. Tube feet dispersed without apparent order over bivium and trivium. Body wall rough to the touch, only 1 mm thick. Calcareous ring with radial pieces with well-developed posterior bifurcation and more than twice as long as the interradial plate. Tentacle ampullae large (> half body length); number could not be determined. Polian vesicle single, large (> half body length). Stone canal(s) and madreporite(s) could not be found. Gonad present, very large, extensively ramified. Longitudinal muscles narrow, not attached laterally. Cuvierian tubules present.

The ossicle assemblage, with very low tables and nodulous small buttons, together with the distinctive morphology of the calcareous ring and the presence of Cuvierian tubules leave no doubt that *H. cadelli* must be removed from the synonymy of *H. scabra*. Instead, the species clearly belongs to the holothurian subgenus *Theelothuria*. We prefer not to assign its specific status until a complete taxonomic revision of *Theelothuria* is carried out.

Holothuria gallensis Pearson, 1903

Taxonomic decision for synonymy: Panning (1935).

Type data: Status and whereabouts of three syntypes undetermined; type locality Reef Galle, Ceylon (= Sri Lanka)

Taxonomic description: Cf. Pearson, 1903: 203, pl. III, figs 46–50.

Remarks: As the types of this species have thus far not been located – Pearson provides no indication as to where they have been deposited (Calcutta? Madras?) – it is difficult to judge whether *H. gallensis* is indeed a synonym of *H. scabra*. Fortunately, the description is rather accurate and thus serves as a guide. Pearson (1903: 204) notes that 'The yellow transverse stripes on the dorsal surface and the mottling on the ventral side are very characteristic'. *H. scabra* as defined here through the neotype, however, does not present 'yellow' but greenish transverse bands. Whitish bands have, however, been described for *H. scabra* by various authors. Selenka (1867), for instance, describes and superbly illustrates them for at least one of the specimens he identifies as *H. tigris* Brandt, 1835, but from which of the localities he lists [Carolinen (Martens), Zanzibar, Amboina, Java] it has been collected from is not clear. More recently other authors also illustrated this coloration pattern as being typical of *H. scabra* (among others: James *et al.*, 1994: 5, fig. II, 6, fig. III, 32: fig. XV; James & James,

1994: 26, fig. XI; Conand, 1999: 23, pl. 3F; Samyn, 2003: 149, pl. 3A). It must be noted that these illustrations all are of specimens from the Indian Ocean.

The taxonomic status of *H. gallensis* will remain doubtful until more material from the Indian Ocean becomes available for morphological and molecular determination. If the Indian Ocean form does prove to represent a valid species then the name *gallensis* is the oldest subjective synonym available, but needs to be stabilized, taxonomically, by the establishment and description of a neotype.

***Holothuria tigris* Brandt, 1835**

Taxonomic decision for synonymy: Panning (1935).

Type data: Status and whereabouts undetermined; type locality Uleai Is., Caroline Archipelago.

Taxonomic description: Cf. Brandt, 1835: 55 (in Latin).

Remarks: The original description clearly states that the dorsum has transverse dorsal stripes that can be interrupted. As this conforms with *H. scabra*, *H. tigris* best remains a junior subjective synonym.

***Holothuria saecularis* Bell, 1887**

Type data: Two syntypes, NHM 1866.4.13.5 with type locality Angola; largest specimen (150 mm long, NHM 1866.4.13.5a) here designated lectotype; paralectotype with collection number NHM 1866.4.13.5b.

Taxonomic description: Cf. Bell, 1887b: 534, pl. XLV, fig. 6.

Examination of the gross morphology and the ossicle assemblage leaves no doubt that this name should be put in the synonymy of *H. scabra.* The type locality (Angola, West Africa) is, however, very problematic as this implies that *H. scabra* is also present in the Atlantic Ocean. We can only conclude that this is an error of Bell.

Remarks: Bell (1887b) stated that no tables were to be found; our (re-)examination, however, did reveal tables, in size and shape identical to those of *H. scabra*.

DISCUSSION

It is remarkable that the taxonomy of one of the most valuable of tropical commercial species has remained so chaotic, despite recent monographs on the species (Bai, 1980; Hamel *et al.*, 2001). The main problem has been the lack of name-bearing types for two of the three Indo-Pacific sandfish species now recognized, which has led to a lack of understanding of the original concept of those species based on erroneous, subjective identifications from original descriptions.

The golden sandfish has in the past been referred to under the infrasubspecific name *Holothuria* (*Metriatyla*) *scabra* var. *versicolor*, proposed by Conand (1986) on the basis of comparative ecological and reproductive studies. Conand erected this name because her data suggested that studied populations were different from *H.* (*Metriatyla*) *scabra* Jaeger, 1833, although ossicle assemblages appeared broadly similar. Later Conand (1989) raised the variety *versicolor* to subspecific rank. Uthicke *et al.* (2005) utilized allozymes and 16S mtDNA sequence data to show that *H. scabra* and *H. scabra* var. *versicolor* are distinct, but young biological and phylogenetic species and suggested that *H. scabra* var. *versicolor* should be raised to species rank. However, as *versicolor* was named as a variety (=an infrasubspecific name), it is not available for a specific name (ICZN Art 15.2), nor can it be raised by subsequent action (such as 'elevation in rank') except by a ruling of the Commission (ICZN Art 45.5). Moreover, as neither the criteria of publication (ICZN Arts 7–9) nor the provisions of availability (ICZN Arts 10–20) were met, the name *versicolor* is a *nomen nudum*.

The next, apparent, available name for the 'golden sandfish', cf. above, is Lesson's (1830) *H. timama*. This, also, is unacceptable, however, as the name had been suppressed in 1966 (see Opinion 762, 1966), following a case submitted by Clark (1963) in order to defend the validity of the species *Holothuria aculeata* Semper, 1868, which was thought, at the time to be threatened following Cherbonnier's (1951b) rediscovery of and redescription of *H. timama*. Cherbonnier (1951b) considered *aculeata* to be a synonym of *timama*. It is all the more unjustified, and confusing, that as recently as 1995, Rowe (in Rowe & Gates, 1995) appeared to have overlooked Opinion 762 (1966) and to have resurrected *timama* on the basis of Cherbonnier's (1951b) conclusions. This error has been followed by both Samyn (2003) and Marsh & Morrison (2004).

Although it is possible to request, through a new ruling of the ICZN, the reinstatement of a suppressed name, we believe this would be unwise as the only remaining, and purported, type material of *timama* is a virtually unidentifiable anterior, internal fragment (including the calcareous ring and associated tissues, see Fig. 1F); the name *H. timama* is thus a *nomen dubium* (ICZN Art 75.5).

As there are no other available synonyms or type specimens from which to establish a named species, we have provided a new name, *Holothuria* (*Metri-*

Table 2. Morphological characters distinguishing the three species discussed

Character	*H. lessoni*	*H. aculeata*	*H. scabra*
Body length	250–480 mm	95 mm	150–200 mm
Body shape	Distinctly flattened ventrally	Mildly flattened ventrally	Mildly flattened ventrally
External coloration	Beige-brown or black, mottled or blotched, lighter ventrally	Blotched	Grey-brown, grey-green, or black, with or without dark transversal bands
Body wrinkles (living specimens)	No transverse body wrinkles, or only on average 0.5 mm (±0.3 SD) deep	Not applicable	Transverse body wrinkles, on average 3.1 mm (±0.7 SD) deep
Coloration of dorsal appendages	Black, bordered by a black circle	Deep brown	Light grey, bordered by a whitish circle
Distribution of dorsal appendages	Numerous (±30 cm^{-2})	Sparse (±15 cm^{-2})	Sparse (±20 cm^{-2})
Length dorsal appendages (living specimens)	Long, on average 3.2 mm (±0.8 SD) (range: 2.0–4.4 mm)	Not applicable	Short, on average 1.5 mm (±0.3 SD) (range: 1.2–2 mm)
Table: disc edge	Spiny	Smooth	Smooth
Table diameter	55–70 μm	45–55 μm	60–95 μm
Large table with reduced pillars	Up to 110 μm	Up to 80 μm	Up to 120 μm
Table height	55–85 μm	40–45 μm	45–55 μm
Table crown	Large, acute spines	Small, blunt spines	Medium, blunt spines
Perforated plate of cloaca	60–130 μm, 9 to > 30 holes	40–65 μm, 2–4 large holes,	80–140 μm, 4–17 holes
Rods of cloaca	Present, 60–130 μm	Absent	Absent
Anal papillae rod shape	Numerous, with large central perforated process	Anal papillae not observed	Few, without large central perforated process

atyla) *lessoni*, with a type specimen collected close to the type locality of *H. timama*.

Finally, we have also established the correct name for the 'sandfish' as *Holothuria* (*Metriatyla*) *scabra* Jaeger, 1833 by describing a neotype specimen, which unambiguously establishes its taxonomic identity. Further investigation is required to determine whether the Indian Ocean form fits within the concept of *scabra* that we have defined or requires recognition as a separate species, for which the name *Holothuria gallensis* Pearson, 1903 may be available.

Of further interest is hybridization between *H. scabra* and *H. lessoni*, initially suggested after intermediate phenotypes had mtDNA from either of the two species (*H. lessoni* as *H. scabra* var. *versicolor*), and allozyme (as nuclear markers) frequencies intermediate between them (Uthicke *et al.*, 2005). Further statistical analyses of those data suggested that all hybrids investigated were from the F1 generation, and no further gene exchange between the two species was detected. Intermediate phenotypes (from the same location) investigated here with morphological data supported the hypothesis that the species are hybridizing.

Table 2 summarizes the main characters that allow recognition of the three species treated here.

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