New species of *Desmanthus* (Porifera, Demospongiae) with a discussion of its ordinal relationships

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**ABSTRACT**

*Desmanthus meandroides* n. sp. is described from São Sebastião, SW Brazil and *D. levii* n. sp. from the Pacific coast of Panama. Assignment of the new species to the “sublithistid” genus *Desmanthus* Topsent, 1893 followed after critical comparison of species of *Desmanthus* with *Lophacanthus rhabdophorus* Hentschel, 1912. In addition to ectosomal erect styles and a basal mass of undifferentiated desmas I, the new species share the possession of subectosomal desmas II provided with prominent outward-facing rhabdomes with *L. rhabdophorus*. However, desmas II with a less prominent but nevertheless clearly developed rhabdome were also discovered in the type species of *Desmanthus*, *D. incrustans* (Topsent, 1889). The alleged difference between the two genera appeared thus to be a matter of grade and a clear discriminatory character was found lacking. Accordingly, it is proposed to consider *Lophacanthus* a synonym of *Desmanthus*. The genus *Desmanthus* now contains six species, together occurring in all tropical regions as well as in the cooler waters of the Mediterranean (one species) and in South East Atlantic (one species). The latter species, *D. macphersoni* Uriz, 1989, has peculiar ectosomal spicules and is suspected to belong to a separate undescribed genus. The
higher taxa classification of Desanthidae is controversial because of lack of similarity to other lithistid groups and the inclusion by some authors of a second genus with characters similar to those of Desmanthus, i.e. Lithobubaris Vacelet, 1969. Type material of L. tenens and a Caribbean specimen assigned to the same species by Van Soest & Stentoft 1988 were studied to determine the degree of similarity with Desmanthus. L. tenens sensu Van Soest & Stentoft, 1988 was distinguished from L. tenens at the species level and a new species L. leviorum n. sp. was erected. The ordinal relationships of the genera Desmanthus and Lithobubaris are considered and various alternative positions are discussed, including Vacelet’s (1969) proposal to assign Lithobubaris to the halichondrid family Bubaridae. A tentative assignment of Desmanthus and Lithobubaris to a single family Desmanthidae Topsent, 1893 in the “lithistid” group of Anoplia is preferred pending further new data.

RÉSUMÉ
INTRODUCTION

The “sublithistid” sponges, i.e. those sponges with desmas that do not form a massive desma skeleton in combination with a prominent presence of normal megascleres, present a challenge for the classification of Demospongiae. The desmas are shared with several groups of mostly tetractinellid recent sponges and a much larger groups of fossil sponges. However, it is commonly accepted that desma-bearing sponges are polyphyletic and should be classed among desma-free orders and families. The normal megascleres of sublithistid sponges and their arrangement may form a clue to their affinities. The genus Desmanthus Topsent, 1893 is an example of a desma-bearing sponge demonstrating similarities with desma-free sponges through the possession and characteristic arrangement of the normal megascleres. Its species form thin encrustations with single styles erect on a basal mass of tetracrepid desmas, a feature which is closely similar to the arrangement in desma-free genera such as Bubaris Gray, 1867 and Monocrepidium Topsent, 1898, where the basal spicule mass is composed of vermiform diactinal spicules. Nevertheless, Topsent (1893) erected a family Desmanthidae in the order Lithistida, suborder Anoplia, for D. incrustans, because the notion that desma-bearing sponges may be polyphyletic had not yet developed at that time.

Hentschel (1912) erected a lithistid genus Lophacanthus for L. rhabdophorus which shared most of its morphological characters with Desmanthus, but possessed a special category of tetracrepid desmas with distinct cladome and rhabdome, interpreted as modified triaenes. Hentschel refrained from assigning this genus to family Desmanthidae in the order Lithistida, suborder Anoplia, for D. incrustans, because the notion that desma-bearing sponges may be polyphyletic had not yet developed at that time.

New species of Desmanthus

ABBREVIATIONS USED

MNHN Muséum national d’Histoire naturelle, Paris;
MNRJ Museo Nacional, University of Rio de Janeiro;
SMF Senckenberg Museum, Frankfurt;
ZMA Zoölogisch Museum, University of Amsterdam.

MATERIAL AND METHODS

Specimens studied are listed under the appropriate species headings.
Methods include the usual preparation of sections, spicule mounts and SEM following e.g. Lehnert & Van Soest 1996. Spicule dimensions are based on measurements of 25 spicules for each spicule category and for each specimen, unless otherwise indicated.

OBSERVATIONS

Comparison of desma shapes, position in the skeleton and sizes led to the conclusion that the seemingly clear-cut differences between Desmanthus and Lophacanthus, i.e. the occurrence in the latter of special rhabd-bearing desmas next to more normal shaped desmas, are transitional. The type specimen and other material of Desmanthus
incrustans was found to possess also two size categories of desmas, the larger of which often bear a small, weakly developed but nevertheless clearly present conical rhabd (Fig. 2A-D). This observation makes recognition of a genus Lophacanthus a matter of grade, and accordingly it is proposed here to consider Lophacanthus a junior synonym of Desmanthus.

The two new species described below are of the “Lophacanthus” type in possessing rather pronounced rhabd-bearing desmas, here dubbed desma II. All other species and specimens recorded under Desmanthus and Lophacanthus, as well as those of Lithobubaris have been reviewed, partly from study of original material, and brief descriptions of their morphological characters are given in a separate section below.

SYSTEMATICS

Family DESMANTHIDAE Topsent, 1893

DEFINITION. — Lithistida (?) forming thin, finely hispid encrustations. The skeleton consists of a basal mass of desmas upon which single monactinal spicules (styles and/or tylostyles) are disposed perpendicularly, heads located in the open spaces between interlocked desmas, points directed outward.

Genus Desmanthus Topsent, 1894

Lophacanthus Hentschel, 1912

TYPE SPECIES. — Aciculites incrustans Topsent, 1889 by subsequent designation (Topsent 1894).

DEFINITION. — Desmanthidae with desmas differentiated into two distinct types: basal desmas without unbranched rhabdome (desmas I) and peripherally located rhabdome-bearing desmas (II), rhabdomes pointing outward. Desmas are tetracrepid.

Desmanthus meandroides n. sp. (Fig. 1A-E)


Saco do Frade. Ilha de São Sebastião, São Paulo State, 23°55.3'S, 45°27.3', 24 m, 16.I.1996, coll. E. Hajdu (WDZUSP 148, 151 and 166), Schizotype from holotype ZMA POR13400.

ETYMOLOGY. — Named after the meandroid system of superficial canals.

DISTRIBUTION. — South East Brazil, encrusting on rocks, barnacles and polychaete tubes, in 7-24 m depth.

DESCRIPTION

Thinly encrusting specimens covering rocks and various calcareous substrates (e.g. polychaete tubes, barnacles, gastropods). The area covered may be larger than 200 cm². Live colour is an intense orange. Discrete subectosomal aquiferous channels clearly visible resulting in a very characteristic meandriform surface (Fig. 1A).

Skeleton

The surface is pierced by the numerous curved styles which stand erect on the substrate, heads in between the desmas II. No specialized ectosomal skeleton is apparent. Choanosomal skeleton composed of a basal layer of rhabdome-free desmas I forming an irregular interlocked mass with moderate zygosis. On top of this basal layer a further layer of desmas II is present (Fig. 1B). These desmas have their cladomes facing down, and the prominent rhabdomes pointing outwards to, but not reaching the sponge surface. The rhabdomes of the desmas II alternate with single erect styles.

Spicules

Smooth desmas I (Fig. 1D), relatively more branched and thinner than desmas II, dimensions: 155-291 × 5-6 μm. Smooth, more robust desmas II (Fig. 1C), with cladomes disposed in a concave manner, irregularly tuberculate, of similar dimensions, but with thicker branches, dimensions: 155-267 × 8-17 μm. Rhabdomes often slightly curved, most are smooth, but sometimes end in a crown of conules, dimensions: 49-204 × 10-30 μm. Smooth rather robust styles (Fig. 1E), slightly thicker at the base, with sharp point, most often slightly bent in the basal quarter. Very variable in size, but without distinct categories, dimensions: 126-834 × 8-10 μm.
Fig. 1. — **A–E**, *Desmanthus meandroides* n. sp.; **A**, habit of holotype, MNRJ 341, photographed *in situ*; **B**, from holotype, partly cleaned section of desma II skeleton showing forest of outward-pointing rhabdomes; **C**, from holotype, desma II showing prominent rhabdome; **D**, from holotype, desma I; **E**, from holotype, style; **F–I**, *Desmanthus levii* n. sp.; **F**, from holotype ZMA 13398, uncleaned section shown sideways. Arrows indicate desma II rhabdomes protruding into the surface membrane among the styles; **G**, from holotype, desma II showing prominent rhabdome and concave cladome; **H**, from holotype, desma I; **I**, from holotype, style (scale bar: bar shared with Fig. 1E = 100 µm). Scale bars: A, 1 cm; B–I, 100 µm.
Remarks

On account of the prominent rhabds, the new species is probably closest to *Desmanthus rhabdophorus* (Hentschel, 1912 as *Lophacanthus*) from eastern Indonesia and *D. levi* n. sp. from the East Pacific (cf. below). Differences are the size of desmas I (smaller in both other species, dimensions: respectively 150-160 µm and 87-112 µm) and the length of the rhabdome of desmas II (184-256 µm in *L. rhabdophorus* exceeding that of *D. meandroides* n. sp., and 78-116 µm in *D. levi* n. sp., clearly smaller on average than that of *D. meandroides* n. sp.).

This species is common in the São Sebastião area, SP, SE Brazil, where it occurs on semi-vertical walls exposed to good illumination.

*Desmanthus levi* n. sp.
(Fig. 1F-I)

Holotype. — NW side of Uva Island. W side of bay, Contreras Islands, Gulf of Chiriqui, Pacific coast of Panama, on boulders, 5 m, coll. W. H. de Weerdt, #12-XII-90-1-1 (ZMA POR13398).

Paratype. — NW side of Uva Island. Rocky Point, Contreras Islands, Gulf of Chiriqui, Pacific coast of Panama, on fishing net, 3 m, coll. W. H. de Weerdt, #10-XII-90-1-1 (on verongid) (ZMA POR13399).

Etymology. — Named in honor of Prof. Claude Lévi in recognition of a lifetime devoted to sponge biology.

Distribution. — Pacific coast of Panama, shallow water, 3-5 m.

Description

Thin crusts, up to 1 mm in thickness, covering up to 20-25 cm² in area (only a few cm² were collected). Colour bright orange. Surface smooth, fine-grained, no special markings were noted. Structure compact.

Skeleton

In dehydrated sections (Fig. 1F), the surface appears pierced by the numerous curved styles which stand erect between the rhabdomes of desmas II. Some styles may lie loosely, tangentially to the surface. The choanosomal skeleton is composed of a thin basal layer of desmas I with moderate zygosis. On top of this layer is a thick continuous layer or alternatively several layers of desmas II. The upper layer or most proximally situated desmas II have some of the rhabdomes (see arrows in Fig. 1F) protruding beyond the surface among the styles. All cladomes are facing down.

Spicules

Smooth desmas I (Fig. 1H), with thin multiply branched cladi, dimensions: 90-112 × 5-10 µm (n = 12). Smooth, more robust desmas II (Fig. 1G), with cladomes strongly concave and strongly tuberculate, dimensions: 94-136 × 12-20 µm. Rhabdomes conical and fairly straight, mostly smooth, dimensions: 47-141 × 15-23 µm. Smooth, curved, relatively thin styles (Fig. 1I), thicker at the base, with sharp points, most often slightly bent on the basal part, dimensions variable but in single size category, dimensions: 136-460 × 4-12 µm.

Remarks

This species resembles *D. rhabdophorus* (Hentschel, 1912 as *Lophacanthus*) and *D. meandroides* n. sp. in many morphological aspects, and it is likely they are closely related. Its specific characters are the distinctly smaller desmas I which are concentrated in an unusually thin layer at the base, and the rhabdomes of desmas II which are on average shorter than those of the other two species. In view of this, it is unlikely that *D. levi* n. sp. constitutes a disjunct population of either of these.

Comparison with other species of Desmanthidae

The following species described by previous authors are assigned to the family Desmanthidae. Their spicular characters are presented in Table 2.

*Desmanthus incrustans* (Topsent, 1889)
(Fig. 2A-F; Table 1)

*Aciculites incrustans* Topsent, 1889: 32.


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Fig. 2. — A-F. Desmanthus incrustans; A, overview of uncleaned section of the type specimen, MNHN D.T. 1853 showing styles and rhabdomes of desmas II (arrows) protruding through the organic ectosome; B, detail of Fig. 2A showing the protruding rhabdomes of desmas II; C, Bonaire specimen ZMA 8491, desma II; D, Bonaire specimen ZMA 8491, desma II; E, Bonaire specimen ZMA 8491, desma I; F, Bonaire specimen ZMA 8491, style; G-H, Desmanthus topsenti, from type specimen SMF 1560; G, desma II; H, desma I.

Scale bars: A, B, F-H, 100 µm; C-E, 10 µm.
**Table 1.** — Spicule sizes (µm) reported for *Desmanthus incrustans*.

<table>
<thead>
<tr>
<th>Reference</th>
<th>Desmas I cladome</th>
<th>Desmas II cladome</th>
<th>Desmas II rhabdome</th>
<th>Styles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Topsent 1889 (Caribbean)</td>
<td>not recorded</td>
<td>not recorded</td>
<td>not recorded</td>
<td>300-400</td>
</tr>
<tr>
<td>Kobluk &amp; Van Soest 1989 (Caribbean)</td>
<td>100-140</td>
<td>70-120</td>
<td>20-30</td>
<td>340-510 × 3.5-8</td>
</tr>
<tr>
<td>Topsent 1894</td>
<td>not recorded</td>
<td>not recorded</td>
<td>not recorded</td>
<td>330-1000 × 13-25</td>
</tr>
<tr>
<td>Pulitzer-Finali 1970 (Mediterranean)</td>
<td>not recorded</td>
<td>up to 200</td>
<td>not recorded</td>
<td>370-1100 × 15-26</td>
</tr>
<tr>
<td>Pouliquen 1972 (Mediterranean)</td>
<td>not recorded</td>
<td>not recorded</td>
<td>not recorded</td>
<td>280-1100 × 10-30</td>
</tr>
<tr>
<td>Vacelet et al. 1976 (Indian Ocean)</td>
<td>not recorded</td>
<td>100</td>
<td>80-175 × 20-30</td>
<td>300-550 × 10-20</td>
</tr>
<tr>
<td>Pulitzer-Finali 1983 (Mediterranean)</td>
<td>80-130</td>
<td>not recorded</td>
<td>not recorded</td>
<td>300-560 × 8-26</td>
</tr>
<tr>
<td>Lévi &amp; Lévi 1989 (Philippines)</td>
<td>not recorded</td>
<td>300-400</td>
<td>110 × 30</td>
<td>350-1100 × 30</td>
</tr>
<tr>
<td>Pulitzer-Finali 1996 (Papua New Guinea)</td>
<td>240</td>
<td>not recorded</td>
<td>70-150 × 15-30</td>
<td>180-300 × 9-16</td>
</tr>
</tbody>
</table>

**Table 2.** — Spicule dimensions (µm) reported for all Desmanthidae species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Desmas I cladome</th>
<th>Desmas II cladome</th>
<th>Desmas II rhabdome</th>
<th>Styles</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Desmanthus incrustans</em></td>
<td>100-240</td>
<td>70-400 × 15-30</td>
<td>20-30 × 10-30</td>
<td>180-1100 × 3.5-30</td>
</tr>
<tr>
<td><em>Desmanthus macphersoni</em></td>
<td>not present ?</td>
<td>330-490</td>
<td>120-170 × 35-45</td>
<td>440-2750 × 28-60</td>
</tr>
<tr>
<td><em>Desmanthus meandroides</em> n. sp.</td>
<td>155-291 × 5-6</td>
<td>155-267 × 8-17</td>
<td>49-204 × 10-30</td>
<td>126-834 × 8-10</td>
</tr>
<tr>
<td><em>Desmanthus levi</em> n. sp.</td>
<td>90-112 × 5-10</td>
<td>94-136 × 12-20</td>
<td>47-141 × 15-23</td>
<td>131-460 × 4-12</td>
</tr>
<tr>
<td><em>Desmanthus rhabdophorus</em></td>
<td>150-160 × 15</td>
<td>104-192</td>
<td>184-256 × 25-30</td>
<td>264-640 × 7-16</td>
</tr>
<tr>
<td><em>Desmanthus topsenti</em></td>
<td>240-270 × 19-25</td>
<td>200-310 × 30-45</td>
<td>not recognizable</td>
<td>224-1000 × 14-31</td>
</tr>
<tr>
<td><em>Lithobubaris leviorum</em> n. sp.</td>
<td>200-300 × 15-35</td>
<td>not present</td>
<td>not present</td>
<td>up to 1500 × 48-63</td>
</tr>
<tr>
<td><em>Lithobubaris tenens</em></td>
<td>150-200 × 20-35</td>
<td>not present</td>
<td>not present</td>
<td>1250-3000 × 45-60</td>
</tr>
</tbody>
</table>

* Possibly a complex of several closely similar species.

**DISTRIBUTION.** — Caribbean (Banc Campêche, Bonaire), apparently also in the Mediterranean and the Indian and Pacific Oceans, but these records need critical re-examination. From Table 2 containing spicule sizes reported for various records of the species, it is clear that these are longer and more robust in samples described outside the Caribbean. Kobluk & Van Soest (1989) suggested the Indian Ocean specimens could be *Desmanthus topsenti*, rather than *D. incrustans*. Pulitzer-Finali’s (1996) from Papua New Guinea is probably referable to *D. rhabdophorus* in view of the large rhabdomes of desmas II figured by this author.

**ECOLOGY.** — In deep-reef habitats and caves, 12-30 m.

**DESCRIPTION**

Thinly encrusting, following the contours of the substrate, thickness usually less than 1 mm, lateral size 2 × 1 cm. Pale or darker yellow in colour. Surface strongly hispid due to the numerous projecting styles (Fig. 2A). In between the styles piercing the surface, there are occasional low pro-
trusions of rhabdomes of desmas II (see black arrows in Fig. 2A and detail in Fig. 2B).

**Skeleton**
The usual arrangement of basal desmas upon which single styles are erected. Desmas II, distinguished primarily on their more robust shape, appear to have a peripheral position in accordance with those of the species described above. Desmas I make up the layer at the base.

**Spicules**
Desmas I with thinly branched cladi (Fig. 2E), dimensions: 100-140 µm. Desmas II (Fig. 2C-D), slightly smaller but more robust, mostly with a vestigial rhabdome only, dimensions: 70-120 µm, with rhabdome 10-30 µm. Styles (Fig. 2F) curved at the base, dimension: 300-400 µm in length in the type, 340-510 × 3.5-8 µm in Bonaire specimens.

**REMARKS**
Several specimens were examined, including a slide from the type and specimens from Bonaire. The rhabdomes of the desmas II are clearly present although considerably shorter than those of the species described above. Nevertheless, both desma types are recognizable and appear to be arranged similarly as in the previously described specimens. This constitutes the main evidence for the synonymy of *Desmanthus* and *Lophacanthus*.

**Desmanthus topsenti** Hentschel, 1912

(Fig. 2G, H)

**Holotype.** — Aru Islands. Stn 77, Merton coll. (SMF 1560).

**Distribution.** — Aru Islands (eastern Indonesia), on rocks at 20 m.

**Description**
Thinly encrusting, about 0.5 mm thick and 1.7 cm long. Surface hispid. Colour grey or brownish grey in alcohol. Structure compact.

**Skeleton**
The main skeleton consists of an irregular layer of desmas on which monactinal spicules are erected.

**Spicules**
Desmas which can be separated in basally arranged smaller desmas (Fig. 2H), presumably desmas I, with more tuberculate cladi, dimensions: 240-270 × 20 µm, and peripherally arranged more robust desmas (Fig. 2G), presumably desmas II, dimensions cladome: 200-310 × 30-45 µm. They are not clearly separated morphologically and the larger desmas lack a distinct rhabdome. Monactinal spicules are styles and rhabdostyles, variable in form, size and curvature, the smaller sizes tend to be rhabdostyles, dimensions: 224-1000 × 14-31 µm.

**Remarks**
Hentschel (1912) states that this species differs from *D. incrustans* mainly in the absence of clear rhabdomes in the desmas. A syntype specimen from the Senckenberg Museum was re-examined (SMF 1560, from stn 77 of the Merton collection described by Hentschel). The rhabdomes are certainly inconspicuous, but nevertheless there is a clear division in thinner and more robust desmas. So far no other specimens of this species have been recorded, but it is possible that some of the Indian Ocean records of *D. incrustans* are referable to this species.

**Desmanthus rhabdophorus** (Hentschel, 1912) n. comb.


**Material examined.** — None.

**Distribution.** — Aru Islands (eastern Indonesia), on stones at 8-16 m; S Korea; possibly Papua New Guinea.

**Description**
Encrusting, 1 mm in thickness, 9.5 cm in widest expansion. Colour grey-white or bluish grey. Surface hispid.

**Skeleton**
A thin basal layer of desmas I on top which there is a relatively prominent layer of tightly inter-
locked desmas II. Basally curved styles are lodged head-first in the space between neighbouring desmas and their shafts are obscured by the prominent rhabds of the desmas II.

Spicules

REMARKS
Sim et al. (1990) recorded this species from Cheju Island, S Korea. The spicule sizes were reported to be considerably larger than those of the type, dimensions : desmas I: 173-287 × 20-27 µm, desmas II: 226-300 × 11-27 µm and styles 639-865 × 3-20 µm. This is treated as infraspecific variation until further data will become available.

Desmanthus (?) macphersoni Uriz, 1988

MATERIAL EXAMINED. — None.

DISTRIBUTION. — Namibia, on rocks in deeper water, 160 m.

DESCRIPTION
Thinly or thickly encrusting sponge covering extensions of up to 25 cm² on rock, and attaining a thickness of 8 mm. Consistency stony. Surface extremely hispid, traversed by grooves acting as surface current channels. Oscules 1-1.5 mm in diameter, usually located at the confluence of two subectosomal canals. Colour translucent grayish blue in life, cream in alcohol.

Skeleton
Ectosome conspicuous, easily detachable where it lines the subectosomal aquiferous canals. Densely packed with tangential, triactinal desmas. Choanosomal skeleton composed of several overlapping layers of fused, tetracrepid desmas (II) with the cladi pointing towards the substratum and the rhabdome pointing upwards. Curved styles with the head resting on the upper layer of desmas, piercing the ektosome perpendicularly.

Spicules

REMARKS
The description of Uriz (1988) mentions rhabds in both desma types, which are differentiated apparently mostly in size, the peripheral ones being smallest. The latter are also packed in the ectosomal region which is distinctly different from the arrangement in e.g. D. meandroides n. sp. Moreover, these ectosomal “desmas” do not appear to be proper desmas. Judging from the excellent illustrations provided by Uriz, they resemble large microscleres dubbed acanthamphiasters (Wiedenmayer 1994), such as found in e.g. Alectona (Hadromerida, Clionidae). Further examination is necessary to determine whether these spicules are really proper to the sponge; if so then it probably belongs to an undescribed genus. This suggestion is strengthened by the large size of the styles which is unusual for the genus Desmanthus. The presence of acanthamphiaster-like spicules in an otherwise obviously desmanthid sponge would provide a distinct clue to the affinities of the family (cf. below).

Genus Lithobubaris Vacelet, 1969

Diagnosis. — Desmanthidae (?) with large, stout styles (over 1000 µm long) and interlocked basal mass of desmas. Desmas monocrepid with special style-encircling branches.

Lithobubaris tenens Vacelet, 1969 (Fig. 3A)

MATERIAL EXAMINED. — Holotype, Cassidaigne, 250 m (MNHN DJV 7).

DISTRIBUTION. — Western Mediterranean, encrusting corals at 250 m.
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FIG. 3. — A, Lithobubaris tenens, from type specimen MNHN DJV 7, styles encircled by desmas (arrows); B-C, Lithobubaris leviorum n. sp., from holotype; B, broken desma showing tuberculated surface and hole in which style head is lodged; C, detail of desma hole; D, Monocrepidium vermiculatum, overview of surface and basal mass of vermiform spicules. Photo J. Vacelet. Scale bars: A, B, D, 100 µm; C, 10 µm.
DESCRIPTION
Thin, small, circular crusts of 1-2 cm diameter, whitish in alcohol. Protruding styles make the surface look hairy.

Skeleton
A basal crust of monocrepid desmas of 300 µm thickness, difficult to separate from the substrate. Styles long and robust, their heads encircled by the branches of the desmas (arrows in Fig. 3A).

Spicules
Apparently monocrepid desmas with outgrowths proliferated to form circular holes, smooth but provided with tubercles and swellings, dimensions: 200-300 µm in diameter with branches 15-35 µm in thickness. Styles: long straight or curved at the blunt end, robust, dimensions: 1250-3000 × 45-60 µm.

REMARKS
The species was recorded also from the Caribbean (Van Soest & Stentoft 1988), but spicule sizes in this specimen differ so much that conspecificity is now judged to be unlikely. Accordingly, this material is described as a new species below.

Lithobubaris leviorum n. sp.
(Fig. 3B, C)

Lithobubaris tenens – Van Soest & Stentoft 1988: 72, fig. 35 (not: L. tenens Vacelet, 1959)

HOLOTYPE. — Off Paynes Bay. Barbados, 216 m (ZMA POR5265).

ETYMOLOGY. — Named after Claude and Pierrette Lévi in recognition of their contributions towards the elucidation of deep-water sponges.

DISTRIBUTION. — Barbados, Caribbean, encrusting dead lithistids and corals in deep water.

DESCRIPTION
Thinly encrusting, round patches on dead corals and lithistid remains, appearing as a “hairy” crust; size several cm². Colour (dry) grey.

Skeleton
Huge single styles erect on a basal interlocked mass of desmas which overlies the substratum. Desmas arranged loosely, zygois not well-developed. Style bases fit into the circular outcrops of branches of the desmas.

Spicules
Desmas with circular side holes (Fig. 3B, C), covered with smoothly rounded swellings and tubercles, dimensions: diameter of desma 150-200 µm, thickness of branches 20-35 µm, diameter of holes 50-60 µm. Styles, robust, dimensions: only up to 1500 µm in length and 48-63 µm in thickness.

REMARKS
The Barbados specimen differs clearly from Mediterranean L. tenens in the size of the styles which are about half as short in the longest sizes. In view of the geographic separation it is likely the Caribbean material represents a separate species.

DISCUSSION
This comparative study of “sublithistid” sponges with styles arranged singly on a basal layer of desmas reveals a number of conflicting aspects which prevents a firm conclusion over their affinities. The position taken in this study, i.e. assignment of treated taxa to two genera of a single family associated with “lithistids” s.l., can be defended on the following arguments:

The morphological similarities of all these sponges are a basal mass of weakly interlocked desmas in combination with styles anchored in peripheral perpendicular position, producing a uniformly hispid surface. Among the lithistids s.l. this is a unique feature and to assume two or more separate independent developments towards such a skeleton in the absence of firm contradictory evidence violates principles of parsimony. The fact that the desmas are tetracrepid in one genus and monocrepid in the other is not unusual, since both types of desmas occur among broad lithistid assemblages unrelated to recent scheme of higher taxa classification. Since tetracrepid desmas are presumably derived from a tetractine spicule, it is reasonable to assume that the Desmanthidae are of tetractinellid stock. The tetractinellid origin of
Desmanthus is perhaps strengthened by the synonymy with Lophacanthus, here proposed. The desma II morphology can be explained as directly derived from triaenes. Several lithistid families have ectosomal triaenes with proliferated or disc-shaped cladomes (phyllothriaenes, discotriaenes) which may be easily derived from dichotriaenes, which occur in both lithistid and non-lithistid sponges. The desma II of Desmanthus could also be assumed to derive from a dicho- or phyllotriaene spicule, thus firmly establishing the link with non-lithistid astrophorid families. However, the homology of the desma II with those triaenes is compromised by the orientation of their rhabdomes, which is the perpendicular position.

The desma II morphology can be explained as directly derived from dichotriaenes, which are assumed to have originated independently. This classification seems less parsimonious because the obvious morphological similarities of Desmanthus and Lithobubaris are assumed to have originated independently.

A third alternative would be the assignment of the whole of Desmanthidae with the presently proposed contents to the order Halichondrida as a sister-group to Bubaridae. Members of that family (Bubaris, Monocrepidium, Skeizia, Cerbaris, Hymerhabdia) possess a similar form and architecture in having a mass of crooked or curved megascleres in contact with the substrate upon which single styles are erected, points out and with their base embedded in the basal spicule mass. The crooked or curved spicules are clearly monaxonic and do not take the form of desmas, hence merging of the families is unwarranted. Bubaridae appear also linked to certain Axinellidae genera such as Acanthella, Auletta and Phakellia, which possess sinuously curved megascleres. One major objection exists to this proposal, i.e. the undoubtedly tetracrepid nature of the Desmanthus desmas, suggesting a tetractinal origin. However, there are examples of tetractine spicules in untested ceractinomorph sponges, in raspailiid Gymnactis and Triientorion. It is conceivable that Desmanthus desmas derived from tetractines originated independently in halichondrid sponges. Further support is found in the fact that not a single truly tetractinellid sponge (i.e. belonging to the order Astrophorida or to triaene-bearing lithistids) possesses a complement of smooth curved styles in perpendicular position.

On the other hand, however, the skeletal architecture of Lithobubaris (and Desmanthus) may look similar to that of some Bubaridae, but among ceractinomorph sponges there are many comparable structures in unrelated sponge groups: e.g. leptoclathrid...
condition in Microcionidae, hymedesmioid condition in Hymedesmiidae, in which thinly encrusting sponges possess single erect monactinal spicules often protruding through the surface membrane with their pointed ends. This condition is apparently easily acquired independently, and the structure itself may not be a reliable indicator of affinity.

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