

# 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

## KEY WORDS

Porifera,  
sublithistid,  
*Desmanthus*,  
*Lophacanthus*,  
*Lithobubaris*,  
new species.

higher taxa classification of Desmanthidae 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

*Espèces nouvelles de Desmanthus (Porifera, Demospongiae) avec discussion sur les affinités du genre.*

*Desmanthus meandroides* n. sp. est décrit de São Sebastião, sud-ouest du Brésil et *D. levii* n. sp. de la côte Pacifique de Panama. L'allocation des nouvelles espèces au genre de « sublithistides » *Desmanthus* Topsent, 1893 résulte d'une comparaison critique des espèces de *Desmanthus* avec *Lophacanthus rhabdophorus* Hentschel, 1912. Les nouvelles espèces ont en commun avec *L. rhabdophorus* la possession de desmes II subectosomiques pourvus de rhabdomes dépassant vers l'extérieur, en plus de styles ectosomiques dressés et d'une masse basale de desmes indifférenciés. Cependant, des desmes II avec un rhabdome moins proéminent mais néanmoins nettement développé ont été aussi découverts dans l'espèce type de *Desmanthus*, *D. incrustans* (Topsent, 1889). La différence invoquée entre les deux genres apparaît ainsi être une question de degré et on n'a pas trouvé de caractère clairement discriminant. En conséquence, on propose de considérer *Lophacanthus* comme un synonyme de *Desmanthus*. Le genre *Desmanthus* inclut maintenant six espèces, réparties dans toutes les régions tropicales ainsi que dans les eaux plus froides de la Méditerranée (une espèce) et de l'Atlantique Sud-Est (une espèce). Cette dernière, *D. macphersoni* Uriz, 1989, a des spicules ectosomiques particuliers et pourrait appartenir à un genre différent non décrit. La classification des Desmanthidae à un niveau plus élevé est sujette à controverse en raison du manque de similitude avec les autres groupes de lithistides et l'inclusion par quelques auteurs d'un second genre avec des caractères semblables à ceux de *Desmanthus*, *Lithobubaris* Vacelet, 1969. Le matériel-type de *L. tenens* et un spécimen caraïbe attribué à la même espèce par Van Soest & Stentoft 1988, ont été examinés pour déterminer leur degré de similitude avec *Desmanthus*. *Lithobubaris tenens* sensu Van Soest & Stentoft, 1988 est distinct de *L. tenens* au niveau spécifique et une nouvelle espèce, *L. leviorum* n. sp., est proposée. Les relations des genres *Desmanthus* et *Lithobubaris* au niveau de l'ordre sont examinées et diverses positions possibles sont discutées, y compris la proposition de Vacelet (1969) d'attribuer *Lithobubaris* à la famille Bubaridae dans les halichondrides. Dans l'attente de nouvelles données, on préfère l'attribution provisoire de *Desmanthus* et de *Lithobubaris* à une seule famille Desmanthidae Topsent, 1893 dans le groupe de « lithistides » Anoplia.

### MOTS CLÉS

Porifera,  
sub-lithistides,  
*Desmanthus*,  
*Lophacanthus*,  
*Lithobubaris*,  
espèces nouvelles.

## 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, but it is obviously similar to *Desmanthus* in its possession of single styles erect on the basal mass of desmas. This similarity induced Pulitzer-Finali (1996) to synonymize *L. rhabdophorus* with *D. incrustans*, implicitly making *Lophacanthus* a junior synonym.

The similarities of *Desmanthus* and *Lophacanthus* with *Bubaris* and *Monocrepidium* may be interpreted as indication of close relationship, and further evidence of that is the existence of the genus *Lithobubaris* Vacelet, 1969, which combines a

similar skeleton with rather peculiarly shaped, apparently monocrepid, desmas of which outgrowths form rounded holes into which the bases of the styles fit tightly. Vacelet, on the basis of the resemblance to *Bubaris*, assigned *Lithobubaris* to the axinellid family Bubaridae, but left *Desmanthus* among the Lithistida. Van Soest & Stentoft (1988) assigned Caribbean specimens of *Lithobubaris* to Vacelet's species *L. tenens* and decided that this fits better in the lithistid family Desmanthidae.

Thus there are opposing views for the affinities of *Desmanthus*, *Lophacanthus* and *Lithobubaris*. Discovery of two new species of Desmanthidae, which will be described below, induced us to review all species of *Desmanthus*, *Lophacanthus* and *Lithobubaris*, and to reconsider the phylogenetic position of these “sublithistid” sponges.

### ABBREVIATIONS USED

- MNHN Muséum national d'Histoire naturelle, Paris;  
 MNRJ Museo Nacional, University of Rio de Janeiro;  
 SMF Senckenberg Museum, Frankfurt;  
 ZMA Zoologisch 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)

HOLOTYPE. — **Celada**. Baía de Castelhanos, Ilha de São Sebastião, São Paulo State, 23°50.3'S, 45°14.6'W, c. 7 m, 25.I.1996, coll. E. Hajdu and G. Muricy (MNRJ 341).

PARATYPES. — **Saco da Serraria**. Ilha de São Sebastião, São Paulo State, 23°48.5'S, 45°14.5'W, 13 m, 11.I.1996, coll. E. Hajdu (MNRJ 109, 114 and 119).

**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 cm<sup>2</sup>. 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.

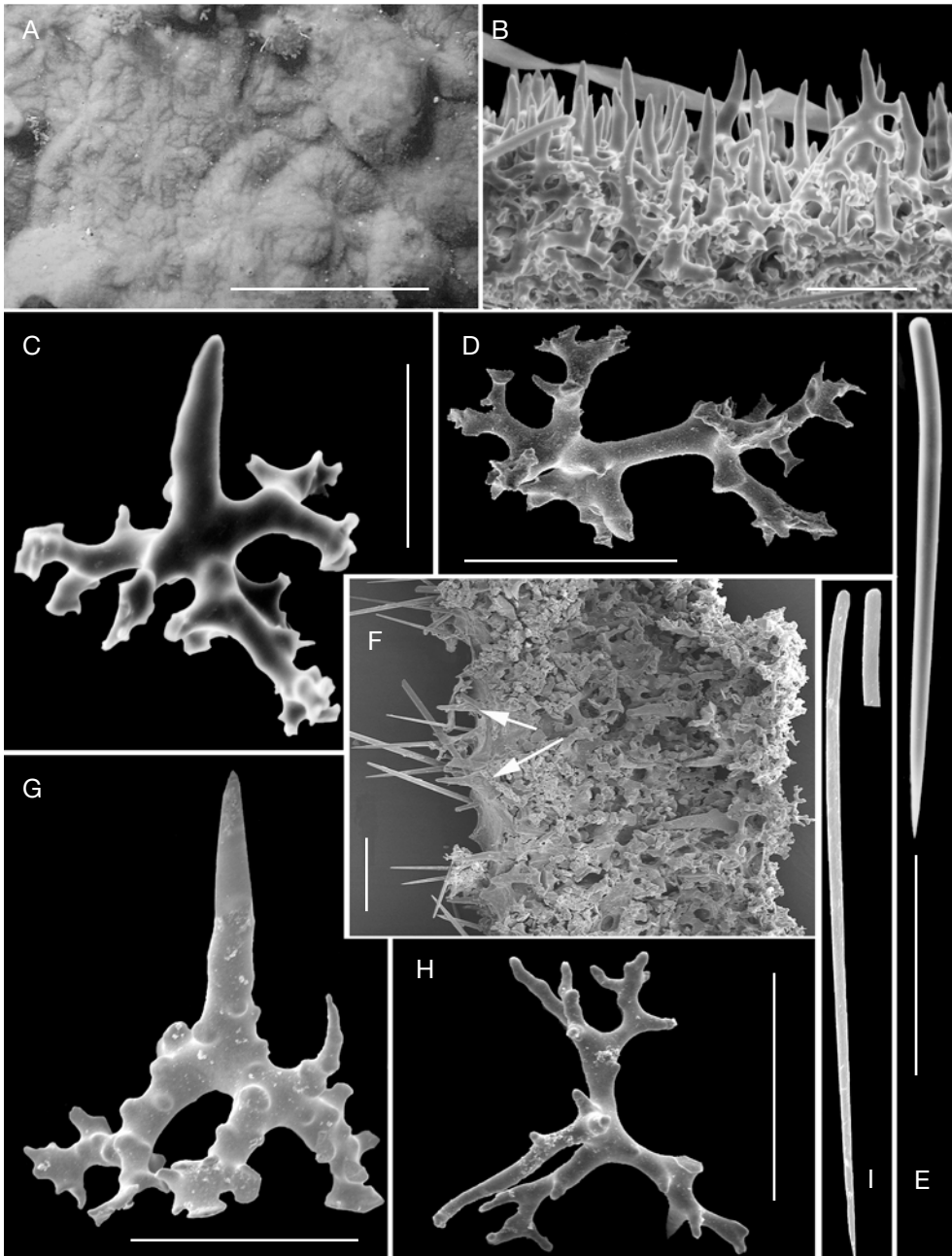


FIG. 1. — **A-E**, *Desmanthus meandroides* n. sp.; **A**, habit of holotype, MNRJ 341, photographed *in situ*; **B**, from holotype, partly cleaned section of desma II skeleton showing forest of outward-pointing rhabdomes; **C**, from holotype, desma II showing prominent rhabdome; **D**, from holotype, 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  $\mu$ m). Scale bars: A, 1 cm; B-I, 100  $\mu$ m.

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. levii* 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. levii* 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 levii* 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 Weerd, #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 Weerd, #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 cm<sup>2</sup> in area (only a few cm<sup>2</sup> 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 zygos. 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. levii* 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.

*Desmanthus incrustans* – Kobluk & Van Soest 1989: 1212.

HOLOTYPE. — Banc de Campêche. Caribbean Mexico, Bonaire, all from reef cavities, 12-30 m, 1984, coll. D. R. Kobluk (MNHN DT 1853) (ZMA POR8491, 8492, 8493).

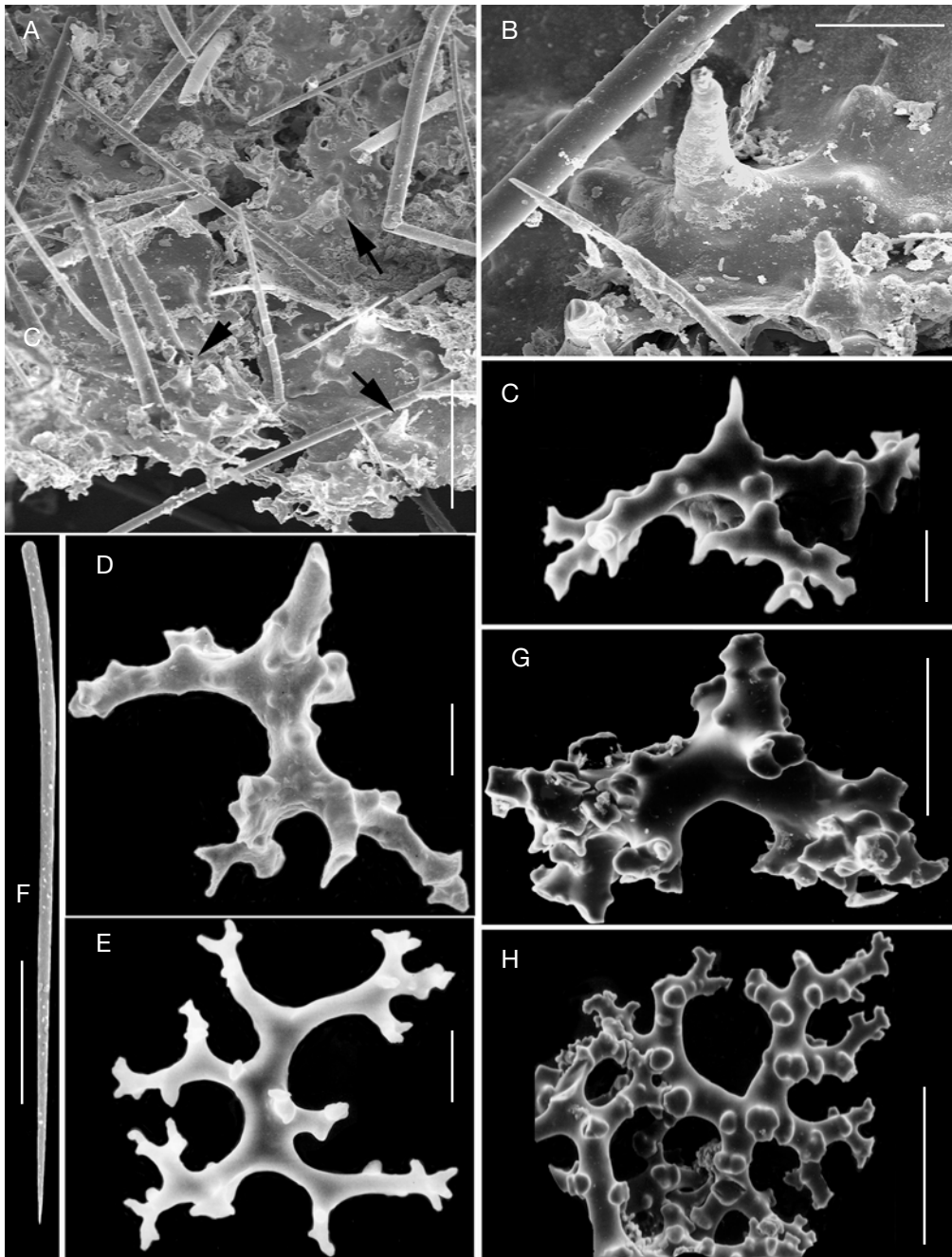


FIG. 2. — **A-F**, *Desmanthus incrustans*; **A**, overview of uncleaned section of the type specimen, MNHN D.T. 1853 showing styles and rhabdomes of desmas II (arrows) protruding through the organic ectosome; **B**, detail of Fig. 2A showing the protruding rhabdomes of desmas II; **C**, Bonaire specimen 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  $\mu$ m; C-E, 10  $\mu$ m.

TABLE 1. — Spicule sizes ( $\mu\text{m}$ ) reported for *Desmanthus incrustans*.

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

TABLE 2. — Spicule dimensions ( $\mu\text{m}$ ) reported for all Desmanthidae species.

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

\* 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  $\times$  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  $\mu\text{m}$ . Desmas II (Fig. 2C-D), slightly smaller but more robust, mostly with a vestigial rhabdome only, dimensions: 70-120  $\mu\text{m}$ , with rhabdome 10-30  $\mu\text{m}$ . Styles (Fig. 2F) curved at the base, dimension: 300-400  $\mu\text{m}$  in length in the type, 340-510  $\times$  3.5-8  $\mu\text{m}$  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  $\times$  20  $\mu\text{m}$ , and peripherally arranged more robust desmas (Fig. 2G), presumably desmas II, dimensions cladome: 200-310  $\times$  30-45  $\mu\text{m}$ . 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  $\times$  14-31  $\mu\text{m}$ .

#### 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.

*Lophacanthus rhabdophorus* Hentschel, 1912 : 306, pl. XVIII, fig. 1. — Sim *et al.* 1990: 126, pl. 5, figs 1-2.

? *Desmanthus incrustans* sensu Pulitzer-Finali, 1996: 105, fig. 4.

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*

Desmas I smooth with relatively thin cladi, dimensions: 150-160 × 15 µm. Desmas II robust with prominent rhabdome, cladome 104-192 µm, rhabdome, dimensions: 184-256 × 25-30 µm. Styles smooth, mostly with slightly curved blunt end, of widely variable size: 264-640 × 7-16 µm.

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 cm<sup>2</sup> 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 ectosome perpendicularly.

*Spicules*

Basal, tetracrepid desmas II with irregularly branching, tuberculate cladi and a short rhabdome, dimensions cladome: 330-490 µm; rhabdome, dimensions: 120-170 × 35-45 µm. Ectosomal desmas (?), highly tuberculate, with lightly spined tubercles, dimensions: 80-190 µm. Styles, very large, variably curved, sharp apex, dimensions: 440-2750 × 28-60 µm.

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.

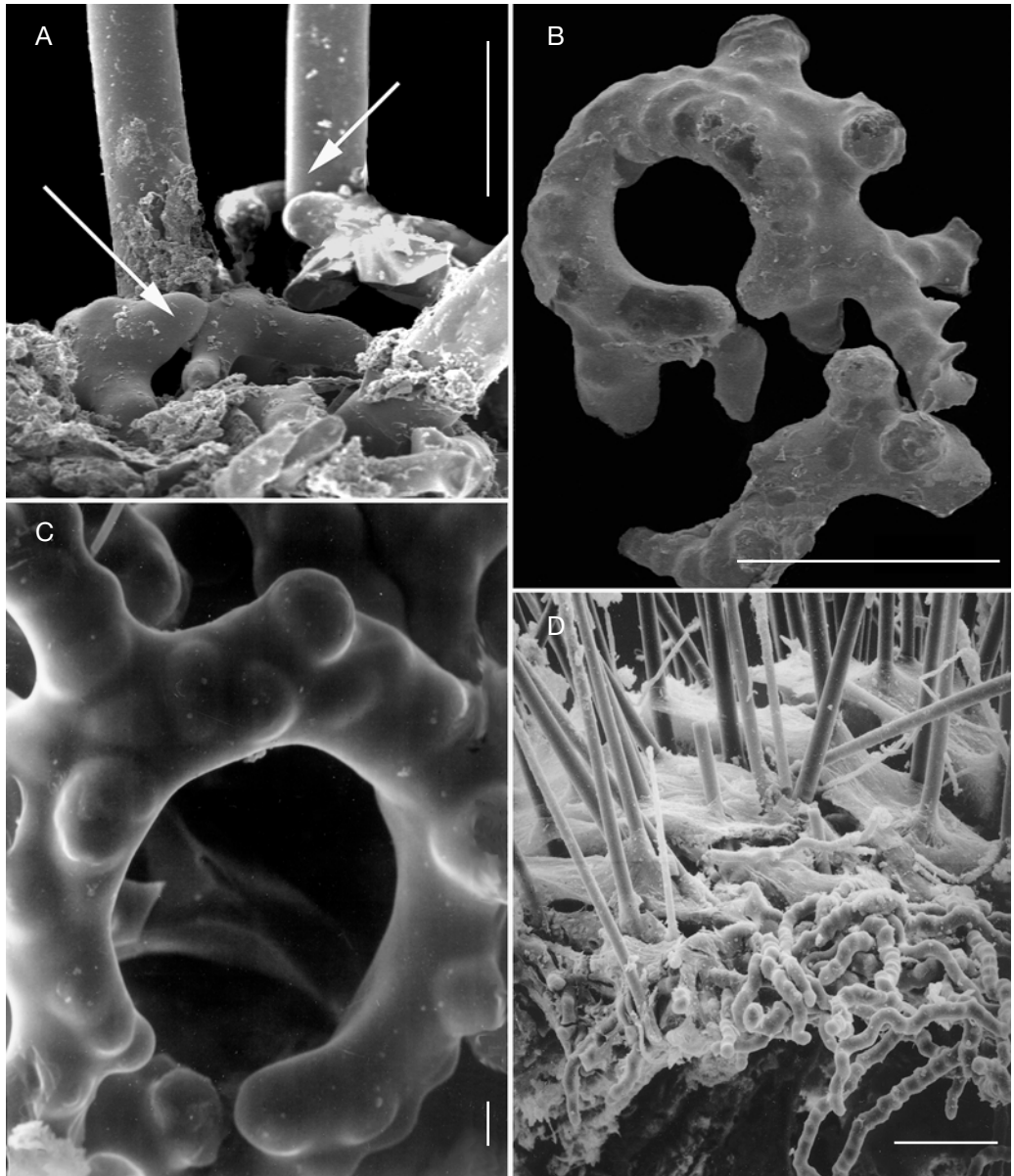


FIG. 3. — **A**, *Lithobubaris tenens*, from type specimen MNHN DJV 7, styles encircled by desmas (arrows); **B-C**, *Lithobubaris leviorum* n. sp., from holotype; **B**, broken desma showing tuberculated surface and hole in which style head is lodged; **C**, detail of desma hole; **D**, *Monocrepidium vermiculatum*, overview of surface and basal mass of vermiform spicules. Photo J. Vacelet. Scale bars: A, B, D, 100  $\mu$ m; C, 10  $\mu$ m.

#### 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 cm<sup>2</sup>. Colour (dry) grey.

#### *Skeleton*

Huge single styles erect on a basal interlocked mass of desmas which overlies the substratum.

Desmas arranged loosely, zygosis 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 (phyllotriaenes, 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 opposite of that of almost all triaenes both in lithistids and in non-lithistids. In all these, perhaps with the exception of *Kaliapsis incrustans* (Lithistida, Theonellidae, cf. Vacelet *et al.* 1976), the rhabdomes are invariably facing inwards, with the cladomes carrying the ectosomal skeleton and microscleres. Monocrepid spicules – if the *Lithobubaris* desmas are indeed monocrepid – presumably derived from monaxones, but these occur widely in both tetractinellids and ceractinomorpha, so their significance as a clue for the affinity of *Lithobubaris* seems low. To further narrow down the affinities of Desmanthidae appears to be problematic, since no other “lithistid” family seems morphologically close. Much will depend of further study of the enigmatic spicules found in *Desmanthus macphersoni*. Possibly, these will connect Desmanthidae with non-lithistid *Alectona*, at present classed among the Hadromerida, but with suspected tetractinellid affinities.

For the time being and by elimination the anoplid family Siphonidiidae may be indicated as a possible sister-group of Desmanthidae, because some of its genera (*Siphonidium*, *Gastrophanella*) possess monactinal ectosomal megascleres in perpendicular position.

An alternative classification has been adopted by Vacelet (1969). He pointed out the similarities between *Lithobubaris* and bubarid genera *Monocrepidium* and *Bubaris*. These genera do not possess desmas, but they have peculiar vermiform spicules arranged in a basal mass, upon which single styles are positioned in perpendicular position. Since *Lithobubaris* desmas are monocrepid, and their undulating, smoothly tuberculate branches

(Fig. 3C) are reminiscent of these vermiform spicules, especially those of *Monocrepidium* (Fig. 3D), Vacelet assigned *Lithobubaris* to Bubaridae (now recognized as belonging to the order Halichondrida). Because the tetracrepid desmas of *Desmanthus* were judged to be evidence of tetractinellid affinities, *Desmanthus* was retained in a “lithistid” family Desmanthidae. A further argument to support this position is the presence in the order Halichondrida of another genus of “sublithistid” sponges possessing monocrepid desmas, i.e. *Petromica* (currently considered a member of the family Halichondriidae). In the absence of definite independent support, 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*, *Hymnerhabdia*) 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 uncontested ceractinomorph sponges, in raspailiid *Cyamon* and *Trikenrion*. 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 Hymedesmidae, 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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