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LISSODENDORYX SPECIES OF THE INDO-MALAYAN ARCHIPELAGO (DEMOSPONGIAE: POECILOSCLERIDA)

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ABSTRACT

A brief history of the genus *Lissodendoryx* Topsent, 1892 is given and the Indo-Malayan representatives are described based on material collected by the Siboga Expedition (1899-1900) and the Indonesian-Dutch Snellius II Expedition (1984-1985), on reexamination of previously described specimens from the area, and on the literature. Previously, ten species assigned to *Lissodendoryx* were reported from this area. Two of these, *L. baculata* Topsent, 1897 and *L. tawiensis* Wilson, 1925, do not conform to the presently employed definition of the genus *Lissodendoryx*. One, *L. sinensis* Brøndsted, 1934, is considered a junior synonym of *L. ternatensis* (Thiele, 1903). *L. grata* (Thiele, 1903) is a valid species of *Lissodendoryx*, with *L. oxytes* De Laubenfels, 1954 of the adjacent Palau Islands as a junior synonym. Indo-Malayan records of *L. isodictyalis* (Carter, 1882) appear to belong to one of the other described species and it is now no longer considered a member of the Indo-Malayan fauna. *L. paucispinata* (Ridley & Dendy, 1886) is a further Indo-Malayan species of the genus. The species variously known as *Halichondria aspera* Bowerbank, 1875, and *Crella, Damiria* or *Damiriana schmidti* sensu Ridley, 1884 is here assigned to *Lissodendoryx*, its name being established as *L. aspera*. Unpublished material of the Siboga and Snellius II expeditions contained six species of the genus, viz. *L. aspera, L. similis* Thiele, 1903, *L. grata, L. ternatensis, L. timorensis* n.sp., and *L. microchelifera* n.sp. This brings the total number of Indo-Malayan *Lissodendoryx* species to seven. A key to the species of the Indo-Malayan area is provided. Several of the species appear to be endemic to the Indo-Malayan area, others have a more widespread occurrence over the Indo-West Pacific region.

INTRODUCTION

The marine sponge genus *Lissodendoryx* Topsent, 1892 (Demospongiae: Poecilosclerida) is recorded from most oceans and seas. The total number of nominal species found in the literature is 80. Only 31 of these conform to a restricted definition of *Lissodendoryx* (cf. below). In this paper a taxonomic review of the Indo-Malayan *Lissodendoryx* species is given based on an analysis of

material recently collected during the Snellius II Expedition, of older unpublished material of the Siboga Expedition, of specimens previously described from the area, and of descriptions in the literature. Until now descriptions of the Indo-Malayan sponge fauna are scattered. Major publications on the Indo-Malayan sponge fauna are: Topsent (1897), revised by Desqueyroux-Faundez (1981), Kieschnick (1896, 1900), Lindgren (1898), Thiele (1899, 1903), Hentschel (1912), Brøndsted (1929, 1934). Recently (Van Soest, 1989, 1990) renewed attention was given to the sponges of Indonesia. In a status report on the Indonesian sponge fauna (Van Soest, 1989) it was estimated that this fauna, with about 830 nominal species, is the richest of the world's oceans. As a modest contribution to the description of this rich fauna, the present paper revises the Indo-Malayan species of the Poecilosclerid genus *Lissodendoryx* .

MATERIAL AND METHODS

Methods of collecting, preservation and preparation of specimens for light microscopy followed Van Soest (1984) and Hooper (1986). All spicule data are based on 25 measurements per spicule category per specimen.

The following abbreviations of institutions are used in the text.

BMNH	- The Natural History Museum, London;
MNHN	- Muséum National d'Histoire Naturelle, Paris
SMF	- Senckenberg Museum Frankfurt;
USNM	- National Museum of Natural History, Smithsonian Institution, Washington;
ZMA	- Zoölogisch Museum Amsterdam.

STUDIED MATERIAL

Ectyodoryx arenaria (Burton, 1936): BMNH 1935: 10:21:5, holotype (as *Lissodendoryx*).

Ectyodoryx bifacialis (Lévi & Lévi, 1983): ZMA POR 9318, 9327, 9147.

?Echinostylinos stylophora (Lévi & Lévi, 1983): MNHN DCl.2870, holotype (as *Lissodendoryx*).

L. grata (Thiele, 1903) : SMF 1783, holotype (as *Dendoryx*); ZMA POR 8389; USNM 22929, holotype of *L. oxytes* De Laubenfels, 1954.

L. jacksoniana (Von Lendenfeld, 1888): BMNH 1887:4: 27:95, holotype (as *Myxilla*); BMNH 1936:11:26:33, Burton's 1936 material labeled *Lissodendoryx isodictyalis* var. *jacksoniana*..

L. paucispinata (Ridley & Dendy, 1986): BMNH 1887:5:2:50-51, holotype and additional specimen (as *Myxilla*).

L. aspera (Bowerbank,1875): SMF 1584, Hent-schel's 1912 specimen, (as *Dendoricella schmidti*); SMF 1780, Thiele's 1903 specimen (as *Dendoryx schmidti*); ZMA POR 851, 857, 2705, 6267 (= fragment of holotype of *Damiriana hawaiia-na*, USNM 22737), ZMA POR 7968; USNM 22215, holotype of *Zetekispongia zonea* De Laubenfels, 1936b.

L. similis Thiele, 1899: ZMA POR 2838.

L. ternatensis Thiele, 1903: ZMA POR. 1518; BMNH 1932:7: RS:38, Burton's 1933 specimen (as *L. sinensis*).

L. timorensis n.sp.: ZMA POR.1471, holotype.

L. microchelifera n.sp.: ZMA POR.8041, holotype.

Myxilla (Ectyomyxilla) arenaria Dendy, 1905: BMNH 1954:2:23:109, holotype.

Damiriella pygmaea (Burton, 1931, as *Myxilla*): type material, BMNH 1933:7:4:16

SYSTEMATIC DESCRIPTIONS

Order Poecilosclerida Topsent, 1928
Family Coelosphaeridae sensu Hajdu et al.,1994

GENUS *LISSODENDORYX* TOPSENT, 1892

Synonymy:

Lissodendoryx Topsent, 1892: 96; Topsent, 1894: 34; Topsent, 1902: 19; Topsent, 1904: 173; Lundbeck, 1905: 153; Hentschel, 1914: 101; Topsent, 1925: 701; Wilson, 1925: 431; Topsent, 1928: 53; Burton, 1929: 436; Burton & Rao, 1932: 331; De Laubenfels, 1932: 75; De Laubenfels, 1950: 73; De Laubenfels, 1954: 132; Burton, 1959: 232; Hechtel, 1965: 40; Simpson, 1968: 108; Van Soest, 1984: 54.

Paramyxilla Dendy, 1905: 233;

Xytopsihis De Laubenfels, 1936a: 54;

Zottea De Laubenfels, 1936a: 64;

Waldoschmittia De Laubenfels, 1936a: 95;

Zetekispongia De Laubenfels, 1936b: 446;

Damiriana De Laubenfels, 1950: 13.

TYPE SPECIES

Tedania leptoderma Topsent, 1889 (= junior synonym of *Halichondria isodictyalis* Carter 1882), designation by Topsent, 1894.

DIAGNOSIS

Encrusting to massive Coelosphaeridae with uneven surface and soft consistency; with ectosomal smooth tylotes, monactinal or diactinal smooth or acanthose choanosomal megascleres

arranged in a renieroid reticulation; microscleres include arcuate isochelas and sigmas; rhaphides may be present (emended after Van Soest, 1984).

REMARKS

Van Soest (1984) emended the definition to accomodate *Lissodendoryx sigmata* (De Laubenfels, 1949) and his new species *L. strongylata*, which are both obvious close relatives of *L. isodictyalis*, but have diactinal (tylotes and strongyles) spicules as structural choanosomal spicules. Emphasis is now being placed on the combination of a renieroid choanosomal reticulation, smooth ectosomal tylotes, and arcuate isochelas and sigmas for microscleres. Raphides may be present. The combination of ectosomal tylotes, renieroid reticulation, arcuate isochelas and sigmas is diagnostic for the genus. Singly, these characters are known for other genera also. Other authors allow species without sigmas to fall within the genus, although a separate genus *Damiriella* Burton, 1935 is available for them. Since no such species have been encountered in the present material, we cannot decide whether or not these form a monophyletic group (but see below).

The family assignment of *Lissodendoryx* and relatives is traditionally to the Myxillidae. However, a recent review of Poecilosclerid characters (Hajdu et al., 1994) made a strong case for keeping genera with anchorate chelas separate from those with arcuate chelas at the family level. *Myxilla* falls to a restricted Myxillidae diagnosed a.o. as having anchorate chelas (see also Desqueyroux-Faúndez & Van Soest, 1995), whereas *Lissodendoryx* goes to a widened Coelosphaeridae (cf. also below).

HISTORY OF THE GENUS

The genus *Lissodendoryx* was established by Topsent, first in 1892, as a subgenus of *Dendoryx* (= junior synonym of *Myxilla*), and later, in 1894, raised to an independent genus. He defined the genus in 1894 as follows: "*Dendoryx* with smooth styles as megascleres of the skeleton".

The type species is *Lissodendoryx leptoderma* (Topsent, 1889 as *Tedania*), later (1897) considered to be identical to *Lissodendoryx isodictyalis* (Carter 1882, as *Halichondria*). The character by which Topsent distinguished the genus from his *Dendoryx*, was exclusively the smooth styles distinct from the spined ones in *Dendoryx*. Lundbeck (1905) stated that this character is untenable, as species are found with both slightly spined and entirely smooth styles, and Topsent himself (1928) admits also to this fact. However, according to Lundbeck, there is another character which sharply separates *Lissodendoryx* from the genus *Dendoryx* (= *Myxilla*), without transitions of any kind, viz. the presence of arcuate chelas instead of anchorate chelas. *Dendoryx* - like species with arcuate chelas, accordingly received the name *Lissodendoryx*, while in the genus *Myxilla* , with type species *M. rosacea* Lieberkühn (1869) only species with anchorate chelas were allowed.

Diagnosis by Lundbeck 1905: "The exterior passes through all forms, from incrustations through massive, often more or less lobed forms, to erect, club-shaped, or finally digitate or richly branched forms. The skeleton is somewhat dependent on the form; it may be a diffuse and quite irregular polyspicular reticulation, in the massive forms longer fibres may be found, in the branched forms distinct primary longitudinal fibres may occur, and it may finally be of dendritic type. Spongin is present more or less copiously. Spicula: Megascleres: the skeletal spicules are smooth or spined styli, the dermal spicules are diactinal, tornota, tylota, strongyla, or similar forms, sometimes with spined ends; microscleres are chelae arcuate of one or more forms, and often sigmata. The name *Lissodendoryx* is not exactly a good one by the new limitations of the genus, but it cannot be rejected." By allowing a large variety of ectosomal spicules in *Lissodendoryx* the emphasis was put entirely on the combination of choanosomal styles and arcuate chelas, which occurs in several other genera, notably *Phorbas* and other Anchinoidae (cf. Voultsiadou & Van Soest, 1991)

Diagnosis by Wilson 1925: " Skeletal framework reticular, including sometimes well-marked fibres, or dendritic; spongin present in variable amount. Skeletal megascleres generally smooth styles, but sometimes spined. Special ectosomal megascleres present; these are generally, but not always, diactinal. Microscleres isochelas, never ancoras; these may be accompanied by sigmas, toxas, or trichodragmas". Wilson (1925) not only

allowed a large variation of ectosomal spicules, like Lundbeck (l.c.), but also accepted palmate isochelas, as long as they are not anchorate. He gives *L. tawiensis* Wilson, 1925, *L. tuberosa* Hentschel, 1911, and *L. styloderma* Hentschel, 1914, as examples with monactinal ectosomal megascleres, and *L. tuberosa* and *L. tawiensis* as examples with palmate isochelas. According to recent views it is clear that these belong to a variety of other Poecilosclerid genera. As far as allowing toxas in *Lissodendoryx* Wilson (l.c.) quoted Topsent (1901b: 19) who mentions this also in his review of the genus *Lissodendoryx*. *L. tawiensis*, *L. tibiellifer* (Ridley, 1884 as *Amphilectus*) (reassignment by Topsent, 1897), and *L. spinulosa* Tanita, 1968 are examples of species with toxas assigned to *Lissodendoryx*. These are without doubt members of the family Microcionidae because of their combination of palmate isochelas and toxas. The genus *Megaciella* Hallmann, 1920 is available for such species.

Van Soest (1984) restricted the use of *Lissodendoryx* to species having ectosomal tylotes, reticulate choanosome, arcuate isochelas and sigmas, but allowing various choanosomal megasclere shapes, including strongyles and oxeas. Van Soest redefined the genus to accomodate *L. sigmata* and his new *L. strongylata*, which are both obvious close relatives of *L. isodictyalis*.

Wiedenmayer (1989) stated that sigmas may be absent and longer tracts, sometimes dendritic, may be present. Wiedenmayer does not regard sigmas mandatory in diagnosing *Lissodendoryx*, thus also following Lundbeck (1905) and Topsent (1928). The arcuate chela is the only real distinction from *Myxilla*, which always has anchorate chelas.

In the here employed definition, sigmas are always present. *Lissodendoryx* - like species without sigmas may be assigned to the genus *Damiriella*, although a future character analysis may prove Wiedenmayer right. In that case *Damiriella* could be employed as subgeneric units within the larger genus *Lissodendoryx*.

GENERA ASSOCIATED WITH *LISSODENDORYX*

Coelosphaera Thomson, 1873: 484.

Type species *Coelosphaera tubifex* Wyville Thomson, 1873. Definition by Van Soest (1984: 71): "Coelosphaeridae with smooth tylote megascleres and arcuate isochelae, sigmata, and often raphides for microscleres". The skeletal difference with *Lissodendoryx* is that *Coelosphaera* has megascleres of one type only: smooth tylotes, while *Lissodendoryx*, excepting *L. sigmata* (De Laubenfels, 1949), has megascleres of two types: tylotes in the ectosome and different monactinal or diactinal, smooth or acanthose megascleres in the choanosome. Microscleres of *Coelosphaera* normally include arcuate isochelas and sigmata, often raphides. Because *L. sigmata* is not bladder-like fistulose as *Coelosphaera* species invariably are, the condition of its skeleton is interpreted as a replacement of the choanosomal megascleres by ectosomal tylotes. *Coelosphaera* is generally considered (cf. Lévi, 1973; Hooper, 1991) a member of a separate restricted family Coelosphaeridae which is defined mostly on the fistulose habit. However, recent studies by Lévi & Lévi (1983), Hajdu et al. (1994) and Van Soest et al. (1994), have shown that the Coelosphaeridae in the sense of Topsent are likely to be artificial, demonstrating that fistular body shape is convergent in at least two Poecilosclerid groups. *Cornulum* and related fistular genera possess microspined tylotes, palmate isochelas and toxas, which make them clear members of the suborder Microcionina (cf. Van Soest et al., 1994). *Coelosphaera* and related fistular genera have smooth tylotes, arcuate isochelas and lack toxas, which latter two characters make them clear members of the suborder Myxillina. In spiculation *Coelosphaera* is extremely similar to *Lissodendoryx* and it is here proposed to unite them in the same family, which is named Coelosphaeridae for priority reasons.

Dendoricella Lundbeck, 1905: 126.

Type species *D. rhopalum* Lundbeck, 1905. Lundbeck 's definition: " The form massive, lobate or erect, club-shaped. The skeleton polyspicular, irregular or dendritic; the dermal skeleton consists of more or less erect bundles of dermal spicules. Spongin present or wanting. Spicula: Megasclera: the skeletal spicules diactinal, oxea (or strongyla), the dermal spicules oxea, tornota, or tylota; microsclera: chelae arcuate solely, or

chela arcuate and sigmata". This definition reminds of *Lissodendoryx*, but the type species *Dendoricella rhpalum* Lundbeck 1905 has oxeas, tornotes and arcuate isochelas. The tornotes are real tornotes, not tylotes. Thus the type species of *Dendoricella* is not a *Lissodendoryx* according to our restricted definition, and thus we regard *Dendoricella* as separate from *Lissodendoryx*. Lundbeck included five species in his new genus. Two of these, *Dendoricella schmidti* (Ridley, 1884) and *Dendoricella cavernosa* (Topsent, 1892) are the type species of respectively *Waldoschmittia* De Laubenfels, 1936 and *Damiriella* (Burton, 1935) (cf. below).

Paramyxilla Dendy 1905: 233.

Type species *Halichondria infrequens* Carter 1881. Dendy's definition : "Esperellinae whose principal megascleres are spined oxea, with which are associated smooth tylota. Microscleres tridentate isochelae and sigmata". The type species falls within our definition of *Lissodendoryx* , thus making *Paramyxilla* a synonym of *Lissodendoryx*. Topsent (1928: 53) synonymised *Paramyxilla* with *Dendoricella*, but see above. *Paramyxilla* may be employed as a subgeneric unit for *Lissodendoryx* species possessing spined oxeas as choanosomal megascleres.

Ectyodoryx Lundbeck 1909: 444.

Type species *Hastatus foliatus* Fristedt 1887. Lundbeck's definition: "Sponges with a reticulate skeleton, echinated (more or less sparingly) by accessory spicules. The skeleton spicules spined or smooth styli, the accessory spicules smaller, spined styli; the dermal spicules diactinal; microscleres isochelae arcuatae solely or together with other forms". The type species of Fristedt has been examined by Lundbeck. He found the accessory spicules few in number. We have not been able to examine the type species, but are inclined to consider the presence of echinating spicules as a character distinct from *Lissodendoryx*, although presence or absence of echinating spicules in other groups, e.g. Microcionidae seems to have little phylogenetic significance.

Damiriella Burton, 1935: 404.

Type species *Damiria cavernosa* Topsent 1892. Burton's definition: "Skeleton a reticulation of smooth strongyla, dermal spicules tornota, microscleres chelae unguiferae (or polydentate chelae?)". *Damiria cavernosa* was redescribed in detail from fresh material by Topsent (1936:19) as *Lissodendoryx cavernosa*, with tylotes, strongyles and arcuate chelas of two sizes. Topsent (1936) remarks that in 1892 he was wrong by putting *cavernosa* in the genus *Damiria* , and that it must go to *Lissodendoryx*. Rützler (1965) likewise assign-ed it to *Lissodendoryx*. Pulitzer-Finali (1978: 56) provided a description of the species as *Damiriella cavernosa*. He supported Burton's new genus *Damiriella* as distinct from *Lissodendoryx*, because of the diactinal nature of the choanosomal megascleres. We agree for the time being with Burton and Pulitzer-Finali in keeping *Damiriella* as a separate, though related, genus lacking sigmas. However, we think that not the diactinal nature of the choanosomal megascleres but the lack of sigmas is the discriminating character. Possibly, *Damiriella* may be employed as a subgenus of a wider defined *Lissodendoryx* (cf. above).

Xytopsihis De Laubenfels, 1936a: 54.

Type species *Halichondria aspera* Bowerbank (1875). De Laubenfels' definition: "This species is not very well-known, but seems to have had both oxeas and strongyles for megascleres and chelas of two sizes". However, according to Bowerbank's description the type species has dermal tylotes and choanosomal oxeas, and for microscleres two sizes of chelas and sigmas. Bowerbank (1875) also described choanosomal styles. We suspect that these styles are either not proper to the sponge, or are modified oxeas. The skeletal plan is a more or less multispicular, rather regular network. This makes *Xytopsihis* a synonym of *Lissodendoryx* and *L. aspera* a very likely senior synonym of the species generally known as *L. schmidti* (Ridley, 1884) (cf. below). The possession of oxeas as choanosomal megascleres is possibly found in several related species (if for instance *Damiria australiensis* Dendy, 1896 and *Zetekispongia zonea* De Laubenfels, 1936b would be related but different *Lissodendoryx* species). It is suggested here to employ *Xytopsihis* as a subgeneric unit within a wider defined genus *Lissodendoryx*.

Jones De Laubenfels, 1936a: 79.

Type species *Myxilla amaknakensis* Lambe 1894. De Laubenfels' definition: "This has a spiculation of megascleres very like the preceding" (i.e. *Jelissima* with spiny oxeas and styles)", but has arcuate isochelas of one kind only for microscleres". The type species has small stout entirely spined styles with sharp points forming the main skeleton and sparsely spined tornotes with rather blunt ends (not tylotes), found throughout the main skeleton but chiefly occurring in the dermal skeleton. Microscleres are small arcuate isochelas, with strongly curved shafts. It has the typical renieroid choanosomal reticulation. Bakus (1966: 499) synonymised *Jones* with *Lissodendoryx* because *Myxilla amaknakensis* contains arcuate isochelas. However, the type species does not conform to the restricted definition of *Lissodendoryx* on account of the ectosomal spicule shape and the lack of sigmas. The genus *Jones* may be valid, but its type species needs redescription.

Merriamium De Laubenfels, 1936a: 83.

Type species *Merriamium tortugasensis* De Laubenfels, 1936a. De Laubenfels' definition:
" This group has the characteristic dermal diacts and endosomal more or less spiny monactinal spicules of the family Myxillidae, accompanied by microscleres of only one sort, arcuate chelas. If there were sigmas present, which I cannot find to be the case at present, this would be like the genus *Ectyodoryx* to be discussed below. If the chelas were anchorate instead of arcuiferate "(sic)", it would be of the genus *Myxilla*. If in addition to sigmas being present, it were a very thinly encrusting form, it would belong to the genus *Hymedesmia*. In the absence of any of these diagnostic points, it appears advisable here to establish a new genus." De Laubenfels intended this genus chiefly to include "atypical" species of *Lissodendoryx* and *Ectyodoryx*, lacking sigmas. He considered the genus *Ectyodoryx* to have both arcuate isochelas and sigmas. However, in the same paper he failed to uphold this distinction and placed *Myxilla crelloides* Brøndsted, 1924 in *Ectyodoryx* despite the fact that it has only arcuate isochelas as microscleres. According to Van Soest (1984: 86), the type species, the West-Indian *Merriamium tortugasensis* is a junior synonym of *Phorbas amaranthus* Duch. & Mich. 1864, the type species of the genus *Phorbas* Duch. & Mich. 1864. *Merriamium* is thus a junior synonym of *Phorbas*. Bergquist & Fromont (1988: 89) ignored all this and stated that the diagnosis of *Ectyodoryx* (Lundbeck 1909: 444) and the diagnosis of *Merriamium* are the same, and decided that it is a junior synonym of *Ectyodoryx*.

Waldoschmittia De Laubenfels, 1936a: 95.

Type species *Crella schmidti* Ridley, 1884. De Laubenfels' definition: "This is superficially rather close to the genus *Lissodendoryx* , but the chelas are unusual, perhaps technically to be regarded as arcuate, but not typically so, and in addition to the monactinal principal spicules there are also oxeas in the endosomal skeleton. *Lissodendoryx* has typical arcuate chelas and no endosomal diacts.... Another species that should be referred to this new genus is *Damiria australiensis* Dendy, 1896". The type species conforms to the definition of *Lissodendoryx* , because it has tylotes, arcuate isochelas and sigmas; the styles to which De Laubenfels refers are not present in the type species. Thus the genus *Waldoschmittia* is synonymous with *Lissodendoryx*. Moreover, the type species is a junior synonym of *Halichondria aspera* Bowerbank, 1875, the type of *Xytopsihis* De Laubenfels, 1936 a, which has page priority over *Waldoschmittia*.

Zottea De Laubenfels, 1936a: 64.

Type species *Myxilla grata* Thiele, 1903. De Laubenfels' definition: "Dermal smooth tylotes, principal spicules are lumpy strongyles, microscleres are raphides, sigmas and isochelae arcuatae, but have sharply pointed clads." As will be demonstrated below in the redescription of the type species the "lumpy" strongyles are in fact acanthostrongylostyles obviously homologous to the often spined styles of *L. isodictyalis*. The isochelas are thoroughly normal arcuate chelas with rounded clads. *Zottea* is thus a clear synonym of *Lissodendoryx*.

Zetekispongia De Laubenfels,1936b: 446.

Type species *Z. zonea* De Laubenfels, 1936b. De

Laubenfels' definition : "Structure more reticulate than plumose; special diactinal ectosomal spicules associated with special diactinal endosomal ones of another sort; arcuate chelas and sigmas for microscleres". Van Soest (1984: 59) synonymised *Zetekispongia* with *Lissodendoryx* as the only difference is the oxeote nature of the choanosomal megascleres. All other features (tylote ectosomal megascleres, microscleres, skeletal reticulation) are so similar to those of *L. isodictyalis*, that it is unrealistic to put them in separate genera. *Lissodendoryx zonea* has not been reported from the Indo-Malayan region, but is probably conspecific with *Halichondria aspera* Bowerbank, 1875, the type of *Xytopsihis* De Laubenfels, 1936a.

Damiriana De Laubenfels, 1950: 13.

Type species *Damiriana hawaiiana* De Laubenfels, 1950. De Laubenfels' definition:"With a special dermal skeleton of tylotes over an endosomal skeleton of oxeas, with arcuate chelas among the microscleres". De Laubenfels (l.c.) apparently overlooked the fact that in 1936 he erected a genus *Zetekispongia* with exactly the same characters as the present genus. The type species *Damiriana hawaiiana* has sigmas and conforms to the definition of *Lissodendoryx* , thus making *Damiriana* a synonym of *Lissodendoryx*. *L. hawaiiana* has not been reported from the Indo-Malayan region. Lévi (1958: 30) synonymised *Crella schmidti* (Ridley 1884), *Damiriana australiensis* (Dendy 1896), *Dendoricella schmidti* (Hentschel 1912), and *Damiriana hawaiiana* (De Laubenfels 1950) with *Lissodendoryx schmidti* (as *Damiriana schmidti*). This species (cf. above) is here considered a junior synonym of *Halichondria aspera* Bowerbank, 1875, the type of *Xytopsihis* De Laubenfels, 1936a.

In conclusion, six genera are considered synonymous with *Lissodendoryx*: *Paramyxilla* Dendy 1905; *Xytopsihis* De Laubenfels 1936a; *Zottea* De Laubenfels, 1936a; *Waldoschmittia* De Laubenfels 1936a; *Zetekispongia* De Laubenfels 1936b; *Damiriana* De Laubenfels 1950. However, species with smooth and spined choanosomal oxeas are suggested to belong to subgenera within *Lissodendoryx*, viz. *Xytopsihis* and *Paramyxilla*, but formal implementation of this should await further revisions. For the time being, until a formal character analysis has been made, the genera *Coelosphaera, Dendoricella, Ectyodoryx, Damiriella* and *Jones* are considered distinct from *Lissodendoryx*. However, *Damiriella* Burton, 1935 may turn out to be a useful subgeneric name for *Lissodendoryx*-like species without sigmas. *Merriamium* as a junior synonym of *Phorbas* clearly belongs to a different family.

DESCRIPTION OF INDO-MALAYAN SPECIES

Lissodendoryx grata (Thiele, 1903) Figs. 1-8

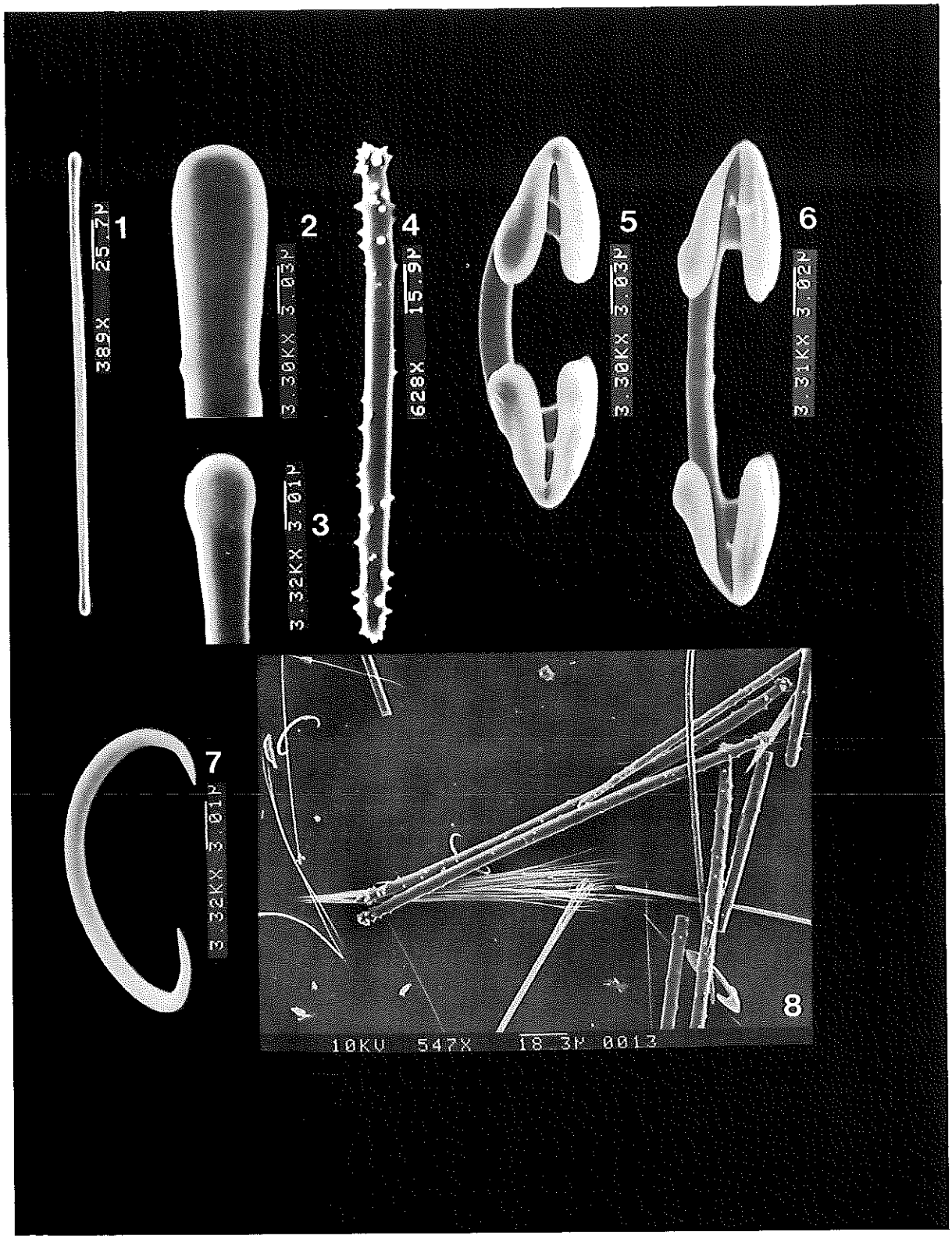
Myxilla grata Thiele 1903: 954, fig. 19.
Zottea grata; De Laubenfels, 1936a: 64.
Lissodendoryx oxytes De Laubenfels, 1954: 132, fig. 83.

MATERIAL EXAMINED

Holotype SMF 1783 (as *Dendoryx*), Thiele 1903, Ternate, Indonesia; holotype of *L. oxytes* USNM 22929, Koror, Palau Isl., West Pacific Ocean, 5 m.
ZMA POR. 8389, Snellius II Exped., 1984, stat. 79, Indonesia, E of Komodo, Selat Linta, 8° 35' S 119°34.2' E, coll. R.W.M. van Soest, SCUBA, depth 4-10 m.

DESCRIPTION

Shape: Thiele described it as a couple of formless fragments of greyish colour in alcohol which possess numerous little stones and other strange objects. The form of the specimen collected during the Snellius II Expedition is massive, friable. Some bits of the specimens of *L. oxytes* De Laubenfels (1954) may be described as encrusting, and at such places it is less than 1 mm thick and it penetrates galleries in coral which appear to have been made by an excavating sponge of the genus *Cliona*. Consistency slimy, soft colloidal. Surface: shiny smooth, with no pores or oscules visible to the naked eye.
Colour: red (ZMA specimen) to extremely dark purple red (USNM specimen) alive, grayish in alcohol (type, Thiele 1903), white in alcohol (ZMA material).



Figs. 1-8: *Lissodendoryx grata* (Thiele, 1903), SEM photographs of spicules. 1. tylote of holotype of *Myxilla grata* Thiele, 1903, SMF 1783, 2. detail of tyle of do., 3. detail of tyle of tylote of holotype of *Lissodendoryx oxytes* De Laubenfels, 1954, USNM 22929, 4. spined style of SMF 1783, 5. chela of do., 6. chela of USNM 22929, 7. sigma of do., 8. overview of spicules of do. showing a.o. raphides.

Table 1. Spicule lengths in µm of *Lissodendoryx grata* specimens. * = original data, ** = our measurements (ac.str.st. = acanthostrongylostyles).

	tylotes	ac.str.st.	isochelas	sigmata	raphides
Thiele 1903*	235	180	23	18	90
SMF 1783**	198-224	134-160	19-32	12-20	128-141
De Laubenfels 1954*	230	165	25	20	35
USNM 22929**	192-205	140-160	16-19	12-26	45-125
ZMA POR. 8389**	198-224	153-173	25-32	12-20	64-103

Ectosome: loosely strewn tylotes.
Choanosome: acanthostrongylostyles, singly or in bundles of 2-3, form an isodictyal reticulation, among which the microscleres lie scattered.
Spicules: The type specimen of Thiele, 1903 (SMF 1783) (cf. Fig. 2) and that of *L. oxytes,* (USNM 22929) (cf. Fig. 3),were reexamined, and both the original values of Thiele and De Laubenfels and the results of the reexamination are given in Table 1.
Ectosomal tylotes (Figs.1-3): smooth, the heads at each end are elongated and only slightly swollen, but well developed, 192-235 x 2-6 µm
Acanthostrongylostyles (Fig. 4): they are mostly inequiended and thus probably style-derived, with many big spines; at the ends there are more spines than in the center of the spicules, and the spines are often grouped into small lumps, 134-180 x 5-16 µm.
Arcuate isochelas (Figs. 5-6): abundant, with relatively long well-developed alae, the flanking ones of which have a slightly indented shape, following the curvature of the shaft, 16-32 µm.
Sigmas (Fig. 7): abundant, 12-26 µm.
Raphides (Fig. 8): very abundant, in long trichodragmas, 45-141 µm.
Ecology: Thiele (1903) mentioned that the type specimen was collected from the littoral. De Laubenfels' specimens was from reefs at 5 m. The specimen collected during the Snellius II Expedition was found at the edge of a very gently sloping coastal reef flat, at 4-10 m. Thus we may conclude that this is a shallow-water reef species.
Distribution: Indonesia: Ternate and Komodo; Palau Isl.

REMARKS

The strongylote nature of the choanosomal styles and their heavy spination, as well as the possession of raphides make this a distinct species. *Lissodendoryx oxytes* De Laubenfels (1954) showed some differences with the type of Thiele: styles were thinner and slimmer in De Laubenfels' material (although generally of the same shape), and raphides were reported to be much smaller. However, reexamination of the type specimen of *L. oxytes* revealed the maximum size of the raphides to be two to three times as long as mentioned by De Laubenfels. There can be little doubt that *L. oxytes* is a junior synonym of *L. grata.*

The species is the type of the genus *Zottea* De Laubenfels, 1936a, but as argued above, this is a clear synonym of *Lissodendoryx.*

Lissodendoryx paucispinata (Ridley & Dendy, 1886) Figs. 9-18

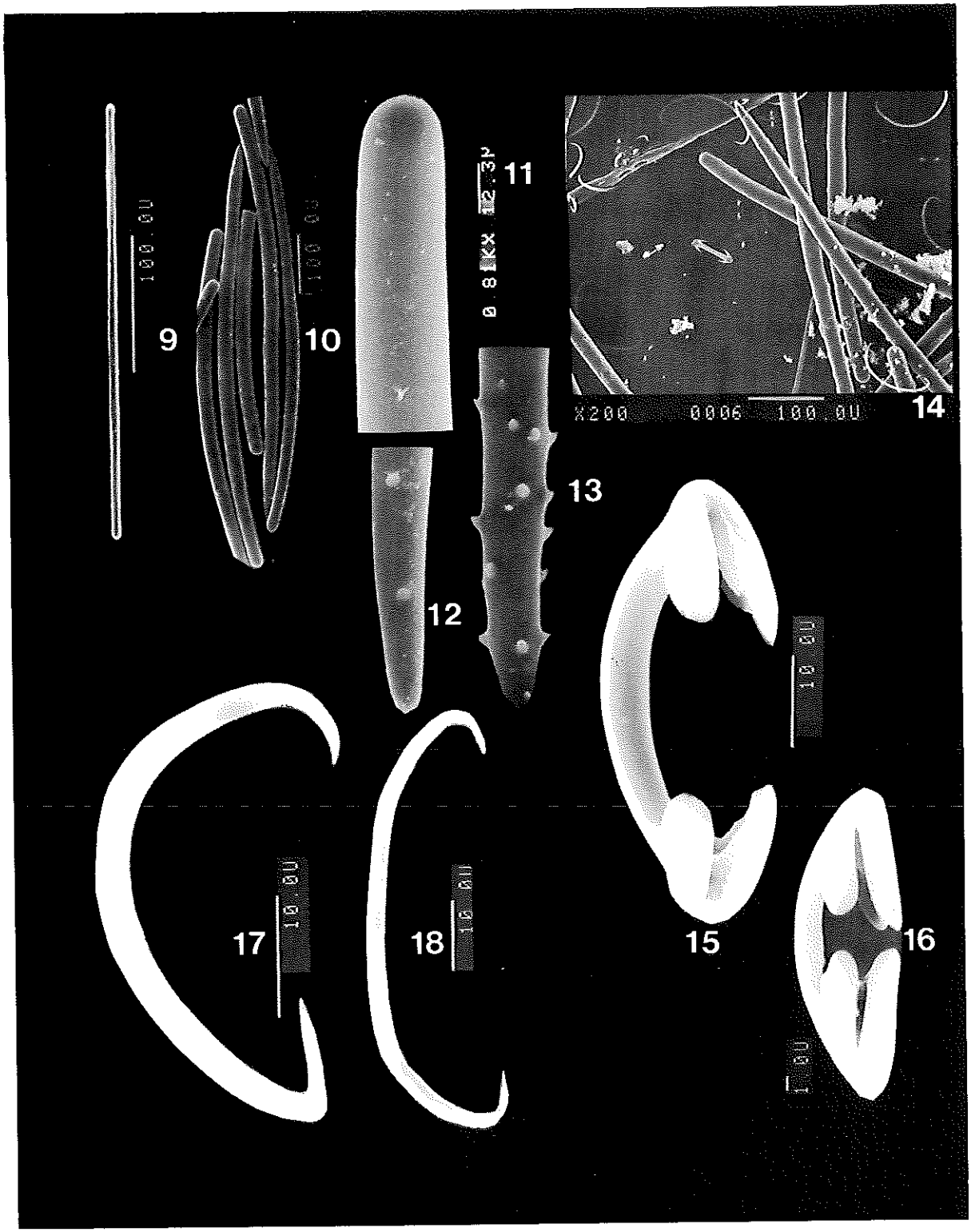
Myxilla paucispinata Ridley & Dendy, 1886: 471; Ridley & Dendy 1887: 132, Pl. 27 fig. 2a-c; Pl. 30 fig. 3.
? Lissodendoryx paucispinata ; Boury-Esnault & Van Beveren, 1982: 82, fig. 23.

MATERIAL EXAMINED

Type BMNH 1887:5:2:50 (as *Myxilla*), Challenger Exped., stat. 192, New Guinea, Ridley & Dendy 1886; additional specimen BMNH 1887: 5:2:51, same data as the holotype.

DESCRIPTION

(mostly condensed from Ridley & Dendy, 1887):



Figs. 9-18: *Lissodendoryx paucispinata* (Ridley & Dendy, 1886), SEM photographs of spicules of holotype, BMNH 1887:5:2:50. 9. tylote, 10. styles, 11. detail of smooth style, 12. detail of lightly spined style, 13. detail of more heavily spined style, 14. overview of spicules showing lightly spined styles, sigmas and two size categories of chelas, 15. larger size category of chela, 16. small chela, 17-18. sigmas.

Table 2. Spicule lengths in µm of *Lissodendoryx paucispinata* specimens. * = original data, ** = our measurements.

	tylotes	styles	isochelas	sigmata
R & D. 1886 (type)*	400	700	50	up to 56
BMNH 1887:5:2:50**	302-346	529-562	16-19/35-47	32-44
R & D 1886 (co-type)*	420	770	63	up to 145
BMNH 1887:5:2:51**	356-389	518-648	23-34/47-59	86-108
Boury-E. & Van Beveren*	326-397	410-480	31-38	28-37

Shape: Sponge massive, amorphous, cavernous.
Texture rather soft, very brittle and fragile.
Surface: very uneven and roughly hispid.
Colour: in spirit pale yellow (R. & D., 1887).
Ectosome: the dermal skeleton consists of thick brushes of tylotes which converge towards the osculum.
Choanosome: irregular but close reticulation of slightly spined styles; spongin scarce.
Spicules: The type specimens of Ridley & Dendy have been reexamined and both their original values and the results of the reexamination are given in Table 2.
Ectosomal tylotes (Fig. 9): smooth, with a fairly straight shaft bearing a distinct, though only slightly developed oval head at each end, 302-420 x 5-8 µm.
Styles (Figs. 10-14): large, stout, mostly curved, with rather blunt apex and often slightly spined. The spination of the styles appears to be very inconsistent in this species, and it is doubtful whether it is of specific value. In the microscopical slides and SEM photos of the type specimen both smooth styles (Figs. 10-11) as well as spined styles (Fig. 12-14) were found. Spines were mostly found on the shaft. Size of styles 518-770 x 10-21 µm.
Arcuate isochelas (Figs. 15-16): with stout, strongly curved shaft. Ridley & Dendy described only one size category, but reexamination of the type material revealed two sizes of arcuate isochelas, the smaller of which is often compact and flattened (Fig. 16). Sizes 16-34 and 35-63 µm.
Sigmas (Figs. 17-18): slender, simple and contort, quite variable in size but not easily divisible in size categories, 32-145 µm.
Ecology: Deep water, 256 m; bottom blue mud.
Distribution: Indonesia, Little Ki Island, near New Guinea, ? Kerguelen Islands.

REMARKS

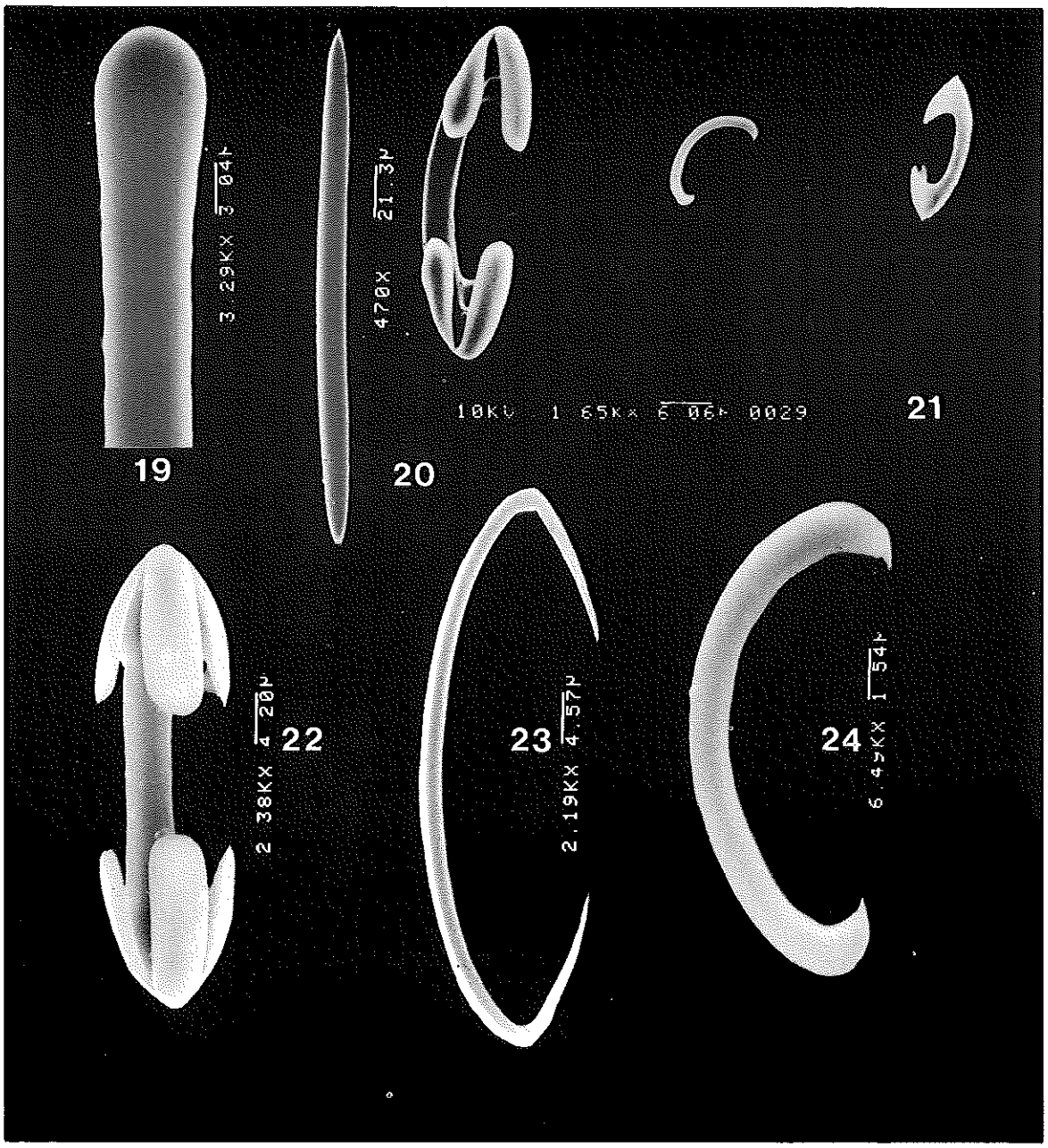
The species was described as *Myxilla*; after reexamination of the type material, we agree with Boury-Esnault & Van Beveren (1982) that this is a *Lissodendoryx*, conforming to the presently employed definition. Characteristic for the species is the variability in spination of the choanosomal styles, and the sizes of both tylotes and styles clearly exceed that of all other Indo-Malayan species.

It is doubtful whether the *Lissodendoryx paucispinata* specimen recorded by Boury-Esnault & Van Beveren (l.c.) is conspecific with the present species. They described their specimen as "flat cushions of 5-8 cm and 4-7 mm thick". The tylotes of their specimen were apparently sometimes spined. The sigmas are smaller and the chelas show only a single size category. The specimen of Boury-Esnault & Van Beveren originated from a cold water area (Kerguelen Archipelago, Southern Ocean), from a basalt and sand bottom at 192 m.

Lissodendoryx aspera (Bowerbank, 1875)
Figs. 19-24

Halichondria aspera Bowerbank, 1875: 287.
Crella schmidti Ridley, 1884: 432, Pl. XLI fig. A.a.
Damiria australiensis Dendy, 1896: 28 (fide Lundbeck, 1905); Lindgren 1898: 25, Pl. 17, fig. 10, Pl. 19, fig. 15.
Damiria schmidti; Topsent, 1897: 455.
Myxilla schmidti; Thiele 1903: 954.
Dendoricella schmidti; Hentschel, 1911: 328, fig. 22;

Erratum:
Figure 21 on page 88 was not fully printed (sigma and smal chela are missing). The corrected plate including its original legend is here added.



Figs. 19-24: *Lissodendoryx aspera* (Bowerbank, 1875), SEM photographs of spicules of SMF 1584 (Hentschels's (1912) specimen of *Dendoricella schmidti*). 19. detail of tylote, 20. oxea, 21. overview of some of the spicules, including large and small category of chelas and small category of sigma, 22. large category of chela, in anterior view, 23. large category of sigma, 24. small category of sigma.

Hentschel, 1912: 342; Dendy & Frederick, 1924: 505.
Waldoschmittia schmidti; De Laubenfels 1936a: 95.
Zetekispongia zonea De Laubenfels, 1936b: 446, Fig. 40.
Damiriana hawaiiana De Laubenfels, 1950: 14, fig. 7; De Laubenfels 1951: 259; Bergquist, 1977: 65.
Damiriana schmidti; Levi, 1958: 30, fig. 25; Levi, 1965: 16, fig. 17; Thomas, 1973: 25, Pl. 1, fig. 13; Thomas 1976: 455, fig. 2i, 1 t/m 6; Thomas, 1979: 22, Pl. 1, fig. 14; Thomas 1981: 21; Desqueyroux-Faundez, 1981: 741, fig. 42.

MATERIAL EXAMINED

SMF 1780 (as *Dendoryx*), Ternate, Indonesia, cf.Thiele, 1903; SMF 1584 (as *Dendoricella*), Indonesia, Aru Isl., Banda Sea, Merton leg. 1908, cf. Hentschel, 1912; ZMA POR. 851, Siboga Exped., stat. 50, Indonesia, Bay of Banjo, W. coast of Flores, dredge, trawl and shore exploration, up to 40 m depth, bottom mud, sand and shells, 16/18-4-1899; ZMA POR. 857, Siboga Exped., stat. 231, Indonesia, Jedan Isl., trawl, dredge and divers, 13 m, bottom sand and shells, 23/26-12-1899; ZMA POR. 2705, Siboga Exped., stat. 7, Indonesia, E. Java, near reef of Batjulmati, 7°33' S 113°36.5' E, dredge and shore exploration, 15 m, bottom coral and stones, 11-3-1899; ZMA POR 6267 = fragment of USNM 22737, type of *Damiriana hawaiiana* De Laubenfels, 1950, Oahu Isl., Hawaii, bottom coral; ZMA POR. 7968, Snellius II Exped., 1984, stat: 52, Indonesia, Sumba, off Melolo, coll. R.W.M. van Soest, 1-4 m.

DESCRIPTION

Shape: massive, with moderately thick lobes pierced by holes 1 to 4 mm in diameter, lined by a smooth surface. Cavernous, repent. Surface covered with narrow longitudinal ridges about 1 mm broad, 5 mm high, and 1 mm apart, rough; ectosomal membrane between ridges smooth, transparant. Ridges conulose, highly pitted, undulating. Texture crumb-of-bread, soft and spongy. Consistency soft to firm, compressible. Oscules up to 2 mm, few, in depressions 1 to 3 mm deep, scattered on projections.
Colour: alive dirty white, (pale) yellow, orange; when dry pale white and yellow; in alcohol light grey brown.
Ectosome: tangentially arranged tylotes and ascending bundles in a plumose arrangement.
Choanosome: main skeleton an irregular reticulation of oxeas, with triangular meshes of 2-4 spicules; in deeper parts tracts of only 1 or 2 spicules.
Spicules: The specimens of Thiele (1903), Hentschel (1912) and De Laubenfels (1950) have been reexamined; both the original spicule size values and the results of the reexamination are given in Table 3.
Ectosomal tylotes (Fig. 19): of dermal tufts, straight, smooth, heads of same thickness as centre of shaft; shaft tapering to necks below heads, necks tapering gradually to the oval heads, 160-264 x 1-8 µm.
Oxeas (Fig. 20): smooth, straight or slightly curved, gradually tapering to sharp points, 147-248 x 4-13 µm.
Arcuate isochelas (Figs. 21-22): only choanosomal; the shaft stout, strongly curved; the teeth strong, well curved inwards, sharp, the two lateral ones united to shaft by falcate expansions. There are two size categories in most specimens, sizes 9-21 and 30-48 µm; sometimes there is a single category of variable size, 12-40 µm.
Sigmata (Fis. 22-24): contort, curve moderate, ends bent sharply inwards. Two size categories, 9-21 and 30-48 µm, but the big size category is not present in every specimen. The smallest sigmata (Fig. 22, 24) are rounded and end in a spine. Since this is found both in Thiele's *Myxilla schmidti* and in the type of *Damiriana hawaiiana* the conspecificity of both is quite likely.
Ecology: Depth: 0-9 m (Ridley, 1884), 45 m (Lindgren, 1898), 14-18 m (Hentschel, 1911), 20-22 m (Thomas, 1976). The Siboga and Snellius II Expedition material came from 1-4 m, 13, 15 and up to 40 m. Habitat: coral (Thiele, 1903), mud and algae (Hentschel, 1911), shells of gastropods (Lévi, 1965), harbour substrata (Thomas, 1976), mud, sand, shells, coral and stones (Siboga and Snellius II Exped. material).
Distribution: Cochin-China, East Africa, Hawaii, Indonesia, Red Sea, Seychelles, South Australia.

REMARKS

As stated above, the similarities between the above described specimens and Bowerbank's

Table 3. Spicule lengths in µm of *Lissodendoryx aspera* specimens. * = original data, ** = our measurements.

	tylotes	oxeas	isochelas	sigmata
Bowerbank, 1875*	not given	not given	10/25	15/190?
Ridley, 1884*	220	220	37	37
Dendy, 1896*	250	200	28	20
Tops., 1897/Desq.*	200	200	40	15
Lindgren, 1898*	216	216	36	12
Thiele, 1903*	?	230	20/40	10
SMF 1780**	160-173	179-205	12-20/25-32	10-13
Hentschel, 1911*	200-264	184-216	19-20/28-34	16-21/30-36
Hentschel, 1912*	192-264	184-248	19-20/27-40	14-21/30-40
SMF 1584**	160-195	166-227	12-20/32-39	10-14/32
Dendy & F., 1923*	310	230	22/34	20/39
De Laub., 1936b*	170-200	210-215	16-24/36	16-24
De Laub., 1950*	170-200	180-230	15/27	13
ZMA POR. 6267**	179-204	166-211	12-19/25-32	13
Lévi, 1958*	200	170	20-23	13-14
Lévi, 1965*	175-225	150-225	20	16-18
Thomas, 1973*	201-218	159-231	up to 33	12/48
Thomas, 1976*	172-234	172-245	24	13
Bergquist, 1977*	200	200	15-30	13
Thomas, 1979*	168-223	182-233	18-32	9-16
ZMA POR. 851**	172-192	172-192	12-20/32	13
ZMA POR. 857**	172-192	166-192	12-26	13
ZMA POR. 2705**	179-199	147-192	12-20/25-32	9-13
ZMA POR. 7968**	173-186	166-180	16-38	13

description of *Halichondria aspera* are so great that there is little doubt all are conspecific. The "acuate" spicules mentioned by Bowerbank are probably modified oxeas. Another discrepancy is the large size of the sigmata (190 µm) quoted by Bowerbank; it is likely there was a misprint involved.

We were able to reexamine a fragment of the type specimen of *Damiriana hawaiiana* De Laubenfels (1950), and there is no doubt this species is a synonym of *Lissodendoryx aspera* Especially on SEM photos the resemblance of the spicules was quite clear. The small sigmas were exactly the same in SMF 1584 (*Dendoricella schmidti* sensu Hentschel 1912) and ZMA POR. 6267 (type fragment of *Damiriana hawaiiana*, De Laubenfels, 1950). Lévi (1958) already syno-nymized *Damiriana hawaiiana* with *Lissodendoryx schmidti* (as *Damiriana schmidti*).

As discussed above, a whole series of generic names is associated with this species: *Xytopsihis* De Laubenfels, 1936a, *Waldoschmittia* De Laubenfels, 1936a, *Zetekispongia* De Laubenfels, 1936 b and *Damiriana* De Laubenfels, 1950. They are all clearly synonyms.

Lissodendoryx similis Thiele, 1899
Figs. 25-27.

Lissodendoryx isodictyalis sensu Topsent 1897: 460 (not: Carter 1882); Hoshino, 1981: 145, fig. 61; Sim & Kim, 1988: 26.

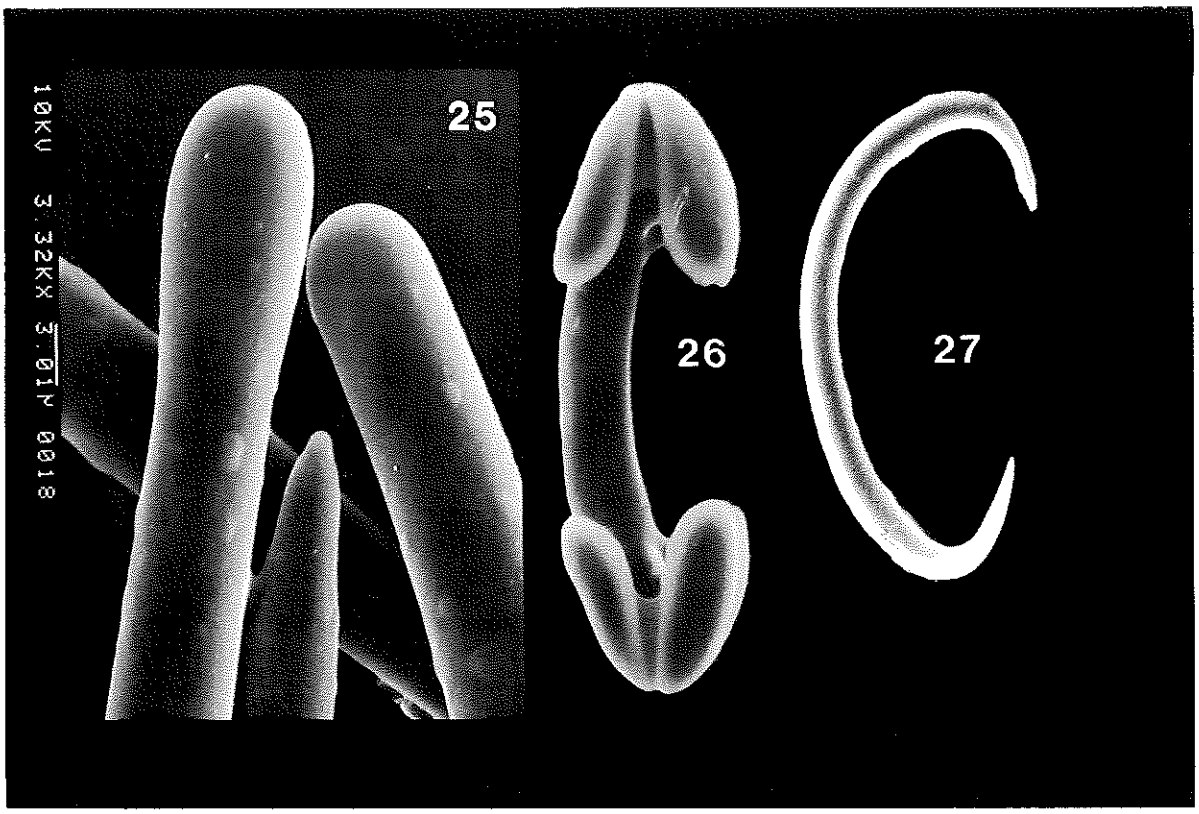
Lissodendoryx similis Thiele 1899: 18, Pl. 5, fig. 10; Burton & Rao, 1932: 331; Ali, 1956: 293, fig. 5.

MATERIAL EXAMINED

ZMA POR 2838, Siboga Exped., Stat. 273, Indonesia, Jedan Isl., trawl, dredge and divers, 13 m, bottom sand and shells, 23/26-12-1899.

DESCRIPTION

Shape: the little fragment of the type specimen of Thiele (1899) was 3-4 mm thick with diameter of 1 cm. The four specimens in the collection of Burton & Rao (1932) were all encrusting, with a



Figs. 25-27: *Lissodendoryx similis* Thiele, 1899, SEM photographs of spicules of ZMA POR. 2838. 25. details of tylote (left) and style (right), 26. chela, 27. sigma.

thin dermal membrane and scattered vents measuring 1-2 mm in diameter. The size of the specimen of Ali (1956) was 65 by 47 mm, the surface is uneven and the texture is very soft and friable. Oscules are small and inconspicuous, scattered all over the surface, about 0.9 mm in diameter.
Colour: light brown when dry (Thiele 1899), in living condition orange, which fades to greyish white in alcohol (Ali, 1956; ZMA POR. 2838).
Ectosome: charged with loosely strewn tylotes, often in whispy bundles.
Choanosome: reticulated fibres made up of styles in bundles; very little spongin.
Spicules (Table 4): Ectosomal tylotes (Fig. 25): smooth, straight, stout, with slightly elongated heads, 148-220 x 5-8 µm.
Styles (Fig. 25): stout, bent slightly near the blunt end, 148-200 x 5-8 µm.
Arcuate isochelas (Fig. 26): with curved shafts, with rounded alas, 18-30 µm.
Sigmas (Fig. 27): few, of the usual shape, 18-30 µm.
Ecology: Found on stones (Thiele, 1899), rock (Burton & Rao, 1932), encrusting on the side walls of the harbour (Ali, 1956), intertidal rocks (Hoshino, 1981); shallow water down to 13 m.
Distribution: Indonesia: Ambon, Celebes; Burma; India: Mergui Archipelago, Madras; Japan; Korea.

REMARKS

Thiele (1899) stated that *L. isodictyalis* Carter (1882) from the West Indies does not resemble the specimen of Topsent (1897) from Ambon, Indonesia. For the latter and his own specimen from Celebes, he erected *L. similis*, which differs from *L. isodictyalis* Carter chiefly in the dimensions of the spicules, particularly the larger microscleres, and the presence of chelas with

Table 4. Spicule lengths in µm of *Lissodendoryx similis* specimens. * = original data, ** = our measurements.

	tylotes	styles	isochelas	sigmata
Topsent, 1897*	215	190	30	30
Thiele, 1899*	220	200	30	22
Burton & Rao, 1932*	148-177	148-164	18-22	18-22
Ali, 1956*	176	176	30	20
Hoshino, 1981*	207-236	175-190	20-23	15-20
ZMA POR. 2838**	185-199	160-180	19-26	19

rounded rather than pointed ends, based on drawings provided by Carter. These supposed differences were cited again by Burton & Rao (1932: 331) to justify the use of the name *L. similis* Thiele for Indian populations. Topsent (1925, 1936) considered chela shape insignificant, and a variable characteristic within *L. isodictyalis*, and pronounced that *L. isodictyalis* is a good example of a cosmopolitan sponge. Hechtel (1965: 40) observed that *L. similis* has spicule sizes similar to those of *L. isodictyalis* and also considered them synonymous. We prefer to follow Thiele and Burton & Rao, in emphasizing differences in shape and size of the microscleres (particularly the chelas with round rather than pointed ends, and single size categories of both chelas and sigmata) and the presence of only smooth styles for choanosomal megascleres in *L. similis*.

The presence of *L. isodictyalis* in Japan and Korea is likewise doubtful. Hoshino (1981) and Sim & Kim (1988), recorded *L. isodictyalis* from resp. the Inland Sea of Japan and Korea. Sim & Kim (1988) only mentioned the locality and some synonyms. Hoshino (1981) described the specimen fully. The choanosomal spicules of his material are only styles (175-190 µm), smooth, straight or slightly bent, nearly constant in width throughout their length, base rounded, and with the opposite end sharply pointed. The chelas are arcuate isochelas (20-23 µm); he did not further consider the shape of the teeth. The sigmas (15-20 µm) are C-shaped or occasionally twisted S-shaped. The tylotes (207-236 µm) are smooth, almost straight or slightly sinuous, very slightly tapering from one end to the other, with each end elongated and slightly swollen. These data resemble *L. similis* Thiele.

Lissodendoryx ternatensis (Thiele, 1903)
Figs. 28-33.

Halichondria isodictyalis; Carter, 1886: 52 (not: Carter, 1882)
Myxilla isodictyalis; Dendy, 1896: 30
Hamigera ternatensis Thiele, 1903: 952, fig. 18
Lissodendoryx sinensis Brøndsted, 1929: 288, fig. 5; Burton, 1933: 240; Burton, 1937: 26, fig. 19.
Lissodendoryx ternatensis; Burton & Rao, 1932: 331; Lévi, 1963: 41, fig. 46; Lévi, 1969: 962.

MATERIAL EXAMINED

BMNH 1932:7: RS:38, South Africa, Stil Bay, cf. Burton 1933 (as *Lissodendoryx sinensis*); ZMA POR. 1518, Indonesia, Balikpapan, Borneo (now Kalimantan), coll. T. van Pakot, #SE 3040 Va, labeled "*Lissodendoryx isodictyalis*".

DESCRIPTION

Shape (Thiele, 1903): cavernous, massive, compressible. Texture: soft, friable. Surface: smooth, irregularly wrinkled, ectosome cavernous. Many small, scattered, oval oscules, up to 1 mm. in diameter. Burton (1937) described his *L. sinensis* as: branching, repent, with cylindrical branches; surface uneven, minutely hispid.
Colour: slate-brown (Carter, 1886), wax yellow (Dendy, 1896), darkbrown-grey (Brøndsted, 1929 and Burton, 1937), grey (Lévi, 1963), bright brown (Lévi, 1969).
Ectosome: whispy multispicular bundles of tylotes, radiating towards the surface and scattered in the dermal membrane.
Choanosome: isodictyal reticulation of tracts of smooth styles, connected by spongin.
Spicules (Table 5, Fig. 30): Ectosomal tylotes

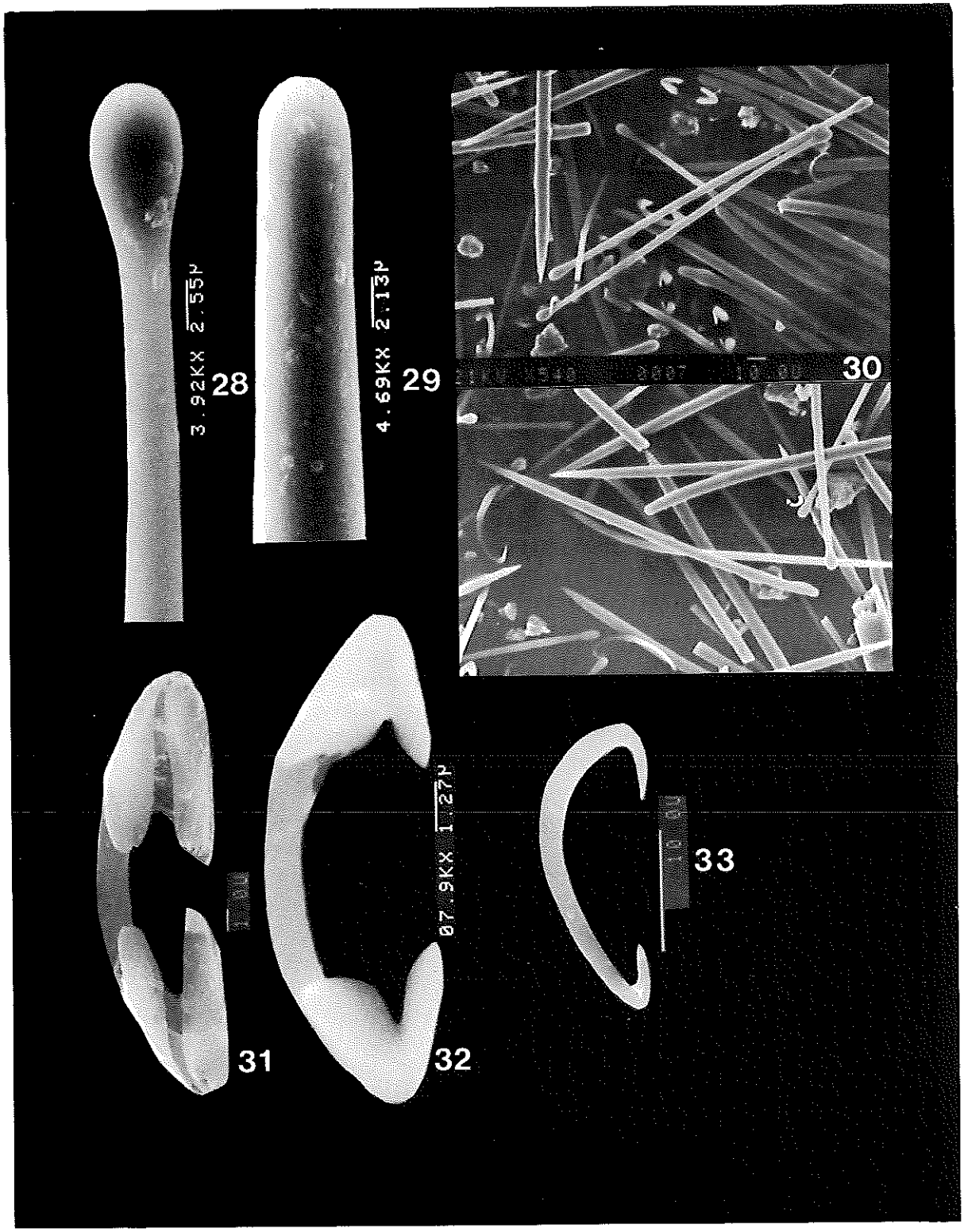
(Figs.28, 30): smooth, straight shaft, with rounded well-developed heads, 151-175 x 3-8 µm.
Styles (Figs. 29-30): smooth, with short sharp pointed end and a little bent towards the proximate end. The styles of the reexamined material from Burton (1933) are thicker in the middle of the shaft than at the rounded end, 110-200 x 5-9 µm.
Arcuate isochelas (Figs. 30-32): usual shape, two size categories, 10-16 (Fig. 32) and 20-28 µm (Fig. 31).
Sigmas (Figs. 30, 33): usual shape, two size categories, 12-21 (Figs. 30, 33) and 28-47 µm (Fig. 30).
Ecology: Intertidal down to 36 m (Lévi, 1963), on rocks (Lévi, 1969).
Distribution: Indonesia: Ternate; South Australia; Amoy, Formosa Strait; India: Krusadai Island, Gulf of Mannar, Madras + Vizagapatam, Bay of Bengal; South Africa, Stil Bay, Port Elizabeth; South Atlantic Ocean, Vema Seamount.

REMARKS

Burton & Rao (1932) reexamined *Halichondria isodictyalis* sensu Carter, 1886 and *Myxilla isodictyalis* Dendy, 1896, both from Port Philip Heads, South Australia, and found these two practically identical and to agree with the sponge described by Thiele (1903) from Ternate as *Hamigera ternatensis*. They observed that the Indo-Australian specimens differ from the holotype of *L. isodictyalis* from the West Indies in having chelas and sigmas differentiated into two sizes. Burton & Rao (1932) separated the two Indo-Pacific species *L. similis* Thiele (1899) and *L.ternatensis* Thiele (1903), by having one or two size categories of the microscleres. Burton & Rao (l.c.) also added *Lissodendoryx sinensis* Brøndsted (1929), as a synonym of *L. ternatensis* . Burton (1937) used *L. sinensis* as a valid species name, without referring to Burton & Rao (1932), in which this species was synonimized with *L. ternatensis*. We agree with Burton & Rao (1932) that *L. ternatensis* differs from *L. similis* in having two size categories of microscleres, instead of only one. In this respect *L. ternatensis* is close to *L.isodictyalis* which according to Van Soest (1984) also has two size categories of microscleres. Differences in shape of the chelas (compare with Van Soest, 1984: pl. V fig. 3), and the invariably smooth condition of the choanosomal styles in *L. ternatensis* are sufficient for the distinction of both as discrete species.

Lévi (1963, 1969) observed that *Myxilla pygmaea* Burton (1931: 34) from Kelso Junction, Natal, South Africa, resembles the type specimen of *Lissodendoryx ternatensis* from Ternate and his specimen from the Vema Seamount off South Africa reported as *L. ternatensis* . However, according to Burton (1931), *Myxilla pygmaea* has only one category of sigmas, while *Lissodendoryx ternatensis* has two categories. Lévi (1963, 1969) reported also only one category of sigmas. As in *L. ternatensis*, the chelas are divided into two size categories (21-27 and 12 µm). The other spicules (tylotes 150 x 6 µm, styles 105 x 4 µm), and characters resemble *Lissodendoryx ternatensis*. We were able to examine type material of *Myxilla pygmaea* Burton, 1931, BMNH 1933.7.4.16, and could not find any chelas at all in the microscopical slides; the sigmas we found were not divided into two categories (21-27 µm). The other spicules (tylotes 164-212 x 5-7 µm, styles 116-185 x 5-7 µm) are in accordance with the description. Possibly, the South African material belongs to a closely related but separate species which would then be named *Damiriella* or *Lissodendoryx pygmaea*.

Another species associated with *L. ternatensis* is *Myxilla jacksoniana* Von Lendenfeld (1888) from East Australia. Hallmann (1914) redescribed this species as *Lissodendoryx jacksoniana*. Burton (1936) reported it from South Africa as *Lissodendoryx isodictyalis* var. *jacksoniana*. Lévi (1963) suggested that this latter record should be assigned to *Lissodendoryx ternatensis*. Hechtel (1965: 40) remarked that *L. jacksoniana* differs sufficiently from *Lissodendoryx isodictyalis* to warrant its retention as a separate species, because its choanosomal skeleton includes small strongyles in addition to the usual styles. The description of *L. jacksoniana* by Von Lendenfeld is as follows: "Massive, lobose sponges with conspicuous oscula. The skeleton consists of a very regular network of single spicules, which only here and there combine to form loose and irregular bundles of two or more series of spicules. The supporting spicules are styli, slightly curved, sharp, and abruptly pointed at one end, and very slightly thickened at the other; they attain a length of 200 µm and a thickness of



Figs. 28-33: *Lissodendoryx ternatensis* (Thiele, 1903), SEM photographs of spicules of ZMA POR. 1518. 28. detail of tylote, 29. detail of style, 30. overviews of spiculation showing tylotes (upper picture), styles (lower picture), large and small chelas (upper picture), small sigmas (upper picture) and large sigmas (lower picture), 31. larger category of chela, 32. small category of chela (note that scale is about 2.5 x that of larger chela), 33. small category of sigma.

Table 5. Spicule lengths in µm of *Lissodendoryx ternatensis* specimens. * = original data, ** = our measurements.

	tylotes	styles	isochelas	sigmata
Thiele, 1903*	175	180	12/20	17/35
Lévi, 1963*	160-180	115-190	15-16/22-24	30
Lévi, 1969*	175-190	110-140	10-11/20-22	24-30
Brøndsted, 1929*	160-200	160-200	12-15/27	12/35
Burton, 1937*	160-280	160-200	12/27	12/35
BMNH 1932:7:RS:38**	151-184	140-184	10-14/23-29	19-21/28-33
ZMA POR. 1518**	188-202	155-195	14/28	18/46

7 µm. Besides these also a few tylota are found, which, however, are very scarce; these are 200 µm long and 4 µm thick. Their ends are very slightly thickened, some of them might in fact be regarded as strongyla. Microscleres are very abundant throughout the whole of the sponge; these are sigmata and chelae. The sigmata are prevalent and have very abruptly recurved pointed ends; they are on average 40 µm long and 2 µm thick. The chelae are about a third as large as the sigmata". We were able to examine Von Lendenfeld's material of *Lissodendoryx jacksoniana* (BMNH 1887.4.27.95), and Burton's material of *Lissodendoryx isodictyalis* var. *jacksoniana* (BMNH 1936.11.26.33). These two specimens are probably conspecific. The choanosomal skeleton includes smooth styles (148-170 x 4-7 µm), and strongylote modifications of the choanosomal styles (90-154 x 4-7). The ectosomal spicules are the usual tylotes (151-207 x 3-6 µm). Microscleres are two size categories of arcuate isochelas (10-11 and 16-23 µm) and one rather variable size category of sigmas (37-64 µm), bigger than the chelas. This makes it close to *L. ternatensis*, but pending further information we refrain from synonymization on account of the strongyles and the single sigma category.

Lissodendoryx timorensis n. sp. Figs. 34-37

MATERIAL EXAMINED

Holotype, ZMA POR 1471, Siboga Exped., Stat. 282, Indonesia, anchorage between Nusa Besi and the NE-point of Timor, trawl, dredge and reef exploration, 27-54 m; bottom sand, coral and lithothamnion.

DESCRIPTION

Only a dry specimen is available which makes it difficult to make an adequate description. The specimen is fragmented and consists of a mass of anastomosing little branchlets, which could represent a macerated skeleton of spicule tracts. Total size approximately 3 by 3 cm; individual branchlets 2-3 mm in diameter, but at the points of anastomosis flattened masses of 5 mm wide are formed. The colour is whitish grey. The ectosomal spicules are masses of microscleres and some tylotes in bundles. The choanosomal architecture is a coarse reticulation of thick tracts of smooth styles forming large, irregular meshes. Possibly, a finer reticulation of thinner tracts has been present, originally. Microscleres extremely numerous, crowding the tracts. Single size categories of arcuate isochelas and sigmata.

Spicules: Ectosomal tylotes (Fig. 34): smooth, with barely developed heads, sometimes inequiended, 280-360 x 8-10 µm.

Styles (Fig. 35): smooth, curved, often tapering, 395-560 x 16-22 µm.

Arcuate isochelas (Fig. 36): with sharp teeth, almost unguiferate: 16-23 µm.

Sigmas (Fig. 37): large, thick, strongly curved, somewhat angular, occasionally flagellar: 56-93 µm.

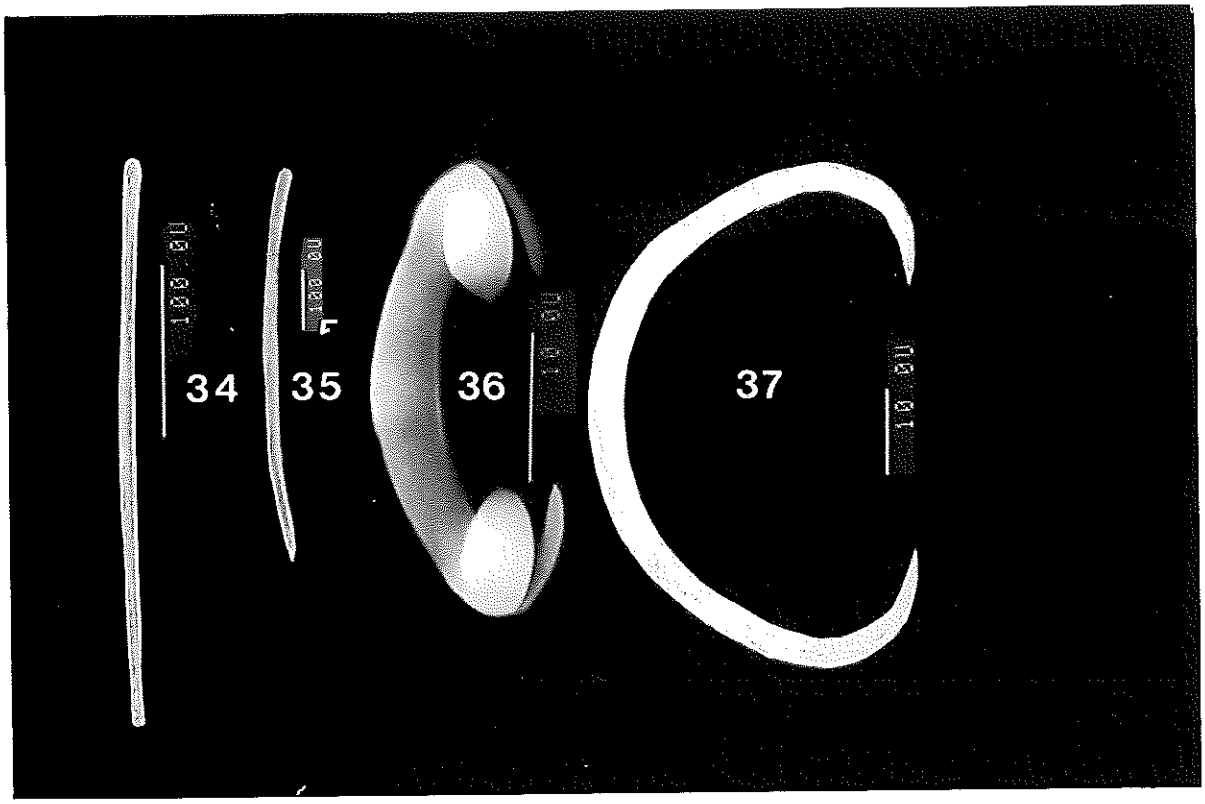
Ecology: Habitat sand, coral and lithothamnion, at 27-54 m.

Distribution: Timor, Indonesia.

Etymology: named after the type locality.

REMARKS

The present specimen belongs to a group of



Figs. 34-37: *Lissodendoryx timorensis* n.sp., SEM photographs of spicules of the holotype, ZMA POR. 1471.34. tylote, 35. style (note that scale is approximately 3 x larger than 34), 36. chela, 37. sigma.

Lissodendoryx species with large sizes of the tylotes, styles and sigmas. Among the Indo-Malayan species, *L. paucispinata* is closest. It differs in having spined styles and a larger category of isochelas. A nearby related species is New Caledonian *L. catenata* Lévi, 1993; this has two sizes of chelas and clearly smaller sigmas.

Lissodendoryx microchelifera n.sp.
Figs 38-42.

MATERIAL EXAMINED

Holotype ZMA POR. 8041, Snellius II Exped. stat.96/II/17, Indonesia, N Cape Komodo, 1-4 m depth, coll. R.W.M. van Soest, 19-IX-1984.

DESCRIPTION

The specimen inhabits holes in a massive knoll-shaped bryozoan. There is at least one bigger round hole which may have served as an oscule. The new species manifests itself as a thin crust barely 2 mm in thickness investing the hollow inside of the bryozoan. The surface of it appears smooth.

Ectosome: charged with bundles of tylotes, both tangentially and perpendicularly arranged. In between numerous microscleres are found.

Choanosome: the bundles of tylotes are progressively replaced by a rather confused reticulation of bundles of strongyles, 2-3 in diameter.

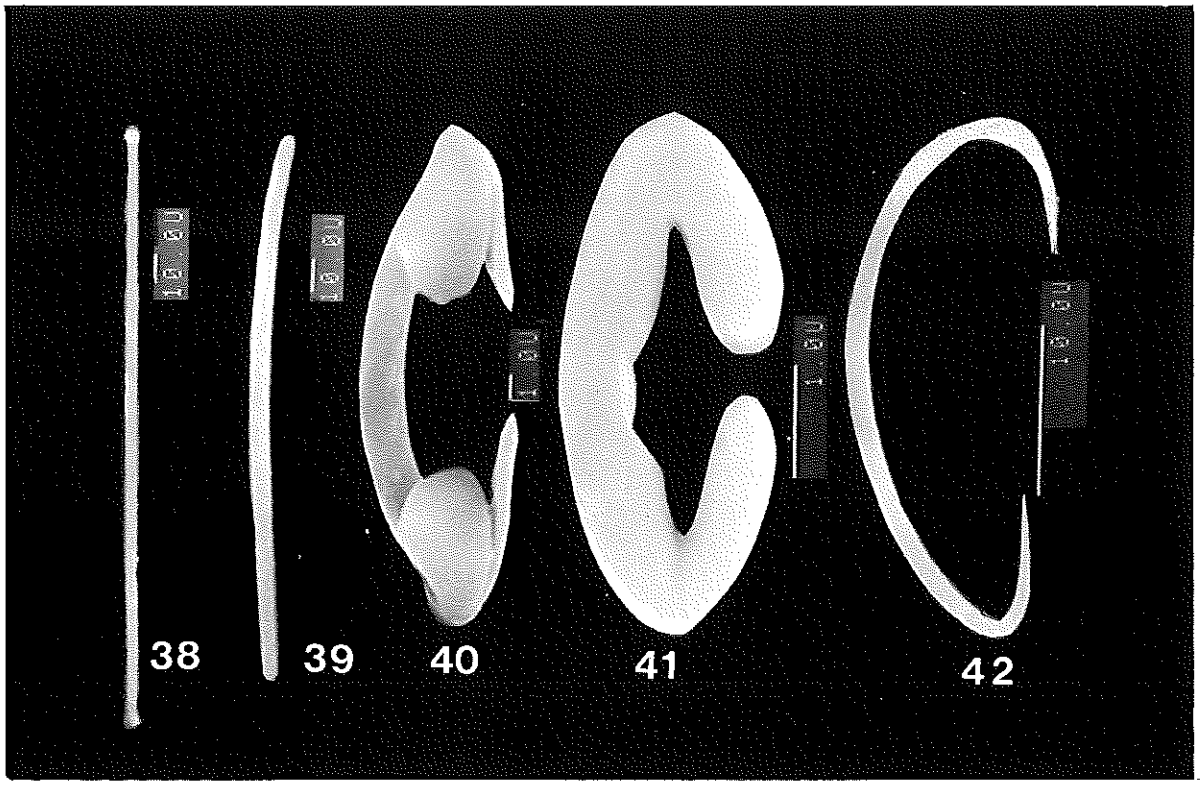
Spicules: Tylotes (Fig. 38), smooth, with clearly developed perfectly rounded tyles: 174 - 211 by 4 - 9 μm.

Strongyles (Fig. 39), smooth, equally thin over their whole length: 169 - 183 by 4 - 5 μm.

Arcuate isochelas (Figs. 40-41) in two size categories, both very small: 4 - 6 (Fig. 41) and 11 - 18 μm (Fig. 40).

Sigmas (Fig. 42) of common shape: 27 - 30 μm.

Etymology: the name refers to the unusually



Figs. 38-42: *Lissodendoryx microchelifera* n.sp., SEM photographs of the holotype, ZMA POR. 8041. 38. tylote, 39. strongyle, 40. large category of chela, 41. small category of chela (note that scale is approximately 4 x smaller than 40), 42. sigma.

small chelas.
Ecology and distribution: cryptic habitat (inside bryozoan knoll) in shallow reefs. Only known from the type locality on the north coast of Komodo Island, Indonesia.

REMARKS

The new species stands out among the known Indo-Pacific species of *Lissodendoryx* by its possession of choanosomal smooth strongyles. In this respect the new species seems related to the West-Indian *Lissodendoryx strongylata* Van Soest, 1984. The habit and remaining spicules of the latter, however, differ rather strongly, so close relationship is uncertain. The tiny chelas are quite characteristic and not found in any other *Lissodendoryx*; technically they are palmate rather than arcuate. However, their shape is unlike the usual palmates of microcionid or mycalid Poecilosclerida and we assume they constitute a parallel development.

KEY TO THE INDO-MALAYAN SPECIES OF *LISSODENDORYX*

1 - Choanosomal spicules not including styles 2
- Choanosomal spicules including (acantho)styles 3
2 - Choanosomal spicules oxea ..... *L. aspera*
- Choanosomal spicules strongyles..... ..... *L. microchelifera* n.sp.
3 - Styles always with spines; raphides present ....*L. grata*
- Choanosomal spicules include smooth styles 4
4 - Choanosomal spicules include both smooth and spined styles ..... *L. paucispinata*
- Choanosomal spicules only smooth 5
5 - Styles > 300 µm .....*L. timorensis* n.sp.
- Styles < 230 µm 6
6 - One size category of microscleres ..... *L. similis*
- Two size categories of microscleres ..... *L. ternatensis*

BIOGEOGRAPHY

From Table 6 it is apparent that several species so far seem to be endemic to the Indo-Malayan

area. *L. paucispinata* has been reported from Indonesia and Kerguelen Island, but the latter may be a misindentification. *L. grata* is almost confined to the area, but occurs also slightly to the north in the Palau Islands. *L. timorensis* and *L. microchelifera* are known only from their Indonesian type localities. The other species, notably *L. aspera* and *L. ternatensis,* appear to be widespread in the Indo-West Pacific area, often including peripheral areas as South Africa and South Australia. Close (morphological) relationships with species from other areas are apparent for *L. similis* and *L.ternatensis* (close to West Indian *L. isodictyalis*) and *L. microchelifera* (close to West Indian *L. strongylata*).

DISCUSSION

Comments on other Indo-West Pacific *Lissodendoryx* records:

Lissodendoryx arenaria (Dendy, 1905)

Myxilla arenaria Dendy (1905: 169; Dendy 1916: 127; Dendy 1922: 89, from Ceylon, Beyt Isl., and Cargados Carajos Isl., Indian Ocean) and *Lissodendoryx arenaria* sensu Lévi (1969: 962, fig. 6b; Vacelet et. al. 1976: 62, fig. 41, from South Africa and Madagascar) do not conform to the restricted definition of *Lissodendoryx*. Having reexamined the type material of *Myxilla arenaria* we conclude that these specimens probably belong to the genus *Ectyomyxilla* , because they have (aniso)strongyles, echinating acanthostyles and anchorate isochelas.

Lissodendoryx arenaria Burton, 1936

Burton (1936: 143, fig. 1), described *Lissodendoryx arenaria* n.sp. from St. James, South Africa. The skeleton was described as a mass of sand grains echinated by acanthostyli (70 x 7 µm) with strongylote to subtylote tornota (110 x 3 µm). These tornota look like tylotes in his drawing, as the ends are swollen. Also the chelas (10-21 µm) look like typical *Lissodendoryx* chelas, as they are drawn like arcuate isochelas. The sigmas (21-29 µm) were not pictured. We reexamined the type material of *Lissodendoryx arenaria* sensu Burton 1936, and we conclude that it is a valid species of the genus *Ectyodoryx* with sand grains replacing the choanosomal styles. Our measurements: tylotes (98-126 x 1.5 -3 µm), echinating acanthostyles (45-54 x 7-8 µm), two size categories of arcuate isochelas (11 and 16-23 µm) and one size category of sigmas (22-31 µm).

Lissodendoryx baculata Topsent, 1897

Lissodendoryx baculata Topsent 1897 from Ambon, Indonesia, does not conform to the present definition of *Lissodendoryx,* because it has tornostrongyles instead of ectosomal tylota. The other spicules are smooth styles, arcuate isochelas, sigmata and raphides. There is only one record of *L. baculata* . In 1981, Desqueyroux-Faundez has revised the sponges collected by M. Bedot and C. Pictet(1890) which were described by Topsent (1897), but no specimen of *L. baculata* was found in the collection.

Lissodendoryx bifacialis Lévi & Lévi, 1983

This species, originally described from New Caledonia is a suspected *Ectyodoryx*, because specimens collected in Indonesia by the Snellius II Exped. (ZMA POR. 9147, 9318, 9327, all from stat. 51, NE coast of Sumba, E. of Melolo, 9° 53.5' S 120° 42.7' E., depth 75-90 m) answering in all details to Lévi & Lévi's specimen, possessed echinating acanthostyles resembling the larger choanosomal acanthostyles but smaller in size. The arcuate chelae verge toward the unguiferate condition. A second record of this species from New Caledonia is mentioned in Lévi (1993).

Lissodendoryx infrequens (Carter, 1881)

Halichondria infrequens Carter, 1881, was made the type of the genus *Paramyxilla* Dendy (1905), but is here considered a member of *Lissodendoryx*. It has choanosomal acanthoxea with the usual complement of ectosomal megascleres and microscleres. Possibly, *Paramyxilla* may be employed as a subgenus of *Lissodendoryx*. Locality: Gulf of Mannaar, India.

Table 6: World distribution of Indo-Malayan *Lissodendoryx* species.

Species	Source	Locality
grata	Thiele, 1903	Ternate, Indonesia
	De Laubenfels, 1954	Koror, Palau Isl., West Pacific Ocean
	present paper	East of Komodo, Indonesia
paucispinata	Ridley & Dendy, 1886	New Guinea, Little Ki Isl., Indonesia
	Boury-Esnault, 1982	Kerguelen Isl., Subantarctic
aspera	Bowerbank, 1875	Straits of Malacca
	Ridley, 1884	Port Jackson, New South Wales, Australia
	Dendy, 1896	Sorrento Reef,Port Phillip Bay, Victoria, Australia
	Topsent, 1897	Ambon, Moluccas, Indonesia
	Lindgren, 1898	Cochin-China, S. Vietnam, Indo-China.
	Thiele, 1903	Ternate, Moluccas, Indonesia
	Hentschel, 1911	Port Royal, Fremantle, Western Australia
	Hentschel ,1912	Aru-Isl., Indonesia
	Dendy & Frederick, 1923	Wooded Isl., Abrolhos, Western Australia
	De Laubenfels, 1936b	Pacific coast of Panama
	De Laubenfels, 1950	Oahu Isl., Hawaiian Islands
	De Laubenfels, 1951	Hawaiian Islands
	Lévi, 1958	Abu Latt Isl., nearby Al Lith, Red Sea
	Lévi, 1965	Dahlak Archipelago, Red Sea
	Thomas, 1973	Mahé Isl., Seychelles, W Indian Ocean
	Thomas, 1976	Zanzibar harbour, Zanzibar Isl., Tanzania
	Bergquist, 1977	Hawaiian Islands
	Thomas, 1979	Inhaca Isl., Maputo Bay, Mozambique
	Thomas, 1981	Mahé Isl., Seychelles, W Indian Ocean
	present paper	Flores + Jedan Isl., Aru Isl. + Java, Sumba, Indonesia
similis	Thiele, 1899	Kema, Celebes, Indonesia
	Topsent, 1897	Ambon, Moluccas, Indonesia
	Burton & Rao, 1932	Mergui Arch, Bay of Bengal, Burma
	Ali, 1956	Madras, Bay of Bengal, India
	present paper	Jedan Isl., Aru Isl., Indonesia
ternatensis	Thiele, 1903	Ternate, Moluccas, Indonesia
	Carter, 1886	Port Phillip Bay, Victoria, Australia
	Dendy, 1896	Sorrento Reef, Port Phillip Bay, Victoria, Australia
	Brøndsted, 1929	Amoy (Xiamen), Formosa Strait, China
	Burton & Rao, 1932	Madras + Vizagapatam, Bay of Bengal, India
	Burton, 1933	Stil Bay, South Africa
	Burton, 1937	Krusadai Isl., India, Gulf of Mannar, India
	Lévi, 1963	Port Elizabeth area, South Africa
	Lévi, 1969	Vema Seamount, South Atlantic Ocean
	present paper	Balikpapan, Kalimantan, Indonesia
timorensis	present paper	NE of Timor, Indonesia
microchelifera	present paper	N Cape Komodo, Indonesia

Lissodendoryx roxasi De Laubenfels (1935)

Lissodendoryx roxasi De Laubenfels (1935: 330, pl. I fig. 3) is an irregular cavernous sponge, 2 x 6 cm, with elastic consistency. The skeletal architecture is very coarse with (spicule?-) tracts of 1 mm diameter and meshes of 2 mm. The ectosomal tylotes are 220 x 3 µm. Choanosomal megascleres are acanthostyles 155 x 8 µm, many of them echinating the choanosomal tracts. Microscleres arcuate isochelae of two sizes, 36 and 16 µm, and rare sigmas of 70 µm. Locality Puerto Galera, Philippines.

On paper this sounds as an *Ectyodoryx*, but a specimen ZMA POR. 2228 collected by the Siboga Expedition, stat. 125 (off Sawan, Siau Island, Indonesia), identified as *Stylostichon roxasi* by Burton (MS), and conforming in many details to De Laubenfels' description, probably belongs to the anchinoid genus *Phorbas*. No sigmas were found in the Indonesian species, but sizes and categories of the remaining spicules, as well as the cavernous structure, are similar. It is unlikely that De Laubenfels' species belongs to *Lissodendoryx* in the restricted sense used here.

Lissodendoryx tawiensis Wilson, 1925

This species described from the Philippines does not conform to the present definition of *Lissodendoryx* . It has no sigmas and no ectosomal tylotes; microscleres are toxas and palmate isochelas. It conforms to the genus *Antho* Gray, 1867 of the family Microcionidae.

Lissodendoryx catenata Lévi, 1993

A deep-water species from New Caledonia with large spicules, similar to *L. timorensis* n.sp. It differs from the Indonesian species by having two sizes of isochelas and clearly smaller sigmata.

Lissodendoryx stylophora Lévi & Lévi, 1983

A deep-water species from New Caledonia, which does not answer to the here employed definition of *Lissodendoryx*, as it lacks ectosomal tylotes in stead of which it has bouquets of small subtylostyles over a choanosomal skeleton of longer styles. We were able to examine a paratype of this species. Its spiculation is similar to that of *Echinostylinos reticulatus* Topsent, 1928, described also from New Zealand by Bergquist & Fromont (1988). It is quite possible that the New Zealand record and the New Caledonian species are conspecific and that both are different from the Azorean type of *E. reticulatus*, in which case *E. stylophora* would be the correct name for this species.

Lissodendoryx tubiformis Lévi, 1993

A deep-water species from New Caledonia, which does not answer to the here employed definition of *Lissodendoryx*, as it lacks ectosomal tylotes in stead of which it has bouquets of small subtylostyles over a choanosomal skeleton of longer styles. Like the previous species, its generic allocation seems to be the genus *Echinostylinos*.

MEMBERSHIP OF THE GENUS *LISSODENDORYX*

Out of 80 nominal species found in the literature, the following species conform to the presently employed definition of the genus *Lissodendoryx* :
L. aspera (Bowerbank, 1875); *L. catenata* Lévi, 1993; *L. colombiensis* Zea & Van Soest, 1986; *L. complicata* Hansen, 1885; *L. cratera* Row, 1911; *L. damirioides* Burton, 1959; *L. firma* Lambe, 1894; *L. fusca* Ridley & Dendy, 1886; *L. grata* Thiele, 1903; *L. hawaiiana* (De Laubenfels 1950 = junior synonym of *L. aspera*); *L. indistincta* Fristedt, 1887; *L. infrequens* (Carter, 1881); *L. isodictyalis* Carter, 1882; *L. isodictyalis paucispinata* Topsent , 1928; *L. jacksoniana* Lendenfeld 1888; *L. microchelifera* n.sp.; *L. mollis* Ridley & Dendy, 1886; *L. monticularis* Baer, 1906; *L. noxiosa* De Laubenfels, 1930; *L. oxytes* De Laubenfels 1954 (=junior synonym of *L.grata*); *L. paucispinata* Ridley & Dendy, 1886; ?*L. pygmaea* (Burton 1931); *L. schmidti* (Ridley, 1884)(= junior synonym of *L. aspera*); *L. sigmata* (De Laubenfels 1949); *L. similis* Thiele, 1899; *L. sinensis* Brøndsted, 1929 (= junior synonym of *L. ternatensis*); *L. stephensoni* Burton, 1936; *L. strongylata* Van Soest, 1984; *L. ternatensis* Thiele 1903; *L. timorensis* n.sp.; *L. vicina* Lundbeck, 1905.

The following species found in literature do have

smooth tylotes and arcuate isochelas, but lack the sigmas. These species answer to the definition of the genus *Damiriella* Burton 1935, but may eventually be considered *Lissodendoryx* which lost their sigmata:

L. behringi Koltun, 1958; *L. buchanani* Topsent, 1913; *L. cavernosa* Topsent, 1892; *L. ciocalyptoides* Burton, 1959a; *L. digitata* Ridley & Dendy, 1886; *L. kyma* De Laubenfels, 1930; *L. laxa* De Laubenfels, 1935; *L. lobosa* Lundbeck, 1905; *L. papillata* Dendy, 1922 (as *Hamigera*, is a *Lissodendoryx* according to Wiedenmayer 1989); *L. papillosa* Koltun, 1958; *L. rarus* Hoshino, 1981; *L. simplex* Topsent, 1904; *L. sophia* Fristedt, 1887; *L. stipitata* Arnesen, 1903; *L. tubicola* Burton, 1959a.

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