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New species of *Zyzzya*, *Cornulella*, *Damiria*, and *Acheliderma* (Porifera: Poecilosclerida), with a review of fistular genera of Iophonidae

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Keywords: Caribbean coral reefs, Seychelles reefs, sponges, Poecilosclerida, Iophonidae, fistule growth form, excavating growth form

Abstract

New sponge species belonging to the closely related fistular genera *Zyzzya*, *Cornulella*, *Damiria*, and *Acheliderma* are described from reef habitats off the coasts of Colombia, Bonaire and Curaçao in the southern Caribbean. With very few exceptions these sponges are small to tiny specimens inhabiting crevices and other cryptic habitats; some may be excavating. For comparison both published and unpublished material belonging to these genera from other parts of the world was examined, and this yielded several nomenclatorial changes and a further three new species from the Indian Ocean. The new species are: *Zyzzya invemar* (Caribbean), *Cornulella santamartae* (Caribbean), *C. tyro* (Seychelles), *C. amirantensis* (Seychelles), *Damiria leonorae* (Caribbean), *D. toxifera* (Seychelles) and *Acheliderma lisannae* (Caribbean). All species belonging to these genera, as well as to the closely related Indo-Pacific genus *Paracornulum*, are briefly diagnosed. The genera and species of this group are found to be distributed over tropical and subtropical waters of all three oceans. The five genera were so far of controversial systematic allocation, although their close relationship with *Cornulum* was generally accepted. The recently revived family Iophonidae is demonstrated to be the likely assemblage for them. A brief survey of Iophonidae genera is presented and a preliminary phylogenetic analysis of the fistular genera is attempted. Although several parts of the phylogenetic relationships remain unsolved, it is nevertheless clear that in all genera the closest relatives are not found in adjacent areas, but are often disjunct.

Résumé

De nouvelles espèces de Spongiaires appartenant aux genres fistuleux et nettement apparentés *Zyzzya*, *Cornulella*, *Damiria* et *Acheliderma* sont décrites d'habitats récifaux au large des côtes de Colombie, Bonaire et Curaçao (Caraïbes du Sud). A très peu d'exceptions près, ces Spongiaires sont des exemplaires petits ou minuscules peuplant des crevasses et d'autres habitats cryptiques; il est possible que certains puissent perforer le substratum. Du matériel publié ou inédit d'autres parties du monde, appartenant à ces genres, a été examiné en vue de comparaisons, ce qui a abouti à plusieurs changements nomenclatoriels et à la découverte de trois autres nouvelles espèces de l'Océan Indien. Les nouvelles espèces sont: *Zyzzya invemar* (Caraïbes), *Cornulella santamartae* (Caraïbes), *C. tyro* (Seychelles), *C. amirantensis* (Seychelles), *Damiria leonorae* (Caraïbes), *D. toxifera* (Seychelles), et *Acheliderma lisannae* (Caraïbes). Pour toutes les espèces appartenant à ces genres ainsi qu'au genre Indo-Pacifique prochement apparenté *Paracornulum*, on donne des diagnoses succinctes. Genres et espèces de ce groupe sont distribués dans les eaux tropicales et subtropicales des trois océans. La position systématique des cinq genres a été jusqu'à présent controversée; cependant, leur proche parenté avec *Cornulum* avait généralement été acceptée. On démontre que c'est la famille des Iophonidae (récemment ressuscitée) qui pourrait vraisemblablement regrouper ces genres. On passe brièvement en revue les genres de cette famille, avec un essai d'analyse phylogénétique préliminaire des genres fistuleux. En dépit du fait que les relations phylogénétiques restent en partie obscures, it est clair que dans tous ces genres les relations de proche parenté dépassent les limites des zones marines contiguës: elles sont souvent disjointes.

Introduction

Shallow-water marine distributions of sponge genera may be summarized into four patterns, viz. Tethyan, Indo-Australian, northern cold waters and southern cold waters (Van Soest, 1994). Tropical sponge genera are either disjunct Tethyan, viz. occurring in the West-Indian-Caribbean-Brazilian areas, potentially in Tropical West Africa, potentially in the East Pacific and in the Indo-West Pacific, or they have their centre in Indo-Australian waters extending outwards to the Red Sea and East

Africa and to the Central Pacific. The former pattern is the more numerous. These patterns are explained as having originated from the former shallow Tethys Ocean on the one hand and from a former isolated Australia on the other. Two closely related iophonid genera, viz. *Zyzzya* and *Cornulella*, up to now are classed as Indo-Australian, because they are known from Indian Ocean and Indo-Australian localities but have not been reported from any Atlantic area. However, during a minutely executed quantitative survey of the sponge and coral faunas of Caribbean Colombian reefs by the third author, specimens of both Indo-Pacific genera were discovered. Additional material from Bonaire and Curaçao was found by students of the University of Amsterdam (cf. Meesters et al., 1991). This shows both genera to belong to the Tethyan distribution pattern, which was also established for the closely related genus *Damiria*, and indeed the majority of the warm-water sponge genera.

The distributions of the genera *Acheliderma*, *Astylinifer*, and *Fusifer* are so far considered ill-known since only single records are known. Recently, Ms. Lisanne Arts picked up a species of fistular Iophonidae uniting characters of these three genera and accordingly it is proposed below to unite them. Combined, distribution records of the genus *Acheliderma* s.l. fall now into the Tethyan pattern as well.

The status and family assignment of *Zyzzya*, *Cornulella*, *Acheliderma*, and *Damiria* is controversial. Since all have fistules and tylote ectosomal megascleres, they were traditionally included in the family Coelosphaeridae (Topsent, 1928). Lévi & Lévi (1983) separated coelosphaerids with palmate isochelae from those possessing arcuate isochelae, and erected a family Cornulidae for the former. They were followed by Bergquist & Fromont (1988) (though not by Hooper & Krasochin, 1989). Finally, Hajdu et al. (1994) extended Lévi & Lévi's Cornulidae to include also non-fistular genera (e.g., *Acarnus*, *Iophon*). Arguments are, that these genera compromise an otherwise homogeneous composition of the family they are usually assigned to, i.e., Myxillidae s.l. The latter assemblage contains predominantly sponges lacking toxas, and possessing "tridentate" chelas (arcuate and anchorate chelas) and sigmas. *Acarnus* has palmate isochelas and abundant toxas, *Iophon* has palmate anisochelas lacking the toxas; both share with the above-mentioned Cornulidae the lack of sigmas and the possession of ectosomal tylotes with spined heads. For reasons of priority the Cornulidae + *Iophon* + *Acarnus* assemblage will have to be named Iophonidae Burton, 1929.

It is the purpose of this study to describe new southern Caribbean material of *Zyzzya*, *Cornulella*, *Acheliderma*, and *Damiria*, and compare it with Indian Ocean specimens of these genera recently collected during the Indian Ocean Program of the Netherlands Foundation of Sea Research. This comparison yielded the discovery of several new species from the Indian Ocean as well.

The phylogenetic position of these genera is considered in a discussion of all closely related fistule-bearing genera of the family Iophonidae.

Material and methods

Caribbean specimens described below were collected by Ms. M. Kielman, S. Zea and Ms. Lisanne Aerts in the course of surveys of the sponge and coral communities of the Santa Marta area, the Islas del Rosario reefs in the Cartagena area, and the Curaçao reefs (1988–1994). In addition, several specimens were collected by students of the University of Amsterdam studying the sub-rubble communities of Bonaire and Curaçao (cf. Meesters et al., 1991). Material was often very limited, because all new species are small (a few millimeters in size), so microscopic sections and spicule mounts are important additional type material. All specimens and preparations are stored in the Zoölogisch Museum of the University of Amsterdam (ZMA); additional microscopic preparations are kept in the Instituto de Investigaciones Marinas (INVEMAR) Porifera collection (INV-POR).

For comparison, fistular iophonid specimens collected by R. van Soest in the reefs of Curaçao, Indonesia, the Seychelles (Indian Ocean) and off the Cape Verde Islands and Mauritania were studied, all incorporated in ZMA. In addition, the type specimens of *Suberites fuliginosus* Carter, 1879 (BMNH 1846:8:5:8), *Dyscliona davidi* Kirkpatrick, 1900 (BMNH 1900:10:19:2), *Cornulum dubium* Hentschel, 1912 (SMF 964), *Damiria simplex* Keller, 1891 (ZMB 310b) and *Heterocornulum virguliferum* Lévi & Lévi, 1983 (paratype, MNHN DCl. 2964) were borrowed from the London, Frankfurt, Berlin, and Paris museums, respectively. Slides of *Acheliderma lemniscata* Topsent, 1892 (D.T. 170) and *Astylinifer planum* Topsent, 1927 (D.T. 1288) were examined in the Paris museum.

Sections and spicule mounts were prepared in the usual way (cf. Van Soest et al., 1991). Spicule measurements are based on

25 spicules per category per specimen, unless otherwise indicated.

Systematic descriptions

Order Poecilosclerida Topsent, 1928

Suborder Microcionina Hajdu et al., 1994
Definition: Poecilosclerida with special ectosomal spicules with microspined heads; microscleres, if present, include palmate chelas and toxas, often in several categories of size and form.

Family Iophonidae Burton, 1929 sensu Hajdu et al., 1994
Definition: Microcionina with ectosomal terminally spined tylotes.

Genus *Zyzzya* De Laubenfels, 1936

Type species (by original designation): *Plocamia massalis* Dendy, 1922 (= jun. syn. of *Suberites fuliginosus* Carter, 1879, cf. below).
Definition (emended from Hooper & Krasochin, 1989): Iophonidae with verticillately-spined strongyles. Massive burrowing or cryptic encrusting growth form, with solid apical fistules or blind papillae. Ectosome consists of thick detachable crust of tangentially orientated tylotes bearing microspined heads. Choanosomal skeleton contains irregular, widely spaced multispicular tracts of tylotes ascending to the surface, between which is dispersed an irregular isodictyal reticulation of verticillately-spined strongyles. Microscleres, if present, are palmate isochelas and toxas.

Remarks. – The definition is slightly extended to include specimens with toxas (cf. below). The generic status separate from related genera such as *Cornulum*, *Cornulella*, and *Paracornulum*, is now confirmed by the discovery of an unequivocal second species. A possible threat of the generic name was posed by the description of Kirkpatrick (1900) of an excavating sponge *Dyscliona davidi*, which on paper looked almost certain to be a close relative of, if not conspecific with, *Zyzzya massalis* (Dendy, 1922) (and its senior synonym *Z. fuliginosa* (Carter, 1879)). However, reexamination of the type specimen of *Dyscliona davidi* made it clear that the principal spicules of that species are strongyles without any ornamentation (despite Kirkpatrick's allusion to occasional spines on them). The verticillately-spined spicules have not been found again in the specimen, and presumably are not proper to the sponge. It is our estimate that *Dyscliona davidi* is either an *Aka*, or more likely, the remnants of a bigger sponge such as *Oceanapia*. The verticillately-spined spicules likely would have been isolated spicules of an excavating sponge of the genus *Dotona*. There are at least two other excavating sponges of the genus *Cliona* present in the sample.

Verticillately-spined megascleres are already known from the Early Oligocene (Hinde & Holmes, 1892), but these are not likely to give evidence that the genus *Zyzzya* was already extant at that time. Similar spicules occur in unrelated genera, such as *Dotona* (Order Hadromerida?), *Agelas* (Order Agelasida), and *Hymeraphia* (family Raspailiidae). It is assumed that these spicules have evolved convergently in the different groups.

Description of the Caribbean species

Zyzzya invemar n. sp.
(Figs. 1, 7–14)

Holotype: ZMA POR. 10803, Pavitos, Islas del Rosario, off Cartagena, Colombian Caribbean, approx. 10°10′N 75°45′W, 25 m, coll. M. Kielman, field no. S116, 17-X-1990. Paratype: ZMA POR. 10804, same data as holotype, field no. S132. In addition to the type specimens there are 12 microscopic slides, both cuts and spicule mounts, incorporated in ZMA (6 slides of the holotype, 1 of the paratype) and INV-POR (3 slides of the holotype, 3 slides of the paratype).

Diagnosis. – Black excavating sponges; above-substrate growth form encrusting and fistular. Ectosomal skeleton consisting of a feltwork of tangentially arranged tylotes. The choanosomal skeleton is a mass of tylotes and acanthostrongyles. Microscleres are palmate isochelas and uncommon wide-curved toxas.

Description. – Both specimens are overgrown by the ubiquitous orange encruster *Eurypon laughlini* Díaz et al., 1987. The specimens were not discovered until rough cuts were examined in the lab for routine identification. The cuts revealed the presence of verticillately-spined acanthostrongyles, so far unknown from Caribbean sponges, next to the well-known spiculation of *E. laughlini*. Subsequent removal of the crusts of *E. laughlini* revealed the presence of a small black sponge sticking several fistules out of a crust covering a piece of coral debris. The sponge was found to have invaded the coral mass, and may tentatively be considered an excavating sponge. Galleries in the coral are irregular, not definitely identifiable. The fistules are somewhat swollen, hollow, with parchment-like smooth skin. The fistules are blind; no exhalant openings were observed. The whole sponge is delicate, easily damaged (and in fact broke into several pieces during manipulation). Size of largest fragment (Fig. 1) 70 mm^2, fistules up to 9 mm high, 2 mm in diameter.

Colour: Black, both immediately after collection and in preservation. The alcohol in which the specimen is kept shows a dark brown discolouration.

Ectosomal skeleton: A feltwork of crisscrossing tangential spicules, several layers thick.

Choanosomal skeleton: The upper parts of the fistules are devoid of spicular skeleton. The lower parts of the fistules and the endolithic parts contain a reticulate mass of spicules. The reticulation is unispicular, irregular, tight; in places the reticulation is absent and a mass of spicules remains. The spicules are of two types: tylotes and acanthostrongyles, both intermingled, seemingly without localization.

Spicules (Table I): Tylotes (Figs. 8, 11–12): most are more or less evenly thick along the entire shaft, smooth except for the heads. The heads are prominently spined over most of their length. In many cases, if not all, there is a distinct difference in the shape and spination of either end of a single spicule, possibly indicating a stylote ancestry. Size: 235–301 by 4–8 µm.

Acanthostrongyles (Figs. 7, 13–14): Without exception regularly verticillately-spined. A whorl has 6–8 spines; average number of whorls is 26 (range 20–34). Size: 173–215 by 4–10 µm.

Chelas (Fig. 9): Palmate isochelas with short alas, rare; size 19–23 µm.

Toxas (Fig. 10): Peculiarly wide-angled, resembling a thin version of the *Acarnus*-"oxhorn" toxa; size 49–71 µm long and 21–30 µm high.

Etymology. – Named after the host institute of S. Zea and M. Kielman, from where many sponge research projects have been and are being carried out.

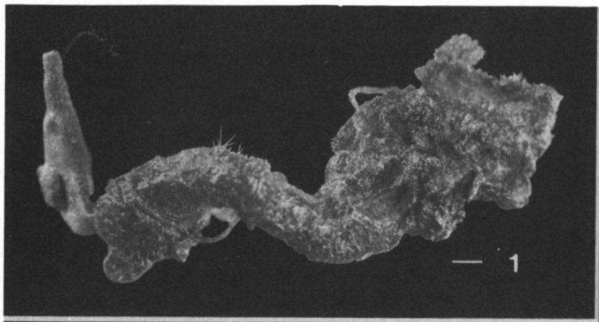
Ecology and distribution. – Deep reef cryptic habitats, so far known only from the Islas del Rosario.

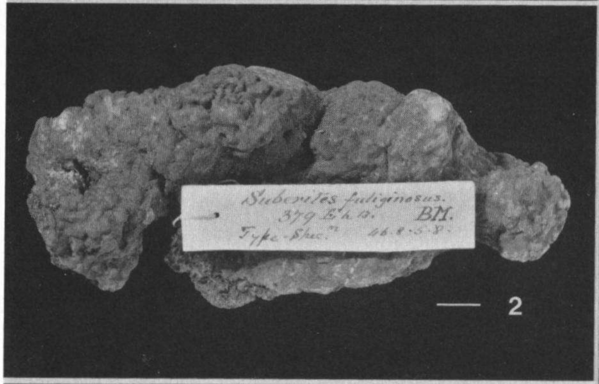
Remarks. – The new species differs clearly from the Indo-Pacific *Zyzzya* (cf. below) in the possession of toxas next to the chelas. In view of the fact that in related genera (e.g., *Cornulum*, *Cornulella*, *Acarnus*) toxas are common, this is not surprising, and it is not considered to be of enough weight to erect a separate genus for it next to *Zyzzya*. Nevertheless, the particular shape of the toxas is unusual, and with the exception of *Acarnus*, unknown from any Caribbean sponge. Careful comparison with sympatric *Acarnus* species (*A. nicoleae* Van Soest et al., 1991, *A. deweerdtae* Van Soest et al., 1991, and *A. innominatus* Gray, 1867) made it clear that there is some superficial resemblance with the category I toxa ("oxhorn") of that genus, but none of the three contain precisely similar toxas. This ruled out the possibility that the toxas might have been a contamination. Further corroboration for this is that both the holotype and the paratype had the toxas.

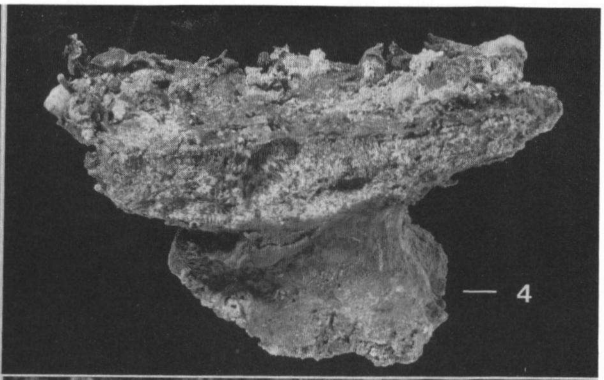
Further, more subtle differences lie in the shape of the tylote heads, which are more pronounced in the Caribbean species, and the more regularly spaced verticils of the acanthostrongyles. In most specimens from the Indo-Pacific, the acanthostrongyles are longer and thicker (Table I).

Review of Indo-Pacific Zyzzya *specimens*

Below brief descriptions of Indo-Pacific specimens are given, with an emphasis on specimens not treated by Hooper & Krasochin (1989):







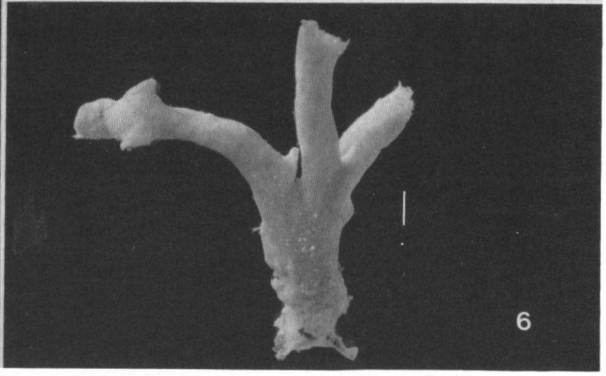


Fig. 1. Zyzzya invemar n. sp., fragment of holotype, ZMA POR. 10803, from the Islas del Rosario, Colombian Caribbean (scale bar: 1 mm) (photo: L.A. van der Laan).

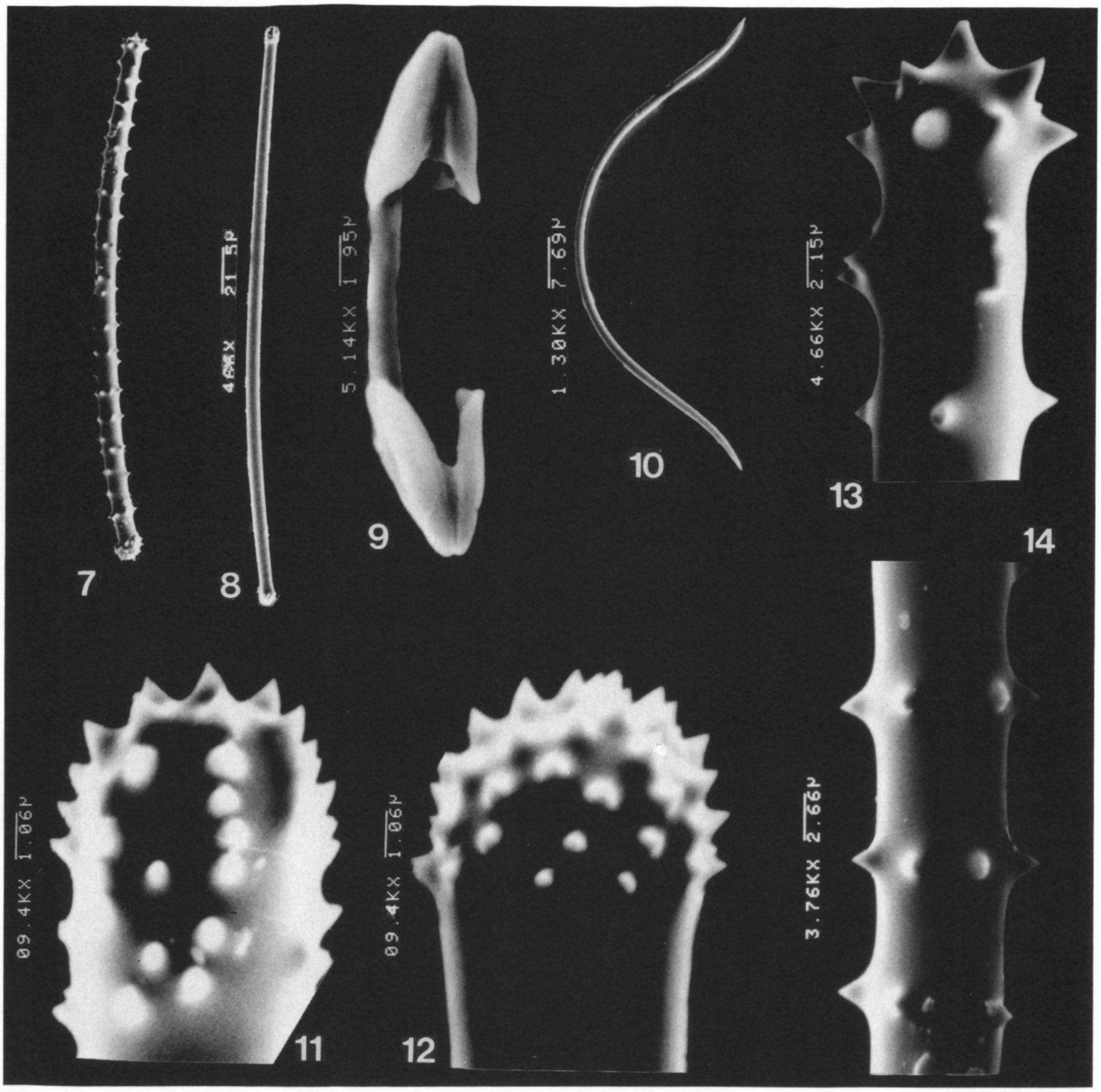
Fig. 2. Holotype of *Suberites fuliginosus* Carter, 1879, BMNH 1846:8:5:8, from Torres Straits, North Australia (scale bar: 10 mm) (photo: L.A. van der Laan).

Fig. 3. Cornulella tyro n. sp., fragmented holotype, ZMA POR. 10520, from the Seychelles (scale bar: 1 mm) (photo: L.A. van der Laan).

Fig. 4. Zyzzya fuliginosa (Carter, 1879), specimen ZMA POR. 10811, from the Seychelles, excavating and encrusting a plate-like coral; note black fistules on the upper surface of the coral (scale bar: 20 mm) (photo: L.A. van der Laan).

Fig. 5. Zyzzya fuliginosa (Carter, 1879), specimen ZMA POR. 10811, from the Seychelles, detail of excavated coral shown in Fig. 4 (scale bar: 1 mm) (photo: L.A. van der Laan).

Fig. 6. Damiria toxifera n. sp., fragment of holotype, ZMA POR. 10807, from the Seychelles (scale bar: 2.5 mm) (photo: L.A. van der Laan).



Figs. 7–14. Zyzzya invemar n. sp., holotype, SEM photos of spicules: 7, verticillately-spined acanthostrongyle; 8, tylote; 9, palmate isochela; 10, bow-shaped toxa; 11, detail of tylote head; 12, detail of opposite head of same tylote; 13, detail of distal part of verticillately-spined acanthostrongyle; 14, detail of middle part of verticillately-spined acanthostrongyle.

Suberites fuliginosus Carter, 1879: 347.
(Figs. 2, 15–17)

Type specimen: BMNH 1846:8:5:8 examined. Locality: Torres Straits, North Australia. A dry, black mass of 11 by 6 by 6 cm. No fistules or other projections; no substrate. The ectosomal skeleton is a feltwork of tylotes. The choanosomal skeleton is an irregular mass of tylotes intermingled with single acanthostrongyles. These are irregularly spined (Fig. 15), and often have a mucronate end. The heads of the tylote (Figs. 16–17) are mostly of unequal swelling and spination. Tylote size: 231–353 by 4–9 µm. Acanthostrongyles: 206–300 by 9–18 µm; 28–36 whorls of spines. No microscleres.

Comment: In view of the variability of the acanthostrongyle thickness and spination (cf. below), and in view of the black massive growth form, there is little doubt that this specimen is conspecific with and senior to Dendy's *Plocamia massalis*.

Table I. Spicule sizes (range, mean and standard deviation, in µm) of *Zyzzya* specimens. Data based on 25 measurements per specimen per spicule category unless otherwise indicated. For data derived from the literature only the range is given.

Specimen	tylotes	acanthostrongyles	no. verticils	chelas	toxas
Zyzzya invemar n. sp. Colombia, ZMA 10803	258-280.5(11.46)-301 / 4-5.2(1.13)-8	173-190.1(11.90)-215 / 5-7.6(1.25)-10	20-25.8-34	19-20.0(1.41)-23 (n=6)	49-58.4(6.53)-71 (n=10)
Zyzzya invemar n. sp. Colombia, ZMA 10804	235-255.9(13.17)-281 / 4-4.8(0.60)-6 (n=10)	167-183.0(10.67)-197 / 4-5.8(1.03)-7(n=10)	26-28-30 (n=3)	20-20.5-21 (n=2)	39 (n=1)
Suberites fuliginosus Carter N. Australia, BM 1846:8:5:8	231-303.3(29.79)-353 / 4-6.4(1.18)-9	206-260.2(24.20)-300 / 9-12.6(2.51)-18	28-31.9-36	not found	absent
Plocamia massalis Dendy Mauritius	286-408 / 6-14	155-232 / 4-15	unknown	14-20	absent
Damirina verticillata Burton Zanzibar	298-468 / 5-15	134-256 / 5-20	unknown	not found	absent
Paracornulum atoxa Vacelet et al. Madagascar	180-590 / 2-20	109-285 / 3-15	unknown	12-22	absent
Zyzzya massalis; Bergquist & Fromont, New Zealand	367-402 / 6-12	217-266 / 11-14	unknown	15-16	absent
Zyzzya massalis; Hooper & Krasochin, W. Australia	280-438 / 1.5-12	118-190 / 4-14	24	not found	absent
Zyzzya massalis; Hooper & Krasochin, Seychelles	305-418 / 3-12	148-242 / 5-15	unknown	not found	absent
Zyzzya fuliginosa; this paper ZMA POR. 8441, Fiji	184-267.4(23.31)-305 / 2-4.0(0.82)-5	155-213.2(19.50)-249 / 4-7.7(2.09)-11	unknown	not found	absent
Zyzzya fuliginosa; this paper ZMA POR. 9475, Papua N.G.	245-260.8(13.83)-282 / 5-5.5(0.87)-7 (n=10)	231-253.2(17.08)-289 / 9-10.4(1.07)-12(n=10)	unknown	not found	absent
Zyzzya fuliginosa; this paper ZMA POR. 10537, Seychelles	173-185.2(7.96)-197 / 2-2.4(0.49)-3(n=10)	184-201.0(9.53)-209 / 10-13.8(2.56)-17(n=10)	unknown	not found	absent
Zyzzya fuliginosa; this paper ZMA POR. 10816, Seychelles	192-227.8(16.35)-255 / 2-5.1(1.21)-7	212-230.4(10.42)-258 / 10-20.3(3.66)-28	21-23.1-25	not found	absent
Zyzzya fuliginosa; this paper ZMA POR. 10811, Seychelles	219-258.6(20.92)-292 / 2-4.7(0.92)-6	201-248.4(14.26)-265 / 21-24.9(2.58)-28	22-24.8-28	not found	absent
Damirina papillata Thomas India	159-277 / 1-5	117-176 / 6-12	10-15	absent	absent
Zyzzya papillata; this paper ZMA POR. 10815, Seychelles	166-218.3(18.97)-216 / 3-3.8(0.51)-4.5	150-159.2-168 / 5-5.6(0.57)-7	13-15.8-18	absent	absent

Plocamia massalis Dendy, 1922: 78.

Not examined. Locality: Mauritius, 200 m. Dark chocolate brown, massive, subspherical, with short fistules. The choanosomal skeleton is a subisodictyal reticulation of tylotes and acanthostrongyles; dispersed multispicular tracts occur as well. Spicule sizes (after Hooper & Krasochin, 1989): Tylotes: 286–408 by 6–14 µm; acanthostrongyles: 155–232 by 4–15 µm; palmate isochelas: 14–20 µm.

Comment: This specimen is closely similar to the specimen of *Suberites fuliginosus*, but for the presence of chelas.

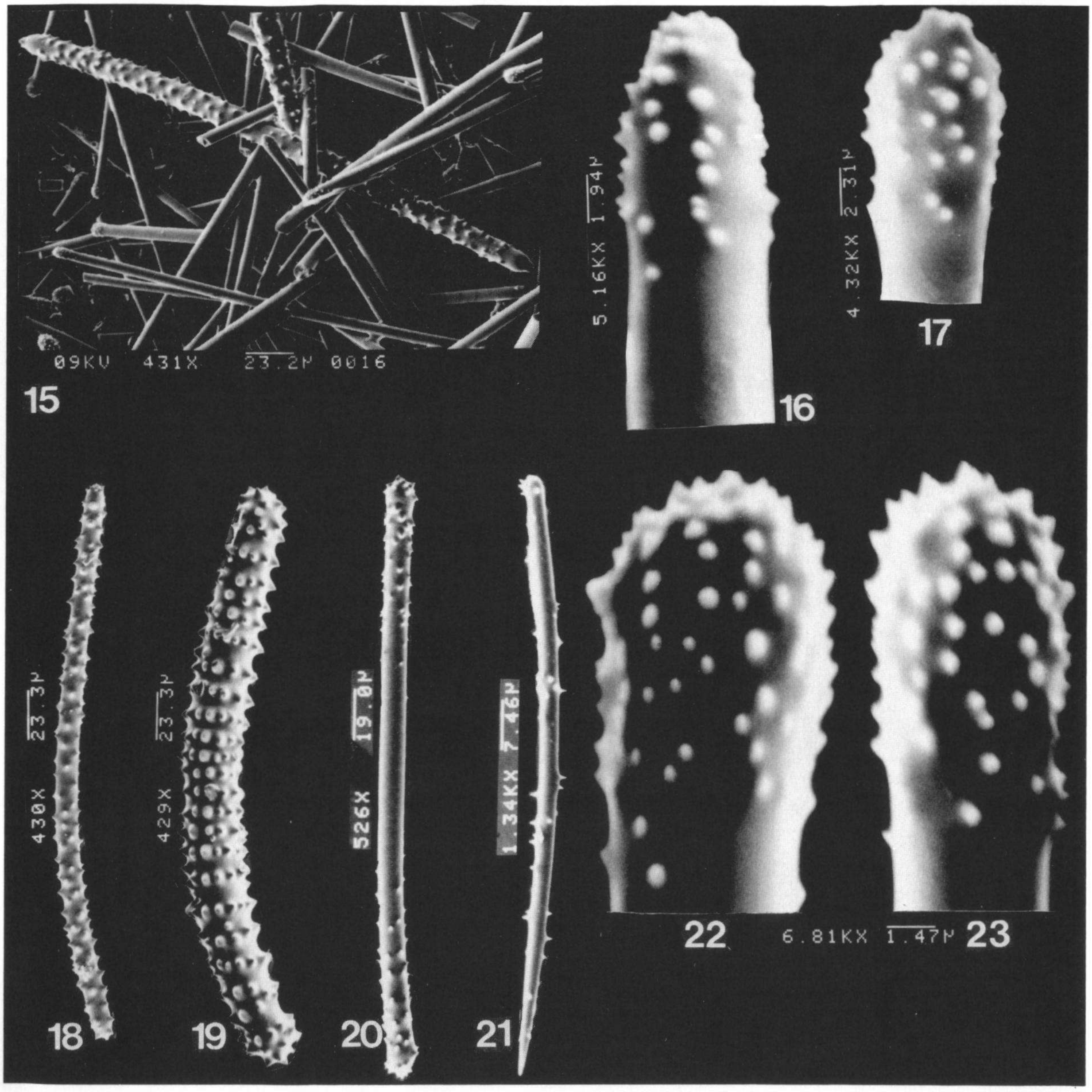
Damirina verticillata Burton, 1959: 240.

Not examined. Locality: Zanzibar, 113 m. Dark brown encrustation in dead coral; fistules present. The choanosomal skeleton is a unispicular reticulation. Spicule sizes (after Hooper & Krasochin, 1989): Tylotes: 298–468 by 5–15 µm; acanthostrongyles: 134–256 by 5–20 µm; no microscleres.

Comment: The robust acanthostrongyles also occur in other specimens (cf. below), and they seem to be graded continuously from thin to robust. In accordance with Hooper & Krasochin we consider this to be a junior synonym of *Z. fuliginosa.*

Damirina papillata Thomas, 1968: 252.

Type specimen not examined. Locality: Gulf of Mannar, India. An elaborate specimen was available for study from the Seychelles, ZMA POR. 10815, IOP-E stat. 792 (bis)/07, St.



Figs. 15–23. Zyzzya fuliginosa (Carter, 1879), SEM photos of spicules of various specimens: 15, acanthostrongyles and tylotes of holotype of *Suberites fuliginosus*; 16, detail of head of tylote; 17, detail of opposite head of same tylote; 18, acanthostrongyle of ZMA POR. 9745; 19, do. of ZMA POR. 10811; 20, do. of ZMA POR. 8441, with weakly developed spination; 21, do., stylote modification; 22, detail of tylote head of ZMA POR. 10811; 23, detail of opposite head of same tylote.

François Atoll, Amirantes, 3 m depth, 07°5′S 52°44′E, 6-I-1993. Several fistules growing erect on a coral rock, with their base rooted deep in the coral. Colour yellow alive, deep brown in alcohol (Thomas's specimen), or transparent (Seychelles specimen). The ectosomal skeleton consists of tangentially arranged tylotes with spined heads. In the type specimen the choanosomal skeleton is described as a reticulation of triangular meshes made by acanthostrongyles; longitudinal multispicular tracts of acanthostrongyles are also present. In the Seychelles specimen the acanthostyles are irregularly distributed, singly or in two's. Spicule sizes: Tylotes: 159–277 by 1–5 µm; acanthostrongyles: 117–176 by 6–12 µm, with 10–15 (up to 18 in Thomas' speci-

men) whorls of spines; no microscleres.
Comment: In the live colour, the small dimensions of the spicules, and the low number of regularly arranged whorls of spines on the acanthostrongyles, these specimens are clearly deviating from the other Indo-Pacific specimens of *Zyzzya*. Consequently, Thomas' and the present specimen constitute a separate species.

Lissodendoryx massalis sensu Thomas, 1973: 32.
Not examined. Locality: Seychelles. Dark brown, thin encrustation with "papery" consistency. The choanosomal skeleton is a confused isodictyal mass. Spicule sizes (after Thomas): Tylotes: 222–260 by 4 µm; acanthostrongyles (called acanthostyles with the observation of these becoming acanthostrongyles when the spination on the ends becomes more dense): 105–142 by 6 µm; palmate isochelas: 16 µm.
Comment: Thomas describes the acanthostrongyles as being more or less uniformly spined, with spines rarely in whorls, but pictures them as clearly verticillately spined. Presumably both kinds of spines occur in his material. With some hesitation this record is assigned to *Z. fuliginosa*.

Paracornulum atoxa Vacelet et al., 1976: 59.
Not examined. Locality: Madagascar, 5.5 m. Dark purple ("marron") encrustations, in and on coral, extending fistules of 10 by 4 mm, which are open at the upper end. The ectosomal skeleton is a feltwork of tylotes; the choanosomal skeleton is confused, with here and there a unispicular reticulation of tylotes and acanthostrongyles. Spicule sizes (after Hooper & Krasochin, 1989): Tylotes: 180–590 by 2–20 µm (Vacelet et al. observed two categories); acanthostrongyles: 109–285 by 3–15 µm; palmate isochelas: 12–22 µm.
Comment: In agreement with Hooper & Krasochin we consider this to be a junior synonym of *Z. fuliginosa*.

Zyzzya massalis sensu Bergquist & Fromont, 1988: 56.
Not examined. Locality: New Zealand, 55–110 m. Dark red-brown, thinly encrusting; no fistules observed. The choanosomal skeleton is a unispicular isodictyal reticulation. Spicule sizes: Tylotes: 367–402 by 6–12 µm; acanthostrongyles: 217–266 by 11–14 µm; palmate isochelas: 15–16 µm.
Comment: The colour is not typical, but in other respects this specimen resembles *Z. fuliginosa*.

Zyzzya massalis sensu Hooper & Krasochin, 1989; Australian specimen.
Not examined. Locality: Houtman-Abrolhos Islands, West Australia, 18–20 m. A dark brown subspherical mass, with at least one third of its base lying in a shallow burrow in soft sediment. The upper surface tapers into a single fistule with a terminal sieve-plate. The ectosomal skeleton is a tangential layer of tylotes. The choanosomal skeleton contains multispicular tracts of tylotes and an irregular subisodictyal reticulation of single acanthostrongyles and occasional tylotes. Spicule sizes: Tylotes 280–438 by 1.5–12 µm (some are stylote); acanthostrongyles 118–190 by 4–14 µm (drawing shows about 24 whorls of spines); no microscleres. This specimen conforms to *Z. fuliginosa*.

Zyzzya massalis sensu Hooper & Krasochin, 1989; Seychelles specimen.
Not examined. Locality: D'Arros Island, Amirantes, Seychelles, 12–20 m. Brown, massive, subspherical sponge; no fistules observed. Spicule syzes: Tylotes: 305–418 by 3–12 µm; acanthostrongyles: 148–242 by 5–15 µm; no microscleres. This specimen likewise conforms to *Z. fuliginosa*.

Zyzzya fuliginosa: undescribed Seychelles material.
(Figs. 4–5, 22–23).
There are three samples collected by R.W.M. van Soest during the Dutch Indian Ocean Project, 1992–1993: ZMA POR. 10537, IOP-E sta. 612/23, Mahé, Anse de Forbans, Seychelles, 1–7 m, 12-XII-1992; ZMA POR. 10816, IOP-E sta. 716/31, N. of Aride Isl., Seychelles, 04°11'S 55°40'E, 40 m, 19-XII-1992, dredge; ZMA POR. 10811, IOP-E sta. 739/18, Mahé, S.E. coast, Seychelles, 35–45 m, 24-XII-1992, dredge. All three specimens were black, excavating corals and extending flattened, tapering fistules above the substrate (Figs. 4, 5); all three were devoid of microscleres. One of the specimens, ZMA 10816, contained numerous large embryos with incipient spiculation of thin tylotes 88–106 µm long. One of the Mahé specimens differed from the other two in having rather feeble spiculation: tylotes 173–197 by 2–3 µm; acanthostrongyles: 184–209 by 10–17 µm. The other two were closely similar both in growth form and in spiculation: tylotes (Figs. 22–23): 219–292 by 2–6 µm and 192–255 by 2–7 µm; acanthostrongyles (Fig. 19): 201–265 by 21–28 µm and 212–258 by 10–28 µm, with 21–28 whorls of spines.
Comment: The latter two specimens are remarkable in having very thick (up to 28 µm) acanthostrongyles (Fig. 19). Possibly, a phenomenon similar to that causing extreme differences in thickness of spicules in the Colombian Caribbean (cf. Zea, 1987) is responsible for this.

Zyzzya fuliginosa: undescribed material from Fiji.
(Figs. 20–21)
ZMA POR. 8441. Voucher fragment of a specimen identified originally as *Damiria* spec. by R.W.M. van Soest, used for a chemical paper (Stierle & Faulkner, 1991). This is a black mass with spiculation dominated by tylotes with spined heads. Closer examination revealed that there are two size categories, the shorter of which frequently showed spination extending some distance along the shaft (Fig. 20). Subsequently, in low proportions, entirely spined acanthostrongyles were found. Some developmental stages were stylote (Fig. 21). Tylotes proper: 184–305 by 2–5 µm; (acantho-)strongyles: 155–249 by 4–11 µm; no microscleres.
Comment: In view of the variation in spination of the acanthostrongyles this material is quite likely conspecific with *Zyzzya fuliginosa*. Chemistry described for this specimen is closely related to that described for *Z. fuliginosa* (cf. Radisky et al., 1993).

Zyzzya fuliginosa: undescribed specimen from Papua New Guinea.
(Fig. 18)
ZMA POR. 9745. Locality: Milford Bay, Eastern Papua New

Guinea, coll. C. Díaz, field no. 90104. Voucher fragment for chemical investigations. This is a dry black mass with typical spiculation: Tylotes: 245–282 by 5–7 µm; acanthostrongyles: 231–289 by 9–12 µm; no microscleres.

Conclusions

Spicule sizes of all specimens are summarized in Table I. It seems clear that the Indo-Pacific specimens fall in at least two distinct species, one dark brown to black with rather irregularly developed verticils of spines on the acanthostrongyles, and one yellow, with very regular verticils. For the time being we concur with Hooper & Krasochin (1989) in considering all Indo-Pacific records, with the exception of *Damirina papillata* Thomas, as belonging to a single, rather variable species.

Diagnoses of valid Indo-Pacific Zyzzya *species*

Zyzzya fuliginosa (Carter, 1879)

Shape, size and consistency: Excavating calcareous substrates and soft sediments. Thinly encrusting, fistular, massive, to pear-shaped. Endolithic parts diffused, invading and "eating away" the calcareous substrate without making distinct galleries or chambers. Above-surface parts a few millimeters to 14 cm high, covering a few mm^2 to 200 cm^2. Fistules may be a few mm high and in diameter to up to 38 mm high and 31 mm in diameter; they tend to have a tapering form. Surface smooth. Fragile consistency in encrusting fistular parts, to firm in massive parts.

Colour: Mostly reported to be dark brown to black-brown alive and in spirit. Smaller encrusting specimens may be lighter coloured (maroon or yellow), but turn brown in alcohol, discolouring it to a dark brown-black.

Ectosomal skeleton: A multi-layered feltwork of intercrossing tangentially arranged tylotes.

Choanosomal skeleton: basically there is a unispicular isodictyal reticulation of acanthostrongyles, with a good proportion of tylotes mixed in. Independent of this there are multispicular tracts which traverse the basal part of the sponge without making a clear reticulation.

Spicules: Tylotes, with well-developed spined heads, more or less straight, often having one well-developed head and the other more strongyle-like; occasionally style-like. Size rather variable (cf. Table I): 173–590 by 1.5–20 µm.

Acanthostrongyles: Verticillately-spined, but more often more uniformly spined to irregularly spined; occasionally parts or the whole of the shaft smooth, or with an occasional spine only; rarely stylote. Size, especially thickness, quite variable: 109–300 by 3–28 µm.

Palmate isochelas: Mostly absent, but found in four of the thirteen known specimens.

Chemistry: The species produces cytotoxic pyrroloiminoquinone alkaloids (Radisky et al., 1993).

Distribution and ecology. – Indo-West Pacific (Torres Straits, Mauritius, Zanzibar, India, Seychelles/Amirantes, New Zealand, Madagascar, Houtman-Abrolhos Islands, Papua New Guinea, Fiji), excavating calcareous substrates at depths of 1–200 m.

Zyzzya papillata Thomas, 1968

Shape, size and consistency: Long and thin fistules sticking out of dead calcareous rubble. Fistules originate from an irregular, partly stolonic encrustation, or directly out of the substrate, in which it forms irregular shallow excavations. Size of individual fistules up to 30 mm long, with a diameter of 2–3 mm. Consistency paper-like, easily damaged.

Colour: Yellow.

Ectosomal skeleton: Tangential, regularly intercrossing single tylotes.

Choanosomal skeleton: An irregular reticulation of single acanthostrongyles, occasionally forming tracts. Many tylotes are strewn among them.

Spicules: Tylotes with microspined heads: 159–277 by 1–5 µm.

Acanthostrongyles: With 10–18 regular whorls of spines: 117–176 by 6–12 µm.

Microscleres: None.

Distribution and ecology. – India, Seychelles, on open reef, 3 m.

Genus *Cornulella* Dendy, 1922

Type species: *Cornulella lundbecki* Dendy, 1922: 103 (by monotypy).
Definition: Very thinly encrusting Iophonidae with long, thin, fistular outgrowths. Ectosomal skeleton a unispicular network of intercrossing tangential tylotes with spined heads. Choanosomal skeleton vestigial, made up of individual tylotes. Accessory megascleres are acanthoxeas, which are distributed singly among the tylotes. Microscleres palmate isochelas and, frequently, toxas.

Remarks. – This definition deviates from that of Dendy in de-emphasizing the microhabd nature of the acanthoxeas. The microrhabds of the type species were indicated as rugose by Dendy, and are demonstrated in a closely related new species, to be thin spined oxeas (cf. Figs. 34–36), differing from those of related species merely in their small size.

Similar species with acanthoxeas so far were assigned to the genus *Paracornulum* Hallmann, 1920. The definition of this genus by Hallmann (l.c.) allowed inclusion of sponges with acanthostyles, acanthoxeas, or acanthostrongyles, thus effectively also including *Zyzzya*. Reexamination of the type specimen of the type species of *Paracornulum*, i.e., *Cornulum dubium* Hentschel, 1912, housed in the Senckenberg Museum at Frankfurt, however, revealed that the acanthostyles of *C. dubium* are true echinating acanthostyles, concentrated at the base of the sponge where they echinate the substrate. It is very unlikely that these spicules are homologous with the acanthoxeas of *C. lundbecki* and the new species described below. It is similarly judged unlikely that they are homologous with the verticillately-spined acanthostrongyles of *Zyzzya*. It is here proposed to limit the use of *Paracornulum* to species with truly echinating acanthostyles, whereby it has to be remarked that *Paracornulum* is barely differentiated from other genera of Iophonidae because echinating acanthostyles are a plesiomorphic feature. It is possibly a junior synonym of *Acheliderma* Topsent, 1892, but this differs from *Paracornulum* in lacking chelas and possessing choanosomal structural styles next to the acanthostyles (see also below).

Description of the Caribbean species

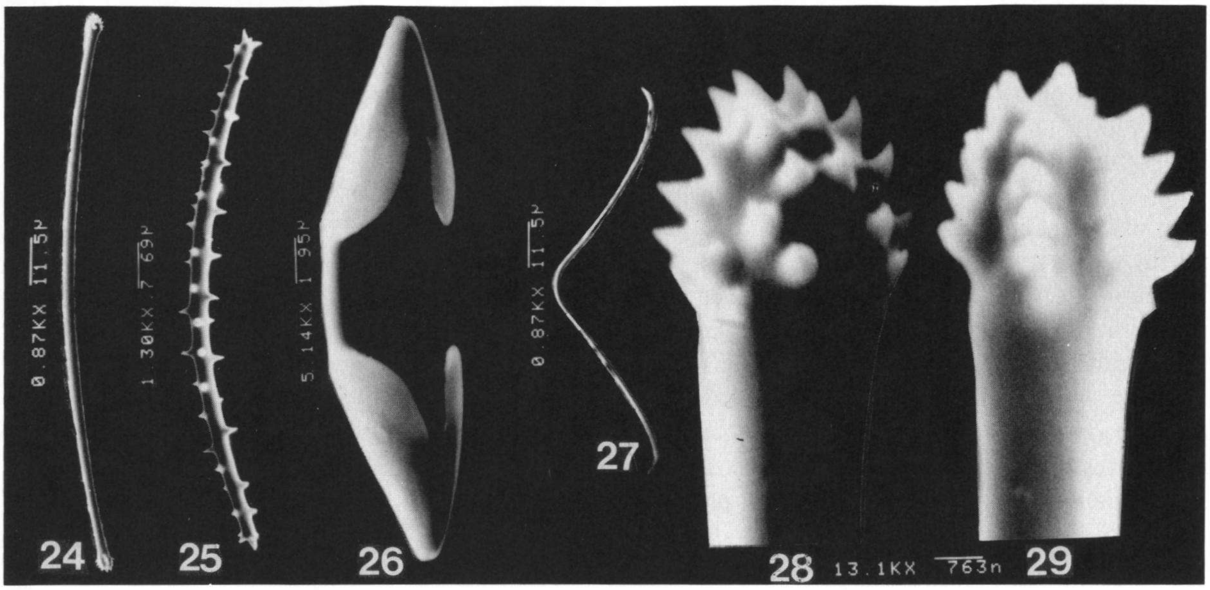
Cornulella santamartae n. sp.
(Figs. 24–29)

Holotype: ZMA POR. 10808, El Morro, Santa Marta area, Colombia, coll. M. Kielman, field no. 410 (fragment INV-POR 0451). Paratype: ZMA POR. 10809, Red Slave, Bonaire, 24 m, under coral rubble, 26-VIII-1987, coll. H.G.J. Pennartz, field no. 237.

Additional material: ZMA POR. 10826, Karpata, Bonaire, 4 m, under coral rubble, 13-VII-1987, coll. G.J. Roebers, field no. 146. Curaçao: Anna Baai & Playa Hundi, 5 m, under coral rubble, coll. E. Meesters & P. Willemse, field nrs. A9B6 (slide only), H13B17 (ZMA POR. 10810), and H51-5 (slide only). Colombia: El Morro, Santa Marta, 4–5 m, on horizontal to inclined rock, 8-III-1988 (slide only, INV-POR. 0451, from sample of *Rhaphidophlus microchelus* Hechtel, 1965).

Diagnosis. – Extremely thin encrustation with tiny erect fistules of 3 mm high. Colour orange. Ectosomal feltwork of tylotes with spined heads. Choanosomal acanthoxeas evenly spined. Robust palmate isochelas. Toxas normally present, but rare or absent in some specimens.

Description. – All specimens are tiny encrustations with very thin and small fistules, which collapse out of the water. Size only a few mm^2 in diameter, fistules 3 mm long at the most, less than 1 mm in cross section. The encrustations and fistules are very fragile. They are also partly overgrown by other encrusters such as *Eurypon laughlini* Díaz et al., 1987. The Curaçao specimens were entirely enclosed in the microscopic slides. The holotype and the paratype were reduced to flimsy fragments by the preparation of the various slides. All slides are considered part of the type series.
Colour: Pale orange or whitish.
Ectosome: A fragile film supported by tangential tylotes in a relatively low density, seemingly forming a loose reticulum. Microscleres and acanthoxeas are dispersed among them.



Figs. 24–29. Cornulella santamartae n. sp., SEM photos of spicules of the holotype: 24, tylote; 25, acanthoxea; 26, palmate isochela; 27, toxa; 28, detail of head of tylote; 29, detail of opposite head of same tylote.

Choanosome: Not observed. Some loose spicules, including a concentration of acanthoxeas, are found in the interior.

Spicules: Tylotes, somewhat variable in shape; in some the tyles are distinct and prominently spined (Figs. 24, 28–29), in others, tyles are less prominent. Sizes are rather uniform (cf. Table II): 111–178 by 1–3 µm.

Acanthoxeas (Fig. 25): Evenly spined all over, slightly curved; not observed in two of the Curaçao specimens. Size: 48–111 by 2–5 µm.

Palmate isochelas (Fig. 26): Robust, with long alas and rather strongly curved shafts. Size: 12–26 µm.

Toxas (Fig. 27): Rare in the holotype, not found in two of the three Curaçao specimens. Size: 39–99 µm.

Distribution and ecology. – Southern Caribbean (Colombian Caribbean, Curaçao, Bonaire), in cryptic reef habitats, or among other sponges in well-lit rocky slopes.

Etymology. – Named after the type locality, the Colombian city of Santa Marta.

Remarks. – The new species has no close relatives in the Caribbean. Three Tropical Western Atlantic species may be similar in habit, viz. *Damiria testis* Topsent, 1928 (cf. below), *Coelosphaerella johnsoni* De Laubenfels, 1934, and "*Artemisina*" *tylota* Boury-Esnault, 1973. However, all three are larger and more elaborate. In addition, the first species lacks any spicules other than the microspined tylotes, and the latter two are members or close relatives of *Cornulum* because they have microspined ectosomal stongyles/tylotes, palmate isochelas and toxas, but lack acanthoxeas. "*A.*" *tylota* from Brazil has smooth styles, making it a certain *Cornulum*; *C. johnsoni* lacks the styles which is a dubious reason for considering it to belong to a genus separate from *Cornulum.*

Species similar to *C. santamartae* in the Indo-West Pacific area are *Cornulella lundbecki* Dendy, 1922, "*Paracornulum*" *minimum* Vacelet et al., 1976, "*Paracornulum*" *purpureum* (Hancock, 1849), and two undescribed species from the Seychelles area. All these are briefly diagnosed below. *C. lundbecki* differs in having much larger tylotes and smaller acanthoxeas; *P. minimum* has twisted palmate isochelas of smaller size than *C.*

Table II. Spicule sizes (range, mean and standard deviation, in µm) of *Cornulella* specimens. Data based on 25 measurements per spicule category per specimen, unless otherwise indicated. For data derived from the literature only the range is given.

Specimen	tylotes	acanthoxeas	chelas	toxas
Cornulella santamartae n. sp. ZMA POR. 10808, Colombia	111-120.8(6.48)-131 / 1-1.9(0.54)-3	57-79.6(7.49)-91 / 2-3.3(0.53)-4	12-14.9(1.64)-17	99 (n=1)
Cornulella santamartae n. sp. INV-POR.0451, Colombia	151-169.7-178 / 2-2.5-3 (n=5)	92-112.0(10.8)-131 / 3-3.7(0.5)-5 (n=10)	21-23.2-25 (n=5)	82 (n=1)
Cornulella santamartae n. sp. ZMA POR. 10809, Bonaire	126-139.5(8.28)-156 / 2-2.5(0.26)-3	81-93.6(6.62)-105 / 3-3.9(0.56)-5	19-22.3(1.62)-26	60-70.1(16.46)-90 (n=5)
Cornulella santamartae n. sp. ZMA POR. 10826, Bonaire	156-168.0(5.50)-177 / 2-2.5(0.39)-3	89-98.0(6.45)-111 / 3-3.4(0.39)-4	16-19.5(1.80)-22	not found
Cornulella santamartae n. sp. ZMA POR. A9 B6, Curaçao	135-151.8(7.85)-162 / 2-2.7(0.32)-3(n=10)	78-96.3(10.26)-108 / 3-3.3(0.40)-4(n=10)	19-19.8(1.45)-23 (n=10)	39-48.5-58 (n=2)
Cornulella santamartae n. sp. ZMA POR. H51-5, Curaçao	123-137.4(7.40)-147 / 2 (n=10)	48-64.0(18.55)-90 / 2-2.3(0.23)-2.5(n=3)	19-21.2(1.07)-23 (n=10)	not found
Cornulella santamartae n. sp. ZMA POR. 10810, Curaçao	144-158.3(10.16)-171 / 2-2.3(0.24)-2.5(n=6)	one broken spicule found	19-20.5(0.76)-21 (n=6)	not found
Cornulella lundbecki Dendy Seychelles	400 / 6	20 / 1	50	120
Cornulella amirantensis n. sp. ZMA POR. 10685, Seychelles	381-416.9(20.79)-466 / 7-11.0(2.19)-15	36-43.5(4.46)-51 / 0.5-0.64(0.22)-1	16-20.6(1.65)-23	absent
Cornulella amirantensis n. sp. ZMA POR. 10805, Seychelles	357-432.5(38.74)-494 / 7-9.6(1.86)-13(n=10)	39-44.3(3.94)-51 / 0.5	18-21.0(1.66)-24	absent
Cornulella purpureum (Hancock) Indo-Pacific	260 / 5	60-170 / 5	18	75
Cornulella minima Vacelet et al. Madagascar	130-250	110-150	12.5-15	1) 20-25 2) 60-175
Cornulella tyro n. sp. ZMA POR. 10520, Seychelles	224-243.1(12.94)-273 / 3-3.7(0.43)-4.5	105-121.0(6.91)-138 / 2-3.1(0.48)-4	13-16.0(1.20)-18	absent

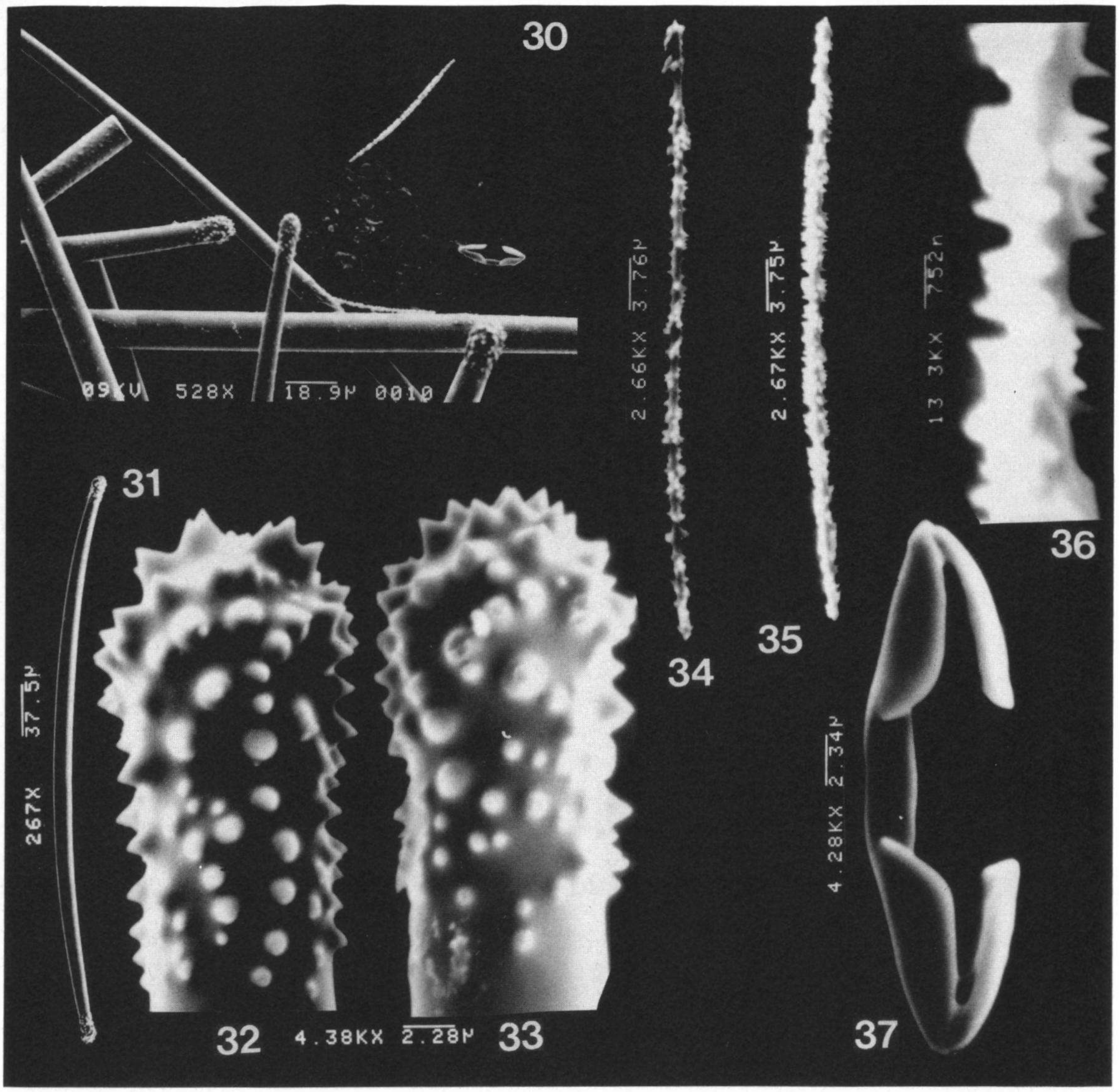
santamartae and the toxas occur in two size categories. *P. purpureum* is different in being purple in colour. The two new species from the Seychelles have no toxas, one has clearly smaller and thinner, the other clearly longer acanthoxeas.

Review of Indo-Pacific Cornulella *specimens*

Below Indo-Pacific specimens belonging to *Cornulella* as defined above are briefly diagnosed. Most previously described specimens are known as *Paracornulum*. However, not all specimens assigned to that genus are here transferred to *Cornulella*. Bergquist & Fromont's (1988) *Paracornulum sinclairi* from New Zealand does not possess entirely spined accessory megascleres and answers to the definition of *Cornulum*. *Paracornulum coherens* Lévi, 1963 from South Africa has true acanthostyles and thus remains in *Paracornulum* along with *P. dubium* Hentschel, 1912.

Cliona purpurea Hancock, 1849.

Not examined. Redescribed by Kirkpatrick (1900; assigned to *Dyscliona*), Topsent (1907: not *Dyscliona*), Hallmann (1920: to *Paracornulum*) and Rützler & Stone (1986: do.). The diagnosis below is based on Rützler & Stone (l.c.) who gave measurements and a photograph of the spicules. Purple fistules, sticking out from a *Tridacna gigas* excavated by the sponge. Ectosomal tylotes with feebly developed spined heads, 260 by 5 µm. Acanthoxeas 60–170 by 5 µm. Robust curved palmate isochelas: 18 µm.



Figs. 30–37. ***Cornulella amirantensis*** **n. sp., SEM photos of spicules of the holotype: 30, tylotes, acanthoxea, and chela; 31, tylote; 32, detail of head of tylote; 33, detail of opposite head of same tylote; 34–35, acanthoxea; 36, detail of acanthoxea; 37, palmate isochela.**

Toxas: 75 µm. Indo-Pacific, locality unknown, shallow water.

Cornulella lundbecki Dendy, 1922.
Not examined. Delicate thin-walled fistules rising from a thin crust occupying irregular depressions of the substrate. Fistules are 2–3 mm in diameter and 13 mm high. Colour purple (due to cyanobacteria?). Ecosomal tylotes up to 400 by 6 µm. Acanthoxeas are small microrhabds, 20 by 1 µm. Microscleres include large palmate isochelas, 50 µm long and 12 µm wide, and rare toxas: 120 by 27 µm. Seychelles, 67 m.
Comment: Dendy also reported sigmas but these are unlikely to be proper. The microrhabd size of the acanthoxeas is shared with *C. amirantensis* (see below).

Cornulella amirantensis n. sp.
(Figs. 30–37)

Holotype: ZMA POR. 10685, IOP-E sta. 766/02, N. of Poivre Isl., Amirantes, 05°44′S 53°20′E, 43–48 m, dredge, coll. R.W.M. van Soest, 29-XII-1992. Paratype: ZMA POR. 10805, IOP-E sta. 755/5B, St. Joseph Atoll, Amirantes, 05°23'S 53°19'E, 60 m, coll. R.W.M. van Soest 26-XII-1992.

Description. – Long yellow fistules of 2–3 mm in diameter and 40 mm in length, issuing from a thinly encrusting base. Fistules may branch occasionally. Papery fragile consistency.
Ecotosomal tylotes (Figs. 30–33): With prominently spined heads; spines extending somewhat along the shaft (Figs. 32–33); shaft distinctly fusiform, i.e., thicker in the middle section. Size: 357–494 by 7–15 µm.
Spined acanthoxeas ("microrhabds") (Figs. 34–36): Small, heavily spined; 36–51 by 0.5–1 µm.
Palmate isochelas (Fig. 37): Robust; 16–24 µm.
Toxas: Not observed.

Distribution and ecology. – Seychelles, 40–60 m.

Etymology. – Named after the island group of which the type locality is one.

Remarks. – The new species is close to *C. lundbecki* in spicule sizes, especially the small size of the acanthoxeas. Differences are the live colour (yellow vs. purple), the size of the chelas (16–24 vs. 50) and the absence of toxas. The latter feature is shared with *C. tyro* n. sp. described below, but it differs clearly from that species in the size of the tylotes (larger in *amirantensis*) and acanthoxeas (much smaller in *amirantensis*).

Paracornulum minimum Vacelet et al., 1976.
Not examined. Transparent white, small fistules of 5 mm high and 1 mm in diameter. No basal encrustation could be found. Ectosomal skeleton a feltwork of tylotes; no choanosomal tissue or skeleton was observed. Tylotes with well-developed spined heads: 130–250 µm. Acanthoxeas, curved, asymmetrical: 110–150 µm. Palmate isochelas, twisted: 12.5–15 µm. Toxas in two size categories: 20–25 µm and 60–175 µm. In addition to this complement, the authors also report the presence in low quantities of small acanthostyles (50–55 µm), with smooth shafts and spined heads. Madagascar, shallow-water reefs.
Comment: If the acanthostyles are proper and if these are echinating, the basis for a distinction between *Paracornulum* and *Cornulella* has disappeared. More evidence for this is needed before such a decision can be made. The two size categories of toxas differentiate this species clearly from the others.

Cornulella tyro n. sp.
(Figs. 3, 38–43)

Holotype: ZMA POR. 10520, IOP-E sta. 717/09, E. of Bird Isl., Seychelles, 03°43'S 55°13'E, coll. J.C. den Hartog, 3 m, 20-XII-1992.

Description. – Yellow-orange fistules (Fig. 3), single or branching dichotomously, up to 16 mm long, less than 1 mm in diameter. Fragile.
Spicules: Tylotes (Figs. 38, 41–42), with feebly developed heads, one end being strongyle-like, with modest spination. Size: 224–273 by 3–4.5 µm.
Acanthoxeas (Figs. 39, 43): With evenly distributed not very dense spination: 105–138 by 2–4 µm.
Palmate isochelas (Fig. 40): 13–18 µm.
Toxas: Not observed.

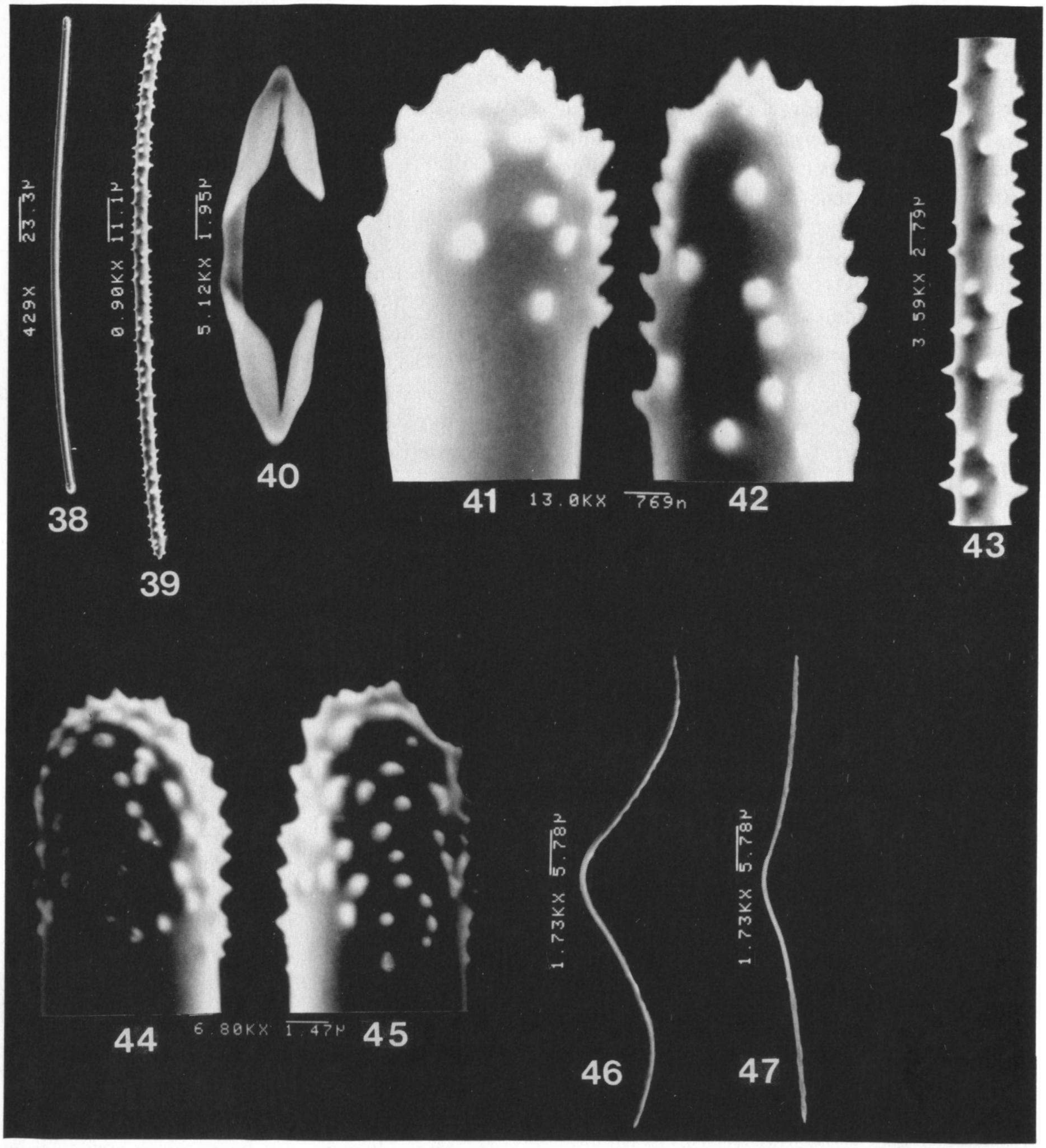
Distribution and ecology. – Seychelles, shallow water.

Etymology. – Named after the Dutch oceanographic research vessel "Tyro", platform for the Indian Ocean Program, 1992–1993.

Remarks. – This species is similar to *Cornulella amirantensis* n. sp. in lacking toxas, but differs clearly from that species in having much smaller tylotes and much longer acanthoxeas. Apart from the lack of toxas and the orange colour, the new species is most similar to *C. purpurea.*

Conclusions

At least six species answer to the emended definition of *Cornulella*, one Caribbean, and five Indo-Pacific. They are all closely similar in habit: thin, transparent, hollow, cylindrical fistules issuing from a thinly encrusting base which seems to either excavate calcareous substrates or agglutinates calcareous sediments. They differ in details of spiculation: *C. tyro* n. sp. has no toxas; *C. lundbecki* may have no toxas either, but has very small (20–40 µm) acanthoxeas; *C. minima* has two size categories of toxas; the remaining two are very similar but *C. purpurea* is purple coloured and *C. santamartae* transparent-orange.



Figs. 38–43. Cornulella tyro n. sp., SEM photos of the holotype: 38, tylote; 39, acanthoxea; 40, palmate isochela; 41, detail of head of tylote; 42, detail of opposite head of same tylote; 43, detail of acanthoxea.

Figs. 44–47. Damiria toxifera n. sp., SEM photos of the holotype: 44, detail of head of tylote; 45, detail of opposite head of same tylote; 46–47, toxas.

A possible seventh species is the Arctic *Histodermella coriacea* Lundbeck, 1910, made the type of a genus *Histodermopsis* by De Laubenfels, 1936 (p. 72). It differs from the very similar *Histodermella ingolfi* in having palmate instead of arcuate chelas and having minute spines on the ectosomal tylotes; both share robust acanthoxeas and lack microscleres. *Histodermella* is a member of the Coelosphaeridae, and the resemblance with *H. coriacea* may be convergent.

Genus *Damiria* Keller, 1891

Type species: *Damiria simplex* Keller, 1891 (by monotypy).
Definition: Fistular Iophonidae possessing tylotes with spined heads, as the only megascleres.

Remarks. – The definition, which usually excludes also microscleres is here slightly widened to allow inclusion of species with at least toxas, to accommodate one of the species described below. The tylote spination is very similar to that found in *Zyzzya* and *Cornulella*, and the genus may be considered the sister group of the latter. Possibly, this is an artificial group representing reduced *Cornulella*-like or *Paracornulum*-like species lacking chelas and acanthose oxeas/styles.

Four species are currently recognized, two are instantly recognizable, either by the possession of toxas (*D. toxifera* n. sp.), or by a single category of tylotes (*D. testis*); the remaining two species differ the thickness of the shorter tylotes, *D. simplex* having these frequently over 10 µm, *D. leonorae* n. sp. normally under 10 µm or at the most up to 11 µm.

Damiria australiensis Dendy (1896) is not a *Damiria* but a clear *Lissodendoryx* (or *Damiriana* if these two are maintained as separate genera); it has smooth tylotes, oxeas and arcuate chelas.

Review of Damiria *species*

Damiria simplex Keller, 1891.
Syn.: *Damiria simplex fistulata* Hentschel, 1912
Not: *D. simplex* var. *fistulata* sensu Sanchez, 1984: 60 (= *D. leonorae* n. sp.)

Type specimen ZMB no. 310b examined. Rather elaborate crust, 2.5 cm thick. Fistules apparently absent in the type specimen, but Hentschel's specimen had robust fistules issuing from a massive base. Consistency stiff, fragile. Colour bright brown. Spiculation includes two distinct sizes of tylotes, one long and thin, the other short and fat, both with extensively spined heads: 300 by 6–10 µm and 250 by 15 µm. Red Sea, Indonesia, shallow-water reefs.
Comment: *Damiria simplex* var. *fistulata* Hentschel, 1912 (not examined) is here assigned to *D. simplex* in view of the similarities in spiculation: it is described as fistular and there are two sizes of tylotes, "slim": 264–296, and "strong, thick": 200–210 µm. However, no mention is made of spination of the tylote heads.

Damiria toxifera n. sp
(Figs. 6, 44–47)

Holotype: ZMA POR. 10807, IOP-E sta. 605, Port Launay National Park, Mahé, Seychelles, 1–7 m, coll. R.W.M. van Soest, 9-XII-1992. Paratype: ZMA POR. 10616, IOP-E sta. 749/20, Ile Moyenne, Mahé, Seychelles, 0–7 m, coll. R.W.M. van Soest, 25-XII-1992. Paratype: ZMA POR. 10817, IOP-E sta. 788/33, Alphonse Atoll, Amirantes, 07°02'S 52°44'E, 6–8 m, coll. R.W.M. van Soest, 4-I-1993.

Description. – Relatively sizeable specimens. The holotype has a massive base from which rise branching, hollow, smooth, fistules (Fig. 6). Size of base 4 cm by 3 cm, 2 cm high, height of fistules 3 cm above the substrate, diameter of the fistules slightly less than 1 cm. Consistency stiffly fragile, parchment-like. The specimen is now fragmented. One paratype is much smaller, consisting of a few, now separated fistules of max. 1 cm high, 3 mm in diameter; the other paratype is fragmented into several partly erect, partly stolonic fistules, up to 5 cm long. The species does not seem to excavate the (often partly living) coral substrate.
Colour: Orange in life, transparent light brown in alcohol.
Ectosomal skeleton: Masses of intercrossing tylotes.
Choanosomal skeleton: In the fistules virtually absent, in the basal mass an isotropic reticulation of spicules arranged in two's and three's or singly. Frequently the reticulation is obscured, and appears confused.
Spicules (Table III): Tylotes (Figs. 44–45) in two

Table III. Spicule sizes (range, mean and standard deviation, in µm) of specimens of *Damiria*. Data based on 25 measurements per spicule category per specimen, unless otherwise indicated. For data derived from the literature only the range is given.

Specimen	tylotes I	tylotes II	toxas
Damiria simplex Keller Red Sea	300 / 6-10	250 / 15	absent
Damiria simplex fistulata Hentschel, 1912, Indonesia	264-296	200-210	absent
Damiria testis Topsent Azores	140-170 / 5	unknown	absent
Damiria leonorae n. sp.* ZMA POR. 4754, Curaçao	231-237.7(8.71)-251 / 3.5-3.8(0.23)-4	174-191.0(14.40)-216 / 5-6.3(1.60)-9	absent
Damiria leonorae n. sp. ZMA POR. 7665, Barbuda	225-248.4(18.06)-296 / 2.5-3.8(0.60)-4.5(n=10)	165-190.7(15.65)-207 / 5-5.4(0.43)-6(n=10)	absent
Damiria leonorae n. sp. ZMA POR. 9425, U.S.Virgin Isl.	240-257.2(8.85)-271 / 3-3.4(0.32)-4(n=10)	189-200.1(9.40)-216 / 6-6.4(0.44)-7(n=10)	absent
Damiria leonorae n. sp. ZMA (micr. slide) C20-6, Curaçao	195-224.9(17.44)-258	123-160.0(23.11)-194 / 2-2.9(0.48)-3.5	absent / 4-4.8(0.40)-5.5
Damiria leonorae n. sp. ZMA (micr. slide), Colombia	192-195.5(4.04)-202 / 2.5-3.1(0.54)-4	145-151.5(4.09)-155 / 7-8.0(0.70)-9	absent
Damiria leonorae n. sp.** Santa Marta, Colombia	222-259 / 2.0-6	177-199 4.3-11	absent
Damiria toxifera n. sp. ZMA POR. 10807, Seychelles	278-294.5(8.89)-308 / 3-4.5(0.65)-5	192-211.5(11.01)-230 / 6-8.1(1.14)-10	60-69.7(6.86)-84
Damiria toxifera n. sp. ZMA POR.10616, Seychelles	239-262.5(12.48)-279 / 3.5-4.0(0.50)-5(n=10)	169-183.3(7.68)-195 / 6-7.5(0.81)-9(n=10)	49-63.3(9.21)-80 (n=6)
Damiria toxifera n. sp. ZMA POR. 10817, Seychelles	240-260.0(16.99)-306 / 3-4.2(0.61)-5	189-206.7(7.27)-217 / 7-9.0(1.00)-10	62-76.7(14.26)-96 (n=3)

* originally as *D. testis* in Van Soest, 1984
** as *D. simplex fistulata* sensu Sanchez (1984),

size categories, long and thin: 239–308 by 3–5 µm, and short and fat: 169–230 by 6–10 µm. The latter are concentrated in the basal mass.

Toxas (Figs. 46–47): Relatively long, with a shallow curve: 49–96 µm.

Distribution and ecology. – So far known only from the Seychelles, in shallow reefs, growing in the open on dead coral substrate.

Etymology. – The name refers to the toxas found in this species.

Remarks. – The new species differs from all *Damiria* in possessing toxas. In view of the great resemblance of the skeleton and the spicules of *D. toxifera* and *D. simplex*, extension of the generic definition of *Damiria* to accommodate this new species is unavoidable. In fact, we searched hard for the occurrence of these toxas in the type specimen of *D. simplex* in the hope of establishing that the Seychelles and the Red Sea specimens would be conspecific. However, there is no trace of toxas in the type specimen of *D. simplex* demonstrating the separate status of the Seychelles specimens.

Damiria testis Topsent, 1928.

(Not: *D. testis* sensu Van Soest, 1984: 74 = *D. leonorae* n. sp.)

Not examined. Specimen thinly encrusting. Tylotes unispicularly arranged; tangential in the ectosome. Topsent gives only a single size of tylotes: 140–170 by 5 µm, but admits that the specimen is damaged and in bad condition. On the Gorringe Bank,

North Artlantic between Portugal and the Azores, deep water: 270 m.
Comment: Van Soest (1984) recorded this species from the reefs of Curaçao, 6–12 m. In view of the differences in geographic origin and habitat, as well as differences in spicule size (cf. below), the latter record is without doubt unjustified. We propose to erect a new species for the Caribbean reef material.

Damiria leonorae n. sp.

Syn.: *Damiria testis* Van Soest, 1984: 74, pl. 6 fig. 6, text-fig. 27; *Damiria simplex* var. *fistulata* sensu Sanchez, 1984: 60, fig. 6.22B.

Holotype: ZMA POR. 4754, Curaçao, Buoy 0, 6–12 m, coll. R.W.M. van Soest.
Additional material: Curaçao, Cornelisbaai, 5 m, coll. E. Meesters & P. Willemsen, field no. C20-6, microscopic slide only (ZMA). Colombia, Santa Marta area, coll. W. Dulfer & M. Rozemeijer, microscopic slide only (ZMA). Barbuda: ZMA POR. 7665, E. of Palmetto Point, 2–7 m, coll. J.J. Vermeulen, field no. 86–184. St. Croix, U.S. Virgin Islands: ZMA POR. 9425, coll. W. Gladfelter.

Description. – Sinuously creeping, hollow encrustations, 2 cm long, 4 mm wide. They seem to be fistules lying on their side, encrusting the substrate, usually corals.
Colour: Yellow.
Ectosomal skeleton: Intercrossing tangential tylotes.
Choanosomal skeleton: A few tracts and loose spicules.
Spicules (Table III): Two size categories of tylotes (treated as a single category in Van Soest's earlier description): long and thin: 192–296 by 2–4.5 µm, and short and thick: 123–216 by 5–9 µm (Sanchez records tylotes up to 11 µm thick).

Distribution and ecology. – Curaçao, Colombian Caribbean, Barbuda, U.S. Virgin Islands, on undersides of coral rubble and dead corals.

Etymology. – Named after Dr. Leonor Botero, director of INVEMAR, Santa Marta, Colombia, host institute of S. Zea and M. Kielman, in recognition of her generous support of Dutch-Colombian sponge research.

Remarks. – The Caribbean species differs from the North Atlantic *D. testis* in the much longer spicules: even the shorter category is longer than the largest spicules of the North Atlantic species. Apparently, there are no size categories in the latter, although this must be verified.

Genus *Acheliderma* Topsent, 1892

Type species: *Acheliderma lemniscata* Topsent, 1892.

Definition. – Fistular Iophonidae with microspined tylotes as ectosomal spicules, microspined styles and echinating acanthostyles as choanosomal spicules. Microscleres characteristically elongated diamond-shaped microxeas and toxas. No chelae.

Remarks. – The diamond-shaped microxeas, which are likely derived from toxas, have been reported in three "genera", viz. *Acheliderma*, *Astylinifer* and *Fusifer*. Topsent (1892) called these "raphides fusiformes" in the original description of *Acheliderma* and this doubtless caused Dendy (1896) to overlook this genus when erecting *Fusifer* with similar spicules. Even Topsent (1927) himself failed to make the connection when he erected *Astylinifer*, again on very similar spiculation. All three "genera" are essentially similar in form and spiculation. The differences between them are of the species level, and it is proposed here to merge them under *Acheliderma* as the oldest name.

Subsequent records of *Acheliderma* and *Astylinifer* by Burton (1932: *Acheliderma topsenti*) and De Laubenfels (1930, 1932: *Astylinifer arndti*) do not conform to the definition of this genus. *A. topsenti* conforms to *Megaciella* (see below), and *A. arndti* is very probably a hymedesmid.

Ectosomal spicules are lacking in one species (*A. fistulatus*) where they may have been replaced by sand. In the new species described below some of the ectosomal spicules are anisotylotes with one end mucronated. In *A. planum* all ectosomal spicules are like that.

The genus *Acheliderma* is intermediate between

Table IV. Spicule sizes (µm) of specimens conforming to the genus *Acheliderma*. Data based on 25 measurements per spicule category per specimen, unless otherwise indicated. For data derived from the literature only the range is given.

Specimen	tylotes	styles	acanthostyles	toxas	microxeas
Acheliderma lemniscata Topsent, 1892, Mediterranean	250-270 (microspined)	420-450 (microspined)	80-175	120	60-70 / 1
Fusifer fistulatum Dendy, 1896, S. Australia	absent	540 (smooth)	70 / 3	present	present
Astylinifer planum Topsent, 1927, Azores	265-315 / 2 (smooth?)	105-455 (not differentiated)		125	30-37 / 2-3
Acheliderma lisannae n. sp. ZMA POR. 10907, Colombia	243-300.8-348 / 3-3.46-4.5 (microspined)	399-440.4-481 / 3-3.90-5 (n=15) (microspined)	67-87.6-101 / 2-3.17-4 (n=2)	101-120.0-136 (n=10)	1) 36-43.5-52 / 1-2.35-3.5 2) 19-25.1-28 / 1-1.42-2

Paracornulum and *Cornulum* in having both echinating acanthostyles and structural styles.

Spicule size data of the four recognized species are given in Table IV.

Review of Acheliderma *species*

Acheliderma lemniscata Topsent, 1892.
Microscopic slide MNHN D.T. 170 examined: Encrusting, with 1 cm long fistules. The ectosomal skeleton consists of microspined tylotes: 250–270 µm. The choanosomal skeleton is a reticulation of styles with microspined heads: 420–450 µm, echinated by short fully spined acanthostyles: 80–175 µm. Microscleres: Toxas: 120 µm, and diamond-shaped microxeas 60–70 by 1 µm. Mediterranean.

Acheliderma planum Topsent, 1927.
Microscopic slide labeled *Fusifer planus*, MNHN D.T. 1288 examined. Flat crust, with ectosomal skeleton to tylotes which are pictured to be smooth, sometimes asymmetrical with one end having a mucron: 265–315 by 2 µm. Choanosomal skeleton consists entirely of acanthostyles, but of various sizes, possibly including echinating ones: 105–455 µm. Microscleres include toxas of 125 µm and diamond-shaped microxeas: 30–37 by 2–3 µm. Azores, deep water.
Comment: This is the type species of the genus *Astylinifer* Topsent, 1927. Topsent's labeling of the type slide indicates his hesitation in considering *Astylinifer* and *Fusifer* synonymous.

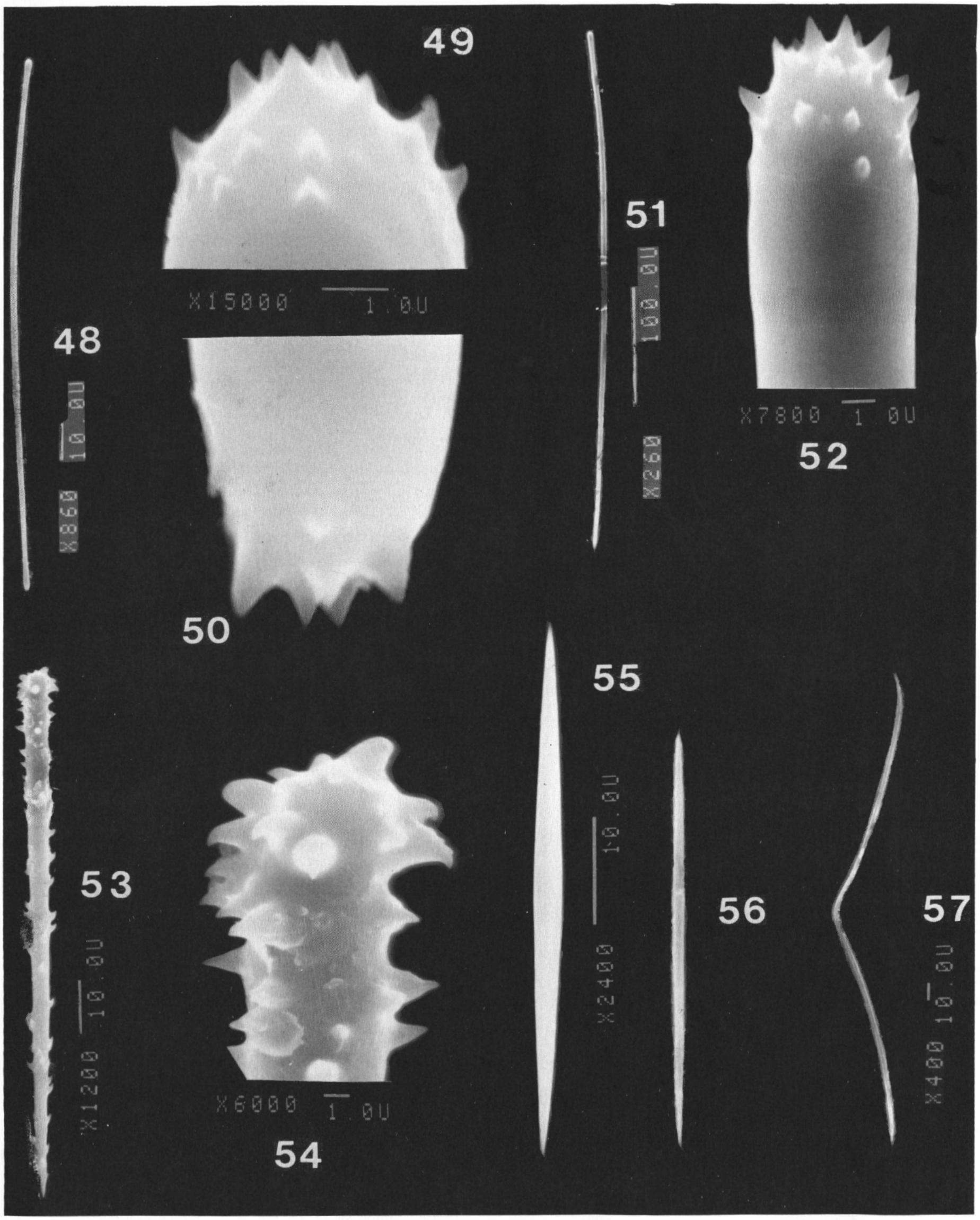
Acheliderma fistulatum (Dendy, 1896).
Not examined. This is one of the many South Australian "sand sponges", i.e., species which have replaced their skeletons partly or wholly by sand grains, a feature which is probably developed convergently. The sponge is a sandy body with short fistules. No ectosomal tylotes. Choanosomal megascleres are smooth tylostyles, 540 by 7 µm, and acanthostyles 70 by 3 µm. Microscleres include diamond-shaped microxeas and toxas. Southeast Australia.
Comment: This is the type species of the genus *Fusifer*. The major synapomorphy for assignment to the Iophonidae, i.e., the spined tylotes, are lacking in this species, but the similarity of the diamond-shaped microxeas makes it very likely that the present species belongs in the genus. The absence of tylotes is explained as replacement by sand grains.

Acheliderma lisannae n. sp.
(Figs. 48–57)

Holotype: ZMA POR. 10907, Punta Betín, 20–23 m, Santa Marta, Colombian Caribbean, 27-XI-1993, coll. L.A.M. Aerts, field no. S174. Furthermore there are in the ZMA POR. collection two microscopic slides and one SEM stub made from the holotype.

Diagnosis. – Small white (?) fistules with papery walls. Ectosomal spicules microspined tylotes or occasionally smooth anisotylotes with one end mucronate. Choanosomal spicules microspined styles and echinating acanthostyles. Diamond-shaped microxeas in two size categories. Long shallowly curved toxas.

Description. – Shape, size and consistency: A single thin, hollow fistule found closely adhering an *Aka cachacrouensis* (Rützler, 1971). Walls of the fistule papery, very fragile, consisting of a feltwork of tylotes. In the basal part of the fistule some tissue was found filling the hollow interior. Size 4 mm long, less than a mm in diameter. The two micro-



Figs. 48–57. Acheliderma lisannae n. sp., SEM photos of the holotype: 48, tylote; 49–50, details of opposite heads of tylote; 51, style; 52, detail of head of style; 53, acanthostyle; 54, detail of head of acanthostyle; 55–56, two sizes of diamond-shaped microxeas; 57, toxa.

scopic slide preparations and the single SEM stub took up a considerable part of the specimen and must be considered part of the type material.
Colour: Recorded as orange, but the species was not recognized in the field as several other sponges were growing over and against it. The specimen is now whitish and there is a possibility that this was also the live colour.
Ectosome: A feltwork of tylotes mixed with microscleres.
Choanosome: A confused mass of styles and tylotes, with a few acanthostyles.
Spicules: Tylotes (Figs. 48–50) with microspined heads: 243–348 by 3–4.5 µm. The smooth anisotylotes with one mucronated end had the same size as the microspined tylotes, which makes it clear that they are structurally the same spicule type.

Styles (Figs. 51–52): With microspined heads, long, thin, with a slight swelling above the pointed end: 399–481 by 3–5 µm.
Echinating acanthostyles (Figs. 53–54): Entirely spined: 67–101 by 2–4 µm.
Microxeas (Figs. 55–56): Elongated diamond-shaped, entirely smooth, in two size classes: (1) 36–52 by 1.5–3.5 µm, and (2) 19–28 by 1–2 µm.
Toxas (Fig. 57): Long, thin, shallowly curved: 101–136 µm.

Etymology. – Named after its collector, Ms. Lisanne A.M. Aerts who is currently studying sponge-coral interactions in the reefs off the Colombian coast.

Ecology and distribution. – On coral debris among other sponges, possibly excavating; known only from the type locality in the Colombian Caribbean.

Remarks. – This specimen bridges the alleged gap between *Acheliderma lemniscata*, described as having microspined tylotes and "fusiform" raphides of 1 µm in thickness, and *Astylinifer planus* with smooth anisotylotes and microxeas of 2–3 µm in thickness.

Related fistular Iophonid genera

Genus *Paracornulum* Hallmann, 1920

Type species: *Cornulum dubium* Hentschel, 1912 (by original designation).
Definition (emended): Encrusting-fistular Iophonidae with ectosomal skeleton consisting of intercrossing tylotes and choanosomal skeleton consisting of similar tylotes. Microscleres palmate isochelas and toxas.

Remark. – This genus shares with *Acheliderma* the possession of proper echinating acanthostyles, but it is otherwise similar to *Damiria*.

Paracornulum dubium (Hentschel, 1912).
Syn.: *Cornulum dubium* Hentschel, 1912.
Type specimen SMF no. 964 examined. Tylotes in two size categories, long and relatively thin: 381–*410.8* (*15.13*)–441 by 4–*8.2* (*1.62*)–11 µm, and short and relatively fat: 201–*234.5* (*15.45*)–264 by 4–*6.2* (*0.91*)– 8 µm; the latter are concentrated at the base of the sponge. Both categories have extensively spined heads. Acanthostyles, with few scattered spines all along the shaft: 87–*104.3* (*19.06*)–153 by 3–*4.1* (*0.67*)–5 µm, likewise concentrated at the base, where they echinate the substrate. Chelas: 12–*14.8* (*1.31*)–17 µm. Toxas: 30–*53.8* (*15.4*)–79 µm. Aru Islands, Indonesia.
Comment: The two tylote categories with extensively spined heads remind of the situation found in several *Damiria* species.

Paracornulum coherens Lévi, 1963.
Not examined. Brick red encrusting sponge, cementing pebbles and shell fragments. No fistules apparent. Ectosomal strongyles with spined heads, apparently in a single category: 250–300 by 10 µm. Robust echinating acanthostyles with spines only on the heads: 150–275 by 12–14 µm. Chelas: 20 µm. In addition there are microrhabds of 12 µm long. South Africa.
Comments: Assignment of this material to *Paracornulum* is tentative, because the robust, smooth acanthostyles and the ectosomal strongyles are rather different from the type species. The possession of acanthostyles unites the two species, but this is a dubious synapomorphy, as these are wide-spread among Microcionina families and genera.

Other species assigned to *Paracornulum* are referred to *Cornulella*, *Cornulum*, and *Zyzzya* (cf. above).

Genus *Anisotylacanthea* Vacelet, 1969

Type species: *A curvata* Vacelet, 1969: 200 (by monotypy).

Not examined. Grey-cream encrustation of 2 cm^2 (dry state). Ectosome not detachable. Spicules are strongyles with spined extremities, in two size categories: the longer with asymmetrical heads, one swollen and spined, the other end smooth: 360–520 by 7.5–12.5 µm, and smaller with likewise only one end spined: 110–190 by 5–7.5 µm. Mediterranean, deep water.
Comment: On paper this genus comes close to *Damiria*, but the spicule sizes do not conform to those of *Damiria* nor to the related genera *Zyzzya*, *Paracornulum*, and *Cornulella*. The relationship of this species remains obscure.

Genera *Cornulum*, *Coelosphaerella*, *Xytopsene*, *Heterocornulum* and *Melonchela*

Genus *Cornulum* Carter, 1876

Type species: *C. textile* Carter, 1876: 309 (by monotypy).
Definition: Fistular Iophonidae with ectosomal skeleton consisting of smooth strongyles or tylotes with microspined apices, choanosomal skeleton consisting of similar spicules to which smooth styles with similar microspined apices are added. Microscleres include palmate chelas and toxas.

Remarks. – It is likely that specimens without styles (genus *Coelosphaerella* De Laubenfels, 1934), without styles and toxas (genus *Xytopsene* De Laubenfels, 1936), with microstrongyles (genus *Heterocornulum* Lévi & Lévi, 1983), and with peculiar anisochelas ("melonchelas": genus *Melonchela* Koltun, 1959) are all members of *Cornulum*. Of course, if more species with such apomorphic characters as microstrongyles and melonchelas would be found, these genera may need to be revived.

Examination of half a dozen *Cornulum* specimens, including a specimen of *Cornulum textile* Carter, 1876 from Mauritania, as well as the type specimen of *Heterocornulum virguliferum* Lévi & Lévi, 1983, has led us to the observation that the above-mentioned genera share with the 8–10 species of *Cornulum* s.l. the microspined condition (occasionally verging towards entirely smooth) of the megascleres as opposed to the more heavy and extensive spination found in the genera described above. It is beyond the scope of this paper to describe all members of *Cornulum* s.l. but Table V gives a preliminary list of species.

Non-fistular Iophonidae

The new concept of the Poecilosclerida classification presented by Hajdu et al. (1994) includes a family Iophonidae comprised by the above-mentioned genera (previously united in the family Cornulidae Lévi & Lévi, 1983) with the addition of three non-fistular genera, viz. *Iophon*, *Acarnus*, and *Megaciella*. A possible fourth member is *Acanthorhabdus* Burton, 1929. For completeness sake, a list of these genera is presented in Table VI and a brief characterization is given here:

Genus *Iophon* Gray, 1867

Syn.: *Alebion* Gray, 1867, *Menyllus* Gray, 1867, *Ingallia* Gray, 1867, *Pocillon* Topsent, 1891, *Iophonota* De Laubenfels, 1936, *Iophonopsis* Dendy, 1924, and *Burtonella* De Laubenfels, 1928.

Type species: *Halichondria scandens* Bowerbank, 1866 (by original designation).
Definition: Massive, branching or encrusting Iophonidae with ectosomal skeleton of intercrossing or scattered tylotes with spined heads, choanosomal skeleton consisting of an isodictyal reticulation of smooth or spined styles, arranged singly or in two's and three's, which may or may not be echinated by acanthostyles. Microscleres include bipocillas and palmate anisochelas.

About 25 species, occurring in cold and temperate waters, or in deeper waters. Not known from the shallow tropics.

Remarks. – The apparent absence of toxas is unusual for the family. The palmate anisochelas are shared with *Melonchela* (see above), *Acanthorhabdus* (see below) and the mycalid genus *Mycale* s.l., but the latter are assumed to have been developed convergently. The genus is traditionally assigned to

Table V. Taxa conforming to the definition of *Cornulum* s.l.

Cornulum textile Carter, 1876; Lundbeck, 1910; Koltun, 1959; Hoshino, 1987; Van Soest, 1993	North East Atlantic
Cornulum fistulatum (Carter, 1880 as *Suberites*; Dendy, 1905 as *Histoderma*; De Laubenfels, 1936 as *Xytopsene*)	Indian Ocean
Cornulum sinclairi (Bergquist & Fromont, 1988 as *Paracornulum*)	New Zealand
Cornulum strepsichela Dendy, 1922; Vacelet et al., 1976; Bergquist & Fromont, 1988	Indian Ocean
Cornulum novaezealandiae Brøndsted, 1924	New Zealand
Cornulum toxifera (Wilson, 1925 as *Coelosphaera*)	Philippines
Cornulum johnsoni (De Laubenfels, 1934 as *Coelosphaerella*); Van Soest, 1984	Caribbean
Cornulum tubiformis Burton, 1935; Hoshino, 1987	North Pacific
Cornulum ciocalyptoides Burton, 1935	North Pacific
Cornulum clathriata (Koltun, 1955 as *Melonchela*)	Arctic
Cornulum tylota (Boury-Esnault, 1973 as *Artemisina*)	Brazil
Cornulum virguliferum (Lévi & Lévi, 1983 as *Heterocornulum*)	New Caledonia
Cornulum spec. Van Soest, 1993	West Africa

Myxillidae, and indeed the skeletal structure of many species reminds of *Myxilla*. However, Myxillidae in the restricted sense of Hajdu et al. possess anchorate chelae and sigmata (although the latter may occasionally be absent).

Genus *Acarnus* Gray, 1867

Syn.: *Acanthacarnus* Lévi, 1952, *Fonteia* Gray, 1867, and *Trefortia* Dezsö, 1880.

Type species: *Acarnus innominatus* Gray, 1867 (by monotypy).
Definition (cf. Van Soest et al., 1991): Massive, branching or encrusting Iophonidae with ectosomal skeleton of scattered tylotes with spined heads, choanosomal skeleton consisting of an isodictyal, isotropic or anisotropic, reticulation of styles and cladotylotes, arranged singly or in tracts of several spicules, which may or may not be echinated by acanthostyles and/or cladotylotes. In thinly encrusting specimens, the choanosomal skeleton is hymedesmioid, i.e., with styles or cladotylotes erect on the substrate. The cladotylotes occur normally in two categories, but exceptionally in three or a single one. Microscleres include up to three categories of toxas, and chelas.

Remarks. – The genus has been extensively revised by Van Soest et al. (1991) and was found to comprise 23 extant species. Since then a 24th species was described by Hooper & Lévi (1993). It was formerly assigned to Myxillidae (e.g., Van Soest, 1984) or to Microcionidae (Van Soest et al., 1991).

Genus *Megaciella* Hallmann, 1920

Type species: *Amphilectus pilosus* Ridley & Dendy, 1886 (by original designation).
Definition: Branching or encrusting Iophonidae with ectosomal brushes of tylotes with spined heads, with a reticulate or confused choanosomal skeleton consisting of smooth styles with spined or smooth heads, arranged singly or in two's or three's. Thinly encrusting specimens have the styles erect on the substrate. Microscleres are palmate isochelas and toxas.

Remarks. – The type species lacks echinating acanthostyles, but similar species with acanthostyles exist. The similarity in spicule characteristics with the microcionid genus *Clathria* is considerable, and future character analysis may show that inclusion in the Microcionidae might be more appropriate. In

Table VI. Nominal genera assigned to the Iophonidae sensu Hajdu et al. (1994). (acanth. = acanthose, acc. = accessory, cat.= category, ch.= choanosomal, ect.= ectosomal, msp.= microspined apices).

Genus	Habit	Ect. spicules	Ch. spicules	Acc. spicules	Chelas	Toxas	Other	Status
Acanthorhabdus Burton, 1929	massive, subspherical	acanthorhabds msp. apices	anisoxeas	absent	aniso- (spurred)	absent	-	valid
*Acarnus** Gray, 1867	massive, ramose	msp. tylotes	styles, cladotylotes	acanthostyles (may be absent)	iso-	3 cat.	-	valid
Acheliderma Topsent, 1892	fistular	msp. tylotes	msp. styles	acanthostyles	absent	present	microxeas	valid
Anisotylacanthea Vacelet, 1969	encrusting	rugose anisotylotes	rugose anisotylotes	absent	absent	absent	-	?jun. syn. *Damiria*
Astylinifer Topsent, 1927	encrusting	smooth? tylotes	?acanthostyles	acanthostyles	absent	present	microxeas	jun. syn. *Acheliderma*
Coelosphaerella De Laubenfels, 1934	fistular	msp. strongyles	msp. strongyles	absent	iso-	present	-	?jun. syn. *Cornulum*
Cornulella Dendy, 1922	fistular	msp. tylotes	msp. tylotes	acanthoxeas	iso-	present	-	valid
Cornulum Carter, 1876	fistular	msp. tylotes	styles	absent	iso-	present (may be spined)	-	valid
Damiria Keller, 1891	fistular	msp. tylotes	msp. tylotes	absent	absent	present (mostly absent)	-	?valid
Fusifer Dendy, 1896	fistular	absent (sandy)	tylostyles (sandy)	acanthostyles	absent	present	microxeas (like *Astylinifer*)	jun. syn. *Acheliderma*
Heterocornulum Lévi & Lévi, 1983	fistular	msp. tylotes	styles	absent	iso-	present	microstrongyles (like *Acarnus*)	?jun. syn. *Cornulum*
Histodermopsis De Laubenfels, 1936	fistular	msp. strongyles	msp. strongyles	acanthostrongyles	absent	absent	-	?jun. syn. *Zyzzya*
*Iophon*** Gray, 1867	massive erect	msp. tylotes	styles (may be acanth.)	acanthostyles (may be absent)	aniso- (spurred)	absent	bipocillae	valid
Megaciella Hallmann, 1920	encrusting	msp. tylotes	styles (may be acanth.)	acanthostyles (may be absent)	iso-	present	-	?valid
Melonchela Koltun, 1955	fistular?	msp. strongyles	msp. styles	absent	aniso- (melonchelas)	present (spined)	-	?jun. syn. *Cornulum*
Paracornulum Hallmann, 1920	fistular	msp. tylotes	msp. tylotes	acanthostyles	iso-	present	-	valid
Xytopsene De Laubenfels, 1936	fistular	msp. tylotes	msp. tylotes	absent	iso-	absent	-	?jun. syn. *Damiria*
*Zyzzya**** De Laubenfels, 1936	fistular	msp. tylotes	msp. tylotes	acanthostrongyles	iso- (may be absent)	present (may be absent)	-	valid

* With generally accepted junior synonyms *Fonteia* Gray (1867) and *Trefortia* Deszö (1880)
** With generally accepted junior synonyms *Alebion* Gray (1867), *Ingallia* (Gray, 1867), *Menyllus* Gray (1867), *Pocillon* Topsent (1893), *Iophonopsis* Dendy (1924), *Burtonella* De Laubenfels (1936), and *Iophonota* De Laubenfels (1936)
***With obvious synonym *Damirina* Burton, 1959 (cf. above)

N.B. Genera with similarities to Iophonid genera, but assigned to other families are: *Cornulotrocha* Topsent (1928) (to Microcionidae), *Damiriopsis* Burton (1928) (to Raspailiidae), *Dyscliona* Kirkpatrick, 1900 (to Phloeodictyidae), and *Tedaniphorbas* De Laubenfels (1936) (to Coelosphaeridae)

that case, convergent development of tylotes must be assumed. In view of the occurrence of these in some families of the suborder Myxillina this is not unexpected.

Genus *Acanthorhabdus* Burton, 1929

Type species: *Acanthorhabdus fragilis* Burton, 1929 (by monotypy).
Definition: Iophonidae with modified styles in the form of anisoxeas often provided with a mucron arranged in a course but ill-defined plumoreticulation. Ectosomal megascleres are acanthorhabds with heavy spines and microspined tylote apices. Microscleres are spurred palmate anisochelas.

Remarks. – Burton (l.c.) placed this rather enigmatic monotypical genus in his Mycaleae on account of its anisochelae, but the presence of the special ectosomal megascleres makes it thoroughly untypical of this group. Spurred anisochelae are characteristic of *Iophon* and the acanthorhabds have spined tylote apices found in all members of the Iophonidae. Accordingly, we propose here to include *Acanthorhabdus* in the family Iophonidae.

Discussion

Phylogenetic relationships

The new concept of the Iophonidae still needs to be more firmly established, as it is based on a combination of characters, viz. ectosomal microspined tylotes, isotropic choanosomal skeletons, palmate chelas and toxas, which are not unique to the group. *Cornulum* and its relatives are traditionally grouped in the Coelosphaeridae, a homogeneous group if the growth form and body organization is taken as a synapomorphy, but an extremely heterogeneous group if spicule characters are taken as synapomorphies. This issue has been debated several times (e.g., Van Soest, 1984; Lévi & Lévi, 1983; Bergquist & Fromont, 1988; Hooper & Krasochin, 1989; Hajdu et al., 1994) with different conclusions. Hajdu et al. (1994) embedded their conclusion – that growth form is more likely to evolve convergently – in an overall discussion of Poecilosclerida characters demonstrating the consequences of adopting different scenarios of character evolution for the classification of genera and families. A leading hypothesis for their conclusion is the higher adaptive constraint of growth form and body organization, and a lower adaptive pressure on microscleres and spicule ornamentation. Thus, spicule (ornamentation) similarities are considered more informative in phylogenetic analysis than growth form and body organization.

Following this reasoning, very similar growth forms found in e.g., *Coelosphaera* and *Cornulum* are not considered firm evidence of family relationship because of lack of spicular similarities (arcuate vs. palmate chelas, smooth tylotes vs. microspined tylotes, presence of sigmas vs. absence, absence of toxas vs. presence). Conversely, strongly different growth forms in e.g., *Acarnus innominatus* and *Zyzzya invemar* do not prevent inclusion of both into the same family, because they share similar spiculation (microspined tylotes, bow-shaped toxas, and palmate chelas).

Character analysis

More studies are needed to link the fistular and the non-fistular genera of the Iophonidae. However, since the fistular genera treated here comprehensively (*Zyzzya*, *Cornulella*, *Damiria*, *Acheliderma*, and *Paracornulum*) show a common feature in the heavy spination of the tylote heads, as opposed to the lighter microspined condition in *Cornulum* s.l., we may safely assume they form a monophyletic group. *Cornulum* shares the fistular growth form with these genera and thus is likely to be the nearest outgroup. These observations make it possible to do a preliminary phylogenetic analysis in order to explore possible evolutionary relationships of the five genera.

Using *Cornulum* s.l. as an outgroup taxon, 14 characters were scored in all known members of the four genera. Character states and their treatment in the analysis are presented in Table VII. This matrix was offered to the computer program PAUP 3.1 (Swofford, 1993) (non-exhaustive heuristics search). If characters are treated unordered and have an equal weight of 1, the analysis yields 24 equally parsimonious trees of 27 steps length and a consistency index of 0.667. The 50% majority consensus tree (Fig. 58), which is identical

Table VII. Characters/states of *Zyzzya, Cornulella, Damiria, Acheliderma* and *Paracornulum* species used for a phylogenetic analysis using PAUP 3.1 (Swofford, 1993), with *Cornulum* s.l. as the outgroup.

Character Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cornulum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Z. invemar	0	1	1	1	0	0	1	1	0	0	0	1	3	0
Z. fuliginosa	0	1	1	1	0	0	1	1	0	1	0	1	3	0
Z. papillata	0	0	0	0	0	0	1	1	1	1	0	1	3	0
C. santamartae	1	0	0	0	0	1	0	1	0	0	0	1	2	0
C. lundbecki	1	0	0	2	0	1	0	1	0	1	0	1	1	0
C. amirantensis	1	0	0	0	0	1	0	1	0	1	0	1	1	0
C. purpurea	1	0	?	2	0	1	0	1	0	0	0	1	2	0
C. minima	1	0	0	0	0	1	0	1	0	0	0	1	2	0
C. tyro	1	0	0	0	0	1	0	1	0	1	0	1	2	0
D. simplex	0	1	0	0	0	0	0	1	1	1	1	1	0	0
D. testis	0	1	0	0	0	0	0	1	1	1	0	1	0	0
D. leonorae	0	1	0	0	0	0	0	1	1	1	1	1	0	0
D. toxifera	0	1	0	0	0	0	0	1	1	0	1	1	0	0
A. lemniscatum	1	0	0	0	1	0	0	0	1	0	0	0	0	1
A. planum	0	0	0	?	1	0	0	0	1	0	0	2	0	1
A. fistulatum	0	0	0	0	1	0	0	0	1	0	0	?	0	1
A. lisannae	1	0	0	?	1	0	0	0	1	0	0	0	0	1
P. dubium	0	1	0	0	1	0	0	1	0	0	1	1	0	0
P. coherens	0	0	0	0	1	0	0	1	0	1	0	1	0	0

Character 1: Growth form: 0 = fistules on top of a massively encrusting base, 1 = fistules either sticking directly out of the substrate or issuing from a very thin crust.
Character 2: Ectosomal skeleton: 0 = unispicular reticulation, 1 = feltwork of spicules.
Character 3: Choanosomal skeleton: 0 = isodictyal reticulation, 1 = mass of spicules.
Character 4: Colour: 0 = orange-yellow, 1 = black, 2 = purple.
Character 5: Presence of echinating acanthostyles: 0 = absent, 1 = present.
Character 6: Presence of acanthoxeas: 0 = absent, 1 = present.
Character 7: Presence of acanthostrongyles: 0 = absent, 1 = present.
Character 8: Presence of structural styles: 0 = present, 1 = absent (loss).
Character 9: Presence of chelas: 0 = present, 1 = absent (loss).
Character 10: Presence of toxas: 0 = present, 1 = absent (loss).
Character 11: Tylote size categories: 0 = single size, 1 = two sizes (one long and thin, one short and thick).
Character 12: Spination of tylote heads: 0 = lightly spined, 1 = extensively spined all over, 2 = not spined (loss).
Character 13: Length of diactinal accessory megascleres: 0 = absent, 1 = <50 μm, 2 = 50–150 μm, 3 = >150 μm.
Character 14: Presence of diamond-shaped microxeas: 0 = absent, 1 = present.

to tree no. 15 of these 24 trees, is chosen as the best representation of the phylogenetic relationships of the species of the five genera. This tree shows several unsolved parts, due to the paucity of characters (states) available for the analysis. Both *Paracornulum* species are shown to be paraphyletic, due to similarities with *Damiria* and the absence of unique characters. The status of *Damiria* and *Paracornulum* as separate genera is not well established. Future studies of the species involved and ongoing phylogenetic studies might eventually result in a rearrangement in this group. *Zyzzya, Cornulella,* and *Acheliderma* seem to be well-established genera, although the relationships of the species within the genera are only partly solved.

Biogeography

Although the results of the character analysis show unsolved parts, several biogeographical conclusions from the tree can nevertheless be made: *Z. invemar* and *Z. fuliginosa* are likely to be sister species dating from the Tethys Sea, with *Z. papillata* being an older, perhaps Indian, element. Similar trends may be observed from *Cornulella*, where sistergroup relationships between Indo-Pacific and Caribbean species (*C. santamartae, C. purpurea,*

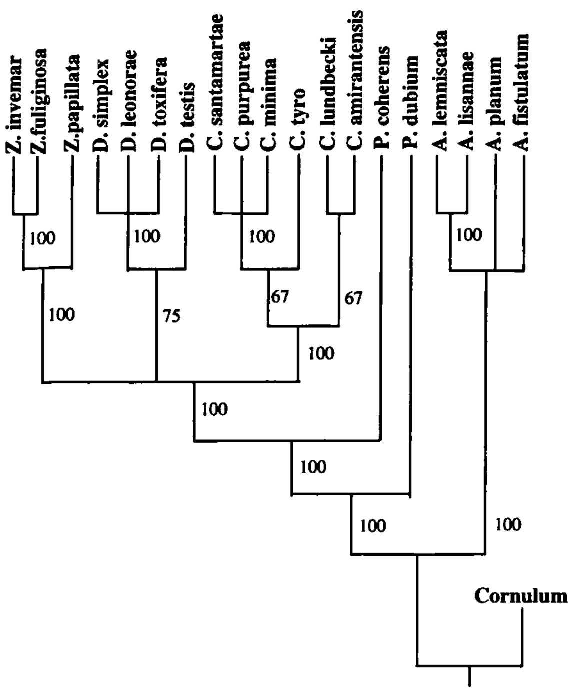


Fig. 58. Phylogenetic relationships of *Zyzzya*, *Damiria*, *Cornulella*, *Acheliderma* and *Paracornulum* species, based on parsimony analysis of characters listed in Table VII, using the computer program PAUP 3.1 (Swofford, 1993). The cladogram represents the 50% majority tree of 24 equally parsimonious trees and is identical to tree number 15 of the PAUP output. Tree length: 27 steps. Consistency index (CI) = 0.667, homoplasy index (HI) = 0.333, retention index (RI) = 0.842, rescaled consistency index (RC) = 0.561. Figures on the branches refer to the percentage of the 24 trees supporting the branching sequence distal to it.

and *C. minima*) are younger than the relationships with several Indian Ocean species (*C. lundbecki*, *C. amirantensis*, and *C. tyro*). In *Acheliderma* the Mediterranean and Caribbean species are closer than each is to the deep-water Azorean and South Australian species. Conclusions on the biogeographic history of *Damiria* and *Paracornulum* are not possible on the basis of the present data.

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