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

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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 For comparison both published and unpublished material belonging to these genera from other parts of the world was examined, and this yielded several nomenclatorial changes and a further three new species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 leonora* (Caribbean), *D. toxifera* (Seychelles) and *Acheliderma lisannae* (Caribbean). All species belonging to these genera, as well as to the closely related Indo-Pacific genus *Paracornulium*, 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 *Cornulium* was generally accepted. The recently revived family Iphionidae is demonstrated to be the likely assemblage for them. A brief survey of Iphionidae 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 récifs au large des côtes de Colombie, Bonaire et Curaçao (Caraïbes du Sud). A très peu d'exceptions près, ces Spongiaires sont des exemples petits ou minuscules peuplant des crevasses et d'autres habitats cryptiques; il est possible que certains puissent perfore 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 nomenclaturaux 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 leonora* (Caraïbes), *D. toxifera* (Seychelles) et *Acheliderma lisannae* (Caraïbes). Pour toutes les espèces appartenant à ces genres ainsi qu'au genre Indo-Pacific prochement apparenté *Paracornulium*, 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 *Cornulium* avait généralement été acceptée. On démontre que c'est la famille des Iphionidae (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, il est clair que dans tous ces genres les relations de proche parenté dépassent les limites des zones marines contiguës: elles sont souvent disjunctes.

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. *Zyzya* 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 minute-ly 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 Curacao 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 estab-

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 *Zyzya*, *Cornulella*, *Acheliderma*, and *Damiria* is controversial. Since all have fistules and tylole ectosomal megaloscleres, 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 isochelae and abundant toxas, *Iophon* has palmate anisocheles lacking the toxas; both share with the above-mentioned Cornulidae the lack of sigmas and the possession of ectosomal tyloles 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 *Zyzya*, *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 Cura
cao reefs (1988–1994). In addition, several specimens were collected by students of the University of Amsterdam studying the sub-rubble communities of Bonaire and Curacao (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 Zoologisch 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 Curacao, Indonesia, the Seychelles (In
do 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 DCI. 2964) were borrowed from the London, Frankfurt, Berlin, and Paris museums, respectively. Slides of *Acheliderma lemnapata* Topsyart, 1892 (D.T. 170) and *Astylinifer planum* Topsyart, 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; micro scleres, if present, include palmate chelae 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 multiporic tracts of tylotes ascending to the surface, between which is dispersed an irregular isodictyal reticulation of verticillately-spined strongyles. Micro scleres, 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 *Dysclonia 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 *Dysclonia 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 *Dysclonia 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* Diaz 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 mm², 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 discoloration.

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: tyloletes and acanthostrongyles, both intermingled, seemingly without localization.

Spicules (Table 1): Tyloletes (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 stylole ancestry. Size: 235–301 by 4–8 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 *Acranrus*—"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, Cornuella, Acranrus*) 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 *Acranrus*, unknown from any Caribbean sponge. Careful comparison with sympatric *Acranrus* species (*A. nicoleae* Van Soest et al., 1991, *A. deweerdtiae* Van Soest et al., 1991, and *A. innominatus* Gray, 1867) made it clear that there is some superficial resemblance with the category I toxas ("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 tylole 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 1).

**Review of Indo-Pacific Zyzzya specimens**

Below brief descriptions of Indo-Pacific specimens are given, with an emphasis on specimens not treated by Hooper & Krasočín (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).
**Suberites fuliginosus** Carter, 1879: 347.

(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*.)

**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.
Table 1. 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.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>tylopes</th>
<th>acanthostygongles</th>
<th>no. verticils</th>
<th>chelas</th>
<th>toxas</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zyzzya invemar n. sp. Colombia, ZMA 10803</td>
<td>258-280.5 (11.46-301) / 4.5-2 (1.13)-8</td>
<td>173-190 (11.90-215) / 5-2.6 (1.25)-10</td>
<td>20-25.8-34</td>
<td>19-20.0 (1.41)-23 (n=6)</td>
<td>49-58.4 (6.53)-71 (n=10)</td>
</tr>
<tr>
<td>Zyzzya invemar n. sp. Colombia, ZMA 10804</td>
<td>235-255.9 (13.17-281) / 4.4-8 (0.60)-6 (n=10)</td>
<td>167-183.0 (10.67-197) / 4.2-8 (1.03)-7(n=10)</td>
<td>26-28-30</td>
<td>20-20.5-21 (n=2)</td>
<td>39 (n=1)</td>
</tr>
<tr>
<td>Suberites fuliginosus Carter N. Australia, BM 1846:8.5:8</td>
<td>231-303.3 (29.79-353) / 4.5-6.4 (1.18)-9</td>
<td>206-260.2 (24.20-300) / 9-12 (2.51)-18</td>
<td>28-31.9-36</td>
<td>not found</td>
<td>absent</td>
</tr>
<tr>
<td>Plocamia massalis Dendy Mauritius</td>
<td>286-408 / 6-14</td>
<td>155-232 / 4-15</td>
<td>unknown</td>
<td>14-20</td>
<td>absent</td>
</tr>
<tr>
<td>Damirina verticillata Burton Zanzibar</td>
<td>298-468 / 3-15</td>
<td>134-256 / 5-20</td>
<td>unknown</td>
<td>not found</td>
<td>absent</td>
</tr>
<tr>
<td>Zyzzya massalis; Bergquist &amp; Fromont, New Zealand</td>
<td>367-402 / 6-12</td>
<td>217-266 / 11-14</td>
<td>unknown</td>
<td>15-16</td>
<td>absent</td>
</tr>
<tr>
<td>Zyzzya massalis; Hooper &amp; Krasochn, W. Australia</td>
<td>280-438 / 1.5-12</td>
<td>118-190 / 4-14</td>
<td>24</td>
<td>not found</td>
<td>absent</td>
</tr>
<tr>
<td>Zyzzya massalis; Hooper &amp; Krasochn, Seychelles</td>
<td>305-418 / 3-12</td>
<td>148-242 / 5-15</td>
<td>unknown</td>
<td>not found</td>
<td>absent</td>
</tr>
<tr>
<td>Zyzzya fuliginosa; this paper ZMA POR. 8441, Fiji</td>
<td>184-267.4 (23.31-305) / 2-4.0 (0.82)-5</td>
<td>155-213.2 (19.50-249) / 4-2.7 (2.09)-11</td>
<td>unknown</td>
<td>not found</td>
<td>absent</td>
</tr>
<tr>
<td>Zyzzya fuliginosa; this paper ZMA POR. 9475, Papua N.G.</td>
<td>245-260.8 (13.83-282) / 5.5-5 (0.87)-7 (n=10)</td>
<td>231-253.2 (17.08-289) / 9-10.6 (1.97)-12 (n=10)</td>
<td>unknown</td>
<td>not found</td>
<td>absent</td>
</tr>
<tr>
<td>Zyzzya fuliginosa; this paper ZMA POR. 10537, Seychelles</td>
<td>173-185.2 (7.96-197) / 2-4.1 (0.49)-3 (n=10)</td>
<td>184-201.0 (9.53-209) / 10-13.8 (2.56)-17(n=10)</td>
<td>unknown</td>
<td>not found</td>
<td>absent</td>
</tr>
<tr>
<td>Zyzzya fuliginosa; this paper ZMA POR. 10816, Seychelles</td>
<td>192-227.8 (16.35-255) / 2-5.1 (1.21)-7</td>
<td>212-230.4 (10.42-258) / 10-20.3 (3.66)-28</td>
<td>21-23.1-25</td>
<td>21-23.1-25</td>
<td>absent</td>
</tr>
<tr>
<td>Zyzzya fuliginosa; this paper ZMA POR. 10811, Seychelles</td>
<td>219-258.6 (20.92-292) / 2-4.7 (0.92)-6</td>
<td>201-248.4 (14.26-265) / 21-24 (2.58)-28</td>
<td>22-24.8-28</td>
<td>not found</td>
<td>absent</td>
</tr>
<tr>
<td>Damirina papillata Thomas India</td>
<td>159-277 / 1-5</td>
<td>117-176 / 6-12</td>
<td>10-15</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Zyzzya papillata; this paper ZMA POR. 10815, Seychelles</td>
<td>166-218.3 (18.97-216) / 3-3.8 (0.51)-4.5</td>
<td>150-159.2-168 / 5-5.8 (0.57)-7</td>
<td>13-15.8-18</td>
<td>absent</td>
<td>absent</td>
</tr>
</tbody>
</table>

Plocamia massalis Dendy, 1922: 78.  

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

Not examined. Locality: Zanzibar, 113 m. Dark brown en-

François Atoll, Amirantes, 3 m depth, 07°5′ S 52°44′ E, 6-1-1993. 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 ecosomal 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 acanthostyles, 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): Tylostyles: 222–260 by 4 μm; acanthostyles (called acanthostyles with the observation of these becoming acanthostyles when the spination on the ends becomes more dense): 105–142 by 6 μm; palmate isochelae: 16 μm.

Comment: Thomas describes the acanthostyles 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 fistsules of 10 by 4 mm, which are open at the upper end. The ectosomal skeleton is a feltwork of tylostyles; the choanosomal skeleton is confused, with here and there a unispiral reticulation of tylostyles and acanthostyles. Spicule sizes (after Hooper & Krasochin, 1989): Tylostyles: 180–590 by 2–20 μm (Vacelet et al. observed two categories); acanthostyles: 109–285 by 3–15 μm; palmate isochelae: 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.


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 tylostyles. The choanosomal skeleton contains multispiral tracts of tylostyles and an irregular subsidical reticulation of single acanthostyles and occasional tylostyles. Spicule sizes: Tylostyles 280–438 by 1.5–12 μm (some are stylostyle); acanthostyles 118–190 by 4–14 μm (drawing shows about 24 whorls of spines); no microscleres. This specimen conforms to *Z. fuliginosa*.

**Zyzzya fuliginosa** sensu Hooper & Krasochin, 1989; Seychelles specimen.


**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 fistsules 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 tylostyles 88–106 μm long. One of the Mahé specimens differed from the other two in having rather feeble spiculation: tylostyles 173–197 by 2–3 μm; acanthostyles: 184–209 by 10–17 μm. The other two were closely similar both in growth form and in spiculation: tylostyles (Figs. 22–23): 219–292 by 2–6 μm and 192–255 by 2–7 μm; acanthostyles (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) acanthostyles (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 tylostyles 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 acanthostyles were found. Some developmental stages were stylostyle (Fig. 21). Tylostyles 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 acanthostyles 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 mm² to 200 cm². 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 tylolets.

Chonosomal skeleton: Basically there is a unispicular isodictyal reticulation of acanthostrongyles, with a good proportion of tylolets 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 styloyle-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 styloete. Size, especially thickness, quite variable: 109–300 by 3–28 μm.

Palmate isochellas: 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 tylolets.

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


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 tylo-" 

Notes: Species with acanthoxeas so far were assigned to the genus Paracornulum Hallmann, 1920. The definition of this genus by Hallmann (1.c.) allowed inclusion of sponges with acanthostyles, acanthoxeas, or acanthostrongyles, thus effectively also including Zyzya. 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 Zyzya. 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 syn-

nym of Acliiderma Topsent, 1892, but this differs from Paracornulum in lacking chelas and possessing choanosomal structural styles next to the acan-thostyles (see also below).

Description of the Caribbean species

Cornulella santamartae n. sp.

(Figs. 24–29)


Additional material: ZMA POR. 10826, Karpata, Bonaire, 4 m, under coral rubble, 13-VII-1987, coll. G.J. Roebers, field no. 146. Curação: 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 tylopes 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 mm² 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 Diaz et al., 1987. The Curação 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 tylopes in a relatively low density, seemingly forming a loose reticulum. Microscleres and acanthoxeas are dispersed among them.
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.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>tyloles</th>
<th>acanthoxeas</th>
<th>chelas</th>
<th>toxas</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cornulella santamartae n. sp. ZMA POR. 10808, Colombia</td>
<td>111-120.8/6.48-131</td>
<td>57-79.6(7.49)-91</td>
<td>12-14.8(1.64)-17</td>
<td>99 (n=1)</td>
</tr>
<tr>
<td>Cornulella santamartae n. sp. INV-POR.0451, Colombia</td>
<td>151-169.7/2-178</td>
<td>92-112.0(10.8)-131</td>
<td>21-23.2-25</td>
<td>82 (n=5)</td>
</tr>
<tr>
<td>Cornulella santamartae n. sp. ZMA POR. 10809, Bonaire</td>
<td>126-139.5(8.28)-156</td>
<td>81-93.6(6.62)-105</td>
<td>19-22.3(1.62)-26</td>
<td>60-70.1(16.46)-90 (n=5)</td>
</tr>
<tr>
<td>Cornulella santamartae n. sp. ZMA POR. 10826, Bonaire</td>
<td>156-168.0(5.50)-177</td>
<td>89-98.0(6.45)-111</td>
<td>16-19.5(1.80)-22</td>
<td>not found</td>
</tr>
<tr>
<td>Cornulella santamartae n. sp. ZMA POR. A9 B6, Curaçao</td>
<td>135-151.8(7.85)-162</td>
<td>78-96.3(10.26)-108</td>
<td>19-19.8(1.45)-23</td>
<td>39-48.5-58 (n=2)</td>
</tr>
<tr>
<td>Cornulella santamartae n. sp. ZMA POR. H51-5, Curaçao</td>
<td>123-137.4(7.40)-147</td>
<td>48-64.0(18.55-90</td>
<td>19-21.2(1.07)-23</td>
<td>not found</td>
</tr>
<tr>
<td>Cornulella santamartae n. sp. ZMA POR. 10810, Curaçao</td>
<td>144-158.3(10.16)-171</td>
<td>one broken spicule found</td>
<td>19-20.5(0.76)-21</td>
<td>not found</td>
</tr>
<tr>
<td>Cornulella lundbeckiensis Dendy Seychelles</td>
<td>400 / 6</td>
<td>20 / 1</td>
<td>50</td>
<td>120</td>
</tr>
<tr>
<td>Cornulella amirantensis n. sp. ZMA POR. 10685, Seychelles</td>
<td>381-416.9(20.79)-466</td>
<td>36-43.5(4.46)-51</td>
<td>16-20.6(1.65)-23</td>
<td>absent</td>
</tr>
<tr>
<td>Cornulella amirantensis n. sp. ZMA POR. 10805, Seychelles</td>
<td>357-432.5(38.74)-494</td>
<td>39-44.3(3.94)-51</td>
<td>18-21.0(1.66)-24</td>
<td>absent</td>
</tr>
<tr>
<td>Cornulella purpureum (Hancock) Indo-Pacific</td>
<td>260 / 5</td>
<td>60-170 / 5</td>
<td>18</td>
<td>75</td>
</tr>
<tr>
<td>Cornulella minima Vacelet et al. Madagascar</td>
<td>130-250</td>
<td>110-150</td>
<td>12.5-15</td>
<td>1) 20-25 2) 60-175</td>
</tr>
<tr>
<td>Cornulella pyro n. sp. ZMA POR. 10520, Seychelles</td>
<td>224-243.1(12.94)-273</td>
<td>105-121.0(6.91)-138</td>
<td>13-16.0(1.20)-18</td>
<td>absent</td>
</tr>
</tbody>
</table>

*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) *Paracornu-

*Ciona 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 (I.e.) who gave measurements and a photograph of the spicules. Purple fistules, sticking out from a *Tridacna gigas* excavated by the sponge. Ectosomal tyloles with feebly developed spined heads, 260 by 5 µm. Acanthoxeas 60-170 by 5 µm. Robust curved palmate isochelas: 18 µm.
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 tyloletes 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, JOP-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,

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 tyloletes (Figs. 30–33): With prominently spined heads; spines extending somewhat along the shaft (Figs. 32–33); shaft distinctively 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.

Palmet 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 tyloletes (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 tyloletes; no chaotosomal tissue or skeleton was observed. Tyloletes with well-developed spined heads: 130–250 μm. Acanthoxeas, curved, asymmetrical: 110–150 μm. Palmet 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)


Description. — Yellow-orange fistules (Fig. 3), single or branching dichotomously, up to 16 mm long, less than 1 mm in diameter. Fragile.

Spicules: Tyloletes (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.


Remarks. — This species is similar to Cornulella amirantensis n. sp. in lacking toxas, but differs clearly from that species in having much smaller tyloletes 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, tyloite; 39, acanthoxea; 40, palmate isochela; 41, detail of head of tyloite; 42, detail of opposite head of same tyloite; 43, detail of acanthoxea.

Figs. 44–47. *Damiria toxifera* n. sp., SEM photos of the holotype: 44, detail of head of tyloite; 45, detail of opposite head of same tyloite; 46–47, toxas.
A possible seventh species is the Arctic *Histoder-mella coriacea* Lundbeck, 1910, made the type of a genus *Histodermopsis* by De Laubenfels, 1936 (p. 72). It differs from the very similar *Histodermella ingolfii* in having palmate instead of arcuate chelas and having minute spines on the ectsomal tylothes; 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 tylothes 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 tylothe 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 oxas/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 tylothes (*D. testis*); the remaining two species differ the thickness of the shorter tylothes, *D. simplex* having these frequently over 10 μm, *D. leonora* 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 tylothes, oxas 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. leonora* 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 tylothes, 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 tylothes, *"slim":* 264–296, and *"strong, thick":* 200–210 μm. However, no mention is made of spination of the tylothe heads.

*Damiria toxifera* n. sp

(Figs. 6, 44–47)


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 tylothes.

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): Tylothes (Figs. 44–45) in two
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. Tylole unisparicularly arranged; tangential in the ectosome. Topsent gives only a single size of tylole: 140–170 by 5 µm, but admits that the specimen is damaged and in bad condition. On the Goring Bank,
North Atlantic between Portugal and the Azores, deep water:
270 m.
Comment: Van Soest (1984) recorded this species from the reefs of Curacao, 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 leonora** 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, Curacao, Buoy 0, 6–12 m, coll. R.W.M. van Soest.


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 tyloles.

Choanosomal skeleton: A few tracts and loose spicules.

Spicules (Table III): Two size categories of tyloles (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 tyloles up to 11 μm thick).

Distribution and ecology. – Curacao, 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 tyloles 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 anisotyloles 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.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>tylostyles</th>
<th>styles</th>
<th>acanthostyles</th>
<th>toxas</th>
<th>microxeas</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acheliderma lemniscata</em> Topsent, 1892, Mediterranean</td>
<td>250-270</td>
<td>420-450</td>
<td>80-175</td>
<td>120</td>
<td>60-70/1</td>
</tr>
<tr>
<td><em>Fusifer fistulatum</em> Dendy, 1896, S. Australia</td>
<td>absent</td>
<td>540</td>
<td>70</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td><em>Asylinifer planum</em> Topsent, 1927, Azores</td>
<td>265-315</td>
<td>105-455</td>
<td>(not differentiated)</td>
<td>125</td>
<td>30-37/2-3</td>
</tr>
<tr>
<td><em>Acheliderma lisannae</em> n. sp. ZMA POR. 10907, Colombia</td>
<td>243-300-8.348</td>
<td>399-440-4.481</td>
<td>67-76.6-101</td>
<td>101-120.0-136</td>
<td>1) 36-43.5-52</td>
</tr>
<tr>
<td></td>
<td>/3-3.46-4.5</td>
<td>/3-3.90-5 (n=15)</td>
<td>/2-3.12-4 (n=2)</td>
<td>/1-1.2-3.5</td>
<td>2) 19-25-1.28</td>
</tr>
<tr>
<td></td>
<td>(microspined)</td>
<td>(microspined)</td>
<td></td>
<td></td>
<td>/1.12-2</td>
</tr>
</tbody>
</table>

**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.

*Acheliderma planum* Topsent, 1927.
Microscopic slide labeled *Fusifer planus*, MNHN D.T. 1288 examined. Flat crust, with ectosomal skeleton to tylostyles 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 *Asylinifer* Topsent, 1927. Topsent’s labeling of the type slide indicates his hesitation in considering *Asylinifer* 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 tylostyles. Choanosomal megascleres are smooth stylestyles, 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 tylostyles, 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 tylostyles 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 tylostyles or occasionally smooth anisotylostyles 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 tylostyles. 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 anisotylo-
totes 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 anisotylo-
totes 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 inter-
crossing tylotes and choanosomal skeleton consisting of similar tylotes. Microscleres palmate isochel-
as 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: 30–33.8 (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.

Comments: Assignment of this material to Paracornulum is ten-
tative, because the robust, smooth acanthostyles and the ecto-
somal 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 cm² (dry state). Ectosome not detachable. Spicules are strongyls 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 *Zyzyya*, *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 strongyls or tyloites 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 microstrongyls (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 microstrongyls 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


Type species: *Halichondria scandens* Bowerbank, 1866 (by original designation).

Definition: Massive, branching or encrusting Iophonidae with ectosomal skeleton of intercrossing or scattered tyloites 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
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


Type species: *Acarnus innominatus* Gray, 1867 (by monotypy).

Definition (cf. Van Soest et al., 1991): Massive, branching or encrusting Iophonidae with ecosomal skeleton of scattered tylostones 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 ecosomal brushes of tylostones 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

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

<table>
<thead>
<tr>
<th>Genus</th>
<th>Habit</th>
<th>Ect. spicules</th>
<th>Ch. spicules</th>
<th>Acc. spicules</th>
<th>Chelas</th>
<th>Toxas</th>
<th>Other</th>
<th>Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthorhabdus</td>
<td>massive, subspherical</td>
<td>acanthorhabds msp. apices</td>
<td>anisoxeas</td>
<td>absent</td>
<td>anisop (spurred)</td>
<td>-</td>
<td>valid</td>
<td></td>
</tr>
<tr>
<td>Burton, 1929</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acarnus* Gray, 1867</td>
<td>massive, ramose</td>
<td>msp. tylopes</td>
<td>styles, cladotylotes</td>
<td>acanthostyles (may be absent)</td>
<td>iso- 3 cat.</td>
<td>-</td>
<td>valid</td>
<td></td>
</tr>
<tr>
<td>Acheliderma Topsen, 1892</td>
<td>fistular</td>
<td>msp. tylopes</td>
<td>msp. styles</td>
<td>acanthostyles</td>
<td>absent</td>
<td>present</td>
<td>microxeas</td>
<td>valid</td>
</tr>
<tr>
<td>Cornulotrocha Dendy, 1922</td>
<td>fistular</td>
<td>msp. tylopes</td>
<td>msp. tylopes</td>
<td>acanthoexes</td>
<td>iso-</td>
<td>present</td>
<td>-</td>
<td>valid</td>
</tr>
<tr>
<td>Cornulum Carter, 1876</td>
<td>fistular</td>
<td>msp. tylopes</td>
<td>msp. tylopes</td>
<td>acanthoexes</td>
<td>iso-</td>
<td>present</td>
<td>-</td>
<td>valid,</td>
</tr>
<tr>
<td>Damiria Keller, 1891</td>
<td>fistular</td>
<td>msp. tylopes</td>
<td>msp. tylopes</td>
<td>absent</td>
<td>absent</td>
<td>-</td>
<td>?valid</td>
<td></td>
</tr>
<tr>
<td>Facifer Dendy, 1896</td>
<td>fistular</td>
<td>absent (sandy)</td>
<td>tylostyles (sandy)</td>
<td>acanthostyles</td>
<td>absent</td>
<td>present</td>
<td>microxeas (like Asylinfer)</td>
<td>?jun. syn. Acheliderma</td>
</tr>
<tr>
<td>Iophon** Gray, 1867</td>
<td>massive erect</td>
<td>msp. tylopes</td>
<td>msp. tylopes</td>
<td>acanthostyles (may be acanth.) (may be absent)</td>
<td>absent</td>
<td>bipocillae (spurred)</td>
<td>valid</td>
<td></td>
</tr>
<tr>
<td>Megaciella Hallmann, 1920</td>
<td>encrusting</td>
<td>msp. tylopes</td>
<td>msp. tylopes</td>
<td>acanthostyles (may be acanth) (may be absent)</td>
<td>iso-</td>
<td>present</td>
<td>-</td>
<td>?valid</td>
</tr>
<tr>
<td>Paracornulotrocha Hallmann, 1920</td>
<td>fistular</td>
<td>msp. tylopes</td>
<td>msp. tylopes</td>
<td>acanthostyles</td>
<td>iso-</td>
<td>present</td>
<td>-</td>
<td>valid</td>
</tr>
<tr>
<td>Zyzya*** De Laubenfels, 1936</td>
<td>fistular</td>
<td>msp. tylopes</td>
<td>msp. tylopes</td>
<td>acanthostrongyles (may be absent)</td>
<td>present</td>
<td>-</td>
<td>valid</td>
<td></td>
</tr>
</tbody>
</table>

* With generally accepted junior synonyms Fonteia Gray (1867) and Trefortia Deszô (1880)
** With generally accepted junior synonyms Alebion Gray (1867), Ingallia (Gray, 1867), Menylus Gray (1867), Pocillon Topsen (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 lophonid genera, but assigned to other families are: Cornulotochus Topsen (1928) (to Microcionidae), Damiriopsis Burton (1928) (to Raspatillidae), Dyschelion Kirkpatrick, 1900 (to Phloeodictyidae), and Tedaniphorbas De Laubenfels (1936) (to Coelosphaeridae)

In that case, convergent development of tyloletes 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 anisoxoeas 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 anisochelae.

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 unypical 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 & Krasochn, 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., Acanthus innominitus 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.

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</table>

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 = isodictyl 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 acanthostrongyles: 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 microscleres: 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 sister-group relationships between Indo-Pacific and Caribbean species (*C. santamartae*, *C. purpurea*, *P. coherens*).
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 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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