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

R.W.M. van Soest1, S. Zee2,3 and M. Kielman1,3
1Institute of Systematics and Population Biology (Zoölogisch Museum), University of Amsterdam, P.O. Box 94766, 1090 GT Amsterdam, the Netherlands; 2Universidad Nacional de Colombia, Depto. de Biología; 3Instituto de Investigaciones Marinas (INVEMAR), Punta de Betín, Apartado Aereo 1016, Santa María, Colombia

Keywords: Caribbean coral reefs, Seychelles reefs, sponges, Pocilloclerida, Iophonidae, fistule growth form, excaving growth form

Abstract

New sponge species belonging to the closely related fistular genera *Zeyzya*, *Cornulella*, *Damiria*, and *Acheliderma* are described from reef habitats off the coasts of Colombia, Bonaire and Curacao in the southern Caribbean. With very few exceptions these sponges are small to tiny specimens inhabiting crevices and other cryptic habitats; some may be overlooked. For comparison both published and unpublished material belonging to these genera from other parts of the world were examined, and this studied several nonsensical changes and a further three new species from the Indian Ocean. The new species are: *Zeyzya zeyza* (Caribbean), *Cornulella zeyzamanum* (Caribbean), *C. zeyzamanum* (Caribbean), *C. zeyzamanum* (Seychelles), *Damiria zeyzamanum* (Caribbean), *D. zeyzamanum* (Seychelles), and *Acheliderma zeyzamanum* (Caribbean). All species belonging to these genera, as well as to the closely related Indo-Pacific genus *Paranormus*, 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 affiliation, although their close relationship with *Carinida* was generally accepted. The recently revived family *Iophonidae* is demonstrated to be the likely assemblage (e.g. *Tomita, 1993*). 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 distant.

Résumé

De nouvelles espèces de *Poroïdées* appartenant aux genres fistulaires et nettement apparentées *Zeyzya*, *Cornulella*, *Damiria* et *Acheliderma* sont décrites d'habitats récifs à large des côtes de Colombie, Bonaire et Curacao (Caribbees du Sud). A très peu d'exceptions près, ces taxons sont des exemples petits ou minuscules peuplant des crevasses et d'autres habitats cryptiques. Il est possible que certains puissent parfois 1er le sub-stratum. Du matériel publié ou inédit d'autres parties du monde, appartenant à ces genres, a été examiné en vue de comparaisons, or qui a abouti à plusieurs changements nomenclaturaux et à la découverte de trois autres nouvelles espèces de l'Océan Indien. Les nouvelles espèces sont: *Zeyzya zeyza* (Caribbees), *Cornulella zeyzamanum* (Caribbees), *C. zeyzamanum* (Seychelles), *Damiria zeyzamanum* (Caribbees), *D. zeyzamanum* (Seychelles), et *Acheliderma zeyzamanum* (Caribbees). Pour toutes les espèces apparentées à ces genres vient qu'au genre Indo-Pacifique pochonnelle apparenté *Paranormus*, on donne des diagnostics succincts. Génres et espèces de ce genre qui distinguent dans les océans tropicaux et subtropicaux des trois oceans. Le passage systématique des cinq genres a été jusqu'à présent controversé; cependant, leur parent proche avec *Cornulella* avait généralement été acceptée. On démontre que ce sont la famille *Poroïdées* (ecmecamment reconnue) qui pouvait vraisemblablement regrouper ces genres. On passe brièvement en revue les genres de cette famille, avec un examen d'analyse phylogénétique préliminaire des genres fistulaires. En plus du fait que les relations phylogénétiques restent en partie obscures, il est clair que dans tous ces genres les relations de parenté parent dépasser les limites des zones marines contiguës; elles sont souvent distantes.

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-Indo-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 pat-
tern is the more numerous. These patterns are ex-
plained as having originated from the former shall-
low Tethys Ocean on the one hand and from a
former isolated lophidion genera on the other. Two closely
related lophidion genera, viz. **Zyzycla** and **Cornulid-
a**, up to now are classed as Indo-Australian, be-
cause 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 *lauas* 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-
lished for the closely related genus **Dorimia**, and in-
deed the majority of the warm-water sponge genera.
The distributions of the genera **Acteliderma**, **Aspidinifer**, and **Pusifer** are so far
considered ill-
known since only single records are known. Recent-
ly, Ms. Lissane Arts picked up a species of fistular
**lophidion** uniting characters of these three genera and
accordingly it is proposed below to unite them. Complied, distribution records of the genera
**Acteliderma** s.l. fall now into the Tethyan pattern as
well.

The status and family assignment of **Zyzycla**,
**Cornulaea**, **Acteliderma**, and **Dorimia** is con-
troversial. Since all have fistules and tylote ec-
osome muscarieté, they were traditionally in-
cluded in the family Coelosphaeridae (Topsent,
1928). Lévi & Lévi (1983) separated coelosphaerids
with palmate isochela from those possessing acu-
rate isochela, and erected a family **Cornulideae** for
the former. They were followed by Bergquist &
Fonscom (1988) (though not by Hooper & Krasso-
chin, 1989). Finally, Hajdu et al. (1994) extended
Lévi & Lévi's **Cornulidae** to include also non-
fistular genera (e.g., **Acarus**, **Iphopon**). Arguments
are, that these genera comprise an otherwise
homogeneous composition of the family they are
usually assigned to, i.e., **Myxillidae** s.l. The latter
assemblage contains predominantly sponges lack-
ing toxi, and possessing "tridentate" chelas (arcau-
ate and archontonate chelas) and sigmas. **Acarus** has
palmate isochela and abundant toxi, **Iphopon** has palmate anisochela lacking the toxi, both share
with the above-mentioned Corculidae the lack of sigma and the possession of ectosomal tyloses
with spined heads. For reasons of priority the Corculi-
dae + **Iphopon** + **Acarus** assemblage will have to
be named Iphoponidae Burton, 1929.

It is the purpose of this study to describe new
southern Caribbean material of **Zyzycla**, **Cornulide-
ae**, **Acteliderma**, and **Dorimia**, and to compare it with
Indian Ocean specimens of these genera recently
discovered 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 con-
sidered in a discussion of all closely related fistu-
less-bearing genera of the family **lophidionidae**.

**Material and methods**

Caribbeam specimens described below were collected by Ms. M. Korfman, S. Zia and Ms. Lissane Arts in the course of surveys of the sponge and coral communities of the Santa Marta area, the Islas del Rosario reefs in the Curaguana area, and the Cur-
acao reefs (1988-1994). In addition, several specimens were col-
lected by students of the University of Amsterdam studying the
sub-tropical 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 micrometric sec-
tions and spicule mounts are important additional types material.
All specimens and preparations are stored in the Zoologicheski Museum of the University of Amsterdam (ZMA); additional
micrometric preparations are kept in the Instituto de Invesiga-
tiones Marinas (INIVEMAR) Pacifica collection (INV-POR).

For comparison, fistular Iphopon specimens collected by R.
van Soest in the reefs of Curacao, Indonesia, the Seychelles (In-
dian Ocean) and off the Cape Verde Islands and Mauritania
were studied, all incorporated in ZMA. In addition, the type
specimens of **Suberites fulgurans** Carse, 1879 (BMNH 1848:S.5.); **Suberites destruens** Kirkpatrick, 1900 (BMNH
1900:10:19:2), **Coelosphaerium Houtoulu**, 1912 (SMF 1964),
**Dorimia simplex-Keller, 1983 (ZMB 3105) and Heilinspongia
**vulgaris** Lévi & Lévi, 1983 (paratype, MNHN 3109). were
tobecripted from the London, Frankfurt, Berlin, and Paris
museums, respectively; Slides of **Acteliderma cornucrassae** Top-
sent, 1892 (D.T. 170) and **Acteliderma planidors** Topsent, 1927
(D.T. 1288) were examined in the Paris museum.

Sections and spicule mounts were prepared in µa usual way
(G. Van Soest et al., 1991). Spicule measurements are based on
25 spicules per category per specimen, unless otherwise indicated.

Systematic descriptions

Order Pocilloclerida Topsen, 1928
Suborder Microcionitina Hajdu et al., 1994
Definition: Pocilloclerida 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, 1925 sensu Hajdu et al., 1994
Definition: Microcionitina with ectosomal terminally spined tyloles.

Genus Zyzza De Laubenfels, 1936

Type species (by original designation): Plocamia massa/I Carter, 1879, cf. below).

Definition (emended from Hooper & Krasochin, 1989): Iophonidae with veritcally-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 tyloles bearing microspined heads. Chaonoasomal skeleton contains irregular, widely spaced multispecific tracts of tyloles ascending to the surface, between which is dispersed an irregular incoital reticulation of vertically-spined strongyles. Microscleres, if present, are palmate isochelae 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 Dyisciona davisii, which on pape looked almost certain to be a close relative of, if not conspecific with, Zyzza massa/I (Carter, 1879) (and its senior synonym Z. fuliginosa (Carter, 1879)). However, reexamination of the type specimen of Dyisciona davisii 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 vertically-spined spicules have not been found again in the specimen, and presumably are not proper to the sponge. It is our estimate that Dyisciona davisii is either an Aka, or more likely, the remnants of a larger sponge such as Oceanapia. The vertically-spined spicules likely would have been isolated spicules of an excavating sponge of the genus Dotonia. There are at least two other excavating spongs of the genus Cliona present in the sample. Vertically-spined megascleres are already known from the Early Oligocene (Hinde & Holmes, 1892), but these are not likely to give evidence that the genus Zyzza was already exant at that time. Similar spicules occur in unrelated genera, such as Dotonia (Order Hadromeridae), Agelas (Order Agelasidae), and Hymerophilia (family: Raquillidiae). It is assumed that these spicules have evolved convergently in the different groups.

Description of the Caribbean species

Zyzza invenar n. sp.

(Figs. 1, 7–14)

Holotype: ZMA POR. 10803, PavoIts, Isla del Rosario, off Cartagena, Colombian Caribbean, approx. 10°10'N 74°35'W, 25 m, coll. M. Kidman, field no. 5118, 17-X-1990. Paratypes: ZMA POR. 10804, same data as holotype, field no. 5122. In addition to the type specimens there are 12 microspined slat, both casas and acetose mounts, incorporated in ZMA (5 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 feltswork of tangentially arranged tyloles. The chaonoasomal skeleton is a mass of tyloles and acet莩regenerated Microscleres are palmate isochelae and uncommon wide-curved toxas.
Description. — Both specimens are overgrown by the ubiquitous orange encrustor *Euphyllia latissi*ma Díaz et al., 1987. The specimens were not discovered until rough cuts were examined in the lab for routine identification. The cut revealed the presence of vertically-spined acanthostyongles, so far unknown from Caribbean sponges, next to the well-known spiculation of *E. lauhini*. Subsequent removal of the crusts of *E. lauhini* revealed the presence of a small black sponge sticking several *fusules* 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 *fusules* are somewhat swollen, hollow, with parchment-like smooth skin. The *fusules* 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, *fusules* 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.

Exoskeletal skeleton: A feltwork of crossing tangential spicules, several layers thick.

Chonannosal skeleton: The upper parts of the *fusules* are devoid of spicular skeleton. The lower parts of the *fusules* and the endolithic parts contain a reticulate mass of spicules. The reticulation is unipicirular, irregular, tight; in places the reticulation is absent and a mass of spicules remains. The *fusules* are of two types: tyloes and acanthostyongles, both intermingled, seemingly without localization.

*Spicules* (Table 1): Tyloes (Figs. 8, 11–12): most are more or less evenly thick along the entire shaft, smooth except for the head. 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 spinulation of either end of a single spicule, possibly indicating a stylole ancestry. Size: 235–301 by 4–8 µm.


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

Tossas (Fig. 10): Peculiarly wide-angled, resembling a *tossa* version of the Acanthus "*ooshn*" tossa; size 49–71 µm long and 21–30 µm high.

Etymology. — Named after the host institute of S. Zea and M. Kiemel, 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 *Zezyya* (cf. below) in the possession of tossas next to the chelas. In view of the fact that in related genera (e.g., *Cornulina*, *Cornuella*, *Acanthus*) tossas 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 *Zezyya*. Nevertheless, the particular shape of the tossas is unusual, and with the exception of *Acanthus*, unknown from any Caribbean sponge. Careful comparison with sympatric *Acanthus* species (*A. nicoleae Van Soest et al., 1951, A. dewerdiae Van Soest et al., 1991, and A. innominitus Gray, 1867*) made it clear that there is some superficial resemblance with the category I tossa ("*ooshn*") of that genus, but none of the three contain precisely similar tossas. This ruled out the possibility that the tossas might have been a contamination. Further corroboration for this is that both the hetotype and the paratype had the tossas.

Further, more subtle differences lie in the shape of the tyloes heads, which are more pronounced in the Caribbean species, and the more regularly spaced projections of the acanthostyongles. In *most* specimens from the Indo-Pacific, the acanthostyongles are longer and thicker (Table 1).

Review of Indo-Pacific *Zezyya* specimens

Below brief descriptions of Indo-Pacific specimens are given, with an emphasis on specimens not treated by Hooper & Kraschín (1989):
Fig. 1. *Zyzza textilis* n. sp., fragment of holotype, ZMA POR. 10803, from the Islas del Rosario, Colombian Caribbean (scale bar: 10 mm) [photo: L.A. van der Laan].

Fig. 2. Holotype of *Sarcosta fulgida* (Carter, 1879), BMNH 1846.8.5.8, from Torres Straits, North Australia (scale bar: 10 mm) [photo: L.A. van der Laan].

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

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

Fig. 5. *Zyzza fulgida* (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. *Darmiee tenuifera* 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. *Zetzuw inornat* n. sp., holotype; SEM photos of spicules: 7, verticillato-spined acanthostreus; 8, tylohy; 9, palmate isochela; 10, bow-shaped tox; 11, detail of tylohy head; 12, detail of opposite tylohy of same tylohy; 13, detail of distal part of verticillato-spined acanthostreus; 14, detail of middle part of verticillato-spined acanthostreus.

Subgenus *fulgissas* Carter, 1879: 347.

(Figs. 2, 15–17)

Type specimen: BMNH 1846.0.5.8 examined. Locality: Torres Strait, North Australia. A dry, black mass of 11 by 6 by 6 cm. No frustules or other projections; no substrate. The ectosomal skeleton is a network of tylohes. The chaostomal skeleton is an irregular mass of spines intermingled with single acanthostreus.

These are irregularly spined (Fig. 15), and often have a mucronate end. The head of the tylohy (Figs. 16–17) are mostly of unequal twining and spination. Tylohy size: 231–333 by 4–9 μm. Acanthostreus: 206–300 by 9–18 μm; 28–56 whorls of spine. No microspheres.

Comment: In view of the variability of the acanthostreus head 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 *Phoronia nasuta*. 

---

*Note:* The text contains references to figures (e.g., Figs. 2, 15–17) which are not visible in the provided image. The description of the specimen is based on SEM photos showing various spicules, specifically focusing on the morphology of tylohy, acanthostreus, and the chaostomal skeleton.
Table 1. Specific sizes (range, mean and standard deviation, in µm) of Zoosperma species. Data based on 25 measurements per species per specific category unless otherwise indicated. For data derived from literature only the range is given.

| Species          | Elytra | Acrosternum | no. verticales | chelae | manus |
|------------------|--------|-------------|----------------|--------|-------|--------|
| Zoosperma innesi sp. Colombiana, ZMA 1063 | 259-301 (321.460-301) / 2.2 (1.13-3.8) | 175-200 (191.900-205) / 5-26 (25-35-10) | 20-22 (18) | 19-20 (1.41-23) | 39-44 (46-55-31) |
| Suberosa flaviscutata Carter, N. Assembl, BM 19608:838 | 201-300 (2.78-333) / 2.2 (1.18-9) | 155-232 / 14-15 | 15-16 (15-16) | 19-20 (1-20) |
| Plocomia maurauda Dendy | 286-408 | 16-14 | unknown | 14-20 | absent | 100-110 |
| Domirina murallica Butor | 208-468 | 15-15 | 134-256 | 5-20 | 20-24 | absent |
| Farcinocolus assai Vaeval et al. Maldives | 367-402 | 6-11 | 27-266 | 11-14 | 15-16 | absent |
| Zoosperma maculatum Berggren & Fronem, New Zealand | 280-415 | 16-15 | 116-190 | 4-16 | 24-25 | absent |
| Zoosperma maculatum Hooper & Krauschin, W. Australia | 305-418 | 13-12 | 148-242 | 5-15 | not found | absent |
| Zoosperma maculatum Hooper & Krauschin, Seychelles | 244-600 (2.74-310) / 2.2 (4.09-2.85) | 155-213 (159.5-249) / 4-1 (5-10) | unknown | not found | absent |
| Zoosperma fuliginosus, this paper | 345-592 (1.83-282) / 2.2 (2.53-178) / 2.2 (96-190) / 2.2 (17-30) | 230-178 (198-209) / 2.2 (22-15) | unknown | not found | absent |
| Zoosperma fuliginosus, this paper | 184-242 (1.30-130) / 2.2 (1.49-150) / 2.2 (17-10) / 2.2 (5-10) | 15-16 (15-16) | 20-25 (20-25) / 2.2 (25-25) | unknown | not found | absent |
| Zoosperma fuliginosus, this paper | 192-222 (1.05-255) / 2.2 (1.21-31) | 212-220 (195-225) / 2.2 (33-64) / 2.2 (25-10) | 18-21 (20-25) | 24-28 | 24-28 | absent |
| Domirina papillosa, this paper | 319-367 (2.90-292) / 2.2 (2.79-263) / 2.2 (2.90-263) / 2.2 (2.79-263) | 19-27 (25-25) / 2.2 (25-25) | 15-16 (15-16) | 10-13 (10-13) |
| Domirina papillosa, this paper | 319-367 (2.90-292) / 2.2 (2.79-263) / 2.2 (2.79-263) / 2.2 (2.79-263) | 19-27 (25-25) / 2.2 (25-25) | 15-16 (15-16) | 10-13 (10-13) |

Plocomia maurauda Dendy, 1902: 78. Not examined: Locality: Mauritius, 200 m. Dark chocolate brown, massive, subspherical, with short filaments. The chitosanoid skeleton is a subisodiametrical reticulation of tyloids and acanthosterniognath; dispersed multiserial teeth occur as well. Spicle size (after Hooper & Krauschin, 1989): Tyloids: 298-468 by 5-15 µm; acanthosterniognath: 134-256 by 5-20 µm; no microdenticles. Comment: The robust acanthosterniognath also occur in other species (cf., below), and they seem to be growth continuously from this to robust. In accordance with Hooper & Krauschin we consider this to be a junior synonym of Z. fuliginosus.

François Assis, Antimines, 3 m depth, 07°55'S 52°41'E, 6.1.1993. Several species growing erect on a coral reef, with their base rooted deep in the coral. Colours: yellow achatin, deep brown in alcohol (Thomas’ specimen), or transparent (Seychelles specimen). The ecosomal skeleton consists of tangentially arranged tylostyles with spined heads. In the type specimen the choanosomal skeleton is described as a reticulation of triangular meshes made by acanthostyles; longitudinal multiplicate streaks of acanthostyles are also present. In the Seychelles specimen the acanthostyles are irregularly distributed, singly or in two’s. Spicle size: Tylostyles 159–277 by 1–5 μm; acanthostyles: 117–176 by 6–12 μm, with 10–15 (up to 16 in Thomas’ speci-
men) whorls of spines; no microscleres.

Comment. In the live colour, the small divisions 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 species of *Zecca*. Consequently, *Zecca* and the group of specimens constitute a separate species.

Linoedendria *nantillus* sensu Thomas, 1975: 32.

Not examined. Locality: Seychelles. Black brown, thin encrustation with "piperia" consistency. The chnosomal skeleton is a cordiform indofucoid man. Spicule size (after Thomas): Tylostyles: 222–350 by 4 μm; acanthostyles (tubate acanthostyles) with the observation of these becoming acanthostyles when the spiculation on the ends becomes more dense: 105–142 by 6 μm; palleumat ischoles: 16 μm.

Comment. Thomas describes the acanthostyles as being more or less uniformly spined, with spines rarely in whorls, but pictures them as clearly ventricously spined. Presumably both kinds of spines occur in his material. With some hesitation this record is assigned to *Z. fuligilus*.

Paracosamutha *struus* Vacelet et al., 1976: 59.

Not examined. Locality: Madagascar, 5.5 m. Dark purple ("mauver") encrustations, in and on coral, extending flexibles of 10 by 4 mm, which are open as the upper end. The ectosomal skeleton is a foliatoey of tylostyles; the choanosomal skeleton is confused, with here and there a stipitulated micula of tylostyles and acanthostyles. Spicule size (after Hooper & Kraaka, 1989): Tylostyles: 180–590 by 20–20 μm (Vacelet et al. observed two categories: acanthostyles: 108–385 by 3–13 μm; palleumat ischoles: 12–22 μm.

Comment. In agreement with Hooper & Kraaka we consider this to be a junior synonym of *Z. fuligilus*.


Comment. The colour is not typical, but in other respects this specimen resembles *Z. fuligilus*.

Zecca *manillis* sensu Hooper & Kraaka, 1989; Australian Museum.

Not examined. Locality: Houtman-Abrolhos islands, West Australia, 18–20 m. A dark brown subepilithic mass, with at least one third of its base lying in a shallow furrow in soft sediment. The upper surface raps into a single furrow with a terminal sieve plate. The ectosomal skeleton is a tangential layer of tylostyles. The choanosomal skeleton contains multiple tracts of tylostyles and an irregular septalindofucoid reticulation of single acan- hostyles and co-axial tylostyles. Spicule size: Tylostyles 200–438 by 1.5–12 μm (some are stylocles); acanthostyles 116–190 by 4–14 μm (drawing shows about 24 whorls of spines; no microscleres. This specimen conforms to *Z. fuligilus*.

Zecca *manillis* sensu Hooper & Kraaka, 1989; Seychelles specimens.


Zecca *fuligilus*: 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 POB. 1057, IOP-E se 4/23, Mahe, André de Forbin, Seychelles, 1–7 m, 12.XII. 1992; ZMA POB. 1081, IOP-E se 716/31, N. of Aldie Isl., *Zecca*, 04/11/ S S 35°00 E, 40 m, 19-XXI-1992, dredge; ZMA POB. 10811, IOP-E sta. 759/18, Mahe, S.E. Sey- chelles, 35–45 m, 24-XXII-1992, dredge. All three specimens were black, encrusted carbon and extending flat- tened, tapering fissures along the substratum (Figs. 4, 5); all were devoid of microscleres. One of the specimens, ZMA POB. 10816, contained numerous large embryos with incipient spiculation of thin tylostyles 88–106 μm long. One of the Mann specimens differed from the other two in having rather fine incipient spiculation: tylostyles 175–197 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 1–6 μm and 192–235 by 2–7 μm; acanthostyles (Fig. 19): 199–201–265 by 21–28 μm and 212–258 by 20–28 μm, with 2–28 whorls of spines.

Comment. The latter two specimens are remarkable in having thick (up to 28 μm) acanthostyles (Fig. 19). Possibly a phenomenon similar to that causing extreme differences in thickness of spicules of the Coloumbia Caribbiana (cf. Zwa, 1987) is responsible for this.

Zecca *fuligilus*: undescribed material from Fiji.

(Figs. 20–21).

ZMA POB. 1641. Voucher fragment of a specimen identified originally as *Dendria* sp. by I.W.M. van Soest, used for a chemical study (Kierle & Faulkner, 1993). This is a black mass with spiculation dominated by tylostyles with spined heads. Close examination revealed that there are two size categories, the shorter of which frequently showed stellate extending some distance along the shaft (Fig. 20). Subsequently, in low propor- tions, entirely spined acanthostyles were found. Some de- cavity of the type was stellate (Fig. 21). Tylostyles proper: 196–305 by 2.5–μm (acanthostyles): 155–249 by 4–11 μm; no microscleres.

Comment. In view of the variation in spiculation of the acan- hostyles this material is quite likely comparable to *Zecca* *fuligilus*. Chemistry described for this species is closely relat- ed to this described for *Z. fuligilus* (cf. Radajčik et al., 1993).

Zecca *fuligilus*: undescribed specimen from Papua New Guinea.

(Fig. 18).

ZMA POB. 975. Locality: Milford Bay, Eastern Papua New
Conclusions
Spicule sizes of all specimens are summarized in Ta-
ble 1. It seems clear that the Indo-Pacific specimens fall in at least two distinct species, one dark brown to black with rather irregularly developed verticals of spines on the acanthonotrygones, and one yellow, with very regular verticals. For the time being we con-
cout with Hooper & Krasochin (1989) in con-
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, fissural, massive, to pear-shaped. Endolithic parts diffused, invading and 'eating away' the calcare-
ous substrate without making distinct galleries or chambers. Above-surface parts a few millimeters to 14 cm high, covering a few mm² to 200 cm². Fissures may be a few mm high and in diameter up to 38 mm high and 31 mm in diameter; they tend to have a tapering form. Surface smooth. Fragile consisten-
cy in encrusting fissural parts, to firm in massive parts. 
Colour: Mostly reported to be dark brown to black-
brown alive and in spirit. Smaller encrusting speci-
mens may be lighter colored (maroon or yellow), but turn brown in alcohol, discolouring it to a dark brown-black. 
Ectosomal skeleton: A multi-layered feltwork of in-
terconnecting tangentially arranged tyloes. 
Chaetosomal skeleton: basically there is a unispicu-
lar isodictyal reticulation of acanthonotrygones, with a good proportion of tyloes mixed in. 
Independent of this there are multispicular tracts which traverse the basal part of the sponge without making a clear reticulation. 
Spicules: Tyloes, with well-developed spined heads, more or less straight, often having one well-
developed head and the other more strongly-like, occassionally style-like. Size rather variable (cf. Ta-
ble 1): 173 - 590 by 1.5 - 20 μm.

Acanthonotrygones: Verticillately-spined, but more often more uniformly spined in irregularly; occassionally parts of the whole of the shaft smooth, or with an occasional spine only; rarely stylole. Size, especially thickness, quite variable: 109 - 300 by 3 - 28 μm. 
Palimate isochelae: Mostly absent, but found in four of the thirteen known specimens. 
Chemistry: The species produces cytotoxic pyr-
rolinoindole alkaloids (Radisky et al., 1993).

Distribution and ecology. - Indo-West Pacific (Torres Straits, Macititus, Zambib, India, Sep-
chelles/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 fisticels sticking out of dead calcareous rubble. Fisticels originate from an irregular, partly zyloleon et-
crustation, or directly out of the substrates. In which it forms irregular shallow excavations. Size of individual fisticels up to 30 mm long, with a dia-
meter of 2 - 3 mm. Consistency paper-like, easily damaged. 
Colour: Yellow.

Ectosomal skeleton: Tangential, regularly inter-
crossing single tyloes. 
Chaetosomal skeleton: An irregular reticulation of single acanthonotrygones, occasionally forming tracts. Many tyloes are strown among them. 
Spicules: Tyloes with microspined heads: 159 - 277 by 1.5 - 5 μm. 
Acanthonotrygones: With 10 - 18 regular whorls of spines: 117 - 176 by 6 - 12 μm. 
Microscelere: None.
Distribution and ecology. - India, Seychelles, on open reef, 3 m.

**Genus Cornulella Dendy, 1922**

Type species: *Cornulella lunulbecki* Dendy, 1922: 103 (by monotypy).

Definition: Very thinly encrusting lophohoridae with long, thin, fiat or outgrowths. Ectosomal skeleton a uniserial network of intercrossing tangential ty-lotes with spined heads. Choanosomal skeleton ves-tigal, made up of individual ty-lotes. Accessory meso- and microscleres are acanthoxaeas, which are distributed singly among the ty-lotes. Microscleres palmate isochelae and, frequently, toxas.

Remarks. - This definition deviates from that of Dendy in de-emphasizing the microscler of the acanthoxaeas. The microscleres of the type spe-cies were indicated as rugose by Dendy, and are demonstrated in a closely related new species, to be this spined oxas (cf. Figs. 34-36), differing from those of related species merely in their small size.

Similar species with acanthoxaeas so far were as-signed to the genus Paracornulum Hallmann, 1920. The definition of this genus by Hallmann (1920) al-lowed inclusion of sponges with acanthostyles, acanthoxaeas, or acanthostroctyles, thus effectively also including *Zyzzya*. Reexamination of the type specimen of the type species of *Paracornulum*, i.e., *Cornulum dibum* Hentschel, 1912, housed in the Senckenberg Museum at Frankfurt, however, re-vealed that the acanthostyles of *C. dibum* are true echnating acanthostyles, concentrated at the base of the sponge where they echinate the substrate. It is very unlikely that these spiculae are homologous with the acanthoxaeas of *C. lunulbecki* and the new species described below. It is similarly judged unlikely that they are homologous with the vertically-spined acanthostroctyles 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 lophohoridae because echinating acanthostyles are a pliesiomorphic feature. It is possibly a junior syno-

nym of *Acanthiderma* Topsent, 1892, but this differs from *Paracornulum* in lacking chelas and posses-sing choanosomal structural styles next to the acanthostyles (see also below).

**Description of the Caribbean species**

*Cornulella santamariae* n. sp. (Figs. 24-29)


Diagnosis. - Extremely thin encrustation with few erect filaments of 3 mm high. Colour orange. Ecto-somal felloptax of ty-lotes with spined heads. Choanosomal acanthoxaeas evenly spined. Robust palmate isochelae. Texas normally present, but rare or absent in some specimens.

Description. - All specimens are thin encrustations with very thin and small felloptox, which collapse out of the water. Size only a few mm in diameter, filaments 3 mm long at the most, less than 1 mm in cross section. The encrustations and felloptox are very fragile. They are also partly overgrown by other encrusts such as *Eurypon lauglini* Diaz et al., 1987. The Curacao specimens were entirely en-closed in the microscopic slide. The holotype and the paratype were reduced to filmy fragments by the preparation of the various slides. All slides are considered part of the type series.

Colour: Blue or orange or whitish.

Ecotope: A fragile film supported by tangential ty-loites in a relatively low density, seemingly form- ing a loose reticulum. Microscleres and acanthoxaeas are dispersed among them.
Choanosome: Not observed. Some loose spicules, including a concentration of acanthoxeas, are found in the interior.

Spicules: Tyloles, somewhat variable in shape; in some the tyloles are distinct and prominently spined (Figs. 24, 28–29), in others, tyloles are less prominent. Sizes are rather uniform (Tab. 11): 111–178 by 1–3 μm.

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

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

Toxas (Fig. 27): Rare in the holotype, not found in two of the 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. *Dactylium tetricum* Topsent, 1928 (cf. below), *Coelophysea johnsonii* De Laubenfels, 1934, and *'Artenuina' tyloea* Boury-Esnault, 1973. However, all three are larger and more elaborate. In addition, the first species lacks any spicules other than the microspined tyloles, and the latter two are members of close relatives of *Corallum* because they have micropined eocnoidal stongyles/tyloles, palmate isochelae and toxas, but lack acanthoxeas. "A." tyloea from Brazil has smooth styles, making it a certain *Corallum*; *C. johnsonii* lacks the styles which is a dubious reason for considering it to belong to a genus separate from *Corallum*.

Species similar to *C. santamartae* in the Indo-West Pacific area are *Corallia leundbecki* Denisy, 1922, "*Paracorallum*" minimum Vacelet et al., 1976, "*Paracorallium*" purpureum (Hancock, 1849), and two undescribed species from the Seychelles area. All these are briefly diagnosed below. *C. leundbecki* differs in having much larger tyloles and smaller acanthoxeas; *P. minimum* has twisted palmate isochelae of smaller size than *C.*
<table>
<thead>
<tr>
<th>Specimen</th>
<th>tyloses</th>
<th>acanthoxas</th>
<th>chelae</th>
<th>toxas</th>
</tr>
</thead>
<tbody>
<tr>
<td>Corenula sanctorum sp. MZA POR. 1008, Colombia</td>
<td>111-120, 98-103</td>
<td>15</td>
<td>12-18, 8-9.4</td>
<td>99</td>
</tr>
<tr>
<td>Corenula sanctorum sp. INV-POOR-061, Colombia</td>
<td>151-165, 7-17</td>
<td>15</td>
<td>21-23, 3-5</td>
<td>82</td>
</tr>
<tr>
<td>Corenula sanctorum sp. MZA POR. 1069, Bonaire</td>
<td>126-139, 32-15</td>
<td>15</td>
<td>19-22, 6-2.5</td>
<td>60-77 (16.6-90)</td>
</tr>
<tr>
<td>Corenula sanctorum sp. MZA POR. 1026, Bonaire</td>
<td>156-168, 0-130</td>
<td>15</td>
<td>16-22, 1.80</td>
<td>117</td>
</tr>
<tr>
<td>Corenula sanctorum sp. MZA POR. A9 B6, Capever</td>
<td>135-141, 0-85</td>
<td>15</td>
<td>19-21, (1.4)</td>
<td>54-56.5 (2)</td>
</tr>
<tr>
<td>Corenula sanctorum sp. MZA POR. 1515.5, Capever</td>
<td>135-141, 0-85</td>
<td>15</td>
<td>19-21, (1.4)</td>
<td>54-56.5 (2)</td>
</tr>
<tr>
<td>Corenula sanctorum sp. MZA POR. 10810, Capever</td>
<td>144-145, 10-160</td>
<td>15</td>
<td>19-20, 0.76</td>
<td>21</td>
</tr>
<tr>
<td>Corenula trinervata sp. SYCCHS, Seychelles</td>
<td>400-750</td>
<td>20</td>
<td>/</td>
<td>120</td>
</tr>
<tr>
<td>Corenula sanctorum sp. MZA POR. 10057, Seychelles</td>
<td>384-416, 0-150</td>
<td>15</td>
<td>/</td>
<td>/</td>
</tr>
<tr>
<td>Corenula sanctorum sp. MZA POR. 10087, Seychelles</td>
<td>357-402, 0-18</td>
<td>15</td>
<td>/</td>
<td>/</td>
</tr>
<tr>
<td>Corenula purpureum (Hinckle) Indo-Pacific</td>
<td>200</td>
<td>/</td>
<td>/</td>
<td>75</td>
</tr>
<tr>
<td>Corenula minima Vuillier et al. Madagascar</td>
<td>130-250</td>
<td>100-150</td>
<td>12.5-15</td>
<td>15-20 (25)</td>
</tr>
<tr>
<td>Corenula tryoni sp. MZA POR. 10120, Seychelles</td>
<td>224-403, 0-240</td>
<td>15</td>
<td>/</td>
<td>/</td>
</tr>
</tbody>
</table>

**Review of Indo-Pacific Corenula species**

Below Indo-Pacific species belonging to *Corenula* as defined above are briefly diagnosed. Most previously described species are known as Paracornula. However, not all species assigned to that genus are here transferred to *Corenula*. Bergquist & Fromont’s (1988) *Paracornula*

*...continues*
Tossia: 75 μm Indo-Pacific, locality unknown, shallow water.

Cornella feedly/Dedy, 1922.

Not examined: Delicate thin-walled filaments rising from a thin crust occupying irregular depressions of the substrate. Filaments are 2–3 mm in diameter and 15 mm high. Colour purple (that on tunicate). Eozonal tubes up to 400 by 6 μm. Acanthom are small microthabs, 20 by 1 μm. Microthabs include large pinnate nothobas, 50 μm long and 12 μm wide, and rare thorns: 120 by 27 μm. Septihab, 67 μm.

Comment: Dedy also reported sigma but these are unlikely to be proper. The microthab size of the acanthom is shared with C. amirantensis (see below).

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

Description. — Long yellow frustules of 2.3–3 mm in diameter and 40 mm in length, issuing from a thinly encrusting base. Frustules may branch occasionally. Papery fragile consistency.

Ecological ytyloles (Figs. 30–33): With prominentely 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 acanthoxaeas ("microrhabdas") (Figs. 34–36): Small, heavily spined; 36–51 by 0.5–1 μm.

Palamate isochelais (Fig. 37): Robust; 16–24 μm.

Toxas: Not observed.

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

Estymology. — Named after the island group of which the type locality is one.

Remarks. — The new species is close to C. lundbecki in spicular sizes, especially the small size of the acanthoxaeas. Differences are the live colour (yellow vs. purple), the size of the isochelas (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 tyloses (larger in amirantisisi) and acanthoxaeas (much smaller in amirantisisi).

Paracoronulum minimum Vacelet et al., 1976. Not exsulted. Transparent white, small frustules of 1 mm high and 1 mm in diameter. No local encrustation could be found. Ecological skeleton a few layers of tyloses; no choanophoral tissue or skeleton was observed. Tyloses with well-developed spined heads: 130–250 μm. Acanthoxaeas, curved, asymmetrical: 110–150 μm. Palamate isochelais, twisted: 13.5–15 μm.

Toxas: There are two size categories: 20–25 μm and 60–75 μm. In addition to this complement, the authors also report the presence in low quantities of small acanthoxaeas (50–55 μm), with smooth shafts and spined heads. Madagascar, shallow-water reef.

Comment: If the acanthoxaeas are proper and if these are echinating, the basis for a distinction between Paracoronulum and Cornulaela has disappeared. More evidence for this needed before such a decision can be made. The two size categories of toxas differentiates this species clearly from the others.

Cornulaela tyro n. sp. (Figs. 3, 8–34)

Holotype: ZMA POR, 10520. ILOPE 78.7.4.1.11 E, coll. J.C. den Talag, 3 m, 20–22-12.

Description. — Yellow-orange frustules (Fig. 3), single or branches dichotomously, up to 16 mm long, less than 1 mm in diameter. Fragile. Spicules: Tyloses (Figs. 38, 42–44), with feebly developed heads, one end being strongylot-like, with modest spination. Size: 224–233 by 3.4–4.5 μm.

Acanthoxaeas (Figs. 39, 43): With evenly distributed very dense spination: 105–138 by 2.4–4 μm.

Palmate isochelais: (Fig. 40): 13–18 μm.

Toxas: Not observed.


Remarks. — This species is similar to Cornulaela amirantisisi n. sp. in lacking toxas, but differs clearly from that species in having much smaller tyloses and much longer acanthoxaeas. 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 Cornulaela, one Caribbean, and five in the Pacific. They are all closely similar in habit: thin, transparent, shallow, cylindrical frustules issuing from a thinly encrusting base which seems to either excavate calcareous substrates or agglutinate calcareous sediments. They differ in details of spiculae: C. tyro n. sp. has no toxas; C. lundbecki may have toxas but is usually small (20–40 μm) acanthoxaeas. C. minima has two size categories of toxas; the remaining two are very similar but C. purpurea is purple coloured and C. antennatae transparent-orange.
A possible seventh species is the Arctic Histodermaella coriacea Lundbeck, 1910, made the type of a genus Histodermapnis by de Laubenfels, 1936 (p. 72). It differs from the very similar Histodermaella ingolfii in having papate instead of accurate chelas and having minute spines on the ecosomal tylos; both share robust acanthoxaeas and lack microscleres. Histodermaella is a member of the Cor-lousphaeridae, 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 tylos 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 tyloate spination is very similar to that found in Zyzygia and Cornulata, and the genus may be considered the sister group of the latter. Possibly, this is an artifical group representing reduced Cornulata-like or Paracornulina-like species lacking chelas and acanthoxae oxysyles.

Four species are currently recognized, two are instantly recognizable, either by the possession of toxas (D. toxifera sp.), or by a single category of tylos (D. testis); the remaining two species differ the thickness of the shorter tylos, 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 tylos, oxes and acanthoxae chelas.

Review of Damiria species

Damiria simplex Keller, 1891.

Syn.: Damiria simplex fistulata Henschel, 1912.

Not: D. simplex var. fistulata var. Flescher, 1864: 60 (~ D. leonora n. sp.)

Type specimen: ZMB no. 3106 examined. Rather elaborate crust, 2.5 mm thick. Fistsules apparently absent in the type specimen, but Ventriculus's specimens had robust fistules rising from a massive base. Consistency stiff, fragile. Colour brownish. Speciules include two distinct sizes of tylos, 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 Henschel, 1912 (not examined) is here assigned to D. simplex in view of the similarities in speciules: it is described as fistular and there are two sizes of tylos, "thin": 264–296, and "strong", "thick": 200–210 μm. However, no mention is made of spination of the tyloate head.

Damiria toxifera sp. (Figs. 6, 44–47)


Description: Relatively small 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 escape the (often partly living) coral substrate.

Colour: Orange in life, transparent light brown in alcohol.

Ecological skeleton: Masses of intercrossing tylos.

Chaonosomal skeleton: In the fistules virtually absent, in the basal mass an isotropic reticulation of spicles arranged in 190° and three or simply. Frequently the reticulation is obscured, and appears confused.

Spicles (Table III): Tylotes (Figs. 44–45) in two
<table>
<thead>
<tr>
<th>Specimen</th>
<th>Tylus d I</th>
<th>Tylus d II</th>
<th>Tuxas</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. simplex</em> Keller</td>
<td>300</td>
<td>200</td>
<td>short</td>
</tr>
<tr>
<td>Red Sea</td>
<td>/</td>
<td>/</td>
<td>/</td>
</tr>
<tr>
<td><em>D. limicola</em> (Koh.): Beach, 1912, beach-sand</td>
<td>264-296</td>
<td>200-210</td>
<td>short</td>
</tr>
</tbody>
</table>

**Damiria litoris** Toppen. 1928.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Tylus d</th>
<th>Tuxas</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avoca</td>
<td>140-170</td>
<td>short</td>
</tr>
</tbody>
</table>

**Damiria litoris n. sp.*

| ZMA POR: 473A, Antwerp | 231-255 (218.73-251) | 174-181 (164.4-210) | short |
| | / | / | / |

**Damiria litoris n. sp.

| ZMA POR: 7883, Barlade | 224-248 (218.06-296) | 165-190 (155.6-207) | short |
| | / | / | / |

**Damiria litoris n. sp.

| | / | / | / |

**Damiria litoris n. sp.

| ZMA POR: 245-248 (17.44-258) | 213-106 (222-113) | 194-200 (186.4-203) | short |
| | / | / | / |

**Damiria litoris n. sp.

| ZMA (micro. slides): Cetmar, Cuenca | 192-195 (204.0-202) | 145.1-159 (139.9-155) | short |
| | / | / | / |

**Damiria litoris n. sp.*

| TMA (micro. slides), Columbia | 255-270 (256.5-270) | 250-270 (256.5-270) | short |
| | / | / | / |

**Damiria litoris n. sp.*

| Sara Mesa, Columbia | 235-259 | 175-199 | short |
| | / | / | / |

**Damiria litoris n. sp.

| ZMA POR: 10007, Seychelles | 278-296 (288.89-308) | 192-211 (211.01-330) | short |
| | / | / | / |

**Damiria litoris n. sp.

| ZMA POR: 10616, Seychelles | 239-262 (218.48-279) | 169.183 (172.68-191) | short |
| | / | / | / |

**Damiria litoris n. sp.

| ZMA POR: 7887, Seychelles | 260-266 (18.69-306) | 280-266 (27.27-217) | short |
| | / | / | / |

**Motility**

| TMA POR: 7887, Seychelles | 250-270 (51-65) | 175-199 | short |
| | / | / | / |

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

**Eymology.** - 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 is 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.

---

*original as *D. rotula* in Van Soest, 1984

*as *D. simplex* Johnson 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: 49-95 µm.

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

**Eymology.** - 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 is 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.
Dariumia leonoraet n. sp.

Syn.: Dariumia testis Van Soest, 1984: 74. pl. 6 fig. 6, text-fig. 27; Dariumia simplex var. ferrugina sensu Sanchez, 1984: 60, fig. 6.22b.

Holotype: ZMA POR. 4759. Curacao, Bonaire. 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 sponges.

Splanes (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: 123–261 by 5–9 μm (Sanchez records tyloles up to 11 μm thick).


Etymology. — Named after Dr. Leonor Betero, director of INVEHAR, 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 longest 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 lasiogena Topsent, 1892.

Definition. — Fistular lophophorae with microspined tyloles as ectosomal spicules, microspined styles and echinating acanthostyles as choanosomal spicules. Micriscles characteristically elongated diamond-shaped microsiscles and toxas. No chela.

Remarks. — The diamond-shaped microsiscles, which are likely derived from toxas, have been reported in three “genera”, viz. Acheliderma, Astylinifer and Fusifer. Topsent (1892) called these “taphopodes fusiformes” in the original description of Acheliderma and this doubtless caused Dundie (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 topsentii) and De Laubenfels (1930, 1932: Astylinifer arndti) do not conform to the definition of this genus. A. topsentii conforms again to Megariella (see below), and A. arndti is very probably a hydmedesid.

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

The genus Acheliderma is intermediate between
Table IV. Spicule states (µm) of specimens conforming to the genus Aechelidora. Data based on 25 spicules per specimen category per specimen, unless otherwise indicated. For data derived from the literature only the range is given.

<table>
<thead>
<tr>
<th>Species</th>
<th>Spicule states (µm)</th>
<th>Acanthostyles</th>
<th>Tosas</th>
<th>Microsclere</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aechelidora amnicola</em></td>
<td>250-270</td>
<td>20-450</td>
<td>95-175</td>
<td>120</td>
</tr>
<tr>
<td>Topset, 1982, Mediterranean</td>
<td>(microspined)</td>
<td>(microspined)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Fusifer fasciatus</em></td>
<td>540</td>
<td>70</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Deny, 1996, S. Australia</td>
<td>(microspined)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acanthaster planus</td>
<td>265-315</td>
<td>106-455</td>
<td>125</td>
<td>30-57 / 2.3</td>
</tr>
<tr>
<td>Topset, 1972, Azores</td>
<td>(microspined)</td>
<td>(not differentiated)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Acanthaster planus</em> n. sp.</td>
<td>394-440</td>
<td>97-274</td>
<td>101</td>
<td>32-45 / 3.5</td>
</tr>
<tr>
<td>ZMA P0R, 10907, Colombia</td>
<td>(microspined)</td>
<td>(n=15)</td>
<td></td>
<td>1/1</td>
</tr>
<tr>
<td><em>Acanthaster planus</em> n. sp.</td>
<td>3,294-3,420</td>
<td>2,671-3,214</td>
<td>(n=15)</td>
<td>23-28</td>
</tr>
</tbody>
</table>

Paracornulina and Cornulina in having both echinating acanthostyles and structural styles. Spicule size data of the four recognized species are given in Table IV.

Review of Aechelidora species

*Aechelidora amnicola* Topset, 1982
Microscopic slide MHN8 D. T. 170 examined: Encrusting, with 1 cm long tusates. The ectosomal skeleton consists of microspined tusates: 250-270 µm. The chaenoskeletal is a recalcification of styles with microspined heads: 420-450 µm, echinated by short fully spined acanthostyles: 80-175 µm. Microscleres: Tusas: 120 µm, and diamond-shaped microscleres 60-70 by 1 µm, Mediterranean.

*Aechelidora planus* Topset, 1927
Microscopic slide labeled Fusifer planus, MHN8 D. T. 1288 examined: Flat crust, with ectosomal skeleton to tusates which are pictured to be smooth, sometimes asymmetrical with one end having a mucron: 265-315 by 2 µm. Chaenoskeletal consists entirely of acanthostyles, but of various sizes, possibly including echinating ones: 195-455 µm. Microscleres include tusas of 125 µm and diamond-shaped microscleres: 30-37 by 2-3 µm. Azores, deep water.
Comment: This is the type species of the genus Acanthaster Topset, 1927. Topset's labelling of the type slide indicates his hesitation in considering Acanthaster and Fusifer synonymous.

*Aechelidora planus* (Deny, 1896)
Not examined. This is one of the rare "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 tusates. No echinating tusates. Chaenoskeletal megascleres are smooth stylostyles, 540 by 7 µm, and acanthostyles 70 by 3 µm.

Microscleres include diamond-shaped microscleres and tusas. Southern Australia.

Comment: This is the type species of the genus Fusifer. The major synapomorphy for assignment to the Lophistidae, i.e., the spined tusates, are lacking in this species, but the similarity of the diamond-shaped microscleres makes it very likely that the present species belongs in the genus. The absence of tusates is explained as replacement by sand grains.

*Aechelidora lisannae* n. sp.
(Figs. 48-57)
Holotype: ZMA P0R, 10907, Ponta Beira, 20-23 m, Santa Marra, Colombian Caribbean, 25-X-1993, coll. L. A. M. Aerts, field no. 5174. Furthermore there are in the ZMA P0R collection two microscopic slides and one SEM stub made from the holotype.


Description. - Shape, size and consistency: A single thin, hollow fistule found closely adhering an Aka cacochroennis (Rützler, 1971). Walls of the fistule papery, very fragile, consisting of a feldwork of tusates. 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. *Achelatisema faamum* n. sp., SEM photos of the holotype: 48, tylostyle; 49–50, details of opposite heads of tylostyle; 51, seta; 52, detail of head of style; 53, acanthostyle; 54, detail of head of acanthostyle; 55–56, two sizes of diamond-shaped microscales; 57, costa.
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.

Ecology: A weltwork of tylostyles mixed with microscleres. 

Chaoansome: A confused mass of styles and tylostyles, with a few acanthostyles. 

Spicules: Tylostyles (Figs. 48–50) with microspined heads; 243–348 by 3–4.5 µm. The smooth anistylostyles with one mucronated end had the same size as the microspined tylostyles, 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. 

Microscleres (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. 

Etyymology. – Named after its collector, Miss 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 Achetoderma lemniscata, described as having microspined tylostyles and "fusiform" raphides of 1 µm in thickness, and Astylinafer planus with smooth anistylostyles and microscleres of 2–3 µm in thickness. 

Related fistular lophonid genera 

Genus Paracornus Hallmann, 1920 

Type species: Cornusium dubium Hentschel, 1912 (by original designation). 

Definition (emended): Encrusting-fistular lophoni- dae with ectosomal skeleton consisting of inter- crossing tylostyles and chaoansomal skeleton consist- ing of similar tylostyles. Microscleres palmate isco- las and toxas. 

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

Paracornus dubium (Hentschel, 1912). 

Syn.: Cornusium dubium Hentschel, 1912. 

Type specimen SMF no. 964 examined. Tylostyles in two size categories, long and relatively thin: 381–416 (15.12)–441 by 4–8.2 (1.60)–11 µm, and short and relatively fat: 201–234.5 (13.45)–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 (19.00)–113 by 3–4.4 (1.67)–5 µm, likewise concentrated at the base, where they eliminate the substrata. 

Chelas: 12–14.8 (1.33)–17 µm. 

Toxas: 30–53.8 (15.4)–79 µm. 

Aruba Islands, Indonesia. 

Comment. The two tylostyle categories with extensively spined heads remind of the situation found in several Damiriia species. 


Comments: Assignment of this material to Paracornus is ten- tative, because the robust, smooth acanthostyles and the ec- toosomal spines 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 Paracornus are referred to Cornusella, Cornusium, and Zycya (cf. above).
Genus Anistrotylaconthra Vaccéet, 1969
Type species: *A. curvata* Vaccéet, 1969: 200 (by monotypy).

Not examined. Grey-craym encrustation of 2 cm² (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 end spined: 110–190 by 5–7.5 μm. Mediterranean, deep water.

Comment: On paper this genus comes close to *Dumiola*, but the spicule sizes do not conform to those of *Dumiola* nor to the related genera *Fecitoa, Paraecinulum*, and *Cornulum*. The relationship of this species remains obscure.

*Genera Cornulum, Coelospheraella, Xystopsene, Heterocornulum and Melonchela*

*Genus Cornulum Carter, 1876*
Type species: *C. textile* Carter, 1876: 399 (by monotypy).

Definition: Fistular Iophonidae with ectosomal skeleton consisting of smooth strongyles or tyloes with microspined apices, chaonosomatal skeleton consisting of similar spicules to which smooth styles with similar microspined apices are added. Microceres include palmate cheilas and toxas.

Remarks. — It is likely that specimens without styles (genus *Coelospheraella De Laubenfels, 1934), without styles and toxas (genus *Xystopsene De Laubenfels, 1936*), with microstrongyles (genus *Heterocornulum* lévi & lévi, 1983), and with peculiar anisochelas ("meclonchelas": genus *Meclonchela Kolturn*, 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 revised.

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, Acanthar*, and *Megenia*. A possible fourth member is *Acanthorhabda* 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 tyloes with spined heads, chaonosomatal skeleton consisting of an isodictic reticulation of smooth or spined styles, arranged singly or in two's and three's, which may or may not be echinated by acanthostyles. Microceres include bipociles 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), *Acanthorhabdae* (see below) and the mycoidal genus *Myxcole* s.l., but the last are assumed to have been developed convergently. The genus is traditionally assigned to
Table V. Taxa conforming to the definition of "Corallum s.l."

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Scientific Name</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cornalum tuscum</td>
<td>Carter, 1876; Lundbeck, 1910; Kolten, 1919; Hoshino, 1982; Van Soest, 1993</td>
<td>North East Atlantic</td>
</tr>
<tr>
<td>Cornalum sarcinatum</td>
<td>Carter, 1880; Salavone; Dendy, 1905; H. K. H. Lebedeff, 1930; E. S. E. P.</td>
<td>Indian Ocean</td>
</tr>
<tr>
<td>Cornalum incrustatum</td>
<td>Berggren &amp; Frey, 1988; as Paracorallum</td>
<td>New Zealand</td>
</tr>
<tr>
<td>Cornalum sp.</td>
<td>Leo, 1922; Vacelet et al., 1976; Berggren &amp; Fromont, 1988</td>
<td>New Zealand</td>
</tr>
<tr>
<td>Cornalum stenacanthus</td>
<td>Breitner, 1924</td>
<td>Philippines</td>
</tr>
<tr>
<td>Cornalum stoloniferum</td>
<td>(Wilcox, 1925 as Coccophyllum)</td>
<td>Caribbean</td>
</tr>
<tr>
<td>Cornalum johnsonii</td>
<td>(De Laubenfels, 1934 as Coccophyllum); Van Soest, 1984</td>
<td>North Pacific</td>
</tr>
<tr>
<td>Cornalum rubrum</td>
<td>Burton, 1935; Hoshino, 1987</td>
<td>North Pacific</td>
</tr>
<tr>
<td>Cornalum rubrum</td>
<td>Burton, 1935; Hoshino, 1987</td>
<td>Brazil</td>
</tr>
<tr>
<td>Cornalum rubrum</td>
<td>Burton, 1935; Hoshino, 1987</td>
<td>New Zealand</td>
</tr>
<tr>
<td>Cornalum rugosum</td>
<td>Burton, 1935; Hoshino, 1987</td>
<td>West Africa</td>
</tr>
</tbody>
</table>

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

**Genus Acanthus Gray, 1867**

**Syn.:** Acanthocorallum Lévi, 1952; Fontaine Gray, 1867; and Trefonlatia Gray, 1880.

Type species: *Acanthus inomnissatus* Gray, 1867 (by monotypy).

Definition (cf. Van Soest et al., 1991): Massive, branching or encrusting lophonidaceae with exocuticular skeleton of scattered ooids with spined heads, chomosomal skeleton consisting of an isodictyal, isotropic or anisotropic, reticulation of styles and cladozyttes, arranged singly or in tracts of several spicules, which may or may not be echinated by acanthostyles and/or cladozyttes. In thin encrusting specimens, the chomosomal skeleton is hymedemoid, i.e., with styles or cladozyttes erect on the substrate. The cladozyttes occur normally in two categories, but exceptionally in three or a single one. Microcleres 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 Lévi & Lévi (1993). It was formerly assigned to Myxillidae (e.g., Van Soest, 1984) or to Microcionidae (Van Soest et al., 1991).

**Genus Megacorallia Hallmann, 1920**

Type species: *Amphilectes plowes* Ridley & Dendy, 1886 (by original designation).

Definition: Branching or encrusting lophonidaceae with exocuticular brushes of ooids with spined heads, with a reticulate or confused chomosomal 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. Microcleres are palmate isochelas and toxas.

Remarks. – The type species lacks echinating acanthostyles, but similar species with acanthostyles exist. The similarity in spicle characteristics with the microcionid genus *Chocoria* is considerable, and future character analysis may show that inclusion in the Microcionidae might be more appropriate. In
<table>
<thead>
<tr>
<th>Genus</th>
<th>Habitat</th>
<th>Ect. spicules</th>
<th>Ch. spicules</th>
<th>Acc. spicules</th>
<th>Chelae</th>
<th>Tegula</th>
<th>Other</th>
<th>Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthohalbus</td>
<td>Barrie, 1929</td>
<td>massive</td>
<td>massive</td>
<td>absent</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Acanthohalbus</td>
<td>Barrie, 1929</td>
<td>spherobental</td>
<td>spherobental</td>
<td>absent</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Acanthus*</td>
<td>Gray, 1867</td>
<td>massive</td>
<td>massive</td>
<td>absent</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Acanthus*</td>
<td>Gray, 1867</td>
<td>ramose</td>
<td>ramose</td>
<td>absent</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Achelosoma</td>
<td>Tappert, 1892</td>
<td>finicular</td>
<td>finicular</td>
<td>present</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Aureliaeclatidum</td>
<td>Tappert, 1927</td>
<td>encrusting</td>
<td>encrusting</td>
<td>present</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Caelolampasella</td>
<td>De Laubenfels, 1934</td>
<td>finicular</td>
<td>finicular</td>
<td>present</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Cormidella</td>
<td>Dendy, 1922</td>
<td>finicular</td>
<td>finicular</td>
<td>present</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Cornuda</td>
<td>Case, 1876</td>
<td>finicular</td>
<td>finicular</td>
<td>absent</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Daubenyae</td>
<td>Kofler, 1891</td>
<td>finicular</td>
<td>finicular</td>
<td>absent</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Forsteri</td>
<td>Dendy, 1896</td>
<td>finicular</td>
<td>finicular</td>
<td>present</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Heterconodroma</td>
<td>Lévi et Lévi, 1983</td>
<td>finicular</td>
<td>finicular</td>
<td>present</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Heterocladus</td>
<td>De Laubenfels, 1936</td>
<td>finicular</td>
<td>finicular</td>
<td>present</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>lucus</td>
<td>Gray, 1867</td>
<td>massive</td>
<td>massive</td>
<td>absent</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Megacrisella</td>
<td>Hoffmann, 1920</td>
<td>encrusting</td>
<td>encrusting</td>
<td>present</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Megacrisella</td>
<td>Hoffmann, 1920</td>
<td>encrusting</td>
<td>encrusting</td>
<td>present</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Paraconodroma</td>
<td>Hoffmann, 1920</td>
<td>finicular</td>
<td>finicular</td>
<td>present</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Xenospongus</td>
<td>De Laubenfels, 1936</td>
<td>finicular</td>
<td>finicular</td>
<td>present</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
<tr>
<td>Zygopora</td>
<td>De Laubenfels, 1936</td>
<td>finicular</td>
<td>finicular</td>
<td>present</td>
<td>-</td>
<td></td>
<td></td>
<td>valid</td>
</tr>
</tbody>
</table>

| * With generally accepted junior synonyms: Fonnie Gray (1867) and Tappert Dendey (1890) |
| ** With generally accepted junior synonyms: Alkton Gray (1861), Ingallia (Gray, 1867), Megacrisella (Gray, 1867), Pucoles Tappert (1893), Cponodroma Dendey (1926), Baranckya De Laubenfels (1936), and Zygopora De Laubenfels (1936) |
| *** With other synonyms: Dameria Burrias, 1939 (cf. above) |

N.B. Genera with synonyms to lepidol purpurea, a genus assigned to other families are: Conululaha Tappert (1928) (to Microstilidae), Dameria Burrias (1939) (to Rhopaliaidae), and Tridactylius De Laubenfels (1936) (to Caelolampasidae) for the exclusion 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: Lophonidae with modified styli in the form of annuleses often provided with a mucron arranged in a course but ill-defined plumometallization. Ectosomal megascleres are acanthorhabdoids with heavy spines and microspined tylole apices. Micro scleres are spurred palpate anisochelae.

Remarks. — Burton (1929) 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 unusual of this group. Spurred anisochelae are characteristic of *Lophon* and the acanthorhabdoids have spined tylole apices found in all members of the lophonidae. Accordingly, we propose here to include *Acanthorhabdus* in the family lophonidae.

**Discussion**

**Phylogenetic relationships**

The new concept of the lophonidae still needs to be more firmly established as it is based on a combination of characters, viz.: ectosomal microspined tylole, isotropic chaomosomal skeletons, palpate chelas and toxas, which are not unique to the group. *Cornulum* and its relatives are traditionally grouped in the Coelosphaeridae, a homogenous group if the growth form and body organization is taken as a synapomorphy, but an extremely heterogenous group if spined characters are taken as synapomorphies. This issue has been debated several times (e.g., Van Soest, 1984; Lévi & Lévi, 1983; Bergquist & Fromont, 1988; Hooper & Kraschin, 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 spicle ornamentation. Thus, spicle (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 (acrunae vs. palpate chelas, smooth tylole vs. microspined tylole, presence of sigma vs. absence, absence of toxas vs. presence). Conversely, strongly different growth forms in e.g., *Acanthorn nomenclatus* and *Zygopy ivemor* do not prevent inclusion of both into the same family because they share similar spication (microspined tylole, bow-shaped toxas, and palpate chelas).

**Character analysis**

More studies are needed to link the lophonate and the non-figular genera of the lophonidae. However, since the lophonate genera treated here comprehensively (*Zygopy ivemor, Cornulum, Damiria, Achelderma*, and *Para cornulum*) show a common feature in the heavy spination of the tylole heads, as opposed to the lighter microspined condition in *Cornulum s.l.*, we may safely assume they form a monophyletic group. *Cornulum* shares the lophonate 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 54% majority consensus tree (Fig. 58), which is identical
Table VII. Characters/states of *Zyccya, Cornelia, Damiria, Achietaerma and Paracornulum* species used for a phylogenetic analysis using PAUP 3.1 (Swofford, 1993), with *Cornelia* s.l. as the outgroup.

<table>
<thead>
<tr>
<th>Character</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Taxa</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cornulum</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Z. invermor</em></td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Z. fuliginosus</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td><em>Z. papillata</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td><em>C. santamariae</em></td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td><em>C. landbeckii</em></td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>C. amodorogil</em></td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><em>C. purpurea</em></td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td><em>C. minuta</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>C. ryff</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>D. simplex</em></td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>D. testa</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>D. leonora</em></td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>D. spongia</em></td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>A. leucoma</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>A. plumaria</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>A. renuaria</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>A. lissanae</em></td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td><em>F. diadum</em></td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Character 1: Growth form: 0 = frutic - at top of a massively encrusting base, 1 = frutic - either sticking directly out of the substrate or tending from a very thin crust.

Character 2: Extensile skeleton: 0 = uniplicate reticuloid, 1 = reticulum of spicles.

Character 3: Choanocellular skeleton: 0 = indistinct reticuloid, 1 = mass of spicles.

Character 4: Colour: 0 = orange-yellow, 1 = black, 2 = purple.

Character 5: Presence of penultimate acrocentryttes: 0 = absent, 1 = present.

Character 6: Presence of ascenclones: 0 = absent, 1 = present.

Character 7: Presence of ascenclonotyles: 0 = absent, 1 = present.

Character 8: Presence of penultimate acrocentryttes: 0 = absent, 1 = present (loss).

Character 9: Presence of a calyx: 0 = present, 1 = absent (loss).

Character 10: Presence of isocyst: 0 = present, 1 = absent (loss).

Character 11: Tylocele size categories: 0 = single size, 1 = two sizes (one long and thin, one short and thick).

Character 12: Spination of tylocele: 0 = lightly spined, 1 = extensively spined all over, 2 = not spined (loss).

Character 13: Length of diaphragm accessory megascleres: 0 = absent, 1 = ≤ 50 µm, 2 = 50–150 µm, 3 = > 150 µm.

Character 14: Presence of diaphragm-shaped microscleres: 0 = absent, 1 = present.

to tree no. 15 of these 24 treess, 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 paraparlytic, 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. *Zyccya, Cornelia, and Achietaerma* 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. invermor* and *Z. fuliginosus* are likely to be species dating from the Yohle Sea, with *Z. papillata* being an older, perhaps Indian, element. Similar trends may be observed from *Cornelia*, where sister group relationships between Indo-Pacific and Caribbean species (C. santamariae, C. purpurea,

...
and *C. minima* are younger than the relationships with several Indian Ocean species (*C. landbeckii, C. amarantensis*, and *C. tyro*). In *Achelidera* the Mediterranean and Caribbean species are closer to each other than to the deep-water Azorean and South Australian species. Conclusions on the biogeographic history of *Domiria* and *Paracornularia* are not possible on the basis of the present data.

**Acknowledgements**

We acknowledge support from the Netherlands Organisation for Tropical Research (WOTRO), grants W84-276 (to R.W.M. van Soest and Ms. M. Kielman), W84-381 (to R.W.M. van Soest), from the Netherlands Science Organisation (NWO) grant 884-342 (to S. Zea), from the Tenth Society (to S. Zea), and from the Foundation for Sea Research (SOZ) (to R.W.M. van Soest), which enabled us to make the various trips and visits, necessary for this cooperative project. Jan Vermeulen made the SEM photos and assisted with the mounting of the planks. Loans of specimens borrowed from the museums of London (Ms. C. Valentine, British Museum [Natural History] [BMNH]), Berlin (Dr. D. Kühnlein, Zoologisches Museum der Humboldt Universität [ZMB]), Frankfurt (Dr. M. Grasノフ, Senckenberg Museum [SMF]), and Paris (Prof. C. Levi, Muséum National d'Histoire Naturelle [MNHN]) are gratefully acknowledged. Two anonymous reviewers contributed to this study.

**References**


Received: 29 April 1994
Revised: 23 September 1994