

# BEAUFORTIA

INSTITUTE OF TAXONOMIC ZOOLOGY (ZOOLOGICAL MUSEUM)  
UNIVERSITY OF AMSTERDAM

Vol. 42, no. 3

September 10, 1991

## TAXONOMY, PHYLOGENY AND BIOGEOGRAPHY OF THE MARINE SPONGE GENUS *ACARNUS* (PORIFERA: POECILOSCLERIDA)

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### ABSTRACT

Cosmotropical species reported in the genus *Acarnus*, viz. *A. innominatus* Gray (1867), *A. tortilis* Topsent (1892) and *A. souriei* Lévi (1952), are demonstrated to show small, but consistent interregional morphological differences, leading to the conclusion that these "species" are very probably complexes of closely related species derived from former widespread (Tethyan and/or Gondwanan) ancestors. On the basis of this analysis, six regional *Acarnus* forms are described as new species, viz. *A. claudae* n.sp. from South East Africa (formerly described as *A. innominatus* by Lévi, 1963), *A. hoshinoi* n.sp. from NW Australia (formerly described as *A. innominatus* by Hooper, 1986) *A. deweerdtiae* n.sp. from the West Indian region (newly discovered material related to *A. tortilis* and *A. toxcata*), *A. bergquistae* n.sp. from the Indo-West Pacific region (formerly described as *A. tortilis* by various authors), *A. nicoleae* n.sp. from the West Indian region (formerly described as *A. souriei* by various authors) and *A. peruanus* n.sp. (undescribed U.S.N.M. material from Peru related to *A. souriei*). The confused taxonomy of some species is clarified on the basis of reexamination of type specimens. The phylogenetic history of the genus is reconstructed with cladistic techniques, using morphological characters of original as well as unpublished material together covering almost all described taxa from all over their known ranges. The resultant cladogram is used for a discussion of the biogeographic history of the genus. Some disjunct patterns are apparent, which are possibly in conflict with the currently accepted history of the world oceans.

### INTRODUCTION

Recently, (Hooper, 1986, Hiemstra & Hooper, 1991, Van Soest, in press) attention was focussed on the phylogenetic relationships of *Acarnus* (Porifera, Poecilosclerida), a genus well-established as a monophyletic taxon because of its unique synapomorphy of the cladotylote megascleres, but otherwise of problematic status through its intermediate plesiomorphous characters linking it to both Microcionidae (see Lévi, 1973) and Myxillidae (Van Soest, 1984, Hooper, 1986). In a review

of the genus (Hooper, 1986 with additional data in Hiemstra & Hooper, 1991) it was suggested that three of the 15 described species had extremely widespread distributions. *A. innominatus* Gray (1867) has been reported from the West Indies (Gray, 1867, and many other authors, see Hooper, 1986:79), South Africa (Lévi, 1963) and North West Australia (Hooper, 1986). *A. tortilis* Topsent, 1892 has been reported from the Mediterranean (Topsent, 1892 and other authors, see Hooper, 1986:82), Atlantic coasts of Spain (Duran & Solorzano, 1982), Azores (Topsent, 1904,

Boury-Esnault & Lopes, 1985), Cape Verde Islands (Topsent, 1928), Indian Ocean (e.g. Dendy, 1916 and Vacelet et al., 1976), Indonesia (Topsent, 1897, Desqueyroux, 1981) and North West Australia (Hooper, 1986). *A. suoriei* (Lévi, 1952 as *Acanthacarnus*) has been reported from West Africa (Lévi, 1952, 1959; Van Soest, in press), Mediterranean (Vacelet, 1961), West Indies (Hechtel, 1965; Van Soest, 1984), Indian Ocean (Thomas, 1970, 1973).

Significantly, among the 12 remaining described species there are seven which appear to be very close to one of those three widespread species, viz. Californian *A. erithacus* De Laubenfels (1927) to *A. innominatus*, Mediterranean *A. polytylus* Pulitzer-Finali (1983) and Brazilian *A. toxata* Boury-Esnault (1973) to *A. tortilis*, Mediterranean *A. levii* (Vacelet, 1960), Brazilian *A. radovani* (Boury-Esnault, 1973), Japanese *A. tener* Tanita (1963) and *A. bicladotylota* (Hoshino, 1980) all to *A. suoriei*. The specific status of some of these forms has been questioned (Vacelet, 1961; Van Soest, 1984; Hiemstra & Hooper, 1991), and one might well ask whether these seven species are not in reality merely regional forms of the three widespread ones. This would lead to a considerable reduction in species, leaving only *A. tenuis* Dendy (1896), *A. topsenti* Dendy (1922), *A. ternatus* Ridley (1884), *A. thielei* sensu Hooper, 1986, *A. primigenius* Hiemstra & Hooper, 1991, and the three widespread ones, as good species, with an even wider distribution than recognized at present.

On the other hand, these regional forms may be expected to have been genetically isolated from one another for considerable periods of time. Their small morphological differences may be a mere reflection of little environmental pressure on their morphology, and effectively hide a considerable genetic difference. There is growing evidence in various marine organisms for morphologically conservative inter-ocean isolates showing no or insignificant morphological divergence but considerable genetic divergence as measured by genetic differences (see for algae e.g. Olsen, et al., 1987). Based on that evidence, there is a strong encouragement

to emphasize inter-ocean differences and where possible describe these as separate species. Cryptic-morphological differences indicating genetically distinct species may be more widespread amongst the morphologically conservative Porifera than previously recognized (cf. Hooper, et al. 1990).

It is the purpose of the present study to review the status of the regional forms of the three widespread species and demonstrate that such widespread distributions do not really exist in *Acarnus*. Comparisons with an extensive collection of *Acarnus* taxa was possible thanks to the cooperation of many colleagues. The revised status of several *Acarnus* species which will be presented below demanded also an adaptation of the classification of Hooper (1986) and later additions by Hiemstra & Hooper (1991) and Van Soest (in press). Finally, an attempt is made to explain the biogeographic patterns which are found in the present day diversity.

## MATERIAL AND METHODS

The studied material consisted of type and other previously described specimens incorporated in several scientific institutions, and of new material, with few exceptions incorporated in the Zoölogisch Museum Amsterdam. The institutions are abbreviated in the text in the following manner:

BMNH: Natural History Museum, London, Great Britain

MHNG: Muséum d'Histoire Naturelle de Genève, Switzerland

MNHN: Muséum National d'Histoire Naturelle, Paris, France

NTM: Northern Territory Museum of Arts and Sciences, Darwin, Australia

QM: Queensland Museum, Brisbane, Australia

USNM: National Museum of Natural History, Smithsonian Institution, Washington, U.S.A.

ZMA: Zoölogisch Museum, University of Amsterdam, the Netherlands

ZMB: Zoologisches Museum, Humboldt Universität, Berlin, Germany

Studied material of *Acarnus* taxa considered as separate entities:

*A. tenuis* Dendy, 1896: lectotype and para-

- lectotype microscopic preparations, BMNH 1902:10:18:62 and 375, both from Port Philip Heads, South Australia (for a redescription cf. Hiemstra & Hooper, 1991)
- A. erithacus* De Laubenfels, 1927: holotype USNM 21430, Monterey Bay, South California; ZMA POR. 8799, do., coll. L. Hunter, don. M.C. Diaz; fragment of specimen from the Berlin Museum from California, ZMA POR. 8286.
- “*A. innominatus*” sensu Lévi, 1963, South Africa: microscopic slides in MNHN DCL. 239, 521, 522, 523, 524.
- A. innominatus* Gray, 1867 s.s.: specimens from Curaçao, ZMA POR. 309 (see Arndt, 1927), 3606 (see Van Soest, 1984).
- “*A. innominatus*” sensu Hooper, 1986, North Australia: specimen in NTM Z2234 (E.P.21) (Darwin area)
- A. thielei* Lévi, 1958, Red Sea holotype fragment (MNHN Abulat # A.107).
- A. wolffgangi* Keller, 1891: fragment of type from ZMB (from the Red Sea); microscopic slide of MNHN DCL. 1297, labeled “*A. ternatus*” from the Red Sea (see Lévi, 1958); microscopic slide of MNHN DCL. 1495 labeled “*A. ternatus*” from Nosy Bé, Madagascar; ZMA specimens from Indonesia (POR 310, 311, 312, 313, 314 (Siboga Exped., all labeled “*A. ternatus*”, from stat. Jedan Island, Aru Islands, 06°S 134°E, and stat. 310, 08°S 119°E), POR. 8767 (Snellius II Exped. stat. 231: Taka Bone Rate, 06°S 121°E); “*A. thielei*” sensu Hooper, 1986, NTM Z855 (Darwin area, North Australia, cf. Hooper, 1986:73)
- A. ternatus* Ridley, 1884: specimen in NTM (Z. 1584) from North Australia (see Hooper, 1986).
- A. topsenti* Dendy, 1922: one of the type specimens BMNH 1921:7:84, from Cargados Carajos in the Indian Ocean (see redescription in Hooper, 1986).
- “*A. topsenti*”: Lobos de Afuera, North Peru, USNM. 23264 (unpublished material, id. of De Laubenfels).
- A. toxcata* Boury-Esnault, 1973 s.s.: 2 microscopic slides of type material, MNHN DNBe 1037, from Brasil, 18°S 38°W.
- “*A. tortilis*” West Indies: ZMA specimens from Curaçao (microscopic slides C 16-C 10 and C 20-7), Bonaire (POR. 8761, 8762), Barbados (ZMA POR. 3833), and North East Colombia (microscopic slide # 207).
- “*A. tortilis*” sensu Topsent, 1897: specimens from Ambon, Indonesia, ZMA 6218 (= small fragment of MHNG C12/28), and microscopic slide MNHN DT.1835; specimen from Great Barrier Reef, North East Australia, NTM Z1538.
- A. tortilis* Topsent, 1892: microscopic slide of the holotype, MNHN DT 271, labeled *A. tortilis* n.sp. “136”, Banyuls, S France (see Topsent, 1892), microscopic slides MNHN DT. 319, Naples (see Topsent, 1925, 1929), DT. 998, Azores, (see Topsent, 1904); microscopic slides from North West Spain (Duran & Solorzano, 1982). West Africa: specimen from Santo Antão, Cape Verde Islands ZMA POR. 7617, microscopic slides of MNHN DT 1203 from the Cape Verde Islands (see Topsent, 1928, 1929); *A. polytylus* Pulitzer-Finali, 1983: microscopic slide of the holotype Ist. Zool. Univ. Genova DC.84) from Porto Cesareo, Southern Italy (Ionian Sea).
- A. primigenius* Hiemstra & Hooper, 1991: holotype ZMA POR. 7693 from Indonesia (cf. Hiemstra & Hooper, 1991).
- A. “souriei”* sensu e.g. Van Soest, 1984: specimens in the ZMA collection from Curaçao (POR. 3327, 3677, 8763), Bonaire (8548), Barbados (3830) North East Colombia (6460, 8768)
- A. bicladotylota* Hoshino, 1980: ZMA POR. 315, 316 (labelled “*A. tortilis*”), and 317 (labeled “*A. topsenti*”), Siboga Exped. specimens from Indonesia, stat. 81 (Borneo-bank, 02°S 117°E) and 225 (Lucipara Islands, 07°S 127°E); one microscopic slide MNHN, DT 1739, labeled “*A. tortilis*” from the Maldive Islands.
- A. tener* Tanita, 1963: three microscopic slides: MNHN, DT. 1890, labeled *A. spec.* Gambier Island, Polynesia, and DT 2590 (2 slides), labeled *A. spec.* from unknown

whereabouts but from *Tridacna* as substrate.

- A. souriei* Lévi, 1952: holotype slide MNHN DCL. 1259 (4) from Senegal; microscopic slide MNHN DCL. 1352 (West Africa, see Lévi, 1959); CANCAP 7 Exped. specimens from the Cape Verde Islands (ZMA POR. 6962, 7031, 7038, 7079, 7082, 7096, 7142, 7238, 7357).
- A. levii* Vacelet, 1960: holotype fragment from "Prés. Th. Tissier" Exped. stat. K. 204; microscopic slides labeled "*A. souriei*" from Corsica, "Antedon" stat. 1657, 1671, 1695 (Vacelet, 1961)
- A. radovani* Boury-Esnault, 1973: 2 microscopic slides of type material, MNHN DNBe 963 from Brasil, 08°S 34°.

All known species of *Acarnus* are represented in the studied material. No type material was studied of *A. ternatus* (but see redescription in Hooper, 1986), *A. innominatus*, *A. bicladotylota*, and *A. tener*; topotypical material, answering to almost all described details of the type specimens was, however, studied of *A. innominatus*, and *A. ternatus*. Of all the remaining species the type material was studied.

Specimens were sectioned and spicule slides were prepared in the usual way (see e.g. Van Soest, 1978, 1980).

#### ACKNOWLEDGEMENTS

The following persons contributed to this study by complying to our request for the loan or donation of material: Miss S.M. Stone (BMNH, London), Prof. C. Lévi (MNHN, Paris), Dr K. Rützler/Miss K. Smith (USNM, Washington), Dr D. Kühlmann (ZMB, Berlin), Miss M.C. Diaz (UCSC, Santa Cruz, USA), Dr R. Desqueyroux-Faundez (MHNG, Genève), Dr M. Solorzano (Santiago de Compostela, Spain), Dr J. Vacelet (Marseille). Mr J.J. Vermeulen assisted in the collecting and preparation of ZMA specimens. This paper benefited from the comments of two anonymous reviewers.

#### SYSTEMATIC DESCRIPTIONS

Systematic descriptions below are intended primarily to emend Hooper's (1986) monographic treatment of the genus. In the present study emphasis is laid on the re-examination of the widespread species *A. innominatus* s.l., *A. tortilis* s.l. and *A. souriei* s.l. For completeness sake the other species are briefly commented upon, but for descriptions and illustrations one is referred to Hooper's study. Only where necessary, new or additional illustrations are here presented. Spicule dimensions of all studied specimens are given in Tables 1-5.

##### 1. "INNOMINATUS" SPECIES GROUP

###### *Acarnus innominatus* s.l.

Specimens assigned to this "species" by various authors share with *A. ternatus*, *A. thielei*, *A. thielei* sensu Hooper, 1986 (= *A. wolffgangi*) and *A. erithacus* thick styles with a characteristic rather abrupt curve in the distal half of the shaft (Hiemstra & Hooper, 1991; this feature was not emphasized by Van Soest (1984) but subsequent reexamination confirmed its presence in most *A. innominatus* styles); with these species it also shares the smooth style heads, the predominantly smooth shaft of the larger cladotylote category, and the absence in these of distinct hooks on the distal extremity (tylote base or tyle), although some of them have lobes. The skeletal architecture often shows a renieroid-isotropic condition, although in some species this is obscured by an anisotropic condition. The group of species referred to above was conveniently indicated as *innominatus*-group (Hooper, 1986), and this concept is retained and revised here.

Specimens assigned to this "species" differ from the related species *A. ternatus* and *A. wolffgangi* in their massively incrusting habit (the latter are lobate or thickly fan-shaped, respectively, in their adult stage) and by the absence of thick, straight, barely curved toxa. They also differ from *A. erithacus* by their softer consistency and hispid surface (against the firm

condition and smooth surface of the Californian species); the latter characters also differentiate them from *A. thielei*.

Specimens assigned to this "species" are reported from three disjunct regions, viz. West Indies (*A. innominatus* s.s.), South Africa (*A. innominatus* sensu Lévi, 1963) and North West Australia (*A. innominatus* sensu Hooper, 1986).

The South African specimens (all five examined slides) differ from the West Indian specimens in the possession of strongly lobate cladotylote tyles (against entirely round in *A. innominatus* s.s.), their cladomes have 3 clads (against 4), part of the styles are minutely spined (in *A. innominatus* s.l. entirely smooth), and the long straight thin toxa are much shorter (250  $\mu\text{m}$  against 450  $\mu\text{m}$ ). The lobate tyles are shared with *A. erithacus* and *A. thielei*.

The North West Australian specimens are much more similar to *A. innominatus* s.s., but differ in the more squarish, flattened condition of many cladotylote tyles and unusually small chelae (9  $\mu\text{m}$  against 14-20 in *A. innominatus* s.s.); like in the South African specimens, clads of the cladotylotes number invariably 3 (not 3-4 as Hooper (1986) stated).

In view of the disjunct distribution it is decided here to describe each as a separate species, with West Indian *A. innominatus* as the nominal one, and two new species described below.

### ***Acarnus innominatus* Gray, 1867**

*Acarnus innominatus* Gray, 1867: 544 (based on unnamed spicule drawings of Bowerbank, 1864: pl. 3 figs. 73-76 and pl. 18 fig. 292); Carter, 1871: 269; Arndt, 1927: 145, pl. 3 fig. 5; De Laubenfels, 1936: 93, pl. 12 fig. 2; Alcolado, 1976: 5; Van Soest, 1984: 61, fig. 22, pl. 5 figs. 6-9.

*Acarnus carteri* Ridley, 1884: 354, footnote.

Not: *A. innominatus* sensu Lévi, 1963 (see below)

Not: *A. innominatus* sensu Hooper, 1986 (see below)

Material: Curaçao: ZMA POR. 309 and 3606.

Diagnosis (taken from Van Soest, 1984):

Thinly to massively (up to 1 cm thick) incrusting, surface smooth, no apparent oscules, consistency soft.

Colour red.

Skeleton: tangential ectosomal tylotes; plumose choanosomal tracts interconnected by renieroid isotropic tracts, fair amount of spongin.

Spicules: Microspined ectosomal tylotes: 180-280 by 2.5-4  $\mu\text{m}$ .

Styles: smooth, curved: 280-460 by 11-22  $\mu\text{m}$ .

Cladotylotes: Mostly smooth large cladotylotes with perfectly rounded tyles and cladomes with four clads: 200-300 by 6-12  $\mu\text{m}$ ; rare, sparingly spined small cladotylotes with perfectly rounded tyles and cladomes with four clads 80-115 by 2-3  $\mu\text{m}$ .

Chelae: 9-16-24.

Toxa: "Oxhorn" toxas (toxa I in Boury-Esnault's and Hooper's terminology, see Plate 3 figs. 19-20) in a large size range: 50-160 by 2-4  $\mu\text{m}$  (the larger may in fact be thicker toxa of the next category; that is difficult to decide); thin deeply curved toxa (toxa II, see Plate 3 fig. 21): 35-150  $\mu\text{m}$ ; "acolada" toxa, long thin, shallowly curved (toxa III, see Plate 3 fig. 23): 200-450  $\mu\text{m}$ .

Distribution: West Indian region (Florida, Curaçao, Cuba; so far not known from the western part of the region).

Remarks: the species stands out among its relatives by the rarity or absence of the smaller cladotylotes, the perfectly rounded smooth cladotyles, and the four-claded opposite ends of the cladotylotes.

### ***Acarnus claudeni* n.sp.**

Fig. 1

*Acarnus innominatus*; Lévi, 1963: 48, fig. 55.

Holotype: MNHN DCL. 524, South Africa, Mossel Bay # 78K.

Paratypes: MNHN DCL. 521 (South Africa, Cape, # 455G), 522 (Mossel Bay, # 44Q), 523 (Mossel Bay, # 18L).

Additional material: MNHN DCL. 239, South Africa, Pt. Elisabeth (from the BMNH collection, bearing an unpublished manuscript name).

Diagnosis (partly from Lévi, 1963):

Massive, rather firm, consolidating calcareous

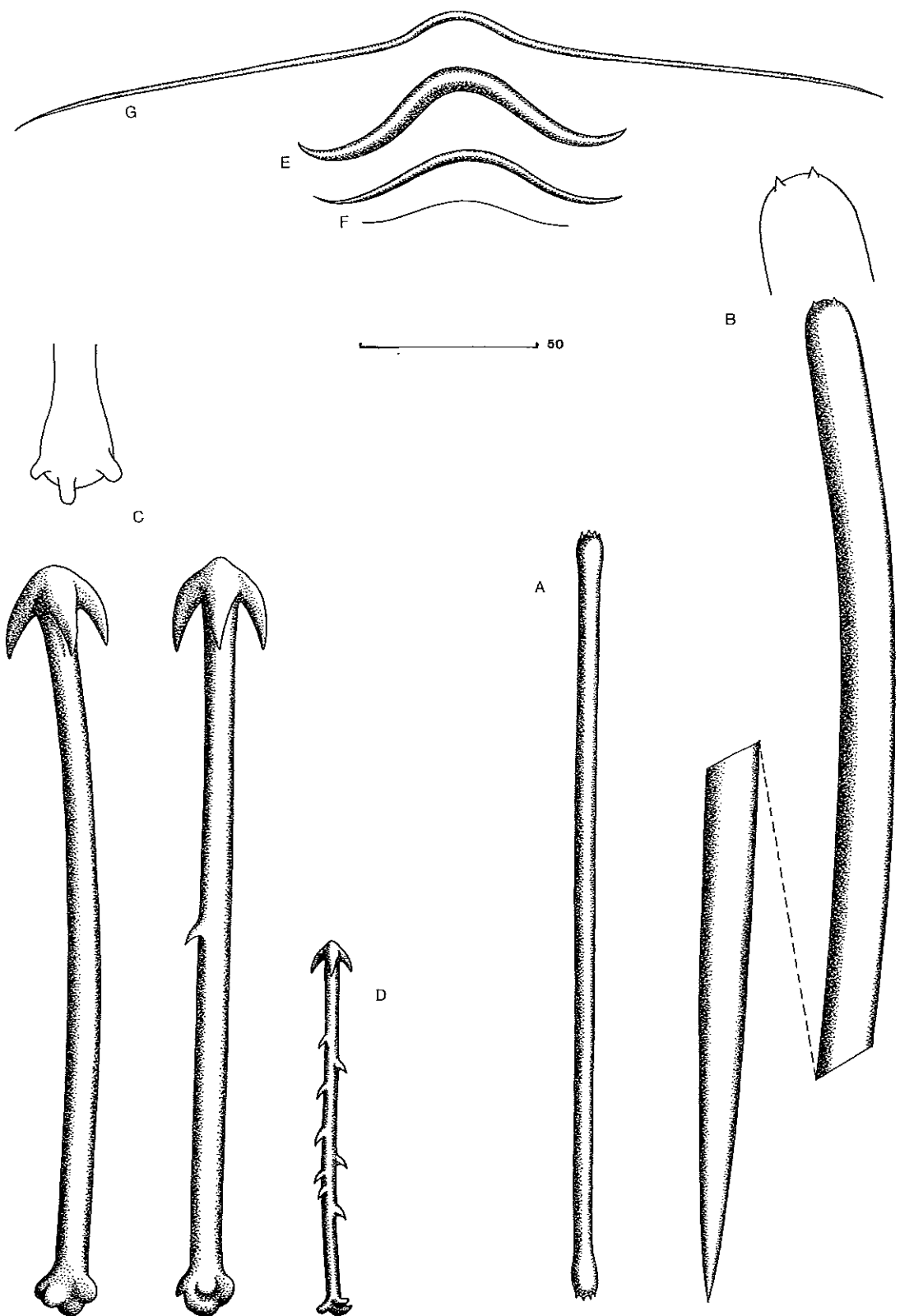


Fig. 1. *Acarnus claudei* n.sp., spicules drawn from the holotype slide MNHN DCI. 524, A. tylole, B. style, C. large cladotylotes (I), D. small cladotylote (II), E. oxhorn toxa (I), F. thin deeply curved toxa (II), G. accolada toxa (III).

algae, size 30-40 mm. Surface even, very slightly hispid. Oscules raised, 2 mm.

Colour: scarlet reddish.

The ectosomal skeleton consists of tangential tyloles. The choanosomal skeleton is dense and composed of paucispicular anastomosing spongin fibres, echinated by abundant cladotylotes.

Spicules: Microspined ectosomal tyloles (Fig. 1A): 130-230 by 3-4  $\mu\text{m}$ .

Styles curved, mostly entirely smooth, but occasionally with minutely spined heads (Fig. 1B): 175-400 by 6-20  $\mu\text{m}$ , but these include immature spicules.

Cladotylotes: large cladotylotes (cladotylotes I) (Fig. 1C), with cladomes provided with mostly three clads, tyloles flattened and provided with lobes and blunt protrusions, shaft normally entirely smooth, but an occasional spine was noticed: 160-230 by 8  $\mu\text{m}$ ; small cladotylotes (cladotylotes II) (Fig. 1D), tyloles likewise flattened and provided with blunt protrusions, shaft entirely spined: 80-110  $\mu\text{m}$  by 2  $\mu\text{m}$ .

Chelae: 11-18  $\mu\text{m}$ .

Toxa: Oxhorn toxa (toxa I) (Fig. 1E) of a large size range: 50-200 by 3-5  $\mu\text{m}$ ; thin deeply curved toxa (toxa II) (Fig. 1F): 50-140  $\mu\text{m}$ ; accolada toxa (toxa III) (Fig. 1G): 200-250  $\mu\text{m}$ . Distribution: South Africa: Cape Town, Mossel Bay and Pt. Elisabeth.

Etymology: named after Prof. Dr Claude Lévi who reported this material and in honour of his life time devoted to sponges.

Remarks: There is a possibility that the second *Acarinus* specimen described by Thiele (1903) (as *A. ternatus*) belongs to the present species, because Thiele describes and pictures lobate cladotyles; other spicules have sizes comparable to the South African material. This would mean that the species has a disjunct distribution in the Indian Ocean.

As remarked above this species differs rather widely from nominate *A. innominatus* in the habit and the shape of the cladotyles, both of which are perhaps shared with Californian *erithacus* (see below) and Red Sea *A. thielei*, and the size of the accolada toxa. Less important differences are the higher frequency and more

heavy spination of the smaller cladotylotes, the three-claded cladomes (four in *A. erithacus*) and the occasionally microspined style heads (always smooth in *A. thielei*)

#### *Acarinus hoshinoi* n.sp.

*Acarinus innominatus*; Hooper, 1986: 76, figs. 10-18, 44.

?*Acarinus thielei* sensu Thomas, 1970: 43, figs. 3-4.

Holotype: NTM Z2234, Dudley Point Reef, Darwin, Northern Territory, Australia, intertidal, 8-III-1985 (holotype slide in ZMA).

Diagnosis (mostly condensed from Hooper, 1986):

Thickly incrusting, covering 45 cm<sup>2</sup>. Surface irregular, shaggy, hispid. Longitudinal grooves, 1.6 mm wide, meander across the surface. Abundant, slightly raised oscules, 1-3 mm in diameter.

Colour: bright orange-red.

Ectosome: tangential layer of tyloles, with large cladotylotes extending beyond the surface.

Choanosome: a confused renieroid reticulation of spicule tracts and single spicules, which may become plumose in the subectosomal region; tracts are bound by some spongin and echinated by cladotylotes.

Spicules: Microspined ectosomal tyloles: 240-280 by 3-4  $\mu\text{m}$ .

Styles: thick, curved, heads smooth: 260-450 by 16-25  $\mu\text{m}$  (Hooper: 267-453 by 6-21  $\mu\text{m}$ , because thinner growth stages were included).

Cladotylotes: large cladotylotes with mostly somewhat flattened asymmetrical cladotyles, with cladomes with three clads (very rarely 4), smooth shafts: 195-280 by 6-15  $\mu\text{m}$ ; small cladotylotes, cladotyles similar to large cladotylotes, cladome predominantly three-claded, shaft spined: 70-140 by 3-5  $\mu\text{m}$ .

Chelae: 6-9-10  $\mu\text{m}$ .

Toxa: Oxhorn toxa (toxa I) wide ranged: 45-250 by 2-5  $\mu\text{m}$ ; thin deeply curved toxa (toxa II) 25-170  $\mu\text{m}$  (Hooper: 20-80  $\mu\text{m}$ , but this was a difference of category assignment, because the thinness/thickness is the only criterion of

assignment of the larger toxa of both categories); *accolada*-toxa (toxa III): 190-590 by 1-3  $\mu\text{m}$ .

Distribution: known only from the type locality, Darwin area, intertidal.

Etymology: named after Dr T. Hoshino, formerly of the Hiroshima University, Japan, whose untimely death prevented the fulfillment of a promising career as sponge taxonomist.

Remarks: Possibly, Thomas' (1970) record of *A. thielei* concerns a specimen of this species, because of shared spicule sizes, especially the small chelae. Cladotylote tyles in this species are rounded but occasionally (as in the holotype) asymmetrical and flattened, perhaps homologous to the lobate condition of *A. thielei* s.s. and *A. claudei* n.sp., and like in those the cladomes are normally three-claded, whereas those of *A. innominatus* are normally four-claded. The frequency of the smaller cladotylotes is much higher than in *A. innominatus*, and they appear to be more heavily spined. The renieroid reticulation of the choanosomal spicule tracts is shared with *A. innominatus*, *A. thielei* and *A. wolffgangi*; other members of the "innominatus-group" (*A. claudei* n.sp., *A. ternatus* and *A. erithacus*) have anisotropic skeletons. The new species resembles both *A. innominatus* and *A. wolffgangi* rather strongly in spicule sizes, but it has distinctly smaller chelae.

#### **A. ternatus** Ridley, 1884.

For a redescription of the type specimen and diagnosis of the species, cf. Hooper, 1986: 83. This species stands out among its relatives by possessing only a single (?larger) category of cladotylotes and the plumoreticulate skeleton of spongin fibres. We disagree with the generally accepted conspecificity of *A. wolffgangi*. The type specimen of that species was found to contain the small category of lightly spined or smooth cladotylotes in a low proportion.

Ridley & Dendy's (1887) record from Tahiti needs verification as the description is inadequate. Dendy's (1905) Indian record needs re-examination, but may for the time being be

considered correctly assigned; possibly the (rare) small cladotylotes have been overlooked and then it belongs to *A. wolffgangi* to which it shows considerable likeness in habit (cf. Dendy's pl. VIII fig. 4). Thiele's (1903) (and thus Kieschnick's (1896) *A. wolffgangi*) Indonesian record needs to be reexamined, but on paper it seems to conform best to *A. claudei*. Hentschel's (1912) Indonesian records are referred to *A. wolffgangi*. Also, Lévi's Red Sea record of this species must be referred to *A. wolffgangi* on the basis of its possession of a smaller cladotylote category discovered in the slide. It shares with *A. thielei* s.s. the relatively smooth surface (not grooved or ridged), and with *A. innominatus*, *A. hoshinoi* and "*A. thielei*" sensu Hooper, 1986 (= *A. wolffgangi*, cf. below) the rounded cladotyles. The distribution so far seems restricted to North Australia and India.

#### **A. wolffgangi** Keller, 1889

(Plate 1 figs. 1-2)

This is Hooper's (1986) *A. thielei*, which differs from the type of that species in having much more robust megascleres (compare Hooper's description with the redescription of *A. thielei* below; cf. also Table I). Thiele's (1903) record (and thus Kieschnick's (1896) record) of this species needs to be reexamined, but on paper may be correctly assigned. Although we did not study Thomas' (1970) material which he called *A. thielei* we suspect it is conspecific with *A. hoshinoi* n.sp. (cf. above) rather than with the present species based primarily on the small chelae of the former. The species is widely distributed: Red Sea, Indonesia, North Australia.

#### **A. thielei** Lévi, 1958

This has been misinterpreted by various authors, emphasizing the two categories of cladotylotes as the distinguishing feature of this species; however, the possession of two categories of cladotylotes is the rule rather than the exception in *Acamus*. In other features, such as spicule sizes, specimens assigned to this



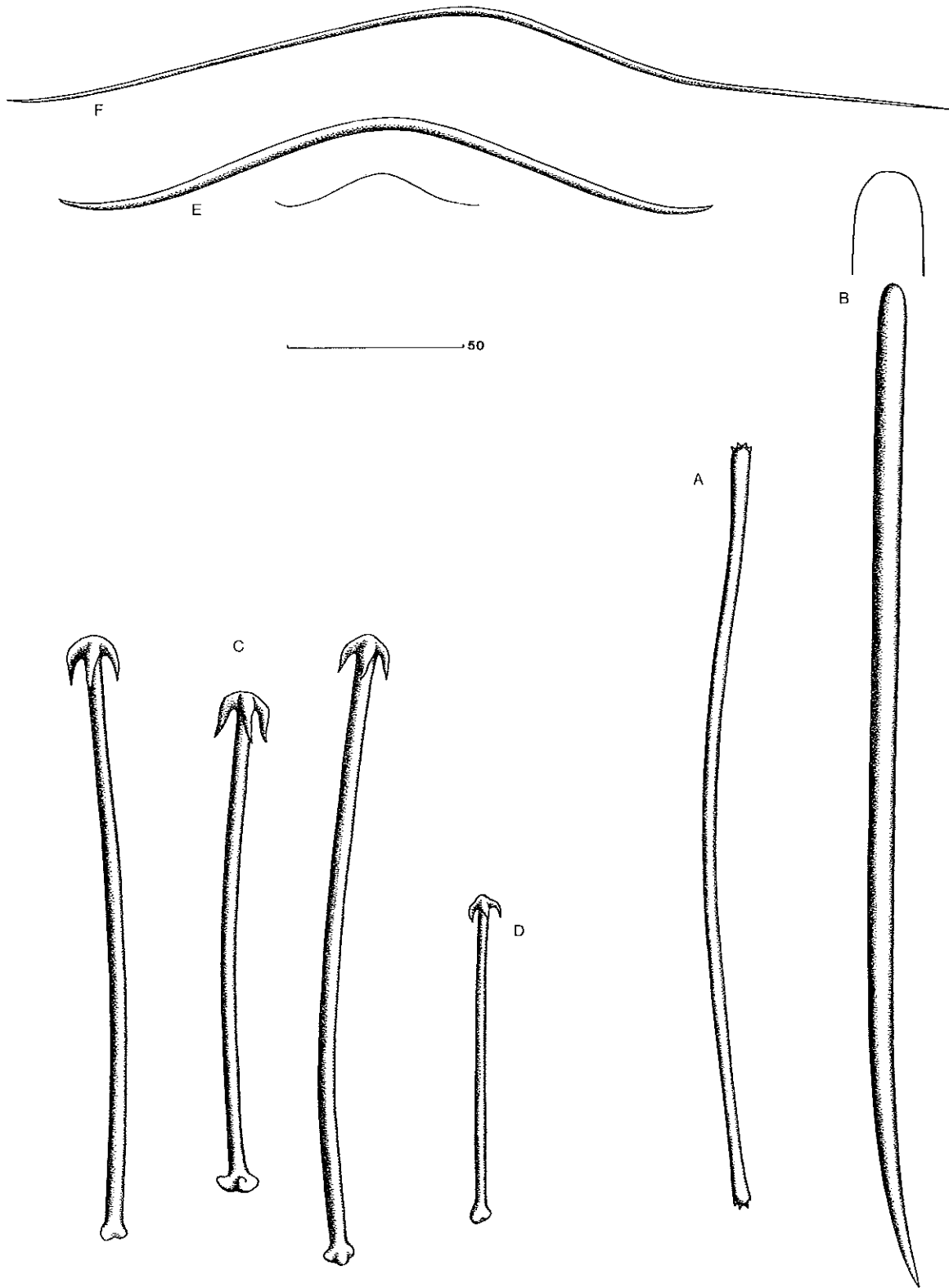


Fig. 2. *Acarnus thielei* Lévi, 1958, spicules drawn from a slide made from the holotype MNHN Abulat, # A. 107 A. tylote, B. style, C. cladotylotes I, D. cladotylote II, E. toxa I-II, F. toxa III.

Table 1. Spicule categories and sizes ( $\mu\text{m}$ ) of species of the *innominatus*-group (*Acarnus* spp. with cladotyles smooth or lobate, not provided with hooks); for more details on studied specimens cf. text.

Species	tylotes	styles	cladotylote I	cladome dim.	clad. no.	cladotylote II	chelae	toxa I	toxa II	toxa III
<i>innominatus</i> (West Indies)	180-280 /2.5-4	280-460 /11-22	200-300 /6-12	40/50	4	80-115 /2-3	9-24	50-160	35-150	200-450 (acco.)
<i>hoshinoi</i> (holotype)	240-280 /3-4	260-450 /6-25	195-280 /6-14	35/35	3	70-140 /3-5	6-10	45-250	25-175	430-590 (acco.)
<i>hoshinoi</i> ( <i>thielei</i> Thomas, 1970)	207-283 /2-4	301-452 /13-24	188-245 /12-16	37/37	3	75-96 /3-4	8-10	25-155	?84	up to 584 (?)
<i>wolffgangi</i> (holotype)	210 /2	286-300 /13	216 /10	60/47	3	110 /3	15-20	80	?	510-900 (straight)
<i>wolffgangi</i> (Siboga specimens)	250-290 /3-4	340-445 /21-33	220-277 /10-16	45/50	3	80-108 /2-3	19-24	40-150	20-200	350-1000 (straight)
<i>wolffgangi</i> ( <i>thielei</i> Hooper, 1986)	194-313 /3-9	178-464 /14-30	85-270 /3-15	48/41	3	75-97 /2-4	18-25	33-151	34-?	up to 960 (straight)
<i>wolffgangi</i> (sensu Thiele, 1903)	260 /4	450 /25	275 /25	?	3	not recorded	22	60	250	900 (straight)
<i>wolffgangi</i> (MNHN, Madagascar)	220 /-	340 /20	150-200 /10	?	3	90-110 /2-3	20	70	150	720 (straight)
<i>wolffgangi</i> (Red Sea, Lévi, 1958)	240 /1-2	280 /6	180-235 /-	-	3	90-110 /2-3	17	70-120	80-150	up to 700 (straight)
<i>ternatus</i> (holotype, cf. Hooper)	224-268 /3-4.5	128-419 /7-14	63-233 /2-11	23/21	3	absent	8-22	12-?	up to 233	up to 708 (straight)
<i>ternatus</i> (NTM Z. 1584)	250 /4	288 /15	135-166 /4	15/12	3	absent	20	75-110	50-150	up to 800 (straight)
<i>thielei</i> (holotype)	206-225 /2-3	230-296 /5-6	130-188 /3-4.5	18/12	3	61-79 /1-2	7-9	60-200	25-70	240-420 (acco.)
<i>claudei</i> (holotype)	130-230 /3-4	175-340 /6-20	160-230 /9	20/20	3	80-110 /2	11-18	50-200	50-140	200-250 (acco.)
“ <i>ternatus</i> ” (sensu Thiele, 1903)	230 /4	350 /15	160 /6	-	3	90 /2	20	?	125	? (?)
<i>erithacus</i> (topotypical material)	170 /4	330 /16	155 /8	24/19	4	85-110 /3	12-26	80-110	80	300 (acco.)
<i>tenuis</i> (syntype series)	96-176 /2	152-205 /2	80-152 /2	-	4-5	absent	absent	absent	absent	absent

species differ rather strongly. Prof. Lévi kindly enabled us to study a fragment of the holotype, which shows the following features:

Smooth surface, renieroid reticulation, little or no spongin; tylotes (Fig. 2A) 206-225/2-3  $\mu\text{m}$  (against 210-290/2-4  $\mu\text{m}$  in *A. thielei* sensu Hooper, 1986); styles (Fig. 2B) 230-296/5-6  $\mu\text{m}$  (against 286-445/13-33  $\mu\text{m}$ ); cladotylote I (Fig.

3C) 130-188/3-4.5  $\mu\text{m}$  (against 186-280/6-14  $\mu\text{m}$ ), with cladomes 12  $\mu\text{m}$  high/18  $\mu\text{m}$  wide (against 50-60  $\mu\text{m}$  high/45-47  $\mu\text{m}$  wide), and tyles lightly quadrilobate (against entirely rounded); cladotylote II (Fig. 3D) 61-79/1-2  $\mu\text{m}$  (against 80-108/2-3  $\mu\text{m}$ ); chelae 7-9  $\mu\text{m}$  (against 15-24  $\mu\text{m}$ ); toxa I (Fig. 2E) 60-200  $\mu\text{m}$  (against 80-150  $\mu\text{m}$ ), grading into toxa II 25-70  $\mu\text{m}$

(against 20-200  $\mu\text{m}$ ); toxa III (Fig. 2F) (acolada-like, softly curved) 240-420  $\mu\text{m}$  (against 350-1000  $\mu\text{m}$ , straight).

Distribution: so far restricted to the Red Sea. Other records of *A. thielei* are referred to *A. wolffgangi* (e.g. Hooper, 1986) or *A. hoshinoi* (e.g. Thomas, 1970).

#### *A. erithacus* De Laubenfels, 1927.

This forms tough masses with relatively smooth surface and big raised oscules (for a colour photograph cf. Bakus & Abbot, 1980: fig. 2.8). The spicular density is unusually high and the cladotylotes have characteristic irregularly lobate tyles; in the studied specimens both its acolada toxa and the tylotes are unusually small compared to those of the other members of the group. Spicule sizes quoted by Hooper (1986) were incorrect. Distribution: boreal and subtropical West Coast of North America.

#### *A. tenuis* Dendy, 1896

For an extensive redescription of this peculiar species cf. Hiemstra & Hooper, 1991. It differs from all other *Acamus* in the lack of microscleres, the lack of spines on tyles of the ectosomal tylotes and the possession of a confused skeletal architecture. Hiemstra & Hooper (l.c.) for this reason placed this species at the base of the phylogeny of *Acamus*, unrelated to any other species. However, when judged on the positive characters alone (smooth spicules, rounded cladotyles) the species belongs to the *innominatus*-group. Distribution: known only from the type locality, Port Phillip Bay, Victoria, Australia.

## 2. "TORTILIS" SPECIES GROUP.

### *Acamus tortilis* s.l.

Like members of the "*Acamus souriei*-group" (sub-genus *Acanthacarnus* (Lévi, 1952), as well as *A. toxcata* Boury-Esnault (1973), *A. polytylus*

Pulitzer-Finali (1983) and *A. topsenti* Dendy (1922), this "species" shares the spined condition of all cladotylotes (but this could very well be a plesiomorphous character, see below). Many species (but regrettably not all) of the *A. souriei*-group have their style-heads slightly swollen and often rugose, i.e. the surface is heavily spined all-over and they are often irregular in outline, whereas those of *A. tortilis* and the other mentioned species, (together conveniently named the *tortilis*-group by Hooper, 1986), are merely microspined, which condition is assumed to be plesiomorphous. The *tortilis*-group also lacks the echinating acanthostyles of the *souriei*-group, but this is shared with all other members of *Acamus*.

From *A. topsenti* this "species" (and indeed also *A. toxcata*) differs in the habit (ramose in the former, incrusting in the latter), in the consistency and the surface condition (firm and smooth against soft and irregular), in the skeletal architecture (spongin fibres cored by styles and echinated by cladotylotes against simple plumose columns of styles and larger cladotylotes echinated by larger and smaller cladotylotes); *A. topsenti* lacks the larger cladotylotes.

From *A. toxcata* this "species" differs in the absence of extremely long toxa and relatively lightly spined larger cladotylotes; from *A. polytylus* it differs only in the absence of a polytylote condition of the megascleres, but other details are so similar that conspecificity with *A. tortilis* s.s. is likely.

Specimens assigned to this species are reported from widely different areas: Mediterranean, North Spain, Azores, Cape Verde Islands, Madagascar, India, Indonesia; North West Australia. Specimens similar to and somewhat intermediate between both *A. tortilis* and *A. toxcata* can now be reported also from the West Indies (recently collected in Bonaire and Curaçao cryptic reef habitats). For that reason, we will include *A. toxcata* in our comparisons and diagnoses of *A. tortilis* s.l.-forms reported from the various localities. Like with *A. innominatus*, we propose to raise these regional forms to specific status:

## *Acarinus tortilis* Topsent, 1892

*Acarinus tortilis* Topsent, 1892: xxiv; Topsent, 1904: 171, pl. 14 fig. 8; Topsent, 1925: 661; Topsent, 1928: 302; Topsent, 1929: 19 (in part); Topsent, 1934: 72; Topsent & Olivier, 1943: 2; Sarà, 1960: 461; Rützler, 1965: 32; Boury-Esnault, 1971: 323; Duran & Solorzano, 1982: 61, fig. 11; Pansini, 1987: 171.

*Acarinus polytylus* Pulitzer-Finali, 1983: 574, fig. 70.

Not: *A. tortilis* sensu Topsent, 1897: 450 (and Desqueyroux, 1981: 758); Dendy, 1916: 130; Vacelet et al., 1976: 74; Hooper, 1986: 79 (see below).

Material: Microscopic slide of holotype MNHN DT 271 (Banyuls), and slides labeled MNHN DT 319 (Naples), MNHN DT. 998 (Azores), 2 microscopic slides MNHN DT 1137, (Boavista, Cape Verde Islands, 91 m), 2 microscopic slides Galicia, North West Spain (La Coruña and Pontevedra, sublittoral), ZMA POR. 7617 (Porto Novo, 500 m W of pier, Santo Antão, Cape Verde Islands, 6 m, 23-I-1986, coll. J.J. Vermeulen, # 86-88). Microscopic slide of holotype of *A. polytylus* Pul.-Fin., Mus. Genova DC 84 (Ionian Sea, Southern Italy).

### Diagnosis:

Massively to thinly incrusting, often agglutinating substrate particles or algae. Consistency soft, surface smooth except where large megascleres pierce the dermis, sticky.

Colour: orange alive, brown in spirit.

Ectosome: a feltwork of tylotes producing a smooth detachable "skin".

Choanosome: plumose columns of styles echinated by cladotylotes rise up from a basal plate of spongin; smaller cladotylotes echinate lower parts and basal plate, larger cladotylotes echinate upper parts of the columns.

Spicules: Microspined tylotes with swollen tyles: 250-400 by 3-6  $\mu\text{m}$ .

Styles, straight, with microspined (occasionally smooth) apices: 295-550 by 5-16  $\mu\text{m}$ .

Cladotylotes: large ones, with cladome provided with 4 (sometimes 5) clads, with heavy spines along the shaft, and often with rather characteristic blunt spines on the tyles, which adhere closely to the shaft: 113-220 (Topsent, 1904: up to 270, but examination of his slide

could not confirm this) by 3-6  $\mu\text{m}$ ; small ones, similar to the large ones, tyles often irregular: 55-110  $\mu\text{m}$  by 1-3.5  $\mu\text{m}$ .

Chelae: 11-22  $\mu\text{m}$ .

Toxa: Oxhorn toxa (toxa I) and thin deep-curved toxa (II) not differentiated, intergrading completely: 20-190 by 0.5-5  $\mu\text{m}$ ; accolada toxa (III) absent, or more precisely: modified in the form of thin straight toxa, lacking the sharp-angled central curve and recurved wings: 170-600  $\mu\text{m}$ .

Distribution: Western Mediterranean, Azores, Atlantic coast of North Spain, Cape Verde islands, 6-91 m.

Remarks: Synonymization of sympatric *A. polytylus* and *A. tortilis* is based on the arguments that apart from the polytylote condition of some of the megascleres of the single specimen of *A. polytylus* there are no other differences; moreover, quite a large proportion of the spicules is "normal". Polytylote spicules occur in other sponges (e.g. *Clathria*, *Polymastia*), and are likely an individual rather than a specific character.

This species differs from *A. toxata* (cf. below), *A. deweerdtiae* (cf. below) and *A. bergquistae* (cf. below) in the straight modification of toxa III: many specimens especially from the Mediterranean show a persistent occurrence of blunt spines on the cladotyles, but Atlantic representatives have normal sharp spines.

Duran & Solorzano (1982) recorded *A. tortilis* from the Atlantic coast of North Spain. Thanks to Dr Solorzano we were able to study material of this northernmost record of the genus in the East Atlantic. They report only a single category of cladotylotes (74-103  $\mu\text{m}$ ), but we found two, viz. 65-94 by 1-2  $\mu\text{m}$  and 108-145 by 3-4  $\mu\text{m}$ ; style sizes reported (217-331  $\mu\text{m}$ ) are outside the range of Mediterranean *A. tortilis* (subsequent reexamination showed the majority of styles to be between 295 and 345  $\mu\text{m}$ ) and the toxa III category (although not reported) is only up to 195  $\mu\text{m}$  long. Style heads are frequently somewhat swollen and relatively heavily spined. If acanthostyles would have been present, then the specimens would be similar to *A. souriei* and *A. levii* (cf. below).

Topsent's (1904) Azores specimen largely

conforms to Mediterranean specimens (even including the blunt spines on the cladotyles), but again the toxa III category reaches only 220  $\mu\text{m}$ .

Cape Verde specimens (Topsent, 1928 and ZMA material) approach the specimens from North Spain in the relatively small-cladotylote I size (123-174  $\mu\text{m}$ ), and again the toxa III are relatively short (up to 404  $\mu\text{m}$ ). It appears as if the Atlantic specimens share the short toxa III and possibly represent a separate taxon. However, in view of the adjacent distributions, the absence of further consistent differences and the large variability in many features, all Eastern Atlantic specimens are assigned to *A. tortilis*.

Indo-Pacific records of *A. tortilis* are referable to a new species *A. bergquistae*; for a survey of the differences cf. below.

#### ***Acarnus bergquistae* n.sp.**

*A. tortilis* sensu Topsent, 1897: 454, pl. 24 fig. 24 (and Desqueyroux, 1981: 758); Dendy, 1916: 130; Vacelet et al., 1976: 74; Hooper, 1986: 79, figs. 19-27, 45.

Holotype: QM GL706 (fragment in NTM Z1538), Outer Barrier, East of Lizard Island, North East Queensland, Australia, 10 m.

Paratype: MHNG, C12/28, Ambon, Indonesia; fragment in ZMA (POR. 6218) (microscopic slides in MNHN, DT. 1835, and ZMA).

Diagnosis (mostly condensed from Hooper, 1986, to which one is referred for illustrations of the spicules):

Thickly incrusting, up to 4 by 7 cm and 4 mm in thickness; agglutinating detritus; surface rough, hispid.

Colour: grey-brown in alcohol.

Ectosome: tangential bundles of tylotes and cladotylotes projecting through the dermis.

Choanosome: riddled with detritus bound by a confused reticulation of bundles of styles echinated by cladotylotes.

Spicules: Microspined tylotes with clearly swollen ends: 183-363 by 3-7  $\mu\text{m}$ .

Styles short, thick, with microspined heads (thinner young stages are smooth): 197-334 by 7-16  $\mu\text{m}$ .

Cladotylotes: Larger ones, cladomes three- or four-claded, shaft heavily spined, tyle with short rounded "spines" closely adhering to the shaft base: 118-212 by 4-8  $\mu\text{m}$ ; small ones relatively thick, similar to large ones: 58-109  $\mu\text{m}$  by 3-5  $\mu\text{m}$ .

Chelae: 7-16  $\mu\text{m}$ .

Toxa: Oxhorn toxa (I): 44-110  $\mu\text{m}$ ; thin deep-curved toxa (II): 80-265  $\mu\text{m}$ ; accolada toxa (III) (or varieties thereof) absent.

Distribution: Indo-West Pacific (North East Australia, Indonesia, India, Madagascar).

Etymology: named after Prof. Patricia R. Bergquist, to honour her invaluable contributions to our knowledge of sponges.

Remarks: This species may be distinguished from *A. tortilis* by the absence of the toxa III category and the relatively short and thick styles. Most cladomes of *A. bergquistae* show 3 clads, against normally 4 or 5 in *A. tortilis*.

#### ***Acarnus dewerdtiae* n.sp.**

Fig. 3, Plate 1 Fig. 3.

Holotype: ZMA POR. 8761, Bonaire, Karpata, 5 m, under coral rubble, V-IX-1988, coll. R. Pennarts & G.J. Roebbers # 42 (scanty material, but with 3 microscopical slides which are important as additional voucher material).

Paratypes: ZMA POR. 8762, Bonaire, 20 m, under coral rubble, V-IX-1988, coll. R. Pennartz & G.J. Roebbers ("R2 1306GR"); 3833, Barbados, 100 m, coll. P. Wagenaar Hummelinck.

Additional material: microscopic slides "C20-7", Curaçao, Cornelisbaai, 5 m, under coral rubble, coll. E. Meesters & P. Willemsen; "C16-C10", do. Microscopic slide "207" Colombia, Santa Marta area, coll. M. Kielman & C. Hofman.

Diagnosis:

Thinly (1 mm) incrusting undersides of coral rubble; surface smooth; no apparent oscules. Consistency soft, easily damaged. Size indefinite, but in the available specimens smaller than 2 cm<sup>2</sup>.

Colour: orange-red.

Ectosome: a feltwork of tangential tylotes.

Choanosome: plumose bundles of styles echinated by cladotylotes of all sizes; smaller ones concentrated at the base and echinating the basal spongin plate.

Spicules: Microspined ectosomal tylotes (Fig. 3A): 290-350/3-5  $\mu\text{m}$ .

Styles (Fig. 3B) microspined, slim and straight: 400-566/5-6  $\mu\text{m}$

Cladotylotes in three (in stead of the usual two) categories: largest, characterized by a low number of spines on the shaft (sometimes spines are entirely absent, Fig. 3C), and three-claded cladomes: 190-279/5-8  $\mu\text{m}$ ; intermediate, fully spined ones (Fig. 3D), four-claded cladomes: 105-128/2-4  $\mu\text{m}$ ; smallest, fully spined, four-claded cladomes (Fig. 3E): 67-86  $\mu\text{m}$ /1-2  $\mu\text{m}$ .  
Chelae: 15-20  $\mu\text{m}$ .

Toxa: Oxhorn toxa (toxa I): absent; thin deep-curved toxa (toxa II) (3F): 40-180  $\mu\text{m}$ ; accolada toxa (toxa III): 160-400  $\mu\text{m}$  (Fig. 3G).

Distribution: West Indian region (Bonaire, Curaçao, Barbados, North East Colombia).

Etymology: named after Ms Wallie de Weerd in recognition of her contribution to our understanding of Haplosclerid phylogeny.

Remarks: The distinctive character of the new species is the occurrence of three instead of the usual two categories of cladotylotes. This species was overlooked in recent surveys of Caribbean Poecilosclerids, although indications of its existence were given in the noted occurrence of "*A. souriei*" specimens "without acanthostyles". From comparison with other members of the *tortilis*-group it is clear that the new species is similar to *A. toxcata* from Brazil, but differs from this in the absence of extremely long accolada toxa, and of course of the mentioned three categories of cladotylotes. With *A. toxcata* it shares the retention of the accolada-toxa (replaced by straight thin toxa in *A. tortilis*), and the sparingly spined largest cladotylotes. Although the hooks on the cladotyles in the present species are somewhat angular and robust, they are not as blunt as those in *A. tortilis* s.s. and the nominal species "*A. polytylus*". Cladotylotes of *A. toxcata* have up to 6 clads on their cladomes.

### *Acarus toxcata* Boury-Esnault, 1973

*Acarus toxcata* Boury-Esnault, 1973: 285, fig. 44.

Material: 2 Microscopic slides MNHN DNBe. 1037 of the holotype from Brazil (08°S 38°W).

Diagnosis (from Boury-Esnault, 1973):

Thinly (0.5-2 mm) incrusting, slightly hispid; size several  $\text{cm}^2$ ; live colour described as maroon.

Ectosome finely detachable. No information on choanosomal structure.

Spicules: Microspined tylotes with barely swollen heads: 213-472 by 3-9  $\mu\text{m}$ .

Styles long, slightly curved, with microspined, but also occasionally smooth heads: 378-727 by 12-16  $\mu\text{m}$ .

Cladotylotes: large ones, lightly spined, cladomes with 4-6 clads: 250-395 by 3-9  $\mu\text{m}$ ; smaller, heavily spined, with 4-6 clads: 56-162 by 3  $\mu\text{m}$ .

Chelae: 12-14  $\mu\text{m}$ .

Toxa: Oxhorn toxa (I) and thin deeply curved (II) grading into one another: 28-265  $\mu\text{m}$ ; accolada toxa (III) extremely long: 500-945  $\mu\text{m}$ .

Distribution: known only from the type locality at 18°09'S 38°30'W off the Brazil coast.

Remarks: This species differs clearly from other members of the *A. tortilis* group in spicule size; especially the choanosomal styles, the larger cladotylotes and the accolada toxa exceed those of the other species significantly. With *A. deweerdtae* this species shares the lightly spined larger cladotylotes and the retention of normal accolada toxa; the size of the larger cladotylotes of *A. deweerdtae* comes nearest of all species to that of *A. toxcata*.

### *A. topsenti* Dendy, 1922

For an extensive redescription of this species cf. Hooper, 1986: 90. It stands out among all *Acarus* by the growth form, which is ramose, with a relatively smooth surface. The consistency is tough, like that of species of the *innominatus*-group. The spiculation, however, is more similar to that of the *tortilis*-group and the

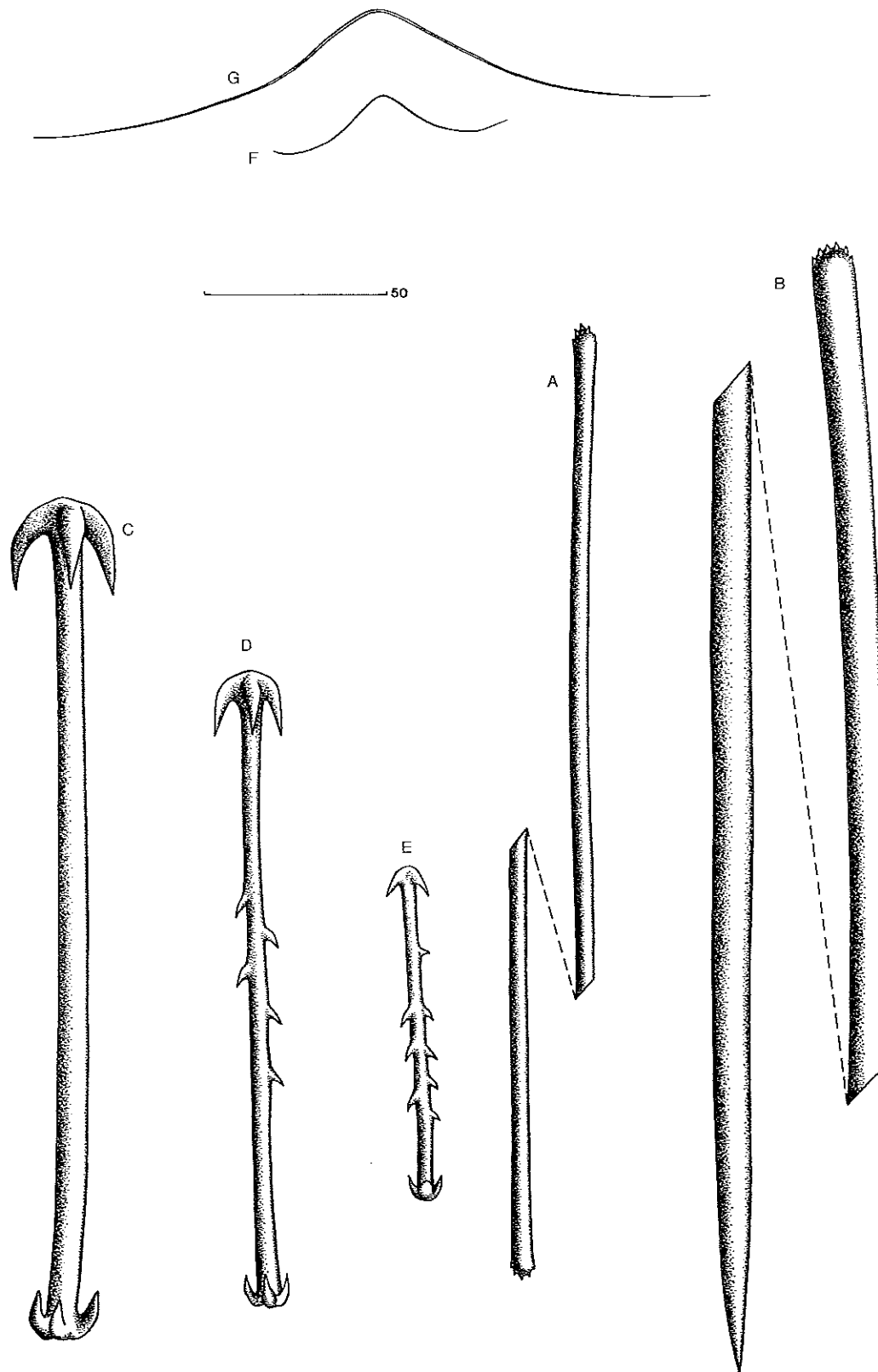


Fig. 3. *Acarus deweerdtiae* n.sp., spicules drawn from a slide made from the holotype, ZMA POR. 8761, A. tylote, B. style, C. cladotylote I, D. cladotylote II, E. cladotylote III, F. toxa II, G. toxa III.

Table 2. Spicule categories and sizes of species of the *tortilis*-group (*Acarnus* species with microspined style heads, but without acanthostyles); including the paraphyletic *A. topsenti*.

Species	tylotes	styles	clado-tylote I	clad no.	clado-tylote II	chelae	toxa I	toxa II	toxa III
<i>tortilis</i> (holotype Banyuls)	380 /5	550 /10	200 /5-6	4-5	100 /3.5-5	15	20-150		600 (straight)
<i>tortilis</i> (MNHN Naples)	260 /4-5	470 /13	150-170 /5	-	90 /3	18	up to 150		present (straight)
<i>tortilis</i> ( <i>polytylus</i> P.F.)	240-350 /4-5	290-430 /11-14	110-170 /4.5-7	-	55-84 /2-3.5	18-20	46-180		up to 600 (straight)
<i>tortilis</i> (Atlantic Spain)	183-240 /3-4	282-345 /7-10	129-138 /3	4	78-91 /1-2	15-18	36-120		120-195 (straight)
<i>tortilis</i> (Azores, MNHN DT. 998)	330-440 /5	400-500 /8-10	125-170 /4-5	4-5	110 /5	15-17	up to 200		220 (straight)
<i>tortilis</i> (Cape Verde, MNHN DT. 1203)	290/5 /9/-	390-420 /-	170 /-	-	90 /-	?	90		250-420 (straight)
<i>tortilis</i> (Cape Verde, ZMA 7617)	235-268 /4	295-345 /5-11	122-174 /3-5	4-5	61-94 /1	11	30-122		211-404 (straight)
<i>bergquistae</i> (holotype)	222-360 /3-4	210-330 /9-16	151-212 /5	3-4	58-109 /3	11-13	40-265		absent
<i>bergquistae</i> (paratype)	180-190 /3	197-220 /7-11	118-160 /5	3(-4)	80-120 /3	16-18	30-260		absent
<i>bergquistae</i> (Vac. Vass. & Lévi)	250-350 /3.5-6	300-450 /5-10	up to 225 /up to 5	3?	down to 65 /down to 2.5	8-10	60-80	15-160	?absent
<i>toxata</i> (holotype)	213-472 /3-9	378-727 /12-16	250-395 /3-9	4-6	56-162 /3	12-14	28-265		500-945 (acco.)
<i>deweerdtae</i> (holotype)	350 /3	400 /6	109-265 (2 cat.) /5-8	3	67-86 /1-2	15	40-180		235 (acco.)
<i>deweerdtae</i> (paratypes series)	290-350 /3-5	400-566 /4-6	105-279 (2 cat.) /5-8	3	67-86 /1-2	12-19	40-180		160-400 (acco.)
<i>topsenti</i> (holotype)	220 /3	220-250 /7	absent	4-5	60-110 /4	11	50-200		absent

*souriei*-group. There is only one size category of (small?) spined cladotylotes which profusely echinate the skeletal spongin fibres which are arranged in a plumoreticulate way. The toxa I and II categories intergrade, whereas the toxa III category appears to be absent. Burton's (1959) record needs verification, because he did not provide a description.

Distribution: Western Indian Ocean.

### 3. "SOURIEI" SPECIES GROUP.

*Acarnus souriei* s.l.

This "species" shares the possession of acanthostyles with *A. bicladotylota*, *A. peruanus* n.sp.

(cf. below), *A. tener*, *A. radovani*, *A. levii* and *A. primigenius*. However, this character is a suspect synapomorphy, since it occurs in many genera and families of the Poecilosclerida and in the related Raspailiids. It is likely that ancestral *Acarnus* possessed acanthostyles, which were subsequently lost in many representatives. Possibly, the acanthostyles of all but one species of *Acarnus* are modified from an ancestral type, because they display an unusually fine dense spination in all but *A. primigenius*, a species which stands out among the other members of the genus by its peculiar cladotylotes and reduced spiculation. The densely spined acanthostyles might be considered a synapomorphy



for most of the *souriei*-group sensu Hooper, 1986 (nominal genus *Acanthacarnus* Lévi, 1952). The choanosomal styles of many species of the *souriei*-group (exceptions are *A. peruanus* n.sp., *A. bicladotylota* and *A. levii*) share a more heavily spined ("rugose") head.

Mediterranean *A. levii* was synonymized with *A. souriei* by Vacelet (1961), but in view of the differences in spicule sizes and categories this seems unjustified. *A. souriei* was originally described from West Africa and subsequently reported from the West Indies, and the Indian Ocean. It will be demonstrated below that the West Indian form differs rather significantly from the West African populations, and that the Indian Ocean form is similar to *A. bicladotylota*. Whether or not *A. tener* and *A. bicladotylota* are synonymous (Hiemstra & Hooper, 1991) is left here undecided, because the type specimens of these species could not be found (Dr Y. Watanabe (Tokyo), *in litteris*). However, acanthostyle-bearing *Acanus* specimens with single and those with the usual two categories of cladotylotes are both known to occur elsewhere in the Indo-Pacific. As with the other wide-spread "species" it is proposed here to consider the regional forms of "*souriei*" as separate related species.

#### ***Acanus souriei* (Lévi, 1952) s.s.**

Fig. 4

*Acanthacarnus souriei* Lévi, 1952: 54, fig. 19; Lévi, 1959: 132.

Not: Vacelet, 1961 (= *A. levii*); Hechtel, 1965 & Van Soest, 1984 (= *A. nicoleae* n.sp.); Thomas, 1970, 1973 (= *A. bicladotylota*).

Material: Microscopic slide of the holotype from Senegal: DCL. 1259; microscopic slide of the Calypso specimen from Principe and St Anna Island (Gulf of Guinea): DCL. 1352. ZMA POR. 6962, 7031, 7038, 7079, 7082, 7096, 7142, 7238, 7357: all specimens from Cancap 7 Exped. to the Cape Verde Islands, 1-30 m, coll. R.W.M. van Soest.

#### Diagnosis:

Thinly (<1 cm, mostly ca. 2 mm) incrusting; lateral size indefinite (holotype: 3 cm<sup>2</sup>).

Surface irregular. Consistency soft.

Colour: red.

Ectosome: some tangential tyloles.

Choanosome: plumose tracts of styles rising up from a basal plate of spongin, echinated by acanthostyles (at the base) and cladotylotes.

Spicules: Microspined tyloles (Fig. 4A), with clearly swollen heads: 230-310 by 3-5 µm.

Styles (Fig. 4B), curved, sometimes slightly flexuous, with rugose heads: 160-350 by 4-9 µm.

Acanthostyles (Fig. 4C): in two size categories, larger (I): 100-165 by 4-6 µm, and smaller (II): 63-90 by 2-3 µm. Acanthostyle lengths of individual specimens are listed in table 3.

Cladotylotes (Fig. 4D), heavily spined (spines on the shaft number 11-15-20), only the ?larger ones present, with 4-cladad cladome: 80-200 by 4-6 µm. Cladotylote lengths of individual specimens are listed in table 3.

Chelae: 12-20 µm.

Toxa: Oxhorn toxa (I) (Fig. 4E): 30-78; thin deeply curved (II) (Fig. 4F): 50-150 µm; accolada-toxa (III) (Fig. 4G), relatively straight (like those of *tortilis* barely recurved, but unlike those with distinct sharp-angled curve): 160-200 µm.

Distribution: Senegal, Cape Verde Islands, Gulf of Guinea, 0.2-25 m.

Remarks: Lévi's (1952) description of the type specimen is inadequate, as he did not mention the diversity in three toxa categories. *A. souriei* s.s. differs from almost all other described *Acanus* in the absence of the smaller cladotylote category and the presence of two size categories of acanthostyles, instead of a single one. These characters are possibly shared with *A. radovani*, since this species has a large range of acanthostyles (81-141 µm) and only large cladotylotes have been found. However, the scanty material of the latter species contained in the microscopic slides studied did not permit a definite conclusion. To facilitate comparison a brief diagnosis of *A. radovani* is presented below. The single cladotylote category is also shared with *A. tener* (for a brief diagnosis see below) and with *A. primigenius* (see Hiemstra & Hooper, 1991), but these have only a single category of

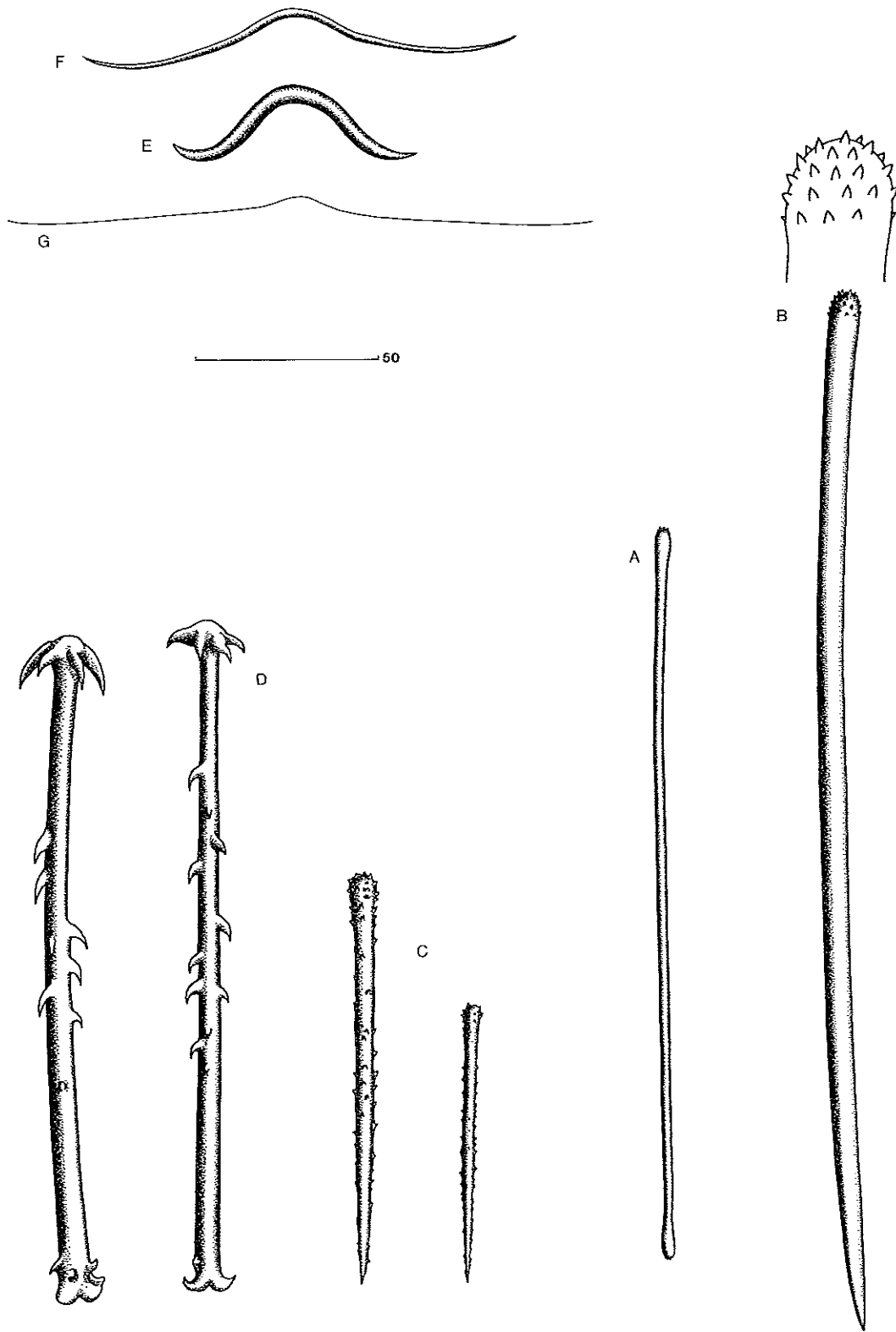


Fig. 4. *Acarnus soureii* Lévi, 1952, spicules drawn from the holotype slide MNHN DCI. 1259, A. tylote, B. style, C. acanthostyles I and II, D. cladotylote I, E. toxa I, F. toxa II, G. toxa III.

Table 3. Acanthostyle and cladotylote lengths of individual specimens of *Acarus soureii*:

Acanthostyle I	Acanthostyle II	Cladotylote
100-135	67-87	160-200
100-165	67-80	120-180
100-105	75-80	105-160
115-120	75-80	130-140
100-105	75-80	80-120
100-120	63-75	150-170
130-160	75-80	120-140
100-130	63-75	100-150
115-120	63-75	130-150
115-120	75-80	150-170
100-150	70-90	140-160
110-130	60-78	120-140

acanthostyles in addition to other apomorphies.

Most specimens of *A. soureii* we examined are very thin incrustations (<2mm), but Lévi's holotype (not examined) apparently was 1 cm in thickness and 3 cm<sup>2</sup> in lateral expansion.

Vacelet (1961) synonymized *A. levii* Vacelet, 1960 with *A. soureii*, but in view of its possession of two categories of cladotylotes, generally more robust and longer spicule sizes, and other details this is incorrect, cf. below.

***Acarus levii* (Vacelet, 1960)**  
(Plate 1 Fig. 4)

*Acanthacarus levii* Vacelet, 1960: 267, fig. 5  
*Acanthacarus soureii* sensu Vacelet, 1961: 42

Material: Holotype fragment from "Président Théodore Tissier" cruise station K.204, E. of Cap Corse, Mediterranean; microscopic slides of specimens collected by the "Antedon" cruises stats. 1657, 1671, 1695, near Bonifacio, Corsica, Mediterranean.

Diagnosis (mostly from Vacelet, 1960, 1961): Thinly incrusting to massive, up to 1.5 cm thick and 6 by 4.5 cm in lateral expansion.

Surface irregular, no apparent oscules. Consistency soft.

Colour: bright red to maroon-red.

Ectosome: difficult to peel off, charged with tangential tylotes.

Choanosome: plumose fibres consisting of styles bound by some spongin, echinated by acanthostyles and cladotylotes.

Spicules: Microspined tylotes with only slightly swollen heads: 260-460 by 3-4.5 µm.

Styles, curved, heads with relatively few clearly visible spines, not rugose as in *A. soureii*: 315-480 by 6-9 µm.

Acanthostyles with shaft extremities heavily and finely spined, in a single category: 55-115 by 3-5 µm.

Cladotylotes: large ones with relatively few spines on the shaft (0-11), expanded basal part of the shaft, 4-claded cladomes: 180-210 by 4.5-6 µm; small ones, similar to the large ones, but more heavily spined: 100-140 by 2-4 µm (the third "reduced" cladotylotes pictured by Vacelet, 1960, are thinner growth stages of the large cladotylote category).

Isochelae: 13-16 µm.

Toxa: oxhorn toxa (I) grading into thin deeply curved (II) toxa: 20-140 µm by 0.5-3 µm; accolada toxa (III) not found; Vacelet records thin very evenly and shallowly curved toxa of 75-195 by 1.5 µm, but the only comparable forms found in his slides were thin growth stages of the choanosomal styles and these may be equivalent to Vacelet's "toxa".

Distribution: Western Mediterranean (Corsica), 47-55 m.

Remarks: From *A. soureii* s.s. and *A. radovani* this species differs in having two cladotylote categories, distinctly longer tylotes and styles, microspined but not rugose choanosomal style heads, integrading toxa I and II categories, and the absence of clear toxa III. The latter character, as well as the megasclere sizes, also differentiates it from the Caribbean *A. nicoleae* (see below). The distinctness of *A. levii* from *A. soureii* is also enhanced by the considerable geographic gap between the areas from where both have been reported: Corsica and West Africa. Extensive investigations off the coast of Mauritania (Van Soest, unpublished data) did not yield any *Acarus* specimens; Cruz' record (personal communication) of *A. soureii* from the Canary Islands remains unconfirmed by any extant specimens.

*A. levii* shares the expanded basal part of the cladotylote shaft with *A. bicladotylota* and *A. peruanus* n.sp.; from the former it differs in the reduced spination of cladotylote I, from the latter in the decidedly plumose skeletal architecture against the plumoreticulate structure of *A. peruanus* n.sp.

***Acarnus radovani*** (Boury-Esnault, 1973)

*Acanthacarnus radovani* Boury-Esnault, 1973: 284, fig. 43

Material: 2 microscopic slides (MNHN D.NBE 963 i-ii) of the type specimen, from Brasil, 08°S 34°W.

Diagnosis (mostly after Boury-Esnault, 1973): Incrusting, brown-violet, hispid.

Skeleton not described; spicules in the slides attached to worm tubes in plumose-erect groups.

Spicules: microspined tylotes with barely swollen heads: 350-473 by 3-4  $\mu\text{m}$ .

Styles, with heads varying from microspined to very rugose (they were not differentiated from the echinating acanthostyles in the original description, but Dr Boury-Esnault informed us in a letter that a line mentioning the presence of styles and their size was omitted in the final print of her article): up to 350 by 5-8  $\mu\text{m}$  (measured in the microscopic slides).

Acanthostyles, more heavily spined near the extremities and somewhat less so in the middle part of the shaft: 81-141  $\mu\text{m}$  (Boury-Esnault gives 80-213 by 3-9  $\mu\text{m}$ , but we suspect she included some of the smaller choanosomal styles; indeed the two spicule categories seem to grade into each other in this species).

Cladotylotes, only large ones present, heavily spined, with four-claded cladome: 172-218 by 4-6  $\mu\text{m}$ .

Chelae: 18-22  $\mu\text{m}$

Toxa: Oxhorn toxa (I): 77-104 by 3-6  $\mu\text{m}$ ; thin deeply curved (II): 50-204  $\mu\text{m}$ ; accolada (III), with rather straight wings: 150-309  $\mu\text{m}$ .

Distribution: known only from the type locality off the Brazilian coast at 08°23'S 34°42'W.

Remarks: as remarked above, this species is

more similar in spiculation to *A. souriei* s.s. from West Africa than to "*souriei*" specimens reported from the West Indies or from the Indian Ocean. However, spicule sizes of the Brazil specimens generally exceed those of the West African specimens, especially the tylotes which also display only barely swollen heads whereas those of *A. souriei* are clearly swollen. The grading of choanosomal styles into echinating acanthostyles is also peculiar to the Brazil specimen. The oxhorn toxa are clearly larger than in *A. souriei*, but in view of the similarity between that spicule category and the thickest spicules of toxa II, that difference is of dubious value.

***Acarnus nicoleae*** n.sp.

*Acarnus souriei* sensu Hechtel, 1965: 40; Van Soest, 1984: 63, fig. 23; Hofman & Kielman (in the press).

Not: *Acarnus souriei* Lévi, 1952, 1959; Vacelet, 1961; Thomas, 1973.

Material: Holotype ZMA POR. 8768, El Morro, Colombia, coll. M. Kielman & C. Hofman,

Paratypes: ZMA POR. 8768, El Morro, Colombia, coll. M. Kielman & C. Hofman. Paratypes: ZMA POR. from Curaçao (POR. 3327, 3677, 8763), Bonaire (8548), North East Colombia (POR. 6460) Barbados (POR. 3830).

Diagnosis:

Thinly incrusting dead corals, and also excavating these to a shallow depth (see Hofman & Kielman, in the press). Surface irregular but smooth. Oscules not apparent.

Size indefinite. Consistency soft.

Colour: red.

Ectosome: tangential tylotes.

Choanosome: little spongin, but echinated plumose tracts are nevertheless formed, rising up from the substrate; also echinating spicules are singly erect on the substrate.

Spicules: Microspined tylotes with well developed heads: 119-380 by 3-7  $\mu\text{m}$ .

Styles with rugose heads: 240-381 by 5-7  $\mu\text{m}$ .

Table 4. Acanthostyle lengths of individual specimens of *Acanthus nicoleae* n.sp.

80-115
60-110
60-70
55-70
70-90
75-87
63-77
77-110
70-90
68-104
55-63

Acanthostyles in a single category: 55-115 by 1-5  $\mu\text{m}$ . Acanthostyle lengths of individual specimens are listed in table 4.

Cladotylotes: large ones, heavily spined, with 4-5 clads: 140-205 by 3-5  $\mu\text{m}$ ; small ones, heavily spined, with 4-5 clads, often rare: 70-117 by 1-2  $\mu\text{m}$ .

Chelae: 14-21.

Toxa: Oxhorn toxa (I) small: 50-90 by 2-4  $\mu\text{m}$ ; thin deeply curved (II): 40-300  $\mu\text{m}$ ; accolada toxa (III) with almost straight, barely recurved wings: 140-330  $\mu\text{m}$ .

Distribution: West Indian region.

Etymology: named after Dr Nicole Boury Esnault, in recognition of her original contributions to sponge biology.

Remarks: This species differs from other Atlantic members of the *souriei*-group in the retention of two sizes of cladotylotes, and the relatively small upper size of the acanthostyles. It is similar to Mediterranean *A. levii*, but that species has clearly larger styles (390-480 by 6-9  $\mu\text{m}$ ) and larger small cladotylotes (100-140 by 3.5-4  $\mu\text{m}$ ); also the accolada toxa seem to be absent in that species. *A. bicladotylota* is also similar, but it has a characteristic distal thickening of the cladotylote shaft and irregularly spined cladotyles. The excavating behaviour has not been reported for other *Acanthus* species.

#### *Acanthus bicladotylota* (Hoshino, 1981)

*Acanthacarnus souriei*; Thomas, 1973: 46, figs. 1, 2a-h.

*Acanthacarnus bicladotylota* Hoshino, 1981: 142, text fig. 60, pl. 6 fig. 4.

Material: ZMA POR. 315, 316 and 317, all from Indonesia, Siboga Exped. stat. 81 (Pulu Sebangkatan, Borneobank, 02°S 117°E) and 225 (Lucipara Islands, Banda Sea, 05°S 127°E) (variously labeled *A. tortilis* and *A. topsenti*; microscopic slide MNHN DT. 1739 from the Maldive Islands (labeled *A. spec.*).

Diagnosis:

Incrusting, often agglutinating calcareous debris or barnacles. Surface covered with foreign material, hispid; no apparent oscules.

Colour: red-orange (Hoshino), blood-red (Thomas).

Ectosome: feltwork of tangential tyloles.

Choanosome: plumose bundles of styles echinated by acanthostyles and cladotylotes rise up from a basal plate of spongin, which is echinated by single acanthostyles.

Spicules: Microspined tyloles with distinct heads: 143-404 by 3-6  $\mu\text{m}$ .

Styles: normally rugose, but occasionally almost smooth: 195-460 by 4-12  $\mu\text{m}$ .

Acanthostyles: slim, finely spined, often with flattened head: 70-127 by 1.5-5  $\mu\text{m}$ .

Cladotylotes: larger ones with characteristic thickening of the distal half of the shaft and frequently irregularly spined cladotyle, with four-clad cladome: 140-210 by 3-7  $\mu\text{m}$  (Thomas gives 80-187  $\mu\text{m}$ ); smaller cladotylotes similar to the large ones: 38-110 by 0.5-6  $\mu\text{m}$ .

Chelae: 14-20  $\mu\text{m}$ .

Toxa: Oxhorn toxa (I): 48-75  $\mu\text{m}$ ; thin deeply curved (II): 30-212  $\mu\text{m}$ ; accolada (III) with recurved wings: 150-250  $\mu\text{m}$ .

Distribution: Indo-West Pacific (Japan, Indonesia, Maldives, Seychelles).

Remarks: The thickened almost conical distal part of the cladotylotes (which is also pictured by Hoshino) and the retention of the microspined condition of the choanosomal style heads is shared with *A. levii* and *A. peruanus* n.sp., but the species differs from these in the frequent thoroughly irregular cladotyles (also mentioned by Hoshino) and the more or less uniform spination of the cladotylote I category (reduced spination in *A. levii* and *A. peruanus* n.sp.).

**Acarnus tener** Tanita, 1956

*Acarnus tenerus* Tanita, 1956: 123, fig. 2, pl. 4 fig. 2.

Material: Microscopic slide MNHN DT. 1890 (Gambier Isl., labeled *Acarnus* spec.); 2 microscopic slides MNHN DT. 2590 (labeled *Acarnus* spec. from unknown origin, but taken from *Tridacna*, which points to Indo West-Pacific origin).

Diagnosis (largely from Tanita):

Massive, up to 2 cm thick and 5 by 4 in lateral expansion (based on Tanita's 3 specimens). Surface rough owing to the presence of ingrown algae; oscules inconspicuous. Consistency soft.

Colour: dull reddish brown (formalin).

Ectosome: tangential tyloles.

Choanosome: plumose multispicular fibres running at right angles to the surface, echinated densely by cladotylotes and acanthostyles.

Spicules: Microspined tyloles with well-developed heads: 180-330 by 2.5-5  $\mu\text{m}$ .

Styles: "minutely and sparingly" spined at the base (Tanita), rugose in the MNHN slides: 260-340 by 8-10  $\mu\text{m}$ .

Acanthostyles: covered with small spines: 70-130 by 4-6  $\mu\text{m}$ .

Cladotylotes: only large ones (both Tanita's specimens and the MNHN slides), with four-cladomed cladome, and irregularly spined type: 130-190 by 5-6  $\mu\text{m}$ .

Chelae: 12-18  $\mu\text{m}$ .

Toxa: Oxhorn toxa (I) and thin deeply curved (II) grading into one another: 70-110  $\mu\text{m}$ ; accolada toxa (III) (not mentioned by Tanita): 160-230  $\mu\text{m}$ .

Distribution: Japan, Central Pacific (Gambier Isl.).

Remarks: The distinctness of *A. tener* is based primarily on the absence of the smaller cladotylotes, which is common to all above mentioned specimens. Apart from the apparent absence of accolada toxa the MNHN slides fit in well with Tanita's description, so we assume that they have been overlooked. The loss of the small cladotylotes is shared with *A. souriei* and *A. radovani*; in contrast to *A. souriei* the present

species and *A. radovani* have a limited size range of the cladotylotes, but this may be simply a reflection of the number of studied specimens.

**Acarnus peruanus** n.sp.

Fig. 5, Plate 1 Fig. 5

Material: Holotype U.S.N.M. 23264, (Islas Lobos de Afuera, North Peru, 07°S 80°W, on wave washed rocks, (unpublished material, id. as "*A. topsenti* by De Laubenfels) (fragment and microscopic slide in ZMA).

Diagnosis:

Massive mat of "several sq ft." in lateral expansion, up to 2 cm thick. Surface hispid, irregular, shaggy. No apparent oscules in preserved specimen, which is fragmented.

Consistency toughly spongy, resilient.

Colour: brown in spirit.

Ectosome: tangential single tyloles.

Choanosome: plumoreticulate skeleton with primary tracts of styles, 2-5 in cross section, and interconnecting styles, singly or in pairs; no visible spongin; cladotylotes and occasional acanthostyles echinating the primary tracts. Distance of primary tracts 330-370  $\mu\text{m}$ , of interconnecting spicules 250-350  $\mu\text{m}$ .

Spicules: microspined tyloles (Fig. 5A) with elongate heads: 211-282 by 3-4  $\mu\text{m}$ .

Choanosomal styles (Fig. 5B), with microspined heads (not rugose): 244-371 by 9-12  $\mu\text{m}$ .

Acanthostyles (Fig. 5C): finely spined, relatively rare: 82-97 by 4  $\mu\text{m}$ .

Cladotylotes: large ones (I) (Fig. 5D), with thickened basal shaft, showing reduced spination (2-11 spines): 121-141 by 4-5  $\mu\text{m}$ , small ones (II) (Fig. 5E): 66-75 by 3  $\mu\text{m}$ .

Chelae: 13-17  $\mu\text{m}$ .

Toxa: oxhorn (I), apparently absent; thin deeply curved (II), rare: 35-40  $\mu\text{m}$ ; accolada (III) (Fig. 5F), with median sharp-angled curve, but straight wings: 188-211 by 0.5  $\mu\text{m}$ .

Distribution: known only from the type locality: islands on the continental platform off the coast of North Peru, at the edge of the East

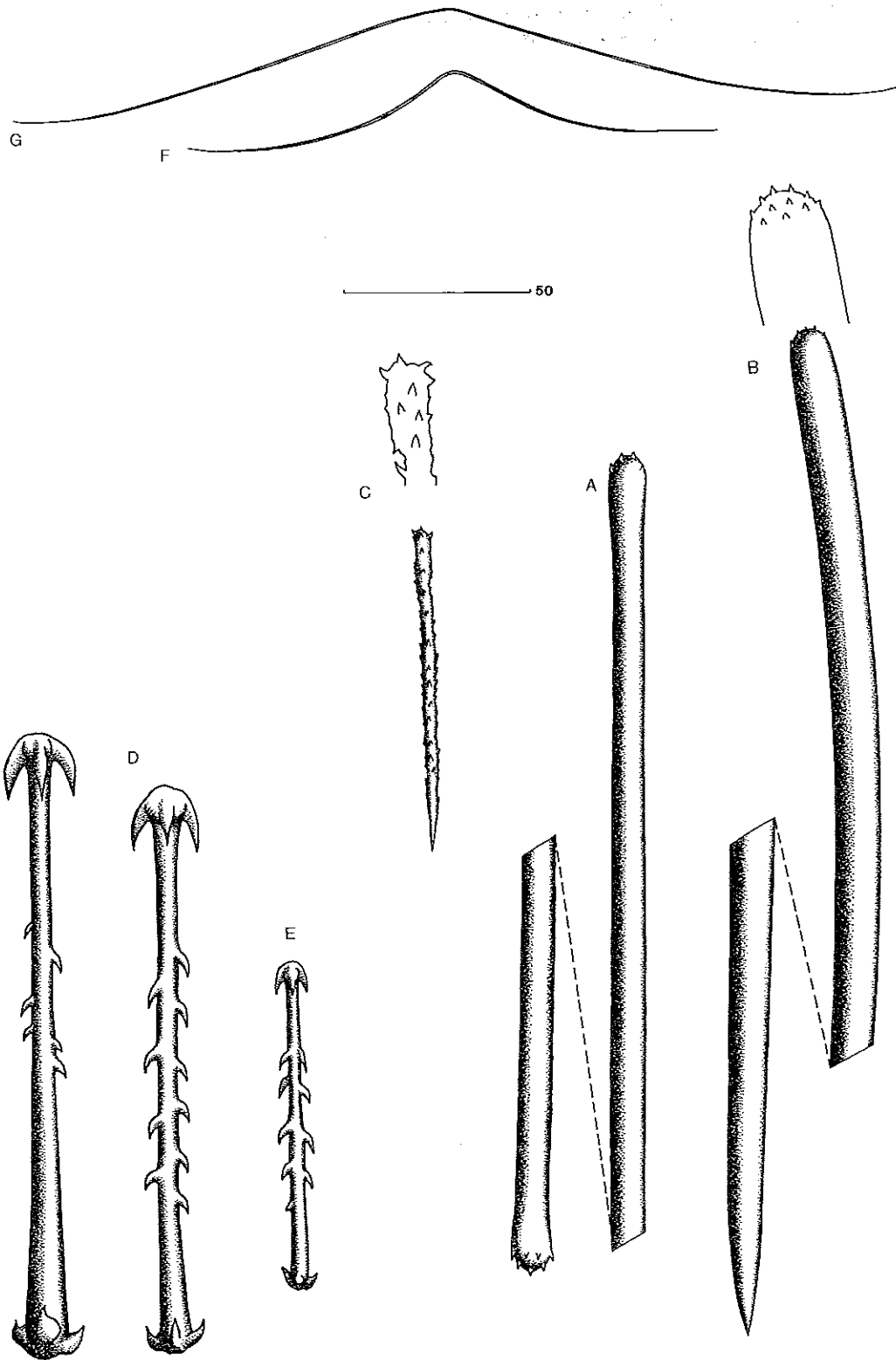


Fig. 5. *Acarnus peruanus* n.sp., spicules drawn from a slide made of the holotype USNM 23264, A. tylote, B. style, C. acanthostyle, D. cladotylote I, E. cladotylote II, F. toxa II, G. toxa III.

Table 5. Spicule categories and sizes of species of the *souriei*-group (*Acanus* species with acanthostyles), including the paraphyletic *A. primigenius*.

Species	tylotes	styles	acantho- style(s)	clado- tylote I	clado- tylote II	chelae	toxa I	toxa II	toxa III
<i>souriei</i> (holotype)	210-270 /3	180-230 /3-10	100-165 (I) 67-80 (II)	105-160 /5	absent	14	80	150	190 (acco.)
<i>souriei</i> (Gulf of Guinée)	270-300 /3-5	300-350 /9	100-135 (I) 67-87 (II)	120-180 /4-6	absent	13-15	30	150	? (acco.)
<i>souriei</i> (Cape Verde Isl.)	230-400 /3	160-350 /4-5	100-160 (I) 65-90 (II)	80-160 /4-6	absent	11-14	50-75	50-140	160-200 (acco.)
<i>radovani</i> (holotype)	350-380 /3-4	50 /3-9	95-141 (I) 75-82 (II)	170-220 /4-6	absent	18-22	70-105	50-204	150-310 (acco.)
<i>tener</i> (Tanita's data)	180-320 /2.5-5	260-340 /8-10	80-130 /5-6	130-190	absent	12-14		70-110	?
<i>tener</i> (Gambier Isl.)	300 /4	310 /4	80-100 /4	138-165 /6	absent	18	?	70	160 (acco.)
<i>tener</i> (no locality)	330 /4	300 /7	70-95 /4	130 /6	absent	?	?	present	230 (acco.)
<i>bicladotylota</i> (Hoshino's data)	205-300 /3-6	195-385 /8-12	80-95 /3-5	140-175 /4-7	80-95 /2-6	12	?	60-110	130-210 (?acco.)
<i>bicladotylota</i> ("souriei" sensu Thomas)	143-284 /4	201-282 /4-8	93 /3-5	80-187 /4-6	54-71 /2	14-16	?	81-168	?
<i>bicladotylota</i> (Maldives)	380 /4-5	410 /10	70 /2	210 /5	90 /2	20	?	100	250 (acco.)
<i>bicladotylota</i> (Siboga spec.)	249-404 /4-6	315-460 /5-9	80-120 /1-2.5	155-193 /4-5	38-70 /1-2	15-20	48-75	30-212	150-220 (acco.)
<i>nicoleae</i> (holotype)	300-330 /4	325-350 /6	60-110 /23	180-200 /4-5	80-100 /2	14-18	45-75	60-150	200-235 (acco.)
<i>nicoleae</i> (paratypes)	200-350 /3-4	280-350 /5-7	55-117 /2-3	163-200 /4-5	75-117 /2	14-18	45-90	40-300	150-235 (acco.)
<i>nicoleae</i> (Hechtel's specimens)	119-357 /?	240-381 /3-7	68-104 /3-5	up to 205 /3-5	down to 70 /?	17-21	50	?	330 ?
<i>levii</i> (holotype)	280-410 /3-4.5	390-480 /6-9	100-110 /3-4.5	180-210 /4.5-6	100-140 /3.5-4	15		20-140	absent
<i>levii</i> (Vacclet, 1961)	260-460 /3-4	315-430 /6-9	55-115 /3.5-4.5	180-210 /6	80-140 /2-4	13-16		40-140	absent
<i>peruanus</i> (holotype)	211-282 /3-4	244-371 /9-12	82-97 /4	121-141 /4-5	66-75 /3	13-17	absent	35-40	188-211 (acco.)
<i>primigenius</i> (holotype)	137-184 /2-5	99-240 /4-6	60-68 /5	absent /5	54-67	14-21.5	14-46	absent	absent

Pacific tropical area (from which no other *Acanus* species are known).

Remarks: East Pacific subtropical *A. erithacus* is not known south of Southern California and differs so widely (smooth surface with large oscules, no acanthostyles, a densely spiculate

choanosomal skeleton, cladotylotes with peculiarly lobate cladotyles) that it cannot be mistaken for the present species. This is the only member of the *souriei*-group with a plumoreticulate rather than a plumose choanosomal skeleton, doubtlessly related to the thicker and



more elaborate growth form; also, the style heads are merely microspined rather than rugose, and together with the apparently absent oxborn toxa, this species is a rather deviating member of the group. However, the acanthostyles are fairly typical in their fine and dense spination. The new species shares the microspination of the styles and the thickened basal shaft of the cladotylote I with *A. bicladotylota* and *A. levii*; it shares the reduced shaft spination of cladotylote I with the latter species.

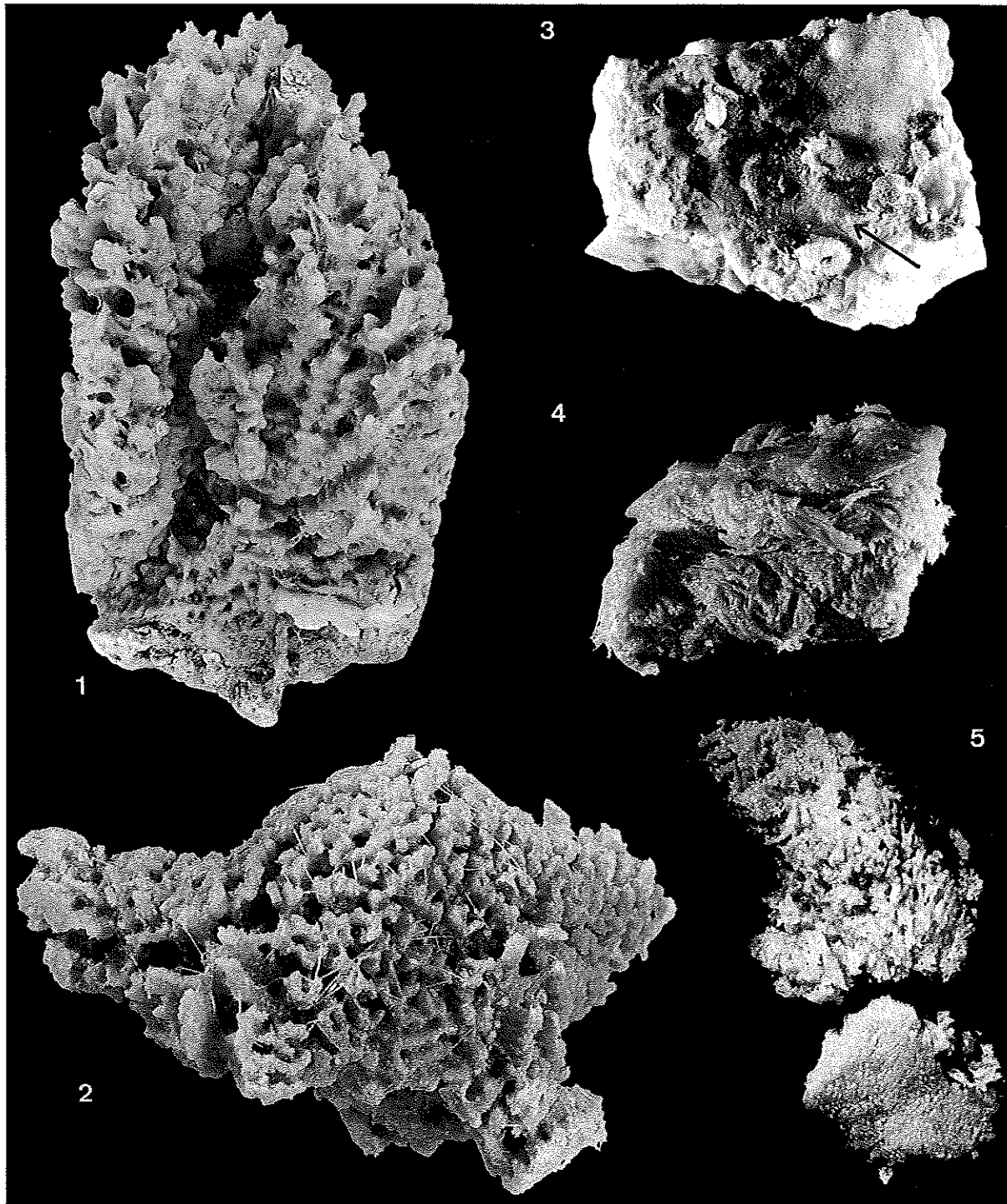
**A. primigenius** Hiemstra & Hooper, 1991.  
This peculiar species stands out from all other *Acarus* by its possession of acanthostyles intergrading into cladotylotes. It is also unique to the genus in having a hymedesmioid growth form with spicules erect on the substrate. The ectosomal spicules are very thin anisotylotes.

KEY TO THE SPECIES OF ACARNUS

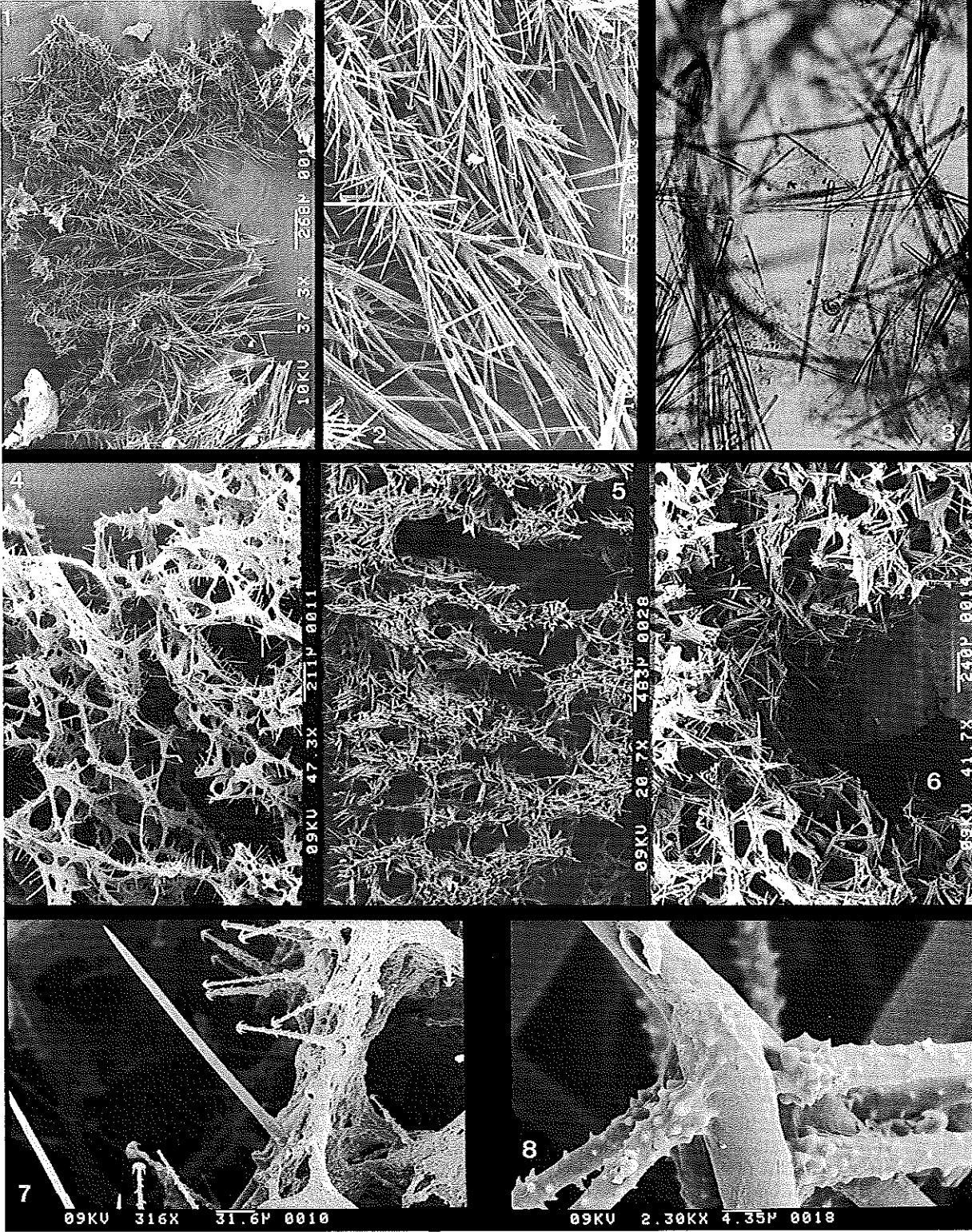
Habit characteristics, skeletal architecture and spicule types mentioned in the keys are illustrated in Plates I-III. Short diagnoses of all keyed-out species are given above.

- 1. -Acanthostyles present ..... 2  
-Acanthostyles absent ..... 9
- 2. -Only a single category of cladotylotes present ..... 3  
-Two categories of cladotylotes ..... 6
- 3. -Cladotylotes small (<70 µm), resembling acanthostyles ..... *primigenius* ..... (see Hiemstra & Hooper, 1991)  
-Cladotylotes >80 µm (mostly over > 130 µm)..... 4
- 4. -Cladotylotes in a large size range may be as small as 80 and as large as 200 µm; acanthostyles in two categories.....*souriei* (see above)  
-Cladotylotes > 130 µm ..... 5
- 5. -Ectosomal tylotes > 350 µm .....*radovani* (see above)  
-Ectosomal tylotes < 330 µm.....*tener* (see above)

- 6. -Distal part of cladotylotes characteristically thickened; choanosomal style heads microspined..... 7  
-Shaft of cladotylotes uniform in thickness; choanosomal style heads rugose and heavily spined.....*nicoleae* (see above)
- 7. -Spines on cladotylote shaft 15-22 (more or less distributed regularly along the shaft); tyles irregularly spined/hooked .....  
.....*bicladotylota* (see above)  
-Spination on cladotylote shaft reduced, only 2-11 spines, concentrated in the middle part; tyles with 4-5 regular hooks ..... 8
- 8. -No oxborn (I) toxa; plumo-reticulate skeleton; majority of the choanosomal styles < 380 µm.....*peruanus* (see above)  
-No accolada (III) toxa; plumose skeleton; majority of the choanosomal styles > 380 µm .....*levii* (see above)
- 9. -Microscleres (toxa, chelae) absent.....  
.....*tenuis* (see Hiemstra & Hooper, 1991)  
-Microscleres present..... 10
- 10. -Large cladotylotes with spined tyles .. 11  
-Large cladotylotes with smooth, rounded, flattened or lobate tyles ..... 15
- 11. -Only a single category of cladotylotes present (small); growth form is ramose ...  
.....*topsentii* (see Hooper, 1986)  
-Two or more categories of cladotylotes; growth form incrusting or massive ..... 12
- 12. -Toxa III extremely long (up to 900 µm) .....  
.....*toxata* (see above)  
-Toxa III, if present, 300-600 µm ..... 13
- 13. -Three size categories of cladotylotes; shaft of largest is lightly spined and often entirely smooth .....*deweerdtae* (see above)  
-Only two categories of cladotylotes ... 14
- 14. -Toxa III absent; styles only up to 335 µm .....  
.....*bergquistae* (see above)  
-Toxa III present; styles up to 500 µm or more.....*tortilis* (see above)
- 15. -Cladotyles of larger cladotylotes irregularly lobate; tylotes generally shorter than 200 µm ..... 16  
-Cladotyles of larger cladotylotes not irregularly lobate, although they may be slightly and regularly quadrilobate or



PL. I, Habits of *Acarnus* spp., 1. Flabelliform habit of *A. wolffgangi* from Indonesia (ZMA POR. 314) showing irregular clathrate-lumpy surface, 2. Irregularly massive-plate like habit of *A. wolffgangi* from Indonesia (ZMA POR. 8767) with grooved-holed surface, 3. Dead-coral incrusting habit of *A. deweerdae* n.sp. (holotype ZMA POR. 8761), 4. Massive habit of *A. levii* (fragment of holotype "Prés. Th. Tissier" stat. K.204), 5. Massive fragments of large cake-shaped expansion of *A. peruanus* n.sp. (pieces of holotype USNM 23264).



- flattened..... 17
16. -Cladome of cladotylotes three-claded; a proportion of the choanosomal style heads are microspined .....*claudei* (see above)  
-Cladome four-claded; all styles smooth .....*erithacus* (see De Laubenfels, 1927)
17. -Toxa III modified into thick straight oxeotes with abrupt shallow-angled median area ..... 18  
-Toxa III the usual accolada-type..... 19
18. -A single category of cladotylotes .....  
.....*ternatus* (see Hooper, 1986)  
-Two categories of cladotylotes..*wolffgangi* (see above)
19. -Cladotylote tyle flattened, asymmetrical or lobate; cladome of cladotylote I three-claded ..... 20  
-Cladotylote tyle of smaller cladotylotes perfectly rounded; cladome of cladotylote I 4-claded .....*innominatus* (see above)
20. -Styles only up to 6  $\mu\text{m}$  in thickness; cladome of cladotylote I about 18 by 12  $\mu\text{m}$  in dimension .....*thielei* (see above)  
-Styles up to 25  $\mu\text{m}$  in thickness; cladome of cladotylote I about 35 by 35  $\mu\text{m}$  in dimension .....*hoshinoi* (see above)

REGIONAL DISTRIBUTION OF ACARNUS SPECIES:

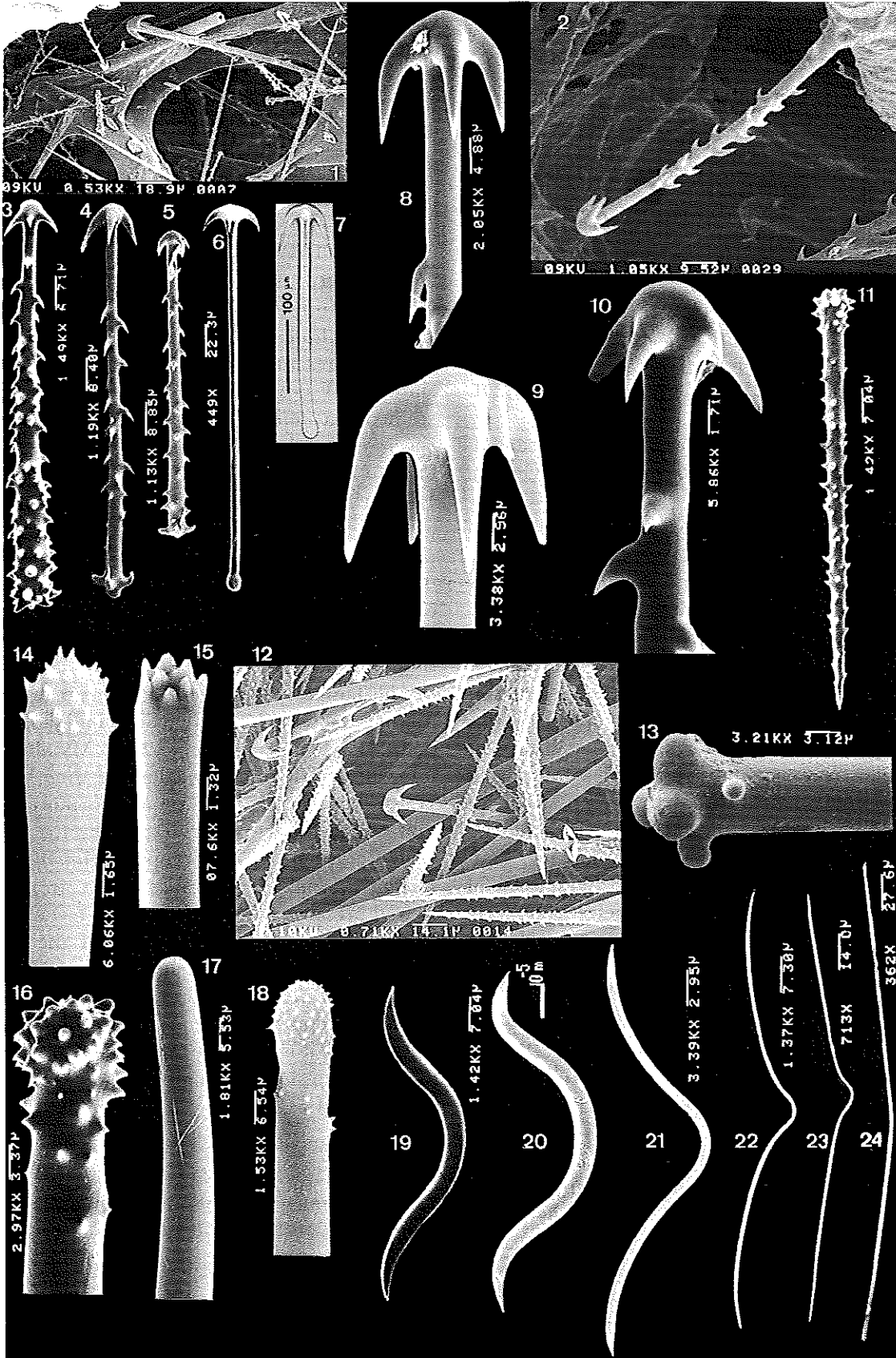
The regional forms of *Acarnus*, here described as discrete species, are distributed over the various shallow-water hard-substrate biogeographic regions of the world oceans. To facilitate quick local identification of *Acarnus* a review of the species occurring in these regions is presented: Mediterranean-Atlantic region (British Isles to Morocco, Azores to Eastern Mediterranean): *Acarnus levii* (acanthostyles,) and *A. tortilis* (no acanthostyles). West Africa (Morocco to Angola): *A. souriei* (acanthostyles, single

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PI.II, Skeletal architecture of *Acarnus* spp. (all photos made by SEM, unless indicated otherwise), 1. Plumose skeletal columns of *A. souriei* (made from a Cape Verde Islands specimen), 2. Detail of 1, 3. Plumoreticulate architecture of *A. peruanus* n.sp. (light microscope) (from holotype USNM 23264), 4. Plumoreticulate architecture with high spongin content of *A. topsenti* (made from one of the syntypes, BMNH 1921: 11: 7: 84), 5. Plumoreticulate architecture with high spicule content of *A. erithacus* (made from the holotype USNM 21430), 6. Renieroid architecture of *A. wolffgangi* (made from ZMA POR. 314), 7. Detail of skeleton of *A. topsenti* (made from one of the syntypes, BMNH 1921: 11: 7: 84) to show echinating cladotylotes, 8. Detail of skeleton of *A. souriei* (made from a Cape Verde Islands specimen) to show echinating acanthostyles.

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PI.III, Spicules of *Acarnus* spp. (all photos made by SEM unless otherwise indicated), 1. small and large cladotylote as well as acanthostyles of *A. bicladotylota* (made from ZMA POR. 315), 2. small cladotylote of *A. erithacus* in echinating position (made from holotype USNM 21430), 3. cladotylote of *A. primigenius*; note its resemblance to acanthostyle (made from the holotype, ZMA POR. 7693), 4. small cladotylote of *A. erithacus* (made from ZMA POR. 8799), 5. small cladotylote of *A. bicladotylota* (ZMA POR. 315), 6. cladotylote of *A. ternatus* (made from NTM Z. 1584), 7. cladotylote I from *A. wolffgangi* (light microscope, from ZMA POR. 314), 8. Detail of 3-claded cladome of *A. deweerdtiae* (from holotype ZMA POR. 8761), 9. Detail of 4-claded cladome of *A. innominatus* (from ZMA POR. 309), 10. Detail of 4-5 claded cladome of *A. primigenius* (from holotype ZMA POR. 7693), 11. Acanthostyle of *A. primigenius* (from holotype), 12. Larger and smaller acanthostyles of *A. souriei* (from a Cape Verde Islands specimen), 13. Lobate tyle of cladotylote I of *A. erithacus* (from ZMA POR. 8799), 14. Tylote head of *A. souriei* (from Cape Verde Islands specimen), 15. Tylote head of *A. topsenti* (from one of the syntypes BMNH 1921: 11: 7: 84), 16. Style head of *A. primigenius* (from the holotype), 17. Style head from *A. hoshinoi* n.sp. (from the holotype NTM Z. 2234), 18. Style head of *A. souriei* (from a Cape Verde Islands specimen), 19. Oxhorn toxa (I) of *A. souriei* (from a Cape Verde Islands specimen), 20. Oxhorn (I) toxa of *A. innominatus* (from ZMA POR. 309), 21. Thin deeply curved toxa (II) of *A. hoshinoi* n.sp. (from the holotype), 22. Accolada toxa (III) of *A. erithacus* (from ZMA POR. 8799), 23. Accolada toxa (III) of *A. souriei* (from Cape Verde Islands specimen), 24. Toxa III of *A. ternatus* (from NTM Z. 1584).



category of cladotylotes), and *A. tortilis* (no acanthostyles, two categories of cladotylotes). Carribbean (Florida to Trinidad): *A. nicoleae* (acanthostyles), *A. deweerdtiae* (no acanthostyles, spined tyles on cladotylotes, which occur in three categories), *A. innominatus* (no acanthostyles, cladotylote tyles smooth and round; rare small cladotylotes).

Brazil (Amazon mouth to Rio de Janeiro): *A. radovani* (acanthostyles), *A. toxata* (no acanthostyles, huge toxa III).

East Pacific (California to Peru): *A. peruanus* (acanthostyles), *A. erithacus* (no acanthostyles, lobate cladotylotes).

South Australia (Freemantle to Brisbane): *A. tenuis*.

Indo-Pacific (Japan to Brisbane and Freemantle, Red Sea and Cape Town to Central Pacific):

*A. bicladotylota* (acanthostyles, two categories of cladotylotes), *A. tener* (acanthostyles, only large cladotylotes), *A. primigenius* (acanthostyles, only small cladotylotes which resemble acanthostyles), *A. topsenti* (no acanthostyles, cladotylote tyles spined, only small cladotylotes present, habit ramose), *A. bergquistae* (no acanthostyles, cladotylote tyles spined, two categories of cladotylotes, habit incrusting), *A. hoshinoi* (no acanthostyles, tyles of larger cladotylotes smooth and rounded, shaft of cladotylotes generally smooth), *A. thielei* (no acanthostyles, cladotyles quadrilobate, shaft smooth), *A. claudeni* (no acanthostyles, tyles of larger cladotylotes smooth, but irregularly lobate, shaft of larger cladotylotes smooth), *A. wolffgangi* (no acanthostyles, tyles of larger cladotylotes rounded elongately and their shaft smooth, tyles of smaller cladotylotes irregular and shaft spined, habit irregularly and thickly fan-shaped), *A. ternatus* (no acanthostyles, tyles of cladotylotes rounded and smooth, cladotylotes in a single category).

*Acarnus* occurs normally in tropical and subtropical shallow-water habitats around the world, but is absent (or not recorded as yet) in the following areas: Mediterranean east of Greece, Hawaii Islands; the occurrence in New Zealand is limited to the Eocene/Oligocene

(Hinde & Holmes, 1891). One species, viz. *A. erithacus*, penetrates into boreal waters as far north as Alaska.

## PHYLOGENETIC ANALYSIS

Hooper (1986) made a cladistic analysis of *Acarnus*, which was emended in Hiemstra & Hooper (1991), because of the discovery of new material. That emended classification was subsequently used in a preliminary area-cladistic study involving four sponge genera including *Acarnus* (Van Soest, in the press).

In the present study we have reexamined the status of all described species and records and studied an almost comprehensive series of specimens and microscopic slides, and it was only to be expected that some emendations of Hooper's original (1986) classification are again necessary. A full character analysis is presented below, using most of Hooper's original characters as well as some new ones, especially those involving the shape and presence of certain toxa categories, and the shape of the cladotylote tyles.

The familial assignment of *Acarnus* remains problematic (Lévi, 1973: Microcionidae, Van Soest (1984) and Hooper (1986): Myxillidae), but will be left undecided for the time being. However, it has become more and more clear that Microcionidae, more especially the genus *Clathria*, are better outgroups of *Acarnus* than certain Myxillidae, because apart from the shared presence of tylotes there are few characters in common with members of the latter family, whereas the diversity of toxa as well as the shape of the megascleres and the chelae are closely similar to those in Microcionidae. In view of this, it is judged unwise to narrow-down the outgroup since no single *Clathria* species can be indicated as a sister group of *Acarnus*.

## LIST OF CHARACTERS AND THEIR DISTRIBUTION OVER THE VARIOUS SPECIES OF ACARNUS:

Based on the studied specimens listed in the Materials section, on above descriptions and on

descriptions in Hooper (1986) and Hiemstra & Hooper (1991), characters (see Plates I-III for illustrations of characters) are discussed and polarities determined using outgroup comparison and ingroup-compatibility. The discussed characters have been subsequently selected for a Wagner-tree analysis using PAUP (version 3.0), and for a manual analysis involving a certain amount of subjective character weighting.

1. *Habit*: Outgroup (*Clathria*) habits include thin crusts, massive, ramose and flabellate forms, so no polarity decision can be made from that. However, most *Acarinus* are flattened masses or crusts of variable thickness. The thicker crusts (Plate 2 Figs. 4-5) are presumed to be the primitive state (1a), with thinner (Plate 2 Fig. 3) growth stages (1b) as the most common derived stage (*A. nicoleae* is thinly incrusting and excavating). Only occasionally more elaborate growth forms occur: flabellate (1c) (*A. wolffgangi*; Plate 2 Figs. 1-2) or ramose (1d) (*A. topsenti*), which are apparently autapomorphies.

2. *Surface characteristics*: Hispid or irregular surfaces are characteristic for most *Clathria* and indeed for most *Acarinus*, too. A fairly smooth surface (2b) characterizes *A. erithacus*, *A. thielei* and *A. claudeni* (with the smooth surfaces of *A. topsenti* and *A. ternatus* as separate autapomorphies), whereas *A. innominatus* and *A. hoshinoi* have characteristic groove-patterns (2c), and *A. wolffgangi* (Plate 2 Figs. 1-2) has irregular lumps and clathrous surface patterns (2d).

3. *Consistency*: This character is related to the development of the skeleton (spicular density) and amount of spongin. Again, outgroup conditions are variable, but in *Acarinus* tough or even hard consistencies are found in *A. ternatus*, *A. topsenti*, *A. erithacus*, *A. innominatus*, *A. hoshinoi*, *A. claudeni*, *A. wolffgangi*. These are all forms which are fairly elaborate and have either plumoreticulate or renieroid skeletons. For the mentioned species tough consistency may be a synapomorphy (3b), the softer conditions (3a) being more common in the outgroup.

4. *Ectosome*: *Clathria* s.s. has ectosomal spicules arranged in paratangential bundles. In *Acarinus* these are almost invariably arranged tangen-

tially, thus the situation in *Acarinus* is probably synapomorphic (4b) for the genus.

5. *Tylote nature of ectosomal spicules*: In *Clathria* the ectosomal spicules are subtylostyles. In most *Acarinus* they are true amphitylotes (5c), but in *A. primigenius* a fair proportion of anisotyloles (5b) are found. The amphitylotes are considered a synapomorphy for all *Acarinus* but *primigenius*.

6. *Spined apices in ectosomal tyloles*: Most *Acarinus*, with the exception of *A. tenuis*, have spined apices (Plate 3 Figs. 14-15) on the tyloles. The ectosomal subtylostyles of *Clathria* very often also have microspined apices. It is assumed that this condition represents the ancestral state, and that the smooth apices in *A. tenuis* constitute an autapomorphy (6b).

7. *Choanosomal skeletal architecture*: in the outgroup all conditions found in the various *Acarinus* species (plumo-reticulate, renieroid, plumose and hymedesmioid) are also found, making a polarity decision difficult. The plumo-reticulate (anisotropic) condition (Plate 2 Figs. 3-5) perhaps represents a general Poccilosclerid condition and as such could be the ancestral condition, but not necessarily the condition found in the outgroup. From the plumo-reticulate condition two apomorphic developments are assumed, one leading to plumose (7b) (*A. souriei* (Plate 2 Figs. 1-2), *A. nicoleae*, *A. radovani*, *A. levii*, *A. bicladotylole*, *A. tener*, *A. tortilis*, *A. texeata*, *A. deweerdtiae*, and *A. bergquistae*), and hymedesmioid (7c) (*A. primigenius*) skeletons and another leading to confused (7d) (*A. tenuis*) or renieroid (7e) skeletons (*A. innominatus*, *A. hoshinoi*, *A. thielei* and *A. wolffgangi* (Plate 2 Fig. 6)). The conditions found in the remaining species, although classed as "plumo-reticulate" (Plate 2 Figs. 3-5) are sufficiently different, to consider possession of such a skeleton as basic, not pointing necessarily to close phylogenetic relationship.

8. *Acanthostyles*: As indicated above, the possession *per se* is shared with the outgroup and indeed with many other Poccilosclerids. The type found in *A. primigenius* (Plate 3 Fig. 11) is a very general one and it is here assumed that it is primitive. However, all other acanthostyle-

bearing *Acarnus* have a rather characteristic type: thin, densely spined all-over with very fine spines (Plate 3 Fig. 1, 12); moreover the heads frequently have a "cut-off" appearance. It is assumed here that these acanthostyles are a synapomorphous condition (8b) for *A. souriei* (in two distinct size categories), *A. radovani*, *A. nicoleae*, *A. bicladotylota*, *A. tener*, *A. levii* and *A. peruanus*. Also the complete loss of any type of acanthostyles maybe considered a synapomorphy (8c) of the remaining *Acarnus* spp., although loss of acanthostyles has occurred frequently in the outgroup also, and there is no logical reason why it could not happen independently in various larger or smaller species groups. The function of the acanthostyles (echinating the lower parts of the choanosomal tracts (Plate 2 Fig. 8) and the basal plate of spongin) is taken over by the smaller cladotylotes (Plate 2 Fig. 7, Plate 3 Fig. 2). In fact, the latter may be hypothesized to be derived from acanthostyles in view of their close similarity and intergrading observed in *A. primigenius* (see Hiemstra & Hooper, 1991 and Plate 3 Fig. 3).

9. *Acanthostyle size categories*: In the outgroup as well as in acanthostyle-bearing *Acarnus* there is usually a single category of acanthostyles. In two species, *A. souriei* and *A. radovani*, the echinating acanthostyles can be divided in two distinct size categories (Plate 3 Fig. 12), which is assumed to be a synapomorphy (9b) for the two.

10. *Choanosomal style shape*: In the outgroup this is normally more or less straight; in *A. innominatus*, *A. hoshinoi*, *A. thielei*, *A. ternatus*, *A. wolffgangi*, *A. claudeni* and *A. erithacus* the robust styles are rather characteristically curved (Plate 3 Fig. 17). This is considered a synapomorphy (10b) for the group.

11. *Choanosomal style head ornamentation*: The conditions found in *Acarnus*: smooth microspined and rugose (i.e. irregular in shape and fairly heavily spined) are also found in various *Clathria* and thus polarity decision is difficult. Compatibility with other characters (e.g. acanthostyles, curvature of the styles, cladotylotes shape) suggests that the microspined condition

is distributed widely over the various groups of *Acarnus*, and thus might represent the ancestral condition, with independent modifications to rugose (11b) (*A. souriei* (Plate 3 Fig. 18), *A. radovani*, *A. nicoleae*, and *A. tener*; the condition in *A. primigenius* (11d) (Plate 3 Fig. 16) is considered separately derived), and entirely smooth (11c) (*A. tenuis*, *A. innominatus*, *A. hoshinoi* (Plate 3 Fig. 17), *A. erithacus*, *A. wolffgangi*, *A. thielei* and *A. ternatus*). In *claudeni* occasionally styles with a few tiny spines occur; this is considered the retention of an ancestral condition.

12. *Cladotylote categories*: Since no cladotylotes occur in the outgroup, only in-group analysis can be done. With few exceptions *Acarnus* species have two cladotylote size categories (Plate 3 Fig. 1): I (length between 80 and 250  $\mu\text{m}$ ) and II (length 30-110  $\mu\text{m}$ ). The *A. primigenius* cladotylotes (Plate 3 Fig. 3, 10) are unique in the genus for their close similarity to and intergrading with the acanthostyles. It is assumed here, that they represent the ancestral condition, and that the development of a second category (12b) is derived. A few species subsequently lost either the larger (12c) (*A. topsenti*) or the smaller (12d) category (*A. souriei*, *A. radovani*, *A. tener*); in the case of the latter three species we may suppose a synapomorphous loss. It is unclear which of the two categories is present in *A. tenuis*, so this is left undecided.

13. *Shaft spination of cladotylotes*: all smaller and part of the larger cladotylotes have hook-shaped spines along the shaft, and presumably this represents the ancestral condition. *A. deweerdtiae*, *A. toxata*, *A. levii* and *A. peruanus* n.sp. share the paucity of such spines in cladotylote I. It is assumed to be two (homoplastic) synapomorphies (13b) for the two sister pairs *deweerdtiae/toxata* and *levii/peruanus*. In the group of *A. innominatus*, *A. hoshinoi*, *A. wolffgangi* (Plate 3 Fig. 7), *A. thielei*, *A. claudeni* and *A. ternatus* (Plate 3 Fig. 6) cladotylote shafts are completely smooth (13c).

14. *Number of clads in cladotylotes heads*: the number is variable between 3 and 6, but 4 clads (Plate 3 Fig. 9) are perhaps most widely distributed within the genus; apomorphous



reductions to 3 (14b) (*A. deweerdtiae* (Plate 3 Fig. 8), *A. hoshinoi*, *A. wolffgangi*, *A. thielei*, *A. ternatus*, *A. claudei*) occur, and it is assumed that it is a homoplastic synapomorphy for both the groups *A. hoshinoi*-*A. wolffgangi*-*A. ternatus* and *A. thielei*-*A. claudei*. In *A. toxeatu*s clads may number up to 6 (14c).

15. *Cladotyle ornamentations in cladotylote I*: the most widespread condition is the tyle bearing four or more strong hooks (Plate 3 Figs. 4-5), which may be closely adhering the shaft or may be directed outwards. The opposite extreme situation is a completely smooth round tyle found only in cladotylote I of *A. tenuis*, *A. innominatus*, *A. hoshinoi*, *A. wolffgangi* (Plate 3 Fig. 7) and *A. ternatus* (Plate 3 Fig. 6) (as well as in cladotylote II in *innominatus* and *hoshinoi*). In cladotylote I (and II) of *A. erithacus* (Plate 3 Fig. 13), *A. claudei* (as well as in cladotylote II of *A. hoshinoi* and *A. wolffgangi*) the tyles are lobate-irregular. In *A. thielei* the tyles are quadrilobate, but regular. It is possible that these conditions form states of a transformation series from tyles with distinct hooks (plesiomorphous) through blunt-rounded (15b) (synapomorphy for *A. tortilis* and *A. bergquistae*), lobate (15c) (with perhaps the quadrilobate condition as 15c1) (synapomorphy for *A. erithacus*, *A. claudei* and *A. thielei*) to completely smooth rounded tyles (15d) (synapomorphy for *A. tenuis*, *A. innominatus*, *A. ternatus*, *A. wolffgangi*, *A. hoshinoi*). However, compatibility with other characters is not very strong unless occasional reversals are assumed.

16. *Cladotylote I shaft thickness*: in three species (*A. levii*, *A. bicladotylota*, *A. peruanus* n.sp.) there is a noticeable thickening of the shaft just above the tyle (16b) (Plate 3 Fig. 5).

17. *Toxa I and II*: These toxa types, especially the thin deeply curved (II) (Plate 3 Fig. 21), occur also in a comparable form in several species of *Clathria*. We may assume that at least the thin deeply curved ones are plesiomorphous, and probably also the thick short toxa I ("oxhorn": Plate 3 Figs. 19-21) because they are found rather widely distributed over various groups of *Acarnus*, in a large size range. A restricted size of "oxhorn"-toxa is

characteristic of many members of the *souriei*-group and presumably constitute a synapomorphy (17b) for the group. An intergrading between toxa I and II (17c) is characteristic for most of the species of the "tortilis-group" (*A. tortilis*, *A. bergquistae*, *A. toxeatu*s). Finally the "oxhorn" may be absent (lost independently or not found?) (in *A. peruanus*, *A. tenuis*, and *A. deweerdtiae*).

18. *Toxa III*: The modification known as "accolada" with a sharp central curve, curving wings with recurved tips, is unique for *Acarnus*, but not found in all species, and if present shows various modifications. In its pure form (18c) it is found in *A. innominatus*, *A. hoshinoi*, *A. claudei*, *A. thielei*, *A. erithacus* (Plate 3 Fig. 22), *A. toxeatu*s, *A. deweerdtiae*. A more simple, possibly ancestral condition (18b) in which the wings are

Table 6. Character states (a-d) of 19 characters observed in the species of *Acarnus* and its outgroup *Clathria*, used for a character analysis with PAUP. Unknown characters states are coded as "?". States were treated unordered except for: 2, 11, 17, 18, 19 (ordered), and 3, 4, 5, 8, 9, 10, 16 (irreversible: a → b → c, etc.). For a discussion of character states and decisions on treatment cf. text.

Character	0									1									
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
Taxon																			
Clathria	?	a	a	a	a	a	?	a	a	a	a	?	?	?	?	?	a	a	a
primigenius	b	a	a	b	b	a	c	a	a	d	a	a	a	a	b	b	a	a	a
peruanus	a	a	a	b	c	a	a	b	a	a	a	b	b	a	a	b	?	b	a
bicladotylota	a	a	a	b	c	a	b	b	a	a	a	b	a	a	a	b	b	b	a
levii	a	a	a	b	c	a	b	b	a	a	a	b	b	a	a	b	b	b	a
nicoleae	b	a	a	b	c	a	b	b	a	a	b	b	a	a	a	a	b	b	a
souriei	b	a	a	b	c	a	b	b	b	a	b	d	a	a	a	a	b	b	a
radovani	b	a	a	b	c	a	b	b	b	a	b	d	a	a	a	a	b	?	a
tener	a	a	a	b	c	a	b	b	a	a	b	d	a	a	a	a	b	b	a
deweerdtae	b	a	a	b	c	a	b	c	?	a	a	b	b	b	a	a	?	c	b
toxeatu	b	a	a	b	c	a	b	c	?	a	a	b	b	c	a	a	c	c	b
bergquistae	a	a	a	b	c	a	b	c	?	a	a	b	a	a	b	a	c	?	?
tortilis	b	a	a	b	c	a	b	c	?	a	a	b	a	a	b	a	c	d	b
topsenti	d	a	b	b	c	a	a	c	?	a	a	c	a	a	a	a	a	a	a
claudei	a	b	b	b	c	a	a	c	?	b	a	b	c	b	c	a	a	c	a
erithacus	a	b	b	b	c	a	a	c	?	b	c	b	a	a	c	a	a	c	a
thielei	a	b	b	b	c	a	e	c	?	b	c	b	c	a	c	a	a	c	a
ternatus	a	a	b	b	c	a	a	c	?	b	c	b	c	b	d	a	a	e	a
wolffgangi	c	d	b	b	c	a	e	c	?	b	c	a	c	b	d	a	a	e	a
hoshinoi	a	c	b	b	c	a	e	c	?	b	c	b	c	b	d	a	a	c	b
innominatus	a	c	b	b	c	a	e	c	?	b	c	b	c	a	d	a	a	c	b
tenuis	b	a	a	b	c	b	d	c	?	a	c	?	c	a	d	a	?	?	?

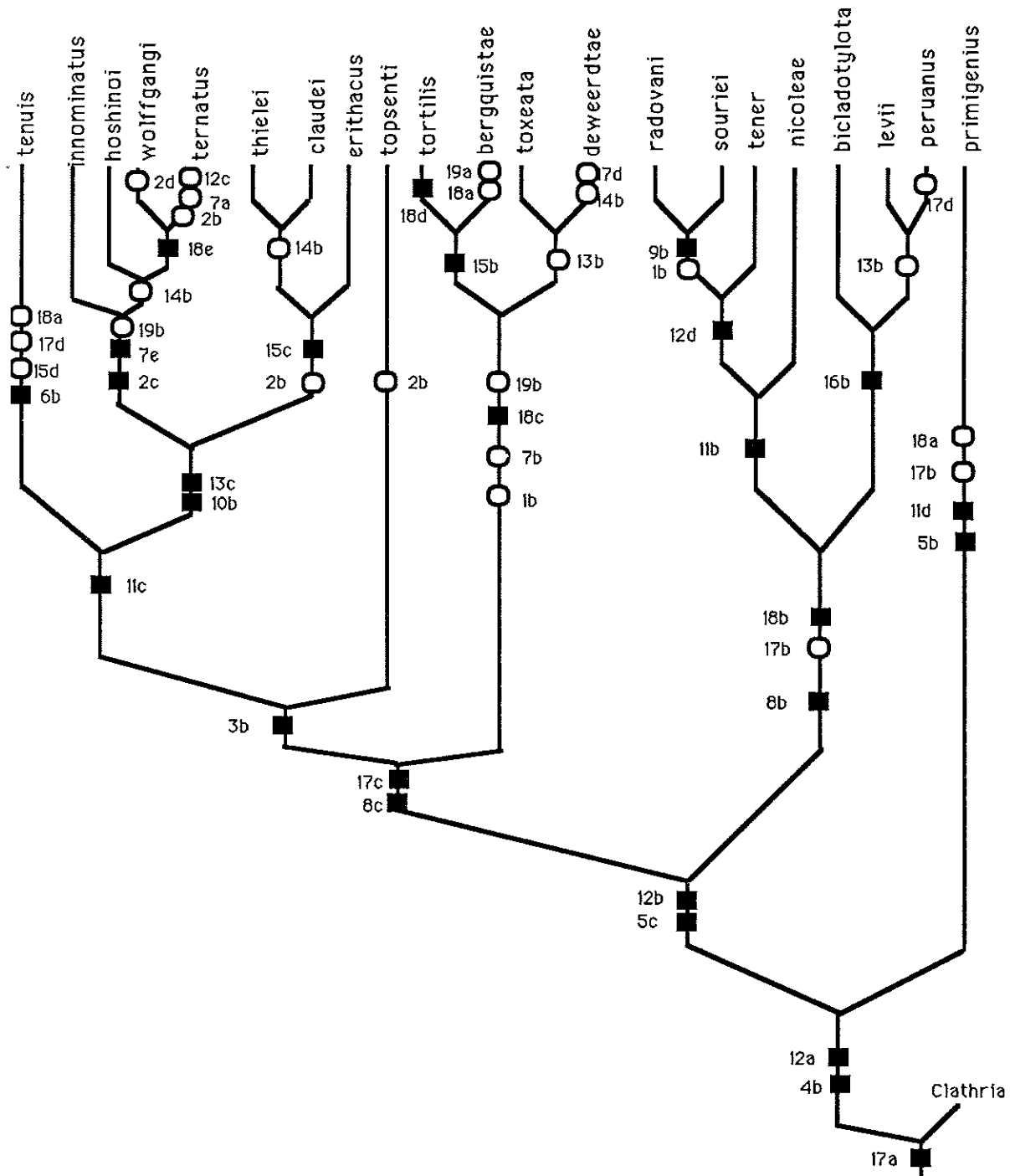


Fig. 6. Cladogram depicting the hypothesized phylogenetic relationships of the recent members of the genus *Acarnus*, based on a character analysis using the computer program PAUP. Black boxes indicate (syn-)apomorphies, open circles homoplasies (assumed parallel developments and/or reversals). Numbers refer to characters listed in Table 6 and discussed in the text.

straight, not (re-)curved, is found in *A. souriei* (Plate 3 Fig. 23), *A. nicoleae*, *A. bicladotylota*, *A. levii*, *A. tener*, *A. peruanus*; an even more simple condition (18d), in which the sharp central curve is absent, is found in *A. tortilis*. An ?unrelated modification consisting of oxea-like barely curved thick toxa (18e) occurs in both *A. ternatus* (Plate 3 Fig. 24) and *A. wolffgangi*. Toxa III are absent (18a) in *A. tenuis*, *A. primigenius*, *A. topsenti* and *A. bergquistae*.

19. *Length of toxa III*: Although lengths of the toxa III vary considerably infraspecifically, several species show unusually long ones (> 400  $\mu\text{m}$ ) (19b): *A. deweerdtae*, *A. toxata*, *A. tortilis*, *A. innominatus*, *A. hoshinoi*, *A. wolffgangi* and *A. ternatus*. Presumably these are aut- or synapomorphic conditions derived from a toxa III size of 150-250  $\mu\text{m}$ .

Wagner-tree analysis, with unweighted character states and those characters ordered which seem to show clear transformation series (see above and Table 6), yielded three equally parsimonious trees (length 61 steps, consistency index 0.77). A consensus tree leaves the relationships between *A. claudesi*, *A. erithacus* and *A. thielei* unsolved. However, one of the three trees coincided with the manually constructed tree, in which *A. thielei* and *A. claudesi* are considered more closely related on the basis of the three-claded cladomes (a homoplastic character found also in *A. hoshinoi*-*A. wolffgangi*-*A. ternatus*). This tree (Fig. 6) is considered the best representation of *Acarnus* phylogenetic relationships. The three species-groups (*innominatus*-, *tortilis*- and *souriei*-groups) are reasonably well established by synapomorphies. The positions of *A. topsenti* and *A. primigenius* as isolated species outside these groups is confirmed. Despite its deviating characters *A. tenuis* is now assumed to be a member of the *innominatus*-group; (Hiemstra & Hooper (1991) placed it at the base of the cladogram).

## BIOGEOGRAPHY

The emended cladogram (Fig. 6) can be used to speculate upon the distributional history (historical biogeography) of the genus and its

members: cladistic biogeography (Humphries & Parenti, 1986; Wiley, 1988; Humphries et al., 1988). Marine examples among the various analytical biogeography methods (see for a review Rosen, 1988) are found in De Weerd (1989: Chalinid sponges), Hoeksema (1989: mushroom corals), Blum (1989: Chaetodontid fishes), Howes (1990: Muraenolepidid fishes) and Reid (1990: Littorinid gastropods). However, the necessary objective distinction between dispersal/extinction phenomena and vicariant events is not really possible in the absence of a detailed general area cladogram of the tropical/subtropical marine areas of endemism, although a rather general relationship between parts of the world oceans was put forward by Nelson (1985).

An attempt to arrive at a first approximation of a more detailed general area cladogram of 12 tropical/subtropical areas (East Pacific, West Indies, Brasil, West Africa, Mediterranean, Red Sea, western Indian Ocean, Central Indian Ocean, Indo-Australian area, Japan, Central Pacific, and South Australia) using phylogenies of four sponge genera (including an earlier version of the *Acarnus* phylogeny in which widespread species were not split-up into regional forms) was made by Van Soest (in the press). Results indicate a general correspondence with major Tertiary geological events: Mediterranean-West African biota show a closer relationship with Indo-West Pacific biota than both do with American biota, which may be assumed to reflect the early Tertiary separation of Atlantic biota by the origination of a deep water barrier, while shallow-water connections still existed between the Mediterranean and the Indian Ocean until the late Tertiary. However, this first attempt to arrive at a general area cladogram is still lacking in detail, e.g. peripheral areas as East Pacific, South Australia are united in an unsolved polytomy at the base of the cladogram. There is still a possibility that older Mesozoic or Paleozoic patterns may eventually emerge from the general area cladogram with the accumulation of phylogenetic data.

In the cladogram of Fig. 6, the three larger

clada (*innominatus*-group, *souriei*-group, and *tortilis*-group) show wholly or partly overlapping distributions (Figs. 7-9) each covering more or less the distribution of the genus as a whole. Two of the species not firmly established as a member of a group, viz. *A. topsenti* and *A. primigenius* show central distributions in the Indo-West Pacific. This picture can be

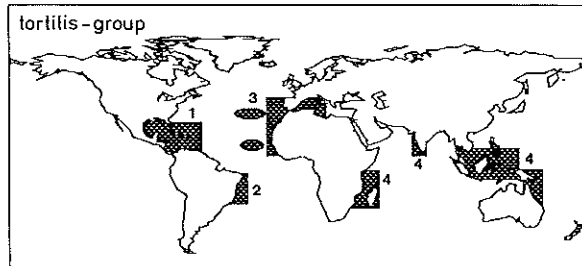


Fig. 7. Schematic distribution map of the *tortilis*-group: 1. *A. deweerdtae* n.sp., 2. *A. toxcata*, 3. *A. tortilis*, 4. *A. bergquistae* n.sp.

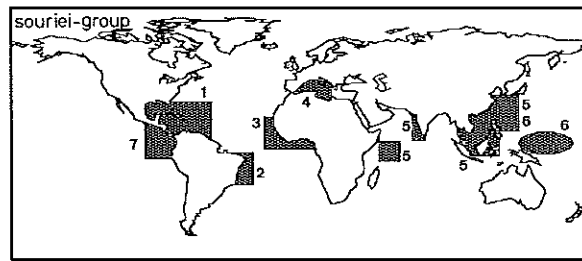


Fig. 8. Schematic distribution map of the *souriei*-group: 1. *A. nicoleae* n.sp., 2. *A. radovani*, 3. *A. souriei*, 4. *A. levii*, 5. *A. bicladotylota*, 6. *A. tener*, 7. *A. peruanus* n.sp.

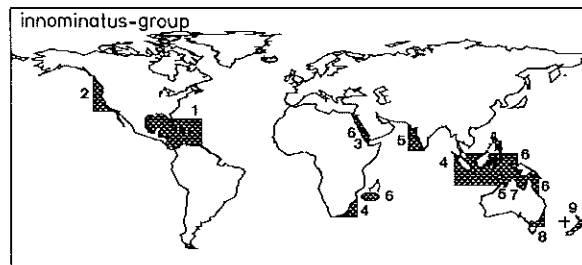


Fig. 9. Schematic distribution map of the *innominatus*-group: 1. *A. innominatus*, 2. *A. erithacus*, 3. *A. thielei*, 4. *A. claudaei* n.sp., 5. *A. ternatus*, 6. *A. wolffgangi*, 7. *A. hoshinoi* n.sp. 8. *A. tenuis*, 9. *A. spec.* (extinct remains).

explained by assuming that in the late Mesozoic before the deep-water barriers between former parts of Gondwana arose, there were already ancestral *innominatus*-, *souriei*- and *tortilis* species and relatives of *A. primigenius* and *A. topsenti* (or even the species themselves) with (partly) overlapping distributions. In fact, the distributions of the *tortilis*- (Fig. 7) and *souriei*- groups (Fig. 8) are overlapping to such an extent that one may assume that they were sympatrically distributed in the tropical Tethys, in a period when it extended from California to Japan. To demonstrate the likelihood of this, recent distributions are plotted over paleogeographic maps provided by Barron et al. (1981): cf. Figs. 10 and 11.

By comparing the phylogenetic relationships (Fig. 6) with the Recent distributions (Figs. 7-8) and with the paleogeographic continental situations (Figs. 10-11), it can be seen, that smaller clada within these two groups in some cases show congruence with the Tethys break-up: the sister-species *A. tortilis* and *A. bergquistae* point to Mediterranean- Atlantic and Indian Ocean recent history, and the West-Atlantic *A. toxcata*-*A. deweerdtae* point to fairly recent differentiation of Brazil and West Indian faunas. The group as a whole may be considered to reflect the relatively remote divergence of West Atlantic and East-Atlantic/Indian Ocean areas (opening-up of the Atlantic Ocean at the beginning of the Cenozoic). These clada can be indicated as evidence for vicariant events.

Patterns in the *souriei*-groups are less compatible: the pair *A. radovani*-*A. souriei* is in conflict with the vicariant events, because its close relationship defies a long history of separation of their areas of distribution (Brazil and West Africa), whereas related species in areas with a more recent shared history (e.g. *nicoleae* in the West Indian region, and *levii* in the Mediterranean) are more distant from both. This close relationship between *radovani* and *souriei* may be a case of fairly recent dispersal. The nearest species to these two is *tener* which shows an unusual distribution in being restricted to the Pacific (Japan/Micronesia); a further West Indian relative is then a potential relict from the

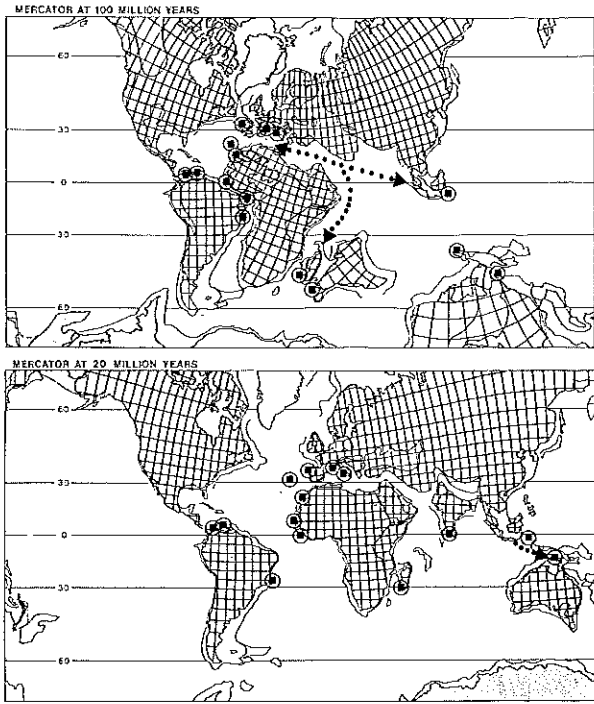


Fig. 10. Distribution of the *tortilis*-group (*A. tortilis*, *A. toxcata*, *A. bergquistae* n.sp., *A. deweerdtae* n.sp.) plotted over paleogeographic maps (modified from Barron et al., 1981) of 100 my BP (top) and 20 my BP (bottom), to demonstrate its likely Tethyan origin.

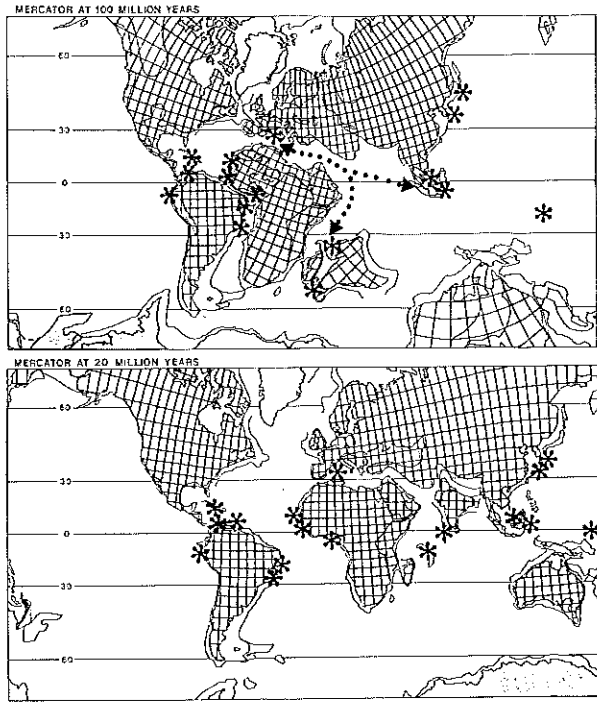


Fig. 11. Distribution of the *souriei*-group (*A. souriei*, *A. levii*, *A. radovani*, *A. nicolae* n.sp., *A. peruanus* n.sp., *A. bicladotylota*, *A. tener*) plotted over paleogeographic maps (modified from Barron et al., 1981) of 100 my BP (top) and 20 my BP (bottom), to demonstrate its likely Tethyan origin.

early separation of the western Atlantic. The trio *A. peruanus*-*A. levii*-*A. bicladotylota* shows some peculiar disjunctions in Mediterranean, Indo-West Pacific and East Pacific localities; this can be only explained if extinction of a related form is assumed in the West Atlantic. Possibly, the depicted relationships of the *souriei*-group are influenced by the fact that the original material of two of the species (*A. tener* and *A. bicladotylota*) could not be studied by us, and their characters only surmised from the literature.

The distribution of the *innominatus*-group (which is lacking from Brasil, West Africa, Mediterranean, Japan, see Fig. 9) is sufficiently different from both above treated species groups to assume that it was especially abundant in the southern waters surrounding adjacent parts of Gondwana. Such a hypothesis is

likely if one plots the Recent distributions in paleogeographic maps (Fig. 12). Apart from this, some presently inexplicable area relationships emerge from the phylogeny of this group (Fig. 6), e.g. the group *A. innominatus*-*A. hoshinoi*-*A. wolffgangi*-*A. ternatus* indicates a past relationship between the eastern parts of the West Indian region and North Australia/Indonesia/India, and the trio *A. erithacus*-*A. claudei*-*A. thielei* indicates that the west coast of North America and the east coast of Africa/Indonesia have biota in common. These disjunct distributions do not seem to be the product of (recent) faunal exchange as the species concerned are not known from intermediate areas. A vicariant explanation is a distinct possibility, since all areas where members of the *innominatus*-group occur were adjacent or at least linked by shallow seas in the

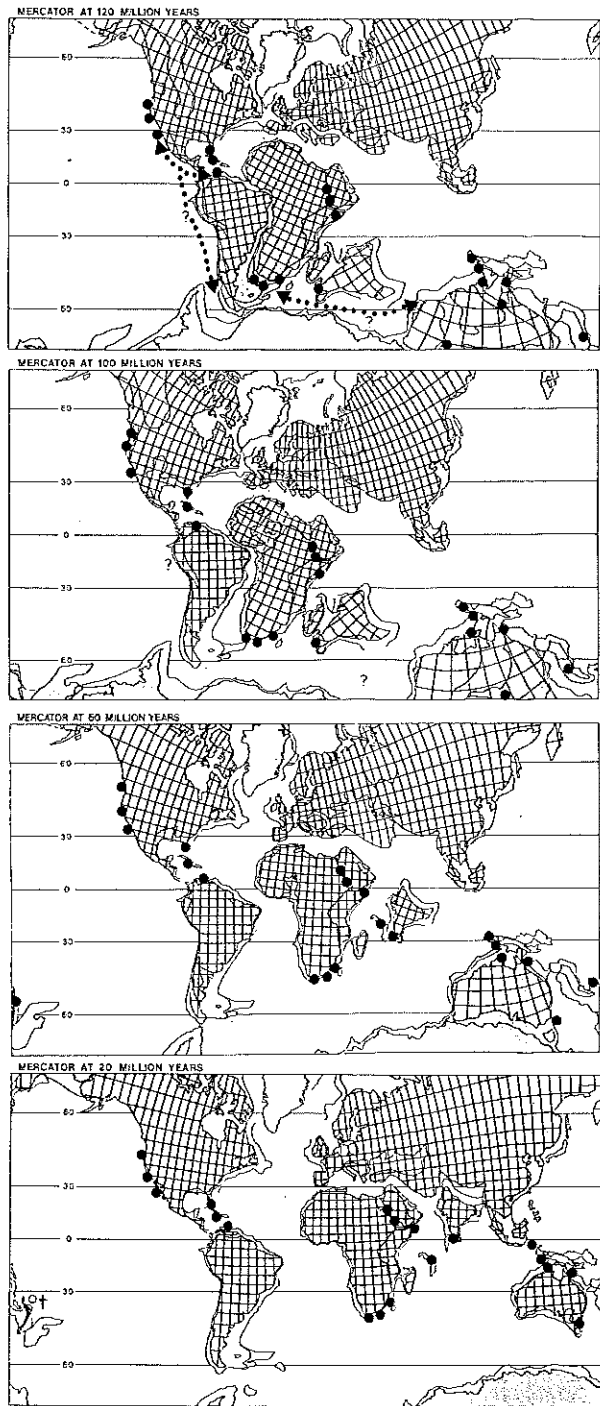


Fig. 12. Distribution of the *innominatus*-group (*A. innominatus*, *A. erithacus*, *A. thielei*, *A. claudeni* n.sp., *A. wolffgangi*, *A. ternatus*, *A. hoshinoi* n.sp., *A. tenuis*) plotted over paleogeographic maps (modified from Barron et al., 1981) of 120 my BP (top), 100 my BP (next one down), 60 my BP (next), and 20 my BP (bottom), to demonstrate its likely Gondwanan origin.

Mesozoic Gondwana-situation (cf. Fig. 12, top). Subsequent break-up of Gondwana and extinctions in many areas might conceivably yield the pattern derived from the phylogeny of the species group. A further support for this idea is found in the fact that the only fossil evidence of *Acarinus* (Early Tertiary of New Zealand, cf. Hinde & Holmes, 1891) concerns cladotylotes of the *innominatus*-group recognizable on their smooth rounded tyles. Significant is also the fact that Recent representatives of the genus so far have not been reported from New Zealand (they are not reported in the Pocilosclerid monograph of Bergquist & Fromont, 1988) and the genus now appears to be extinct in that area. Hinde & Holmes (1891) also report the occurrence of isolated "grapnel" spicules of *Acarinus* in deep sea sediments dredged off the coasts of South West Australia, again an area where *Acarinus* at present seems to be absent.

The vicariant (?) event that separated *A. wolffgangi* and *A. ternatus* may never be unraveled because the species are now largely sympatric over a large area of the Indian Ocean.

Some of these clada might also be explained in the light of amphi-Pacific vicariant events (island integration (Rotondo et al., 1981), "Pacifica" (Melville, 1981) or "Expanding Earth" (see e.g. discussion in Owen, 1983)), but since there is insufficient geological evidence for these hypotheses, we refrain from further speculation along these lines.

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Received: March 16, 1991