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ADDITIONS TO THE INDO-AUSTRALIAN REPRESENTATIVES OF *ACARNUS* GRAY (PORIFERA: DEMOSPONGIAE: POECILOSCLERIDA), WITH DESCRIPTION OF A NEW SPECIES

FREERK HIEMSTRA AND JOHN N.A. HOOPER

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The poorly known species *Acarnus tenuis* from southern Australian waters is redescribed and illustrated for the first time. A new species from Sumbawa in Indonesian waters is described, bringing the total number of species known for Indo-Australian waters to seven, and a key for Indo-Australian species is given. 14 species of *Acarnus* are now recognized worldwide, and a brief synopsis of the genus is given. Phylogenetic relationships of the genus proposed by Hooper (1987) are re-evaluated and five species-groups are proposed. □ *Porifera, Demospongiae, Acarnus, new species, Australia, Indonesia.*

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Recent collections undertaken by the *Snellius II* expedition in southern Indonesia discovered a thinly incrusting, previously undescribed species of *Acarnus*, bringing the total number of species known for the genus to 14. Given the close proximity of the type locality (Sumbawa) to the north coast of Australia, it is possible that this new species may also be a part of the tropical Australian sponge fauna, since other species of *Acarnus* known to occur in Australian waters, recorded by Hooper (1987), have also been found in southern Indonesia (ZMA collections, van Soest, personal communication; van Soest 1989). In addition, the *Snellius II* collections in Amsterdam also contain specimens of *A. souriei* (Lévi, 1952) from Indonesian waters, which extends its known distribution further eastwards from Palk Bay, India (Hooper, 1987, fig. 39).

Through the efforts of Miss Shirley Stone, type material of the poorly known *A. tenuis* Dendy from southern Australian waters was made available from the BMNH collections, and the species is re-described here. Although 'syntypes' of the species held in the NMV were examined during a comprehensive revision of the genus (Hooper, 1987), no trace of the species was found on any of the incrusting sponge substrates. *Acarnus tenuis* was subsequently treated as a *species inquirenda*, and its characters, as described by Dendy (1896), were declared circumspect until

the remaining BMNH microscope slides (reported by Ayling *et al.*, 1982) became available. In this paper *A. tenuis* is redescribed and illustrated for the first time. Its phylogenetic relationships with other members of the genus were merely speculated upon by Hooper (1987), but these are now re-evaluated. A key is also presented for identification of the seven Indo-Australian *Acarnus* species, and illustrations comparing these species are presented.

METHODS

Methods of collection, preservation and preparation of specimens for examination under light microscopy are described elsewhere (Hooper, 1986). Spicule measurements, based on 25 units, are presented as lower range–~~mean~~–upper range of lengths x widths. Preparation of material for scanning electron microscope examination is described by Buizer and van Soest (1977). The following abbreviations are used in the text: BMNH, British Museum (Natural History), London; MNHN, Muséum National d'Histoire Naturelle, Paris; NMV, Museum of Victoria, Melbourne; NTM, Northern Territory Museum, Darwin; ZMA, Zoological Museum Amsterdam.

SYSTEMATICS

Order POECILOSCLERIDA Topsent
 Family MYXILLIDAE Topsent
Acarnus Gray, 1867

Acarnus Gray, 1867:544 [type species and full synonymy given by Hooper, 1987].

DIAGNOSIS

Ectosomal spicules are tylotes; choanosomal spicules are smooth styles, with or without microspined bases, echinated by cladotylotes and sometimes by acanthostyles; microscleres are palmate isochelae and toxas, the latter usually including a category which is thick and evenly curved, with recurved points ('oxhorn' shaped).

REMARKS

Species are easily recognizable as belonging to the order Poecilosclerida in having chelate microscleres, and as members of the genus *Acarnus* by their possession of cladotylotes. The recurved apical spines or clads of these spicules show some similarities with some Raspailiidae (e.g. *Ectyoplasia*, *Endectyon*) and tetractinal spicules of the Tetractinomorpha, but these are obviously analogous structures. Evidence for the origin of cladotylotes is conflicting. On the one hand (e.g. *A. primigenius* sp. nov.) the tetractinal modifications to cladotylotes in *Acarnus* appear to be highly derived forms of normal acanthostyle stock. This is illustrated by the series of spicules described in Figure 2a. This situation is thought to be similar to the origin and modification of acanthoplagiatrienes (monact, diact, triact, tetract and pentact forms) in the Raspailiidae genera *Cyamon* and *Trikentrion* (Hooper 1991b). Conversely, there is also a sequence demonstrated in *A. tenuis* (Fig. 1a,b) which suggests that larger, smooth-shaft forms of cladotylotes at least may be derived from ectosomal tylotes. In this regard *A. tenuis* is atypical of other species, and for reasons discussed further below, it may eventually be moved from *Acarnus* altogether.

Another character which appears to be characteristic for the genus *Acarnus* is the possession of thick toxas with greatly rounded central curvature and reflexed tips, resembling a pair of "oxhorns" (e.g. Fig. 2c). These sorts of spicules are shared by most, but not all species (absent in *A. tenuis* and apparently absent in *A. bicladotylotus*), but they are not unique to the genus, also occurring in some species of *Clathria*

of the Microcionidae (e.g. *C. (Axociella) cylindrica*, *C. (Clathria) inanchorata*; Hooper, in preparation).

The family placement of *Acarnus* is less easily decided. Van Soest (1984) transferred the genus from its traditional placement with the Microcionidae to the Myxillidae, based on the possession of ectosomal diactinal spicules (tylotes), which are apomorphic for the family. Hooper (1987:72) summarizes the arguments presented by various authors in favour of each system, and he chose to include the genus with the Myxillidae on the basis that the possession of ectosomal tylotes provides the only consistent character and clear differentiation between the two families (Hooper, in prep.). However, it is true that there are many characters shared between *Acarnus* and the Microcionidae, especially the geometry of microscleres. For the purposes of the present study the Microcionidae are considered to be an outlying sister-group of Myxillidae such as *Acarnus*. This argument is developed further below.

Acarnus tenuis Dendy, 1896
 (Figs 1, 3a,b)

Acarnus tenuis Dendy, 1896:50–51. Hooper, 1987: 87–90, table 5.

MATERIAL EXAMINED

LECTOTYPE: BMNH 1902.10.18.62 (RN974) (microscope slide): vicinity of Port Phillip Heads, Melbourne, Victoria, 38°20'S, 144°42'E; date and depth of collection unknown, J.B. Wilson, dredge [NMV G2456 now consists only of a specimen of the sponge *Plumohalichondria arenacea*, upon which *A. tenuis* incrusts, and from which the BMNH microscope slide preparation was made, but no trace of the incrusting sponge was found].

PARALECTOTYPE: BMNH 1902.10.18.375 (RN991) (microscope slide): same locality [NMV G2457 is a specimen of *Tedania digitata*, upon which *A. tenuis* incrusts, and from which the BMNH slide was made, but the incrusting species is no longer present].

PARALECTOTYPE: BMNH 1902.10.18.323 (RN1072): same locality [this BMNH specimen was not examined, nor is there any material with Dendy's RN number present in the NMV, supposedly incrusting on *Clathria typica*. Ayling *et al.* (1982) reported that the BMNH material consisted only of a microscope slide preparation, but this is unconfirmed, and it is still possible that the entire specimen is housed in the BMNH collection].

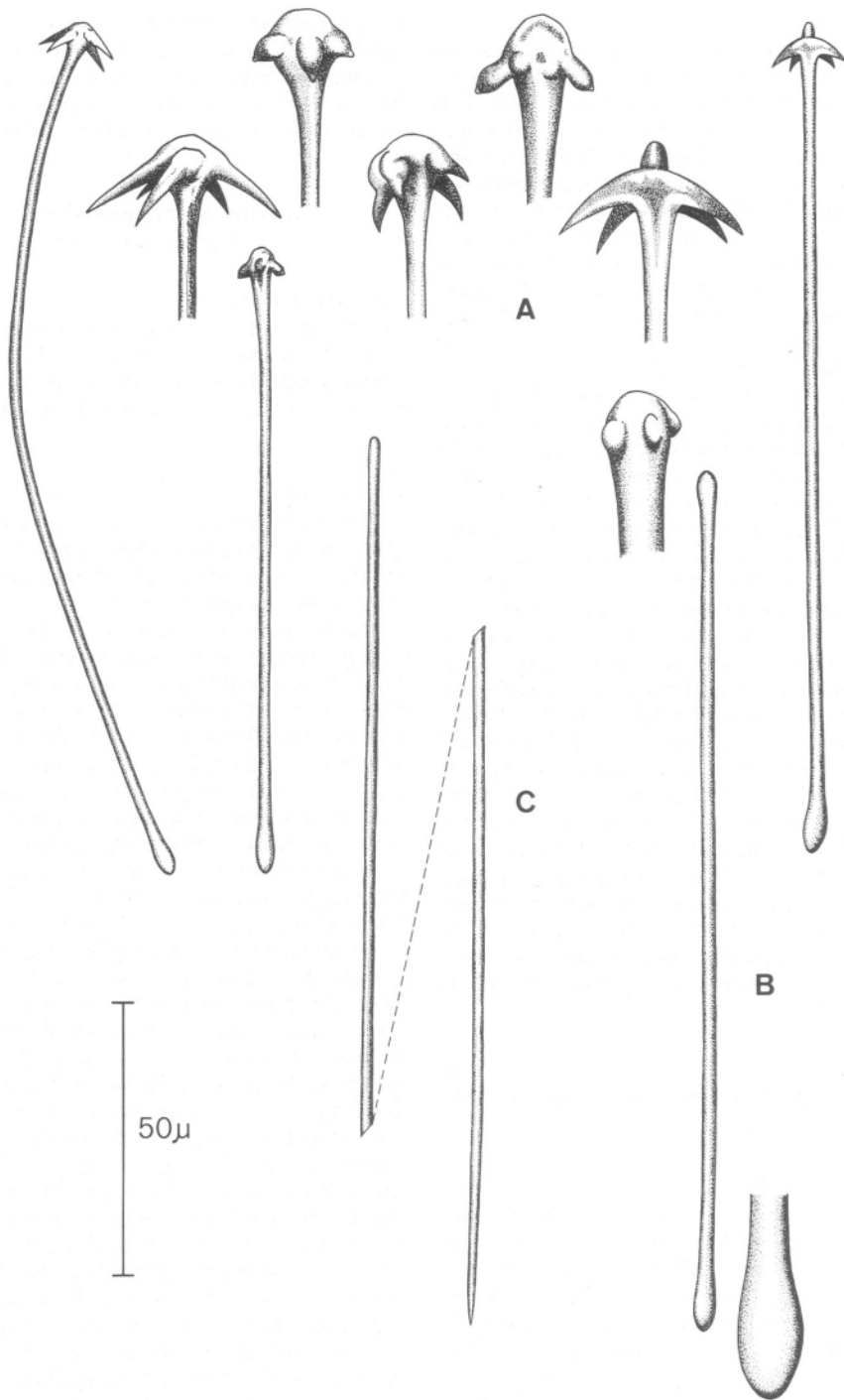


FIG. 1. *Acarnus tenuis*. A., cladotylotes, different growth stages and malformations. B., ectosomal tylote. C., choanosomal style.

DESCRIPTION

The only extant material seen of this species consists of two microscope slide mounts of whole pieces. Nevertheless, they were enough to make the species recognizable, whereas Hooper (1987) had to rely on Dendy's (1896) brief and uninformative description. The specimens appear as pale yellowish blobs, flattened under the cover glass. They contain no visible spongin, and as a consequence, their skeleton is very lax, composed of loose bundles containing a mixture of cladotylotes orientated parallel to the surface and tylotes of equal size. The skeleton may be described as confusedly isotropic. The megascleres are of three types: tylotes (96–142–176 μm x 2 μm) which are dominant and for the most part lying in bundles consisting of 15–20 spicules, together with cladotylotes of similar size (80–137–152 μm x 2 μm), which seem to occur in all stages ranging from spicules resembling tylotes up to clear cladotylotes, and in this species at least they appear to be derived from tylotes. Cladotylotes are also abundant, generally lying in mixed bundles, although not all with the cladome in the same direction. Many cladotylotes are situated just under the surface of the sponge, piercing through it. Styles are not frequent (152–184–205 μm x 2 μm). They do not occur in bundles, but are separately arranged in the skeleton. As noted by Dendy (1922), these spicules are stylote, strongylote, or sometimes subtylostylote, and in fact all these forms can be found in the preparations. Moreover, they seem to be modifications of one type, which is essentially a style. There are no microscleres. Numerous apparently unorganized spherical cells were also observed dispersed throughout the choanosome.

DISTRIBUTION

Known only from the type locality of Port Phillip Heads, Victoria.

REMARKS

Except for the possession of cladotylotes, this species would not have been assigned to the genus *Acarinus*, as it differs considerably from the other species in the genus. In fact Dendy (1922) suggested that a new genus might be created for *A. tenuis*. He considered that the key difference was the absence of chelate microscleres, but this is no longer considered of sufficient importance at the generic level (e.g. van Soest, 1984). However, other differences may vindicate his suggestion. For the time being

we propose to keep this species in the genus *Acarinus*, if for nothing else than convenience, and with affinities to the other species indicated by cladotylotes, but the species is readily differentiated from other members of the genus.

***Acarinus primigenius* sp. nov.**
(Figs 2, 3d,e,f, 4c)

MATERIAL EXAMINED

HOLOTYPE: ZMA Por. 7693: Bay of Sangara (Teluk Sengari), Sumbawa, Indonesia, 8°17'S, 118°15'E, 18m depth, 21 September 1984, coral reef, coll. H.A. ten Hove, *Snellius II* expedition, stn. 114/V/05.

DESCRIPTION

The single specimen occurs as a thin hairy crust on the surface of a *Seriatopora* sp. (needle coral). In life it was bright orange, and in spirit it has a grey-purplish colour.

The skeleton is composed of a basal plate of spongin with erect plumose spongin fibres arising in microcionid pattern, and fibres are cored with styles and echinated by acanthostyles and cladotylotes. Cladotylotes are of the same size as acanthostyles (54–62.5–67 μm x 5 μm at the base), and occur in all stages from true acanthostyles through all intermediate stages to true cladotylotes (Figs 2a, 3d,e). Apparently, the transformation from acanthostyles to cladotylotes starts with an increase in spine size at the tip of acanthostyles. The next step appears to be a progressive blunting of the pointed apex, resulting in a cladotylote. All cladotylotes, however, remain tapering from the base to the tip like regular acanthostyles, and these are as such readily distinguishable from other *Acarinus* cladotylotes which have a definitely tylole-like basal form. However, the tylole base (swelling) of the present species, from which the clads sprout, remains relatively small.

Styles are long (99–166–240 μm x 4–5.5–6 μm), somewhat curved, and towards the tip they are slightly recurved. They possess a distinct base, which is heavily spined (Fig. 4c). Juvenile styles seem to be smooth and thin with a knob-like head. Acanthostyles are of a single size category only (60–66–68 μm x 5 μm at the base). The head is provided with spines curved in the direction of the tip, whereas the spines on the shaft are curved in the opposite direction. They appear to have the same function as the cladotylotes, since both are echinating. The ectosomal spicules consist of anisotylotes (137–156–184 μm x 2.5 μm in size),

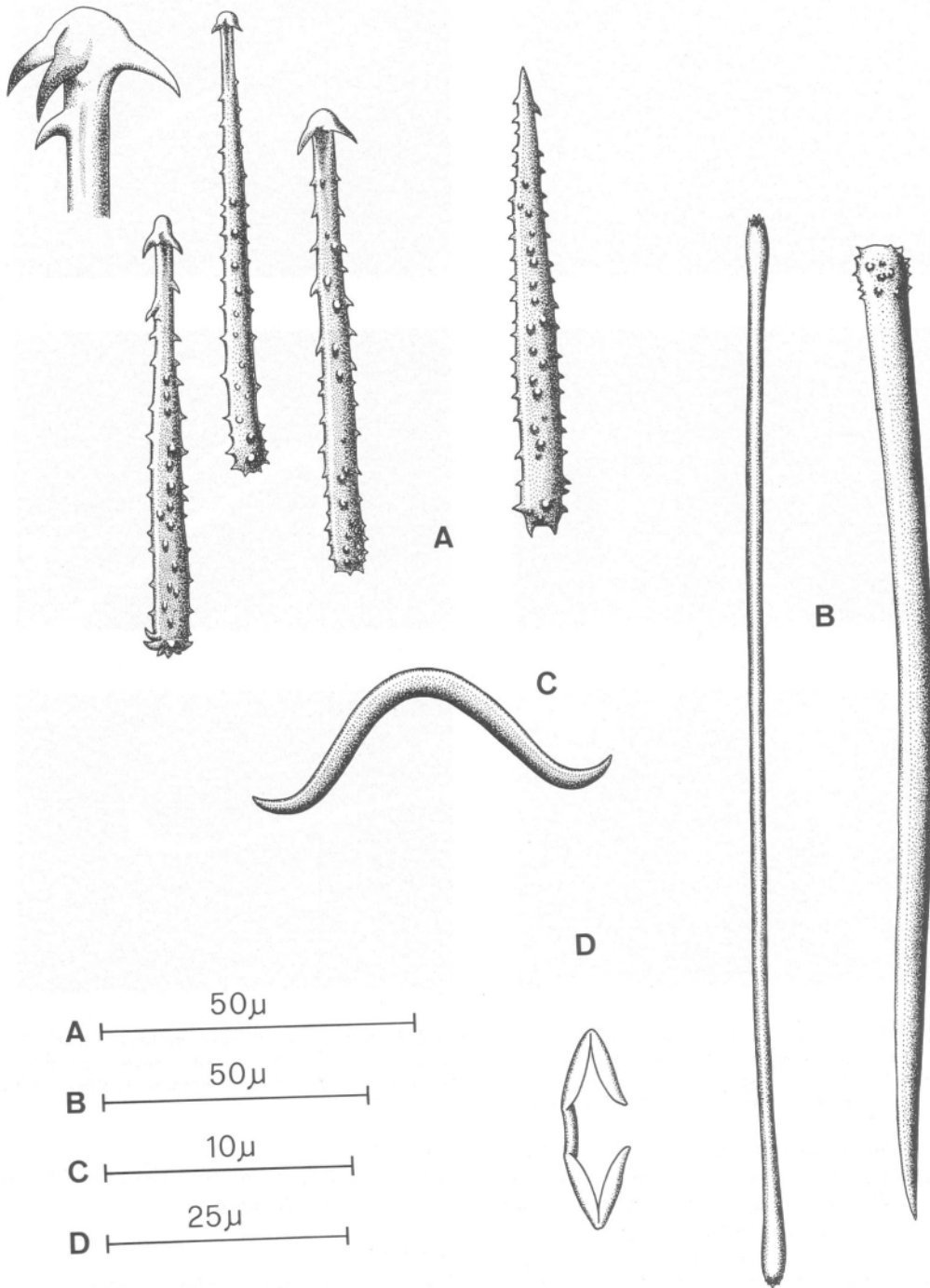


FIG. 2. *Acarnus primigenius*. A, cladotylotes and acanthostyle, different growth stages. B, tylote and style. C-D, toxa.

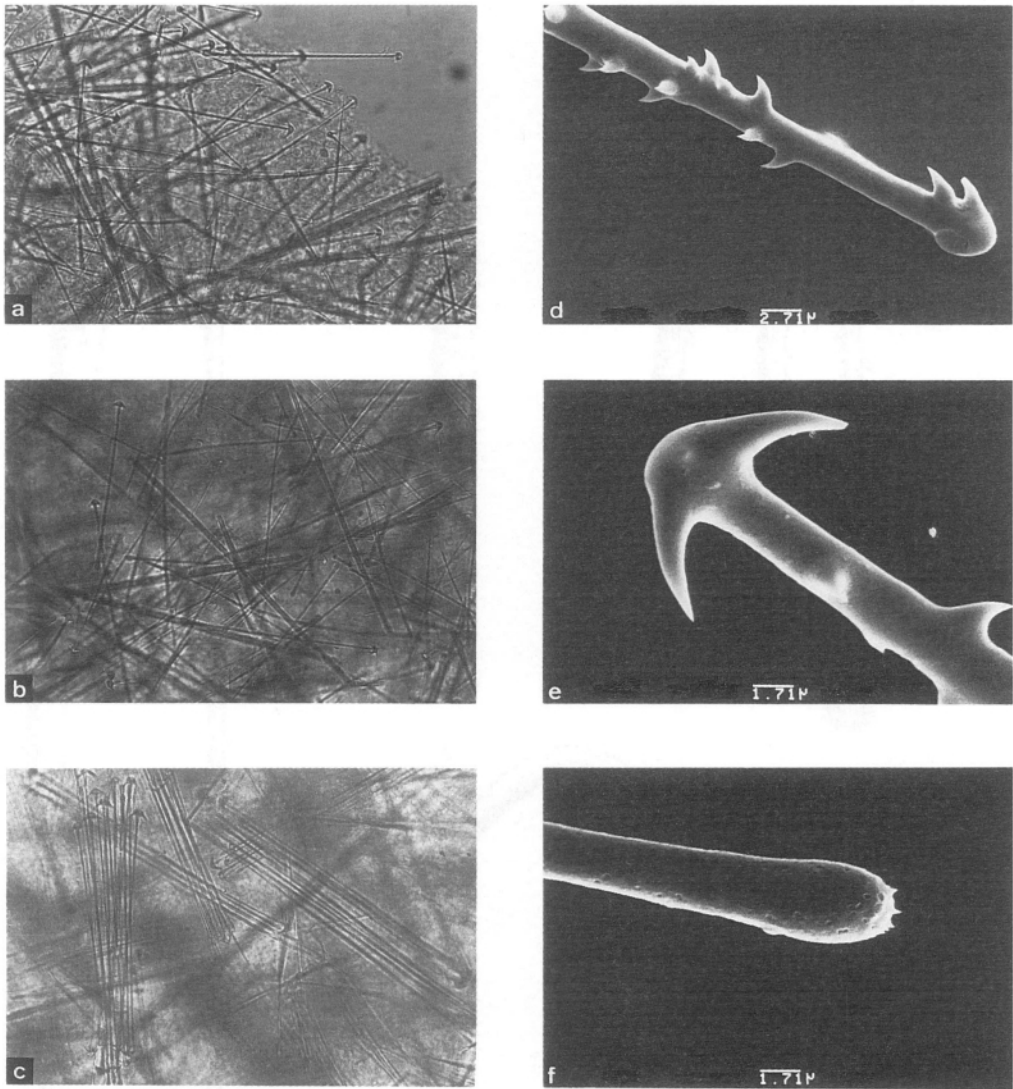


FIG. 3 A-C. *Acarnus tenuis*. A, cladotylotes protruding through the skin and the loose formation of round cells, not seen in other species of the genus. B, spicules of *A. tenuis* intermingled with those of its substrate *Tedania*; C, bundles of cladotylotes and tylotes. FIG. 3D-F, *Acarnus primigenius*. D-E, different growth stages of the basal clads. F, microspined base of the tylote spicule.

which appear smooth-based under the light microscope, but scanning electron microscopy (Fig. 3f) reveals microspines common to all *Acarnus* species (with the exception of *A. tenuis*).

Microscleres palmate isochelae (14-17.5-21.5 μ m), toxas of a single type, having characteristic "oxhorn"-like shape common to the genus (14-30-46 μ m x 1.5-3-4 μ m in size) (Fig. 2c).

DISTRIBUTION

Known only from the type locality of Sumbawa, southern Indonesia.

ETYMOLOGY

For the many plesiomorphic character states.

REMARKS

This new species is easily differentiated from

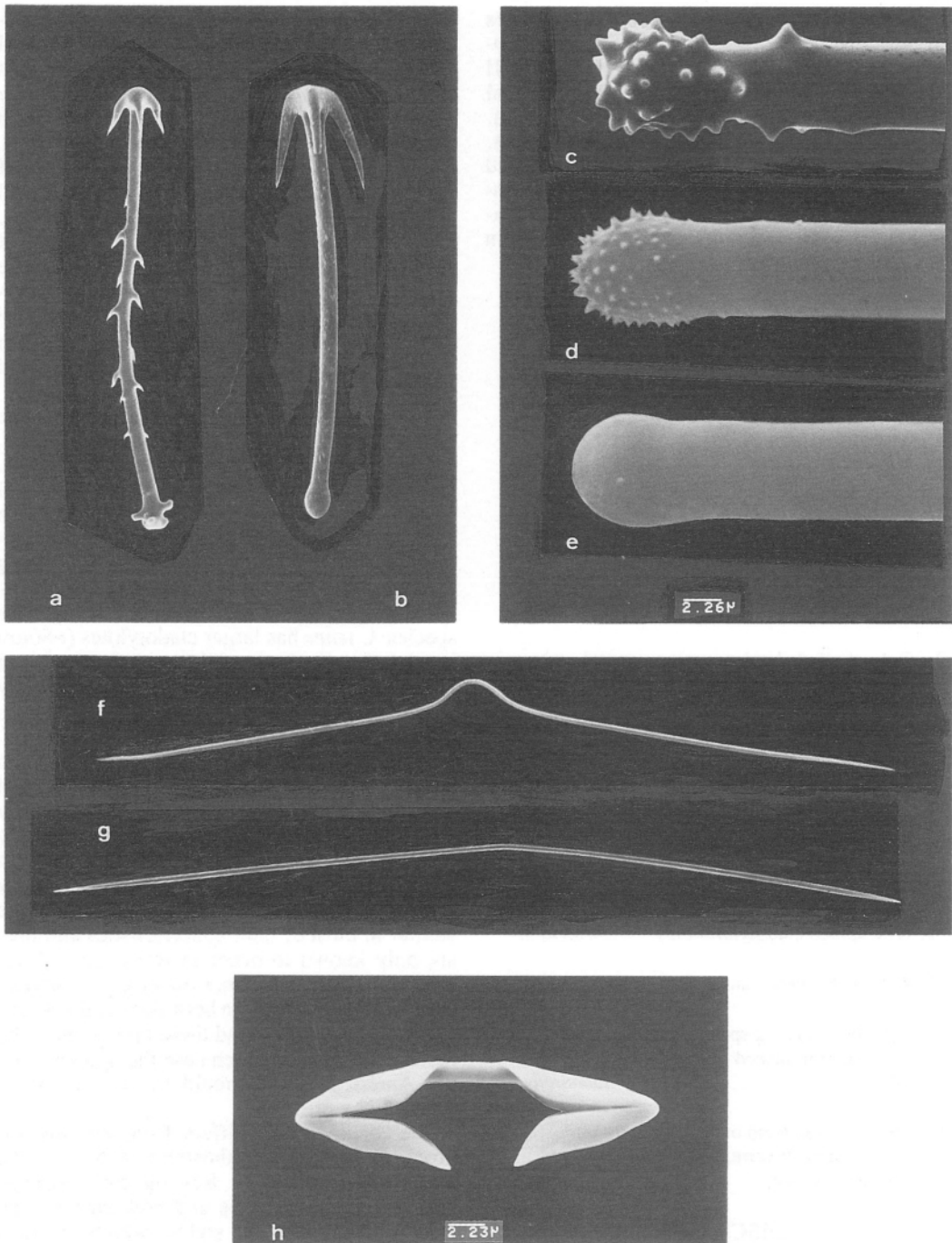


FIG. 4. Comparison between spicules of Indo-Australian *Acarnus* species. A,B, cladotylote varieties with microspined shaft and basal clads (A, *A. souriei*), and smooth shaft and swollen base (B, *A. ternatus*). C-E, variation in microspination of the bases of styles, *A. primigenius* (C), *A. tortilis* (D,E). F,G, longer toxas, showing the centrally curved (F, *A. innominatus*) and the slightly V-shaped types (G, *A. thielei*).

other *Acarus* in having only small cladotylotes in combination with acanthostyles. *Acarus topsenti* Dendy, 1922 also has only small cladotylotes but lacks acanthostyles. Skeletal structure also differs, being plumose in *A. primigenius* and isotropic/plumo-reticulate in *A. topsenti* (Hooper, 1987, fig.37). It is speculated that the plumose skeleton may represent an ontogenetic growth stage, occurring in more mature specimens, similar to the sequence found in *A. souriei* Lévi, 1952.

KEY TO THE INDO-AUSTRALIAN SPECIES OF ACARNUS

- 1a. No microscleres, spicule bundles consist of tyloses and cladotylotes only . . . *A. tenuis*.
- 1b. Microscleres present 2.
- 2a. Acanthostyles present 3.
- 2b. No acanthostyles present, larger cladotylotes usually with basal tylose swelling (Fig. 4b) 4.
- 3a. Only small cladotylotes present (<100 µm) long *A. primigenius*.
- 3b. Both small (<100 µm) and large cladotylotes present (>100µm), which have a cladome at their base (Fig. 4a) *A. souriei*.
- 4a. No small cladotylotes *A. ternatus*.
- 4b. Both large and small cladotylotes 5.
- 5a. With spined cladotylotes only . . . *A. tortilis*.
- 5b. With both smooth and spined cladotylotes 6.
- 6a. Thickly incrusting sponge, with long toxas bearing pronounced central curvature (Fig. 4f) *A. innominatus*.
- 6b. Elaborate vasiform or flabellate growth form, coarse texture, long toxas slightly v-shaped (Fig. 4g) *A. thielei*.

DISCUSSION

Acarus tenuis Dendy, 1896 differs from all other *Acarus* species in lacking microscleres, in having a lax skeleton, apparently without spongin fibres, and in lacking basal spination on

choanosomal styles. *Acarus primigenius* differs from most species in having only small cladotylotes. The acanthostyles distinguish it from *A. topsenti* Dendy, 1922, together with the possession of a microcionid basal and dendroid choanosomal skeleton, an incrusting habit, larger tyloses, and heavy spines on the heads of styles (Fig. 4c). In having acanthostyles as well as cladotylotes echinating skeletal tracts, *A. primigenius* shows similarities with a group of species such as *A. souriei* (Lévi, 1952). These species were previously referred to *Acanthacarus* Lévi, 1952, but Hooper (1987) supported their merger into a single genus on the basis that acanthostyles are primitive, and as such could not be used to define a genus.

Acarus souriei and other members of the *souriei*-group (viz. *A. bicladotylotus* Hoshino, 1981, *A. radovani* (Boury-Esnault, 1973), and *A. tener* Tanita, 1963) differ from other species in having cladotylotes of two sizes, both of which have spined shafts, a dendritic skeletal architecture, in addition to the presence of echinating acanthostyles. Within the *souriei*-group, however, the differences are less clear. The Japanese species *A. tener* has larger cladotylotes (>80µm long) (whereas those of *A. souriei* are <80µm long). Similarly, *A. bicladotylotus* apparently has no large "oxhorn"-shaped toxas, but it is otherwise poorly differentiated from *A. souriei*. These differences require confirmation through re-examination of the original Japanese material (which unfortunately has now become virtually unobtainable for loan, following the untimely death of our colleague Takaharu Hoshino in 1988). Speculatively, however, it seems unlikely that the two species are distinct, since they are similar in most of their characteristics and they are only known to occur in restricted and adjacent localities in Japan. Conversely, *A. souriei* specimens reported from both sides of the Atlantic do seem to differ, and these may prove to be distinct species, in which case the species from the American shelf should be referred to *A. radovani* by priority.

The *tortilis*-group differs from the *souriei*-group in lacking acanthostyles, and from the *innominatus*-group in having only spined varieties of cladotylotes and both smooth and microspined bases on styles, which are also more-or-less straight. Other than *A. tortilis* Top-sent, 1892, other species included in the *tortilis*-group are *A. topsenti*, *A. toxeatatus* Boury-Esnault, 1973, and *A. polytylus* Pulitzer-Finali, 1983. *Acarus topsenti* is easily differentiated from

other species in this group in having only small cladotylotes, whereas others have both small and large varieties of these spicules. The Brazilian *A. toxeatius* is distinguished in having its larger category of cladotylotes being very long and many-claded; the Mediterranean *A. polytylus* has polytylote examples of ectosomal and choanosomal spicules, but these may be merely malformations of normal ones found in *A. tortilis*, and the two species may prove to be conspecific.

The *innominatus*-group differs from other groups in having generally smooth shafts on the larger variety of cladotylotes, which also have a smooth basal tylote swelling. In addition, all members (viz. *A. erithacus* de Laubenfels, 1927, *A. innominatus* Gray, 1867, *A. thielei* Lévi, 1958, and *A. ternatus* Ridley, 1884) possess more-or-less abruptly curved styles which have smooth bases. *Acarnus ternatus* (which was not previously included with this group of species, but was placed in a group with *A. tenuis*; Hooper 1987) has only a single, larger size of cladotylotes, whereas the other species have two size categories of these spicules; *A. innominatus* has centrally curved long toxas (Fig. 4f) whereas both *A. thielei* and *A. erithacus* have their long toxas slightly v-shaped (Fig. 4g). The latter two species differ mainly in shape: *A. thielei* has a flabellate growth form, whereas *A. erithacus* is more massive.

PHYLOGENETIC REMARKS

The genus *Clathria* of the Microcionidae and the genus *Megaciella* of the Myxillidae are chosen as outgroups of *Acarnus*, representing both more-distantly and more-closely related taxa, and criteria for judging the apomorphic state of characters are listed below. This system essentially follows the findings of van Soest (1984) and Hooper (1987), but the conclusions of those authors are developed further in the following analysis.

Cladotylotes: small acanthostyle-like spined cladotylotes are plesiomorphic. Since the cladotylotes of *A. tenuis* seem to have a different origin, these are considered to be an apomorphy for this taxon, and it is speculated that its plesiomorphic state must have been the possession of a dermal layer of tylotes only. In *A. tenuis* all stages from tylotes to cladotylotes can be found, both of which have smooth shafts, and it seems unlikely that spicules with spined shafts have ever been present.

Acanthostyles: the possession of acanthostyles is considered to be plesiomorphic, since there is a tendency to lose acanthostyles (also throughout various groups of Poecilosclerida) and replace them with cladotylotes serving as echinating spicules.

Styles: the presence of microspines on the bases of the choanosomal styles is considered here to be plesiomorphic; apomorphy is the occurrence of smooth styles together with microspined ones, or completely replacing them.

Tylotes: the possession of a dermal layer of tylotes is the plesiomorphic state for the genus, since the character is shared by all myxillids. No apomorphic tendencies of this character were recorded for the genus.

Skeletal architecture: a reticulate or plumo-reticulate (dendroid) skeleton is considered to be plesiomorphic, and a plumose architecture is one of several possible derived conditions.

Microscleres: toxas do not seem to be of great importance in defining groups; in fact there seems to be random distribution in the loss of toxa categories (which was also found for the Microcionidae; Hooper, 1991a, and in preparation), whereas the most closely related advanced species seem to have kept all three categories of toxas. The loss of isochelae is probably a derived feature of the genus.

Based on this analysis of characters, the four species-groups proposed by Hooper (1987) are modified as follows:

GROUP I: *A. tenuis* - group has derived its cladotylotes from dermal tylotes, and is supposed to have lost the other spined spicules and microscleres. *Acarnus tenuis* is the only representative of this group.

GROUP II: *A. primigenius* - group has a dendritic skeletal architecture, one category only of toxas, and styles with distinctly spined bases. *Acarnus primigenius* is the only representative of this group.

GROUP III: *A. souriei* - group has retained the dendritic skeletal architecture, with echinating acanthostyles, and styles mainly with microspined bases. This group includes *A. souriei*, *A. radovani*, *A. tener* and *A. bicladotylotus*.

GROUP IV: *A. tortilis* - group has an isotropic skeleton, both microspined and smooth styles, but it has lost the acanthostyles. Representatives are *A. tortilis*, *A. topsenti*, *A. polytylus* and *A. toxeatius*.

GROUP V: *A. innominatus* - group also has a derived isotropic skeleton but has lost the

microspined styles, whereas larger cladotylotes show a strong tendency towards a smooth shaft and a smooth basal swelling. This group is represented by *A. innominatus*, *A. erithacus*, *A. thielei* and *A. ternatus*.

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