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NEW RECORDS OF *ACARNUS* GRAY (PORIFERA : DEMOSPONGIAE : POECILOSCLERIDA) FROM AUSTRALIA, WITH A SYNOPSIS OF THE GENUS

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ABSTRACT

Five species of *Acarnus* are now known for Australian waters. *Acarnus thielei, A. innominatus, A. tortilis*, and *A. ternatus* are redescribed from recent northern Australian material, three of which represent new locality records for this region. *Acarnus tenuis* from southern Australia is poorly known, and apparently the type-specimens no longer exist. A redescription of *A. ternatus* and *A. topsenti* based on type-material, and a synopsis of other species is given, including diagnoses from the literature. Twelve species are recognised. A cladistic analysis of *Acarnus* species supports the abandonment of a generic subdivision based mainly on the presence or absence of acanthostyles (subgenus *Acanthacarnus*), in favour of a taxonomy based mainly on cladotylote morphology. Four species groups are recognized on that basis: *ternatus, tortilis, souriei* and *innominatus* groups. The zoogeography of species is discussed.

INTRODUCTION

The marine sponge genus *Acarnus* is easily diagnosed on account of the unique cladotylote megascleres, but specific identifications based on morphological characters are less easily made.

The present study redescribes material collected recently from northern Australian waters, including three new records for the region, and provides a synopsis from the literature of all species currently placed in the genus.

The genus is cosmopolitan, with records from most oceans and seas, although species of the nominal subgenus *Acanthacarnus* have been recorded mainly from the northern hemisphere. Species are found predominantly in shallow-water, but one species from California has an extensive bathymetric distribution extending from the intertidal zone to a depth of 700 metres (de Laubenfels 1932). Previous records of the genus from Australia are restricted to *A. tenuis* Dendy from Port Phillip, Victoria and *A. ternatus* Ridley from Torres Strait, northern Queensland.

METHODS

Methods of collection, preservation and preparation of specimens for light microscopy are described elsewhere (Hooper 1984).

The following abbreviations are used in the text, and refer to specimen holding institutions: AM — Australian Museum, Sydney; BM — British Museum (Natural History), London; NMV — Museum of Victoria, Melbourne; NTM — Northern Territory Museum, Darwin; QM — Queensland Museum, Brisbane.

SYSTEMATICS

Order POECILOSCLERIDA Topsent, 1928

Family MYXILLIDAE Topsent, 1928

Genus **Acarnus** Gray, 1867

Acarnus Gray, 1867, p. 544. [type-species; *Acarnus innominatus* Gray by monotypy].

Fonteia Gray, 1867, p. 544. [type-species; *Fonteia anomala* Gray by monotypy. Gray (1867, p. 544) established this genus for a sponge figured by Bowerbank (1864, figs 73-76), and he attributed the specific name to Bowerbank also. No record of that name was found in any of Bowerbank's monographs on British Sponges, and furthermore the figures referred to by Gray (viz. 73-76) are those of *Acarnus innominatus* (which has page priority)].

? *Trefortia* Dezsö, 1880. [according to de Laubenfels (1936, p. 92); neither the genus nor the type-species were gazetted by the Zoological Record].

Acanthacarnus Lévi, 1952, p. 54. [type-species: *Acanthacarnus souriei* Lévi by monotypy. The genus was placed into synonymy with *Acarnus* by Van Soest (1984), on the basis that the acanthostyles of *Acanthacarnus* represent the retention of an ancestral character, which therefore cannot be used as a character to separate genera. Van Soest retains the taxon at the subgeneric level].

DIAGNOSIS

The most recent definition of *Acarnus* (Van Soest 1984, p. 60) is here expanded.

Ectosomal skeleton with a tangential layer of amphitylotes, and with a more-or-less hispid surface produced by styles from ascending fibres and cladotylotes poking through the surface. Choanosomal skeleton with a renieroid reticulation of spongin fibres cored by styles, or with a reduced plumo-reticulate skeleton, or further reduced to a plumose-halichondroid skeleton in encrusting forms. Fibres composed of moderate to very light spongin, and echinated by smooth and/or spined cladotylotes, and sometimes by small acanthostyles. Light spongin with or without auxiliary styles strewn between fibres. Microscleres palmate isochelae and diverse forms of toxas.

REMARKS

The genus *Acarnus* was established by Gray (1867, p. 544) for *Acarnus innominatus*, based on figures of an unidentified sponge of Bowerbank (1864). These figures were also used to erect *Fonteia anomala* Gray (1867, p. 544), which becomes *nomina nuda*.

Originally included with the Tethyadae by Gray (1867) on the basis that cladotylotes were related to tetraxonid spicules, Ridley (1884) placed the genus in the family Ectyonidae, because he considered that the cladotylotes of *Acarnus* resemble acanthostyles of *Clathria* Schmidt and *Echinodictyum* Ridley. Various minor reorganizations occurred in the taxonomic placement of *Acarnus*, such as with the old family Desmacidonidae, subfamily Ectyoninae (e.g. Dendy 1905; Hentschel 1912), but Thiele (1903) adopted Topsent's (1894) system of classification in placing the genus with the family Poeciloscleridae, later to become the order Poecilosclerida.

Several more recent schemes have been proposed for the placement of *Acarnus*.

(1) Dendy (1922) established the section Acarneae for this genus as distinct from his subdivisions Clathreae and Myxilleae, to include species having echinating cladotylotes (which he suggested were merely modified acanthostyles), ectosomal amphitylotes, palmate isochelae and toxas. In his opinion, *Acarnus* did not fit with either the Myxilleae (which have arcuate isochelae), or the Clathreae (which have monactinal ectosomal megascleres). Topsent (1928) raised Dendy's groups to family level, and several other authors have since used that system (de Laubenfels 1932; Lévi 1952, 1963; Sarà 1960; Ruetzler 1965). Boury-Esnault (1971, 1973) placed *Acarnus* in the Acarnidae also, but attributed the family to de Laubenfels (1936). The family Acarniidae de Laubenfels was erected for Gray's genus *Acarnia*, and several other small or poorly known genera (de Laubenfels 1936, p. 79), and is characterized by the presence of spiny megascleres only, which may be entirely diactinal, or a combination of diactinal and monactinal. Acarniidae de Laubenfels is neither a valid taxon (containing some freshwater Spongillidae together with marine axinellids) nor closely related to Acarnidae Topsent.

(2) Burton (1959) placed *Acarnus* with genera such as *Clathria, Plocamilla* Topsent, and *Echinodictyum* in a subfamily Clathriinae. Lévi (1973) and Vacelet *et al.* (1976) follow this system, and include the genus with the Family Clathriidae Hentschel (= Microcionidae Carter) on the basis that the microsclere complement of *Acarnus*, and the acanthostyles of *Acanthacarnus* are similar to those of clathriid genera.

(3) de Laubenfels (1936) included *Acarnus* with the family Tedaniidae Ridley and Dendy, placing emphasis on the presence of ectosomal diactinal megascleres, and he was followed by Tanita (1963), Hechtel (1965), Thomas (1970, 1973) and Hoshino (1981). De Laubenfels (1936) notes also that the Tedaniidae are closely related to the Myxillidae Hentschel, both of which have ectosomal diactinal megascleres, but he retains the families as separate. He suggests that the Tedaniidae have mainly smooth choanosomal megascleres and a higher degree of skeletal and fibre organization than the Myxillidae.

(4) Bakus (1966) and Van Soest (1984) consider that the ectosomal characteristics are of greater systematic importance than the megasclere or microsclere complement at the familial level of classification, and accordingly adopt de Laubenfels (1935) scheme. Both authors place *Acarnus* with the family Myxillidae, which includes the Tedaniidae as a subfamily only (after Topsent 1928). In support of this scheme, Van Soest (1984) notes that apart from the ectosomal characters shown by *Acarnus*, the reticulate skeletal architecture is close to other myxillids such as *Lissodendoryx* Topsent. He suggests further that the presence of acanthostyles does not necessarily confer a close affinity between taxa which possess them, because they are probably an unstable taxonomic character, and moreover they occur (independently) in several other families also. The use of ectosomal characters in sponge

taxonomy is consistent with the current differentiation of a large number of genera, particularly poecilosclerids, and even within the family Microcionidae (e.g. *Clathria*, *Dendrocia* and *Rhaphidophlus*).

AUSTRALIAN SPECIES

Acarnus thielei Lévi, 1958
(Figs 1–9, 40–43, Table 1)

Acarnus thielei Lévi, 1958, p. 35, text-fig. 33. Thomas, 1970, p. 43–6, text-figs 3a–g, 4.
Acarnus ternatus (in part): Thiele, 1903, pp. 960–61, fig. 27. Hentschel, 1912, pp. 372–73.

MATERIAL EXAMINED

NTM Z855, Z876: Channel Island, Middle Arm, Darwin, NT, 12°32.7'S, 130°52.5'E, 12–13 m depth, 20 August 1982, P. Alderslade, SCUBA.

DESCRIPTION (2 specimens)

SHAPE: Semi-vasiform to fan-shaped, 100–130 mm high, 110–200 mm wide (edge-to-edge), 3–20 mm thick. Basal attachment discoid, 45 mm in diameter, 10 mm thick.

COLOUR: Light yellow-brown alive (Munsell 2.5Y 8/4). A similar colour is maintained upon preservation.

SURFACE DETAILS: The external surface (exterior of 'vase') is roughened, with corrugations, ridges and semi-papillate projections, 4–10 mm high, pointed apically, usually bifurcate, occasionally rejoined (reticulated) and forming a more-or-less longitudinal array of raised ridges (appearing net-like). The entire external surface is optically hispid. The apical edge has a serrated appearance. The inner surface (interior of 'vase') is relatively optically smooth, with occasional folding, and bearing numerous oscula, 0.8–4.0 mm in diameter. Overall external appearance of these sponges is relatively thin but cavernous.

ECTOSOME: Microscopically the surface is moderately hispid, with cladotylotes extending beyond the surface (with clads pointing outwards), and with styles from the ascending fibres poking through the surface (mainly on the apices of ridges and corrugations). Occasionally smaller cladotylotes appear on the ectosome, at right angles to the surface, but these are confined mainly to the choanosome.

Lying on or just below the surface are amphitylotes, occurring in bundles or singly, sometimes absent from areas of the ectosome. Ectosomal spongin is moderate to light, slightly granular and containing numerous microscleres interdispersed with the amphitylotes.

Ectosomal layer varies from 25 to 90 μm in thickness.

CHOANOSOME: Skeletal architecture is clearly reticulate, consisting of ascending plumose multispicular tracts, ending blindly at the surface, and interconnected by a sub-renieroid reticulation of uni- or paucispicular tracts. Occasionally large multispicular tracts run parallel to the surface in some sections. Fibres are lightly invested with spongin, but heavily cored by styles (2–10 spicule widths in major tracts, 1–4 spicule widths in minor tracts). The sub-renieroid reticulation forms ovoid chambers, 80–550 μm in diameter; containing abundant interfibril spongin, and heavily invested with microscleres, smaller cladotylotes and auxiliary (smaller, thinner) styles. The fibres are echinated by cladotylotes in moderate numbers, with their clads projecting into the chambers. The smaller category of cladotylote is more abundant within the choanosome than is the larger variety.

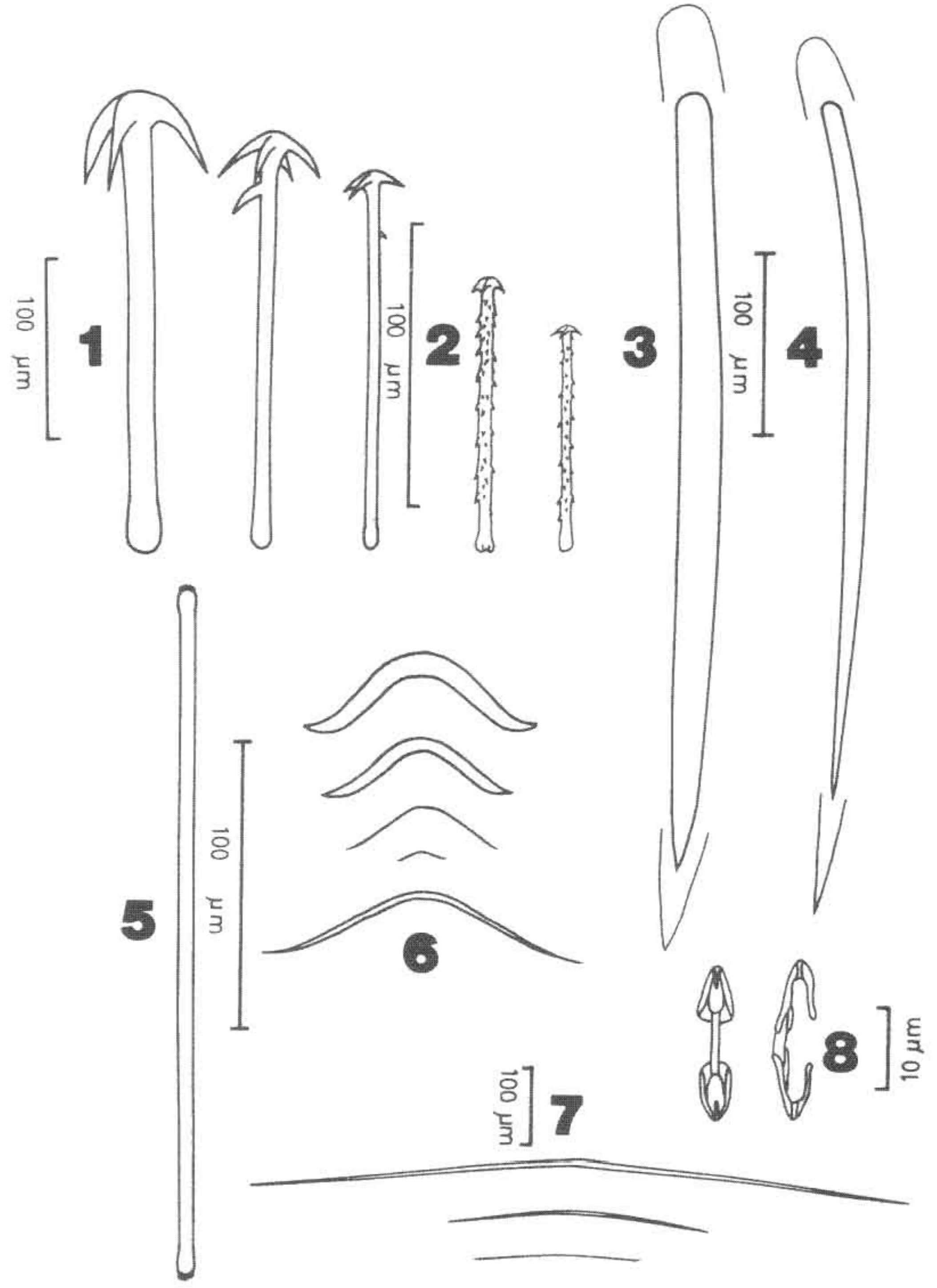
MEGASCLERES: Principal styles — moderately long, thick, hastate, sharply pointed, with rounded bases. Styles are often slightly bent near the base, but sometimes straight. Dimensions (N = 50): 407.1 μm long (mean) (range 319–464 μm), 21.6 μm wide (14–30 μm).

Auxiliary styles — moderately long, thin hastate to very faintly subtylote, slightly bent near the base, or straight. Dimensions (N = 50): 321.3 μm long (mean) (range 178–401 μm), 7.5 μm wide (2–11 μm).

Amphitylotes — moderately short, thin, straight, tylote ends rounded, slightly swollen, with microspined tips. Dimensions (N = 50): 250.1 μm long (mean) (range 194–313 μm), 4.4 μm wide (3–9 μm).

Cladotylotes I — moderately long, thick, straight, mostly smooth shaft, occasionally with few large spines on shaft; tylote base rounded, swollen; 3 clads on apical end. Dimensions (N = 50); 233.6 μm shaft length (mean) (range 85–270 μm), 9.5 μm shaft width (3–15 μm), 41.7 μm clad chord length (5–70 μm), 47.9 μm wide at clad end (10–70 μm).

Cladotylotes II — small, thin, straight, moderately but consistently spined shaft; tylote bases rounded or obtuse, often bearing small spines (giving the appearance of double ended cladotylotes); 3 clads on apical end, occasionally 4. Dimensions (N = 50); 86.3 μm shaft length (mean) (range 75–97 μm), 3.4 μm shaft width (2–4 μm), 3.3 μm clad chord length (2–5 μm), 7.4 μm wide at clad end (4–11 μm).



FIGS 1-8: *Acarnus thielei*; **1**. smooth cladotylotes (I); **2**. spined cladotylotes (II); **3**. principal style (inset: enlarged view of extremities); **4**. auxiliary choanosomal style (inset: enlarged view of extremities); **5**. ectosomal amphitylote; **6**. toxas (I); **7**. toxas (II), **8**. isochelae.

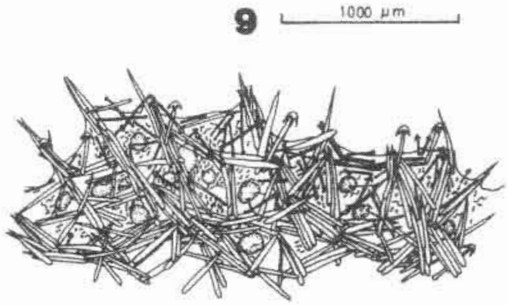


FIG. 9: *Acarnus thielei*, perpendicular section of peripheral skeleton.

MICROSCLERES: Toxas I — relatively small and thick, generous central bend, tricurvate with reflexed tips. Dimensions (N = 50): 76.6 µm chord length (mean) (range 33–151 µm), 4.9 µm wide at centre (1–9 µm).

Toxas II — small to very large, always thin, slightly bowed to almost straight (oxeote), tips not reflexed. Dimensions (N = 50): 341.6 µm chord length (mean) (range 34–960 µm), 2.4 µm wide at centre (0.5–7 µm).

Isochelae — small palmate. Dimensions (N = 50): 21.1 µm long (mean) (range 18–25 µm).

ECOLOGY

Both specimens were found on a rock reef which was covered completely by mud and sand, and in an area of high turbidity, with currents of up to 6 knots. There is some morphological variation between the two specimens described here. In particular, Z876 has a strikingly reticulated appearance due to the prominence of regular longitudinal striations on the surface (Fig. 41), whereas Z855 has an irregular raised surface (Fig. 40), and closely resembles *Echinodictyum mesenterinum* (Lamarck) in external appearance. Specimen Z876 has fewer echinating cladotylotes of either variety than does Z855. From the present observations and published records, it appears that *A. thielei* is a shallow-water species, with bathymetric distribution extending from the intertidal zone to 13 metres depth.

TABLE 1. Comparison between published records of *Acarnus thielei*. All measurements are given in micrometres, and denoted as length × width.

CHARACTER	AUTHOR				
	Lévi (1958) type-specimen	Thomas (1970)	Thiele (1903)	Hentschel (1912)	Present study
Colour alive:	orange	orange	?	light brown	light yellow brown
Shape:	massive, volumous, irregular	digitate on broad base	?	bulky, cylindrical or plate-like	fan-like to semi-vasiform
Skeleton:	renieroid reticulation	sub-renieroid reticulation	?	?	sub-renieroid reticulation
Styles:	260–270 × 6	301–452 × 13–24	350 × 15	300–384 × ?	178–464 × 2–30
Amphitylotes:	230 × 1	207–283 × 2–4	230 × 4	220–304 × ?	194–290 × 3–9
Cladotylotes I: (smooth)	150 × 4	188–245 × 8–12	160 × 2	160–272 × ?	85–270 × 3–15
Cladotylotes II: (spined)	90 × 2	75–96 × 3–4	90 × ?	95 × ?	75–97 × 2–4
Toxas I:	30–375 × ?	25–155 × 8	125 × ?	72–176 × ?	33–151 × 1–9
Toxas II:		84–584 × 3		658–948 × ?	34–960 × 0.5–7
Isochelae:	8–9	8–10 (scarse)	20	19–29	18–25
Locality:	Abulat, Red Sea	Palk Bay, Bay of Bengal, Indian Ocean	Ternate, Banda Sea, Indonesia	Aru I., Arafura Sea, Indonesia	Darwin, Australia

DISTRIBUTION

This species is restricted to the Indian Ocean (Indo-Australian) region. Localities are: Darwin, Australia (present study), Aru Island and Ternate, Molluccas, Indonesia (Thiele 1903, Hentschel 1912), Palk Bay, Bay of Bengal, India (Thomas 1970), and Abulat, Red Sea (Lévi 1958).

REMARKS

This species is diagnosed as *A. thielei* in having 2 different forms of cladotylote megascleres, the larger (mostly) smooth, the smaller invariably spined, at least two distinct forms of toxas, in specific details of spicule measurements, and in overall habit.

There are certain details of spicule dimensions found in the present material which differ from published records of *A. thielei* (Table 1). In particular, the Darwin specimens have a smaller category of style, here denoted as the auxiliary styles, which is mainly found outside the fibres. These are probably young forms of the larger, or principal styles, and both forms are combined and considered together in the following Tables. *Acarnus thielei* sensu lato has a broad range of isochelae sizes. Specimens from the western Indian Ocean (Lévi 1958; Thomas 1970) have small isochelae (8–10 μm long), whereas eastern Indian Ocean specimens (Thiele 1903; Hentschel 1912; present study) have larger isochelae (19–29 μm long). It is probable that this difference between the two populations is of little taxonomic significance, and indeed Lévi (1958, p. 36) in synonymizing Thiele's (1903) and Hentschel's (1912) specimens of *A. ternatus* with *A. thielei* considers that cladotylote morphology and size are more important diagnostic characters than the size of isochelae.

Thomas (1970) notes that the smaller cladotylotes of the Indian specimen have smooth bases whereas those of the Darwin specimens are frequently spined, occasionally resembling double-ended cladotylotes.

Acarnus thielei has close affinities with two other species, *A. erithacus* and *A. innominatus* in having both larger smooth and smaller spined varieties of cladotylotes. On that basis Lévi (1963) assigned all 3 species to his group III *Acarnus*. It is difficult to separate these 3 species by their spicule dimensions alone. All show considerable intraspecific variability and consequently overlap in their ranges of spicule measurements (Table 5). Generally, *A. thielei* may be differentiated from the other 2 species by its habit (massive, flabellate, plate-like or digitate, versus encrusting, sometimes massively encrusting, respectively). *Acarnus erithacus* has predominantly acanthose cladotylotes, which differentiates it from *A. innominatus* (see below) (Van Soest 1984).

Acarnus innominatus Gray, 1867
(Figs 10–18, 44, Table 2)

unidentified sponge, Bowerbank, 1864, pp. 23, 33, 122, 239, pl. 3, figs 73–76, pl. 18, fig. 292.
Acarnus innominatus Gray, 1867, p. 544. Carter, 1871, pp. 269, 273–4. Arndt, 1927, pp. 133–53, pl. 3, fig. 5. de Laubenfels, 1936, pp. 92–93, pl. 12, fig. 2. Lévi, 1963, pp. 48–49, text-fig. 55, pl. 7G. Alcolado, 1976, p. 5. Randall and Hartman, 1968, pp. 218, 219, 223. Van Soest, 1984, pp. 61–3, text-fig. 22, pl. 5, figs 6–9.
? *Fonteia anomala* Gray, 1867, p. 544.
Acarnus carteri Ridley, 1884, pp. 453–4 (footnote).

MATERIAL EXAMINED

NTM Z2234: Dudley Point Reef, East Point Fish Reserve, Darwin, NT, 12°25.0'S, 130°49.1'E, intertidal, 8 March 1985, J.N.A. Hooper.

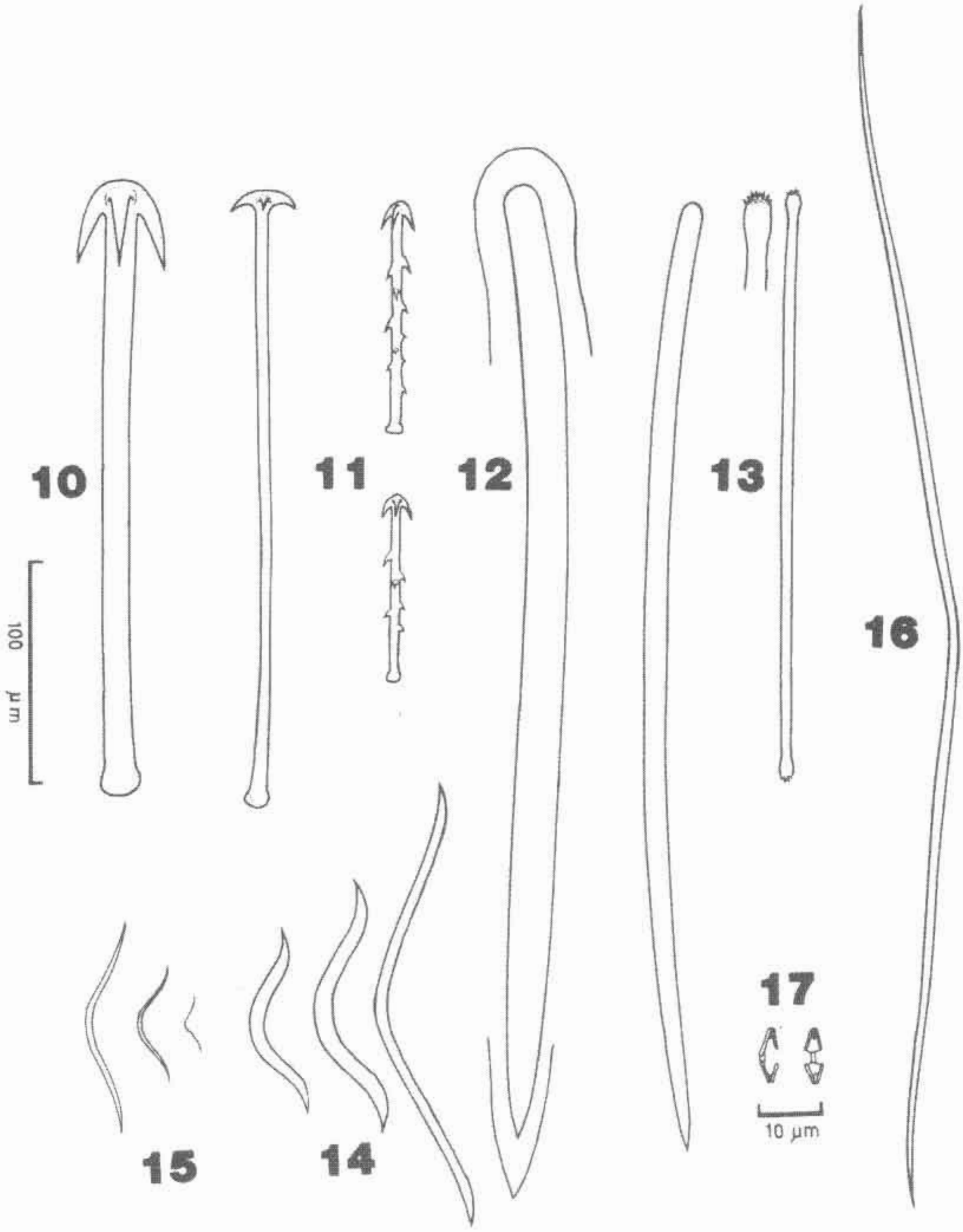
DESCRIPTION

SHAPE: Thickly encrusting, sprawling across dead coral substrate, covering an area of approximately 45 cm^2.

COLOUR: Bright orange-red alive (Munsell 5R 5/12), yellow-brown in ethanol (5YR 7/10).

SURFACE DETAILS: Surface is of variable thickness, shaggy, with irregular papillose projections up to 3 mm high and 3 mm in diameter, which are optically hispid. Longitudinal grooves meander across the surface, often with a membraneous ectosomal covering, approximately 1.6 mm wide and of variable depth. Oscula are abundant, scattered, slightly raised above the surface, 1.1–3.4 mm in diameter, sometimes with a trace of silt around the margins of the lip.

ECTOSOME: Microscopically the surface is microconulose and hispid, with the clad-ends of the large cladotylotes extending beyond the surface. Few principal styles poke through the ectosome. The ectosome has a prominent but often confused tangential layer of amphitylotes lying mainly parallel with the surface, occasionally at right angles to it. Amphitylotes predominantly occur in bundles of up to 5 spicules abreast, sometimes lying singly. Ectosomal spongin is light, yellow-brown, granular and contains numerous microscleres, often arranged in tracts just below the surface. Small particles of detritus (silt, sand grains) are included in parts of the ectosome, but generally the area is clear of inorganic debris. Ectosomal layer varies from 15 to 40μm in thickness.



FIGS 10–17. *Acarnus innominatus*. **10**. smooth cladotylotes (I); **11**. spined cladotylotes (II); **12**. choanosomal styles (inset: enlarged view of extremities); **13**. ecotosomal amphitylote (inset: enlarged view of extremity); **14**. thick toxas (I); **15**. short, thin toxa (II); **16**. long, thin toxa (III); **17**. isochelae.

CHOANOSOME: Skeletal architecture consists of a confused renieroid reticulation of spicule tracts or single spicules. No spongin fibres are visible, but it is possible they are extremely light and cannot be differentiated from the abundant type B mesohyl spongin. Tracts containing 1–5 principal styles abreast are bound together by abundant, loose interfibril spongin at their nodes, and surrounded by relatively heavy deposits of type B spongin. Smooth (I) and spined (II) cladotylotes echinate tracts, particularly at the nodes. Choanosomal renieroid reticulation becomes semi-plumose in the subectosomal region, with single spicule tracts ascending to the surface, ending blindly in microconules, and producing radiating tufts of cladotylotes protruding through the ectosome. Choanosomal spongin is mainly clear of detritus, and meandering tracts of granular spongin, collagenous spongin and microscleres form chambers and canals of variable size (range 70–150 μm in diameter).

MEGASCLERES: Principal styles — moderately long, thick, mostly hastate, occasionally slightly fusiform or even subtylote, usually slightly curved near the basal end, sometimes straight; bases smooth. Dimensions (N=25): 391.5 μm long (mean) (range 267–453 μm), 16.8 μm wide (6–21μm).

Amphitylotes — moderately short, thin, straight, tylote ends swollen, with microspined tips. Dimensions (N=25):265.5μm long (mean) (range 247–283μm), 3.7μm wide (3–4μm).

Cladotylotes I — moderately long, thick, straight shaft, always smooth; tylote ends with rounded or slightly asymmetrical bases; 3–4 clads on apical end. Dimensions (N=25): 258.9μm shaft length (mean) (range 222–283μm), 11.0μm shaft width (6–14μm), 41.0μm clad chord length (18–49μm), 38.3μm wide at clad end (19–46μm).

Cladotylotes II— small, thin, straight, with lightly spined shafts and large spines; rounded or asymmetrical bases; 4 clads on apical end. Not common; rare or absent in areas of very thin encrustation. Dimensions (N=25): 99.6μm shaft length (mean) (range 72–141μm), 3.9μm shaft width (3–5μm), 13.7μm clad chord length (9–22μm), 14.3μm wide at clad end (11–18μm).

MICROSCLERES: Toxas I — relatively small, thick, generously rounded at centre, sometimes almost straight, with reflexed tips. Moderately common. Dimensions (N=25): 90.6μm chord length (mean) (range 45–249μm), 3.2μm wide at centre (2–5μm).

Toxas II — small, thin, of similar morphology as previous category; possibly a developmental stage of that category. Very common. Dimensions (N=25): 39.7μm chord length (mean) (range 21–79μm), 1.3μm wide at centre (1–2μm).

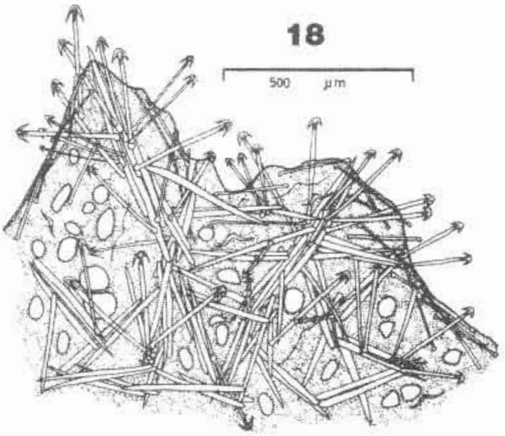


FIG. 18: *Acarnus innominatus*, transverse section of peripheral skeleton.

Toxas III — long, moderately thick, mostly straight with small-angled central curvature, and with reflexed tips. Moderately common. Dimensions (N=25): 430.3μm chord length (mean) (range 192–586μm), 2.2μm wide at centre (1.5–3 μm).

Isochelae — very small, palmate. Abundant. Dimensions (N=25): 8.6μm long (mean) (range 6–10μm).

ECOLOGY

Found on the undersurface of a dead coral boulder, on an intertidal coral platform, close to the shoreline, and in an area of high sedimentation (mud, silt). Associated with (growing next to) sponges (*Rhaphidophlus* and *Haliclona* spp.), an encrusting coralline algae, and colonial ascidians (possibly *Pycnoclavella*). Previous records of *A. innominatus* suggest that the species is probably restricted to dead corals, with a bathymetric distribution extending from the intertidal zone to 29 metres depth (de Laubenfels 1936; Lévi 1963; Van Soest 1984).

DISTRIBUTION

The present record considerably extends the known distribution of *A. innominatus*. Further studies may show that the species is cosmopolitan, but current records indicate a patchy distribution: Gulf of Mexico and Caribbean Sea (Curaçao,

TABLE 2. Comparison between published records of *Acarnus innominatus*. All measurements are given in micrometres, and denoted as length × width.

CHARACTER	AUTHOR					
	Carter (1871)	Ridley (1884)	deLaubenfels (1936)	Lévi (1963)	Van Soest (1984)	Present study
Colour alive:	?	?	bright orange to red	scarlet and reddish	red	bright orange-red
Shape:	encrusting, flat, spiculous	?	massive, amorphous, encrusting	massive encrusting	thinly to massively encrusting	thickly encrusting
Skeleton:	polyhedral (renieroid)	?	ascending plumose, rarely anastomosing	anastomosing paucispicular fibres	renieroid reticulation, plumose tracts	confused renieroid reticulation and semi-plumose tracts
Styles:	340.3 × ?	present	280–300 × 12–13	175–340 × 6–20	340–459 × 11–22	267–453 × 6–21
Amphitylotes:	?	280 × 4.5	180 × 2	130–230 × 3–4	217–262 × 2.5–4	247–283 × 3–4
Cladotylotes I: (smooth)	244.9 × ?	present	200 × 6	180–230 × 8	217–294 × 7–12	222–283 × 6–14
Cladotylotes II: (spined)	95.3 × ?	absent?	80 × 2	85–90 × 2	110–115 × 3 not common	72–141 × 3–5 not common
Toxas I:	81.7 × ?	130 × 4.2	40–400 × 1–3	70–80 × 3–5	57–158 × 2–4	45–249 × 2–5
Toxas II:					38–68 × ?	21–79 × 1–2
Toxas III:				present	200–402 × ?	192–586 × 1.5–3
Isochelae:	13.6	16–24	12–15	11	9–18	6–10
Locality:	West Indies	West Indies	Tortugas, Florida	South Africa	Curaçao	Darwin

Cuba, Florida, West Indies) (Gray 1867; Carter 1871; Ridley 1884; Arndt 1927; de Laubenfels 1936; Alcolado 1976; Randall and Hartman 1968; Van Soest 1984), South Atlantic-Indian Oceans (Cape Town and Mossel Bay, South Africa) (Lévi 1963), and Arafura Sea, Indo-Pacific (Darwin, Northern Territory).

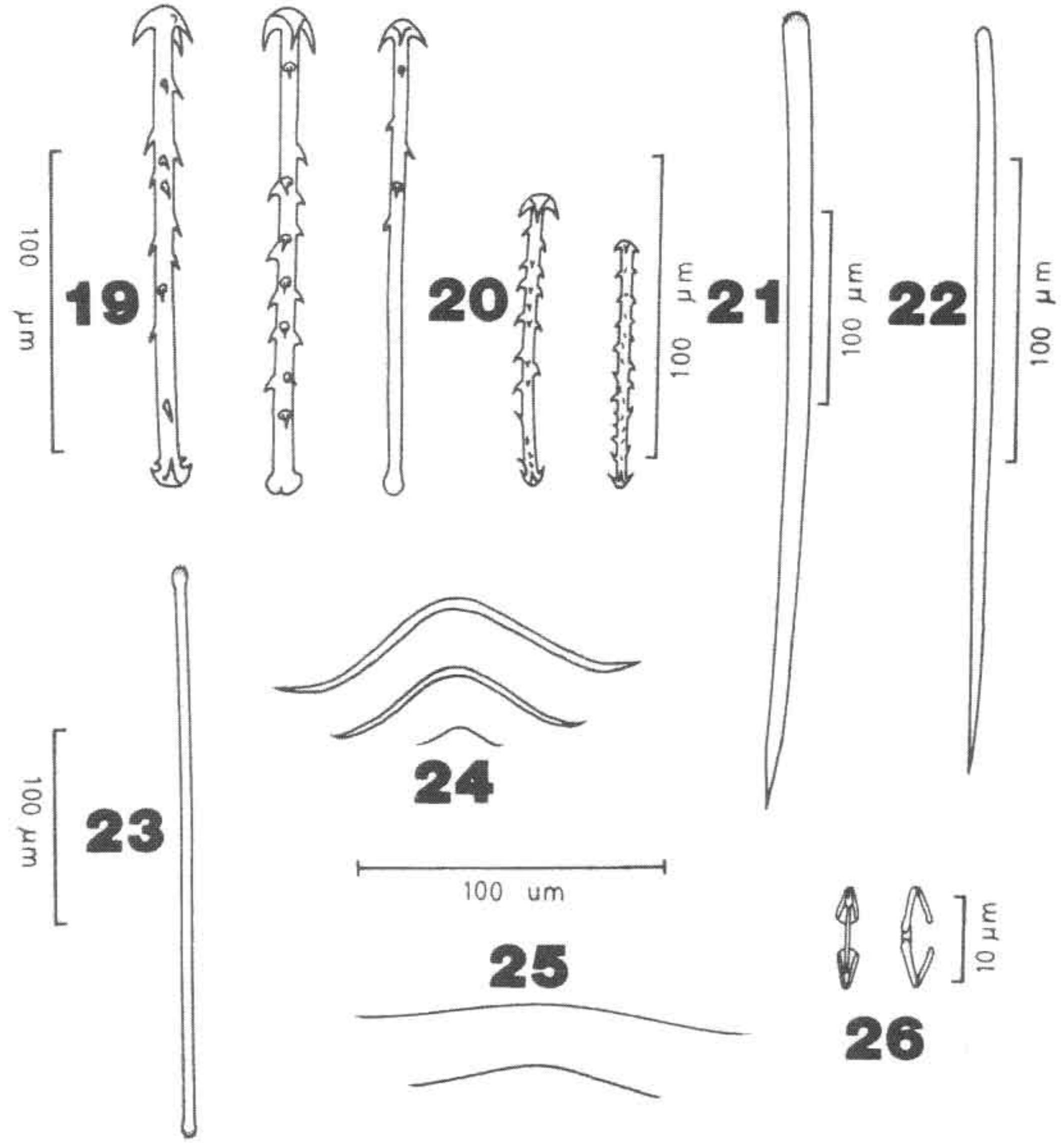
REMARKS

This specimen is easily placed in Levi's group III *Acarnus* in having both smooth and spined cladotylotes, and on the basis of published descriptions the specimen is diagnosed as *A. innominatus* (refer to Table 2). The species is closest to *A. erithacus*, which has predominately acanthose cladotylotes, but which are rare in *A. innominatus* (Van Soest 1984). Records of *A. erithacus* show a large size range for all spicule categories, and on that basis alone the two species cannot be separated reliably. Details such as the proportion of smooth and spined cladotylotes, and the form of the longer variety of toxa offer a tentative basis for differentiating these closely related species. Similarly, *A. innominatus* is difficult to distinguish from *A. thielei* on the sole basis of spicule size, and a tentative character used for the separation of those two species is growth form (see above). On that basis I have little hesitation in separating the Darwin specimens of *A. innominatus* and *A. thielei*, which have quite distinct gross morphologies. However, a study on the ecophenotypic variability of all three species (*A. innominatus, A. erithacus*, and *A. thielei*) may show them to be conspecific.

Acarnus tortilis Topsent, 1892

(Figs 19–27, 45, Table 3)

Acarnus tortilis Topsent, 1892, pp. 24–5. Topsent, 1897, p. 450. Topsent, 1904, p. 171, pl. 14, fig. 8. Dendy,



FIGS 19–26: *Acarnus tortilis*. **19**. spined cladotylotes (I); **20**. spined cladotylotes (II); **21**. principal choanosomal styles; **22**. auxiliary choanosomal styles; **23**. ectosomal amphitylote; **24**. toxas (I); **25**. toxas (II); **26**. isochelae.

1916, pp. 130–31. Topsent, 1925, pp. 661–2. Topsent, 1929, pp. 19–20, text-figs 1–2. Topsent, 1934, p. 72. Topsent and Olivier, 1943, p. 2. Sarà, 1960, p. 461. Ruetzler, 1965, p. 32. Boury-Esnault, 1971, p. 323. Vacelet *et al.*, 1976, pp. 74–5, text-fig. 50. Desqueyroux-Faundez, 1981, p. 758, Table 2.

MATERIAL EXAMINED

QM GL706 (fragment NTM Z1538): Outer Barrier, East of Lizard Island, Northeast Queensland, 14°42.0'S, 145°45.0'E, 10 m depth, September 1979, Queensland Fisheries Service, trawl.

DESCRIPTION

SHAPE: Flat, thick, sprawling, plate-like encrustation; fragmented; rounded smooth margins, 43 × 75 mm, approximately 4 mm thick.

COLOUR: Grey-brown in ethanol (Munsell 7.5YR 6/2).

SURFACE DETAILS: Surface is rough, where intact, and mostly obscured by detritus incorporated into sponge. The texture is easily crumbled in the preserved state.

ECTOSOME: Microscopically the surface is rough, slightly hispid due to the presence of large cladotylotes projecting outwards, and mainly encrusted with detritus. Amphitylotes are found in loose bundles lying parallel to the surface, lying on or just below the ectosome and in no apparent order, occuring haphazardly throughout the choanosome also. Ectosomal spongin is light brown, non-fibrous, granular, and mostly encrusted with debris.

CHOANOSOME: Skeletal architecture is loosely reticulate, verging on halichondroid due to the reduced, encrusting habit of the sponge. The distinctive feature of the choanosome is the presence of large quantities of detritus incorporated into the skeleton. The size of inorganic particles varies considerably, and particles are bonded together by light spongin. Where visible, spongin fibres are light, forming a loose reticulation containing ovoid chambers, 100-180μm in diameter. Spongin fibres are 50-80μm thick, clearly lamellated, yellow-beige in colour, and cored with principal styles in paucispicular tracts, lying 1-4 spicules abreast. Spongin between the fibres is light, slightly granular, abundant in places, and contains microscleres and smaller (auxiliary) styles. Isochelae are found scattered throughout the choanosome, in association with interfibril spongin, but occur in extremely heavy concentrations in places, particularly lying just below the ectosome. Spongin fibres are echinated by cladotylotes of both varieties. Cladotylotes are seen in interfibril spongin, and adhering to the surface of detrital particles also.

MEGASCLERES: Principal styles — moderately long and thin, mostly straight or very slightly curved near the apical end, hastate, sharply pointed, with evenly rounded bases. Bases are smooth or have numerous microspines on basal extremities. Dimensions (N = 25): 293.8μm long (mean) (range 214-334μm), 11.4μm wide (9-16μm).

Auxiliary styles — moderately long, thin, hastate, sharply pointed, with evenly rounded smooth bases. Dimensions (N = 25): 248.6μm long (mean) (range 215-279μm), 5.2μm wide (3-7μm).

Amphitylotes — long, thin straight, slightly swollen tylote ends, with numerous microspines covering extremities, or occasionally smooth. Dimensions (N = 25): 288.4μm long (mean) (range 222-363μm), 5.3μm wide (4-7μm).

Cladotylotes I — moderately small, thin with straight shafts. Shaft is invariably echinated by moderately large spines (3-10μm in length). Clads occur on one or both ends. Principal clads are variable in size and 4 in number. The basal end has small clads (1-4μm long if present), or has a rounded bulbous smooth tylote base. Dimensions (N = 25): 175.9μm shaft length (mean) (range 151-212μm). 6.2μm shaft width (4-8μm), 16.0μm clad chord length (12-22μm), 18.2μm wide at clad end (12-22μm).

Cladotylotes II — straight, short, thin, mostly heavily echinated with small spines along the shaft. Spines 1-3μm long. Clads occur on 1 or both ends, and are similar in morphology to those of the larger variety. Main clads are variable in length, and 4 in number. Dimensions (N = 25): 80.7μm shaft length (mean) (range 58-109μm), 3.8μm shaft width (3-5μm), 8.2μm clad chord length (4-12μm), 11.2μm wide at clad end (8-17μm).

MICROSCLERES: Toxas I — relatively thick, generously curved, tricurvate, with reflexed tips: moderately uncommon. Dimensions (N = 25): 68.4μm chord length (mean) (range 44-110μm), 2.4μm wide at centre (1-4μm).

Toxas II - thin, long, almost oxeote or only slightly curved, with a slight central bend; tips not reflexed. Very rare. Dimensions (N = 5): 162.5μm

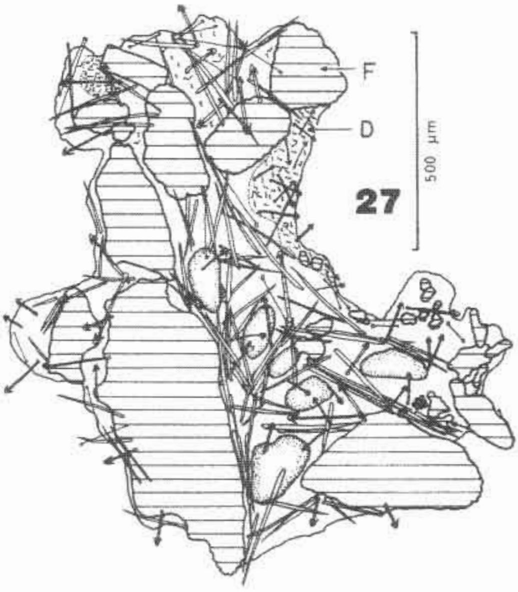


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FIG. 27: *Acarnus tortilis*; perpendicular section through choanosome. D: Deposits of heavy loose spongin, cored by microscleres; F: foreign particles incorporated into skeleton.

chord length (mean) (range 150–265μm), 1.5μm wide at centre (1–2μm).

Isochelae — small, palmate, very abundant. Dimensions (N = 25): 11.1μm long (mean) (range 7–13μm).

ECOLOGY

This specimen was apparently associated with a dead coral and sand substrate. From published records and present observations, the bathymetric distribution of *A. tortilis* extends from the intertidal zone to 54 metres depth.

DISTRIBUTION

Acarnus tortilis is a widely distributed, almost cosmopolitan species, recorded from the North Atlantic and Indian Oceans (Topsent 1904, 1929; Vacelet *et al.* 1976), Mediterranean, Adriatic, Arabian, Banda, Biban and Oman Seas (Boury-Esnault 1971; Dendy 1916; Ruetzler 1965; Sarà 1960; Topsent 1892, 1897, 1925, 1929, 1934; Topsent and Olivier 1943). The specimen described above is the first record for the species in the Pacific Ocean.

REMARKS

This species is easily diagnosed as *A. tortilis* in having two varieties of cladotylotes, both of which have profusely spined shafts, an encrusting habit incorporating foreign particles into the skeleton, and in specific details of spicule dimensions (Table 3).

Lévi (1963) placed *A. tortilis* in his group II *Acarnus* on the basis of having spined cladotylotes only. *Acarnus tortilis* is closest to *A. topsenti* in this respect, and differs from that species mainly by its habit (encrusting versus flabellate-digitate, respectively), in having two categories of cladotylotes, and by the specific dimensions of spicules (Table 4). The stability of those diagnostic characters is presently unknown, particularly with regard to known intraspecific geographic variation in spicule dimensions, with some spicule categories overlapping between the species (Table 5).

TABLE 3. Comparison between published records of *Acarnus tortilis*. All measurements are given in micrometres, and denoted as length × width.

CHARACTER	AUTHOR				
	Topsent (1892) type-specimen	Topsent (1904)	Topsent (1925)	Vacelet *et al.* (1976)	Present Study
Colour alive:	brown	blackish	reddish	red	(grey-brown in ethanaol)
Shape:	thinly encrusting	encrusting	encrusting	encrusting	encrusting
Skeleton:	loosely reticulate	?	?	?	loosely reticulate to halichondroid
Styles:	500 × 10	400–450 × 8–10	515–550 × ?	300–450 × 5–10	214–334 × 3–16
Amphitylotes:	400 × ?	370–440 × 4–5	307–360 × ?	250–350 × 3.5–6	222–363 × 4–7
Cladotylotes I: (spined)	up to 220 × 5	125–170 × 4–5	75–160 × ?	65–225 × 2.5–5	151–212 × 4–8
Cladotylotes II: (spined)					58–109 × 3–5
Toxas I:	present	100 × 4	130 × ?	60–80 × 4–5	44–110 × 1–4
Toxas II:	present	220 × 1	210 × ?	15–160 × ?	150–265 × 1–2
Isochelae:	15	15	22	8–10	7–13
Locality:	Cape Abeille, Gulf of Lyon Mediterranean	Terceira I., Azores, North Atlantic	Nisida, Gulf of Naples, Mediterranean	Tuléar, Mozambique Channel, Indian Ocean	East of Lizard I., GBR, NE Queensland

Another character which differentiates these allied species is the degree of development of the fibrous skeleton. *Acarnus topsenti* has strongly developed horny fibres, whereas those of *A. tortilis* are reduced and are invested with light spongin only. The taxonomic value and stability of that character remains to be determined, as it is possible that the reduction of horny fibres in *A. tortilis* is related to its reduction in growth form.

As an indication of their close affinities, and supporting a possible combination of the two species, is the fact that the bases of the principal styles in both species frequently have a light covering of microspines. This character is consistent throughout the entire geographic range of *A. tortilis* (Topsent 1892, 1897, 1904, 1925; Dendy 1916; Vacelet *et al.* 1976; present study), and Dendy (1922) records it for *A. topsenti* also. No other species of *Acarnus (Acarnus)* have this characteristic, although it is present in *Acarnus (Acanthacarnus)* species. It is clear that the relationship between *A. tortilis* and *A. topsenti* is closely analogous to that of *A. thielei* and *A. innominatus*, as discussed above. Unfortunately the type-specimen of *A. tortilis* is presently unavailable for re-examination, requiring a visit to the Paris Museum (Lévi pers. comm.). Consequently it is not possible to make a firm decision on whether or not the two species are conspecific. Vacelet *et al.* (1976) recommended that the two species should be maintained as separate, and his decision is supported here on a tentative basis through comparison between the Queensland specimen of *A. tortilis* and the syntype of *A. topsenti* (see below).

De Laubenfels (1927) and Bakus (1966) suggest that *A. erithacus* is closely related to *A. tortilis* in skeletal architecture, but this affinity may be a result of a reduced skeletal architecture of both species, owing to their encrusting habits. *Acarnus erithacus* is easily differentiated from *A. tortilis* by the presence of a larger category of smooth cladotylote megasclere, and in having a heavier fibrous skeleton.

Acarnus toxeatus should be included in Lévi's (1963) group II *Acarnus* also, in having spined cladotylotes only, but differs from *A. tortilis* in having larger spicules of most categories (except isochelae), and three distinct categories of toxas (Table 5).

Acarnus ternatus Ridley, 1884

(Figs 28–36, 46–48, Table 4)

Acarnus ternatus Ridley, 1884, pp. 453, 615, pl. 42, figs b,b'. Ridley and Dendy, 1887, p. 159. Dendy, 1905, p. 177, pl. 8, fig. 4. Lévi, 1958, p. 35, text-fig. 32. Bruce, 1976, p. 128.

non *Acarnus ternatus*: Thiele, 1903, pp. 960–61, fig. 27. Hentschel, 1912, pp. 372–3.

Acarnus wolffgangi Keller, 1889, pp. 399–400, pl. 24, figs 53–58. Kieschnick, 1896, p. 533. Thiele, 1903, pp. 960-61, fig. 26.

MATERIAL EXAMINED

SYNTYPE: BM 1882.2.23.248: West Island, Torres Strait, North Queensland, 10°22'S, 142°04'E, 14 m depth, ? April–October, 1881. H.M.S. 'Alert', dredge.

OTHER MATERIAL: QM GL2773 (fragment NTM Z1584), QM GL2777 (fragment NTM Z1590): 20 kilometres northeast of Green Island, off Cairns, Great Barrier Reef, northeast Queensland, 16°43.0'S, 146°03.0'E, 80 m depth, 21 February 1979, L. Cannon and B. Goeden (stn. W5 Cairns preliminary inter-reef survey), dredge. QM GL715 (fragment NTM Z1532): Hall-Thompson Reef, East of Innisfail, Great Barrier Reef, Northeast Queensland, 17°34.0'S, 146°27.5'E, 66 m depth, date of collection unknown, Queensland Fisheries Service, dredge or trawl.

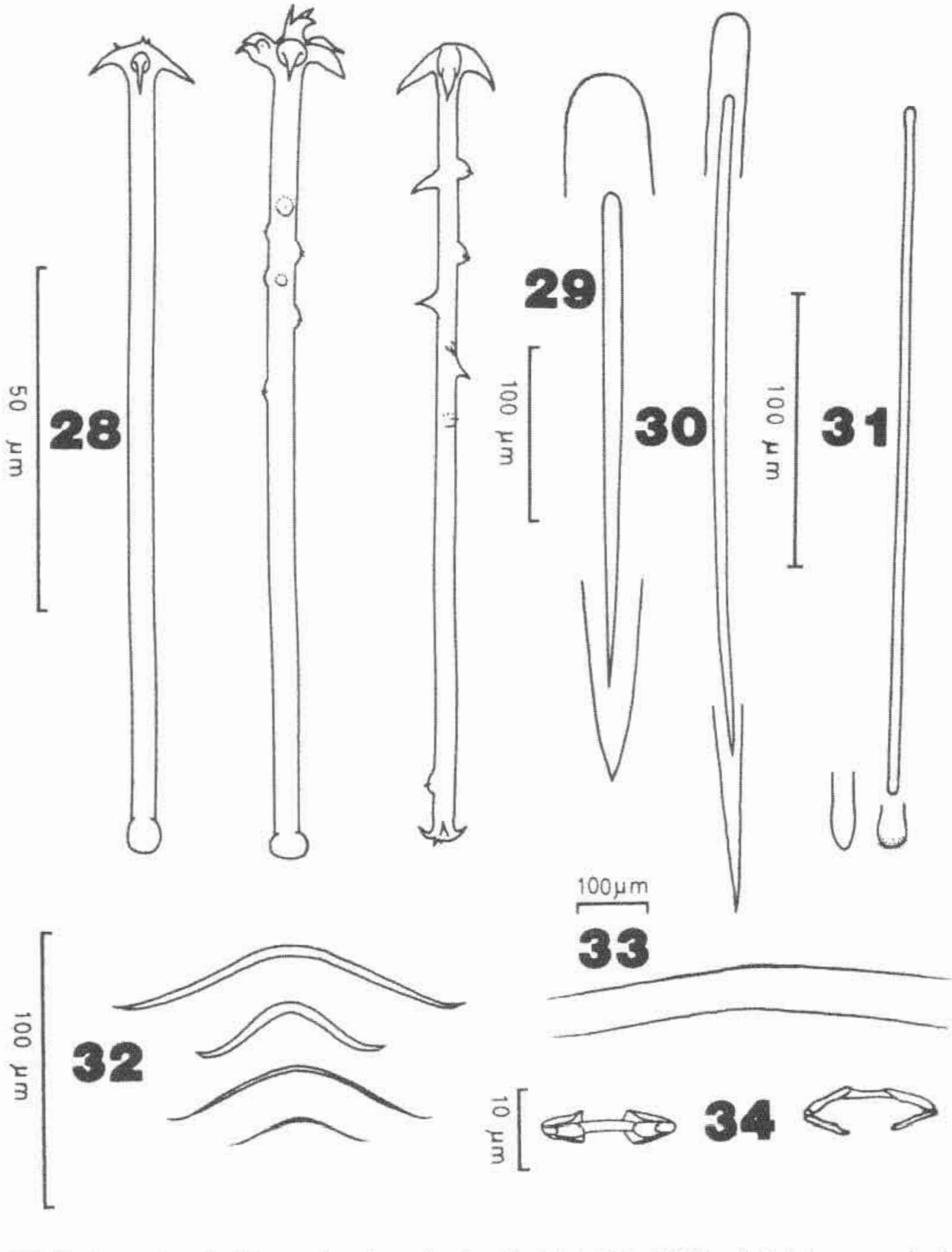
REDESCRIPTION OF TYPE-SPECIMEN

DETAILS OF EXTERNAL MORPHOLOGY: refer to Ridley (1884, p. 453).

ECTOSOME: The ectosomal region has a multispicular, sometimes confused, but mostly tangential layer of amphitylotes lying on or just below the surface. The surface is raised into conules in places, and is lightly hispid from the tips of cladotylotes and occasionally styles poking through the ectosome.

CHOANOSOME: The skeletal architecture is a heavy renieroid to sub-renieroid reticulation of thick fibres (35–120 μm in diameter), cored by uni- to multi-spicular tracts which do not occupy the entire diameter of fibres. Major tracts appear to run longitudinally, cored by 5–10 spicules abreast, and are interconnected by smaller ascending tracts, containing 1–5 spicules abreast. There is only slight plumose divergence of fibres in the subectosomal region, and fibres are predominantly anastomosing. Chambers formed by the fibre reticulation are subrectangular to ovoid, 112–435 μm in diameter. Cladotylotes are not abundant, variable in size, and echinate fibres at right angles to spicule tracts. The mesohyl matrix has heavy deposits of debris scattered between the fibres, but there are also many large cavernous chambers formed by fibre anastomoses clear of debris and spicules. Loose, granular spongin between the fibres is mostly paucispicular.

MEGASCLERES (N = 25): Principal styles — robust, hastate, slightly curved at the centre, entirely smooth shafted, and with evenly rounded bases having little or no tylote swelling; tips taper



FIGS 28-34: *Acarnus ternatus*. **28.** smooth and occasionally-spined cladotylotes (I); **29.** principal choanosomal style (inset: enlarged view of extremities); **30.** auxiliary choanosomal style (inset: enlarged view of extremities); **31.** ectosomal amphitylote (inset: enlarged view of spined and smooth ends); **32.** toxas (I); **33.** toxas (II): **34.** isochelae.

to sharp points, or are sometimes blunt or rounded. 325.8 μm long (mean) (range 265–419 μm), 11.8 μm wide (7–14 μm).

Auxiliary styles — not abundant; of thinner and shorter dimensions than the previous category, and probably young forms of those spicules. 201.4 μm long (mean) (range 128–285 μm), 2.4 μm wide (2–4 μm).

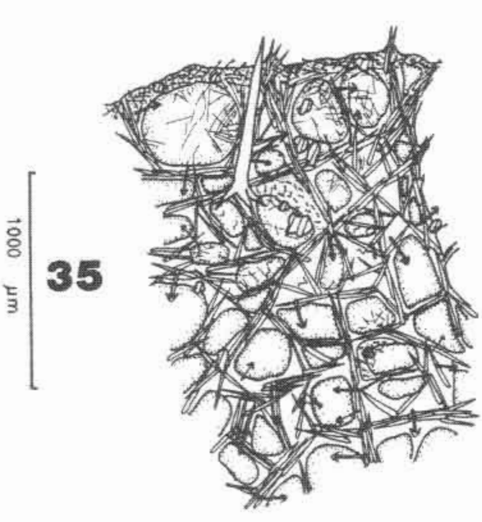
Amphitylotes — thin, moderately long, straight, with only slightly tylote bases, and with very few or no microspines on apices. 248.4 μm long (mean) (range 224–268 μm), 3.5 μm wide (3-4.5 μm).

Cladotylotes — variable in size, and not abundant; straight or slightly curved shaft, mostly smooth, but some spicules have occasional, isolated spines on the shaft; bases are prominently tylote, mostly smooth and evenly rounded, or sometimes with apical spines or tuberculate; 3 clads on apical end, which are of variable length; the apex of the clad end is mostly smooth and evenly rounded. 182.2 μm shaft length (mean) (range 63–233 μm), 7.0 μm shaft width (2–11 μm), 21.8 μm clad chord length (2–34 μm), 23.7 μm wide at clad end (5–36 μm).

MICROSCLERES (N = 25): Toxas I — short to moderately long, variable in thickness, mostly generously curved at the centre, and reflexed at the tips. 112.9 μm long (mean) (range 12–233 μm), 3.5 μm wide (0.8–6 μm).

Toxas II — short to very long, moderately thin, only slightly curved at the centre, and only slightly reflexed, sometimes oxeote. 262.2 μm long (mean) (range 19–708 μm), 2.0 μm wide (0.5–5 μm).

Isochelae — palmate, variable in size. 16.4 μm long (mean) (range 8–22μm).



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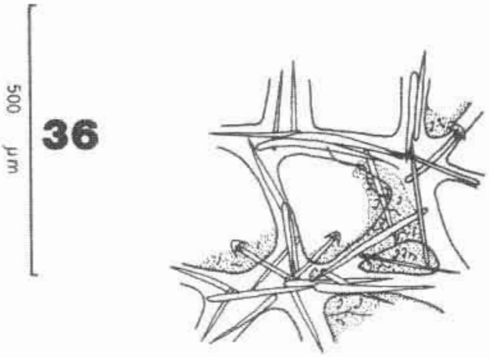

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FIGS 35–36: *Acarnus ternatus*. **35**. perpendicular section of peripheral skeleton; **36**. enlarged view of choanosomal fibres.

DESCRIPTION OF OTHER SPECIMENS

SHAPE: plate-like, thickly flabellate, probably semi-vasiform, fragmented, basal attachment not collected. 50–110 mm wide edge-to-edge, 55–83 mm high, 3.5–5 mm thick. One smaller atypical specimen (QM GL715) has solid tubulo-digitate projections arising from a semi-encrusting, bulbous base, and is growing on a bivalve shell and pebbles. Base 35 mm wide, 54 mm high at highest point; digits short, twisted, 10–18 mm high, 4–13 mm in diameter.

COLOUR: light brown (Munsell 2.5Y 8/4) to brown-grey in ethanol (10R 6/2).

SURFACE DETAILS: External surface of sponge (exterior of 'vase' or 'plate') is roughened, with numerous surface projections, which are mostly low and rounded, extending not more than 20 mm from the sponge surface, and forming irregular meandering tracts. The internal surface (interior of 'vase' or 'plate') is optically smooth, and contains many oscula of 1–6 mm in diameter. The entire surface is optically hispid, and the overall flabellate/vasiform habit resembles closely that of *Acarnus thielei* from Darwin. The smaller specimen has a dusty appearance due to sand debris embedded in the ectosome.

ECTOSOME: The ecotosome is mostly even microscopically, with few conules formed by fibre endings from the choanosomal skeleton poking through the surface, and with the tips of styles rendering the surface hispid. Few cladotylotes were observed poking through the ectosome. The ectosome has a thin tangential layer of amphitylotes lying on or just below the surface. The ectosome also has a thin layer of detritus

TABLE 4. Comparison between published records of *Acarnus ternatus*. All measurements are given in micrometres, and denoted as length × width.

CHARACTER	AUTHOR					
	Ridley (1884)* type-specimen	Keller (1889)	Thiele (1903)	Dendy (1905)	Lévi (1958)	Present Study
Colour alive:	reddish-brown (preserved)	matt blue	?	brown (dry)	red	light brown-grey brown (preserved)
Shape:	clathrous, rounded, anastomosing tubes	massive, rounded rough exterior surface	?	thickly flabellate, lobed margins, to irregularly branched	massive irregular, folded surface	flabellate-vasiform to tubulo-digitate semi-encrusting rough surface
Skeleton:	heavy renieroid to sub-renieroid reticulation	reticulate, strongly developed fibres	?	strongly developed fibres	reticulate	renieroid to sub-renieroid reticulation
Styles:	128–419 × 2–14	305–320 × 15	450 × 25	300 × 16.4	275–310 × 6	139–281 × 2–14
Amphitylotes:	224–268 × 3–4.5	approx. 220 × ?	260 × 4	220 × 3.5	240 × 1.5	200–280 × 2–5
Cladotylotes I: (smooth)	63–233 × 2–11	200–220 × 10	275 × 12	210 × 12	180–200 × 5	85–205 × 2–6
Toxas I:	12–233 × 0.8–6	up to 600 × 3	60–250 × ?	up to 152 × 8	35–130 × 1–3	41–266 × 1–6
Toxas II:	19–708 × 0.5–5		900 × ?	740 × 4	375–600 × ?	80–770 × 0.5–5
Isochelae:	8–22	15	22	20	18	9–22
Locality:	Torres Strait, Australia. (Also ?Bombay, India, and Amirante Is.)	Sudan, Red Sea	Ternate, Banda Sea, Indonesia	Gulf of Manaar, Indian Ocean	Abulat, Red Sea	Great Barrier Reef, Queensland

*Morphology cited by Ridley (1884, p. 453) as close to *A. innominatus*.
Values given here are from the redescription of the syntype B.M. 1882.2.23.248.

overlaying the skeleton, consisting of non-contort spined spiraster-like spicules, large quantities of sand and shell debris.

CHOANOSOME: The overall skeletal architecture is a renieroid to sub-renieroid reticulation of relatively heavy, pale yellow spongin fibres, 20–130 µm in diameter, moderately cored by bi- or multispicular tracts of principal styles. Major spicule tracts run longitudinally through sections, are cored with 3–8 spicules abreast, and are connected by vertical, ascending spicule-spongin tracts, with 1–3 spicules abreast. The reticulation in deeper parts of the choanosome is regular, renieroid, whereas closer to the surface the ascending (secondary) spicule tracts become plumose. The fibre reticulation forms ovoid to subrectangular chambers, 120–450 µm in diameter. Fibres are echinated by cladotylotes of 1 variety only, which vary in abundance between specimens (few in larger specimens, common in the smaller specimen). Spongin between the fibres is scarce, and where present, is cored with auxiliary styles and microscleres. Amphitylotes also occur in loose bundles in the choanosome, lying mainly at right angles to the surface. Moderate quantities of detritus, mostly sand grains occur in the choanosome also, particularly in the smaller specimen.

MEGASCLERES: Principal styles — moderately stout, straight or slightly curved at midsection, hastate, tapering to a sharp point; smooth rounded base with very little or no tylote swelling. Dimensions (N = 75): 248.2 μm long (mean) (range 203–281 μm), 10.3 μm wide (mean) (7–14 μm).

Auxiliary styles — abundant, relatively short, thin, hastate, tapering to a sharp point, smooth rounded base, some slightly subtylote. Dimensions (N = 75): 218.1 μm long (mean) (range 139–252 μm), 4.9 μm wide (2–7 μm).

Amphitylotes — moderately long, thin, straight, evenly rounded (only slightly swollen) tylote ends; few microspines on apical ends, occasionally smooth. Dimensions (N = 75): 235.2 μm long (mean) (range 200–280 μm), 3.6 μm wide (2–5 μm).

Cladotylotes I — relatively short, thin, straight, mostly with smooth shafts, some with occasional (isolated) spines along stem (1–4 μm long); 3 clads, occasionally 4 on the apex; clads recurved or only slightly curved, variable in length, and sometimes bearing 1 or more spines on apex. Bases tylote, smooth, sometimes tuberculate or with small clads. Dimensions (N = 100): 133.3 μm shaft length (mean) (range 85–205 μm), 4.5 μm shaft width (2–6 μm), 12.1 μm clad chord length (4–22 μm), 15.4 μm wide at clad end (5–23 μm).

MICROSCLERES: Toxas I — short, relatively thick, tricurvate, generously curved at midsection and with reflexed tips. Dimensions (N = 75): 79.3 μm chord length (mean) (range 41–266 μm), 2.9 μm wide at centre (1–6 μm).

Toxas II — long, thin, only slightly curved at midsection, some entirely oxeote, tips not reflexed. Dimensions (N = 75): 359.7 μm chord length (mean) (range 80–770 μm), 2.5 μm wide at centre (0.5–5 μm).

Isochelae — palmate. Dimensions (N = 100): 17.0 μm long (mean) (range 9–22 μm).

ECOLOGY

The present specimens were collected from a sand-gravel substrate. Previous records indicate that *A. ternatus* is generally found associated with sand and coral (Ridley 1884; Ridley and Dendy 1887; Keller 1889). The bathymetric distribution of this species extends from the intertidal zone (Lévi 1958) to a maximum depth of 80 metres (present study).

DISTRIBUTION

Acarnus ternatus appears to be widespread throughout the Indo-Pacific region, extending from the Red Sea (Keller 1889; Lévi 1958), Amirante Islands (Ridley 1884) and Kenya (Bruce 1976), to India and Sri Lanka (Ridley 1884; Dendy 1905), Indonesia and northeastern Australia (Ridley 1884; Kieschnick 1896; Thiele 1903; present study), to Tahiti (Ridley and Dendy 1887).

REMARKS

The specimens from Queensland are identified as *Acarnus ternatus* on the basis of having smooth cladotylotes of one category only. There is a close correspondence between that material and Ridley's syntype. Although several cladotylotes were observed with occasional scattered or single large spines on the shaft, this character was certainly unusual, and the majority of these spicules had smooth shafts. That condition was observed in the syntype also, although not recorded by Ridley (1884). Cladotylotes of the Queensland specimens were also unusual in sometimes having one or more small spines on the apex of clads, resembling multiple-clad spicules, and many having small clads only. These atypical characters were most evident in the smaller specimen (QM GL715), which also differed from the larger examples in shape (Fig. 47) (tubulo-digitate on a semi-encrusting base, versus flabellate semi-vasiform respectively), in having larger quantities of detritus on the ectosome and in the choanosome, and in the relative abundance of cladotylotes. The peculiar characteristics of the cladotylotes, the incorporation of numerous foreign particles into the skeleton and the atypical habit of specimen QM GL715 is probably of small consequence only, and on the basis of comparison with the type-specimen does not justify the separation of these 2 forms into distinct taxa. The details of skeletal architecture and fibre development, and the dimensions of spicules in all 3 specimens from the Great Barrier Reef correspond with details of the type-specimen and other records of *A. ternatus* within a reasonable range of variation (Table 4).

In having only one category of cladotylote, which is predominantly unspined, *A. ternatus* is placed in Lévi's (1963) group I *Acarnus*, to which may be added *A. tenuis* (see below).

Acarnus tenuis Dendy, 1896
(Table 5)

Acarnus tenuis Dendy, 1896, pp. 50–51.

MATERIAL EXAMINED

NMV G2456 (Dendy's RN 974), G2457 (RN 991): vicinity of Port Phillip Heads, Melbourne, Victoria, 38°20'S, 144°42'E; date of collection unknown, J.B. Wilson, dredge, (NMV G2456, encrusting on *Plumohalichondria arenacea*; G2457, encrusting on

TABLE 5. Comparison between published records of all species of *Acarnus*, showing extreme ranges of spicule dimensions. Refer to text for sources of information. All measurements are given in micrometres, and denoted as length × width.

CHARACTER	SPECIES					
	A. thielei Lévi	*A. tortilis* Topsent	*A. topsenti* Dendy	*A. ternatus* Ridley	*A. tenuis* Dendy	*A. erithacus* deLaubenfels
Colour alive/ (preserved):	light brown to orange	blackish to red	(dull grey)	blue, red to brown	(pale yellow)	red to bronze
Shape:	massive, digitate to lamellate/ vasiform	encrusting	digitate to flabellate	massive, rounded flabellate to branched on semi-encrusting base	thinly encrusting	encrusting
Skeleton:	renieroid to sub-renieroid	loosely reticulate	plumo-reticulate	renieroid to sub-renieroid reticulation	loosely reticulate	loosely reticulate
Styles:	178–464 × 2–30 smooth base	214–550 × 3–16 smooth and spined bases	204–287 × 3–12 smooth and spined bases	128–450 × 2–25 smooth base	180 × 2	220–790 × 7–43 smooth base
Acanthostyles:	absent	absent	absent	absent	absent	absent
Amphitylotes:	194–304 × 1–9	222–440 × 3.5–7	205–262 × 2–3.5	192–280 × 1.5–5	? absent	170–434 × 3–8
Cladotylotes I:	85–272 × 2–15 smooth shaft	151–225 × 3–5 spined shaft	absent	63–275 × 2–12 smooth shaft	160 × 2 smooth shaft	180–472 × 8–36 smooth shaft
Cladotylotes II:	75–97 × 2–4 spined shaft	58–109 × 2.5–4 spined shaft	53–97 × 3–8 spined shaft	absent	absent	80–182 × 3–7 spined shaft
Toxas I:	25–176 × 1–9	44–130 × 1–5	32–191 × 1–4	12–266 × 0.8–8	absent	40–645 × 2–7
Toxas II:	34–960 × 0.5–7	15–265 × 1–2	absent	19–900 × 0.5–5	absent	
Isochelae:	8–29	7–22	9–12	8–22	absent	12–26
Locality:	Western Indian Ocean to Indo-Australian	Atlantic, Pacific and Indian Oceans	Western Indian Ocean	Indo-Pacific	Port Phillip, Victoria	Pacific Coast, North America

TABLE 5 (Cont.).

CHARACTER	SPECIES					
	A. innominatus Gray	*A. toxeatus* Boury-Esnault	*A. bicladotylotus* Hoshino	*A. souriei* Lévi	*A. tener* Tanita	*A. radovani* Boury-Esnault
Colour alive/ (preserved):	orange to red	maroon	red-orange	bright orange to red	(red-brown)	(deep violet)
Shape:	encrusting	encrusting	thinly encrusting	thinly encrusting	oval mass	encrusting
Skeleton:	renieroid reticulation	?	irregular reticulation	plumose, halichondroid	plumo-reticulate	?
Styles:	175–459 × 6–22 smooth base	378–727 × 12–16 smooth base	195–394 × 6–12 spined base	170–381 × 3–10 spined base	260–340 × 8–10 spined base	80–213 × 3–9 spined base
Acanthostyles:	absent	absent	80–95 × 3–5	6–145 × 2–5	80–130 × 4–6	
Amphitylotes:	130–283 × 2–6.3	213–472 × 3–9	205–310 × 3–6	119–357 × 2–7	180–320 × 2.5–5	350–473 × 3–4
Cladotylotes I:	180–295 × 6–14 smooth shaft	250–395 × 3–9 lightly spined	140–180 × 3–7 spined shaft	54–236 × 2–6 spined shaft	130–190 × 5–6 spined shaft	210–218 × 4.5–6 spined shaft
Cladotylotes II:	72–141 × 2–5 rare, spined shaft	56–162 × 3 heavily spined shaft	80–110 × 2–6 spined shaft	absent	absent	absent
Toxas I:	21–249 × 1–5	28–75 × ?	60–110 × 1–2	45–330 × 2–4	70–110 × 2	a. 78–104 × 3–6 b. 143–204 × 1.5–3
Toxas II:	192–586 × 1.5–3	a. 218–265 × ? b. 500–945 × 2	130–210 × 2–3		absent	230–309 × 1.5
Isochelae:	6–24	12–14	15	12–21	12–14	19–22
Locality:	West Indies, South Africa, North Australia	Coast of Brazil, South Atlantic	Kyushu, Japan, East China Sea	Widespread, Northern Hemisphere	Noto Peninsula, Sea of Japan	Coast of Brazil, South Atlantic

Tedania digitata). These specimens were noted as syntypes by Ayling *et al.* (1982) (see below).

Missing from collection: RN 1072, encrusting on *Clathria typica* (Ayling *et al.* 1982, p. 106; personal observation).

ECOLOGY

Unknown.

DISTRIBUTION

This species has been recorded only once, from Port Phillip Bay, Victoria.

REMARKS

Extensive examination of the two specimens held at the Museum of Victoria failed to discover any trace of the encrusting type specimens of *Acarnus tenuis*. Dendy (1896) notes that *A. tenuis* occurs as a small, thin, pale yellow crust on the surface of three sponges. Crusts do exist in quite extensive patches on the surface of G2456 and G2457 (*Crella incrustans* and *Tedania digitata*, respectively), but in all cases these encrustations consist of usual ectosomal spicules for these species (viz. oxeas, acanthoxeas and arcuate isochelae, and erect amphitylotes, respectively). It is apparent therefore that the type-specimens of *A. tenuis* no longer exist, at the Museum of Victoria.

Ayling *et al.* (1982) note that the British Museum (Natural History) holds three microscope slide preparations of each syntype (1902:10:18:62, 323, 375). Until these spicule mounts are re-examined, a definition of *A. tenuis* can be drawn from Dendy's (1896) description only (Table 5). This species may be differentiated from other *Acarnus* in having no microscleres, no fibres, a very loose irregular reticulation of styles or subtylostyles (189 × 2 μm), and scattered or loose bundles of cladotylotes (160 × 2 μm), bearing 5 clads (approximately 4 μm in length) with unspined shafts. Amphitylotes are apparently absent also.

Lévi (1963) omits *A. tenuis* from his subdivision of the genus, but on the basis of the cladotylote morphology it would fit with his group I *Acarnus*, together with *A. ternatus*. Dendy (1922) suggests that the absence of chelate microscleres in this species may be cause to erect a separate genus for *A. tenuis*, but such a move could not be justified for such a poorly known species.

SYNOPSIS OF OTHER SPECIES

Brief diagnoses are given below of other species of *Acarnus* not found in the Australian region. Table 5 provides a summary of the main diagnostic characters for each.

Acarnus erithacus de Laubenfels, 1927
(Table 5)

Acarnus erithacus de Laubenfels, 1927, pp. 258–60, 262, text-figs 1,2,9,10,11. de Laubenfels, 1930, p. 104. de Laubenfels, 1932, pp. 104–7, text-fig. 63. Dickinson, 1945, p. 20. Bakus, 1966, pp. 468–71, text-figs 14a–j. Schwab and Shore, 1971, pp. 125–36. Shore, 1972, pp. 689–98. Carter and Rinehart, 1978, pp. 4302–4. Hofknecht, 1978, pp. 53–4.

DIAGNOSIS

Brilliant red to bronze, thinly to massively encrusting sponge with an irregular, microconulose, hispid surface and an irregular, loosely reticulate skeleton of ascending spicule tracts. Spongin fibres are light, cored by styles (200–790 × 7–43 μm), and echinated by cladotylotes of 2 varieties: I— (180–472 × 8–36 μm) have 3–4 clads and smooth shafts; II— (80–182 × 3–7 μm) have spined shafts. Tangential ectosomal amphitylotes (170–434 × 3–8 μm) with microspined tips. Toxas of 2 sizes: I— small, thick and reflexed; II— long, thin and mostly straight or only slightly curved (both 40–645 × 2–7 μm). Palmate isochelae (12–26 μm) core light spongin between the fibres.

Source: de Laubenfels (1927, 1932), Bakus (1966).

ECOLOGY

Associated with rock, dead corals, and living or dead barnacles; extensive bathymetric range from the intertidal zone to 700 metres depth.

DISTRIBUTION

Pacific coast to North America (California, Washington).

REMARKS

Acarnus erithacus was placed in group III *Acarnus*, together with *A. thielei* and *A. innominatus* on the basis of its smooth and spined cladotylotes (Lévi 1963). It is close to *A. tortilis* in skeletal architecture, but differs from that species in cladotylote morphology and spongin content (Bakus 1966) (Table 5). The affinities of this species, and arguments for a possible combination of Lévi's group III species have been presented earlier.

Acarnus topsenti Dendy, 1922
(Fig. 37, Table 5)

Acarnus topsenti Dendy, 1922, pp. 98–9, pl. 4, fig. 3a–b, pl. 15, fig. 8a–e. Burton 1959, p. 253.

MATERIAL EXAMINED

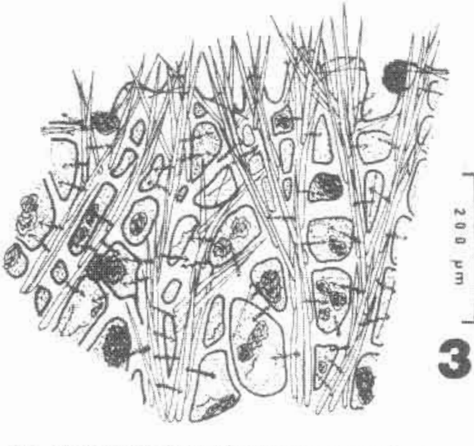
SYNTYPE: BM 1921.11.7.84: Cargados Carajos, north of Mauritius, Indian Ocean, 16°25'S, 59°36'E, 60 m depth, 29 August 1905, H.M.S. 'Sealark', dredge.

REDESCRIPTION OF TYPE-SPECIMEN

DETAILS OF EXTERNAL MORPHOLOGY: Digitate to flabellate sponge with digitiform processes and microconules on the surface. Surface is roughened and microscopically hispid. Ectosome has a thin, translucent membraneous covering, and small oscula on the margins of branches. Texture is compressible, fibrous and fairly tough. Colour in ethanol ranges from dull grey to reddish or purplish (Dendy 1922, p. 98).

ECTOSOME: Choanosomal fibres ascend to the ectosomal region and form erect microconulose projections. Ascending fibres are cored by plumose tracts of styles, with the ultimate brushes poking through the surface and forming an irregular, erect palisade of spicules. In addition to a hispid ectosomal layer of styles, there is a fine tangential ectosomal layer of amphitylotes, in bundles of up to 10 spicules abreast or scattered singly. The tangential ectosomal layer is conspicuous in some areas, but difficult to observe in other areas due to the presence of relatively heavy deposits of detritus on the ectosome. Amphitylotes are scattered throughout the mesohyl of the choanosome also.

CHOANOSOME: The overall choanosomal skeletal architecture is plumo-reticulate, with distinctive ascending fibre tracts (30-50 μm in diameter), which diverge in plumose fashion towards the subectosomal region (Fig. 37). Fibres consist of relatively heavy spongin, resembling those of the Spongiidae. Ascending fibres are cored by plumose tracts of principal styles, 4-10 spicules abreast, occasionally singly, which ultimately protrude through the ectosome, and are echinated by cladotylotes in moderate concentrations. Ascending (cored) fibres are connected in a loose reticulation by transverse uncored fibres of similar diameter. Transverse fibres are only lightly echinated by cladotylotes or not at all. The mesohyl matrix contains relatively heavy deposits of granular spongin bearing microscleres and scattered amphitylotes. No styles were observed outside spongin fibres. Meshes formed by anastomosing fibres are variable in diameter, 90-290 μm. Detritus is moderately abundant between fibres, and consists mainly of sand grains.



37

FIG. 37: *Acarnus topsenti*, syntype; perpendicular section of peripheral skeleton.

MEGASCLERES (N = 25): Principal styles — hastate, tapering to a sharp point, relatively straight or only slightly curved at the centre, with evenly rounded or only slightly subtylote bases; bases smooth or very lightly microspined. 223.7 μm long (mean) (range 204-287 μm), 7.8 μm wide (3-12 μm).

Amphitylotes — relatively long, thin, straight, with slightly swollen tylote bases bearing microspines on their tips. 227.4 μm long (mean) (range 205-262 μm), 2.5 μm wide (2-3.5 μm).

Cladotylotes — relatively small, thin, straight, thicker near base than on clad end, with profusely microspined shafts and a bare anterior area immediately below clads; clads are relatively short, and number 4 to 5; bases are slightly subtylote, with 3-4 large recurved spines. 76.7 μm shaft length (mean) (range 53-97 μm), 5.1 μm shaft width (3-8 μm), 6.3 μm clad chord length (3-11 μm), 8.9 μm wide at clad end (5-14 μm).

MICROSCLERES (N = 25): Toxas I — short to long and thick, generously curved at the centre, with recurved tips, 112.2 μm long (mean) (range 32-191 μm), 2.3 μm wide (1-4 μm).

Isochelae— small, thin, palmate, 10.7 μm long (mean) (range 9-12 μm).

ECOLOGY

A moderately deeper-water species, with a bathymetric distribution of 38-165 metres; apparently associated with a red algae (*Lithothamnion*) (Burton 1959).

DISTRIBUTION

Western Indian Ocean (Coast of Oman, Arabian Sea; Cargados Carajos, north of Mauritius, Indian Ocean).

REMARKS

Dendy (1922, p. 15, fig. 8) provides adequate drawings of the spicule morphology of *A. topsenti*, and those do not need to be repeated here. Fig. 37 shows the skeletal architecture of this species, which has not been illustrated previously. The supposed absence of a tangential ectosomal skeleton of amphitylotes, reported by Dendy (1922) was not supported by the re-examination of the type-specimen, and in that respect *A. topsenti* does not differ from other *Acarnus* species.

Acarnus topsenti is placed in Lévi's (1963) group II *Acarnus* by the presence of spined cladotylotes only, and in this respect the species has affinities with *A. tortilis* and *A. toxeatus*. Arguments have been presented above in support of maintaining *A. topsenti* and *A. tortilis* as distinct species, despite their very close similarities.

Acarnus toxeatus Boury-Esnault, 1973
(Table 5)

Acarnus toxeata Boury-Esnault, 1973, p. 285, text-fig. 44.

DIAGNOSIS

Maroon, thinly encrusting sponge with a delicate detachable ectosomal crust. Surface is hispid. Choanosomal skeletal architecture is unknown, but presumably greatly reduced as a result of its thin habit. Styles have slightly swollen, smooth bases (378–727 × 12–16 μm). Ectosomal amphitylotes (213–472 × 3–9 μm) with spined extremities. Cladotylotes of 2 varieties: I— (250–395 × 3–9 μm) have 6 clads and a lightly spined shaft; II— (56–162 × 3 μm) have a heavily spined shaft. Toxas of 3 varieties: I— (28–75 μm) short, relatively thick, with reflexed tips and generously curved centrally; II— (218–265 μm) moderately long, slightly reflexed and curved at centre; III— (500–945 μm) relatively thin, long, straight, not reflexed at tips. Palmate isochelae 12–14 μm long.

Source: Boury-Esnault (1973).

ECOLOGY

Habitat unknown. Collected from 50 depth.

DISTRIBUTION

Single locality, off Governador Valadares, Brazil, South Atlantic.

REMARKS

Acarnus toxeatus is placed in Lévi's (1963) group II *Acarnus* in having spined cladotylotes only. The species is distinctive in the extreme size of toxas (Table 5), but the division of toxas into three varieties may be artificial. Toxa II probably represents an intermediate between the smaller, curved form and the long, straight form.

Acarnus bicladotylotus Hoshino, 1981
(Table 5)

Acarnus bicladotylota Hoshino, 1981, pp. 142–3, text-fig. 60, pl. 6, fig. 4.

DIAGNOSIS

Thinly encrusting, red-orange sponge, with a smooth surface containing foreign particles. Ectosome with a confused tangential layer of amphitylotes (205–310 × 3–6 μm) bearing spines on extremities. Choanosomal skeletal architecture irregularly reticulate with ascending spicule tracts cored by styles (195–394 × 6–12 μm), and echinated by cladotylotes of 2 varieties: I— (140–180 × 3–7 μm); II— (80–110 × 2–6 μm), both with spined shafts. Acanthostyles (80–95 × 3–5 μm) erect on basal membrane of sponge. Toxas of 2 varieties, both thin and reflexed: I— (60–100 × 1–2 μm); II— (130–210 × 2–3 μm).

Arcuate (?) isochelae (15 μm) coring abundant spongin between the fibres.

Source: Hoshino (1981).

ECOLOGY

Associated with barnacles (*Acasta*); located in the intertidal zone to shallow subtidal regions.

DISTRIBUTION

East China Sea (Matsushima Maeshima, Ariake Sea, Kyushu, Japan).

REMARKS

In habit and skeletal structure (ascending plumose tracts), *A. bicladotylotus* resembles *A. erithacus*, but differs from that species and other *Acarnus* by the dimensions and composition of the skeletal components (Table 5).

This species is a member of the nominal subgenus *Acanthacarnus* by virtue of a basal layer of acanthostyles in the skeleton, acanthose cladotylotes only, and thin styles. Although Hoshino (1981) records the isochelae as arcuate, his figure (60f) suggests that they are probably palmate, which is consistent with other species of *Acarnus*.

Acarnus souriei (Lévi, 1952)
(Table 5)

Acanthacarnus souriei Lévi, 1952, p. 54, text-figs 18–19. Lévi, 1959, pp. 132–3, text-fig. 25. Vacelet, 1961, p. 42. Hechtel, 1965, p. 40. Thomas, 1970, pp. 46–50, text-figs 1–2a–h. Thomas, 1973, p. 30, pl. 2, fig. 2.

Acanthacarnus levii Vacelet, 1960, pp. 267–9, text-fig. 5.

Acarnus souriei: Van Soest, 1984, pp. 63–5, text-fig. 23.

DIAGNOSIS

Bright orange to red, thinly encrusting sponge, with an optically smooth, microscopically hispid surface. Ectosome with an irregular tangential layer of amphitylotes (119–357 × 2–7 μm) bearing terminal spines. Choanosome skeletal architecture lightly reticulate only and more markedly halichondroid, with ascending plumose spiculo-spongin fibres. Spongin fibres are light, cored by styles (170–381 × 3–10 μm) and echinated by acanthostyles (60–145 × 2–5 μm) and cladotylotes of 1 variety only, with 4 clads and spined shafts (54–236 × 2–6 μm). Toxas of at least 2 varieties: I— with reflexed tips, generously curved, and of variable thickness; II— thin, angular central curvature, long (both: 45–330 × 2–4 μm). Palmate isochelae (12–21 μm).

Source: Lévi (1952, 1959), Hechtel (1965), Thomas (1970, 1973), Van Soest (1984).

ECOLOGY

Apparently restricted to dead coral and rock substrate; bathymetric distribution from the intertidal zone to 10 metres depth.

DISTRIBUTION

Predominantly northern hemisphere, widespread; Mediterrean (Corsica), North Atlantic Ocean, West Africa (Senegal, Gulf of Guinea), Indian Ocean (Seychelles, Palk Bay, Gulf of Manaar), Caribbean (Curaçao, Barbados, Puerto Rico, Jamaica).

REMARKS

Acarnus souriei s.l. has a wide range of spicule measurements, particularly for the cladotylotes. Vacelet (1960) and Thomas (1970, 1973) divide cladotylotes of specimens from the Mediterranean and Indian Ocean (respectively) into two size categories, both of which are spined (I— 80–210 × 4.5–6 μm; II— 54–140 × 2–4 μm), but other authors group these spicules into a single (albeit variable) category (Vacelet 1961; Hechtel 1965; Van Soest 1984). Van Soest (1984) notes other differences in skeletal components between the various populations of *A. souriei*. It is evident that the species is highly variable over its large geographical range, and consequently it is difficult to isolate any single character which separates this species from others (Table 5). Van Soest (1984) suggests that *A. bicladotylotus* may be distinguished from *A. souriei* in having 2 sizes of cladotylotes (see Table 5), but both forms fall well within the range of those of *A. souriei*. The same argument applies for all spicule components of *A. tener*. *Acarnus radovani* is maintained here as a separate species, with question, in having larger amphitylotes with only slightly swollen ends, although Van Soest (1984) suggests that it is close to, and probably synonymous with *A. souriei*. That distinction is tenuous, and probably artificial, but the combination of *A. radovani* and *A. souriei* would provide sufficient reason to synonymize all *Acarnus (Acanthacarnus)* species on the basis of similarities in spicule morphology and size. This problem of clearly and objectively differentiating *Acarnus* species has been encountered earlier (*A. innominatus* and *A. thielei*, *A. topsenti* and *A. tortilis*), and on the basis of morphological characters alone no easy solution is presently available. Combinations of specific characters, such as habit, architecture and spicule morphology must be used together in distingushing species, taking into account known ecophenotypic differences between populations, and in some cases subjective criteria are as equally important (e.g. colour, texture, gross morphology and the appearance of the ectosome).

Acarnus radovani (Boury-Esnault, 1973)
(Table 5)

Acanthacarnus radovani Boury-Esnault, 1973, p. 284, text-fig. 43.

DIAGNOSIS

Deep violet (in preserved state), encrusting sponge, with hispid surface. Ectosomal and choanosomal skeletal structure is unknown. Ectosomal amphitylotes with only slightly swollen ends which are terminally spined (350–473 × 3–4 μm). Styles with spined bases, slightly subtylote acanthostyles abundant with numerous small spines on shaft (both styles and acanthostyles: 80–213 × 3–9 μm). Cladotylotes of 1 variety, with spined shafts (210–218 × 4.5–6 μm). Toxas of at least 2 varieties: I— with reflexed tips, a generous central curvature and relatively thick (78–104 × 3–6 μm); II— thin, oxeote, with slight central arch (230–309 × 1.5 μm). A third variety of toxa, probably an intermediate stage is recorded (143–204 × 1.5–3 μm). Palmate isochelae abundant in heavy deposits of spongin (19–22 μm).

Source: Boury-Esnault (1973).

ECOLOGY

Habitat unknown; collected from 51 metres depth.

DISTRIBUTION

Tropical Atlantic Ocean (off Recife, Brazil, South Atlantic).

REMARKS

Boury-Esnault (1973) differentiates this species from other *Acarnus (Acanthacarnus)* by the large size of the spicules and by the presence of 3 sizes of toxas. A comparison with other species (Table 5) shows that most spicule forms fall within the upper size range of most other species, particularly the widespread *A. souriei*. Van Soest (1984) records *A. souriei* with similar categories of toxas as *A. radovani*, which supports his suggestion that the two may be synonymous, but they are presently maintained as distinct species for reasons discussed above. In general, *A. radovani* has larger amphitylotes and cladotylotes than does *A. souriei*.

Acarnus tener Tanita, 1963
(Table 5)

Acarnus tenerus Tanita, 1963, pp. 123–4, pl. 4, fig. 2, text-fig. 2. Hoshino, 1981, p. 144.

DIAGNOSIS

Dull reddish-brown (in preserved state), oval sponge, more-or-less 'dorso-ventrally' compressed, with a lightly hispid surface. Surface is rough; ectosome with a tangential layer of amphitylotes, with terminal swellings and spines on apices (180–320 × 2.5–5 μm). Choanosomal skeletal architecture is plumo-reticulate, and slender fibres are cored by styles with basal spination (260–340 × 8–10 μm). Fibres echinated by numerous acanthostyles (80–130 × 4–6 μm) and cladotylotes of 1 variety, with spined shafts and 4 clads (130–190 × 5–6 μm). Toxas generously curved at cente with reflexed tips (70–110 × 2 μm). Palmate isochelae 12–14 μm long.

Source: Tanita (1963).

ECOLOGY

Growing amongst seaweed (*Laurencia*); depth recorded as shallow to moderately shallow water.

DISTRIBUTION

Japan (Noto Peninsula, Sea of Japan).

REMARKS

Tanita (1963) erected this species on the basis of its shape and the presence of echinating acanthostyles. Those characters are now of little value in separating species, but *A. tener* can be differentiated from *A. bicladotylotus* in having only a single category of cladotylote and toxa (Table 5). It is close to *A. souriei* s.l. but differs from that species in skeletal architecture.

DISCUSSION

The intraspecific variability in morphological characters shown by some *Acarnus* makes the specific taxonomy of this group difficult and unreliable. Limited studies have shown that some characters in some species are unstable. Most significantly, de Laubenfels (1932), Thomas (1970) and Van Soest (1984) found that cladotylotes were sometimes absent from specimens of *A. erithacus* and *A. souriei*. Furthermore, Van Soest (1984) noted that acanthostyles were absent from one Caribbean specimen of *A. souriei*. Those authors were able to assign aberrant specimens to a specific taxon through morphological comparisions with other material from the same localities. Although atypical specimens are reportedly not abundant, there exists the possibility that records of single specimens from isolated localities, such as *A. innominatus* from Darwin, represent specimens with reduced characteristics. Unfortunately there is no solution to this problem on the basis of known material, and in using a limited number of morphological characters of undetermined stability. Populations of *Acarnus* species are not abundant in any locality, with the possible exception of *A. erithacus* from the Pacific coast of North America, so it is unlikely that a study of intraspecific variability, would be successful for this group.

Nevertheless, accepting the limitations of the data, it is possible to speculate further on species relationships and the zoogeography of *Acarnus*. Conclusions derived from these analyses cannot be fully corroborated because conspecificity has been assumed from the literature, and not in comparison with type-specimens (e.g. Wiedenmayer 1977). That material was not available to the author.

In following with current taxonomic procedures, the important diagnostic characters for the genus are the size, morphology and distribution of the echinating cladotylotes, toxas, and ectosomal amphitylotes, the basal feature of choanosomal styles, the presence or absence of echinating acanthostyles, the overall skeletal architecture, and the gross morphology of the sponge. Other more subjective criteria, such as the colour alive, the macroscopic appearance of the ectosome, and the degree of infiltration of detritus into the choanosome are also important in distinguishing allied species. On this basis, it is possible to separate 12 species. However, many of those species are encrusting in habit, with a concomitant reduction in skeletal architecture, and consequently the value of some diagnostic characters is diminished. As a result, the morphology of the cladotylote megasclere remains the principal characteristic for differentiating species. Lévi's (1963) proposal for subdividing *Acarnus* on the basis of cladotylote form offers a convenient and practical method to faciliate identifications. He omits *A. tenuis* from his scheme, possibly with good reason due to the poorly known characteristics of that species, but it is included here on a provisional basis, as it represents the only record of the group from temperate Australian waters.

GROUP I: with only smooth shafts on cladotylotes
- *A. ternatus* Ridley
- *A. tenuis* Dendy

GROUP II: with only spined shafts on cladotylotes
- IIA— without echinating acanthostyles
  - *A. tortilis* Topsent
  - *A. topsenti* Dendy
  - *A. toxeatus* Boury-Esnault
- IIB— with echinating acanthostyles (subgenus *Acanthacarnus*)
  - *A. bicladotylotus* Hoshino
  - *A. souriei* (Lévi)
  - *A. radovani* (Boury-Esnault)
  - *A. tener* Tanita

GROUP III: with both smooth and spined cladotylotes
- *A. erithacus* de Laubenfels
- *A. innominatus* Gray
- *A. thielei* Lévi

It is clear that some species are more closely related than others. Using a restricted set of morphological characters (Table 6), it is possible to construct a cladogram to illustrate these relationships (Fig. 38). Each number on the cladogram indicates an evolutionary change of the corresponding character from a relatively plesiomorphic to a relatively apomorphic state. The apomorphic character states were judged on a number of criteria (Table 6, mainly after Van Soest 1984, pp. 65, 151), the most significant of which are the reduction of cladotylote and acanthostyle megascleres.

From Fig. 38, the basic separation of the three groups is indicated (characters 1,2), which corresponds to Lévi's (1963) subdivision of the genus. From this particular analysis, it is suggested that species formerly included in the genus *Acanthacarnus* are more closely related to *Acarnus* group IIA species than previously recognized when using the presence or absence of acanthostyles as the primary characteristic for subdividing the genus. Supporting evidence for this opinion is suggested by the synplesiomorphy of basal spination of choanosomal styles, and the synapomorphy through reduction of the smooth cladotylote megascleres.

Group III species are subdivided on the basis of growth form (No. 3; a character of undetermined stability and questionable importance), and the proportion of acanthose and smooth cladotylote megascleres (No. 4). *Acarnus erithacus* and *A. innominatus* are more plesiomorphic than *A. thielei*. Synplesiomorphic characters which unite Group IIB species (viz. the possession of acanthostyles, spined cladotylotes only, and the basal spination of styles) are more obvious than any apomorphic separation of that group. Synapomorphy for *A. tener* and *A. radovani* is the possession of one category of spined cladotylote spicule only (No. 6). No derived characters are presently known to separate those two species in this analysis, because the ectosomal and choanosomal characteristics of *A. radovani* are unknown. *Acarnus topsenti* and *A. tortilis* (Group IIA) are related to Group IIB species by the retention of ancestral characters (Nos. 2,8), which is not clear from this analysis, whereas *A. toxeatus* seems to have lost the basal spination on styles. That condition may have arisen independently, as it is synapomorphic for *Acarnus* Groups I and III.

Five *Acarnus* species are now known from Australian waters, three of which represent new locality records (*A. thielei*, *A. innominatus*, and *A. tortilis*). *Acarnus ternatus* is well known throughout the Indo-Pacific region, but its distribution in Australia is restricted to the tropics. *Acarnus tenuis* was recorded from the Tasman Sea, but the species is poorly known. Until redescriptions are made of the presently missing type-specimens, or more preferably, redescriptions based on fresh material, *A. tenuis* becomes a species inquirenda.

Several zoogeographical patterns are indicated for *Acarnus* species (Fig. 39). Of Group I species, *A. ternatus* shows a separation into two disjunct populations: Western Indian Ocean, and Indo-Pacific, but conspecificity of the two populations seems to be clear on the basis of morphological characteristics. In following with standard taxonomic procedures, Group I species should be referred to as the *ternatus* species group.

The major component of Group IIA species, *A. tortilis* has three discontinuous populations,

TABLE 6. Characters used in the construction of Fig. 38. Criteria for judging apomorphy are listed below.

PLESIOMORPHIC STATE	APOMORPHIC STATE
1. At least one category of cladotylote megascleres with spined shafts	1. A single category of cladotylote megascleres with smooth shafts only
2. Two varieties of cladotylotes (spined and smooth)	2. Smooth cladotylotes not present
3. Growth from encrusting	3. Digitate, flabellate, or vasiform habit
4. Cladotylote megascleres are predominantly acanthose	4. Acanthose cladotylotes are rare
5. Acanthostyles present	5. Acanthostyles absent
6. Two size-categories of acanthose cladotylotes	6. One size-category of acanthose cladotylotes
7. Toxa microscleres are diverse in form and size, with at least 3 categories	7. Reduced complement of toxas, and relatively thin
8. Choanosomal styles or subtylostyles with microspined bases	8. Styles or subtylostyles with smooth bases
9. Strongly developed (horny) spongin fibres	9. Fibres reduced, lightly invested with spongin only
10. Ectosomal amphitylotes form a more-or-less tangential layer	10. Amphitylotes absent

Cladotylotes: In the plesiomorphic state, cladotylotes have both smooth and spined shafts, representing 2 separate categories of megascleres, and in the apomorphic state one of the varieties is lost. A reduction in the proportion of spined versus smooth cladotylotes, and the number of varieties of spined cladotylotes is considered here as a further derived condition.

Acanthostyles: The retention of acanthostyles echinating a layer of basal spongin and/or spiculo-spongin tracts is interpreted as an ancestral condition (Van Soest 1984).

Styles: The presence of microspines on bases of choanosomal styles or subtylostyles is considered here as a plesiomorphic condition.

Amphitylotes: The possession of a tangential ectosomal skeleton of tylote megascleres is shared with other myxillids, and at least one other family of Poecilosclerida (Van Soest 1984), and is probably an ancestral character. Synapomorphy is the secondary reduction or loss of amphitylotes.

Habit: An encrusting growth form is considered here as plesiomorphic, and development of digitate, flabelliform or vasiform habit is probably a derived condition. This distinction may be illusory, as the stability of this character has not been determined in any study, and ecophenotypic factors and individual maturation must be considered (see text).

Skeletal architecture and fibre development: Van Soest (1984, p. 151) suggests that a reticulate or plumo-reticulate skeletal architecture is probably an ancestral condition, shared with several outgroups of the Poecilosclerida. Similarly, skeletal fibres which are heavily invested with type B spongin is interpreted here as the plesiomorphic state. The importance of this character is debatable (see text), as ecophenotypic factors influencing growth form and the consequent skeletal development are probably critical.

Microscleres: Synapomorphy for the Poecilosclerida s.s. are the chelate microscleres, but synplesiomorphy is probably a full and diverse complement of other microscleres, including toxas (Van Soest 1984, p. 151). A reduction in heterogeneity of non-chelate microscleres is considered here as an apomorphic condition.

extending into both northern and southern hemispheres: North Atlantic-Mediterranean, Western Indian Ocean, and Indo-Pacific populations. It is difficult to determine any intraspecific variability corresponding to these zoogeographical populations, on the basis of known material, because only few published accounts of *A. tortilis* describe morphological characteristics (see Table 3). There appears to be a trend in size reduction of styles from the Mediterranean to Indo-Pacific populations (400–515, 300–450, 214–334 μm long respectively for the three populations), but that pattern requires confirmation from additional data.

The distribution of *A. topsenti* is sympatric with the Western Indian Ocean population of *A.*

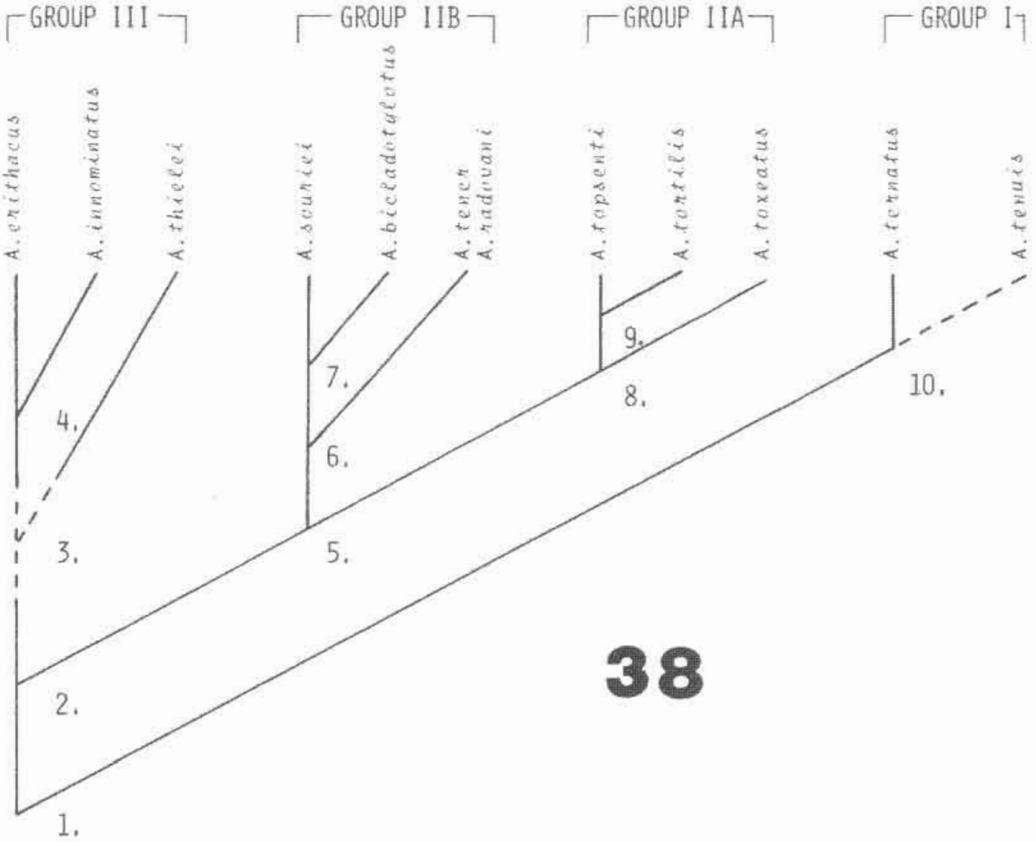


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FIG. 38: Cladogram of the relationships between species of *Acarnus*. Each number on the cladogram indicates an evolutionary change of the corresponding character (Table 6) from a relatively plesiomorphic to a relatively apomorphic state.

tortilis, which is further evidence in support of a possible combination of the two species (cf. above, and Vacelet *et al.* 1976). *Acarnus toxeatus* is known from a single locality only (tropical South Atlantic Ocean). *Acarnus* group IIA species should be referred to as the *tortilis* species group.

Group IIB species are found predominantly in the northern hemisphere. *Acarnus souriei* has a disjunct zoogeography, with the separation of three populations: Caribbean, Mediterranean-West African, and central Western Indian Ocean. Van Soest (1984, p. 64) suggests that the Caribbean and Mediterranean-West African populations are clearly conspecific, although he notes that the Mediterranean specimens have larger styles and amphitylotes than the tropical specimens. The Indian Ocean population is recorded as having a lower size range of cladotylote megasclere than the Atlantic region populations (54–187, 70–236 μm respectively), but this is probably of minor taxonomic significance. Isochelae microscleres are relatively homogeneous in size throughout the entire geographical range of this species. Van Soest (1984) also supports a possible combination of *A. radovani* and *A. souriei* on the basis that spicule sizes for both species correspond closely. Populations of *A. souriei* which are geographically closest to *A. radovani* (viz. Caribbean and West African specimens) have significantly smaller amphitylotes (119–357, 350–473 μm long respectively), and in that respect *A. radovani* is most similar to Mediterranean specimens of *A. souriei* (which have amphitylotes 280–408 μm long). It is possible that the variability is taxonomically insignificant, and that the two species are conspecific, but for reasons discussed

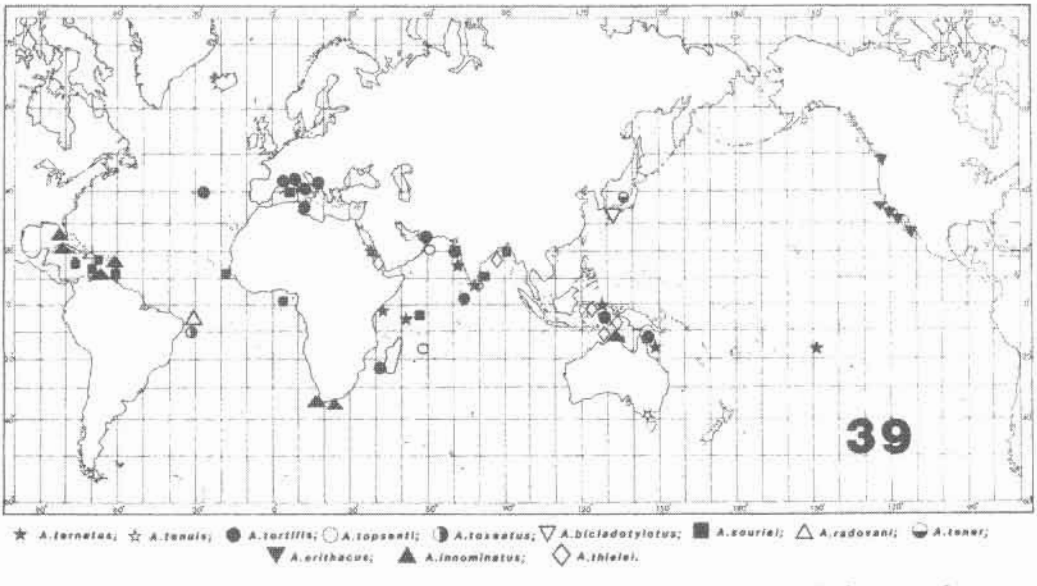

FIG 39: Zoogeography of *Acarnus* species. Conspecificity is assumed from the literature. Refer to text for sources of information.

earlier their specific separation is maintained here. Other species in Group IIB, *A. bicladotylotus* and *A. tener* are known only from the Japan region. Group IIB species should be referred to as the *souriei* species group in preference to subgenus *Acanthacarnus*, as the latter term implies a greater degree of taxonomic distance than recognized here.

Group III is represented by one endemic species, *A. erithacus* from the Pacific Coast of North America, and two other species with more widespread distributions. *Acarnus innominatus* is widely separated with three discontinuous populations: Carribean-Gulf of Mexico, temperate South Atlantic-Indian Ocean, and Indo-Pacific. There is a relatively homogeneous distribution of morphological characteristics throughout the range of this species, although the specimen from the Arafura Sea region is more similar to the Caribbean population than to the South African specimens in spicule sizes. More detailed studies on encrusting sponge faunas throughout the Indian Ocean region may show that this species has a more extensive distribution than is presently known. *Acarnus thielei* has a relatively contiguous distribution across the western Indian Ocean to the Indo-Pacific, but there seems to be two populations within that range. Indian Ocean specimens have small isochelae (8–10 μm long), whereas isochelae of the Indo-Pacific specimens are larger (18–25 μm long) (see also Lévi 1958). *Acarnus innominatus* is most representative of Group III species, and that group should be known as the *innominatus* species group.

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LITERATURE CITED

ALCOLADO, P., 1976. Lista de nuevos registros de Poriferos para Cuba. *Acad. Sci. Cuba, Ser. Oceanol.* **361**: 1–11.

ARNDT, W., 1927. Kalk- und Kieselschwämme von Curaçao. *Bijdr. Dierk. Amsterdam.* **25**: 133–58, 3 pls., 18 figs.

AYLING, A.L., STONE, S., and SMITH, B.J., 1982. Catalogue of types of sponge species from southern Australia described by Arthur Dendy. *Rep. National Mus. Victoria* **1**: 97–109.

BAKUS, G.J., 1966. Marine poeciloscleridan sponges of the San Juan Archipelago, Washington. *Jour. Zool. London.* **149**: 415–531, 24 figs.

Boury-Esnault, N., 1971. Spongiaires de la zone rocheuse de Banyuls-sur-mer. II-Systématique. *Vie Milieu*. **22**(2), Sér.B: 287–350, 8 pls.

1973. Campagne de la Calypso au large des côtes Atlantiques de l'Amerique du Sud (1961–1962). I. 29 Spongiaries. *Ann. Inst. Oceanogr., Paris*. **49** (Suppl.): 263–95, 49 figs., 3 pls.

Bowerbank, J.S., 1864. 'A Monograph of the British Spongiadae, Vol. 1.' (Ray Society: London). 290 pp., 37 pls.

1866. 'A Monograph of the British Spongiadae, Vol. 2.' (Ray Society: London). 388 pp.

1874. 'A Monograph of the British Spongiadae, Vol. 3.' (Ray Society: London). 360 pp.

1882. 'A Monograph of the British Spongiadae, Vol. 4.' (Ray Society: London). 250 pp, 17 pls.

Bruce, A.J., 1976. *Discias mvitae* sp. nov. a new sponge associate from Kenya (Decapoda, Natantia, Disciadidae). *Crustaceana* **31**(2): 119–30.

Burton, M., 1959. Sponges. *Scient. Rep. John Murray Exped.*, **10**(5): 151–281, 41 figs.

Carter, G.T., and Rinehart, K.L. Jr., 1978. Acarnidines, novel antiviral and antimicrobial compounds from the sponge *Acarnus erithacus* (de Laubenfels). *Jour. Am. Chem. Soc.* **100**(13): 4302–4.

Carter, H.J., 1871. On two undescribed sponges and two Esperiadae from the West Indies; also on the nomenclature of the Calcisponge *Clathrina*, Gray. *Ann. Mag. nat. Hist.* (ser.4). **7**: 268–83, 1 pl.

Dendy, A., 1896. Catalogue of non-calcareous sponges collected by J. Bracebridge Wilson in the neighbourhood of Port Phillip Heads. Part 2. *Proc. R. Soc. Vict.* **2**(8): 14–51.

1905. Report on the sponges collected by Prof. Herdman at Ceylon in 1902. *Rep. Ceylon Pearl Oyster Fish. Gulf of Manaar*. **3** (Suppl. 18): 57–246, 16 pls.

1916. Report on the non-calcareous sponges collected by Mr James Hornell at Okhamandal in Kattiawar in 1905–1906. *Rep. Government of Baroda on the Marine Zool. of Okhamandal*, (ser. 2). **17**: 96–146, 4 pls.

1922. Report on the Sigmatotetraxonida collected by H.M.S. 'Sealark' in the Indian Ocean. *Trans. Linn. Soc. London, Zool.* **18**: 1–164, 18 pls.

Desqueyroux-Faundez, R., 1981. Révision de la collection d'éponges d'Amboine (Moluques, Indonésie) constituée par Bedot et Pictet et conservée au Muséum d'histoire naturelle de Genève. *Rev. Suisse Zool.* **88**(3): 723–64, 132 figs.

Dickinson, M.G., 1945. Sponges of the Gulf of California. *Univ. S. Calif. publs. Alan Hancock Pac. Exped.* **11**(1): 1–252, 97 pls.

Gray, J.E., 1867. Notes on the arrangement of sponges, with description of some new genera. *Proc. Zool. Soc. London*. 1867: 492–558, 2 pls.

Hechtel, G., 1965. A Systematic study of the Demospongiae of Port Royal, Jamaica. *Bull. Peabody Mus. nat. Hist.* **20**: 1–103, 8 pls, 15 figs.

Hentschel, E., 1912. Kiesel- und Hornschwämme der Aru- und Kei-Inseln. *Abh. Senckenb. Naturf. Ges.* **34**: 294–448, 9 pls.

Hofknecht, G., 1978. Description and key to the intertidal sponges of the Puerto Penasco area in the Gulf of California. *Jour. Ariz. Nev. Acad. Sci.* **13**(2): 51–6.

Hooper, J.N.A., 1984. *Sigmaxinella soelae* and *Desmacella ithystela*, two new desmacellid sponges (Porifera, Axinellida, Desmacellidae) from the Northwest Shelf of Western Australia, with a revision of the Family Desmacellidae. *Northern Territory Mus. Arts. Sci. Monog. Ser.* **2**: 1–58, 18 figs.

Hoshino, T., 1981. Shallow-water Demosponges of Western Japan, I, II. *Jour. Sci. Hiroshima Univ., Ser. B (Div.1 Zool.)* **29** (1–2): 47–205, 11 pls, 86 figs, 207–76, 7 pls., 38 figs.

Keller, C., 1889. Die Spongienfauna des rothen Meeres. *Z. wiss. Zool.* **48**: 311–406, 5 pls.

Kieschnick, O., 1896. Silicispongiae von Ternate nach den Sammlungen von Herrn Prof. Dr. W. Kukenthal. *Zool. Anz.* **19**: 526–34.

1900. Kieselschwämme von Amboina. *In*: Semon, R. 'Zoologische Forschungsreisen in Australien und dem Malayischen Archipel ... ausgefuhrt in den Jahren 1891–1893.' 5. *Denskschr. med. natw. Ges. Jena*. **8**: 545–582, 1 pl.

Laubenfels, M.W. De, 1927. The red sponges of Monterey Peninsula, California. *Ann. Mag. nat. Hist.* Ser. 9. **19**: 258–66.

1930. The sponges of California. *Standford Univ. Bull.* **5**(98): 24–9.

1932. The marine and freshwater sponges of California. *Proc. U.S. Nat. Mus. Washington.* **81**(4): 1–140, 79 figs.

1936. A discussion of the sponge fauna of the Dry Tortugas in particular, and the West Indies in general, with material for a revision of the families and orders of the Porifera. *Papers Tortugas Lab.* **30**: 1–225, 22 pls.

Lévi, C., 1952. Spongiaries de la côte du Sénégal. *Bull. Inst. français Afrique noire.* **14**: 34–59, 20 figs.

1958. Resultats scientifiques des campagnes de la 'Calypso'. Fasc. III. Spongiaries de Mer Rouge. *Ann. Inst. Océan. Monaco*. **34**: 3–46, 37 figs.

1959. Resultats scientifiques des campagnes de la 'Calypso'. Fasc. IV. (5). Golfe de Guinée. Spongiaries. *Ann. Inst. Océan. Monaco*. **37**: 115–41, 2 pls., 31 figs.

1963. Spongiaries d'Afrique du Sud. (1) Poecilosclérides. *Trans. R. Soc. S. Africa*. **37**(1): 1–72, 10 pls, 75 figs.

1973. Systématique de la classe des Demospongiarias (Démosponges). *In*: Grassé, P.P. (Ed.). 'Traité de Zoologie.' **3**: 577–631. (Masson et Cie: Paris).

Randall, J.E. and Hartman, W.D., 1968. Sponge-feeding fishes of the West Indies. *Mar. Biol.* **1**(3): 216–25.

Ridley, S.O., 1884. Spongiida. *In*: 'Reports on the Zoological collections made in the Indo-Pacific Ocean during the voyage of H.M.S. "Alert" 1881–

1882'. (British Museum (Natural History), London, 366–484, 582–630, 7 pls.

Ridley, S.O., and Dendy, A., 1887. Report on the Monaxonida collected by H.M.S. 'Challenger' during the years 1873–1876. *Rep. Sci. res. Voy. "Challenger", Zool.* **20**: 1–275, 51 pls.

Ruetzler, K., 1965. Systematik und ökologie der Poriferen au Litoral-Schattengebieten der Nordadria. *Z. Morph. Ökol. Tiere.* **55**: 1–82, 41 figs.

Sarà, M., 1960. Poriferi del litorale dell'isola d'Ischia e loro ripartizions per ambienti. *Pubbl. Staz. Zool. Napoli.* **31**: 421–72, 2 pls., 11 figs.

Schwab, D.W. and Shore, R.E., 1971. Fine structure and composition of a siliceous sponge spicule. *Biol. Bull. mar. biol. Lab. Woods Hole.* **140**: 125–36, 5 pls.

Shore, R.E., 1972. Axial filaments of siliceous sponge spicules, its organic components and synthesis. *Biol. Bull. mar. biol. Lab. Woods Hole.* **143**(3): 689–98, 5 pls., 2 figs.

Soest, R.W.M. Van, 1984. Marine sponges from Curaçao and other Caribbean localities. Part III. Poecilosclerida. *Stud. Fauna Curaçao Caribb. Isl.* **66**(199): 1–167, 10 pls., 58 figs.

Tanita, S., 1963. Report on the non-calcareous sponges in the Museum of the Biological Institute of the Tohoku University. Part II. *Sci. Rep. Tohoku Univ., Ser. 4.* **29**(2): 121–30, 1 pl., 5 figs.

Thiele, J., 1903. Kieselschwämme von Ternate, II. *Abhandl. Senckenb. Naturf. Ges.* **25**: 933–68. 1 pl.

Thomas, P.A., 1970. Studies on Indian Sponges — VI. Two new records of siliceous sponges (Poecilosclerida : Tedaniidae) from the Indian region. *Jour. mar. biol. Ass. India.* **12**(1–2): 43–50, 4 figs.

1973. Marine Demospongiae of Mahe Island in the Seychelles Bank (Indian Ocean). *Ann. Mus. roy. Afr. Centr. (ser.8 Sci. Zool.)* **203**: 1–96, 8 pls.

Topsent, E., 1892. Diagnoses d'Eponges nouvelles de la Méditerranée et plus particulièrment de Banyuls. *Arch. Zool. exp. gén. (Sér. 2). Notes et Revue.* **10**: xvii–xxx.

1892b. Contribution à l'étude des spongiaries de l'Atlantique Nord. *Rés. camp. Sci. Albert Ier Monaco.* **2**: 1–165, 11 pls.

1894. Une réforme dans la classification des Halichondrina. *Mem. Soc. Zool. France.* **7**: 5–26.

1897. Spongiares de la baie d'Amboine (Voyage de MM M. Bedot et C. Pictet dans l'archipel Malais). *Rev. Suisse Zool.* **4**: 421–87, 4 pls.

1904. Spongiares des Açores. *Rés. Camp. Sci. Albert Ier Monaco.* **25**: 1–263, 18 pls.

1925. Étude des spongiaires du Golfe de Naples. *Arch. Zool. exp. gén.* **63**: 623–725, 8 pls., 27 figs.

1928. Spongiaires de l'Atlantique et de la Méditerranée provenant des croisières du Prince Albert Ier de Monaco. *Rés. Camp. Sci. Albert Ier Monaco.* **74**: 1–376, 11 pls.

1929. Phénomènes de styloprothèse chez des Poecilosclérines. *Arch. Zool. exp. gén., Notes et Revue.* **68**: 19–32, 14 figs.

1934. Étude d'éponges littorales du Golfe de Gabès. *Bull. Stat. Aquiculture et Pêche, Castiglione.* **1932**: 71–102.

Topsent, E. and Olivier, M., 1943. Éponges observées dans les parages de Monaco (fin). *Bull. Inst. Océanog. Monaco.* (854): 1–12.

Vacelet, J., 1960. Éponges de la Méditerranée nord-occidentale récoltées par le 'President Théodore-Tissier' (1958). *Rev. Trav. Inst. Pêches Marit.* **24**: 257–72, 5 figs.

1961. Spongiaries (démosponges) de la région de Bonifacio (Corse). *Rev. Trav. Sta. Mar. Endoume, Bull.* **22**(36): 21–45, 4 figs.

Vacelet, J., Vasseur, P. and Lévi, C., 1976. Spongiaries de la pente externe des récifs coralliens de Tuléar (sud-oest de Madagascar). *Mem. Mus. Nat. Hist. nat., n.s., A. Zool.* **99**: 1–116, 10 pls, 78 figs.

Wiedenmayer, F., 1977. 'Shallow-water sponges of the Western Bahamas.' (Birkhauser, Basel: Stüttgart). 287 pp., 43 pls.

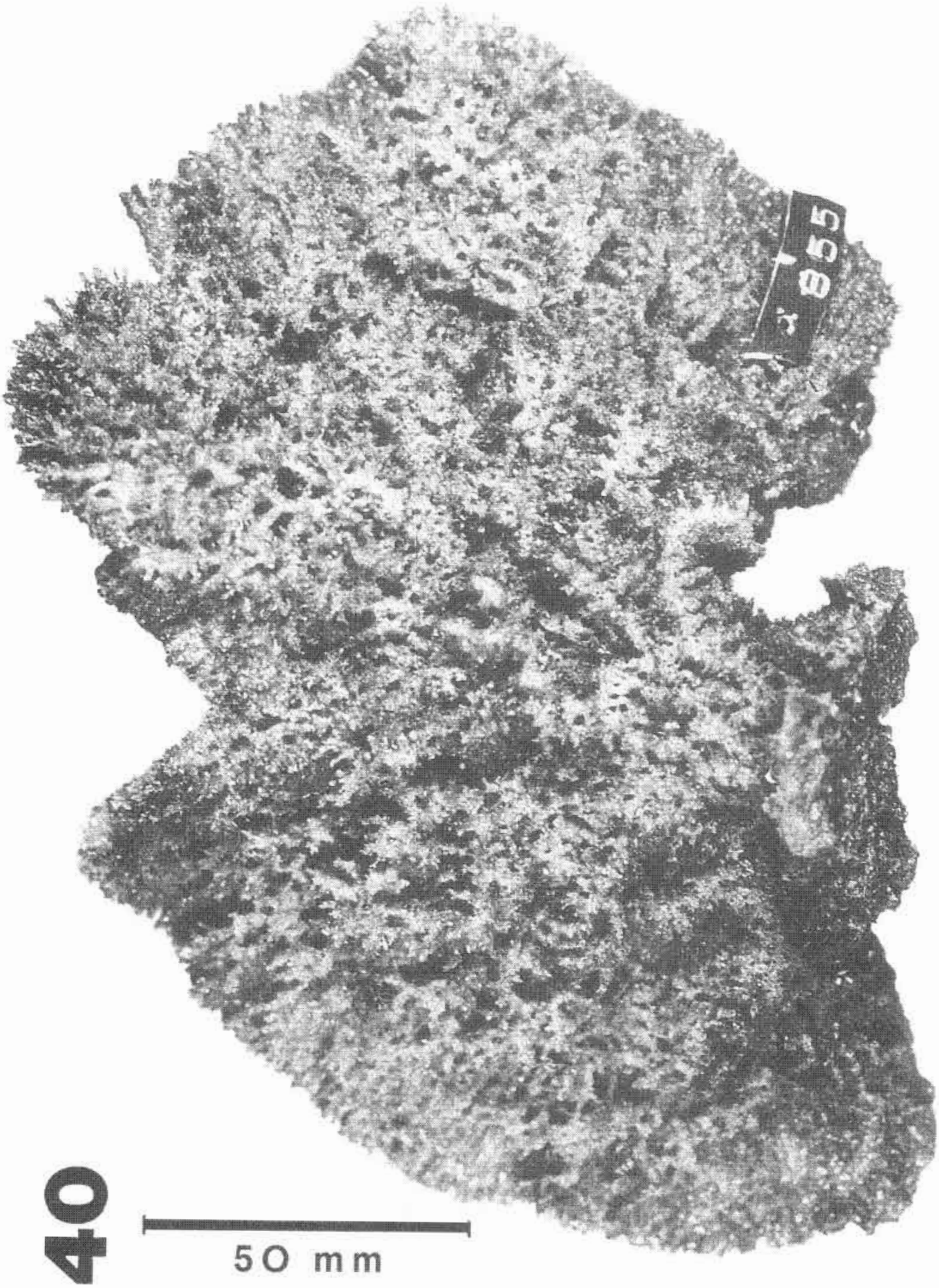

FIG. 40: *Acarnus thielei*; exterior surface of specimen NTM Z855, showing numerous raised surface projections.

41

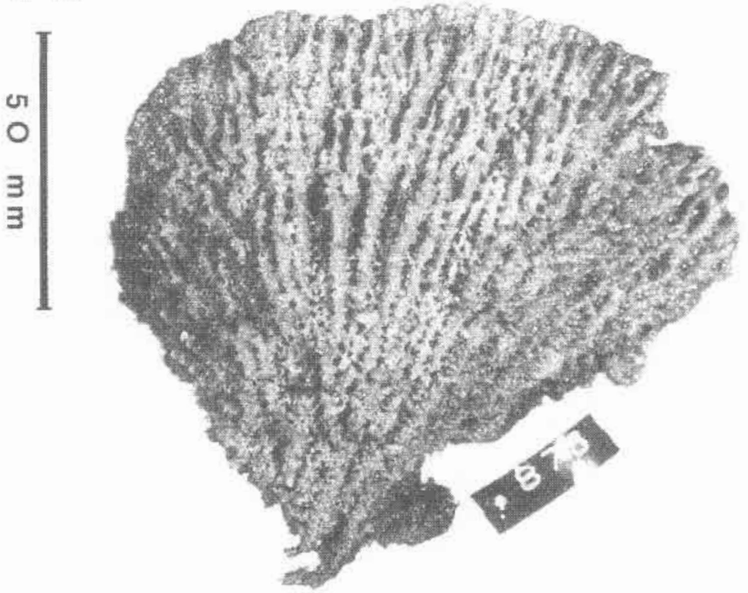

FIG. 41: *Acarnus thielei*; exterior surface of specimen NTM Z876, showing raised longitudinal surface ridges.

42

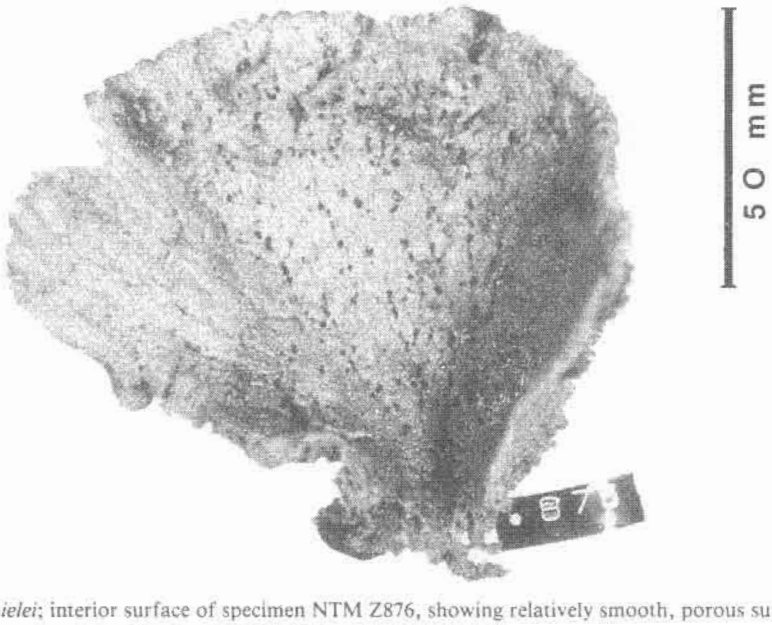

FIG. 42. *Acarnus thielei*; interior surface of specimen NTM Z876, showing relatively smooth, porous surface.

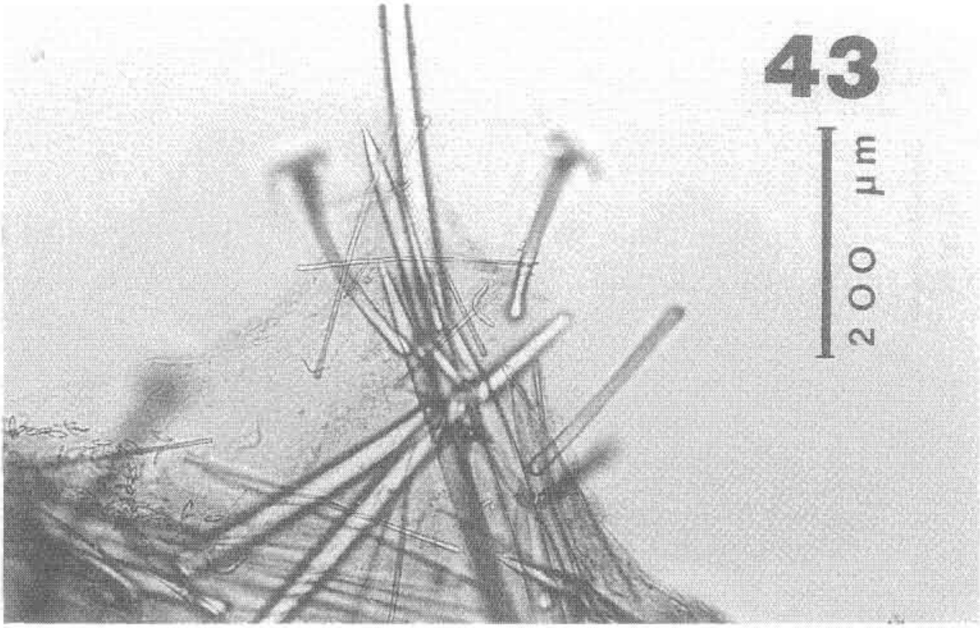

FIG 43. *Acarnus thielei*; photomicrograph of perpendicular section through choanosome of specimen NTM Z876.

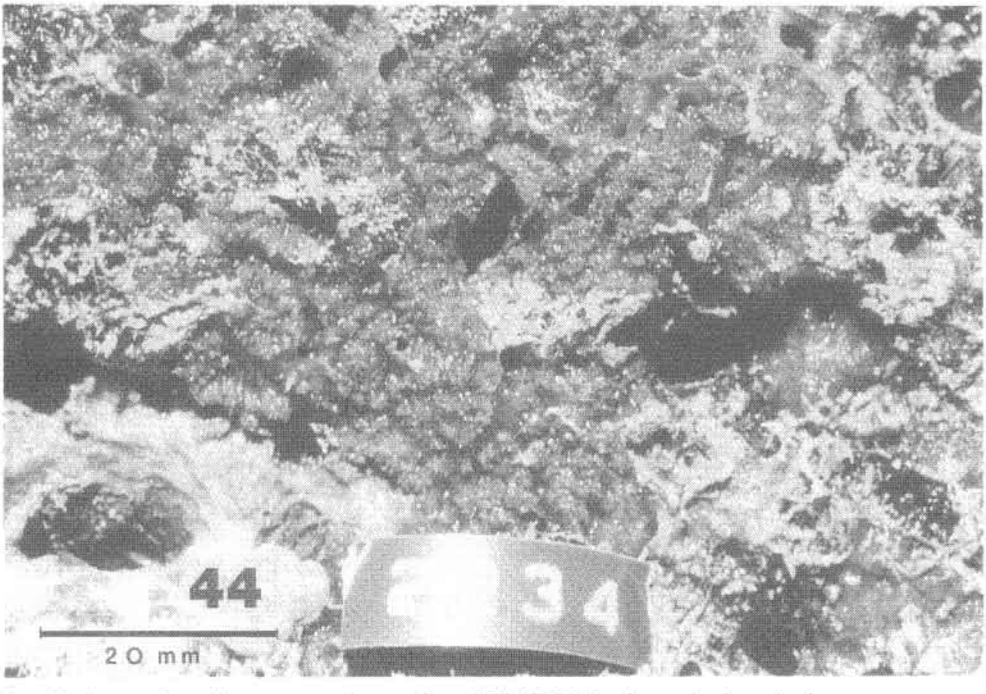

FIG. 44. *Acarnus innominatus*; encrusting specimen NTM Z2234 *in situ* on dead coral substrate.

45

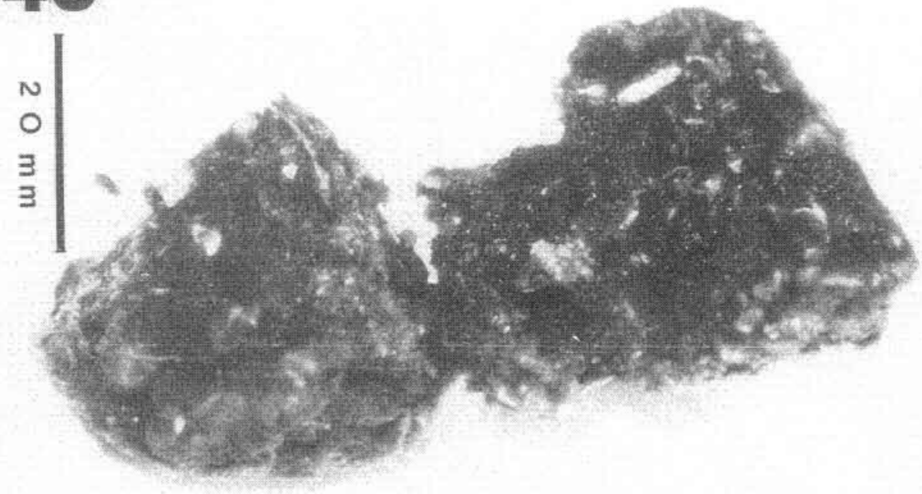

FIG. 45. *Acarnus tortilis*; encrusting specimen QM GL1538.

46

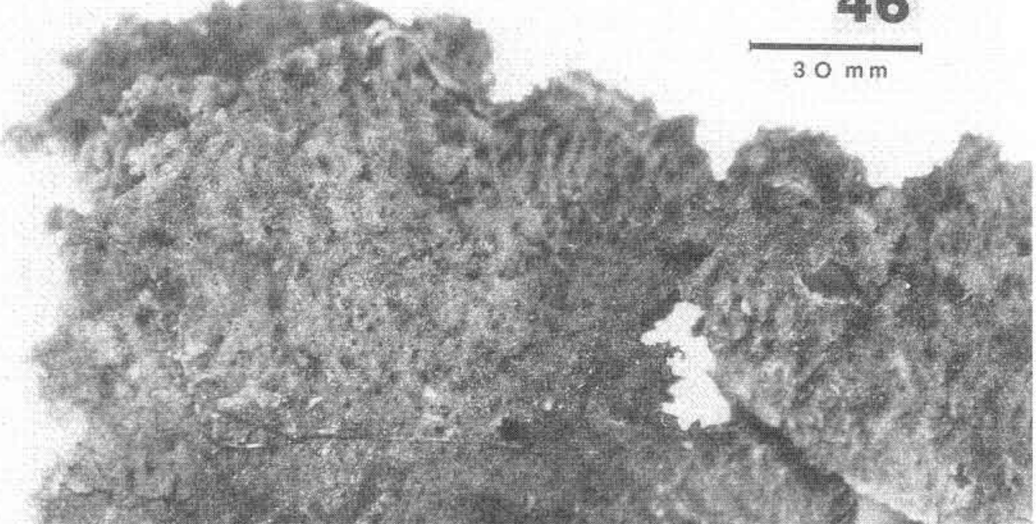

FIG. 46. *Acarnus ternatus*; exterior surface of lamellate specimen QM GL2773.

FIG. 47. *Acarnus ternatus*; atypical bulbous-digitate specimen QM GL715.

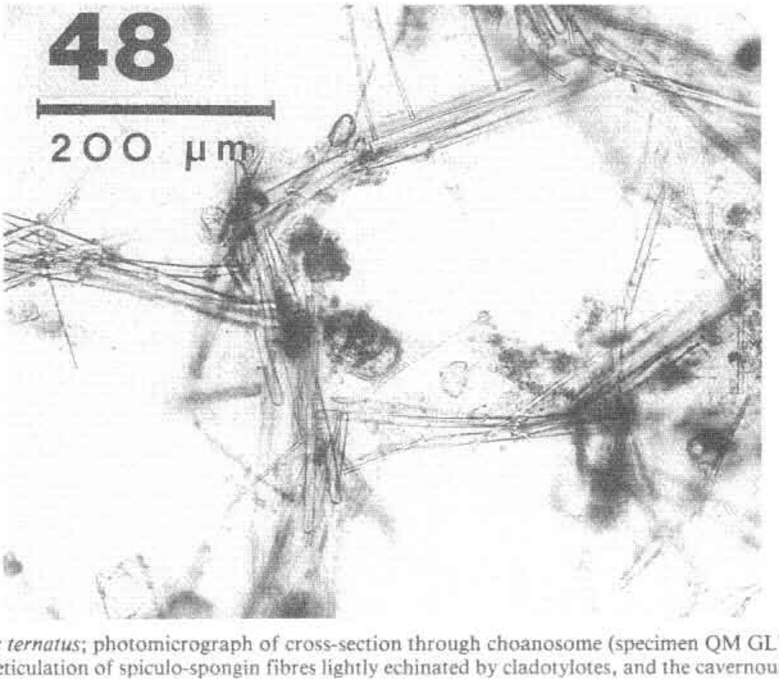

FIG 48. *Acarnus ternatus*; photomicrograph of cross-section through choanosome (specimen QM GL715), showing isodictyal reticulation of spiculo-spongin fibres lightly echinated by cladotylotes, and the cavernous architecture.