Systema Porifera: A Guide to the Classification of Sponges, Edited by John N.A. Hooper and Rob W.M. Van Soest

Family Trachycladidae Hallmann, 1917

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Trachycladidae Hallmann (Demospongiae, Hadromerida), contains two genera with at least nine species, all having an axial (or basally) compressed skeleton, and an extra-axial plumo-reticulate skeleton, with megascleres predominantly oxeas, less often strongyles and/or (tylo-)styles, in spongin-enforced multispicular tracts, or in the case of encrusting species, megascleres erect on the substrate (in hymedesmioid arrangement). Ectosomal skeleton is a crust of spinispirae (spined vermiform spiraster-like spicules), with smooth microrhabds and/or spinispirae dispersed throughout the mesohyl. The two genera are differentiated on the basis of fundamental differences in spinispirae morphology. Species are known from the shallow subtidal to about 220 m depth, distributed from temperate Australia, New Zealand and New Caledonia, Indonesia, East Africa and South Africa, Mediterranean and the western North Atlantic.
Keywords: Porifera; Demospongiae; Hadromerida; Trachycladidae; *Rhaphidhistia*; *Trachycladus*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Trachycladidae Hallmann, 1917c: 673. [Spirophorellinae] Lendenfeld, 1889b (*nomen nudum*). Rhaphidistiinae de Laubenfels, 1936a.

Definition

Hadromerida with spined vermiform spinispirae and smooth microrhabds, with a differentiated axial and extra-axial skeleton cored by oxeas, strongyles and/or (tylo-)styles.

Diagnosis

Encrusting, massive or branching growth forms. Oscules are small (less than 1 mm diameter) and ostia are scattered singly or grouped. Skeleton is condensed in the axial region and plumo-reticulate in the extra-axial region, with ascending multispicular tracts joined at infrequent intervals by single spicules. Encrusting species have a hymedesmioid architecture. Skeletal tracts are composed of spongin fibres enclosing oxeas, strongyles and/or (tylo-)styles. Microscleres are smooth microstrongyles (microrhabds) and/or spined vermiform spiraster-like spirules (spinispirae), with either a curled shaft bearing longitudinal rows of spines along its length, or a straight shaft bearing concentric spiral rows of spines around its circumference and length.

Remarks

Trachycladus was allocated to Axinellidae as 'Axinellidae with microscleres', but nevertheless recognised as anomalous (Hallmann, 1916a: 454), and later (in postscript) allocated to a monogeneric subfamily Trachycladinae (Hallmann, 1917c: 673). Topsent (1928c) overlooked or ignored Hallmann's new subfamily in his revision of Demospongiae, and retained the genus in Axinellidae. Hallmann (1916a: 454) remarked on the obvious derivation of spinispirae from spirasters of *Spirastrella*, the fact that microrhabds occur commonly in hadromerids, and (less convincingly) that some Spirastrellidae (e.g., *S. dilatata* Kirkpatrick) have megascleres united into spongin-enforced tracts reminiscent of *Trachycladus*. Conversely, he noted that *Trachycladus* had skeletal structure reminiscent of sigma-bearing poecilosclerids (which we now know as Desmacellidae), and thus supposedly represented a link between Spirastrellidae and Poecilosclerida. Brøndsted (1924b) also stressed the close relationship between *Trachycladus* and Spirastrellidae and *Latrunculia*, although the latter taxon is no longer widely included in this relationship (see chapters on Latrunculiidae and Podospongiidae, this volume). Similarly, Trachycladidae was included in the polyphyletic order Axinellida by Bergquist (1970, 1978), Lévi (1973), Hartman (1982) and others, as opposed to an allocation in Hadromerida, implicitly based on possession of an axially compressed and extra-axially plumo-reticulate skeletal structure, spongin-enforced spicule tracts, bright colouration, arborescent growth form (Lévi, 1973). Unfortunately there is no corroboratory evidence to support a close relationship between typical axinellids (e.g. *Axinella*) and *Trachycladus* (e.g., oviparous mode of reproduction, parenchymella larvae), and in the absence of this evidence Trachycladidae is included in Hadromerida. Conceivably, however, it could justifiably be merged in Spirastrellidae given the fundamental similarities in their microscleres, although with equally fundamental differences in patterns of spination, hypothesised to reflect ontogenetic differences in their respective development.

Scope and biology

Four nominal genera have been included, or potentially included in the family, of which two are considered here to be valid, *Trachycladus* and *Rhaphidhistia*. There are 17 nominal species or subspecies referred to the family at one time or another, of which only nine are probably valid: seven allocated to *Trachycladus*, and two to *Rhaphidhistia*. These are: (1) *T. laevispirulifer* Carter (the type species, from E, SE, S and SW Australia, including as synonyms: *digitata* Lendenfeld, 1888; *scabrosus* Hallmann, 1916a; *fastigatus* Hallmann, 1916a; *gracilis* Hallmann, 1916a; *clavatus* Hallmann, 1916a, *reteporosus* Hallmann, 1916a; and *pustulosus* Hallmann, 1916a); (2) *T. strongylatus* Hallmann, 1916a (as *T. digitatus strongylatus*, from Victoria)

including *T. digitatus* sensu Lévi & Lévi, 1983b (from New Caledonia); (3) *T. stylifera* Dendy, 1924 (from northern and southern New Zealand, Bergquist, 1970); (4) *T. cervicornis* Burton, 1959a (from east Africa); (5) *T. tethyoides* Burton, 1959a (from east Africa and Indonesia, Van Soest, unpublished); (6) *T. 'spinispirulifer' sensu* Carter, 1879b (as *Suberites*) from E, SE, S and SW Africa (Carter, 1886a; Dendy, 1897; Burton, 1959a; Lévi, 1959); and Indonesia (as *Spirastrella dilatata*; Kieschnick, 1896; Thiele, 1900); and *T. 'spinispirulifer'* sensu Bergquist, 1970, from N New Zealand, and Uriz (1987) (from SW Africa)) – the two groups of '*spinispirulifer*' potentially also not conspecific; (7) *T. minax* (Topsent, 1888) (as *Hymeraphia*) from the Mediterranean, NW Africa and the coast of France (Topsent, 1900; Burton, 1956; Sarà, 1958, 1961; Cabioch, 1968b; Pulitzer-Finali, 1977); (8) *Rhaphidhistia spectabilis* Carter, 1879b; and (9) *R. mirabilis* (Dendy, 1924) from N New Zealand (as *Dotonella*). Hallmann (1916a, plate 24) mentions another species (*T. formosus*), but this appears to be a manuscript name and thus *nomen nudum*.

Trachycladus laevispirulifer from southern Australia was discovered to have organohalogen compounds (trachycladine) with highly cytotoxic activity against the P388 leukemia cell line (Searle & Molinksy, 1995; Gribble, 1998), but few other biological or chemical data are yet known for any species of the family.

Reviews

Topsent (1928c: 37), Bergquist (1970: 22; 1978), Brien *et al*. (1973), Wiedenmayer (1989: 53), Hartmann (1982), Hooper & Wiedenmayer (1994: 444).

Distribution

Species are known from the shallow subtidal to depths of at least 220 m (Hartman, 1982), distributed in southern, western and eastern Australia, New Zealand and New Caledonia, Indonesia, East Africa and South Africa, Mediterranean and the western North Atlantic.

KEY TO GENERA

(1) Spinispirae with spines forming regular longitudinal rows running the length of the stem, with the spicule itself (not the spines) curled or contorted into twisted shapes; only one size class of spinispirae ..... ***Trachycladus***
Main spinispirae with a long and straight shaft, but with spines forming a complete full turn around the circumference of the shaft, producing concentric spiral rows along its length; a second smaller, curly size class of spinispirae may also be present ..... ***Rhaphidhistia***

TRACHYCLADUS CARTER, 1879

Synonymy

Trachycladus Carter, 1879b: 343. [*Spirophora*] Lendenfeld, 1887c: 794 (preocc.). *Spirophorella* Lendenfeld, 1888: 236. Taxonomic decision for synonymy Hallmann, (1914: 429).

Type species

Trachycladus laevispirulifer Carter, 1879b (by monotypy).

Definition

Trachycladidae with spines on the spinispirae forming regular rows that run longitudinally along the stem of the spicule, and the spicule itself (not the spines) contorted into curled shapes. Smooth or occasionally faintly centrotylote microrhabds are also typically present.

Diagnosis

Tubulo-digitate, arborescent, whip-like to flabellate, rarely encrusting growth forms. Ectosome with a distinct cortex packed with spinispirae. Choanosomal skeleton compressed in the axial region, plumoreticulate in the extra-axial region, with paucispicular connecting fibres. Fibres fully cored by oxeas, but also including styloid or strongyloid modifications resembling strongyloxeas, anisoxeas, mucronated anisoxeas, true styles or strongyles, and in one species tylostyles. Microscleres are 'spinispirae', smooth or minutely spined, with spines forming longitudinal rows along the shaft, and the geometry of the shaft ranging from simply curved, c-shaped, to twisted with up to two complete turns, and also with microrhabds, smooth or occasionally faintly centrotylote.

Remarks

Spirophorella Lendenfeld (with type species *Spirophora digitata* Lendenfeld, 1887c, by subsequent designation, Wiedenmayer in Hooper & Wiedenmayer, 1994: 444), was undoubtedly proposed as a replacement name for [*Spirophora*] Lendenfeld (a junior homonym of *Spirophora* Milne-Edwards, 1836 (Bryozoa), and [*Spirophora*] Zopf, 1884 (Protozoa)), although Lendenfeld (1888) was not explicit about this.

Reviews

The genus has been reviewed by Hallmann (1916a: 453), Topsent (1928c: 37), Bergquist (1970: 22), Lévi & Lévi (1983b: 942) and Wiedenmayer (1989: 53).

Description of type species

Trachycladus laevispirulifer Carter, 1879b (Fig. 1).

Synonymy. *Trachycladus laevispirulifer* Carter, 1879b: 343, pl. 28, figs 1–5. *Spirophora bacterium* Lendenfeld, 1887c: 795. *Spirophora digitata* Lendenfeld, 1887c: 794. *Trachycladus digitata*; Hallmann, 1916a, pl. 22 fig. 2. *Trachycladus digitatus clavatus* Hallmann, 1916a: 474, fig. 6, pl. 22 fig. 4, pl. 23 fig. 3, pl. 25 fig. 2, pl. 27 fig. 3, pl. 28 fig. 5, pl. 29 fig. 1. *Trachycladus digitatus gracilis* Hallmann, 1916a: 472. *Trachycladus fastigatus* Hallmann, 1916a: 462. *Trachycladus pustulosus* Hallmann,

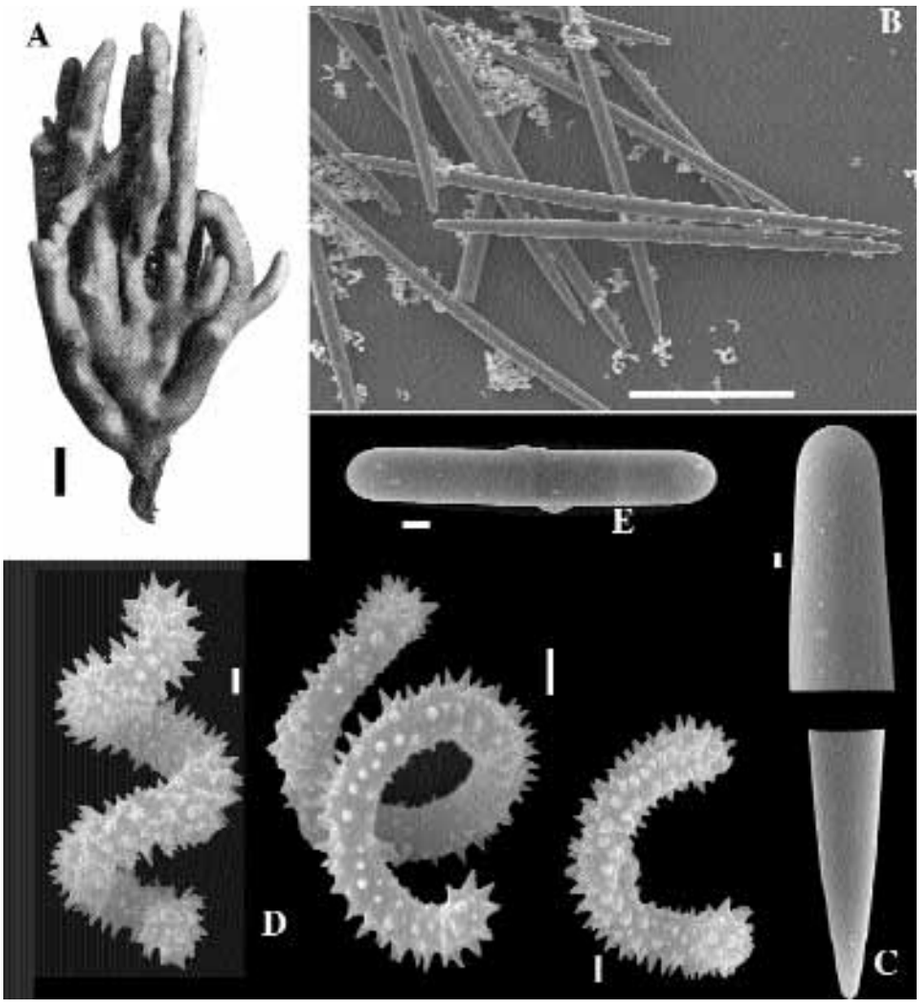

Fig. 1. *Trachycladus laevispirulifer* Carter, 1879b. A, habit of *Trachycladus digitatus* Hallmann, 1916a (jun.syn. of the type species) (reproduced from his plate XXII fig. 2; (scale 1 cm). B, SEM overview of spicules of holotype of *T. laevispirulifer*, BMNH unregistered (scale 100 μm). C, details of stylote megasclere of the same (scale 1 μm). D, spinispirae (scale 1 μm). E, microrhabd (scale 1 μm).

1916a: 486, fig. 9, pl. 21 fig. 5, pl. 26 figs 5, 8, pl. 27 fig. 6, pl. 39 figs 6, 7, pl. 39 figs 6, 7. *Trachycladus reteporosus* Hallmann, 1916a: 479, pl. 21 figs 2, 3, pl. 23 figs 5–8, pl. 24 figs 1–3, pl. 25 fig. 1, pl. 26 figs 1, 4, 7, pl. 27 fig. 5, pl. 28 figs 1–4, pl. 29 fig. 2. *Trachycladus scabrosus* Hallmann, 1916a: 459. Not *Trachycladus digitatus strongylatus* Hallmann, 1916a: 477. Not *Trachycladus stylifer* Dendy, 1924: 377. Refer to Wiedenmayer (1989: 53) for more complete synonymy citations.

Material examined. Lectotype: BMNH unregistered dry. Paralectotype: BMNH 1883.1.25.10 – South Australia. Other type material. Holotype of *S. bacterium*: BMNH 1887.4.27.31 (slide AM G3476) – Westernport Bay, Victoria, Australia. Lectotype of *S. digitata*: AM Z488 – Port Jackson, NSW. Paralectotype AM Z1333 – Encounter Bay, South Australia. Holotype of *T. digitatus clavatus*: AM Z1270 – Port Phillip Bay, Victoria, Australia. Holotype of *T. digitatus gracilis*: AM Z963 – Port Jackson, NSW. Holotype of *T. fastigatus*: AM E3710 – Great Australian Bight. Holotype of *T. pustulosus*: AM Z1761 – Port Phillip Bay, Victoria. Holotype of *T. reteporosus*: AM Z1620 – Port Phillip Bay and Heads, Victoria. Holotype of *T. scabrosus*: AM Z1501 – off Port Jackson, NSW. Additional material. QM collections and Fromont (1999b: 177). Comparative material. Holotype of *T. digitatus strongylatus*: AM Z1760 – Port Phillip Bay, Victoria. Holotype of *T. stylifer*: BMNH 1923.10.1.158 – Three Kings Is., New Zealand. Syntypes of *T. spinispirulifera* (Carter, 1879b): BMNH 1871.5.12.1, BMNH 1954.3.9.443, ZMB 3039 – Port Elizabeth, South Africa.

Description. Highly polymorphic growth form, ranging from tubulo-digitate, shrub-like to simple arborescent, di- or polychotomous branching sponge, rarely unbranched whip-like or flabellate. Branches variable in length between specimens, ranging from: relatively short, club-like, thickened more towards their apex than at their point of attachment to the stalk, with tapering rounded or club-shaped terminations, often bifurcate at the extremities; to long thin tendrils tapering to fine points. Branches fleshy in life. Stalk relatively firm and thin compared to branch diameter. Oscules small, up to 3 mm diameter (living material), or <1 mm diameter when preserved (if visible at all), scattered either on lateral (less often terminal) parts of branches, in vague longitudinal rows, or clustered into poriferous areas on the distal parts of branches. Texture compressible, rubbery in life, firm and harsh

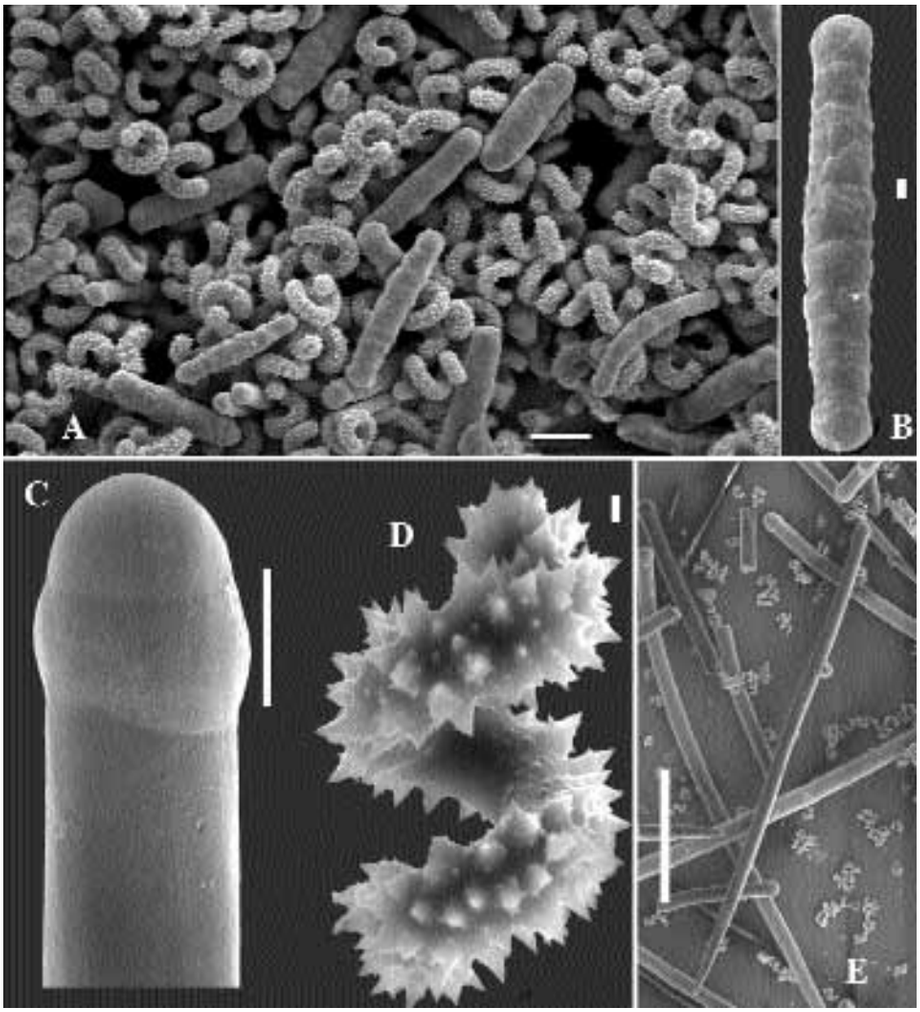

Fig. 2. A–B, *Trachycladus stylifer* Dendy, 1924. A, SEM overview of microscleres of ZMA 13000, from 695–798 m off New Zealand (scale 10 μm). B, detail of microrhabd of the same (scale 1 μm). C–E, *Trachycladus spinispirulifer* (Carter, 1880 as *Suberites*), SEM images of the holotype BMNH 1871.5.12.1. C, detail of tylostyle (scale 10 μm). D, spinispira (scale 1 μm). E, overview of spicules (scale 100 μm).

when preserved. Surface macroscopically smooth and even in life but microscopically conulose due to ascending fibres terminating at the surface. When preserved the surface is porous and highly conulose, with prominent sharp conules ('scopuliform process') corresponding to the lines of reticulate fibres below the surface, but this is certainly not a feature of the living sponge. Subdermal canals clearly visible below surface when detached. Colour red, red-orange, vermilion to pale pinkish alive, beige in ethanol with a distinctly white surface membrane that largely disintegrates after preservation. Ectosome with a distinct and detachable cortical region packed with spinispirae. Choanosomal skeleton axially compressed, with axis occupying at least half of branch diameter, composed of longitudinally directed multispicular tracts interconnected by short, oblique lateral tracts together forming a dense reticulation, becoming more plumose towards the periphery of the axis. Ascending fibres arising from the central axis are radial, plumose, becoming increasingly thinner towards the surface, with primary multispicular ascending fibres and paucispicular lateral connecting fibres, the former extending to just below the cortex. Fibres fully cored by tracts of mostly oxeas, but also including styloid or strongyloid spicules, with many also scattered irregularly between fibres. Mesohyl heavily collagenous, with scattered spinispirae and microrhabds, the latter often clustered, and sarcode permeated with large aquiferous canals near the surface, becoming increasingly smaller and converging as they approach the axial region. Megascleres predominantly oxeas, symmetrically curved at centre with varying terminations ranging from slightly fusiform, gradually tapering to abruptly pointed with telescoped points; occasionally styloid resembling strongyloxeas, anisoxeas, mucronated anisoxeas, true styles or strongyles, 230–315 × 5–7 μm. Microscleres 'spinispirae', resembling spirulae, toxaspires and sigmaspires, smooth or minutely spined, with spines forming regular rows that run longitudinally along the stem; the spicule itself (not the spines) are curly, ranging from simply curved, c-shaped, to contorted and forming up to two complete turns of the shaft, 6–15 × 1–2 μm; microrhabds smooth, occasionally faintly centrotylote, 6–16 × 1–4 μm.

Remarks. Wiedenmayer (1989) notes that there are so many descriptions of the type species (and its synonyms) that it comprises one of the most prolifically and thoroughly described and illustrated of sponges in the Australian fauna (refer to literature citations in Wiedenmayer, 1989: 53–54). It has a confirmed distribution from

coastal waters of southern Queensland (J.N.A. Hooper, unpublished collections), NSW, Victoria, South Australian and southern Western Australia (to the Houtman Abrolhos) (refer to records cited by Wiedenmayer, 1989). Other records included in synonymy with the type species by Wiedenmayer (1989) are excluded here and now considered valid species: *T. stylifer* from New Zealand (Dendy, 1924: 377; Bergquist, 1970: 21), and *T. 'digitatus' sensu* Lévi & Lévi from deeper waters off New Caledonia (Lévi & Lévi, 1983b: 942). *Suberites spinispirulifer sensu* Carter, 1879b from Africa has been traditionally assigned to *Spirastrella* but has curly 'spirasters' that closely resemble those of Trachycladidae, in addition to having tylostyles for megascleres and encrusting growth form, substantially expanding the definition of the genus.

RHAPHIDHISTIA CARTER, 1879

Synonymy

Rhaphidhistia Carter, 1879b: 300. *Dotonella* Dendy, 1924: 379.

Type species

Rhaphidhistia spectabilis Carter, 1879b (by monotypy).

Definition

Trachycladidae with long straight spinispirae, with a straight shaft and spines forming spiral rows along the length of the shaft, each forming a complete full turn around the circumference of the shaft. A second category of smaller, curly spinispirae may also be present, forming an ectosomal cortex.

Diagnosis

Thinly or thickly encrusting growth forms, with 1–2 size categories of spinispirae, and if both are present, the smaller forming an ectosomal cortex. Choanosomal skeletal architecture ranges from loosely dispersed megascleres in vaguely plumose arrangement to hymedesmioid architecture, consisting of erect megascleres embedded in the substratum and protruding through the surface. Megascleres are oxeas or tylostyles. Microscleres are spinispirae in one or two size categories, the larger with a long straight shaft and bearing concentric spiral rows of spines forming a complete turn around the circumference of the shaft, producing a smooth inner curve, and the smaller with similar spination but with the shaft curled into c-, s- or contorted-shapes.

Remarks

See remarks for type species below.

Description of type species

Rhaphidhistia spectabilis Carter (Fig. 3).

Synonymy. *Rhaphidhistia spectabilis* Carter, 1879b: 300–301, pl. 26, figs 10, 13, 14 (by monotypy).

Material examined. Holotype: BMNH 1877.5.21.1877a (slide) – Mauritius. Other material. Holotype of *Dotonella mirabilis* Dendy, 1924: BMNH 1923.10.1.159 (fragment and 3 slides) – Three Kings Island, New Zealand, 'Terra Nova' Expedition, 180 m depth.

Description of Rhaphidhistia spectabilis (partly from Carter, 1879b and holotype slide; Fig. 3A–D). Lamelliform, extremely thinly encrusting, size up to 2.5 cm in lateral expansion, whitish yellow in dry condition, texture delicate. Surface smooth, even, with oscules raised on monticular processes. Choanosomal skeleton described as consisting of a delicate sarcode with 'loosely' arranged oxeas and large lacunae (Carter, 1879b). In fact the skeletal preparation consists of a tissue tease which contains plumose bundles of oxeas packed with spinispirae, and it is possible that these bundles may have been erect on the surface of the living sponge. This feature is not possible to verify based on existing museum material. Oxeas large, slightly curved, slightly asymmetrical, abruptly pointed or slightly tapering, occasionally with rounded blunt tips, 440–648 × 11–22 μm. Microscleres are long, straight or irregularly curved spinispirae, up to 28–75 × 4–9 μm, with up to 10 spiral twists of spines running around the circumference of the spicule forming concentric spiral rows along its length. Spinispirae are not apparently restricted to any particular region of skeleton but are heavily clustered throughout the entire skeleton.

Description of Dotonella mirabilis Dendy (partly from Dendy, 1924 and holotype; Fig. 3E–I). Thinly encrusting sponge, about 22 × 16 mm in dimensions, cream-white in preserved condition, with a strongly hispid surface (although now abraded due to transportation and handling). Basal skeleton, in contact with substratum, has a dense layer of larger spinispirae, and likewise the ectosomal skeleton has a dense layer of smaller spinispirae (slides of the holotype suggest that the ectosome is a removable cortex), and with a hymedesmioid skeleton of large tylostyles embedded in the basal layer and points protruding a long way through the ectosomal layer and beyond the surface, producing the hispid appearance. Megascleres are tylostyles with well-developed basal tyle, a somewhat curved shaft, and gradually tapering to sharp or abrupt points, 800–1000 × 14–24 μm (although the exact length is difficult to measure since most spicules are broken in the slide preparations), with rounded heads 20–24 μm diameter. Microscleres consist of two distinct size categories of spinispirae, both with tight spiral concentric whorls of spines over the spicule; the larger basal ones have a long, thick and straight shaft, 90–135 × 10–19 μm, with concentric spiral spination; and the smaller ones are tightly curled, varying from c-shapes to up to two complete twists, or sometimes recurved upon itself forming commas, and resembling those of the type of *T. laevispirulifer*, 9–14 × 4–7 μm, and are densely covered by tiny spines.

Remarks. *Rhaphidhistia*, including *Dotonella* Dendy (previously referred to Spirastrellidae), stands apart from *Trachycladus* in having long straight spinispirae (as opposed to curly ones), and also with quite different patterns of spination on spinispirae. In *Rhaphidhistia* spinispirae are even more distinct from typical spirasters of Spirastrellidae than are those of *Trachycladus*, having a straight shaft with spines forming concentric spiral rows, with each row forming a complete full turn around the circumference of the shaft, and producing a smooth inner curve (see Fig. 3). By comparison, spines on the spinispirae of *Trachycladus* (see Figs 1–2) form regular rows that run longitudinally along the stem of the spicule, and the spicule itself (not the spines) forming a contorted curl or twist. We consider these differences may represent fundamental ontogenetic processes in the formation of microscleres and hence justify differentiating these two genera.

Dotonella (type species *Dotonella mirabilis* Dendy, 1924: 379, pl. 15, figs 43–45; by monotypy), differs from *Rhaphidhistia s.s.* in

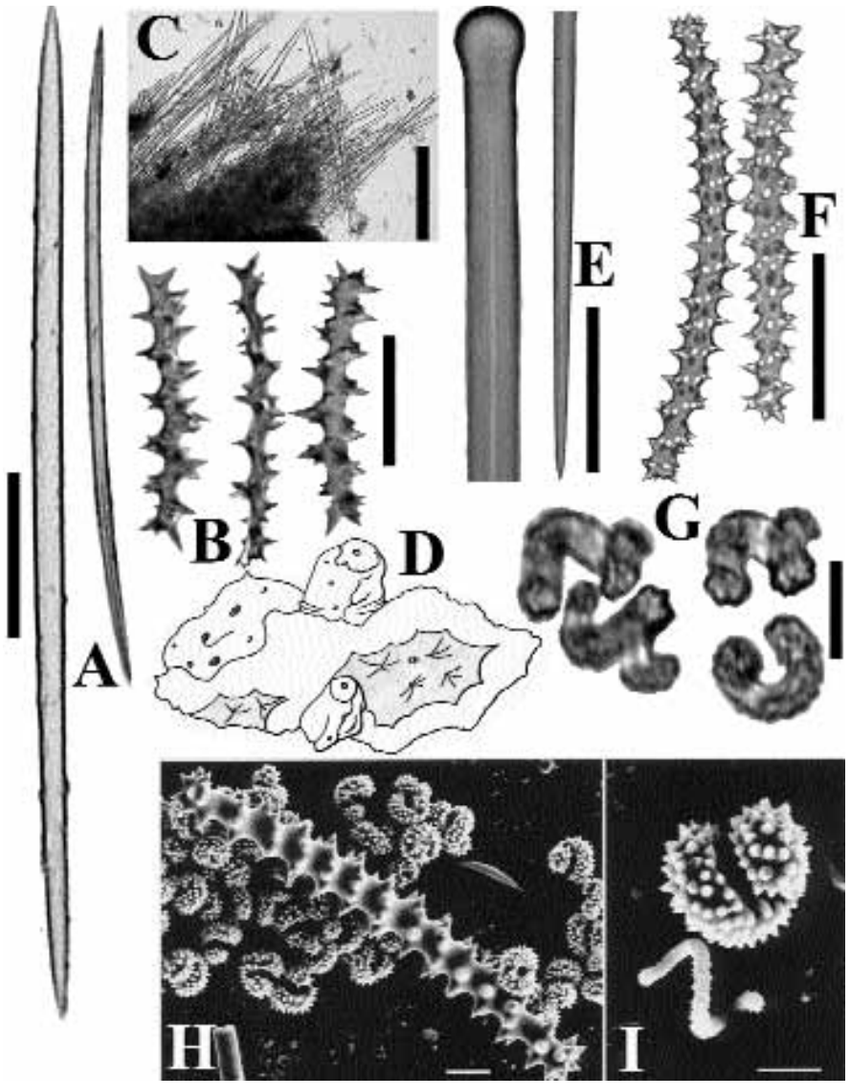

Fig. 3. A–D, *Rhaphidhistia spectabilis* Carter, 1879b. A, oxeas (scale 100 μm). B, large spinispirae (scale 25 μm). C, ectosomal skeleton (scale 200 μm). D, drawing of encrusting specimen (from Carter, 1879b). E–I, *Rhaphidhistia mirabilis* (Dendy, 1924 as *Dotonella*). E, ends of tylostyles (scale 50 μm). F, larger spinispirae (scale 50 μm). G, smaller spinispirae (scale 5 μm). H, large microrhabd surrounded by spinispirae (scale 10 μm). I, spinispirae (two types or one developing stage), enlarged (scale 10 μm). H–I, courtesy of Klaus Rützler.

having a differentiated deeper layer of large straight spinispirae and a superficial layer of much smaller curly spinispirae, and with megascleres consisting of tylostyles (as opposed to oxeas). There are also reported differences in their respective choanosomal skeletal structures (hymedesmioid versus 'loosely arranged'), but these might plausibly be attributed to relative differences in the thicknesses of their respective growth forms. Dendy (1924) also remarked on the similarities between its microscleres with those of *Rhaphidhistia spectabilis* Carter and *Spiroxya heteroclita* Topsent, 1900: 280, although he discounted any inferred relationship between these groups based on the fact that both the latter have oxeas for megascleres. However, it is not certain that the skeleton of *Rhaphidhistia spectabilis* is 'loosely arranged', as quoted by Carter (1879b), where slide preparations reveal distinct plumose bundles of oxeas, which are obviously flattened in slide preparations, but potentially these bundles might have formed erect hymedesmioid or microcionid architectures in the living sponge, similar to the hymedesmioid arrangement seen in *Dotonella*. Dendy (1924) compared *Dotonella* to *Trachycladus* and *Dotona* (an excavating Clionaidae), suggesting that only the small spinispirae of *D. mirabilis* resembled those of *Trachycladus*, and the larger ones were more coarsely spined than corresponding spicules in *Dotona*, implying a close relationship between Trachycladidae, Clionaidae and Spirastrellidae – but perhaps also inferring it was one related to their respective growth forms/habits. We reject this assumption, instead regarding that the characteristics of spinispirae are more informative to this hypothesized phylogeny than are modifications to megascleres (with *Rhaphidhistia* having either oxeas or tylostyles, and *Trachycladus* having megascleres that range from oxeas, strongyloxeas, anisoxeas, mucronated anisoxeas, true styles, strongyles or tylostyles). Dendy (1924) included *Dotonella* in the family Clavulidae, subfamily Spirastrellinae, and considered its type species an equivalent to *Dotona pulchella* Carter in the Clionaidae. It is feasible that *Dotonella* and *Rhaphidhistia* could be

assigned to Spirastrellidae (as redefined by Rützler, this volume), but this hypothesis is also rejected given the profound similarities in microsclere geometries to those of *Trachycladus*.

Although de Laubenfels (1936a) subsequently referred *Spirastrella aculeata* Topsent (1890b: 69; 1892: 127) to *Rhaphidhistia*, that species has strongyloxeas (or tornotes) and spirasters typical of spirastrellids (and quite unlike those of the two Trachycladidae genera – clearly indicating that it should remain in *Spirastrella*). Dendy (1924) suggests that *Spiroxya heteroclita* Topsent, 1900 also belongs in *Rhaphidhistia*, having two kinds of spinispirae, although quite different from those of the New Zealand sponge, but this assertion has not yet been tested from examination of relevant type material. He also notes that Hinde & Holmes (1892: pl.7 fig. 38) illustrated a spinispira resembling, but much larger than that of *Dotonella mirabilis*, from the Tertiary deposits of Oamaru, South Island, New Zealand. It is also theoretically feasible that *Spirastrella*-like encrusting species which all have tylostyles should be differentiated from *Trachycladus* proper (with oxeas/strongyles/styles), except for the existence of species like *Dotonella mirabilis* with both tylostyles and *Rhaphidhistia*-like long straight spinispirae microscleres. Thus, there are potentially more species of thinly encrusting 'spirastrellids' that may belong to this genus, but no decision is possible without careful re-examination of respective type material.