Clarification of dictyoceratid taxonomic characters, and the determination of genera

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Abstract: Distinguishing between dictyoceratid families is relatively straight forward, but distinguishing genera and subgenera within some of those families can be difficult. Dictyoceratid genera are characterised by the presence, structure and organisation of skeletal elements, surface characters, choanocyte chambers, collagen, cortical armour and by their general form. There are published instances of misunderstood characters leading to unnecessary and erroneous reassignments or generic mis-diagnoses. There are also situations where authors have redefined genera to accommodate new species, to the point where generic descriptions become too broad, making the character boundaries of the genus indistinct. These factors have led to confusion when attempting to allocate dictyoceratid specimens to some genera. Previously published work by the author attempted to clarify some of these problems, but the aim here is to consolidate those clarifications of dictyoceratid characters into a single paper. Keys and descriptions of dictyoceratid genera are provided.

Keywords: Characters, Dictyoceratida, genera, keys, taxonomy

Introduction

Dictyoceratid families are relatively easy to distinguish, with fine collagenous filaments in the irciniids, the homogeneous skeletal fibres of spongiids, eurypylous choanocyte chambers in dysideids, and the opposite of these characters in thorectids, i.e. diplodal choanocyte chambers, pithed and laminated fibres, and an absence of fine filaments. However, distinguishing genera and subgenera within some of these families can be difficult.

Genera are defined in terms of their skeletal architecture, mucus production, and whether or not they are armoured. Skeletal characters include the presence of primary, secondary or tertiary fibres, fascicular fibres, foreign coring, fibre diameter, skeletal density, collagen deposition, and general skeletal morphology and distribution. Published instances of misunderstood characters, e.g. cortical armour, have led to incorrect generic reassignments or mis-diagnoses, and situations where authors have massaged generic definitions to the point where they become ill-defined and largely meaningless within the context of the appropriate family, e.g. the thorectid *Cacospongia*.

Taxonomic and systematic research based on New Zealand Dictyoceratida encountered a number of ambiguities in morphological characters used to distinguish between some taxa. The following three pairs of genera, one from each of three different families, provide examples where ambiguities in generic diagnoses had resulted in species being incorrectly assigned to genera, or where genera have become a "catch-all" for species that approximate the generic characters.

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Cacospongia vs *Scalarispongia*

Cacospongia, as historically diagnosed, admitted any thorectid sponge with cored primary fibres, uncored secondary fibres, and an unarmoured and finely conulose surface (Bergquist 1980, Desqueyroux-Faúndez and van Soest 1997). While the New Zealand sponges could be "pigeon-holed" into *Cacospongia*, they did not quite "fit". Closer inspection of *Cacospongia* found that the diagnosis was too loose, and that species displayed two different skeletal morphologies – a well-developed secondary fibre skeleton (Fig. 1), in contrast to a simpler, more ladder-like skeleton (Fig. 2), epitomised respectively by *Cacospongia mollior* Schmidt, 1862 (type species of *Cacospongia*) and *Cacospongia scalaris* Schmidt, 1862. Consequently, *Cacospongia* was redefined and amended to provide a less ambiguous taxon, which more closely conformed to the morphology of the type species *Cacospongia mollior* Schmidt, 1862. A new genus, *Scalarispongia*, was established (Cook and Bergquist 2000) for sponges previously assigned to *Cacospongia*, but with a more ladder-like skeleton, with *Cacospongia scalaris* Schmidt, 1862 designated as the type species.

Spongia vs *Hippospongia*

Hippospongia was traditionally distinguished from the very similar *Spongia* by the relative rarity of primary fibres, the presence of large canals, subdermal lacunae and vestibules within the mesohyl, and the firmly attached dermis (de Laubenfels and Storr 1958, Vacelet 1959, Wiedenmayer 1977, van Soest 1978, Bergquist 1980). Historically, the definition of *Hippospongia* became too loose, largely because of the

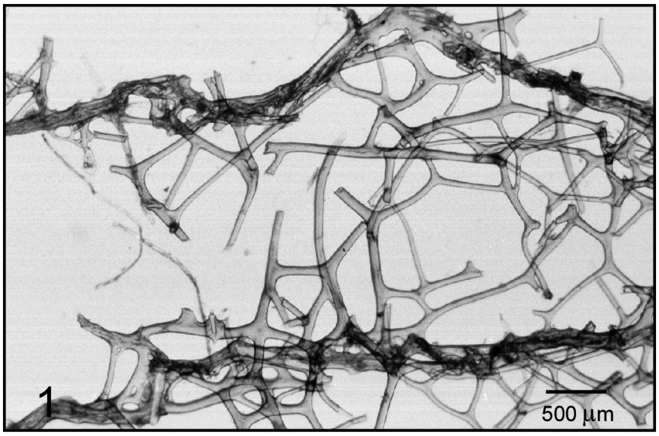

Fig. 1: Cored primary fibres and well-developed secondary fibre reticulum of *Cacospongia mollior* (Mediterranean).

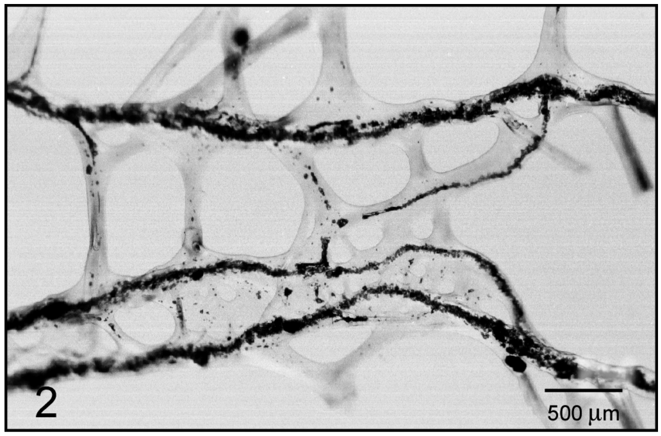

Fig. 2: Cored primary fibres and the more sparse, ladder-like skeleton of *Scalarispongia scalaris* (Mediterranean).

published works of von Lendenfeld, who focused closely on the presence of subdermal lacunae as the distinguishing feature of *Hippospongia* (see Cook and Bergquist 2001 for a full discussion). Examination of dry, macerated specimens, and published photos of *Spongia* (Fig. 3) and *Hippospongia* (Fig. 4) species, led to an emended diagnosis of *Hippospongia* that expands and emphasises the diagnostic characters within specified limits (Cook and Bergquist 2001).

Ircinia vs *Psammocinia*

Within the Irciniidae, distinguishing between *Ircinia* and *Psammocinia* can be difficult – while dermal armouring characterises *Psammocinia*, specimens of *Ircinia* can have a dermal dusting of foreign debris that has been interpreted as armouring. There has been a tendency to diagnose *Psammocinia* solely on the basis of fine filaments and apparent armouring, without due regard for other relevant characters. This has led to some confusion, and historically some authors have chosen to ignore *Psammocinia* or to synonymise it with *Ircinia* (e.g. Wiedenmayer, 1977). For specimens that are difficult to place in either *Ircinia* and *Psammocinia*, the presence and magnitude of fascicular primary fibres is a useful character. *Psammocinia* species have simple primary fibres, sometimes showing moderate fasciculation (Fig. 5), whereas *Ircinia* species typically have massive, sometimes spectacular fascicular fibres (Fig. 6). If a specimen has a significant amount of sand in its ectosome, but does not appear to form a distinct armoured crust, and has heavily fascicular fibres, it should be classified as *Ircinia*. Using this method, all New Zealand specimens so far encountered have been able to be placed within one genus or the other without difficulty.

Clarification of dictyoceratid characters

Fibre forms

Simple fibres are essentially undivided fibres (Fig. 7).

Coalescing fibres are created where two or more fibres converge and coalesce into a single, often larger fibre (Fig. 8).

Fascicles are defined as a bundle or bunch, and the term is used to describe a fibre, usually primary, that shows multiple diverging and converging tracts within a single fibre axis; fascicles can range in size and complexity, from minor to massive; fascicles also vary in form, from a well-defined meshwork to a tangled mass (Figs. 5 and 6, 9 and 10).

Secondary webs are broad, web-like structures stretched between primary fibres where secondary fibres would normally be seen, that are distinct from a fascicle; secondary webs resemble stretched plastic, may be entire or perforate, and may also be observed in the V-shaped space created where a single primary fibre bifurcates into two diverging primary fibres (Figs. 9 and 10).

Skeletal fibre types

Dictyoceratids have an anastomosing fibre skeleton, usually organised into a hierarchy reflecting size and orientation:

Primary fibres are typically orientated at right angles to the surface; distally they usually terminate at the sponge surface, and support conules in those species that have them; they may be simple, coalescing or fascicular, and they may be axially to fully cored with foreign inclusions, e.g. sand, spicules (Figs. 7-10, 12).

Secondary fibres interconnect primary fibres; they are simple or compound, and at their simplest, they resemble the rungs of a ladder; they may be axially to fully cored with foreign inclusions (Figs. 7-9, 11-12).

Tertiary fibres typically interconnect secondary fibres; they are uncored, usually very fine, and are recognised as fibres of very small diameter in relation to secondary fibres, usually forming a fine mesh-work within the meshes of the secondary reticulum, e.g. as seen in *Luffariella* (Fig. 11); in one genus, *Carteriospongia*, they are more vermiform and wandering.

Pseudo-tertiary fibres are finer than secondary fibres, but are not as fine as those typically called tertiary fibres. While this name is inadequate, the authors (Cook and Bergquist 2001) considered it best to use an interim term, until such time as

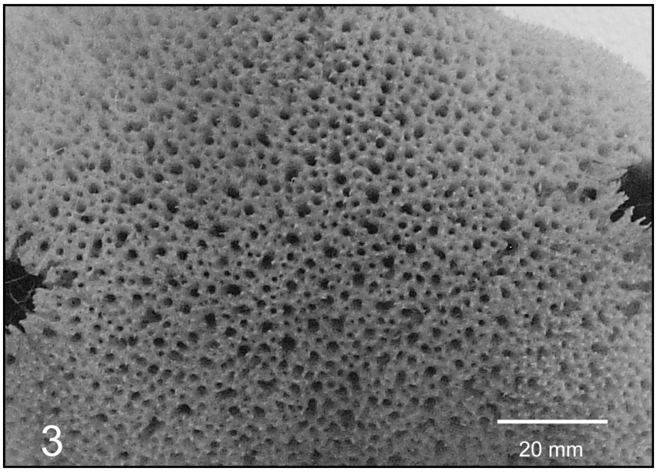

Fig. 3: Surface of macerated *Spongia officinalis.*

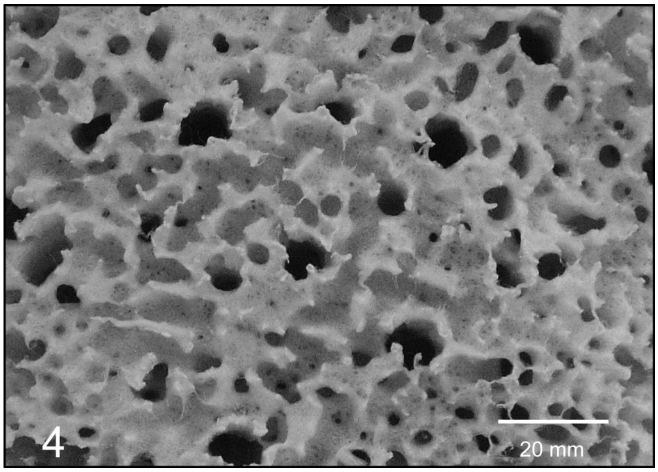

Fig. 4: Surface of macerated *Hippospongia communis.*

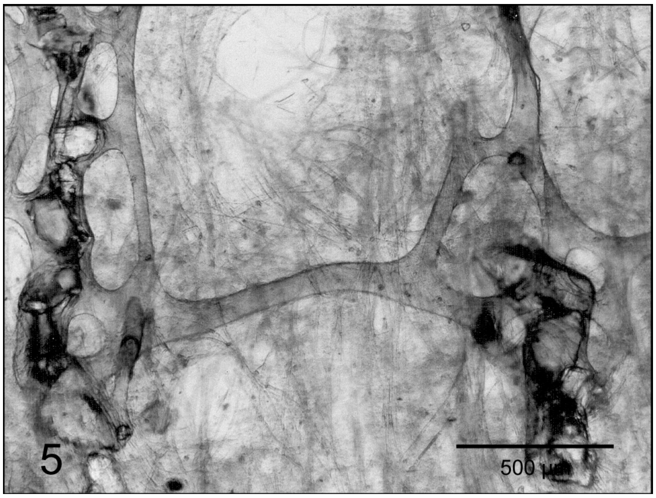

Fig. 5: Lightly fasciculated fibre of *Psammocinia hawere* (New Zealand).

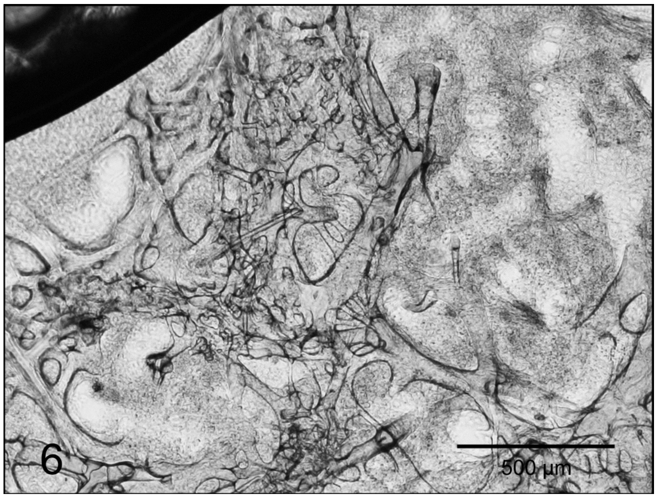

Fig. 6: Heavily fasciculated fibre of *Ircinia irregularis* (Torres Strait).

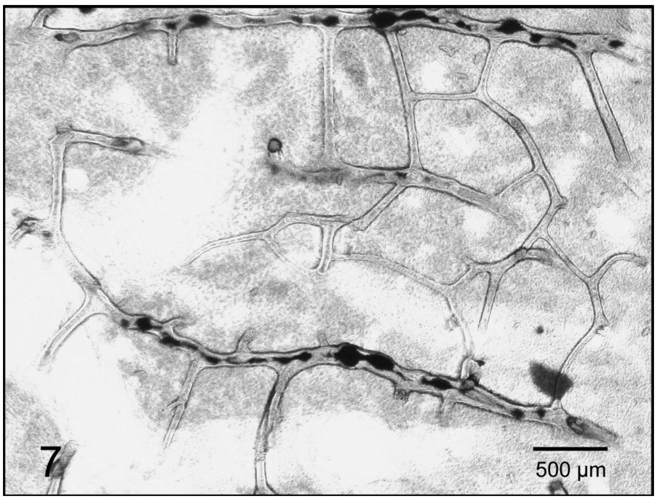

Fig. 7: Simple cored primary fibres and uncored secondary fibres of *Thorecta reticulata* (New Zealand).

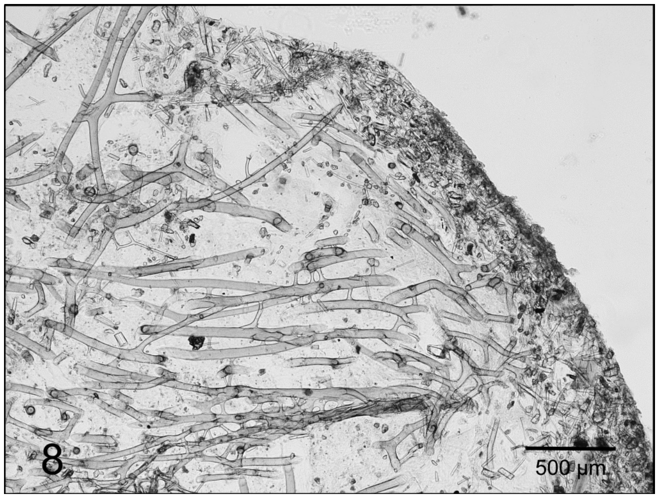

Fig. 8: Coalescing primary fibre of *Spongia gorgonocephalus* (New Zealand); sand in dermis is inconsistent over sponge surface.

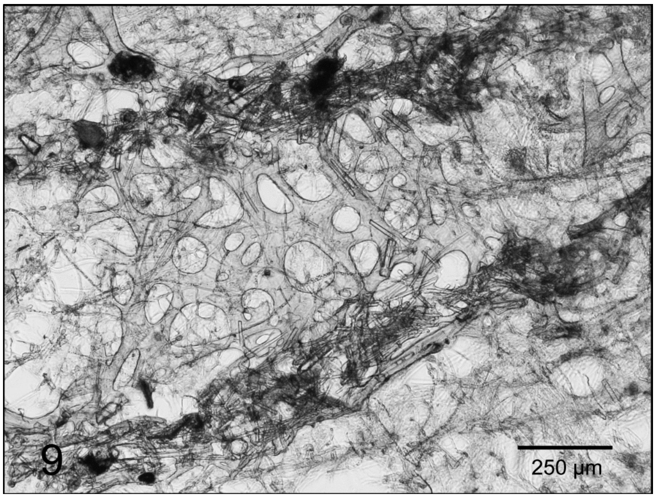

Fig. 9: Cored primary fibre fascicles and perforate secondary webbing of *Ircinia subaspera* (New Zealand).

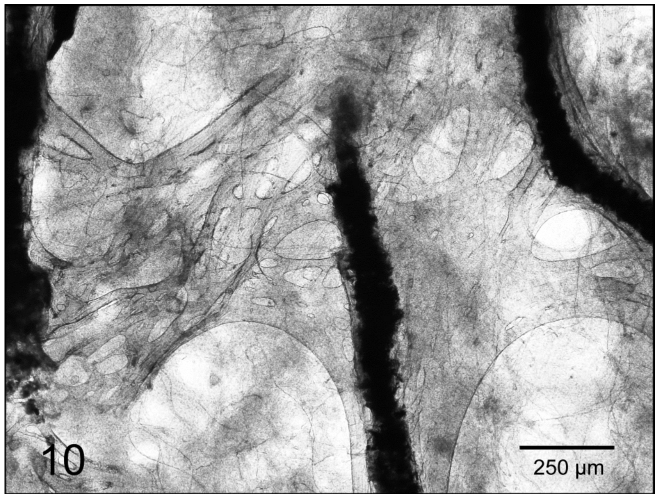

Fig. 10: Cored primary fibre fascicles and secondary webbing of *Ircinia aucklandensis* (New Zealand).

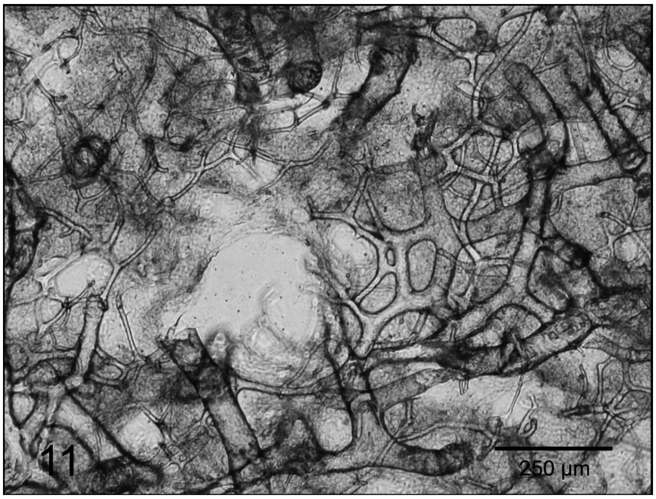

Fig. 11: Secondary and fine tertiary fibre network of *Luffariella variabilis* (Gt Barrier Reef).

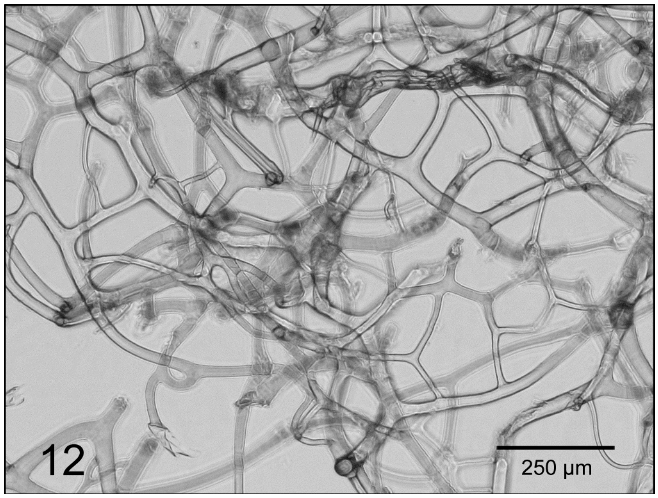

Fig. 12: Cored primary fibre, secondary fibre network and thinner pseudo-tertiary fibres of *Spongia cristata* (New Zealand).

their diagnostic significance within the relevant family can be more accurately determined (Fig. 12).

Fine filaments are not skeletal fibres, but they add support and strength to irciniid sponges. They are long, thin collagenous threads that may be relatively sparse, to forming thick bundles within the mesohyl. Filaments are easily recognisable by their swollen tips (Figs. 13 and 14).

Fibre construction

The construction of skeletal fibres is used as a familial character, principally, whether or not fibres are laminated and pithed. Primary and secondary fibres are laminated (Fig. 15) in the Dysideidae, Irciniidae and the Thorectidae. The primary fibres of these sponges are also pithed, though this can be difficult to see, particularly in those genera with a core of foreign material. Unlike the verongids, the pith is somewhat diffuse, and blends with the surrounding fibre, rather than having a distinct boundary between pith and fibre. Note however that in some specimens fibre laminations can be difficult to see. When this occurs, look carefully for evidence of laminations and pith in the primary fibres, particularly near the sponge surface, and if necessary where there is a gap in foreign coring material (Fig. 15). In some cases, e.g. *Psammocinia halmiformis* (Fig. 16), this may not be possible and other characters have to be employed. This highlights the importance of knowing the morphological range of taxonomic characters. In spongiids, the skeletal fibres are not laminated when viewed under a light microscope, i.e. they are homogeneous, and are unpithed.

Dermal armour

There are clearly some genera that are able to produce an organised armoured dermal layer (Fig. 16). There is evidence that some species exercise active selection of particles for

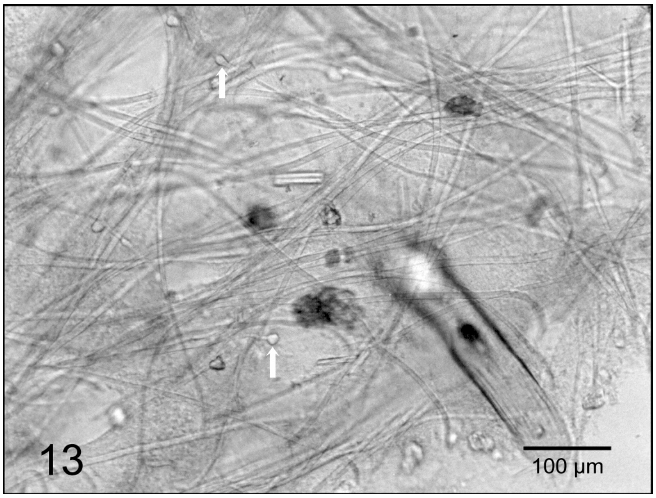

Fig. 13: Fine filaments with swollen tips (arrowed), characteristic of the Irciniidae, from *Psammocinia beresfordae* (New Zealand).

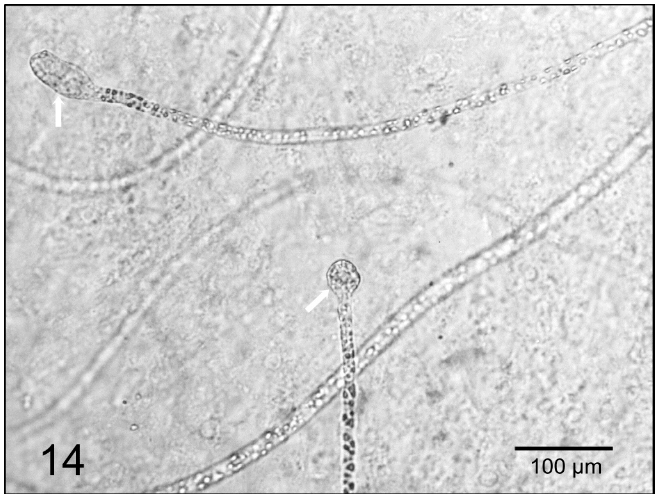

Fig. 14: Detail of fine filaments from *Ircinia aucklandensis* (New Zealand), with swollen tips arrowed. The granular appearance of filaments is due to a coating of lepidocrocite granules.

their armour. For example, *Psammocinia halmiformis* (Fig. 16) and *Coscinoderma* spp. (Fig. 17) have a uniformly fine-grained surface armour, whereas other species consistently use coarse particles. The transport of foreign particles in sponges has been studied in the dysideid *Dysidea etheria* (Teregawa 1986a, 1986b). These studies demonstrated active transport of foreign particles to specific sites on the surface and within the sponge body. Observations suggested "that coordinated migration of groups of mesohyl cells control particle transport to conules and that patterns of cell migration are associated with the structural organization of the dermal membrane" (Teregawa 1986b). However, newly grown areas may have thinner or poorly-developed sand crusts that may confound diagnosing the presence of a dermal armour. This remains the subject of a separate study. Note also the work of Cerrano *et al.* (2007), on how and why sponges incorporate foreign material.

Mesohylar collagen

The mesohyl of dictyoceratid genera includes collagen in varying degrees of density. Thin section microscopy, with a suitable stain, e.g. Mallory-Heidenhain, can be used to determine the relative volume of collagen that occurs in a specimen. This is used as a character in some genera, e.g. *Aplysinopsis*, or to assist in distinguishing between some otherwise similar genera, e.g. *Scalarispongia* and *Semitaspongia* (Fig. 18).

Determination of dictyoceratid families and genera

Dictyoceratida incorporates four families that are relatively easy to distinguish from one another. When producing histological slides of specimens, it is useful to take thin sections (12 µm is a good thickness), as well as thicker ones (often hand sections), to assist in the diagnosis. Stained with Mallory-Heidenhain, or similar, these thin sections facilitate determining the proportion of collagen in the sponge, and the type of choanocyte chambers, i.e. whether they are diplodal or eurypylous.

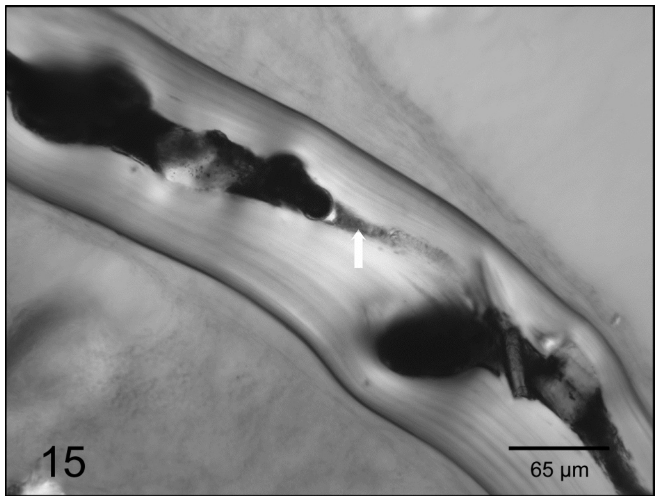

Fig. 15: Laminated primary fibre of *Thorecta reticulata* (New Zealand), showing a section of pith where there is a break in foreign coring.

Important: the keys below are not suitable for use on their own and should, at a bare minimum, be used in conjunction with the generic descriptors that follow.

Key to dictyoceratid families

1. Fine filaments absent 2
   Fine filaments present .... Irciniidae

2. Skeletal fibres concentrically laminated 3
   Skeletal fibres homogeneous, without
   laminations .... Spongiidae

3. Choanocyte chambers small and spherical
   (diplodal) .... Thorectidae

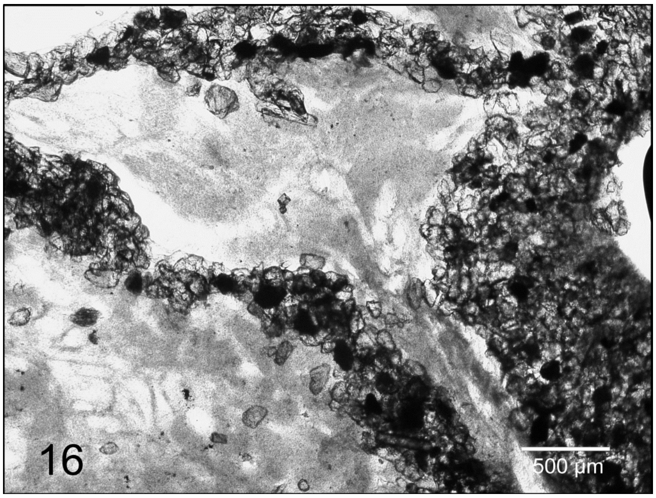

Fig. 16: Heavily armoured dermis and cored primary fibre of *Psammocinia halmiformis* (New South Wales).

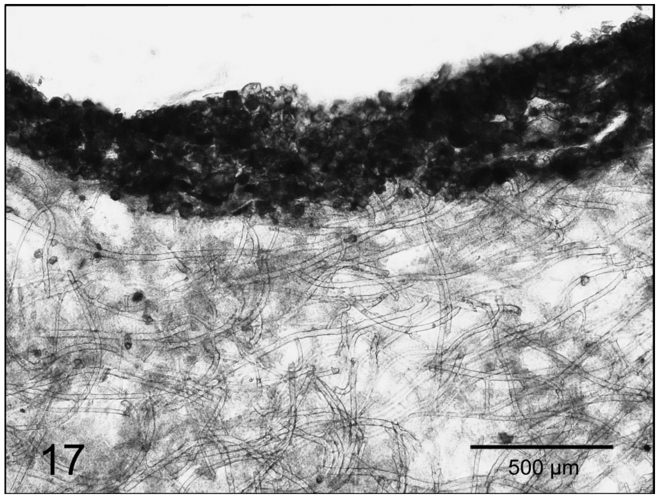

Fig. 17: Armoured dermis and cored primary fibre of *Coscinoderma* sp. (Chuuk, FSM).

Choanocyte chambers large and oval (eurypylous)..Dysideidae

Dysideidae – Dictyoceratida with laminated skeletal fibres and eurypylous choanocyte chambers.

Irciniidae – Dictyoceratida with unique fine collagenous filaments in the mesohyl, and diplodal choanocyte chambers.

Spongiidae – Dictyoceratida with homogeneous skeletal fibres, i.e. without distinct laminations, a skeleton dominated by sub-primary fibres, and diplodal choanocyte chambers.

Thorectidae – Dictyoceratida with laminated skeletal fibres and diplodal choanocyte chambers.

Family Irciniidae

This family is characterised by the presence of fine collagenous filaments within the body of the sponge. Filaments occur in varying density and organisation, from scattered through the mesohyl, to forming thick bundles. In the past, the presence of very thin filaments (0.5-5 µm) has been used as a diagnostic character for *Sarcotragus* (Vacelet 1959, Bergquist 1980), but subsequently, very thin filaments have also been observed in some species of *Psammocinia* from New Zealand, Australia and South Korea (Cook and Bergquist 1996, 1998, Sim and Lee 1998).

Key to irciniid genera

1. Dermis unarmoured..2
   Dermis armoured with an organised layer ....*Psammocinia*
2. Primary fibres form minor fascicles, lightly cored or uncored..3
   Primary fibres form massive fascicles, cored with foreign debris..*Ircinia*
3. Primary fibres form minor fascicles, lightly cored or uncored...*Sarcotragus*
   Primary fibres form minor uncored fascicles, with secondary web...*Bergquistia*

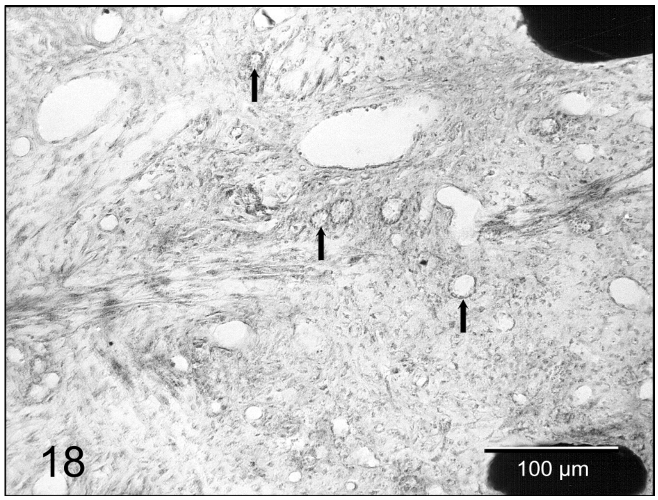

Fig. 18: Stained thin section of *Semitaspongia incompta* (New Zealand), with heavy collagen deposition, showing several small, spherical diplodal choanocyte chambers (arrowed). Collagen is a lot easier to observe when selectively stained (and in colour)

Bergquistia – unarmoured irciniids, with slightly fascicular and uncored primary fibres, though there may be some coring near the surface. In some areas, primary fibres are connected by secondary webs (Sim and Lee 2002). The distinction between this genus and *Sarcotragus* requires clarification or revision.

Ircinia – unarmoured irciniids with massive fascicular primary fibres, that are usually cored with foreign debris. Primary fibres may be connected by secondary webs.

Psammocinia – armoured irciniids, with minor fascicles, usually near the surface. Primary fibres are cored and secondary fibre coring is variable, from uncored to fully cored. Primary fibres may be connected by secondary webs.

Sarcotragus – unarmoured irciniids in which the primary fibres are simple or form relatively minor fascicles, compared to *Ircinia*, and are uncored or have only light, intermittent coring.

Family Spongiidae

Spongiids have a well-developed skeleton of primary, secondary, and in a group of Australasian sponges, distinct fine secondary or pseudo-tertiary fibres. Primary fibres can be sparse. All fibres are unpithed, and are homogeneous when viewed with light microscopy, i.e. they show little or no sign of concentric laminations within the fibres. Sometimes very fine laminations can be seen in the fibres, typically at stress points, e.g. fibre junctions, but they are tightly adherent, and not as obvious as seen in other dictyoceratid families. Spongiids are characterised by a dense secondary fibre reticulum that dominates the skeleton, though this character is not unique to spongiids. Choanocyte chambers are diplodal, and spherical to oval in shape. In some species, the mesohyl and ectosome are supported by heavy deposits of collagen.

Key to spongiid genera

1. Dermis armoured 2
   Dermis unarmoured 3

2. Dense secondary skeleton of thick, branching secondary fibres .... *Leiosella*
   Dense secondary skeleton of very fine, intertwined fibre network .... *Coscinoderma*

3. Sponge body or ectoderm lacunose 4
   Sponge not lacunose 5

4. Primary fibres common .... *Hyattella*
   Primary fibres uncommon to rare .... *Hippospongia*

5. Primary fibres form long, minor fascicles .... *Rhopaloeides*
   Primary fibres are simple, not forming fascicles .... *Spongia*

Coscinoderma – thinly armoured spongiid, with a dense skeleton of simple, cored primary fibres and dominated by characteristic very fine, meandering, uncored secondary fibres.

Hippospongia – these unarmoured spongiids have large diameter oscules and associated canals, rendering the sponge body lacunose. Primary fibres are uncommon to rare, and surface conules are usually produced by a tuft of emergent fibres.

Hyattella – unarmoured spongiid, with a lacunose body. The fibre skeleton consists of primary fibres, which are cored with foreign material, a dense regular network of uncored secondary fibres, plus a fine, dermal fibre network.

Leiosella – lightly armoured spongiids, with lightly cored primary fibres, and a dense secondary skeleton of characteristically thick, uncored fibres.

Rhopaloeides – massive, upright sponges, with an unarmoured surface, bearing thick tuberculate conules. These sponges could easily be mistaken for *Spongia* species, but are distinguished by the presence of fascicular primary fibres, particularly near the sponge surface.

Spongia – unarmoured spongiids, with relatively few simple, cored primary fibres and uncored secondary fibres. Some species may also have a superficial fibre net supporting the pinacoderm.

Family Thorectidae

Dictyoceratida with an anastomosing skeleton of concentrically laminated primary, secondary, and sometimes tertiary fibres. Primary fibres have an axial, granular pith that may extend into secondary fibres. Foreign material is often incorporated as a core within the fibres, obscuring the pith when coring material is abundant. The anastomosing fibre skeleton is regular and varies in arrangement from rectangular to disorganised. Fibres range in form, from simple fibres to strong, complex fascicles. Primary fibres may be reduced, and are not apparent in one genus. Zones of disjunction between successive fibrous layers remain tightly adherent, producing an overall solid structure with visible contiguous laminae, in contrast to the skeletal fibres of some dendroceratids, where fibre laminations are not tightly adherent and may gape slightly in histological sections. Thorectids have small, spherical and diplodal choanocyte chambers. The cortex may be armoured with foreign material, but when not armoured, the surface is always coarsely to micro-conulose. There are two subfamilies in the Thorectidae, Thorectinae and Phyllospongiinae.

Key to thorectid subfamilies

1. Foliose, thin lamellate or folio-digitate; tertiary fibres present (except in one genus) .... Phyllospongiinae
   Variable form; tertiary fibres in only two non-folio-lamellate genera .... Thorectinae

Phyllospongiinae – foliose, thin lamellate or folio-digitate, sponges, with tertiary fibres in the skeleton (except in one genus).

Thorectinae – variable form. Fibre skeleton comprised of primary and secondary fibres, except for *Luffariella* and *Fenestraspongia*, which also have tertiary fibres but are not foliose, lamellate or folio-digitate.

Key to Thorectinae genera

1. Dermis armoured 2
   Dermis unarmoured 6

2. Armour moderate to heavy and consistent over whole sponge 3
   Armour light, patchy, restricted to specific areas (may form crust, not armour) 4

3. Large diameter fibres; excess mucus when live .... *Thorectandra*
   Fibres not of large diameter; without excess mucus .... *Thorecta*

4. Massive forms, not lamello-digitate or foliose 5
   Thin-walled lamello-digitate or foliose sponges; upper part of sponge may have sand crust; primary fibres parallel to surface; surface fibre network present .... *Collospongia*

5. Hard and incompressible; dense secondary skeleton .... *Petrosaspongia*
   Firm, compressible and collagenous .... *Aplysinopsis*

6. Fine tertiary fibres supplement fibre skeleton 7
   Without tertiary fibres 8

7. Fenestrate or ridged surface; strongly fascicular primary fibres .... *Fenestraspongia*
   Conulose surface; primary fibres simple (vague fascicles may be seen) .... *Luffariella*

8. Uncored primary and secondary fibres 9
   Primary or secondary fibres with core of foreign debris 12

9. Dense, branching fibre network 10
   Axially-concentrated skeleton .... *Thorectaxia*

10. Surface with coarse irregular conules 11
    Surface microconulose, though may appear smooth .... *Narrabeena*

11. No distinction between primary and secondary fibres .... *Dactylospongia*
    Ascending primary fibres and a network of secondary fibres .... *Smenospongia*

12. Secondary fibres uncored 13
    Secondary fibres heavily cored .... *Hyrtios*

13. Primary fibres strongly fascicular throughout sponge 14
    Primary fibres not strongly fascicular (slight subsurface fascicles possible) 15

14. Very thick fibres; collagenous throughout mesohyl .... *Fascaplysinopsis*
    Thick fibres; prominent central exhalant canals and subdermal lacunae; heavy dermal collagen .... *Fasciospongia*

15. Low forms 16
    Upright form, on a basal stalk .... *Taonura*

16. Primary and secondary fibres in approximately equal proportion 17
    Secondary fibre skeleton well-developed .... *Cacospongia*

17. Heavily collagenous mesohyl; irregular skeleton .... *Semitaspongia*
    Low to moderate mesohyl collagen; very regular skeleton .... *Scalarispongia*

Aplysinopsis – thinly armoured thorectid, with a relatively sparse fibre skeleton of simple, cored primary fibres and an irregular network of uncored secondary fibres. The mesohyl of these species is characteristically collagenous.

Cacospongia – unarmoured thorectid, with a well-developed branching uncored secondary fibre skeleton, cored primary fibres, and low to moderate collagen deposition.

Collospongia – unarmoured thorectids, but the surface may be encrusted with sand patches. The skeletal characters of this genus are unique within the Dictyoceratida, particularly the arrangement of the primary fibres, and the presence of a tangential dermal reticulum. Lightly cored primary fibres are arranged parallel to the surface, within the lamellae of the sponge, with primary fibre fascicles and secondary fibres curving out towards both surfaces. Near the surface, fascicles divide into finer fibres, forming a tangled network that supports a regular dermal fibre network.

Dactylospongia – unarmoured thorectids, with a relatively dense skeleton of uncored fibres and no clear distinction between primary and secondary fibres.

Fascaplysinopsis – unarmoured thorectids, with a sparse skeleton of relatively large diameter, cored primary and uncored secondary fibres, producing coarse, widely-spaced conules at the surface. Primary fibres can be either fasciculate or laddered. The mesohyl is characteristically gelatinous or fleshy.

Fasciospongia – unarmoured, and with strong central or subdermal exhalant canals. The skeleton consists of relatively large diameter primary and secondary fibres. Primary fibres are cored and fascicular, secondary fibres are uncored, and there are heavy deposits of ectosomal collagen, usually including a dermal band.

Fenestraspongia – unarmoured thorectids, with a fenestrate surface. The skeletal reticulum is comprised of heavy primary and secondary fibres, and very fine tertiary fibres. Primary fibres are cored with foreign material and fascicular, while secondary and tertiary fibres are uncored and form a relatively dense reticulum.

Hyrtios – unarmoured thorectids with heavily cored primary and secondary fibres.

Luffariella – unarmoured thorectids with a skeletal reticulum of simple cored primary (though coring thin in one species), and uncored secondary and fine tertiary fibres.

Narrabeena – unarmoured thorectids with a well-developed skeletal reticulum of uncored fibres, with no clear distinction between primary and secondary elements. These sponges also have a micro-conulose surface with a slimy texture, and light collagen deposition throughout the sponge.

Petrosaspongia – unarmoured thorectids, with a dense secondary reticulum of uncored fibres, rendering these sponges hard and incompressible. Primary fibres are limited in number, but are present in the ectosome where they are formed by converging secondary fibres. Primary fibres merge into a fenestrated spongin plate, from which primary elements extend to the surface.

Scalarispongia – unarmoured thorectids, with a regular, rectangular fibre skeleton of simple cored primary fibres and uncored secondary fibres that occasionally form light webbing. There is moderate collagen deposition in the mesohyl.

Semitaspongia – unarmoured thorectids, with an irregular to regular skeletal reticulum, slightly fascicular, cored primary fibres and uncored secondary fibres. There is moderate to abundant collagen deposition in the mesohyl.

Smenospongia – unarmoured, with a characteristic honeycombed surface. The relatively dense secondary fibre skeleton may sometimes obscure the primary fibres. There is only minor collagen deposition in the mesohyl.

Taonura – soft, unarmoured thorectids, upright in form with a basal stalk. They possess a regular skeleton of cored primary and uncored secondary fibres.

Thorecta – armoured thorectids, with a regular skeleton of simple cored primary and uncored secondary fibres, fine to moderate in diameter.

Thorectandra – armoured thorectids, with simple, large diameter, cored primary and uncored secondary fibres. This genus characteristically exudes copious amounts of mucus when collected.

Thorectaxia – unarmoured thorectids, with a characteristic axially concentrated skeleton, and uncored, loosely laminated fibres.

Key to Phyllospongiinae genera

1. Dermis moderately to heavily armoured 2
   Dermis unarmoured, or with patchy sand crust
   (not armoured) 4

2. Tertiary fibres supplement fibre skeleton....................................3
   Without tertiary fibres; bright white .... *Candidaspongia*

3. Stellate pattern of exhalant canals around
   each oscule .... *Strepsichordaia*
   Without stellate pattern of exhalant canals......... *Carteriospongia*

4. Sand crust (not armour) on one or both faces;
   primary fibres perpendicular to surface;
   tough and flexible .... *Phyllospongia*
   Fasciculate primary fibres; primary fibres
   meandering; soft and fleshy..................................*Lendenfeldia*

Candidaspongia – heavily armoured thorectids, that are characteristically brilliant white in colour. These sponges have simple, cored primary fibres and uncored secondary fibres, but do not have tertiary fibres.

Carteriospongia – heavily armoured thorectids, with an undulating surface. The fibre skeleton is relatively dense, and is comprised of heavily cored primary fibres, cored or uncored secondary fibres, that can be difficult to identify, and a tangled network of vermiform tertiary fibres.

Lendenfeldia – unarmoured thorectids, producing lamellate forms. These sponges have tertiary skeletal fibres, and have a soft, fleshy consistency.

Phyllospongia – unarmoured Phyllospongiinae, but with a sand crust. Regular fibre skeleton of primary, secondary and vermiform tertiary fibres.

Strepsichordaia – heavily armoured thorectids, of lamellate or foliose forms, with a characteristic stellate exhalant and oscular system. The skeleton is dominated by tertiary fibres, and these sponges are firm, tough and flexible.

Family Dysideidae

Dictyoceratida with an anastomosing skeleton of concentrically laminated primary and secondary fibres. The skeletal fibres are pithed, and may be uncored to fully cored with foreign material, the latter situation obscuring details within the fibres. Choanocyte chambers are large, usually oval, and eurypylous. These sponges are typically soft and compressible, though are rendered firmer by the presence of foreign interstitial material, e.g. sand.

Key to dysideid genera

1. Primary and secondary fibres cored with foreign debris 2
   Primary fibres cored, secondary fibres clear................................3

2. Skeleton regular, with primary fibres perpendicular
   to surface 4
   Skeleton irregular, without a clear hierarchy of
   primary and secondary fibres .... *Lamellodysidea*

3. Encrusting, massive or branching, very soft
   and collapsible.. *Euryspongia*
   Lamellate or digitate, dense, soft and pliable .... *Citronia*

4. Sponge thin, encrusting, fragile, with secondary
   skeleton sparse or absent ....*Pleraplysilla*
   Sponge massive, with secondary fibre skeleton
   well-developed .... *Dysidea*

Citronia – Dysideidae with cored primary fibres and uncored secondary fibres. Consistency is soft, but dense and pliable.

Dysidea – Dysideidae in which primary and secondary fibres are cored with foreign material.

Euryspongia – Dysideidae in which the primary fibres are cored and the secondaries are clear of foreign coring. Secondary fibres form a well-developed reticulum, which has been likened in appearance to the development seen in *Spongia*.

Lamellodysidea – massive, lamellate to digitate dysideids, with a thin, encrusting basal plate; the skeleton is irregular, without clear distinction between primary and secondary fibres; all skeletal fibres are cored with foreign material.

Pleraplysilla – encrusting Dysideidae with cored fibres, and a secondary skeleton that, where present, is weak.

Discussion

When determining dictyoceratid genera, the easiest way to minimise errors and avoid confusion is to ensure that all diagnostic characters required for generic diagnosis are present, not just the obvious ones – if they are absent, determine why. If in doubt, do your homework – understand the character ranges for any given taxa, as some genera or species can be problematic to distinguish accurately, and a successful diagnosis can be confounded by the observer not being fully aware of character ranges. While these suggestions may seem like “stating the obvious” to some, examples of these errors entering the literature still occur.

Not intended as an example of the errors mentioned above, but as a taxonomic update, in recent research Schmitt *et al.* (2005) proposed that *Smenospongia* be reassigned to the Aplysinidae. The genus *Smenospongia* Wiedenmayer, 1977 was originally described to accommodate *Aplysina aurea* Hyatt, 1875 within the Aplysinidae. *Smenospongia* has characters that align it with both the Thorectidae (Dictyoceratida) and the Aplysinidae (Verongida), with an anastomosing fibre skeleton of primary and secondary fibres, and displaying a pronounced very dark colour change on death or exposure to air, respectively.

Van Soest (1978) considered that *Smenospongia* was an aplysinid, but with remarkable similarities to some dictyoceratid genera. Subsequently, Bergquist (1980) placed *Smenospongia* in the Thorectidae, based on the presence of secondary metabolites identical to those found in other thorectids, and which had never been found in members of the Verongida. Also, all tested verongids yielded bromotyrosine derivatives, and were consequently considered to characterise the order, but they had not been recorded from any other taxa, including *Smenospongia*.

However, recent research suggests reassigning *Smenospongia* back to the Aplysinidae, as proposed by

Schmitt *et al.* (2005), based on molecular research. In addition, bromotyrosine derivative compounds have now been found in other non-keratose sponge taxa, e.g. *Agelas* spp. (van Soest and Braekman 1999) and *Jaspis* spp. (Kim *et al.* 1999), and are no longer considered exclusive to the verongids, as evidenced by the review of sponge chemosystematics by Erpenbeck and van Soest (2006).

Note also that the new species of *Smenospongia* described from Korea by Lee and Sim (2005) is clearly not a member of this genus. The published images show a pale alcohol-preserved specimen, where *Smenospongia* would have turned a very dark colour, and the fibre skeleton bears a very strong resemblance to that of *Cacospongia* (see Fig. 1 above).

Given the difficulty associated with dictyoceratid taxonomy, and the very real possibility of specimen contamination, mislabeling, and other confounding issues, it is suggested that *Smenospongia* remain within the Thorectidae, until such time as all *Smenospongia* species are thoroughly reviewed morphologically, and verified as species of *Smenospongia*.

Acknowledgements

To the Auckland University of Technology (AUT) and the Faculty of Health & Environmental Sciences Travel Grant, for assistance with travel expenses to the Seventh International Sponge Symposium (Búzios, Brazil); Brid Lorigan and Olive Sykes (AUT) for assistance with numerous mundane requests, and Debbie Blake, Claire Stockman and Steve Henry for access to microscopy equipment; Brent Beaumont (Department of Anatomy, University of Auckland) for micrographs and Emma Beatson (AUT) for the underwater photographs, used in the conference presentation. This manuscript was improved by the valuable comments of two anonymous referees.

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