## Family Thorectidae Bergquist, 1978

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Thorectidae Bergquist (Demospongiae, Dictyoceratida) is divided into two subfamilies (Thorectinae, Phyllospongiinae), containing 23 valid genera and 129 species worldwide. Thorectids range from low and encrusting to massive in growth form. They occur throughout tropical and temperate oceans but are not recorded from polar waters. They are differentiated from other members of the Dictyoceratida by their diplodal choanocyte chambers, strongly laminated skeletal fibres, and the absence of fine skeletal filaments (characteristic of Irciniidae). Thorectid genera are differentiated by the presence or absence of a cortical armour, skeletal morphologies and the characteristic growth forms of some genera.

**Keywords:** Porifera; Dictyoceratida; Thorectidae; Thorectinae; Phyllospongiinae; *Cacospongia*; *Hyrtios*; *Taonura*; *Thorecta*; *Aplysinopsis*; *Thorectandra*; *Luffariella*; *Fasciospongia*; *Dactylospongia*; *Smenospongia*; *Fenestraspongia*; *Fascaplysinopsis*; *Collospongia*; *Petrosaspongia*; *Thorectaxia*; *Scalarispongia*; *Semitaspongia*; *Narrabeena* gen. nov.; *Phyllospongia*; *Carteriospongia*; *Lendenfeldia*; *Strepsichordaia*; *Candidaspongia*.

## **DEFINITION, DIAGNOSIS, SCOPE**

## Synonymy

Thorectidae Bergquist, 1978.

## Definition

Dictyoceratida with laminated skeletal fibres and diplodal choanocyte chambers.

### Diagnosis

Wide range of growth forms, from encrusting pads to massive, upright, lobose, caliculate or digitate structures. The surface may be armoured, and is frequently thrown into ridges and hollows. Where unarmoured the surface is typically conulose. The skeleton comprises primary, secondary and sometimes tertiary fibres. The skeletal reticulum is usually regular, frequently with almost perfectly rectangular meshes. The spongin fibres making up the anastomosing skeleton are laminated in cross-section, with clear zones of disjunction between successive layers. The central region of each fibre is a diffuse pith that is not sharply disjunct from the denser investing layer, as is the pith in the Verongida, but merges into the outer layer. A pith is always evident in the primary fibres, though it may be obscured by an axial core of foreign material within fibres, and may extend into the secondary elements of the skeleton. Some fibres can become extremely stout, and in some genera may form light and simple, to strong, complex fascicles. Primary fibres can be greatly reduced in number, or difficult to distinguish from sub-primary fibres. Thorectids do not possess the fine filaments seen in Irciniidae species. Choanocyte chambers are spherical to oval, and diplodal. The mesohyl is more collagenous than in the Spongiidae, and macroscopically can appear fleshy. Its cellular composition can be complex, and some secretory cell types, the spherulous cells, resemble those of the Verongida.

## Scope

Two subfamilies are currently recognised containing 23 genera in total. They occur throughout the world, from tropical to temperate regions but cannot yet be confirmed from polar waters (existing identifications questionable). Most thorectids are found from the intertidal zone to around 100 m depth. A checklist of described thorectid species is available on the internet (Cook, 2001).

## History and biology

Thorectidae was erected by Bergquist (1978) to accommodate sponges with distinctly laminated and pithed fibres, which included *Ircinia* and the other filamentose genera. Bergquist (1980b) revised the Dictyoceratida and restructured the higher family level taxa to include three families: Spongiidae, Thorectidae and Dysideidae. However, inclusion of *Ircinia* in Thorectidae contravened the rules of the ICZN Art. 40 (Anon., 1999) regarding the priority of Irciniidae Gray, 1867a over Thorectidae Bergquist, 1978. By including the genera *Ircinia* and *Thorecta* (type genera of Irciniidae and Thorectidae, respectively) within a single taxon, the name Irciniidae had seniority. This was corrected by Hooper & Wiedenmayer (1994), where they used Irciniidae in place of Thorectidae. Bergquist (1995) subsequently assigned the three filamentose genera to Irciniidae, leaving all non-filamentose dictyoceratids with laminated fibres and diplodal choanocyte chambers in Thorectidae.

## Remarks

It is suspected that some generic diagnoses have been stretched to accommodate new species, to the point where the original concepts of these genera have been lost, misunderstood or ignored, and the character-limits of the genus have become confused, (e.g., *Dactylospongia* and *Smenospongia*). Some progress has been made towards remedying these problems (e.g., *Cacospongia* cf. *Scalarispongia*; Cook & Bergquist 2000), but there are probably others, and there are certainly still many undescribed species.

## **Previous Reviews**

Lendenfeld, 1889a; de Laubenfels, 1948; Bergquist, 1965; Bergquist, Ayling & Wilkinson, 1988; Bergquist, 1980b; Bergquist, Sorokin & Karuso, 1999; Cook & Bergquist, 2000.

## **KEY TO SUBFAMILIES**

## SUBFAMILY THORECTINAE BERGQUIST, 1978

#### Synonymy

Thorectinae Bergquist, 1978: 176.

## Definition

Variable growth form. Fibre skeleton comprises primary and secondary fibres, except for *Luffariella* and *Fenestraspongia* which also have tertiary fibres. These are massive, often lobose, globose or digitate sponges, not lamellate or folio-digitate (except for *Collospongia* which is a spreading plate).

## Diagnosis

Variable growth form, from low and pad-like to a range of upright forms. The fibre skeleton comprises primary, secondary and sometimes tertiary elements. Fibres are distinctly concentrically laminated. Primary fibres, where apparent, are cored with foreign

#### **KEY TO GENERA**

(1)	Dermis armoured	
	Dermis unarmoured	6
(2)	Dermal armour moderate to heavy and consistent over whole sponge	
	Dermal armour light, patchy or restricted to specific areas (may form only a crust, not a discrete armour)	
(3)	Large diameter fibres; excess mucus	Thorectandra
	Fibres not of large diameter; without excess mucus	Thorecta
(4)	Thin-walled lamello-digitate or foliose sponges; upper part of sponge may have sand crust; primary fibres paral	llel to surface; surface
	fibre network present	Collospongia
	Massive forms, not lamello-digitate or foliose	5
(5)	Hard and incompressible; dense secondary skeleton	Petrosaspongia
	Firm, compressible and collagenous	Aplysinopsis
(6)	Fine tertiary fibres supplement fibre skeleton	
	Without tertiary fibres	
(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	
	Primary or secondary fibres with core of foreign debris	11
(9)	Axially-concentrated skeleton	Thorectaxia
	Dense, branching, non-hierarchical fibre network	10
(10)	Surface with irregular truncate conules	Dactylospongia
	Surface smooth	Narrabeena
(11)	Secondary fibres uncored	
	Secondary fibres heavily cored	Hyrtios
(12)	Primary fibres strongly fascicular throughout sponge	
	Primary fibres not strongly fascicular (slight subsurface fascicles possible)	

## Distribution

Tropical and temperate seas.

material and may form fascicles. Secondary and tertiary fibres are uncored, except in the genus *Hyrtios* which has heavily cored primary and secondary fibres. There is low to moderate collagen deposition in most genera, but high collagen content in one, *Aplysinopsis*.

## Scope

There are currently 18 genera in this subfamily, with 98 species.

## Remarks

This heterogeneous group of sponges is difficult to objectively define other than to include all those sponges which do not belong to Phyllospongiinae. They display a wide range of characters, many of which cross-over with the Phyllospongiinae. In other words, while Phyllosponiinae forms a monophyletic taxon Thorectinae remains a catch-all for other thorectids, and may require further subdivision at the subfamily level as evidence comes to hand.

(13)	Very thick fibres; collagenous throughout mesohyl	Fascaplysinopsis
	Thick skeletal fibres; prominent subdermal lacunae and central exhalant canals; heavy dermal collagen	Fasciospongia
(14)	Upright growth form, on a basal stalk	Taonura
	Low growth forms	15
(15)	Secondary fibre skeleton well-developed	
	Skeleton comprises primary and secondary fibres in equal proportion	
(16)	Honeycomb pattern at surface; colour darkens upon collection	Smenospongia
	Without honeycomb pattern; colour does not change	Cacospongia
(17)	Heavily collagenous mesohyl; irregular skeleton	Semitaspongia
	Low to moderate mesohyl collagen; very regular skeleton	Scalarispongia

## CACOSPONGIA SCHMIDT, 1862

## Synonymy

*Cacospongia* Schmidt, 1862: 26; de Laubenfels, 1948: 91; Vacelet, 1959: 81; Bergquist, 1980b: 460; Cook & Bergquist, 2000: 385.

## Type species

*Cacospongia mollior* Schmidt, 1862 (by subsequent designation; de Laubenfels, 1936a).

## Definition

Unarmoured Thorectinae with well-developed, branching secondary fibre skeleton, and low to moderate collagen deposition.

## Diagnosis

Massive sponges, with an unarmoured and conulose surface. The skeleton comprises relatively fine, concentrically laminated, primary and secondary fibres. Primary fibres are cored, and may form slight fascicles near the sponge surface; secondary fibres are uncored. A granular pith is visible in primary fibres, where not obscured by the coring material, sometimes extending into the secondary fibres. The secondary reticulum is well developed (Fig. 1B–C), relative to primary fibres, branching and irregular. The sponge surface is finely and evenly conulose, and externally *Cacospongia* resembles *Spongia*. However, because of the harsh, brittle nature of the stratified fibres *Cacospongia* is easily torn, and thus should never be confused in the field with *Spongia*, which is tough and elastic. The consistency of the sponge is soft to firm, and compressible; the surface is never armoured. There is low to moderate collagen deposition in the ecto-some, and surrounding larger canals throughout the mesohyl.

#### **Previous reviews**

Vacelet, 1959; Cook & Bergquist, 2000.

## **Description of type species**

Cacospongia mollior Schmidt (Fig. 1A-B).

Synonymy. Cacospongia mollior Schmidt, 1862: 27; de Laubenfels, 1936a: 24, 1948: 92; Vacelet, 1959: 84; Bergquist, 1980b: 460, figs 2c, 7d; Cook & Bergquist, 2000: 385, figs 1a–b, 2a–b. Euspongia irregularis var. mollior Lendenfeld, 1889a: 256, pl. 22, fig. 11.

*Material examined.* Lectotype: LMJG 15405. Other material. See Cook & Bergquist (2000).

**Description.** See generic diagnosis above. *Cacospongia mollior* is massive, relatively compact and undulating, with a finely conulose surface. The exterior is black, and the interior is off-white to pale grey.

**Remarks.** Cacospongia is readily distinguished from other thorectids by its well-developed secondary fibre reticulum, a feature that is often missed or ignored by authors, but which is fundamental to Schmidt's (1862) original diagnosis for the genus. Currently there are only two valid species, *C. mollior* and *C. serta.* Other published names require revision.

#### Distribution

Only currently recognised from the Mediterranean (type locality) and New Zealand.

## HYRTIOS DUCHASSAING & MICHELOTTI, 1864

#### Synonymy

Hyrtios Duchassaing & Michelotti, 1864: 74; de Laubenfels, 1936a: 30, 1948: 160; Bergquist, 1980b: 460; Hooper & Wiedenmayer, 1994: 230; Oligoceras Schulze, 1879: 34; Dysideopsis Lendenfeld, 1888: 155; Heteronema Keller, 1889: 339; Duriella Row, 1911: 369; Thorectopsamma Burton, 1934a: 577; de Laubenfels, 1948: 96; Inodes de Laubenfels, 1957: 249.

## Type species

*Hyrtios proteus* Duchassaing & Michelotti, 1864 (by subsequent designation; de Laubenfels, 1936a).

#### Definition

Unarmoured Thorectinae with heavily cored primary and secondary fibres.

## Diagnosis

Upright, tubular or digitate thorectids (Fig. 1D–F) in which both primary and secondary fibres are fully charged with detritus (Fig. 1G–H) to an extent which, in some species, can obscure the stratified nature of the spongin. The primary skeleton can show some fasciculation near the surface. The surface of the sponge always retains a distinctly conulose appearance, despite the presence in some species of extraneous detritus throughout the matrix. Primary fibres terminate in the conules, and as a consequence of the sandy inclusions these can appear whitish against the dark sponge surface. The texture of the sponge ranges from compressible to



Fig. 1. Cacospongia and Hyrtios. A–B, C. mollior. A, in situ (3288) (photo R. Pronzato). B, fibre skeleton showing cored primary fibres and characteristic secondary fibre reticulum (PRB coll.). C, C. serta, SDCC/NZ076, fibre skeleton. D, Hyrtios proteus, Curaçao (ZMA Por 3880). E, H. erecta, BMNH 1912.2.1.82. F, H. reticulata, New Caledonia. G, H. proteus, skeletal detail. H, H. reticulata, fibre skeleton. (D, G, reproduced with permission from Van Soest, 1978).

quite firm, even brittle, reflecting the degree of development of the skeleton, which in some species can be irregular and reduced, and the extent to which matrix debris is accumulated.

## **Previous reviews**

Van Soest, 1978; Bergquist, 1980b, 1995.

## **Description of type species**

Hyrtios proteus Duchassaing & Michelotti (Fig. 1D, G).

*Synonymy. Hyrtios proteus* Duchassaing & Michelotti, 1864: 74; de Laubenfels, 1936a: 30, 1948: 160; redescribed by Van Soest, 1978: 46; Bergquist, 1980b: 462. *Polyfibrospongia echina* de Laubenfels, 1934: 25.

*Material examined.* Schizolectotype: BMNH 1828.11.12.29. Other material. Authors collections, including: SDCC/ RF031 (*reticulata*); SDCC/RF049 (*erecta*).

**Description (from Van Soest, 1978).** Cake-shaped, with protruding lobes. The surface is regularly conulose, with conules 1-2 mm high and 2-5 mm in diameter. The consistency is very spongy and difficult to tear. This species is a very distinctive black externally, alive and preserved, though old specimens may turn slightly brownish, and are light brown internally. When preserved in formalin, a violet exudate was produced. The fibre skeleton is a regular reticulation of primary and secondary fibres, with a mesh width of 2000  $\mu$ m. Skeletal fibres are cored with foreign debris. Primary fibres are 200–400  $\mu$ m in diameter and secondary fibres are 70–150  $\mu$ m in diameter. Rarely, small sections of secondary fibre are free of inclusions, revealing clear laminations.

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## Porifera • Demospongiae • Dictyoceratida • Thorectidae

Choanocyte chambers are indistinct (in formalin preserved specimens), oval and up to 40  $\mu$ m across.

*Remarks. Hyrtios* is easily recognisable within the Thorectinae with its heavily cored secondary fibres. Seventeen species are known.

#### Distribution

Australia, Indo-Pacific, Mediterranean, West Indies (type locality).

#### TAONURA CARTER, 1882

## Synonymy

Taonura Carter, 1882b: 108; Bergquist, 1980b: 472. Paraspongia Carter, 1885c.

#### Type species

Taonura flabelliformis Carter, 1882b (by monotypy).

## Definition

Soft, unarmoured Thorectinae, upright in form, with a regular skeleton of cored primary and uncored primary fibres.

## Diagnosis

Stipitate, caliculate and occasionally foliaceous forms, arising from a basal stalk (Fig. 2A–D). The unarmoured surface is finely conulose, and typically is gently undulating. The fibre skeleton is regular and approximately rectangular, comprising simple, cored primary fibres and uncored, branching secondary fibres (Fig. 2E). The consistency is characteristically soft and compressible.

#### **Previous reviews**

Bergquist, 1980b.

#### **Description of type species**

Taonura flabelliformis Carter (Fig. 2A-B).

Synonymy. Taonura flabelliformis Carter, 1882b: 108; Bergquist, 1980b: 472, figs 11c–d, 12d. *Thorecta radiatus* Lendenfeld, 1889c: 40, 1889a: 350. De Laubenfels (1948) incorrectly reduced *T. flabelliformis* Carter to a junior synonym of *Phyllospongia pesleonis* (Lamarck). This latter species is now recognised as a species of the spongiid genus *Coscinoderma* (Bergquist, 1980b).

*Material examined.* Lectotype: BMNH 1844.9.13.3 (dry). Other material. Authors collections, including: SDCC/RF014 (cf. *colus*); SDCC/RF022 (*colus*); SDCC/RF023 (*colus*); SDCC/RF024 (*flabelliformis*); SDCC/RF070 (*marginalis*).

**Description (from Carter, 1882b).** Fan-shaped, thick, stipitate, and circular, with an obtuse margin. It is more convex on one side than the other. The stem is short, thick, hard, gnarled, and is sometimes branched and naked for a short distance before the flabellate expansion begins. The surface is smooth, and covered with shallow depressions, that are smaller and more numerous towards the circumference. Oscules are large in diameter, and are arranged along the margin. The skeleton is organised radially, and consists of cored primary fibres and uncored secondary fibres. Colour yellowamber. The consistency is soft and resilient.

**Remarks.** The external form of these sponges appears to be consistent within the genus, and is an important diagnostic character. However, *Taonura* can be a difficult genus to distinguish based solely on skeletal preparations. The skeletal morphology could be considered a hybrid of skeletal morphologies seen in Cacospongia, Semitaspongia and Scalarispongia. Taonura does not have the welldeveloped secondary fibre reticulum of Cacospongia and the fibre skeleton is more regular, and sometimes ladder-like. Taonura has finer fibres and a more developed secondary fibre network than either Scalarispongia or Semitaspongia, and a more regular fibre skeleton than Semitaspongia. In addition, Taonura species are upright, and do not form encrusting pads. Paraspongia Carter (type species Paraspongia laxa Carter, 1885c (by monotypy), lectotype BMNH 1886.12.15.230), is included into synonymy here following examination of all specimens in the BMNH and AMS collections. Lendenfeld (1889) gave an accurate description of Paraspongia laxa and referred the species to Chalinopsilla as C. paraspongia Lendenfeld, 1889. This action was unnecessary and is an unjustified replacement name. The extremely regular skeleton, fine conulose surface, an undulating overall surface morphology, marginal oscules and flexible texture are all features shared with Taonura. Eleven species are known.

#### Distribution

Australia (type locality), Indian Ocean.

## THORECTA LENDENFELD, 1888

#### Synonymy

[*Geelongia*] Carter, 1885c: 306 (in part). *Thorecta* Lendenfeld, 1888: 142; Lendenfeld, 1889a: 336; de Laubenfels, 1948: 107; Bergquist, 1980b: 468. *Antheroplax* Lendenfeld, 1889a: 171.

#### Type species

*Thorecta exemplum* var. *tertia* Lendenfeld, 1888 (by subsequent designation; de Laubenfels, 1948).

#### Definition

Armoured Thorectinae, with cored primary and uncored secondary fibres, of fine to moderate diameter.

## Diagnosis

Stalked, globular, fan-shaped or cylindrical upright growth forms (Fig. 2F–G), in which the primary fibres are cored with a regular axial column of debris and the secondary fibres are clear. The skeleton forms a regular, almost perfectly rectangular mesh (Fig. 2H) in which the spaces between the fibres may be quite large (2 mm is common). The surface is always armoured, not conulose. These sponges are firm and compressible.

### **Previous reviews**

De Laubenfels, 1948; Wiedenmayer, 1977b; Bergquist, 1980b; Hooper & Wiedenmayer, 1994.

## **Description of type species**

Thorecta latus (Carter) (Fig. 2F-H).

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Fig. 2. Taonura and Thorecta. A–B, Taonura flabelliformis. A, lectotype, BMNH1844.9.13.3. B, BMNH 1866.8.27.157. C, T. marginalis, AM G8875. D, T. colus, AM G3985. E, T. marginalis, SDCC/RF070. F, Thorecta cf. exemplum, AM Z552. G, T. vasiformis, holotype, BMNH 1886.12.15.227. H, Thorecta sp., South Australia, SDCC/RF069, note armoured surface at top.

Synonymy. Stelospongus latus Carter, 1885c: 306; Stelospongus cribrocusta Carter, 1886c: 371; Thorecta exemplum var. tertia Lendenfeld, 1888: 145; Lendenfeld, 1889a: 359; Wiedenmayer, 1977b: 70; Bergquist, 1980b: 468, 470, figs 9c–d; Thorecta latus Hooper & Wiedenmayer 1994: 242.

*Material examined.* Holotype: BMNH 1886.8.27.188. Other material. Authors collections.

**Description (from Lendenfeld, 1888).** Massive, conical, irregular pedunculate sponges, 100–150 mm high. The peduncle is cylindrical, straight or curved, and consistently about 4 mm in diameter; it is generally short, though may be indistinguishable, to 200 mm long. The surface in large specimens is generally covered with a network of broad, high ridges. Oscules are confined to the upper surfaces. Primary fibres are axially cored with large sand grains and spicule fragments, and are 60–70  $\mu$ m in diameter. Secondary fibres are simple, and 35–40  $\mu$ m in diameter. Towards the surface, some secondary fibres may branch.

**Remarks.** Histologically *Thorecta* and *Thorectandra* are similar. Live specimens of *Thorectandra* can easily be distinguished by the excess mucus they produce. The two genera can also be separated by the size of the fibres. In *Thorectandra* they are

large and heavy, and the fibre skeleton is relatively sparse, whereas *Thorecta* has much finer fibres and more of them. Twenty species are known.

## Distribution

Australia (type locality), New Zealand, West Indies (identification questionable).

## APLYSINOPSIS LENDENFELD, 1888

## Synonymy

Aplysinopsis Lendenfeld, 1888: 149; Lendenfeld, 1889a: 374; Bergquist, 1980b: 476.

## Type species

Aplysinopsis elegans Lendenfeld, 1888 (by subsequent designation; Burton, 1932b).



Fig. 3. Aplysinopsis, Thorectandra and Luffariella. A–B, Aplysinopsis elegans. A, reproduced from Lendenfeld, 1888, as A. digitata. B, AM G8847. C–D, Thorectandra choanoides, C, in situ. D, AM G1056. E–H, Luffariella variabilis. E, elongate specimen. F, massive specimen. G, fibre skeleton (E–G, reproduced from Poléjaeff, 1884). H, fibre skeleton, holotype BMNH 1885.8.8.52. I–J, L. caliculata. I, fibre skeleton with fine tertiary fibres visible in lower left. J, holotype QM G304686.

## Definition

Armoured Thorectinae, with a relatively sparse fibre skeleton and collagenous mesohyl.

#### Diagnosis

Upright and tubular, lobose or digitate sponges, with a thin, regular surface armour, and rounded conules or tubercles. The comparatively sparse fibre skeleton comprises simple, cored primary fibres and an irregular reticulum of uncored secondary fibres. Primary and secondary fibres are of similar diameter, with smaller diameter branching of the secondary fibres. The mesohyl of these sponges is characteristically fleshy or collagenous, in contrast to the more fibrous mesohyl of genera such as *Cacospongia, Thorecta* and *Scalarispongia*.

#### **Previous review**

Bergquist, 1980b.

## **Description of type species**

Aplysinopsis elegans Lendenfeld (Fig. 3A-B).

Synonymy. Aplysinopsis elegans Lendenfeld, 1888: 149; Burton, 1932b: 203; Lendenfeld, 1889a: 379; Bergquist, 1980b: 476, figs 15b–e; Hooper & Wiedenmayer, 1994: 226. Aplysinopsis digitata Lendenfeld, 1888: 150, pl. 12; Lendenfeld, 1889a: 381. *Aplysinopsis pedunculata* Lendenfeld, 1889c: 42; Lendenfeld, 1889a: 380, pl. 27 fig. 4. *Thorecta elegans* de Laubenfels, 1948: 113, pl. 19 fig. 37.

*Material examined.* Lectotype: BMNH 1886.8.27.3 (as *Aplysina rigida* var. *digitata* MS name). Other material. Authors collections, including: SDCC/RF068 (*elegans*).

**Description.** Monospecific (see generic diagnosis). These sponges are flesh-coloured to light red on the surface, and yellowish or dirty greyish white internally. Primary fibres are  $180-300 \,\mu\text{m}$  in diameter and secondary fibres are approximately  $140-160 \,\mu\text{m}$  in diameter. The consistency is firm and compressible. Choanocyte chambers are roughly spherical, and  $33-36 \,\mu\text{m}$  in diameter

*Remarks.* The most characteristic feature of this genus is its fleshy, collagenous matrix. Currently monotypic.

## Distribution

Australia (type locality).

#### THORECTANDRA LENDENFELD, 1889

#### Synonymy

[*Halispongia*] Bowerbank, 1872b: 123 (preocc.) (not *Halispongia* de Blainville, 1830). *Thorectandra* Lendenfeld, 1889c: 41; Bergquist, 1980b: 472; Hooper & Wiedenmayer 1994: 245.

#### Type species

*Thorectandra corticatus* Lendenfeld, 1889 (by subsequent designation; de Laubenfels, 1936a).

## Definition

Armoured Thorectinae, with large diameter, cored primary and uncored secondary fibres. These genera characteristically exude copious amounts of mucus when collected.

#### Diagnosis

Thorectidae in which the primary fibres are cored with an axial column of debris and the secondary fibres are clear. The skeleton is almost perfectly rectangular with huge mesh spaces (commonly up to 4.0 mm) and thick fibres (0.3 mm for primary fibres being frequent). The surface is heavily armoured and thrown into a series of ridges and hollows. The shape is always stalked, globular, fanshaped or tubular (Fig. 3C–D), with apical or fringing oscules. The fibre skeleton is relatively sparse, so the whole sponge inside the cortical armour is soft, easily crumbled, and collapsible. Excessive mucus production characterises those species thus far observed in the field.

## **Previous reviews**

Bergquist, 1980b; Hooper & Wiedenmayer, 1994.

#### **Description of type species**

Thorectandra boletus (Lamarck) (Fig. 3C-D).

Synonymy. Alcyonium boletus Lamarck, 1814: 332. Thorectandra corticatus Lendenfeld, 1889c: 42. Thorecta boleta de Laubenfels, 1948: 107. Thorectandra boletus Bergquist, 1980b: 472; Hooper & Wiedenmayer, 1994: 245.

*Material examined.* Holotype: Unknown (Hooper & Wiedenmayer, 1994). Other material. Authors collections, including: SDCC/RF016 (cf. *excavatus*).

Description (from Lendenfeld, 1889a). Pedunculate, pyriform sponges, which attain a height of 120 mm, and a width, in the central thickest part, of 40-60 mm. The surface is protected by a stout sand-cortex, and appears very uneven. Irregular ridges, on an average 5 mm high, project from the surface, and anastomose to form a pretty regular network with irregular or polygonal meshes. There is a single osculum, about 8 mm wide, which is situated terminally. The living sponge is grey. The skeleton is bright chestnut-brown, soft, and elastic. The main fibres of the supporting skeleton are 300 µm thick, and contain an irregular axial column of sand grains. The connecting fibres are 200 µm thick, simple, and mostly straight. The meshes are for the most part more or less regularly square, 3 mm broad (the distance between the main fibres), and 1.5-2 mm high (the distance between the connecting fibres). All the fibres, but particularly the connecting fibres, are very conspicuously stratified. In the latter, an axial granular thread, 15 µm thick, is observed.

*Remarks.* See remarks for *Thorecta*. Seven species are known.

#### Distribution

Australia (type locality), New Zealand. Possibly also Inland Sea of Japan (Hoshino, 1981a).

#### LUFFARIELLA THIELE, 1899

#### Synonymy

*Luffariella* Thiele, 1899: 25; Bergquist, 1980b: 464, 1995: 14; Hooper & Wiedenmayer, 1994: 236.

## Type species

*Luffaria variabilis* Poléjaeff, 1884 (by subsequent designation; Thiele, 1899).

## Definition

Thorectinae with a skeletal reticulum of simple primary, secondary and fine tertiary fibres.

#### Diagnosis

Massive to upright, producing caliculate, cylindrical-tubular and lobed forms (Fig. 3E–F, J). The surface is conulose and unarmoured. The moderately dense, regular to irregular skeleton comprises branching primary, secondary and fine tertiary fibres (Fig. 3G–I). Primary fibres are cored with foreign debris, although this is known to be sparse in one species, and tend to bifurcate near the surface, becoming almost fascicular. Secondary and tertiary fibres are uncored. These sponges are moderately firm and barely compressible.

## **Previous reviews**

Bergquist, 1965, 1980b, 1995; Hooper & Wiedenmayer, 1994.

#### **Description of type species**

Luffariella variabilis (Poléjaeff) (Fig. 3E-I).

Synonymy. Luffaria variabilis Poléjaeff, 1884: 69, pl. 9 figs 1–6; Lendenfeld, 1889a: 387; Luffariella variabilis Thiele, 1899: 25, Bergquist, 1965: 128; 1980b: 464, figs 8a–c. Thorecta variabilis de Laubenfels, 1948: 112.

*Material examined.* Holotype: BMNH 1885.8.8.52 (slide). Other material. Authors collections, including: SDCC/RF058 (*variabilis*), SDCC/RF143 (*variabilis*).

**Description.** (See generic diagnosis above). Low and massive, to upright and digitate, with the surface covered by coarse conules. Outer surface greyish, mesohyl yellow and dirty-greyish white. Primary fibres are 200  $\mu$ m in diameter and secondary fibres are around 67  $\mu$ m in diameter, and tertiary fibres are 10  $\mu$ m in diameter.

**Remarks.** The very fine tertiary fibres of this species provide the benchmark in defining tertiary fibres within the Dictyoceratida; the diameter of these tertiary fibres is approx. 20% of the diameter of secondary fibres. However, examples have been found in other families where some fibres are distinctly thinner than secondary fibres, but not to the same degree as those seen in *Luffariella* (e.g., Cook & Bergquist, 2001). Some species of *Luffariella* may be difficult to distinguish from *Fenestraspongia*, based solely on skeletal characters, though typically *Fenestraspongia* has strong fascicular primary fibres, in contrast to the simple fibres of *Luffariella*. The external features of *Fenestraspongia* are also an important diagnostic character. Four species are known.

## Distribution

Vanuatu (type locality), South Pacific.

## FASCIOSPONGIA BURTON, 1934

#### Synonymy

[Stelospongos] Schmidt, 1870: 29; Hyatt, 1877: 528–529 (nomen nudum, no type species designated). [Stelospongia] Schulze, 1879: 613 (in part) (nom. nov. for Stelospongos Schmidt; unjustified emendation); Lendenfeld, 1889a: 468. [Stellospongia] Marshall, 1880: 118 (? lapsus for Stelospongia Schulze, 1879). [Stelospongus] Ridley, 1884a: 383 (in part) (nom. nov. for Stelospongos Schmidt; unjustified emendation). Fasciospongia Burton, 1934a: 602; de Laubenfels, 1948: 118; Bergquist, 1980b: 472.

## Type species

*Stelospongia australis* var. *fovea* Lendenfeld, 1888 (by original designation); jun. synonym of *Spongia turgida* Lamarck, 1814: 377 (Bergquist, 1980b: 470).

## Definition

Unarmoured Thorectinae, with strong central or subdermal exhalant canals. Primary fibres are fascicular and there are heavy deposits of ectodermal collagen.

## Diagnosis

Usually globular, tubular, caliculate or thickly foliose, with distinct central exhalant canals and characteristic subdermal lacunae (Fig. 4A–F). The sponge surface is unarmoured, and has a shiny, plastic appearance, reflecting heavy collagen deposition in the ectoderm. The skeleton is composed of solid, large diameter primary and secondary fibres. Primary fibres are cored with foreign debris and form strong fascicles or ladders, which produce truncate conules on the surface. Secondary fibres are uncored and branching. These sponges are firm and compressible, and the dermal region is supported by a band of collagen.

#### Previous reviews

Bergquist, 1980b; Hooper & Wiedenmayer, 1994.

#### **Description of type species**

Fasciospongia turgida (Lamarck) (Fig. 4A-C).

Synonymy. Spongia turgida Lamarck, 1814: 377. Stelospongos levis Hyatt, 1877: 530. Stelospongos levis rotundus Hyatt, 1877: 530, pl. 17 figs 23–24. Stelospongia australis var. fovea Lendenfeld, 1888: 170, pl. 11. Stelospongia australis var. conulata Lendenfeld, 1888: 168. Stelospongia australis var. conulissima Lendenfeld, 1888: 172. Stelospongia australis var. villosa Lendenfeld, 1888: 166–167. Stelospongia australis Lendenfeld, 1888: 166–167. Stelospongia australis Lendenfeld, 1889a: 513, pl. 23 fig. 1, pl. 24 fig. 8, pl. 25 figs 3–4, pl. 29 fig. 3, pl. 30 figs 12–13, pl. 31 figs 2, 7–9, pl. 32 figs 7, 9. Stelospongia australis var. canaliculata Lendenfeld, 1888: 166. Fasciospongia turgida Burton, 1934a: 602; de Laubenfels, 1948: 118, pl. 21 fig. 40; Bergquist, 1980b: 474, figs 3b, 13a–d; Hooper & Wiedenmayer, 1994: 228.

*Material examined.* Holotype: MNHN LBIM DT548 (var. beta). Other material. Authors collections, including: SDCC/RF012 (*turgida*); SDCC/RF055 (*cavernosa*); SDCC/RF066 (*cavernosa*); SDCC/RF105 (*turgida*).

pedunculate Description. Massive, roughly globose, sponges. The peduncle forms a basal plate, with which it attaches to the substratum. The surface is coarsely conulose and unarmoured. Conules are arranged in lines, producing a uniform polygonal pattern. This sponge characteristically has 1-2 large diameter apical oscules, that are raised about the sponge surface. Oscules are always surrounded by frills of longitudinal fascicles. The exterior of this species is light purple-brown externally, and greyish yellow internally. The fibre skeleton consists of thin and broad band-shaped fascicles, which are joined by a loose network of secondary fibres. The band-shaped fascicles curve towards the surface, where they measure  $1000 \times 6000 \,\mu\text{m}$ . Secondary fibres are around 40–80  $\mu\text{m}$ in diameter, but secondary fibres which interconnect between the fascicles are 80-100 µm thick.

**Remarks.** The type species, *Fasciospongia turgida* (Lamarck), is a very distinctive sponge, with very heavy fibres (simple, non-fascicular sections of primary fibre were measured around 200  $\mu$ m in diameter). Specimens of two other species, *F. cavernosa* (Schmidt, 1868) and *F. pikei* (Hyatt, 1877), were also available, both of which displayed very different skeletal morphology. There is some suspicion that *Fasciospongia* species from the Mediterranean are not congeneric with *Fasciospongia* species from the Southern Hemisphere, (e.g., the type species). Unfortunately, there was insufficient material available to review the genus. Twelve species are known.



Fig. 4. Fasciospongia, Dactylospongia and Smenospongia. A–C, Fasciospongia turgida. A, AM Z915. B, surface of dry skeleton, AM G8871. C, internal section, showing fasciculate fibre columns. D, F. cycni. AM Z1139. E, F. flabellum, holotype BMNH 1886.12.15.213. F, F. rimosa, BMNH 1886.8.27.137. G–I, Dactylospongia elegans. G, holotype. H, specimen USNM 23707. I, skeleton (H–I, reproduced from Bergquist, 1965). J–L, Smenospongia aurea. J, in aquarium, B873 (reproduced with permission from Wiedenmayer, 1977b). K, alcohol preserved specimen. L, dry skeleton, BMNH 1939.1.30.3.

#### Distribution

Australia (type locality), Indo-Pacific, Mediterranean, Red Sea and possibly northern New Zealand.

## DACTYLOSPONGIA BERGQUIST, 1965

## Synonymy

Dactylospongia Bergquist, 1965: 127; Bergquist, 1980b: 452.

## Type species

Luffariella elegans Thiele, 1899 (by original designation).

## Definition

Unarmoured Thorectinae, with uncored fibres and no clear distinction between primary and secondary fibres.

#### Diagnosis

The type specimen of this genus consists of thin, elongate, anastomosing straps (Fig. 4G–H), with an unarmoured surface, bearing irregular, truncate conules. The only other known species, *D. metachromia* (de Laubenfels, 1954), forms a compact cushion (de Laubenfels, 1954). The fibre skeleton is a dense network of solid, uncored, branching and interconnecting fibres, with no clear distinction between primary ascending and secondary connecting fibres (Fig. 4I) as typically seen in the Thorectidae, where primary fibres can be identified by their orientation to the surface, or the presence of a debris core. Conules are formed by a denser mass of fibres, that are smaller in diameter and more dichotomous or fascicular. The conules are separated by lacunae, covered over by the pinacoderm. This sponge is firm and only slightly compressible.

#### Previous reviews

De Laubenfels, 1954; Bergquist, 1965, 1980b.

## **Description of type species**

Dactylospongia elegans (Thiele) (Fig. 4G-I).

*Synonymy.* Luffariella elegans Thiele, 1899: 25, pl. 3, fig. 4, pl. 5, fig. 20. *Dactylospongia elegans* Bergquist, 1965: 127, figs 1a–b; Bergquist, 1980b: 452, figs 2a, 4b.

*Material examined.* Holotype: ZMB 2838 (fragment). Other material. Authors collections, including: SDCC/RF047 (*metachromia*).

**Description.** (See generic diagnosis above). The branches of this sponge are 0.5-1.5 cm wide, up to 32 cm long, and may anastomose several times along its length. The unarmoured surface is coarsely conulose, with the irregular, multi-tuberculate conules tending to be aligned in rows, between which the dermal membrane is stretched. Oscules are scattered over the surface of the branches. The skeleton consists of an irregular reticulation of clear, yellowbrown fibres. Primary or ascending fibres are only distinguishable immediately below the surface. Fibres,  $20-54 \,\mu\text{m}$  in diameter, show some evidence of concentric lamination, and a diffuse pith is seen occasionally. Isolated foreign inclusions may be seen but the fibres are essentially uncored. The fibre surface is also characteristically granulated. The small, spherical choanocyte chambers are  $24-30 \,\mu\text{m}$  in diameter. This sponge is extremely tough and elastic.

**Remarks.** This genus was originally proposed within the family Spongiidae (Bergquist, 1965, 1980b). *Dactylospongia* is now considered correctly assigned to the Thorectidae, because of its apparent similarity to *Smenospongia*, and the presence of pithed and stratified fibres, as indicated in the original description. These sponges are yellow externally, and after collection the colour changes to dark purple or reddish brown. This yellow colouration and subsequent pigment change is unusual in Dictyoceratida, but characteristic of sponges of the order Verongida and some Dendroceratida. (See also remarks for *Smenospongia*). Two species are known.

## Distribution

Sulawesi (type locality), and Palau.

#### SMENOSPONGIA WIEDENMAYER, 1977

## Synonymy

*Smenospongia* Wiedenmayer, 1977b: 69; Bergquist, 1980b: 478; Hooper & Wiedenmayer, 1994: 238.

#### Type species

Aplysina aurea Hyatt, 1875 (by monotypy).

#### Definition

Unarmoured Thorectinae with a well-developed secondary fibre reticulum, low collagen deposition, and surface which displays a characteristic honeycomb pattern.

## Diagnosis

Massive, semi-encrusting, amorphous to lobate (Fig. 4J-L). Similar to *Dactylospongia* but the skeletal reticulum is clearly divided into cored ascending primary fibres and a regular and relatively dense network of uncored, simple or branching, secondary fibres. The distinction between primary and secondary fibres may at times be obscured by the density of the secondary fibre network. The fibre skeleton produces a distinctly honeycomb arrangement near the surface that is not evident deeper in the mesohyl. Primary fibres are essentially simple, but may form slight fascicles or ladders near the surface, or in association with adjacent secondary fibres. The fibre reticulum becomes less organised or somewhat tangled at the surface where conules are formed, each conule has a cored primary fibre projecting from its tip. There is only limited collagen deposition within the mesohyl.

#### **Previous reviews**

Wiedenmayer, 1977b; Bergquist, 1980b; Hooper & Wiedenmayer, 1994.

#### **Description of type species**

Smenospongia aurea (Hyatt) (Fig. 4J-L).

Synonymy. Aplysina aurea Hyatt, 1875: 404. Stelospongus cribriformis var. typica Hyatt, 1877: 531, pl. 15 fig. 14. Smenospongia aurea Wiedenmayer, 1977b: 69; Van Soest, 1978: 64; Bergquist, 1980b: 478, figs 16e–f, 17a–b.

*Material examined.* Syntypes: MCZ 7332; MCZ 7245. Other material. Authors collections.

Description (after Wiedenmayer, 1977b). Semi-encrusting to massive, and amorphous, tending to be lobate. The interior is often coarsely cavernous or hollow. Colour in life is light brown, commonly with reddish and purplish tinges, especially towards the base, or occasionally olive or yellow-green; internally this species is bright lemon-yellow. The sponge typically turns black on exposure to air, and becomes slimy after death. These sponges are firm and compressible. The ostia are contractile, and are crowded in surficial depressions. Oscules are large and conspicuous, 5-10 mm in diameter, usually on top of mounds. The skeleton is characterised by wide, trellised primary systems. They consist of crowded primary fibres, connected to each other by very short secondaries. Secondary fibres are commonly arranged in continuous planes, outlining triangular to hexagonal prisms: hence the characteristic honeycombed aspect of the surface in dried specimens. In some specimens, distinction between primary systems and secondary fibres is difficult because the secondaries are often very crowded and anastomose profusely. Fibres are regularly stratified, and their axial region is darker, but devoid of pith. No foreign inclusions were seen, either in fibres or in the dermis. Primary fibres range in diameter from 40–180 µm.

**Remarks.** Consideration was given to the possibility of combining *Smenospongia* and *Dactylospongia* into a single genus, but owing to the limited, well-fixed material available, this will have to await further study. Histological information is particularly difficult to obtain. The original description of *Smenospongia* refers to aerophobic properties typical of verongid sponges, and as also seen in the two species of *Dactylospongia*. This is similar to the oxidation sequence seen in Verongida. *Smenospongia* has a more distinct demarcation between the inner and outer regions of individual skeletal fibres, than seen in any other member of the Dictyoceratida. Aplysinopsin and related compounds have been isolated from *S. aurea*, which are identical to those found in *Fascaplysinopsis* and *Thorectandra*, indicating the relationship of *Smenospongia* to the Thorectidae. No member of this group of tryptophane-derived compounds has ever been found in the Verongida (Bergquist, 1980b). Four species are known.

#### Distribution

West Indies (type locality).

#### FENESTRASPONGIA BERGQUIST, 1980

#### Synonymy

*Fenestraspongia* Bergquist, 1980b: 474; Hooper & Wiedenmayer, 1994: 230.

#### Type species

Hircinia intertexta Carter, 1885c (by original designation).

## Definition

Unarmoured Thorectinae, with a fenestrate surface. The skeletal reticulum is comprised of heavy primary and secondary fibres, and very fine tertiary fibres.

## Diagnosis

Upright, thickly lamellate or cylindrical and tubular forms. The surface is unarmoured, conulose and raised into characteristic intersecting, plate-like ridges (Fig. 5A), i.e., fenestrate. These sponges have a fibre skeleton made up of primary, secondary and tertiary fibres (Fig. 5B). Primary fibres are cored, and form strong fascicles that curve towards the surface. Secondary fibres are uncored and branching, and form a moderately dense reticulum. Tertiary fibres are uncored, very fine, and occur within the meshes of the secondary fibre reticulum.

#### **Previous reviews**

Bergquist, 1980b; Hooper & Wiedenmayer, 1994.

## **Description of type species**

Fenestraspongia intertexta (Carter) (Fig. 5A-B).

*Synonymy. Hircinia intertexta* Carter, 1885a: 120, Carter, 1885c: 312. *Fenestraspongia intertexta* Bergquist, 1980b: 474, figs 14d–e, 15a; Hooper & Wiedenmayer, 1994: 230.

*Material examined.* Holotype: BMNH 1886.12.15.238 (dry). Other material. Authors collections, including: SDCC/RF028 (*intertexta*).

**Description (from Carter, 1885c).** Specimen wet. Oblong, erect, like "a piece of board an inch thick", slightly thinning towards the sides and upper border, whose margins are rounded and irregularly undulated, sessile, spreading below. Consistence firm and resilient, very light when dry. Colour, when fresh, grey, now brownish grey. Surface on both sides uniformly covered with monoticular, single-pointed conuli averaging 1 mm apart and about the same in height above sunken intervening dermis, which unites them together more or less linearly; dermis consisting of beautifully reticulated, soft, grey fibre without foreign objects, which

dries light brown, and whose interstices are tympanised by a thin transparent sarcode in which the pores are situated, supported by another subjacent reticulation of amber-coloured keratose fibre, which, resting on the ends of the arenaceous vertical filaments, thus together form the conuli and support the dermis. Vents large, chiefly on the upper margin. Internal structure consisting of a mass of reticulated fibre of three kinds, like the dermis, viz., (1) large, scanty, cored with foreign objects, vertical; (2) middle-sized, exclusively amber-coloured keratine, lateral; (3) microscopic, soft when fresh, hard and transparent when dry, intertextural, whose interstices, tympanised by thin poriferous sarcode, occupy the rest of the space and, traversed by the branches of the excretory canalsystem, complete the parenchyma. Size of specimen 300 mm high by  $90 \times 38$  mm. horizontally in its greatest dimensions. As a slice has been cut from one side perpendicularly, the probability is that this specimen was much wider, perhaps double the present width, when entire. The most striking feature in this specimen is the presence of the microscopic, intertextural fibre filling up the interstices of the skeleton.

**Remarks.** Within the Thorectidae there are only two genera with fine tertiary skeletal fibres, *Luffariella* and *Fenestraspongia*. The conulose surface and usually simple or branching primary fibres of *Luffariella*, are readily distinguishable from the fenestrate or ridged surface and strongly fascicular primary fibres of *Fenestraspongia*. Two species are known.

## Distribution

Southeastern Australia (type locality).

#### FASCAPLYSINOPSIS BERGQUIST, 1980

#### Synonymy

Fascaplysinopsis Bergquist, 1980b: 478.

## Type species

Aplysinopsis reticulata Hentschel, 1912 (by monotypy).

## Definition

Unarmoured Thorectinae, with a sparse skeleton of massive primary and secondary fibres.

#### Previous reviews

Bergquist, 1980b; Hooper & Wiedenmayer, 1994.

## **Description of type species**

Fascaplysinopsis reticulata (Hentschel) (Fig. 5C–F).

*Synonymy. Aplysinopsis reticulata* Hentschel, 1912: 437, pl. 15, fig. 1, pl. 16, fig. 9. *Fasciospongia cavernosa* de Laubenfels, 1948: 119. *Fascaplysinopsis reticulata* Bergquist, 1980b: 478, figs 3a, 16a–c; Hooper & Wiedenmayer, 1994: 226.

*Material examined.* Syntypes: SMF 904 (two specimens). Other material. Authors collections, including: SDCC/RF017 (*reticulata*); SDCC/RF021 (*reticulata*).



**Fig. 5.** *Fenestraspongia, Fascaplysinopsis* and *Collospongia.* A–B, *Fenestraspongia intertexta.* A, specimen AM Z3866. B, secondary fibres and very fine tertiary fibre skeleton. C–E, *Fascaplysinopsis reticulata.* C, surface view showing distinctive, wide-spaced conules. D, internal cross-section. E, SDCC/RF017, showing massive fibres and fascicles. F, *in situ*, New Caledonia, ORSTOM R1344. G–I, *Collospongia auris.* G, holotype AM Z5035. H, cross-section through whole lamella. I, fibre skeleton, with horizontal primary fibre (G–I, reproduced with permission from Bergquist *et al.*, 1990a).

**Description.** Upright, lobose form (Fig. 5C, F). The surface is unarmoured, with large, widely-spaced conules, reflecting the underlying fibre skeleton, and creating a pitted appearance. The fibre skeleton comprises very large diameter primary and secondary fibres (Fig. 5D–E). Primary fibres are fasciculate, or sometimes ladder-like, and cored with foreign debris. Secondary fibres are uncored, and form an irregular, branching network. The mesohyl is characteristically gelatinous or fleshy, but the consistency is firm and compressible, becoming hard and stiff in alcohol.

#### Distribution

Northern Great Barrier Reef and Northern Australian coast, Indonesia (type locality).

#### COLLOSPONGIA BERGQUIST, CAMBIE & KERNAN, 1990

## Synonymy

*Collospongia* Bergquist, Cambie & Kernan, 1990a: 349; Hooper & Wiedenmayer, 1994: 226.

### Type species

Collospongia auris Bergquist, Cambie & Kernan, 1990a (by monotypy).

#### Definition

Unarmoured Thorectinae, 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 fasciculate and lightly cored primary fibres and uncored secondary fibres, and the presence of a tangential dermal reticulum.

#### Diagnosis

Thin lamellae to multi-caliculate sponges (Fig. 5G), with an unarmoured, micro-conulose surface. The upper part of the sponge may have a sand crust, rendering the surface smooth, but this does not form a consistent armour over the whole sponge. The fibre skeleton comprises fasciculate and lightly cored primary fibres, and uncored secondary fibres (Fig. 5H–I). Primary fibres are arranged parallel to the surface, within the thin lamellae or walls of the sponges, with fibre fascicles curving out towards both surfaces. The secondary fibres are arranged similarly. Close to the surface the fascicular primaries repeatedly subdivide into finer fibres, forming a fascicular and tangled fibre mass which supports a tangential dermal skeleton of fine fibres with a regular meshwork. These sponges are firm, tough and flexible.

## **Previous reviews**

Bergquist, Cambie & Kernan, 1990a; Hooper & Wiedenmayer, 1994.

#### **Description of type species**

Collospongia auris Bergquist, Cambie & Kernan (Fig. 5G–I). Synonymy. Collospongia auris Bergquist, Cambie & Kernan, 1990a: 349, figs 1–5.

*Material examined.* Holotype: AM Z5035. Other material. Authors collections, including: SDCC/RF128 (*auris*); SDCC/ RF131 (*auris*) (see also Bergquist, Cambie & Kernan, 1990a).

**Description.** Monospecific (see generic diagnosis). A thin spreading sponge, with a slightly cupped, lamellate form. The sponge body is 1–4 mm thick, with a tough, flexible and collage-nous consistency. Oscules, 0.5–0.7 mm in diameter, are regularly spaced over the upper surface of the lamellae. They are only slightly elevated in life and become flush with the surface in fixed specimens. This species varies in colour from greyish white to maroon on upper surfaces, and dark maroon on lower surfaces.

**Remarks.** Superficially this genus would appear to be aligned with the Phyllospongiinae, rather than the Thorectinae, but *Collospongia* has a unique skeletal structure and does not possess the bishomoscalarane secondary metabolites, which characterise the subfamily. Monospecific.

## Distribution

Great Barrier Reef (type locality), Australia.

#### PETROSASPONGIA BERGQUIST, 1995

#### Synonymy

Petrosaspongia Bergquist, 1995: 13.

#### Type species

Petrosaspongia nigra Bergquist, 1995 (by monotypy).

## Definition

Unarmoured Thorectinae, with a dense secondary fibre reticulum, rendering these sponges hard and incompressible.

#### Diagnosis

Large, massive and spreading, with thick interlacing lobes arising from a spreading base. The surface is finely conulose, each conule with a fine projecting fibre. The dense skeletal reticulum is dominated by tightly interlocking, strongly laminated, uncored secondary fibres. Some finer secondary fibres occur, which in places almost constitute a tertiary fibre network. Cored primary fibres are greatly reduced in number, but may be seen in the ectosomal region, where they are produced by the convergence of many secondary fibres, and form a fenestrated spongin plate, from which primary elements extend to the surface. Coring material is regular and occupies approximately half of the fibre diameter. The surface is encrusted by a fine, evenly dispersed sand layer, that does not form an armoured crust. The external pigmentation is black, whereas the interior is beige to pale yellow. As a result of the density of the secondary network and the incorporation of moderate amounts of interstitial debris throughout the sponge, the texture is extremely hard and incompressible. There is light deposition of collagen through the matrix, and choanocyte chambers are small, diplodal and spherical.

#### **Previous review**

Bergquist, 1995.

#### **Description of type species**

Petrosaspongia nigra Bergquist (Fig. 6A-C).

*Synonymy. Petrosaspongia nigra* Bergquist, 1995: 13, figs 6a–c.

*Material examined.* Holotype: QMG304685. Other material. Authors collections.

Description. Large, massive and spreading, with thick interlacing lobes arising from a spreading base. Oscules are small, 1.0-2.5 mm in diameter, flush with the surface, and scattered over the body. The surface is finely conulose, each conule with a fine projecting fibre. The dense skeletal reticulum is dominated by tightly interlocking, strongly laminated, uncored secondary fibres. Some finer secondary fibres occur, which in places almost constitute a tertiary fibre network. Primary fibres, 90-110 µm thick, are short, cored and arise only 800-1000 µm below the surface where sectors of the secondary skeleton fuse to form a fenestrated spongin plate, from which primary elements extend to the surface. The predominant secondary fibres are 25-60 µm in diameter, but some very fine fibres 8-10 µm in diameter also occur, and in places almost constitute a tertiary network. The fine fibres do not occur throughout the skeleton. Colour in life, and in alcohol, is jet black externally, pale yellow to beige internally. The consistency is hard, incompressible, and the surface has a brittle, rough aspect. There is light deposition of collagen through the matrix, and choanocyte chambers are small, 20–25 µm in diameter, diplodal and spherical.

**Remarks.** Petrosaspongia is closest to Hyrtios, from which it differs in the density of the irregular skeletal reticulum, having uncored secondary fibres which form a very dense network, in the absence of coring material in the secondary fibres, and in having distinct but reduced, primary cored fibres. Two species are known.



Fig. 6. Petrosaspongia, Thorectaxia, Scalarispongia and Semitaspongia. A–C, Petrospongia nigra. A, holotype QM G304685. B, in situ. C, skeleton. D–F, Thorectaxia papuensis. D, specimen P. 42. E, axial skeleton. F, ascending skeleton structure (D–F, reproduced with permission from Pulitzer-Finali & Pronzato, 1999). G–I, Scalarispongia scalaris. G, specimen SDCC/RF083. H, skeleton. I, histological detail, with low collagen. J, Semitaspongia incompta, holotype NMNZ Por.459. K, S. bactriana, holotype NMNZ Por.458. L, S. glebosa, holotype NMNZ Por.457, skeleton. M, S. nigracorda, holotype NMNZ Por.456, skeleton. N–O, S. incompta. N, skeleton. O, histological detail showing collagenous mesohyl.

## Distribution

New Caledonia (type locality), Fiji. Likely to occur at other localities in the Southwest Pacific region.

#### THORECTAXIA PULITZER-FINALI & PRONZATO, 1999

## Synonymy

Thorectaxia Pulitzer-Finali & Pronzato, 1999: 596.

## Type species

*Thorectaxia papuensis* Pulitzer-Finali & Pronzato, 1999 (by monotypy).

## Definition

Unarmoured Thorectinae, with an axially concentrated skeleton, and loosely laminated fibres.

## Diagnosis

Upright, cylindrical, digitate form, with an unarmoured, conulose surface. The sponge is supported by an axially concentrated skeleton consisting of fasciculated main fibres, irregularly connected by secondary fibres. From this structure, single main fibres diverge toward the surface up to the conules (Pulitzer-Finali & Pronzato, 1999). All fibres are uncored, and appear loosely laminated. This latter feature is unique within the Thorectidae.

## **Recent reviews**

Pulitzer-Finali & Pronzato, 1999.

#### **Description of type species**

*Thorectaxia papuensis* Pulitzer-Finali & Pronzato (Fig. 6D–F). *Synonymy. Thorectaxia papuensis* Pulitzer-Finali & Pronzato, 1999: 596, fig. 4.

#### Material examined. None.

Description (from Pulitzer-Finali & Pronzato, 1999). Monospecific (see generic diagnosis). The specimen is erect, cylindrical, 1-1.5 cm thick, 10 cm long, the base is missing. This sponge is white in life, and greyish-brown in alcohol. The consistency is tough, not resilient. The surface is irregularly, finely granulated, and conulose, the conules being about 1.5 mm high and 3-4 mm apart. The oscules are few, oval, cribriform, and about 2mm wide. The sponge surface is clearly organized, with an ectosomal region, about 100 µm thick, easily separable. The fibre skeleton can be viewed as two different regions. An axial skeleton consists of stout primary fibres 180-260 µm thick, densely connected by secondary fibres 20-80 µm thick. This is concentrated in the centre of the sponge, where it occupies about one third, in diameter, of the body. From this axis single primary fibres, devoid of connections, diverge obliquely and run toward the surface, where they produce surface conules. Skeletal fibres are laminated, free from inclusions, amber coloured with an irregular, blackish, empty or granular pith. Choanocyte chambers are numerous, roundish, 10-25 µm wide, diplodally organized.

#### Distribution

Papua New Guinea (type locality).

#### SCALARISPONGIA COOK & BERGQUIST, 2000

#### Synonymy

Scalarispongia Cook & Bergquist, 2000: 388.

## Type species

*Cacospongia scalaris* Schmidt, 1862 (by original designation).

#### Definition

Unarmoured Thorectinae, with a regular, rectangular fibre skeleton, simple primary fibres, and moderate collagen deposition.

#### Diagnosis

Massive sponges, forming regular to irregular, pads or cushions. The surface is unarmoured, and covered with fine to coarse conules. The skeleton is made up of a spongin fibre reticulum of concentrically laminated primary and secondary fibres, arranged in a regular, ladder-like pattern. The meshes of the skeletal reticulum are often, though not always, precisely rectangular, with secondary fibres forming almost perfect right-angles to primary fibres. Primary fibres are cored with foreign material and secondary fibres are clear. Primary fibres do not form fascicles, but some secondary fibres may form light webbing, rather than discrete secondary fibres, in between the primary fibres. The mesohyl is moderately and evenly infiltrated with collagen.

#### Previous reviews

Vacelet, 1959; Cook & Bergquist, 2000.

#### **Description of type species**

Scalarispongia scalaris (Schmidt) (Fig. 6G–I).

*Synonymy.* Cacospongia scalaris Schmidt, 1862: 27, pl. 3 fig. 4; de Laubenfels, 1948: 93; Vacelet, 1959: 82; Bergquist 1980b: 460, fig. 2c, 7d; *Stelospongia scalaris* Lendenfeld, 1889a: 491. *Aplysinopsis massa* Szymanski, 1904: 448.

*Material examined.* Lectotype: LMJG 15416 (dry). Other material. Authors collections, including: SDCC/RF054 (*scalaris*); SDCC/RF083 (*scalaris*); SDCC/RF090 (*scalaris*); SDCC/RF137 (*scalaris*); SDCC/RF142 (*scalaris*); SDCC/RF145 (*scalaris*), SDCC/RF159 (*linteiformis*).

**Description.** (See generic diagnosis). Massive, irregular, and amorphous or slightly lobose, with an unarmoured, conulose surface. Oscules are scattered over the sponge surface, usually on raised areas of the sponge surface. Most oscules are surrounded by a wider, flattish or slightly depressed velum of pinacoderm. Externally *S. scalaris* is light to medium grey on upper areas of the sponge, though can range to dark grey-black, fading to greyish off-white in lower areas. Internally this species is off-white to cream.

*Remarks.* See Cook & Bergquist (2000). Six species are known.

#### Distribution

Mediterranean (type locality), Galapagos, West Indies.

#### SEMITASPONGIA COOK & BERGQUIST, 2000

#### Synonymy

Semitaspongia Cook & Bergquist, 2000: 389.

#### Type species

*Semitaspongia incompta* Cook & Bergquist, 2000 (by original designation).

#### Definition

Unarmoured Thorectinae, with an irregular to regular skeletal reticulum, slightly fascicular primary fibres, and moderate to abundant collagen deposition.

#### Diagnosis

Sponges forming regular to irregular pads, blunt fingers, lobes, or cushions (Fig. 6J–K). The surface is conulose and unarmoured. The skeleton is an irregular to regular reticulum of primary and secondary fibres (Fig. 6L, N). Primary fibres are cored and may be slightly fascicular (Fig. 6M), typically just beneath the cortex; secondary fibres are clear. A central pith is visible in primary fibres, though it may be obscured where fibres are cored, and can

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sometimes be seen extending into secondary fibres. The consistency is soft to firm, compressible and is easily torn. There is moderate to abundant collagen deposition, up to 40% of the mesohyl volume, in subdermal regions and around canals.

#### **Previous review**

Cook & Bergquist, 2000.

## **Description of type species**

Semitaspongia incompta Cook & Bergquist (Fig. 6J, N-O).

Synonymy. Semitaspongia incompta Cook & Bergquist, 2000: 389, fig. 3.

*Material examined.* Holotype: NMNZ Por.459 (=SDCC/ NZ031). Other material. Refer to Cook & Bergquist (2000).

Description. A highly irregular pad-like sponge, comprising living tissue and exposed fibre network. The surface is conulose, each conule with long dendritic emergent terminal fibres. Thin ridges are stretched between some adjacent conules on coarsely conulose specimens. Internally, apparently solid areas of sponge have internal pockets of unfleshed fibre skeleton. The sponge is soft to moderately firm, and compressible. Colour is light to medium grey externally and light grey to brownish grey internally. The three specimens used in the original description are ca. 60-80 mm in diameter and 5-20 mm thick. The skeleton ranges from regular, rectangular and low to moderate density, to a tangled, relatively high density network. Primary fibres are axially to fully cored, and secondary fibres are uncored. Pith is visible in primary, and some secondary fibres. In places, fibres form complex, tangled fascicles, and vary greatly in diameter. Primary fibres are 87-825 µm in diameter, secondary fibres are 29-146 µm in diameter. The spherical to oval choanocyte chambers are diplodal. They are loosely scattered throughout the mesohyl, and in some places arranged in tracks through beds of collagen (Fig. 6O). Choanocyte chambers are 23-39 µm in diameter. The mesohyl is heavily impregnated with collagen. Typically an irregular and unkempt looking species, which may contribute to it being overlooked, but which is readily distinguishable.

**Remarks.** This genus is closest to *Cacospongia*, but is distinguished by the equal abundance of primary and secondary fibres, and its enhanced collagen deposition. *Aplysinopsis*, which also has a collagenous mesohyl, is differentiated from this genus by its sparse skeleton, in relation to the mesohyl, and its thin, regular sand cortex. Five species are known.

### Distribution

New Zealand (type locality).

#### NARRABEENA GEN. NOV.

#### Type species

Smenospongia lamellata Bergquist, 1980b (here designated).

#### Definition

Unarmoured Thorectinae, with a well-developed skeletal reticulum of uncored fibres, and no clear distinction between

primary and secondary elements. These sponges also have a microconulose surface, and light collagen deposition throughout the sponge.

## Diagnosis

Sponge composed of multiple intersecting lamellae (Fig. 7A), and has a microconulose surface with a slimy texture. It is compressible, pliable and tough. The skeleton is a well-developed, irregular, interlocking mesh in which there is no distinction between primary and secondary fibres (Fig. 7B). The skeletal branching pattern has no fixed orientation to the surface except where fibres extend into conules. Skeletal fibres are concentrically laminated, and have a small, but distinct axial pith.

#### **Previous review**

Bergquist, 1980b.

## **Description of type species**

Narrabeena lamellata (Bergquist) (Fig. 7A-B).

*Synonymy. Smenospongia lamellata* Bergquist 1980b: 478, figs 17c–f; Hooper & Wiedenmayer, 1994: 238.

Material examined. Holotype: AM Z3867. Paratypes: AM.

**Description.** (See generic diagnosis). The lamellae making up the sponge body are each 3–8 mm thick and up to 30 cm high, arising from an attachment base 9–12 cm long. In life, external colouration is dark black-green to yellow-green, and pale creamy yellow internally. Skeletal fibres are 15–70  $\mu$ m in diameter, and the diplodal choanocyte chambers are 20–40  $\mu$ m in diameter.

**Remarks.** Narrabeena lamellata was originally described as a Smenospongia, based on the presence of tryptophane-based compounds in both S. lamellata and S. aurea (see remarks for Smenospongia), and on the skeletal organisation, but it has never sat comfortably within that genus. This sponge has a welldeveloped skeleton, with pithed fibres, whereas the skeletal fibres of S. aurea show only traces of pith. Narrabeena is also similar to Dactylospongia, but that genus has a dense skeleton, conulose surface, long subdermal lacunae and is uniformly pigmented, in contrast to Narrabeena's more open mesh skeleton, differential colouration, and slimy microconulose surface. Monotypic.

## Distribution

Southern New South Wales coast, Australia (type locality).

#### Etymology

The name *Narrabeena* is derived from the Narrabeen region on the New South Wales coast of Australia, where this sponge was found.

### SUBFAMILY PHYLLOSPONGIINAE KELLER, 1889

#### Synonymy

Phyllosponidae Keller, 1889: 349. Phyllospongiinae Bergquist, Sorokin & Karuso, 1999: 57.



Fig. 7. Narrabeena, Phyllospongia and Carteriospongia. A–B, Narrabeena lamellata. A, holotype AM Z3867. B, skeleton. C–D, Phyllospongia papyracea. C, typical form, AM Z5014. D, digitate branching form, AM Z5025. E–F, P. lamellosa. E, in situ, Great Barrier Reef, Australia. F, simple lamellate form. G–H, Carteriospongia foliascens. G, neotype BMNH 1925.11.1.411. H, specimen BMNH 1872.9.25.1. I, C. pennatula, BMNH 1946.11.25.444. J, C. contorta, surface showing complex lamellae (A–B, D, G, reproduced with permission from Bergquist et al., 1988).

## Definition

Thorectidae consisting of foliose, lamellate or folio-digitate growth forms, with tertiary fibres in the skeleton (except in one genus).

## Diagnosis

Foliose or folio-digitate sponges in which the spongin fibres making up the anastomosing skeleton are finely laminated and contain a differentiated pith. Zones of disjunction between successive fibrous layers remain tightly adherent, producing an overall homogeneous structure with visible contiguous laminae. The pith is not sharply disjunct from the investing spongin fibre but rather merges into it. Secondary fibres show a surface striation. The skeleton is made up of cored primary and uncored secondary fibres to which uncored vermiform or reticulate tertiary elements are added in most genera. Choanocyte chambers are large, spherical and diplodal. The matrix is only very lightly infiltrated with collagen and appears fibrous macroscopically rather than fleshy. Cyanobacteria are always incorporated. Phyllospongiinae are also characterised by a secondary metabolite compliment which includes a series of unique bishomoscalaranes (Bergquist, Sorokin & Karuso, 1999).

## Scope

There are 5 genera in this subfamily, with 31 nominal species.

## KEY TO GENERA

(1)	Dermis moderately to heavily armoured	2
	Dermis unarmoured, or with patchy sand crust (but not true armour)	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 distinct armour) present on one or both faces; primary fibres perpendicular to surface; tough and	
	flexible	Phyllospongia
	Fasciculate primary fibres; primary fibres meandering; soft and fleshy	Lendenfeldia

## PHYLLOSPONGIA EHLERS, 1870

## Synonymy

*Phyllospongia* Ehlers, 1870: 30; Bergquist, 1980b: 454; Bergquist, Ayling & Wilkinson, 1988: 302. *Mauricea* Carter, 1877d: 174.

## Type species

*Spongia papyracea* Esper, 1806 (by subsequent designation; Burton, 1934a).

## Definition

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

## Diagnosis

Lamellate, vasiform, digitate or foliose sponges (Fig. 7C–F), typically thin-walled, with an unarmoured, smooth, irregularly corrugated, micro-conulose surface. The fibre skeleton comprises a regular reticulation of primary ascending, secondary connecting, and vermiform tertiary fibres. Primary fibres are axially cored with foreign debris, secondary and vermiform tertiary fibres are uncored. Secondary fibres may dominate the fibre skeleton in some species, particularly those with a thicker habit. Vermiform tertiary fibres are sometimes dispersed throughout the mesohyl, but are more typically arranged as an axial skeleton, particularly in the base and stalk. In digitate forms they can form fascicles, arranged in a similar orientation to secondary fibres. A sand cortex is usually present on one or both surfaces, but it never becomes a distinct sand armour, as seen in *Carteriospongia* and *Strepsichordaia*. The consistency is tough and flexible.

## **Previous reviews**

Bergquist, 1980b; Bergquist, Ayling & Wilkinson, 1988; Hooper & Wiedenmayer, 1994.

## **Description of type species**

Phyllospongia papyracea (Esper) (Fig. 7C-D).

Synonymy. Spongia papyracea Esper, 1806: 38. Phyllospongia papyracea Ehlers, 1870: 22; Hyatt, 1877: 543; Ridley, 1884a: 593; Lendenfeld, 1889a: 184; Dendy, 1905: 21; Burton, 1934a: 572; de Laubenfels, 1948: 45, pl. 8 fig. 17; Bergquist, 1980b: 454; Bergquist, Ayling & Wilkinson, 1988: 304, figs 13–17, 29. *Phyllospongia coriacea* Thiele, 1899: 27.

*Material examined.* Holotype: BMNH 1931.4.1.1a (dry – fragment). Other material. Authors collections, including: SDCC/ RF009 (*lamellosa*) (see also Bergquist, Ayling & Wilkinson, 1988).

**Description (from Bergquist, Ayling & Wilkinson, 1988).** Extremely thin body, 1.0–2.0 mm thick, typically flat, strap-like lamella, with many lamellae arising from a single stalk up to approximately 20 mm in diameter. Another common growth form is a stalked fan which produces the rounded strap-like extensions marginally. The sponge surface is always smooth, never macroscopically showing any grooves or organised pore areas. The oscules are small and flush with the surface which, under low magnification, is regularly conulose. Externally, this species is beige to fawn, turning white in alcohol. (See generic diagnosis for skeletal details).

**Remarks.** The term 'tertiary fibres', applied to the fine vermiform fibres, is used here in a different sense to its more traditional application, in which case it refers to the very fine fibres which occur with the meshes of the secondary fibre reticulum, as seen in genera such as *Luffariella* and *Fenestraspongia*. In Phyllospongiinae they are tertiary fibre filaments arising from the secondary skeleton and meandering throughout the mesohyl. Six species are known.

## Distribution

India (type locality), Indo-Pacific, Red Sea.

#### CARTERIOSPONGIA HYATT, 1877

#### Synonymy

*Carteriospongia* Hyatt, 1877: 540; Bergquist, 1980b: 454; Bergquist, Ayling & Wilkinson, 1988: 294. *Polyfibrospongia* Bowerbank, 1877: 459. [*Carterispongia*] Ridley, 1884a: 385 (lapsus).

## Type species

Spongia foliascens Pallas, 1766 (by subsequent designation; Burton, 1934a).

## Definition

Heavily armoured Phyllospongiinae, with an undulating surface, and unorganised vermiform tertiary fibres in the mesohyl.

## Diagnosis

Lamellate, foliose, caliculate and spreading forms are typical (Fig. 7G–I), though variable. The surface is heavily armoured with foreign debris and displays a characteristic pattern of mounds or ridges (Fig. 7J), that tend to be more pronounced on the oscular face. The relatively dense, irregular fibre skeleton comprises primary, secondary and tertiary fibres. Primary fibres are heavily cored, and may form strong fascicles in the subsurface region; primary fibres do not necessarily comprise the ascending component of the skeleton, at times tending to be more disorganised. The secondary fibres may be difficult to distinguish, being without orientation to primary fibres, and are either cored or uncored. More prominent are long, thin vermiform tertiary fibres which branch and rejoin, creating a tangled network of fine fibres. These vermiform fibres meander throughout the sponge without any apparent orientation. The consistency is coarse and flexible.

#### **Previous reviews**

Bergquist, 1980b; Bergquist, Ayling & Wilkinson, 1988; Hooper & Wiedenmayer, 1994.

#### **Description of type species**

Carteriospongia foliascens (Pallas) (Fig. 7G-H).

Synonymy. Spongia foliascens Pallas, 1766: 365. Spongia otahitica Esper, 1797: 209. Carteriospongia otahitica Hyatt, 1877: 541; Ridley, 1884a: 385. Phyllospongia foliascens Lendenfeld, 1889a: 196, pl. 5 fig. 3, pl. 6 figs 1, 3–4, 10, pl. 7 fig. 11, pl. 14 fig. 2, pl. 24 fig. 6; de Laubenfels, 1948: 48, pl. 10 fig. 20; Bergquist, 1965: 131, figs 3a–b. Carteriospongia foliascens Burton, 1934a: 573; Bergquist 1980b: 454, figs 5e–f; Bergquist, Ayling & Wilkinson, 1988: 294, figs 2–5; Hooper & Wiedenmayer, 1994: 378.

*Material examined.* Neotype: BMNH 1925.11.1.411. Other material. Authors collections, including: SDCC/RF003 (*contorta*); SDCC/RF018 (*contorta*) (see also Bergquist, Ayling & Wilkinson, 1988).

Description (from Bergquist, Ayling & Wilkinson, 1988). Easily recognised by the coarse, verrucose nature of both inhalant and exhalant surfaces of the lamellate body. These surface nodules or verrucae, which are formed by brushes of short primary fibres, break the surface into uneven sand-encrusted islands between which exhalant and inhalant canals run. This fibre conformation and resultant fibre morphology occurs on both surfaces, but the nodules are more pronounced on the oscular surface. The skeleton consists of coarse irregular primary fibres that break into brushes near the surface, but which otherwise are disposed with irregular orientation to the surface. There is a very reduced secondary skeleton of uncored fibres and these connect primary elements. Thin elongate vermiform fibres arise from both primary and secondary fibres and form a tangled web throughout the sponge.

**Remarks.** Hooper & Wiedenmayer (1994) regard the neotype designation as invalid, (under ICZN Article 75d(3); Anon., 1999), as Burton failed to present his reasons for believing the holotype was lost; no alternative to this specimen was however proposed. We were also unable to locate the holotype, despite several searches of the Natural History Museum (London) collections since 1965. Consequently, the neotype designation made by Burton (1934a) is reaffirmed here. A notable difference from *Phyllospongia* is the density and tangled nature of the accessory skeleton (Bergquist, 1980b). Eleven species are known.

## Distribution

India (type locality), Indo-Pacific, Red Sea.

#### LENDENFELDIA BERGQUIST, 1980

#### Synonymy

Lendenfeldia Bergquist, 1980b: 456.

## Type species

*Phyllospongia dendyi* var. *frondosa* Lendenfeld, 1889 (by original designation).

#### Definition

Unarmoured Phyllospongiinae of lamellate form. These sponges have tertiary skeletal fibres of the usual thorectid type, and have a soft, fleshy consistency.

## Diagnosis

Lamellate or lamello-digitate forms (Fig. 8A–B), with an unarmoured, finely conulose surface. The skeleton comprises primary, secondary and tertiary fibres (Fig. 8C). Primary fibres are cored with debris, are often fasciculate, and tend to be meandering, rather than clearly arranged as ascending fibres. Secondary and tertiary fibres are uncored, and form an irregular mesh. The tertiary fibre skeleton is not as fine as that of *Fenestraspongia*, nor as dense as in either *Luffariella* or *Fenestraspongia*. The consistency is soft, compressible and fleshy.

#### **Previous reviews**

Bergquist, 1980b; Hooper & Wiedenmayer, 1994; Bergquist, Sorokin & Karuso, 1999.

#### **Description of type species**

Lendenfeldia frondosa (Lendenfeld) (Fig. 8A).

Synonymy. Phyllospongia (Antheroplax) dendyi var. frondosa Lendenfeld, 1889a: 178, pl. 14 fig. 5. Lendenfeldia frondosa Bergquist, 1980b: 456, fig. 6a.

*Material examined.* Lectotype: BMNH 1877.5.21.1697. Other material. Authors collections, including: SDCC/RF088 (*chondrodes*).

**Description (See generic diagnosis).** There is no full description of this species available. While *L. frondosa* is readily identifiable, the lectotype is dry, and the species has not apparently been collected for some time. A full redescription will not be possible until fresh specimens become available.

*Remarks.* Wiedenmayer (in Hooper & Wiedenmayer, 1994) suggested that the type species, *Phyllospongia dendyi* var. *frondosa* Lendenfeld, 1889, may be a synonym of *Spongia plicata* Esper, 1806, another species now recognised as *Lendenfeldia*, although



**Fig. 8.** Lendenfeldia, Strepsichordaia and Candidaspongia. A, Lendenfeldia frondosa, holotype BMNH 1877.5.21.1697. B, L. torresia, BMNH 1893.3.4.14. C, L. typica, fibre skeleton, showing fine tertiary fibres. D–F, Strepsichordaia lendenfeldi. D, holotype AM Z5026. E, paratype AM Z5027, showing characteristic stellate pattern of exhalant canals. F, fibre skeleton, SDCC/RF004. G–I, Candidaspongia flabellata. G, holotype QM G25081. H, flat specimen. I, fibre skeleton (G–I, reproduced with permission from Bergquist, Sorokin & Karuso, 1999).

no reason was given. This view is not upheld here. Ten species are known.

#### Distribution

Indo-West Pacific.

# STREPSICHORDAIA BERGQUIST, AYLING & WILKINSON, 1988

## Synonymy

*Strepsichordaia* Bergquist, Ayling & Wilkinson, 1988: 314; Hooper & Wiedenmayer, 1994: 394.

## Type species

*Strepsichordaia lendenfeldi* Bergquist, Ayling & Wilkinson, 1988 (by original designation).

## Definition

Heavily armoured Phyllospongiinae, 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.

## Diagnosis

Caliculate, lamellate or foliose sponges (Fig. 8D–E), with a characteristically smooth, heavily armoured surface. Small, flush

oscules are evenly distributed over the oscular face, each at the centre of a stellate pattern created by superficial exhalant canals. The poral face is smooth. The irregular fibre skeleton comprises primary, secondary and tertiary fibres (Fig. 8F). Primary fibres are simple and branching, not fasciculate, and are heavily cored with foreign debris. Secondary fibres are similar in size and coring to the primary fibres, and are only distinguishable by their orientation to the surface. The long, uncored, vermiform tertiary fibres arise from both primary and secondary, forming a dense mat which dominates the fibre skeleton. These fibres meander for considerable distances without branching, have no fixed orientation, do not form fascicles, and only occasionally interconnect. The consistency is firm, tough, flexible, and barely compressible.

#### **Previous reviews**

Bergquist, Ayling & Wilkinson, 1988; Hooper & Wiedenmayer, 1994; Bergquist, Sorokin & Karuso, 1999.

#### **Description of type species**

*Strepsichordaia lendenfeldi* Bergquist, Ayling & Wilkinson (Fig. 8D–F).

*Synonymy. Strepsichordaia lendenfeldi* Bergquist, Ayling & Wilkinson, 1988: 314, figs 30–32; Hooper & Wiedenmayer, 1994: 395.

*Material examined.* Holotype: AM Z5026. Other material. Authors collections, including: SDCC/RF127 (*lendenfeldi*).

Description. Upright lamellae or bowls, up to 400 mm high; lamellae walls are 4-5 mm thick. The poral surface is smooth, while the oscular surface is patterned with regularly-spaced oscules 0.5-2.0 mm in diameter, each with exhalant canals radiating in a stellate pattern. The surface is armoured, and the cortex is reinforced with collagen deposits. Primary fibres are simple, heavily cored with coarse debris, and arranged on a quasi-rectangular plan; primary fibres extend into microconules at the surface. Secondary fibres are distinguishable only in their relation to the surface, not on their dimensions or coring. Primary and secondary fibres dimensions vary with the nature of coring material between 50-250 µm. Thin, cylindrical, homogeneous (unlaminated), vermiform fibres,  $15-30 \,\mu\text{m}$  in diameter, which arise from both primary and secondary fibres, are a dominant element of the skeleton and run throughout the sponge as a dense intertwined skeleton. The choanocyte chambers, 30-50 µm in diameter, are oval and diplodal. The sponge is firm and pliable, but incompressible. External colouration is pale grey to beige, while internally they are fawn.

**Remarks.** The features stressed in recognising *Strepsichor*daia are the oscular surface morphology, with a regular stellate pattern of exhalant canals in conjunction with lamellate to vasiform shape, and a dominant, filamentous vermiform fibre skeleton ramifying through the entire sponge. This genus may be difficult to distinguish from *Coscinoderma*. In this case, the most distinctive recognition character is the consistency, where *Strepsichordaia* is firm, tough and flexible in contrast to the soft and compressible *Coscinoderma*, and fibre structure. Three species are known.

## Distribution

Great Barrier Reef, Australia (type locality), Madagascar, Philippines.

## CANDIDASPONGIA BERGQUIST, SOROKIN & KARUSO, 1999

#### Synonymy

Candidaspongia Bergquist, Sorokin & Karuso, 1999: 59.

## Type species

*Candidaspongia flabellata* Bergquist, Sorokin & Karuso, 1999 (by original designation).

## Definition

Heavily armoured Phyllospongiinae, that are brilliant white in colour. These sponges are without tertiary fibres.

#### Diagnosis

Lamellate sponges, with a slightly roughened oscular face and a finely conulose poral face (Fig. 8G–H). The surface is heavily armoured with sand, which is consistent in its size and composition, producing a brilliant white colour. The regular fibre skeleton comprises cored, simple primary fibres, and uncored secondary fibres which form a polygonal network (Fig. 8I). The consistency is firm, flexible and compressible. The wide mouthed, spherical choanocyte chambers are notably large for Thorectidae.

#### **Previous review**

Bergquist, Sorokin & Karuso, 1999.

## **Description of type species**

*Candidaspongia flabellata* Bergquist, Sorokin & Karuso (Fig. 8G–I).

*Synonymy.* Candidaspongia flabellata Bergquist, Sorokin & Karuso, 1999: 59.

*Material examined.* Holotype: QMG25081. Other material. Authors collections.

Description. Monospecific (see generic diagnosis). The sponge is a slightly concave, erect fan or a concave plate with a broad base of attachment. The lamella is most frequently simple but small fan-like accessory lobes are sometimes located near the base. The body is 3.0-4.5 mm thick, up to 25 cm high and 35 cm wide. Oscular and poral faces are differentiated. The oscular face is thrown into very low rounded mounds. The poral surface is very finely conulose with rows of conules following the line of the underlying primary fibre tracts. Near the edge of the fan this produces a very regular pattern which is enhanced in dry specimens. Oscules are flush with the surface, 0.1-1.5 mm diameter and scattered evenly over the entire face. The pores make up an even delicate network over the entire poral face and are 0.1-0.3 mm diameter. The colour in life is brilliant white out of water and in ethanol, golden brown internally. A slight purplish tinge can develop, resulting from leaching cyanobacteria pigments. Dry specimens are cream externally, pale golden brown internally. The texture is firm, pliant and compressible, dry to the touch with no mucus exuded in life or on collection. The skeleton is a network of slender, uncored secondary fibres with irregular mesh extending between thin, cored primary fibres which are evenly spaced 1-2 mm apart and which run from the attachment base to the margin of the sponge. Primary fibres are 65–120  $\mu m$  in diameter, and secondaries are 30–69  $\mu m$ . The surface of the secondary fibres has a fine braided texture. These sponges are only lightly infiltrated with collagen. Choanocyte chambers are spherical to oval, 50–90  $\mu m$  in longest dimension, with a wide mouth.

## Distribution

Great Barrier Reef, Australia (type locality). There are also unverified reports of this sponge from the Philippines (Bergquist *et al.*, 1999).