

## Revision of the marine sponge genus *Caulospongia* Saville Kent, 1871 (Demospongiae: Hadromerida). Part 1. Morphological and skeletal characters

Jane Fromont

Department of Aquatic Zoology, Western Australian Museum, Francis Street, Perth,  
Western Australia 6000, Australia. Email: fromont@museum.wa.gov.au

**Abstract** – The sponge genus *Caulospongia* is reviewed and redefined to accommodate eight closely related species that belong to the genus. Four new species, *Caulospongia amplexa*, *C. reticulata*, *C. venosa* and *C. biflabellata* are described, and *C. pennatula* (Lamarck, 1814), *C. perfoliata* (Lamarck, 1814), and *C. plicata* Saville Kent (1871) are redescribed with reference to the type specimens and new material. *C. elegans* (Lendenfeld, 1888) is redescribed from the type material. The scope of the genus is discussed with respect to morphological and skeletal characters and its location within the family Suberitidae is confirmed in the light of these characters. As a consequence of examination of type material the synonymy of the genus *Plectodendron* Lendenfeld (1888) with *Caulospongia* Saville Kent (1871) is confirmed. A preliminary assessment is made of the biogeography of the genus, which is predominantly Western Australian.

### INTRODUCTION

In 1814, Lamarck described *Spongia perfoliata* and *S. pennatula*, two species of stalked sponges with an unusual foliaceous morphology. Their common feature was to have a sponge body composed of leaf-like lobes around a central stem. Subsequently, Saville Kent (1871) established a new genus *Caulospongia* for two species he described: *C. verticillata* and *C. plicata*. He established the genus for sponges with a central stem surrounded by leaf-like whorls or spiral convolutions and with a skeleton of fibre and spicules.

Saville Kent did not mention the material described by Lamarck (1814) and it is assumed that he was unaware that species had previously been described that were congeneric with *C. verticillata* and *C. plicata*. Bowerbank (1876) also failed to refer to previous publications that described species with this unusual morphology when he described a specimen collected from Fremantle, Western Australia as *Chalina verticillata*. Topsent (1932) noted this incredible lack of knowledge of earlier published references by both Saville Kent and Bowerbank when he redescribed Lamarck's species.

Meanwhile, in 1888, Lendenfeld had defined another new genus *Plectodendron* with the type species *P. elegans* collected on the New South Wales coast. This genus was closely related to *Caulospongia* as it had tylostyles for spicules and fibre in the skeleton, but in this genus the sponge body extended from a central stalk into a regular

branching network, and bore no resemblance to the three dimensional whorls characteristic of *Caulospongia*. When Hallmann (1914) redescribed *P. elegans* he synonymised *Plectodendron* with *Caulospongia* on the basis of identical skeletal and spicule morphology. Since this time no further work has been carried out on these unusual sponges. Hooper (1984) mentioned a specimen of *C. perfoliata* collected from the Timor Sea, and Hooper and Wiedenmayer (1994) retain the synonymy of *Plectodendron* with *Caulospongia* and list three valid species,

1. *C. elegans* (Lendenfeld, 1888)
2. *C. pennatula* (Lamarck, 1814)
3. *C. perfoliata* (Lamarck, 1814) with the synonyms:  
*C. plicata* Saville Kent, 1871  
*C. verticillata* Saville Kent, 1871  
*Chalina verticillata* Bowerbank, 1876

Some questions became obvious as a consequence of the review of the literature on these sponges summarised above.

- Should the genus *Plectodendron* remain synonymised with *Caulospongia*?
- How many valid species of *Caulospongia* are there?
- Is the family Suberitidae, order Hadromerida, the most appropriate taxon for the genus?

Examination of the collections at the Western Australian Museum found 12 wet specimens and numerous dry specimens of *Caulospongia*; the latter are beachwash material and in a condition too poor for descriptive purposes. Beachwash specimens of

*Caulospongia* are regularly found on local Perth beaches after winter storms. Five additional wet specimens have since been added to the collection, with good *in situ* colour photographs and habitat descriptions. Four of these specimens were collected from the South West coast (K. Bancroft and CALM; J. Fromont) and the other from the Abrolhos Islands (J. Fromont). The abundance of preserved material indicated the prevalence of the genus in WA waters, and prompted a redescription and re-evaluation of species. This examination immediately indicated a suite of problems, the first being to determine how many species were represented in the WAM collections, with the second and related problem being the ability to discriminate precisely between these morphologically similar species. Finally, defining the boundaries of the genus *Caulospongia* also appeared to be very complex. As an aid to resolving these problems additional material was loaned from the Northern Territory Museum of Arts and Sciences, the South Australian Museum, and the Queensland Museum. The total number of wet specimens available for examination was 37, and all available type material was also examined (Table 1).

#### MATERIALS AND METHODS

Material from various museums (listed at the end of this section) was examined during the course of this study. Wet specimens were preserved in 70% ethanol. Skeletal structure and spicule morphology were examined using light microscopy. Spicules were prepared by boiling small pieces of sponge, including ectosome and choanosome, in

concentrated nitric acid, followed by two consecutive washes of distilled water and two of absolute alcohol. Spicule extracts were dried on a glass slide and mounted in DePeX, Gurr Products. Spicule measurements are based on 15 spicules per specimen selected at random. The skeleton was prepared by cutting a representative section at right angles to the surface of the sponge, dehydrating it through an ascending ethanol series, clearing in xylene and infiltrating in paraffin wax (Histoplast, Shandon Elliot) using an automatic tissue processor on a nine hour cycle. The sponge tissue was further infiltrated with paraffin under a vacuum of 635mm Hg for 30 minutes prior to embedding. Blocks were sectioned at 90 µm thickness with a Leitz slide microtome, and section rolling was eliminated by placing filter paper, moistened with distilled water, on top of the paraffin block. Sections were placed on a glass slide smeared with egg albumin for adhesion, dried overnight at 60°C and dehydrated in two changes of xylene. They were mounted with Eukitt, Agar Scientific.

Abbreviations used in the text: AIMS/NCI, Marine Bioproducts Group, Australian Institute of Marine Science, (Zoological collections now housed in the QM, Brisbane); AM, Australian Museum, Sydney; BMNH Natural History Museum, London; CALM, Department of Conservation and Land Management, Perth; MNHN, Museum National d'Histoire Naturelle, Paris; NTM, Northern Territory Museum of Arts and Sciences, Darwin; QM, Queensland Museum, Brisbane; SAM, South Australian Museum, Adelaide; WAM, Western Australian Museum, Perth.

**Table 1** Type material relevant to this study.

SPECIES	AUTHOR/YEAR	LOCALITY	MATERIAL EXAMINED	NOTES
<i>Spongia perfoliata</i>	Lamarck, 1814	Seas of Australia (Peron & Leseur)	Holotype: MNHN LMIM DT 3368, dry	
<i>Spongia pennatula</i>	Lamarck, 1814	Shark Bay, WA (Peron & Leseur)	Holotype: MNHN LBIM DT 583, dry	
<i>Caulospongia verticillata</i>	Saville Kent, 1871	North Australia	Not examined, Type destroyed	
<i>Caulospongia plicata</i>	Saville Kent, 1871	No locality data	Holotype: BMNH 1870:12:22:2, dry	Beachwash specimen
<i>Chalina verticillata</i>	Bowerbank, 1876	Fremantle, WA	Holotype: BMNH 1877:5:21:6, dry	Beachwash specimen
<i>Plectodendron elegans</i>	Lendenfeld, 1888	Broughton Island, NSW	Lectotype: AM G9186, wet	
<i>Plectodendron elegans</i>	Lendenfeld, 1888	Port Jackson, NSW	Paralectotype: AM Z5221, wet	
<i>Plectodendron elegans</i>	Lendenfeld, 1888	Port Jackson, NSW	Paralectotype: AM Z5271, dry	fragments

## SYSTEMATICS

## Order Hadromerida

## Diagnosis

Megasclere skeletons composed of monactinal spicules which are usually tylostyles, subtylostyles, or styles. A size and locational distinction is usually found in the megascleres with peripheral megascleres smaller than choanosomal ones. A radial construction occurs in the outer layers but may not occur internally. Microscleres, if present, are euasters or derivatives thereof [abbreviated from Hartman (1982)].

## Remarks

The Hadromerida is a relatively well defined order although in some families the simplicity of skeletal characters makes lower taxonomic level determinations difficult due to the paucity of characters with which to work. The Suberitidae is the least complex family of the order in terms of skeletal architecture.

## Family Suberitidae Schmidt, 1870

## Diagnosis

The radial arrangement of the skeleton is evident only at the surface. The spicules have confused orientation in the deeper regions of the sponge, but in a few cases may assume a loose axial orientation. Species of this family do not commonly have a differentiation of megascleres into size categories or a restriction of megascleres to particular localities in the sponge.

## Remarks

Lendenfeld (1888) located *Plectodendron* in the Suberitidae and Hallmann (1914) did the same with the genus *Caulospongia*. The definition of this family has recently been examined by Voultziadou-Koukoura and van Soest (1993) where they noted that the majority of previous authors who had defined the family on morphological characters agreed that the confused orientation of the choanosomal skeleton was characteristic. However, they noted that the skeletons of *Rhizaxinella* spp. and of *Suberites massa* are well organised with an axial component. An organised choanosomal skeletal arrangement also occurs in the genus *Caulospongia*. There are additional skeletal characters that *Caulospongia* has in common with other genera of the Suberitidae. For instance, surface brushes of spicules found in *Suberites* and *Laxosuberites*, and two characters found in most genera of this family: a single megasclere size category, and a lack of surface papillae. *Caulospongia* is one of the few genera in the Suberitidae that has erect growth forms, the others

being some species of *Suberites* such as *S. massa* which is branching and erect and the genus *Rhizaxinella* which has a globular, ovoid, cylindrical, or branching morphology with a basal stalk. Most of the genera of this family are small mounds or balls (e.g. *Aptos*) massive forms (e.g. some species of *Laxosuberites* and *Suberites*) or thin encrustations (e.g. *Terpios*, *Prosuberites*, and some species of *Laxosuberites*). Rützler and Smith (1993) noted that the family Suberitidae contained genera distinguished by shape of the adult sponge, by skeleton structure, and by spicule orientation, type and distribution.

In summary, the genus *Caulospongia* is most appropriately located within the family Suberitidae. The genus has simple spiculation, one size category of tylostyles, and surface brushes of spicules. The genus is unusual within this family in having a well organised choanosomal skeleton of fibre and spicules with a central axial component.

*Caulospongia* Saville Kent

*Caulospongia* Saville Kent, 1871: 616.

*Plectodendron* Lendenfeld, 1888: 66.

## Type species

of *Caulospongia*: *Caulospongia verticillata* Saville Kent, 1871 (junior synonym of *Caulospongia perfoliata* (Lamarck, 1814)) by subsequent designation of Hallmann (1914).

of *Plectodendron*: *Plectodendron elegans* Lendenfeld, 1888 by monotypy.

## Diagnosis

Sponges of erect morphology with a solid basal stem and either a lobed or interlocking, reticulate branching morphology, or erect fans. Spicules are a single category of tylostyles; there are no microscleres. The choanosomal skeleton is a plumo-reticulate or reticulate network of fibre cored with spicules; interstitial spicules are present. The ectosomal skeleton consists of spicule fans or brushes with a narrow or diffuse layer of spicules parallel to the surface and overlying the brushes.

## Remarks

Burton (1930) designated *Caulospongia plicata* as "genoelectotype" but this is an invalid designation, which was predated by Hallmann (1914) who designated *C. perfoliata* as the type of the genus. *C. elegans*, the sole species described in the genus *Plectodendron*, has identical skeletal characters to species assigned to the genus *Caulospongia*. It differs from species of *Caulospongia* only in its external morphology. In this study the redefinition of the genus *Caulospongia* accommodates sponges

with a reticulate branching structure previously assigned to the genus *Plectodendron*.

*Caulospongia perfoliata* (Lamarck)

Figures 1a–d; 2a–d; 3

*Spongia perfoliata* Lamarck, 1814: 439.

*Caulospongia perfoliata* (Lamarck): Hallmann, 1914: 306, plate 18, figure 1; Topsent, 1932: 85, plate 3, figure 4; Hooper and Wiedenmayer, 1994: 405.

*Caulospongia verticillata* Saville Kent, 1871: 616, pl. 48, figure 1.

*Chalina verticillata* (Saville Kent): Bowerbank, 1876: 769, pl. 79.

**Material Examined**

*Holotype*

MNHN LBIM DT 3368, "Australian seas" (precise locality unknown).

*Other material*

**Australia: Western Australia:** BM 1877:5:21:6, specimen of *Chalina verticillata* (Bowerbank, 1876), Fremantle, 32°04'S, 115°45'E; WAM Z57 West of City Beach, Station 12, 31°56'S, 115°38'E, 29 m depth, 12 October 1976, coll. L. Marsh *et al.* on RV Flinders; WAM Z58 Point Hood Reef, 33°57'S, 120°06'E, 26.8 m depth, 18 March 1997, coll. K. Bancroft, SCUBA; WAM Z59 Stream Bay, 34°29'S, 119°17'E, 11.5 m depth, 13 March 1997, coll. K. Bancroft, SCUBA; QM G310964 N. side 0.5 nm NW Charlotte Pt., Rottnest Is. 31°59'S, 115°29'E, 16 m depth, 14 March 1989, coll. AIMS/NCI, SCUBA.

**Diagnosis**

This species is characterised by having large and irregular lobes that are thick and firm. The surface has an adherent dermal membrane. The lobes of *C. perfoliata* circumvolve a central axial hollow stem and they do not encircle the axis in one complete whorl as found in *C. amplexa*. A consistent character for this species is that the lobes turn upwards at their outer edges. This species is most like *C. amplexa* and *C. reticulata*. However, the former species has more regular, smaller and softer lobes, and the latter species is characterised by having branches that form reticulate cross branches, not seen in either *C. perfoliata* or *C. amplexa*.

**Description**

*Shape:* Sponges with firm, basal stems and wide, spreading, irregularly shaped lobes (Figure 1a–d). Stem within lobes is hollow. Lobes slope upwards towards the apex of the sponge.

*Dimensions:* 30–36 cm in height, stem below lobes

5.5–13 cm in length, sponge body with lobes 20–25 cm x 6–9 cm across at the widest point in the middle of the sponge body axis. Lobes are 0.3–0.5 cm thick.

*Colour:* Cream, yellow or pale yellow orange, QM G310964 pale salmon pink alive darkening to orange on collection; fawn in alcohol.

*Oscules:* Oscular canals visible over basal stem. Both surfaces of the lobes are porous, with more pores on the lower surface.

*Texture and surface characteristics:* Specimens are very firm but compressible. The surface has a dermal membrane.

*Ectosome and subectosome:* Fans consisting of a few spicules occur at the surface with a thick parallel layer of spicules beneath. This surface skeleton is 90–150 µm thick.

*Choanosome:* Beneath the ectosomal layer, tracts of spicules support the fans and in the centre of the sponge the skeleton becomes plumoreticulate (Figure 2a–d). Thick primaries, 60 µm across, are packed with ~5 spicules and surrounded by a fibre sheath. Some dark pigment occurs over the primary fibre. The secondary fibres are 30 µm wide and cored by 2–4 spicules. The basal stem has a dense fibre skeleton with dark pigmentation over yellow fibre. Fibres are up to 320 µm wide and are sparsely cored by spicules. Some of the fibres are fasciculate. Secondary fibres in the basal stem are thinner, 40–60 µm wide. A dense layer of spicules occurs parallel to the surface of the stem with few spicule fans.

*Megascleres:* (Figure 3). Tylostyles with flat nail heads frequently double or multi-bulbed. See Table 2 for dimensions.

**Remarks**

Material of this species that had been described by previous authors was examined, and conformed to the redescription presented above. Only a fragment of the type material (MNHN LBIM DT3368) was available and included the basal stalk and first basal lobe (Figure 1a). This specimen has an ectosomal skeleton of spicules at right angles to the surface with a layer of tangential spicules beneath, and towards the centre of the sponge fibre

**Table 2** Spicule measurements (µm) of specimens of *Caulospongia perfoliata* are given as minimum-mean-maximum (n=15).

Material	Tylostyles
MNHN LBIM DT 3368	118–166–200 x 2.5–5.0–7.5
BM 1877:5:21:6	130–179–208 x 4–4.9–5.0
WAM Z57	135–179–205 x 5–5.8–8.5
WAM Z58	145–179–203 x 5–6.5–10
WAM Z59	140–175–210 x 4–6.5–9
QM G310964	175–197–215 x 6.5–7.9–10

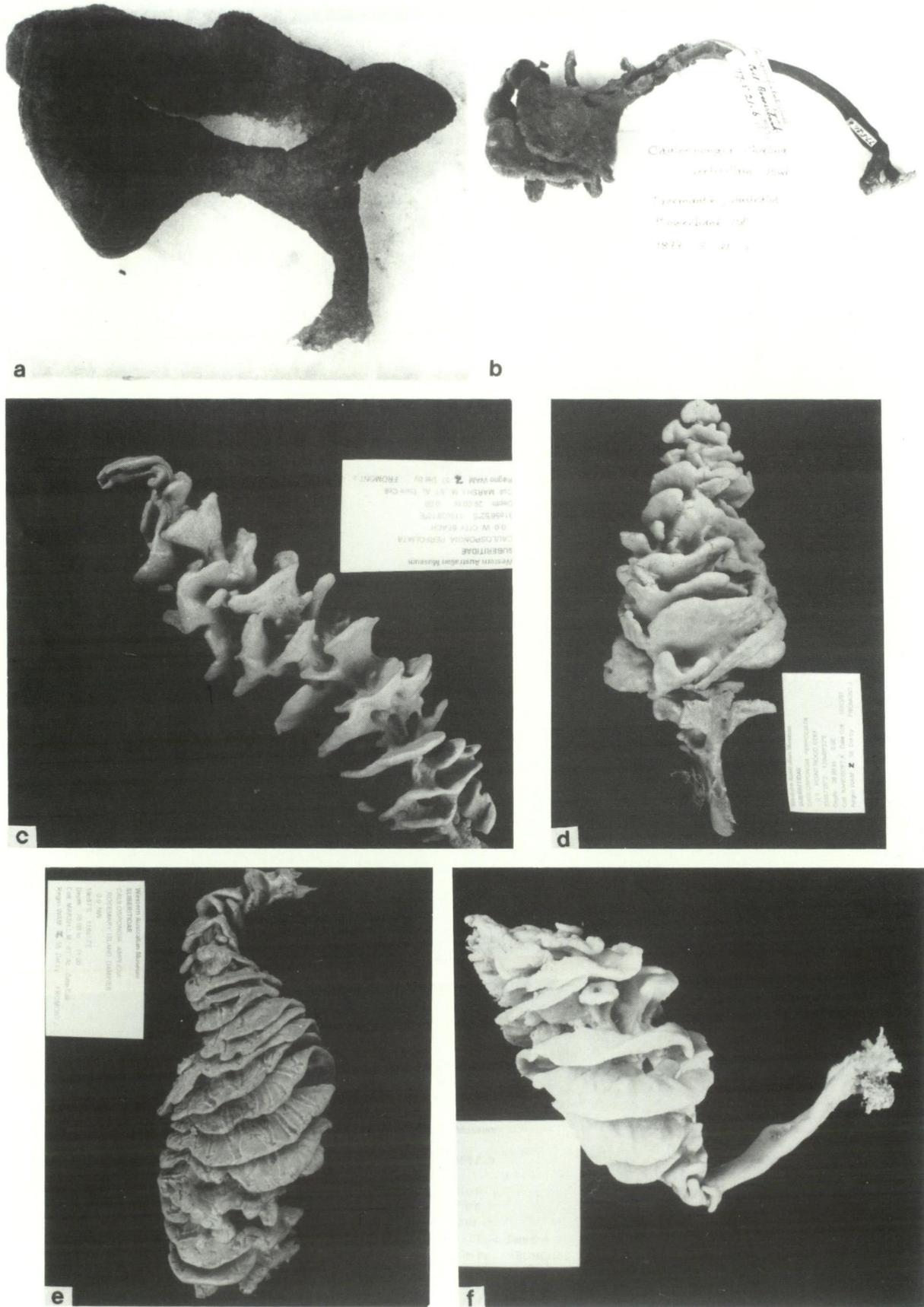
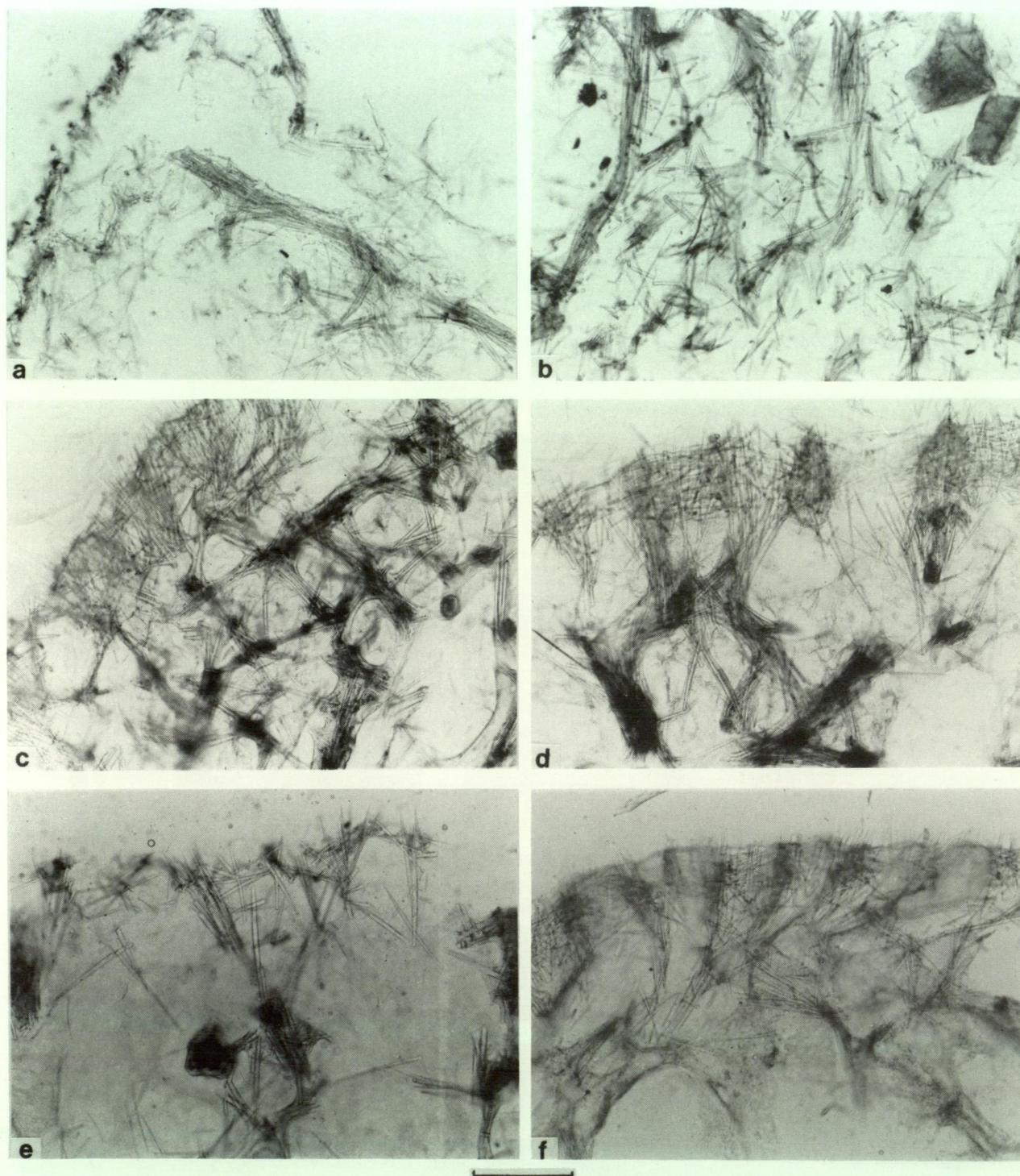


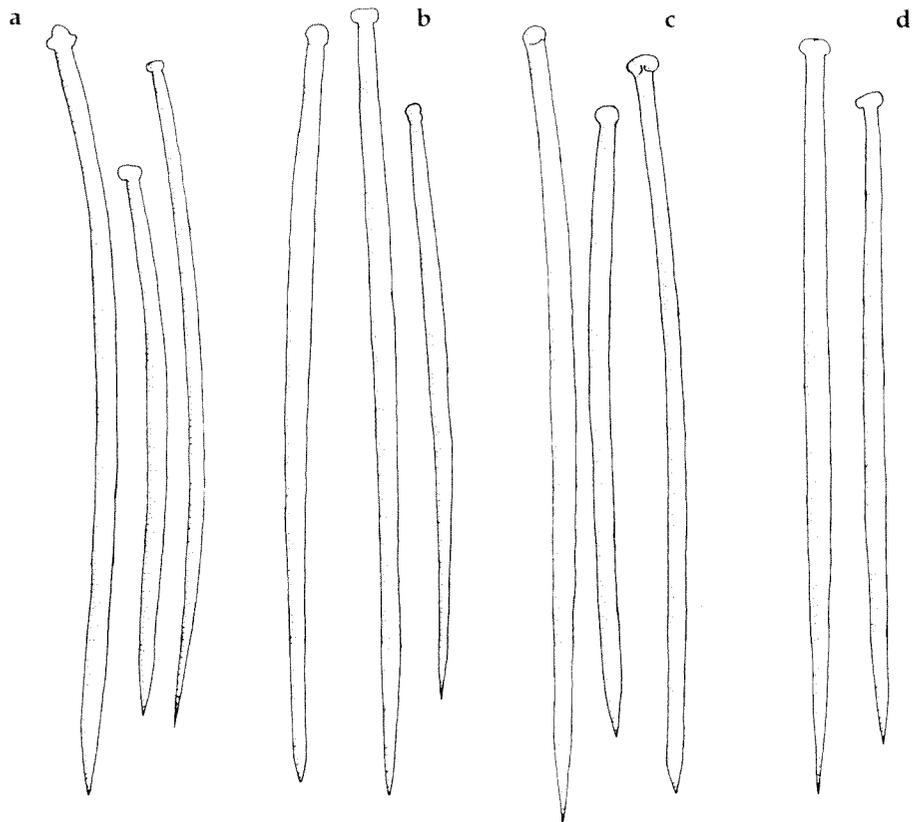
Figure 1 Photographs of whole specimens: a, *Caulospongia perfoliata* (Lamarck, 1814), MNHN LBIM DT 3368, fragment of basal lobe with stalk; b, *Caulospongia perfoliata* (Lamarck, 1814), specimen of *Chalina verticillata* of Bowerbank, 1876 BM 1877:5:21:6, part of lobes and stalk; c, *Caulospongia perfoliata* (Lamarck, 1814) WAM Z57, with upward directed lobes; d, *Caulospongia perfoliata* (Lamarck, 1814) WAM Z58, with upward directed lobes; e, *Caulospongia amplexa* sp. nov., holotype WAM Z55, showing downturned lobes; f, *Caulospongia amplexa* sp. nov. Paratype WAM Z56, with downturned lobes.



**Figure 2** Photographs of skeletal organisation: a, *Caulospongia perfoliata* (Lamarck, 1814), Holotype, MNHN LBIM DT 3368, showing surface on lhs and fibre development beneath; b, *Caulospongia perfoliata* (Lamarck, 1814), specimen of *Chalina verticillata* of Bowerbank, 1876 BM 1877:5:21:6, reticulate spicule and fibre skeleton; c, *Caulospongia perfoliata* (Lamarck, 1814) WAM Z57, with well developed surface spicule brushes and fibre reticulation beneath; d, *Caulospongia perfoliata* (Lamarck, 1814) WAM Z58, layer of spicules parallel to surface overlies surface spicule fans; e, *Caulospongia amplexa* sp. nov., holotype WAM Z55, surface skeleton uppermost with fibre development beneath; f, *Caulospongia amplexa* sp. nov., paratype WAM Z56, surface skeleton at top and tracts beneath. Scale bar = 200  $\mu$ m.

development is apparent with fibres that are 80  $\mu$ m thick and cored by 5–10 spicules. The skeleton is plumoreticulate and sometimes fasciculate centrally. The tylostyles have flattened, or

occasionally, "knobbly" heads, frequently curved along the shaft and thickest in mid-axis. The drawing of the complete specimen in Topsent (1932: plate 3, Figure 4) is of an erect sponge with



**Figure 3** Spicules of *Caulospongia perfoliata* (Lamarck, 1814): a, MNHN LBIM DT 3368; b, Spicules of *Caulospongia perfoliata* (Lamarck, 1814), specimen of *Chalina verticillata* of Bowerbank, 1876 BM 1877:5:21:6; c, Spicules of *Caulospongia perfoliata* (Lamarck, 1814), WAM Z57; d, WAM Z58. Scale bar = 50  $\mu$ m.

irregular lobes that slope upwards at their outer edges. This morphology is characteristic of *Caulospongia perfoliata*.

Bowerbank's specimen (BM 1877:5:21:6) was re-examined and is dry, soft and fragile. It is a beachwash specimen with sandgrains visible throughout the lobes of the sponge. The specimen is not complete but consists principally of the basal stalk and some of the basal sponge lobes (Figure 1b). It is 19 cm long with a 12 cm long basal stalk. The lobes surround the stem in a circular fashion but are wide and frequently irregular in shape. The internal skeleton is plumose to plumo-reticulate with fibres 55  $\mu$ m wide, centrally cored by 4–10 spicules. Other spicules occur without order throughout the mesohyl. The surface of the sponge has been worn away and the structure of the ectosomal skeleton could not be determined. The tylostyles have flattened heads, some have stylote modifications or knobby ends. The spicules are slightly curved below the head. The drawing in the publication by Bowerbank (1876: plate 79, figure 1) is of the complete specimen and depicts the lobes curving upwards at the edges, a principal distinguishing characteristic of *C. perfoliata*.

The type material of *Caulospongia verticillata*

Saville Kent, 1871 is lost but from the drawing in Saville Kent (1871: plate 48, Figure 1) it too has lobes turning upwards at their outer edges. The exact locality where this specimen was collected is not known. Saville Kent (1871) noted the locality as North Australia.

#### Habitat Description

WAM Z58 was found on granite boulders with *Ecklonia*; WAM Z59 was shaded on sloping rock beneath granite boulders; WAM Z57 was with *Posidonia* and dead shells; and QM G310964 was on rocky ledges covered with algae.

#### Associated Fauna

WAM Z58 contained ophiuroids, a crinoid, isopod and a shrimp; WAM Z57 contained ophiuroids and shrimps.

#### *Caulospongia amplexa* sp. nov.

Figure 1e–f; 2e–f; 4

#### Material Examined

*Holotype*

WAM Z55: NW of Rosemary Island, Dampier

Archipelago, Station SO1/79/33, Western Australia, Australia, 19°57'S, 116°17'E to 19°67'S, 116°16'E, 70–71 m depth, 4 October 1979, coll. S. Slack Smith and L. Marsh on RV Soela, otter trawl.

#### Paratypes

**Australia: Western Australia:** WAM Z53: Goss Passage off Beacon Island, 28°44'S, 113°46'E, 15 m depth, 20 March 1997, coll. J. Fromont, SCUBA. WAM Z54: Serventy Island, Easter Group, Abrolhos Islands, 28°29'S, 113°46'E, 25–30 m depth, 16 March 1987, coll. L. Marsh, SCUBA. WAM Z56: W. coast N of Boulder Cliff, Dorre Island, Station 13, 25°09'02"S, 11°05'19"E, 12–22 m depth, 16 May 1995, coll. S. Slack Smith and M. Hewitt *et al.*, SCUBA.

#### Other Material

**Australia: Western Australia:** QM G306005 NE of Dampier, 19°34'S, 117°14'E, 74 m depth, 31 August 1995, coll. S. D. Cook on RV Southern Surveyor, trawl. NTM Z1803 West of Pt. Hedland, 19°02'S, 119°00'E, 85 m depth, 29 August 1983, coll. T. Ward. NTM Z1791 West of Pt. Hedland, 19°04'S, 118°57'E, 84 m depth, 29 August 1983, coll. T. Ward. NTM Z2446 NW of Amphinone Shoals, 19°12'S, 118°36'E, 76–80 m depth, 1 June 1985, coll.

observers. NTM Z1769 W. of Pt. Hedland, 19°03'S, 118°49'E, 82 m depth, 29 August 1983, coll. T. Ward. NTM Z1882 W. of Pt. Hedland, 19°02'S, 118°04'E, 84 m depth, 1 September 1983, coll. T. Ward. NTM Z1490 Bonaparte Archipelago, 13°59'S, 124°43'E, 86 m depth, 27 March 1981, coll. C. C. Lu on RV Hai Kung. QM G311623 NW side Goss Passage, Wallabi Grp, Abrolhos 28°29'S, 113°36'E, 19 m depth, 13 September 1990, coll. AIMS/NCI.

#### Diagnosis

Sponges of *Caulospongia amplexa* have regularly and evenly shaped lobes that circumvolve the central stem as one entire whorl. The edges of the lobes are regular and rounded. A dermal membrane is always associated with the surface, and can be peeled away in small sections. The lobes of this species consistently slope downwards at their outer edge. This species is most similar to *C. perfoliata* which has fairly wide, thick lobes circumvolving a central hollow stalk, and an adherent dermal membrane. The lobes of *C. amplexa* are relatively thick, up to 0.3 cm, but not as thick as those of *C. perfoliata* which can be 0.5 cm thick. *C. perfoliata* has irregular shaped lobes that slope upwards at their outer edge which is in marked contrast to the lobes of *C. amplexa* which slope downwards.

#### Description

**Shape:** The sponges consist of a series of downturned lobes that circumvolve the central stem of the sponge. The lobes are widest in the central region of the sponge and narrow toward the base and apex of the sponge (Figure 1e, f). The central stalk is hollow internally except for the solid basal stem below the lobed region of the sponge.

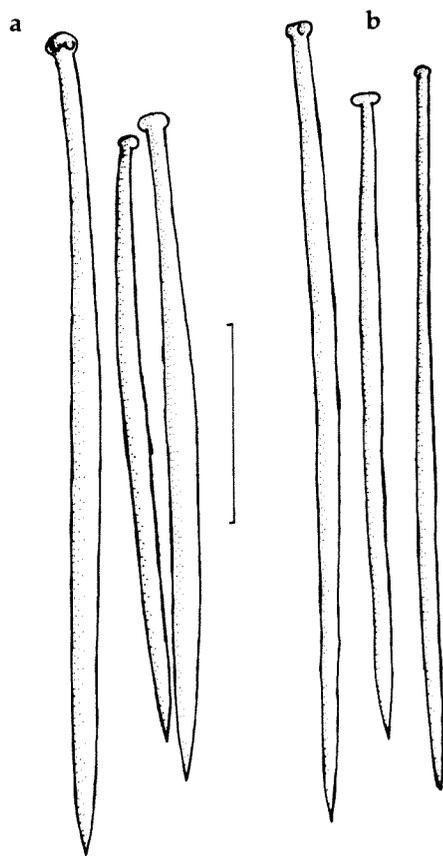
**Dimensions:** 20–42 cm tall, stem below lobes 8–11 cm long, sponge body with lobes 13–31 cm x 4–5 cm wide at the widest point in the centre of the sponge body axis. The lobes are 0.2–0.3 cm thick.

**Colour:** WAM Z53 and QM G311623 salmon to orange pink, QM G306005 and NTM Z1791 yellow, NTM Z1769, Z1803 and Z1882 yellowish brown alive; in alcohol WAM Z53 fawn to dull orange, other specimens fawn or light brown to dark brown in alcohol.

**Oscules:** The undersurfaces of the lobes are always finely porous; the upper surfaces are porous but the pores are less visible because of the presence of a dermal membrane.

**Texture and surface characteristics:** Soft compressible sponges, with firm, incompressible basal stems. The surface is smooth, finely hispid, with a dermal membrane that peels away from the underlying tissue.

**Ectosome and subectosome:** All specimens have a detachable dermal membrane that is most obvious



**Figure 4** Spicules of *Caulospongia amplexa* sp. nov. a, Holotype WAM Z55; b, Paratype WAM Z56. Scale bar = 50  $\mu$ m.

on the upper surfaces of the lobes. Spicule fans, with the spicules loosely packed, occur at right angles to the surface. The pointed ends of the spicules extend slightly above the surface. A layer of spicules, parallel to the surface and also loosely packed, underlie the spicule brushes. This combined ectosomal skeleton is 250 µm wide. In WAM Z53 the ectosome is heavily pigmented with numerous orange cells so the structure of the skeleton is difficult to determine. NTM Z1791, Z2446, Z1769, Z1882 and Z1490 have foreign material at the surface and in superficial canals.

**Choanosome:** Beneath the fans are primary tracts of spicules, 40–45 µm wide, with the spicules loosely packed (Figure 2e, f). Between the tracts are sub-dermal spaces which are approximately 85 µm wide. Towards the centre of the lobes is a plumoreticulate skeleton consisting of fibre centrally and sparsely cored by spicules. Fibre development is most pronounced towards the centre of the sponge lobe. The stem of the sponge has a reticulate fibre skeleton with thick primary fibres, 100–200 µm thick, with 5–10 spicules loosely packed within, and with some central fasciculation. The secondary fibres are 30 µm wide and cored by approximately 5 spicules. There is dense mesohyl with interstitial spicules.

**Megascleres:** (Figure 4). Tylostyles with flat nail-like heads generally straight or very slightly curved apically, tapering towards the head, thickest centrally, and with a large range of lengths. Thin forms occur. There is no differentiation of spicule sizes into particular regions of the skeleton. QM G311623 has longer spicules than the other specimens examined. See Table 3 for dimensions.

#### Remarks

WAM Z55 (collected 4 December 1979), NTM Z1803 and NTM Z1791 (both collected 29 August 1983) and WAM Z53 (collected 20 March 1997) are

**Table 3** Spicule measurements (µm) of specimens of *Caulospongia amplexa* are given as minimum-mean-maximum (n=15).

Material	Tylostyles
WAM Z53	155–209–260 x 4–6–7.5
WAM Z54	138–194–238 x 4–5.4–7.5
WAM Z55	148–192–245 x 4.5–7.6–10
WAM Z56	118–171–208 x 4.8–5.7–7.5
QM G306005	160–212–238 x 7.5–10–12.5
NTM Z1803	150–202–235 x 5–8.5–10
NTM Z1791	120–192–230 x 5–8–10
NTM Z2446	165–214–25– x 6–8–10
NTM Z1769	155–201–235 x 7.5–8.7–10
NTM Z1882	130–193–230 x 5.5–9.2–10
NTM Z1490	133–188–215 x 5–8–10.5
QM G311623	168–220–255 x 5–6.3–8

reproductive. The first three specimens contain oocytes that are ~90 µm in diameter. The latter specimen contains larvae that are 500–700 µm wide.

#### Habitat Description

WAM Z53 and WAM Z54 occur in full light on reef outcrops surrounded by algae, hard corals and some ascidians. WAM Z56 was found on limestone reef, and QM G311623 was collected on a steep slope to 40m with coral rubble.

#### Associated Fauna

Numerous spionid worms cover the surface of WAM Z53; ophiuroids were found on WAM Z55, WAM Z56 and QM G306005. WAM Z56 contained a shrimp within the hollow part of the central stem and WAM Z55 had specimens of *Calliostoma* sp. associated with it.

#### Etymology

This species is named for the encircling habit of the sponge lobes around the central stem of the sponge. From the Latin amplexus: surrounding, encircling.

#### *Caulospongia pennatula* (Lamarck)

Figure 5a, b; 6a, b; 7

*Spongia pennatula* Lamarck, 1814: 440.

*Caulospongia pennatula* (Lamarck): Hallmann, 1914: 306; Topsent, 1932: 87, plate 4, figure 3, text figure 1; Hooper and Wiedenmayer, 1994: 405.

Not *C. pennatula* (Lamarck): Lendenfeld, 1889: 193.

#### Material Examined

##### Holotype

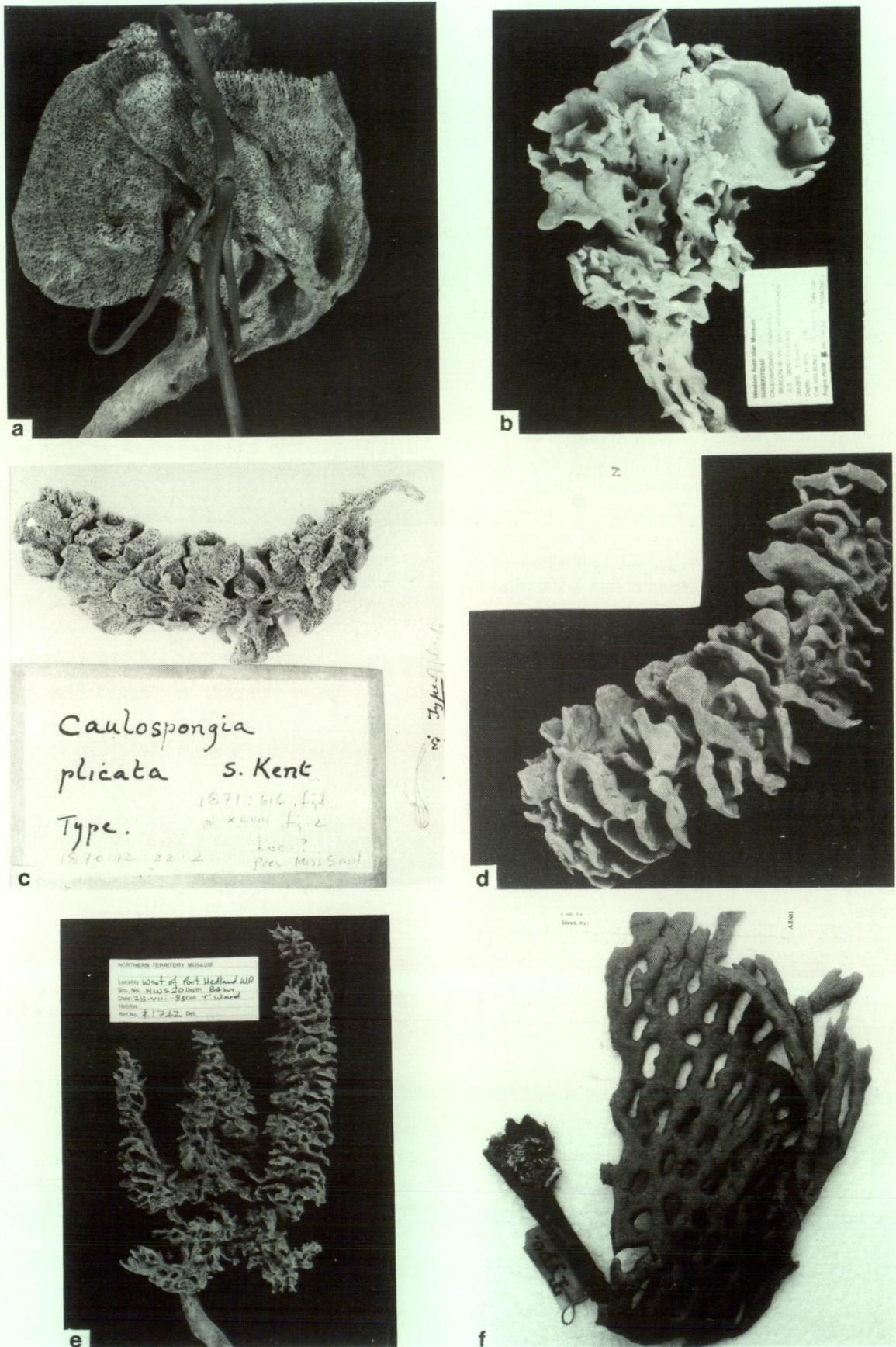
MNHN LBIM DT 583, Locality: Shark Bay (estimated lat. and long.: 25°13'S, 113°43'E), Western Australia, Australia.

##### Other material

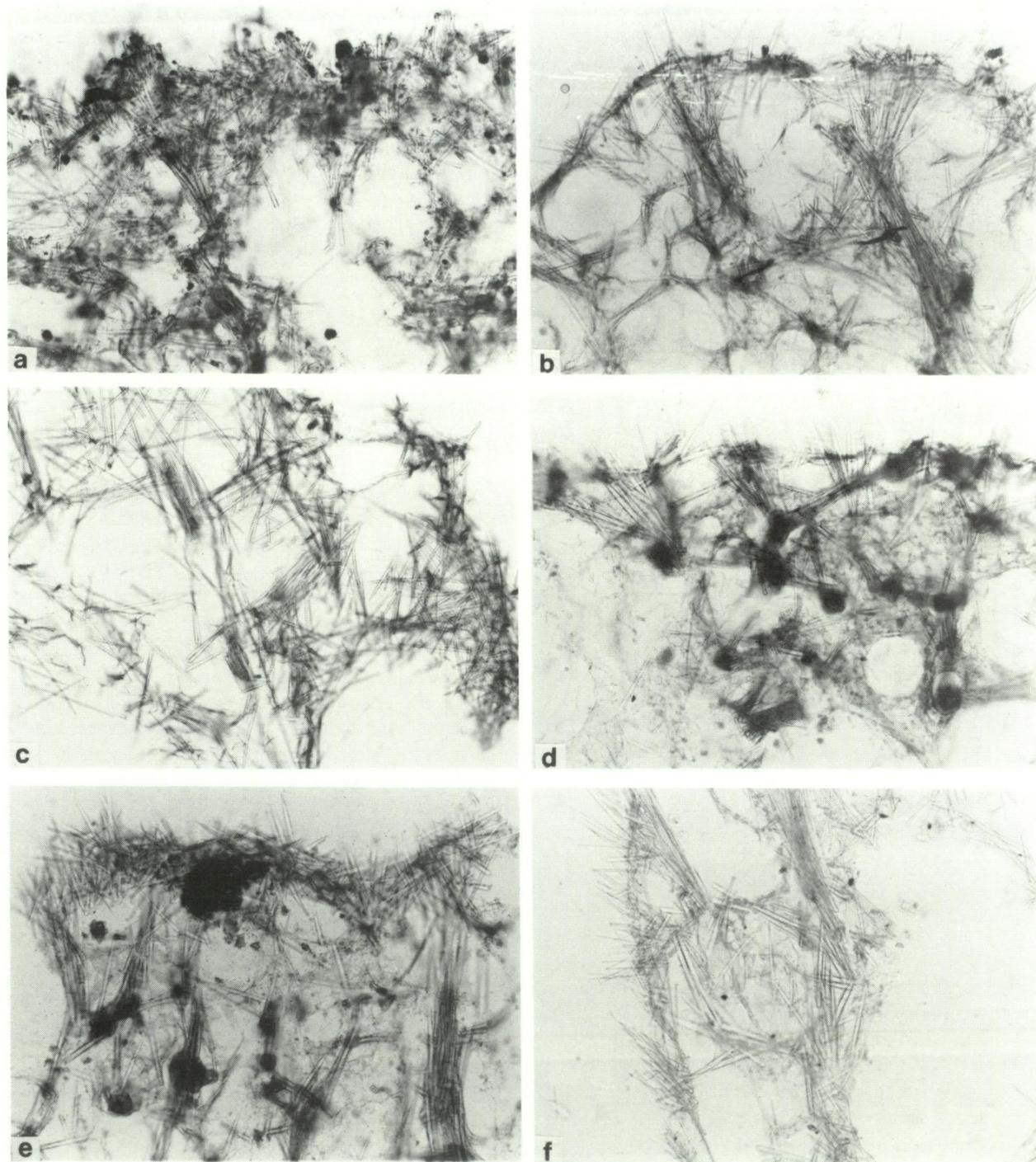
**Australia: Western Australia:** WAM Z60 Goss Passage, Beacon Island, Abrolhos, 28°29'S, 113°46'E, 31 m depth, 6 April 1978, coll. B.R. Wilson, D. Devaney (sponge 17), SCUBA. WAM Z61, Quobba, Shark Bay, 24°24'S, 113°24'E, no depth information, 7 July 1962, coll. on FRV Peron, (sponge 26). NTM Z2970 W. of Carnarvon, 24°55'S, 112°50'E, 80–85 m depth, 14 July 1987, coll. J.N.A. Hooper.

#### Diagnosis

This species has very wide leafy lobes with a thin adherent membrane and obvious pores visible on both surfaces. The leaves are thin; never thicker than 0.3 cm. This species is characterised by large,



**Figure 5** Photographs of whole specimens: a, *Caulospongia pennatula* (Lamarck, 1814), holotype MNHN LBIM DT 583, showing wide lobes dried vertically; b, *Caulospongia pennatula* (Lamarck, 1814) WAM Z60, showing wide horizontal lobes; c, *Caulospongia plicata* Saville Kent (1871), holotype BM 1870:12:22:2, whole specimen showing frilly lobes; d, *Caulospongia plicata* Saville Kent (1871) WAM Z65, single branched form (label upside down); e, *Caulospongia plicata* Saville Kent (1871), NTM Z1742, multi-branched form; f, *Caulospongia elegans* (Lendenfeld, 1888), lectotype AM G9186, showing reticulate branches.



**Figure 6** Photographs of skeletal organisation: a, *Caulospongia pennatula* (Lamarck, 1814), holotype MNHN LBIM DT 583, showing surface skeleton; b, *Caulospongia pennatula* (Lamarck, 1814) WAM Z60, with surface skeleton and internal tracts; c, *Caulospongia plicata* Saville Kent (1871) Holotype BM 1870:12:22:2, with surface on rhs and choanosomal skeleton forming tracts beneath it; d, *Caulospongia plicata* Saville Kent (1871), WAM Z65, single branched form, surface brushes and reticulation beneath; e, *Caulospongia plicata* Saville Kent (1871), NTM Z1742, multi-branched form, surface brushes and reticulation beneath; f, *Caulospongia elegans* (Lendenfeld, 1888), lectotype AM G9186, with surface brushes on lhs. Scale bar = 200  $\mu$ m.

flat, slightly upturned leaves which are very wide unlike the lobes of the morphologically similar species *Caulospongia perfoliata* and *C. amplexa*.

#### Description

*Shape*: Sponges consist of large, flat, slightly

upturned leaves which are very wide (Figures 1, 5a, b). The leaves are porous with a patterned surface produced by the outline of the underlying canals. There is a thin attached membrane superficially.

*Dimensions*: (specimens not complete) 17–26 cm



**Figure 7** Spicules of *Caulospongia pennatula*: a, holotype MNHN LBIM DT 583; b, WAM Z60. Scale bar = 50  $\mu\text{m}$ .

tall. Stem below leaves 6–15 cm long and 2 cm wide consisting of 3–4 stems coalesced. Leafy upper region of sponge 11 cm tall  $\times$  12 cm wide to 26 cm tall and 5 cm wide. Leaves are 0.1 cm thick, 0.3 cm thick in NTM Z2970.

**Colour** NTM Z2970 yellowish fawn; in alcohol cream or beige to orange or medium brown.

**Oscules:** Oscular canals visible beneath the fine membrane and leaves porous on both sides.

**Texture and surface characteristics:** Thin surface membrane but missing in parts so the surface is hispid. Soft, compressible sponge.

**Ectosome and subectosome:** Spicule brushes occur at the surface but the spicules are not tightly packed together within them. A layer of spicules, parallel to the surface, underlie the spicule brushes, 70  $\mu\text{m}$  wide. In some specimens pigment cells occur at the surface and throughout the mesohyl.

**Choanosome:** Beneath the brushes are primary tracts of spicules with strong fibre development, 60–100  $\mu\text{m}$  wide, cored by 5–8 spicules (Figure 6a, b). Secondary fibres are 20–40  $\mu\text{m}$  wide and cored by 1–4 spicules. The strongest fibre development occurs centrally, and primary and secondary fibres

form a plumoreticulate skeleton curving out to the surface spicule brushes. Dark coloured grainy cells, possibly pigment, overlie the central fibres. NTM Z2970 has some foreign material in the canals within the choanosome.

**Megascleres:** (Figure 7). Tylostyles with reduced development of the head end which is slightly rounded or flat. Spicules have long tapering points and are thickest in the middle of the shaft. See Table 4 for dimensions.

### Remarks

The holotype is dried and mounted and consists of a sponge with a basal stalk 11 cm long and the lobed part of the sponge 12 cm long (Figure 5a). The lobes of this specimen are very large, up to 9 cm wide and 0.1–0.3 cm thick. In the dried state it is difficult to determine the surface features but there are numerous fine pores as noted by Lamarck (1814). The lobes are orientated vertically but this may not have been the correct orientation of them when the sponge was alive. The sponge is a medium brown colour. At the surface there is a dense skeleton with spicules at right angles to the surface as well as horizontal, forming a layer 175  $\mu\text{m}$  wide. The thickest fibre tracts, 50–60  $\mu\text{m}$  wide, run parallel to the surface and centrally within the sponge. The skeleton tends to be plumoreticulate. The tylostyles have flat nail heads with some stylote modifications, and are widest above the pointed end.

The other specimens examined differ from the holotype in lacking a vertical orientation to the lobes, however in life the lobes of the holotype may have had a more horizontal orientation. The intact edges of the lobes of the type are regular but both WAM Z60 and NTM Z2970 have more irregular edges to the lobes. Only the lobes of NTM Z2970 are as thick as the thickest lobes of the holotype, the other two specimens examined have lobes that are <0.2 cm in thickness. The skeleton is less ordered in the holotype than in the other specimens examined. In all other aspects the new material conforms to the holotype.

### Habitat Description

WAM Z60 on bottom of channel, with sand and

**Table 4** Spicule measurements ( $\mu\text{m}$ ) of specimens of *Caulospongia pennatula* are given as minimum–mean–maximum ( $n=15$ ).

Material	Tylostyles
MNHN LBIM DT 583	148–197–220 $\times$ 5–7.7–9.5
WAM Z60	150–200–248 $\times$ 5–5.9–7.5
WAM Z61	140–180–213 $\times$ 4.5–6.9–9.5
NTM Z2970	150–215–255 $\times$ 6–9–10.5

coral rubble and rippling from current, and NTM Z2970 on sand and shell grit.

*Caulospongia plicata* Saville Kent

Figure 5c–e; 6c–e; 8

*Caulospongia plicata* Saville Kent, 1871: 616, plate 48 Figure 2; Hallmann, 1914: 306; Burton, 1930: 673; Topsent, 1932: 88; Hooper and Wiedenmayer, 1994: 405.

**Material Examined**

*Holotype*

BMNH 1870:12:22:2 Locality unknown, probably North Australia.

*Other material*

**Australia: Western Australia:** WAM Z62 46 nautical miles WNW Port Hedland, 19°58'S, 117°50'E to 20°01'S, 117°50'E, 40 m depth, 8 August 1982, coll. J. Marshall on Soela (Stn SO4B/82/08), Frank and Bryce trawl. WAM Z63 41 nautical miles North of Port Hedland, Station SO/82/60, 19°38'S, 118°30'E, approx. 30 m depth, 17 April 1982, coll. L. Marsh on RV Soela, Frank and Bryce trawl. WAM Z64 Shark Bay, 24°49'S, 113°33'E, 10 m depth, 13 May 1982, coll. B. Bruce on RV Sprightly, dredge. WAM Z65 27 nautical miles NNE of Cape Lambert, Station SO5/82/09, 20°11'S, 117°23'E to 20°13'S, 117°24'E, 37–39 m depth, 27 September 1982, L. Marsh and M. Bezant on Soela, Otter trawl. WAM Z66 NE of Monte Bello Islands, Station SO1/79/22, 19°54'S, 116°02'E to 19°55'S, 116°00'E, 76–78 m depth, 3 December 1979, coll. S. Slack Smith and L. Marsh on Soela, Otter trawl. NTM Z3053 NW Amphinome Shoals, 19°19'S, 119°08'E, 50 m depth, 19 July 1987, coll. J.N.A.Hooper. NTM Z1816 W of Pt. Hedland, 19°26'S, 118°54'E, 50 m depth, 30 August 1983, coll. T. Ward. NTM Z1742 W. of Pt. Hedland, 19°05'S, 118°47'E, 84 m depth, 28 August 1983, coll. T. Ward. NTM Z1408 NE of Pt. Hedland, 19°01'S, 119°25'E, 80 m depth, 19 April 1983, coll. R. Williams on Pair trawler Tung Mao 1. QM G310450, NW corner of Flat Island, 21°35'S, 114°36'E, 13 m depth, 20 August 1988, coll. AIMS/NCI, SCUBA.

**Diagnosis**

This species is characterised by small, thin (<0.2 cm), and narrow lobes with undulating or "frilled" edges. This species is distinguished from other species of *Caulospongia* by the small size of the lobes and their frilled appearance. The two morphs of this species are distinguished by either having single branches (shallow water forms) or multiple branches (deep water forms). Both forms have the characteristic frilled lobes that distinguish this species from all other species of *Caulospongia*.

**Description**

*Shape:* Two morphs of this species occur. Those that occur in shallow water have a single branch (WAM Z63, Z64, Z65 and QM G310450) while those that occur in deep water (NTM Z3053, Z1816, Z1742, Z1408) are multibranched (Figure 5d, e). This species has the classic *Caulospongia* shape of a central hollow stem with whorls arrayed around the outside. In this species the leaf-like extensions are more convoluted than other species of *Caulospongia*. The fronds are either perpendicular to the stem or turn upwards at their outer edge (Figure 5c–e). The fronds of this species are small and narrow, approximately 1 cm wide and <0.2 cm thick. In QM G310450, a shallow water form, the lobes are very small, often only 0.5 cm wide and some branches interconnect. The deepwater specimens are multibranched (NTM Z3053, Z1816, Z1742, Z1408) and have a single basal, solid stem with 3–5 branches extending above this in a candelabra fashion.

*Dimensions:* Single branched specimens 13–22 cm tall, 3.5–6 cm wide; multibranched specimens 33–60 cm tall, basal stem 8–11 cm long, each branch 3–5 cm wide.

*Colour:* WAM Z63 orange, QM G310450 peach-pink to orange, NTM Z3053 and Z1742 yellow, NTM Z1816 deep yellow-orange alive; in alcohol



**Figure 8** Spicules of *Caulospongia plicata*: a, holotype BM 1870:12:22:2; b, WAM Z65; c, NTM Z1742. Scale bar = 50  $\mu$ m.

cream to beige, fawn or yellowish light brown or dark red brown.

*Oscules*: Not apparent.

*Texture and surface characteristics*: A very fine microhispid surface that is shiny and reflective. A thin membrane is attached to the underlying tissue, and pores are faintly apparent or not visible. The sponge has dense texture, is firm, spongy and compressible, except for the basal part of the stem which is solid and incompressible.

*Ectosome and subectosome*: Spicule fans occur at right angles to the surface with the pointed ends of the spicules projected outwards, forming the hispid surface. A layer of spicules 30–60 µm wide, parallel to the surface, underlie the spicule brushes.

*Choanosome*: Beneath the spicule fans are primary fibres with spongin development, 30–80 µm wide and centrally cored by 6–10 spicules. Secondary fibres occur that link the primary fibre in a plumoreticulate or ladder-like fashion (Figure 6c–e). The secondary fibres are 20 µm wide cored by 1–3 spicules. Towards the centre of the sponge leaves or in the central stem of the sponge the primary fibres are thick (80 µm wide), have dense spongin, and run parallel to the surface. In some specimens fasciculation of the primary fibres occurs. Interstitial spicules present, without order. No differentiation of size categories of spicules throughout the skeleton. Some specimens (WAM Z66 and NTM Z1742) incorporate some foreign material into the superficial regions.

*Megascleres*: (Figure 8). Tylostyles with a large range of widths and lengths, but generally short and thick. The head is flat and nail-like, or rounded. The spicules are straight or slightly curved, tapering to long points. See Table 5 for dimensions.

#### Remarks

The holotype was dry and consequently brittle and fragile and its colour was fawn to light brown.

**Table 5** Spicule measurements (µm) of specimens of *Caulospongia plicata* are given as minimum–mean–maximum (n=15).

Material	Tylostyles
BM 1870:12:22:2	150–199–225 × 4–5.2–6.5
WAM Z63	115–153–205 × 4.5–6.9–11
WAM Z64	115–185–240 × 3–5–7.5
WAM Z65	125–178–205 × 5–7.5–10
WAM Z62	125–173–200 × 5.5–8.1–10
WAM Z66	140–197–225 × 5–8.6–10.5
NTM Z3053	155–184–213 × 5–7.5–10
NTM Z1816	128–169–200 × 5–7.7–10
NTM Z1742	130–172–200 × 5–8–10
NTM Z1408	130–190–210 × 6–8.6–10.5
QM G310450	155–198–215 × 6.5–8.7–10

It is probably a beachwash specimen judging from the amount of foreign material in the mesohyl microscopically, and macroscopically the sand distributed over the surface and throughout the body of the sponge. Part of the stem of the specimen is missing. The sponge measures 12 cm in length and is 3.5 cm at its widest point. Leaf-like structures surround the stem in whorls but are convoluted giving the sponge a “frilly” appearance (Figure 5c). The ectosomal skeleton of the holotype consists of tylostyles at right angles, as well as parallel to the surface, forming a layer 80 µm wide. In the centre of the sponge the plumose skeleton is strengthened with fibre development, 60–85 µm wide, cored by up to 5 spicules. Surrounding this region the spicules occur in tracts forming a reticulate skeleton with fibre that is not as dense as it is centrally. Interstitial spicules occur without order. The spicules are tylostyles with flattened heads, slightly curved below the head (Figure 8).

*Caulospongia plicata* was previously synonymised with *C. perfoliata* by Hallmann (1914). This is clearly a good species and the name is here removed from synonymy.

#### Habitat Description

WAM Z63 collected with gorgonians and branching sponges; WAM Z66 collected with large sponges and soft corals, WAM Z65 on sand, NTM Z3053 and WAM Z62 on shell substrate and sand and shell grit, QM G310450 on subtidal reef flat with sediment layer, sea whips and sponges, WAM Z64 found attached to stems of seagrass in shallow water.

#### Associated Fauna

NTM Z3053 with ophiuroids.

#### *Caulospongia elegans* (Lendenfeld)

Figure 5e; 6e; 9

*Plectodendron elegans* Lendenfeld, 1888: 66.

*Caulospongia elegans* (Lendenfeld): Hallmann, 1914: 306, plate 18, figure 1; Topsent, 1932: 88; Hooper and Wiedenmayer, 1994: 404.

#### Material Examined

##### *Lectotype*

AM G9186 (wet), Broughton Island, New South Wales, Australia, 32°37'S, 152°19'E.

##### *Paralectotypes*

**Australia: New South Wales:** AM Z5221 (wet) Port Jackson, 33°51'S, 151°16'E; AM Z5271 (dry), Port Jackson, 33°51'S, 151°16'E.

#### Diagnosis

This species is characterised by having a two

dimensional reticulate branching morphology. The branches intermesh at right angles, giving a lattice-like appearance to the sponges. It does not have a hollow stem through the centre of the sponge as lobed species do, but does have a solid basal stalk found in all species of *Caulospongia*. This species has the same skeletal layout as other species of the genus. It is most similar morphologically to *C. reticulata* but it does not have lobes which are characteristic of the latter species.

### Description

*Shape*: An erect branching sponge with branches interlocking at right angles, giving a reticulate, lattice morphology (Figure 5f). Basal stalk tough and solid.

*Dimensions*: Intact Pt. Jackson specimen (AM Z5221) is 17 cm tall with an incomplete basal stem. Individual branches are 0.9 x 0.6 cm. AM Z5271 is numerous dry fragments, some of which have the branching reticulate morphology characteristic of the species. The material is porous without an obvious membrane, which has probably worn off.

*Colour*: No live colour; in alcohol fawn to medium brown.

*Texture and surface characteristics*: The surface is smooth with an attached membrane, with pores faintly visible beneath.

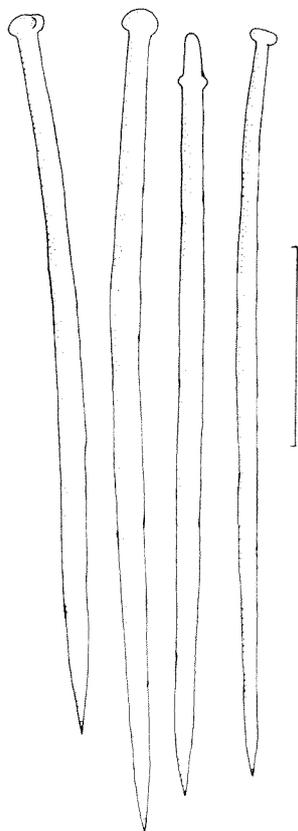


Figure 9 Spicules of *Caulospongia elegans*. Lectotype AM G9186. Scale bar = 50  $\mu$ m.

*Ectosome and subectosome*: Dense spicule brushes at the surface with a layer of spicules orientated horizontally to the surface overlying the brushes.

*Choanosome*: An irregular plumoreticulate skeleton with tracts of spicules surrounded by spongin fibre, 30–40  $\mu$ m wide, and cored by 4–6 spicules (Figure 6f). The sponge skeleton is most compact centrally. Spicules also occur haphazardly in the mesohyl.

*Megascleres*: (Figure 9). Tylostyles with thickest dimension in centre of spicule, somewhat rounded tylote head. Large size range. See Table 6 for dimensions.

### Remarks

There were three syntypes of this species in the Australian Museum. AM G9186, which has been designated lectotype in this paper, is in good condition with part of the basal stem and all of the branches intact (Figure 5f). The paralectotype from Pt. Jackson (AM Z5221) was previously registered as AM Z778, a number shared with another sponge species *Polymastia bicolor*. The register number AM Z778 has now been exclusively allocated to the specimen of *P. bicolor* and the specimen of *C. elegans* has been given the new number AM Z5221 (P. Berents, pers.comm.) This specimen is in good condition and is a large fragment with some of the basal stem and branches. Some dry material, previous registration number AM Z508, consists of numerous fragments (<1.5 cm long) that were thought to be a mixture of fragments of *Hircinia gigantea* and *C. elegans*. However, the larger fragments are of *C. elegans* and all the fragments look identical. The condition of this material is a consequence of it being attacked by rats in 1941. A large intact wet specimen of *H. gigantea* has been assigned the number AM Z508 and the fragments of *C. elegans* have been given the new registration number AM Z5271 (P. Berents, personal communication). Only these three specimens exist in the Australian Museum, not four, as suggested by Hooper and Wiedenmayer (1994), who thought the label referring to two specimens on one of the jars, was referring to two specimens of *C. elegans* (J. Hooper, personal communication). However, these sponges were one of the mixed lots described above.

Table 6 Spicule measurements ( $\mu$ m) of specimens of *Caulospongia elegans* are given as minimum-mean-maximum (n=15).

Material	Tylostyles
AM G9186	148–183–220 x 5–7.4–10
AM Z5221	145–198–223 x 6.5–9–10
AM Z5271	140–183–200 x 7.5–9.4–12.5

*Caulospongia reticulata* sp. nov.

Figure 10a,b; 11a,b; 12

**Material Examined***Holotype*

WAM Z67, Reef off mouth of Capel River, Western Australia, Australia, 33°46'S, 115°08'E, 3–6 m depth, 19 February 1984, coll. L. Marsh.

*Paratypes*

**Australia: South Australia:** SAM IS403 Southern Gulf of St. Vincent, 35°13'S, 138°15'E, 20–40 m depth, May–June 1987, coll. S. Corigliano on FV Rivoli Queen. SAM IS402 (NTM Z3116) 15.5 miles NNE of Rapid Head, Gulf of St. Vincent, 35°31'S, 138°10'E, 37 m depth, 6 June 1987, coll. K. Gowlett-Holmes, S. Corigliano on FV Rivoli Queen, prawn trawl by catch.

**Diagnosis**

In this species specimens may have lobes with interconnections that circumvolve a central stem, or lobes that are much reduced in dimensions and form a lattice reticulation, without a central stem, that has similarities to *C. elegans*. This species differs from *C. elegans* in retaining lobes, while specimens of *C. elegans* have branches that lack lobes of any form and are rounded, smooth and interconnected.

**Description**

*Shape:* WAM Z67 is an erect sponge with reticulate branches and small lobes, flattened into two dimensions (Figure 10a). SAM IS403 has a lobed reticulation like WAM Z67 but the upper 6 cm of the sponge is flattened into vertical plates. SAM IS402 is a series of interconnected short blunt nodes with a hollow central stem, but some of the leaf-like appendages form connections in a reticulate manner (Figure 10b).

*Dimensions:* WAM Z67: 16–29 cm long with a basal stem 10 cm long, branched region of sponge 19 cm, at widest point: 7–11 x 2 cm wide. Thickness of networked branches; 0.2–0.5 cm.

*Colour:* Live colour unknown, cream, beige or fawn in alcohol.

*Texture and surface characteristics:* Firm but compressible. Pores over surface faintly visible macroscopically beneath an adherent dermal membrane.

*Ectosome and subectosome:* Spicule fans or brushes and a layer of parallel spicules overlying these, 70–100 µm wide. Ectosomal skeleton of South Australian specimens more diffuse than the WAM Z67 material from Capel River.

*Choanosome:* Beneath the ectosomal layer is a plumoreticulate fibre skeleton with strong fibre development (Figure 11a, b). Primary fibres are 50–

**Table 7** Spicule measurements (µm) of specimens of *Caulospongia reticulata* are given as minimum–mean–maximum (n=15).

Material	Tylostyles
WAM Z67	140–172–200 x 5–7.2–9.5
SAM IS403	165–194–220 x 4–4.9–6
SAM IS402 (NTM Z0003116)	155–194–223 x 3.5–4.5–5

80 µm wide cored by 4–6 spicules, secondary fibres 20–50 µm wide cored by 1–3 spicules. Interstitial spicules present. In the basal stem of the sponge the fibre component of the skeleton extends to the ectosomal spicule brushes.

*Megascleres:* (Figure 12). Tylostyles usually with flat nail heads, some rounded stylote or knobby modifications. See Table 7 for spicule dimensions.

**Remarks**

The three specimens described above form a transition series from the lobed forms, with central hollow stem typical of most species of *Caulospongia* and found in SAM IS403, to the reticulate morphology characteristic of *C. elegans* and to an extent seen in WAM Z67. SAM IS402 is intermediate, having reticulate processes connecting the lobes which link it with the morphologies of the other two specimens. *C. reticulata* is a transitional morphology between typical *Caulospongia* with lobes, and reticulate branching, two dimensional forms seen in *C. elegans*.

The spicules of the South Australian specimens are longer and thinner than those of the South West Australian specimen.

**Habitat Description**

No details available.

**Etymology**

This species is named for the connections that form between the lobes giving a lattice component to the external morphology. From the Latin reticulatus: made like a net.

*Caulospongia venosa* sp. nov.

Figure 10c; 11c; 13

**Material Examined***Holotype*

SAM IS405 (NTM Z3742) 8 km NNW of Pt. Riley, Spencer Gulf, South Australia, Australia, 33°48'S, 137°34'E, 20 m depth, 13 December 1988, coll. K. Gowlett-Holmes and P. Briggs on FV Kara George.

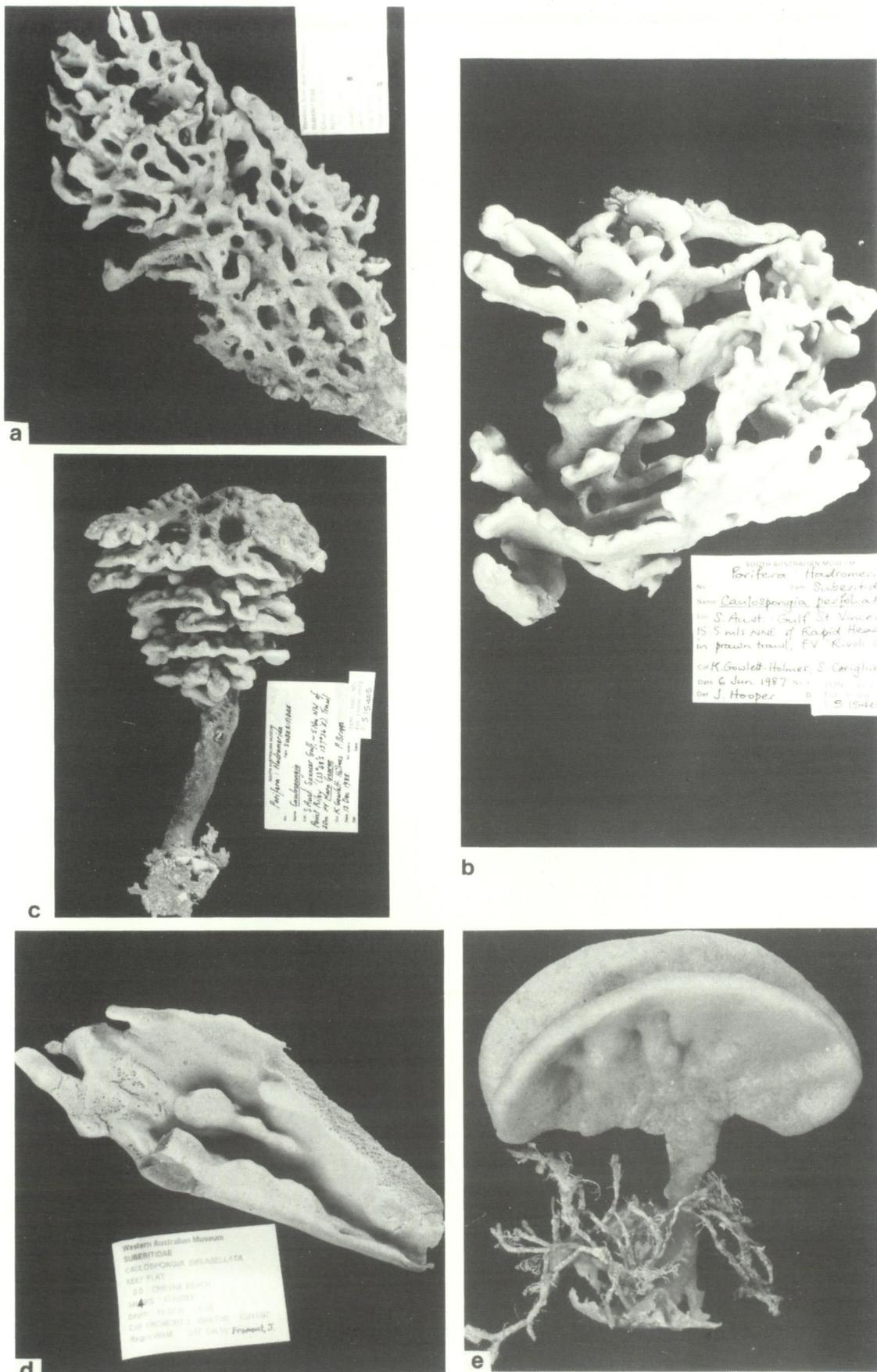
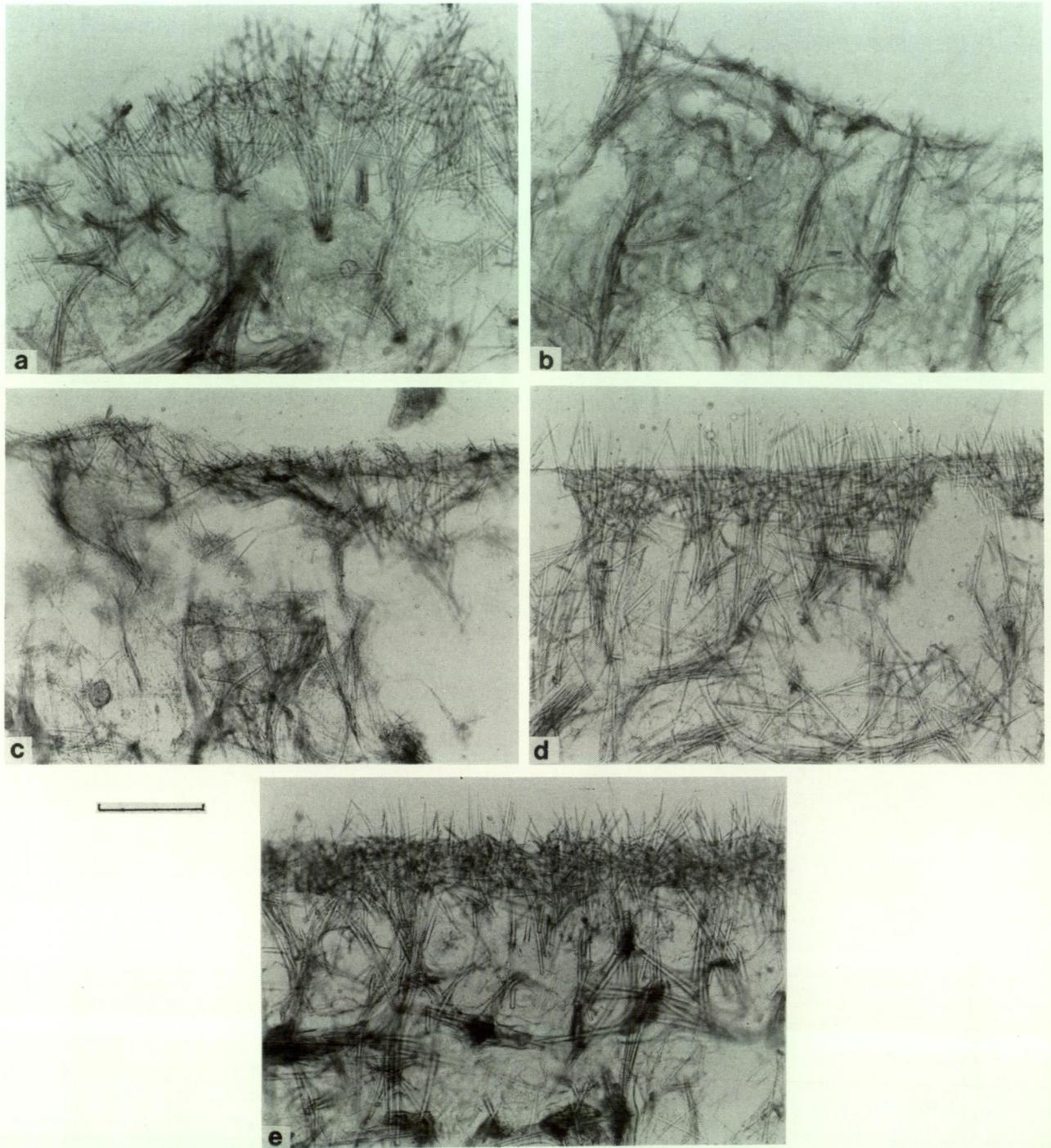


Figure 10 Photographs of whole specimens: a, *Caulospongia reticulata* sp. nov., holotype WAM Z67, with reticulations and lobes; b, *Caulospongia reticulata* sp. nov., SAM IS402, with lobes that interconnect; c, *Caulospongia venosa* sp. nov., holotype SAM IS405, showing veins on lobes; d, *Caulospongia biflabellata* sp. nov., holotype WAM Z267, fragment of fan showing lobes; e, *Caulospongia biflabellata* sp. nov., QM G311009, whole specimen showing bilobed form of fan.



**Figure 11** Photographs of skeletal organisation: a, *Caulospongia reticulata* sp. nov., holotype WAM Z67, showing fibre development beneath surface; b, *Caulospongia reticulata* sp. nov., SAM IS402, surface and underlying fibre development; c, *Caulospongia venosa* sp. nov., holotype SAM IS405, showing surface and internal skeleton; d, *Caulospongia biflabellata* sp. nov., holotype WAM Z267, showing thick surface skeleton and internal reticulation; e, *Caulospongia biflabellata* sp. nov., QM G311009, showing thick surface skeleton and internal reticulation. Scale bar = 200  $\mu$ m.

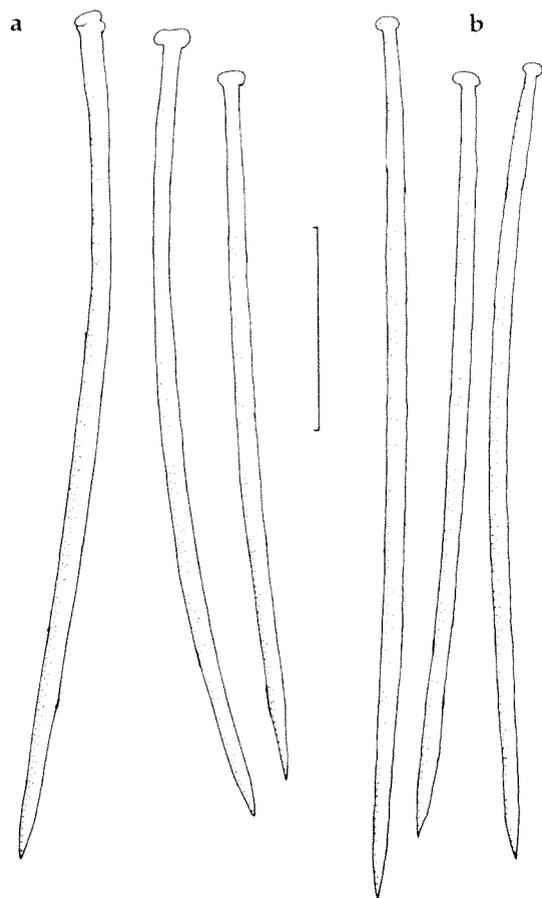
### Diagnosis

This species is distinctive from all other species of *Caulospongia* in having plumose lines on the surface of the lobes, very porous lobes with an open texture, and a knobby upper surface. The layout of the skeleton is similar to other species of *Caulospongia* although it is not as dense and compact as some species like *C. biflabellata*. No

other species of *Caulospongia* have the veined lobes characteristic of this species.

### Description

*Shape*: This is an erect sponge with the classic *Caulospongia* shape of whorls of sponge around a central axial hollow stem. However, the thick, large lobes have major superficial differences from other



**Figure 12** Spicules of *Caulospongia reticulata* sp. nov.: a, holotype WAM Z67; b, SAM IS402. Scale bar = 50  $\mu$ m.

species of *Caulospongia*. Extending from the central stem to the outer edge of the lobes are plumose lines that look like the leaf veins of plants (Figure 10c). The upper surface of the sponge is irregular and convoluted with small nodes or veins. The underside of the lobes have large pores.

**Dimensions:** Specimen incomplete; overall size 27cm; stalk 12 cm incomplete lobed part of sponge 15 cm, lobes 5 cm wide, 0.4 cm thick.

**Colour:** Live colour unknown, beige with pinkish tinge in alcohol.

**Texture and surface characteristics:** Soft, compressible, spongy. Surface porous, in some areas with an attached dermal membrane, otherwise hispid.

**Ectosome and subectosome:** Spicule fans or brushes at the surface form a loose palisade up to 200  $\mu$ m wide. The layer of parallel spicules overlying these is thin and the spicules are sparse. There is some thickening of the mesohyl at the outer surface edge and around the canals.

**Choanosome:** Beneath the ectosomal layer is a reticulate fibre skeleton cored with spicules (Figure 11c). Primary fibres are 40  $\mu$ m wide cored by ~7

**Table 8** Spicule measurements ( $\mu$ m) of specimens of *Caulospongia venosa* are given as minimum-mean-maximum (n=15).

Material	Tylostyles
SAM IS405 (NTM Z3742)	143-180-223 x 4-4.6-5

spicules, secondary fibres 10-20  $\mu$ m wide cored by 1-3 spicules. The fibres are thicker toward the centre of the lobes and the skeleton more plumoreticulate with the thickest fibres running parallel to the surface. Primary fibres are 70  $\mu$ m wide cored by up to 10 spicules, secondary fibres are 40-70  $\mu$ m wide and cored by 1-3 spicules. Interstitial spicules present.

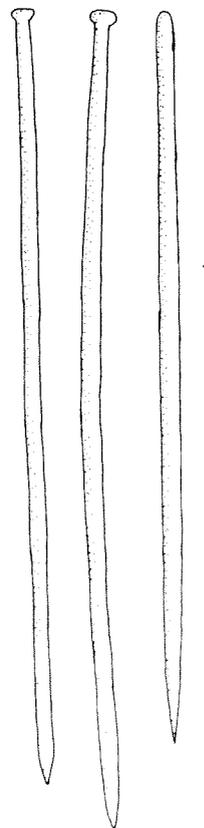
**Megascleres:** (Figure 13). Tylostyles thin, gently curved along their length, with flattened nail-like heads or with small knobbed or stylote modifications. See Table 8 for spicule dimensions.

#### Remarks

This specimen was reproductive with oocytes 40  $\mu$ m wide visible in the mesohyl (date of collection: 13 December 1988).

#### Habitat Description

Trawl grounds.



**Figure 13** Spicules of *Caulospongia venosa* sp. nov., holotype SAM IS405. Scale bar = 50  $\mu$ m.

### Etymology

This species is named for the veins, plumose lines of thickened tissue, that occur on the lobes. From the Latin *venosus*: veined.

### *Caulospongia biflabellata* sp. nov.

Figure 10d, e; 11d, e; 14

### Material Examined

#### Holotype

WAM Z267 Limestone reef flat, Cheyne Beach, Western Australia, Australia, 34°48'S, 118°00'E, 10 m depth, 2 November 1997, coll. J. Fromont, SCUBA.

#### Paratype

**Australia: Western Australia:** WAM Z268 Limestone reef flat, Cheyne Beach, 34°48'S, 118°00'E, 10 m depth, 2 November 1997, coll. J. Fromont, SCUBA.

#### Other Material

**Australia: Western Australia:** QM G311009 Sunken oil rig near Lancelin, 31°10'60"S, 115°11'40"E, 30 m depth, 19 March 1989, coll. AIMS/NCI, (cross ref. Q66C2754-K), SCUBA. QM G310451 NW Corner of Flat Island, NW Cape, 21°35'20"S, 114°36'40"E, 13 m depth, 20 August 1988, coll. AIMS/NCI, (cross ref. Q66C1371-H), SCUBA. QM G311044 Bay at Western end of Breaksea Island, Albany, 35°03'70"S, 118°02'50"E, 20 m depth, 25 March 1989, coll. AIMS/NCI, (cross ref. Q66C2853-R), SCUBA.

### Diagnosis

This species is distinctive from all other species of *Caulospongia* in having a fan-shaped morphology with a solid basal stalk. Ectosomal spicule brushes extend beyond the surface in a palisade. The skeletal arrangement remains identical to typical lobed species of *Caulospongia*. This species does not have lobes or a reticulate branching structure which is found in other species of *Caulospongia*.

### Description

**Shape:** These sponges are erect fans, commonly bilobed, with basal stalks (Figure 10d, e). Specimens may have additional lobes on the outer surfaces, either as irregular raised ridges, <1 cm high, as seen in QM G311044, or as long fingerlike lobes seen in the holotype (Figure 10d).

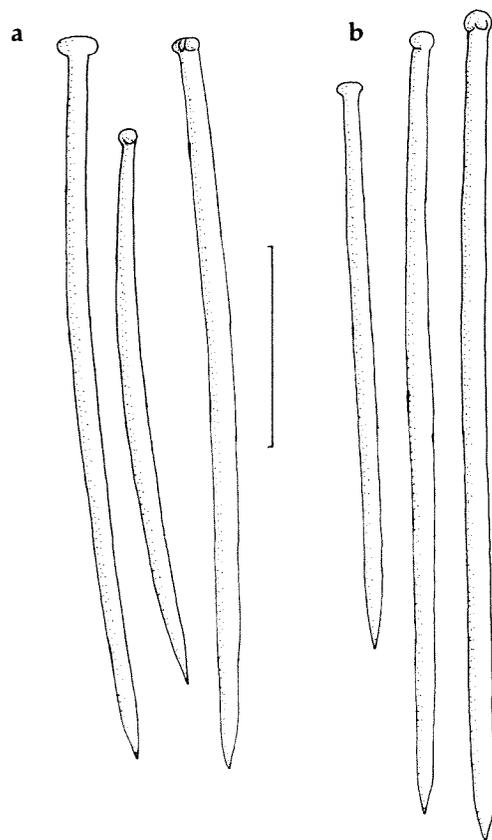
**Dimensions:** Specimens are 9–40 cm tall with a stalk 4.5–12 cm long. The fans are 8.5–24 cm wide and split into two lobes approximately 6–8 cm above the stalk. Some of the specimens are pieces only.

**Colour:** WAM Z267 and Z268 pale peach–orange with slightly more yellow–orange interior, QM G311009 pale pink, QM G310451 pinkish white, QM G311044 peach/pink alive, in alcohol cream to beige or fawn.

**Texture and surface characteristics:** Firm, compressible. Surface porous with an adherent dermal membrane. Oscules visible on the edges of the fans and lobes, small pores <1 mm wide, abundant on outer side of fan.

**Ectosome and subectosome:** Spicule fans and a layer of parallel spicules overlying these form a thick surface skeleton. The parallel layer of spicules is 140 µm wide and is dense and compact. The sharp end of the spicule fans protrude beyond the parallel layer by 50–100 µm and form a palisade.

**Choanosome:** Beneath the ectosomal layer the primary fibres spread into wide fans or brushes and below this region fibre development occurs (Figure 11d, e). It is a reticulate fibre skeleton becoming more plumoreticulate centrally, where the thickest fibres are oriented parallel to the surface. Primary fibres are 150–180 µm wide centrally cored by ~12 spicules. Secondary fibres are 30–50 µm wide cored by 1–5 spicules. Interstitial spicules present. The skeleton is dense



**Figure 14** Spicules of *Caulospongia biflabellata* sp. nov., a, holotype WAM Z267; b, *Caulospongia biflabellata* sp. nov. QM G311009. Scale bar = 50 µm.

**Table 9** Spicule measurements ( $\mu\text{m}$ ) of specimens of *Caulospongia biflabellata* are given as minimum-mean-maximum ( $n=15$ ).

Material	Tylostyles
WAM Z267	138-177-200 x 5-7-9
WAM Z268	140-192-215 x 5-6.8-10
QM G311009	200-222-245 x 6-8-10
QM G310451	168-182-195 x 6-6.7-8
QM G311044	175-203-223 x 6-8.6-10

and compact compared to other species of *Caulospongia* (Figure 11d, e).

**Megascleres:** (Figure 14). Tylostyles with flattened nail heads to bulbous and stylote modifications. Spicules gently curved and thickest centrally along length. See Table 9 for spicule dimensions.

#### Remarks

The wide geographic distribution of the specimens examined may indicate a future separation into distinct species.

#### Habitat Description

Vertical or horizontal limestone reef with a component of either coral or kelp.

#### Associated Fauna

Barnacles within sponge tissue visible by small apertures and slightly raised surrounding surface. Ophiroids on the surface.

#### Etymology

This species is named for the bilobed fan shaped external morphology. From the Latin bi: two, double; flabellum, fan-shaped.

### DISCUSSION

This is the first work redescribing species of the genus *Caulospongia* since Topsent's (1932) revision of Lamarck's collections. *Caulospongia plicata*, *C. pennatula*, *C. perfoliata* and *C. amplexa* comprise "typical" morphotypes of the genus with circumvolving lobes around a hollow central stem and with a solid basal stalk. This morphology is consistent with the first description of the genus by Saville Kent (1871). The remaining four species described in this paper do not have this characteristic lobed morphology. *C. venosa* has lobes that are thick, perforated, and have dendritic veins, which is a very different morphology from the "typical" species. *C. reticulata* has lobes but there is a tendency for a reticulation to form between the lobes. *C. biflabellata* does not have lobes but has a double fan shape, and *C. elegans* has a reticulate branching morphology. The tendency

to reticulation in *C. reticulata* is transitional between the lobed species and the interconnected branching morphology of *C. elegans*, the latter previously assigned to *Plectodendron*. This morphological gradation between species that were originally placed in separate genera supports the retention of the synonymy of *Plectodendron* with *Caulospongia*.

Recognition of a diversity of morphotypes, not previously included in the genus, but which otherwise have identical skeletal characters, necessitates broadening the generic definition of *Caulospongia*. Species of this genus have few skeletal characters but they consistently have the following attributes: one type of megasclere in a single size category, no microscleres, and no localisation of spicule categories within the skeleton. All the species described have surface brushes of tylostyles with a layer of tylostyles, parallel to the surface, overlying the brushes. The choanosomal skeleton always contains fibre cored by tylostyles. Some variation between species is apparent in the thickness of the parallel layer of spicules, the density of the spicules within the surface brushes, the proximity of the brushes to each other, and the degree of fibre development internally.

There are two possible explanations for the diversity of morphotypes found within this genus. One is that there is a single species with extreme variation in external morphology that occurs over a lengthy latitudinal gradient (Northern Territory border along the west and south coasts of Australia to New South Wales). The second is that the morphological characteristics are indicative of fixed differences at the species level. The first explanation was rejected when the phenotypic differences were found to be consistent and invariable. These morphological features identify a suite of sibling species defined by a range of phenotypic characters, primarily their consistently recognisable external growth forms. Differences were also noted in membrane development, thickness of the sponge lobes, and sizes of the spicules (Table 10). *C. plicata* is characterised by narrow lobes with frilled edges, a fine adherent surface membrane, thin lobes and medium sized spicules; *C. pennatula* has very wide leafy lobes, a fine adherent surface membrane, thin porous lobes and long spicules; *C. perfoliata* has irregularly shaped thick lobes, a thick membrane, and medium sized spicules; *C. amplexa* has thick regular lobes, a detachable membrane and long thick spicules; *C. biflabellata* has a fan shaped morphology and long spicules, while *C. venosa* and *C. reticulata* have veined lobes and interconnected lobes respectively, and both species have thin spicules.

For some marine phyla the endemic component of the southwestern Australian fauna has been

**Table 10** Characteristics of the species of *Caulospongia*.

Species	Growth form	Membrane	Lobes	Spicule size (mean)	Distribution
<i>C. plicata</i>	narrow lobes with frilled edges	thin adherent	thin, faintly porous	153–199 $\mu\text{m}$ long, 5–8.7 $\mu\text{m}$ wide	North of Port Hedland to Shark Bay
<i>C. pennatula</i>	wide leafy lobes	thin adherent	thin porous	180–215 $\mu\text{m}$ long, 5.9–9 $\mu\text{m}$ wide	Carnarvon to Abrolhos
<i>C. perfoliata</i>	thick irregular lobes	thick adherent	thick, slope upwards	166–197 $\mu\text{m}$ long, 4.9–7.9 $\mu\text{m}$ wide	Perth coast to Fitzgerald River
<i>C. amplexa</i>	thick regular lobes	thick, detachable	thick, slope downwards	171–220 $\mu\text{m}$ long, 5.4–10 $\mu\text{m}$ wide	Bonaparte Archipelago to Abrolhos
<i>C. venosa</i>	thick irregular lobes	thick adherent	thick, veined	180 $\mu\text{m}$ long, 4.6 $\mu\text{m}$ wide	Spencer Gulf, Sth Aust.
<i>C. reticulata</i>	lobes with reticulation	thick, adherent	thick, connected	172–194 $\mu\text{m}$ long, 4.5–7.2 $\mu\text{m}$ wide	Capel River to Gulf of St. Vincent, SA
<i>C. biflabellata</i>	fan shape	thick, adherent	–	182–222 $\mu\text{m}$ long, 6.7–8.6 $\mu\text{m}$ wide	North West Cape to Albany
<i>C. elegans</i>	branched network	thin adherent	–	183–198 $\mu\text{m}$ long, 7.4–9.4 $\mu\text{m}$ wide	Pt. Jackson and Broughton Is.

reported to have affinities with the southern Australian fauna (Hooper and Lévi 1994), and some authors suggest a 'Western Australian Province' may occur on this coastline (Knox 1980). To date, species of the genus *Caulospongia* have only been collected from Australian seas, and predominantly from Western Australia. Only two species, *C. elegans* and *C. venosa* have distributions that do not extend into Western Australian state waters; *C. elegans* is reported from Broughton Island and Pt. Jackson in New South Wales and *C. venosa* from Spencer Gulf in South Australia. The biogeographic implications of these distribution patterns are interesting, but prior to concluding that *Caulospongia* is indigenous to Western Australia with incursions and subsequent speciation in southern and eastern seas, further collection from adjacent waters must be made.

A Western Coast Overlap Zone between the tropical fauna of the Northern Australian tropical province and the Southern Australian Warm temperate province, is thought to be a region of transition of species with a gradual replacement of a tropical fauna in the north by a predominantly temperate fauna in the south (Wilson and Allen, 1987). In this study, none of the North Western species occur further south than the Abrolhos Islands and the southern *C. perfoliata* is not found

further north than the Perth metropolitan coastline (Figure 15). It is not yet known if these distributions are an artifact of the limited collecting undertaken on the species to date, or whether there is some zone of transition between the northern and southern species between the latitudes of Perth and the Abrolhos.

The exception to species with either a northern or southern location is the distribution of *C. biflabellata*. Few specimens of this species have been collected but presently its distribution extends from North West Cape in the northwest to Albany in the southwest (Figure 15). This distribution may be influenced by the south flowing Leeuwin current moving along the Western Australian coastline which enables many tropical species to colonise southern localities such as Rottnest Island off the Perth metropolitan coastline (Morgan and Wells, 1991). Alternatively, this may be a composite species that with future collecting will be split into geographically separated species. There is emerging evidence that species of giant clams formerly thought to have a widespread Indo-Pacific distribution may be instead a number of cryptic species each with a more restricted range (Benzie and Williams, 1997). Only further collection of the *Caulospongia* species within Western Australian waters will assist in resolving the

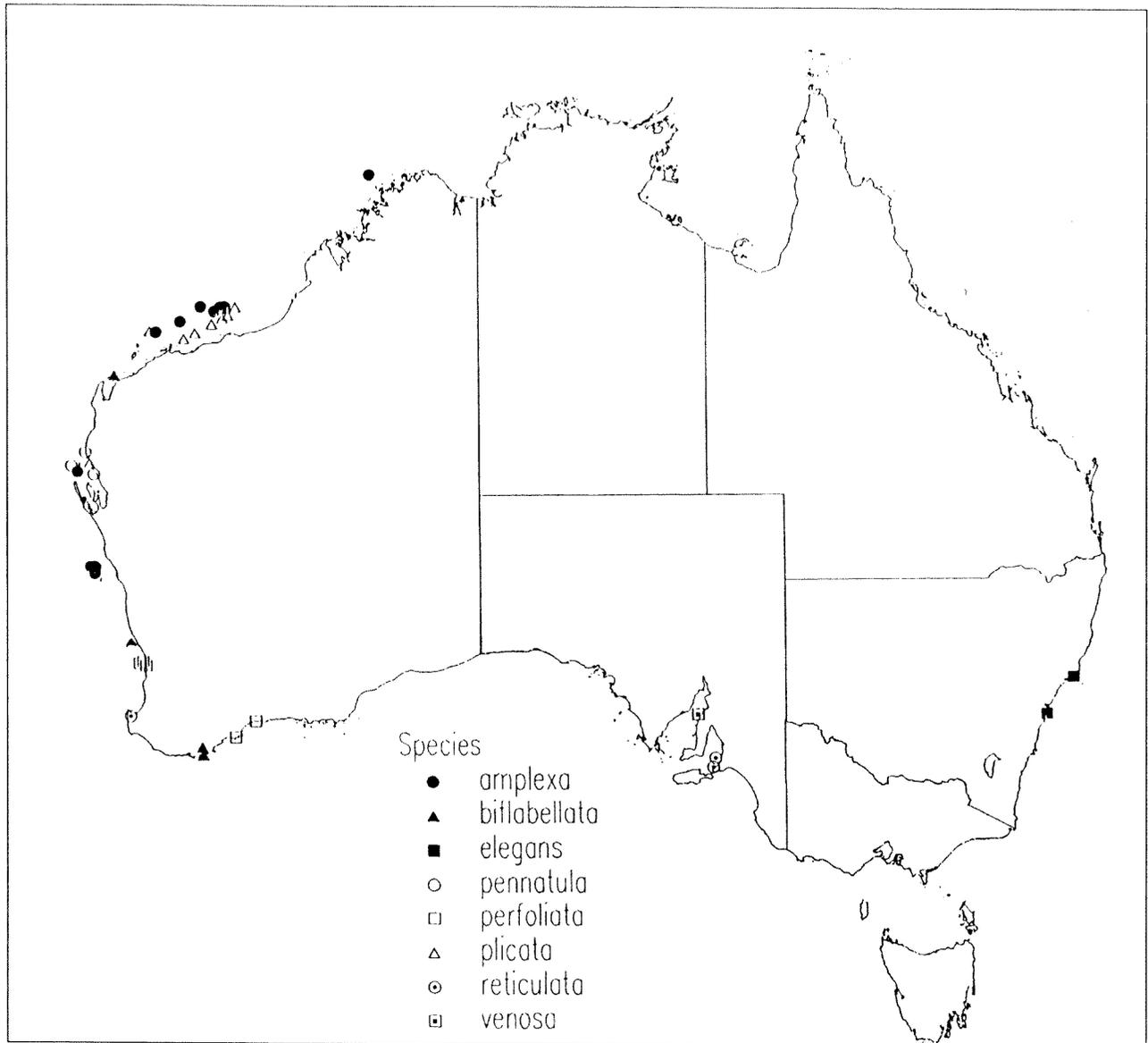


Figure 15 Map of Australia showing the locality of the specimens examined in the study.

geographical boundaries of the species as defined in this paper.

Within species of *Caulospongia* it is possible that populations may have patchy distributions. For example, only one specimen of *C. amplexa* was seen at the Abrolhos during a dive of one hour duration (0–20 m), but when collecting in Albany, *C. biflabellata* was one of the most common sponges encountered, with a specimen recorded approximately every 2 metres on the reef edge during a dive of similar duration (depth 0–10 m) (J. Fromont, unpub. observ.).

The almost complete reliance in this study on preserved Museum material, and therefore the determination of species solely on morphological and skeletal characters of preserved sponges, has highlighted the great need for the continuing use of additional data sets in sponge taxonomy as previously suggested by other authors (e.g.

Bergquist 1978; Bavastrello *et al.* 1994). Such data sets include chemotaxonomy, molecular systematics, enzyme electrophoresis, cytology and reproductive biology, statistical analyses of skeletal characters, as well as reliable ecological data and field descriptions. These alternative characters can be essential in the determination of species boundaries and relationships at generic and higher taxonomic levels.

As more material of the genus *Caulospongia* is collected and preserved using alternative methods, other characters will be examined and applied to the systematics of this group of sponges. There is a need to supplement field descriptions and gather ecological data for each species, and to analyse their biogeographical distributions.

One of the first tasks when frozen material is available will be to examine the chemistry of the species for the presence of the sterol aaptamine.

Bergquist *et al.* (1991) reported the occurrence of aptamine from *Aaptos aaptos* and a species of *Suberites*, and suggested that this may be a taxonomic marker for sponges within the family Suberitidae. To date it is not known whether or not this compound occurs in *Caulospongia*.

Genetic studies have been particularly useful in separating closely related species. Enzyme electrophoresis (Sole Cava *et al.* 1991) and molecular studies (Kelly Borges *et al.* 1991) have both assisted with species determinations and higher order systematics respectively. Similar studies should be undertaken on species of *Caulospongia* once new material is collected.

Skeletal differences can be influenced by environmental conditions. Palumbi (1986) examined sponges of the same species and found that specimens from high wave force habitats had spicule sizes and content that were greater than those from low wave force habitats. In this study, *C. biflabellata* had high spicule content with a thick parallel layer of surface spicules and dense spicule brushes. Collection of specimens of this species from within the same habitat and from other locations would allow for statistical comparisons of spicule size and degree of silification of the skeleton. In turn this would determine if these factors varied between specimens from different localities, or if this species was characterised by a dense skeleton irrespective of environmental factors.

Some of the species in this study have overlapping distributions, such as the North Western species *C. pennatula*, *C. plicata*, and *C. amplexa* (Figure 15). If more than one species is found at a locality in reasonable numbers, then examination of their reproductive biology will assist with the determination of species boundaries. Studies of reproduction in sympatric species of *Xestospongia* demonstrated reproductive isolation by differences in timing of the spawning events, and reinforced the morphological distinctions that separated the species (Fromont and Bergquist 1994).

In summary, this study differentiated eight species of *Caulospongia* on the basis of consistent morphological characters. The identification of a species of *Caulospongia* with interconnecting nodes supported the synonymy of the genus *Plectodendron* (established for a sponge with reticulate branches) with the genus *Caulospongia* (established for species with circumvolving lobes). On the basis of spicule complement and skeletal characters examined here the location of the genus within the family Suberitidae is confirmed. Future studies will examine biochemical, reproductive, molecular and genetic characters of this genus and confirm the morphological systematics presented here.

## ACKNOWLEDGEMENTS

Many thanks to Dr L. Matz, Mr Bruce Beaney and staff of the Histopathology Lab. of Royal Perth Hospital for allowing me the use of microtomes, Mr Kevin Bancroft and CALM for the Fitzgerald River material and photographs, Department of Fisheries, Geraldton, for use of their facilities at the Abrolhos Islands, The Marine BioProducts Group, Australian Institute of Marine Science for photographs, Christine Hass, University of Western Australia, for constant assistance as a dive buddy, David Sutton for assistance with photography in the field.

The following staff of the WAM provided assistance: Mark Salotti for technical assistance, databasing and photography, Alex Bevan for use of his photo microscopy equipment, Clay Bryce for photographic assistance, and Mark Cowan for assistance with maps.

I thank workers at the following Museums for their assistance with providing Type and other sponge material that greatly facilitated this study: Penny Berents, Australian Museum, Sydney; Claire Valentine, Museum of Natural History, London; Claude Lévi, Museum National d'Histoire Naturelle, Paris; Karen Coombes, Northern Territory Museum of Arts and Sciences, Darwin; John Hooper, Queensland Museum, Brisbane; and Thierry Laperousaz, South Australian Museum, Adelaide.

I thank Professor Dame Pat Bergquist and Dr. John Hooper for useful comments on the manuscript.

This study was funded by ABRS (Australian Biological Resources Study) and carried out at the Museum of Natural Science, Perth, Western Australia.

## REFERENCES

- Bavestrello, G., Pansini, M. and Sarà, M. (1994). The variability and taxonomic status of different *Petrosia*-like sponges in the Mediterranean Sea. In Soest, R.W.M. van, Kempen, T.M.G. van and Braekman, J.-C. (eds). *Sponges in Time and Space*: 83-92. Balkema, Rotterdam.
- Benzie, J. A. H. and Williams, S. T. (1997). Genetic structure of giant clam (*Tridacna maxima*) populations in the West Pacific is not consistent with dispersal by present-day ocean currents. *Evolution* **51**: 768-783.
- Bergquist, P. R. (1978). *Sponges*. 268 pp. Hutchinson, London.
- Bergquist, P. R., Cambie, R. C. and Kernan, M. R. (1991). Aptamine, a taxonomic marker for sponges of the order Hadromerida. *Biochemical Systematics and Ecology* **19**: 289-290.
- Bowerbank, J. S. (1876). Contributions to a general history of the Spongiadae. Part viii. *Proceedings of the Zoological Society, London* **1876**: 768-775.

- Burton, M. (1930). Additions to the sponge fauna of the Gulf of Manaar. *Annals and Magazine of Natural History* (10)5: 665–676.
- Fromont, J. and Bergquist, P. R. (1994). Reproductive biology of three sponge species of the genus *Xestospongia* (Porifera: Demospongiae: Petrosida) from the Great Barrier Reef. *Coral Reefs* 13: 119–126.
- Hallmann, E. F. (1914). A revision of the monaxonid species described as new in Lendenfeld's 'Catalogue of the sponges in the Australian Museum'. Part 1. *Proceedings of the Linnæan Society of New South Wales* 39: 263–315.
- Hartman, W. D. (1982). *Porifera*. In Parker, S. P. (ed), *Synopsis and classification of living organisms*, 1: 640–666. McGraw-Hill, New York.
- Hooper, J. N. A. (1984). A new genus and two new species of haplosclerid sponges (Porifera: Demospongiae) from the Timor Sea, Northwest Australia. *Proceedings of the Royal Society of Victoria* 96: 55–60.
- Hooper, J. N. A. and Lévi, C. (1994). Biogeography of Indo-west Pacific sponges, Microcionidae, Raspailiidae, Axinellidae. In Soest, R.W.M. van, Kempen, T.M.G. van and Braekman, J.-C. (eds), *Sponges in Time and Space*: 191–212. Balkema, Rotterdam.
- Hooper, J. N. A. and Wiedenmayer, F. (1994). *Porifera*. *Zoological Catalogue of Australia* 12: 1–621. CSIRO, Melbourne.
- Kelly-Borges M, Bergquist P.R. and Bergquist P.L. (1991). Phylogenetic relationships within the order Hadromerida (Porifera, Demospongiae, Tetractinomorpha) as indicated by ribosomal RNA sequence comparisons. *Biochemical Systematics and Ecology* 19: 117–125.
- Kent, W. Saville (1871). On a genus of sponges from North Australia. *Proceedings of the Zoological Society, London* 1871: 615–616.
- Knox, G. A. (1980). Plate tectonics and the evolution of intertidal and shallow water benthic biotic distribution patterns of the southwest Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology* 31: 267–297.
- Lamarck, J. B. P. A. de Monet (1813–1814). Sur les polypiers empates. *Annales Museum Histoire Naturelle Paris* 20: 294–312 (1813), 370–386, 432–458 (1814).
- Lendenfeld, R. von (1888). *Descriptive Catalogue of the Sponges in the Australian Museum*. Sydney. 260 pp. Taylor and Francis, London.
- Lendenfeld, R. von (1889). *A monograph of the horny sponges*. 936 pp. Trubner and Company, London.
- Morgan, G. J. and Wells, F. E. (1991). Zoogeographic provinces of the Humboldt, Benguela and Leeuwin current systems. *Journal of the Royal Society of Western Australia* 74: 59–69.
- Palumbi, S. R. (1986). How body plans limit acclimation: responses of a Demosponge to wave force. *Ecology* 67: 208–214.
- Rützler K. and Smith K.P. (1993). The genus *Terpios* (Suberitidae) and new species in the 'Lobiceps' complex. *Scientia Marina* 57: 381–393.
- Schmidt, E. O. (1870). *Grundzüge einer spongien-fauna des Atlantischen Gebietes*. 88 pp. Engelmann, Leipzig.
- Sole Cava, A. M., Klautau, M., Boury-Esnault, N., Borojevic, R. and J. P. Thorpe. (1991). Genetic evidence for cryptic speciation in allopatric populations of two cosmopolitan species of the calcareous sponge genus *Clathrina*. *Marine Biology* 111: 381–386.
- Topsent, E. (1932). Eponges de Lamarck conservees au Museum de Paris. Deuxieme partie. *Archives Museum Nationale Histoire Naturelle Paris*. (6)8: 61–124.
- Voultsiadou-Koudoura, E. and Soest, R.W.M. van. (1993). Suberitidae (Demospongiae, Hadromerida) from the North Aegean Sea. *Beaufortia* 43: 176–186.
- Wilson, B. R. and Allen G. R. (1987). Major components and distribution of marine fauna. In Fauna of Australia. General Articles. Dyne, G. R. and Walton, D. W. (eds), 1A: 43–68. Australian Government Publishing Service, Canberra.