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SYSTEMATICS AND BIOGEOGRAPHY OF THE GENUS *IANTHELLA* (DEMOSPONGIAE: VERONGIDA: IANTHELLIDAE) IN THE SOUTH-WEST PACIFIC.

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ABSTRACT

Three new species of *Ianthella* Gray (Demospongiae; Verongida; Ianthellidae) from Papua New Guinea and north-western Australia are described. *Ianthella flabelliformis* Gray and *I. basta* Gray are redescribed following reference to type material and to new material. Diagnostic characters of *Ianthella* species are stated and subjected to phylogenetic analysis in order to evaluate the uniformity of the genus. The systematics and biogeography of *Ianthella* are reviewed.

KEYWORDS: Porifera, Demospongiae, Verongida, Ianthellidae, *Ianthella*, new species, taxonomy.

INTRODUCTION

The verongid family Ianthellidae contains sponges in which the fibre skeleton is most commonly compressed into two dimensions, in an arrangement which is always a reticulation of primary fibres radiating from a constricted base of attachment and supported by abundant connecting fibres. The genera *Ianthella* Gray and *Anomoianthella* Bergquist differ in the degree of regularity, fasciculation, and coarseness of the fibre skeleton. Fibres consist of a diffuse pith surrounded by a concentrically laminated bark, into which spongocytes are incorporated. The choanosomal construction of all Ianthellidae is cavernous, but the region can be reinforced locally with collagen. Choanocyte chambers are eurypylous, sometimes markedly elongate.

The genus *Ianthella* contains thin, frequently large fan or vase-shaped sponges, which display the typical verongid range of colours, yellow, orange, green, blue and purple. In *Ianthella* the skeleton, which makes up the bulk of the sponge body, is developed in two dimensions; it can be a complex reticulation of fascicles, or an anastomosing network of single fibres. Extensions of the fibres at right angles to the two dimensional plane of the sponge are present in several species.

Six species of *Ianthella* have been described by Lendenfeld (1889) and Poléjaeff (1884). Of these species, only *I. flabelliformis* (Pallas) and I. basta (Pallas) were considered to be valid (Bergquist 1980), although there is considerable confusion in the past literature regarding the diagnostic characters that differentiate these easily recognised species. *Ianthella ianthella* de Laubenfels has been transferred to the genus Verongula (Wiedenmeyer 1977), and *Ianthella ardis* de Laubenfels is a synonym of *Aiolochroia crassa* (Bergquist 1980, 1995). *Ianthella concentrica* Hyatt and *I. homei* Gray have been declared unrecognisable by Bergquist (1980). In this communication we report three new species of *Ianthella* from northern Australia, eastern Australia and Papua New Guinea, and redescribe *I. flabelliformis* and *I. basta*.

METHODS

Colour notation for preserved and living specimens follow Munsell (1942). Collections were made by the authors unless otherwise stated. To examine skeletal structure, sections of sponge tissue were macerated in 10 % sodium hypochlorate for 2-5 minutes, washed thoroughly in water and stored in 70 % ethanol. Skeletons were mounted on aluminium stubs and sputter-coated with 10 nm gold. Skeletons were examined and photographed using a Phillips 505 scanning electron microscope at 20 kV. The holotype of *Ianthella reticulata* sp. nov. has been deposited in the Australian Museum (AM), Sydney, Australia, and the registration numbers are cited in the text. The holotypes of *Ianthella labyrinthus* sp. nov. and *I. quadrangulata* sp. nov. are in the Northern Territory Museum (NTM), Darwin, Australia, and the Natural History Museum (BMNH), London, United Kingdom, respectively. Other abbreviations - MNHN: Muséum National d'Histoire Naturelle, Paris, France; AIMS: Australian Institute of Marine Sciences, Townsville, Australia; UAZA: Zoology Department, University of Auckland, Auckland, New Zealand; NSRC (UPNG): Natural Science Resource Centre, University of Papua New Guinea, Port Moresby, Papua New Guinea; CRRF: Coral Reef Research Foundation, Micronesia; 0CDN: specimen sample numbers for United States National Cancer Institute shallow-water collection program contracted to CRRF. A complete collection of all 0CDN specimens is located at the Smithsonian Institution (United States National Museum); Q66C: specimen sample numbers for United States National Cancer Institute shallow-water collection program previously contracted to AIMS. This latter collection is destined to be located at the Queensland Museum, Brisbane, Australia.

SYSTEMATICS

Order Verongida Bergquist
Family Ianthellidae Hyatt
Genus *Ianthella* Gray

Ianthella Gray, 1869: 49; Hyatt, 1875: 407; Poléjaeff, 1884: 37; Lendenfeld, 1888: 23, 1889: 683; Wilson, 1925: 474; de Laubenfels, 1936: 31, 1948: 154, Bergquist, 1980: 443-503.

Basta Oken, 1815: 77; Burton, 1934: 596.

Haddonella Sollas, 1903: 557.

Type species. *Spongia flabelliformis* Pallas 1776: 380 (by subsequent designation, Topsent 1905).

Diagnosis. Ianthellidae in which the fibre skeleton is compressed in a single plane to produce a single, bilamellate or multilamellate fan or vase, frequently of very large size. The skeleton makes up the bulk of the sponge body and can be a rectangular reticulation of fascicles crosslinked by secondary fibres, or a simple reticulation of anastomosing fibres, developed in two dimensions. Fibre outgrowths at right angles to the basic two dimensional reticulum are present in several species. Fibres are deep reddish purple and typically consist of bark with spongocytes in concentric annuli, which surround a pith that makes up between 20 to 50% of the total fibre diameter. The bark immediately surrounding the pith is compact and contains the great bulk of the spongocytes. The outer region of the fibre is less compact, and contains fewer spongocytes. The choanosome is cavernous with large, sac-shaped eurypylous choanocyte chambers. The mesohyl of the choanosome is usually lightly to moderately reinforced with collagen, but the ectosomal region has strong collagen deposition. Sand and detritus can be incorporated into the choanosome of some species, but are absent from the fibres of all species. Sponges are intense yellow, green, orange, blue, and purple in colour.

Ianthella basta (Pallas)
(Fig. 1a-e, Pl. 1a-b, 2a-b, 3a)

Restricted synonymy.

Spongia basta Pallas, 1766: 309.

Spongia striata Lamarck, 1814: 364.

Ianthella flabelliformis; de Laubenfels, 1948: 155.

Ianthella basta Gray, 1869: 51; Bergquist, 1980: 498.

Material examined. UAZA 15.3, 15.11, 15.12, 15.14, 15.17, AM Z5091: Aidler's Bay, Port Moresby, Papua New Guinea, 10 m, 12 January 1986; NSRC (UPNG) 20: Motupore Island, Bootless Inlet, Papua New Guinea, 12 m, 22 June 1984; NSRC (UPNG) 24: Buna Motu Islet, Bootless Inlet, Papua New Guinea, 18 m, 23 March 1985; UAZA 15.30: Apra Harbour, Guam, 15 m, collector C. Birkland, 26 November 1985; AM Z5092, UAZA 20.1: Marie-Helene Reef, Walinde, West New Britain, Papua New Guinea, 26 m, 22 October 1991; UAZA 20.6: Cape Lambert, West New Britain, Papua New Guinea, 20 m, 18 October 1991; Q66C-4357-A: Nagada Harbour, Madang, Papua New Guinea,

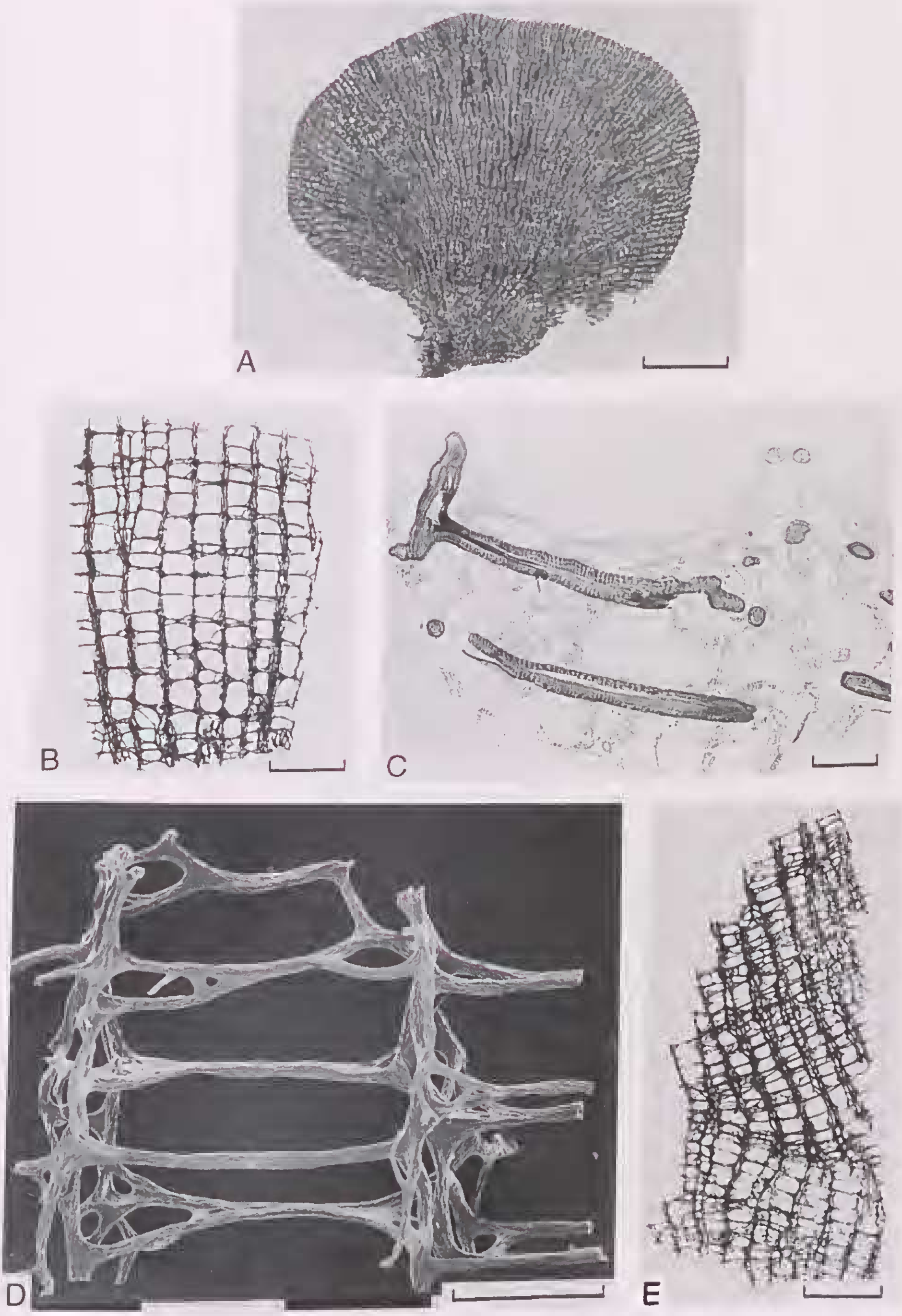


Fig. 1. *Ianthella basta* (Pallas). **A**, preserved specimen showing radiating rows of fine, regularly spaced conules, scale = 2 cm; **B**, the skeleton is a complex rectangular reticulation of fibre fascicles joined by regularly spaced secondary connecting fibres, oriented within a single plane. Note that the fascicles consist of up to four fibres aligned one above the other, perpendicular to the plane of the sponge, scale = 0.5 cm; **C**, soft tissues are cavernous with large sac-like, spherical or slightly oval choanocyte chambers set in a sparse mesohyl. Fibres consist predominantly of bark, scale = 200 μm; **D**, scanning electron micrograph of the skeleton. Note the short, sharply pointed fibres that extend outwards from the edges of the fibre fascicles, scale = 300 μm; **E**, differential growth rates are evident in the lamella in bands of very closely spaced connecting fibres laid down in new directions, scale = 0.5 cm.

20 m, 4 September 1990; UAZA 4.1, 6.2: Davies Reef Lagoon, Great Barrier Reef, Australia, 20 m, 18 August 1982; UAZA 6.1: Darwin Harbour, Northern Territory, Australia, May 1984.

Additional material. MNHN DT578 (82): *Spongia basta* Pallas; MNHN DT523 (48): *Spongia striata* Lamarck.

Description. Elongate fan or vase, occasionally with basal fanlets, up to 1500 cm in height and width, 1-3 mm thick. Sponges are attached to the substrate at a constricted base which is thickened and strengthened by crowded fibre fascicles (Fig. 1a). Small specimens are semicircular and attached along the base of the lamella; vase-shaped specimens can be attached by a solid or circular base. Large specimens are undulate with waves along the vertical, and occasionally, the horizontal axis of the sponge (Pl. 1a,b, 2a,b). The surface is extremely regular with radiating rows of sharply pointed conules, 0.5-1.0 mm high, 1.0-2.5 mm apart. Oscules are 0.5-1.0 mm diameter, and inhalant pores are separated on opposite sides of the sponge lamella; scattered within the depressions between the fibre meshes.

The sponge is flexible, and the surface is fleshy but slightly harsh to the touch due to projecting fibre tips. In life, the external and internal colouration of the sponge is most commonly bluish violet (P6/6-5/6) in the basal three quarters of the sponge, gradually becoming lighter, to greyish magenta (RP7/4) in the outer regions of the sponge. Sponges can also be mimosa yellow (Y7/10), copper green (G7\8-GY7/8), mandarin orange (YR6/10), opal green (BG5/6-6/6), or vivid blue (PB7/6). Deep reddish-purple fibres can be seen through the tissue at the sponge surface. On exposure to air and in ethanol, the sponge rapidly turns dark reddish purple (RP5/2). *Ianthella basta* is oviparous. UAZA 15.12, collected on the 26 January 1986, contains unfertilised eggs 62-94 µm diameter with nuclei and prominent nucleoli. No choanocyte chambers remain intact in this specimen.

Skeleton. The skeleton is a complex rectangular reticulation of fibres oriented within one plane, radiating from the base to the margin of the sponge (Fig. 1b, Pl. 2a,b). Through the vertical plane of the lamella, 1-2 mm wide fascicles composed of two to four fibres 20-100 µm wide, aligned one above the other perpendicular to the plane of the sponge, run 1-3 mm apart and parallel to each other (Fig. 1d). The fasciculi are connected at regular intervals of 1 mm by single, or occasionally tracts of two or three fibres (Fig. 1d). Differential growth rates are evident across the lamella, as bands of very closely spaced connecting fibres that are laid down in new directions (Fig. 1e). Short, sharply pointed fibres extend outwards from the edges of the fascicles (Fig. 1d). The bark component of the fibres is strongly laminated and incorporates spongocytes in concentric arrays, pith makes up approximately one third of the fibre diameter.

Soft tissue. The soft tissues of *Ianthella basta* are uniformly cavernous, with slightly ovate choanocyte chambers 80-100 µm in longest dimension, and large ramifying exhalant canals (Fig. 1c). There is little mesohyl surrounding the chambers. A narrow ectosome 21-73 µm deep is distinguished from the underlying choanosome by a lack of chambers, greater tissue density and collagen reinforcement.

Ecology. *Ianthella basta* is found singly or in groups, on inshore silty patch and fringing reef slopes that experience good tidal or current flow. Marie-Helene Reef in West New Britain, and Aidler's Bay in Port Moresby, Papua New Guinea, support a spectacular growth of 2-3 sponges per m^2, many of which are up to 1.5 m in height.

All specimens examined were infested with an unidentified polychaete which occupies the exhalant canals. A small brown and white striped apodid holothurian, *Synaptula lamperti*, has been recorded in densities of >200 per m^2 on *Ianthella basta* on the Great Barrier Reef, Australia. These have also been recorded in West New Britain. Hammond and Wilkinson (1985) have shown that *Synaptula lamperti* ingests organic exudates from the sponge surface and metabolises these compounds for incorporation into the body wall.

Remarks. *Ianthella basta* is the best known and most easily recognised species of *Ianthella*. This is in part due to its wide distribution in the Indo-West Pacific, and thus its presence in older collections, but it is mainly due to the morphology of the sponge. The thin, two dimensional, fan or vase-like form of *Ianthella basta* is very distinctive, and the fine reticulation of fibres in very regular rectangular meshes, is striking.

Ianthella basta has been well illustrated and described by Lendenfeld (1889) and Topsent (1931). In all specimens examined, there is no evidence of the development of fibrous extensions of the basic two-dimensional skeleton. *Ianthella basta* exhibits the full range of verongid colouration, but no differences in fibre construction or arrangement can be detected between specimens with differing coloration.

De Laubenfels (1948) synonymised *Spongia striata* Lamarck with *Ianthella flabelliformis*. *Spongia striata* has been examined and is definitely a specimen of *I. basta* Pallas, having the fine regular rectangular network characteristic of the species.

Distribution. Northern Australia, Torres Straits, Papua New Guinea, Guam, Mascarene Islands, Indian Ocean.

Ianthella flabelliformis (Pallas)
(Fig. 2a-e, Pl. 4a-b, 5a-b)

Restricted synonymy.

Spongia flabelliformis Pallas, 1766: 380; Lamarck 1814: 550.

Verongia flabelliformis Ehlers, 1870: 11.

Ianthella flabelliformis Gray, 1869: 50; Lendenfeld, 1888: 23; Lendenfeld, 1889: 683 (in part, see *I. quadrangulata* sp. nov.); Poléjaeff,1884: 37; Wilson, 1925: 474; Bergquist, 1980: 497.

Material examined. UAZA 15.10, 15.13, 15.16, AM Z5093: Aidler's Bay, Port Moresby, Papua New Guinea, 10 m, 12 January 1986; Q66C-4771-A: north side of Cumberland Strait, Wessel Islands, Northern Territory, Australia, 16 m, 14 November 1990; UAZA 29: Aidler's Bay, Port Moresby, Papua New Guinea, 15 m, 8 January 1984; Q66C-4532-R: Mananouha (Lion) Island, Bootless Inlet, Papua New Guinea, 22 m, 15 September 1992; NTM Z1410: north-east of Port Hedland, Station NWS 17, 80 m, 19 April 1983; NTM Z908: Dudley Point, Darwin, Northern Territory, Australia, Station EP8, 10 m, 31 August, 1982, collector J. N. A. Hooper; NSRC (UPNG) 114, Q66C-4532-R: Mananouha (Lion) Island, Bootless Inlet, Papua New Guinea, 22 m, 7 March 1985; NTM Z689: West Buccaneer Archipelago, Western Australia, Station DON 19, 35 m, 28 April 1982; NTM Z850: Channel Island, Darwin, Northern Territory, Australia, Station CI3, 12-13 m, 20 August 1982, collector J. N. A. Hooper; NTM Z1072: Fish Reef, Bynoe Harbour, Northern Territory, Australia, Station FRI, 10-12 m, 24 November 1982, collector J. N. A. Hooper; BMNH 1930.8.13.164: Great Barrier Reef, Australia; BMNH 1885.8.8.1: south of New Guinea, 9° 59'S, 139°42'E. Station 188, 56 m, 10 September 1874.

Additional material. AM - G9980 Lord Howe Island, Australia; AM - G9975: Lord Howe Island, Australia; AM - G9981: Manly Beach, Australia; AM - G8905: Port Jackson, New South Wales; NTM Z2557; MNHN DT534, DT3448, DT3449: *Spongia flabelliformis* Lamarck.

Description. Symmetrical single or bilamellate fan (Fig. 2a, Pl. 4a,b), up to 1000 cm high, 10-15 mm thick in the centre, 1-3 mm on the outer edge of the lamella. Small sponges are elevated by a fibrous stalk. In large sponges the base is broad and thickened by robust fibre fascicles. The surface is raised into narrow irregular ridges 2-5 mm high, except in the outer 40-50 mm of the lamella. Oscules, 1-2 mm wide, are located on one face of the sponge. The texture is harsh. In life the external and internal colour of the sponge is most commonly greenish yellow (GY8/10), occasionally vivid blue (PB7/6) with a whitish cast due to the presence of sand grains in the dermal tissue. Reddish purple fibres (RP3/10) are clearly seen in the surface of the sponge. On exposure to air or ethanol, the sponge is dark reddish purple. *Ianthella flabelliformis* is oviparous, eggs are present in specimen Q66C 4771-A, collected on 10 November 1990. Eggs are 15-73 μm in diameter, ovoid, and grouped in clumps within the choanosome (Fig. 2b, Pl. 5a,b).

Skeleton. The skeleton is a semi-regular reticulation of fibres, 120-500 μm thick, oriented in one plane and radiating from the base to the margin of the sponge (Fig. 2d,e). Primary fibres are loosely fasiculated and interconnected by smaller fibres to form irregular polygonal meshes 2-5 mm wide and 5-7 mm high; variants of this basic pattern occur. In specimen NTM Z1410, the reticulation is irregular and anastomosing, with primary and secondary fibres barely distinguishable. In NSRC (UPNG) 114, the secondary fibres dominate the skeleton and coalesce in places to form a fibrous plate.

Outgrowths from the plane of the lamella are regularly spaced 5-10 mm apart and are composed of fasciculate extensions of the primary fibres that coalesce at the apex to form a round flattened knob up to 5 mm in diameter; the apex of the knob is minutely conulose (Fig. 2c,e). Several adjacent bosses may coalesce to form a surface pattern of meandering, often interconnected ridges. Knobs are more pronounced towards the centre and lower portions of the sponge, and on the poral face.

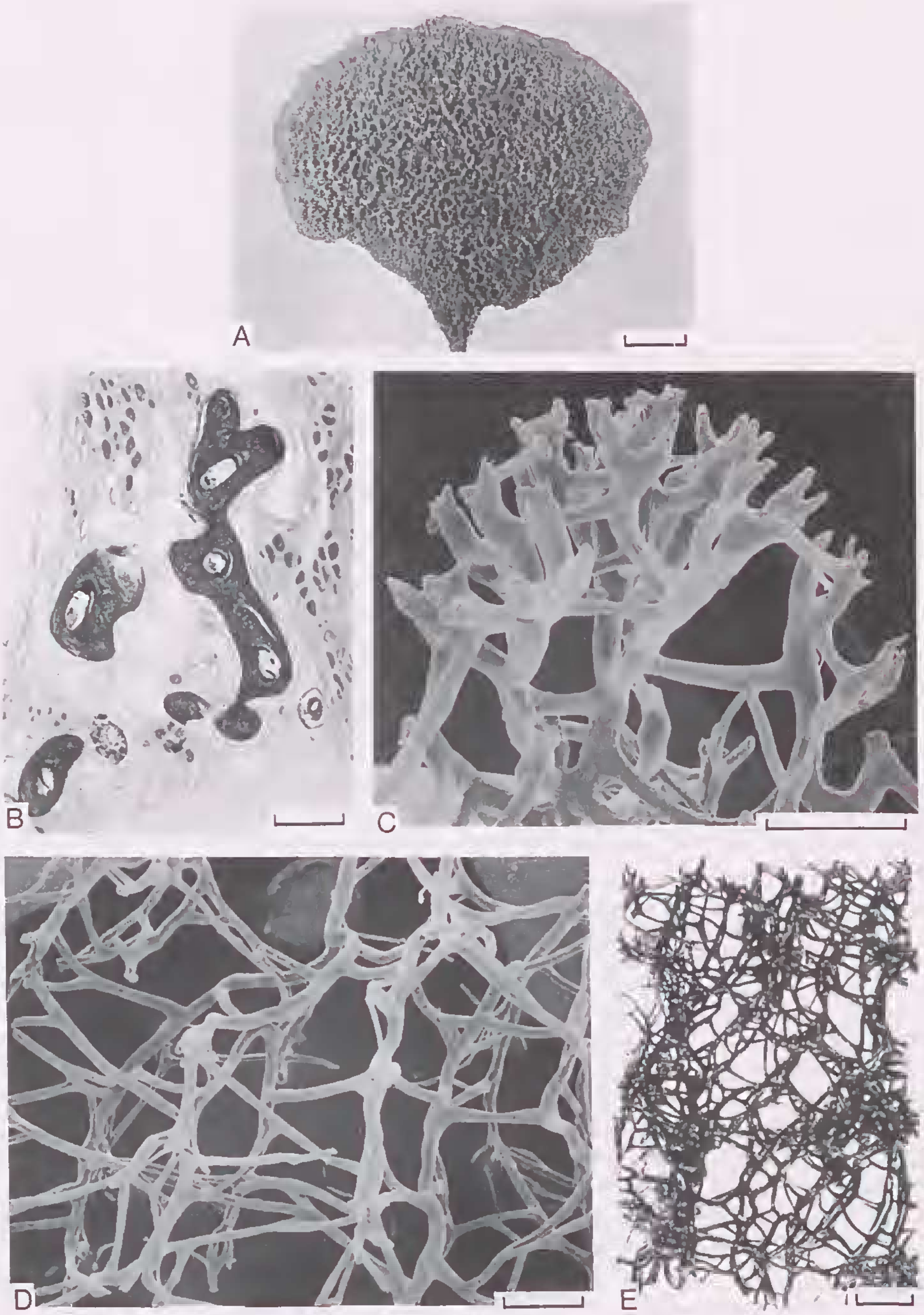


Fig. 2. *Ianthella flabelliformis* (Pallas). **A**, preserved specimen showing narrow irregular interconnected ridges, scale = 3 cm; **B**, the choanosome is cavernous, the choanocytes are grouped within a thick collagenous mesohyl. Fibres are thick, the pith comprising approximately 10 % of the volume of the fibre. Note oocytes grouped in choanosome, scale = 300 µm; **C**, scanning electron micrograph of fibrous skeletal outgrowths. These are composed of fasciculated extensions of the primary fibres that coalesce at the apex to form a round flattened knob, the apex of which is minutely conulose, scale = 100 µm; **D**, scanning electron micrograph of the skeleton which is a semi-regular reticulation of fibres oriented in a single plane, radiating from the base to the margin of the sponge. The primary fibres are loosely fasciculated and interconnected by smaller fibres to form irregular polygonal meshes, scale = 200 µm; **E**, adjacent fibrous outgrowths may coalesce to form a surface pattern of meandering ridges, scale = 0.5 cm.

The bark component of the fibres is strongly laminated and incorporates spongocytes in concentric arrays, pith comprises approximately 10 % of the volume of the fibre.

Soft tissue. The choanosome is cavernous, but choanocyte chambers lie in a moderately thick mesohyl (Fig. 2b). The ectosomal region is heavily reinforced with collagen and is 100-170 µm deep. Sand grains are scattered throughout the ectosome and outer choanosome.

Ecology. The sponge occurs on coral reef slopes in oceanic or inshore waters which experience good current movement. An unidentified polychaete is almost always present in the exhalant canals.

Remarks. Examination of fresh specimens of *Ianthella flabelliformis* from Papua New Guinea and Australia confirm the major features of fibre construction and the choanosome as described by Lendenfeld (1889) and Poléjaeff (1884). This species differs from *I. basta* in having a much less regular skeletal arrangement, as well as in having complex fasciculated fibre extensions perpendicular to the two dimensional plane of the sponge. In *I. basta*, these extensions are short sharp spikes, and the sponge lamella is much thinner as a result. The surface of *I. flabelliformis*, is much less regular than that of *I. basta* and the choanosome can contain sand and detritus.

Our observations of the architecture of surface extensions of *Ianthella flabelliformis* differ in detail from the descriptions given by Lendenfeld (1888), Poléjaeff (1884) and Wilson (1925). The fibres perpendicular to the surface of the sponge have been described as being "ramified in a dendritic manner" emanating from the junction of the primary radial and secondary connecting fibres (Lendenfeld 1888). These fibres in fact arise at irregular intervals along the primary radial fibres and form blunt fasciculations.

There are differences in colouration and the degree of flexibility of the sponge, between specimens of *Ianthella flabelliformis* described here and those described in older literature. The rigidity of the skeleton is dictated by the robustness of the individual fibres, the degree of fasciculation of the primary and secondary fibres, and the presence of surface extensions. The amount of sand incorporated in the sponge tissue will also affect the pliability of the sponge. Bergquist (1980) noted considerable variation among specimens labelled as this species in the London Natural History Museum collections. In particular, some specimens had very thick basal fibres. Many of these specimens, mainly dry, can be assigned to two of the new species described below. Lendenfeld's specimen labelled as *Ianthella flabelliformis* (BMNH 1886.7.8.13) from Port Jackson has very large fibres and is the holotype of *I. quadrangulata*, described below.

Ianthella flabelliformis is common in southern Papua New Guinea and along the eastern and northern coasts of Australia, and is reported to extend as far south as Port Jackson. This southern record rests on an identification by Lendenfeld (1889) of a specimen collected by Ramsay. It was only after publication of this work that Lendenfeld realised that another species, *I. quadrangulata*, could be recognised. It is probable therefore that the true southern limit of *I. flabelliformis* is the southern Great Barrier Reef. This species is most easily recognisable in the field by its frequently bilamellate construction, harsh texture, and irregular embossed surface.

Distribution. Western, northern, eastern and south-eastern coasts of Australia, Torres Straits, southern Papua New Guinea.

Ianthella labyrinthus sp. nov.
(Fig. 3a-c)

Type material. HOLOTYPE - NTM Z691: west of Buccaneer Archipelago, Western Australia, Station DON 19, 35 m, 28 April 1982.

Description. Highly symmetrical circular fan, 140 mm wide and 165 mm high, attached to the substrate by a thick flattened stem 20 mm in diameter and 50 mm high (Fig. 3a). The lamella is 12-14 mm thick basally and 2-3 mm thick at the margin. The surface is thrown into meandrine ridges, which are rounded apically and minutely conulose. Ridges are 1-4 mm wide and 2-5 mm high on the face, and have a roughly concentric arrangement on the oscular face. The outer 7-15 mm of the fan is regularly and minutely conulose. The lamella is flexible, firm and just compressible, the texture rough. In life, the internal and external colouration is greenish yellow (GY8/10), with reddish purple fibres visible through the surface tissue. In ethanol the tissue is deep reddish purple (P3/8).

Skeleton. Primary fibres are irregularly fasciculated in groups of three to five fibres, each 70-200 µm in diameter, interconnected by slightly finer secondary fibres to form small irregular

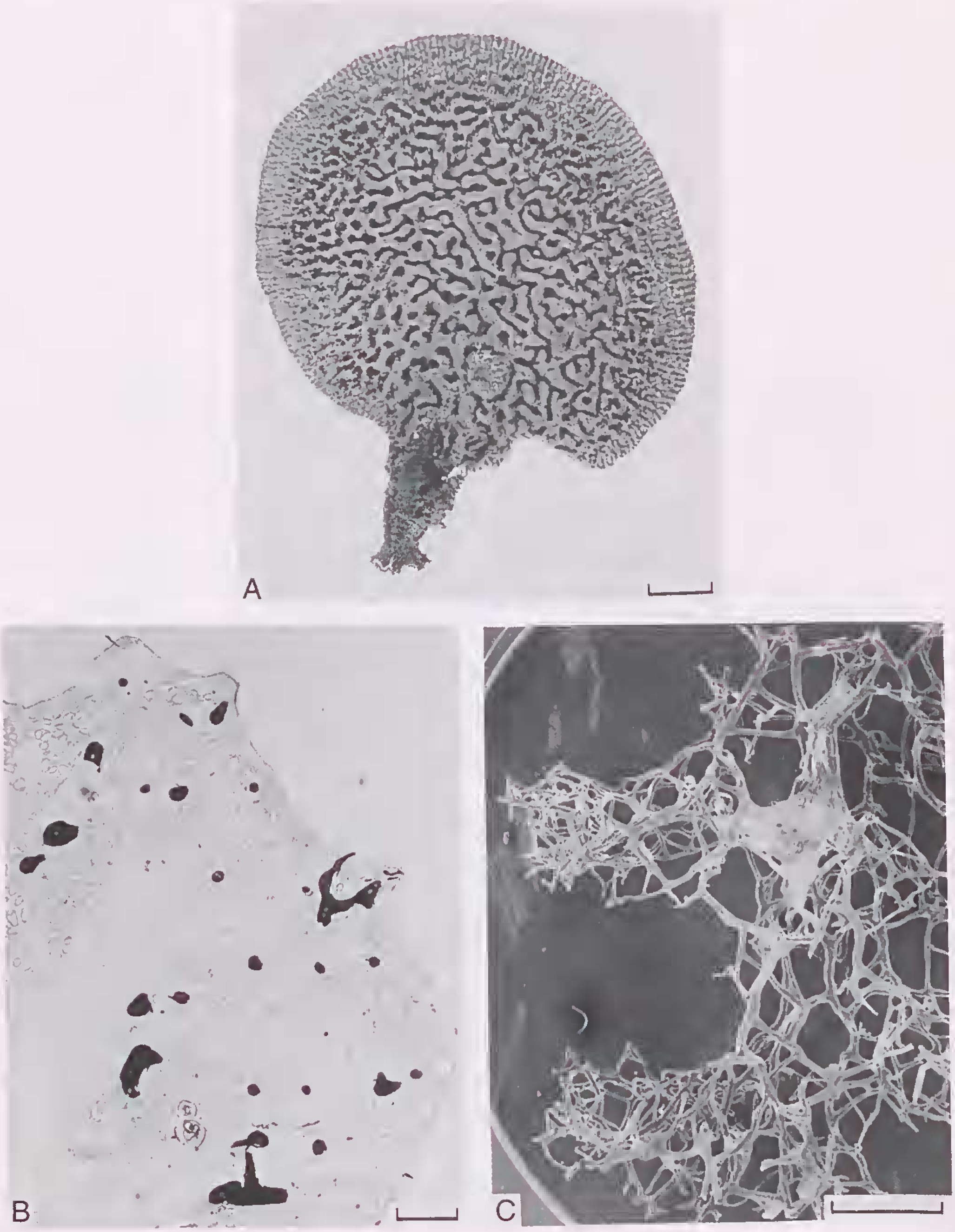


Fig. 3. *Ianthella labyrinthus* sp. nov. **A**, preserved specimen (holotype, NTM Z691) showing the meandrine, interdigitating, rounded minutely conulose ridges, scale = 2 cm; **B**, choanocyte chambers are grouped in a thick mesohyl, the cortex is heavily reinforced with collagen, and sand and spicular debris is scattered within the cortex. Fibres are fine and consist predominantly of bark, scale = 200 µm; **C**, the skeleton consists of fine irregularly fasciculated fibres that are connected by finer secondary fibres to form small polygonal meshes. Complex irregular outgrowths consisting of fine anastomosing fibres extend outward from the sponge lamella, coalescing to form a labyrinthine surface pattern, scale = 300 µm.

polygonal meshes 1-2 mm wide and 5-7 mm high (Fig. 3c). At intervals of 5-10 mm along the fascicular columns, the fascicle broadens and complex outgrowths arise and these coalesce to form elaborate surface ridges. The ridges are arranged approximately concentrically toward the sponge margin, or in a labyrinthine pattern towards the centre of the sponge. The surface extensions are made up of fine irregularly anastomosing fibres 20-50 µm diameter (Fig. 3c). The outer 10-15 mm of the sponge margin is very thin and the skeleton in that region is more regular than at the centre of the sponge lamella.

Individual fibres are up to 200 µm thick and have a very reduced pith. It makes up 5-10 % only of the fibre diameter. The bark is loosely laminated with spongocytes incorporated in concentric arrangement.

Soft tissues. Choanocyte chambers are grouped in a dense mesohyl (Fig. 3b). The ectosome is heavily reinforced with collagen and is 70-120 µm deep. Sand and spicular debris is scattered within the ectosome.

Ecology. The sponge was found attached to a sand-covered rock surface at 35 m.

Etymology. The surface patterning of the sponge is like a maze.

Remarks. *Ianthella labyrinthus* is comparable to *I. flabelliformis* in that the basic two-dimensional skeleton of the sponge is supplemented with fibrous extensions that form an elaborate surface pattern of ridges and knobs. The two species are also greenish yellow and both have a stalked, roughly circular lamella. However, there are differences in skeletal arrangement and resultant surface patterns between the two sponges. The surface of *I. flabelliformis* has very firm squat knobs that render the surface harsh and irregular, while the surface extensions of *I. labyrinthus* form soft microconulose concentric ridges. The fibres of *I. labyrinthus* are much finer than those of *I. flabelliformis* and the pith component of the former species is greatly reduced in comparison. *Ianthella labyrinthus* has a much thicker body than *I. flabelliformis* and this permits development of a dense mesohyl.

The characteristic features of *Ianthella labyrinthus* are the surface patterning and the fine, slightly irregular rectangular reticulation at the outer margin. The skeleton and resultant surface pattern of the outer margin resembles the surface of *I. basta*, although the mesh is not as regular and the radial fascicles are wider.

Ianthella quadrangulata sp. nov.
(Fig. 4a-c, Pl. 6a-b)

Type material. HOLOTYPE - BMNH 1886.7.8.13: Port Jackson, New South Wales (misidentified as *Ianthella flabelliformis* by R. von Lendenfeld).

Additional material. UAZA 25: Fairlight Harbour, Sydney, New South Wales, Australia, 2 February 1964; AM G8906: Port Jackson, New South Wales; FN1334: Port Jackson, New South Wales; BMNH 1844.9.13.32: Illawarra, New South Wales, Australia, presented by J. B. Jukes Esq, collected by H. M. S. *Fly*; BMNH 39.2.4.1: Lord Howe Island, Australia, presented by L. B. Moore; BMNH 1925.11.1.883: Manly Beach, Australia; BMNH 1938.5.2.10: Western Australia, presented by D. L. Serventy, Perth; NTM Z 1784B: west side of Russell Island, Frankland Island Group, Western Australia, 23-26 m; QM G303784: Long Reef, Sydney, New South Wales, Australia, 50 m, collector D. Roberts, 16 August 1993; QM G301211: Pig Is., Port Stephens, New South Wales, Australia, 10 m, collector M. Garson, 1989. QM G304088: Lazarette Gutter, Peel Island, Moreton Bay, Queensland, Australia, 4 m, Collector N. Coleman, 6 October 1993; QM G300027: Outer Gneerings Shoals, off Mooloolaba, Queensland, Australia, 20 m, collector J. N. A. Hooper, 10 December 1991; QM G303942: Jew Shoals, Noosa Head, Queensland, Australia, 20 m, collector J. N. A. Hooper, 9 February 1994.

Description. The sponge is an elongate fan, 10-16 cm high and wide, and 3-5 mm thick with basal fanlets. It has a slightly constricted base of attachment which is strengthened by thick, interlocking primary fibres. The surface is smooth and the lamella is flexible across the horizontal axis only. In life the external and internal colouration is mimosa yellow (Y8/12). On exposure to air, and in ethanol, the sponge turns dark reddish purple (RP5/2).

Skeleton. The skeleton is a simple reticulation of robust vertical fibres 0.5-2.5 mm in diameter, anastomosing to produce a net-like skeleton. The shape of the meshes is elongate and polygonal, measuring up to 20 mm long by 7 mm wide. Finer secondary fibres, 0.2-0.5 µm wide are common, irregularly distributed, and are oriented diagonally across the fan. Fibre pith occupies more than 50 % of the fibre diameter and the bark is laminated, charged with spongocytes in concentric array.

Plate 1. A, *Ianthella basta*, Papua New Guinea, *in situ*, specimen 1.0 m high; **B**, *Ianthella basta*, Papua New Guinea, *in situ*, specimen 1.5 m high.

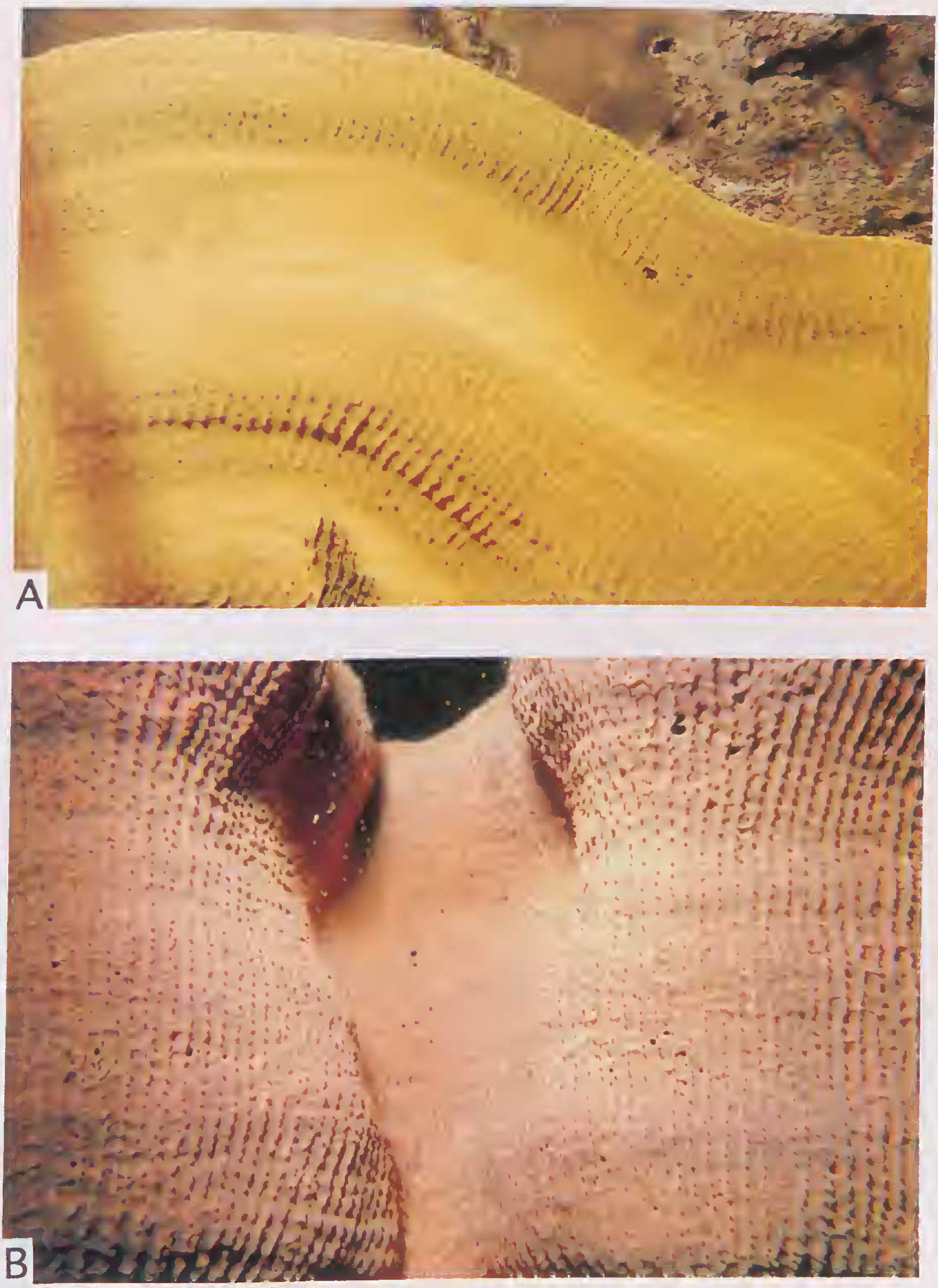


Plate 2. A, *Ianthella basta*, Papua New Guinea, close up of regular rectangular skeleton in the living sponge, natural size; **B**, *Ianthella basta*, Papua New Guinea, close up of undulating body structure, natural size.

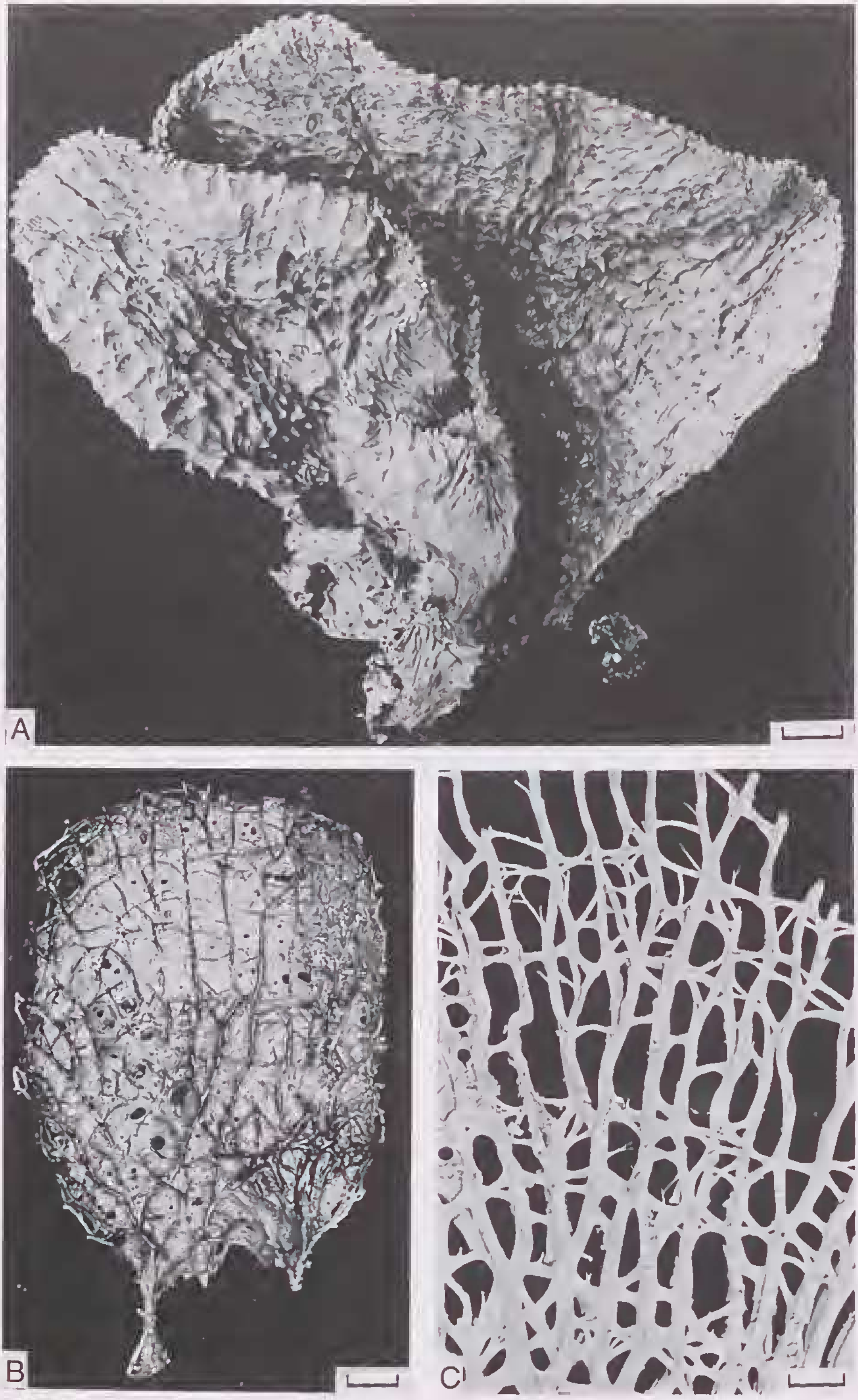


Figure 4. *Ianthella quadrangulata* sp. nov. A, preserved specimen (holotype, BMNH 1886.7.8.13) showing widely spaced sharply pointed surface conules, scale = 2 cm; **B**, preserved specimen showing the large anastomosing primary fibres interconnected by smaller secondary fibres, scale = 1 cm; **C**, the skeleton is a simple reticulation of robust vertical fibres anastomosing to produce a net-like skeleton with elongate to quadrangulate meshes, scale = 1 cm.

Soft tissue. Choanocyte chambers are grouped in a strongly collagenous mesohyl. A large portion of the tissue volume is taken up by broad tracts of collagen that run vertically through the sponge, and surround the fibres.

Ecology. *Ianthella quadrangulata* is found predominantly within harbours and in turbid coastal waters, down to 50 m.

Etymology. The species name describes the shape of the meshes produced by anastomosis of the huge vertical fibres in this species.

Remarks. The major characters that distinguish *Ianthella quadrangulata* from other species of *Ianthella* are the detail of skeletal structure and the extremely collagenous mesohyl. The skeleton is a network of extremely thick anastomosing fibres which lack complex lateral outgrowths. The fibres in *I. quadrangulata* are very thick, and appear to be hollow on drying due to the substantial pith volume.

Ianthella quadrangulata is the southernmost species of this genus and is known to extend only as far north on the east coast of Australia as Hervey Bay in Queensland where it overlaps with *I. flabelliformis* at its southern limit around the Fraser Island and Tweed Heads regions (J. N. A. Hooper, pers. comm. 1995). Both species have a similar depth distribution.

Bergquist (1980) noted that in the collections labelled as *Ianthella flabelliformis* in London's Natural History Museum and the Australian Museum, there were dry specimens that had unusually large fibres. In particular, a group of specimens labelled *Ianthella flabelliformis* (AM G9976) from New South Wales contained a number of fragmentary specimens of *Ianthella* from the *Thetis* collection from Lord Howe Island, all of which had large fibres. Although positive identification was not possible due to the state of the specimens, it is likely that they represent additional records of *Ianthella quadrangulata*.

In an unpublished manuscript held by the Natural History Museum, London, Lendenfeld described specimens of *Ianthella* from various southern New South Wales collections that are very similar to the specimens described above. Lendenfeld suggested that the New South Wales specimens be given the species name *quadrangulata*, which accurately reflects the shape of the skeletal meshes in his specimens and those specimens examined in this study. We have chosen to formally adopt the species name *quadrangulata*, and have designated a further good Lendenfeld specimen labelled *I. flabelliformis* (BMNH 1886.7.8.13) as the holotype of *I. quadrangulata*.

Ianthella reticulata sp. nov.
(Fig. 5a-e, Pl. 3b)

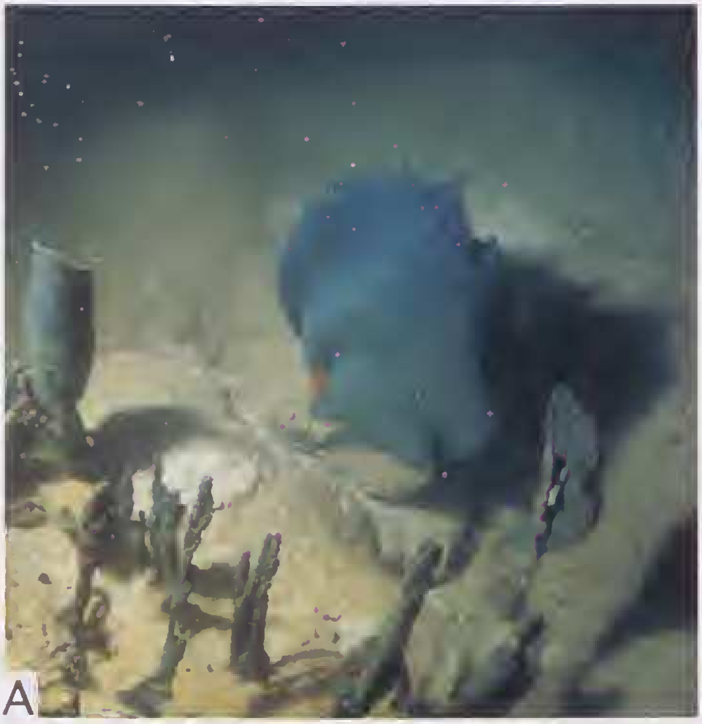
Dendrilla aerophoba; Pulitzer-Finali 1982: 136.

Type material. HOLOTYPE - AM Z5094: Aidler's Bay, Port Moresby, Papua New Guinea, 10 m, 12 January 1986 (UAZA 15.15).

Additional material. UAZA 15.4, 15.8, AM Z5095: Aidler's Bay, Port Moresby, Papua New Guinea, 10 m, 12 January 1986; UAZA 30: Aidler's Bay, Port Moresby, Papua New Guinea, 15 m, 8 January 1984; NSRC (UPNG) 26: Buna Motu Islet, Bootless Inlet, Papua New Guinea, 18 m, 22 August 1984; UAZA 15.GBR: Davies Reef, Great Barrier Reef, Australia, 10 m, 30 October 85; NSRC (UPNG) 70: Mananouha (Lion) Island, Bootless Inlet, Papua New Guinea, 20 m, 17 August 1985; AIMS PA 23: Pandora Reef, Great Barrier Reef, 12 m, 28 May 1984, collector C. R. Wilkinson; UAZA 31, 32, 33, 34: Davies Reef Lagoon, Great Barrier Reef, 20 m, 18 August 1982, collector C. R. Wilkinson; AM Z4113 (Roche FN1915): Russell Is., 12-20 m; AM Z4137: Escape Reef, Great Barrier Reef, 20 m; BMNH 1993.11.19.1 (0CDN 2048-L): Kar Kar Island, north of Madang, Papua New Guinea, 20 m, collector P. L. Colin, CRRF, 19 November 1993.

Description. Semi-circular or irregularly shaped fan, 10-25 cm high and wide, and 5-10 mm thick, frequently prostrate or curled over, attached along the entire length of the lamella (Fig. 5a). The surface is raised into prominent well spaced multiple conules, 5-7 mm high, and 3-8 mm apart, the surface is spikey but very smooth and fleshy between the conules. The texture is elastic and compressible. Oscules 0.5-1.0 mm wide, are regularly distributed on one surface of the sponge. In life the external and internal colouration is mandarin orange (YR6/10), mimosa yellow (Y8/12) or bluish violet (P6/6-5/6). On exposure to air, and in ethanol, the sponge is dark reddish purple (RP5/2).

Skeleton. The skeleton is a simple reticulation of uniform anastomosing fibres, 0.5-1.5 µm in diameter, in a net-like arrangement (Fig. 1c). The primary fibres are zigzagged in the vertical plane, and, through the plane of the lamella, the meshes formed are diamond-shaped and 10-15 mm long by 1-5 mm wide. Fine short secondary fibres 0.2-0.5 µm wide, are oriented diagonally across the fan but only connect between a few



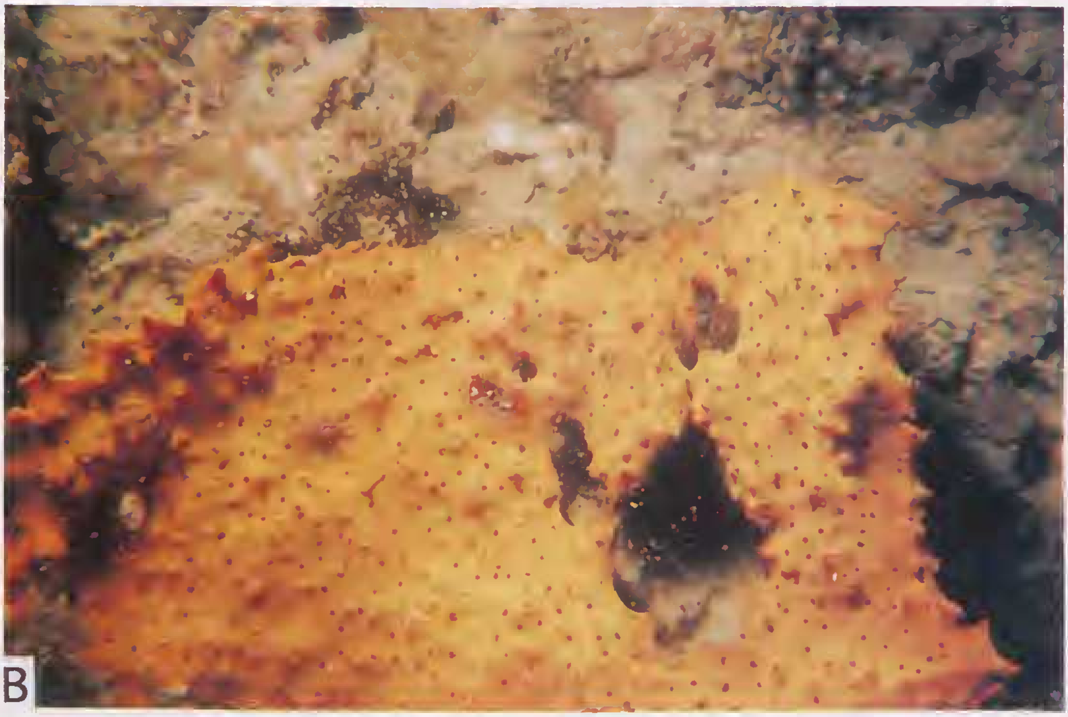


Plate 3. A, *Ianthella basta*, Guam, *in situ*, specimen 1 m high; **B**, *Ianthella reticulata*, Papua New Guinea, close up view of fleshy surface and irregular skeletal pattern, natural size.

Plate 4. A, *Ianthella flabelliformis*, Papua New Guinea, *in situ*, specimen 40 cm high; **B**, *Ianthella flabelliformis*, Papua New Guinea, *in situ*, specimen 30 cm high.

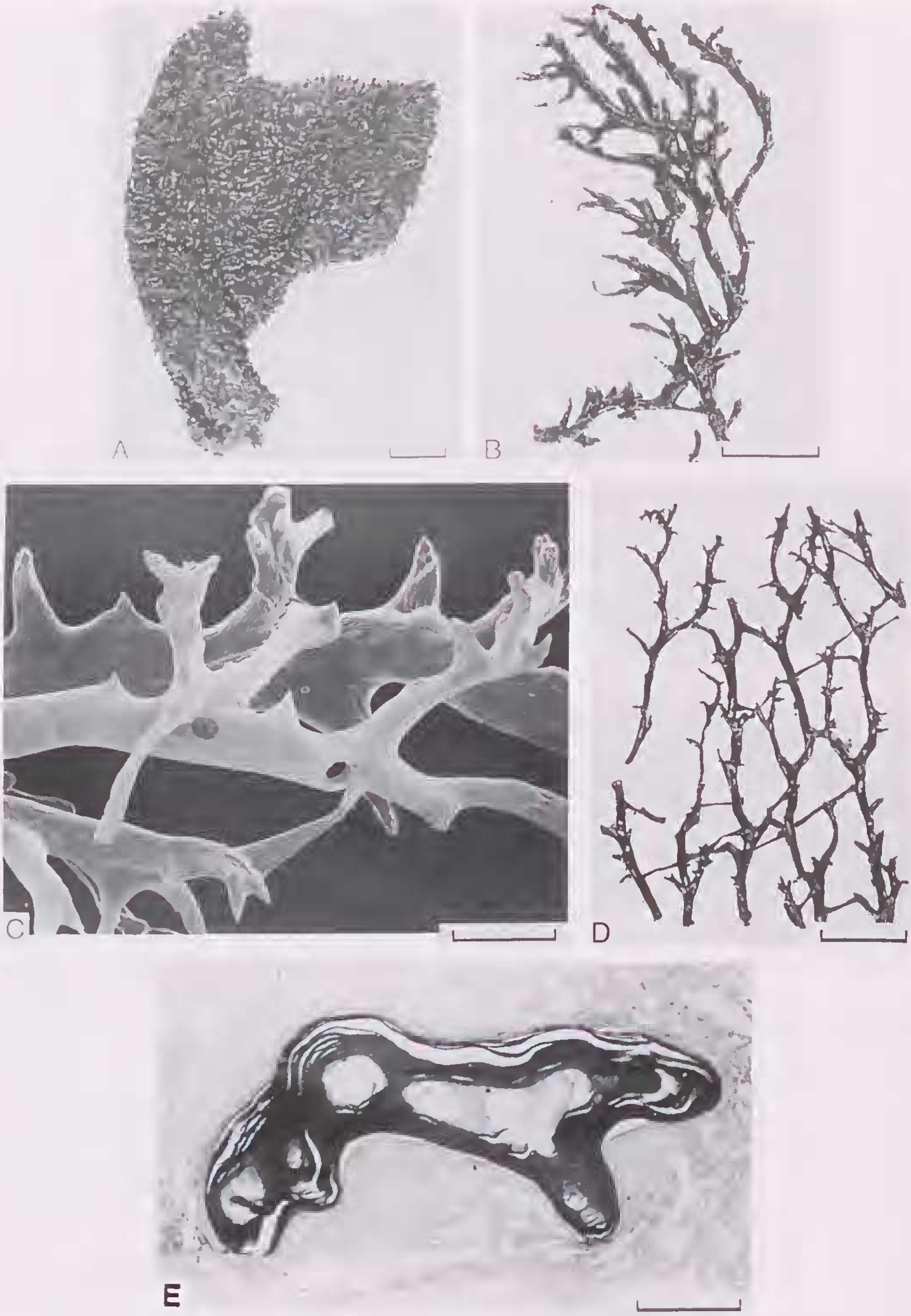


Fig. 5. *Ianthella reticulata* sp. nov. **A**, preserved specimen showing the prominent, well-spaced multiple conules, scale = 1.5 cm; **B**, dendritic spikes extend outwards from zigzagged primary fibres, evident in this lateral view of the skeleton. The oscular face of the sponge is on the right, scale = 0.5 cm; **C**, scanning electron micrograph of the dendritic skeletal outgrowths, scale = 100 µm; **D**, the skeleton is a simple reticulation of uniform anastomosing fibres that is net-like in arrangement. Note the fine diagonal fibres, scale = 0.5 cm; **E**, choanocyte chambers are large, spherical or elongate and are grouped in a mesohyl heavily reinforced with collagen. Pith occupies approximately 50 % of the fibre width, and fibres are sheathed with collagen, scale = 200 µm.

adjacent fibres. These fibres are patchy in occurrence. Dendritic spikes extend outwards from the zigzagged primary fibres; this is evident in the lateral view of the skeleton (Fig. 5c,d), and are more pronounced on the poral face of the sponge. The fibre pith occupies up to 75 % of the fibre width and the bark laminae are charged with spongocytes in concentric array. Often multiple pith elements are surrounded by a common bark layer.

The rigidity of the skeleton varies with the robustness of the fibres, and the degree of their interconnection. Sponges also vary in the degree of lateral ornamentation of the fibre.

Soft tissue. Choanocyte chambers are large, oval or elongate, and the mesohyl is heavily reinforced with collagen. Collagen surrounds the fibres as a sheath. The ectosome on the poral face of the sponge is 147-367 µm deep, strongly collagenous, and honeycombed with inhalant apertures 62-135 µm wide. The ectosome on the oscular surface is compact, 50-170 µm deep and also heavily reinforced with collagen.

Ecology. *Ianthella reticulata* is moderately common, and found on inshore fringing reef slopes. Specimens may be heavily infested with a commensal barnacle, *Acasta porata*, which becomes embedded in the sponge body and attached basally to the fibrous skeleton of the sponge.

Etymology. The skeleton is reticulated like the mesh of a net.

Remarks. *Ianthella reticulata* is closely related to *I. quadrangulata*, which also has anastomosing fibres, an unstalked body and a choanosome that is heavily reinforced with collagen; both possess fibres that are similar in size, structure, and arrangement. They differ in the shape of the skeletal meshes, however, which are zigzagged and polygonal in *I. reticulata*, and flattened and polygonal in *I. quadrangulata*. *Ianthella reticulata* possesses well developed dendritic spikes in a plane perpendicular to the surface of the sponge; these are absent in *I. quadrangulata*. Secondary fibres are quite variable in their distribution within *I. reticulata*, while in *I. quadrangulata* the secondary fibre network is better developed. The two species are geographically separated: *I. quadrangulata* occurs in southern Australian waters, and *I. reticulata* is found in north-eastern Australian waters, southern Papua New Guinea, and occasionally on the north coast of Papua New Guinea.

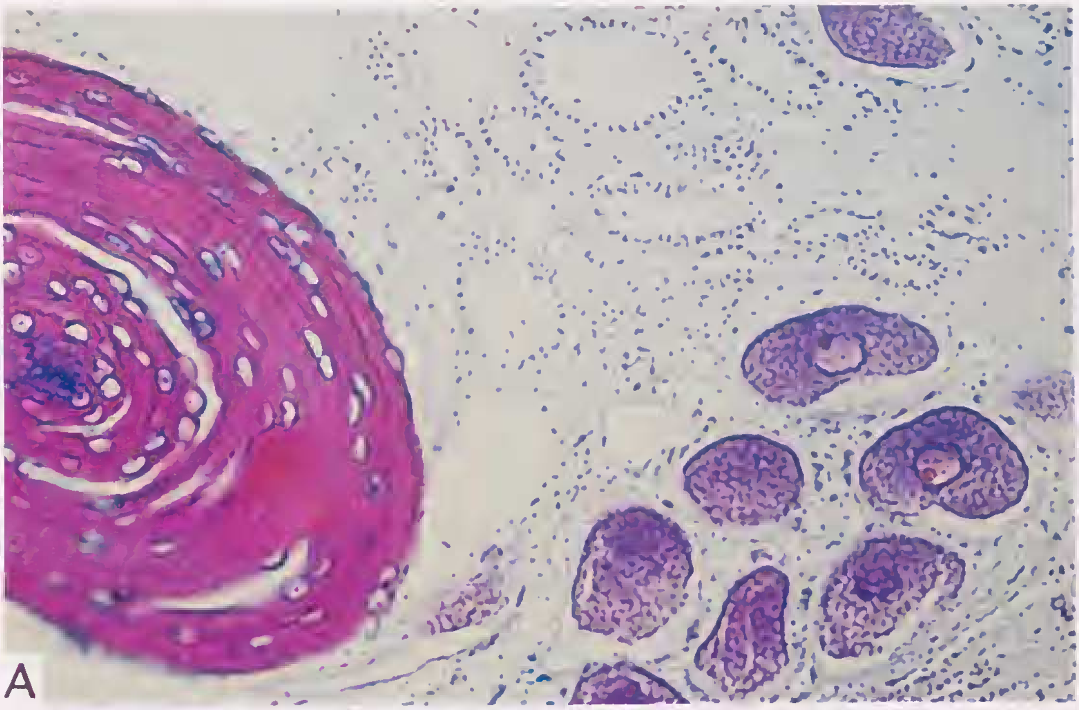
Pulitzer-Finali (1982) identified a fan-shaped yellow sponge from the Great Barrier Reef as *Dendrilla aerophoba* Lendenfeld. *Dendrilla aerophoba* was originally described from Port Philip in Southern Australia, and is described as having strange grooved fibres, and a highly structured cortical armour of clionid chips (Lendenfeld 1889). These novel features are not mentioned in Pulitzer-Finali's brief recent description of the sponge. The Great Barrier Reef specimen is described as being a 10 mm thick fan with a dendritic, anastomosing skeleton of dark laminated fibres, with fibrous offshoots perpendicular to the main skeleton. There is no doubt from this information and from photographs of the specimen that it is *Ianthella reticulata*. *Dendrilla aerophoba* Lendenfeld is unrecognisable on the basis of present collections except as belonging to the Ianthellidae.

Hyatt (1875) described *Ianthella concentrica* from the Fiji Islands, a sponge that was "probably irregularly frondose" and 3-6 mm thick. The skeleton consisted of what appear to be thick fibres 1-3 mm in diameter, "compound and ornamented with thick short spines and minute wart-like prominences". Hyatt also noted that "the fibres are almost always double, contained within common layers of horny material and externally appearing as one stem" which is reminiscent of the multiple piths seen in *Ianthella reticulata* fibres. The skeletal mesh is described as being "quite irregular in size and shape, varying from 12 mm to only 5 mm in length". It is possible that *I. concentrica* is synonymous with *Ianthella reticulata*, but there are no specimens, other than the type which has been declared unrecognisable, available to permit precise identification.

Among species of *Ianthella*, the skeletal structure of *Ianthella reticulata* and *I. quadrangulata* come closest to that of *Anomoianthella*, but the latter sponge has a definite and well developed three dimensional interlocking skeletal structure. Lendenfeld (1888, 1889) placed Western Australian specimens of a thick-walled, cup-shaped sponge with clumped oscules and huge fibres in *Ianthella concentrica* (BMNH 1886.2.19.13). These specimens belong to *Anomoianthella* (Bergquist 1980).

DISCUSSION

The range of morphologies known within the genus *Ianthella* has been extended with the description of three new species and by redescription of *Ianthella flabelliformis* and *I.*



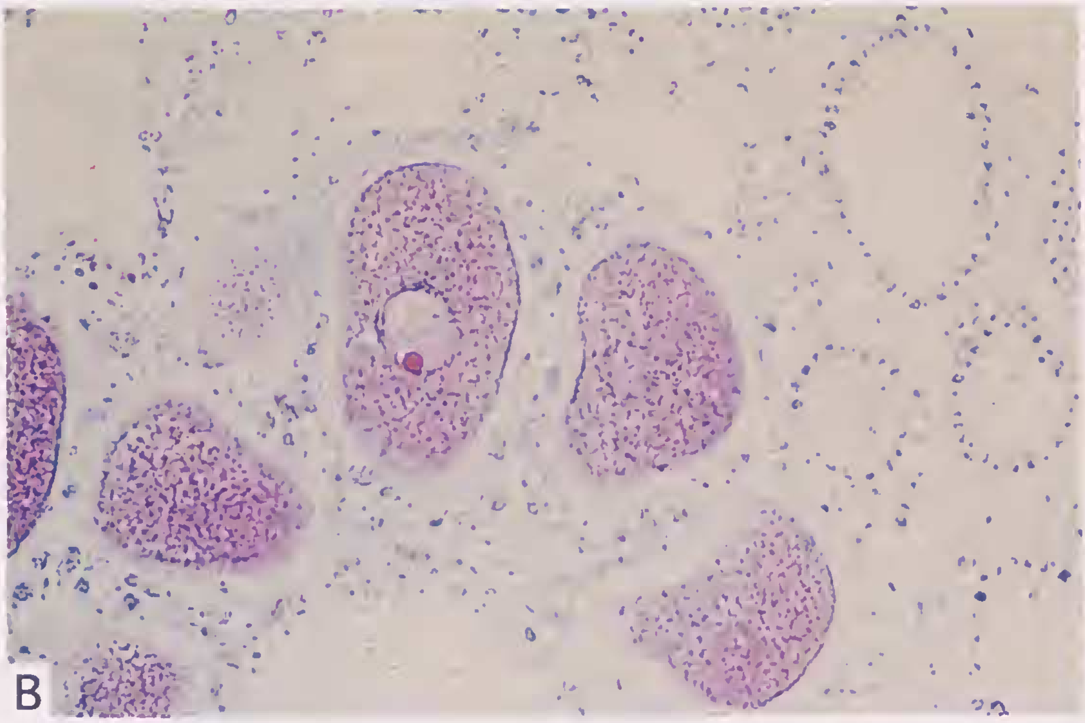


Plate 5. A, *Ianthella flabelliformis*. Photomicrograph to show fibre structure, eurypylous choanocyte chamber structure and developing eggs x 200; **B**, *Ianthella flabelliformis*. Photomicrograph to show detail of egg structure x 600.

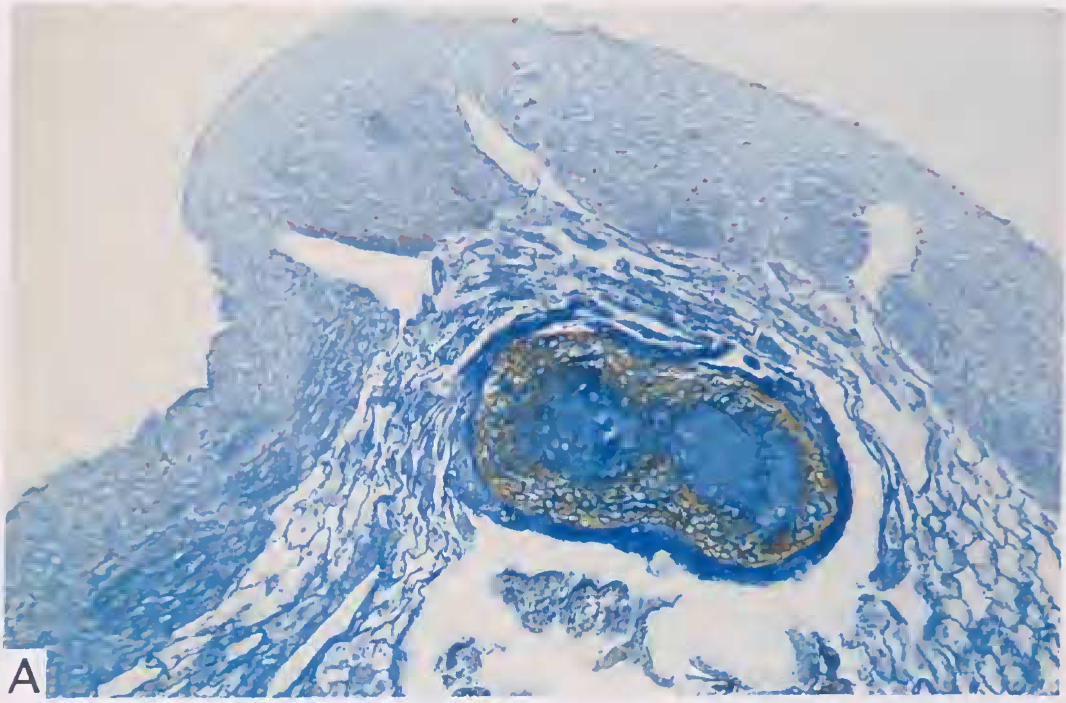


Plate 6. A, *Ianthella quadrangulata*. Holotype. Low power photomicrograph to show strong ectosomal development and fibre structure x 150. This specimen has been preserved since 1889 and the choanosomal tissue has deteriorated; **B**, *Ianthella quadrangulata*. Mooloolaba, Queensland, Australia, *in situ*, specimen 70 cm high.

Table 1. Characters and character states of *Ianthella*. [1] Character states are unique to the species listed. [2] Ianthellid characters 13 and 14, and 15 do not apply to the outgroups, as *Psammaplysilla purpurea* and *Pseudoceratina durissima* do not possess reticulate skeletons, and their skeletons are not compressed into two dimensions as they are in *Ianthella*. Outgroup character states 13, 14 and 15 were thus coded as absent. Character states in italics are unique to the outgroups. [3] Although species of *Ianthella* are relatively uniform in thickness, the surface is frequently ornamented with ridges, knobs and conules, and specimens are often thicker in the centre of the lamella. Character states in character 1 are thus defined as the maximum thickness, including ornamentation, in the centre of the lamella. [4] It is difficult to distinguish between the various hues of yellow that are found within *Ianthella* and the aplysinellid outgroups. Yellow pigmentation ranges from golden or mimosa yellow to lemon in *Ianthella* and *Pseudoceratina*, to greenish yellow or yellow tinged with bright green in *Psammaplysilla* and *Ianthella*. Only clearly defined colours are included in the character list. *A. popae* = *Anomoianthella*; *I.* = *Ianthella*.

MORPHOLOGY

1. Thickness of lamella[3]
- a. 1-3mm: *I. basta*[1]
- b. 5-10mm
- c. 10-15mm
- d. >20mm: *A. popae*[1]
- e. *non-lamellate*

2. Attachment to substrate
- a. distinct stalk or basal constriction of fasciculated primary fibres
- b. stalk absent with only a slight restriction of sponge base

3. Morphology
- a. single fan
- b. bilamellate: *I. flabelliformis*[1]
- c. principal fan plus smaller additional fans
- d. *knob-shaped*
- e. *complex encrusting*

COLOURATION[4]

4. blue violet
- a. present
- b. absent

5. mandarin orange
- a. present
- b. absent

6. vivid blue
- a. present
- b. absent

SKELETAL STRUCTURE

7. Body compressed in a two planes
- a. present
- b. absent

8. General organisation
- a. fibro-reticulate
- b. *dendritic*

9. Fibre:soft tissue volume
- a. fibre dominates
- b. *sparse fibre*

FIBRE CONSTRUCTION

10. Proportion of bark in fibre
- a. significant component of fibre
- b. *absent or reduced to patches*

11. Spongocytes in bark
- a. present;
- b. *absent*

SKELETAL ARCHITECTURE

12. Primary fibres
- a. fasciculated in a plane perpendicular to the plane of the fan, very regular: *I. basta*[1]
- b. irregular non-aligned fascicles
- c. single and anastomosing
- d. *single and dendritic*

SKELETAL ARCHITECTURE (cont.)

13. Mesh shape [2]
- a. extremely regular and rectangular: *I. basta*[1]
- b. vaguely rectangular to elongate
- c. anastomosing primaries form quadrangulate to oval meshes
- d. *absent*

14. Mesh size (av. Hgt x Wdth)[2]
- a. 1x3mm: *I. basta*[1]
- b. 7x3mm
- c. 20x10mm
- d. >20mmx10: *A. popae*[1]
- e. *absent*

15. Outgrowths on the two-dimensional skeleton[2]
- a. boss-like fasciculated outgrowths that render the sponge surface ridged and knobbed
- b. dendritic outgrowths forming multiple surface conules: *I. reticulata*[1]
- c. sharply pointed single spikes forming a very regular conulose surface: *I. basta*[1]
- d. *absent*

16. Maximum fibre thickness
- a. 150um
- b. 500um
- c. 2500um
- d. >2500um: *A. popae*[1]

SOFT TISSUES

17. Density stratification
- a. cavernous; chambers set in sparse mesohyal: *I. basta*[1]
- b. chambers grouped in a moderately dense matrix; collagen evenly distributed.
- c. choanosome heavily infiltrated with collagen, often in tracts
- d. *heavily infiltrated with collagen, extremely dense*

18. Average cortex depth
- a. 70um: *I. basta*[1]
- b. 120-170um
- c. >300um

19. Cortex structure
- a. collagen reinforced
- b. fibrous cuticle: *A. popae*[1]

20. Choanocytes
- a. eurypylous, sac-shaped
- b. eurypylous, elongated and occasionally branched: *A. popae*[1]
- c. *diploidal, spherical and small*

BIOCHEMISTRY

21. Aplystane sterols
- a. *present*;
- b. absent

Table 2. Character state matrix for *Ianthella*. Characters and states are described in Table 1. When a character state is unknown for a particular species, the character is coded with a question mark. Asterisks indicate outgroups. Data for outgroups *Psammaplysilla purpurea* and *Pseudoceratina durissima* were obtained from Kelly-Borges and Bergquist (1988), Bergquist (1965), and Bergquist (1980), respectively. Note that character 19 is uninformative in a cladistic sense, but it is included here for completeness of the character set and for potential information in future work. According to parsimony criteria, a character is informative only if, for the given set of taxa, at least two taxa differ in their assigned character state from the remainder of the set. This is a putative synapomorphic character. Uninformative characters such as the autapomorphic character 19 occur when a character state is different in only one taxon in the entire group for that character. These characters do not illuminate ingroup relationships but are indicative of evolutionary rate or "uniqueness" of the taxon (Swofford, 1991b).

Species	Characters 1-21																				
Order Verongida																					
Family Ianthellidae																					
Ianthella basta	A	A	C	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	B
Ianthella labyrinthus	C	A	?	?	?	B	A	A	A	A	A	B	B	B	A	A	B	B	A	A	B
Ianthella flabelliformis	C	A	B	A	?	A	A	A	A	A	A	B	B	B	A	B	B	B	A	A	B
Ianthella reticulata	B	A	A	A	A	B	A	A	A	A	A	C	C	C	B	C	C	C	A	A	B
Ianthella quadrangulata	B	A	C	B	B	B	A	A	A	A	A	C	C	C	D	C	C	C	A	A	B
Anomoianthella popeae	D	B	A	B	A	B	B	A	A	A	A	C	C	D	D	D	?	C	B	B	B
Family Aplysinellidae																					
*Pseudoceratina durissima**	E	B	D	B	B	B	B	B	B	B	B	D	D	E	D	C	D	C	A	C	A
*Psammaplysilla purpurea**	E	B	E	B	B	B	B	B	B	B	B	D	D	E	D	B	C	?	A	C	A

basta. Traditional diagnostic characters for *Ianthella* have been re-evaluated and details of skeletal architecture, fibre construction, and pigmentation have been given consideration. In particular, we emphasise the pattern of reticulation of the primary radiating fibres, the nature of the secondary connecting fibres, and the development of outgrowths of the skeleton from the plane of the lamella, in redefinitions of taxonomic characters and thus, distinction between species.

A phylogenetic analysis of morphological characters (Tables 1-2) described here, was carried out to examine inter-species relationships within *Ianthella*. Additionally, data for *Anomoianthella popae* Bergquist was included within the analysis, in order to explore further the position of this genus within the Family Ianthellidae. There is no evidence of compression of the skeleton into a single plane in *Anomoianthella*, as there is in *Ianthella*, and the fibrous skeleton forms an irregular anastomosing reticulum (Bergquist 1980). The choanocyte chambers of *Anomoianthella* are eurypylous but elongate and occasionally branched.

In order to obtain a directed phylogenetic analysis, two members of the verongid family Aplysinellidae, *Pseudoceratina durissima* Carter and *Psammaplysilla purpurea* Carter, were chosen as outgroups. The characters that separate these aplysinellid species from *Ianthella* are possession of a sparse, three dimensional dendritic skeleton composed of fibres that do not contain cellular elements, and in which the bark component is significantly reduced or absent. These aplysinellid genera also contain aplystane sterols which are absent in the Ianthellidae (Bergquist et al. 1991). Contention over the correct family name to apply to our outgroup genera has been addressed by Bergquist (1995) and the name Aplysinellidae is upheld.

The analysis was carried out using PAUP Version 3.0 (Swofford 1991a) (Tables 2-3) as described in Bergquist and Kelly-Borges (1991). The data were unordered, unweighted, and the *branch and bound* option was used to ensure that all minimum length trees were obtained. Two equally parsimonious trees were obtained for the data set, each of length 53, and each with a high consistency index (CI) of 0.868. These trees differed only in their placement of *Ianthella quadrangulata* and *Ianthella reticulata* in relation to each other. Hypothetical relationships within *Ianthella* and within the Family Ianthellidae are presented in Figure 6.

The phylogenetic tree indicates that the Ianthellidae is monophyletic with respect to the Aplysinellidae, as represented by the outgroups. The major synapomorphies of the Ianthellidae, or the changes that occur between nodes 1 and 2 in Figure 6, are the possession of a reticulate rather than a dendritic fibrous skeleton (character 8B->A) in which fibres have a significantly amplified bark component (10B->A) and which contain spongocytes in annuli (11B->A). Fibre dominates in volume over soft tissue in Ianthellidae (9B->A). The choanocyte chambers in the Ianthellidae are eurypylous and sac-shaped (20C->B) and these sponges lack aplystane sterols (21A->B).

Anomoianthella is placed with *Ianthella* in the Ianthellidae as it shares features of fibre and soft tissue construction. It also has a similar skeletal structure to *Ianthella quadrangulata* and *I. reticulata*, although the construction is three dimensional. *Anomoianthella* differs, however, from the genus *Ianthella* in that the body is not compressed into a thin fan (7B->A), and the sponge body is not stalked or basally constricted (2B->A). A fibrous cuticle (19A->B) is unique to *Anomoianthella* and choanocyte chambers are elongated and occasionally branched (20A->B).

Ianthella is monophyletic, with *I. basta*, *I. flabelliformis* and *I. labyrinthus* being more closely related to each other than to *I. reticulata* and *I. quadrangulata*, which are situated basally on the tree above *Anomoianthella popae*. Major characters that differentiate species within the *Ianthella* group include the arrangement of the primary fibres, the mesh shape and size, and the nature of the surface skeletal outgrowths. The skeletal factors that separate *I. quadrangulata* and *I. reticulata* (nodes 3 to 4) from other species are essentially the differences in the nature of the surface ornamentation of the sponges. *I. reticulata* has dendritic outgrowths of the skeleton, while in *I. quadrangulata* these are limited to occasional small spikes. Synapomorphies for *I. basta*, *I. flabelliformis*, and *I. labyrinthus* (nodes 4 to 5) include a complex development of the skeleton with primary fibre fascicles (12C->B) in *I. flabelliformis*, *I. labyrinthus* and *I. basta*, and smaller more regular meshes (13C->B, 14C->B) in *I. quadrangulata* and *I. reticulata*. In *I. quadrangulata* and *I. reticulata*, the primary fibres form a loose anastomosing network, connected by small diagonally oriented fibres. Fibres in *I. basta*, *I. flabelliformis* and *I. labyrinthus* are also much thinner (16C->A). Tissue density is reduced in these later three species, and there is less collagen reinforcement of the matrix. The choanosome of *Ianthella* ranges in density from cavernous in *I. basta*, *I. flabelliformis* and *I. labyrinthus*, to heavily reinforced with collagen in *I. quadrangulata* and *I. reticulata*.

Table 3. Data from phylogenetic analysis of species of *Ianthella*. The characters given in Table 1 are listed with the number of character states. The column headed *Status* refers to the a priori definition of the character as questionable (characters that are susceptible to coding errors by misinterpretation), or well defined (characters that can be assigned with confidence to discrete character states, see Bergquist and Kelly-Borges, 1991). The character states of the basal branch of all *Ianthella* species is given along with the pleisiomorphic states of the ingroup *Ianthella*.

Character states	Number	Status	Consistency value	Basal branch of states for *Ianthella*
1	5	Q	1.000	B
2	2	Q	1.000	A
3	5	Q	0.750	A/C
4	2	WD	1.000	A/B
5	2	WD	0.500	A
6	2	WD	1.000	B
7	2	WD	1.000	A
8	2	WD	1.000	A
9	2	WD	1.000	A
10	2	WD	1.000	A
11	2	WD	1.000	A
12	4	WD	1.000	C
13	4	WD	1.000	C
14	5	Q	1.000	C
15	4	WD	1.000	D
16	4	Q	0.750	C
17	4	WD	1.000	C
18	3	Q	1.000	C
19	2	WD	1.000	A
20	3	WD	1.000	A
21	2	WD	1.000	B

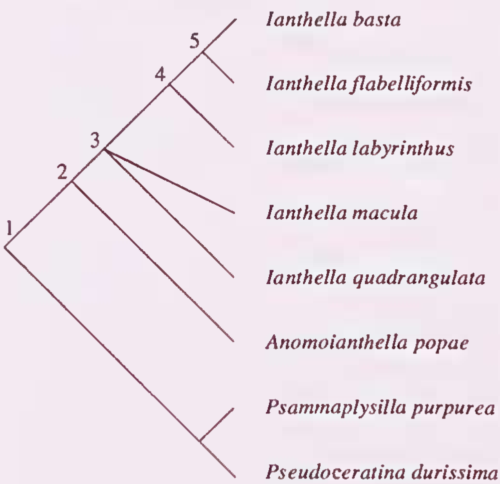


Fig. 6. Hypothetical relationships within the genus *Ianthella* and within the Family Ianthellidae (Demospongiae: Verongida). The hypothesised changes in character states along each branch are as follows. Characters are as in Table 1 and nodes have been given the reference numbers 1-5: nodes 1->2 (5b->a; 3d->a; 1e->b; 8b->a; 9b->a; 10b->a; 11b->a; 12d->c; 13d->c; 14e->c; 20b->a; 21a->b); nodes 2->3 (3a->c; 2b->a; 7b->a); nodes 3->4 (4b->a; 15d-> a); nodes 4->5 (1b->c; 12c->b; 13c->b; 14c->b; 16c->a; 17c->b); nodes 5->6 (6b->a); node 1-> *Pseudoceratina* (17c->d); node 1->*Psammaplysilla* (16c->b); node 2->*Anomoianthella* (1b->d; 14c->d; 16c->d; 19a->b; 20a->c); node 4->*I. reticulata* (15a->b); node 6->*I. flabelliformis* (3c->b; 16a->b); node 6->*I. basta* (1c->a; 12b->a; 13b->a; 14b->a; 15a->c; 17b->a; 18b->a).

Figure 7. Zoogeographic distribution of *Ianthella* and *Anomoianthella* (Family Ianthellidae) within the major Australian marine faunal provinces (Bennet and Pope 1953; Hooper 1991), and a hypothesised evolutionary scenario for diversification of the Ianthellidae.

The differentiation of species of *Ianthella* and their monophyly are well supported by morphological data; characters that largely determine the topology of the tree being the structure of the skeleton, the nature of the fibres and density of the soft tissues. The phylogenetic hypothesis suggests that speciation of the genus *Ianthella* has proceeded from a three dimensional ancestral sponge whose skeleton is a simple anastomosing semi-dendritic network of very large fibres, with dense collagenous tissue, towards a progressively more laterally compressed body plan, with complex fibro-reticulation of small regular meshes, ornamented surface outgrowths, and diversity of pigmentation.

Models proposed for delineation of Australian marine zoogeographic regions by Bennet and Pope (1953), recognise five major divisions which include two tropical provinces (Dampierian and Solanderian), two warm-temperate provinces (Flindersian and Peronian) and a cool-temperate province (Maugean) (Fig. 7).

Table 4. Zoogeographical distribution of Ianthellidae. Species distributions are listed within the major Australian marine provinces (Bennet and Pope 1953) and other locations. The physical localities encompassed within these regions can be found in Fig. 7. IND =Indian Ocean; SE ASIA=Southeast Asia, WCP=West Central Pacific.

	IND	SE ASIA	WCP	AUSTRALIA			
				Dampierian	Solanderian	Flindersian	Peronian
Anomoianthella popae				×			
Ianthella labyrinthus			×				
Ianthella flabelliformis				×	×		×
Ianthella quadrangulata						×	×
Ianthella reticulata					×(+south and north PNG)		
Ianthella basta	×	×	×(Guam)	×	×		

Recent interpretations of this model (Wilson and Allen 1987; Hooper 1991) recognise broad regions of overlap between zones as well as narrow areas of endemism.

The known biogeographic distribution of *Ianthella* and *Anomoianthella* in the Australasian and Indo-West Pacific regions is given in Table 4. Data were obtained from published literature and from London's Natural History Museum, the Northern Territory Museum and Australian Museum collections, McCauley *et al.* (1992), and the authors' unpublished collections. In the absence of complete collections from the faunal regions in question, a biogeographic discussion can be given with minimal confidence. However, the opportunity exists to make some suggestions on speciation events within the Ianthellidae, as the species in this group have well defined and frequently discrete distributions. Locality records have been verified where possible by examination of material, and a reconstruction of the phylogeny of the organisms is available.

The Dampierian region (mid-west to north-west Australian) has the greatest diversity of Ianthellidae with two apparently endemic species, *Anomoianthella popae* and *Ianthella labyrinthus* (Table 4). From the Dampierian region, *I. basta* extends north into Southeast Asia and the West Central Pacific, and east across the top of Australia into the Solanderian province (Great Barrier Reef). This is the most widely distributed species of *Ianthella*. Unlike *I. basta*, the northern limit of *I. flabelliformis* is the south coast of Papua New Guinea. It also extends east and south into the Solanderian region, and may occur further south in the cooler warm-temperate Peronian region (NSW coast), although as mentioned earlier, this record is questionable. *Ianthella quadrangulata* is restricted to cool-temperate southern waters of the Flindersian province, and the Peronian province where it overlaps in distribution with *I. flabelliformis*. *Ianthella reticulata* is restricted in distribution to the Solanderian region but extends north onto the south coast of Papua New Guinea with *I. flabelliformis*, with a single record north of the Papua New Guinea mainland.

These distributions suggest speciation and dispersal of the genera *Anomoianthella* and *Ianthella* through an ancestor from the mid-west to north-western Australia (Dampierian region), with *I. basta* and *flabelliformis* dispersed into northern and eastern waters, and *I. quadrangulata* into southern waters. The absence of *I. reticulata* from the Dampierian suggests that this species resulted later from a northward dispersal event along the eastern coast of Australia, through isolation from *I. quadrangulata* by cooling southern waters. These two species are very closely related morphologically. This southward dispersal event has parallels in several microcionid genera (Hooper and Lévi 1994).

The contention that the Dampierian region might have been the centre of diversification of *Ianthella* and *Anomoianthella* is supported by an exhaustive study of the Raspailiidae of Australia by Hooper (1991). Hooper found that the fauna of the Dampierian province was extremely diverse as compared with the fauna of the adjacent Solanderian province, and the southern Flindersian province, having many endemic species. Lévi (1979) also contends that the southern Indonesian-northern Australian region has the highest diversity for Indo-Pacific biogeographical provinces, and is the centre for dispersal for Indo-Pacific sponges.

It is interesting to consider the hypothesised phylogeny of relationships within the Ianthellidae (Fig. 6) in the light of these zoogeographic distributions. The phylogenetic reconstruction also hypothesises that a common ancestor to *Ianthella* and *Anomoianthella* first led to the derivation of both *I. reticulata* and *I. quadrangulata;* which of these species came first is equivocal in the analysis. A common ancestor to the *quadrangulata-reticulata* group gave rise to the endemic *labyrinthus*, and then to the most recently derived and most widely distributed *basta* and *flabelliformis*. Historical events that might go towards explaining the later speciation event are the warming of northern Australian waters during the Tertiary "journey" northwards, and renewal of shallow-water contact between Australia and Southeast Asia during the Miocene.

FIELD KEY TO *IANTHELLA*

1 a. Symmetrical single or bilamellate fan, can be stalked, up to 1m high, 10-15 mm thick, irregular rugose, knobbed surface, texture harsh, compressible, yellow-green or blue. 2

b. Elongate fan or vase, occasional basal fanlets, surface smooth to microconulose 3

c. Surface smooth and fleshy between well spaced conules, sponge 5-10 mm thick, fleshy, highly elastic and flexible, blue-purple, yellow, orange and lilac, found on the north-eastern Great Barrier Reef, and predominantly in southern Papua New Guinea. ....*Ianthella reticulata*

2 a. Surface covered in squat firm knobs and very irregular ridges, sponge firm and harsh to the touch, yellow-green or blue with a whitish sheen, found in western, northern, and eastern Australia and southern Papua New Guinea. .... *Ianthella flabelliformis*

b. Surface outgrowths form concentric or labyrinthine microconulose ridges, surface soft and sponge pliable, stalked, found in western Australia only *Ianthella labyrinthus*

3 a. Surface smooth , huge vertical rib-like anastomosing fibres can be seen through lamella, sponge fairly rigid in horizontal plane, yellow, found in southern and western Australian waters, and extends eastwards to Lord Howe Island...... *Ianthella quadrangulata*

b. Elongate fan or vase, occasionally with basal fanlets, up to 1.5 m high, 1-3 mm thick, very regular micro-conules forming a ladder-like surface pattern, frequently wavy, purple, green, yellow, orange or blue, found throughout Australia, the Indian Ocean and the Indo-West Pacific ... .*Ianthella basta*

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