



## The most common sponges on the Great Barrier Reef seabed, Australia, include species new to science (Phylum Porifera)

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### Abstract

We describe two new species amongst the most common sponges living on the seabed (inter-reef) of the Great Barrier Reef (GBR) collected during a multi-agency survey (GBR Seabed Biodiversity Project 2003–2006) of the shelf benthic biota using a trawl and dredge at 1254 sites. More than 1,200 sponge morphospecies (operational taxonomic units or OTUs) were recognised, many of which are potentially new species. This paper describes five of the most common sponges, two of which are new to science, *Dercitus xanthus* **sp. nov.** and *Paracornulum fistulosum* **sp. nov.** Taxonomic revisions of the three other most common species (*Coscinoderma nardorus* (Lendenfeld, 1886), *Sphēciospongia vagabunda* (Ridley, 1884) and *Xenospongia patelliformis* Gray, 1858), reveal new characters not previously recorded. Extensive distribution maps are provided for these species within the GBR Marine Park. Analysis of the physical data associated with the biota revealed these species had strong preference for sand and carbonate sediments. As colonisers of the soft seabed these most prevalent species provide important habitat stabilisation, enabling succession communities to more readily establish on the seabed. This wide-scale study along the length and breadth of the GBR provides a concise and encompassing view of the distribution and diversity of the seabed benthos, and has significant implications for the conservation and management of the GBR World Heritage Area.

**Key words:** Demospongiae, *Dercitus*, *Coscinoderma*, *Paracornulum*, *Sphēciospongia*, *Xenospongia*, inter-reef, new species, predicted distribution, taxonomy

### Introduction

The Great Barrier Reef (GBR), Australia, is the world's largest reef ecosystem and forms part of the largest World Heritage Area (GBRWHA). The GBR consists of a network of nearly 3,000 coral reefs rising from a continental shelf area of 224,000 km<sup>2</sup>, stretching 2,300 km north to south along its outer perimeter, and extending 23 to 260 km eastwards from the Queensland coast (Hopley 2008). Within the GBRWHA coral reefs occupy only about 7% of the area, whereas the area in between these reefs on the continental shelf (known as the inter-reef or seabed (or reefless seafloor; Hopley 2008), and herein referred to as the seabed), makes up approximately 61% of the GBRWHA (Great Barrier Reef Marine Park Authority, 2009).

The seabed is predominantly shallow, ranging from 20 to 40 m depth in the inshore and wider portions of the shelf, sloping down to about 100 m depth in some places at the edge of the shelf (Hopley 2008), and contains a wide diversity of habitats, such as seagrass beds, submerged patch reefs, sponge gardens and bryozoan mats. Although far more poorly known than the adjacent coral reefs (e.g. see overview of current knowledge of the GBR in Hutchings *et al.*, 2008), this vast seabed area is fundamental to the coral reef ecosystem in providing passages of connectivity between individual reefs and reef systems, and contributes a significant ecological role to the biodiversity of the entire GBR. The seabed is also highly significant for supporting large commercial and recreational fisheries and other activities whose sustainability is dependent on its continuing health, yet until recently knowledge of the seabed was far more rudimentary than the emergent coral reefs.

Consequently, in 2003–2006 a consortium of eight marine research and conservation agencies embarked on the monumental Great Barrier Reef Seabed Biodiversity Project (GBRSBD). The project mapped seabed habitats, sampled and documented their associated biodiversity across the length and breadth of the shelf seabed. Over four years 1,382 sites were documented and sampled using towed video and digital cameras, baited remote underwater video stations (BRUVS), digital echo-sounder, epibenthic sled and research trawls. Huge quantities of data and samples were amassed and processed, including ~600 km of towed video, 100,000 photos, 1150 BRUVS videos, 140 GB of digital echograms, 1,200 sediment samples, and 140,000 records of 5,300 species of invertebrates, plants and fishes sorted from 14,000 benthic sample lots and 4,000 fish sample lots (Pitcher *et al.*, 2007: with a detailed plain English summary found at <http://www.reef.crc.org.au/resprogram/programC/seabed/final-report.htm>).

Sponges were a dominant taxon within the seabed fauna, recorded from about 72% of all sites, and comprising more than 1200 morphospecies (operational taxonomic units or OTUs) that represent 28% of biomass of all invertebrates processed (Pitcher *et al.*, 2007). 38% of species occur in more than 5 sites, 36% from 2–5 sites, and 26% were rare (singletons) encountered only once. This trend corresponds to equivalent analyses of the reefal sponge faunas (Hooper & Ekins 2004). However, from preliminary taxonomic evaluation of the collection so far, 63 of the “top 100” most prevalent sponges were found to be potentially new species. More significantly, of the five most common species (with abundance >230 specimens collected) two are reported here to be new to science. This is an astounding statistic given the history of significant sponge collections from the adjacent coral reef faunas over the past two decades (Queensland Museum collections, Hooper & Ekins 2004), and the near-saturation of the species accumulation/ rarefaction curves that suggested adequacy of sampling was indicative of presumed true species diversity on the GBR (Hooper & Ekins 2004). Clearly the inter-reef fauna differs significantly from the reefal fauna, and it is a telling statistic about what we still do not know from the increasingly well-explored GBR biome.

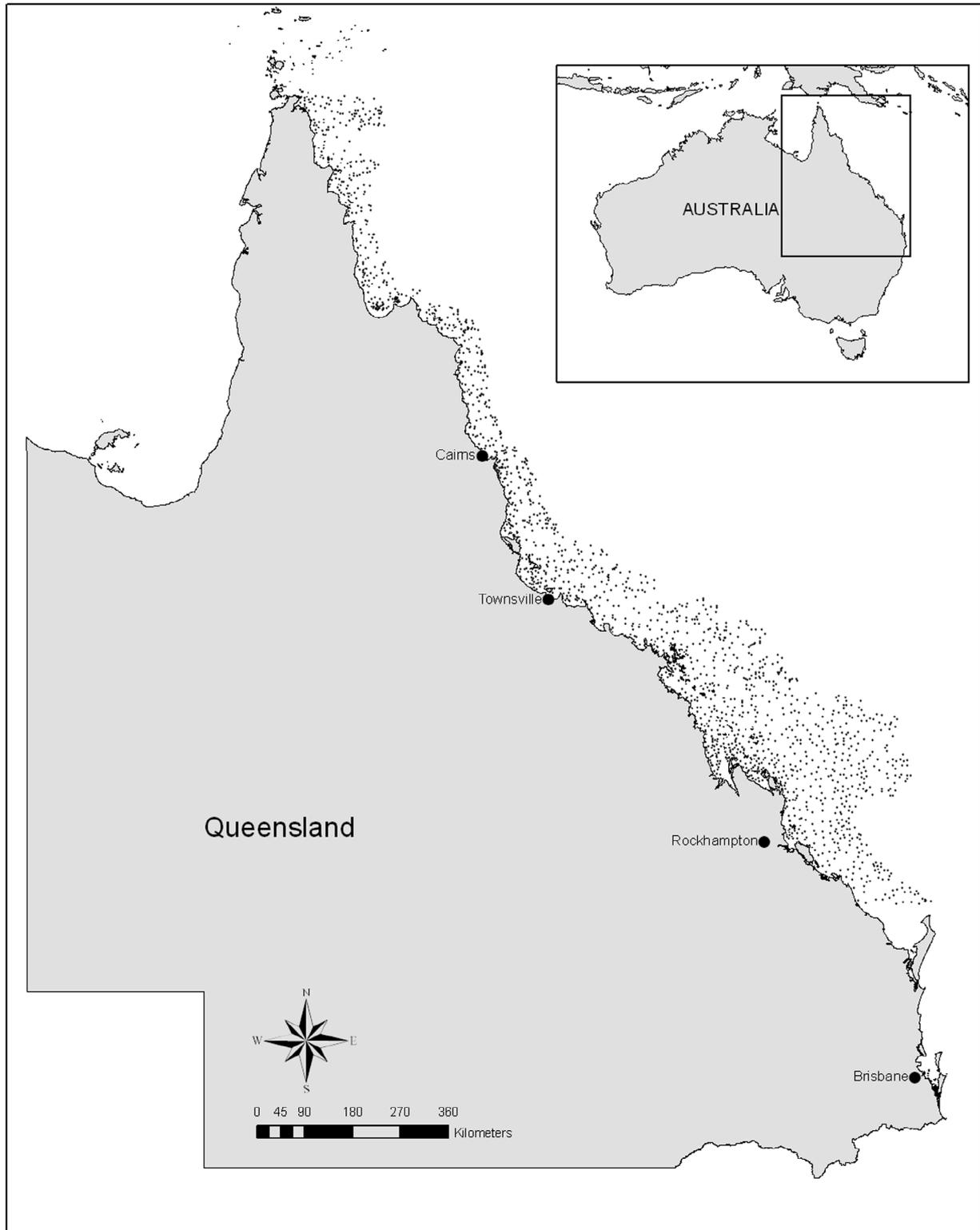
There have been a number of studies on sponge biodiversity, ecology, chemistry and molecular systematics from the GBR region (e.g. Degnan *et al.* 2008; Erpenbeck *et al.* 2007; Hooper & Van Soest 2006; Pöppe *et al.*, 2010, Wörheide *et al.* 2005; Wörheide *et al.* 2008), but our knowledge of sponge biodiversity and distribution is still very incomplete, and until the GBRSBD Project, virtually non-existent for the seabed fauna (Pitcher *et al.* 2007). To date, approximately 400 sponge species have been described from seas adjacent to Queensland, including the Great Barrier Reef, Southeast Queensland and the Coral Sea Territories, yet more than 2000 species remain unnamed in museum collections (Hooper *et al.*, 2008). The Queensland Museum alone houses a collection of sponges representing almost 5000 nominal species or OTUs. The majority of these are undescribed, yet in some instances are commonly found (e.g. Degnan *et al.* 2008; Hooper & Van Soest 2006), illustrating the enormity of the task ahead to describe them within the Linnaean classification to provide a strong comparative basis for faunal composition and distribution worldwide. Although these museum collections are only partly resolved taxonomically, and hence their uniqueness or commonality within the Indo-West Pacific remains unresolved, they have been used extensively to develop our understanding of sponges within the GBR, their distribution and diversity.

This present study begins to document the inter-reef seabed species to assess concordance in ecological trends with reefal species. In this first paper, we describe five of the most common species found on the GBR seabed, with two species being new to science and to our knowledge, not present in any previous collections. We also provide additional records for the previously described species *Coscinoderma nardorus* (Lendenfeld, 1886), *Xenospongia patelliformis* Gray, 1858 and *Sphaciospongia vagabunda* (Ridley, 1884), revising taxonomy, describing habitat preferences and extending known distribution within the GBR.

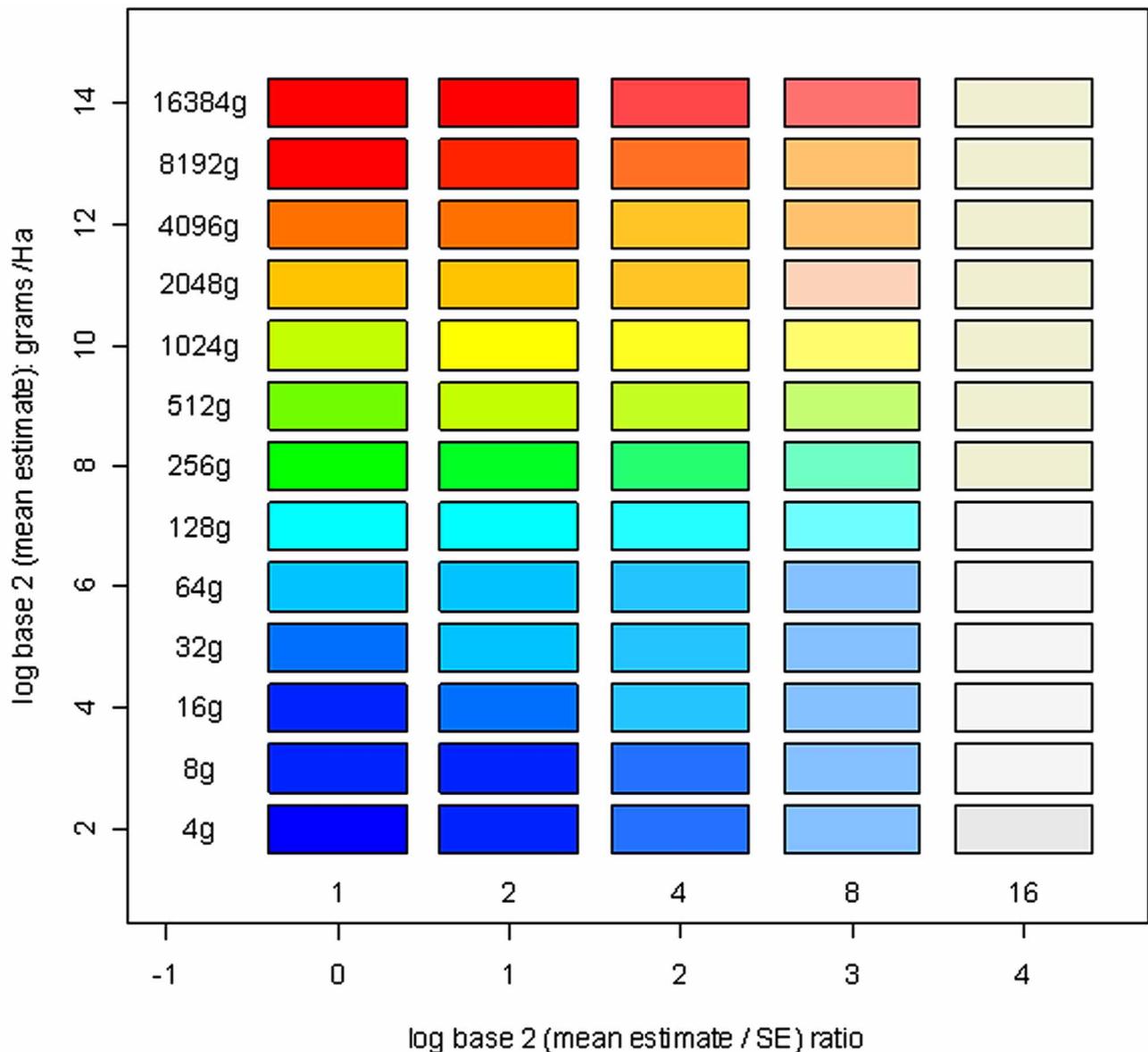
## Materials and methods

**Great Barrier Reef Seabed Biodiversity Project (GBRSBD) Sampling.** Specimens were collected from 457 trawl sites and 1189 epibenthic sled sites (Figure 1) as part of the GBRSBD (Pitcher *et al.*, 2007). Six voyages were conducted on the AIMS research vessel, *RV Lady Basten* from September 2003 to November 2005. A 1.5 m epibenthic sled was deployed at each collecting site and towed at a constant bearing and speed

of ~2 knots over a distance of 200 m. Four voyages were also conducted on the QDPIF research trawler *FRV Gwendoline May* from November 2003 to December 2005. Collections were made using an 8 fathom prawn otter trawl net, towed in a relatively straight line for a distance of 1 km at a speed of about 2.7 knots. All catches from both vessels were photographed on deck, sub-sampled as necessary and sorted into higher taxonomic groups. Sponges were initially preserved by freezing and subsequently sorted in the laboratory, catalogued, voucher specimens preserved in 70% ethanol and the remainder refrozen. Sampling and processing protocols are provided in detail by Pitcher *et al.* (2007).



**FIGURE 1.** Map of the sites sampled from the GBR seabed as part of the Seabed Biodiversity Project.



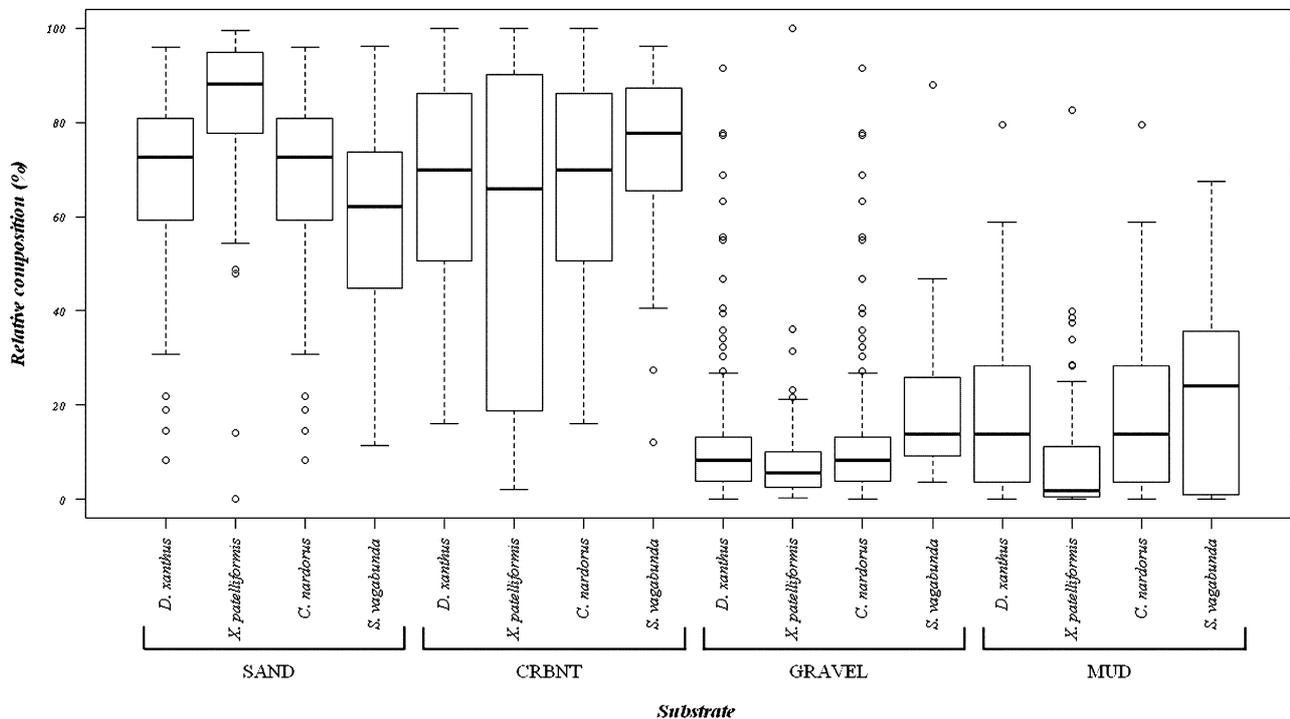
**FIGURE 2.** Colour coding used for defining biomass and standard error for species distribution maps as depicted in figures 4, 6, 8 and 10.

**Species descriptions.** Of the five most abundant sponges encountered on the GBR, a subset of specimens was prepared for light (LM) and scanning electron (SEM) microscopy. Sections were prepared for LM by taking thin cross sections of tissue using a scalpel blade, soaking them in a xylene-phenol solution overnight, subsequently mounting them on a slide in Durcupan Fluka. Spicules were prepared for LM by boiling a fragment of the sponge in nitric acid over a low heat on one end of a microscope slide. Nitric acid was added incrementally as needed, until all of the organic material was digested. In cases where the concentration of spicules was particularly high, ethanol was added to disperse the spicules, and placed over a very low heat to evaporate the remaining ethanol. The spicules were then mounted in Canada Balsam and the slide placed in an oven at 40°C overnight. For SEM spicule preparation, tissue was soaked in bleach, rinsed in demineralised water twice and ethanol twice, centrifuging between each stage. Spicules were then transferred to a stub, left to air dry and coated in gold. Thick sections were soaked in bleach to remove organic material, rinsed gently in water and ethanol, mounted on a stub, air dried and coated in gold also.

Measurements of spicules were based on a representative set of 30 of each spicule type, with the length and width recorded in micrometres ( $\mu\text{m}$ ) as ranges with means in parenthesis.

**Predictive modelling.** The distributions of each species over the full GBR shelf area were predicted using statistical modelling. A selection of up to 28 physical environment variables for which gridded coverages were available for the region was used. These were a collation of 22 datasets from CSIRO Marine Research, The Great Barrier Reef Marine Park Authority, Royal Australian Navy Hydrographic Office, James Cook University, Sydney University, Geoscience Australia and Queensland Department of Primary Industries and Fisheries. Data were also collected during the Seabed Biodiversity Project, using baited remote underwater video (BRUVS), sediment sampling, single-beam acoustics and a towed video camera for habitat mapping. Sediment types were recorded using the standard terms used by Geosciences Australia: % Carbonate (calcium carbonate CaCO<sub>3</sub> composition); % Gravel (> 2 mm), % Sand (2mm–63 μm), % Mud (< 63 μm) based on grain size and dominant substrate constituents. These are referred to throughout this paper simply as carbonate, gravel, sand and mud. The towed camera apparatus was also fitted with a CTD (Conductivity-Temperature-Depth) instrument to record salinity, temperature, oxygen, chlorophyll, turbidity, light and depth. Biomass was recorded for each specimen in the laboratory, as total wet weight in grams. A detailed list of included datasets and sampling apparatus used during the seabed project can be found in Pitcher *et al.* (2007).

Full details of the generalized linear modelling (GLM) method is provided in Pitcher *et al.* (2007). Most species were present at few sites, and thus a two-stage GLM approach was used. The first stage modelled the presence/absence of species at sites, using stepwise logistic regression with bayesian information criterion (BIC), and the second stage modelled the distribution of the biomass of species at sites where present, using stepwise log-linear regression with BIC. Both stages involved two-passes where the first allowed selection of physical variables in the 1<sup>st</sup>-order linear terms and, from this set, the second pass allowed selection of additional 2<sup>nd</sup>-order and interactions terms. The predicted biomass distributions were mapped with the same colour ramp (Figure 2) for all species, and standard errors of predictions were represented by colour intensity.



**FIGURE 3.** Substrate composition plot, showing the relative composition of sand, carbonate, gravel and mud for four species (*Dercitus xanthus* sp. nov., *Xenospongia patelliformis* Gray, 1858, *Coscinoderma nardorus* (Lendenfeld, 1886) and *Spheciospongia vagabunda* (Ridley, 1884)).

## Systematics

### Phylum Porifera Grant, 1836

### Class Demospongiae Sollas, 1885

### Order Astrophorida Sollas, 1888

### Family Pachastrellidae Carter, 1875

### Genus *Dercitus* Gray, 1867

#### *Dercitus xanthus* sp. nov.

(Figures 4, 5, Tables 1, 2)

**Material examined.** Holotype: QMG329976 (SBD513022), south of Rock Cod Shoal, off Gladstone, Great Barrier Reef, 23° 43' 30" S 151° 39' 53" E, 34 m depth, epibenthic sled, 20 ix. 2004, coll. *FRV Lady Basten*.

Paratypes: QMG329977 (SBD513042), East of Lady Musgrave Island, Great Barrier Reef, 23° 53' 06" S 152° 06' 17" E, 42 m depth, epibenthic sled, 21 ix. 2004, coll. *FRV Lady Basten*., QMG32978 (SBD505424), South of Big Broadhurst Reef, off Townsville, Great Barrier Reef, 19° 24' 18" S 147° 56' 06" E, 42 m depth, epibenthic sled, 27 xi. 2003, coll. *RV Lady Basten*.

**Other material:** 163 specimens distributed from adjacent to Bligh Reef in the far northern GBR to the Swain Reefs in the south (Figure 4). Housed at the Queensland Museum, Brisbane, Australia.

**Description.** *Shape.* Massive, agglutinating sponge where a thin layer of tissue cements biogenic rubble such as worm tubes, small gastropods and bivalve remnants. Usually found in fist sized patches or smaller, and occasionally as massive conglomerations.

*Colour.* Ranging from red to yellow. The bright red colour was predominant in frozen specimens. The sponge emits a very distinctive, profuse and intense yellow dye which stains easily. This eosin-like dye stains the surface of the sponge as it defrosts, masking the original red colour. Upon preservation in ethanol, the sponge loses all colour and becomes white. The ethanol, however, retains a brilliant yellow colour which darkens as the specimen remains immersed in ethanol.

*Oscules.* Oscules or papillae were never observed in this sponge, however, no *in situ* observations were possible.

*Texture and surface characteristics.* The agglutinating nature of this sponge means that it is easily broken, but does not crumble finely due to the large size of the rubble agglutinated by the sponge. The surface layer is uneven due to the presence of the rubble.

*Skeletal structure.* There is no definable structure in either the ectosomal or choanosomal skeletons. Sanidasters are scattered throughout the sponge with no particular organisation, but in high concentrations.

*Megascleres* (Table 1). Two size classes of three rayed calthrops (ie triods) (small: 22–26 µm (mean 25 µm) and large: 49–94 µm (mean 72 µm)) were seen in the paratype QMG329977 and in approximately 20% of other specimens examined, occurring in high densities within these specimens (Figure 5).

**TABLE 1.** Measurement of spicules for *Dercitus xanthus* sp. nov., as range (and mean) of length x width in µm, N=30.

Specimen number	Sanidasters	Calthrops Type I	Calthrops Type II
QMG329976 (SBD513022)	10-17 x 1-2.5 (14 x 1.5)	-	-
QMG329977 (SBD513042)	9-17 x 1-2 (14 x 1.5)	22-26 (25)	49-94 (72)
QMG329978 (SBD505424)	10-20 x 1-2.5 (15 x 2)	-	-

*Microscleres* (Table 1). Sanidasters were universally present in all specimens. They display wide variation in length and width (10–20 µm x 1–2.5 µm), with the shorter, wider examples containing large spines

protruding up to 1  $\mu\text{m}$  from the main shaft. The shaft is straight, and can be completely obstructed from view by the density of the spines present. Spines also vary in structure from conical with straight sides, to bulbous. In more sparsely spined sanidasters, spination is not evenly spaced but nonetheless consistent along the length of the spicule (Figure 5).

**Habitat and distribution.** Distributed throughout the Great Barrier Reef, from the southern extremities adjacent to Rockhampton and the Capricorn Bunker group, extending through to the northern Great Barrier Reef and Torres Strait (Figure 4). Found on sandy bottoms in areas with a high component of calcium carbonate rubble. Depths range from 16 to 86 m, with the highest concentration of specimens found in depths of 30 to 40 m.

**Etymology.** Named for the distinctive yellow dye which exudes profusely from the sponge, derived from the greek word *xanthos*, yellow.

**Remarks.** This new species is assigned to *Dercitus* based on the presence of distinctive sanidasters, triods and the cementing growth form. This species also fits the description currently given for *Stoeba* Sollas 1888, with the only apparent character differentiating *Dercitus* and *Stoeba* being the presence of toxas in *Dercitus*. Toxas, however, are confined only to *D. bucklandi* Bowerbank, 1858, and are absent in the only other species currently assigned to this genus, *D. natalensis* (Burton, 1926) (Van Soest, 2009a). We assign this new species to *Dercitus* rather than *Stoeba*, being the older of the two genera, given the current uncertainty surrounding whether both genera will remain valid in light of recently published comments and a pending revision of the pachastrellids (Maldonado, 2002; Moraes & Muricy, 2007; Van Soest, pers. comm.).

This species differs from the two described species of *Dercitus* in its spicule composition (Table 2). *D. bucklandi* contains toxas, calthrops and short shafted plagiotriaenes with blunt clads; *D. natalensis* has short shafted dichotriaenes. The triod calthrops observed in *D. xanthus* are clearly different from the megascleres in both these other species.

There are 12 currently described species of *Stoeba* (van Soest, 2009b). Eight of these species possess dichotriaenes (*S. dissimilis*, *S. extensa*, *S. loricata*, *S. occulta*, *S. pauper*, *S. plicata*, *S. reptans* and *S. simplex*). Three species also contain monactinal spicules such as oxeads (*S. dissimilis*, *S. exostotica* and *S. lesinensis*), which clearly differ from the spicule composition of this new species. Only two species, *S. latex* Moraes & Muricy, 2007 and *S. syrmatitus* (de Laubenfels, 1930), contain only calthrops and sanidasters and are thus most similar in spicule composition to *D. xanthus*. The major characteristics of all these species are compared in Table 2.

*Stoeba latex* from north east Brazil is a red/brown, thickly encrusting sponge (not in aggregating or filling small cavities as in most described species). It has four-rayed calthrops which can be much larger (42.5–212.5  $\mu\text{m}$ ) than the triods found in *D. xanthus* (22–94  $\mu\text{m}$ ), and sanidasters that are slightly smaller (10–15  $\mu\text{m}$ ) than in the present species (10–20  $\mu\text{m}$ ). *Stoeba syrmatitus* from California has a similar agglutinating growth form as does *D. xanthus* and has similar ranges of spicule sizes, with sanidasters ranging from 8–12  $\mu\text{m}$ , and calthrops 25–80  $\mu\text{m}$  (compared to sanidasters 10–20  $\mu\text{m}$ , and triods 22–94  $\mu\text{m}$ ), but is drab in colour (compared to *D. xanthus* which is yellow to orange, with a prominent deep yellow dye). Megasclere morphology is also the most similar, including some of the four-rayed calthrops in *S. syrmatitus* reduced to triods (compared to all the calthrops in *D. xanthus* being 3-rayed), but their respective microscleres differ substantially. Sanidasters in *S. syrmatitus* were only tentatively referred to as sanidasters (“abundant, discasters (?) or sanidasters”) by de Laubenfels (1930), with the spination confined to two nodes on the shaft of the rhabd. De Laubenfels (1930) also noted that some microscleres were so irregularly spiny they resembled acanthomicrostrongyles, but most were more similar to discorhabds based on the localisation of the spines in two nodes (compared to consistently spined sanidasters, with examples of both large and small spines, in the new species).

This is the first record of a *Dercitus* or *Stoeba* species in the south western Pacific.

**Predicted distributions and biophysical preferences.** *Dercitus xanthus* is distributed along the entire length of the GBR at depths ranging from 16 to 85 m. Specimens were found at 134 sled sites (biomass 12.2 kg) and 23 trawl sites (biomass 3.5 kg) and were most highly concentrated in the Capricorn Bunker, Swain Reefs and Townsville regions (Figure 4). Biomass was calculated as the total wet weight, including all

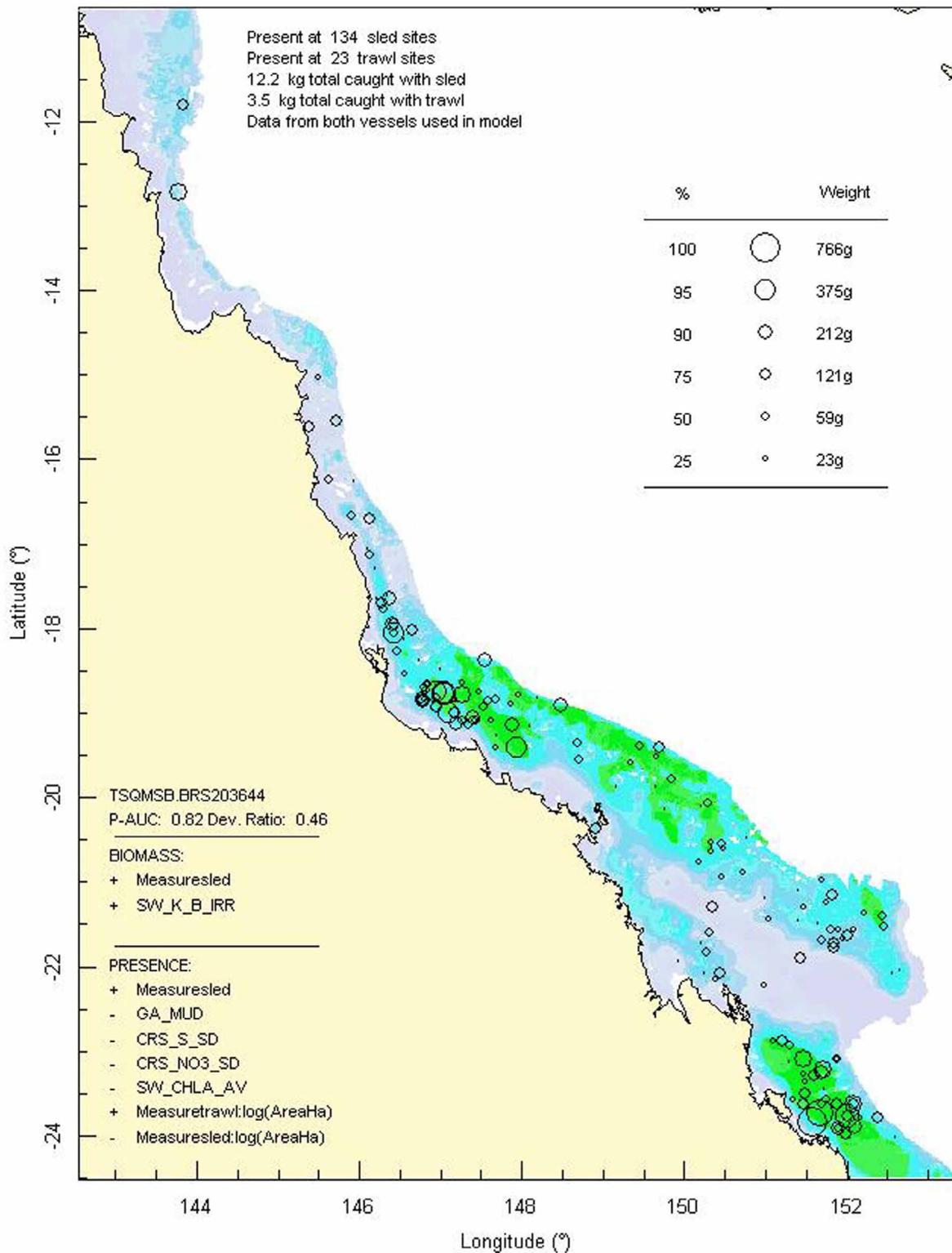
TABLE 2. Comparison between the new and known species of *Dercitus* Gray, 1867 and *Stoeba* Sollas, 1888.

Species	Locality	Source	Morphology	Megascleres	Microscleres
<i>Dercitus bucklandi</i> (Bowerbank, 1858) Type species of <i>Dercitus</i>	NE Atlantic–W Mediterranean	Maldonado, 2002	Massive or cushion-shaped, sometimes filling cavities in hard substrata. Surface finely hispid.	Dichotriaenes absent. Calthrops to short-shafted plagiotriaenes (clads 170–450 x 30–50 µm)	Sanidasters (27–35 x 2–6 µm) covered by minute spines resembling acantho-microstrongyles Toxas (50–110 x 1–1.5 µm) – possibly foreign Sanidasters ataxaster-like, tuberculate microrhabds (5–8 µm), in radial arrangement.
<i>Dercitus natalensis</i> (Burton, 1926)	Natal coast, South Africa	Burton, 1926; Moraes & Muricy, 2007	Thinly incrusting on other sponges	Short-shafted dichotriaenes (shaft 720 x 54 µm, clads 180 µm). Small calthrops rarely present.	
<i>Dercitus xanthus</i> sp. nov.	Great Barrier Reef, Australia	Present study	Agglutinating habit, cementing biogenic rubble; irregular surface, easily broken, yellow- red colour, profuse yellow dye.	Dichotriaenes absent. Two sizes of 3-rayed calthrops (triads) present (22–26 and 49– 94 µm). Short-shafted dichotriaenes (protoclads 30–50x12–60µm; deutroclads 150x35–40 µm; rhabdome 40–225x42–75 µm). Calthrops absent.	Sanidasters, evenly distributed heavy or light spines (10–20 µm x 1–2.5 µm). Sanidasters, reduced spines, twisted thick axis (22–28x4–6 µm).
<i>Stoeba simplex</i> (Carter, 1880) Type species of <i>Stoeba</i>	Gulf of Manaar, Andaman Sea	Maldonado, 2002	Encrusting, filling excavated cavities in calcareous substrata.	Calthrops absent. Dichotriaenes (77–102 µm). 3- and 4- rayed calthrops (175 x 5 µm). Oxeas (65–930 x 1.8–21 µm) Large and small oxeas, tylostyles, amphistrongyles Dichotriaenes absent. Calthrops	Sanidasters (15 x 3–4 µm)  Compressed spheraster- like sanidasters
<i>Stoeba dissimilis</i> (Sarà, 1959)	W Mediterranean,	Sarà, 1959	Incrusting, insinuating cavities, whitish,		
<i>Stoeba exostolica</i> (Schmidt, 1868)	Red Sea	Moraes & Muricy, 2007	Thinly encrusting		
<i>Stoeba extensa</i> Dendy, 1905	Sri Lanka (Ceylon)	Dendy, 1905	Thinly encrusting, extending into cavities of calcitic biogenic rubble; smooth surface; tough consistency; black or pale grey colour.	Short-shafted dichotriaenes (rhabd 136–20 µm; clad 200 µm). Calthrops absent.	Sanidasters, heavily and evenly spined, short spines, slight constriction in middle 20x1.3 µm).

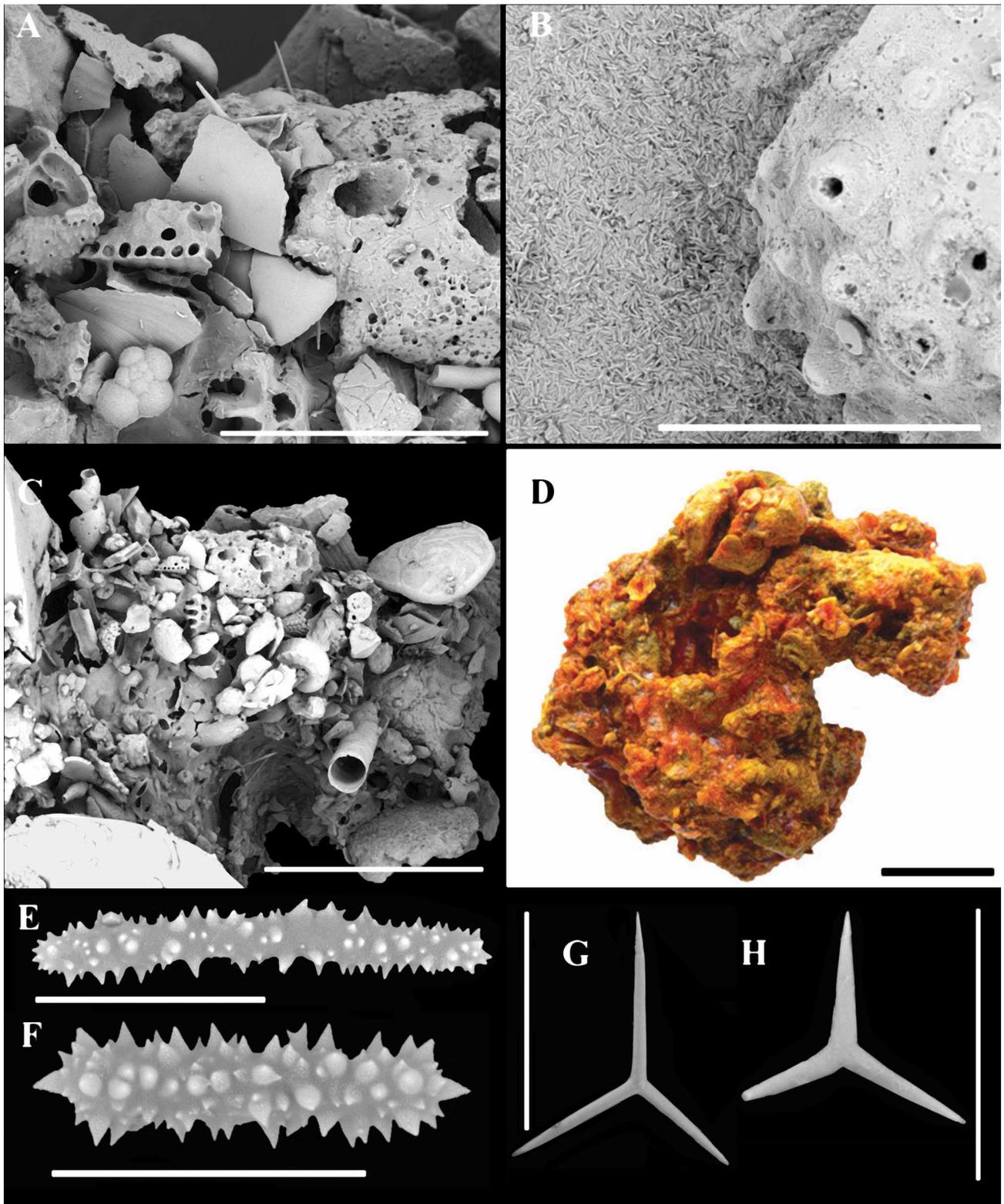
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TABLE 2. (continued)

Species	Locality	Source	Morphology	Megascleres	Microscleres
<i>Stoeba latex</i> Moraes & Muricy, 2007	NE Brazil	Moraes & Muricy, 2007	Thickly encrusting habit, brownish-red colour, rubbery consistency	Dichotriaenes absent. 4-rayed Calthrops (42–213 x 7–25 µm)	Sanidasters, spines well developed and evenly distributed (10–15 x 1 µm)
<i>Stoeba lesinensis</i> (Lendenfeld, 1894)	Lesina, Adriatic Sea	Lendenfeld, 1894	Thinly to thickly encrusting; orange-red colour.	Dichotriaenes absent. Monaxon spicules present including large centrotylote oxeas (up to 4000 x 70 µm), smaller centrotylote oxeas, tylostyles and amphistrongyles (250–300x7–10 µm) 4-rayed calthrops (160x40 µm).	Spined strongyle like sanidasters (15x1.6 µm).
<i>Stoeba occulta</i> (Hentschel, 1909)	Shark Bay, Western Australia	Hentschel, 1909	In cavities in dead coral, barely protruding; vivid brown colour.	Dichotriaenes (rhabdome 86–105x12–18 µm; protoclad 20–28 µm, deutroclad 50–92 µm). Calthrops absent.	Sanidasters, robust with regular spines (16–21x 1.5µm).
<i>Stoeba pauper</i> (Sollas, 1902)	Malay Peninsula	Sollas, 1902	Encrusting band on dead coral; smooth surface, pink colour.	Small dichotriaenes (protoclad 50–60x1 µm; deuteroclad 30 µm; rhabdome 80 µm). Rare calthrops-like 'microtriae' (clads 60–70x3 µm).	Sanidasters, sparsely spined (15–20x1 µm).
<i>Stoeba plicata</i> (Schmidt, 1868)	Mediterranean, eastern Atlantic (Portugal, Azores)	Boury-Esnault & Lopes, 1985	Thinly encrusting, in cavities of calcareous substrata, some with papillae and terminal oscules; white to pinkish or ochre	Dichotriaenes present or absent amongst specimens (rhabd 75–80 µm, clads 44–64 µm). Calthrops also present or absent amongst specimens (30–207x3–30 µm).	Sanidasters evenly spined, heavy spines (11–18x1.5 µm).
<i>Stoeba reptans</i> (Desqueyroux-Faúndez & van Soest, 1997)	Galapagos Is	Desqueyroux-Faúndez & van Soest, 1997	Thin, creeping, stolon-like branches, in places irregularly encrusting the substrate; surface rough, hard consistency; whitish pink preserved.	Short shafted dichotriaenes (clads 156–170 pm, rays 90x 8–9 µm). Large calthrops (clads to 670 µm; rays 344–648x16–50 µm). Dichotriaenes absent.	Sanidasters, irregularly spined (15–74 x 2–8 µm).
<i>Stoeba symmatitus</i> (de Laubenfels, 1930)	California	de Laubenfels, 1930, Moraes & Muricy, 2007	Agglutinating growth form, mass of sand held together by sponge; slimy habit, drab colour; smooth surface; mediocre consistency.	3– to 4-rayed Calthrops (25–80x3–10 µm).	Sanidasters, irregularly distributed, sometimes resembling discorhabds (8–12 µm). Toxas also reported but deemed foreign.



**FIGURE 4.** Model distribution map displaying predicted and actual distribution and biomass of *Dercitus xanthus* sp. nov. from the Great Barrier Reef seabed, displaying: OTU code for this species (TSQMSB.BRS203644), P-AUC: Area Under the Curve performance diagnostic for the Presence/Absence model; Dev. Ratio: Deviance Ratio (P-AUC) performance diagnostic for the Biomass model; Measuresled: a device factor accounting for the difference in sampling rates between devices; Measuretrawl:log(AreaHa) and Measuresled:log(AreaHa): offsets accounting for the swept area sampled by the trawl and sled; and influential predictor variables including: SW\_K\_B\_IRR: relative benthic irradiance, GA\_MUD: mud grainsize fraction (%), CRS\_S\_SD: standard deviation of salinity (psu), CRS\_NO3\_SD: standard deviation of nitrate levels ( $\mu\text{M}$ ), SW\_CHLA\_AV: mean chlorophyll-a ( $\text{mg}/\text{m}^3$ ) concentration.



**FIGURE 5.** *Dercitus xanthus* sp. nov. (QMG329976 (SBD513022)). **A**, Choanosomal structure displaying a high density of foreign material (scale bar 300  $\mu$ m). **B**, Surface of foreign material within the choanosome covered in Sanidasters (scale bar 300  $\mu$ m). **C**, External morphology (scale bar 1 mm). **D**, Holotype (scale bar 2.5 cm). **E**, Sanidaster (scale bar 10  $\mu$ m). **F**, Sanidaster (scale bar 10  $\mu$ m). **G**, QMG329977 (SBD513042). Triod calthrops (scale bar 50  $\mu$ m). **H**, QMG329977 (SBD513042). Triod calthrops (scale bar 50  $\mu$ m).

biogenic rubble incorporated within the body of the sponge, as this was impossible to separate from the tissue. The most important physical covariate affecting the distribution patterns of this sponge using the presence /

absence model was mud. This species was found in habitats with very low mud content present in the substrate, and where there was low variability in salinity and nitrate levels (Figure 4). This species occurs in benthic habitats with high levels of carbonate (biogenic rubble) and sand (Figure 3), accounting for its characteristic habit of incorporating prolific detritus into the skeleton and cementing sand and biogenic rubble. Predicted distributions show overall biomass to be low, with higher predicted presence and biomass in proximity to Townsville and the Capricorn Bunker regions, and within a small section of the Swain Reefs.

## Order Dictyoceratida Minchin, 1900

### Family Spongiidae Gray, 1867

#### Genus *Coscinoderma* Carter, 1883

#### *Coscinoderma nardorus* (Lendenfeld, 1886) comb. nov.

(Figures 6, 7)

*Aphrodite nardorus* Lendenfeld, 1886[1885]: 306.

*Hippospongia nardorus*; Hooper & Wiedenmayer, 1994 (2005 web version): 384.

*Hippospongia aphroditella* Lendenfeld, 1889: 36 [in key, see also Lendenfeld, 1889: 312, pl. 11 figs 11–14, pl. 12 fig. 13]; unjustified replacement name for *Aphrodite nardorus* Lendenfeld, 1885].

*Ceratodendron haeckeli* Marshall, 1892: 5.

**Material examined.** Holotype. BMNH 1886.8.27.105 wet (=AM G3398 slide, figured in Lendenfeld, 1889, pl. 12 fig. 13, Palm Is., Torres Strait, QLD, 10°25'S 142°10'E. Paratype. BMNH 1930.8.13.181 dry.

**New material.** QMG329979 (SBD500371), seabed on outer shelf south of Myrmidon Reef, Great Barrier Reef, 18° 31' 29" S 147° 35' 06" E, 74 m depth, epibenthic sled, 22 ix. 2003, coll. *RV Lady Basten*. QMG329120 (SBD507175), seabed on inner shelf of Swains Reef, adjacent to Herald's Prong No. 2, Great Barrier Reef, 21° 47' 06" S 151° 21' 54" E, 85 m depth, trawl, 7 xii. 2003, coll. *FRV Gwendoline May*. QMG330307 (SBD524660), seabed east of Palm Island, Great Barrier Reef, 18° 42' 17" S 146° 48' 18" E, 35 m depth, epibenthic sled, 30 iv. 2004, coll. *RV Lady Basten*. . QMG330304 (SBD523195), seabed west of Ribbon Reef No. 4, Great Barrier Reef, 15° 25' 30" S 145° 41' 06" E, 48 m depth, trawl, 17 x. 2004, coll. *FRV Gwendoline May*.

**Other material:** 129 specimens collected between the seabed adjacent to MacLennan Reef #2 in the far northern GBR and Swain Reefs in the south (Figure 6). Housed at the Queensland Museum, Brisbane, Australia.

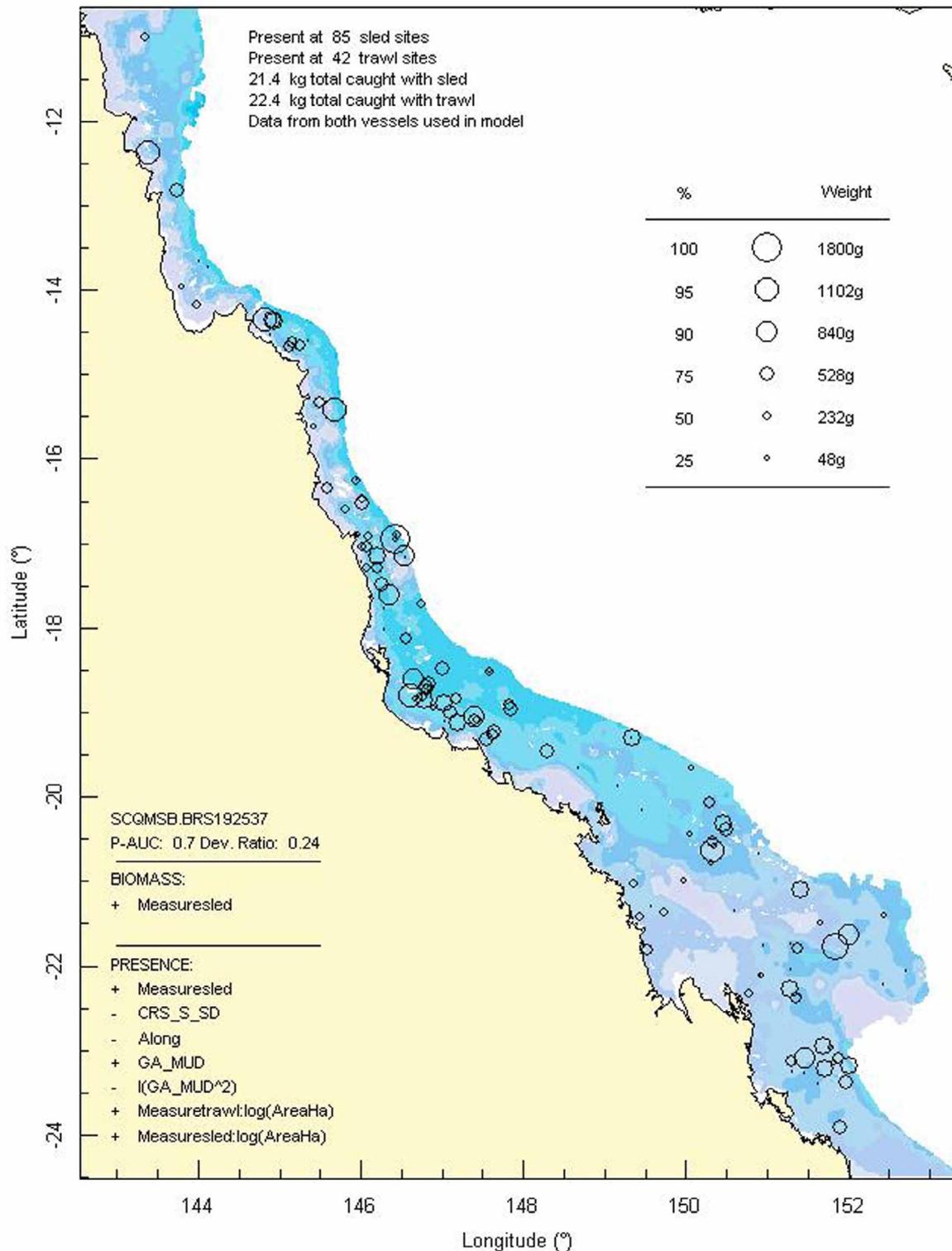
**Description.** *Shape.* Stalked, with long basal root or holdfast. Stalk and root can comprise more than half of the total length of the sponge. The main body of the sponge is globular.

*Colour.* Light pink colour in situ and on deck. Specimens turn beige when preserved in ethanol and stain the ethanol a bright yellow colour. When removed from the water, the sponge emits a fluorescent pink dye.

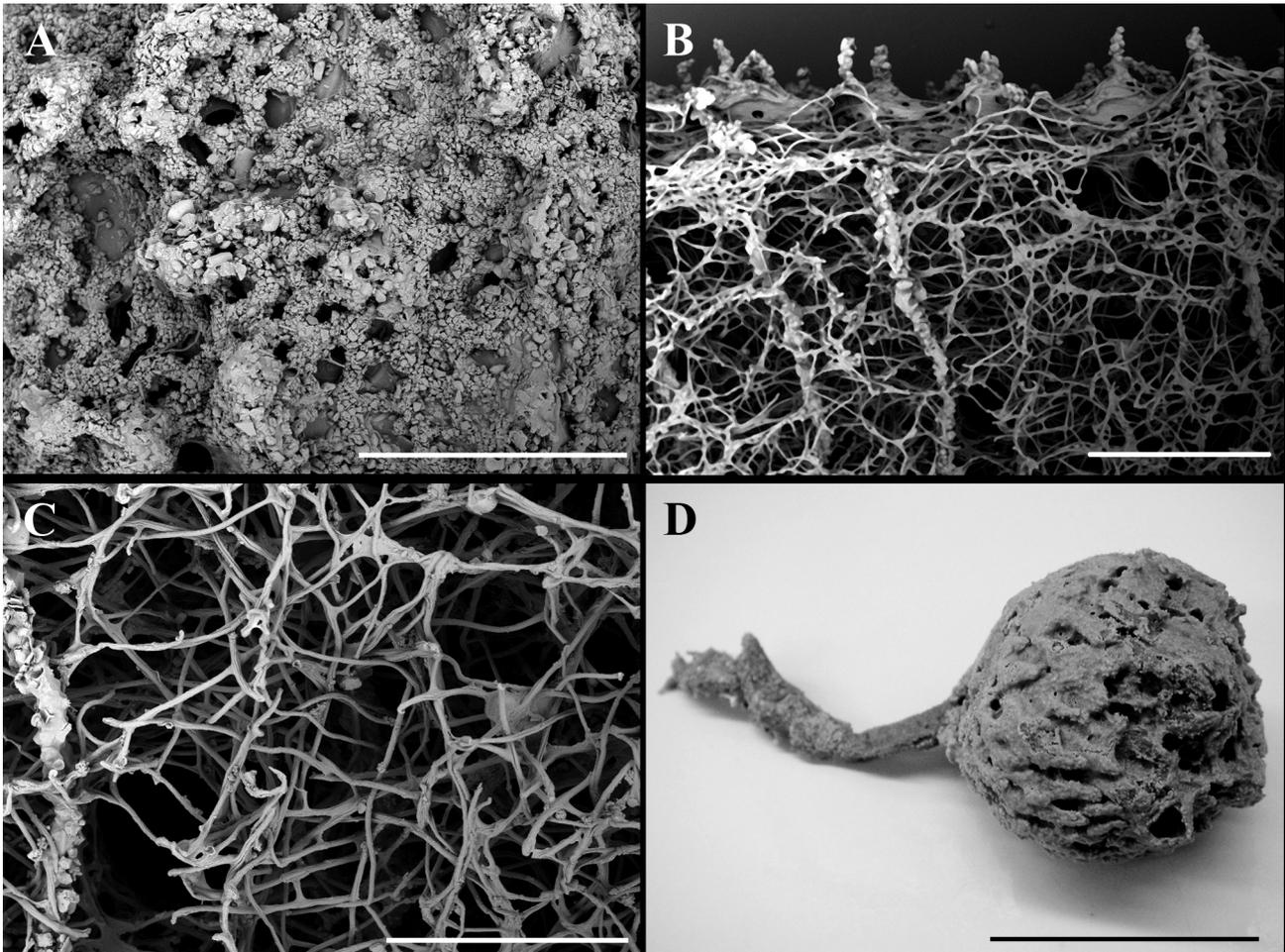
*Oscules.* Terminal to the globular body of the sponge, oscules can be numerous, with up to ten oscules visible in the larger specimens. Each oscule is surrounded by a raised lip to a height of 1–15 mm, depending on the size of the specimen.

*Texture and surface characteristics.* Compressible sponge which is very dense and retains a substantial amount of water within the main body. The surface is almost entirely covered by microconules, raised up to 0.5 mm from the surface, but can be smooth in some areas. Stalk and root are smooth. Internally cavernous, the surface is irregularly pitted with deep channels and large inhalant pores.

*Skeletal structure.* The ectosome is armoured with sand grains. Irregular primary fibres cored with sand can protrude through the ectosome, or become more apparent further within the choanosomal structure. The choanosome is dominated by a dense, confused mass of clear secondary fibres. Small sand grains are lightly scattered throughout the choanosome.



**FIGURE 6.** Model distribution map displaying predicted and actual distribution and biomass of *Coscinoderma nardorus* (Lendenfeld 1886) from the Great Barrier Reef seabed, displaying: OTU code for this species (SCQMSB.BRS192537), P-AUC: Area Under the Curve performance diagnostic for the Presence/Absence model; Dev. Ratio: Deviance Ratio (P-AUC) performance diagnostic for the Biomass model; Measuresled: a device factor accounting for the difference in sampling rates between devices; Measuretrawl:log(AreaHa) and Measuresled:log(AreaHa): offsets accounting for the swept area sampled by the trawl and sled; and influential predictor variables including: CRS\_S\_SD: influential predictor variables of standard deviation of salinity (psu), Along: along shelf gradient, GA\_MUD/ GA\_MUD<sup>2</sup>: mud grain size fraction (%) and its quadratic term.



**FIGURE 7.** *Coscinoderma nardorus* (Lendenfeld, 1886) (QMG329979 (SBD500371)). **A**, Top view of the ectosomal skeleton (scale bar 2 mm). **B**, Cross section of the skeleton, showing cored primary tracts protruding through the ectosome (scale bar 1 mm). **C**, Fibre network within the choanosome (scale bar 500 µm). **D**, QMG330307 (SBD524660). Specimen (scale bar 9 cm).

**Habitat and distribution.** Found in reef areas and sandy bottoms, this sponge is attached to rubble in soft sediment by a holdfast. It is distributed in Torres Strait and throughout the entire length of the Great Barrier Reef seabed (Figure 6) at depths between 12 and 85 m, predominantly in benthic substrates dominated by sand and calcium carbonate material.

**Remarks.** This species is very characteristic and immediately recognisable by its external stalked club-shaped growth form as Lendenfeld's species *Aphrodite nardorus*. Lendenfeld (1889) subsequently transferred it to *Hippospongia*, where it has remained until the present, albeit with virtually no subsequent citation over the past century (see Hooper & Wiedenmayer, 1994 (2005 web version)).

The generic definition of *Hippospongia* was revised in 2001 (Cook & Bergquist, 2001), to clarify misidentifications between *Spongia* and *Hippospongia*. Species were reclassified, new species of *Spongia* were described, and only three species were left assigned to *Hippospongia* (*H. communis* (Lamarck, 1814), *H. gossypina* (Duchassaing & Michelotti, 1864) and *H. lachne* (de Laubenfels, 1936)). The question of the best assignment for the remaining species still classified in *Hippospongia* was left open.

Cook and Bergquist (2001) revised the choanosomal skeleton of *Hippospongia* as containing rare, irregular and sometimes cored primary fibres occurring predominantly near the surface, with secondary fibres dominating. The subdermal lacunose structure is a characteristic feature and the oscular canals are large, retaining approximately the same width throughout the body of the sponge as the oscules themselves. The unarmoured ectosomal layer is also an important primary characteristic in the key to the genera of Spongiidae (Cook & Bergquist, 2002). Consequently, '*nardorus*' does not conform to this revised definition and is more

appropriately allocated to *Coscinoderma* based upon the presence of an armoured ectosome, irregular, cored primary fibres and a thin, unorganised, dense reticulation of secondary fibres. This is in contrast to the only other genus of Spongiidae with an armoured ectosomal layer, *Rhopaloeides*, which contains very thick secondary fibres in the choanosome (Cook & Bergquist, 2002).

The inclusion of the nominal species *C. haeckeli* into synonymy with this species was based on superficial comparison of the respective (mostly dried) type material (Hooper & Wiedenmayer, 1994), not through a modern analysis using fresh material. Hence this reported synonymy should be regarded as a tentative hypothesis given their disparate geographic distributions (Bass Strait versus Torres Strait and the GBR).

**Predicted distributions and biophysical preferences.** *Coscinoderma nardorus* was found consistently along the length of the GBR at depths ranging from 12 to 85 m, with the highest populations found in the Townsville/Cairns regions (Figure 6). Specimens were collected from 85 sled sites (biomass 21.4 kg) and 42 trawl sites (biomass 22.4 kg), living in benthic habitats dominated by sand and carbonate (Figure 3) distributed across the shelf. Analysis of environmental correlates showed preference for low variation in salinity and a negative correlation to high mud substrates (Figure 6). The stalked, root-like base of the sponge allows settlement on mobile substrates.

## Order Hadromerida Topsent, 1894

### Family Tethyidae Gray, 1848

#### Genus *Xenospongia* Gray, 1858

##### *Xenospongia patelliformis* Gray, 1858.

(Figures 8,9, Table 3)

*Xenospongia patelliformis* Gray, 1858: 229; Hooper & Wiedenmayer, 1994 (2005 web version): 427; Fromont, 2003: 408; Sara, 2002: 265.

**Material examined.** Holotype BMNH 1883.1.25.9 dry, Torres Strait, QLD, 10°25'S 142°10'E. Paratypes BMNH unregistered 2 specimens, dry (D.A.38); BMNH unregistered slide 2/57.

**New material.** QMG331025 (SBD513104), seabed north of Heron Island, adjacent to Haberfield Shoal, Great Barrier Reef, 22° 57' 53" S 151° 47' 05" E, 55m depth, epibenthic sled, 22 ix. 2004, coll. *RV Lady Basten*. QMG329286 (SBD537920), seabed between Capricorn-Bunker Group and Swains Reef, Great Barrier Reef, 22° 55' 30" S 151° 58' 29" E, 76 m depth, epibenthic sled, 9 xi. 2005, coll. *RV Lady Basten*. QMG329285 (SBD537858), inner shelf seabed between Herald's Prong No.2 and the mainland, Great Barrier Reef, 22° 12' 17" S 150° 59' 42" E, 22 m depth, epibenthic sled, 10 xi. 2005, coll. *RV Lady Basten*.

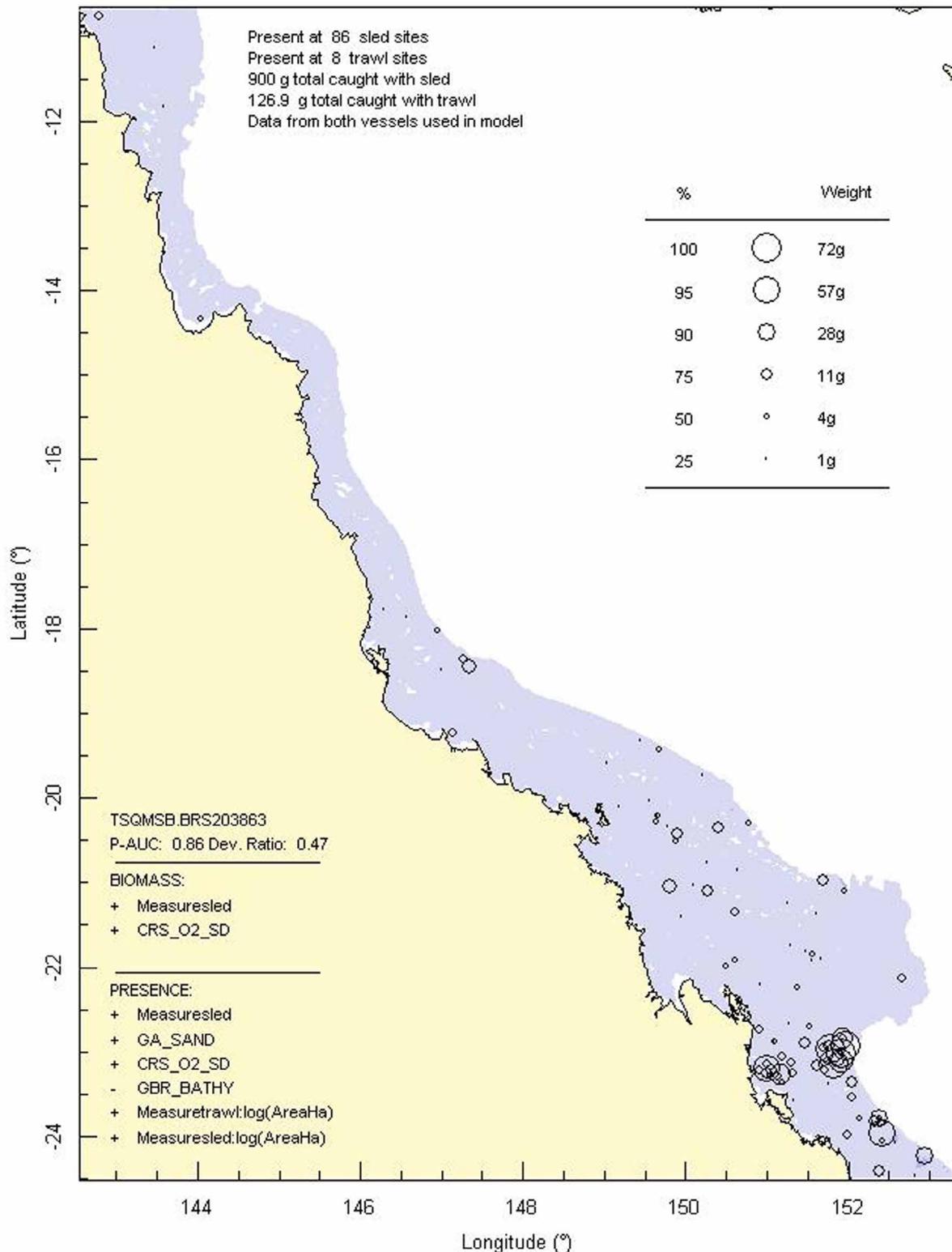
**Other material:** 102 specimens collected between Wyborn Reef at the tip of Cape York to the seabed adjacent to northern Fraser Island in the south (Figure 8). Housed at the Queensland Museum, Brisbane, Australia.

**Description.** *Shape.* Distinctive disc shape, ranging in thickness from 3–6 mm. All specimens show a concave structure, which allows them to be raised above the seabed.

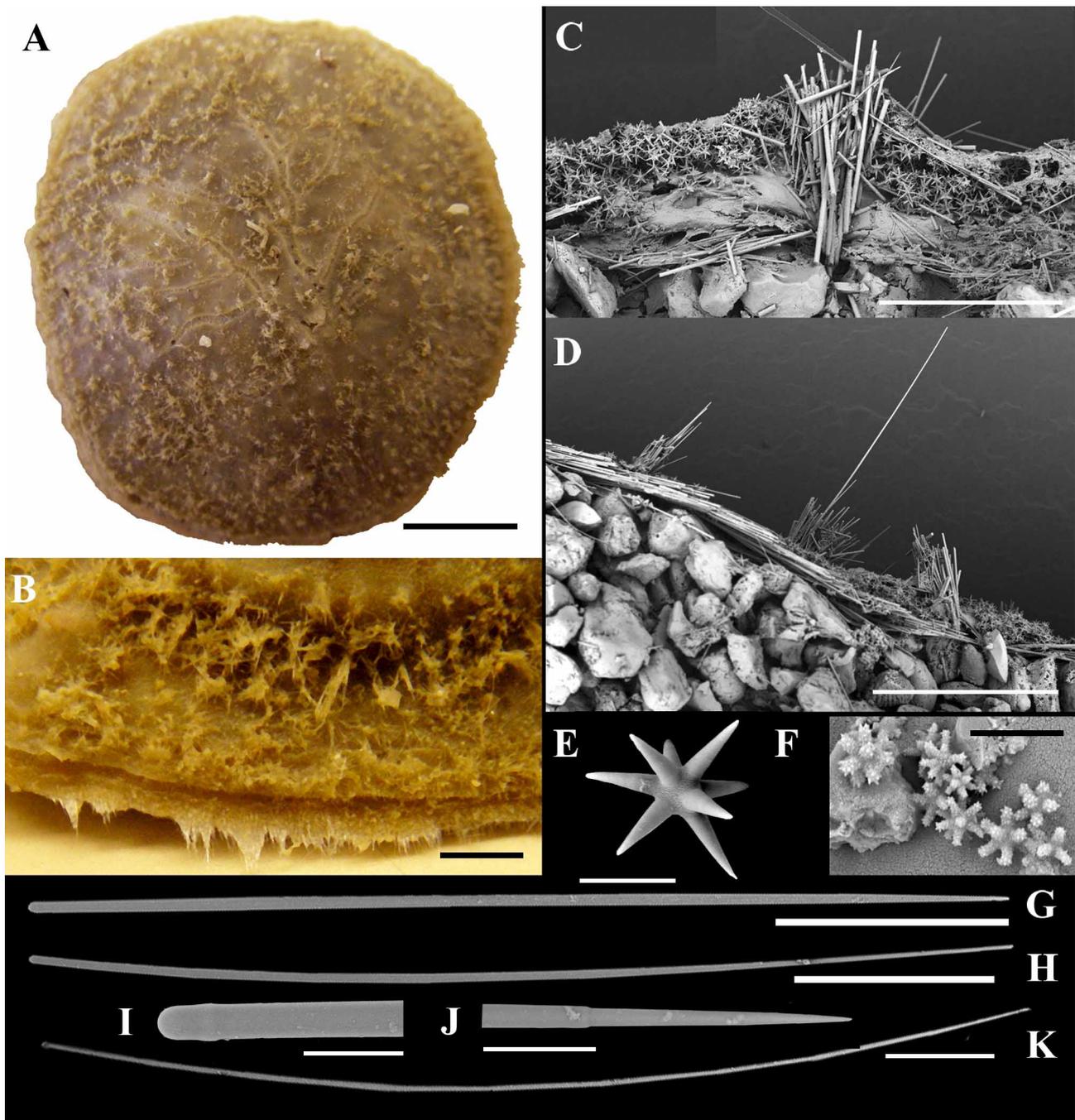
*Colour.* A beige or grey colour on the surface, when the sponge is turned over, the underside is mottled as the incorporated sand grains are more highly visible.

*Oscules.* No oscules were visible in these specimens.

*Texture and surface characteristics.* Flexible due to the thin shape of the specimens, this sponge is otherwise firm, incompressible, easily torn and becomes very brittle when dry. Spicule bundles and large single spicules protrude from the ectosome and give the surface a hispid appearance, although the longer spicules are easily broken. The extremities of the disc also have large spicules echinating through the ectosome, allowing the entire sponge to be raised above the seabed. The surface is frequently grooved. Grooves originate from the apex of the sponge and run to the extremities of the disc, with variable degrees of branching.



**FIGURE 8.** Model distribution map displaying predicted and actual distribution and biomass of *Xenospongia patelliformis* Gray, 1858 from the Great Barrier Reef seabed, displaying: OTU code for this species (TSQMSB.BRS203863), P-AUC: Area Under the Curve performance diagnostic for the Presence/Absence model; Dev. Ratio: Deviance Ratio (P-AUC) performance diagnostic for the Biomass model; Measuresled: a device factor accounting for the difference in sampling rates between devices; Measuretrawl:log(AreaHa) and Measuresled:log(AreaHa): offsets accounting for the swept area sampled by the trawl and sled; and influential predictor variables including: CRS\_O2\_SD: oxygen (ml/l) standard deviation, GA\_SAND: sand grainsize fraction (%), GBR\_BATHY: bathymetry.



**FIGURE 9.** *Xenospongia patelliformis* Gray, 1858 (QMG331025 (SBD513104)) **A**, Specimen (scale bar 5 mm) **B**, Margin of discoid sponge, showing long echinating styles protruding from the tangential ectosomal layer as well as from brushes perpendicular to the surface (scale bar 3 mm). **C**, Ectosome, displaying the high concentration of asters and arrangement surface brushes (scale bar 500  $\mu$ m) **D**, Ectosome in cross section, with long style protruding from ectosomal bundles. Dense, tangential arrangement of styles and highly arenaceous choanosome are also visible (scale bar 1 mm). **E**, Large oxyaster (scale bar 15  $\mu$ m). **F**, Strongylasters (scale bar 10  $\mu$ m). **G**, Style (Type II) (scale bar 50  $\mu$ m). **H**, Style (Type I) (scale bar 200  $\mu$ m). **I**, Style head (Type II) (scale bar 10  $\mu$ m). **J**, Style tip (Type II) (scale bar 20  $\mu$ m). **K**, Style (Type III) (scale bar 250  $\mu$ m).

*Skeletal structure.* Spicules are concentrated almost exclusively in the ectosomal layer on the upper, exposed side. Styles in two size classes are arranged tangentially, forming a matted layer which lies directly below the ectosomal crust of asters. Specialised styles form dense bundles which project through the ectosome, surrounding a single, large, specialised style which extends to a distance of about 1.5 mm. The choanosome is filled almost entirely with sand grains (Figure 9).

*Megascleres* (Table 3). Large styles (Type I) are the most abundant, have smooth heads, rounded tips and can be flexuous. They form the tangential ectosomal layer as well as the dense ectosomal brushes and range from 530–1447  $\mu\text{m}$  in length. The upper length limit of these styles, however, may be very conservative as a result of the fragility of these larger spicules. Smaller, thinner styles (Type II) have slightly swollen heads, approaching subtylote, with sharply pointed tips and a straight shaft. They are also located in the tangential ectosomal layer. Very fine, elongate styles (Type III) are the single styles arising from the centre of ectosomal brushes to a distance of approximately 1.5 mm.

**TABLE 3.** Measurement of spicules for *Xenospongia patelliformis* Gray, 1858, as range (and mean) of length x width in  $\mu\text{m}$ , N=30. Asters are measured by overall diameter from tip of ray to opposing tip of ray.

Specimen number	Styles (Type I)	Styles (Type II)	Styles (Type III)	Oxyasters	Strongylasters
QMG331025 (SBD513104)	535–1275 x 5–13 (1020 x 9)	145–600 x 2–6 (380 x 4)	1500–2600 x 8–12 (2000 x 11)	14–65 (45)	3–11 (5)
QMG329285 (SBD537858)	930–1447 x 8–12 (1100 x 10)	245–485 x 2–4 (330 x 3)	1600–3000 x 9–11 (2100 x 10)	21–65 (38)	3–18 (8)
QMG329286 (SBD537920)	850–2100	205–445 x 4–8 (350 x 5)	1500–3000 x 9–12	20–80 (45)	3–10 (7)

*Microscleres* (Table 3). Oxyasters are large and regular, with a small centrum and smooth, slightly recurved, conical rays. These are slender, uniform asters with approximately 11 rays per aster.

Strongylasters are very compact and robust, with 7–8 stout rays. These have been previously described as tylasters, but our examination shows that the spination is spread along the entire length of the rays, with larger, more sharply pointed spines at the tips of each ray in some asters, giving the appearance of being swollen, thus simply a manifestation of the size of spines and not a true tylaster morphotype. The short tuberculate spines on the shaft of the rays give a warty appearance and can conceal the centrum in smaller asters, due to the shaft width and elaborate spination on the rays.

**Habitat and distribution.** Distributed throughout the Great Barrier Reef, this species has also been recorded from the Torres Strait, Western Australia and allegedly Sri Lanka. Specimens from the GBR were collected in depths ranging from 10 to 87 m, from predominantly sandy and carbonate dominated substrata.

**Remarks.** This species has an unusually distinctive habit which is relatively well known by many marine invertebrate researchers, and as recently as 2003 was recorded from Western Australia (Fromont, 2003), where specimens reach a much larger size than any of those reported here. Type II and Type III styles have not been previously recorded in descriptions of this species. Type III styles were possibly overlooked due to handling of the degraded type specimens causing the larger megascleres to break, giving the false impression that the ectosomal megascleres were the only megasclere component. Smaller, Type II styles were also previously overlooked.

In the original description, Gray (1858) noted that oscules were visible in the surface grooves of the adult specimen, and infrequently situated on the surface of the main body of the sponge. Sollas (1888) agreed and added that small pores could be seen in rows situated externally to the grooves. In the specimens collected as part of the GBRSD no oscules were visible, possibly due to the nature by which they were collected, and preserved frozen.

Although the officially recorded distribution of this species is relatively limited to date, it is possible that it is widespread throughout Australasia on the inter-reef seabed. The holotype was collected in the Torres Strait (Gray, 1858). Dendy (1905) recorded a single specimen from Sri Lanka, but conspecificity has never been confirmed. The older (non GBRSD) collections of the Queensland Museum contain one specimen from the Gulf of Carpentaria, one from Yeppoon (Queensland coastal waters) and six specimens from four sites in Torres Strait. The Western Australian Museum, however, has specimens ranging the West Australian coast from Rottnest Island to Broome (Jane Fromont, pers. comm.), which is a far more southern reaching distribution. Collections from South Australia also suggest an abundant southern distribution, however, identification of these specimens have not been confirmed (Shirley Sorokin, pers. comm.). To our knowledge

at least, there are no other records of this species, despite it being the third most abundant sponge on the GBR seabed, with 415 specimens recorded from 96 sites.

**Predicted distributions and biophysical preferences.** Distributed throughout the northern and southern regions of the GBR, the highest concentrations were found in the southern coastal regions (Figure 8). This species was collected from 86 sled sites (biomass 900 g) and 8 trawl sites (biomass 126.9 g) between 10 and 87m depth in benthic habitats dominated by sandy sediments and carbonate dominated sediments (Figure 3). The low occurrence of this species in the northern regions of the GBR, which has similar benthic habitats to the southern GBR regions (e.g. coastal region in proximity to Townsville), is curious considering that previously known distribution on the East coast was only from these northern regions (Torres Strait and Yeppoon). This high abundance in the southern GBR, as well as records from southern Western Australia, suggest that this species has a stronger distribution in southern regions. *X. patelliformis* showed preference for shallow water, sandy environments with high deviation in oxygen content.

## Family Clionidae D'Orbigny, 1851

### Genus *Sphaciospongia* Marshall, 1892

#### *Sphaciospongia vagabunda* (Ridley, 1884)

(Figures 10,11, Table 4)

*Spirastrella vagabunda* Ridley, 1884: 468; Hooper & Wiedenmayer, 1994 (2005 web version): 375

*Sphaciospongia vagabunda*; Kelly-Borges, 1997: 108.

*Spirastrella vagabunda trincomaliensis* Ridley, 1884: 468.

*Spirastrella cylindrica* Kieschnick, 1896: 534.

*Spirastrella vagabunda tubulodigitata* Dendy, 1905: 123.

*Spirastrella vagabunda fungoides* Dendy, 1905: 124.

*Spirastrella vagabunda gallensis* Dendy, 1905: 124.

**Material examined.** Syntypes BMNH 1882.2.23.307 2 specimens, wet, 7–13 m, Thursday and West Islands, Torres Strait, 10°35'S 142°13'E and 10°22'S 142°02'E; BMNH 1882.2.23.243 wet, 7–13 m, Thursday and West Islands, Torres Strait; BMNH 1882.2.23.243a–307a 4 slides 2/20, 7–13 m, Thursday and West Islands, Torres Strait.

**New material.** QMG329980 (SBD527235), inner shelf, north of Townshend Island, Great Barrier Reef, 22° 10' 30" S 150° 27' 54" E, 35 m depth, epibenthic sled, 10 v. 2004, coll. *RV Lady Basten*. QMG329184 (SBD517192), seabed between South Ledge Reef and Albany Island, northern tip of Cape York, Great Barrier Reef, 10° 44' 05" S 142° 42' 18" E, 21 m depth, epibenthic sled, 2 ii. 2005, coll. *RV Lady Basten*. QMG329166 (SBD513801), inner shelf seabed between Pompey Reef and Mackay, Great Barrier Reef, 21° 02' 42" S 149° 48' 53" E, 21 m depth, epibenthic sled, 29 ix. 2004, coll. *RV Lady Basten*.

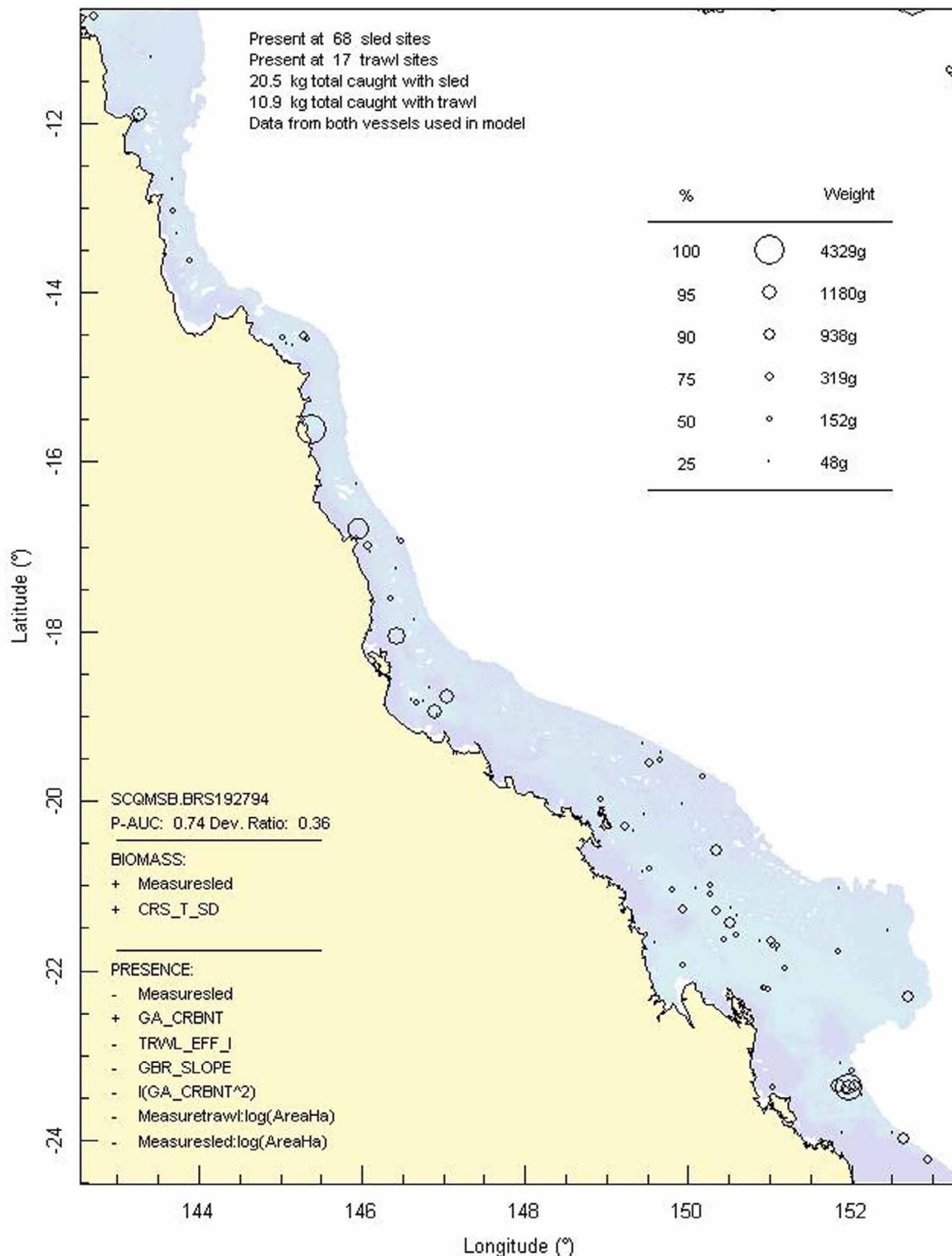
**Other material:** 95 specimens distributed between the seabed north of Wyborn Reef at the tip of Cape York to the seabed north of Fraser Island in the south (Figure 10). Housed at the Queensland Museum, Brisbane, Australia.

**Description.** *Shape.* This species has a highly variable morphology ranging from large cushion shapes to masses buried within the sand, with thick, tapering fistules protruding from the substrate. Nearly all the specimens collected from the GBR SBD project are massive with a large base which is usually buried within the substrate, tapering to thick fistules with an apical oscule.

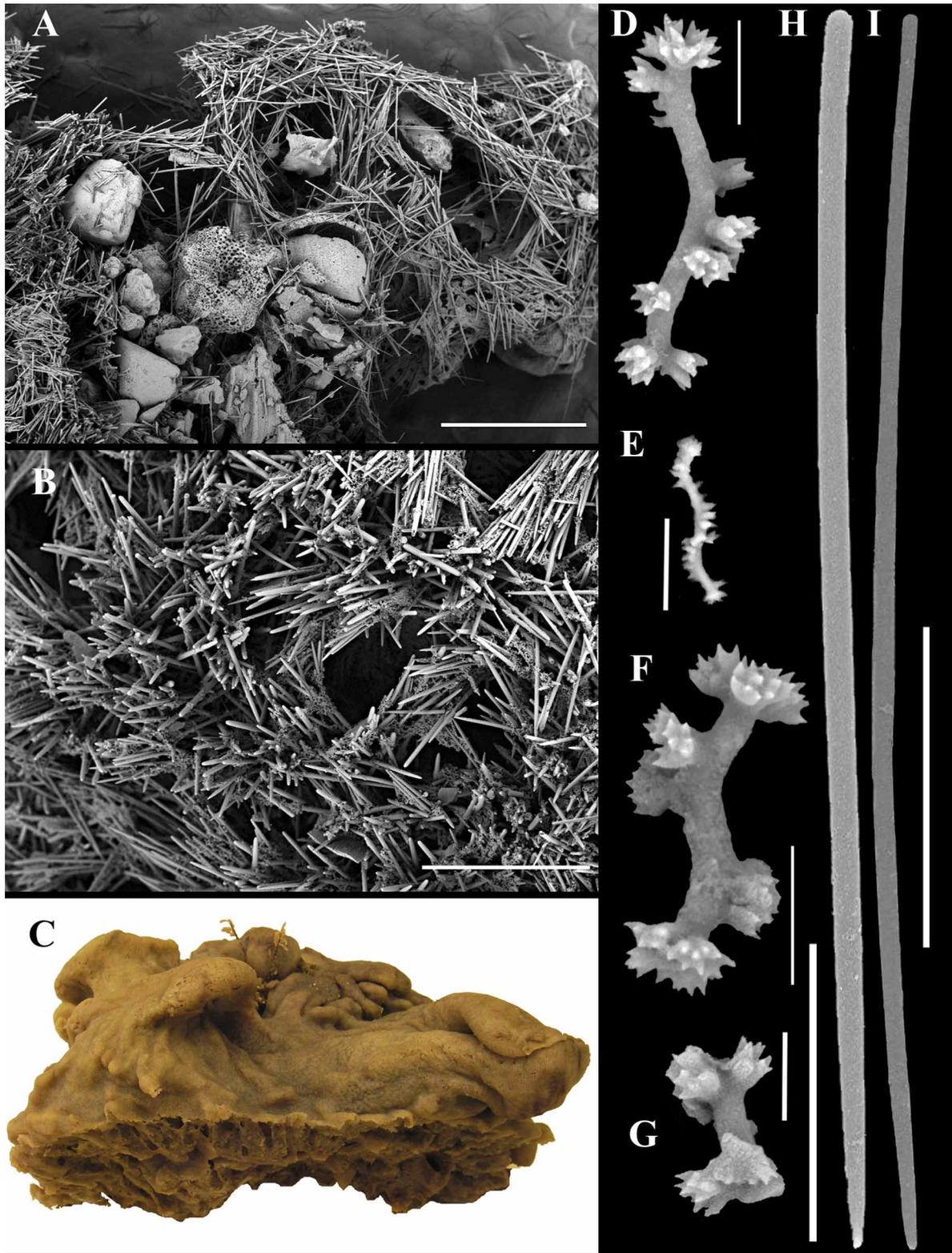
*Colour.* Grey/khaki colour when frozen and in ethanol. In situ coloration was not recorded.

*Oscules.* Protruding fistules are open, with a single, large oscule rimmed by a thick, firm layer of dense spongin, spicules and sand.

*Texture and surface characteristics.* This is an extremely dense sponge containing a large proportion of sand in the basal skeleton. It is easily cut or torn, and the internal texture is rough where the sand grains and other foreign material are exposed. The surface is smooth but not uniform, and firm to touch.



**FIGURE 10.** Model distribution map displaying predicted and actual distribution and biomass of *Spheciospongia vagabunda* (Ridley, 1884) from the Great Barrier Reef seabed, displaying: OTU code for this species (SCQMSB.BRS192794), P-AUC: Area Under the Curve performance diagnostic for the Presence/Absence model; Dev. Ratio: Deviance Ratio (P-AUC) performance diagnostic for the Biomass model; Measuresled: a device factor accounting for the difference in sampling rates between devices; Measuretrawl:log(AreaHa) and Measuresled:log(AreaHa): offsets accounting for the swept area sampled by the trawl and sled; and influential predictor variables including: CRS\_T\_SD: temperature (°C) standard deviation, GA\_CRBNT/ GA\_CRBNT^2: carbonate (%) and its quadratic term, TRWL\_EFF\_I: weighted average annual trawl effort, GBR\_SLOPE: slope.



**FIGURE 11.** *Spheciospongia vagabunda* (Ridley, 1884) (QMG329980 (SBD527235)). **A**, Section through the choanosome (scale bar 250  $\mu\text{m}$ ). **B**, View of spicule arrangement at the ectosome (scale bar 250  $\mu\text{m}$ ). **C**, Specimen (scale bar 8 cm). **D**, Spiraster (Type II) (scale bar 5  $\mu\text{m}$ ). **E**, Spiraster (Type II) (scale bar 20  $\mu\text{m}$ ). **F**, Spiraster (Type I) (5  $\mu\text{m}$ ). **G**, Spiraster (Type I) (scale bar 8  $\mu\text{m}$ ). **H**, Style (Type II) (scale bar 50  $\mu\text{m}$ ). **I**, Style (Type I) (scale bar 120  $\mu\text{m}$ ).

*Skeletal structure.* Small ectosomal tylostyles form distinct and dense brushes, with a crust of spirasters present at the base of these brushes. The choanosome is cavernous and consists of dense, seemingly random

tracts of larger tylostyles. Elongated spirasters were rare in our material, seen mainly in the buried portion of the basal skeleton.

*Megascleres* (Table 4). Two size classes of tylostyles are present. Ectosomal tylostyles are small and fine (135–430 µm), commonly with a straight or slightly curved shaft, some more gently recurved. Choanosomal tylostyles are larger and more robust (350–750µm), with most but not all having at least slightly curved shafts. Swollen tyloles range from flattened to evenly rounded, and some are simply styles with no subtylote swelling. Points range from sharp and evenly pointed, to heavily telescoped. There is a high amount of morphological variation in both size classes of megascleres.

**TABLE 4.** Measurement of spicules for *Sphaciospongia vagabunda* (Ridley, 1884), as range (and mean) of length x width in µm, N= 30.

Specimen number	Tylostyles ( Type I)	Tylostyles (Type II)	Spirasters (Type I)	Spirasters (Type II)
QMG329980 (SBD527235)	455–550 x 8–15 (500 x 10)	135–420 x 2.5–9.5 (255 x 7)	4–12 x 3–7 (9 x 5)	4–20 x 2 (11 x 2)
QMG329184 (SBD517192)	450–750 x 7–15 (550 x 10)	200–430 x 3–12 (300 x 7)	10–25 x 3–5 (13.8 x 4)	10–24 x 2–4 (14 x 2)
QMG329166 (SBD513801)	350–510 x 7–14 (400 x 9)	160–350 x 3–7 (250 x 5)	10–20 x 3–5 (11.3 x 5)	15–39 x 1–3 (17 x 2)

*Microscleres* (Table 4). Spirasters are present in two size classes. The shorter (Type I) spirasters have curved shafts showing thick, regular spination concentrated along the upper side of the shaft. Longer, thinner spirasters (Type II) are coiled with up to 4 rotations and exhibit evenly distributed spines concentrated in one line only which follows the coiling of the shaft.

**Habitat and distribution.** This species was collected from sites distributed along the entire GBR, in depths ranging from 14 to 92 m, mainly in habitats dominated by carbonate and sandy substrates. It was previously known from Torres Strait, Sri Lanka, Papua New Guinea, Indian Ocean, Philippines, the Central Pacific and tropical Australia (from the Great Barrier Reef to the Houtman Abrolhos, Western Australia).

**Remarks.** This current dataset confirms the commonality of this species within the Great Barrier Reef seabed as well as adjacent reefal areas. It often burrows within the substrate and can be easily missed when sampling. Published descriptions have also varied due to the large morphological variability across its broad geographic range. Spicule composition has also varied, with previous descriptions including only one size class of tylostyles, and microscleres including from one type – spirasters - (Bergquist, 1965, Bergquist & Tizard, 1967) to two, including spinispires (Kelly Borges & Bergquist, 1988). Our current definition identified two size classes of tylostyles, spirasters and rarely more elongate spirasters, as described as spinispires in the description by Kelly Borges and Bergquist (1988).

We have left this species in the genus *Sphaciospongia* for the time being, however, we recommend that the boundaries between *Sphaciospongia* and *Cervicornia* Rützler & Hooper, 2000 need to be resolved and that a revision of Clionidae and Spirastrellidae is needed.

**Predicted distributions and biophysical preferences.** *Sphaciospongia vagabunda* is evenly distributed along the length of the GBR, with no latitudinal regionalisation evident. Specimens were collected from 68 sled (biomass 20.5 kg) and 17 trawl sites (biomass 10.9 kg) between 14 and 92 m depth. Most populations appear to be located closer to the mainland, with very few specimens occurring towards the outer barrier reef areas. There may be cross shelf variation between populations given that *S. vagabunda* displays a wide range of gross morphological variability, however, this apparent cross shelf variation may simply be an artefact of the division of this species at OTU level, reflecting the different morphotypes. This species has a distribution which is negatively correlated with slope (Figure 10) and is found in sediments with a high carbonate content (Figure 3). This is expected given that the main body of this sponge is buried within the sediment, which thus needs to be relatively friable.

## Order Poecilosclerida Topsent, 1928

### Suborder Microcionina Hajdu, Van Soest & Hooper, 1994

#### Family Acarnidae Dendy, 1922

#### Genus *Paracornulum* Hallmann, 1920

##### *Paracornulum fistulosum* sp. nov.

(Figure 12, Tables 5, 6)

**Material examined.** Holotype: QMG329109 (SBD504571), seabed near Arlington Reef, Cairns, 16° 42' 17" S 146° 07' 30 E, 47m depth, epibenthic sled, 30 ix. 2003, coll. *RV Lady Basten*.

Paratypes: QMG329280 (SBD537201), seabed between mainland and Gould Reef (No. 1), 19° 37' 30" S 148° 05' 05 E, 45 m depth, epibenthic sled, 28 xi. 2005, coll. *RV Lady Basten*. QMG329191 (SBD518733), seabed near Noddy Reef No. 3, Cape York, 13° 37' 30" S 143° 53' 42 E, 31m depth, epibenthic sled, 8 ii. 2005, coll. *RV Lady Basten*.

**Description.** *Shape.* Small, elongated globules from 5 to 15 cm in length observed. Thin papery fistules rise to a distance of approximately 1–2 cm from the body surface.

*Colour.* Dark brown detachable ectosome, uniform in colour. Main body of sponge is also brown, some specimens with a slightly yellow interior, oxidising to brown.

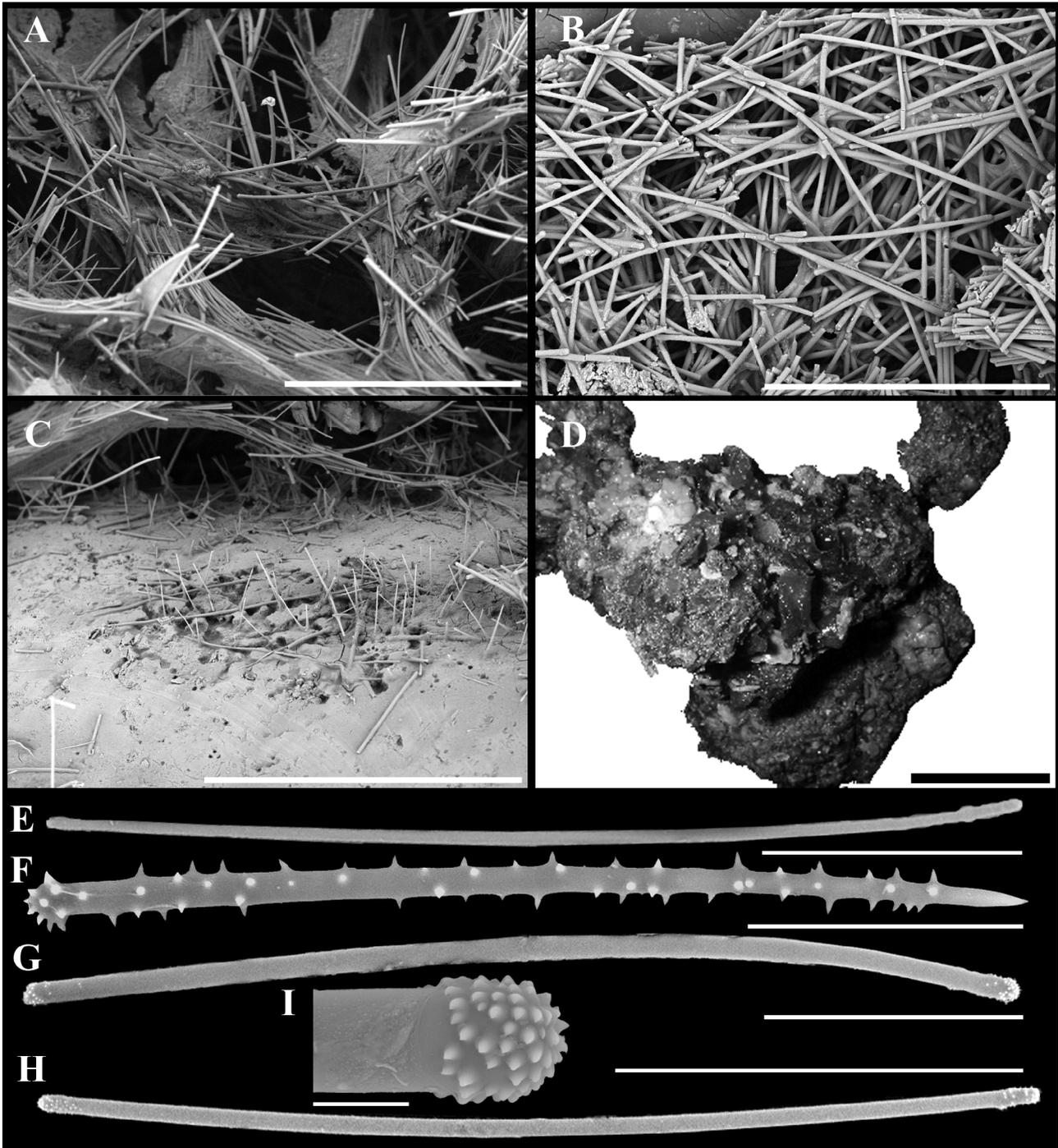
*Oscules.* Papery fistules are erect on the upper surfaces of globules. Fistules are open with a terminal oscule approximately 3 mm in diameter, composed of a thin wall less than 1 mm thick. Fistules collapse when preserved, but still recognised in most specimens, flattened along the surface of the sponge.

*Texture and surface characteristics.* Surface covered with a paper-like detachable crust of tangential tylotes. Specimens are brittle and easily broken due to the dominance of sand within the choanosome.

*Skeletal structure.* Given its small, agglutinating growth form the skeletal structure can only be determined accurately using untreated or barely treated histological preparations under scanning electron microscopy. The basal skeletal architecture is hymedesmioid with acanthostyles erect and embedded in a basal layer of spongin coating the biogenic coralline substrate. These acanthostyles appear to be patchy, as observed under SEM (presumably related to the distribution of basal spongin) with acanthostyles barely present in some places, but forming dense clumps in other places, such as areas where bioerosion of the calcite appears to be occurring (see Figure 12C showing a worm tube with pitted surface and paratangential acanthostyles conforming with these cavities). Arising from this hymedesmioid basal skeleton are dense tracts of tylotes forming the majority of the choanosomal skeleton, also with some thinner tylotes (Type I) incorporated. Spicule tracts loosely ascend to the surface, with a less well-developed reticulate component. Under SEM many tracts appear to be paratangential (e.g. Figure 12A), but this is possibly due to compression of the choanosomal skeleton during preservation (e.g. collapse of the fistules), and chemical preparation for histology. The ectosomal skeleton is a dense feltwork of tangentially arranged, apically spined tylotes forming a thin layer, clearly distinct from the choanosomal skeleton (Figure 12B), producing the parchment-like ectosomal peel. Both choanosomal and ectosomal skeletons are highly spiculose with a poorer spongin component.

*Megascleres* (Table 5). Apically spined tylotes (Type II) are the primary spicules of this species, found in both the ectosomal and choanosomal skeletons. Terminal and subterminal spination is variable, ranging from large, irregular spines concentrated in the tyle region, to finer, more blunt spines extending partially down the shaft (Figure 12G, H). Smooth tylotes (Type I) are also incorporated within the choanosomal skeleton, are much thinner than the Type II tylotes and differ only from strongyles by the presence of slight terminal swelling (Figure 12E).

Acanthostyles are heavily spined at the head, with irregularly spaced but nonetheless continuous spines along the length of the shaft. Tips of the acanthostyles may be spiny or smooth, usually mirroring the degree of spination on the shaft.



**FIGURE 12.** *Paracornulum fistulosum* sp. nov. (QMG329109 (SBD504571)). **A**, Multispicular tracts forming plumoreticulation throughout the choanosome (scale bar 300  $\mu$ m). **B**, View of spicule arrangement at the ectosome (scale bar 300  $\mu$ m). **C**, Acanthostyles echinating the basal skeleton coating biogenic substratum with evidence of bioerosion (scale bar 500  $\mu$ m). **D**, Holotype (scale bar 3 cm). **E**, Tylote (Type I) with smooth tips (scale bar 100  $\mu$ m). **F**, Acanthostyle (scale bar 25  $\mu$ m). **G**, Tylote (Type II), heavily spined at both ends (scale bar 50  $\mu$ m). **H**, Tylote (Type II) (scale bar 100  $\mu$ m). **I**, Tylote (Type II) head, showing detailed spination (scale bar 5  $\mu$ m).

*Microscleres.* Absent.

**Habitat and distribution.** This species was collected from depths greater than 30 m in the central and northern Great Barrier Reef.

**Etymology.** Named for the fistules which are characteristic and protrude from the upper surface of the sponge.

**TABLE 5.** Measurement of spicules for *Paracornulum fistulosum* sp. nov., as range (and mean) of length x width in  $\mu\text{m}$ , N=30.

Specimen number	Tylotes (Type I)	Tylotes (Type II)	Acanthostyles
QMG329109 (SBD504571)	200–400 x 3–8 (300 x 5)	300–450 x 2–6 (400 x 4)	70–130 x 2–5 (95 x 3)
QMG329280 (SBD537201)	145–400 x 4–10 (235 x 5)	350–470 x 3–7 (400 x 5)	90–130 x 2–5 (100 x 3)
QMG329191 (SBD518733)	200–400 X 4–8 (350 X 6)	330–400 X 3–7 (350 X 4)	65–150 X 2–3 (88 X 3)

**Remarks.** Allocation of this species within the family Acarnidae remains problematic, showing similarities to three genera

*Cornulum* Carter, 1876 (type species *Cornulum textile* Carter, 1876) has a plumo-reticulate skeletal structure slightly similar to the new species, but lacks acanthostyles and has palmate isochelae. The genus was recently redefined to exclude *Cornulotrocha* (type species *Cornulotrocha cheliradians* Topsent, 1927) by Hajdu *et al.* (2006). Hooper (2002) had allocated *Cornulotrocha* as a synonym of *Cornulum*, based on similarities in skeletal structure and also on the original published description whereby megascleres were described as diactinal. Hajdu *et al.*, (2006) subsequently found that these megascleres were actually monactinal, and together with possession of acanthostyles reallocated it to Microcionidae as *Clathria* (*Cornulotrocha*). In the present species the tylotes are clearly diactinal, and together with the presence of acanthostyles, the species does not fit well with *Cornulum*.

*Zyzya* is excavating, with a choanosomal skeletal structure consisting of irregular or plumose and widely spaced tracts of tylotes. Palmate isochelae may be present or absent (absent in the holotype of the type species, *Z. fuliginosa*, but otherwise present in other populations; Hooper, 2002: 431), interpreted as a secondary loss, common amongst other poecilosclerids (e.g. Hooper, 1996). *Zyzya* has a strong apomorphy in the form of characteristically verticillate-spined acanthostrongyles that form a prominent secondary isodictyal reticulate skeleton. These acanthostrongyles are quite different to the category of echinating acanthostyles in the new species described here, forming the hymedesmioid basal skeleton. Van Soest *et al.* (1994) reported on a Fiji specimen allocated to *Z. fuliginosa* that had rare acanthostyles and no proper verticillated acanthostrongyles, with its allocation to *Z. fuliginosa* confirmed by the common possession of makaluvamines, a pyridoacridine alkaloid class of compound typical of this species. Consequently we checked the chemical profile of our new species, which was found not to contain makaluvamines (Mary Kay Harper & Chris Ireland, pers.comm.). Thus, its potential allocation to *Zyzya* is tenuous at best, lacking the primary *Zyzya* apomorphy of verticillate-spined acanthostrongyles in isodictyal reticulation but having an unequivocal basal hymedesmioid skeleton of echinating acanthostyles.

This new species appears to fit best with *Paracornulum* on the basis that amongst Acarnidae it possesses true acanthostyles and diactinal spicules. The new species is similar in this respect to the type species, *P. dubium*, (Hentschel, 1912), with acanthostyles echinating a basal spongin skeleton, but differs from all other *Paracornulum* in lacking microscleres (interpreted as a secondary loss), and having a choanosomal skeleton that is plumose but compressed and therefore plumo-reticulate rather than radial. A comparison of spicule composition and sizes between this new and the known species of *Paracornulum* is provided in Table 6.

Initial collections of this species from the GBR seabed included two other, cryptically similar species within a single OTU, which subsequent more detailed taxonomy revealed as a heterogeneous species complex. Although extremely similar in external morphology, the spicule components and skeletal structures were found to be clearly different. We have therefore not included associated widespread GBR distribution and biophysical data for *P. fistulosum* until all of the many hundreds of specimens originally included within this OTU have been examined and assigned to an appropriate taxon.

**TABLE 6.** Comparisons in spicule composition and size ranges for species of *Paracornulum* Hallmann, 1920 (data from original descriptions).

	Tylotes	Acanthostyles	Styles	Chelae	Toxas	Microrhabds
<i>P. dubium</i> (Hentschel, 1912) (type species)	216–440 µm (Two size classes)	96–152 µm	absent	14–16 µm	80–150 µm	absent
<i>P. coherens</i> Levi, 1963	250–300 x 10 µm	150–275 x 12–14 µm	absent	20 µm	absent	12 µm
<i>P. fistulosum</i> sp. nov.	145–400 x 3–10 µm (Type I) 300–470 x 2–7 µm (Type II)	65–150 x 2–5 µm	absent	absent	absent	Absent
<i>P. sinclairae</i> Bergquist & Fromont, 1988	205–260 x 5.5–7 µm	absent	285–515 x 7.5–16 µm (Type I) 160–215 x 6–11 µm (Type II) 295–340 x 4–6.5 µm (Type III)	23–26 µm	70–140 x 1–2.5 µm (Type I) 113–125 (Type II)	Absent
<i>P. strepsichela</i> (Dendy, 1922) (also reported in Bergquist & Fromont, 1988)	380 x 9 µm	absent	absent	16 µm	absent	Absent

## Discussion

Aside from the intrinsic value of discovering two new species amongst the five most common sponges on the GBR, the most significant contribution this study has made is to tell us how much we still do not know about the now relatively well-explored GBR. It is clear that our previous understanding of sponge biodiversity within the GBR is predominantly based on the reefal faunas, which comprise only about 7% of the GBRWHA. These five most common sponges exhibit widespread distributions and are predominantly located in sand or calcium carbonate dominated benthic habitats, as opposed to muddy, patch reef or rocky outcrop benthic habitats.

The presence of species such as *D. xanthus* that incorporate detritus into the skeleton, becoming a major structural component of the sponge, provides stabilisation to the benthos as it spreads through the sediment, agglutinating the biogenic rubble and inorganic substrata. This has an important follow-on effect of providing a new habitat for other species to subsequently colonise. By its very fragile nature and relatively shallow depth this community is at significant risk through both anthropogenic and naturally caused impacts. The potential loss of these habitat stabilising species through activities such as trawling, will have compounding effects on other species, with a conservation management implication. Thus, the GBR Seabed Biodiversity Project has collected data crucial to the conservation and management strategies of the GBRWHA.

Of the several environmental covariates recorded in this study, depth was found to have little relative correlation with species distributions. Conversely, substrate composition was repeatedly a highly influential factor in determining the presence of these species. For example it was mostly the presence of mud, sand or carbonate that correlated positively or negatively with particular species distributions. This contrasts with a previous study (Cleary *et al.*, 2005) of the benthos of the Spermonde Archipelago, Indonesia, which concluded that coral reef associated sponges had differing community structures between inshore and offshore reefs, with depth being the most important physical characteristic defining variation in diversity. However, similar to the seabed fauna of the GBR, the foraminifera, which can live in sandy, inter reef seabed habitats, were broadly distributed across the shelf and were more affected by exposure and habitat. Thus, our prior generalisations concerning trends in the distributions of sponges in coral reef ecosystems, and the environmental and physical parameters that influence these distributions, are incomplete and therefore not entirely correct.

This prior knowledge of sponge distributions shows they are highly spatially heterogenous (e.g. see summary in Hooper & Ekins, 2004). While this spatial variation cannot be completely explained by environmental variability, general influences include substrate type (e.g. Duckworth *et al.* 2008), reproductive methods and dispersal capabilities (e.g. Uriz *et al.* 1998), depth and distance from shore, where factors such as light intensity, turbidity, nutrient and sediment content are influential (e.g. Wilkinson & Cheshire 1989; de Voogt *et al.* 2006). Neighbouring coral reef systems have been found to have up to 85% dissimilarity in species composition, with relatively few species displaying widespread distributions. The most highly correlated factor determining the distribution of widespread species was the presence/absence of niche habitats, such as caves, reef flats, spurs and grooves or particular inter reef regions (eg. Hooper, 1994; Hooper *et al.*, 1999).

Despite the significance of numerous environmental variables on the distribution of sponges at smaller scales, analysis of sponge diversity of the tropical Australian fauna at the continental scale found the tropical east coast to constitute a single province, with the Great Barrier Reef showing transitional zones only at Mackay/Townsville and in the far Northern region (Hooper & Ekins 2004). This has been supported by genetic differences found within populations of the widespread species *Leucetta chagosensis*, which showed significant differences between haplotypes at a line between the Whitsunday Islands and the Swain Reefs (Wörheide *et al.* 2002). Most of these conclusions are based on coral reef species data.

While patch reefs and rocky outcrops are interspersed throughout the continental shelf of the GBR, they are disjointed and often isolated, sometimes with little or haphazard connectivity between them as seen previously for local sponge populations (e.g. Hooper, 1994). In contrast, seabed habitats have a far higher level of continuity over large distances, where there are no well-defined physical barriers. In the GBRSD study predicted distributions of these species are based on analyses of the most influential physical parameters thought to affect the known distributions of seabed populations. These maps show that with the exception of *D. xanthus*, the predicted presence and biomass of these species are largely continuous along a latitudinal gradient. This suggests that continuous areas of similar seabed habitats provide corridors for widespread species distribution, at least for those species that are adapted to live in these inter-reef habitats.

Based predominantly on the previously known coral reef associated faunas, it was shown that the Great Barrier Reef could be divided into regions based on species distributions and species 'turnover points' (beta-diversity) (Hooper & Ekins, 2004), with a latitudinal turnover of the sponge fauna at the Townsville/Mackay region and in the far north of the GBR. Few coral reef associated species exhibited widespread distributions, with less than 20 reef species found in more than 12 locations (0.1%). In significant contrast to the reef-associated faunas, the inter-reef seabed species' distributions occupy genetically connected corridors along the entire length and breadth of the GBRWHA, not previously known for any of the GBR sponges. These combined reef and inter-reef datasets represent a valuable and globally unique future research resource.

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