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Two new records of *Geodia* (Porifera: Astrophorida: Geodiidae) from the Johor Straits, Singapore

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Abstract. Two new records of sponges in the genus *Geodia* were identified from Singapore in the estuarine Johor Straits. The white, encrusting, cushion-like *G. distincta* Lindgren was common in shallow water from the intertidal zone to 20 m deep, whilst the larger *G. picteti* Topsent was collected from the shallow subtidal and possessed upright, finger-like processes extending from a base that is attached to gravel and sand. An identification key to all 11 species recorded from the South China Sea is presented. Inherent difficulties associated with *Geodia* identification are highlighted and discussed.

Key words. Taxonomy, *Geodia*, Johor Strait, Singapore, South China Sea, Indo-Pacific

INTRODUCTION

The genus *Geodia* is a large group of astrophorid sponges with a worldwide distribution and occurs from the shallow littoral zone to bathyal depths. *Geodia* species are typically globular or irregularly massive sponges possessing a diverse range of spicules and are distinctive in having a prominent cortex made up of sterrasters. The sterraster is the single autapomorphic character that distinguishes members of the family Geodiidae from other sponges, although the sterrasters has been secondarily lost many times independently in some Geodiidae (Cárdenas et al., 2011). Molecular phylogenetic analyses have led to the synonymisation of the genera *Isops* and *Sidonops* with *Geodia* (Cárdenas et al., 2010) and to the abandonment of oscule / pore morphology as a diagnostic character for Geodiidae genera (Uriz, 2002). Hitherto, there are some 164 valid *Geodia* species worldwide (Van Soest et al., 2014).

There are about 100 *Geodia* species recorded from the Indo-Pacific Ocean, compared to the 60 or so species known from the Atlantic Ocean. To date, nine species have been described and recorded from the South China Sea: *Geodia arripiens* Lindgren, 1897 from Vietnam; *G. distincta* Lindgren, 1897 and *G. nigra* (Lindgren, 1897) from the Java Sea; *G. ostracomorpha* (Lévi & Lévi, 1989), *G. japonica spherulifera* Wilson, 1925 and *G. philippinensis* Wilson, 1925 from the Philippines; *G. spherastrosa* (Wilson, 1925) from Shantou, southern China; *G. microspinosa* (Wilson, 1925) and G. *sparsa* Wilson, 1925 from eastern Borneo. These have been recorded from depths of between 45 m (*Geodia arripens*) to 256 m (*Geodia spherastrosa*). The rest of the *Geodia* species are shallow-water species recorded from less than 100 m depth except *G. ostracomorpha* (137 m). They range from 1 cm to 50 cm in size, exhibiting a diverse morphology including spherical or subspherical forms (*G. ostracomorpha* and *G. arripiens*), vase-shaped forms (*G. philippinensis* and *G. microspinosa*), massive irregular or cushion-shaped forms (*G. japonica spherulifera* and *G. spherastrosa*), to massive forms with cylindrical processes (*G. sparsa*) and encrusting forms (*G. distincta* and *G. nigra*). These tropical species all have a diverse repertoire of spicules and overlapping size ranges, which have resulted in a somewhat incomplete and confused taxonomy.

Descriptions of two new Singapore records, *Geodia distincta* and *G. picteti*, are provided in this paper. Discrepancies in the original species descriptions are highlighted and discussed. These specimens were compared with published descriptions of *Geodia* species from the Indo-Pacific and an identification key to the South China Sea species of *Geodia* is provided.

MATERIAL & METHODS

Sponge specimens were collected in the Johor Straits off Pulau Ubin using a beam trawl towed by R/V *Galaxea* during the Johor Straits International Workshop in October 2012. They were preserved in 95% denatured ethanol within six hours. Type material was deposited at the Zoological Reference Collection (ZRC) at the Lee Kong Chian Natural History Museum (LKCNHM, formerly Raffles Museum of Biodiversity Research), National University of Singapore. To examine skeletal architecture, paraffin-embedded sponge tissue was sectioned either by hand or by using a microtome. The sections were then cleared in 1:1 v/v phenol-xylene mixture and mounted in Dpex® on glass slides. Spicule preparations were made on a glass slide by dissolving a small piece of the specimen in a few drops of concentrated nitric acid over an alcohol flame. These were mounted either in

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Dpex® on glass slides for light microscopy or transferred onto brass stubs for SEM (scanning electron microscopy). SEM mounts were platinum-coated and viewed using JEOL JSM-6510 scanning electron microscope. Spicule measurements (25 for each type, unless stated otherwise) were made by light microscopy and from SEM images. Spicule size range was estimated and presented as lowest value-mean-highest value of both length and width. Asters were measured based on its maximum diameter.

The classification of *Geodia* used here follows Cárdenas et al. (2010), which has been accepted by the World Porifera Database (Van Soest et al., 2014).

SYSTEMATICS

Class Demospongiae

Order Astrophorida

Family Geodiidae

Genus *Geodia* Lamarck, 1815

Geodia distincta Lindgren, 1897
(Figs. 1, 2)

Material. ZRC.POR.0277. East Johor Strait, Singapore, 5–20 m depth, 1°23.912'N; 103°58.577'E; coll. 29 October 2012 using a beam trawl; S. C. Lim.

Description. Encrusting, irregular to cushion-shaped sponge. Size 7 cm by 5 cm, about 1 cm in height (Fig. 1). Living animal is white and colour remains unchanged in ethanol. Surface is even and smooth. Pointed spicules 1–2 mm in length can be observed with the naked eye protruding from the surface sparsely. Pores and oscules are not visible in preserved specimens. Fairly fragile and breaks easily.

Skeletal structure. Cortex is about 0.8 mm in thickness, consisting of spherical sterrasters (Fig. 2A), strongylasters (Fig. 2B), oxyasters I (Fig. 2C), oxyasters II (Fig. 2D), spherasters (Fig. 2E) and oxeas (Fig. 2F). The cortex is densely packed with sterrasters. There are abundant strongylasters on the surface of the cortex that is mostly one spicule thick. Numerous spherasters are interspersed in cortex; oxyasters I and oxyasters II are present in much lower numbers. Oxeas I are mostly arranged perpendicularly to the surface.

Choanosome consists of oxeas II, orthotriaenes, protriaenes and anatriaenes, in addition to the cortical spicules. Orthotriaenes are found mostly near the cortex, supporting the cortical sterraster layers with the cladome. Oxeas II are the dominant megascleres and they form radiating spicule bundles with orthotriaenes and rare pro- and anatriaenes.

These are arranged randomly within the interior of the choanosome. All cortical spicules are interspersed in the choanosome. Oxyasters II (Fig. 2E) occur in much higher density in the choanosome compared to the cortex.

Spicules (Fig. 2).

1. Sterrasters (Fig. 2A), 75–80.3–85 µm, mostly perfectly spherical in shape.
2. Strongylasters (Fig. 2B), 4–5.2–6 µm, rays short, truncated and spiny.
3. Oxyasters I (Fig. 2C), 16–18.5–20 µm in diameter, number of rays 11–>18. Large robust spines around the tip of rays.
4. Oxyasters II (Fig. 2D), 37.8–49.6–65.5 µm, 4–7 rays. Recurved spines around the tips of ray.
5. Spherasters (Fig. 2E), 24–25.9–28 µm. rays short, truncated with spiny terminal.
6. Oxeas I (Fig. 2F), 230–252.5–280 µm × 5 µm, smooth, straight or slightly curved.
7. Oxeas II, 1464–1897.8–2400 µm × 22–30.4–40 µm, smooth, straight or slightly curved, very abundant. Only present in choanosome.
8. Orthotriaenes, 2000–2215–2500 µm × 40–51–60 µm; cladi, 180–201.7–240 µm × 35–38.8–40 µm. Less abundant than oxeas II. Only present in choanosome.
9. Anatriaenes: 3500–4156–5000 µm × 10–13.6–20 µm; cladi, 40–50.6–60 µm (N = 10). Only present in choanosome. Considerably less abundant than orthotriaenes.
10. Protriaenes: 3200–3500–3750 µm × 18–20.8–25 µm (N = 5). Only present in choanosome. Less abundant than anatriaenes.

Ecology and distribution. Common in shallow water from the intertidal zone to 20 m in a highly sedimented environment; encrusting on rocks, stones and gravel, with aggregating coral rubble and shells at the base. This species was also previously documented in Singapore from the intertidal zone as *Geodia* sp. (Lim et al., 2012). *Geodia distincta* appears to be a widespread species distributed across the Indonesian archipelago.

Remarks. *Geodia distincta* has a spiculation of sterrasters, strongylasters, spherasters, oxyasters I and II, oxeas I and II, orthotriaenes, protriaenes and anatriaenes. The characters present in the Singapore material are comparable to those of *G. distincta* in Lindgren (1898). The only discrepancies are that anatriaenes and protriaenes are common in the specimen described by Lindgren (1897, 1898), whilst these spicules appear to be rare in Singapore material. We consider such discrepancies to fall within the range of intraspecific variation of *G. distincta*.

The spiculation in *Geodia hirsuta* (Sollas, 1886) and *G. japonica spherulifera* Wilson, 1925 are quite similar to *G. distincta*. However, *G. hirsuta* can be distinguished by its large sterrasters (161–306 µm) and the presence of dichotriaenes. *Geodia japonica spherulifera* is very similar to *G. distincta* and the former has all the spicule types with slight size variation. It might be a synonym of *G. distincta* but further morphological examination and molecular work

Fig. 1. *Geodia distincta* Lindgren, 1897. ZRC.POR.0277. Ethanol preserved specimen from East Johor Strait, Singapore.

Fig. 3. *Geodia picteti* (Topsent, 1897). ZRC.POR.0276. Ethanol preserved specimen from East Johor Strait, Singapore.

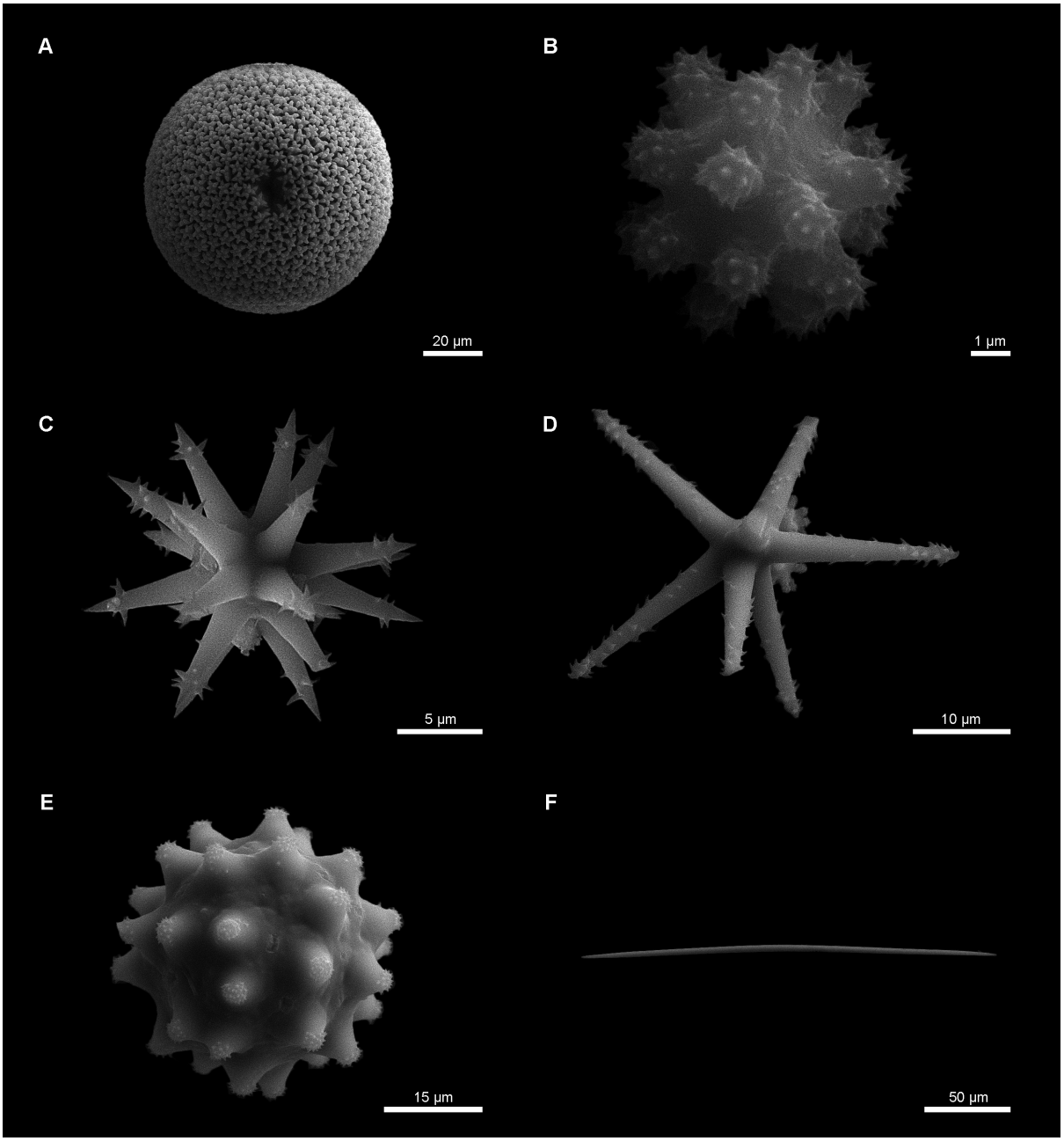

Fig. 2. Spicules of *Geodia distincta*. A, sterraster. B, strongylaster. C, oxyaster I. D, oxyaster II. E, spheraster.

are required to ascertain this. Wilson (1925) also stated that *Geodia japonica spherulifera* is sufficiently close to *G. japonica*, but *G. japonica* lacks a second category of oxyasters and protriaenes (Sollas, 1888).

Geodia picteti (Topsent, 1897)

(Figs. 3, 4)

Material. ZRC.POR.0276 preserved in 95% ethanol. East Johor Strait, Singapore, 5–20 m depth, 1°23.912'N, 103°58.577'E; collected 29 October 2012 using beam trawl, S. C. Lim.

External morphology. Sponge massive, 8 cm wide and 15 cm in height with upright finger-like processes rounded terminally, 5–7 cm in length and 2 cm in diameter (Fig. 3). Colour is white when alive and unchanged in ethanol. Surface appears even and smooth but is rough to the touch and hispid under close examination. Uniporal oscules (ca. 1 mm in diameter each) are gathered in an area about 2 cm in diameter. Ostia are not visible to the naked eye after preservation. The sponge resists tearing due to the 1.5–2.5 mm thick cortex. Interior is soft and pulpy.

Skeletal structure. Cortex is 1.5–2.5 mm thick, consisting of sterrasters (Fig. 4A), strongylasters (Fig. 4B) and styles (Fig. 4C). Densely packed sterrasters make up the bulk of the cortex, which is supported by cladomes of orthotriaenes in the choanosome. Single spicule thick strongylasters form a dermal layer (ectocortex) on top of sterraster crust. Abundant styles are arranged perpendicular to and protrude from cortical surface. Only styles are present, other kinds of monaxones absent.

Choanosome consists of oxeas, orthotriaenes and oxyasters (Fig. 4D) in addition to the cortical spicules. Oxeas and orthotriaenes are arranged perpendicularly to the surface of the cortex but become confused towards the interior. The cladome of orthotriaenes lie just below the cortex with the rhabdome directed inwards. The remaining spicule types (oxyasters, sterrasters, strongylasters and styles) are interspersed throughout the choanosome.

Spicules (Fig. 4).

1) Sterrasters (Fig. 4A), 110–141.9–160 μm × 100–120.6–140 μm in diameter, subspherical.
2) Strongylasters (Fig. 4B), 5–5.6–6 μm in diameter (N = 10), highly, irregular, short spiny rays, large centrum.
3) Styles (Fig. 4C), 180–212.5–240 μm × 3.5–3.9–4 μm.
4) Oxeas, 1625–2370–2750 μm × 25– 35.7–45 μm, straight or slightly curved and acerated. Only present in choanosome.
5) Orthotriaenes, rhabdome straight, 2000–2416–2750 μm × 42.5–47.5–50 μm. Cladi, 320–518.9–620 μm × 35–39.4–45 μm (N = 10). Only present in choanosome.

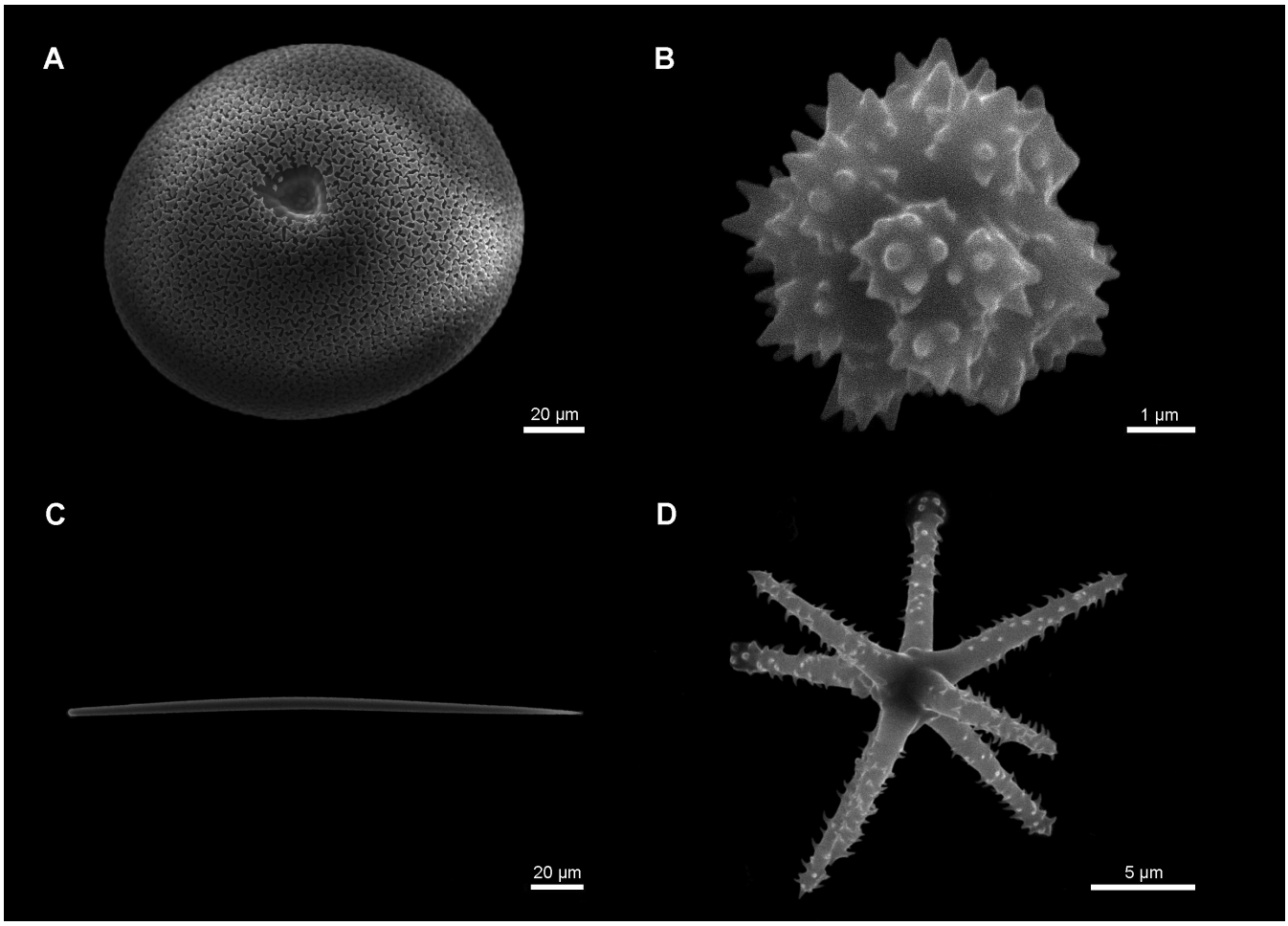

Fig. 4. Spicules of *Geodia picteti*. A, sterraster. B, strongylaster. C, style. D, oxyaster.

Table 1. Spicule composition of 11 *Geodia* species known to occur in the South China Sea. * sensu Lindgren 1898.

Geodia species	Sterrasters	Strongylasters	Sphaerasters	Oxyasters	Microstyles	Microoxeas	Oxeas	Orthotriaenes	Anatriaenes	Protriaenes	Plagiotriaenes	Dichotriaenes
arripiens	72 × 88 μm	8–12 μm (chiaster)	–	36 μm	–	–	+	–	+	+	–	+
*berryi**	68 × 80 μm	8 μm (chiaster)	12–15 μm	16–20 μm	–	+	+	+	+	+	–	–
distincta	56 × 68 μm	8 μm	28 μm	16; 44 μm	–	+	+	+	+	+	–	–
japonica spherulifera	80 × 85 μm	4–6 μm	24–32 μm	16–20 μm; 44–60 μm	–	+	+	+	+	+	–	–
microspinosa	56 × 48 μm	–	6–8 μm	8 μm; 16–28 μm	–	–	+	+	–	–	–	–
nigra	52 × 62 μm	–	20 μm	24 μm	–	–	+	–	–	–	+	–
ostracomorpha	95 × 130 μm	–	15 μm (spheroxyasters)	15–180 μm (five categories)	–	–	+	+	–	–	–	–
philippinensis	124 × 104 μm	–	–	4–6 μm; 24–36 μm	–	+	+	–	+	+	–	+
*picteti**	120 × 160 μm	–	4 μm (pynasters)	20–48 μm	+	–	+	+	+	+	–	–
sparsa	144 × 196 μm	–	–	4 μm; 24–40 μm; 32–40 μm	–	+	+	–	+	+	+	–
spherastrosa	130 × 200 μm	12–14 μm	8 μm	30–32 μm	–	–	+	–	–	–	–	–

6) Oxyasters (Fig. 4D), 25–31.1–35 µm, entire rays microspined. Number of rays 7–9. Only present in choanosome.

Ecology and distribution. Occurs in shallow waters (5–20 m) in a highly sedimented environment, attached to gravel and coarse sand. *Geodia picteti* appears to be a widespread species distributed across the Indonesian archipelago.

Remarks. Topsent (1897) might have made a number of mistakes in the description of *G. picteti*. Examination and observation of the *G. picteti* type material (both holotype and paratype) by Cárdenas (pers. comm.) revealed that: 1) larger sterrasters (105–145 × 100–130 µm) are present compared to the size range (97–85 µm provided by Topsent (1897); 2) styles are present, although stated to be absent in Topsent (1897); 3) large oxeas (1800–2300 µm in length) are present, 500–600 um in Topsent (1897); 4) orthotriaenes with long rhabdomes (1850 µm in length) are present, 500–600 um in Topsent (1897).

Interestingly, Lindgren (1898) presented a description similar to Cárdenas' recent observations of *G. picteti*. These are significant differences but Lindgren (1898) did not explain the discrepancies between his material and those of Topsent.

Anatriaenes and protriaenes were absent in Singapore material but the absence could be due to environmental conditions (Cárdenas, pers. comm.). It remains possible that they could be very rare in the skeleton. However, the significance of the absence of these spicules remains speculative and requires confirmation based on material from elsewhere within its geographical range (Cárdenas, pers. comms.).

DISCUSSION

The genus *Geodia* is a large and diverse group worldwide but surprisingly has only a small presence in the South China Sea. The two new records of *Geodia* species from Singapore were from shallow depths less than 20 m. The shallowest depth recorded of a *Geodia* species from the South China Sea prior to this study was *G. arripiens* from a depth of 45 m off the Vietnamese coast.

All 11 species of *Geodia* known to occur in the South China Sea can be distinguished based on previous descriptions (see Table 1 and identification key). Both *G. spherastrosa* and *G. sparsa* possess large sterrasters 144–200 µm in diameter, but *G. spherastrosa* can be distinguished from *G. sparsa* in having 8 µm dermal spherasters while *G. sparsa* has 4 µm dermal oxyasters. *Geodia microspinosa* has the smallest sterrasters, which are about 56 × 48 µm in size. *Geodia ostracomorpha* has the highest number of categories of oxyasters (six categories). Only *G. arripiens* and *G. philippinensis* have dichotriaenes and *G. philippinensis* can be distinguished from *G. arripiens* in having two categories of oxeas (3 mm × 50 µm; 370–500 × 6–8 µm). *Geodia nigra* has the fewest categories of megascleres i.e., it only has oxeas and plagiotriaenes. Lastly, *G. japonica spherulifera* and *G. distincta* have similar spicule types with slight size variation. There is a possibility that they are conspecific, and further morphological examination and molecular comparisons are needed to determine if they are indeed the same species.

Identification of *Geodia* species based solely on the original descriptions may not be entirely reliable even though they seem sufficiently detailed at first glance. Re-examination of type material can provide additional and critical information, as shown in the case of *G. picteti* in this study. Many species were described in the last century without the benefit of a scanning electron microscope, and observations based solely on the light microscope may not be sufficiently detailed to differentiate contemporary *Geodia* fauna. For instance, it is difficult to categorise asters less than 10 µm in diameter as strongylasters, oxyasters or spherasters under the light microscope, let alone determine if spines are present on their surfaces. Another common problem is that the full extent of spicule size range is often not provided. The presence or absence of triaenes such as anatriaenes, protriaenes and plagiotriaenes cannot be taken into serious consideration for species determination as they can be very rare in skeleton, or may be absent altogether, due to environmental factors (see Cárdenas & Rapp, 2013). This is further confounded by the increasing realisation that many *Geodia* species in the Indo-Pacific are indeed very similar. Many spicule characters overlap and it becomes necessary to utilise a large suite of characters to distinguish congeners apart. All the above variables and problems make identification of *Geodia* very difficult.

Identification key to *Geodia* species in the South China Sea

1. Sterrasters 100 µm and above in diameter 2
– Sterrasters less than 100 µm in diameter 6
2. Spherasters over 10 µm in diameter present ..... *G. ostracomorpha* (Lévi & Lévi, 1989)
– Spherasters over 10 µm in diameter absent 3
3. Orthotriaenes present 4
– Orthotriaenes absent 5
4. Micro-styles present ..... *G. picteti* (Topsent, 1897)
– Micro-styles absent ..... *G. spherastrosa* (Wilson, 1925)
5. Dichotriaenes present ..... *G. philippinensis* Wilson, 1925
– Dichotriaenes absent ..... *G. sparsa* Wilson, 1925
6. Orthotriaenes present 8
– Orthotriaenes absent 7
7. Spherasters present ..... *G. nigra* (Lindgren, 1897)
– Spherasters absent ..... *G. arripiens* Lindgren, 1897
8. Spherasters present ..... *G. distincta* Lindgren, 1897/*G. japonica spherulifera* Wilson, 1925
– Spherasters absent 9
9. Ana- and pro-triaenes present ..... *G. berryi* (Sollas, 1888) sensu Lindgren 1897
– Ana- and pro-triaenes absent ..... *G. microspinosa* (Wilson, 1925)

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LITERATURE CITED

Cárdenas P & Rapp HT (2013) Disrupted spiculogenesis in deep-water Geodiidae (Porifera, Demospongiae) growing in shallow waters. Invertebrate Biology 132(3), 173–194.

Cárdenas P, Rapp HT, Schander C & Tendal OS (2010) Molecular taxonomy and phylogeny of the Geodiidae (Porifera, Demospongiae, Astrophorida) - combining phylogenetic and Linnaean classification. Zoologica Scripta, 39: 89–106.

Cárdenas P, Xavier JR, Reveillaud J, Schander C & Rapp HT (2011) Molecular phylogeny of the Astrophorida (Porifera, Demospongiae) reveals an unexpected high level of spicule homoplasy. PLoS ONE, 6: e18318.

Carter HJ (1880) Report on specimens dredged up from the Gulf of Manaar and presented to the Liverpool Free Museum by Capt. W. H. Cawne Warren. Annals and Magazine of Natural History (5)6(31): 35–61, pls IV–VI; 129–156, pls VII, VIII.

Dendy A (1916) Report on the Homosclerophora and Astrotetraxonida collected by H.M.S. 'Sealark' in the Indian Ocean. Reports of the Percy Sladen Trust Expedition to the Indian Ocean in 1905, Volume 6. Transactions of the Linnean Society of London (2), 17(2): 225–271, pls 44–48.

Hooper JNA, Kennedy JA & van Soest R (2000) Annotated checklist of sponges (Porifera) of the South China Sea region. The Raffles Bulletin of Zoology, Supplement 8: 125–207.

Kirkpatrick R (1900) On the Sponges of Christmas Island. Proceedings of the Zoological Society of London, 1900: 127–141, pls. XII-XIII.

Lamarck JBP De Monet, Comte De (1815 [1814]) Suite des polypiers empâtés. Mémoires du Muséum d'Histoire naturelle, Paris 1: 69–80, 162–168, 331–340.

Laubenfels MW De (1951) The sponges of the Island of Hawaii. Pacific Science, 5: 256–271.

Lendenfeld R Von (1910) The Sponges. 1. The Geodidae. Reports on the Scientific Results of the Expedition to the Eastern Tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer 'Albatross', from October, 1904, to March, 1905, Lieut. Commander L.M. Garrett, U.S.N., Commanding, and of other Expeditions of the Albatross, 1888-1904. (21). Memoirs of the Museum of Comparative Zoology at Harvard College 41(1): 1–259, pls. 1–48.

Lévi C & Lévi P (1989) Spongiaires (MUSORSTOM 1 & 2). In: Forest J (ed.), Résultats des Campagnes MUSORSTOM, Volume 4. Mémoires du Muséum national d'Histoire naturelle (A, Zoologie) 143. Pp. 25–103.

Lim SC, de Voogd NJ & Tan KS (2012) Biodiversity of shallow water sponges (Porifera) in Singapore and description of a new species of *Forcepia* (Poecilosclerida: Coelosphaeridae). Contributions to Zoology, 81: 55–71.

Lindgren NG (1897) Beitrag zur Kenntniss der Spongienfauna des Malaiischen Archipels und der Chinesischen Meere. Zoologische Anzeiger, 547: 480–487.

Lindgren NG (1898) Beitrag zur Kenntniss der Spongienfauna des Malayischen Archipels und der chinesischen Meere. Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Thiere, 11: 283–378, pls. 17–20.

Sollas WJ (1886) Preliminary account of the Tetractinellid sponges dredged by H.M.S. 'Challenger' 1872–76. Part I. The Choristida. Scientific Proceedings of the Royal Dublin Society (new series) 5:177–199.

Sollas WJ (1888) Report on the Tetractinellida collected by H.M.S. Challenger, during the years 1873–1876. Report on the Scientific Results of the Voyage of H.M.S. Challenger, 1873–1876. Zoology, 25(63): 1–458, pls. I–XLIV, 1 map.

Topsent E (1897) Spongiaires de la Baie d'Amboine. (Voyage de MM. M. Bedot et C. Pictet dans l'Archipel Malais). Revue suisse de Zoologie, 4: 421–487, pls 18–21.

Uriz MJ (2002). Family Geodiidae Gray, 1867. In: Hooper JNA & Van Soest RWM (eds,), Systema Porifera. A Guide to the Classification of Sponges. Kluwer Academic / Plenum Publishers, New York, USA. Pp. 134–140.

Vacelet J & Vasseur P (1965) Spongiaires des grottes et surplombs des récifs de Tuléar (Madagascar). Recueil des Travaux de la Station marine d'Endoume, 2–4: 71–123.

Van Soest RWM, Boury-Esnault N, Hooper JNA, Rützler K, de Voogd NJ, Alvarez de Glasby B, Hajdu E, Pisera AB, Manconi R, Schoenberg C, Janussen D, Tabachnick KR, Klautau M, Cárdenas P, Picton B, Kelly M, Vacelet J, Dohrmann M & Cristina Díaz M (2014) World Porifera Database. http://www.marinespecies.org/porifera (Accessed 10 October 2014).

Wilson HV (1925) Silicious and horny sponges collected by the U.S. Fisheries Steamer 'Albatross' during the Philippine Expedition, 1907–10. Contributions to the biology of the Philippine Archipelago and adjacent regions. Bulletin of the United States National Museum, 100(2, part 4): 273–532, pls. 37–52.