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Molecular and morphological assessment of tropical sponges in the subfamily Phyllospongiinae, with the descriptions of two new species

MUHAMMAD AZMI ABDUL WAHAB[1,*], NERIDA G. WILSON[2,3], DIANA PRADA[2], OLIVER GOMEZ[2] and JANE FROMONT[2]

[1]*Australian Institute of Marine Science, Arafura Timor Research Facility, Brinkin, NT 0810, Australia*
[2]*Collections & Research, Western Australian Museum, Locked Bag 49, Welshpool, WA 6986, Australia*
[3]*School of Biological Sciences, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia*

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Sponges in the subfamily Phyllospongiinae are important components of coral reefs. However, significant taxonomic inconsistencies exist in this group due to the lack of useful morphological characters for species delineation. This study assesses the systematics of some common phyllospongiinids in the genera *Carteriospongia*, *Phyllospongia* and *Strepsichordaia* from tropical Australia and the Red Sea, by using a multigene approach that utilizes the Internal Transcribed Spacer 2, the complete ribosomal 18S rRNA and three 28s rRNA gene regions (D1–D2, D3–D5 and D6–D8), which produced a phylogenetic framework in which complementary morphological taxonomic assessments were performed. Type specimens were included, where available, and six species clades were recovered, including the well-established *Phyllospongia papyracea* and *Strepsichordaia lendenfeldi*. *Carteriospongia foliascens*, the type species for the genus *Carteriospongia,* is transferred to the genus *Phyllospongia*, resulting in *Carteriospongia* becoming a synonym of *Phyllospongia*. Consequently, *Carteriospongia flabellifera* is removed from *Carteriospongia* and is reinstated to its original designation of *Polyfibrospongia flabellifera*. Two new species, ***Phyllospongia bergquistae* sp. nov.** and ***Polyfibrospongia kulit* sp. nov.**, are described. With phyllospongiinid sponges increasingly used as models for assessing the effects of climate change and anthropogenic stressors, this study provides a reliable systematics framework for the accurate identification of common phyllospongiinids across the Indo-Pacific.

ADDITIONAL KEYWORDS: 18S – 28S – Dictyoceratida – Indo-Pacific – ITS2 – Keratosa – morphology – Porifera – sponge – taxonomy.

INTRODUCTION

Sponges are important components of marine ecosystems and provide key ecological functions (Wulff, 2006; Bell, 2008). Although the diversity and abundance of sponges can be significant at some locations (Van Soest *et al*., 2012), challenges exist for the identification and taxonomy of sponges; in particular, in the order Dictyoceratida Minchin, 1900.

Sponges in the subfamily Phyllospongiinae Hyatt, 1877 (Demospongiae Sollas, 1885: Dictyoceratida: Thorectidae Bergquist, 1978) comprise aspiculate species having foliose, lamellate or foliodigitate growth forms (de Cook & Bergquist, 2002). Members of Phyllospongiinae can be phototrophic and may rely on their cyanobacterial symbionts for up to 50% of their energetic requirements (Wilkinson, 1983; Pineda *et al.*, 2016). These sponges occupy intertidal to shallow emergent reef habitats to deeper mesophotic environments (Wilkinson & Evans, 1989; Bridge *et al.*, 2011; Abdul Wahab *et al.*, 2014d). Despite the ecological importance of phyllospongiinids (holobionts) for primary production, benthic habitat structure and biomass, much confusion exists around species

*Corresponding author. E-mail: m.abdulwahab@aims.gov.au
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delineation in this group, in part due to the large morphological variability resulting from environmental plasticity, and the lack of taxonomically informative skeletal structures, such as spicules (Abdul Wahab *et al.*, 2014d; Galitz *et al.*, 2018).

Historical review of Phyllospongiinae

The genera examined in this study have a long, rich and complicated taxonomic history. The Phyllospongiinae comprise four genera, and species from three genera are the focus of this study: *Carteriospongia* Hyatt, 1877; *Phyllospongia* Ehlers, 1870 and *Strepsichordaia* Bergquist *et al.*, 1988. In order of date established, *Phyllospongia* is the oldest genus of this group of foliose sponges.

Ehlers (1870) erected the genus *Phyllospongia* for *Spongia papyracea* Esper (1806), and Burton (1934) designated the type specimen (NHMUK 1931.4.1.1a). The emphasis for describing this genus was the paper-thin body, leaf-like shape, homogeneity of the fibre skeleton and absence of large oscules (Bergquist *et al.*, 1988). However, some authors (Burton, 1934; Bergquist *et al.*, 1988) considered that others, in particular Lendenfeld (1889), erroneously treated the genus as a repository for many thin fan, leaf or cup-shaped sponges lacking spicules that are not true *Phyllospongia*. Lendenfeld (1889) established three subgenera in *Phyllospongia*: *Antheroplax*, *Spongionella* and *Carterispongia* (*Carteriospongia*). *Antheroplax* and *Spongionella* are no longer upheld and *Carteriospongia* Hyatt, 1877 was considered a valid genus with characters distinctive from *Phyllospongia*, namely that some of the fibres, usually those vertical to the surface, are cored with sand grains (Burton, 1934). At the time of this publication, there are nine valid species of *Phyllospongia* (Van Soest *et al.*, 2020).

Carteriospongia is the second-oldest genus name in this group. The type species for this genus, *Spongia foliascens* Pallas, 1766, was also designated by Burton in 1934 (NHMUK 1925.11.1.411). However, Hyatt (1877) did not mention *C. foliascens* (Pallas, 1766) when he erected the genus *Carteriospongia*. The first species Hyatt (1877) refers to after establishing the new genus is *Spongia otahitica* Esper, 1797. Although it would perhaps have been more appropriate to designate the type of *S. otahitica* as the type of *Carteriospongia* (the specimen is still in the Natural History Museum, London, NMHUK 1872.9.25.1), this may also have caused misunderstanding as Hyatt (1877) had partly incorrectly cited Esper's figures, referring to the figure number for the type of *S. lamellosa* (Esper, 1794: pl. XLIV, fig.1), not the type of *S. otahitica* (Esper, 1797: 209, pl. LXI, fig. 8). In addition, a second specimen of *S. otahitica* (Esper, 1797: 209, pl. LXI, fig. 7; NMHUK 1931.6.25.17) is also in the Natural History Museum, London, but labelled as *Halispongia ventriculoides* Bowerbank, 1874 (T. White, personal communication). There is no doubt this also conforms to *C. foliascens*. Three specimens were first figured in Ellis & Solander (1786: pl. 59, figs 1–3) as sponges from Otaheite (Tahiti).

Burton (1934) justified establishing a neotype for *C. foliascens* by noting that Pallas (1766) did not provide figures of *S. foliascens*, but Pallas referred to figures from earlier publications, e.g. Petiver (1712: pl. XIX, fig. 4) *S. foliata* and Rumphius (1705: pl. XC, fig. 1) *S. infundibuli*. Hooper & Wiedenmayer (1994) regarded this neotype designation as invalid because Burton (1934) failed to present reasons for the designation and his assumption that the type specimen was lost (de Cook & Bergquist, 2002). However, as outlined above, the type specimen of *S. otahitica* does exist. Examination of Petiver's (1712) figure affirms that the concept Pallas (1766) had of *S. foliascens* is consistent with the figure of *S. otahitica* in Esper (1797) and with the neotype designated by Burton (1934). Consequently, the general acceptance that *C. foliascens* and *C. otahitica* are conspecific is upheld here.

There are currently ten valid species of *Carteriospongia* (Van Soest *et al.*, 2020), with *Polyfibrospongia* Bowerbank, 1877 being accepted as a synonym of this genus.

Strepsichordaia Bergquist *et al.*, 1988 is a much more recent genus without a complicated history. The genus currently has five valid species, with *S. lendenfeldi* Bergquist *et al.*, 1988 being the type of the genus (Bergquist *et al.*, 1988; Van Soest *et al.*, 2020). Bergquist *et al.* (1988) recognized *S. radiata* (Hyatt, 1887) as a good species of *Strepsichordaia*. Two other species, *Carteriospongia caliciformis* Carter, 1885 and *Halispongia stellifera* Bowerbank, 1877, which Bergquist *et al.* (1988) did not recognize as belonging to this genus, have later been transferred to *Strepsichordaia* (Van Soest *et al.*, 2020). Formerly, *Phyllospongia aliena* Wilson, 1925 was synonymized with *Carteriospongia caliciformis* by Hooper & Wiedenmayer (1994). However, Van Soest *et al.* (2020) noted that there is insufficient evidence for the synonymy of the two taxa and retained them as two species.

The fourth genus in Phyllospongiinae, *Lendenfeldia*, is characterized by a complex lamellate or lamellodigitate morphology, cored, often fasciculate, primary fibres lacking orientation and an irregular fibre network formed by secondary and tertiary fibres. It lacks a sand cortex and the surface is conulose, the texture fleshy and soft (Bergquist, 1980). Bergquist *et al.* (1988) suggested that after additional study of *Lendenfeldia*, these four genera may form a subfamily. There are currently six valid species of *Lendenfeldia* (Van Soest *et al.*, 2020).

Hyatt (1877) established the family Phyllospongiadae for the two genera *Phyllospongia* and *Carteriospongia*, noting that they were forms of Spongiidae Gray, 1867 with leaf-like or frondose forms. Keller (1889), following Hyatt (1877), recognized Phyllospongidae as a separate family to Spongiidae, defined by the complete lack of conuli in the former group, but this was not adopted by later authors. For example, Burton (1934) continued to place *Phyllospongia* and *Carteriospongia* in Spongiidae. Bergquist *et al.* (1988) also placed them in Spongiidae but discussed some of their characters, such as the laminate, pithed fibres being more characteristic of Thorectidae, the surface morphology of the vermiform fibres being similar to the surface of collagenous filaments found in *Ircinia* Nardo, 1833 and the similarity of braided structures in *Ircinia oros* (Schmidt, 1864) and *Carteriospongia flabellifera* suggesting that these two genera, along with *Strepsichordaia*, may be better placed in the family Thorectidae. They also noted the terpene chemistry of these three genera and that *Lendenfeldia* has some affinity to *Cacospongia* Schmidt, 1862 and *Hyrtios* Duchassaing de Fonbressin & Michelotti, 1864 in Thorectidae (Bergquist *et al.*, 1988).

Bergquist *et al.* (1999) placed the subfamily Phyllospongiinae within Thorectidae for foliose or foliodigitate sponges with finely laminated fibres with a differentiated pith. They did not comment on the earlier works (Hyatt, 1877; Keller, 1889) that had recognized the group at family level. According to the ICZN (1999), the author and date of a family name remain unchanged when the taxon denoted by the name is raised or lowered in rank, hence the subfamily Phyllospongiinae is attributed to Hyatt, 1877 (ICZN, 1999: Art. 35.4.2).

The genera included in the subfamily by Bergquist *et al.* (1999) were: *Candidaspongia* Bergquist *et al.*, 1999; *Carteriospongia*; *Lendenfeldia*; *Phyllospongia*; and *Strepsichordaia*. Bergquist *et al.* (1999) considered the laminated fibres to be representative of a homogenous structure with the zones of disjunction between the laminations being tightly adherent, and the pith not sharply disjunct from the spongin fibre. These features differentiated this subfamily from the Spongiidae where the fibres are homogenous.

Erpenbeck *et al.* (2012) sequenced members of Spongiidae and Thorectidae but could not get an unambiguous signal from *COI* and 28S gene trees to separate the two families. Erpenbeck *et al.* (2020) noted that morphological characters traditionally used to differentiate dictyoceratid genera, including fibre lamination, fibre coring and surface armour, lack phylogenetic signal at the order level.

Erpenbeck *et al.* (2020) re-evaluated the intra-order phylogeny of the Dictyoceratida and highlighted several discrepancies in the systematics of Thorectidae using a multigene dataset. Including type specimens and other well-identified specimens used as reference taxa for the *Systema Porifera* (Hooper & Van Soest, 2002), the study redefined the subfamily Phyllospongiinae to exclude *Candidaspongia* (now transferred to the family Dysideidae Gray, 1867). They noted that *Lendenfeldia* requires revision as the sequencing of the type species was unsuccessful. The Phyllospongiinae concept, at present, includes *Carteriospongia, Lendenfeldia*, *Phyllospongia* and *Strepsichordaia* and is sister to Spongiidae (Erpenbeck *et al.*, 2020).

The finding of Erpenbeck *et al.* (2020) that morphological characters traditionally used to differentiate dictyoceratid genera lacked phylogenetic signal at the order level, highlights the need for a complementary and multifaceted taxonomic approach that utilizes both a multigene molecular phylogenetic framework in which to assess relevant interspecific morphological characters and intraspecific morphological variation for species in Phyllospongiinae.

In a previous molecular phylogeny of Phyllospongiinae, non-monophyly of two of the three included genera was detected (*Carteriospongia* and *Phyllospongia*, with a monophyletic *Strepsichordaia*) (Abdul Wahab *et al.*, 2014d). To address these taxonomic issues, this study aims to expand the molecular dataset to five gene regions (three parts of 28S, full length 18S and ITS2), in conjunction with morphological analyses, assessment of type material and study of original species descriptions to reassess the systematics of species in three genera: *Carteriospongia*, *Phyllospongia* and *Strepsichordaia*.

MATERIAL AND METHODS

Sample collections

Samples of tropical foliose phyllospongiinid sponges, including those identified as *Carteriospongia foliascens* (Pallas, 1766), *C. flabellifera* (Bowerbank, 1877), *Phyllospongia papyracea* (Esper, 1806), *P. lamellosa* (Esper, 1794) and *Strepsichordaia lendenfeldi* Bergquist *et al.*, 1988 from Abdul Wahab *et al.* (2014d), were used for the study. In addition, sponge specimens from the Western Australian Museum (WAM), identified as species of the genera *Carteriospongia*, *Phyllospongia* and *Strepsichordaia*, and a range of outgroups were included. A total of 207 specimens were included for molecular and morphological assessments. The collection locality for these specimens ranged from the central to west Indo-Pacific, including tropical regions of Australia and the Red Sea. The full metadata for specimens used

in this study are provided in Supporting Information, Material S1.

Molecular systematics

DNA extraction, polymerase chain reaction (PCR) amplification and sequencing

DNA extraction was carried out with a DNeasy blood and tissue kit (Qiagen) on preserved tissue following the manufacturer's instructions. Five gene regions were chosen for analysis based on information content from previous works. These included the highly variable nuclear Internal Transcribed Spacer 2 (ITS2) region, suitable for species-level phylogenetic constructions in keratose sponges (Worheide *et al.*, 2004; Abdul Wahab *et al.*, 2014d), three gene regions known to be suitable for taxonomic delineation in sponges from the nuclear ribosomal 28S rRNA (D1–D2, D3–D5 and D6–D8) (Borchiellini *et al.*, 2004; Thacker *et al.*, 2013; Carballo *et al.*, 2018) and complete ribosomal 18S rRNA (Schmitt *et al.*, 2005; Redmond *et al.*, 2013). Amplifications were carried out with 1–2 µL genomic DNA or with a dilution series, with conditions and primers listed in Table 1. Amplified products were outsourced to the Australian Genome Research Facility (Perth) for bidirectional sequencing.

Sequence alignment, model selection and phylogenetic analyses

Bidirectional sequences were assembled in GENEIOUS v.11 (Kearse *et al.*, 2012) and edited by eye, if necessary. Consensus sequences for specimens were aligned using MAFFT (Katoh *et al.*, 2002) implemented in GENEIOUS using the auto option (coding genes) and the E-ISI-i option (rRNA genes). Each gene fragment (with primers trimmed away) was analysed separately in a maximum likelihood (ML) framework (data not shown) and then concatenated but partitioned by gene, applying the optimal models of evolution simultaneously estimated and selected with the Bayesian information criterion in ModelFinder (Kalyaanamoorthy *et al.*, 2017) in IQ-TREE (Nguyen *et al.*, 2015). To estimate support at each node, we used the ultrafast bootstrap function, implementing 1000 replicates using a maximum of 1000 iterations and a minimum correlation coefficient of 0.99 as a stopping rule (Hoang *et al.*, 2018). All models and partitions are shown in Supporting Information, Material S2.

Trees were rooted with members of the subfamily Thorectinae Bergquist, 1978 [*Hyrtios* sp. SS2 Duchassaing & Michelotti, 1864 and *Dactylospongia elegans* (Thiele, 1899)] and Dysideidae Gray, 1867 [*Dysidea* sp. 2 Johnston, 1842 and *Lamellodysidea herbacea* (Keller, 1889)]. We also carried out an ML analysis, as above, using only ITS2 to include the neotype of *Carteriospongia foliascens* [combining the two different length sequences submitted to GenBank by Galitz *et al.* (2018) and Erpenbeck *et al.* (2020)], and the holotype and paratype of *Strepsichordaia lendenfeldi*, and to integrate our dataset with that provided in Abdul Wahab *et al.* (2014d). To minimize missing data for the concatenated tree, we included taxa with data available for at least ITS2 and partial 18S, but allowing for one of the three fragments of 28S to be missing (see Supporting Information, Material S1). New DNA sequences produced in the study were accessioned to GenBank (Supporting Information, Material S1).

Morphological assessments

The gross morphology, surface characteristics and microscopic skeletal characteristics of the sponge specimens were assessed at the Western Australian Museum (see Supporting Information, Material S3 for a catalogue of all specimen assessed, herein, and their gross morphology). Subsamples of tissue, 5 mm wide and 20 mm long at right angles to the edge of the sponge lamellae, were sampled from specimens and preserved in 70% ethanol. Dried tissue samples from type specimens were rehydrated in 70% ethanol at least overnight prior to performing histological processing. Samples were processed using a graded ethanol dehydration and xylene clearing procedure, followed by paraffin impregnation in a vacuumed tissue processor. Thick sections at right angles to the sponge surface (~90 µm) were cut with a Leitz slide microtome. Sections were de-waxed in histolene and the unstained section mounted using Shandon EZ-Mountant.

RESULTS

Phylogenetic analyses

ITS2 sequences in this study were used to produce an inclusive phylogenetic tree comprising 186 ingroup and four outgroup sequences. This included sequences for the neotype of *Carteriospongia foliascens*, the holotype and paratype of *Strepsichordaia lendenfeldi*, the holotype and paratype of the new species *Polyfibrospongia kulit* Abdul Wahab & Fromont, and a paratype of the new species *Phyllospongia bergquistae* Abdul Wahab & Fromont (see Supporting Information, Material S1 for the full specimen list). The ITS2 tree recovered six well-supported species level

Table 1. Details of ITS2, 28S and 18S primers and PCR conditions used for this study

Primer name	Primer sequence	Program	Reference
ITS2 *N143: SP58bF* *N144 SP28cR*	5'-AATCATCGAGTCTTTGAACG-3' 5'-CTTTTCACCTTTCCCTCA-3'	94–95 °C 3–5 min (94–95 °C 20–30 s, 45–56 °C 30 s, 72 °C 40 s) ×35, 72 °C 5 min	Thacker & Starnes, 2003 Thacker & Starnes, 2003
28S D1-D2 *N137: Por28S-15F* *N138: Por28S-878R*	5'-GCGAGATCACCYGCTGAAT-3' 5'-CACTCCTTGGTCCGTGTTTC-3'	95 °C 3 min (95 °C 20 s, 60 °C 30 s, 72 °C 40 s) ×35, 72 °C 5 min 94 °C 5 min (94 °C 30 s, 55–50 °C (TD) 30 s, 72 °C 30 s) ×10, (94 °C 30 s, 53 °C 30 s, 72 °C 30 s) ×25, 72 °C 5 min	Morrow *et al.*, 2012. Morrow *et al.*, 2012.
28S D3-D5 *N139: Por28S-830F* *N140: Por28S-1520R*	5'-CATCCGACCCGTCTTGAA-3' 5'-GCTAGTTGATTCGGCAGGTG-3'	95 °C 3 min (95 °C 20 s, 60 °C 30 s, 72 °C 40 s) ×35, 72 °C 5 min 94 °C 5 min (94 °C 30 s, 55–50 °C (TD) 30 s, 72 °C 30 s) ×10, (94 °C 30 s, 53 °C 30 s, 72 °C 30 s) ×25, 72 °C 5 min	Morrow *et al.*, 2012. Morrow *et al.*, 2012.
28S D6-D8 *N141: Por28S-1490F* *N142: Por28S-2170R*	5'-AACTCACCTGCCGAATCAAC-3' 5'-CCAATCCTTTTCCCAARGTT-3'	95 °C 3 min (95 °C 20 s, 56 °C 30 s, 72 °C 40 s) ×35, 72 °C 5 min 94 °C 5 min (94 °C 30 s, 55–50 °C (TD) 30 s, 72 °C 30 s) ×10, (94 °C 30 s, 51 °C 30 s, 72 °C 30 s) ×25, 72 °C 5 min	Morrow *et al.*, 2012. Morrow *et al.*, 2012.
18S *N32: 18S1F* *N35: 18S5R* *N326: SP18aF* *N327: 600R18S*	5'-TACCTGGTTGATCCTGCCAGTAG-3' 5'-CTTGGCAAATGCTTTCGC-3' 5'-CCTGCCAGTAGTCATATGCTT-3' 5'-CGAGCTTTTTAACTGCAA-3'	95 °C 3 min (95 °C 20 s, 49–50 °C 30 s, 72 °C 40 s) ×35, 72 °C 5 min –[N32/35] 94 °C 5 min (94 °C 60 s, 48 °C 30 s, 72 °C 60 s) ×30, 72 °C 10 min [N326/327]	Giribet *et al.*, 1996. Giribet *et al.*, 1996. Redmond *et al.*, 2013. Redmond *et al.*, 2007.
18S *N33:* 18s3F *N36:* 18Sbi *N328: 400F18S* *N329: 1350R18S*	5'-GTTCGATTCCGGAGAGGGA-3' 5'-GAGTCTCGTTCGTTATCGGA-3' 5'-CCTGAGAAACGGCTACCACA-3' 5'-CGGGACTAGTTAGCAGGTTAA-3'	95 °C 3 min (95 °C 20 s, 49–50 °C 30 s, 72 °C 40 s) ×35, 72 °C 5 min [N33/36] 94 °C 5 min (94 °C 60 s, 48 °C 30 s, 72 °C 60 s) ×30, 72 °C 10 min [N328/329]	Giribet *et al.*, 1996. Giribet *et al.*, 1996. Redmond *et al.*, 2007. Redmond *et al.*, 2007.
18S *N34:* 18sa2.0 *N37:* 18S9R *N330: 1200F18S* *N331: SP18gR*	5'-ATGGTTGCAAAGCTGAAAC-3' 5'-GATCCTTCCGCAGGTTCACCTAC-3' 5'-TAATTTGACTCAACACGGG-3' 5'-CCTTGTTACGACTTTTACTTCCTC-3'	95 °C 3 min (95 °C 20 s, 49–50 °C 30 s, 72 °C 40 s) ×35, 72 °C 5 min [N34/37] 94 °C 5 min (94 °C 60 s, 48 °C 30 s, 72 °C 60 s) ×30, 72 °C 10 min [N330/331]	Giribet *et al.*, 1996. Giribet *et al.*, 1996. Redmond *et al.*, 2007. Redmond *et al.*, 2013.

clades, and the inclusion of types allowed the clear application of the genus names *Carteriospongia* and *Strepsichordaia* (Supporting Information, Material S4). The concatenated phylogeny, derived from the ITS2, 18S and 28S sequence alignments, consisted of 142 ingroup and four outgroup sequences. The concatenated reconstruction produced a statistically well-supported tree (ML bootstrap values > 88) within and between clades and recovered *Strepsichordaia* as sister to *Polyfibrospongia* + *Phyllospongia* (Fig. 1). A total of 968 new ITS2, 28S and 18S sequences (including their gene partitions) were produced in this study (Supporting Information, Material S1).

The application of genus names on the phylogeny was tested for the included genera, with *Strepsichordaia* supported by the type material of *S. lendenfeldi* (holotype and paratype) (Fig. 1; Supporting Information, Material S4). *Strepsichordaia lendenfeldi* is the sister-group to the rest of the Phyllospongiinae, with the other generic clades recovered as polyphyletic, using the previously accepted taxonomy (as *Carteriospongia* species).

A clade containing members of *Carteriospongia foliascens*, identified by a sequence from the neotype, recovers as sister to the new species *Phyllospongia bergquistae*, which together are sister to *P. papyracea* (Fig. 1; Supporting Information, Material S4). *Carteriospongia foliascens* is the type species for the genus *Carteriospongia* and *P. papyracea* is the type species for the genus *Phyllospongia*. As *Phyllospongia* has publication seniority, *C. foliascens* is, therefore, reclassified here as ***Phyllospongia foliascens* comb. nov.** and the genus *Carteriospongia* is here synonymized with *Phyllospongia*. Consequently, *Carteriospongia flabellifera* is removed from *Carteriospongia* and reinstated to its original designation of *Polyfibrospongia flabellifera* Bowerbank, 1877, which itself is the type species for the genus *Polyfibrospongia*. A new species, *Polyfibrospongia kulit*, is recovered as sister to *P. flabellifera* and it is thus also placed in the genus *Polyfibrospongia* (Fig. 1). In summary, three genera are recovered and recognized from the analysis: *Phyllospongia*, *Polyfibrospongia* and *Strepsichordaia*. Generic reclassification, synonymies and novel species discovery are elaborated in greater detail in the following 'Systematics' section.

In addition to species relationships and new species recovered from the phylogeny, phylogeographic structure between east and west Australia is also evident from the concatenated tree (Fig. 1). This east–west Australia phylogeographic structure was apparent in *P. flabellifera*, *S. lendenfeldi*, *P. papyracea* and *P. foliascens* (Fig. 1).

Systematics

Class Demospongiae Sollas, 1885

Subclass Keratosa Grant, 1861

Order Dictyoceratida Minchin, 1900

Family Thorectidae Bergquist, 1978

Subfamily Phyllospongiinae Hyatt, 1877

Amended subfamily diagnosis

Thin, foliose, digitate, lamellate, cup-shaped or encrusting sponges. Primary and secondary fibres finely laminated with a central, differentiated pith. Primary fibres are cored, secondaries are cored or uncored. Uncored tertiary fibres may be vermiform, reticulate, narrow lattice-like or form fascicules. Surface lightly to heavily armoured, collagen may occur subdermally in some species. Primary fibres may form surface brushes in some species.

Key to genera

1a. Tertiary fibres form lattice-like complexes to fascicules in lamella; surface membranous ..... *Polyfibrospongia*
1b. Tertiary fibres do not form lattice-like complexes or fascicules; surface not membranous 2
2a. Tertiary fibres vermiform or reticulate, rare in upper lamellae ..... *Phyllospongia*
2b. Tertiary fibres dominate in lamella, reticulate with rare cross connections ..... *Strepsichordaia*

Genus *Phyllospongia* Ehlers, 1870

Synonymy

Carteriospongia Hyatt, 1877: 540–541 *Mauricea* Carter, 1877: 172–176

Type species

Spongia papyracea Esper, 1806, by subsequent designation Burton (1934); Cotype NHMUK 1931.4.1.1a from southern India (not located in NHMUK collections in 2018).

Amended generic diagnosis

Lamellate, digitate, cup-shaped or foliose fans or ridges up to 5 mm thick, that may have single or multiple lamellae and basal attachments. Surface variable – in the type of the genus it is smooth, and in other species it can be verrucose. Oscules are small (0.2–1.0 mm), flush with the surface or slightly raised, they may be

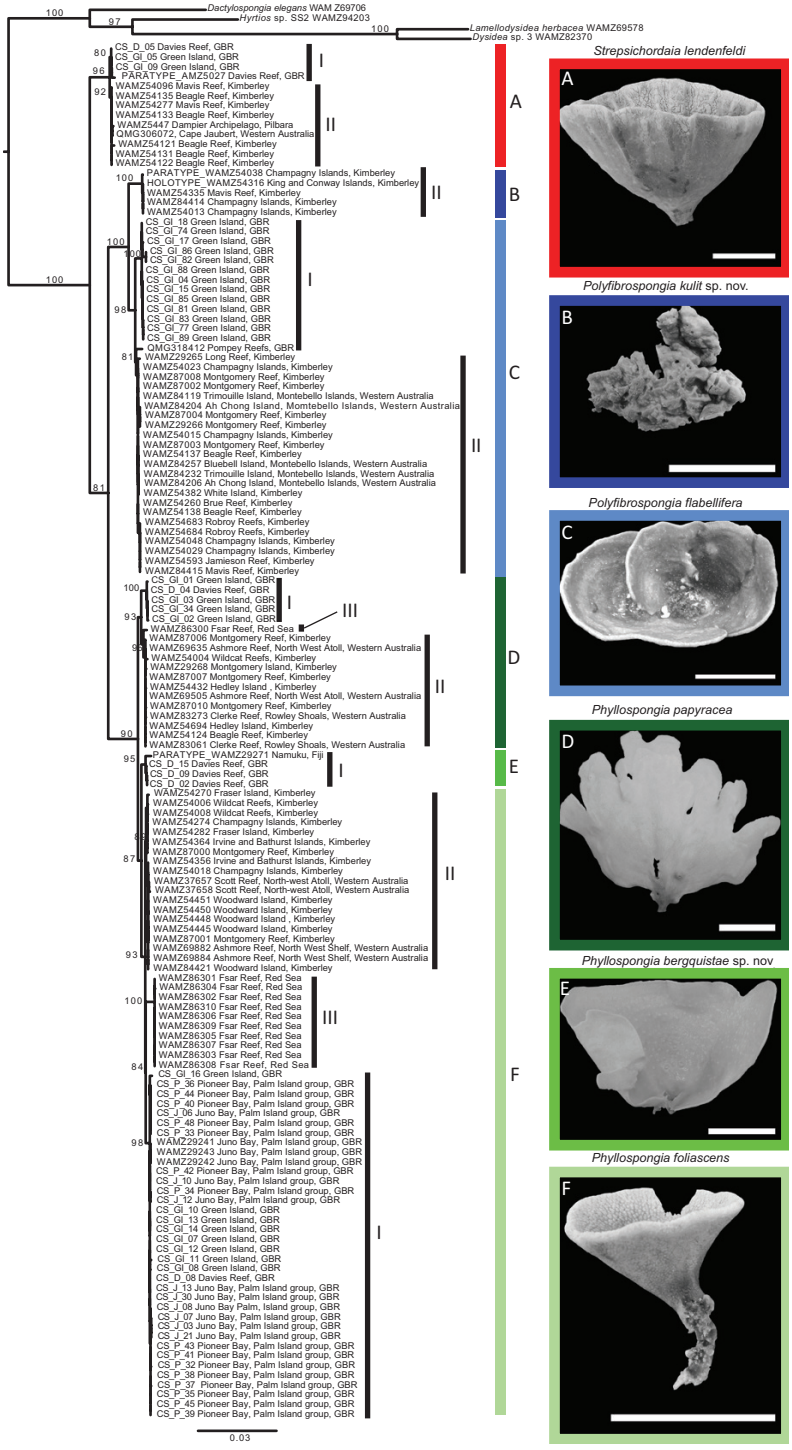

Figure 1. Concatenated phylogenetic tree of ITS2, 18S and 28S sequence alignments, for specimens identified as *Strepsichordaia, Polyfibrospongia* and *Phyllospongia*. Note that names post-generic reclassification are shown here for *Polyfibrospongia flabellifera* (formerly *Carteriospongia flabellifera*) and P*hyllospongia foliascens* (formerly *Carteriospongia foliascens*). Coloured vertical bars on the right correspond to the clades corresponding to species. Representative images of the sponge species are bounded by the colour of the clades (Scale bar = 5 cm). The geographic locations where specimens were collected are indicated as bars next to the samples: I, West Pacific Ocean; II, East Indian Ocean; III, Red Sea.

apical on ridges and are often only on one surface. An organized sand cortex is usually present on one or both surfaces, it may be thinner on one side and can become a pronounced crust. Texture is incompressible. Colour is light to dark brown when alive and cream to fawn in ethanol. The skeleton is a reticulation of primary and secondary fibres with vermiform tertiary elements not always apparent except basally. Primary and secondary fibres are laminated. The primary fibres are usually cored, reticulate centrally and at right angles at the surface. Primary fibres form subdermal brushes in one species. Secondary fibres can be cored or uncored and can be most visible condensed beneath the lamella surface. Tertiary fibres are uncored, vermiform basally and some may be visible as part of the reticulate skeleton superficially.

Remarks

With *Phyllospongia foliascens* and the new species *P. bergquistae* supported by the molecular phylogenetic analyses and now included in the genus (Fig. 1), the diagnosis provided by Bergquist *et al.* (1988) has been amended to include more pronounced verrucose surface patterning, a more pronounced sand cortex, differentiated oscular and poral surfaces, and primary fibres forming subdermal brushes. Bergquist *et al.* (1988) recorded that the skeletal reticulation could become more irregular in thicker specimens of this genus, and this is seen consistently in *P. foliascens* and *P. bergquistae*, both species with thicker morphology. The fine, meandering surface patterning is characteristic for *Phyllospongia papyracea* and a verrucose surface is characteristic for *P. foliascens*.

KEY TO SPECIES OF *PHYLLOSPONGIA* INCLUDED IN THIS STUDY

1a. Surface verrucose; surface brushes; skeleton plumoreticulate ..... *P. foliascens*
1b. Surface not verrucose; no surface brushes; skeleton reticulate 2
2a. Surface finely patterned; collagenous superficially ..... *P. bergquistae*
2b. Surface smooth; not collagenous superficially ..... *P. papyracea*

PHYLLOSPONGIA PAPYRACEA (ESPER, 1806)

(FIGS 2, 3, 4A, B)

Restricted synonymy

Spongia papyracea Esper, 1806: 38–40, pl. 65, fig. 1, 2, 3; pl. 65A, fig. 1, 2.

Spongionella holdsworthi Bowerbank, 1873: 25–32, pl. 5, fig. 1, 2.

Spongia laciniata Lamarck, 1814: 445.

Material examined

Thirty-four specimens, including syntype, ethanol-preserved specimens, dried specimens, slides, DNA, and photographs and illustrations (see Supporting Information, Material S1 for the detailed specimen metadata). *Syntypes* (of *Spongionella holdsworthi* Bowerbank, 1873): NHMUK 1873.7.21.1 (specimen) and NHMUK 1873.7.21.1a (slide); NHMUK 1873.7.21.2a (slide); NHMUK 1873.7.21.3a (slide); NHMUK 1873.7.21.4a (slide); NHMUK 1873.7.21.5a (slide); NHMUK 1873.7.21.6a (slide), Pearl Banks, Ceylon (8°51.943'N, 79°50.307'E).

Type data: Spongia papyracea Esper, 1806, pl. 65, 1, 2, 3; pl. 65A, 1, 2, by subsequent designation Burton (1934); Cotype NHMUK 1931.4.1.1a from southern India (Bergquist *et al.* 1988) (not located in NHMUK collections in 2018).

SPECIES REDESCRIPTION

Syntype

Morphology: The two microscope slides of the *P. papyracea* cotype NHMUK 1931.4.1.1a described in Bergquist *et al.* (1988) could not be located, therefore a dried specimen of the syntype of *Spongionella holdsworthi* Bowerbank, 1873: NHMUK 1873.7.21.1 and syntype slides NHMUK 1873.7.21.1a–6a, from specimens collected from the region of the type locality [syntypes – Sri Lanka (Ceylon), cotype – southern India], were used for comparison with specimens in this study. The syntype conforms to illustrations of the lost holotype described by Esper (1806: pl. 65, figs 1, 2, 3, and pl. 65A, figs 1, 2) (see Fig. 2A, B). It is a whole, dried specimen (Fig. 2B), with a fan thickness of 1 mm, 35 mm high and 111 mm wide, has a single stalk, apically rounded lobes, an oscular surface with oscules flush with the surface, drainage canals not clearly visible and some low ridging (~1–2 mm). Oscules were not present on the edge of the lamellae. The specimen is vertically compressed and may have been dried flat.

Skeleton: A thin (< 60 µm) sand cortex is present on both sides of the lamella. Primary fibres are both lightly cored and uncored. Secondary fibres are always uncored and condensed under the surface of the lamella. Tertiary fibres are fine, uncored, not common and found at the base of the lamellae. Fibres are laminated. Primary fibre diameter 40–50 µm, secondary fibre diameter 20–25 µm, tertiary fibre

diameter 8–10 µm. Mesh configuration is regular, with primary to primary fibre mesh size 160 µm wide and secondary to secondary fibre mesh size 80 µm wide. Syntype slides NHMUK 1873.7.21.2a–6a conformed to the skeletal characters described for NHMUK 1873.7.21.1, except that NHMUK 1873.7.21.4a has a thin sand cortex on one side and NMHUK 1873.7.21.5a has a sand cortex on both sides of the lamellae.

Additional material

Morphology: Erect, thin to thick strap-like single or multiple lamellae, occasional cups or thick truncated vertical lobes (Fig. 2A–G). Single or multiple short stalks. Sponge thickness ranged from 0.5–3 mm; height 60–190 mm; width 110–170 mm. Fine veining of drainage canals with spidery stellate patterning leading to oscules or canals are present but may not be visible in thicker specimens (Fig. 3B, C, F). Surface either smooth (Figs 2D, E, 3A–F) or with low ridges of ~1–2 mm (Figs 2F, G, 3H), with no distinct conules in both intertidal and subtidal specimens. Specimens are incompressible in both intertidal and subtidal specimens. Oscules always visible as pin pricks with a diameter of ~0.2–1 mm, usually on one surface, but may be on both surfaces and on the edge of lamellae in thicker specimens (Fig. 3H). Oscules usually flush with the surface, however they may be raised ~2–3 mm above it in some thicker specimens, e.g. in WAM Z5409 and WAM Z3992 (Fig. 3G). Ostial pores occur as pin pricks and are more pronounced in lamellate forms. Live coloration is brown and cream to fawn in ethanol.

Skeleton: Primary fibres are cored, sometimes uncored and occur at right angles to the surface (Fig. 4A). Secondary fibres are usually uncored, although they may have light coring (Fig. 4A, B). Secondary fibres are abundant and are most visible and condensed beneath the lamella surface (Fig. 4B). Tertiary fibres are uncored, vermiform, central and/or basal in lamellae and found in the stalk. Vermiform tertiary fibres can extend to the edge of the lamellae in thick, vertically truncated morphologies (Fig. 4B). Fibres are laminated, and primary and secondary fibres are arranged as a neat and compact reticulation. Occasionally, a fine pith or graininess can be observed centrally in tertiary fibres (e.g. WAM Z54694 and WAM Z54124; Fig. 4B). Primary fibre diameter 40–100 µm, secondary fibre diameter 20–70 µm, and tertiary fibre diameter 8–20 µm. Primary to primary fibre mesh width 160–350 µm, secondary to secondary fibre mesh width 80–180 µm. The sand cortex can be fine or coarse grained, is present on one or both sides of the lamella, and often thicker on one surface (40–150 µm) (Fig. 4A).

Distribution

Specimens in this study were from the east and west shallow tropical seas of Australia and the Red Sea. The species is considered to be widespread Indo-Pacific [eastern Australia, Bergquist *et al.* (1988); South Africa, Hyatt (1877); Sulawesi, Thiele (1899); New Caledonia, Bergquist (1995); Philippines, Levi (1961); Madagascar, Barnes & Bell (2002)], but reassessment of specimens, including molecular data, is essential for determining the true extent of distribution of this species.

Remarks

As the type slides for this species were not found, the syntypes of the synonymized species *Spongionella holdsworthi* Bowerbank, 1873, were examined. They were collected in Sri Lanka (Ceylon) not India, which is the type locality of *Phyllospongia papyracea* Esper, 1806. The dried syntype specimen NHMUK 1873.7.21.1 conforms to the illustration in Esper, 1806 (Fig. 2A, B) of the type specimen designated by Burton (1934) but was not found in the museum in Erlangen. It also conforms to the redescription of the species by Bergquist *et al.* (1988), as do all the other specimens of *P. papyracea* examined in this study.

Bergquist *et al.* (1988) described considerable variation in this species, and this was also found in this study (see Supporting Information, Material S2 for a photo catalogue displaying the range of morphology for all specimens assessed in this study). Although the classic morphology of the species is a paper-thin lamella, some specimens can be up to 5 mm thick, and may have truncated short, squat lobes, apparently a result of living in the intertidal region (Fig. 2G). Usually, the surface is entirely smooth, but it may have low corrugations or ridges (Fig. 2F, G). The oscules usually occur on one surface but can be found on both surfaces and along the edge of the lamellae (Fig. 3H). Oscules may be flush with the surface or slightly raised (2–3 mm), they are always tiny (pin prick size, 0.2–1 mm). Fine, irregular, stellate or meandering drainage canals may (Fig. 3B, C, F), or may not, be present (Fig. 3A, D, E). In addition, the amount of sand in the surface cortex varies in thickness from 40 to 150 µm and may be on one or both surfaces (Fig. 4A). Primary fibres are rarely uncored and coring can be light or heavy. Secondary fibres are usually uncored, although occasionally some light coring was noted; tertiary fibres are always uncored. Fibre diameters are variable, they are laminated and may be lightly pithed. The primary fibres align at right angles beneath the surface (Fig. 4A, B). The meshes are more regular and the secondaries more condensed at the surface, features that can be difficult to see if the sand cortex

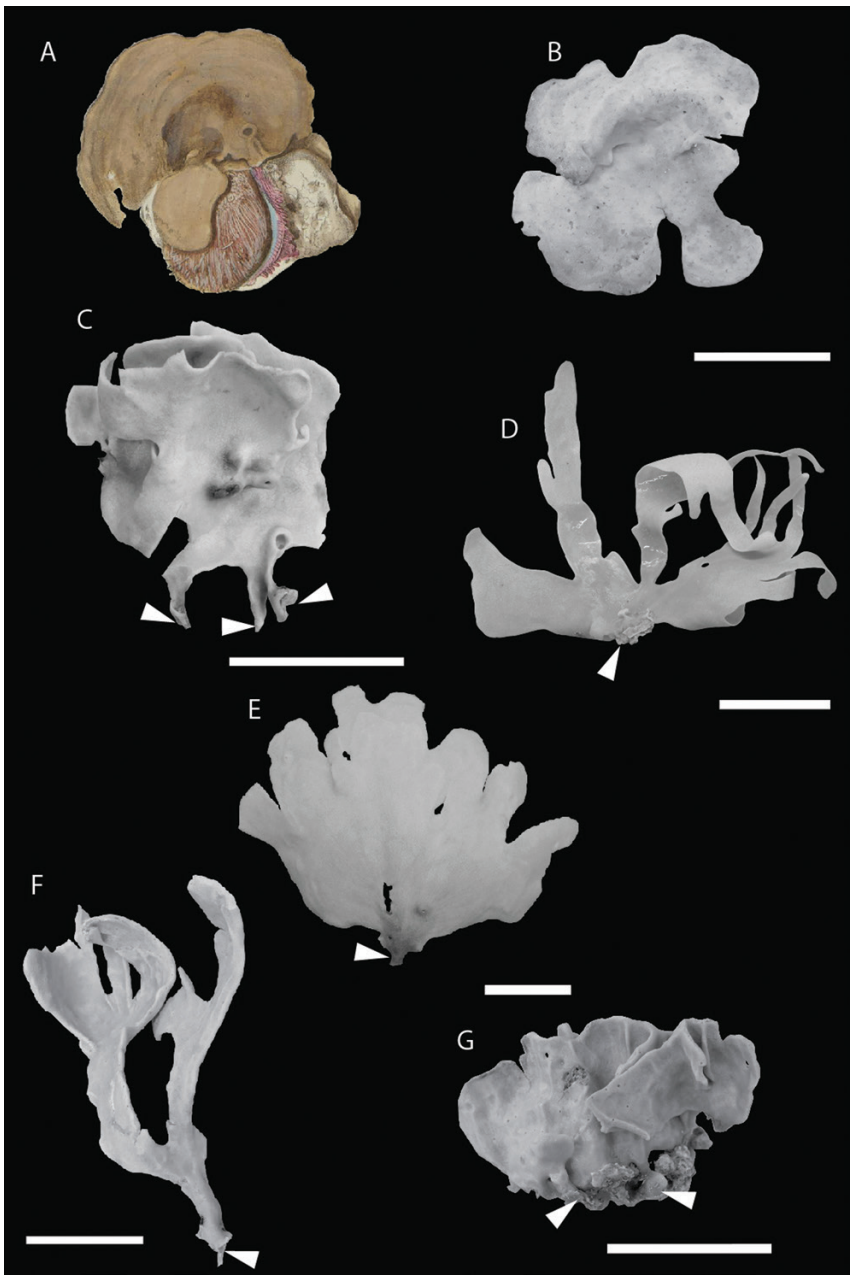

Figure 2. A, *Spongia papyracea* holotype. Illustration from Esper (1806: pl. 65, fig. 1). Thin erect wide cup morph. Dried specimen. No scale bar provided in original description. B, *Spongionella holdsworthi* syntype Bowerbank, 1873, thick, erect, wide cup morph, Sri Lanka, NHMUK 1873.7.21.1. Top view, single stalked. Collection depth unknown. Dried specimen. Scale bar = 5 cm. C, *Phyllospongia papyracea*, intertidal erect lamellate morph, Montgomery Reef, Kimberley, WAM Z87007. Collection depth = 0 m. Ethanol-preserved specimen. White arrows indicate multiple stalks. Scale bar = 5 cm. D, *Phyllospongia papyracea*, subtidal, thin, erect, lamello-digitate morph, Beagle Reef, Kimberley, WAM Z54124. Collection depth = 16 m. Ethanol-preserved specimen. White arrow indicates a single stalk. Scale bar = 5 cm. E, *Phyllospongia papyracea*, subtidal, thin, erect, lamellate morph, John Brewer Reef, central Great Barrier Reef, AM Z4987. Described in Bergquist *et al.* (1988: 304–305, fig. 14) (mislabelled as AM Z4087). Collection depth = 22 m. Ethanol-preserved specimen. Arrow indicates a single stalk. Scale bar = 5 cm. F, *Phyllospongia papyracea*, intertidal, thick, erect, lamello-digitate morph, Ashmore Reef, North-West Australian Shelf, WAM Z69635. Collection depth = 0 m. Ethanol-preserved specimen. Arrow indicates a single stalk. Scale bar = 5 cm. G, *Phyllospongia papyracea*, intertidal, thick, truncated, vertical lobes morph, Hedley Island Kimberley, WAM Z54432. Collection depth = 0 m. Ethanol-preserved specimen. Arrows indicate multiple substrate attachment points. Scale bar = 5 cm.

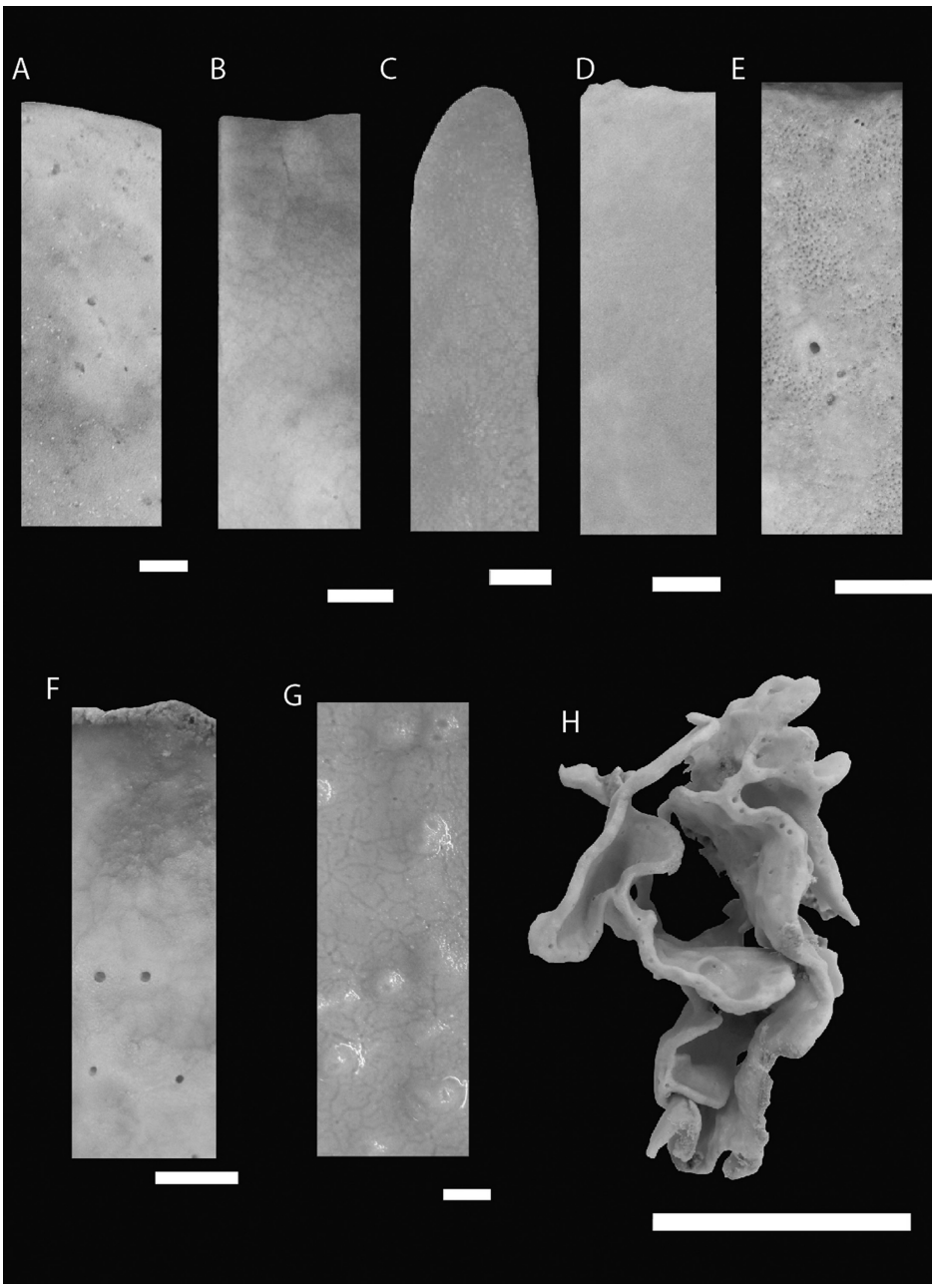

Figure 3. A, *Spongionella holdsworthi* syntype Bowerbank, 1873, close up of smooth surface, Sri Lanka (Ceylon), NHMUK 1873.7.21.1. Collection depth unknown. Dried specimen. Scale bar = 5 mm. B, *Phyllospongia papyracea*, close up of smooth surface showing drainage canals, Montgomery Reef, Kimberley, WAM Z87007. Collection depth = 0 m. Ethanol-preserved specimen. Scale bar = 5 mm. C, *Phyllospongia papyracea*, close up of smooth surface showing drainage canals, Beagle Reef, Kimberley, WAM Z54124. Collection depth = 16 m. Ethanol-preserved specimen. Scale bar = 5 mm. D, *Phyllospongia papyracea*, close up of smooth surface, John Brewer Reef, central Great Barrier Reef, AM Z4987. Described in Bergquist *et al.* (1988: 304–305, fig. 14) (mislabelled as AM Z4087). Collection depth = 22 m. Ethanol-preserved specimen. Scale bar = 5 mm. E, *Phyllospongia papyracea*, close up of smooth porous surface, Ashmore Reef, North-West Australian Shelf, WAM Z69635. Collection depth = 0 m. Ethanol-preserved specimen. Scale bar = 5 mm. F, *Phyllospongia papyracea*, close up of smooth oscular surface showing drainage canals, Hedley Island, Kimberley, WAM Z54432. Collection depth = 0 m. Ethanol-preserved specimen. Scale bar = 5 mm. G, *Phyllospongia papyracea*, close up of surface showing raised oscules and drainage canals, Dampier Archipelago, WAM Z3992. Collection depth = 0 m. Ethanol-preserved specimen. Scale bar = 5 mm. H, *Phyllospongia papyracea*, top view showing oscula openings on the edge of lamellae, Hedley Island, Kimberley, WAM Z54432. Collection depth = 0 m. Ethanol-preserved specimen. Scale bar = 5 cm.

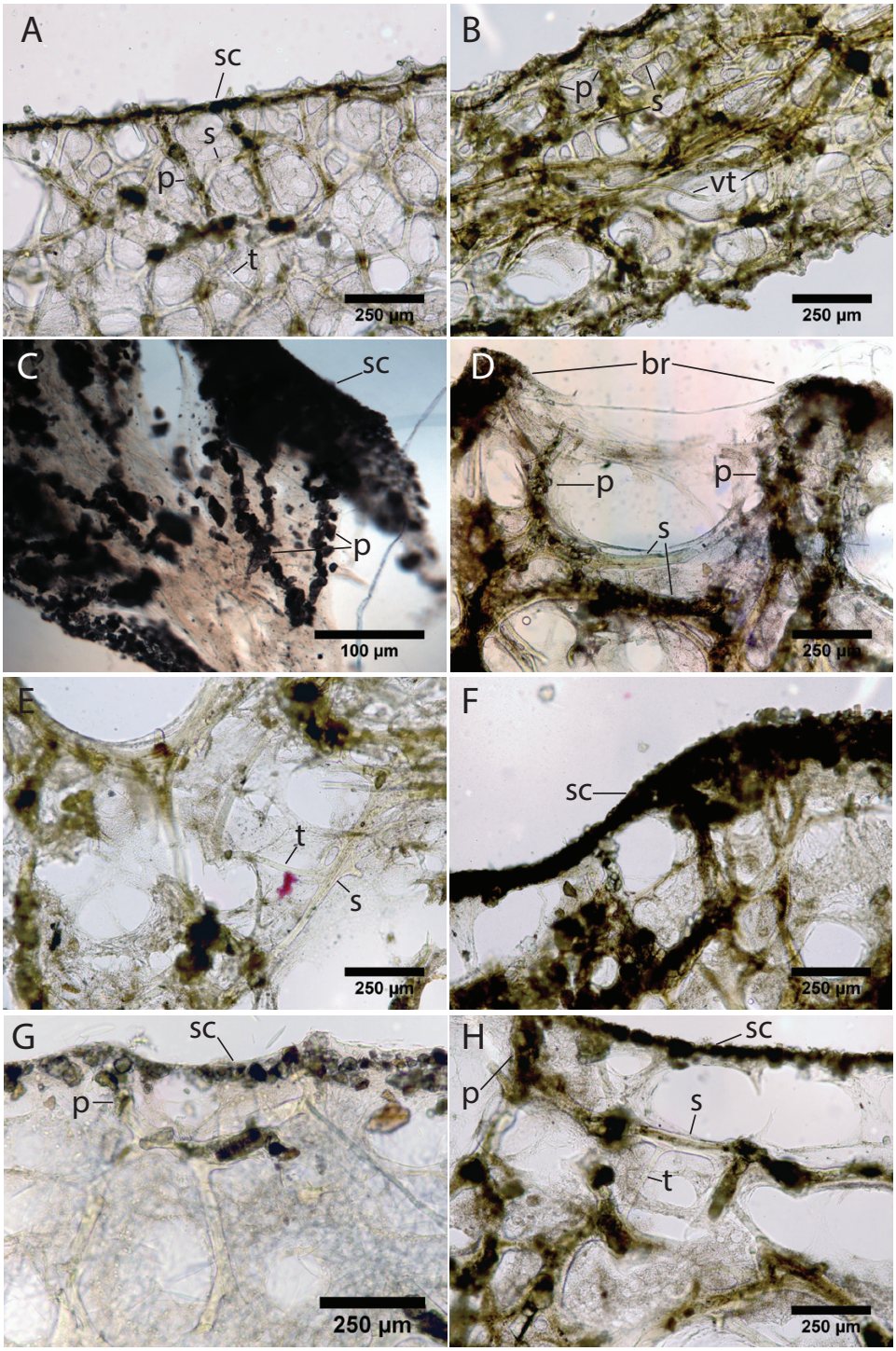

Figure 4. A, *Phyllospongia papyracea*, Davies Reef, Great Barrier Reef, CS_D_4. Micrograph of a thick histological section (90 µm) showing cored primary (p), uncored secondary (s) and tertiary (t) fibres, and a sand cortex (sc). Collection depth = 12 m. Scale bar = 250 µm. B, *Phyllospongia papyracea*, Beagle Reef, Kimberley, WAM Z54124. Micrograph of a thick histological section (90 µm) showing the regular skeletal mesh configuration, and the primary (p), secondary (s) and axial vermiform tertiary (vt) fibres. Fine pithing can be seen in the vermiform tertiary fibres. Collection depth = 16 m. Scale bar = 250 µm. C, *Phyllospongia foliascens*, neotype, Coin Peros, NHMUK 1925.11.1.411. Described in Bergquist *et al.* (1988: 294–297, figs 2–5). Micrograph of a thick histological section (90 µm) showing cored primary fibres (p) and a plumoreticulate fibre

is pronounced. Vermiform tertiary fibres are usually only visible at the base of the lamellae or in the stalk. The outstanding feature of *Phyllospongia papyracea* is the regular reticulation of the primary and secondary skeletons (Fig. 4A, B).

In our study, we noted three differences from the Bergquist *et al.* (1988) redescription: (1) occasionally, the primary fibres are irregular as a consequence of coring, but there is always a spongin sheath, (2) the secondary fibres may occasionally be lightly cored and (3) truncated gross morphologies may occur.

Phyllospongia papyracea has a neater, more compressed secondary skeleton compared to *P. foliascens*, and the dermal sand crust is much reduced. *Phyllospongia bergquistae* also has a compressed secondary skeleton and reduced sand crust, a feature that is intermediate between *P. papyracea* and *P. foliascens*.

PHYLLOSPONGIA FOLIASCENS (PALLAS, 1766)

(FIGS 4C–F, 5, 6)

Restricted synonymy

Carteriospongia foliascens (Pallas, 1766: 395).

Carteriospongia otahitica (Esper, 1797: 209, pls L–LXI, fig. 8).

Phyllospongia lamellosa (Esper, 1794:270; pl. XLIV, figs 1, 2).

Spongia fissurata Lamarck, 1814: 382.

Halispongia ventriculoides Bowerbank, 1874: 307, pl. XLVII, figs 1, 2.

Spongia polyphylla Lamarck, 1814: 441.

Material examined

Eighty-eight specimens including neotypes, syntype, schizotype, ethanol-preserved specimens, dried specimens, slides, DNA, and photographs and illustrations (see Supporting Information, Material S1 for detailed metadata). Neotype *Spongia foliascens* Pallas, 1766: NHMUK 1925.11.1.411, Coin Peros, Indian Ocean. *Other material:* Neotype *Spongia lamellosa* Esper, 1794: NHMUK 1881.10.21.273; *Spongia lamellosa* Esper, 1794: NHMUK 1881.10.21.274, Port Molle, Queensland, Australia. Syntype *Spongia otahitica* Esper 1797: NHMUK 1872.9.25.1, Tahiti.

Type data: Spongia foliascens Pallas, 1766 by subsequent designation Burton (1934). Neotype NHMUK 1925.11.1.411 from Coin Peros, Indian Ocean (5°21.430'S, 71°51.688'E).

SPECIES REDESCRIPTION

Neotypes

Morphology: Neotype NHMUK 1925.11.1.411 is a whole ethanol-preserved specimen, an erect cup with a single stalk (69 mm wide, 49mm high, 5 mm thick). The specimen has differentiated surfaces with the inner cup distinctly verrucose and the oscular, outer cup smoother than the inner cup (Fig. 5A, B). Oscules (< 1 mm diameter) are flush with the surface, drainage canals are not visible. Oscules are not present apically on the cup wall. The verrucose surface of the lamella is distinctive with rectangular conules and a heavy sand crust (Fig. 4C). Neotype *Spongia lamellosa* Esper, 1794 NHMUK 1881.10.21.273; is a whole, dried, erect, multilobed fan with a single stalk (165 mm wide, 148 mm high, 3 mm thick; Fig. 5C). It also has differentiated surfaces with the inner cup distinctly verrucose and oscular, and the outer cup surface smoother than the inner one. The verrucose surface is distinctive with rectangular conules. Oscules are flush with the surface and drainage canals are not visible.

Skeleton: Neotype NHMUK 1925.11.1.411. A sand cortex is on both sides of the lamella, 180–200 μm thick (Fig. 4C). The fibres are faintly laminated, the primary fibres are cored, secondary fibres uncored and interconnected with uncored tertiary fibres. Tertiary fibres are central and vermiform without pith. Primary fibres are 100–150 μm diameter. Secondary fibre diameter consistently 30 μm and tertiary fibre diameter ranged from 10 to 15 μm. The mesh

skeleton. Scale bar = 100 μm. D, *Phyllospongia foliascens*, eastern Australian intertidal/shallow water erect cup morph, Juno Bay, Fantome Island, central Great Barrier Reef, CS_J_ 7. Micrograph of a thick histological section (90 μm) showing cored primary fibres (p) and cored and uncored secondary fibres (s). Parallel primary fibres reach the sponge surface as brushes (br). Collection depth = 0 m. Scale bar = 250 μm. E, *Phyllospongia foliascens*, Fraser Island, Kimberley, WAM Z54270. Micrograph of a thick histological section (90 μm) showing uncored secondary fibres (s), and tertiary fibres (t) that form part of the skeletal reticulation. Collection depth = 0 m. Scale bar = 250 μm. F, *Phyllospongia foliascens*, Wildcat Reefs, Kimberley, WAM Z54006. Micrograph of a thick histological section (90 μm) showing a thick sand cortex (sc). Collection depth = 0 m. Scale bar = 250 μm. G, *Phyllospongia bergquistae* holotype, John Brewer Reef, Great Barrier Reef, AM Z5021. Micrograph of a thick histological section (90 μm) showing a cored primary fibre (p) and the sand cortex (sc). Collection depth = 22 m. Scale bar = 250 μm. H, *Phyllospongia bergquistae*, Davies Reef, Great Barrier Reef, CS_D_10. Micrograph of a thick histological section (90 μm) showing cored primary (p), uncored secondary (s) and tertiary (t) fibres, and the sand cortex (sc). Collection depth = 12 m. Scale bar = 250 μm.

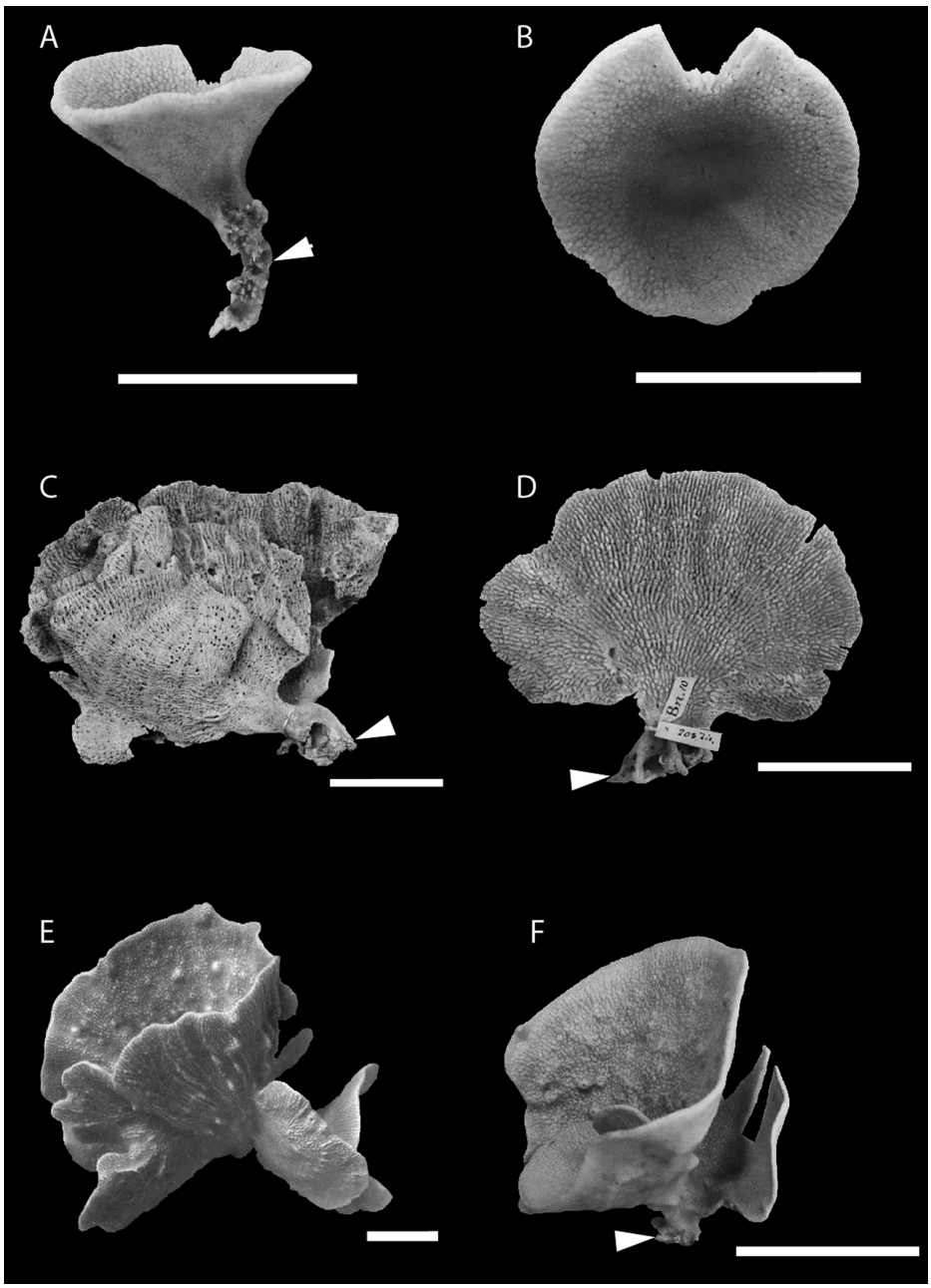

Figure 5. A, *Phyllospongia foliascens* neotype, erect, cup morph, Coin Peros, NHMUK 1925.11.1.411. Described in Bergquist *et al.* (1988: 294–297, figs 2–5). Side view. Ethanol-preserved specimen. White arrow indicates stalk. Scale bar = 5 cm. B, *Phyllospongia foliascens* neotype, erect, cup morph, Coin Peros, NHMUK 1925.11.1.411. Described in Bergquist *et al.* (1988: 294–297, figs 2–5). Top view. Ethanol-preserved specimen. Scale bar = 5 cm. C, *Phyllospongia foliascens*, intertidal/shallow water, erect, convoluted cup morph, Port Molle Queensland, NHMUK 1881.10.21.273. Dried specimen. Previously designated as neotype of *Phyllospongia lamellosa*. White arrow indicates stalk. Scale bar = 5 cm. D, *Phyllospongia foliascens*, subtidal, erect, lamellate morph, Tahiti, NHMUK 1872.9.25.1. Dried specimen. Originally described as *Spongia otahitica* in Ellis & Solander (1786: pl 59, fig 1). White arrow indicates stalk. Scale bar = 5 cm. E, *Phyllospongia foliascens*, intertidal/shallow water, erect, cup morph, Juno Bay, Fantome Island, central Great Barrier Reef, CS_J_13. Collection depth = 1 m. Live sponge in situ. Scale bar = 5 cm. F, *Phyllospongia foliascens*, intertidal/shallow water, erect, cup morph, Woodward Island, Kimberley, WAM Z54445. Collection depth = 0 m. Ethanol-preserved specimen. White arrow indicates stalk. Scale bar = 5 cm.

configuration is irregular, the primary to primary mesh size 450 µm wide and secondary to secondary 190 µm wide.

Neotype: Spongia lamellosa Esper, 1794 NHMUK 1881.10.21.273. A sand cortex is on both sides of the lamella. Primary fibres are fully cored. Secondary fibres are present but not pronounced and some are pithed. Tertiary fibres form meshes with secondaries. Vermiform tertiary fibres are rare in the slide, there is some evidence of pithing. Fibres are faintly laminated. The primary fibre diameter is 90–120 µm, the secondary fibre diameter 20–30 µm and the tertiary fibre diameter 10–15 µm. The mesh configuration is irregular, the primary to primary mesh size is 450 µm wide, and the secondary to secondary 190 µm wide. The specimen of *Spongia lamellosa* Esper, 1794 NHMUK 1881.10.21.274 is similar to NHMUK 1881.10.21.273 and also belongs to *P. foliascens*.

Additional material

Morphology: Phyllospongia foliascens comprises erect fans, which may have multiple fronds or cups, with single or multiple short stalks (Figs 5A–F, 6A–C). The sponge lamellae are generally thicker in intertidal specimens, ranging from 1.5 to 5.5 mm, compared to subtidal specimens that reach a maximum thickness of ~3 mm. Maximum sponge dimensions are 150 mm height and 165 mm width.

The sponge is incompressible. Surfaces are always sand-encrusted (180–200 µm thick) and differentiated, with the inner surface more verrucose than the outer surface. The inner surface consists of well-defined ridges and narrow grooves. Oscules are small (< 1 mm), found on the inner surface of cups and are, in general, flush with the lamellae surface. However, they can be raised on mounds ~2 mm wide and 2–3 mm high in specimens from shallow depths or the intertidal (e.g. Fig. 5E, F). Drainage canals are not visible and are in grooves between verrucae. Oscules are rarely present apically on the cup wall, except in some intertidal specimens (e.g. WAM Z54364). The verrucose surface is distinctive with rectangular conules and a heavy sand crust (Figs 6E–K, 4C, F). The lamella surface may appear waxy and is due to a surface membrane (e.g. pronounced in WAM Z29241; Fig. 6D). The edge of the lamella may be regular or scalloped. Ridging of the lamella is present in intertidal specimens (Fig. 5C, E) but was not observed in subtidal specimens. Live coloration is brown and in ethanol cream to fawn.

Skeleton: Skeletal fibres are arranged in an irregular, plumoreticulate pattern with the primary fibres oriented centrally, forming a central plumose lattice that diverges near the surface as brushes (Fig. 4C, D). These brushes form the verrucose surface patterning. Primary fibres are dominant and densely cored (Fig. 4C, D). Secondary fibres are cored or uncored, and tertiary fibres uncored (Fig. 4D, E). Tertiary fibres are not pithed and are part of the skeletal reticulation (Fig. 4E), however they can occur as vermiform elements centrally near the base of the sponge and may be abundant. Tertiary fibres can be tangled around the central fibres. Fibres are faintly laminated. Primary fibres range from 70 to 140 µm in diameter. Secondary fibres are reduced in number, from 20 to 90 µm diameter and tertiary fibres are 10–25 µm diameter. The skeletal mesh is irregular (Fig. 4C), the primary to primary mesh size is 450 µm wide, and secondary to secondary 190 µm wide.

Distribution

Phyllospongia foliascens (and synonymized species) is widely distributed across the Indo-Pacific, and has been recorded from the Red Sea, Indian Ocean and Pacific Ocean (Van Soest *et al.*, 2020; Bergquist *et al.*, 1988). Specimens in this study were from northern, eastern and western shallow tropical seas of Australia, Fiji and the Red Sea.

Remarks

The two neotypes examined in this study: the neotype of *Spongia foliascens* Pallas 1766 was designated by Burton (1934) and discussed in Bergquist *et al.* (1988), and the neotype of *Spongia lamellosa* Esper 1794 was designated by Bergquist *et al.* (1988). The ITS2 sequence of the neotype of *Spongia foliascens* (NHMUK 1925.11.1.411), which is the type of the genus *Carteriospongia*, grouped with other specimens identified as *C. foliascens* from the Great Barrier Reef, northern Western Australia and the Red Sea (Supporting Information, Material S4). These sequences formed a sister-clade to specimens of *Phyllospongia papyracea* (Fig. 1; Supporting Information, Material S4). All specimens examined in this study conformed morphologically to the neotype. However, as a consequence of the sister-relationship with *P. papyracea*, these specimens can no longer be separated at the genus level from *Phyllospongia*.

As *Spongia foliascens* is the type of the genus *Carteriospongia*, this genus (*Carteriospongia*) is no longer valid and the name can no longer be used. According to the Principle of Priority (IZCN, 1999), *Phyllospongia* Ehlers 1870, as the older established name, has priority over *Carteriospongia* Hyatt, 1877. Here, we formally synonymize *Carteriospongia* with *Phyllospongia*. The diagnosis of the genus

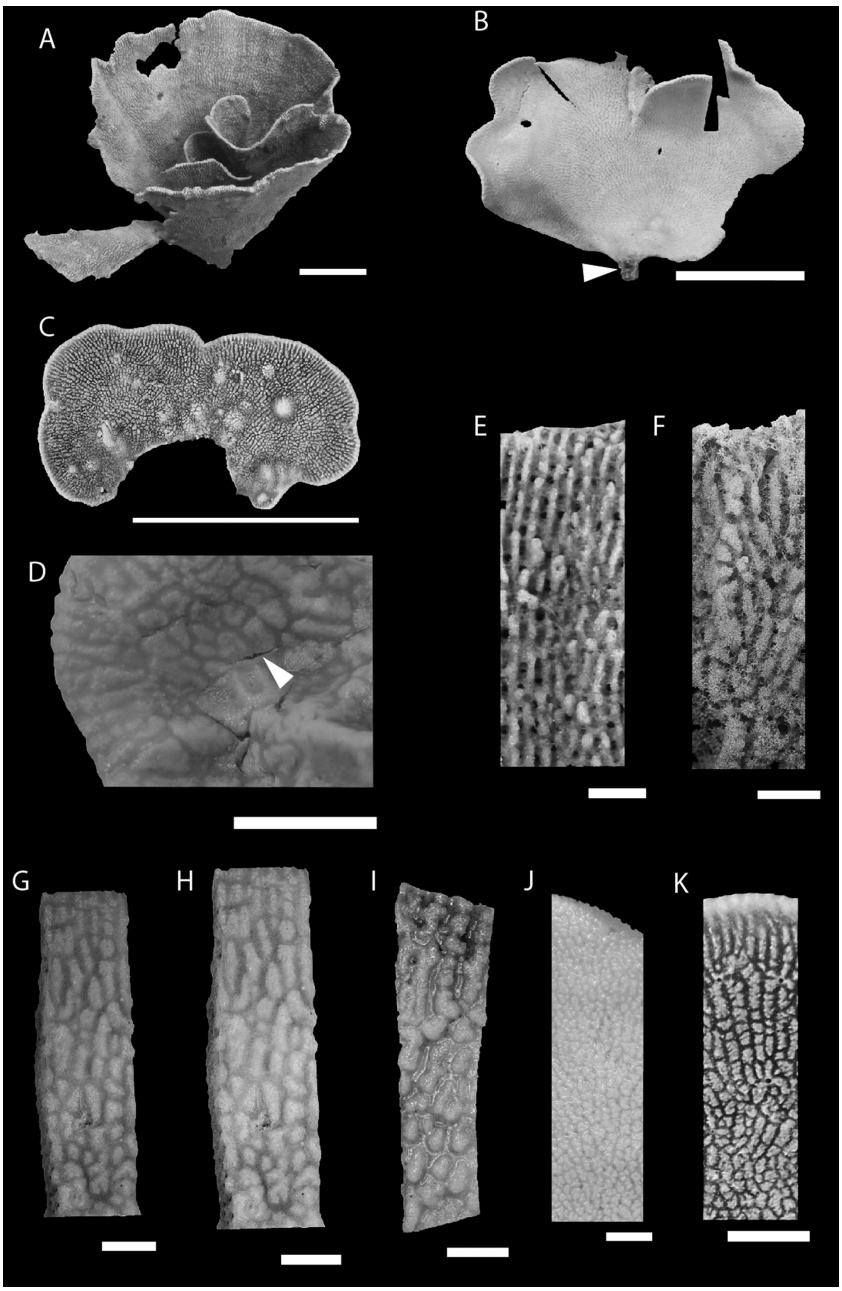

Figure 6. A, *Phyllospongia foliascens*, subtidal, erect, cup morph, Green Island, northern Great Barrier Reef, CS_GI_10. Collection depth = 10 m. Live sponge *in situ*. Scale bar = 5 cm. B, *Phyllospongia foliascens*, subtidal, erect, lamellate morph, Scott Reef, North-West Australian Shelf, WAM Z37657. Collection depth = 12.8m. Ethanol-preserved specimen. White arrow indicates stalk. Scale bar = 5 cm. C, *Phyllospongia foliascens*, subtidal, erect, lamellate morph, Red Sea, WAM Z86304. Collection depth = 5–10 m. Live sponge in situ. Scale bar = 5 cm. D, *Phyllospongia foliascens*, close up of surface with membrane, intertidal/shallow water, erect, lamellate morph, Juno Bay, Fantome Island, central Great Barrier Reef, WAM Z29241. Arrow shows a tear in the surface membrane. Collection depth = 0 m. Ethanol-preserved specimen. Scale bar = 5 cm. E, *Phyllospongia foliascens*, close up of verrucose sponge surface, Tahiti, NHMUK 1872.9.25.1. Dried specimen. Originally described as *Spongia otahitica* in Ellis & Solander (1786: pl 59, fig 1). White arrow indicates stalk. Scale bar = 5 cm. F, *Phyllospongia foliascens*, close up of verrucose sponge surface, Port Molle Queensland, NHMUK 1881.10.21.273. Dried specimen. Previously designated as neotype of *Phyllospongia lamellos*a. White arrow indicates stalk. Scale bar = 5 mm. G, *Phyllospongia foliascens*, close up of verrucose sponge surface, intertidal/shallow water, Juno Bay, Fantome Island, central Great Barrier Reef, CS_J_13. Collection depth = 1 m. Live sponge *in situ*. Scale bar = 5 mm. H, *Phyllospongia foliascens*,

Phyllospongia has been amended to accommodate this change.

A syntype of *Spongia otahitica* NHMUK 1872.9.25.1 was also examined (Fig. 5D). This is one of the specimens figured by Ellis & Solander (1786: pl. 59, fig. 1) and reproduced by Esper (1797: 209, pl. LXI, fig. 8) when he described the species. This specimen also conforms to the description of *P. foliascens*. The other syntype specimen of this species is also in the type collection: NHMUK 1931.6.25.17 labelled *Halispongia ventriculoides* Bowerbank, 1874 (T. White, personal communication). This specimen was not examined.

In addition, the neotype specimen of *Phyllospongia lamellosa* (NHMUK 1881.10.21.273) is identical to intertidal morphs of *Phyllospongia foliascens* (Fig. 5C, E, F). The specimen is fan-shaped, with the distinctive verrucose surfaces found in *P. foliascens* (Fig. 6E–K). The skeleton also conforms to *P. foliascens* with a pronounced sand cortex, primary fibres forming brushes at the surface and with fully cored primaries, few secondaries and vermiform tertiary fibres. Consequently, in this study *P. lamellosa* is synonymized with *P. foliascens*. Other specimens assigned to *P. lamellosa* (*sensu* Bergquist *et al.*, 1988) have been examined and given a new species name, *Phyllospongia bergquistae*.

Morphological variability in *Phyllospongia foliascens* is pronounced but it is based on habitat and depth to a degree and is predictable. From the assessment of 88 specimens collected from the intertidal (0 m) to subtidal habitats (up to 13 m; Supporting Information, Material S3), this study found the eastern and western Australian intertidal specimens had rectangular, verrucose surface patterning (Figs 5, 6). Specimens from eastern Australia had a well-defined surface rugosity that is clearly visible in both intertidal and subtidal specimens (e.g. Fig. 6I), while on the west coast the sponge surfaces are less rugose with increasing depth (e.g. Fig. 6J). Subtidal specimens from the Red Sea exhibit similar morphology to east coast subtidal specimens, although they have more tertiary fibres.

Regardless of the degree of development of the verrucose surface, it is always more pronounced on the oscular surface. The verrucose nature of the surface is a consistent character for the species. Other distinctive species characters are the formation of brushes at the sponge surface, the greater mesh size in *P. foliascens* compared to *P. papyracea* (primary 450 µm in the former, < 350 µm in the latter), the more irregular plumoreticulate skeleton in *P. foliascens* and the tertiary vermiform fibres tending to be more abundant centrally in the lamella. Secondary fibres are less common than in *P. papyracea*.

PHYLLOSPONGIA BERGQUISTAE ABDUL WAHAB & FROMONT, SP. NOV.

(FIGS 4G, H, 7A–F)

Zoobank registration: urn:lsid:zoobank.org:act:C308BA14-936C-4E39-A8AA-BBF08C3E9A60

Material examined

Seventeen specimens including holotype, paratype, ethanol-preserved specimens, slides, DNA and photographs (see Supporting Information, Material S1 for the detailed metadata).

Type data: Holotype AM Z5021 John Brewer Reef (18°38.382'S, 147°2.865'E), 22m, collector Thompson, J. E.. Paratypes AM Z5020 Davies Reef (18°49.024'S, 147°37.939'E), 20 m, collector Wilkinson, C. R.; AM Z5017 Flinders Reef (26°58.745'S, 153°29.290'E), 5 m, collector Kinsey, K.; AM Z5016 Flinders Reef (26°58.745'S, 153°29.290'E), 2 m, collector Wilkinson C.R.; WAM Z29271, Namuku Fiji (16°9.920'S, 179°40.931'E), depth unknown, collector Capon, R.

SPECIES DESCRIPTION

Holotype

Morphology: Holotype AM Z5021 is an ethanol preserved whole erect fan with two attachment points. The lamella surfaces are smooth, or with low ridges, with the outer fan surface smoother than the inner surface (Fig. 7A). The inner oscular surface has raised oscules to 1 mm high. There is fine patterning over the oscular surface similar to *P. foliascens* but not raised into regular rectangular ridges and grooves (Fig. 7F), the outer surface has fine linear patterning. The sponge is incompressible.

Skeleton: There is a sand cortex on both sides of the fan 50–60 µm with associated thickened collagen deposition. Primary fibres are cored, secondary fibres uncored and

close up of verrucose sponge surface, intertidal/shallow water, Woodward Island, Kimberley, WAM Z54445. Collection depth = 0 m. Ethanol-preserved specimen. White arrow indicates stalk. Scale bar = 5 mm. I, *Phyllospongia foliascens*, close up of verrucose sponge surface, subtidal, Green Island, northern Great Barrier Reef, CS_GI_10. Collection depth = 10 m. Live sponge *in situ*. Scale bar = 5 mm. J, *Phyllospongia foliascens*, close up of less rugose sponge surface, Scott Reef, North-West Australian Shelf, WAM Z37657. Collection depth = 12.8m. Ethanol-preserved specimen. White arrow indicates stalk. Scale bar = 5 mm. K, *Phyllospongia foliascens*, close up of verrucose sponge surface, Red Sea, WAM Z86304. Collection depth = 5–10 m. Live sponge *in situ*. Scale bar = 5 mm.

some are pithed, tertiary fibres are uncored and rare in slide. Fibres are laminated. Primary fibre diameter 75–90 µm, secondary fibre diameter 40–50 µm, tertiary fibre diameter 10–15 µm. The mesh configuration is irregular, the primary to primary mesh size is 220 µm wide and secondary to secondary 80–150 µm. Secondary fibres are condensed beneath the surface.

Additional material

Morphology: Erect, foliose, lamellate lobes, cups or fans (e.g. AM Z5021; Fig. 7A), which may have multiple fronds e.g. WAM Z29271; Fig. 7D). It has single or multiple basal attachments (Fig. 7B, C). The sponge lamellae are thin; 1–3 mm thick; height 50–110 mm; width 65–90 mm. The cortex has a light sand coring and thickened collagen deposition of 50–200 µm thick, differentiated from the inner surface, which has a heavier sand cortex (Fig. 4G, H). The ocular surface has raised oscules to 1 mm height (Fig. 7A, B) and may have ridges 2 mm high (Fig. 7D). Oscules may be on ridges (e.g. WAM Z29271; Fig. 7D). The outer poral surface is smoother than the inner surface (e.g. AM Z5020; Fig. 7B, C). The inner surface has fine patterning due to narrow underlying meshes, which are not rectangular (Fig. 7E, F). The surface patterning is flat and irregular, except apically where it may form regular, low, parallel ridges with oscules on the apical edge (e.g. AM Z5017; see Bergquist *et al.* 1988: fig. 20). The outer surface is smooth with faint meandering lines and small pores 1–2 mm wide. AM Z5021 and Z5020 have smoother surfaces than other specimens of this species and are thinner; these sponges were both collected from deeper depths.

Skeleton: The primary fibres are cored, the secondary fibres uncored and there are uncored tertiary fibres (Fig. 4G, H). Tertiary fibres form part of the reticulation but are rarely observed in slides. The fibres are laminated. Primary fibre diameter is 70–100 µm, secondary fibres dominate in thicker fans, diameter 30–50 µm, tertiary fibre diameter 10–15 µm. The mesh configuration is irregular centrally, but the primary fibres are at right angles to the surface at the edges of the fan (Fig. 4H). Primary to primary mesh size up to 230 µm wide, secondary to secondary mesh up to 190 µm wide but can be much smaller and form a dense skeleton superficially at right angles to the surface.

Distribution: The type locality is on the central Great Barrier Reef with a paratype found eastwards in Fiji. Specimens have only been collected from the West Pacific Ocean.

Etymology: Bergquist *et al.* (1988) redescribed *Phyllospongia lamellosa* (Esper, 1794) and designated a neotype specimen for the species, NHMUK 1881.10.21.273. However, the type specimen conforms to *Phyllospongia foliascens* (Pallas, 1766) and we synonymize it with that species. This action means that a new name is required for specimens assigned to *P. lamellosa* in Bergquist *et al.* (1988). We, therefore, name this species *P. bergquistae*, in recognition of Dame Professor Patricia Bergquist (deceased) and her substantial contribution to the systematics of the Phyllospongiinae.

Remarks

The specimens examined here do not conform to the neotype specimen of *P. lamellosa* NHMUK 1881.10.21.273. The neotype has the rectangular verrucose surface patterning characteristic of *P. foliascens*, hence its reassignment as a synonym of *P. foliascens*.

Specimens of *P. bergquistae* have smoother surfaces with fine, irregular patterning, not rectangular or verrucose. The surface characters of this species are intermediate between the smooth surfaces seen in *P. papyracea* and the rugose, rectangular patterning characteristic of *P. foliascens*. This is, in part, due to differences in mesh sizes seen in the species, e.g. *P. bergquistae* has smaller primary mesh sizes than *P. foliascens* (230 µm compared to 450 µm, respectively). In addition, the cortex is thinner in *P. bergquistae* (50–60 µm vs. 180–200 µm). The primary fibres do not form brushes at the surface, characteristic of *P. foliascens*, and instead have secondary fibres that become dense and compact beneath the surface, showing some similarity to *P. papyracea* (Fig. 4A–H). This species has currently only been reported from the Western Pacific Ocean.

Bergquist *et al.* (1988) redescription of *P. lamellosa* included some other species in synonymy: *S. laciniata*, *S. polyphylla*, *P. palmata* and *P. sweeti*. We have assessed the descriptions of these species and reassigned them as follows. *Spongia laciniata* from the Indian Ocean does not conform to *P. bergquistae*. It has the delicate morphology of *P. papyracea* and we assign it in synonymy to this species. *Spongia polyphylla* is also an Indian Ocean species, but it has the ribbed surface morphology and fibre details characteristic of *P. foliascens* and we synonymize it with that species. *Phyllospongia sweeti* Kirkpatrick, 1900 is currently assigned to *Spongia* (*Spongia*) *sweeti* (Van Soest *et al.*, 2011) due to the presence of a continuous anastomosing mass of secondary fibres that are characteristic of the genus *Spongia*. *Phyllospongia palmata* is a valid species of *Phyllospongia*, and morphological comparisons to *P. bergquistae* are provided below.

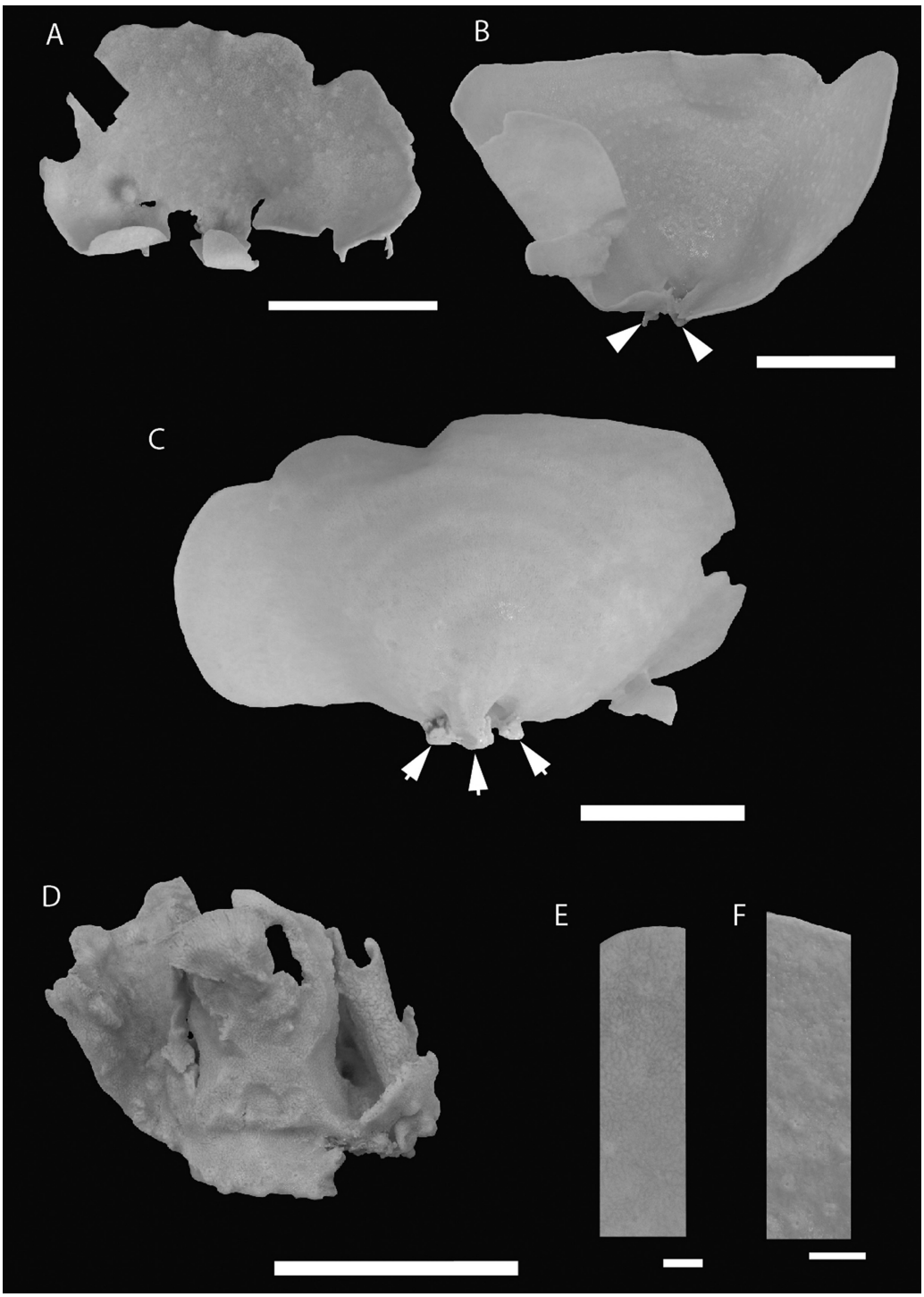

Figure 7. A, *Phyllospongia bergquistae*, holotype, erect, fan morph, John Brewer Reef, Great Barrier Reef, collected from 22 m depth, AM Z5021. Described in Bergquist *et al.* (1988: 306–309) as *Phyllospongia lamellosa*. View of inner fan. Ethanol-preserved specimen. Scale bar = 5 cm. B, *Phyllospongia bergquistae*, paratype, erect, fan morph, Davies Reef, Great Barrier Reef, collected from 20 m depth, AM Z5020. Described in Bergquist *et al.* (1988: 306–309, fig. 22) as *Phyllospongia lamellosa*. View of inner fan. Ethanol-preserved specimen. White arrows indicate attachment points. Scale bar = 5 cm. C, *Phyllospongia bergquistae*, paratype, erect, fan morph, Davies Reef, collected from 20 m depth, Great Barrier Reef, AM Z5020. Described in Bergquist *et al.* (1988: 306–309, fig. 22) as *Phyllospongia lamellosa*. View of outer fan. Ethanol-preserved specimen. White

Phyllospongia bergquistae is unlike any other described *Phyllospongia* species. It is morphologically closest to *P. alcicornis* (Esper, 1794) in that these are the only two *Phyllospongia* species with a collagenous subsurface layer. However, *P. alcicornis* has a distinctive branching morphology and dense vermiform tertiary fibres that form fascicules centrally (Bergquist *et al.* 1988); both characters are not seen in *P. bergquistae*. The fasciculate nature of the tertiary fibres in *P. alcicornis* suggests this species could be a *Polyfibrospongia*, but sequencing of type or fresh topotype material is necessary to resolve its generic assignment.

Both *P. macropora* Lendenfeld, 1889 and *P. schulzei* Lendenfeld, 1889 are temperate species, from New Zealand and South Africa, respectively. *Phyllospongia macropora* is a thick cup-shaped sponge (10 mm thick) with a thick sand cortex (500 µm) markedly different from the 3 mm thick fan and 50–60 µm sand cortex of *P. bergquistae*. *Phyllospongia schulzei* has fibres cored with spicule fragments and a pitted and grooved internal surface, it is also 10 mm thick, all characters not seen in *P. bergquistae*. *Phyllospongia cyathina* (Lamarck, 1814) is from Shark Bay, Western Australia, Indian Ocean. It is cup-shaped but otherwise the description by Lamarck, 1814 provided few other characters. Because *P. bergquistae* has not been recorded from Western Australia, it is not considered to be this species. Three other tropical species of *Phyllospongia* are currently recognized. *Phyllospongia ectoscula* Lévi, 1961 was described from the Philippines and is cup-shaped, has an irregular skeletal reticulation and a distinctive internal surface resembling 'cracked mud' when dry. *Phyllospongia bergquistae* has a consistently smooth to fine patterned inner surface with an underlying condensed secondary reticulation. The primary fibres of *P. ectoscula* are 40 µm wide, the secondaries 15 µm wide, while in *P. bergquistae* both fibre types are much larger, 70–100 µm and 30–50 µm, respectively. *Phyllospongia supraoculata* Ridley, 1884 from the Seychelles is unusual in having cored primary fibres superficially only, whereas in *P. bergquistae* cored primary fibres are not restricted to a particular part of the sponge. In addition, the primary to primary meshes are 100 µm in *P. supraoculata* and 220–230 µm in *P. bergquistae*. *Phyllospongia palmata* Thiele, 1889 from Sulawesi, Indonesia, has leaf-shaped fronds and an unusual surface layer like a cuticle that the fibres end beneath. The fronds are the same thickness as *P. bergquistae* (3 mm thick) but the primary fibres are bigger, 100–150 µm, in *P. palmata* compared to 70–100 µm in *P. bergquistae* and uncored secondaries 20–40 µm compared to 30–50 µm.

Most specimens of *P. bergquistae* were from the Great Barrier Reef with one specimen from Fiji. This study examined molecular sequences of a total of 124 specimens of the genus *Phyllospongia*, of which 39 were from tropical Western Australia, and yet this species was not recorded on the west coast, thus at this stage it appears to be a tropical West Pacific Ocean species. The distribution of *P. bergquistae* is comparatively restricted compared to *P. papyracea* and *P. foliascens*, which are found extensively across the West Pacific Ocean, Indian Ocean and the Red Sea.

Specimens of *P. bergquistae* occur sympatrically with those of *P. foliascens* and *P. papyracea* that are abundant and densely distributed on parts of the GBR, including the holotype, and a paratype location, i.e. John Brewer Reef and Davies Reef (Wilkinson 1988). All these species potentially have high fecundity, high fertilization success (due to a brooding developmental mode) and a year-round reproductive season, as reported for *P. foliascens* (Abdul Wahab *et al.*, 2014a, c). These biological and community characteristics of *Phyllospongia* species populations on the GBR, are conducive for facilitating hybridization between two closely related species and it is possible that *P. bergquistae* is a hybrid between *P. foliascens* and *P. papyracea*, which could explain its intermediate morphological characters and position on the current molecular phylogeny. Few studies have examined the potential for hybridization in sponges (Riesgo *et al.*, 2016), and formal investigations in the future, using more advanced molecular techniques (e.g. single nucleotide polymorphisms, Bouchemousse *et al.*, 2016), are necessary to test the presence of this process in species of *Phyllospongia*.

Genus *Polyfibrospongia* Bowerbank, 1877

Type species

Polyfibrospongia flabellifera Bowerbank, 1877: 459–460, by original designation. Holotype lodged in the Dresden Museum. Two slides from the holotype are

arrows indicate attachment points. Scale bar = 5 cm. D, *Phyllospongia bergquistae*, paratype, erect, multiple frond morph, near Namuku, Fiji, WAM Z29271. Ethanol-preserved specimen. Scale bar = 5 cm. E, *Phyllospongia bergquistae*, holotype, close up of sponge inner surface showing fine, irregular patterning, John Brewer Reef, Great Barrier Reef, collected from 22 m depth, AM Z5021. Described in Bergquist *et al.* (1988: 306–309) as *Phyllospongia lamellosa*. Ethanol-preserved specimen. Scale bar = 5 mm. F, *Phyllospongia bergquistae*, paratype, close up of sponge inner surface showing fine, irregular patterning, Davies Reef, Great Barrier Reef, collected from 20 m depth, AM Z5020. Described in Bergquist *et al.* (1988: 306–309, fig. 22) as *Phyllospongia lamellosa*. Ethanol-preserved specimen. Scale bar = 5 mm.

in the British Natural History Museum NHMUK 1877.5.21.1302 from Geelvink Bay, Papua New Guinea.

Amended diagnosis

Fans, cups, ridges or plates always thin, 0.5–2 mm thick, with multiple or single basal attachments. Characterized by a pronounced sand cortex, which may be thinner on one side, and longitudinal surface patterning. The surface may be shiny if the sand cortex is reduced. Oscules small (< 0.2 mm), rare, flush with the surface. Primary fibres are light to heavily cored, at right angles to the surface with irregular fibre diameters due to coring, secondary fibres are rare to absent and rarely cored, tertiary fibres are abundant, pithed, uncored and form a lattice-like reticulation with short connecting fibres, associated with the primary fibres in the centre of the sponge, and sometimes beneath the surface. The texture is incompressible and brittle, the colour cream to fawn.

Remarks

Polyfibrospongia was originally established by Bowerbank in 1877 with the type species *P. flabellifera*; the genus was later synonymized with *Carteriospongia* Hyatt, 1877 by Bergquist (1980). Interestingly, it appears that *Carteriospongia* Hyatt, 1877 was published on 8 June 1877 and *Polyfibrospongia* Bowerbank, 1877 on 5 June 1877. Consequently, *Polyfibrospongia* should have been the senior name when the genera were synonymized.

With the determination in this publication that the type species of *Carteriospongia*, *C. foliascens,* belongs in *Phyllospongia* and thus *Carteriospongia* is no longer a valid genus name, *C. flabellifera* reverts to its original generic determination, and *Polyfibrospongia* is here thus reinstated as a valid genus. This was supported by both morphological and molecular assessments of the type material (morphological only for the *P. flabellifera* holotype) and additional sponges from the Great Barrier Reef and Western Australia that conform to the original description of the species by Bowerbank, 1877 (Figs 1, 8A–C, 9A–C) and support this species as distinct from any species in *Phyllospongia* and *Strepsichordaia*.

The outstanding feature of the genus *Polyfibrospongia* is the concentrated and greatly emphasized tertiary fibre complexes around the primary fibres; these tertiary fibres form a lattice-like reticulation in the centre of the sponge lamella around the primary fibres, and superficially in the new species *P. kulit*. This degree of development of tertiary fibres is not seen in the lamella of *Phyllospongia* species. These fibres are visible in the type slides and were referred to by Bowerbank (1877) as 'continuous fasciculi'. He did not recognize these as tertiary fibres, but as primary and secondary elements. Bergquist *et al.* (1988) examined the type slides and noted these distinctive tertiary fibres and that they could form complex tresses. In preparations sectioned at 90 µm the abundant tertiary fibres form a tight lattice-like reticulation with short cross-connecting fibres and are associated with the primary fibres centrally within the lamella of the sponge (Fig. 9A–C). In contrast, tertiary fibres are rare in the upper lamellae of *Phyllospongia* and the base or the stalks need to be examined to see an abundance of tertiary fibres in that genus. Bergquist *et al.* (1988) also noted that primary fibres never form brushes at the surface in *P. flabellifera*, but this absence is also seen in some species of *Phyllospongia*.

Other distinguishing features of the genus are the surface details. Species of *Polyfibrospongia* never have the verrucose surface seen in *Phyllospongia foliascens* and this is likely to be due to the rarity of the secondary skeleton and, therefore, a primary–secondary reticulation being largely absent in this species. Specimens can be fleshy as a result of collagen in the ectosome, a character also seen in *Phyllospongia bergquistae.* There is always a sand cortex in *Polyfibrospongia* but this varies in degree, being lighter in *P. kulit*.

KEY TO THE SPECIES OF *POLYFIBROSPONGIA*

1a. Heavily cored primary fibres; pronounced surface sand armour..... *P. flabellifera*
1b. Lightly cored or uncored primary fibres; fine sand cortex..... *P. kulit*

POLYFIBROSPONGIA FLABELLIFERA BOWERBANK, 1877

(FIGS 8A–C, G, H, 9A–C)

Synonymy

Carteriospongia flabellifera (Bowerbank, 1877)

Material examined

Forty-four specimens, including holotype, ethanol-preserved specimens, slides, DNA and photographs (see Supporting Information, Material S1 for the detailed metadata).

Type data: Polyfibrospongia flabellifera Bowerbank, 1877, NHMUK 1877.5.21.1302 two slide preparations from the holotype lodged in the Dresden Museum. From Geelvink Bay, Papua New Guinea (2°37.416'S, 135°15.102'E).

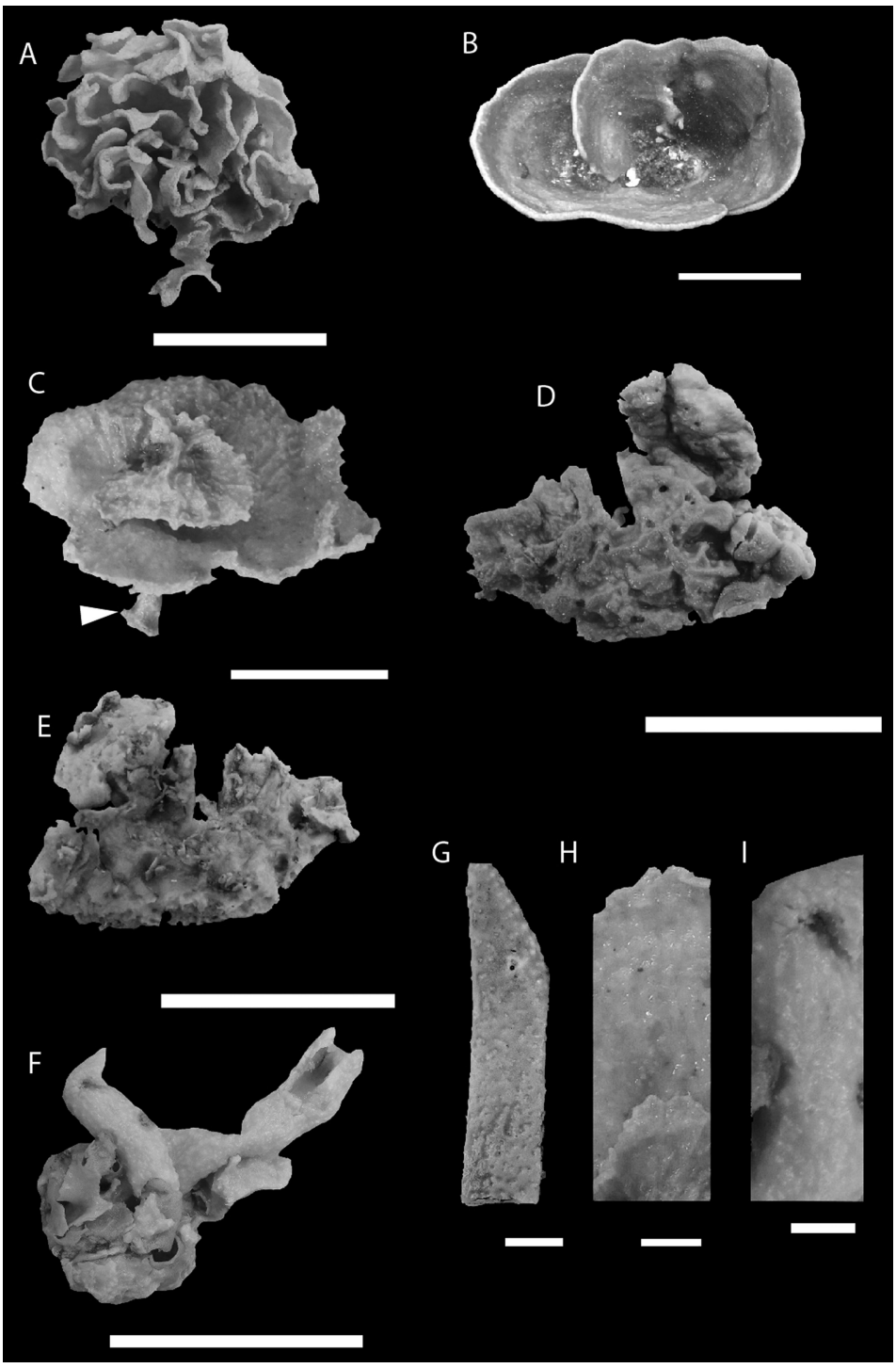

Figure 8. A, *Polyfibrospongia flabellifera*, intertidal, contorted, lamellate morph, Montgomery Reef, Kimberley, WAM Z87008. Collection depth = 0 m. Ethanol-preserved specimen. Scale bar = 5 cm. B, *Polyfibrospongia flabellifera*, eastern Australian, subtidal, erect, cup morph, Green Island, northern Great Barrier Reef, CS_GI_74. Collection depth = 10 m. Live sponge *in situ*. Scale bar = 5 cm. C, *Polyfibrospongia flabellifera*, western Australian, subtidal, erect, wide, cup morph, Beagle Reef, Kimberley, WAM Z54137. Collection depth = 16 m. Ethanol-preserved specimen. Scale bar = 2 cm. D, *Polyfibrospongia kulit*, holotype, intertidal, thick encrusting morph, top surface, King and Conway Islands, Kimberley, WAM Z54316. Collection depth = 0 m. Ethanol-preserved specimen. Scale bar = 5 cm. E, *Polyfibrospongia kulit*, holotype,

Species redescription

Morphology: Species morphology is predominantly thin fans or cups, usually with multiple attachments, but attachment can be single. Shape variable with flattened cups and ridges, or walls in intertidal forms (Fig. 8A–C). The cups can be convoluted, and the edges may be serrated; irregular flanges or ridges may occur (Fig. 8A–C). The sponge is always thin 0.5–2 mm thick; height 55–100 mm; width 70–150 mm. There is a pronounced sand cortex 30–170 µm. Oscules are small and inconspicuous (< 0.2 mm); pores may occur between surface vertical lines. The surface is smooth or microconulose, with fine, vertical lines on both surfaces, stronger lines may occur closer to the fan edge. These are less visible with a more pronounced sand cortex. Occasional surface ridges are ~5 mm high. There is a fine membrane over the whole surface, which gives a fleshy appearance, except in those with a heavy sand cortex. The sponges are incompressible. The colour when live is dark to reddish-brown and fawn in ethanol.

Skeleton: The primary fibres are heavily cored and they may be pithed, 100–150 µm wide; the secondary fibres are uncored or lightly cored, rare, and 30 µm wide; the tertiary fibres are abundant, uncored and may have pith. Tertiary fibres form lattice-like reticulations with short connecting fibres and are associated with primary fibres centrally. They are 12–18 µm wide. In thick sections they may look like tresses or fascicules to 80 µm wide (Fig. 9A–C). The primary fibres at right angles to the surface form the external raised lines (Fig. 9A). The skeletal mesh has primary fibres generally at right angles to the surface. The primary to primary mesh size is 250–450 µm wide, the secondary to secondary 50 µm wide, and the tertiary 10–30 µm.

Distribution

Specimens in this study were from northern, eastern and western shallow tropical seas of Australia. This species has been reported from south-east Papua New Guinea and the eastern Philippines (Bowerbank, 1877; Longakit *et al.*, 2005), the Great Barrier Reef and eastern Indian Ocean (Abdul Wahab *et al.*, 2014d).

Remarks

The molecular phylogenies presented here (ITS2 or concatenated ITS2 + 18S + 28S) showed strong support for the delineation of *P. flabellifera* from species of *Phyllospongia* and *Strepsichordaia lendenfeldi* (Fig. 1; Supporting Information, Material S4). A specimen of *Carteriospongia contorta* Bergquist *et al.*, 1988 (QM G318412) was sequenced here and aligned with specimens of *P. flabellifera*. *Carteriospongia contorta* was recognized as being closely related to *P. flabellifera* when the species was first described, and the skeletons of both species are similar. The holotype (AM Z3937) and paratype (AM Z4986) of *C. contorta* were examined in this study, as well as non-type material from the Queensland Museum. All specimens showed skeletal features that fall within the range of those found in *P. flabellifera*, but with sandy elements more pronounced in *C. contorta*. The external morphology of *C. contorta* is ornately sculptured and lamellate. Due to the morphological and molecular support of *C. contorta* aligning with characters of *Polyfibrospongia* as a result of this study, the species is assigned to the genus *Polyfibrospongia*, thus becoming *P. contorta*. However, whether *P. contorta* represents another morphotype within *P. flabellifera,* or is a unique species, requires the assessment of more *P. contorta* specimens and additional molecular analyses, particularly of the type specimens or from the type locality (Milln Reef, Great Barrier Reef). Until this is done, we retain *P. contorta* as a valid species, conforming to the genus *Polyfibrospongia*.

Polyfibrospongia flabellifera is distinguished from the new species *P. kulit* by the presence of thin, brittle lamella, a dense sand cortex and a large amount of foreign material in the skeleton. *Polyfibrospongia kulit* is fleshier and has a thinner sand cortex composed of fine sand grains.

POLYFIBROSPONGIA KULIT ABDUL WAHAB & FROMONT, SP. NOV.

(FIGS 8D–F, I, 9A–C)

Zoobank registration: urn:lsid:zoobank.org:act:8378C887-1FCD-4A81-997E-62806221B5B2

Material examined

Five specimens, including holotype, paratype, ethanol-preserved specimens, slides and DNA (see Supporting Information, Material S1 for the detailed metadata).

intertidal, thick encrusting morph, bottom substrate surface, King and Conway Islands, Kimberley, WAM Z54316. Collection depth = 0 m. Ethanol-preserved specimen. Scale bar = 5 cm. F, *Polyfibrospongia kulit*, intertidal encrusting-columnar form, Champagny Islands, Kimberley, WAM Z54013. Collection depth = 0 m. Ethanol-preserved specimen. Scale bar = 5 cm. G, *Polyfibrospongia flabellifera*, close-up of sand encrusted surface, Green Island, northern Great Barrier Reef, CS_GI_74. Collection depth = 10 m. Live sponge *in situ*. Scale bar = 5 mm. H, *Polyfibrospongia flabellifera*, close up of the microconulose sponge surface, Beagle Reef. Kimberley, WAM Z54137. Collection depth = 16 m. Ethanol-preserved specimen. Scale bar = 5 mm. I, *Polyfibrospongia kulit*, close up of the finely microconulose sponge surface, Champagny Islands, Kimberley, WAM Z54013. Collection depth = 0 m. Ethanol-preserved specimen. Scale bar = 5 cm.

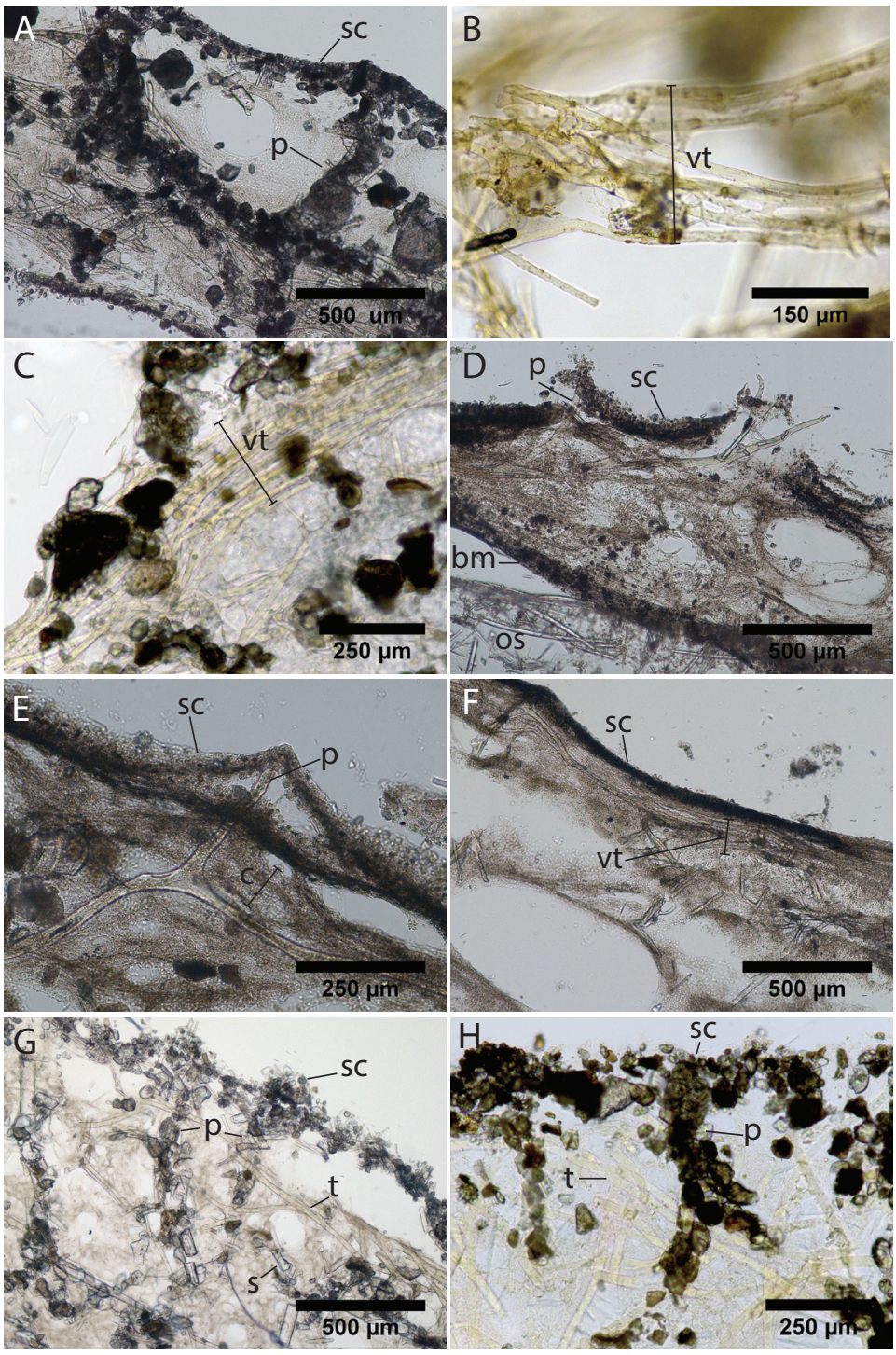

Figure 9. A, *Polyfibrospongia flabellifera*, Robroy Reefs, Kimberley, WAM Z54683. Micrograph of a thick histological section (90 µm) through the entire sponge lamella, showing heavily cored primary (p) fibres, and a sand cortex (sc). Collection depth = 13.3 m. Scale bar = 500 µm. B, *Polyfibrospongia flabellifera*, holotype, Geelvink Bay, Papua New Guinea, NHMUK 1877.5.21.1302. Described in Bergquist *et al.* (1988: 298–300, figs 6–8). Micrograph of a thick histological section from one of two slides from the holotype, showing tertiary fibres (vt) that form characteristic lattice-like reticulations. Scale bar = 150 µm. C, *Polyfibrospongia flabellifera*, Hook Reef, Whitsunday Group, Great Barrier Reef, AM Z4984. Described in Bergquist *et al.* (1988: 298–300, figs 6–8). Micrograph of a thick histological section (90 µm) showing characteristic tertiary

Type data: Holotype WAM Z54316 King and Conway Islands, Kimberley (15°52.203'S, 123°39.910'E), 0 m, collector Gomez, O. A.; paratypes WAM Z54038 and WAM Z54013 Champagny Islands, Kimberley (15°19.842'S, 124°13.014'E), 0 m, collector Gomez, O. A.

Species description

Holotype

Morphology: Holotype WAM Z54316. The specimen has a thick, encrusting morphology, 1–20 mm thick, has an irregular convoluted shape, or may be flat and spreading and form a regular mat (Fig. 8D, E), with multiple attachment points. Dimensions – breadth 70 mm, length 64 mm, height to 20 mm above substrate. Colour cream or fawn to light brown in ethanol. Texture is compressible, springy and resilient, the sponge can be torn. Fleshy, shiny, membranous surface, with fine, low conules in clusters in some areas, or ridges to < 0.5 mm height, surface not homogenous, it is irregular and uneven. The surface may be finely microconulose from underlying primary fibres. Oscules are rare, flush with the upper surface and small – 0.5–1.0 mm wide. There is a sand cortex on the apical surface of fine sand grains, thin and occasionally intermittent. The basal surface has a collagenous layer with sparse sand grains. Barnacles associated with this species form small mounds on the sponge surface. The sponge is partly overgrowing a spicule containing demosponge.

Skeleton: A sand cortex with fine grains is 40–150 µm thick. A collagenous layer, clear of sand, occurs beneath the cortex and is 50–100 µm thick. The primary fibres are lightly cored or uncored, pithed, at right angles to the surface and slender (40–60 µm thick); the secondary fibres are rare, uncored, lightly pithed and 20–50 µm thick; and the tertiary fibres are uncored and 18–20 µm thick. They form a slender, lattice-like reticulation centrally, and these may extend to beneath the surface. Overall, the skeleton is open, not dense and clear of sand inclusions in the mesohyl. The primary to primary mesh size is 200–370 µm wide, the secondary to secondary 200–250 µm wide and the tertiary to tertiary 10–40 µm. Basally, a collagenous layer is 50–60 µm thick.

Additional material

Morphology: Thin to thick encrusting (1–20 mm), irregular spreading, overgrowing coral reef substrate and other demosponges. Multiple substrate attachment points. Surface irregular and uneven, finely hispid (Fig. 8I), with symbiotic barnacles forming small mounds on the surface of some specimens. A fine membrane covering the surface makes the sponge appear shiny. Sponge compressible and springy. Colour brown when alive and cream to fawn to light brown in ethanol.

Skeleton: Sand cortex with fine sand grains (40–150 µm) with a collagenous layer beneath the surface that is free of sand (50–100 µm; Fig. 9D). Primary fibres lightly cored or uncored, secondary fibres rare, uncored and with light pithing and tertiary fibres uncored (Fig. 8D). Primary fibres are at right angles to the surface and slender (40–60 µm), forming a microconulose surface (Fig. 8D, E). Secondary fibres are rare (20–50 µm). Tertiary fibres (18–20 µm), lattice-like with narrow interconnections, also occurring beneath the surface (Fig. 8F). Skeletal matrix sparse, reticulation large, primary to primary mesh size 200–580 µm, secondary to secondary mesh 200–250 µm.

Distribution

Known from the King and Conway Islands (north of Macleay Island) and Champagny Island, all within

fibre lattice-like reticulations. Collection depth = 10 m. Scale bar = 250 µm. D, *Polyfibrospongia kulit*, Champagny Islands, Kimberley, WAM Z54013. Micrograph of a thick histological section (90 µm) showing a primary fibre (p) elevating the fine sand cortex (sc). The basal mesohyl (bm) shows the sponge overgrowing another sponge (os) as indicated by the underlying spicule mass. Collection depth = 0 m. Scale bar = 500 µm. E, *Polyfibrospongia kulit*, Champagny Islands, Kimberley, WAM Z54013. Micrograph of a thick histological section (90 µm) showing a primary fibre (p) at right angles to the surface, elevating the sand cortex (sc) that forms the microconulose surface. A layer of collagen (c), clear of sand, is found beneath the surface. Collection depth = 0 m. Scale bar = 250 µm. F, *Polyfibrospongia kulit*, Champagny Islands, Kimberley, WAM Z54038. Micrograph of a thick histological section (90 µm) showing a sand cortex (sc) and tertiary fibres (vt) forming a slender lattice-like reticulation beneath the sponge surface. Collection depth = 0 m. Scale bar = 500 µm. G, *Strepsichordaia lendenfeldi*, Beagle Reef, Kimberley, WAM Z54122. Micrograph of a thick histological section (90 µm) showing a sand cortex (sc), cored primary fibres (p), cored secondary fibres (s) and tertiary fibres (t). Collection depth = 16 m. Scale bar = 500 µm. H, *Strepsichordaia lendenfeldi*, paratype, Davies Reef, Great Barrier Reef, WAM Z5027. Described in Bergquist *et al.* (1988: 312–316, figs 30–32). Micrograph of a thick histological section (90 µm) showing a close-up view of a sand cortex (sc), cored primary fibres (p) and tertiary fibres (t).

the Kimberley region of Western Australia, eastern Indian Ocean.

Etymology: The epithet is taken from Malay, the senior author's mother tongue. *Kulit* translates as *skin* and is treated here as a noun in apposition. This species is named for its unique encrusting and skin-like growth form within the Phyllospongiinae.

Remarks

Polyfibrospongia kulit is characterized by a compressible and springy texture, which distinguishes it from *P. flabellifera*. The species has an encrusting habit, with a shiny, extremely fleshy surface, the irregular, undulating habit of the sponge may be related to substrate characteristics (Fig. 8D–F). It contains distinctive lattice-like tertiary fibres with narrow interconnections characteristic of the genus, but these are not as common as in *P. flabellifera and* can occasionally be seen beneath the surface. *Polyfibrospongia kulit* does not have the dense sand complement seen in *P. flabellifera*, the primary fibres are lightly cored and the surface has a much reduced sand-grain cortex, consisting of much finer grains. Overall, there is reduced foreign material in the matrix of this species compared to *P. flabellifera.* This species has currently only been reported from the Kimberley region, Western Australia.

Morphological and skeletal characters of *P. kulit* differ substantially from other species assigned to *Carteriospongia*. Eight other species are currently assigned to *Carteriospongia*, and these were assessed against the species examined in this study. As mentioned previously, the type material of *C. contorta* will need to be reviewed and compared with *P. flabellifera*, but from molecular data of non-type material it is a *Polyfibrospongia*. *Polyfibrospongia kulit* is distinguished from *P. contorta* by a fleshier lamella characterized by a reduced sand cortex, and this was further supported by the molecular phylogeny. *Carteriospongia delicata* Pulitzer-Finali, 1982 also appears to be a *Polyfibrospongia* as Pulitzer-Finali (1982) describes it, as having uncored secondary fibres that are tangled and sometimes fasciculate. These would be tertiary fibres misinterpreted as secondary fibres because the latter were probably rare. The distinctive honeycomb surface of this species separates it from *P. kulit*. The type of *C. delicata* (MSNG 46953) is formalin-fixed. The species was originally collected from Lizard Island, Great Barrier Reef, but was not found in this study, although collections were made from other parts of the reef complex. Fresh material from the type locality is essential for sequencing and subsequent generic placement of the species.

We have assigned the remaining currently recognized *Carteriospongia* species to a genus, but these require thorough re-examination (Table 2). However, these species were all morphologically distinct, and/ or geographically separated, from *P. kulit*. *Carteriospongia mystica* Hyatt, 1877 is irregularly cup-shaped with a hispid surface and is a temperate species from southern Australia. Unfortunately, no internal characters were provided in the original description. The external morphology and temperate location preclude *P. kulit* from being assigned to this species and without knowledge of the internal characters, it cannot be assigned to a genus. A similar circumstance exists for *C. perforata* Hyatt, 1877, which is also a temperate species that is flabellate with a ridged surface, and no description was provided of internal characters. *Carteriospongia silicata* (Lendenfeld, 1889) is a flat cup with a smooth outer surface and an inner membranous surface with radial grooves. It has primary fibres cored with spicule fragments, distinctive from the sand grains and other debris usually found in Phyllospongiinae. It has uncored secondary fibres and the description does not mention tertiary fibres. This makes it unlikely to be a *Polyfibrospongia* because the tertiary fibres are dominant and clearly visible in the lamella in this genus. A similar situation occurs for *C. vermicularis* (Lendenfeld, 1889), where tertiary elements are not included in the description. This species was recorded from the west coast of Australia but has a distinctive external morphology of numerous slender, digitate branches. *Carteriospongia fissurella* (de Laubenfels, 1948) was originally described by Lendenfeld (1889) as *Phyllospongia fissurata*; de Laubenfels renamed the species *P. fissurella* because *Spongia fissurata* Lamarck, 1814 was transferred to *Phyllospongia*. de Laubenfels (1948) did not redescribe the species but suggested it was a typical variety of *P. papyracea.* The original description by Lendenfeld (1889) is of a large, erect, cup-shaped sponge with primary and secondary fibres only. The sponge may well be a species of *Phyllospongia* as tertiary fibres were not seen in the lamella. Re-collection of specimens from the type locality would provide fresh material for sequencing to guide generic assignment. *Spongia fissurata* Lamarck, 1814 is considered a synonym of *Phyllospongia foliascens*.

A summary of proposed genus transfers is provided in Table 2, but because of the synonymy of *Carteriospongia* with *Phyllospongia*, all species previously assigned to *Carteriospongia* will need to be carefully re-examined with accompanying molecular analyses to determine if they are species of *Phyllospongia* or *Polyfibrospongia*.

Table 2. Summary of existing species names, corrected names, and the level of confidence of these corrections were made based on different lines of evidence used in this study for *Phyllospongia*, *Carteriospongia* and *Strepsichordaia*. Asterisks in front of species names indicate the type species for the genus

Existing name	Corrected name	Confidence
Phyllospongia Ehlers, 1870		
Phyllospongia alcicornis (Esper, 1794)	*Polyfibrospongia alcicornis* (Esper, 1794)	Not physically assessed in this study, based on previously described morphological descriptions
Phyllospongia cyathina (Lamarck, 1814)	*Phyllospongia cyathina* (Lamarck, 1814)	Not physically assessed in this study, based on previously described morphological descriptions
Phyllospongia ectoscula Lévi, 1961	*Phyllospongia ectoscula* Lévi, 1961	Not physically assessed in this study, based on previously described morphological descriptions
Phyllospongia lamellosa (Esper, 1794)	*Phyllospongia foliascens* (Pallas, 1766)	Based on morphological evidence of type specimen of *P. lamellosa* conforming to *P. foliascens*
	Phyllospongia bergquistae sp. nov. Abdul Wahab & Fromont	Based on specimens first assigned in Bergquist *et al.* 1988 as *P. lamellosa*, morphological and molecular evidence including type specimen (morphological and molecular)
Spongia laciniata Lamarck, 1814	*Phyllospongia papyracea* (Esper, 1806)	Was synonymized with *P. lamellosa*, here synonymized with *P. papyracea*, due to delicate morphology like *P. papyracea*
Spongia polyphylla Lamarck, 1814	*Phyllospongia foliascens* (Pallas, 1766)	Was synonymized with *P. lamellosa*, here synonymized with *P. foliasens*, due to ribbed surface morphology and fibre characteristic of *P. foliascens*
Polyfibrospongia sweeti Kirkpatrick 1900	*Spongia (Spongia) sweeti*	Was synonymized with *P. lamellosa*. Genus transfer to *Spongia (Spongia)* by Van Soest *et al.* (2011), no change
Phyllospongia macropora Lendenfeld, 1889	*Phyllospongia macropora* Lendenfeld, 1889	Not physically assessed in this study, based on previously described morphological descriptions
Phyllospongia palmata Thiele, 1899	*Phyllospongia palmata* Thiele, 1899	Not physically assessed in this study, based on previously described morphological descriptions
* *Phyllospongia papyracea* (Esper, 1806)	*Phyllospongia papyracea* (Esper, 1806)	Based on morphological and molecular evidence from this study, including from type specimens (morphological)
Phyllospongia schulzei Lendenfeld, 1889	*Phyllospongia schulzei* Lendenfeld, 1889	Not physically assessed in this study, based on previously described morphological descriptions
Phyllospongia supraoculata Ridley, 1884	*Phyllospongia supraoculata* Ridley, 1884	Not physically assessed in this study, based on previously described morphological descriptions
Carteriospongia Hyatt, 1877		
Carteriospongia contorta Bergquist, Ayling & Wilkinson, 1988	*Polyfibrospongia contorta* (Bergquist, Ayling & Wilkinson, 1988)	Based on morphological evidence of tertiary fibre characteristics in type specimens, including molecular evidence from a non-type specimen
Carteriospongia delicata Pulitzer-Finali, 1982	*Polyfibrospongia delicata* (Pulitzer-Finali, 1982)	Based on morphological evidence of tertiary fibre characteristics from original species descriptions

Table 2. Continued

Existing name	Corrected name	Confidence
Carteriospongia fissurella (Laubenfels, 1948)	*Phyllospongia fissurella* (Laubenfels, 1948)	Not physically assessed in this study. Original description of species did not mention prominent occurrence of tertiary fibres. Likely a *Phyllospongia*, however requires physical examination of type specimen or recollection from type locality to confirm.
Carteriospongia flabellifera (Bowerbank, 1877)	*Polyfibrospongia flabellifera* Bowerbank, 1877	Based on morphological evidence of tertiary fibre characteristics and molecular evidence, including from type specimen (morphological)
* *Carteriospongia foliascens* (Pallas, 1766)	*Phyllospongia foliascens* (Pallas, 1766)	Based on morphological and molecular evidence, including from type specimens (morphological and molecular)
Carteriospongia mystica Hyatt, 1877	*Phyllospongia mystica* (Hyatt, 1877)	Not physically assessed in this study. Internal characters were not provided in original descriptions. Assigned to *Phyllospongia*, following reassignment of the *Carteriospongia* type species, *P. foliascens,* until morphological and/ or molecular assessment of type specimen could indicate positioning in *Polyfibrospongia* or otherwise
Carteriospongia pennatula sensu Ridley, 1884	*Polyfibrospongia pennatula* (sensu Ridley, 1884)	Not physically assessed in this study, based on previously described morphological descriptions. Has a sand cortex and coring in the superficial primary fibres. Requires a new species name according to Van Soest *et al.* (2020)
Carteriospongia perforata Hyatt, 1877	*Phyllospongia perforata* (Hyatt, 1877)	Not physically assessed in this study. Internal characters were not provided in original descriptions. Assigned to *Phyllospongia*, following reassignment of the *Carteriospongia* type species, *P. foliascens*, until morphological and/ or molecular assessment of type specimen could indicate positioning in *Polyfibrospongia* or otherwise
Carteriospongia silicata (Lendenfeld, 1889)	*Phyllospongia silicata* Lendenfeld, 1889	Not physically assessed in this study. Original description of species did not mention prominent occurrence of tertiary fibres. Likely a *Phyllospongia*, however require physical examination of type specimen or recollection from type locality to confirm
Carteriospongia vermicularis (Lendenfeld, 1889)	*Phyllospongia vermicularis* Lendenfeld, 1889	Not physically assessed in this study. Original description of species did not mention prominent occurrence of tertiary fibres. Likely a *Phyllospongia*, however require physical examination of type specimen or recollection from type locality to confirm
Strepsichordaia Bergquist, Ayling & Wilkinson, 1988		
Strepsichordaia aliena (Wilson, 1925)	*Strepsichordaia aliena* (Wilson, 1925)	Not physically assessed in this study, based on previously described morphological descriptions
Strepsichordaia radiata (Hyatt, 1877)	*Strepsichordaia radiata* (Hyatt, 1877)	Not physically assessed in this study, based on previously described morphological descriptions
Strepsichordaia caliciformis (Carter, 1885)	*Strepsichordaia caliciformis* (Carter, 1885)	Not physically assessed in this study, based on previously described morphological descriptions

Table 2. Continued

Existing name	Corrected name	Confidence
* *Strepsichordaia lendenfeldi* Bergquist, Ayling & Wilkinson, 1988	*Strepsichordaia lendenfeldi* Bergquist, Ayling & Wilkinson, 1988	Based on morphological and molecular evidence (including type specimens)
Strepsichordaia stellifera (Bowerbank, 1877)	*Strepsichordaia stellifera* (Bowerbank, 1877)	Not physically assessed in this study, based on previously described morphological descriptions, but polyfibrous nature of fibres in the type description should be checked

GENUS *STREPSICHORDAIA* BERGQUIST *ET AL.*, 1988

Type species

Strepsichordaia lendenfeldi Bergquist *et al.*, 1988: figs 30, 31, 32, by original designation, holotype AM Z5026.

Diagnosis

Bergquist *et al.* (1988) described the species *Strepsichordaia lendenfeldi* as containing sponges that are cup- or fan-shaped, always macroscopically smooth, with a sand-reinforced surface marked by evenly dispersed, small, flush oscules, each surrounded by prominent, superficially extending exhalant canals. This produces a stellate pattern over the otherwise microconulose oscular surface. The poral surface is macroscopically smooth. A thick organized sand cortex is present on both surfaces. The skeleton is irregular with heavily cored primary fibres, simple not fasciculate but branching in irregular fashion. Secondary elements are not distinct from primary fibres in diameter or coring, only in disposition. Uncored, cylindrical tertiary elements dominate the skeleton; they arise from both primary and secondary cored fibres and form a dense mat throughout the sponge. These fibres meander for a considerable distance, without branching, have no fixed orientation with respect to the surface or attachment base, they do not form fascicles and only occasionally interconnect. The sponge texture is firm, flexible and not easily compressible.

Remarks

The primary and secondary fibres are difficult to tell apart and, as mentioned by Bergquist *et al.* (1988), they are differentiated by orientation. In some of the specimens in this study, the secondary fibres were thinner. The tertiary fibres were not seen to form a pronounced dense mat, rather they formed an open reticulation, but our sections were cut at 90 µm, which are thinner than the hand-cut sections of Bergquist *et al.* 1988. Perhaps the tertiary fibre density referred to by those authors is not visible in thinner sections. For this reason, the original diagnosis has not been amended.

STREPSICHORDAIA LENDENFELDI BERGQUIST *ET AL.*, 1988 (FIGS 9G, H, 10A–D, 11A–G)

Material examined

Fifteen specimens, including holotype, paratype, ethanol-preserved specimens, slides, DNA and photographs (see Supporting Information, Material S1

for the detailed metadata). Holotype AM Z5026, Davies Reef, Great Barrier Reef (18°49.024'S, 147°37.939'E), 15–20 m. Paratype AM Z5027, Davies Reef (18°49.024'S, 147°37.939'E), 15–20 m.

Species redescription

Morphology: Cup, fan or lamellate sponges, lamella may be multiple (WAM Z54135, WAM Z5447) and fans may be bilobed (WAM Z54121; Figs 10A–D, 11A). They are attached to the substrate by single or multiple stalks basally. Oscules are flush with the surface, membranous, small (~1 mm), and may have a distinctive stellate pattern, otherwise both surfaces are microconulose (Fig. 11E–G). Conule alignment tends to be longitudinal and, particularly near the attachment point, the surface may be ridged (WAM Z54131; Fig. 11D). Fan thickness is variable 2–5 mm, sponge size variable from small (breadth 60 mm, width 40 mm, height to 60 mm) to large (breadth 210 mm, width 150 mm, height 140 mm). There is a heavy surface armour, consistent on both sides of the sponge, but it may be lighter on one surface; 200–350 µm thick on oscular surface, 80–150 µm thick on poral surface. Texture firm, slightly compressible. Colour cream to light brown in ethanol.

Skeleton: Irregular skeletal reticulation, primary and secondary fibres indistinguishable, except in orientation to the surface and narrower width of the latter (Fig. 9G, H). Extended primary fibres form the microconulose surface. Primary fibres fully cored, they can be irregular in outline 130–200 µm wide; secondary fibres always cored 20–130 µm wide; and tertiary fibres uncored, pithed, 3–20 µm wide (Fig. 9G, H). Mesh sizes for primary to primary fibres are 120–550 µm wide, secondary to secondary 180 µm wide and tertiary to tertiary 15–150 µm wide. Tertiary fibres form wide, meandering meshes.

Distribution

This species is found in shallow tropical seas of eastern and western Australia.

Remarks

The main difference from Bergquist *et al.*'s (1988) description of *Strepsichordaia lendenfeldi* is that a microconulose surface frequently occurs and stellate patterning is only found in some specimens. Two of the Western Australian specimens had unusual morphology: WAM Z54122 has tapering finger-like extensions apically (Fig. 11B) and WAM Z54135 has unusual scalloped edges to the fans with a stellate canal system (Fig. 11C). The tertiary fibres are abundant but not as densely packed as in *Polyfibrospongia*; in this species they form a meandering reticulation, rather than a narrow lattice-like structure.

Strepsichordaia lendenfeldi has only been collected subtidally, unlike *Phyllospongia foliascens*, *P. papyracea* and *Polyfibrospongia flabellifera*, which also occur in intertidal habitats. Based on gross external morphology, this species can be distinguished from species of *Phyllospongia* and *Polyfibrospongia* by its thicker lamellae (up to 5 mm) and fine, microconulose surface that does not form the elongate rectangular ridges seen in *P. foliascens* (Figs 5, 6) or the fine reticulated surface seen in *P. flabellifera* (Fig. 8). A layer of pink coloration directly below the surface in freshly collected specimens is probably due to symbionts. Specimens of this species may contain barnacles.

Other species currently assigned to *Strepsichordaia* are *S. radiata* (Hyatt, 1877), *S. caliciformis* (Carter, 1885), *S. aliena* (Wilson, 1925) and *S. stellifera* (Bowerbank, 1877). None of these species were found during this study.

DISCUSSION

This study provided a reassessment and reassignment of genera and species of sponges in the subfamily Phyllospongiinae. Here the sample size was almost doubled (N = 207) compared to that utilized by Abdul Wahab *et al.* (2014d) (N = 112). The molecular results, based on three gene regions, including the highly variable ITS2, three of the 28S-D subregions and 18S, provided a robust phylogenetic hypothesis against which complementary morphological data were tested. The generic reassignment of *Carteriospongia foliascens* is confirmed, thus the genus *Carteriospongia* is synonymized with *Phyllospongia* and the genus *Polyfibrospongia* is resurrected. Two new species are described comprising *Phyllospongia bergquistae* and *Polyfibrospongia kulit*. *Strepsichordaia* remains unchanged, with the type species the only one examined in this study.

The generic reclassification of *P. foliascens* is important in ensuring accurate taxonomic reporting of future work utilizing this species. Notably, *P. foliascens* is distributed widely across the Indo-Pacific, from the West Pacific to the Red Sea, and is an important model species commonly used for assessing the effects of climate and anthropogenic stressors (Bennett *et al.*, 2017; Pineda *et al.*, 2017; Abdul Wahab *et al.*, 2019), patterns of microbial symbioses (Luter *et al.*, 2015), and population dynamics and connectivity (Abdul Wahab *et al.*, 2014c; Shaffer *et al.*, 2020). Through assessments of the original descriptions of species, it was also clear that *Carteriospongia* was paraphyletic with species

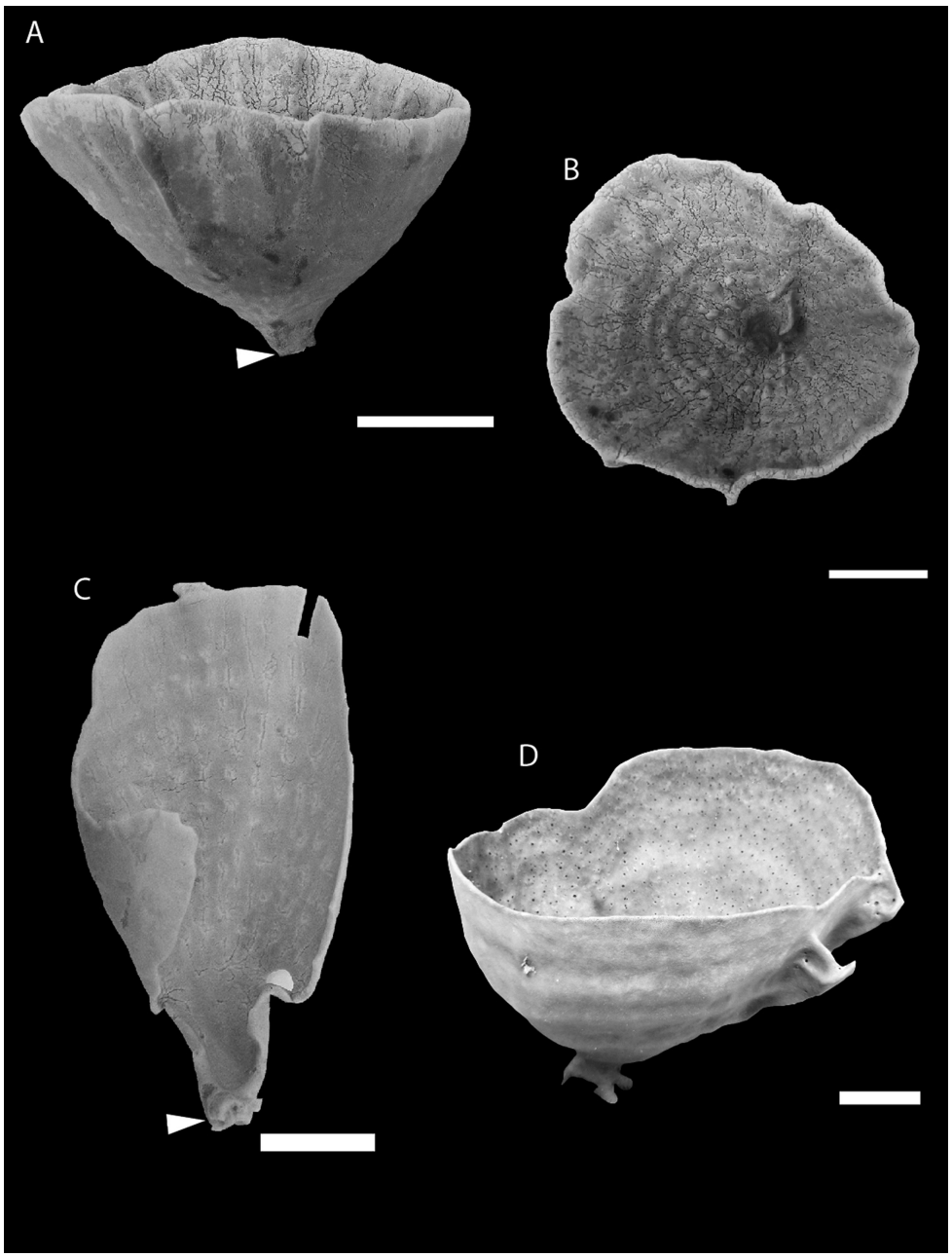

Figure 10. A, *Strepsichordaia lendenfeldi*, holotype, subtidal erect cup morph, Davies Reef, central Great Barrier Reef, AM Z5026. Original description in Bergquist *et al.* (1988: 312–316, fig. 30). Side view. Collection depth = 15–20 m. Ethanol-preserved specimen. White arrow indicates stalk. Scale bar = 5 cm. B, *Strepsichordaia lendenfeldi*, holotype, subtidal, erect, cup morph, Davies Reef, central Great Barrier Reef, AM Z5026. Original description in Bergquist *et al.* (1988: 312–316, fig. 30). Top view. Collection depth = 15–20 m. Ethanol-preserved specimen. Scale bar = 5 cm. C, *Strepsichordaia lendenfeldi*, paratype, subtidal erect lamellate morph, Davies Reef, central Great Barrier Reef, AM Z5027. Original description in Bergquist *et al.* (1988: 312–316, figs 31–32). Side view. Collection depth = 15–20 m. Ethanol-preserved specimen. White arrow indicates stalk. Scale bar = 5 cm. D, *Strepsichordaia lendenfeldi*, subtidal, erect, cup morph, Davies Reef, central Great Barrier Reef, CS_D_5. Collection depth = 12 m. Live sponge in situ. Scale bar = 5 cm.

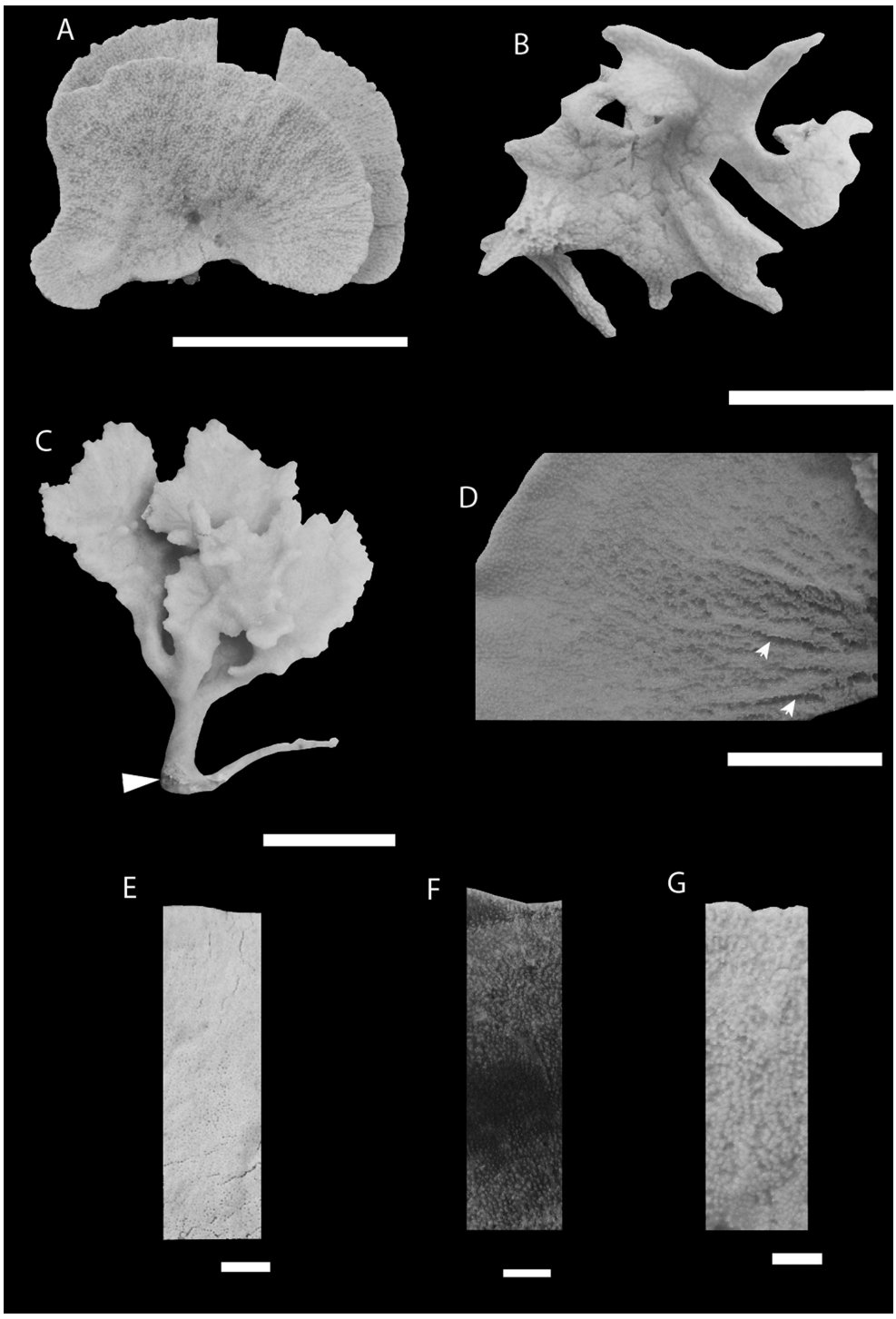

Figure 11. A, *Strepsichordaia lendenfeldi*, subtidal, erect, lamellate morph, Beagle Reef, Kimberley, WAM Z54121. Collection depth = 16 m. Ethanol-preserved specimen. Scale bar = 5 cm. B, *Strepsichordaia lendenfeldi*, subtidal, erect, finger-like apical extension morph, Beagle Reef, Kimberley, WAM Z54122. Collection depth = 16 m. Ethanol-preserved specimen. Scale bar = 2 cm. C, *Strepsichordaia lendenfeldi*, subtidal, erect with scallop-edged fan and stellate canal system, Beagle Reef, Kimberley, WAM Z54135. Collection depth = 16 m. Ethanol-preserved specimen. Scale bar = 2 cm. D, *Strepsichordaia lendenfeldi*, subtidal, erect, lamellate morph, Beagle Reef, Kimberley, WAM Z54131. Arrows show the ridges on the sponge surface. Collection depth = 16 m. Ethanol-preserved specimen. Scale bar = 2 cm. E, *Strepsichordaia*

conforming to either *Phyllospongia* (*P. foliascens*) or *Polyfibrospongia* (*P. flabellifera* and *P. contorta*). This study was unable to physically assess all ten species formerly classified as *Carteriospongia*. Nevertheless, we provided corrected names for all species in this genus (also for *Strepsichordaia* and *Phyllospongia*; Table 2) based on their descriptions, to ensure that species previously assigned to *Carteriospongia* were not left without a generic placement. Specifically, *Polyfibrospongia* species are defined by obvious lattice-like reticulations of tertiary fibres in the lamella that are never seen in *Phyllospongia*. For any ambiguous *Carteriospongia* species without detailed tertiary fibre descriptions, we have tentatively placed them in *Phyllospongia* following the genus transfer for the type *P. foliascens*. Therefore, it is important that any future work on these species test their generic placement using the morphological and molecular methodology described in this study.

It is challenging to define evolutionary relevant characters in keratose sponges, particularly as they lack mineral components, such as spicules. Nevertheless, a clear character that defines the Phyllospongiinae is the presence of tertiary fibres. Of note, tertiary fibres have been proposed to have undergone convergent evolution and have been observed in other related sponge lineages (Erpenbeck *et al.*, 2020). It will be of great interest to expand the study to assess the placement of other Thorectinae genera with tertiary fibres, such as *Luffariella* Thiele, 1899. Although tertiary fibre variations can be useful in delineating taxa at the generic level, taxonomic confusion could arise at the inter- and intraspecific levels. For example, there can be large variations in Phyllospongiinae external features in response to the environment, with the morphology of *Phyllospongia papyracea* ranging from the classical paper-thin lamella in subtidal habitats, to short, squat lobes in specimens from the intertidal. Prior to this study, which interrogated a large sample set of specimens from variable habitats and geographic regions and that utilized molecular-based evidence to formulate a phylogenetic hypothesis, intertidal *P. papyracea* could have been taxonomically misidentified, potentially as a new species, due to non-conformity to *P. papyracea* or to any other *Phyllospongia* species.

Erpenbeck *et al.* (2020) additionally noted that a problem exists for Keratosa in the lack of robust morphological apomorphies, and that characters currently used for defining Thorectidae species, such as the possession of surface armour and coring or non-coring of fibres, do not provide sufficient phylogenetic signal for the delineation of species. This study highlights the importance of assessing species across a broad suite of habitats (e.g. intertidal vs. subtidal, hydrodynamic regimes, etc.) and geographic locations to capture the range of morphological variability due to local environmental adaptations. In addition, it is essential to use a multifaceted approach (e.g. morphology coupled with molecular, chemistry, ecology, etc.) to delineate species for highly plastic taxa that lack informative evolutionary characters (e.g. spicules), such as is seen in Phyllospongiinae or, more broadly, Dictyoceratida.

In addition to providing clarity to the revised systematics for the Phyllospongiinae, the molecular analyses also identified some phylogeographic signal in the data, particularly for *P. foliascens*, *P. papyracea* and *P. flabellifera*, which showed some degree of separation between the West Pacific and East Indian Ocean. This observation was likewise reported by Abdul Wahab *et al.* (2014d) through ITS2 analysis. They suggested that glacial cycles affecting the intermittent opening and closing of the Torres Strait land bridge could be responsible for rounds of population fragmentation and speciation in the Phyllospongiinae (Mirams *et al.*, 2011). The use of two additional genes (28S-D and 18S) in this study, as expected, did not provide any further resolution to the pattern that was observed. It is intriguing that species having short planktonic duration and restricted population connectivity, such as *P. foliascens* (Abdul Wahab *et al.*, 2014b; Shaffer *et al.*, 2020), should have such a wide-ranging Indo-Pacific distribution from Fiji to the Red Sea. Likewise, other biological and community characteristics of Phyllospongiinae species, such as high density and abundance in some habitats, and high fecundity and high likelihood for endogenous recruitment, seem to suggest that interspecific processes, such as hybridization, could occur, as found in other co-occurring organisms, such as corals (Richards & Hobbs, 2015). As such, future work employing the use of more powerful and relevant molecular techniques (e.g. SNPs) may provide further insights into population processes, such as the potential for hybridization (e.g. *P. bergquistae*) in Phyllospongiinae.

lendenfeldi, paratype, close up showing microconulose surface, Davies Reef, central Great Barrier Reef, AM Z5027. Original description in Bergquist *et al.* (1988: 312–316, figs 31–32). Collection depth = 15–20 m. Ethanol-preserved specimen. White arrow indicates stalk. Scale bar = 5 mm. F, *Strepsichordaia lendenfeldi*, close up showing microconulose surface, Green Island, northern Great Barrier Reef, CS_GI_9. Collection depth = 10 m. Live sponge on deck of boat. Scale bar = 5 cm. G, *Strepsichordaia lendenfeldi*, close up showing microconulose surface, Beagle Reef, Kimberley, WAM Z54121. Collection depth = 16 m. Ethanol-preserved specimen. Scale bar = 5 cm.

CONCLUSION

This study provides a revised systematics for a common and abundant group of tropical Indo-Pacific sponges in the subfamily Phyllospongiinae. The work results in a significant reassignment of species, the genus *Carteriospongia* is synonymized with *Phyllospongia* and *Polyfibrospongia* is resurrected. *Strepsichordaia* remains unchanged. In addition, two new species are described: *Phyllospongia bergquistae* and *Polyfibrospongia kulit*. The resolution of the three genera in Phyllospongiinae presented here must be considered a first step in a framework on which to reassess species in this subfamily that occur around the globe, and future work should similarly use both molecular and morphological information, including type specimens or topotype material, where possible. To aid morphological identification of genera and species, keys to both have been developed and these may be refined as more species are examined.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Supplementary Material 1. Metadata of all specimens assessed in the study including those used in the ITS2 and ITS2+18S+28S concatenated molecular phylogenetic analyses, and physical and image-based morphological assessments. The original specimen id, confirmed id from this study, specimen registration number, specimen location, collector, taxonomic details, and collection location and depth are provided. Cells marked with "X" indicate where samples and data were available for each of the specimen. Published Genbank accession numbers for ITS2, 28S and 18S sequences used in the study are provided under the "DNA" columns. Both ingroup and outgroup information are included. For individual images of these specimen, please refer to Supplementary Material 3: Photo catalogue.

Material S2. Data partitions and substitution models used in concatenated phylogenetic analyses.

Material S3. Photo catalogue of specimens that were assessed from the subfamily Phyllospongiinae.

Material S4. ITS2 phylogenetic reconstruction of specimens identified in the study as *Strepsichordaia lendenfeldi*, *Polybrospongia kulit*, *P. flabellifera*, *Phyllospongia papyracea*, *P. bergquistae* and *P. foliascens*. Maximum likelihood bootstrap values are shown. Vertical coloured bars represent the supported species clades.