



Research article

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A new deep-water *Tethya* (Porifera, Tethyida, Tethyidae) from the Great Australian Bight and an updated Tethyida phylogeny

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Abstract. A new species of *Tethya* Lamarck, 1815 is described from a depth of 1000 m on the continental slope of the Great Australian Bight (GAB), southern Australia. The GAB slope was explored as part of systematic benthic surveys to understand unexplored communities in the light of current oil and gas exploration activity in the area. *Tethya irisae* sp. nov. was present at 1000 m in six of eight longitudinal depth surveys. Three molecular markers were obtained: COI, 28S (D3–D5) and ITS1–5.8S–ITS2. COI and 28S phylogenetic analyses show that the new species fits clearly within the genus *Tethya*. This is the 28th species of *Tethya* reported from Australia; it is unusual in that it has a stalk. The presence of a stalk as a morphological character to split genera in this family is questioned. The description of this new species is an opportunity to revisit the molecular phylogeny of the Tethyida Morrow & Cárdenas, 2015 using comprehensive datasets of COI and 28S markers. As in previous analyses, four *Tethya* clades were retrieved; we discuss the possibility of using external colour to support some of these clades. Despite unclear phylogenetic relationships amongst Tethyidae Gray, 1848 from Australia, our results suggest that tethyid genera *Tethytimea* Laubenfels, 1936, *Tectitethya* Sarà, 1994, *Laxotethya* Sarà & Sarà, 2002, *Stellitethya* Sarà, 1994, and *Xenospongia* Gray, 1858 derive from species of *Tethya*. We show that asters

have been secondarily lost at least twice in the Hemiasterellidae Lendenfeld, 1889: in *Liosina* Thiele, 1899 and a potential new genus from northern Australia. We formally propose the reallocation of *Liosina* from Dictyonellidae van Soest, Diaz & Pomponi, 1990 to Hemiasterellidae Lendenfeld, 1889.

Keywords. Porifera, Dictyonellidae, Hemiasterellidae, *Liosina*, marine benthos.

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Introduction

The family Tethyidae Gray, 1848, reclassified from the order Hadromerida Topsent, 1894 (order abandoned) to order Tethyida Morrow & Cárdenas, 2015, contains 14 genera of which the genus *Tethya* Lamarck, 1815 is by far the most speciose with 93 accepted species (Van Soest *et al.* 2019). Tethyidae are defined by ‘stylote megascleres mainly stronglyoxeas, generally in radiate tracts and two categories of euasterose microcleres, micrasters and megasters, sometimes rhadbs’ (Sarà 2002). Occurrence and length of a stalk are included as key morphological characteristics in distinguishing some genera of Tethyidae (Sarà 1994, 2002; Sarà & Burlando 1994); although the development of the stalk in the family has been noted as being an adaptation to deep-water, soft sediment habitat (Sarà & Burlando 1994). The taxonomy of the Tethyidae was rearranged by Sarà (1994) into eight genera, with the new genera *Burtonitethya* Sarà, 1994 and *Tethycometes* Sarà, 1994 joining *Halicometes* Topsent, 1898, as stalked genera in the family. Cladistic analysis by Sarà & Burlando (1994) placed Tethyidae into three clades (a) the genus *Tethya*, (b) genera with stalks and (c) massive and encrusting genera.

The Australian Faunal Directory (AFD) (Hooper 2012) lists six genera of Tethyidae in Australia (*Anthotethya* Sarà & Sarà, 2002; *Laxotethya* Sarà & Sarà, 2002; *Oxytethya* Sarà & Sarà, 2002; *Stellitethya* Sarà, 1994; *Tethya* Lamarck, 1815; *Xenospongia* Gray, 1858). A seventh genus *Tethyastra* Sarà, 2002 (*Tethyastra oxyaster* (Burton, 1934), ‘accepted’ (van Soest *et al.* 2019)) is listed in the Codes for Australian Aquatic Biota (Rees *et al.* 1999 onwards); in the AFD this is listed as *Tethya oxyaster*.

The slope of the Great Australian Bight (GAB) was explored in 2010 as part of a preliminary exploration of deep-water communities (Currie & Sorokin 2011) and again in 2015 as part of systematic benthic surveys to understand unexplored communities in the light of current oil and gas exploration activity in the area (MNF 2015; Williams *et al.* 2018). The surveys resulted in the discovery of several new benthic species including sponges. Multiple specimens of a small stalked tethyid were found at 1000 m; here, we describe this new species, using morphological characters and molecular markers (COI, 28S (D3–D5) and ITS1-5.8S-ITS2) to consider how it fits into the family.

The description of this new species is an opportunity to revisit the molecular phylogeny of this group. Heim *et al.* (2007) and Heim & Nickel (2010) produced the first phylogenetic analyses of *Tethya*, combining COI and morphology. Since then, although large Demospongiae trees were produced that led to the creation of the order Tethyida by Morrow & Cárdenas (2015), no phylogenetic studies truly focused on the *Tethya*, Tethyidae or Tethyida. We therefore felt it was time to present an updated molecular phylogeny for COI and ran the first comprehensive 28S phylogenetic analyses focusing on the Tethyida.

Material and methods

Field collection

Tethya irisae sp. nov. was first collected, as only one specimen, in the GAB in 2010 (Currie & Sorokin 2011). More specimens were collected in November and December 2015 as part of systematic epibenthic

surveys of the central GAB slope. Stations were sampled by beam trawl along five longitudinal transects and over depths ranges from 200 m to 5000 m (Fig. 1). Benthic specimens were collected under Australian Commonwealth Area Permit No. AUCOM2015-284 and Commonwealth Marine Reserve Permit No. CMR-15-000344. *Tethya irisae* sp. nov. was found at six out of eight of the 1000 m depth stations. Specimens were photographed on board and fixed in 70% ethanol. Specimens for molecular analysis were fixed in ethanol (> 95%). Most specimens (including the holotype) are lodged at the South Australian Museum (accession prefix SAMA), Adelaide, South Australia; two specimens were deposited at the Queensland Museum (accession prefix QM), Brisbane, Australia; four specimens from lot SAMA S2039 and a thick section are deposited at the Museum of Evolution, Uppsala, Sweden (UPSZTY 178608). Collection information of specimens examined in this study is archived in the open access PANGAEA data repository (<https://doi.pangaea.de/10.1594/PANGAEA.894720>).

Light microscope preparation

To examine the skeleton, thick sections in resin were prepared from a specimen from collection lot SAMA S2039, following the method described by Boury-Esnault *et al.* (2002). Thin sections were also

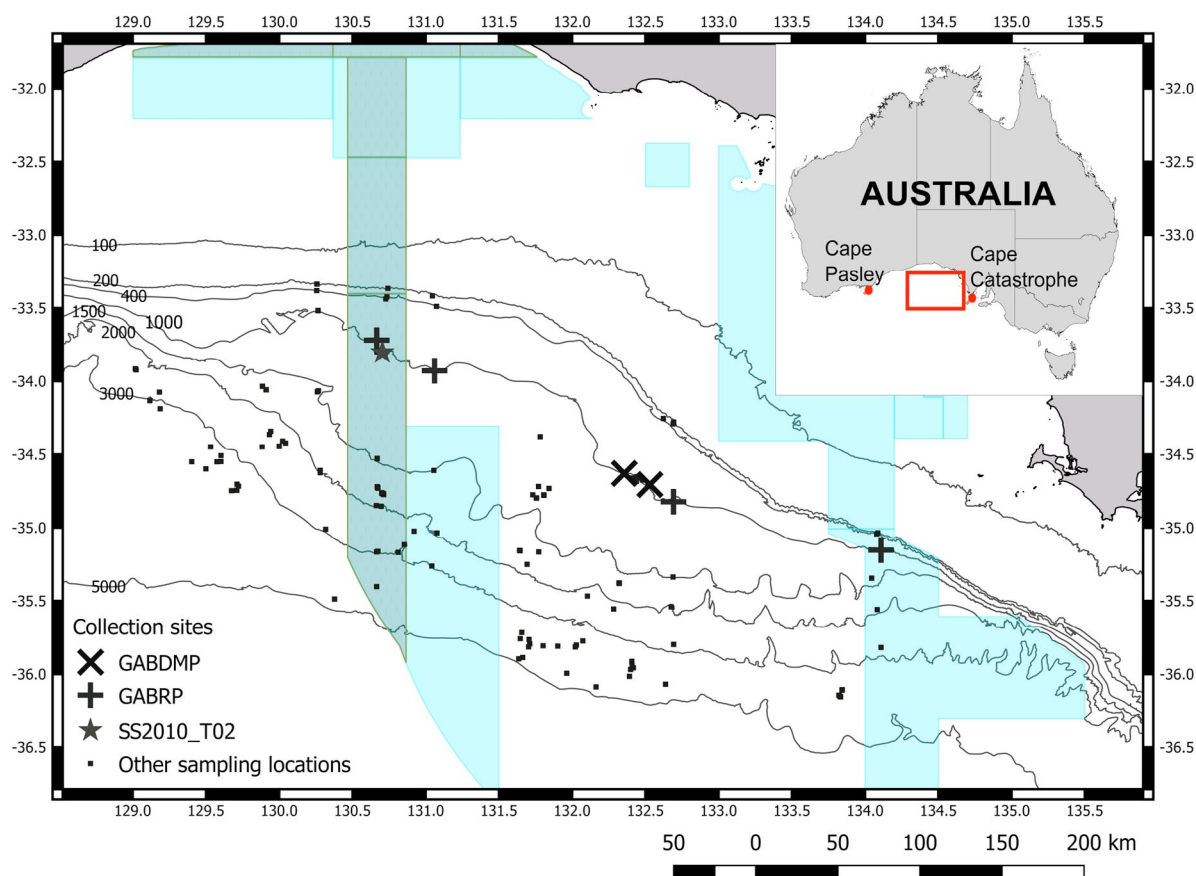


Fig. 1. Sites where *Tethya irisae* sp. nov. was collected in the Great Australian Bight, including sites that were sampled where the sponge was not found. All specimens of *Tethya irisae* sp. nov. were collected along the 1000 m contour. Light shaded polygons show the Australian Commonwealth Marine Reserves. The darker polygon strip is the GAB Marine Park Benthic Protection Zone. The 200 m contour is the edge of the continental shelf. Abbreviations: GABDMP = Great Australian Bight Deepwater Marine Program (MNF 2015); GABRP = Great Australian Bight Research Project (Williams *et al.* 2018). Cruise SS2010_T02 (Currie & Sorokin 2011).

made, with the following protocol: sections were cut perpendicular to the surface with a sharp blade and laid onto a slide, covered with a weighted coverslip and dried on a hot plate. Sections were covered with mounting media (Durcupan™) and dried overnight in an oven at 50°C. Spicule slides were prepared by dissolving a small amount (~ 2 mm²) of sponge tissue in 3.9% sodium hypochlorite. The resultant spicules were rinsed with distilled water three times and with 95% ethanol twice before mounting on a microscope slide with DPX™ mountant.

SEM preparation

Scanning Electron Microscope (SEM) tissue preparations were made by dissolving the tissue in 12.5% sodium hypochlorite to remove the soft tissue. They were then rinsed twice in distilled water, rinsed twice in 70% ethanol and then finally twice in 98% ethanol and then air dried. SEM preparations were sputter coated in gold to improve resolution. The scanning electron micrograph photos were taken using a Hitachi TM-1000 SEM and plates assembled in Adobe Photoshop. Morphometric measurements of the spicules were done using the same Hitachi TM-1000 SEM.

Spicule terminology

Spicule terminology follows that suggested by Bergquist & Kelly-Borges (1991) for the genus *Tethya*.

Molecular studies

Whole genomic DNA was extracted from sponge tissue frozen at -80°C. A conventional hexadecyltrimethylammonium bromide (CTAB)-based protocol (Taylor *et al.* 2004) was used for isolating DNA. Briefly, the sponge tissues were ground under liquid nitrogen. The CTAB extraction buffer was applied to lyse tissues and then combined with polyvinylpyrrolidone (PVP) and β-mercaptoethanol to help remove phenolic compounds and tannins in the extract. To separate the proteins and polysaccharides from nucleic acids, phenol: chloroform: isoamyl alcohol (25:24:1) was utilised before DNA was precipitated with chilled isopropanol. The mitochondrial cytochrome c oxidase subunit 1 (COI) Folmer fragment was amplified using the universal primers LCO1490 and HCO2198 (Folmer *et al.* 1994). The D3–D5 region of 28S rRNA gene was amplified by primers NL4F and NL4R (Nichols 2005). To amplify ITS, we used primers originally designed for a unicellular eukaryote, ITSRA2 (5'-GTC CCT GCC CTT TGT ACA CA-3') and ITS2.2 (5'-CCT GGT TAG TTT CTT TTC CTC CGC-3') (Adlard & Lester 1995), to amplify a 753 bp long sequence including ITS1-5.8S-ITS2 and small fragments of the surrounding 28S and 18S. The thermocycler was programmed following Yang *et al.* (2017). Sequences were assembled and blasted using Geneious® ver. 8.1 (created by Biomatters, <http://www.geneious.com>).

All Tethyidae COI and 28S sequences from GenBank were collected and aligned with our new sequences in AliView 1.18 (Larsson 2014). No ITS alignment was made since only one other Tethyidae ITS was found on GenBank. The full COI and 28S from *Tethya wilhelma* Sarà, Sarà, Nickel & Brümmer, 2001 were assembled from the whole genome, https://bitbucket.org/molpalmuc/tethya_wilhelma-genome/src (courtesy of W.R. Francis). We included Timeidae Topsent, 1928 and Hemiasterellidae Lendenfeld, 1889 (*Adreus* Gray, 1867 and *Axos* Gray, 1867, *Hemiasterella* Carter, 1879, and *Liosina* Thiele, 1899) sequences that seemed to group close to the Tethyidae in our preliminary analyses and previous studies (Erpenbeck *et al.* 2012; Morrow *et al.* 2012; Redmond *et al.* 2013; Thacker *et al.* 2013). *Raspailia australiensis* Ridley, 1884 and *Ceratopsion axiferum* (Hentschel, 1912) 28S sequences were included as possible species of *Adreus*, as suggested by Morrow *et al.* (2019). We discarded the 28S sequence of *Timea lowchoyi* Hooper, 1986 (AY561871) and *Hemiasterella* sp. WAMZ12383 (AY561947), both from Nichols (2005) that seemed to be mis-identifications: BLAST results indicated, respectively, that they were close to *Cymbaxinella* Gazave, Carteron, Chenuil, Richelle-Maurer, Boury-Esnault & Borchiellini, 2010, and a 93% match with *Hymeniacidon heliophila* (Wilson, 1911). *Hemiasterella* sp. 1 (AY561901, QMG315767, OTU QM2839)

from Nichols (2005) was re-identified as *Adreus* sp. on SpongeMaps (<http://www.spongemaps.org>). *Hemiasterella* sp. (AY626310, QM G304645, OTU QM0694) from Kober & Nichols (2007) was re-identified as a tethyid by Morrow *et al.* (2012). *Hemiasterella* sp. UCMPWC1021 (AY56197) from Nichols (2005) was re-examined and re-identified as a *Jaspis* sp. (P. Cárdenas, unpublished data), we included this sequence in our outgroup. Finally, no trustworthy sequences of *Hemiasterella* were left to include in the alignment. We also included 28S (C1–D2) sequences from C. Chombard’s PhD Thesis (Chombard 1998), never published or submitted to GenBank. These were copied ‘by hand’ from the ‘Annexe B2’ from her thesis, and included the following species: *Tethya* sp., *Tethya taboga* (Laubenfels, 1936), *Tectitethya crypta* (Laubenfels, 1949), *Tethya aurantium* (Pallas, 1766) and *Timea* sp. The three first samples were collected by N. Boury-Esnault in Panama in July 1995. Preliminary 28S analyses showed that the Chombard sequence of *T. aurantium* (from Chausey Islands, Normandy, France) had 1 bp difference to *T. citrina* Sarà & Melone, 1965 (HQ379237) from Wales, so we considered that the Chombard specimen had been mis-identified (both species can be difficult to discriminate but are clearly different genetically) and we thus renamed it *T. cf. citrina*. We discarded the 28S (D1–D2) sequence of *T. aurantium* (AY552024) from Borchiellini (2004) because it was 100% identical to that of *T. taboga* 28S (C1–D2) from Chombard (1998) and we suspected a mix-up in the sequence submitted. COI alignments were trimmed to contain only the Folmer fragment (658 bp). The 28S alignment included essentially sequences from the C1–D2, D3–D5 and/or D6–D8 regions or from the full 28S (3376 bp). When we had different 28S regions for the same species, we merged those sequences into a single one using the ‘merge’ option in AliView; we did this for *Timea cf. centrifera*, *Tethya citrina*, *Tethya hibernica* Heim, Nickel, Picton & Brümmer, 2007, *Laxotethya dampierensis* Sarà & Sarà, 2002, *Adreus micraster* (Burton, 1956), *Adreus fascicularis* (Bowerbank, 1866) and *Adreus* sp. Alignment was done using MAFFT (Katoh *et al.* 2002) implemented in AliView, then refined by eye; ambiguous regions were kept. We included in both our datasets sequences of Placospongiidae that are phylogenetically close to the Tethyida, maybe even their sister-group (Morrow *et al.* 2013; Thacker *et al.* 2013). The final COI alignment contained 39 sequences, including five outgroup sequences from *Paratimea* Hallmann, 1917 (Stelligeridae Lendenfeld, 1898), *Jaspis* Gray, 1867 (Ancorinidae Schmidt, 1870) *Cliona* Grant, 1826 (Clionaidae d’Orbigny, 1851) and *Placospongia* Gray, 1867 (Placospongiidae Gray, 1867). The 28S alignment contained 45 sequences, including three outgroup sequences from *Placospongia* and *Trachycladus* (Trachycladidae Hallmann, 1917).

Analyses were conducted with the CIPRES science gateway (<http://www.phylo.org>) (Miller *et al.* 2010): RAXML 8.2.10 (Stamatakis 2014) for maximum likelihood (ML) and MrBayes v. 3.2.6 (Ronquist *et al.* 2012) for Bayesian analyses. For RAXML, 1000 bootstrap iterations were run; bootstrap Bayesian analyses consisted of two runs of four chains, each for 5 000 000 generations and sampled every 1000th tree after a 25% burn-in.

Abbreviations

| | | |
|-------|---|------------|
| bp | = | base pairs |
| diam. | = | diameter |
| h | = | height |
| l | = | length |
| w | = | width |

Collection acronyms

| | | |
|------|---|---|
| ABTC | = | Australian Biological Tissue Collection, South Australian Museum, Adelaide, Australia |
| AM | = | Australian Museum, Sydney, Australia |
| BMNH | = | The Natural History Museum (formerly British Museum of Natural History), London, UK |
| QM | = | Queensland Museum, Brisbane, Australia |

SAMA = South Australian Museum, Adelaide, Australia
UPSZTY = Museum of Evolution, Uppsala, Sweden

Results

Systematics

Class Demospongiae Sollas, 1885
Order Tethyida Morrow & Cárdenas, 2015
Family Tethyidae Gray, 1848
Genus *Tethya* Lamarck, 1815

Tethya irisae sp. nov.

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figs 1–3, 4A

Etymology

Named after the golden-winged Greek goddess Iris, grandchild of Tethys, who could reach all parts of the cosmos including the deep sea; and in memory of marine naturalist Iris Sorokin.

Material examined

Holotype

AUSTRALIA • Size 16.6 mm total height (body 11.9 mm (h) × 11.7 mm (w), stalk 4.7 mm (l) × 1.77 mm diam., raised apical osculum); Great Australian Bight (GAB); 34.822° S, 132.69° E; 1006 m depth; Great Australian Bight Research Project (GABRP) leg.; epibenthic sled; SAMA S3387.

Paratypes

AUSTRALIA • 4 specs; same collection data as for holotype; SAMA S2913, SAMA S3388, QM G305000, QM G305001 • 1 spec.; Great Australian Bight; 33.928° S, 131.06° E; 1027 m depth; GABRP leg.; epibenthic sled; UPSZTY 178608.

Additional material at South Australian Museum (sighted only)

AUSTRALIA • 1 spec.; Great Australian Bight; 33.928° S, 131.06° E; 1027 m depth; GABRP leg.; epibenthic sled; SAMA S2039 • 1 spec.; Great Australian Bight; 35.152° S, 134.109° E; 1021 m depth; GABRP leg.; epibenthic sled; SAMA S2371 • 1 spec.; Great Australian Bight; 33.718° S, 130.66° E; 1005 m depth; GABRP leg.; epibenthic sled; SAMA S2482 • 1 spec.; Great Australian Bight; 34.629° S, 132.35° E; 1021 m depth; Great Australian Bight Deepwater Marine Program (GABDMP) leg.; epibenthic sled; SAMA S2095 • 1 spec.; Great Australian Bight; 34.705° S, 132.53° E; 987 m depth; GABDMP leg.; epibenthic sled; SAMA S2096 • 1 spec.; Great Australian Bight; 33.802° S, 130.70° E; 1000 m depth; D. Currie leg.; epibenthic sled; SAMA S1461.

Comparative material

INDIA • 1 section in slide, holotype of *Burtonitethya gemmiformis* Sarà, 1994; Andaman Islands; depth unknown; BMNH 1957.7.15.1.

AUSTRALIA – New South Wales • 1 spec., syntype and slides of *Tethya fissurata* Lendenfeld, 1888; Port Jackson; “33°51’ S, 151°16’ E [33.85° S, 151.27° E]; depth unknown; AM G.9069 (syntype), Z6053, Z6893 (slides).

NEW ZEALAND • 1 spec., holotype (specimen and slides) of *Tethya bullae* Bergquist & Kelly-Borges, 1991; Alderman Island; “36°58’ S, 176°05’ E [36.97° S, 176.08° E]; 100 m depth; AM Z5074.

DNA barcoding

COI (MH518072), 28S (D3–D5) (MH511148), ITS1-5.8S-ITS2 (MH511149). All sequences came from the same individual from lot SAMA S2913, although this is a different individual than the type specimens. A tissue sample from this voucher is deposited at the Australian Biological Tissue Collection at the South Australian Museum, Adelaide (ABTC145318).

Description

A small, spherical to oval, stalked, sponge (Fig. 2). The sponge body is 11–14 mm diam., with the stalk approximately the same length as the diameter of the sponge. The surface is covered in polygonal plate-like tubercles (2–3 mm diam.) separated by grooves (0.5 mm wide, 0.25–0.5 mm deep). The sponge is firm to hard and spiculate. Grey/white in life and in ethanol. There is a single raised apical osculum. No sign of any budding.

SKELETON. A stalk of dense megascleres supports the sponge. There is a ‘nucleus’ where the stalk meets the centre of the sponge body, and although the stalk may divide and/or flatten and thicken externally it emanates from the same point at the base of the sponge. From the nucleus dense bundles (0.3–0.7 mm in

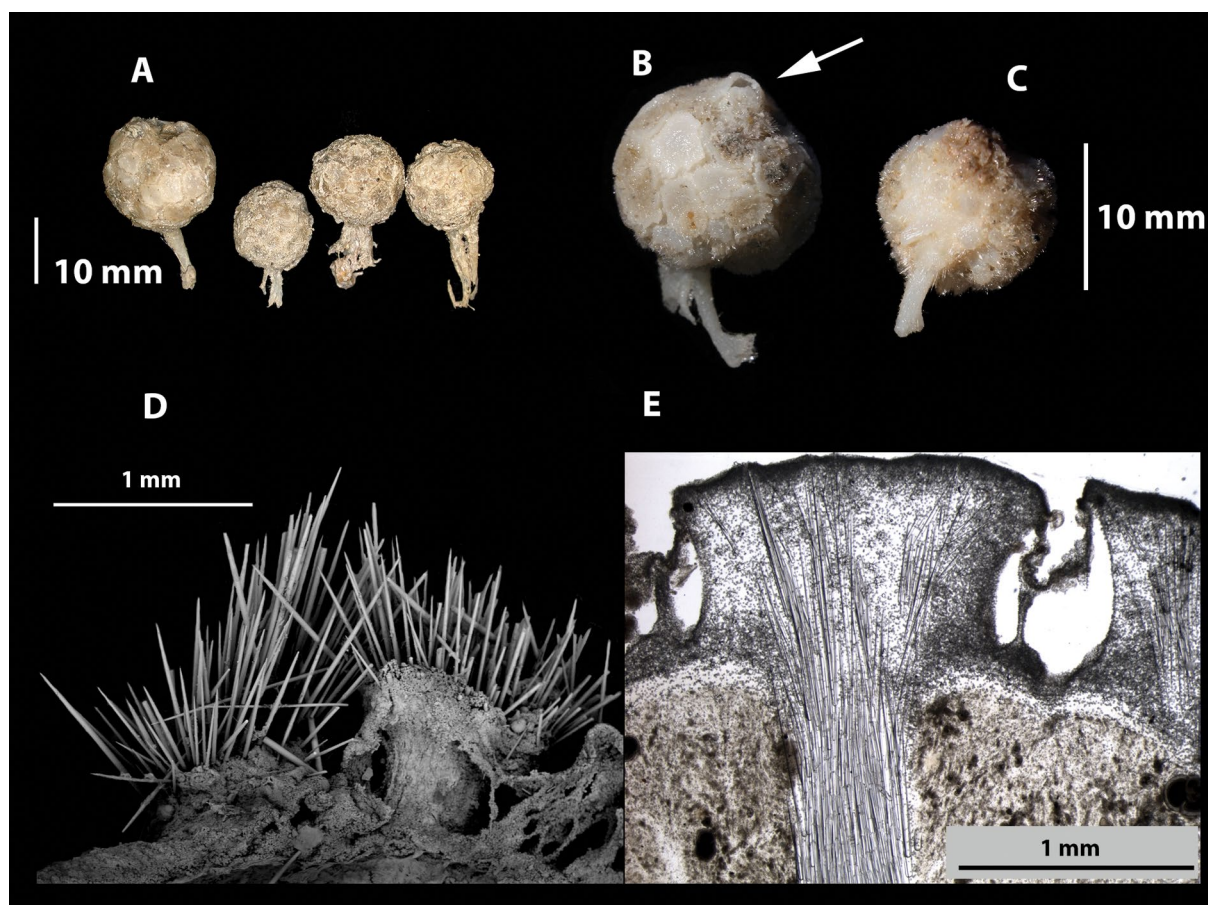


Fig. 2. A. Freshly collected specimens (lot SAMA S2096) of *Tethya irisae* sp. nov. B. Paratype (QM G305000) showing single apical oscule (arrow), and tessellated plate-like polygonal tubercles. C–D. Holotype (SAMA S3387), entire specimen and SEM showing surface tubercles with emerging megascleres. E. Section of UPSZTY 178608, showing the well-developed cortex and cortical canals around the tubercles.

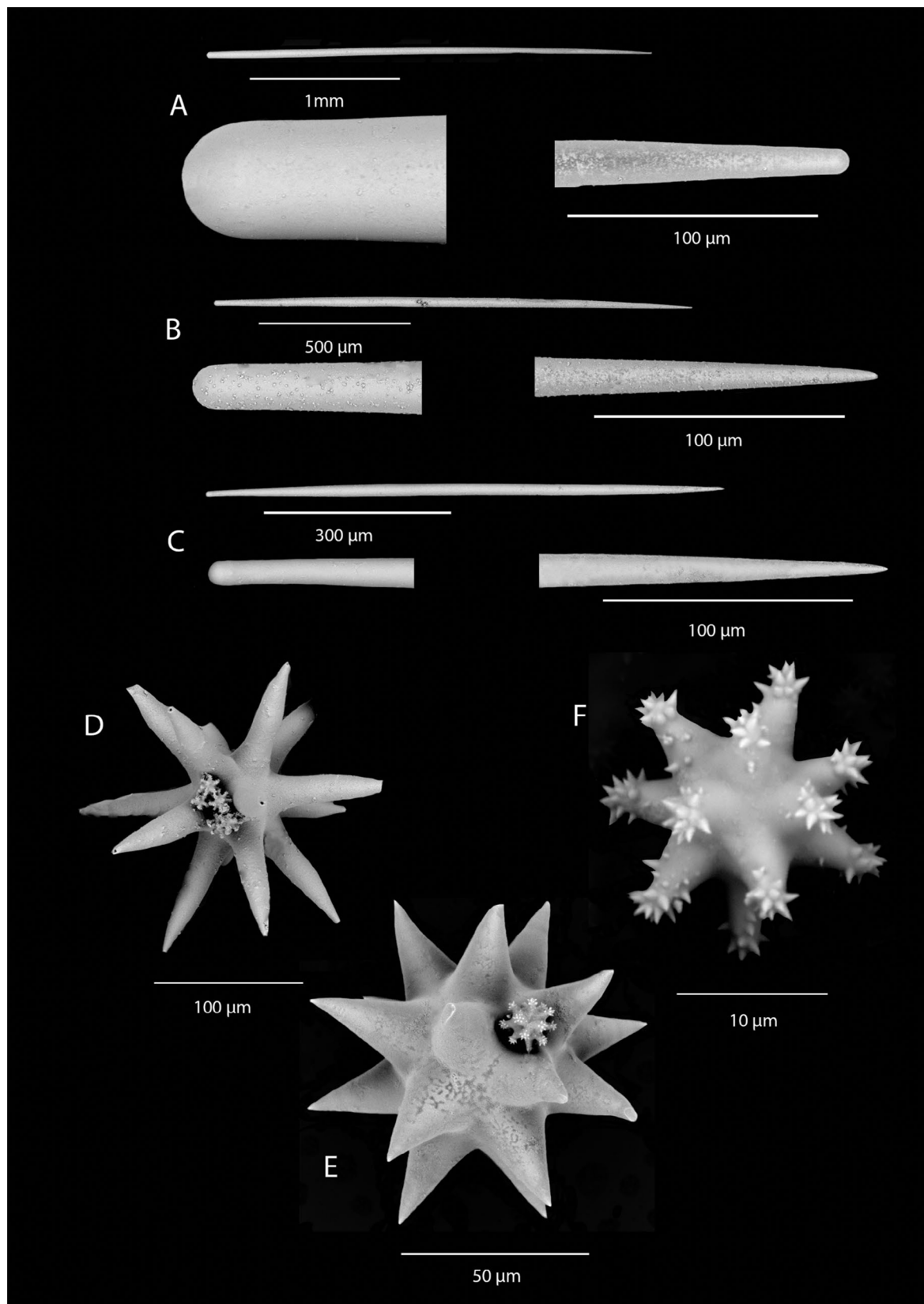


Fig. 3. *Tethya irisae* sp. nov. spicules. **A–B.** Straight style/strongyloxeas. **C.** Subtylostyle. **D.** Long-rayed oxyspheraster. **E.** Short-rayed oxyspheraster with small acanthooxyspheraster. **F.** Acanthooxyspheraster.

diameter) of megascleres radiate through the choanosome to the surface tubercles; the bundles slightly fan out in the tubercles. The cortex is a dense layer of micrasters and oxyspherasters interspersed with megascleres emerging through the tubercles, making the surface microscopically hispid (Fig. 2D–E). The cortex is well developed and follows the contours of the tubercles, 1–1.7 mm thick. Large cortical canals are visible between tubercles (Fig. 2E). A thin fibrous layer is below the cortex, it has micrasters in a much lower density. Large oxyspherasters are especially found at the base of the cortex. The megascleres of the stalk are covered in a layer of micrasters and regularly interspersed with short-rayed oxyspherasters. The choanosome is rich in sediment-like particles; there are some micrasters and rare oxyspherasters. Foraminifera (*Globigerina* d'Orbigny, 1826) and Radiolaria are common in the cortical canals and the choanosome.

SPICULES. Megascleres are straight style/strongyloxeas (size range $900\text{--}3060 \times 17\text{--}52 \mu\text{m}$) (Table 1, Fig. 3A–B) the proximal end is smooth and rounded, the distal end is tapered (not stepped) and either rounded or pointed. There are auxiliary thinner styles to subtylostyles in the medulla between the main styles ($260\text{--}900 \times 7\text{--}22 \mu\text{m}$) (Fig. 3C). Megaster microscleres are two types of oxyspherasters: long-rayed oxyspherasters ($120\text{--}185 \mu\text{m}$) (Fig. 3D) have ~15 rays that can be bent towards the oxete tips (ray profile is conical); short-rayed oxyspherasters ($53\text{--}154 \mu\text{m}$) (Fig. 3E) have a larger centrum ~17 rays with a conical profile and oxete tips. Micraster microscleres are acanthooxyspherasters ($12\text{--}20 \mu\text{m}$) (Fig. 3F), with a centrum and spined tips, and lightly spined on the rays.

Ecology and distribution

Found on the continental slope in the Great Australian Bight at a depth of 1000 m, in soft sediment (clay/silt).

Remarks

The morphology as well as molecular markers confirm that our new sponge is a *Tethya*. Table 2 shows morphological comparisons between other species of *Tethya* from Australia and New Zealand. The external appearance of *Tethya irisae* sp. nov. is similar to *T. fissurata* from Port Jackson, New South Wales, Australia, which is spherical with polygonal tubercles and has a stalk. However, *T. fissurata* differs from *T. irisae* sp. nov. in body size (~4 cm diam.), tubercle shape, and number of oscula (2–4). *Tethya fissurata* has megascleres with stepped ends unlike *T. irisae* sp. nov., which are smooth and *T. fissurata* lacks the short-rayed oxyspherasters seen in *T. irisae* sp. nov. Although we do not know the exact depth at which *T. fissurata* was collected, Port Jackson (viz. Sydney Harbour) is not deeper than 45 m (Johnston *et al.* 2015), so this is presumably a shallow species. *Tethya bullae* is a deep-water (100 m) sponge that is of comparable size to *T. irisae* sp. nov., although it has prominent raised tubercles rather than the flat plate-like tubercles of *T. irisae* sp. nov. (Fig. 4). The holotype from the Australian Museum does not include a stalk but the description and photograph in Bergquist & Kelly-Borges (1991) shows “basal flattened branched rooting processes”. The long-rayed oxyspherasters of *T. irisae* sp. nov. are similar to those of *T. bullae*. The short-rayed oxyspherasters in *T. irisae* sp. nov. do not fork as those of *T. bullae*. *Tethya irisae* sp. nov. has lightly spined acanthooxyspherasters compared to the completely spined acanthooxyspherasters of *T. bullae*. In addition to *T. fissurata* and *T. bullae*, other *Tethya* with rooting processes/stolons are shown in Table 2 (descriptions in bold text). It is difficult to tell how similar the rooting processes are to each other but these species differ in spicule forms and dimensions from *T. irisae* sp. nov. For example: species with megascleres < 2000 μm (*T. acuta* Sarà & Sarà, 2004, *T. bergquistae* Hooper in Hooper & Wiedenmayer, 1994, *T. burtoni* Sarà & Sarà, 2004, *T. dendyi* Sarà & Sarà, 2004, *T. robusta* (Bowerbank, 1873), *T. seychellensis* (Wright, 1881), *T. stolonifera* Bergquist & Kelly-Borges, 1991); species with megasters not of a ‘spheraster’ form (*T. amplexa* Bergquist & Kelly-Borges, 1991, and *T. fastigata* Bergquist & Kelly-Borges, 1991); species with very different micrasters (*T. ingalli* Bowerbank, 1858, *T. flexuosa* Sarà & Sarà, 2004 and *T. monstrosa* (Burton, 1924)).

Table 1. Spicule dimensions of *Tethya irisa* sp. nov. holotype (SAMA S3387) and paratypes (QM G305000, QM G305001).

| Spicule type | Specimen # | n | Size range (µm) |
|------------------------------------|------------|----|---|
| | | | Mean value underlined |
| Strongyloxeas (l × w) | S3387 | 34 | 897– <u>1361</u> –3060 × 17– <u>27</u> –52 |
| | G305000 | 26 | 1110– <u>2310</u> –3130 × 19– <u>42</u> –72 |
| | G305001 | 36 | 1270– <u>2495</u> –3160 × 20– <u>39</u> –64 |
| Styles (l × w) | S3387 | 13 | 262– <u>675</u> –1090 × 7– <u>16</u> –23 |
| | G305000 | 16 | 830– <u>1067</u> –1730 × 11– <u>20</u> –33 |
| | G305001 | 8 | 1250– <u>1525</u> –1970 × 19– <u>27</u> –34 |
| Short-rayed oxyspherasters (diam.) | S3387 | 75 | 53– <u>81</u> –154 |
| | G305000 | 41 | 44– <u>99</u> –177 |
| | G305001 | 59 | 49– <u>98</u> –133 |
| Long-rayed oxyspherasters (diam.) | S3387 | 21 | 120– <u>153</u> –185 |
| | G305000 | 17 | 154– <u>196</u> –253 |
| | G305001 | 2 | 131– <u>134</u> –136 |
| Acanthooxyspherasters (diam.) | S3387 | 55 | 12– <u>15</u> –20 |
| | G305000 | 43 | 13– <u>15</u> –19 |
| | G305001 | 32 | 13– <u>16</u> –19 |

In addition, *T. irisa* sp. nov. is collected at the start of the bathyal zone (~1000 m). The deepest of the *Tethya* is *T. compactus* Bergquist, 1961 (402 m), which has very different external morphology.

It occurred to us that when using the key to genera of Tethyidae (Sarà 2002), *Tethya irisa* sp. nov. appears closest to the monospecific genus *Burtonitethya*, a tethyid with a stalk of equal length to the diameter of the sponge. The type of *Burtonitethya* (*B. gemmiformis*), was collected from the Andaman Sea at an unknown depth (Sarà 1994). *Burtonitethya gemmiformis* was originally assigned to *Tethya* (labelled as *Tethya gemmiformis* Burton & Rao, 1957 on the NHM microscope slide) but was re-assigned to a new genus *Burtonitethya* by Sarà (1994) on account of the stalk, the conspicuous nucleus with strongyles, the reduced lacunar cortex, the specialised surface tubercles and the giant oxyaster megasters. Our new species clearly differs from this species in having different microscleres and does not have the giant megasters present in *B. gemmiformis*. As there is no specimen of the type species of *Burtonitethya* and thus no potential to sequence the sponge, we cannot test if *Burtonitethya* is a junior synonym of *Tethya*.

As seen above, the genus *Tethya* shows many different modes of attachment including basal stolons, basal roots, curved peduncles, flattened rooting processes as well as attachment discs and narrow skirts of tissue. Our results suggest that the stalk may not be a good genus-defining character within the family. Heim *et al.* (2007) in their analysis of *Tethya* species, for which they used morphological characters and molecular markers, suggest that characters pertaining to ecological influences may have developed several times. Similarly, we suggest that some of the external morphological characters used to separate genera of Tethyidae are homoplasious, probably appearing several times in different clades of *Tethya* and we question whether they should be grouped as definitive characters in morphological identifications. In the same way the genus *Amphitethya* Lendenfeld, 1907 (Family Tetillidae Sollas, 1886) was created based on its stalk, but phylogenies show it is a *Cinachyrella* Wilson, 1925 (Szitenberg *et al.* 2013; Schuster *et al.* 2017).

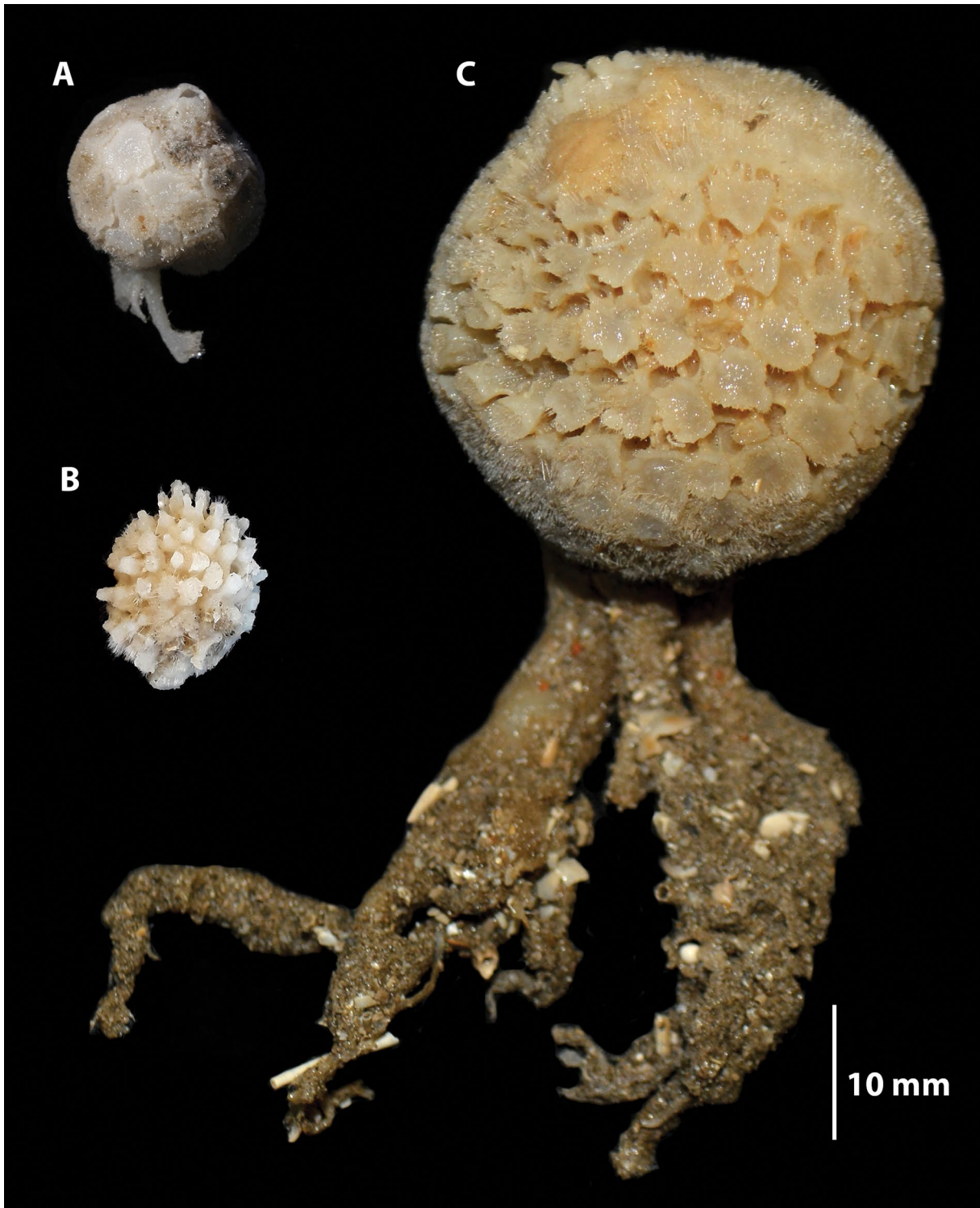


Fig. 4. Comparative sizes and external morphology of species of *Tethya* Lamarck, 1815. **A.** *Tethya irisae* sp. nov., holotype (SAMA S3387). **B.** *Tethya bullae* Bergquist & Kelly-Borges, 1991, part of the holotype (AM Z5074). **C.** *Tethya fissurata* Lendenfeld, 1888, syntype (AM G.9069) Note: the original photo of *T. bullae* (Bergquist & Kelly-Borges 1991) shows rooting processes.

Table 2 (continued on five next pages). Comparison of morphology between species of *Tethya* Lamarck, 1815 from Australia and New Zealand.

| Species | External appearance Significant attachment in bold | Body diam. Colour | Skeletal arrangement in μm & interstitial brushes | Spicules Ms = megascleres, me = megasters, mi = micrasters (size in μm) | Type locality | Depth (m) |
|--|--|----------------------------------|--|---|--|-----------|
| <i>T. irisae</i> sp. nov. | Spherical; plate-like polygonal tubercles separated by grooves; apical osculum; hard. Stalk, same length as body diam. | 11 mm Grey/white | Tracts of megasclere bundles (300–700) are uniform from choanosome to cortex and fan slightly in tubercles. | Ms : strongyloxeas (to 3000×70), styles (to 1970×34). me : long & short-rayed oxyasperasters (44–177) mi : acanthoxyasperasters (12–20) | Great Australian Bight | 1000 |
| <i>T. acuta</i> Sarà & Sarà, 2004 ¹ | Spherical with small, distinct tubercles; firm. Buds and rhizoid protuberances. | 13 mm Unknown* | Thick tracts of megasclere bundles (250) fanning out in the cortex. | Ms : strongyloxeas, anisostromyloxeas, styles (to 1600×20) me : oxyasperasters (15–50) mi : oxyasters (8–20) | Pt Phillip Heads, Victoria, Australia | Unknown** |
| <i>T. amplexa</i> Bergquist & Kelly-Borges, 1991 ² | Spherical to subspherical; surface encrusted with animals. Broad flat tubercles. Apical oscule. Long curved flexible peduncle. | 30–70 mm Yellow | Robust bundles (440–800) diverging into branches in cortex. Brushes of interstitial megascleres. | Ms anisostromyloxeas (to 2300×32) me : oxyasters (16–35) mi : various, incl. acanthoylasters acanthochiasters, acanthoxyasperasters (10–20) | Mimiwhangata, New Zealand | 7 |
| <i>T. bergquistae</i> Hooper in Hooper & Wiedenmayer 1994 ^{1,2} | Spherical to ovate; surface mammillate to tessellated with buds arising on filaments; firm compressible. Oscules in groups of 3–4). Root-like processes. | 20–25 mm Rose pink | Widely separated thin flexuous tracts of megasclere bundles (171– 612) radiating into tertiary branches at surface. Interstitial megasclere brushes. | Ms : anisostromyloxeas (to 1617×18) me : oxyasperasters (18–52), oxyasters (22–31) mi : acanthoylasters/acantho- stromyloxeas (10–17), micro-oxyasters (7–10). | Whitianga, New Zealand | 27 |
| <i>T. bullae</i> Bergquist & Kelly-Borges, 1991 ² | Spherical to ovate; large blunt well separated tubercles. Basal flattened branched rooting processes. | 10–14 mm Yellow grey | Tracts of megasclere bundles (500) uniform from choanosome to cortex, where they radiate slightly to support the raised tubercles. | Ms : anisostromyloxeas (to 2225×30) me : long and short-rayed oxyasperasters mi : completely microspined acanthoxyasperasters & acanthostromyloxeas (11–15), microoxyasperasters (9–10) | Alderman Islands, New Zealand | 100 |
| <i>T. burtoni</i> Sarà & Sarà, 2004 ¹ | Spherical to hemispherical; tubercles conulated, flat or inconspicuous. Sponges clump together. Small marginal stolons. | 10–13 mm Pale orange brown | Tracts of megasclere bundles (500–750) unbranched. Brushes of auxiliary interstitial megascleres. | Ms : strongyloxeas/anisostromyloxeas to (1800×40) + interstitial styles me : oxy-/spherasters (40–80) mi : tylasters (8–14), chiasters or tylote oxyasters (12–15) | Tauranga, New Zealand | 1 |

Table 2 (continued). Comparison of morphology between species of *Tethya* Lamarck, 1815 from Australia and New Zealand.

| Species | External appearance | Body diam. Colour | Skeletal arrangement | Spicules | Type locality | Depth (m) |
|---|--|--|---|---|--|----------------------|
| <i>T. compacta</i> Bergquist, 1961 ³ | Rhomboid, with lateral fan-like projections. Stony. | 8 mm Mid brown (in ethanol) | Tracts (356–722) (in ectosome). Endosome with radiate structure. | Ms: strongyloxeas (to 1574 × 21) me: spherasters (25–43) mi: tylasters (7–12) | Chatham Rise, New Zealand | 402 |
| <i>T. communis</i> Bergquist & Kelly-Borges, 1991 ² | Spherical to subspherical; growing in clumps. | 7–12 mm Dull grey pink (in ethanol) | Flexuous tracts of megasclere bundles (125–300) have elaborate tertiary branching. | Ms: anisostrongyloxeas (to 1225 × 12) me: oxyspherasters (38–55), oxyasters (7–12) mi: includes polyrhabs | Cape Banks, New South Wales, Australia | Intertidal |
| <i>T. dendyi</i> Sarà & Sarà, 2004 ¹ | Body covered in small, flattened tubercles. Rhizoid-like stolons. | 20 mm Pale buff (in ethanol) | Tracts of megasclere bundles (250–500) branch in choanosome and form fans in cortex. | Ms: strongyloxeas and styles (to 980 × 15) me: spherasters 20–30 mi: tylasters/chiasters/oxyasters (10–16) | Pt Phillip Heads, Victoria, Australia | Unknown ^a |
| <i>T. expansa</i> Sarà & Sarà, 2004 ¹ | Irregular shape, very hard, irregular labyrinthine tubercles. | 20–30 mm Unknown | Tracts of megasclere bundles (250–500) form secondary branching in cortex with fans at surface. | Ms: strongyloxeas and anisostrongyloxeas (1400 × 28) me: spherasters/oxyasters (30–50) mi: tylasters/chiasters/oxyasters (7–13) | Alipara Bay, New Zealand | Unknown |
| <i>T. fastigata</i> Bergquist & Kelly-Borges, 1991 ² | Ovoid; 1–3 large raised apical oscules; surface conulose. Short, thick stolons. | 40–60 mm Bright orange | Fine, widely separated tracts of megasclere bundles (275–539) radiate slightly towards surface. | Ms: anisostrongyloxeas (to 2425 × 35) me: oxyasters (18–39) mi: various incl. acanthotylasters/chiasters (9–20) | Poor Knights Isl. New Zealand | 25–40 |
| <i>T. fissurata</i> Lendenfeld, 1888 ^{4,5} | Spherical; tubercles separated by deep grooves. Thick stalk which divides into roots. | 40 mm Beige (in ethanol) | Tracts of megasclere bundles branch in the tubercles, supporting the edge of the tubercles and spicules extend through the surface. | Ms: strongyloxeas (to 4000 × 80) me: short-rayed spherasters (160), long-rayed spherasters (240) mi: oxyasters (55), tylasters (19) | Pt Jackson, New South Wales, Australia | Unknown ^b |
| <i>T. flexuosa</i> Sarà & Sarà, 2004 ¹ | Irregular spherical shape. Tubercles rounded and slightly conical and carry thin filaments. Elastic consistency. Basal rhizoid stolons. | 18–35 mm Brownish white | Tracts of megasclere bundles (250–750) branch into secondary and tertiary branches in cortex. | Ms strongyloxeas and anisostrongyloxeas (to 2600 × 50) me: spherasters & oxyspherasters (30–80) mi: tylasters (10–15), oxyasters (10–50) | NW Australia | 30–62 |
| <i>T. gigantea</i> (Lendenfeld, 1888) ⁴ | Spherical; surface with 7 mm high mounds; tuberculose. | 60–90 mm Orange-red | Widely spaced tracts of megasclere bundles (500–700), separating only slightly in surface tufts. | Ms: strongyloxeas (2000 × 35) me: oxyspherasters (30–60) mi: chiasters/oxyasters (10–20) & polyrhabs | Pt Jackson, New South Wales, Australia | Unknown ^b |

Table 2 (continued). Comparison of morphology between species of *Tethya* Lamarck, 1815 from Australia and New Zealand.

| Species | External appearance | Body diam. Colour | Skeletal arrangement | Spicules | Type locality | Depth (m) |
|--|--|--------------------------------------|---|--|--|----------------------|
| <i>T. gunni</i> Sarà & Sarà, 2004 ¹ | Smooth with small conulated tubercules. | 25 mm Faded purple (in ethanol) | Tracts of megasclere bundles (250–500) branch in the choanosome ending in compact fans in tubercules. | Ms: strongyloxeas (to 1850 × 35), styles (to 800 × 10) me: spherasters (20–55) mi: tylasters/chiasters/oxyasters | Tasmania, Australia | Unknown |
| <i>T. hooperi</i> Sarà & Sarà, 2004 ¹ | Body ellipsoid; smooth surface, no tubercules. | 20–30 mm Ochraceous (in ethanol) | Tracts of megasclere bundles (250–500) radiate in cortex with secondary and tertiary branching. | Ms: strongyloxeas (to 1530 × 20) me: spherasters (30–60) mi: tylasters (8–14) oxyasters (15–25) | Heron, Is. Great Barrier Reef, Australia | 12 |
| <i>T. ingalli</i> Bowerbank, 1858 ¹ | Spherical/sub-spherical; flattened often inconspicuous tubercules. Basal stolons. | 30–50 mm Pinkish | Tracts of megasclere bundles split into secondary and tertiary branches in cortex. | Ms: strongyloxeas/anisostrongyles (to 2130 × 30) me: oxyspherasters (70–90) mi: tylasters (10–15), chiasters, oxyasters (20–30) | SW Australia | 30–50 |
| <i>T. japonica</i> Sollas, 1888 ⁶ | Spherical; conules rounded; gemmiferous. | 13–22 mm Greyish white | [No details on tracts.] | Ms: strongyloxeas (to 1500 × 26) me: spherasters (67) mi: chiasters (12) | Eastern Philippines | 32 |
| <i>T. laevis</i> (Lendenfeld, 1888) ⁴ | Spherical/ovate; surface smooth to tuberculate. | 30–45 mm Light brown (in ethanol) | Tracts of megasclere bundles (500–800) expand to surface tufts. | Ms: strongyloxeas (to 2000 × 36) me: spherasters (30–60) mi: chiasters/oxyasters (10–20), tylasters (10–15), polyrhabs | Pt Jackson, New South Wales, Australia | Unknown ² |
| <i>T. magna</i> Kirkpatrick, 1903 ^{1,7} | Oval or spherical; conulated surface (in young specimens), expanding to polygonal plates. Tree-like rootlets. | 70 mm Purple-brown (in ethanol) | Tracts of stout megasclere bundles (500–1000), unbranched but with terminal fans. | Ms: strongyloxeas (to 4805 × 75) me: spherasters (120) mi: asters (35–45), chiasters (12–17) | Natal, South Africa | 62 |
| <i>T. microstellata</i> Sarà, 1990 ⁸ | Hemispherical/cushion-like; tubercules vary from conules to flat papillae. | 10 mm Brownish/light yellow | Tracts of megasclere bundles in choanosome are accompanied by styles in cortex. | Ms: strongyloxeas (to 1600 × 15) me: spherasters (30–80) mi: tylasters (4–6) & larger ‘other micrasters’ | Pioneer Bay, Orpheus Is, Queensland, Australia | 0–1 |
| <i>T. monstrosa</i> (Burton, 1924) ⁹ | Spherical; sub-glabrous, a few small buds attached. Rooting processes well developed. | 14–25 mm Nut brown (in ethanol) | Radial tracts of megasclere bundles spread out into fans at surface. | Ms: strongyloxeas me: spherasters (48) mi: tylasters (20) & oxyasters (32). Many microscleres have abnormalities where the tyles & spines are reduced to knobs or absent leaving just a sphere. | Tasmania | Unknown |

Table 2 (continued). Comparison of morphology between species of *Tethya* Lamarck, 1815 from Australia and New Zealand.

| Species | External appearance | Body diam. Colour | Skeletal arrangement | Spicules | Type locality | Depth (m) |
|---|--|--------------------------------|---|--|---|------------|
| <i>T. mortoni</i> Bergquist & Kelly-Borges, 1991 ² | Ovoid; low tubercles. Buds on erect filaments. | 6–8 mm Maize yellow | Fine tracts of megasclere bundles (122–490) uniform from choanosome to cortex, expand slightly in cortex. Interstitial spicules radial. | Ms: anisostrongyloxeas (to 1092 × 21) me: long-rayed oxyasperasters (26–62), short rayed oxyasperasters (28–52) mi: incl. acanthostrongyloasters & acanthotyloasters (8–13) | Manukau Harbour, Auckland, New Zealand | 0.5 |
| <i>T. multistella</i> Lendenfeld, 1888 ^{4,1} | Spherical to subspherical; regularly tuberculose. | 20–40 mm Red, flesh or rose | Radial tracts of megasclere bundles (300–500) are trumpet-like in shape and spread to secondary and tertiary branches in tubercles. | Ms: strongyloxeas (to 3500 × 18) me: spherasters (20–50) mi: tyloasters (12–16), oxyasters (5–10) | Pt. Jackson, New South Wales Australia | Unknown |
| <i>T. orphei</i> Sarà, 1990 ⁸ | Subspherical; lengthened but apically flattened tubercles at top of sponge, smooth elsewhere. | 5 mm Brown yellowish | [Tracts/bundles not described.] | Ms: strongyloxeas, (to 1600 × 15) styles (to 1200 × 10) me: spherasters (10–50) mi: chasters & tyloasters (8–12), oxyasters (10–30) | Pioneer Bay, Orpheus Is, Queensland, Australia | 0–1 |
| <i>T. pellis</i> Bergquist & Kelly-Borges, 1991 ² | Flattened subspherical, tubercles divided by pore grooves; firm but compressible. | 40 mm Flesh rose | Tracts of megasclere bundles widely spaced – branch in top third of cortex into fans. | Ms: anisostrongyloxeas (to 2075 × 30) me: oxyasperasters (25–120), oxyasters (20–25) mi: acantho-chasters/tyloasters/oxyasperasters (13–18), microoxyasters (5–11) | Fairlight, Sydney Harbour, New South Wales, Australia | Intertidal |
| <i>T. popae</i> Bergquist & Kelly-Borges, 1991 ² | Irregular subspherical; ill-defined tubercles or smooth; 2–8 apical oscules; sponges can cluster connected by stolons. | 8–16 mm Bright deep orange | Flexuous tracts of megasclere bundles have elaborate tertiary branching. | Ms: anisostrongyloxeas (to 910 × 10) me: oxyasperasters (20–55) mi: acanthochasters & acanthostrongyloasters (7–13), microoxyasters (2–10) | Cape Banks, New South Wales, Australia | Intertidal |
| <i>T. pulitzeri</i> Sarà & Sarà, 2004 ¹ | [No description, species designation from slides only.] | Unknown Unknown | Unknown. | Ms: strongyloxeas, anisostrongyles (to 1100 × 15) me: oxyasperasters (30–50) mi: tyloasters & chasters (8–10), oxyasters (10–15) | Heron Island, Great Barrier Reef, Australia | Unknown |
| <i>T. robusta</i> (Bowerbank, 1873) ¹ | Hemispherical; polygonal areas separated by grooves Attached by short broad robust basal stolons. | 30–50 mm Yellow-grey | Slim tracts of megasclere bundles expand slightly in cortex. | Ms: anisostrongyloxeas (to 1850 × 32) me: oxyasperaster (30–90), oxyasters (11–22) mi: acantho-tyloasters/strongyloasters (7–12), microoxyasperasters (4–5) | Australia | 0.2–30 |

Table 2 (continued). Comparison of morphology between species of *Tethya* Lamarck, 1815 from Australia and New Zealand.

| Species | External appearance | Body diam. Colour | Skeletal arrangement | Spicules | Type locality | Depth (m) |
|--|---|---|--|--|--|------------|
| <i>T. seychellensis</i> (Wright, 1881) ^{1,2} | Spherical or hemispherical; smooth with flattened polygonal tubercles separated by grooves; firm compressible. Attached by fine stolons. | 15–25 mm Brown red | Tracts of megasclere bundles (250–500) have secondary branching in cortex – spicules protrude well beyond surface. | Ms: anisostromyloxeas (to 1500 × 30) me: oxyspherasters (17–76), oxyasters (32–50) mi: acanthochiasters & acanthostromylosters (7–13), microasters (7–17) | Dampier, Western Australia | Intertidal |
| <i>T. stellodermis</i> Sarà & Sarà, 2004 ¹ | [Shape not described]; surface of very flattened tubercles; very hard. | 25 mm Pale purple brown (in ethanol) | Thick tracts of megasclere bundles (300–500) branch into secondary and tertiary tracts in cortex. | Ms: strongyloxeas (to 1400 × 28) me: spherasters/oxyasters (10–40) mi: various incl. tylasters (20–25), oxyasters (5–10) | Pt Phillip Heads, Victoria | Unknown |
| <i>T. stolonifera</i> Bergquist & Kelly-Borges, 1991 ² | Spherical to subspherical; circular or polygonal tubercles; soft compressible. Extensive stolons. | 3–11 mm Reddish yellow | Narrow well separated tracts of megasclere bundles (200–425) radiate in cortex forming conical brushes. | Ms: anisostromyloxeas (to 1225 × 26) me: oxyspherasters (13–76); mi: acanthostromylosters, acanthotylasters (8–14) rare microoxyspherasters (3–10) | Waitemata Harbour, Auckland, New Zealand | 0. 5–1.5 |
| <i>T. tasmaniae</i> Sarà & Sarà, 2004 ¹ | Spherical with small tubercles. | 20 mm Unknown | Tracts of megasclere bundles (500–1000) branch in choanosome and end in cortex as wide cones. | Ms: strongyloxeas/anisostromyloles (to 1200 × 20) me: spherasters 20–50 mi: various e.g. tylasters, oxyasters (3 types), chasters | Blackmans Bay, Tasmania, Australia | Unknown |

Sources. ¹Sarà & Sarà (2004); ²Bergquist & Kelly-Borges (1991); ³Bergquist (1961); ⁴Lendenfeld (1888); ⁵Hallmann (1914); ⁶Sollas (1888); ⁷Kirkpatrick (1903); ⁸Sarà (1990); ⁹Burton (1924).

Notes. * unknown, or not noted in sources. ^a Maximum depth of Pt Phillip Heads is 50 m (Barton *et al.* 2012); ^b Maximum depth of Pt Jackson is 45 m (Johnston *et al.* 2015). *Tethya diploclerma* Schmidt, 1870 is listed as occurring in New Zealand by Kelly *et al.* (2009), but is not included as this is currently shown as inaccurate by van Soest (2019). *Tethya compacta* Bergquist, 1961 is not included in the list of Australia and New Zealand species by Sarà & Sarà (2004) due to its synonymisation by Bergquist with *T. aurantium* (Pallas, 1766), however they note that the taxonomic status of *T. compacta* “remains uncertain”; it is included here as it is shown as accepted by van Soest (2019). The occurrence of *T. aurantium* in New Zealand is shown as inaccurate (van Soest 2019) and is not included here.

Results of the phylogenetic analyses

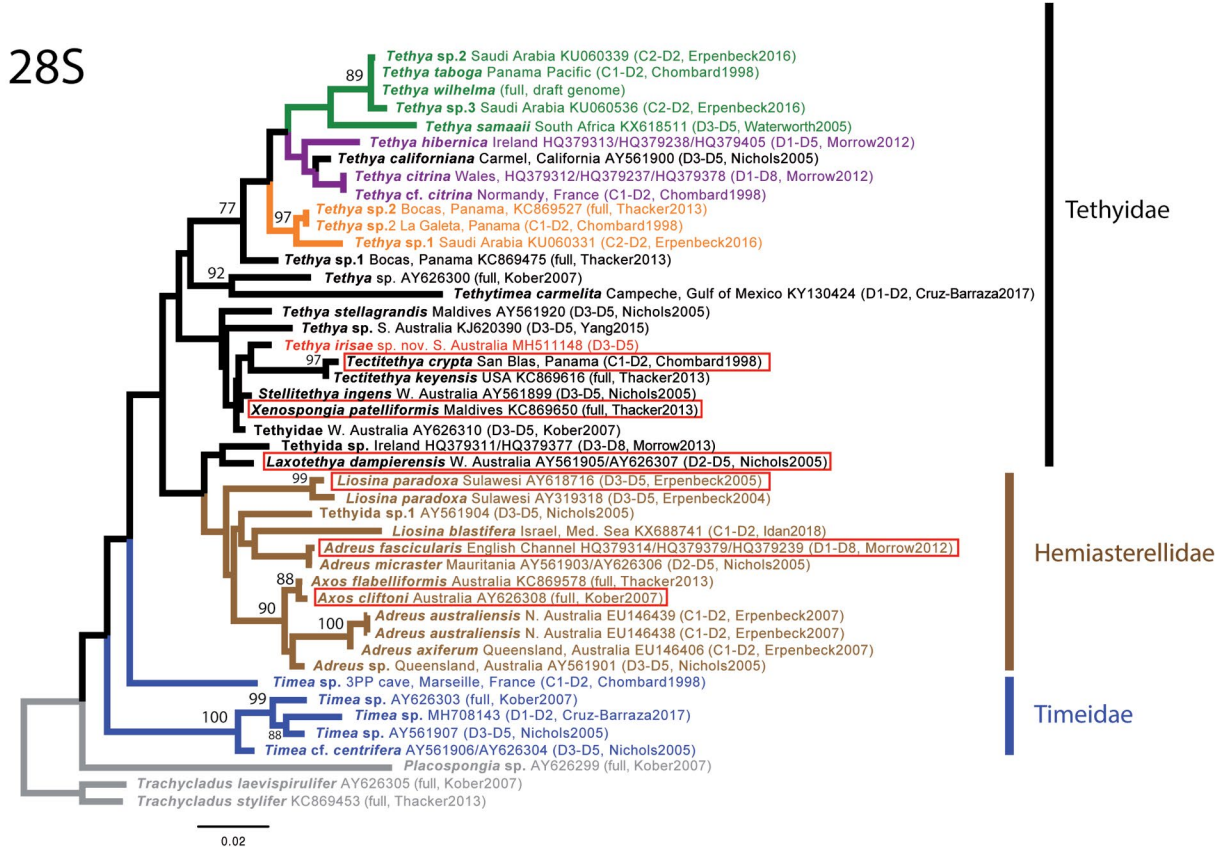
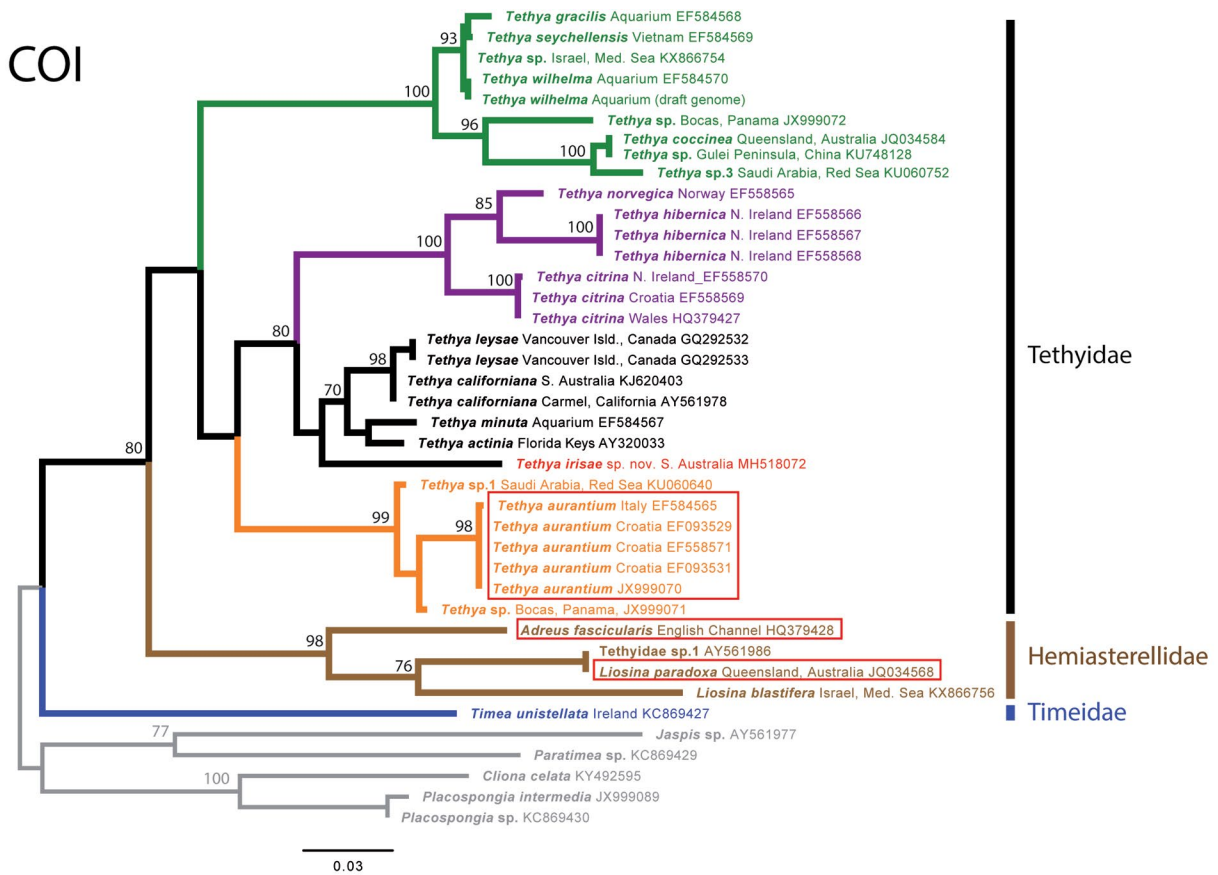
28S and COI trees had similar topologies (Fig. 5). The monophyly of the Tethyida was not supported (28S, bootstrap of 12; COI, bootstrap of 33) with Timeidae sister to a moderately (COI) to poorly supported (28S) Tethyidae + Hemiasterellidae clade. *Timea* sp. from the ‘3PP cave’, La Ciotat, France, (Chombard 1998) did not group with the rest of the Timeidae, but its paraphyletic position was poorly supported. The Hemiasterellidae (*Adreus*, *Axos*, *Liosina*) seemed to group in a moderately to well-supported clade (28S, 69; COI, 98). The 28S tree suggested that the Australian *Laxotethya dampieriensis* (Tethyidae) and a Tethyida sp. from Ireland with no obvious genus assignment (C. Morrow, pers. comm.) had more ambiguous positions: in RaxML analyses they grouped together (poorly supported), while in MrBayes analyses Tethyida sp. branched between the Timeidae and the rest of the Tethyida. *Liosina paradoxa* Thiele, 1899 and *Liosina blastifera* Vacelet, Bitar, Carteron, Zibrowius & Perez, 2007 did not group together in the 28S trees, while *Adreus* was polyphyletic with two clades (one from Australia, the other from the North Atlantic). With COI, where we only have *Tethya* sequences, we could identify four moderately to well-supported clades: 1) the *T. aurantium* clade, 2) the *T. wilhelma* clade, 3) the *T. citrina* clade and 4) the *T. actinia* Laubenfels, 1950 clade. Our new species *T. irisae* sp. nov. branched as the sister taxa to clade 4 (in RaxML and MrBayes) but this is poorly supported. In our 28S dataset where we found the same four clades, all other Tethyidae genera (*Tethytimea* Laubenfels, 1936, *Stellitethya*, *Xenospongia* and *Tectitethya* Sarà, 1994) were mixed with *Tethya* species, especially in clade 4. *T. irisae* sp. nov. grouped with *Tectitethya* in clade 4 (in RaxML and MrBayes analyses) but this is poorly supported. *T. wilhelma* was originally described from a tropical aquarium in Germany but its original geographical location is unknown. In *Tethya* clade 2, we noticed several species were very close genetically to *T. wilhelma*: with COI, *Tethya* sp. from Israel (Mediterranean Sea) had only 1 bp difference with *T. wilhelma*; with 28S, *T. taboga* from Panama had 0–2 bp difference with *T. wilhelma* (uncertainty due to two ambiguous base pairs) while *Tethya* sp. 2 from Saudi Arabia had 1 bp difference with *T. wilhelma*.

Discussion

Tethya irisae sp. nov. is a new and distinctive sponge from the slope of the Great Australian Bight (GAB). This is the 28th *Tethya* species reported from Australia, and the deepest, being found in the bathyal zone at around 1000 m deep. With uncertainties in the validity of genera divisions based on morphological characters e.g., possession of a stalk, a reappraisal of the genera within Tethyidae based on molecular sequencing is needed.

Phylogeny of Tethyidae

The first phylogenetic analyses of *Tethya*, using COI and morphology (Heim *et al.* 2007; Heim & Nickel 2010) revealed four main clades: 1) the *seychellensis-wilhelma* complex, 2 + 3) the *citrinia-actinia* complex divided in two subclades (European species and western Atlantic species + eastern Pacific) and 4) the *aurantium* clade. Our COI and 28S analyses with extended datasets retrieve these four clades, but with a higher biogeographical diversity. The *seychellensis-wilhelma* complex now includes specimens from Israel, Vietnam, Panama, China and Queensland; the *aurantium* clade now includes species from the Mediterranean Sea, the Red Sea and Panama. All clades are well-supported in the COI tree except for clade 3, the western Atlantic/Pacific clade. This is precisely the group joined by the COI sequence of *T. irisae* sp. nov.; its position within this group, however, remains unclear. These same four clades are not as clear in our 28S tree, their inter-relationships are also different, and not supported at all. This may be due to the fact that our 28S alignment is a mix of different 28S domains and different sampling than COI, both of which may influence some of the groupings. The *seychellensis-wilhelma* and *aurantium* clades are well supported with 28S as well. On the other hand, the *citrinia* and *actinia* subclades are unclear, and this is probably due to the addition in this dataset of many different genera of Tethyidae (*Tethytimea*, *Tectitethya*, *Stellitethya*, *Xenospongia* Gray, 1858, *Laxotethya*). As suggested by Sarà *et al.*



(2001) and Heim *et al.* (2007), *Tethya wilhelma* and *T. gracilis* Sarà, Sarà, Nickel & Brümmer, 2001, both described from aquaria in Germany belong to the *seychellensis-wilhelma* complex. There is only 1 bp difference between the COI of *T. wilhelma* and *Tethya* sp. (Mediterranean Sea, Israel) so this specimen should be re-examined to see if it could be conspecific with *T. wilhelma*. Heim *et al.* (2007) showed that the most reliable characters for *Tethya* taxonomy were morphometric spicule data, but none could actually make good morphological synapomorphies for the two *Tethya* clades supported with COI and 28S. New characters (e.g., chemical compounds, specialized cells, associated microbes) must be explored in order to find independent support for these groups.

External colour may be a reliable character to discriminate those clades, as shown previously in some calcareous sponges (Rossi *et al.* 2011). Indeed, most shallow water *Tethya* species have a yellow, orange to red surface colour, probably due to different carotenoids (Tanaka *et al.* 1982) some of which they can synthesise themselves (Liaaen-Jensen *et al.* 1982) and therefore have a genetic basis. All species currently in the *citrina* subclade (*T. norvegica* Bowerbank, 1872, *T. citrina* and *T. hibernica*) are light-yellow coloured. Species from the *actinia* subclade and *aurantium* clade are usually bright yellow to orange to bright orange, except for the ‘aquarium’ species *T. minuta* Sarà, Sarà, Nickel & Brümmer, 2001 (white, in artificial conditions at least). Finally, the *seychellensis-wilhelma* clade seems to include especially bright red/carmine surface-coloured species (*T. seychellensis*, *Tethya* sp. from Bocas, *T. coccinea* Bergquist & Kelly-Borges, 1991, *Tethya* sp. 3 from Saudi Arabia, *T. taboga*, *T. samaaii* Ribeiro & Muricy, 2011), except for the *Tethya* sp. from Israel which was more light orange, and except again for the ‘aquarium’ species (*T. wilhelma* and *T. gracilis*). In red surface-coloured species, the choanosome is usually orange. However, more colours exist: some *Tethya* can be green (e.g., *Tethya brasiliiana* Ribeiro & Muricy, 2004), dark blue (e.g., *Tethya cyanea* Ribeiro & Muricy, 2004), or pink (e.g., *Tethya bergquistae*) but none of these species have been sequenced yet. We can probably dismiss the green colour. It is found in species that can also be orange; Laubenfels (1950) suggested the green colour of *T. actinia* in Bermuda was due to symbiotic algae (a specimen may “turn orange” when fixed in alcohol, as the chlorophyll is extracted). More problematic are species with varying colours, from yellow to orange and red (e.g., *Tethya fastigata*). As for the few deep-sea species of *Tethya*, some have lost their colours (e.g., *Tethya irisae* sp. nov.) while others have retained them: e.g., *Tethya levii* Sarà, 1988 from New Caledonia is light orange, and groups in the *actinia* clade, in accordance with our hypothesis (P. Cárdenas, unpublished data). This grouping-by-colour hypothesis should be further tested with the sequencing of new species of *Tethya*. Other genera of Tethyidae included in our dataset have usually irregular massive forms or are disc-shaped (instead of subspherical forms), and all have dark colours: black-brownish for *Tectitethya* spp., beige-gray for *Xenospongia*, and whitish-brown in ethanol for *Laxotethya* and *Stellitethya* (the live colour is unknown). Since all except *Laxotethya* are sister group to a bright orange *Tethya* sp. from South Australia (possibly in the *actinia* clade) (Fig. 5, 28S tree), we suppose the common ancestor of these other genera lost its yellow-orange colours, and so its capacity to produce carotenoids.

Our COI and 28S dataset include type species of four Tethyidae genera (of the 14 valid genera): *Tethya* (*T. aurantium*, COI), *Tectitethya* (*T. crypta*, 28S), *Xenospongia* (*X. patelliformis*, 28S) and *Laxotethya* (*L. dampierensis*, 28S). In addition to that, two other Tethyidae genera are represented in our 28S tree: *Stellitethya* and *Tethytimea*. All these genera are essentially defined by different skeletal structures and therefore body shape; all these genera have an indistinct or ill-defined cortex (vs a distinct thick cortex for *Tethya*) and an irregular massive or encrusting shape (vs (sub)spherical shape in *Tethya*). Our

Fig. 5 (opposite page). Tethyida COI and 28S maximum-likelihood (RaxML) trees. ML bootstrap supports (1000 bootstrap replicates) > 70 are indicated. After the species name, locality of the specimen is given (when known), followed by the GenBank accession number(s). For 28S, we also indicated the 28S region that was sequenced as well as the first author + date of the publication where the sequence first appeared. Type species of genera are in red boxes while *Tethya irisae* sp. nov. appears in red.

28S tree suggests that *Xenospongia*, *Stellitethya*, *Tectitethya* and *Tethytimea* are grouping with *Tethya* (Fig. 5), while *Laxotethya* groups with Hemiasterellidae, albeit with no support. *Tethytimea carmelita*, *Tectitethya* and *Stellitethya/Xenospongia* evolved independently within *Tethya* thus suggesting that the loss of a distinct cortex and of the subspherical shape happened several times. More sequences from Australian *Tethya* are needed to understand the origin and relationships of these other Tethyidae genera. One clade that is moderately supported (bootstrap of 69) is the sister-group relationship of *Xenospongia* and *Stellitethya*, with a 5–6 bp difference in 28S (D3–D5). Both genera have a poorly defined cortex but different shapes: discoid for *Xenospongia*, massive irregular for *Stellitethya*. These two genera also share megasters reaching large sizes (> 150 µm), as in *T. irisae* sp. nov., grouping nearby (bootstrap of 62) with *Tectitethya* (which does not have very large megasters).

Phylogeny of Tethyida

The Tethyida also include Hemiasterellidae and Timeidae. Since the ex-hemiasterellid genera *Stelligera* Gray, 1867 and *Paratimea* have been reallocated to the Stelligeridae Lendenfeld, 1898, order Axinellida (Morrow *et al.* 2012), the Hemiasterellidae include four genera: *Adreus*, *Axos*, *Hemiasterella* and the monospecific *Leptosastra* Topsent, 1904. The sister position of Hemiasterellidae *Adreus* and *Axos* with the Tethyidae has been repeatedly shown by previous COI (Morrow *et al.* 2012, 2013), 28S (Thacker *et al.* 2013; Cruz-Barraza *et al.* 2017) and 18S analyses (Redmond *et al.* 2013). *Liosina*, a genus with only four species and a loose arrangement of oxeas/styles, had been tentatively assigned to the family Dictyonellidae, order Bubarida (van Soest *et al.* 2002). The grouping of *Liosina paradoxa*, type species, with the Hemiasterellidae was revealed for the first time by Morrow *et al.* (2012) with 28S. Our study confirms this grouping for the first time with COI sequences (*L. paradoxa* and *Liosina blastifera*), as well as a 28S sequence of *L. blastifera*. Its unambiguous grouping with the Hemiasterellidae suggests that species of *Liosina* are in fact Hemiasterellidae that have secondarily lost their euasters. Furthermore, *Liosina* often have a polygonal surface pattern, and/or pores in shallow grooves, a character present in most Tethyidae and Timeidae, which often gives rise to the characteristic surface tubercles. Since we have sequenced the type species of *Liosina*, we formally propose the reallocation of *Liosina* from Dictyonellidae to Hemiasterellidae. However, it is unclear in our trees whether *Liosina* is polyphyletic. The small polygons from *Liosina*, also called tubercles or microconules, are also present in the three *Adreus* species from Australia (*A. australiensis* (Ridley, 1884), *A. axiferum* (Hentschel, 1912) and *Adreus* sp.) thereby confirming their reallocation. These two branching species also share with the Tethyida the typical radial bundles of megascleres fanning out closer to the surface. *Adreus australiensis* and *A. axiferum* were previously grouped in Raspailidae (Hooper 1991) although they lacked echinating megascleres, before Erpenbeck *et al.* (2007) showed with 28S that they clustered instead with Hemiasterellidae and Tethyidae. These two species also secondarily lost their asters, while the vase-shaped *Adreus* sp. from Queensland (QM G315767) still has tylasters. This second case of aster loss in the Tethyida suggests that, similarly as in the Astrophorina (Cárdenas *et al.* 2011), more genera or species without asters, can be expected to be reallocated to the Tethyida once they are sequenced. Since this *Adreus* clade does not cluster with the clade of *Adreus fascicularis* (type species of the genus), they potentially represent a new genus in the Hemiasterellidae. To conclude, the Hemiasterellidae now include *Adreus*, *Axos*, *Hemiasterella*, *Leptosastra*, *Liosina*, and a potential new genus. So far, all GenBank *Hemiasterella* sp. sequences are doubtful and failed to cluster with the Hemiasterellidae (cf. Material and methods). The type specimen of *Hemiasterella typus* Carter, 1879, has not been revised and sequenced so that the phylogenetic position of *Hemiasterella* remains to be tested. We note, however, that *H. typus* does not share with most of the Tethyida 1) a surface with pores in grooves around tubercles/plates or 2) bundles of megascleres fanning out at the surface.

To sum up the main findings of the phylogenetic analysis.

1. Four *Tethya* clades were retrieved (as in previous analyses) for which no synapomorphies are currently known; we, however, discuss the possibility of using external colour to support some of these clades.
2. Despite unclear phylogenetic relationships amongst Tethyidae from Australia, our results suggest that Tethyidae genera *Tethytimea*, *Tectitethya*, *Laxotethya*, *Stellitethya*, and *Xenospongia* derive from species of *Tethya*, which may challenge their validity in the future.
3. Our results suggest that Hemiasterellidae is the sister-group of Tethyidae while the position of Timeidae is still ambiguous (not supported).
4. We show that asters have been secondarily lost at least twice in the Hemiasterellidae: in *Liosina* and a potential new genus from northern Australia. We formally propose the reallocation of *Liosina* from Dictyonellidae to Hemiasterellidae.

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