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Three new species of *Sollasella* (Porifera: Demospongiae: Axinellida: Raspailiidae) from Western Australia

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ABSTRACT – The sponge genus *Sollasella* has three named species, two from eastern Australia, (Queensland and New South Wales) and one from the western Arabian Sea. Using a combination of morphological and molecular data, we describe three new species from northern Western Australia. We sequenced Cytochrome Oxidase I and two different fragments of 28S to reconstruct genealogical relationships among species in the genus. *Sollasella suttonorum* sp. nov. is closest morphologically to the two previously known Australian species: *S. digitata* Lendenfeld, 1888 and *S. moretonensis* van Soest, Hooper, Beglinger and Erpenbeck 2006. However, *S. ananas* sp. nov., and *S. maraca* sp. nov. show a novel clubbed or oval (rather than digitate or lobed) morphology. These two species contain a unique spicule type (anatriaene-like) not previously reported in the Axinellida. As a consequence of this study the species diversity of *Sollasella* is doubled to six species, with all species confined to the Indian and Pacific oceans.

KEYWORDS: morphology, taxonomy, systematics, molecular phylogenetics, sponge

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INTRODUCTION

The genus *Sollasella* was first established by Lendenfeld (1888). He named *S. digitata*, from New South Wales, as the type species for the genus. Subsequently Hallmann (1914) redescribed the species, providing additional details and images of the lectotype from the NHMUK. Van Soest et al. (2006) determined that *Raspailopsis cervicornis* Burton, 1959 was a second species of *Sollasella* and redescribed that species from type material (NHMUK) as well as freshly collected material from the vicinity of Oman, the type locality. They also described a third species, *S. moretonensis* van Soest, Hooper, Beglinger and Erpenbeck, 2006 from Queensland and Western Australia.

At a higher systematic level, the familial and ordinal placement of the genus was resolved when Sollasellidae Lendenfeld, 1887 was synonymised with Raspailiidae Nardo, 1833 (order Poecilosclerida; van Soest et al. 2006). A more recent study provided molecular evidence which confirmed this systematic placement (Erpenbeck et al. 2007). Consequently, three species of *Sollasella* are currently recognised; there is the type species *S. digitata* Lendenfeld, 1888 from New South Wales, *S. moretonensis* van Soest, Hooper, Beglinger and Erpenbeck, 2006 from Queensland and Western Australia, and *S. cervicornis* Burton, 1959 from the western Arabian Sea (van Soest et al. 2021). The genus is therefore only known from the Indian and western Pacific oceans.

In this study we describe three new species from the eastern Indian Ocean, Western Australia. We review the morphological characters used to describe species, highlight the importance of some of these, provide additional data and comparisons between species, and a species key. We report the first finding of an anatriaene-like spicule in the Axinellida and discuss the implications of this.

MATERIAL AND METHODS

Collections of fresh material were made by SCUBA diving, or by trawl or epibenthic sled beyond diving depths, from several localities along the northern Western Australian coast. Specimens were preserved in 70–100% ethanol. Type specimens and slides of *Sollasella digitata* and *S. moretonensis* were borrowed from the Australian and Queensland Museums respectively. A map shows the location of specimens utilised in this study (Figure 1), with sequenced specimens in Table 1.

For freshly-collected material, subsamples were cut at right angles to the surface and processed using a graded ethanol dehydration and histolene clearing procedure. They were then embedded in paraffin, sectioned at right angles to the sponge surface with a Leitz slide microtome, and mounted on glass slides with EZ-mountant to determine the skeletal arrangement. Spicule preparations were made with nitric acid, washed in distilled water, mounted on glass slides and examined with an Olympus BX50 microscope. For SEM (TM 3030Plus), dissociated spicules were dried, mounted on stubs and sputter coated with gold. For each spicule type, 20 spicules were measured per specimen, except when noted otherwise. Spicule measurements are expressed as min–av–max spicule length / min–av–max spicule width in micrometers. In the three new species descriptions an overall min–av–max spicule length / min–av–max spicule width in micrometers is calculated from the holotype measurements and three paratypes for each species.

Subsamples of tissue were also used to extract genomic DNA, using the DNeasy blood and tissue kit (Qiagen) according to the manufacturer's instructions. Extractions were used in PCR reactions, using primers and conditions outlined in Table 2. All reactions were tried with 1ul of neat extraction first, followed by concentration and dilution series (1:20 and 1:50 were often successful). PCR amplicons were outsourced for enzymatic clean-up and sequencing via a capillary sequencer (ABI) at the Australian Genome Research Facility, Perth. Raw sequences were assembled, edited and quality checked in Geneious Prime 2020.2.5. They were then aligned using the MAAFT plug in (Katoh and Standley 2013) and analysed using PopART (Leigh et al. 2015, TCS algorithm Clement et al. 2002) and IQ-tree (Nguyen et al. 2015, Chernomor et al. 2016, Kalyaanamoorthy et al. 2017). The maximum likelihood phylogeny was mid-point rooted and nodes assessed with 1000 ultrafast replicates. The two fragments of COI were assembled as one continuous piece for haplotype networks, but the 28S fragments do not overlap and were analysed separately. Of the nine specimens with existing data for 28SD3D5 (*S. cervicornis, S. moretonensis, S. suttonorum*), we re-sequenced six to ensure veracity.

The following acronyms have been used in this paper:

AMS	Australian Museum (Sydney, New South Wales).
NHMUK	Natural History Museum (London, United Kingdom).
NTM	Museum and Art Gallery of the Northern Territory (Darwin, Northern Territory).
QM	Queensland Museum (Brisbane, Queensland).
WAM	Western Australian Museum (Perth, Western Australia).
ZMA	Zoological Museum (University of Amsterdam, Netherlands).

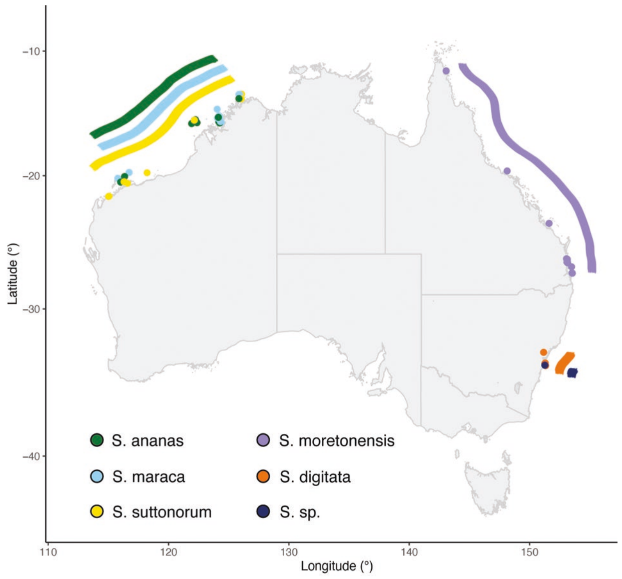

FIGURE 1 Map showing the location of *Sollasella* specimens utilised in this study, excluding *S. cervicornis*, Oman. Dots represent specimens and offset lines represent species distributions.

RESULTS

The haplotype networks showed varying levels of resolution. The COI network (Figure 2) differentiates among all species except *S. ananas* and *S. maracas*, as well as recovering two haplotypes within *S. suttonorum*. The 28S D3–D5 fragment recovers a single haplotype network for all included species and shows 6 mutational steps between *S. ananas* and *S. maracas*. The 28S C-region fragment shows the most resolution and recovers a single haplotype network for all included species as well as 24 mutational steps between *S. ananas* and *S. maracas*.

The concatenated maximum likelihood phylogeny (Supplementary Figure 1) shows two main lineages. One contained the two new species with club-like or oval morphology, and the other lineage contained the rest of the species in *Sollasella*. The single specimen of *Sollasella* sp. from NSW (represented only by a single gene) was nested inside *S. suttonorum*, but with a relatively long branch. All other species formed monophyletic clades, although *S. moretonensis* was not highly supported (BS 56). All other species were better supported where testable (*S. ananas* BS 100, *S. maracas* BS 99, *S. suttonorum* BS 81).

TABLE 1 *Sollasella* specimens sequenced in this study. Holotypes in bold. Depths estimated to nearest metre.

Reg. No.	Species	Location	Depth (m)	Latitude	Longitude	Date	COI	28SD3D5	28S-C
WAMZ88025	*ananas*	Camden Sound, WA	39	-15.376306	124.139547	21 Mar 2015	MZ408260	MZ409557	MZ409584
WAMZ88421	*ananas*	Camden Sound, WA	41	-15.725853	124.166978	23 Mar 2015	MZ408261	MZ409559	MZ409585
WAMZ88431	*ananas*	Camden Sound, WA	16	-15.823992	124.248742	24 Mar 2015	MZ408262	MZ409556	MZ409586
WAMZ90694	*ananas*	Lynher Bank, WA	72	-15.5608	122.234233	29 Oct 2016	MZ408263	MZ409558	MZ409587
WAMZ95018	*ananas*	Eclipse Islands, WA	42	-13.870788	125.849004	8 Mar 2016	MZ408264	MZ409555	MZ409588
ZMAPOR17450	*cervicornis*	Dhofar, Oman	17	16.950433	54.818483	11 Dec 2002	MZ408265	MZ409535	MZ409568
WAMZ87345	*maraca*	Camden Sound, WA	53	-15.376689	124.248319	15 Mar 2015	MZ408266	MZ409550	MZ409576
WAMZ87779	*maraca*	Camden Sound, WA	45	-15.253592	124.203039	19 Mar 2015	MZ408267	MZ409554	MZ409578
NTMZ007749	*maraca*	Camden Sound, WA	36	-15.431364	124.059194	20 Mar 2015	MZ408268	MZ409553	MZ409583
WAMZ87955	*maraca*	Camden Sound, WA	62	-15.446442	124.083022	20 Mar 2015	MZ408269	MZ409552	MZ409579
WAMZ88085	*maraca*	Camden Sound, WA	28	-15.711306	124.315778	22 Mar 2015	MZ40827	MZ409549	MZ409581
WAMZ94066	*maraca*	Maret Islands, WA	33	-14.7208	124.039667	5 Dec 2015	MZ408271	MZ409551	MZ409577
WAMZ95073	*maraca*	Eclipse Islands, WA	23	-13.536462	125.846464	10 Mar 2016	MZ408272	MZ409548	MZ409580
WAMZ95323	*maraca*	Eclipse Islands, WA	27	-13.521582	125.906131	14 Mar 2016	MZ408273	MZ409547	MZ409582
QMG303059	*moretonensis*	Cape Grenville, QLD	31	-11.617	143.069	26 Mar 1993	MZ408274	MZ409536	MZ409567
QMG303205	*moretonensis*	N Stradbroke Is, QLD	25	-27.418	153.551	2 Jun 1993	-	MZ409538	-
QMG303227	*moretonensis*	N Stradbroke Is, QLD	30	-27.401	153.533	4 Jun 1993	-	MZ409534	MZ409566
QMG303996	*moretonensis*	Mooloolaba, QLD	11	-26.602	153.103	9 Feb 1994	-	MZ409537	MZ409562
QMG315719	*moretonensis*	Noosa, QLD	18	-26.376	153.126	12 Oct 1999	-	MZ409529	MZ409560
QMG315759	*moretonensis*	Noosa, QLD	21	-26.346	153.067	13 Oct 1999	-	MZ409530	MZ409561
QMG321402	*moretonensis*	Mooloolaba, QLD	13	-26.645	153.161	18 Aug 2004	-	MZ409531	MZ409563
QMG321796	*moretonensis*	Gladstone, QLD	10	-23.677	151.618	11 Nov 2004	-	MZ409533	MZ409564
QMG329277	*moretonensis*	Ayr, QLD	45	-19.625	148.135	28 Nov 2005	MZ408277	MZ409532	MZ409565

Reg. No.	Species	Location	Depth (m)	Latitude	Longitude	Date	COI	28SD3D5	28S-C
AMSZ5725	*Sollasella* sp.	Malabar, NSW	7	-33.967	151.267	20 Jul 1972	MZ408275	-	-
QMG306153	*suttonorum*	Port Hedland, WA	37	-19.767	118.217	5 Sep 1995	-	MZ409539	MZ409569
WAMZ05487	*suttonorum*	Dampier Archipelago, WA	18	-20.585833	116.593833	2 Sep 1999	-	MZ409542	MZ409570
WAMZ65274	*suttonorum*	Onslow, WA	12	-21.596111	115.060556	26 Mar 2013	MZ408276	MZ409546	MZ409572
WAMZ81703	*suttonorum*	Pilbara Shelf, WA	37	-20.474722	116.307222	25 Jun 2013	-	MZ409544	MZ409573
WAMZ88378	*suttonorum*	Onslow, WA	10	-21.620278	115.011944	10 Jul 2015	-	MZ409543	MZ409574
WAMZ94761	*suttonorum*	Eclipse Islands, WA	25	-13.898364	126.039685	6 Mar 2016	MZ408278	MZ409541	MZ409571
NTMZ007747	*suttonorum*	Eclipse Islands, WA	27	-13.508897	126.078492	3 Mar 2016	MZ408280	MZ409545	-
WAMZ95470	*suttonorum*	Lynher Bank, WA	76	-15.6005	122.141033	29 Oct 2016	MZ408279	MZ409540	MZ409575

TABLE 2 Primers and PCR cycling conditions used in this study.

Primer name	Primer sequence	Program	Reference
COI			
SpongeCOI-F1 /	5’-AGATAGGDACWGCNTTTA-3’/	94°C 3 mi (94°C 30s, 41°C 30s, 72°C 60s) x35,	Vargas et al. 2015
dgHCO2198	5’-TAAACTTCAGGGTGACCAAARAAYCA-3’	72°C 5 mi	Meyer et al. 2005
COI			
SpongeCOI-F1 /	5’-AGATAGGDACWGCNTTTA-3’/	94°C 3 mi, (94°C 30s, 50°C 30s, 72°C 45s) x8,	Vargas et al. 2015
jgLCO1490 v2	5’-TITCIACIAAYCAYAARGAYATTGG-3’	(94°C 30s, 48°C 30s, 72°C 45s) x35, 72°C 5 mi	Geller et al. 2013
COI			
COX1-D2 /	5’-AATACTGCTTTTTTTGATCCTGCCGG-3’/	95°C 2 mi, 50°C 60s, 72°C 2 mi,	Rot et al. 2006
COX1-R1	5’-TGTTGRGGGAAAAARGTTAAATT-3’	(95°C 50s, 48°C 50s, 72°C 2 mi) x35, 72°C 10 mi	Rot et al. 2006
28s D3–D5			
Por28S-830F /	5’-CATCCGACCCGTCTTGAA-3’/	94°C 5 mi (94°C 30s, 55–50°C (TD) 30s, 72°C 30s) x10,	Morrow et al. 2012
Por28S-1520R	5’-GCTAGTTGATTCGGCAGGTG-3’	(94°C 30s, 53°C 30s, 72°C 30s) x25, 72°C 5 mi	Morrow et al. 2012
28s C-region			
28S C2 /	5’-GAAAAGAACTTTGRARAGAGAGT-3’/	95°C 4 mi, 51°C 2mi, 72°C 2 mi,	Chombard et al. 1998
28S D2	5’-TCCGTGTTTCAAGACGGG-3’	(95°C 60s, 51°C 60s, 72°C 60s) x35, 72°C 5 mi	Chombard et al. 1998

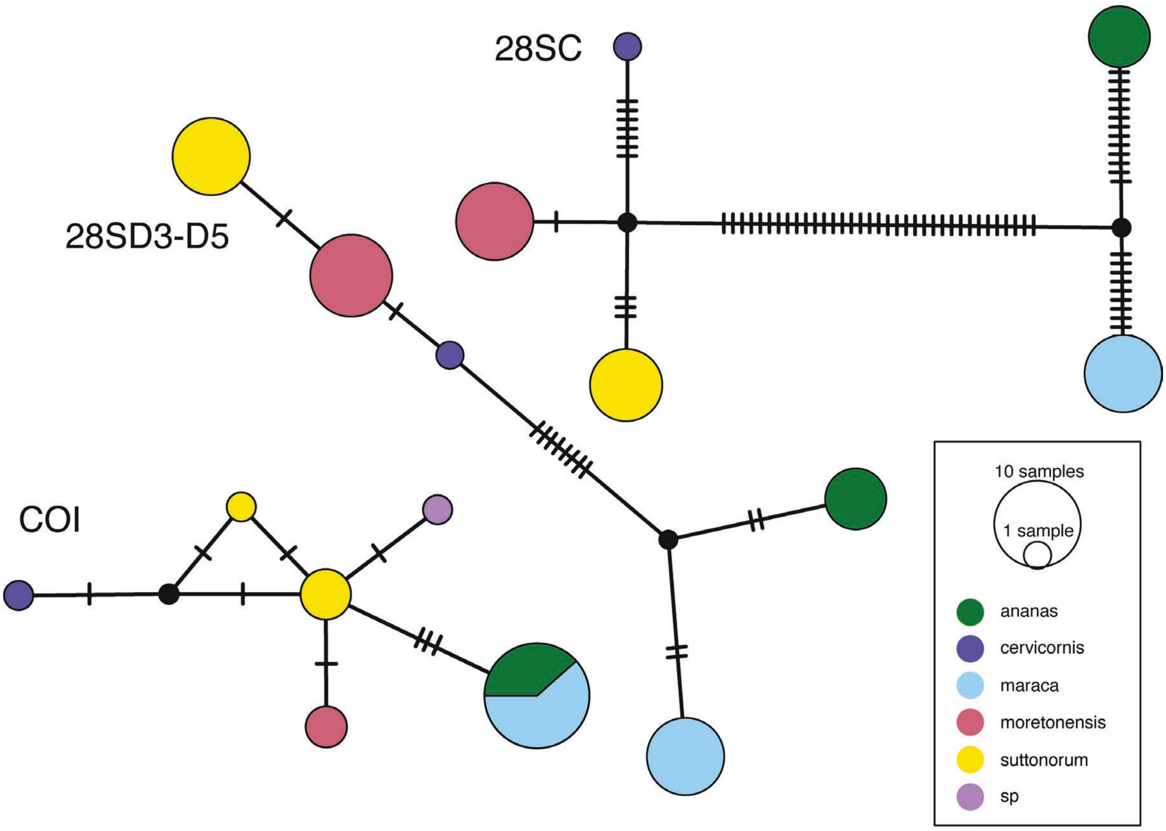

FIGURE 2 Statistical parsimony haplotype network of three gene regions (COI, 28SD3D5, 28S C-region) for species of *Sollasella*. Black circles represent extinct or unsampled haplotypes, hash marks represent one mutational step.

SYSTEMATICS

Class Demospongiae Bergquist, 1978

Order Axinellida Dendy, 1905

Family Raspailiidae Nardo, 1833

Genus *Sollasella* Lendenfeld, 1888

DEFINITION

Emended from van Soest et al. 2006: Raspailiidae with a strong axial column of confusedly aligned oxeas and styles/anisostrongyles with extra-axial columns of short oxeas and long and short styles/anisostrongyles positioned at right angles to the axial column. Branching, vasiform or oval morphology typically with a basal stalk, characterised by polygonal to rectangular surface plates surrounded by pores. Oxeas form a continuous cortical palisade of brushes centrally pierced by long styles/anisostrongyles. A low proportion of short acanthostyles may be present. Anatriaene-like spicules occur in two species.

TYPE SPECIES

Sollasella digitata Lendenfeld, 1888 (by monotypy).

Sollasella suttonorum
Fromont and Wilson, sp. nov.

Suttons' sponge

(Figures 1–2, 3–8, 15; Tables 3–4)

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DEFINITION

Branching *Sollasella* that are dichotomous, rounded apically, stalked basally, with small pores defining the edges of surface polygonal plates. Surface hispid in parts, usually apically or intermittently on the sides of branches. Firm and compressible texture. Spicules are smooth oxeas with a large size range and very large anisostrongyles. Skeleton divided into three parts: axially condensed central core, subcortical region of lower spicule density with spicule brushes crossing from the core to the cortex, and a surface cortical region.

MATERIAL EXAMINED

Holotype

Australia: ***Western Australia*:** Wheatstone, Onslow, Pilbara, 21°37'13"S, 115°00'43"E, 9 m depth, 10 July 2015, J. Fromont, M.A. Wahab, stn. RVS6222/D11-T4, SCUBA, WAMSI Onslow Survey II July 2015 (WAM Z88378^{DNA}).

Paratypes

Australia: ***Western Australia*****:** Enderby Island, Dampier Archipelago, Pilbara, 20°35.15'S, 116°35.63'E, 17 m depth, 2 September 1999, J. Fromont, stn. DA3/99/55, SCUBA, Woodside Dampier Expedition III 1999 (WAM Z5487$^{\mathrm{DNA}}$); Bare Rock, Pilbara, 20°28'29"S, 116°18'26"E, 36–38 m depth, 25 June 2013, E. Morello, G. Fry, M. Miller, D. Thomson, D. Bearham, stn. PMCP/118, sled, CSIRO Pilbara Seabed Biodiversity Characterisation & Mapping survey 2013 (WAM Z81703$^{\mathrm{DNA}}$); Eclipse Islands, Kimberley, 13°53'54.110"S, 126°02'22.867"E, 24 m depth, 6 March 2016, O.A. Gomez, J.A. Ritchie, stn. SOL79/WA079, epibenthic sled, WAMSI Survey 3 Eclipse Islands March 2016 (WAM Z94761$^{\mathrm{DNA}}$); Lynher Bank, Kimberley, 15°36'01.800"S, 122°08'27.720"E, 76 m depth, 29 October 2016, J. Fromont, J.A. Ritchie, stn. SOL20/WA110, epibenthic sled, WAMSI Survey 4 Lynher Bank Oct-Nov 2016 (WAM Z95470$^{\mathrm{DNA}}$); Eclipse Islands, Kimberley, 13°30'32.030"S, 126°04'42.572"E, 26–27 m depth, 3 March 2016, O.A. Gomez, J.A. Ritchie, stn. ECL45/WA072, epibenthic sled, WAMSI Survey 3 Eclipse Islands March 2016 (NTM Z007747$^{\mathrm{DNA}}$).

Other material

Australia: ***Western Australia*****:** SW of Cape Jaubert, -19.7666666666667, 118.216666666667, 37 m depth, 5 September 1995, S. Cook, RV Southern Surveyor, by trawl (QM G306153$^{\mathrm{DNA}}$); Wheatstone, Onslow, Pilbara, 21°35'46"S, 115°03'38"E, 12 m depth, 26 March 2013, J. Fromont, E. Buettner, stn. RVS5737/D10-T4, SCUBA, WAMSI Onslow Survey I March 2013 (WAM Z65274$^{\mathrm{DNA}}$).

Material examined for comparison

Australia: ***New South Wales*****:** *paralectotype Sollasella digitata*, Port Jackson, Sydney, 33°51'S, 151°16'E (AMS G9107); *Sollasella* sp. east of Malabar, Sydney, 33°58'S, 151°16'E, 7 m depth, 20 July 1972, Australian Museum Shelf Benthic Survey (AMS Z5725$^{\mathrm{DNA}}$). ***Queensland*****:** holotype, *Sollasella moretonensis*, Middle Reef, N of North Stradbroke Island, 27.40083°S, 153.53°E, 30 m depth, 4 June 1993, J.N.A. Hooper, J.A. Kennedy, SCUBA (QM G303227$^{\mathrm{DNA}}$); *paratype* (QM G321402$^{\mathrm{DNA}}$) and 7 other specimens (QM G303996$^{\mathrm{DNA}}$, QM G331599$^{\mathrm{DNA}}$, QM G315649$^{\mathrm{DNA}}$, QM G315759$^{\mathrm{DNA}}$, QM G303205$^{\mathrm{DNA}}$, QM G315759$^{\mathrm{DNA}}$, QM G303059$^{\mathrm{DNA}}$; collection details in van Soest et al. 2006).

DESCRIPTION

Stalked branching sponge. Branches rounded apically, frequently dichotomous (Figure 3). Distinctive polygonal plates (largest 3 x 3 mm) over surface, with numerous small pores (0.05 mm) outlining polygon edges. Surface hispid apically and intermittently along sides of branches from spicules extending to 3 mm; stalk and most of branch surfaces not hispid (Figure 4). Consistency firm and compressible (preserved 75% ethanol), or incompressible (100% ethanol).

Dimensions: holotype WAM Z88378 overall height x width x breadth 110 x 75 x 15 mm, stalk height x width x breadth 40 x 25 x 15 mm, branches height x width x breadth 70 x 15 x 13 mm; largest specimen WAM Z95470 overall height x width x breadth 140 x 90 x 17 mm, stalk height x width x breadth 50 x 17 x 15 mm, branches height x width x breadth 90 x 15 x 13 mm. Color *in vivo* reddish brown, in ethanol dull grey, or brown if covered in sediment.

Skeleton: The sponge body is clearly divided into three parts (Figure 5). Oxeas, anisostrongyles and fibre arranged longitudinally, form a dense axial region up to 5 mm wide. At right angles to the surface, oxeas form dense brushes with a central anisostrongyle, forming a cortical region 1 mm wide (Figure 6). Anisostrongyles extend beyond the surface to 3 mm. In between is a subcortical region of lower spicule density, 3 mm wide, with spicule brushes crossing from the core to the surface cortex. Brushes taper from the cortex to the axial core. The skeletal layout is the same in the branches and in the basal stem.

Spicules: Spicules are abundant oxeas with a large size range, usually straight, occasionally curved, rarely wavy, with long hastate tapering points that are occasionally acerate, rare anisostrongyle forms: size 240–$\underline{645}$–1010 x 4–$\underline{16.2}$–35 µm (Figure 7, Tables 3–4). Anisostrongyles that are extremely long, straight: size 2500–$\underline{4609}$–7200 x 22–$\underline{44.6}$–68 µm (Figure 15, Tables 3–4). No acanthostyles.

ECOLOGY

Collected from 9–38 m depth, on low rocky outcrops or reef, can withstand high sediment load in water column. Barnacle on stalk of WAM Z94761.

REPRODUCTION

Reproductive elements were not observed.

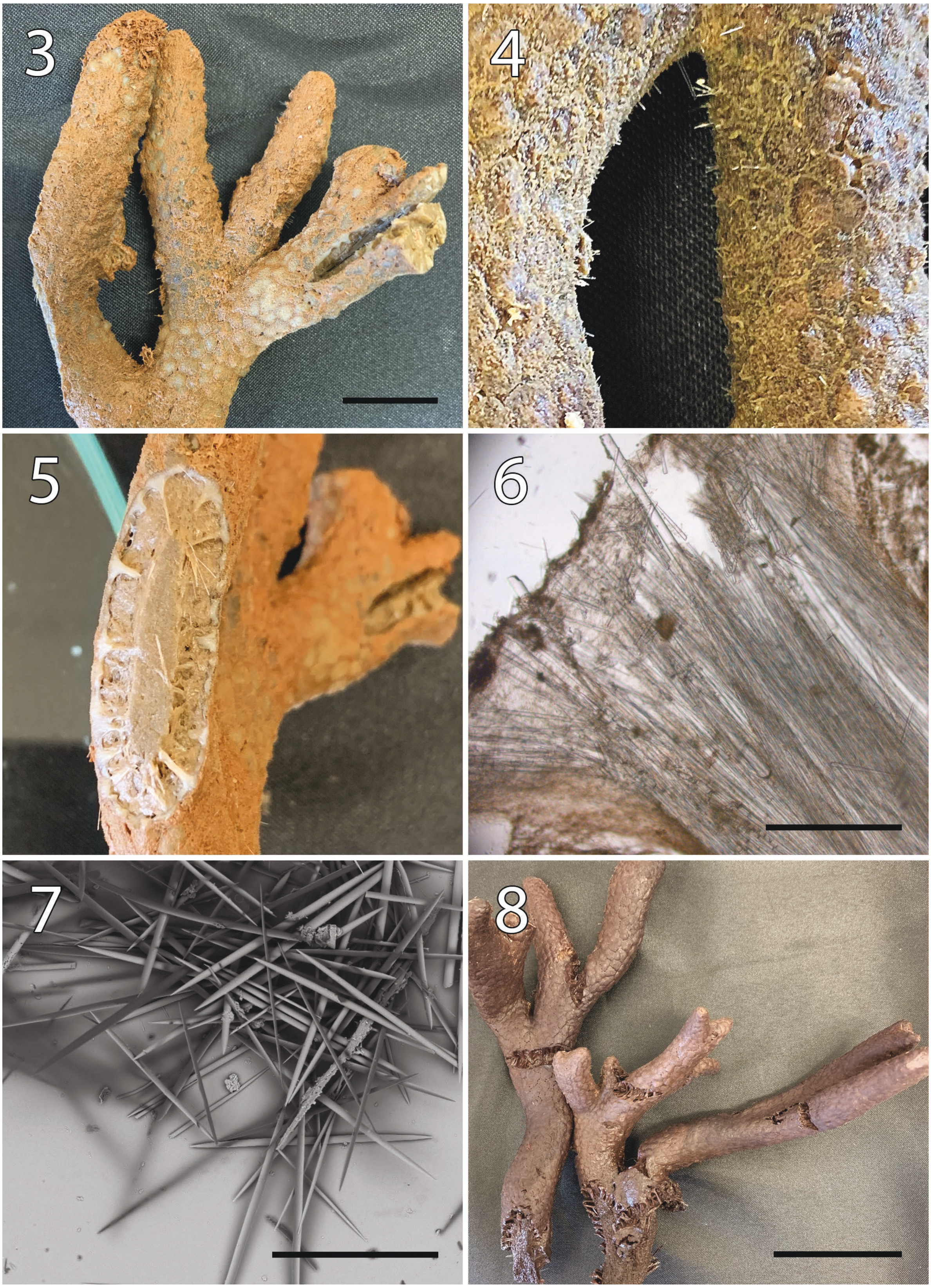
DISTRIBUTION

Sollasella suttonorum sp. nov. is restricted to the tropical Pilbara and Kimberley regions of Western Australia (Figure 1).

REMARKS

Sollasella suttonorum is distinguished from other species of *Sollasella* by its surface polygons and complement and size range of spicules (Tables 3–4). Although all species of *Sollasella* have surface polygons, oxeas and some form of long spicule, it is the combination found in *S. suttonorum* that is unique.

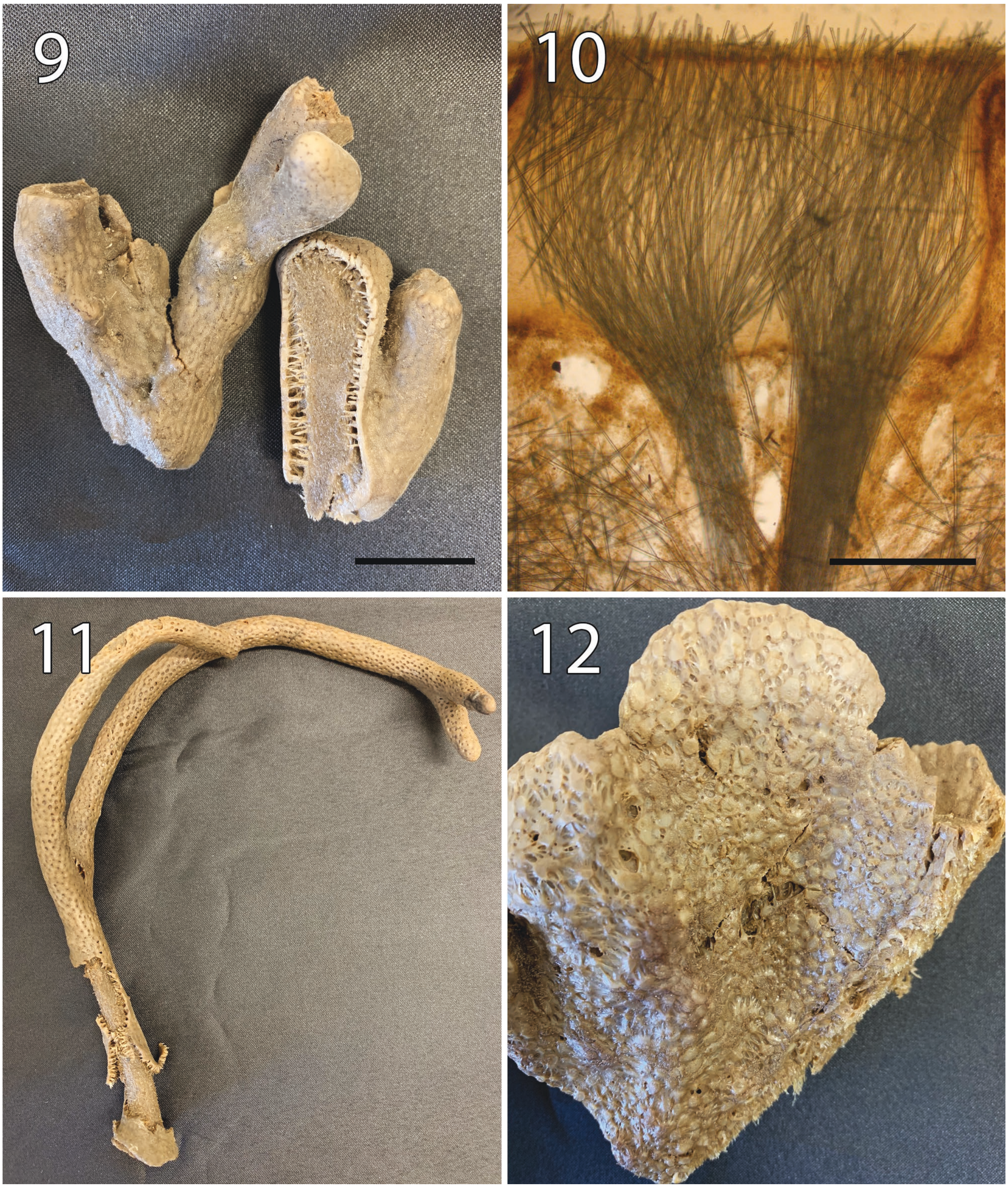
The paralectotype of *S. digitata* (AMS G9107) has oxeas and anisostrongyles (Figure 10) and lacks acanthostyles, as found in *S. suttonorum*. However, the size ranges of the spicules differ with both oxeas and anisostrongyles in *S. digitata* consistently shorter than those in *S. suttonorum* (Table 3, Figures 13, 15). In addition, the surface polygons of *S. digitata* are small



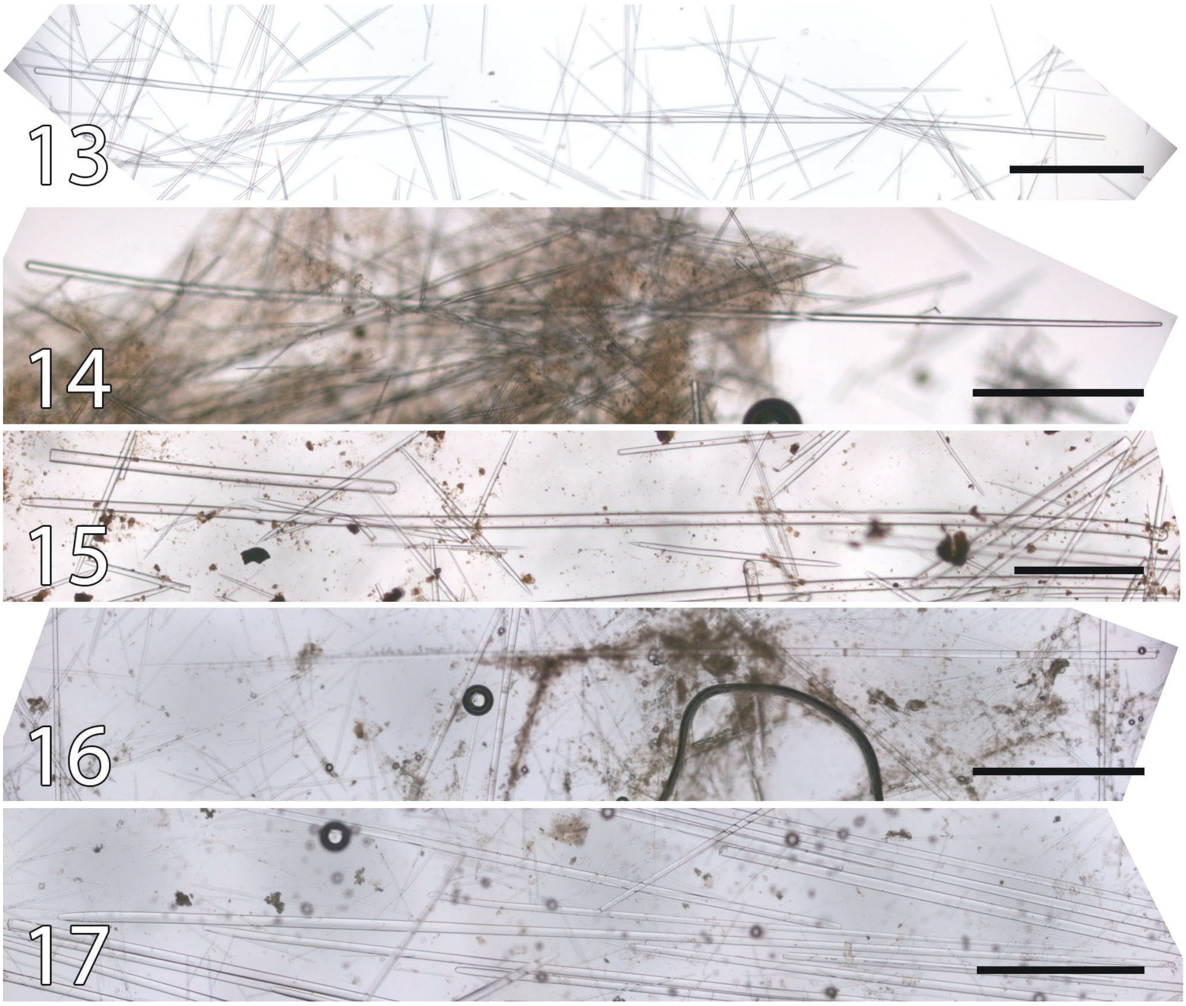
FIGURES 3–8 *Sollasella suttonorum* sp. nov. 3) holotype (WAM Z88378) whole specimen showing rounded apices and polygonal surface plates, scale = 2 cm; 4) paratype (WAM Z95470) close up of surface polygons and hispid sides of branches; 5) holotype (WAM Z88378) longitudinal section through branch showing axially condensed core, subcortical region and cortex; 6) paratype (WAM Z5487) brushes of cortical skeleton showing large central anisostrongyles (broken), scale = 500 µm; 7) paratype (WAM Z94761) SEM image of oxeas showing large size range, scale = 500 µm; 8) (QM G306153) whole specimen showing branching habit and polygonal surface plates without net-like collagen scale = 2 cm.

and elongate (Figure 9). Lendenfeld (1888) reported them to be 1–2 mm wide, and Hallmann (1914) noted that the surface structures in the type specimen were ‘much elongated in the longitudinal direction of the branches’, also measuring them as only 1–2 mm wide, concurring with Lendenfeld (1888) on their narrow width.

Our examination of the paralectotype also found the surface structures are narrow and elongate (Figure 9), markedly different from the polygons of *S. suttonorum* which are 3 x 3 mm wide. The narrow, more rectangular structures in *S. digitata* were not noted by van Soest et al. (2006) but this may in part be due to



FIGURES 9–12 9) *Sollasella digitata* syntype (AMS G9107) whole specimen showing rounded apices and small rectangular surface plates on branches, scale = 2 cm; 10) *S. digitata* syntype (AMS G9107) skeleton showing characteristic cortical brushes of oxea, scale = 500 um; 11) *Sollasella* sp. (AMS Z5725) whole specimen showing long, apically bifurcated branches and small surface plates; 12) *S. moretonensis* holotype (QM G303227) whole specimen showing fan-shaped habit and large polygonal surface plates with net-like collagen.



FIGURES 13–17 Large anisostrongyles characteristic of *Sollasella* species. 13) *Sollasella digitata* syntype (AM G9107) scale = 500 µm; 14) *S. moretonensis* holotype (QM G303227) scale = 500 µm; 15) *S. suttonorum* holotype (WAM Z88378) scale = 500 µm; 16) *S. ananas* holotype (WAM Z88431) scale = 1 cm; 17) *S. maraca* holotype (WAM Z94066) scale = 1 cm.

a non type specimen, figured in Hallmann (1914) and reproduced in van Soest et al. (2006), that appears to have polygonal structures.

Sollasella suttonorum differs from *S. cervicornis* in size of spicules, with *S. suttonorum* having oxeas and anisostrongyles that are longer than those in *S. cervicornis* (Table 3). The latter species also has abundant smooth styles, of a similar size to the oxeas, not seen in *S. suttonorum* or *S. digitata*. *Sollasella cervicornis* has polygons (4 x 2 mm) which are more elongate than those in *S. suttonorum*.

Sollasella suttonorum is very different from *S. moretonensis*. The latter species has larger polygons (≤ 5 x 6 mm), a vasiform, lobate or fan-shaped morphology (Figure 12) and acanthostyles as part of the spicule complement (Table 3). *Sollasella moretonensis* has two size categories of oxeas, with the smaller category restricted to the ectosomal region (van Soest et al. 2006). Combining these two categories gives a similar size range of oxeas to that found in *S. suttonorum*, but in the latter species, oxeas of different sizes are not restricted to distinct parts of the skeleton.

One specimen (QM G306153, Figure 8), previously referred to *S. moretonensis* (van Soest et al. 2006, Hooper et al. 2008), was found to conform to *S. suttonorum* in branching morphology, surface polygonal detail, spicule complement and sizes as well as DNA, and has been transferred to this species.

In summary, the branching morphology and combination of surface polygon shape, spicule complement and sizes, characterise *S. suttonorum*.

ETYMOLOGY

The new species is named for Jane Fromont's family, David, Zollie and Hanna Sutton, in recognition of their constant support during her career as a sponge biologist, museum curator and head of Aquatic Zoology, Western Australian Museum.

Sollasella ananas
Fromont and Wilson, sp. nov.

Pineapple sponge

(Figures 1–2, 16, 18–23; Tables 3–4)

urn:lsid:zoobank.org:act:4AB8A295-2C8D-4FA7-BFA2-8D0E5E4D7391

DEFINITION

Oval *Sollasella* that are stalked basally with conspicuous surface polygonal plates. Centre of polygons may be raised. Pores around polygons not visible. Firm, slightly compressible texture. Cream alive and preserved. Spicules are smooth oxeas with a large size range and very large anisostrongyles, anatriaene-like spicules occur axially. Skeleton divided into three parts: axially condensed central core, subcortical region of lower spicule density with spicule brushes crossing from the core to the cortex, and a surface cortical region.

MATERIAL EXAMINED

Holotype

Australia: *Western Australia*: Camden Sound, Kimberley, 15°49'26.37"S, 124°14'55.47"E, 16 m depth, 24 March 2015, J. Fromont, L. Kirkendale, stn. SOL105/WA037, epibenthic sled, WAMSI Survey 1B Camden Sound March 2015 (WAM Z88431^{DNA}).

Paratypes

Australia: *Western Australia*: Camden Sound, Kimberley, 15°49'26.37"S, 124°14'55.47"E, 16 m depth, 24 March 2015, J. Fromont, L. Kirkendale, stn. SOL105/WA037, epibenthic sled, WAMSI Survey 1B Camden Sound March 2015 (WAM Z88325); Camden Sound, Kimberley, 15°43'33.07"S, 124°10'01.12"E, 40 m depth, 23 March 2015, J. Fromont, L. Kirkendale, stn. SOL77/WA034, epibenthic sled, WAMSI Survey 1B Camden Sound March 2015 (WAM Z88421^{DNA}); Camden Sound, Kimberley, 15°22'34.70"S, 124°08'22.37"E, 39 m depth, 21 March 2015, J. Fromont, L. Kirkendale, stn. SOL160/WA025, epibenthic sled, WAMSI Survey 1B Camden Sound March 2015 (WAM Z88025^{DNA}); Eclipse Islands, Kimberley, 13°52'14.837"S, 125°50'56.414"E, 41–42 m depth, 8 March 2016, O.A. Gomez, J.A. Ritchie, stn. ECLE1/WA084, epibenthic sled, WAMSI Survey 3 Eclipse Islands March 2016 (WAM Z95018^{DNA}); Lynher Bank, Kimberley, 15°33'38.880"S, 122°14'03.240"E, 72 m depth, 29 October 2016, J. Fromont, J.A. Ritchie, stn. SOL21A/WA111, epibenthic sled, WAMSI Survey 4 Lynher Bank Oct-Nov 2016 (WAM Z90694^{DNA}); Lynher Bank, Kimberley, 15°48'14.100"S, 122°22'03.780"E, 45 m depth, 01 November 2016, J. Fromont, J.A. Ritchie, stn. SOL59/WA114, epibenthic sled, WAMSI Survey 4 Lynher Bank Oct-Nov 2016 (WAM Z90856); Lynher Bank, Kimberley, 15°36'01.800"S, 122°08'27.720"E, 76 m depth, 29 October 2016, J. Fromont, J.A. Ritchie, stn. SOL20/WA110, epibenthic sled, WAMSI Survey 4 Lynher Bank Oct-Nov 2016 (NTM Z007748); off Mclennan Bank, Pilbara, 20°29'46.32"S, 116°1'34.32"E, 38 m depth, 3 November 2017, B. Alvarez, stn. W18/535, epibenthic sled, CSIRO RV INVESTIGATOR 2017_05 (WAM Z41922).

Other material

Australia: *Western Australia*: Lynher Bank, Kimberley, 15°52'29.160"S 121°55'07.380"E, 49–50 m depth, 22 October 2016, J. Fromont, J.A. Ritchie, stn. SOL15/WA098, epibenthic sled, WAMSI Survey 4 Lynher Bank Oct-Nov 2016 (WAM Z95480); Camden Sound, Kimberley, 15°22'34.70"S, 124°08'22.37"E, 39 m depth, 16 March 2015, J. Fromont, L. Kirkendale, stn. SOL100/WA008, epibenthic sled, WAMSI Survey 1B Camden Sound March 2015 (WAM Z88429); off Mclennan Bank, Pilbara, 20°29'49.56"S, 116°1'22.44"E, 32 m depth, 4 November 2017, B. Alvarez, stn. W18/543, McKenna trawl, CSIRO RV INVESTIGATOR 2017_05 (WAM Z41559); off Kendrew Island, Pilbara, 20°3'52.92"S, 116°20'49.92"E, 56 m depth, 24 October 2017, B. Alvarez, stn. W84/281, epibenthic sled, CSIRO RV INVESTIGATOR 2017_05 (WAM Z41889).

DESCRIPTION

Oval sponge tapering to short stalk (Figure 18–20). Distinctive polygonal plates (largest 4 x 4 mm) over surface. Centre of polygons may be raised due to central core of anisostrongyles, most visible when the sponge has been preserved in 100% ethanol (Figure 20). Pores around polygons not visible. Consistency firm and slightly compressible (preserved 75% ethanol), or incompressible (100% ethanol). Stalk may be covered in sediment reflecting the habitat of the sponge (Figure 20).

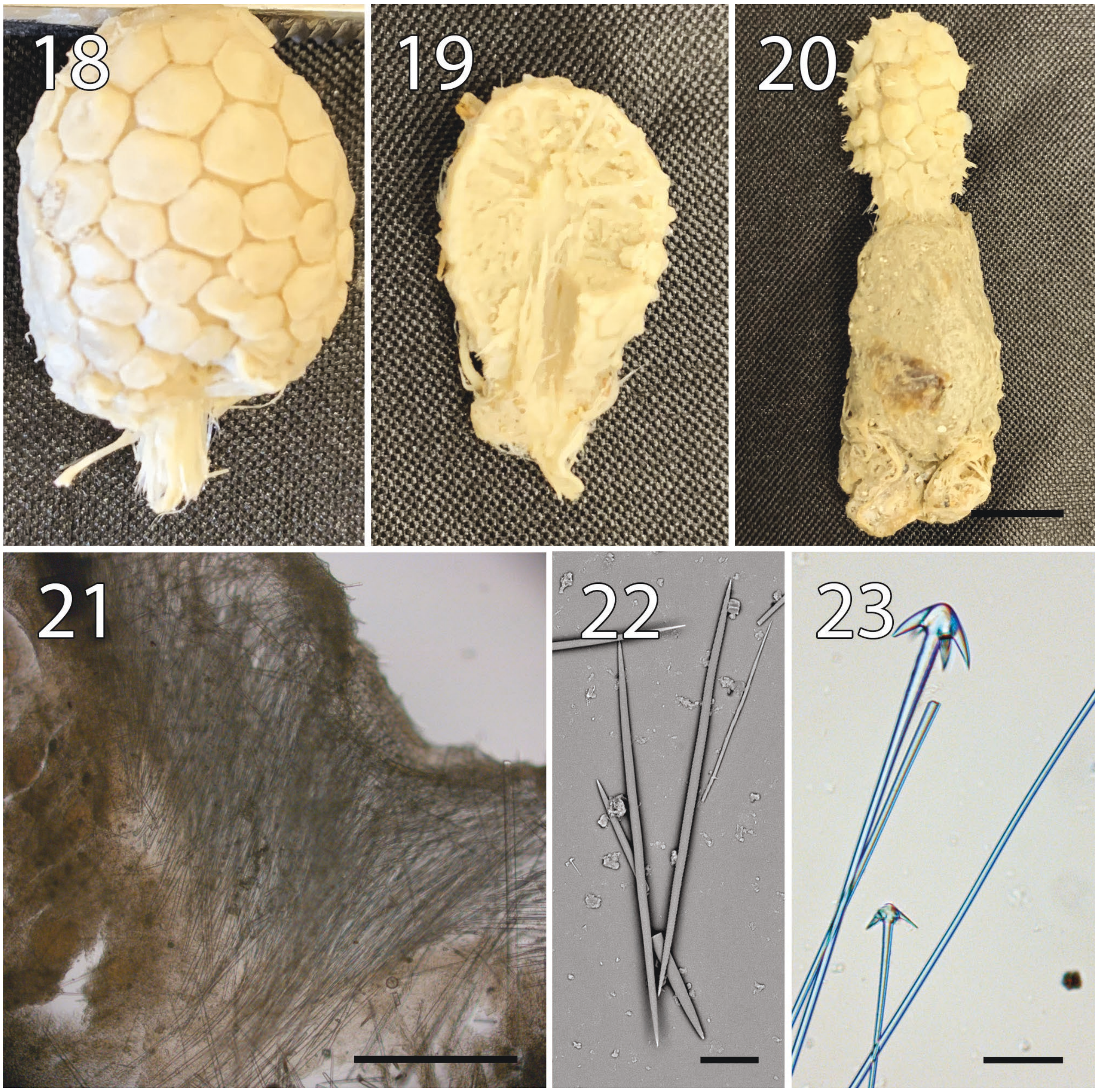
Dimensions: holotype WAM Z88431 overall height x width x breadth 30 x 17 x 16 mm, stalk (incomplete) height 6 x 4 x 4 mm, body height 24 mm; largest specimen WAM Z41889 overall height x width x breadth 48 x 27 x 26 mm, stalk height x width x breadth 11 x 13 x 12 mm, body height 36 mm. Color *in vivo* and in ethanol cream, may have a fine cover of sediment.

Skeleton: The sponge body is clearly divided into three parts (Figure 19). Oxeas and anisostrongyles, arranged longitudinally with some spongin reinforcement, form a dense axial region up to 3 mm wide. At right angles to the surface, oxeas form dense brushes with a central anisostrongyle, forming a cortical region 1 mm wide (Figure 19). In between is a subcortical region of lower spicule density, 4 mm wide, with spicule brushes crossing from the core to the surface cortex (width of skeletal regions from holotype). Brushes taper from the cortex to the axial core. Anisostrongyles extend beyond the surface to 1 mm in specimens preserved in 100% ethanol. The stalk has three skeletal components as found in the body of the sponge but with a reduced width in the subcortical region and anatriaene-like spicules axially. The anatriaene-like spicules are most prevalent at the base of the sponge stalk, also occur in the axial skeleton of the stalk and, albeit rarely, in the axis of the sponge body. The clads originate from a central 'tyle' and are recurved (Figure 23).

Spicules: Spicules are abundant oxeas with a large size range, usually straight or wavy, long hastate tapering points: size 280–710–990 x 5–11.5–20 µm (Figure 22, Tables 3–4). Anisostrongyles that are extremely long, straight: size 3920–6303–9250 x 20–39.8–50 µm (Figure 16, Tables 3–4). Anatriaene-like spicules that are extremely long and thin, often sinuous: size 3020–4799–6900 x 2–2.9–4 µm (Figure 23, Tables 3–4). No acanthostyles.

ECOLOGY

Collected from 16–76 m depth on low rocky outcrops, which may have cover of sediment.



FIGURES 18–23 *Sollasella ananas* sp. nov. 18) holotype (WAM Z88431) whole specimen showing oval morphology, polygonal plates and short stalk; 19) paratype (WAM Z88421) longitudinal section through whole specimen showing cortex, subcortex and axial core; 20) paratype (WAM Z95018) whole specimen showing anisostrongyles extending from centre of polygons and sediment encrusting basal stalk, scale = 1 cm; 21) holotype (WAM Z88431) skeleton showing characteristic cortical brushes of oxea around long anisostrongyloxeas (broken), scale = 500 µm; 22) holotype (WAM Z88431) SEM image of oxeas showing showing long hastate points, scale = 50 µm; 23) holotype (WAM Z88431) light microscope image of long, thin anatriaene-like spicules, scale = 50 µm.

REPRODUCTION

WAM Z88431 is a reproductive female containing oocytes, collected in March 2015.

DISTRIBUTION

Sollasella ananas sp. nov. is restricted to the tropical Pilbara and Kimberley regions of Western Australia (Figure 1).

REMARKS

Sollasella ananas is distinguished from all other species of *Sollasella* by its oval external morphology and large polygons such that it resembles a pineapple, and its cream colour. No pores are visible around the polygon edges. The species is most similar to *S. maraca*, which is also oval, but dark brown to black in colour. The size range of oxeas in *S. ananas* is similar to other species of *Sollasella*, but it lacks stylote or stronglyote forms. The anisostrongyles are larger than in *S. digitata*, *S. cervicornis*, *S. moretonensis* or *S. suttonorum*, and closest in size to those in *S. maraca* (Table 3). A striking character of this species is the presence of anatriaene-like spicules in the central axis of the sponge; they are most prevalent in the stalk, entwined around the anisostrongyles or forming dense tracts.

ETYMOLOGY

The name of the new species derives from its external shape and polygonal surface structures which resemble those of a pineapple. 'Ananas' has been adopted by many languages as the name for the pineapple, apparently derived from the Brazilian Tupi word 'nanas'. The name is to be treated as a noun in apposition.

Sollasella maraca Fromont & Wilson, sp. nov.

Maraca sponge

(Figures 1–2, 17, 24–31; Tables 3–4)

urn:lsid:zoobank.org:act:B4CEF779-D523-4C5C-952C-4EEB98FF8004

DEFINITION

Elongate oval *Sollasella* that are stalked basally with conspicuous surface polygonal plates. Centre of polygons may be raised. Pores around polygons not visible. Firm, slightly compressible texture. Dark brown to black alive and preserved. Spicules are smooth oxeas, occasionally with strongylote tips, with a large size range, and very large anisostrongyles, anatriaene-like spicules occur axially. Spicules form dense tracts longitudinally in the stalk. Skeleton poorly differentiated into three parts: axial central core, subcortical region with pronounced spicule brushes crossing from the core to the cortex and a collagenous surface cortical region.

MATERIAL EXAMINED

Holotype

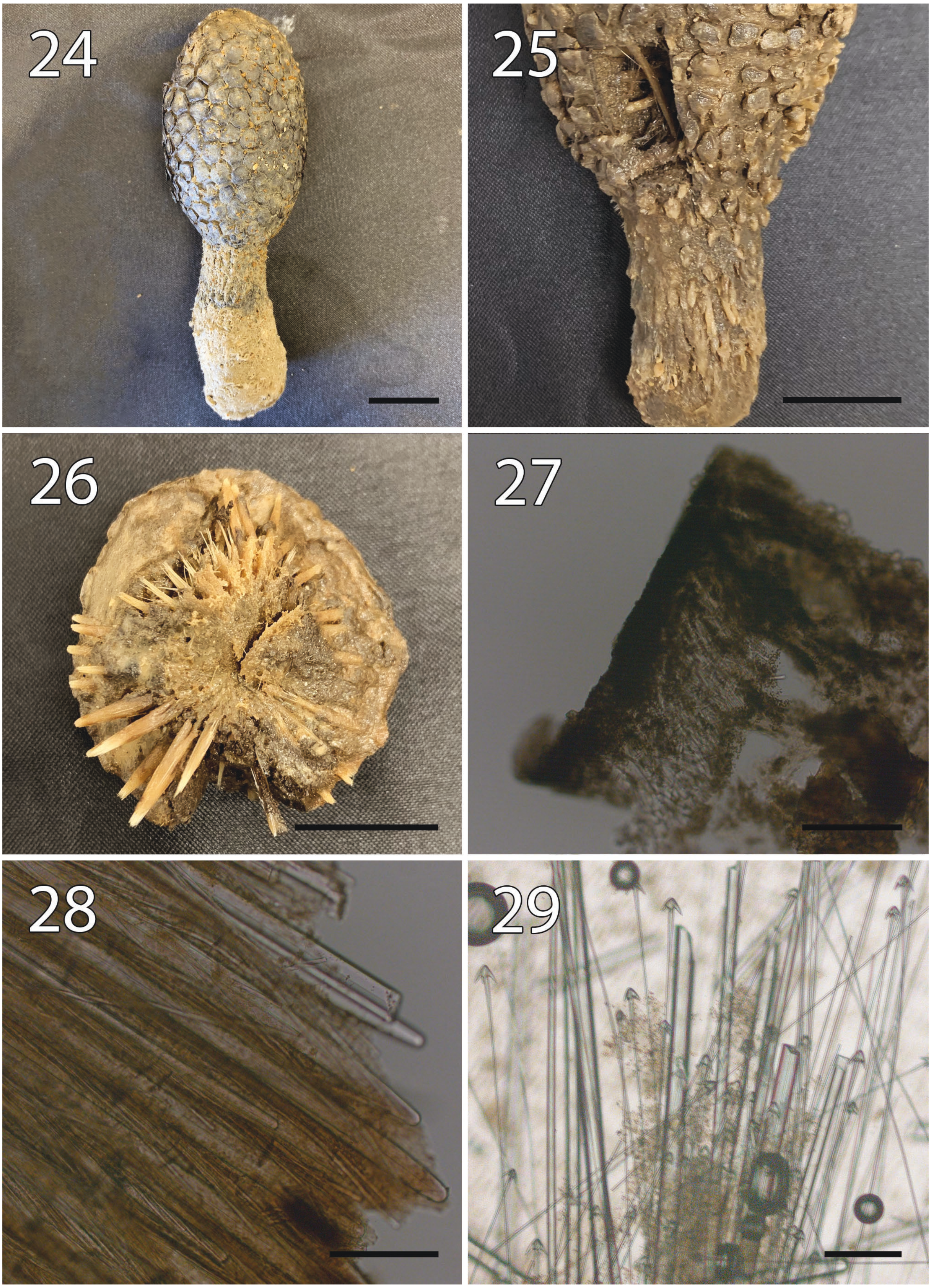
Australia: *Western Australia*: Maret Islands, Kimberley, 14°43.248'S, 125°02.378'E, 32 m depth, 5 December 2015, O.A. Gomez, J.A. Ritchie, stn. SOL52/WA045, epibenthic sled, WAMSI Survey 2 Maret Islands December 2015 (WAM Z94066^{DNA}).

Paratypes

Australia: *Western Australia*: Camden Sound, Kimberley, 15°22'36.08"S, 124°14'53.95"E, 52–53 m depth, 15 March 2015, J. Fromont, L. Kirkendale, stn. SOL120/WA005, epibenthic sled, WAMSI Survey 1B Camden Sound March 2015 (WAM Z87345^{DNA}); Camden Sound, Kimberley, 15°25'52.91"S, 124°03'33.10"E, 36 m depth, 20 March 2015, J. Fromont, L. Kirkendale, stn. SOL84/WA021, epibenthic sled, WAMSI Survey 1B Camden Sound March 2015 (NTM Z007749^{DNA}); Camden Sound, Kimberley, 15°42'40.70"S, 124°18'56.80"E, 27–28 m depth, 22 March 2016, J. Fromont, L. Kirkendale, stn. SOL2/WA030, epibenthic sled, WAMSI Survey 1B Camden Sound March 2015 (WAM Z88085^{DNA}); Eclipse Islands, Kimberley, 13°32'11.264"S, 125°50'47.270"E, 21–24 m depth, 10 March 2016, O.A. Gomez, J.A. Ritchie, stn. ECL38/WA087, epibenthic sled, WAMSI Survey 3 Eclipse Islands March 2016 (WAM Z95073^{DNA}); Eclipse Islands, Kimberley, 13°31'17.695"S, 125°54'22.072"E, 27 m depth, 14 March 2016, O.A. Gomez, J.A. Ritchie, stn. ECL40/WA097, epibenthic sled, WAMSI Survey 3 Eclipse Islands March 2016 (WAM Z95323^{DNA}); off Glomar Shoal, Pilbara, 19°44'44.52"S, 116°43'39.72"E, 51 m depth, 21 October 2017, B. Alvarez, stn. W72/198, McKenna trawl, CSIRO RV INVESTIGATOR 2017_05 (WAM Z41318).

Other material

Australia: *Western Australia*: Camden Sound, Kimberley, 15°15'12.93"S, 124°12'10.94"E, 44–45 m depth, 19 March 2015, J. Fromont, L. Kirkendale, stn. SOL32/WA019, epibenthic sled, WAMSI Survey 1B Camden Sound March 2015 (WAM Z87779^{DNA}); Camden Sound, Kimberley, 15°26'47.19"S, 124°04'58.88"E, 61 m depth, 20 March 2015, J. Fromont, L. Kirkendale, SOL4/WA022, epibenthic sled, WAMSI Survey 1B Camden Sound March 2015 (WAM Z87955^{DNA}); Camden Sound, Kimberley, 15°46'58.31"S, 124°22'40.97"E, 33 m depth, 25 March 2015, J. Fromont, L. Kirkendale, stn. SOL97/WA039, epibenthic sled, WAMSI Survey 1B Camden Sound March 2015 (WAM Z88446); off Violet Island, Pilbara, 20°11'55.32"S, 115°47'21.12"E, 53 m depth, 5 November 2017, B. Alvarez, stn. W49/578, McKenna trawl, CSIRO RV INVESTIGATOR 2017_05 (WAM Z41580).



FIGURES 24–29 *Sollasella maraca* sp. nov. 24) holotype (WAM Z94066) whole specimen showing oval morphology tapering basally, polygonal plates and pleated appearance of stalk, scale = 2 cm; 25) (WAM Z41318) base of whole specimen and stalk showing thick longitudinal tracts of anisostrongyles in stalk, scale = 2 cm; 26) paratype (WAM Z95073) cross section through whole specimen showing collagenous nature of sponge, lack of differentiation between the three skeletal regions and thick tracts of spicules, scale = 2 cm; 27) holotype (WAM Z94066) cortical brushes densely covered in surface pigment cells, scale = 200 µm; 28) holotype (WAM Z94066) skeleton showing end of a thick tract of anisostrongyles, scale = 200 µm; 29) paratype (WAM Z95323) light microscope image of long, thin anatriaene-like spicules, scale = 200 µm.

DESCRIPTION

Dimensions: holotype WAM Z94066 overall height x width x breadth 110 x 36 x 35 mm, stalk height 45 x 25 x 24 mm, body height 60 mm; largest specimen WAM Z41318 overall height x width x breadth 125 x 56 x 56 mm, stalk height x width x breadth 35 x 24 x 20 mm, body height 90 mm. Color *in vivo* and in ethanol dark brown to black, may have a fine cover of sediment.

Skeleton: Elongate oval sponge tapering to stalk (Figure 24–29). Distinctive polygonal plates (largest 5 x 5 mm) over surface. Centre of polygons may have a raised protrusion due to a central core of anisostrongyles (Figure 24). Pores around polygons not visible. Consistency firm and slightly compressible (preserved 75% ethanol), or incompressible (100% ethanol). Relatively long stalk may be covered basally in sediment reflecting the habitat of the sponge (Figure 24). Anisostrongyles form dense tracts longitudinally in the stalk giving a 'pleated' appearance (Figure 24–25). Skeleton poorly differentiated into three parts: axial central core, subcortical region with pronounced spicule brushes crossing radially from the core to the cortex (Figures 26–28) and a collagenous surface cortical pigmented region (Figure 27). The stalk has three skeletal components as found in the body of the sponge but with a reduced width in the subcortical region and anatriaene-like spicules axially (Figure 29). The anatriaene-like spicules are most prevalent at the base of the sponge stalk, also occur in the axial skeleton of the stalk and, albeit rarely, in the axis of the sponge body. The clads originate from a central 'tyle' and are recurved (Figure 29).

Spicules: Spicules are abundant oxeas with a large size range, usually straight or wavy, long hastate tapering points, frequent strongylote modifications, rare stylote: size 270–562–1000 x 4–10.3–18 µm (Figures 30–31, Tables 3–4). Anisostrongyles that are extremely long, straight or slightly curved: size 4250–6589–9600 x 20–55.3–80 µm (Figures 17, 27–28, Tables 3–4). Anatriaene-like spicules that are extremely long and thin, often sinuous: size 4250–6159–6900 x 2–2.9–3 µm (Figure 29, Tables 3–4). No acanthostyles.

ECOLOGY

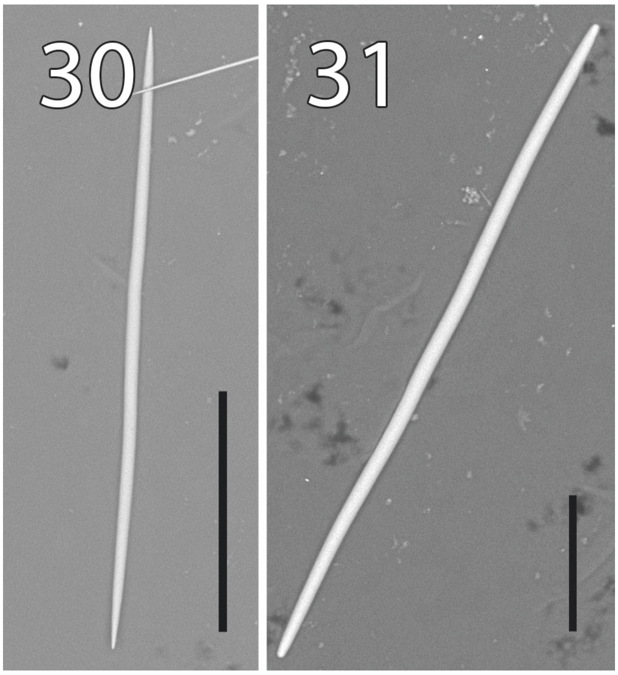
Collected from 24–61 m depth, on low rocky outcrops, which may have cover of sediment.

REPRODUCTION

Reproductive elements were not observed.

DISTRIBUTION

Sollasella maraca sp. nov. is restricted to the tropical Pilbara and Kimberley regions of Western Australia (Figure 1).



FIGURES 30–31 *Sollasella maraca* sp. nov. 30) holotype (WAM Z94066) SEM image of oxea, scale = 250 µm; 31) holotype (WAM Z94066) SEM image of strongylote form, scale = 100 µm.

REMARKS

Sollasella maraca is distinguished from all other species of *Sollasella* by its elongate oval external morphology, sturdy appearance, long stalk, and large polygons with central protrusions. No pores are visible around the polygon edges. The species is most similar to *S. ananas,* which is also oval, but does not attain the same large size or large stalk as *S. maraca* and is distinctively cream in colour, while *S. maraca* is dark brown to black. *Sollasella maraca* and *S. ananas* have the largest anisostrongyles reported for species of *Sollasella* (Tables 3–4). In addition, *S. maraca* has numerous strongylote modifications of the oxeas, a character not seen in any of the other species of *Sollasella*. Both these species contain anatriaene-like spicules in the central skeletal axis, that are most prevalent in the stalk, entwined around the anisostrongyles or forming dense tracts. This is an extremely unusual spicule for a raspailiid genus and has not been reported before in any Axinellida. The presence of this spicule type is discussed in detail below.

ETYMOLOGY

The name of the new species derives from its external shape which resembles a maraca. 'Maraca' is the Brazilian name for a percussion instrument, and the name is to be treated as a noun in apposition.

TABLE 3 Spicule measurements of species of *Sollasella*. Measurements are min–av–max length / min–av–max width, in micrometers, and based on holotype measurements for the three new species. Oxea measurements in *S. maraca* are for both oxeote and strongylote forms, * n=5.

Species	Oxeas I	Oxeas II	Short styles	Subtylostrongyles/styles/ anisostronglyoxeas	Acanthostyles	Anatriaene -like spicules*	References
S. digitata	700 x 8	-	-	2000 x 45	-	-	Lendenfeld, 1888
	340 (450–650) 760 x ≤15–16			2000–≥4000 x 10–35			Hallmann, 1914
	340–760 x 10–16			2000–4000 x 10–35			Van Soest et al., 2006
	430–571–720 x 6–9–10			2500–3541–4250 x 15–23–30			present study
S. cervicornis	710–850 x 20–29	-	495–710 x 18–25	1600–3000 x 32–50	-	-	Van Soest et al., 2006
S. moretonensis	660–940 x 14–20	360–515 x 5–8	-	2500–≥4000 x 20–55	95–165 x 3–5	-	Van Soest et al., 2006
S. suttonorum	240–645–1010 x 7–17–28	-	-	2500–4239–5125 x 38–47–50	-	-	present study
S. ananas	280–528–810 x 5–10–15	-	-	3920–5976–7725 x 20–39–50	-	3020–3875–5040 x 3–3.4–4	present study
S. maraca	330–528–730 x 5–9–13	-	-	4545–6094–7300 x 38–50–58	-	4400–5455–6875 x 2.5–3–3	present study
Sollasella sp.	440–641–900 x 12–17–20 (n=8)	-	-	3450–3575–3700 x 50–53–55 (n=3)	-	-	present study

TABLE 4 Spicule measurements of paratype specimens of the three new species of *Sollasella*. Measurements are min–av–max length / min–av–max width, in micrometers ([1] n=20, [2] n=10, [3] n=5, * both oxeote and strongylote forms measured and grouped under 'oxeas').

Species	Specimen number	Oxeas[1]	Anisostronglyoxeas[2]	Anatriaene-like spicules[3]
S. suttonorum	WAM Z5487	380–657–960 x 8–12–18	3175–4302–5375 x 22–30–40	-
	WAM Z81703	370–635–910 x 8–13–20	3750–4300–4775 x 22–42–50	-
	WAM Z94761	360–679–1000 x 9–22–35	4600–5595–7200 x 55–60–68	-
S. ananas	WAM Z88421	300–641–970 x 6–11–16	5375–6257–7125 x 30–43–50	4500–5180–6300 x 2–2.6–3
	WAM Z95018	310–654–990 x 8–13–20	5000–6950–9250 x 20–39–50	3700–4730–6900 x 2–2.6–3
	WAM Z41922	380–657–960 x 8–12–18	3920–6029–9250 x 20–38–50	4900–5410–6050 x 3–3–3
*S. maraca**	WAM Z87345	370–634–1000 x 4–12–18	4250–6255–9600 x 20–47–70	4250–6165–7500 x 2.5–3–3.5
	WAM Z95073	270–540–790 x 4–10–12	7550–8015–8250 x 60–68–80	5500–5865–6250 x 2.0–2.8–3
	WAM Z95323	320–544–780 x 5–10–12	5000–5990–7225 x 48–56–65	5500–7150–8250 x 2.5–2.9–3

KEY TO SPECIES OF *SOLLASELLA*

1 Branching, lobed or fan-shaped 2

Oval-shaped, anatriaene-like spicules present 5

2 Lobed or fan-shaped, net-like collagenous surface.... ....*S. moretonensis*

Branching, no net-like collagenous surface............. 3

3 Small, narrow (1–2 mm wide) surface meshes, large anisostrongyles (2000–4000 mm) ....*S. digitata*

Polygonal surface meshes, large styles/anisostrongyles (1600–7500 mm) 4

4 Abundant smooth styles (495–710 mm), western Arabian Sea ....*S. cervicornis*

No smooth styles, eastern Indian Ocean ....*S. suttonorum*

5 External colour cream................................ *S. ananas*

External colour dark brown to black .... *S. maraca*

DISCUSSION

We report two remarkable findings from this study. The first is the the presence of anatriaene-like spicules in *S. ananas* and *S. maraca* (Figures 23, 29) and the second is the novel clubbed or oval (rather than digitate or lobed) morphology found in these species. Initially, we speculated that the novel spicules may not have been found previously in raspailiid species because the base of the stalk had not been present on specimens examined. This was the region where the anatriaene-like spicules were most prevalent in this study. All the specimens of *S. ananas* and *S. maraca* were collected by dredge or sled and the majority of the stalk bases were intact with sediment and substrate adhering to them. Alternatively, many of the branching specimens of *S. suttonorum* and *S. moretonensis* had been collected on SCUBA and did not have the stalk base attached; however, those that did were subsequently examined and did not contain anatriaene-like spicules. Consequently, we note that this spicule type is unique to *S. ananas* and *S. maraca* in the genus *Sollasella.* It would be of merit in future studies to examine other raspailiid genera to see if this spicule type is present.

Anatriaene-like spicules have never been reported from the Raspailiidae or the Axinellida. The spicules are extremely long, thin and fragile and occur next to anisostrongyles in the stalks of *S. ananas* and *S. maraca*. They were particularly prevalent at the base of the sponge and were found in all specimens of both species where the stalks were intact. We carefully examined the sediment at the base of the sponge and the axis of the stalk and found that they were not foreign spicules, sourced from the habitat, but intricately associated with the skeleton of the sponge. We consider them to be ‘anatriaene-like’ spicules as they may not be homologous to Tetractinellida anatriaenes. Fromont and Bergquist (1990) were the first to suggest that spicules considered to be of the same structural type, e.g. sigmas, may not be homologous. Erpenbeck et al. (2006) noted detailed functional distinctions of characters are required to disprove convergent evolution in what appear to be identical spicule types. More recently, Vacelet and Cárdenas (2018) reported an example of homoplasy, reporting a spicule similar to a euaster, in a genus in the Poecilosclerida. They concluded that the ‘asters’ may be derived from pseudoastrose acanthostyles but with complete loss of the spicule shaft. Much more detailed structural analysis of the anatriaene-like spicules found in this study will be required to determine if they are true anatriaenes but this is beyond the scope of this study. Consequently, we have not revised the diagnosis of Raspailiidae or Axinellida here.

Species of *Sollasella* can be distinguished by external morphological characters, the types of spicules present and details of spicule morphology. Of the six species of *Sollasella* now known, three have an erect branching morphology, with mostly dichotomous branches: *S. digitata, S. cervicornis* and *S. suttonorum* sp. nov. Among the branching species, *S. cervicornis* is the only one with relatively common small styles in the same size range as oxeas. All six known species have distinctive surface plates that are usually polygonal but can be rectangular (*S. digitata*). All included species are delimited by molecular data, but it bears repeating that the 28S-C region contains much more information than the traditionally used barcoding fragment of the COI gene (including the suggested addition of the second half of COI), as discussed by Erpenbeck et al. (2016). Here it showed great resolution among species, and we encourage this marker to be used more widely addressing species-level problems in sponges.

Sollasella moretonensis is unique within the genus for a number of reasons. This is the only species with a vasiform, lobate or fan-shape. The surface texture of net-like collagenous low ridges between polygons is a synapomorphy for the species. In addition, small acanthostyles are relatively common in this species but have only been rarely reported in *S. cervicornis* and not at all in the four other species. The two new species with oval morphologies, *S. ananas* and *S. maraca*, extend the diagnosis of the genus beyond branching, lobate and fan-shaped morphologies.

The large spicules in this genus have previously been referred to as styles (Lendenfeld 1888; van Soest et al. 2006). However, Hallmann (1914) referred to them as subtylostrongyles and his figure 1a[1] depicted one rounded spicule tip being wider than the other. This figure was reprinted in van Soest et al. (2006) and these authors, although calling the spicules styles, noted that Hallmann (1914) referred to them as ‘tylostrongyles’. Examination of the paralectotype shows the ‘tyle’ (a rounded swelling on a spicule, Boury Esnault and Rützler 1997) barely exists, and in *S. digitata* this spicule is more correctly an anisostrongyle, with both ends rounded, albeit unequally. We also found that the holotype of *S. moretonensis* had anisostronglyes, as did the three new species: *S. suttonorum, S. ananas* and *S. maraca* (Figures 13–17). We were not able to examine material of *S. cervicornis* but recommend this be done in the future. There was also variation in the oxeas found in these species. *Sollasella cervicornis* is reported to have abundant stylote modifications not seen in any other species (van Soest et al. 2006), while we found common strongylote forms in *S. maraca*, a spicule not reported in any other species. In *S. moretonensis*, *S. ananas* and *S. maraca* the oxeas generally have long hastate tapering points, while *S. suttonorum* had some acerate modifications and *S. digitata* has hastate oxeas and others with acerate or stepped tips. These oxeote modifications may be species specific.

We examined an undetermined specimen collected in New South Wales in 1972 (AMS Z5725) and obtained some sequence data (Folmer fragment of COI). However, we could not compare it genetically to *S. digitata,* as the paralectotype of this species did not amplify for any gene regions (AMS G9107, Erpenbeck et al. 2007), but we did see some morphological similarities that suggest it may be this species. It has small, rectangular surface meshes (Figure 11) currently only seen in *S. digitata* and the oxeas and anisostrongyles were similar in length to this species but thicker (Table 3). However, it has much more elongate branches than the paralectotype of *S. digitata*. The recollection of fresh, sequence-able material of *S. digitata* from near the type locality is necessary to establish the identity of the species, as there is still no genetic information available for the type species of the genus. If furnished, this data could provide information on the genetic distances between the species, and allow testing of the monophyly of the genus, the application of the genus name and its relationship to other raspailiid genera.

The original publication listed the type locality of *S. digitata* as 'east coast of Australia' but subsequent publications also clarified this as Port Jackson and Manly Beach; the AMS original hard copy register has 'E. Australia' for one paralectotype (G.3630 — part from British Museum of Natural History specimen) and Port Jackson (G.9107) for another (Stephen Keable, pers. comm.). The paralectotype G.3630 has a note added in the AMS 'Although recorded as a slide by Hooper and Weidenmayer (1994) material was located as a dry fragment in the non-type collection October 2020 and placed with other dry Porifera type specimens. The form of object as a dry fragment is more consistent with the original hard copy register entry from 1901 which indicates the material was presented by Prof. Arthur Dendy and the top of the page indicates fragments of Lendenfeld's types from the British Museum. Possibly this fragment should be considered Schizotype material'.

Bergquist identified two other specimens as *S. digitata* that were collected in NSW in the 1970s and are in the AMS collection. Although we have not physically examined these specimens, images of these (AMS Z15997 and Z4306) indicate they have the small, rectangular surface meshes that are characteristic of this species (Figures 32–33). This is particularly obvious in AMS Z15997 (Figure 32), while in AMS Z4306 (Figure 33) parts of the surface have rectangular surface meshes and others have elongate polygons. These are reminiscent of the figure of *S. digitata* in van Soest et. al (2006) suggesting that surface morphology in *S. digitata* is variable. However, the polygons do not resemble those found on the other four Australian species. It appears that few specimens of *Sollasella* have been collected in NSW, the type specimens in the 1800s and three others in the 1970s, whereas the other Australian species have abundant material.

This study increased the number of *Sollasella* species worldwide from three to six, but this may be an underestimate with sponges in many areas of the world still poorly studied (van Soest et al. 2021). The area of this study was restricted to north Western Australia yet resulted in three new species being discovered. Although the genus is restricted to the Indian and Pacific oceans, the diversity of species is clearly concentrated in the Australian region, with five of the six species recorded there. Furthermore, with the three new species in this publication, the tropical region of Western Australia is the most speciose region globally for the genus. This finding supports earlier reports by Hooper (1991) and Fromont (2003) that northern Western Australia has a disproportionately high number of raspailiid species, with high local endemism. Other sponge genera and families also have high diversity in northern Western Australia e.g. *Ianthella* (Kelly Borges and Bergquist 1995) and *Caulospongia* (Fromont 1998).

As well as being a region of high marine diversity, the north west shelf of Australia is a centre of endemism for many invertebrate groups (Wilson 2013). There is evidence of in situ speciation and radiation of benthic shelf species, especially in genera that lack pelagic larvae (Wilson 2013). This pattern is indicative of a former Tethyan distribution (with the current Indo-West Pacific region the largest remnant of the Sea of Tethys) followed by extinction on the Eurasian shelf (Wilson 2013). In the late Jurassic Period (160 mya) Australia formed part of the supercontinent Gondwana and only the west coast of Western Australia was open to the Tethys Sea, after India had drifted away (Marsh and Fromont 2020). The Australasian continental plate abutted the Indo-West Pacific and consequently the Australian north-western margin became proximal to the world's greatest centre of marine biodiversity (Wilson 2013). Pisera et al. (2017) considered the disjunct distribution of *Vetulina* (Demospongiae: Sphaerocladina: Vetulinidae), with the type species from the Caribbean and the only other two known species reported from northern Western Australia, to be an example of relict faunas that had their origin in the Tethys Sea.

Most species of *Sollasella* have relatively restricted distributions. *Sollasella digitata* is only known from

FIGURES 32–33 *Sollasella digitata*. 32) elongate branching specimen with narrow, elongate surface meshes (AMS G15997), scale = 2 cm; 33) small specimen with small polygonal meshes on some surfaces and irregular elongate meshes on others (AMS Z4306), scale = 2 cm.

New South Wales and has only been collected on three occasions, all in the 1970s, since the type specimens were found. *Sollasella moretonensis* was reported from Queensland and Western Australia, but we found the Western Australian specimen (QM G306153) conformed to *S. suttonorum* in molecular and morphological characters and have transferred the specimen to the new species. This means that *S. moretonensis* only occurs in Queensland. *Sollasella cervicornis* has only been found in the north-western Indian Ocean and *S. suttonorum, S. ananas* and *S. maraca* only from northern Western Australia. The characteristic surface plates make this genus distinctive and hopefully the reporting of these three new species will inspire scientists and divers to look for more. Furthermore, the reporting here of an anatriaene-like spicule in a non-tetractinellid genus may prompt research in testing spicule homologies.

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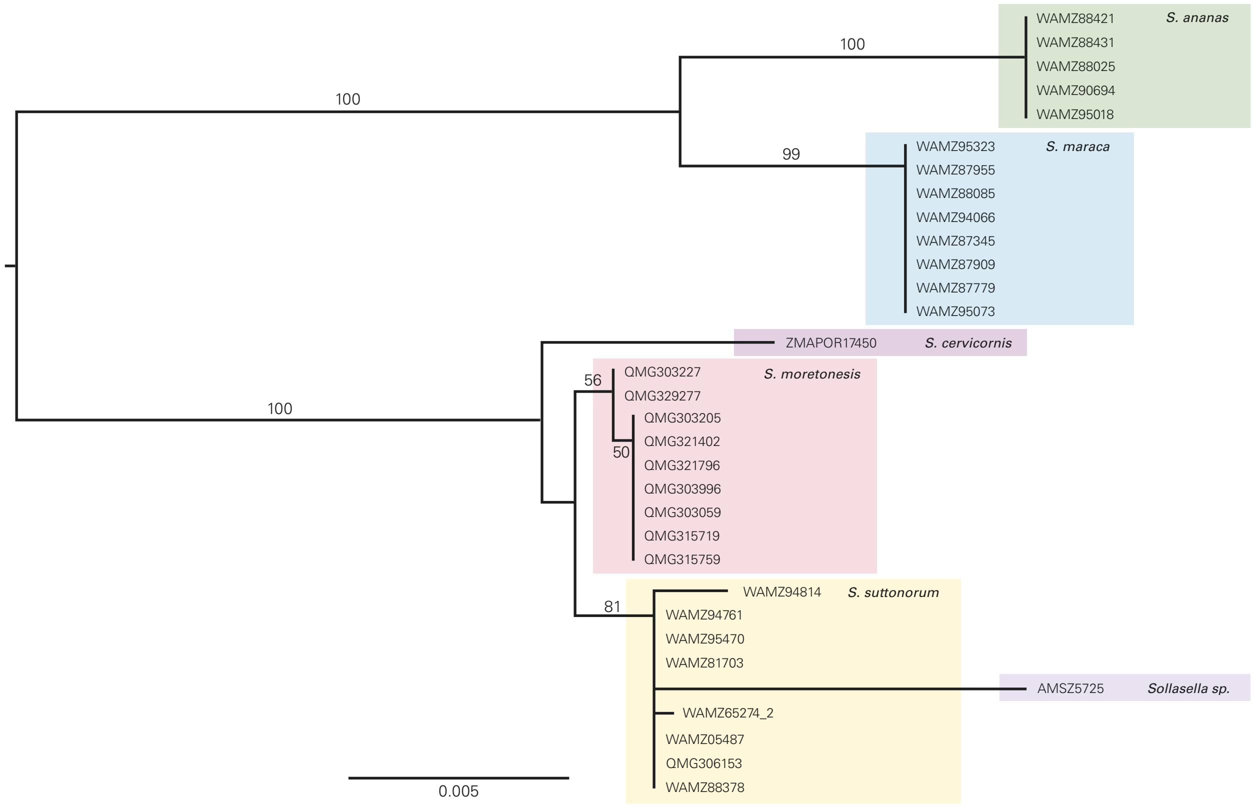
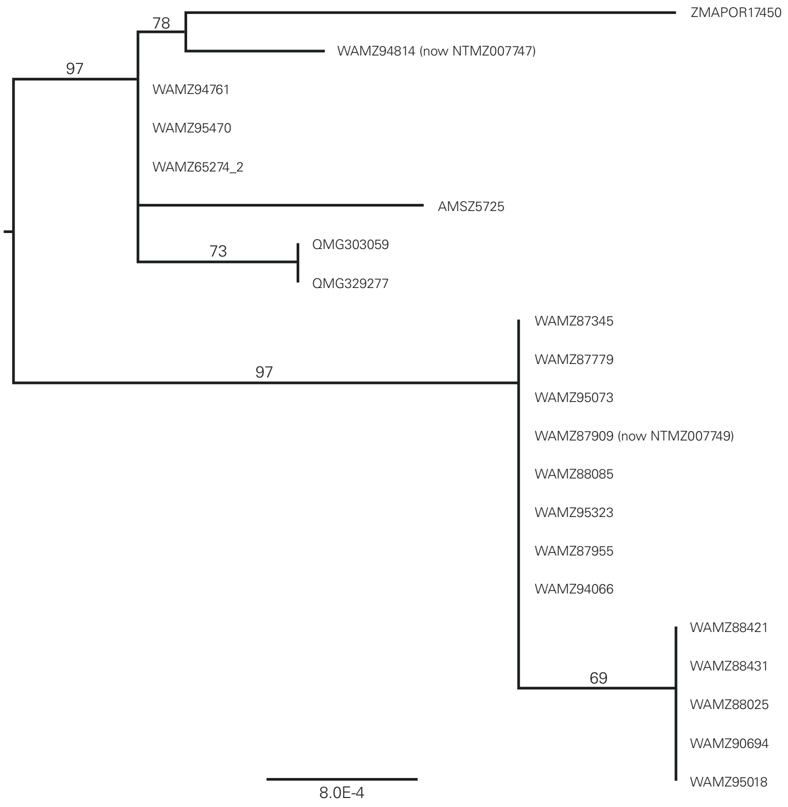
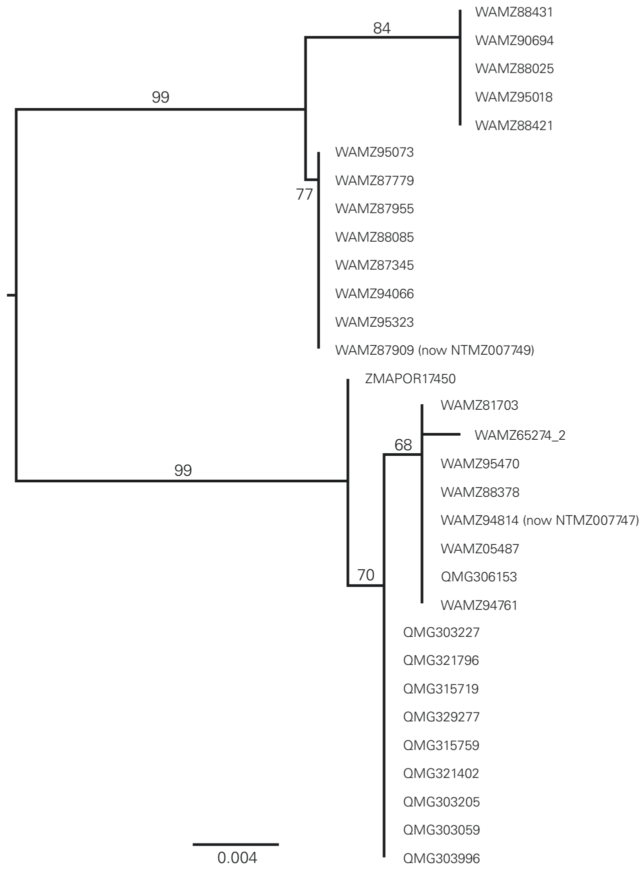


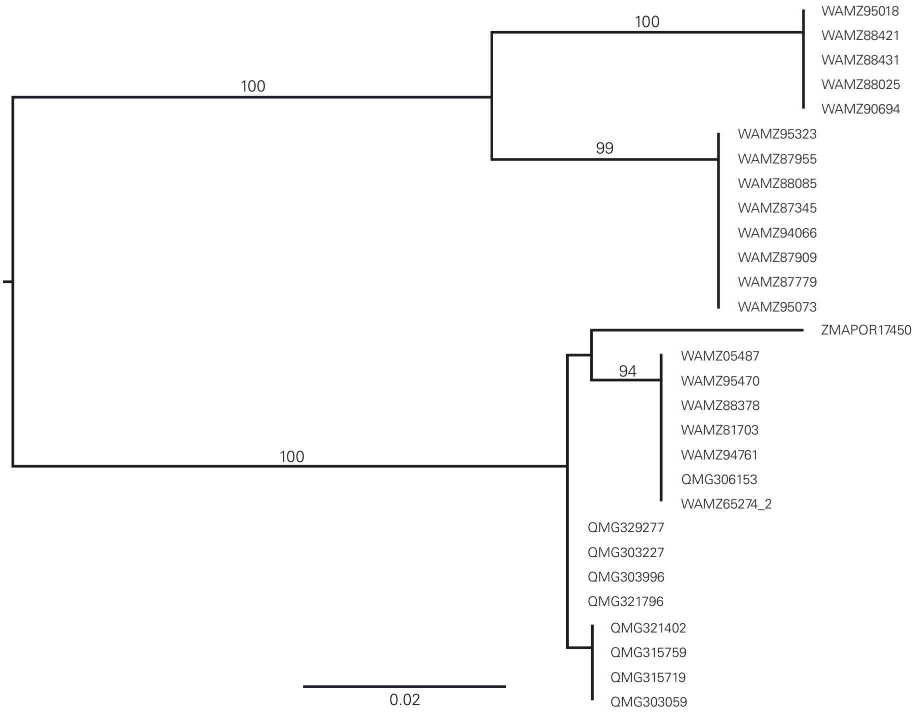
SUPPLEMENTARY FIGURE 1 Maximum likelihood concatenated tree of *Sollasella specimens* (COI, 28S D3D5, 28S C-region) with mid-point rooting.



SUPPLEMENTARY FIGURE 2 Maximum likelihood concatenated tree of *Sollasella* specimens (COI) with mid-point rooting.



SUPPLEMENTARY FIGURE 3 Maximum likelihood concatenated tree of *Sollasella* specimens (28S D3D5) with mid-point rooting.



SUPPLEMENTARY FIGURE 4 Maximum likelihood concatenated tree of *Sollasella* specimens (28S C-region) with mid-point rooting.