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Museum collections as untapped sources of undescribed diversity of sponge-zoantharian associations with the description of six new species of *Umimayanthus* (Zoantharia: Parazoanthidae) from Western Australia and eastern Indonesia

Javier Montenegro | ORCID: 0000-0002-0289-3274
Molecular Invertebrate Systematics and Ecology Laboratory, Graduate School of Engineering and Science, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 903-0213, Japan
Minderoo-UWA Deep-Sea Research Centre, School of Biological Sciences and Oceans Institute, The University of Western Australia, 35 Stirling Highway, Perth, WA 6009, Australia
jmontzalez@gmail.com

Jane Fromont | ORCID: 0000-0002-8887-4452
Collections and Research, Western Australian Museum, Welshpool, Western Australia, 6016, Australia

Zoe Richards | ORCID: 0000-0002-8947-8996
Collections and Research, Western Australian Museum, Welshpool, Western Australia, 6016, Australia
School of Molecular and Life Sciences, Curtin University, Kent St. Bently WA 6102, Australia

Hiroki Kise | ORCID: 0000-0002-4099-6469
Molecular Invertebrate Systematics and Ecology Laboratory, Graduate School of Engineering and Science, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 903-0213, Japan
Geological Survey of Japan, National Institute of Advanced Industrial Science and Technology, AIST, 1-1-1 Higashi, Tsukuba, Ibaraki 305-8567, Japan

Oliver Gomez | ORCID: 0000-0002-9106-6261
Collections and Research, Western Australian Museum, Welshpool, Western Australia, 6016, Australia

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Bert W. Hoeksema | ORCID: 0000-0001-8259-3783
Marine Evolution and Ecology Group, Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands
Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands

James Davis Reimer | ORCID: 0000-0003-0453-8804
Molecular Invertebrate Systematics and Ecology Laboratory, Graduate School of Engineering and Science, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 903-0213, Japan
Tropical Biosphere Research Center, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 903-0213, Japan

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Abstract

The zoantharian genus *Umimayanthus* consists largely of species that live in obligate symbioses with sponges. Although zoantharians have often been overlooked in field collecting campaigns and in research, sponges are usually well-collected, and many natural history museums harbor numerous sponge specimens. Thus, these sponge collections may also include previously overlooked zoantharian species. Such is the case in this research, in which we examined sponge specimens in museum collections from Western Australia and eastern Indonesia. Based on our morphological and molecular analyses, we herein describe six species of *Umimayanthus* new to science, and redescribe another species described over a century ago. These species can be distinguished by their sponge associations, gross polyp and colony morphology, and depth ranges. Based on these findings, it appears that the Central Indo-Pacific region of Western Australia and Indonesia can be considered a hotspot for sponge-associated zoantharian diversity. We provide a key for the identification of all formally described species in the genus, but caution that there are likely more *Umimayanthus* species awaiting discovery.

Keywords

Anthozoa – biodiversity – coral reefs – Porifera – species descriptions

Zoobank: http://zoobank.org/urn:lsid:zoobank.org:pub:19B47378-B015-401D-B011-AD48AFE8F8DD

Introduction

Natural history collections play a crucial societal role as reservoirs of biological information, spanning multiple generations of researchers. The information derived from biological collections impacts a large range of disciplines and provides a solid baseline for evolutionary and biodiversity studies (Suarez & Tsutsui, 2004). Natural history museums generally follow the prime directive to archive and document the diversity of species and their distributions on Earth. In this context, they are an irreplaceable tool for the scientific community, and the value of such collections can only increase with time (Krell & Wheeler, 2014; Rocha et al., 2014; Connelly et al., 2024). Each specimen in a collection is unique and represents a "snapshot" of the environment, location and the taxonomy that was understood at the time it was collected and/or used in a description or analysis (Winker, 2004). Furthermore, with the advances in technology and development of scientific knowledge, museum specimens are increasingly recognized as a unique source of unexplored information (Winker, 2004; Bakker et al., 2020; Nakahama, 2021). In recent years museum collections have been gaining attention as an abundant, convenient, and often unique snapshots in time, source of genetic data (Card et al., 2021; Sampaio et al., 2023), and as a stock of undescribed diversity. They also provide baselines to study changes in the species composition of biota in areas that undergo anthropogenic stress (Hoeksema & Koh, 2009; Van der Meij et al., 2010; Hoeksema et al., 2012; Richards et al., 2014; Drew, 2017).

One of the taxonomic groups that has been demonstrated to have unknown diversity represented in natural history collections is the order Zoantharia Rafinesque, 1815 (Reimer et al., 2014). Zoantharians are benthic hexacorals most closely related to actiniarians (sea anemones) and include taxa from shallow waters to the deep sea. Zoantharians are also recognized as an important components of nearshore cnidarian communities, and as such have a long history of research (Donati, 1765; Ellis, 1768; Fujii & Reimer, 2013; Low, 2016; Montenegro et al., 2020). Valuable and ground-breaking discoveries on zoantharian ecology, systematics and diversity have often stemmed from collections targeting other organisms, with associated zoantharians becoming unintended "bycatch" of this collection (Swain & Wulff, 2007; Montenegro et al., 2020; Kise et al., 2022). This has been particularly true in Porifera (sponge) collections, with sponges often establishing symbiotic associations with at least four genera of zoantharians in two families; *Epizoanthus* Gray, 1867 in the family Epizoanthidae Delage & Hérouard, 1901 and *Parazoanthus* Haddon & Shackleton, 1891, *Bergia* Duchassaing de Fonbressin & Michelotti, 1860, and *Umimayanthus* Montenegro, Sinniger & Reimer, 2015 in the family Parazoanthidae Delage & Hérouard, 1901. By targeting Porifera collections, scientists have discovered species new to science, described emerging ecological and evolutionary patterns in this symbiosis, and made significant progress in the understanding of the systematics and phylogenetics of sponge-zoantharian associations (Swain & Wulff, 2007; Montenegro et al., 2020; Kise et al., 2022).

Within the family Parazoanthidae, the genus *Umimayanthus* has recently been one of the most actively studied groups. First erected by Montenegro et al. (2015), the genus originally consisted of four species; the type species, *U. chanpuru* Montenegro, Sinniger & Reimer, 2015, along with *U. miyabi* Montenegro, Sinniger & Reimer, 2015, *U. nakama* Montenegro, Sinniger & Reimer, 2015, and *U. parasiticus* (Duchassaing de Fonbressin & Michelotti, 1860). Subsequently, Fujii et al. (2021) described *U. kanabou* Fujii, dos Santos & Reimer, 2021 from Amami-Oshima Island in southern Japan. Thus, currently *Umimayanthus* includes five formally described valid species, but it is expected that the diversity of this genus remains largely underestimated. For instance, Sinniger & Häussermann (2009) reported an undescribed species of *Umimayanthus* from the Indian Ocean, and Montenegro et al. (2020) reported another unknown species from the Caribbean Sea. Furthermore, considering that the taxonomy of the genus *Parazoanthus*, a sister group to *Umimayanthus*, has undergone extensive revisions in recent years (Sinniger & Häussermann, 2009; Low & Reimer, 2011; Montenegro et al., 2015, 2016), it is likely that after re-examination, several additional *Parazoanthus* species reported from the South Pacific and Indo-Pacific oceans may be transferred into the genus *Umimayanthus*, such as *P. lividum* Cutress, 1971 and *P. aruensis* Pax, 1911.

In this study we present the results of a survey aiming to describe the hidden diversity of zoantharians within the Porifera collections of the Western Australia Museum (WAM), Naturalis Biodiversity Center (NBC), The Netherlands, and other institutions, which are listed below. Specimens were independently analysed by taxonomists with expertise in sponges and zoantharians using a multidisciplinary approach, including traditional morphological analyses, histological dissections, and DNA sequencing analyses. The results of our survey highlight the value of biological collections not only as archives of reference biological material for comparative analyses, but also as a repository of significant undescribed diversity yet to be revealed. In this study we discover and formally describe six new species within the genus *Umimayanthus* from voucher specimens in the Porifera collections of WAM and NBC. We also discuss the implications of these discoveries on the systematics and taxonomy of the genus *Umimayanthus*, provide a key for identification of *Umimayanthus* species, and give insights into possible future research directions on this genus.

Materials and methods

Abbreviations of museum collections

MV	Museums Victoria Natural History Museum (Melbourne, Australia)
NBC	Naturalis Biodiversity Center (Leiden, The Netherlands)
NHMUK	Natural History Museum (London, UK)
RMNH	Rijksmuseum van Natuurlijke Historie (now at NBC)
SMF	Forschungsinstitut und Natur-Museum Senckenberg
WAM	Western Australian Museum (Perth, Australia)
ZMA	Zoological Museum of Amsterdam (now at NBC)

Specimens

WAM specimens were collected by SCUBA diving, by trawl, or by epibenthic sled beyond diving depths, from several localities along the Western Australian coast between 2007–2018 and preserved in 70–100% ethanol. Additional preserved specimens were loaned from the MV and NHMUK. Specimens were also examined at NBC (RMNH and ZMA collections) in the Netherlands, and SMF in Germany.

DNA extraction, PCR, and sequencing

Total DNA was extracted using the Qiagen DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions for all zoantharian specimens. PCR amplification was performed using a Taq PCR Master Mix Kit (Qiagen, Hilden, Germany) for partial sequences of cytochrome oxidase subunit I (COI-mtDNA) using primers LCO1490: 5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3' and HCO2198: 5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3' (Folmer et al., 1994), and thermal cycling conditions of 35 cycles of 1 min at 94 °C, 1 min at 40 °C, and 90 sec at 72 °C, with a final elongation of 7 min at 72 °C (Reimer et al., 2007a); mitochondrial 16S ribosomal DNA (16S-rDNA) with primers 16SarmL: 5'-GGC CTC GAC TGT TTA CCA AA-3' and 16SBmoH: 5'-CGA ACA GCC AAC CCT TGG-3' (Sinniger et al., 2005; Fujii & Reimer, 2011), and thermal cycling conditions of 35 cycles of 1 min at 95 °C, 1 min at 52 °C, 2 min at 72 °C and followed by a 7 min extension at 72 °C (Fujii & Reimer, 2011); and the nuclear internal transcribed spacer region of ribosomal DNA (ITS-rDNA) using primers Zoan-f: 5'-CTT GAT CAT TTA GAG GGA GT-3' and Zoan-r: 5'-CGG AGA TTT CAA ATT TGA GCT-3', and thermal cycling conditions of 35 cycles of 1 min at 94 °C, 1 min at 50 °C, and 2 min at 72 °C, with a final elongation of 10 min at 72 °C (Reimer et al., 2007b). Successful amplifications were confirmed by 2% agarose gel electrophoresis, cleaned by a mix of ExoI and SAP (cat. 2650A and 2660A, TaKaRa, Japan), and sent for external sequencing in both directions to Fasmac, Kanagawa, Japan.

Phylogenetic analyses

The nucleotide sequences were initially aligned using Geneious Prime 2024.04 (https://www.geneious.com) with the algorithm "Global alignment with free end gaps" and default settings, thereafter sequences were manually curated and flaking positions were trimmed. 127 additional sequences were downloaded from GenBank following Montenegro et al. (2016, 2020) and included in this study (table 1). All sequences were then aligned using the Geneious plugin MAFFT (Katoh & Standley, 2013) with the algorithm L-INS-I. Resultant alignments were trimmed, realigned using the plugin MUSCLE (Edgar, 2004) and manually checked.

Maximum likelihood (ML) and Bayesian posterior probability (BPP) phylogenetic hypothesis were estimated using raxml-ng v0.9.0 (Kozlov et al., 2019), and Mr. Bayes v3.2.6 (Ronquist & Huelsenbeck, 2003), respectively. Phylogeny reconstructions were performed for the concatenated alignment of the regions ITS-rDNA, 16S-rDNA and COI-mtDNA, and with *Epizoanthus arenaceus* as the outgroup. Epizoanthidae it is in a clade sister to Parazoanthidae within Macrocnemina Haddon & Shackleton, 1891 (Sinniger et al., 2005; Reimer et al., 2019), thus giving

TABLE 1 Newly generated and downloaded sequences used in the phylogenetic reconstructions, along with their corresponding GenBank accession numbers.

Fam.	[#]	Species	ITS-rDNA	16S-rDNA	COI-mtDNA
	10	*U.* cf. *aruensis* WAM Z88847	–	PP377648	PP359451
	11	*U.* cf. *aruensis* WAM Z88841	PP377666	–	PP359452
	12	*U.* cf. *aruensis* WAM Z88839	PP377667	–	PP359453
	13	*U.* cf. *aruensis* WAM Z88867	PP377668	–	PP359454
	14	*U.* cf. *aruensis* WAM Z88837	PP377669	–	PP359455
	15	*U.* cf. *aruensis* WAM Z88870	PP377670	PP377649	PP359456
	16	*U.* cf. *aruensis* WAM Z88865	PP377671	–	PP359457
	17	*U.* cf. *aruensis* WAM Z88840	PP377672	–	PP359458
	18	*U.* cf. *aruensis* WAM Z88820	PP377673	PP377650	PP359459
	19	*U.* cf. *aruensis* WAM Z88819	PP377674	PP377651	PP359460
	---	*U.* cf. *aruensis* WAM Z88861	–	–	PP359461
	20	*U. mirnangga* sp. nov. WAM Z88824	PP377675	PP377652	PP359462
	21	*U. mirnangga* sp. nov. WAM Z88817	PP377676	PP377653	PP359463
	22	*U. mirnangga* sp. nov. WAM Z88823	PP377677	PP377654	PP359464
	23	*U. jebarra* sp. nov. WAM Z88825	PP377678	–	PP359465
	24	*U. wunanggu* sp. nov. WAM Z88827	PP377679	PP377655	PP359466
	25	*U. wunanggu* sp. nov. WAM Z88818	PP377680	–	PP359467
	26	*U. wunanggu* sp. nov. WAM Z88826	PP377681	PP377656	PP359468
	27	*U. wunanggu* sp. nov. WAM Z88822	PP377682	PP377657	PP359469
	28	*U. miyabi*	GQ848256	EU591606	EU591625
	29	*U. miyabi* NCShallow3A	GQ848255	GQ848272	GQ848277
	30	*U. miyabi* NCShallow1	EU591568	EU591607	EU591626
	31	*U. miyabi* 70JR	KR092646	KR092454	KR092573
	32	*U. miyabi* 179TF	KR092645	KR092453	KR092570
	33	*U. nakama* 363JR	KR092644	KR092458	KR092577
	34	*U. nakama* 3J	KR092643	KR092457	KR092579
	35	*U. nakama*	GQ464884	GQ464855	AB247352
	36	*U. nakama* Japan1	EU591567	EU591608	EU591630
	37	*U. chanpuru* 16J	KR092678	KR092469	KR092609

TABLE 1 Newly generated and downloaded sequences used in the phylogenetic reconstructions (*cont.*)

Fam.	[#]	Species	ITS-rDNA	16S-rDNA	COI-mtDNA
Parazoanthidae	38	*U. chanpuru* 33J	KR092680	KR092504	KR092594
	39	*U. chanpuru* NCDeep2A	EU591579	EU591609	EU591624
	40	*U. chanpuru* NCDeep1	EU591578	EU591605	EU591623
	41	*U. parasiticus*	GQ848263	AY995938	–
	42	*U. parasiticus*	EU418306	EU828756	EF672663
	43	*U. kanabou* NSMT-C01748	MZ305299	MZ305308	MZ298131
	44	*U. kanabou* KAUM-CN18	MZ305298	MZ305307	MZ298130
	45	*U.* sp.3 Madagascar	EU591576	EF687825	EF672664
	46	*U. discolor* sp. nov. BMNHUK-1931.8.4.57	PP377683	PP377658	PP359470
	47	*U. discolor* sp. nov. BMNHUK-1887.5.21.1865	PP377684	PP377659	PP359471
	48	*U. discolor* sp. nov. WAM Z88616	–	PP377660	PP359472
	49	*U. discolor* sp. nov. WAM Z88626	–	PP377661	–
	50	*U. discolor* sp. nov. Tasmania	–	EU591610	EU591620
	51	*U. lynherensis* sp. nov. WAM Z88821	PP377685	PP377662	PP359473
	52	*U. raksasa* sp. nov. sp.3 Sulawesi	EU591575	AY995937	AB247354
	53	*U. raksasa* sp. nov. RMNH.COEL.46520	PP377686	PP377663	PP359474
	54	*U. raksasa* sp. nov. RMNH.COEL.46521	PP377687	–	–
	55	*U. raksasa* sp. nov. WAM Z88815	PP377688	PP377664	PP359475
	---	*U. raksasa* sp. nov. WAM Z88828	–	PP377665	–
	56	*P. axinellae*	EU591570	AY995935	AB247355
	57	*P. axinellae*	EU591571	AF398921	EF672659
	58	*P. anguicomus* 2	GQ464880	GQ464851	–
	59	*P. anguicomus* 1	EU591574	EF687827	EF672660
	60	*P. capensis* SA262	GQ464881	GQ464852	–
	61	*P. swifti*	EU418332	EU828755	AB247350
	62	*P. swiftii*	GQ848258	NC_046475 (9394–9988bp)	NC_046475 (162–606bp)
	63	*P. darwini*	EU333802	EU333751	MH029314

TABLE 1 Newly generated and downloaded sequences used in the phylogenetic reconstructions (*cont.*)

Fam.	[#]	Species	ITS-rDNA	16S-rDNA	COI-mtDNA
	64	*P. atlanticus* MISEJDR170613-10-61	MT103527	MT103539	MT102222
	65	*P. atlanticus* MISEJDR170613-10-60	MT103528	MT103538	MT102223
	66	*P. elongatus* Chile	EU591565	EF687829	EF672661
	67	*P. elongatus* NZ	EU591564	EF687828	EF672662
	68	*P.* aff. *juanfernandezii* CA128	GQ464877	GQ464849	–
	69	*P.* aff. *juanfernandezii* FRAPC1	GQ464878	GQ464848	–
	70	*B. puertoricense*	EU591584	EU828758	AB247351
	71	*B. puertoricense*	EU418312	AY995933	–
	72	*B. catenularis*	EU418292	EU828757	–
	73	*B. cutressi*	EU418264	EU828759	–
	74	*B.* sp. Senegal	EU591582	EF687820	EF672656
	9	*Parazoanthid* 02–27	EU333810	EU333760	–
	8	*A. macaronesicus*	EU591556	HM130467	–
	7	*C. tsukaharai*	EU035621	EU035627	–
	6	*S. savaglia*	EU346888	AY995925	–
	5	*M. fossii*	EU591545	EF687821	–
	4	*I. giganteus*	GQ464896	GQ464867	–
	3	*E. incrustatus*	GQ464894	GQ464865	–
	2	*E. scotinus*	GQ464899	GQ464870	–
Epizoanthidae	1	*E. arenaceus*	EU591538	AY995926	AB247348

sufficient resolution to establish if all specimens' sequences truly belong within genus *Umimayanthus*, confirming that the genus remains a cohesive taxonomic and evolutionary unit (monophyly).

For each of the molecular markers, the best-fitting model was selected using ModelTest-NG v0.2 (Darriba et al., 2020) for ML reconstructions and MrModeltest2 (Nylander, 2004) for BBP. In both cases the lowest AIC score was used as the selecting criteria. The best-fitting models for ML were TPM3uf+I+G4 for ITS-rDNA, TrN+G4 for 16S-rDNA, and TrN+I for COI-mtDNA. The best-fitting models for BPP were HKY+I+G for ITS-rDNA, SMY+G for 16S-rDNA, and HKY+I for COI-mtDNA.

ML phylogenies were estimated using a 100 initial parsimony trees, 1000 bootstraps, and the evolutionary models selected by ModelTest-NG; distinct substitution rates across partitions, automated optimization of model parameters and branch lengths were allowed. BPP trees were estimated following the models and parameters as indicated by MrModeltest2, 4 MCMC heated chains were run for 10,000,000 generations with a temperature

for the heated chain of 0.2. Chains were sampled every 200 generations. Burn-in length was set to 25% at which point the average standard deviation of split frequency (ASDOSF) was steadily below 0.01.

Specimen identification

All zoantharian specimens were identified by JM, HK or JDR, while associated sponges from MV and WAM were identified by JF. ZMA sponges were identified by B. Alvarez, N.J. de Voogd and R.W.M. van Soest (ZMA.POR.9139, ZMA.POR.20704) in previous publications (Alvarez et al., 2016). NHMUK specimens were identified by E. Hentschel (NHMUK 1931.8.4.57) and H. John Carter (Carter, 1882) (NHMUK 1887.5.21.1865), and reexamined by J. Hooper and JF. Sponge subsamples were cut at right angles to the surface and processed using a graded ethanol dehydration and histolene clearing procedure, sectioned at right angles to the sponge surface either with a Leitz slide microtome or hand cut with a razor blade, and mounted on glass slides with EZ-Mount mountant (Fisher Scientific) to determine the skeletal arrangement (Fromont et al., 2011). Spicule preparations were made with nitric acid or bleach, washed in distilled water, mounted on glass slides and examined with an Olympus BX50 microscope. A calibrated micrometer eyepiece was used to measure skeletal details and spicule sizes (Fromont et al., 2011). Skeletal layout and spicule complements were examined and compared with relevant sponge literature to identify genera and species. (Hooper, 1984,1991, 1996; Van Soest et al., 2012; Alvarez et al., 2016; de Voogd et al., 2023).

Zoantharian specimens were preliminarily grouped based on molecular similarities across the three DNA markers. For all species, where possible, three polyps were randomly selected to measure diameter and height, and the presence or absence of coenenchyma connecting polyps was recorded. Cnidae analyses were performed; one polyp was dissected per species group and undischarged nematocysts from tentacles, column, actinopharynx, and mesenterial filaments were counted and measured under a Nikon Eclipse80i stereomicroscope (Nikon, Tokyo, Japan). Cnidae sizes were measured using ImageJ ver. 1.45s (Rasband, 2012), and classified according to England (1991) and Ryland & Lancaster (2004), to the exception of basitrichs and microbasic mastigophores, which were treated as a single type following Kise et al. (2019). Thus, six cnidae categories were quantified; spirocysts, bastrichs & microbasic b-mastigophores, holotrichs-(L), holotrichs-(M), holotrichs-(S), and microbasic p-mastigophores; additionally special microbasic b-mastigophores were also counted when present.

Serial sections from preserved specimens were also examined for internal morphology. Whole polyps of the specimens were embedded in paraplast after decalcification with Morse solution for 48 h (1:1 vol; 20% citric acid: 50% formic acid) and desilication with 20% hydrofluoric acid for 18–24 h. 10–15 mm thick serial sections were made with a microtome (LEICA RM2145; Leica, Germany) and stained with haematoxylin and eosin. Classification of marginal muscle shapes followed Swain et al. (2015). However serial sectioning was not successful and therefore the internal morphology of the polyps was characterized by direct observation using a dissection stereomicroscope.

Results

Phylogenetic analyses

In total, 34 zoantharian specimens were analysed in this study; 26 from WAM, three from MV, two from NHMUK, two from NBC, and one from SMF (table 2). The specimens were collected from 26 different localities in Australia and Indonesia (table 2, fig. 1). The final concatenated alignment included data from 26 out of the 34 analysed specimens, and included 191 sequences, out of which 64 were newly generated in this study: 23 sequences for ITS-rDNA, 17 sequences for 16S-rDNA, and 24 sequences for COI-mtDNA. The total length of the final concatenated alignments was 1843 bp; consisting of 864 bp for ITS-rDNA, 533 bp of 16S-rDNA, and 446 bp of COI-mtDNA (supplementary data S1–S4).

The genus *Umimayanthus* was supported as a member of the family Parazoanthidae, and was presented as a moderately supported monophyly in ML analyses, and well supported in BPP with a >0.98 posterior probability. All specimens analysed in this study were included within the

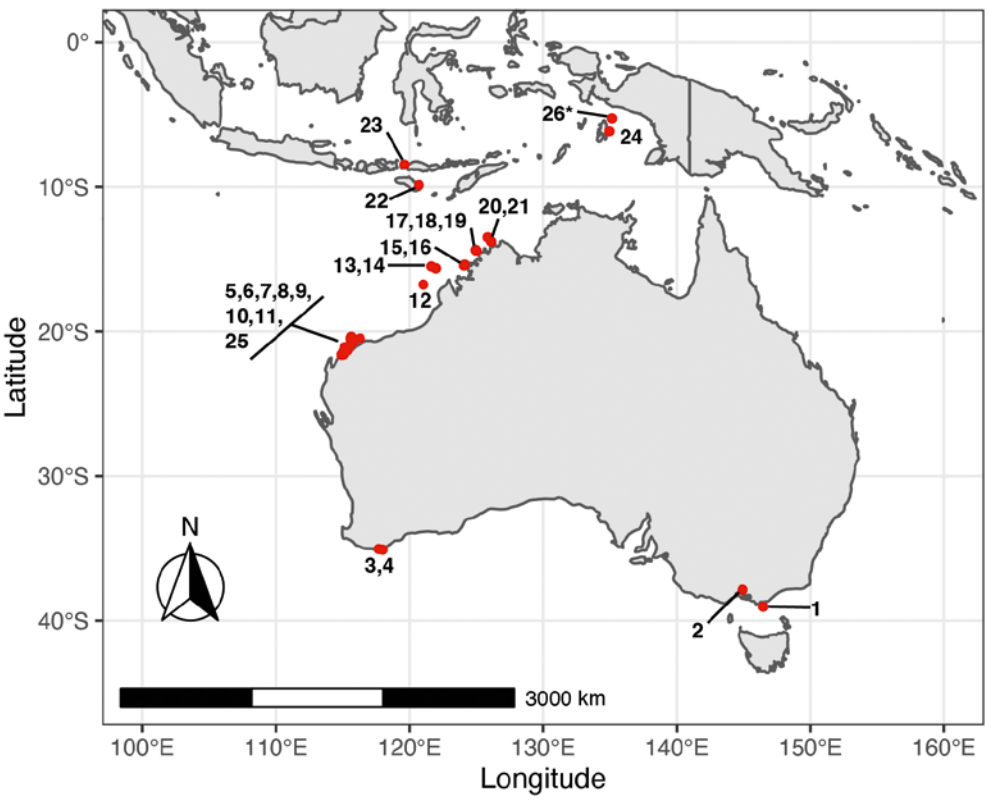

FIGURE 1 Collection location for all samples analyzed. Numbers indicate unique locations. Details in table 2 (*) indicate approximated locations

TABLE 2 Samples and collection metadata for all samples analysed in this study

[#]	Zoantharian voucher#	*Umimayanthus* IDs	Sponge voucher#	Sponge Fam.	Sponge ID s	Country	State	IslandGR	Locality	Date	Lat(dd)	Long(dd)	Loc. ID	Depth (meters)
10	WAM Z88847	*U.* cf. *aruensis*	WAM Z81811	Raspailiidae	*Trikentrion flabelliforme*	Australia	Western Australia	Pilbara Shelf	Bare Rock	Jun.6. 2013	−20.4747	116.3072	11	37
11	WAM Z88841	*U.* cf. *aruensis*	WAM Z81606	Raspailiidae	*Trikentrion flabelliforme*	Australia	Western Australia	Pilbara Shelf	Sultan Reef	Jun.6. 2013	−21.4	115.0897	7	18
12	WAM Z88839	*U.* cf. *aruensis*	WAM Z65319	Raspailiidae	*Trikentrion flabelliforme*	Australia	Western Australia	Onslow	Wheatstone	Mar.3. 2013	−21.6069	114.9331	5	12.2
13	WAM Z88867	*U.* cf. *aruensis*	WAM Z81810	Raspailiidae	*Trikentrion flabelliforme*	Australia	Western Australia	Pilbara Shelf	West Reef	Jun.6. 2013	−21.3122	115.3692	8	14
14	WAM Z88837	*U.* cf. *aruensis*	WAM Z65253	Raspailiidae	*Trikentrion flabelliforme*	Australia	Western Australia	Onslow	Wheatstone	Mar.3. 2013	−21.5961	115.0606	6	12.2
15	WAM Z88870	*U.* cf. *aruensis*	WAM Z84853	Raspailiidae	*Trikentrion flabelliforme*	Australia	Western Australia	Montebello Islands	Ah Chong Island	Apr.4. 2015	−20.4992	115.5897	10	14.5
16	WAM Z88865	*U.* cf. *aruensis*	WAM Z86127	Raspailiidae	*Trikentrion flabelliforme*	Australia	Western Australia	Pilbara Shelf	West Reef	Jun.6. 2013	−20.9783	115.5522	9	14
17	WAM Z88840	*U.* cf. *aruensis*	WAM Z81602	Raspailiidae	*Trikentrion flabelliforme*	Australia	Western Australia	Onslow	Wheatstone	Mar.3. 2013	−21.6069	114.9331	5	12.2
18	WAM Z88820	*U.* cf. *aruensis*	WAM Z88301	Raspailiidae	*Trikentrion flabelliforme*	Australia	Western Australia	Onslow	near Wheatstone	Jul.7. 2015	−21.5961	115.0606	6	12.3
19	WAM Z88819	*U.* cf. *aruensis*	WAM Z88060	Raspailiidae	*Trikentrion flabelliforme*	Australia	Western Australia	Camden Sound	Camden Sound	Mar.3. 2015	−15.3763	124.1395	16	39
–	WAM Z88861	*U.* cf. *aruensis*	WAM Z82539	Raspailiidae	*Trikentrion flabelliforme*	Australia	Western Australia	Pilbara Shelf	The Man in the Boat	Jun.6. 2013	−20.9783	115.5522	9	18

TABLE 2 Samples and collection metadata for all samples analysed in this study (*cont.*)

[#]	Zoantharian voucher#	*Umimayanthus* IDs	Sponge voucher#	Sponge Fam.	Sponge ID s	Country	State	IslandGR	Locality	Date	Lat(dd)	Long(dd)	Loc. ID	Depth (meters)
–	WAM Z88863	*U.* cf. *aruensis*	WAM Z86126	Raspailiidae	*Trikentrion flabelliforme*	Australia	Western Australia	Pilbara Shelf	Sultan Reef	Jun.6. 2013	−21.4	115.0897	7	18
–	WAM Z88853	*U.* cf. *aruensis*	WAM Z86125	Raspailiidae	*Trikentrion flabelliforme*	Australia	Western Australia	Pilbara Shelf	Poivre Reef	Jun.6. 2013	−21.0803	115.18	25	21
20	WAM Z88824*	*U. mirnangga* sp. nov.	WAM Z94034	Raspailiidae	*Ectyoplasia vannus*	Australia	Western Australia	Maret Islands	Maret Islands	Dec.12. 2015	−14.3545	124.9488	19	61
21	WAM Z88817	*U. mirnangga* sp. nov.	WAM Z87200	Raspailiidae	*Endectyon* (*Endectyon*) *fruticosum*	Australia	Western Australia	Camden Sound	Camden Sound	Mar.3. 2015	−15.4464	124.083	15	61
22	WAM Z88823^	*U. mirnangga* sp. nov.	WAM Z94033	Raspailiidae	*Ectyoplasia vannus*	Australia	Western Australia	Maret Islands	Maret Islands	Dec.12. 2015	−14.4244	125.0409	17	55
23	WAM Z88825*	*U. jebarra* sp. nov.	WAM Z94791	Raspailiidae	*Endectyon* sp.	Australia	Western Australia	Eclipse Islands	Eclipse Islands	Mar.3. 2016	−13.4938	125.8516	21	41
24	WAM Z88827	*U. wunanggu* sp. nov.	WAM Z95455	Raspailiidae	*Endectyon* (*Endectyon*) *fruticosum*	Australia	Western Australia	Lynher Bank	Lynher Bank	Oct.10. 2016	−15.6233	121.9722	13	61
25	WAM Z88818^	*U. wunanggu* sp. nov.	WAM Z87958	Raspailiidae	*Endectyon* (*Endectyon*) *thurstoni*	Australia	Western Australia	Camden Sound	Camden Sound	Mar.3. 2015	−15.4464	124.083	15	61
26	WAM Z88826*	*U. wunanggu* sp. nov.	WAM Z94991	Raspailiidae	*Endectyon* (*Endectyon*) *thurstoni*	Australia	Western Australia	Eclipse Islands	Eclipse Islands	Mar.3. 2016	−13.7942	126.1188	20	59

TABLE 2 Samples and collection metadata for all samples analysed in this study (*cont.*)

[#]	Zoantharian voucher#	*Umimayanthus* IDs	Sponge voucher#	Sponge Fam.	Sponge ID s	Country	State	IslandGR	Locality	Date	Lat(dd)	Long(dd)	Loc. ID	Depth (meters)
27	WAM Z88822^	*U. wunanggu* sp. nov.	WAM Z94013	Raspailiidae	*Endectyon* (*Endectyon*) *thurstoni*	Australia	Western Australia	Maret Islands	Maret Islands	Dec.12.2015	−14.4019	124.9441	18	50
46	NHMUK-1931.8.4.57	*U. discolor* sp. nov.	NHMUK-1931.8.4.57	Raspailiidae	*Trikentrion flabelliforme**	Indonesia	Aru Islands	Maluku	East cost of Aru Island	na, 1931	−6.16403	134.9447	24	4~15
47	NHMUK-1887.5.21.1865	*U. discolor* sp. nov.	NHMUK-1887.5.21.1865	Raspailiidae	*Trikentrion flabelliforme**	Australia	South West	–	–	na, 1865~87	–	–	–	na
48	WAM Z88616*	*U. discolor* sp. nov.	WAM Z88473	Microcionidae	*Clathria* (*Thalysias*) *cactiformis*	Australia	Western Australia	Albany	Murray Road boat ramp	Apr.4.2018	−35.0939	117.9639	3	6.4
49	WAM Z88626^	*U. discolor* sp. nov.	WAM Z88474	Microcionidae	*Clathria* (*Thalysias*) *cactiformis*	Australia	Western Australia	Albany	Shelter Island	Apr.4.2018	−35.0497	117.6936	4	8.5
–	MV-F67954	*U. discolor* sp. nov.	–	Microcionidae	*Clathria* (*Thalysias*) cf. *cactiformis*	Australia	Victoria	Wilsons Promontory	South Wall, Sealer Cove	Apr.4.1987	−39.0163	146.4429	1	10
51	WAM Z88821*	*U. lynherensis* sp. nov.	WAM Z90632	Biemnidae	*Sigmaxinella soelae*	Australia	Western Australia	Lynher Bank	Lynher Bank	Oct.10.2016	−15.4937	121.6362	14	95
53	RMNH.COEL.46520*	*U. raksasa* sp. nov.	ZMA-POR-9139	Axinellidae	*Phakelia cf. tropicalis*	Indonesia	Nusa Tenggara	NE coast of Sumba	East of Melolo	Sep.9.1984	−9.89169	120.7117	22	75–90

TABLE 2 Samples and collection metadata for all samples analysed in this study (*cont.*)

[#]	Zoantharian voucher#	*Umimayanthus* IDs	Sponge voucher#	Sponge Fam.	Sponge ID s	Country	State	IslandGR	Locality	Date	Lat(dd)	Long(dd)	Loc. ID	Depth (meters)
54	RMNH.COEL. 46521^	*U. raksasa* sp. nov.	ZMA-POR-20704	Axinellidae	*Phakellia* n.sp.	Indonesia	Nusa Tenggara	Komodo	East of Komodo Field #100	Sep.9. 1984	−8.46833	119.6175	23	91
55	WAM Z88815	*U. raksasa* sp. nov.	WAM Z36122	Axinellidae	*Phakellia* sp. Ng2	Australia	Western Australia	Broome	Broome L25	Jun.6. 2007	−16.7525	121.0467	12	108–100
–	WAM Z88828	*U. raksasa* sp. nov.	WAM Z95466	Axinellidae	*Phakellia* sp. Ng1 cf.	Australia	Western Australia	Lynher Bank	Lynher Bank	Oct.10. 2016	−15.6233	121.9722	13	61
–	SeSam42611_ Cat86*	*U. aruensis*	–	–	n.a	Indonesia	Aru Islands	Aru	–	Apr.4. 1908	−5.29167	135.1586	26+	5
–	MV-F41549*	*P. lividum*	–	Clionaidae	*Spheciospongia* sp.	Australia	Victoria	Port Phillip Bay	Area 6, Loc. 65, Off Williamstown	Jun.6. 1958	−37.877	144.918	2	na
–	MV-F41550^	*P. lividum*	–	Clionaidae	*Spheciospongia* sp.	Australia	Victoria	Port Phillip Bay	Area 6, Loc. 65, Off Williamstown	Jun.6. 1958	−37.877	144.918	2	na

*indicate the holotype, ^paratype specimens, +indicated location of Aru Island.

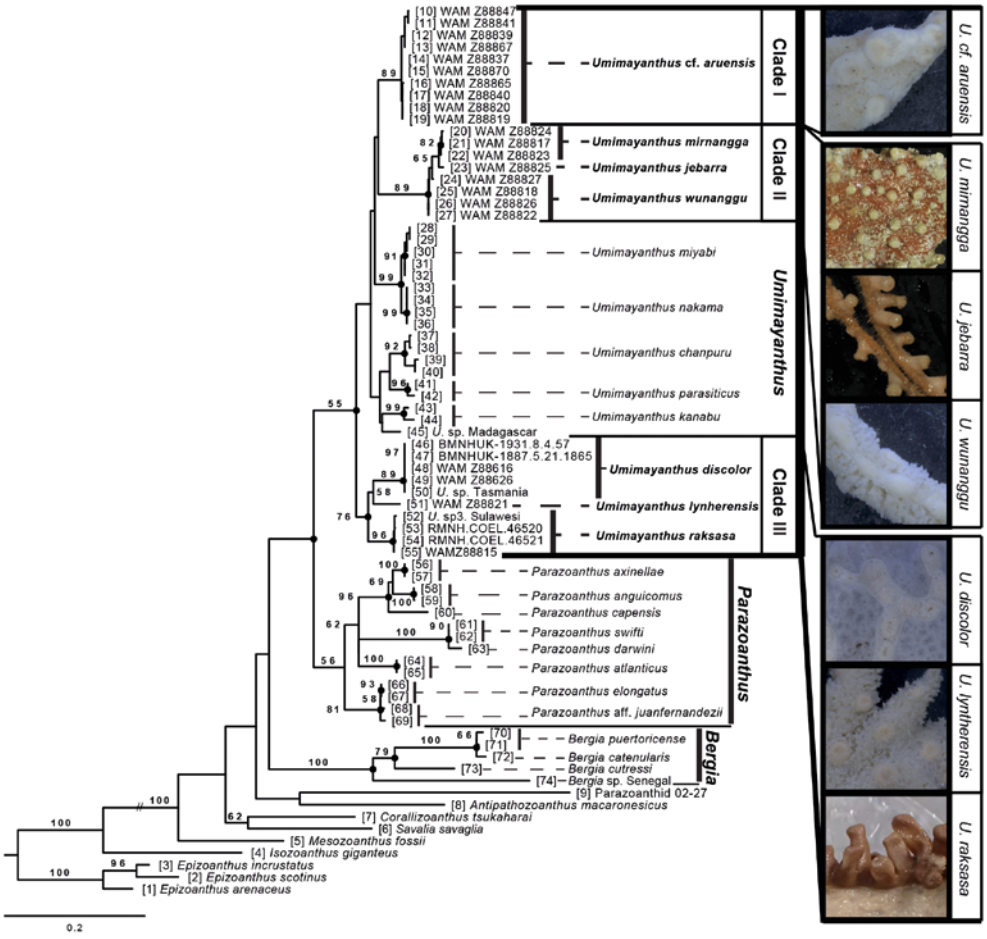

FIGURE 2 Phylogenetic reconstruction based on the concatenated alignments of the ITS-rDNA, 16S-rDNA, and COI-mtDNA. Values at branches indicate ML bootstrap support ≥ 50% and black circles at nodes represent BPP ≥ 0.95. Numbers in brackets correspond to the unique number per taxonomic unit in table 1.

Umimayanthus clade, and grouped into three major clades; designated as clades I, II and III in fig. 2.

Clade III was sister to all other species in the genus *Umimayanthus* while the phylogenetic positions of Clades I and II were less certain. Nonetheless, each of these three clades was well supported in both ML analyses, with bootstrap values of 76–89% for ML and posterior probabilities of ≥0.95 for BPP for Clades II and III. The lack of support from BPP analyses for Clade I may stem from multiple individuals having missing ITS-rDNA or 16S-rDNA sequence data.

Clade III included three closely related clades corresponding to *Umimayanthus discolor* sp. nov., *Umimayanthus lynherensis* sp. nov., and *Umimayanthus raksasa* sp. nov. The clades of *U. discolor* sp. nov.

and *U. lynherensis* sp. nov. were strongly supported as sister species, while *U. raksasa* sp. nov. was found to be basal within Clade III. The relationships between these three sibling species were supported by bootstrap value of 76% for ML and a posterior probability of ≥ 0.95 for BPP in phylogenetic analyses. Interestingly, *U. discolor* sp. nov. was found in association with two distantly related sponge species in families Microcionidae (specimens WAM Z88616 and WAM Z88626) and Raspiliidae (specimens NHMUK-1887.5.21.1865 and NHMUK-1931.8.4.57), while each of its sibling species seems to be restricted to a single family and genus of host sponges.

The monophyly formed by Clade I was strongly supported in ML analyses with a bootstrap value of 89%, however support from BPP was lacking. While minor subclades were present within Clade I their support was weak in ML and not existent in BPP analyses. Clade I was formed by multiple specimens of *Umimayanthus* cf. *aruensis*.

In a similar fashion, Clade II was well supported in ML analyses with a bootstrap value of 89% and posterior probabilities of ≥ 0.95 for BPP in the phylogenetic analysis. However, in contrast to Clade I, Clade II internal subclades were well supported with values ranging from 65% to 89%, and posterior probabilities ≥ 0.95 for BPP for some of these clades. Of these subclades, the most supported monophyly was formed by three specimens of *Umimayanthus mirnangga* sp. nov., followed by a clade formed by four specimens of *Umimayanthus wunanggu* sp. nov., and finally a single specimen of *Umimayanthus jebarra* sp. nov. Specimens in this complex were all hosted by sponges in the genera *Endectyon* and/or *Ectyoplasia* in the family Raspaillidae, supporting the phylogenetic hypothesis of close evolutionary relatedness among these three species.

Systematics

Phylum Cnidaria Hatschek, 1888
Subphylum Anthozoa Ehrenberg, 1831
Class Hexacorallia Haeckel, 1896
Order Zoantharia Rafinesque, 1815
Family Parazoanthidae Delage & Hérouard, 1901

Genus *Umimayanthus* Montenegro, Sinniger and Reimer 2015

urn:lsid:zoobank.org:act:A7C6F356-9128-41EA-B108-271EC70B82F

The genus *Umimayanthus* was initially diagnosed by a unique insertion of 9 bp in length and one 14 bp deletion in the mt 16S-rDNA region. However, relying on deletions, or alignment gaps, as a diagnostic character can be problematic when analysing relationships between distantly related taxa. Therefore, here we revise the generic diagnosis and propose to use a combination of unique insertions and substitutions across the ITS-rDNA and 16S-rDNA molecular markers as follows.

The genus *Umimayanthus* can be distinguished from all other sponge-associated zoantharians by multiple conservative positions across the ITS-rDNA region in our concatenated alignment, as follows: two conservative and unique substitutions in base pair positions 22–23 bp as "TG", and multiple unique combinations

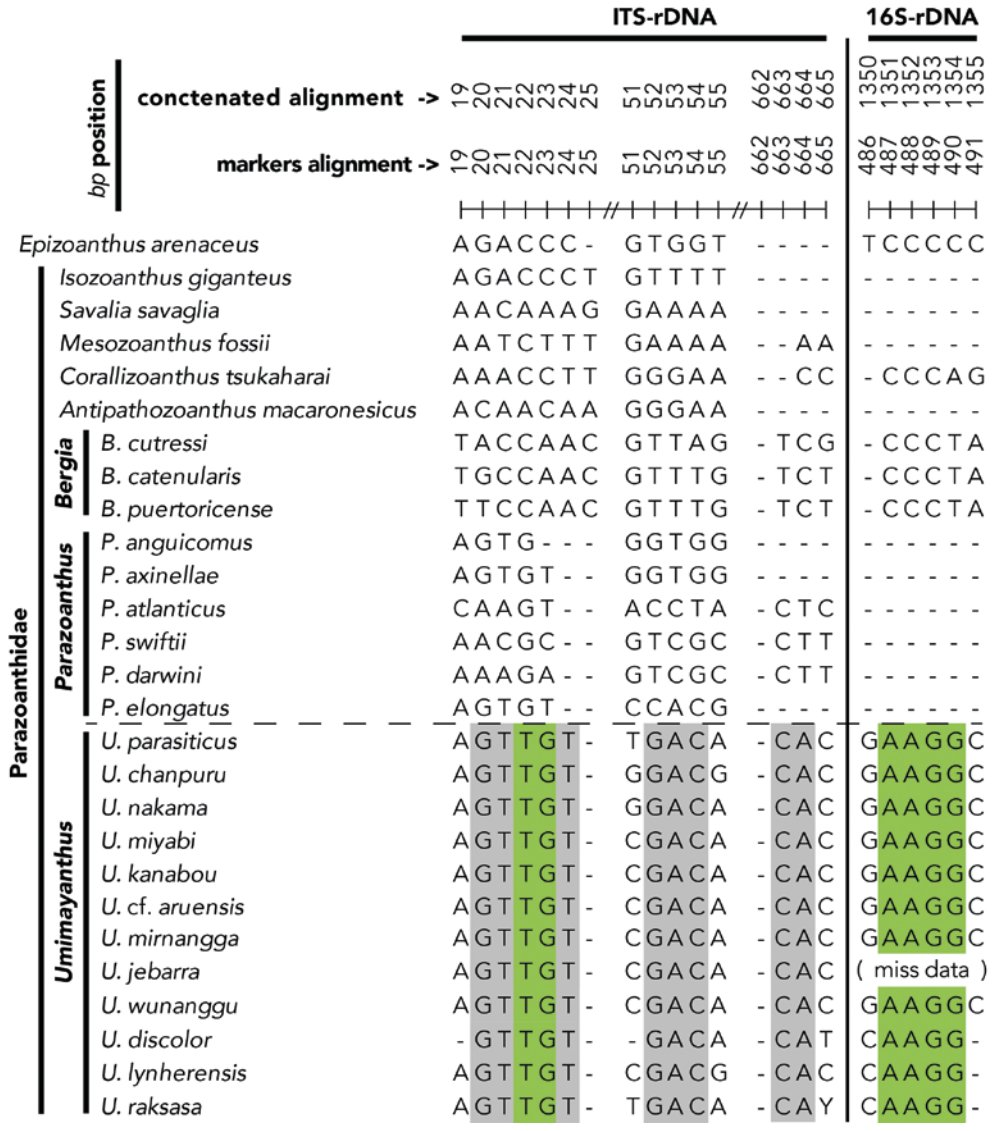

FIGURE 3 Summary chart for the alignments showing relevant nucleotide positions for the molecular diagnosis of genus *Umimayanthus*. Positions in green are unique to genus *Umimayanthus*. Positions in grey indicate regions with a unique combination of nucleotides for *Umimayanthus*.

of substitutions between positions 20–24 bp as "GTTGT", 52–54 bp as "GAC" and 663–664 bp as "CA". Furthermore, between positions 1351–1354 bp in the 16S-rDNA region of our alignment a highly conservative insertion of four base pairs, "AAGG", was also found to be unique to genus *Umimayanthus* (fig. 3).

***Umimayanthus* cf. *aruensis* (Pax, 1911)**

urn:lsid:zoobank.org:act:9310A989-B76E-4096-8BB5-09E348935394

Here we transfer *Parazoanthus aruensis* to the genus *Umimayanthus* based on its general morphology and position of the sphincter muscle, as well as corresponding geographical location, and gross external morphology of the host sponge. *P. aruensis* was originally described by Pax (1911) as a zoantharian "that lives in sponges and forming loose colonies. Polyps 8 mm high, 5 mm wide, connected to each other by narrow flat stolon. Tissue walls incrusted with sponge spicules, 18 septs, sphincter muscle diffuse, endodermal and poorly developed". The holotype specimen of *P. aruensis*, SMF museum, GUID = SeSam 42611, Catalog #86, had polyps of 4.15 mm ± 0.402 mm (σ^2 = 0.161, max. 4.92 mm, n = 10 polyps) in diameter and 4.72 mm ± 0.89 mm (σ^2 = 0.787, max. 6.67 mm, n = 10 polyps) in height, with chains of polyps firmly connected to each other in a reticulate manner over the surface of the host sponge (fig. 4). The morphology of the host sponge was arborescent/branching

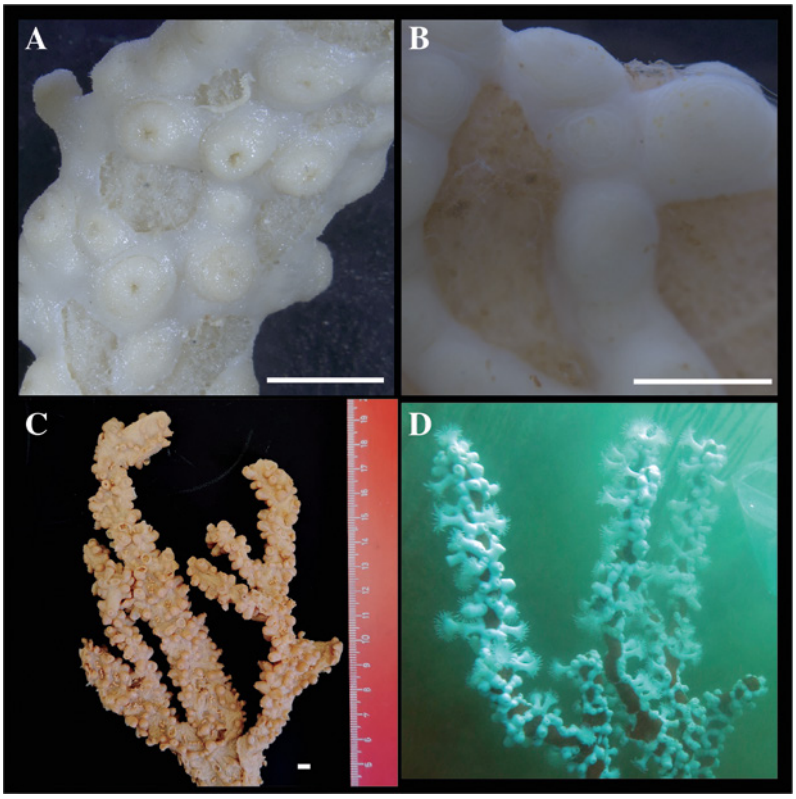

FIGURE 4 Specimens of *Umimayanthus* cf. *aruensis* and holotype of *Umimayanthus aruensis*; (A) WAM Z8881 9 and (B) WAM Z8882 0 specimens of *U.* cf. *aruensis*. (C) SeSam 42611 Cat.86 picture of *U. aruensis* holotype taken by Saskia Dimter, and (D) *in situ* image of *U.* cf. *aruensis*. Scale bars: 5 mm

in shape, although the specific identity remains unknown.

The specimens newly analysed in this study that are attributable to *U.* cf. *aruensis* have polyps that are on average 2.66 mm ± 0.89 mm (σ^2 = 0.79, max. 4.17 mm, n = 29 polyps) in diameter, 0.79 mm ± 0.5 mm (σ^2 = 0.26, max. 2.04 mm, n = 27 polyps) in height. The host sponge in *U.* cf. *aruensis* was identified as *Trikentrion flabelliforme* Hentschel, 1912 (family Raspailiidae Nardo, 1833). All measurements were performed on voucher specimens preserved in ethanol: zoantharian voucher numbers WAM Z88819, WAM Z88820, WAM Z88840, WAM Z88847, WAM Z88841, WAM Z88839, WAM Z88867, WAM Z88837, WAM Z88870, and WAM Z88865.

The *U.* cf. *aruensis* colonies were found to be primarily formed by interconnected polyp chains extending over the surface of the host sponge in a reticulated pattern; exceptionally the polyps were found to be solitary or arranged in groups of two or three. The coenenchyma is clearly visible over the sponge surface and firmly connects multiple polyps by the stolon. Polyps preserved in ethanol are white or cream in color. Capitulary ridges not visible. Tentacles approximately up to 24 in number, in two rows. Preserved tentacles light brown in coloration. Capitulum and scapus heavily encrusted by various particles comprised of sand and silica (spicules of host sponges). The sphincter muscle located in the endoderm. Mesenterial arrangement macrocnemic (fifth mesenteries from dorsal directive complete). Mesenteries approximately up to 24 in number. Ectoderm and mesoglea of capitulum and scapus heavily encrusted by various sand and silica particles. Single siphonoglyph.

In synthesis, *U. aruensis* and *U.* cf. *aruensis* strongly resemble each other in multiple aspects. Both *U. aruensis* and *U.* cf. *aruensis* present colonies form by chains of polyps extending over the surface of the host sponge in a reticulated manner, with a clearly visible coenenchyma. Both were collected from the same region of the Indo-Pacific Ocean and are associated to host sponges of arborescent/branching shapes. Both have sphincter muscle located in the endoderm, and tissue walls incrusted with sponge spicules. However, differences were observed regarding the dimensions of the polyps, *U. aruensis* was 4.15 mm ± 0.402 mm in diameter and 4.72 mm ± 0.89 mm in height, while for *U.* cf. *aruensis* polyps were 2.66 mm ± 0.89 mm in diameter and 0.79 mm ± 0.5 mm in height. It is important to note that differences in height could be related to the level of retraction of the specimens in preservation. Therefore, we consider these facts, along with the fact that no *Parazoanthus* is known from this region of the Indo-Pacific Ocean, sufficient to support that *U. aruensis* should be transferred into *Umimayanthus*. However, given the evident species diversity of *Umimayanthus* in the region as illuminated by the current work, we feel the evidence is not strong enough to be fully ascertain that our relevant specimens represent *U. aruensis*, and conservatively we therefore have decided to use the "*confer*" denomination (cf.) for these specimen's identification (= *U.* cf. *aruensis*).

Molecular characterization. At the molecular level, *U.* cf. *aruensis* can be distinguished from other species in *Umimayanthus* using multiple unique nucleotide substitutions across the ITS-rDNA region as follows: an "A" in positions 49 bp,

378 bp, 387 bp and 441 bp; a "G" in positions 97 bp, 338 bp, 340 bp, 359 bp and 390 bp; a "C" at 113 bp and 128 bp, and "T" at 373 bp. Additionally, unique combinations of nucleotides and deletions were found from 128 bp to 341 bp; and 408 bp to 437 bp (fig. 5).

Cnidae. All cnidae categories were found, but they were differentially distributed across tissues. Spirocysts were numerous and only found in the tentacles, with bastrichs and microbasic b-mastigophores also present. The column presented few cnidae and exclusively (M) and (L) type holotrichs. The pharynx had holotrichs (M) and microbasic b-mastigophores. Filaments presented the largest variety of cnidae with special microbasic b-mastigophores, bastrichs and microbasic b-mastigophores, and microbasic p-mastigophores. For details on sizes, lengths, and widths of each cnidocyte type see table 3 and fig. 6.

Material examined. WAM Z88819, loc. 16 (–15.376306 °S, 124.139547 °E), Camden Sound, Western Australia, 39 m depth, March 21, 2015 by J. Fromont & L. Kirkendale, WAM Z88820, loc. 6 (–21.596111 °S, 115.060556 °E), near Wheatstone, Onslow, Western Australia, 12.3 m depth, July 7, 2015 by J. Fromont & M.A. Wahab, WAM Z88840, loc. 5 (–21.606944 °S, 114.933056 °E), Wheatstone, Onslow, Western Australia, 12.2 m depth, March 29, 2013 by J. Fromont & C.L. Schoenberg, WAM Z88847, loc. 11 (–20.474722 °S, 116.307222 °E), Bare Rock, Pilbara Shelf, Western Australia, 37 m depth, June 25, 2013 by E. Morello, G. Fry, M. Miller, D. Thomson & D. Bearham, WAM Z88841, loc. 7 (–21.4 °S, 115.089722 °E), Sultan Reef, Pilbara Shelf, Western Australia, 18 m depth, June 13, 2013 by E. Morello, G. Fry, M. Miller, D. Thomson & D. Bearham, WAM Z88839, loc. 5 (–21.606944 °S, 114.933056 °E), Wheatstone, Onslow, Western Australia, 12.2 m depth, March 29, 2013 by J. Fromont & C.L. Schoenberg, WAM Z88867, loc. 8 (–21.312222 °S, 115.369167 °E), West Reef, Pilbara Shelf, Western Australia, 14 m depth, June 14, 2013 by E. Morello, G. Fry, M. Miller, D. Thomson & D. Bearham, WAM Z88837, loc. 6 (–21.596111 °S, 115.060556 °E), Wheatstone, Onslow, Western Australia, 12.2 m depth on March 26, 2013 by J. Fromont & E. Buettner, WAM Z88870, loc. 10 (–20.499167 °S, 115.589722 °E), Ah Chong I., Montebello Is., Western Australia, 14.5 m depth on April 16, 2015 by A.M. Hosie & A. Hara, WAM Z88865, loc. 9 (–20.978333 °S, 115.552222 °E), West Reef , Pilbara Shelf, Western Australia, 14 m depth, June 14, 2013 by E. Morello, G. Fry, M. Miller, D. Thomson & D. Bearham, WAM Z88861, loc. 9 (-20.978333 °S, 115.552222 °E), The Man in the Boat, Pilbara Shelf, Western Australia, 18 m depth, June 21, 2013 by E. Morello, G. Fry, M. Miller, D. Thomson & D. Bearham, WAM Z88863, loc. 7 (–21.4 °S, 115.089722 °E), Sultan Reef, Pilbara Shelf, Western Australia, 18 m depth, June 13, 2013 by E. Morello, G. Fry, M. Miller, D. Thomson & D. Bearham, and WAM Z88853, loc. 25, (–21.080278 °S, 115.18 °E), Poivre Reef, Pilbara Shelf, Western Australia, 21 m depth, June 16, 2013 by E. Morello, G. Fry, M. Miller, D. Thomson & D. Bearham.

Associated host. Umimayanthus cf. *aruensis* was found to be host specific, only associated with the host sponge *Trikentrion flabelliforme* (family Raspailiidae). Interestingly, the paralectotype of *T. flabelliforme* (NHMUK 1931.8.4.57, from Aru Islands, Indonesia) and another historical

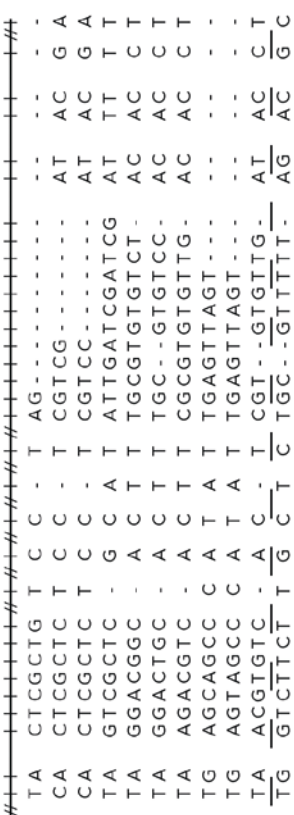

FIGURE 5 Summary chart of the alignments showing nucleotide positions and deletions characteristics to *U.* cf. *aruensis*. across the ITS-rDNA region. Positions in green are unique to *U.* cf. *aruensis* sp. nov. in genus *Umimayanthus*. Positions in grey indicate regions with a unique combination of nucleotides insertion and deletions for *U.* cf. *aruensis*

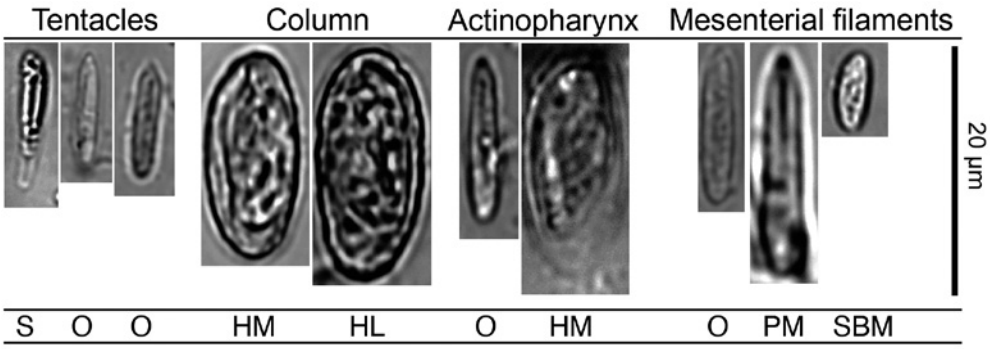

FIGURE 6 Diversity of cnidae found in *U.* cf. *aruensis* across tissues in specimen WAM Z88819. (S) spriocysts, (O) basitrichs and microbasic b-mastigophores, (HM) holotrich medium, (HL) holotrich large, (PM) microbasic p-mastigophores and special (SBM) microbasic b-mastigophores

TABLE 3 Results for the cnidocyte analyses for *Umimayanthus* cf. *aruensis*, holotype specimen WAM Z88819

Tissue	Category	Length (max–min, average)	Width (max–min, average)	*n*	Frequency
Tentacles	Spirocysts	23.6–10.9, 16.8	3.7–1.3, 2.5	163	Numerous
	Bastrichs and microbasic b-mastigophores	20.7–13.6, 16.8	4.0–2.2, 3.3	22	Common
Column	Holotrichs (L)	23.3–20.7, 21.5	11.5–10.6, 11.0	5	Rare
	Holotrichs (M)	18.8–17.6, 18.2	10.3–8.7, 9.6	3	Rare
Pharynx	Holotrichs (M)	19	10.2	1	Rare
	Bastrichs and microbasic b-mastigophores	32.2–14.8, 18.4	3.7–2.1, 2.8	30	Common
Mesenterial Filaments	Special microbasic b-mastigophores	11.6–7.1, 9.0	3.9–1.9, 3.1	18	Common
	Bastrichs and microbasic b-mastigophores	22.8–13.8, 17.5	3.9–1.8, 2.7	24	Common
	Microbasic p-mastigophores	19.9–19.0, 19.5	5.6–5.4, 5.5	2	Rare

specimen (NHMUK 1887.5.21.1865, precise location unknown, southwest Western Australia) were found associated with *Umimayanthus discolor* sp. nov., described below, rather than with *U.* cf. *aruensis*.

Remarks. Specimen WAM Z88865 has an abnormally small polyp diameter and height for *U.* cf. *aruensis*, 0.9 mm in diameter and 0.1 mm in height. It is worth noting that only two polyps were available for examination from this specimen. Nonetheless, molecular evidence clearly determined specimen WAM Z88865 to belong to *U.* cf. *aruensis* (fig. 5).

U. cf. *aruensis* has polyp sizes similar to those of *U. kanabou* as described in Fujii et al. (2021), however *U. kanabou* has been reported to be exclusively in association with gorgonians while *U.* cf. *aruensis* exclusively associates with sponges, and appears to be specific to *Trikentrion flabelliforme*.

Specimen NHMUK 1887.5.21.1865 was referred to *Trikentrion laeve* Carter, 1879 by Carter (1882), being a species described from South Africa. Although the specimen number was not given in the publication, Carter's (1899) description is of a fan-shaped sponge with an anastomosing zoantharian over its surface. Hooper (1991) used Carter's name for the specimen NHMUK 1887.5.21.1865, namely *Trikentrion laeve* var. *flabelliforme*, but Van Soest et al. (2012) noted that the specimen was never formerly described. Re-examination of a fragment of the specimen by J.N.A. Hooper and JF confirmed that this specimen is *T. flabelliforme* based on the spicule complement and skeletal characters. Therefore, the locality of this specimen as southwest Western Australia is potentially incorrect as no specimens of *T. flabelliforme* have since been collected south of Red Bluff near Ningaloo (–24.043611 °S, 113.026944 °E) in Western Australia.

Hooper (1991) redescribed *T. flabelliforme* and commented on the heavy infestation of a white zoantharian that regularly occurs on this species. He noted it was previously referred to as *Bergia* in Carter (1882). *Trikentrion flabelliforme* is common in shallow subtidal tropical waters and has been reported from the Arafura Sea (type locality), and Northern and Western Australia.

Umimayanthus mirnangga sp. nov. Montenegro, Kise & Reimer

urn:lsid:zoobank.org:act:50E0D7DC-D383-45EE-B921-1140F1E29347

Etymology. The specific epithet "mirnangga" is derived from the phoneme used to refer to a young single woman in the Wunambal language. This in reference to the fact that the colonies of *U. mirnangga* sp. nov. are exclusively composed of solitary polyps. "mɨrnangga binya" *n., B-class* young woman. *Syn*: munangga. See Bengmoro et al. (1971) and Boona (2022).

Material examined. Type locality: Maret Is. [loc. 19], Western Australia, -14.35445 °S, 124.9488 °E. *Holotype*: WAM Z88824 (–14.35445 °S, 124.9488 °E, loc. 19, Maret Is., Western Australia, 61 m depth, December 16, 2015 by O.A. Gomez & J.A. Ritchie). *Paratype*: WAM Z88823 (–14.424417 °S, 125.040933 °E, loc. 17, Maret Is., Western Australia, 55 m depth, December 9, 2015 by O.A. Gomez & J.A. Ritchie).

Other material. Other examined specimens belong to the Western Australian Museum; WAM Z88817 (–15.446442 °S,

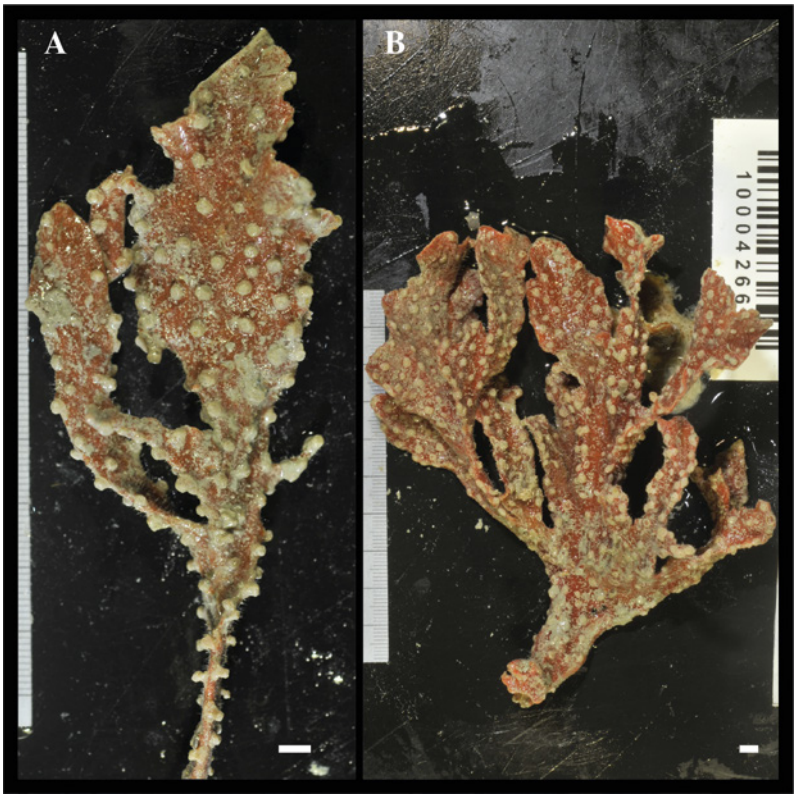

FIGURE 7 Type specimens of *Umimayanthus mirnangga* sp. nov; (A) WAM Z88824 (holotype), (B) WAM Z88823 (paratype). Scale bars: 5 mm

124.083022 °E, loc. 15, Camden Sound, Western Australia, 61 m depth, March 20, 2015 by J. Fromont & L. Kirkendale).

Diagnosis. U. mirnangga sp. nov. can be distinguished from other species in the genus *Umimayanthus* by having colonies exclusively formed of solitary polyps, and by having symbiotic associations with sponges in genus *Endectyon* Topsent, 1920 and *Ectyoplasia* Topsent, 1931; current known hosts are *Endectyon* (*Endectyon*) *fruticosum* (Dendy, 1887) and *Ectyoplasia vannus* Hooper, 1991. Additionally, *U. mirnangga* sp. nov. can be differentiated from all other species in genus *Umimayanthus* by three unique nucleotide substitutions across the ITS-rDNA region as follows: "C" in positions 88 bp and 418 bp, and "G" at position 438 bp (fig. 8).

Description. Size. Preserved polyps were on average 2.41 mm ± 0.23 mm (σ^2 = 0.05, max 2.722 mm, n = 9 polyps) in diameter, and 2.18 mm ± 0.23 mm (σ^2 = 0.05, max 2.506 mm, n = 9 polyps) in height. All measurements were performed of ethanol-preserved specimens: zoantharian voucher numbers WAM Z88824, WAM Z88823, and WAM Z88817.

Morphology. The type specimens are associated with *Ectyoplasia vannus.* The

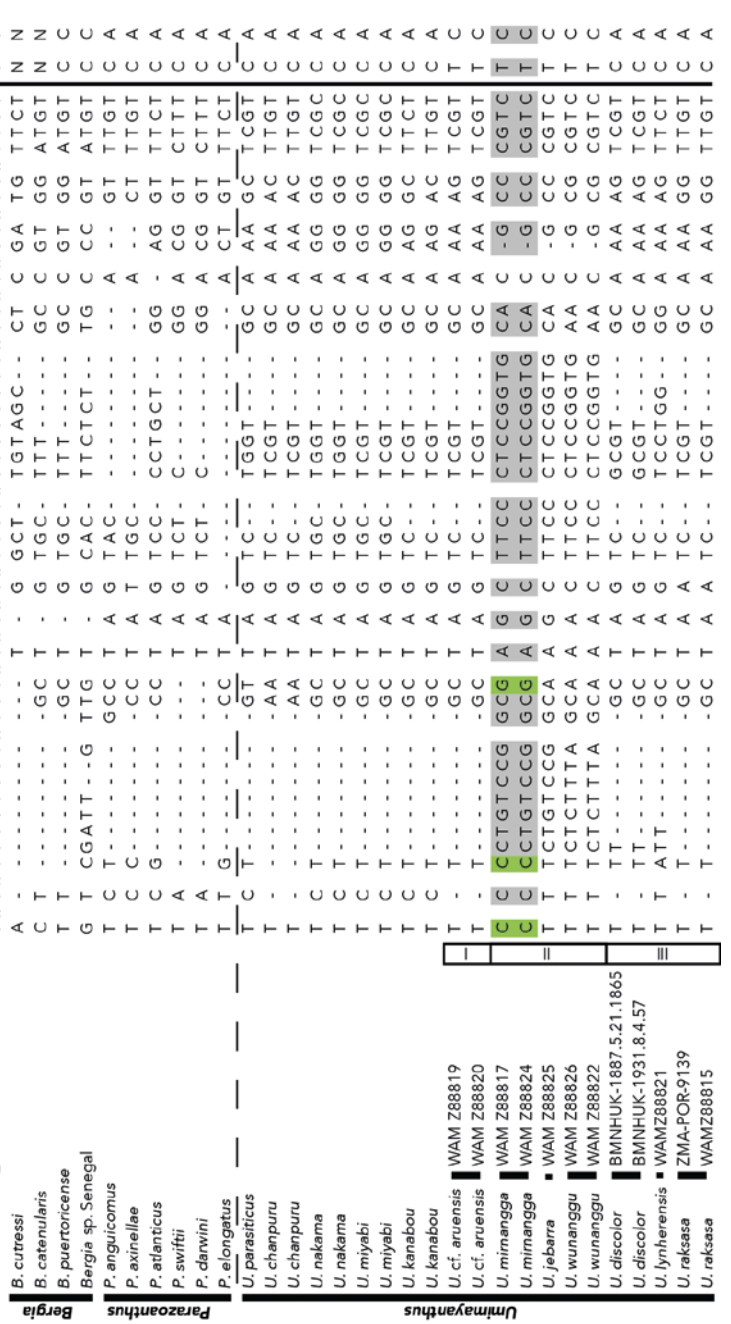

FIGURE 8 Summary chart of the alignments showing nucleotide positions characteristics to *U. mirnangga* sp. nov. across the ITS-rDNA and CO1-mtDNA region. Positions in green are unique to *U. mirnangga* sp. nov. in genus *Umimayanthus*. Positions in grey are characteristic but not unique to *U. mirnangga* sp. nov

species has solitary polyps spread all over the surface of the sponges. The inter-polyp distance is variable, with a minimum distance of 2.35 mm between polyps, and an average of 4.27 mm ± 0.91 mm (σ^2 = 0.83, max. 6.751 mm, n = 44 polyps) between them. Capitulary ridges were visible, 14–16 in number. Polyps preserved in ethanol are yellowish in colour. No cnidae or internal morphological data are available for this species due to the poor condition of the preserved specimens.

Distribution. All specimens analysed were collected along the west coast of Australia. Camden Sound [loc. 15] and Maret Is. [loc. 17, 19] (fig. 1). Specimens were found at depths of 55–61 m.

Associated host. Umimayanthus mirnangga sp. nov. was found associated with two different sponge species, *Ectyoplasia vannus* and *Endectyon* (*Endectyon*) *fruticosum*, both in the family Raspailiidae.

Remarks. Umimayanthus mirnangga sp. nov., *U. wunanggu* sp. nov., and *U. jebarra* sp. nov. are sibling species based on our phylogenetic analyses. Key diagnostic molecular and morphological characters, including the general external morphology of the colonies and the height of the polyps, as well as the different host species, clearly separate these three species from each other.

Out of all the species in *Umimayanthus* the closest resemblances can be found between the sibling species *U. wunanggu* sp. nov., and *U. jebarra* sp. nov., which have similar polyp diameters as *U. mirnangga* sp. nov. Nonetheless, the heights of polyps in *U. mirnangga* sp. nov. are 2.41 mm ± 0.23 mm, twice as large as *U. wunanggu* sp. nov. (0.92 mm ± 0.36 mm), and smaller than *U. jebarra* sp. nov. (3.09 mm ± 0.63 mm). Furthermore, the morphological differences between *U. mirnangga* sp. nov. and *U. wunanggu* sp. nov. are present even though both species were found to establish associations with the same sponge species, *Endectyon* (*Endectyon*) *fruticosum*. Out of the three sibling species, *U. mirnangga* sp. nov. is the only species composed exclusively of solitary polyps.

The type locality of *Ectyoplasia vannus*, the host sponge of *Umimayanthus mirnangga* sp. nov., is Port Essington in the Northern Territory, Australia, and this sponge species has otherwise only been reported from other areas in the Northern Territory and tropical Western Australia.

Umimayanthus jebarra sp. nov. Montenegro, Kise & Reimer

urn:lsid:zoobank.org:act:557A4CDC-8805-4626-854E-C591DB88598C

Etymology. The specific epithet "jebarra" is derived from the phoneme used to refer to the emu in Wunambal language. This in reference to the elongated shape of the polyps in *U. jebarra* sp. nov., which resemble the neck of an emu. As well, the name can act as a memorial to all the emus killed during the Great Emu Wars of 1932 in Western Australia. "jebarra anya" *n., A-class.* emu. *Dromaius novaehollandiae*. *Syn*: garnanganyja; jeebarra. See Mangglamarra (1991) and Karadada et al. (2011).

Material examined. Type locality: Eclipse Is. [loc. 21], –13.493782 °S, 125.851633 °E. *Holotype*: WAM Z88825 (–13.493782 °S, 125.851633 °E, loc. 21, Eclipse Is., Western

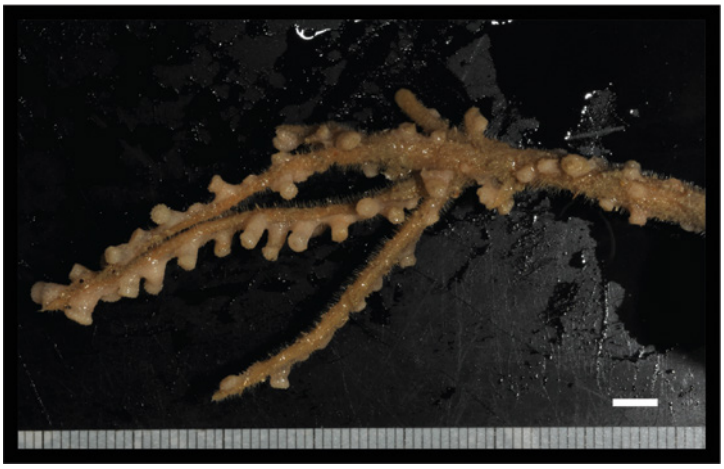

FIGURE 9 Holotype of *Umimayanthus jebarra* sp. nov.; (A) WAM Z88825 (holotype). Scale bars: 5 mm

Australia, 41 m depth, March 2, 2016 by O.A. Gomez & J.A. Ritchie). No other material was available.

Diagnosis. U. jebarra sp. nov. can be distinguished from other species in the genus *Umimayanthus* by having colonies with polyps connected to each other in a linear fashion, and establishing symbiotic associations with sponges in the genus *Endectyon*. Additionally, three unique substitutions in the ITS-rDNA region differentiate *U. jebarra* sp. nov. from all other species in the genus *Umimayanthus*, as follows: "G" in position 367 bp, "C" in position 417 bp and "A" in position 760 bp. Furthermore, a unique combination of nucleotides can be found between positions 417 bp to 425 bp in the ITS-rDNA region (fig. 10).

Description. Size. Preserved polyps were on average 2.34 mm ± 0.02 mm ($\sigma 2$ = 0, max. 2.36 mm, n = 3 polyps) in diameter, and 3.09 mm ± 0.63 mm ($\sigma 2$ = 0.39, max. 3.77 mm, min. 2.53, n = 3 polyps) in height. All measurements were performed on ethanol-preserved specimens: zoantharian voucher WAM Z88825.

Morphology. The holotype specimen is associated with a sponge in the genus *Endectyon*. The colony is formed by a chain of polyps that branches and extends linearly over the surface of the sponge. The coenenchyma connecting the polyps is thin but clearly visible. All polyps were clearly spread over the sponge matrix and the coenenchyma tissue by 3.09 mm ± 0.63 mm on average. Capitulary ridges were visible, and approximately 16 in number. Polyps preserved in ethanol were orange in colour. No cnidae or internal morphological data are available for this species due to the poor condition of the preserved specimen.

Distribution. The specimen analysed was collected along the west coast of Australia. Eclipse Is. [loc. 21] (fig. 1). The specimen was found at a depth of 41 m.

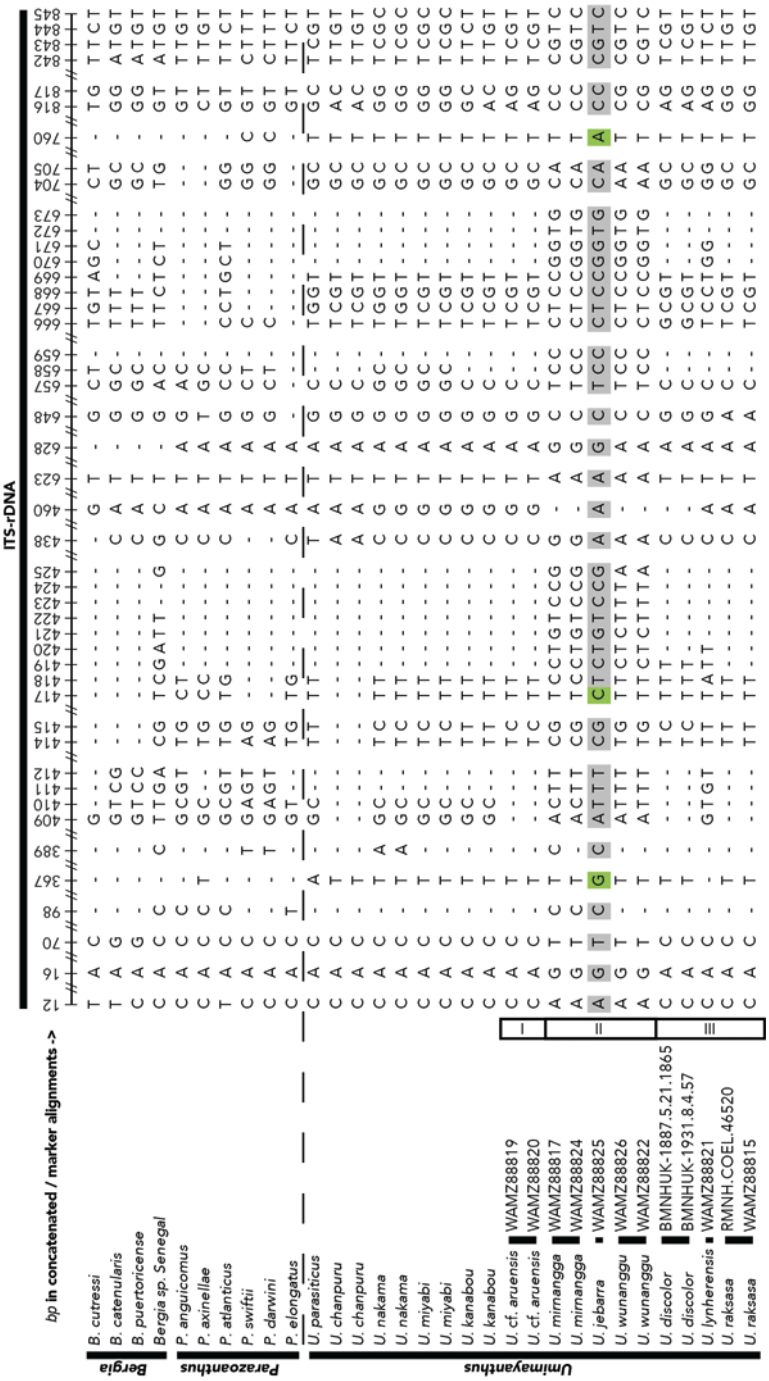

FIGURE 10 Summary chart of the alignments showing nucleotide positions characteristics to *U. jebarra* sp. nov. across the ITS-rDNA region. Positions in green are unique to *U. jebarra* sp. nov. in genus *Umimayanthus*. Positions in grey are characteristic but not unique to *U. jebarra* sp. nov

Associated host. Umimayanthus jebarra sp. nov. was found in association with a sponge in the genus *Endectyon*.

Remarks. U. mirnangga sp. nov., *U. wunanggu* sp. nov., and *U. jebarra* sp. nov. are closely related sibling species. Nonetheless, key diagnostic molecular and morphological characters, including the external morphology of the colonies and the height of the polyps, as well as the different host species, clearly separate these three species from each other.

The sponge specimen voucher WAM Z94791 could only be identified as *Endectyon* sp. The acanthostyles are "cladotylote-like". For now, we have retained this specimen in *Endectyon* but this interesting specimen requires further study for a species-level identification.

While no other species in the genus *Umimayanthus* quite resemble *U. jebarra* sp. nov., the closest similarity is to one of the specimens WAM Z88817 of *U. mirnangga* sp. nov. associated with the sponge *Endectyon* (*Endectyon*) *fruticosum* (sponge voucher WAM Z87200). However, the polyps of *U. mirnangga* sp. nov. are solitary, while the polyps of *U. jebarra* sp. nov. are clearly connected to each other in a linear fashion by a coenenchyma, which is not as well developed as in *U.* cf. *aruensis* or in *U. discolor* sp. nov.

Umimayanthus wunanggu sp. nov. Montenegro, Kise & Reimer

urn:lsid:zoobank.org:act:E0D67C58-5506-4700-9F44-98C4789A27F7

Etymology. The specific epithet "wunanggu" is derived from the phoneme used to refer to the hill white gum tree in Wunambal language. This in reference to *U. wunanggu* sp. nov. forming colonies of white polyps connected by a thin coenenchyma that extends on a linear branching pattern over the sponge surface. "wunanggu winya" *n., W-class.* /wunaŋgu/. hill white gum, tropical red box, *Eucalyptus brachyandra* von Mueller, 1859. See Capell (1941) and Karadada (2011).

Material examined. Type locality: Eclipse Is. [loc. 20], –13.794197 °S, 126.11881 °E, Western Australia (fig. 1).

Holotype. WAM Z88826 (–13.794197 °S, 126.11881 °E, loc. 20, Eclipse Is., Western Australia, 59 m depth, March 7, 2016 by O.A. Gomez & J.A. Ritchie). *Paratype 1*: WAM Z88822 (–14.401883 °S, 124.944067 °E, loc. 18, Maret Is. Western Australia, 50 m depth, December 8, 2015 by O.A. Gomez & J.A. Ritchie). *Paratype 2*: WAM Z88818 (–15.446442 °S, 124.083022 °E, loc. 15, Camden Sound, Western Australia, 61 m depth, March 20, 2015 by J. Fromont & L. Kirkendale).

Other material. One additional examined specimen belonging to the Western Australian Museum; WAM Z88827 (–15.6233 °S, 121.972233 °E, loc. 13, Lynher Bank, Western Australia, 61 m depth, October 28, 2016 by J. Fromont & J.A. Ritchie).

Diagnosis. U. wunanggu sp. nov. can be distinguished from all other sponge-associated zoantharians by its symbiotic associations with sponges in the genus *Endectyon*, and forming colonies of polyps connected by a thin coenenchyma that extends linearly over the host sponge surface; currently known to establish associations with *Endectyon* (*Endectyon*) *fruticosum* and *Endectyon* (*Endectyon*)

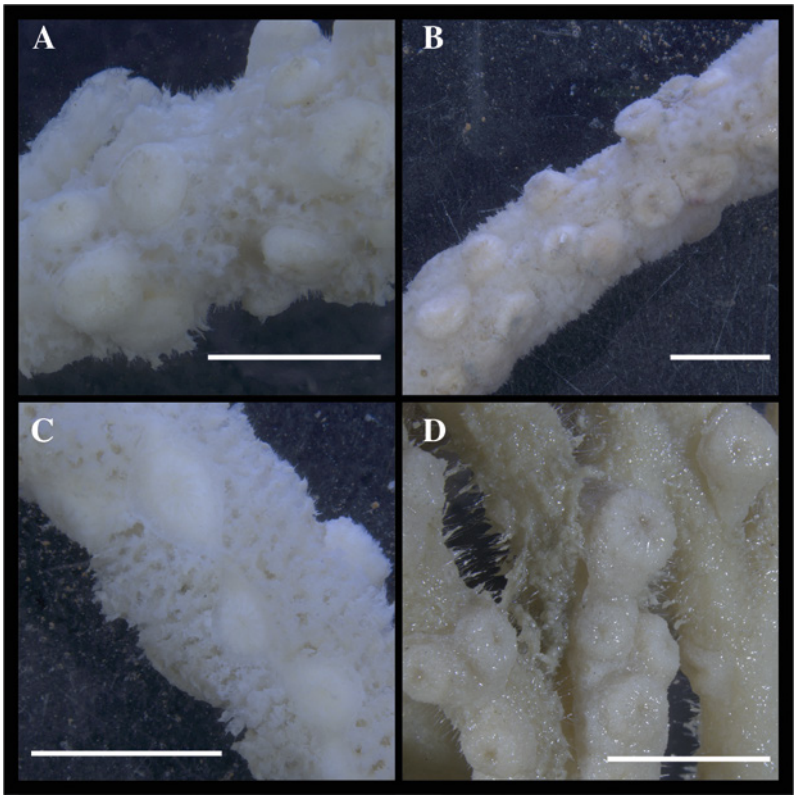

FIGURE 11 Specimens of *Umimayanthus wunanggu* sp. nov.; (A) WAM Z88826 (holotype), (B) WAM Z88822 (paratype), (C) WAM Z88818 (paratype), and (D) WAM Z88827. Scale bars: 5 mm

thurstoni (Dendy, 1887). Additionally, unique substitutions across the ITS-rDNA region set this species apart from other species in the genus *Umimayanthus*, as follows: "C" in positions 360 bp, 421 bp, and 426 bp; "TTAC" from positions 423–426 bp; "A" in position 704 bp; and a unique combination of nucleotides, "AA" between position 704–705 bp, and "CG" in 816–817 bp (fig. 12).

Description. Size: Preserved polyps are on average 2.4 mm ± 0.22 mm (σ^2 = 0.05, max. 2.79 mm, n = 12 polyps) in diameter, and 0.92 mm ± 0.36 mm (σ^2 = 0.13, max. 1.77 mm, n = 12 polyps) in height. All measurements were performed on voucher specimens preserved in ethanol: zoantharian voucher numbers WAM Z88826, WAM Z88822, WAM Z88818, and WAM Z88827.

Morphology. The holotype specimen is associated with *Endectyon* (*Endectyon*) *thurstoni*. The polyp diameter of *U. wunanggu* sp. nov. is remarkably constant, 2.2~2.8 mm across all analysed specimens. All specimens were colonies with polyps extended well over the sponge surface. Most specimens had polyps connected by a well-developed coenenchyma, forming

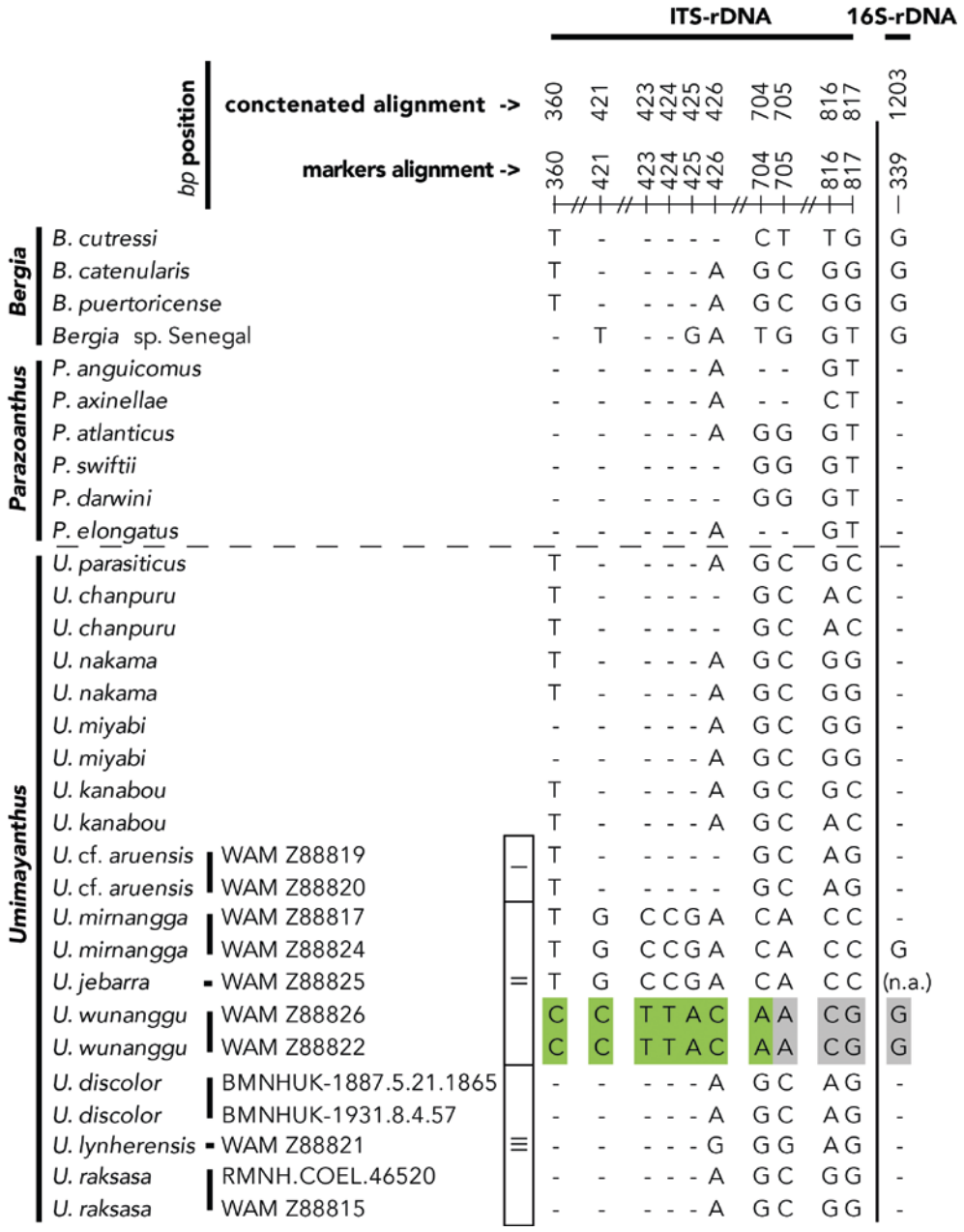

FIGURE 12 Summary chart of the alignments showing nucleotide positions characteristics to *U. wunanggu* sp. nov. across the ITS-rDNA and 16S-rDNA region. Positions in green are unique to *U. wunanggu* sp. nov. in genus *Umimayanthus*. Positions in grey are characteristic but not unique to *U. wunanggu* sp. nov

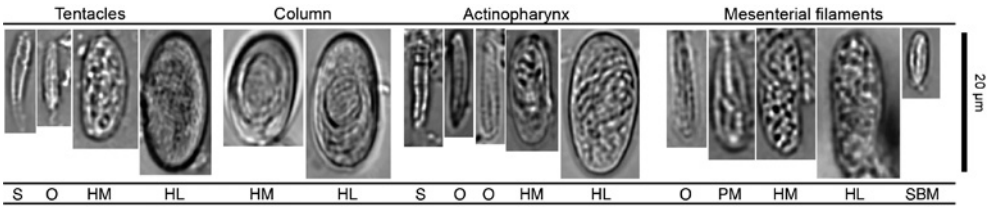

FIGURE 13 Diversity of cnidae found in *Umimayanthus wunanggu* sp. nov. across tissues in specimen WAM Z88826. (S) spriocysts, (O) basitrichs and microbasic b-mastigophores, (HM) holotrich medium, (HL) holotrich large, (PM) microbasic p-mastigophores and (SBM) special microbasic b-mastigophores

chains of polyps in branches rather than in a reticulate pattern, different from *U.* cf. *aruensis*. Capitulary ridges were visible, 14–18 in number. Tentacles were approximately up to 36 in number. Preserved tentacles were light brown in coloration. Capitulum and scapus were heavily encrusted by various particles of sand and silica (= spicules of host sponges). Polyps preserved in ethanol were white or cream in color.

Cnidae. Except for holotrich (S), all categories of cnidae were found. The cnidae composition across tentacles and pharynx was similar and made up of spirocysts, holotrichs (L) and (M), bastrichs and microbasic b-mastigophores. The column had the lowest diversity of cnidae with only holotrichs (L) and (M). In contrast the mesenterial filaments had the largest diversity of cnidae, including holotrichs (L) and (M), microbasic p-mastigophores, bastrichs and microbasic b-mastigophores and special microbasic b-mastigophores. For details on sizes, lengths, and widths of each cnidae type, see table 4 and fig. 13.

Internal morphology. Sphincter muscle was located in the endoderm. Mesenterial arrangement was macrocnemic. Mesenteries were approximately up to 28 in number. Ectoderm and mesoglea of capitulum and scapus were heavily encrusted by various sand and silica particles. Single siphonoglyph.

Distribution. All specimens analysed were collected along the west coast of Western Australia. Lynher Bank [loc. 13], Camden Sound [Loc. 15], Maret Is. [loc. 18] and Eclipse Is. [loc. 20] (fig. 1). Specimens were found at depths of 50–61 m.

Associated host. Umimayanthus wunanggu sp. nov. was associated with four sponges in two species in the family Raspailiidae Nardo, 1833, *Endectyon* (*Endectyon*) *thurstoni* (n = 3) and *Endectyon* (*Endectyon*) *fruticosum* (n = 1). The type locality of *Endectyon* (*Endectyon*) *thurstoni* is India, and this species has also been reported from the Arabian Sea and Western Australia. The type locality of *Endectyon* (*Endectyon*) *fruticosum* is also India and it has additionally been reported from the Aru Islands, Indonesia, the south Andaman Sea, Thailand (Hooper, 1991), and now from the Kimberley region, Western Australia. Based on this wide host sponge distribution, it may be that the distribution of *U. wunanggu* sp. nov. is wider than currently known.

Remarks. Umimayanthus wunanggu sp. nov., *Umimayanthus mirnangga* sp. nov. and *Umimayanthus jebarra* sp. nov. are

TABLE 4 Results for the cnidocyte analyses for *Umimayanthus wunanggu* sp. nov., holotype specimen WAM Z88826

Tissue	Category	Length (max–min, average)	Width (max–min, average)	*n*	Frequency
Tentacles	Spirocysts	22.6–11.6, 29.2	3.3–1.1, 2.2	90	Numerous
	Bastrichs and microbasic b-mastigophores	18.1–9.8, 15.7	3.6–1.9, 3.0	15	Occasional
	Holotrichs (L)	24.1–23.6, 23.8	11.1–9.8, 10.5	2	Rare
	Holotrichs (M)	18.8–11.8, 16.4	8.8–5.9, 7.5	9	Occasional
Column	Holotrichs (L)	29.4–20.0, 23.5	14.3–11.1, 12.4	38	Common
	Holotrichs (M)	19.8–14.7, 17.1	11.0–8.8, 10.0	11	Occasional
Pharynx	Spirocysts	19.5–11.7, 15.7	3.0–1.2, 2.1	16	Common
	Bastrichs and microbasic b-mastigophores	23.1–11.0, 17.3	3.5–1.6, 2.6	80	Numerous
	Holotrichs (L)	23.2–21.0, 21.9	11.8–11.7, 11.8	3	Rare
	Holotrichs (M)	18.5–15.0, 16.6	9.3–7.1, 7.9	8	Occasional
Mesenterial Filaments	Bastrichs and microbasic b-mastigophores	19.9–6.4, 17.6	2.9–.3, 2.6	4	Rare
	Holotrichs (L)	25.0–20.5, 22.6	12.8–7.7, 10.0	4	Rare
	Holotrichs (M)	18.6–17.5, 18.1	7.2–6.9, 7.1	2	Rare
	Microbasic p-mastigophores	18.9–16.0, 17.7	5.5–3.4, 4.5	10	Occasional
	Special microbasic b-mastigophores	11.6–6.4, 9.7	3.7–2.4, 3.1	14	Occasional

sibling species that were shown to be closely related in our phylogenetic analyses. Nonetheless, key diagnostic molecular and morphological characters, including the general external morphology of the colonies and the height of the polyps, as well as the different host species, clearly separate these three species from each other. For details refer to each of the species formal description.

Umimayanthus discolor sp. nov. Montenegro, Kise & Reimer

urn:lsid:zoobank.org:act:7A022F55-32F9-49FA-A395-081BA7240FF3

Synonymy. This specimen was misidentified as *Parazoanthus lividum*, specimen F67954 in the collection of Museum Victoria.

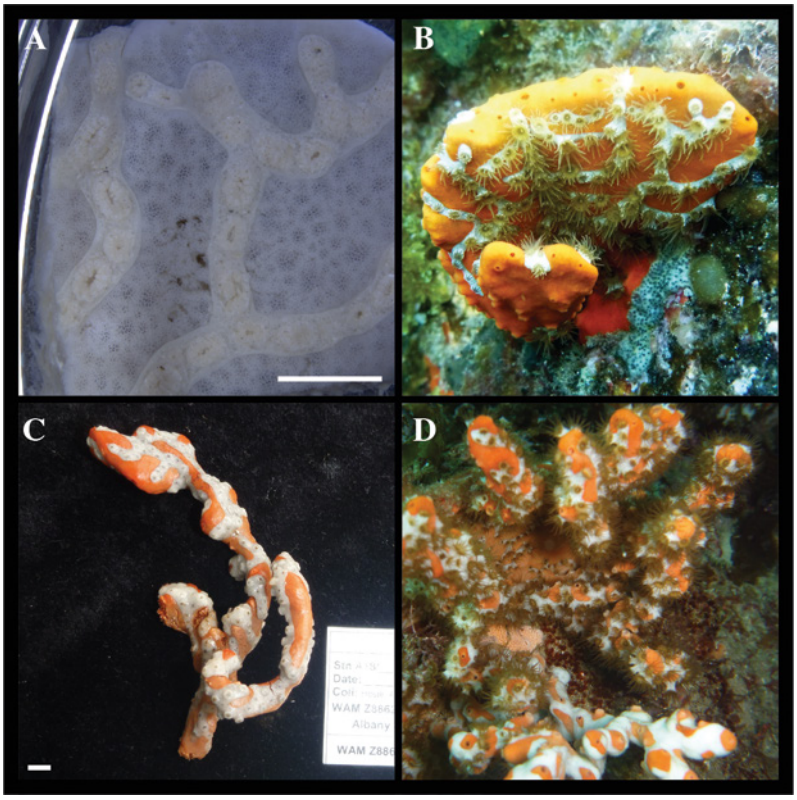

FIGURE 14 Type specimens of *Umimayanthus discolor* sp. nov.; WAM Z88616 (holotype) voucher specimen (A) and in-vivo pictures (B), WAM Z88626 (paratype) voucher specimen (C) and in-vivo pictures (D). Scale bars: 5 mm

Etymology. The specific epithet "discolor" means multiple colors in Latin. This is in reference to *U. discolor* sp. nov. forming colonies of polyps with contrasting colorations between the oral disk and the column, stolon, and coenenchyma.

Material examined. Type locality: Albany [loc. 3], −35.093889 °S, 117.963889 °E. *Holotype*: WAM Z88616 (−35.093889 °S, 117.963889 °E, loc. 3, Murray Road boat ramp, Albany, Western Australia, 6.4 m depth, April 10, 2018 by O.A. Gomez). *Paratype*: WAM Z88626 (−35.049722 °S, 117.693611 °E, loc. 4, Shelter Is., Albany, Western Australia, 8.5 m depth, April 11, 2018 by O.A. Gomez).

Other material (n =3). Other examined specimens belong to the Museum of Natural History and Museums Victoria; NHMUK-1887.5.21.1865 (precise location unknown, southwestern part of Western Australia), NHMUK-1931.8.4.57 (−6.164028 °S, 134.944667 °E, loc. 24, east coast of Aru Is., Maluku, Indonesia, 4–15 m depth), MV-F67954 (−39.016306 °S, 146.442917 °E, loc. 1, South Wall, Sealer Cove, Wilsons Promontory, Victoria, Australia, 10 m depth, April 16, 1987 by Dept. Conservation of Environment).

Diagnosis. U. discolor sp. nov. can be distinguished from other species in the genus *Umimayanthus* by combining the growing pattern and coloration of colonies. *U. discolor* has polyps connected in chains following a branching pattern, but branches are not connected to each other. Different from all other species of *Umimayanthus* in the Indo-Pacific Ocean, *U. discolor* sp. nov. has a disruptive coloration pattern when observed *in-vivo*, with polyps having a dark brown oral disk clearly contrasting against the white-coloured column, stolon, and coenenchyma (fig. 14B–D). Currently known to establish associations with sponges in the genera *Trikentrion* Ehlers, 1870 and *Clathria* Schmidt, 1862; known host species are *Trikentrion flabelliforme* and *Clathria* (*Thalysias*) *cactiformis* (Lamarck, 1814).

Additionally, multiple unique substitutions across the ITS-rDNA, 16S-rDNA and COI-mtDNA markers clearly differentiate this species from all other members of genus *Umimayanthus* in the concatenated alignment, as follows: in the ITS-rDNA there is a "A" in position 9 bp, "TCA" between 42 bp to 44 bp, "T" at 74 bp, 344 bp and 665 bp, "G" at 87 bp, 430 bp, 652 bp, 710 bp, and unique deletions at 51 bp and 455 bp; remarkably substitutions were found in the 16S-rDNA region, "T" at position 1337bp, and COI-rDNA region, "T" at position 1654bp . As well, a unique combination of substitutions and deletions/gabs is present between 132–339 bp in the ITS-rDNA region (fig. 15).

Description. Size. Preserved polyps were on average 2.1 mm ± 0.26 mm (σ^2 = 0.07, max. 2.39 mm, n = 9 polyps) in diameter, and 0.97 mm ± 0.46 mm (σ^2 = 0.21, max. 1.58 mm, n = 8 polyps) in height. All measurements were performed on voucher specimens preserved in ethanol: zoantharian specimen vouchers WAM Z88616, WAM Z88626, and MV-F67954.

Morphology. The holotype specimen is associated with *Clathria* (*Thalysias*) *cactiformis* (Lamarck, 1814). Colonies formed by polyps tightly connected by stoloniferous chains in a branching pattern extending over the surface of the host sponge. Polyp chains branch continuously with branches interconnected. The coenenchyma is clearly visible over the sponge surface and connects multiple polyps by the stolon. Polyps preserved in ethanol are white or cream in color. Capitulary ridges were not visible. Tentacles were approximately up to 22–24 in number. Capitulum and scapus were moderately encrusted by small sand particles.

Cnidae. The diversity of cnidae was relatively low across tissues. Spirocysts, bastrichs and microbasic b-mastigophores were numerous in the tentacles and pharynx. Additionally, holotrichs (L) were found in the pharynx. Mesenterial filaments were populated by numerous microbasic p-mastigophores, while cnidae were rare in the column with only holotrichs (L) found. See table 5 and fig. 16.

Internal morphology. Sphincter muscle was located in the endoderm. Mesenterial arrangement was macrocnemic. Mesenteries were approximately up to 22–24 in number.

Distribution. Analysed specimens were collected from Australia and Indonesia. In Australia, specimens were from Albany [loc. 3, 4] and Wilson's Promontory [loc. 1], and in Indonesia from the Aru Islands

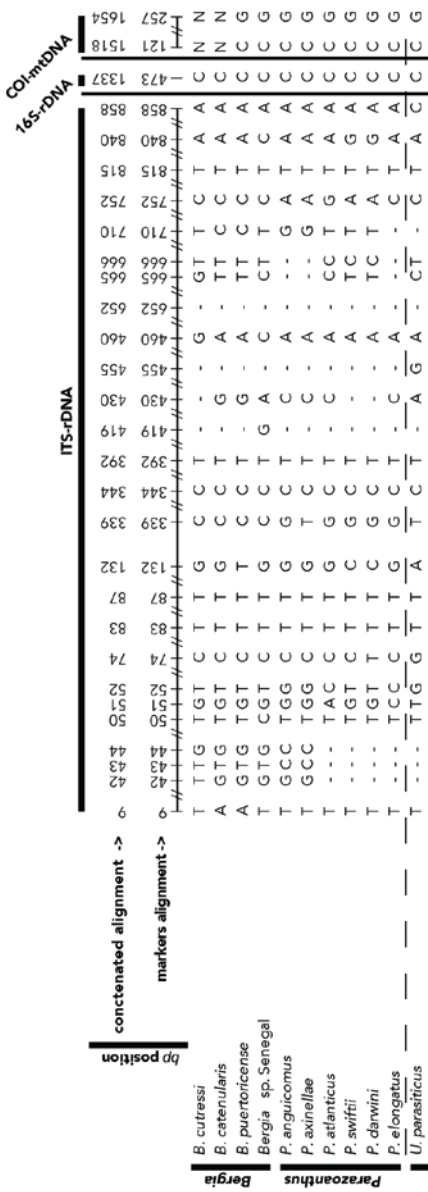

FIGURE 15 Summary chart of the alignments showing nucleotide positions characteristics to *U. discolor* sp. nov. across the ITS-rDNA, 16S-rDNA and CO1-mtDNA region. Positions in green are unique to *U. discolor* sp. nov. in genus *Umimayanthus*. Positions in grey are characteristic but not unique to *U. discolor* sp. nov

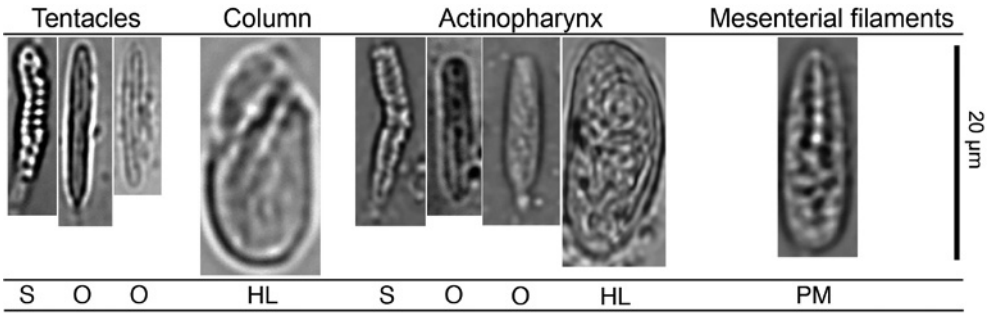

FIGURE 16 Diversity of cnidae found in *Umimayanthus discolor* sp. nov. across tissues in specimen WAM Z88616. (S) spriocysts, (O) basitrichs and microbasic b-mastigophores, (HL) holotrich large and (PM) microbasic p-mastigophores

TABLE 5 Results for the cnidocyte analyses for *Umimayanthus discolor sp. nov.*, holotype specimen WAM Z88616

Tissue	**Category**	**Length (max–min, average)**	**Width (max–min, average)**	***n***	**Frequency**
Tentacles	Spirocysts	26.3–13.5, 19.4	3.6–1.3, 2.3	213	Numerous
	Bastrichs and microbasic b-mastigophores	23.7–15.6, 18.5	3.9–1.0, 2.2	13	Occasional
Column	Holotrichs (L)	22.9	9.5	1	Rare
Pharynx	Spirocysts	23.9–13.5, 17.4	3.4–1.1, 2.2	106	Numerous
	Bastrichs and microbasic b-mastigophores	23.1–13.3, 17.2	4.5–1.7, 2.8	47	Numerous
	Holotrichs (L)	21.9	18.2	1	Rare
Mesenterial Filaments	Microbasic p-mastigophores	24.0–15.2, 19.9	7.0–3.5, 5.3	65	Numerous

[loc. 24] (fig. 1). Specimens were found at depths of 4–15 m.

Associated host. Umimayanthus discolor sp. nov. was found to be associated with two sponge species; *Clathria* (*Thalysias*) *cactiformis*, family Microcionidae Carter, 1875, and *Trikentrion flabelliforme*, family Raspailiidae.

As with *Umimayanthus* cf. *aruensis*, only historic specimens (collected in 1887 and 1931) of *Trikentrion flabelliforme* were shown to host *Umimayanthus discolor* sp. nov., and all more recently collected specimens of this sponge species available to us instead hosted *Umimayanthus* cf. *aruensis*.

Clathria (*Thalysias*) *cactiformis* is in a different sponge family (Microcionidae) from *Trikentrion flabelliforme* (Raspailiidae). The other *Umimayanthus* species described in this study are specific to the same host family, often to the same genus, and in one instance to a single species. Thus, *Umimayanthus discolor* sp. nov. is a more 'host-generalist' species, and the exception among these newly described *Umimayanthus* species.

Remarks. Molecular data and the arrangement of polyps in specimens BMNH-1887.5.21.1865 and BMNH-1931.8.4.57 led us to identify these specimens as *Umimayanthus discolor* sp. nov., and further morphological analyses will be helpful to confirm this decision.

Specimen MV-F67954 was initially identified as *P. lividum*, however based on the general morphology of the colony, with polyps arranged in branching chains, and the association with *Clathria* (*Thalysias*) cf. *cactiformis*, we have amended the identification of this specimen to *Umimayanthus discolor* sp. nov.

U. discolor sp. nov. has polyp diameter sizes similar to those reported for *U. chanpuru*, *U. miyabi*, and *U. nakama*, all from southern Japan. In contrast to these species, *U. discolor* sp. nov. has a well-developed coenenchyma firmly connecting polyps in chains in a branching pattern. These branches remain unlinked and do not form a reticulate pattern over the surface of the host sponge, unlike as in *U.* cf. *aruensis*, and do not form a mat as in *Parazoanthus lividum*.

Umimayanthus lynherensis sp. nov. Montenegro, Kise & Reimer

urn:lsid:zoobank.org:act:5047277C-8846-4965-81E1-53A2D5268A56

Etymology. The specific epithet "*lynherensis*" is derived from the locality where the type specimen was collected, the Lynher Bank sea country north Kimberley, Western Australia, Australia.

Material examined. Type locality: Lynher Bank [loc. 14], –15.493683 °S, 121.636233 °E. *Holotype*: WAM Z88821 (–15.493683 °S, 121.636233 °E, loc. 14, Lynher Bank, Western Australia, 95 m depth, October 25, 2016 by J. Fromont & J.A. Ritchie). No other material was available.

Diagnosis. U. lynherensis sp. nov. can be differentiated from all other species in the genus *Umimayanthus* by combining polyp size, colony morphology and identity of the host sponges. *U. lynherensis* sp. nov. have comparatively the smallest polyp diameter of all the species described in here, 1.58 mm ± 0.17 mm, colonies exclusively composed of solitary polyps, and associate with sponges in *Sigmaxinella*

FIGURE 17 *Umimayanthus lynherensis* sp. nov. specimen WAM Z88821 (holotype). Scale bars: 5 mm

soelae Hooper, 1984 of the order Biemnida Morrow, 2013.

Additionally, there are multiple unique nucleotide substitutions and insertions across ITS-rDNA and CO1-mtDNA in the concatenated alignment, as follows: for ITS-rDNA an "A" in positions 47 bp and 135 bp, a "C" at 65 bp and 354 bp, a "G" at 403 bp, 411bp, 426 bp and 705 bp, a "T" at 756 bp, and one unique insertion of 8 nucleotides "GGTGGGGT" between 695–702 bp. As well, multiple unique substitutions were also found in the CO1 region: a "G" at positions 1442 bp and 1446 bp, a "C" at 1804 bp, and an "A" at 1835 bp (fig. 18).

Description. Size. Preserved polyps were on average 1.58 mm ± 0.17 mm (σ^2 = 0.03, max. 1.74 mm, n = 3 polyps) in diameter, and 0.34 mm ± 0.06 mm (σ^2 = 0, max. 0.39 mm, n = 3 polyps) in height. All measurements were performed on the ethanol preserved zoantharian specimen voucher WAM Z88821.

Morphology. The holotype specimen is associated with *Sigmaxinella soelae*. Colonies formed of solitary polyps, barely extending out from the surface of the sponge. The polyps were distributed all over the surface of the sponge, and inter-polyp distances were relatively constant, 3.58 mm ± 0.44 mm (σ^2 = 0.19, max. 4.56 mm, n = 14 polyps). Capitulary ridges were visible, 10–12 in number. Tentacles up to 24 in number. Polyps preserved in ethanol were white in color.

Cnidae. All dissected tissues had a unique composition of cnidae compared to other species examined in this study (table 6). Spirocysts were only present in tentacles. Bastrichs and microbasic b-mastigophores were found across most tissues except for the column. Special microbasic b-mastigophores were found

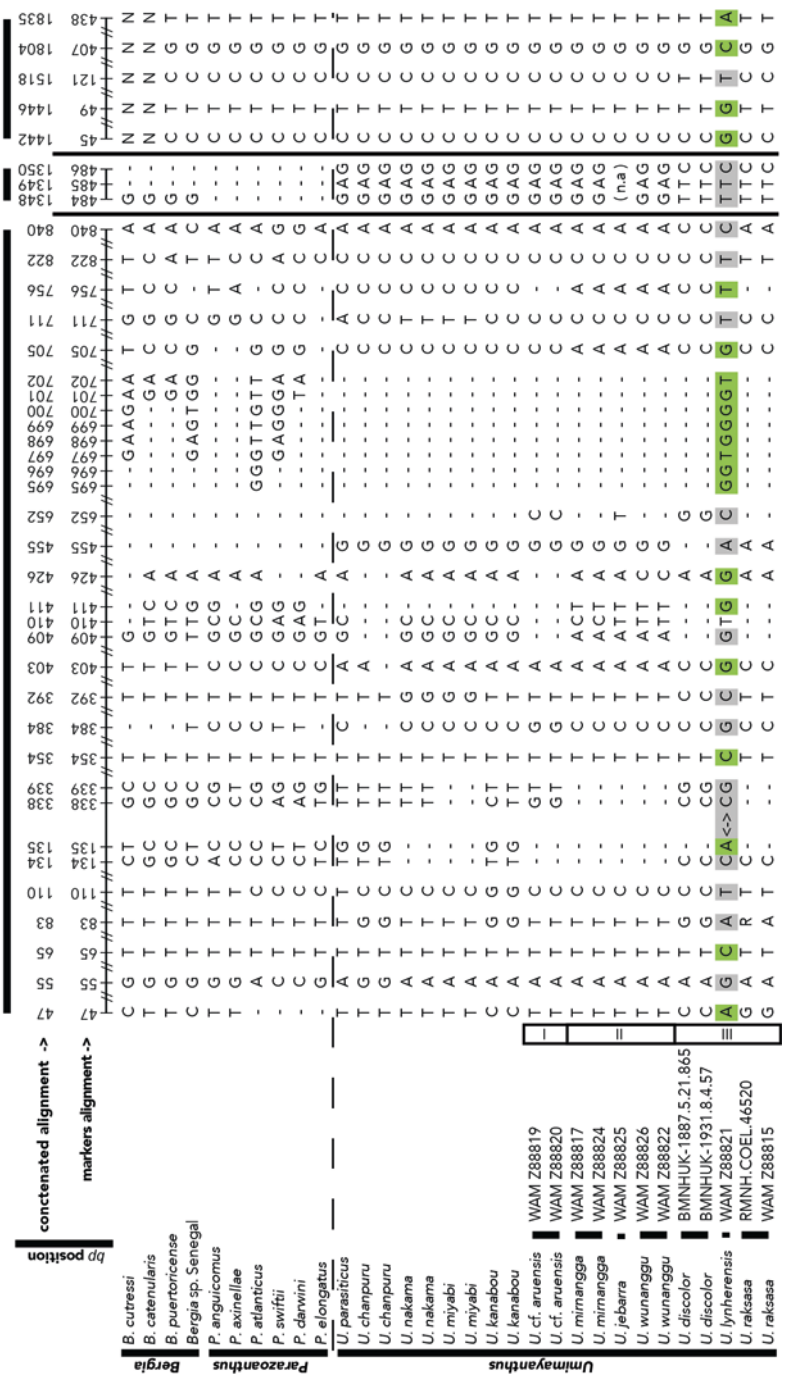

FIGURE 18 Summary chart of the alignments showing nucleotide positions characteristics to *U. lynherensis* sp. nov. across the ITS-rDNA, 16S-rDNA and COI-mtDNA region. Positions in green are unique to *U. lynherensis* sp. nov. in genus *Umimayanthus*. Positions in grey are characteristic but not unique to *U. lynherensis* sp. nov

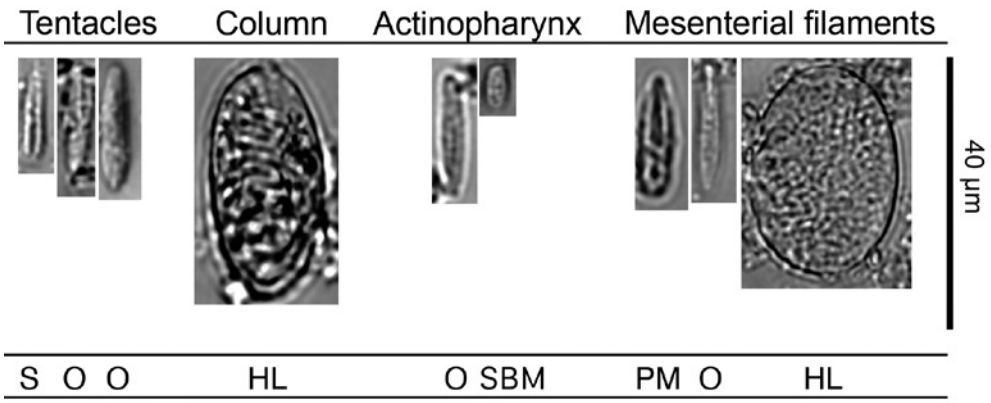

FIGURE 19 Diversity of cnidae found in *Umimayanthus lynherensis* sp. nov. across tissues in specimen WAM Z88821. (S) spriocysts, (O) basitrichs and microbasic b-mastigophores, (HL) holotrich large, (SBM) special microbasic b-mastigophores and (PM) microbasic p-mastigophores

only in the pharynx. Holotrichs (L) were found in the column and filaments. Microbasic p-mastigophores were only present in filaments (fig. 19).

Internal morphology. The sphincter muscle was located in the endoderm. Mesenterial arrangement was macrocnemic. Mesenteries were approximately 20–24 in number. Single siphonoglyph.

Distribution. The single available specimen was collected from Lynher Bank, Australia [loc. 14] (fig. 1). This specimen was found at a depth of 95 m.

Associated host. U. lynherensis sp. nov. is associated with *Sigmaxinella soelae* in the family Biemnidae Hentschel, 1923. The type locality of *Sigmaxinella soelae* is off Port Hedland with originally distribution reported between Exmouth and Broome (Hooper, 1984) in tropical Western Australia. *Sigmaxinella soelae* is now known to be more widespread in Western Australia and occurs between Lynher Bank, Kimberley (–15.493611 °S, 121.63611 °E) in the north and Point Cloates, Ningaloo (–22.603333 °S, 113.609444 °E) on the upper central west coast of Western Australia.

Remarks. Only a single specimen of *U. lynherensis* sp. nov. was available, and the inter-polyp distances and polyp diameters were very consistent across the colony.

The colonies of *U. lynherensis* sp. nov. are formed by solitary polyps spread homogenously across the surface of the host sponge, different from the arrangement of polyps in chains, as in *U. discolor* sp. nov. The diameter of the polyps of *U. lynherensis* sp. nov. are similar to those observed for *U. chanpuru*, *U. nakama*, *U. miyabi*, and *U. parasiticus*. Out of these four species, *U. lynherensis* sp. nov. most closely resembles *U. parasiticus*, however *U. parasiticus* has only been reported from the Atlantic Ocean while *U. lynherensis* sp. nov. was collected from Western Australia in the Indian Ocean. Furthermore, *U. parasiticus* has only been reported in association with sponges in the orders Clionaida Morrow & Cárdenas, 2015, Haplosclerida Topsent, 1928, Scopalinida Morrow & Cárdenas, 2015, and Tetractinellida Marshall, 1876

TABLE 6 Results for the cnidocyte analyses for *Umimayanthus lynherensis* sp. nov., holotype specimen WAM Z88821

Tissue	Category	Length (max–min, average)	Width (max–min, average)	*n*	Frequency
Tentacles	Spirocysts	19.2–13.2, 15.6	3.9–1.3, 2.5	31	Common
	Bastrichs and microbasic b-mastigophores	19.114–14.04, 16.8	4.766–1.513, 3.097625	8	Occasional
Column	Holotrichs (L)	37.3–25.3, 29.2	21.6–12.1, 15.2	14	Occasional
Pharynx	Special microbasic b-mastigophores	8.8–8.6, 8.7	2.6–2.1, 2.4	2	Rare
	Bastrichs and microbasic b-mastigophores	19.3–5.4, 17.5	3.7–1.6, 2.7	11	Occasional
Mesenterial Filaments	Holotrichs (L)	33.3–32.9, 33.1	23.3–13.6, 18.5	2	Rare
	Bastrichs and microbasic b-mastigophores	20.0–15.5, 17.5	3.8–2.3, 3.0	5	Rare
	Microbasic p-mastigophores	19.5–13.1, 16.5	7.7–3.6, 5.4	30	Common

(Montenegro et al., 2020; Swain & Wulff, 2007), while *U. lynherensis* sp. nov. is associated with *Sigmaxinella soelae* in the order Biemnida.

Umimayanthus raksasa sp. nov. Montenegro, Kise & Reimer

urn:lsid:zoobank.org:act:01BCCB92-17CE-4768-AB0E-186C31653238

Synonymy. *Parazoanthus* sp. 3 in Reimer et al. (2014) and *Parazoanthus* in Alvarez et al. (2016).

Etymology. The specific epithet "raksasa", which means "giant" or "gigantic" in Indonesian, refers to the large size of the polyps of this species in comparison to the other members of its genus.

Material examined. Type locality: NE coast of Sumba, Nusa Tenggara Timur, Indonesia [loc. 22], −9.891694 °S, 120.711694 °E.

Holotype. RMNH.COEL.46520 in ZMA.POR.9139, *Phakellia* cf. *tropicalis* Alvarez & Hooper, 2009, (−9.891694 °S, 120.711694 °E, loc. 22, east of Melolo, NE coast of Sumba, Nusa Tenggara Timur, Indonesia,

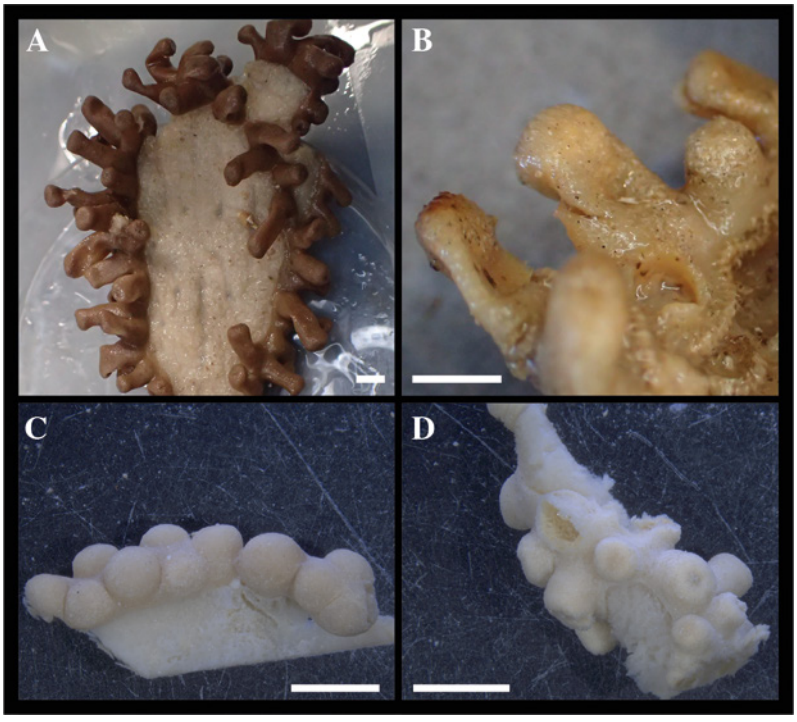

FIGURE 20 Specimens of *Umimayanthus raksasa* sp. nov.; (A) RMNH.COEL.46520 (holotype), (B) RMNH.COEL.46521 (Paratype), (C) WAM Z88815, and (D) WAM Z88828. White bars represent 5mm scales. Note that specimens C and D are tightly contracted in comparation to specimens A and B

75–90 m depth, September 13, 1984. Collected by R.W.M. van Soest, Snellius-II Expedition). *Paratype*: RMNH.COEL.46521 in ZMA.POR.20704, *Phakellia* spec., (–8.468333 °S, 119.6175 °E, loc. 23, east of Komodo Field #100, Nusa Tenggara Timur, Indonesia, 91 m depth, September 19, 1984 Collected by R.W.M. van Soest, Snellius-II Expedition).

Other material (n =2). Other examined specimens belong to the collection of the Western Australian Museum; WAM Z88815 (–16.7525 °S, 121.046667 °E, loc. 12, Broome L25, Broome, Western Australia, 108-100 m depth, June 30, 2007 by M.P. Salotti), WAM Z88828 (–15.6233 °S, 121.972233 °E, loc. 13, Lynher Bank, Western Australia, 61 m depth, October 28, 2016 by J. Fromont & J.A. Ritchie).

Diagnosis. U. raksasa sp. nov. can be differentiated from other members of the genus *Umimayanthus* by presenting comparatively large polyps, colonies with a unique growth pattern, and the identity of host sponge. *U. raksasa* sp. nov. has an average polyp diameter of 2.83 mm ± 0.42 mm and polyp height of 6.53 mm ± 5.58 mm, colonies primarily extended along the edges of the sponge and this species has only been found in association with sponges in the genus *Phakellia* Bowerbank, 1862 (fig. 20A). Additionally, there are multiple unique nucleotide substitution across the ITS-rDNA and 16S-rDNA

regions in the concatenated alignment, as follows: for the ITS-rDNA region a "G" in positions 47 bp, 131 bp, 454 bp and 860 bp, a "T" at 51 bp, 130 bp, 634 bp, 650 bp, 716 bp, 835 bp and 850 bp, an "A" at 648 bp, and a unique combination of substitutions and deletion/gaps between 130–340 bp; and for the 16S-rDNA region there is a "T" at position 1036 bp, a "C" at 1132 bp, and a unique combination of substitutions and deletion/gaps between 1348–1381 bp (fig. 21).

Description. Size. Preserved polyps were on average 2.83 mm ± 0.42 mm (σ^2 = 0.17, max. 3.51 mm, n = 12 polyps) in diameter, and 6.53 mm ± 5.58 mm (σ^2 = 31.17, max. 15.7 mm, n = 12 polyps) in height. All measurements were performed on the ethanol preserved specimen: zoantharian voucher number RMNH.COEL.46520, RMNH.COEL.46521, WAM Z88815, and WAM Z88828. Note that polyps in specimens WAM Z88815 and WAM Z88828 were tightly contracted.

Morphology. The holotype specimen is associated with *Phakellia* cf. *tropicalis* Alvarez & Hooper, 2009. Colonies formed by polyps tightly connected in a single chain, although small branches with 2~3 polyps were also found. All polyps were conspicuously spread over a well-developed coenenchyma. Capitulary ridges were visible, 16 in number. Tentacles were 32 in number. Preserved tentacles were brown in coloration. Capitulum and scapus were heavily encrusted by various particles of sand and silica (spicules of host sponges). The colony developed primarily on the outer edge of the host sponge, and most of the sponge surface remained free of polyps. Polyps preserved in ethanol were brown or white in color.

Cnidae. Tentacles and pharynx had similar cnidae compositions, with spirocysts, bastrichs and microbasic b-mastigophores commonly found. In the column only holotrichs (L) were found at a low frequency. In the mesenterial filaments bastrichs and microbasic b-mastigophores, and microbasic p-mastigophores were found in low frequency. See table 7 and fig. 22.

Internal morphology. Sphincter muscle was located in the endoderm. Mesenterial arrangement was macrocnemic. Mesenteries were approximately up to 32 in number. Ectoderm and mesoglea of capitulum and scapus were heavily encrusted by various sand and silica particles. Single siphonoglyph.

Distribution. The analysed specimens were collected from Australia and Indonesia. In Australia, from Broome [loc. 12], and Lynher Bank [loc. 13], while in Indonesia off Sumba [loc. 22] and Komodo [loc. 23] islands (fig. 1). Specimens were found at depths of 61–108 m.

Associated host. Umimayanthus raksasa sp. nov. appears to be exclusively associated with sponges in the genus *Phakellia*, within the family Bubaridae Topsent, 1894. One of the ZMA specimens was identified as *P.* cf. *tropicalis* (Alvarez et al., 2016), while the WAM sponge specimens were not *P. tropicalis*.

Remarks. Molecular data, identity of the host sponge, and polyp diameter group all specimens here analysed as *Umimayanthus raksasa* sp. nov. It is worth noting that in specimens WAM Z88815 and WAM Z88828 polyps are tightly contracted and therefore it will appear to have smaller heights (1.67 mm ± 0.52 mm, σ^2 = 0.27, max. 2.93 mm, n = 6 polyps) than those

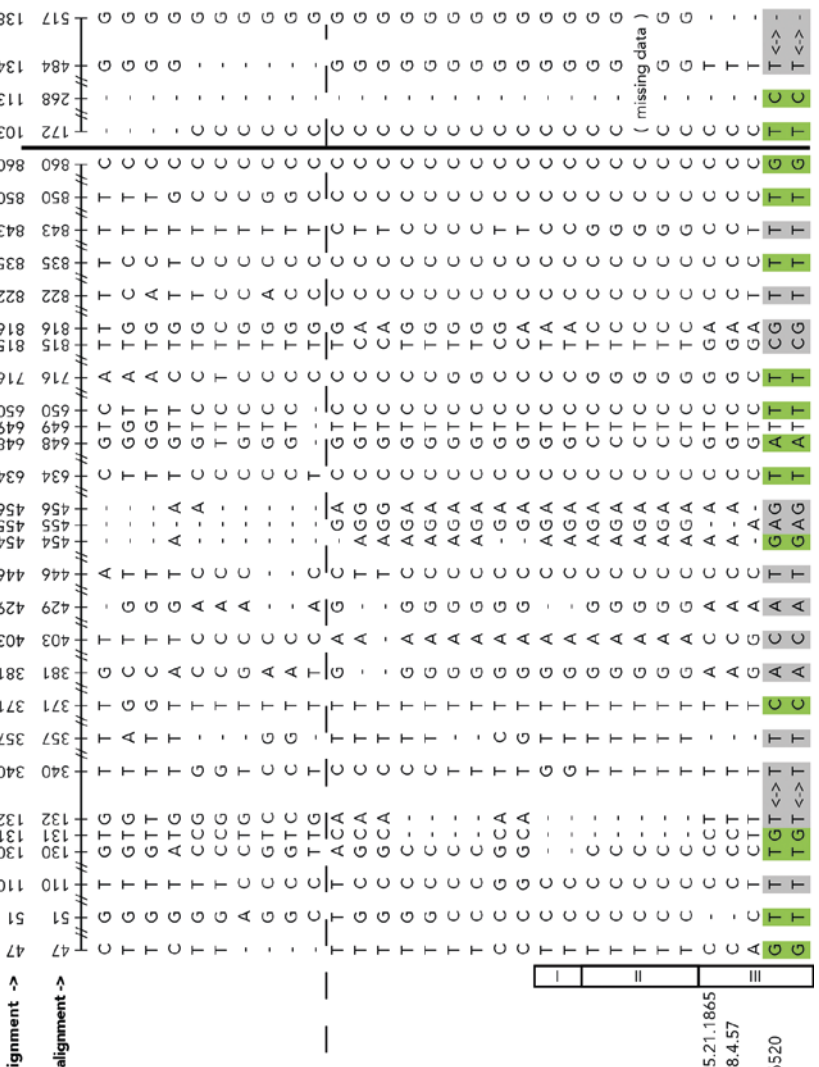

FIGURE 21 Summary chart of the alignments showing nucleotide positions characteristics to *U. raksasa* sp. nov. across the ITS-rDNA and 16S-rDNA region. Positions in green are unique to *U. raksasa* sp. nov. in genus *Umimayanthus*. Positions in grey are characteristic, but not unique, to *U. raksasa* sp. nov

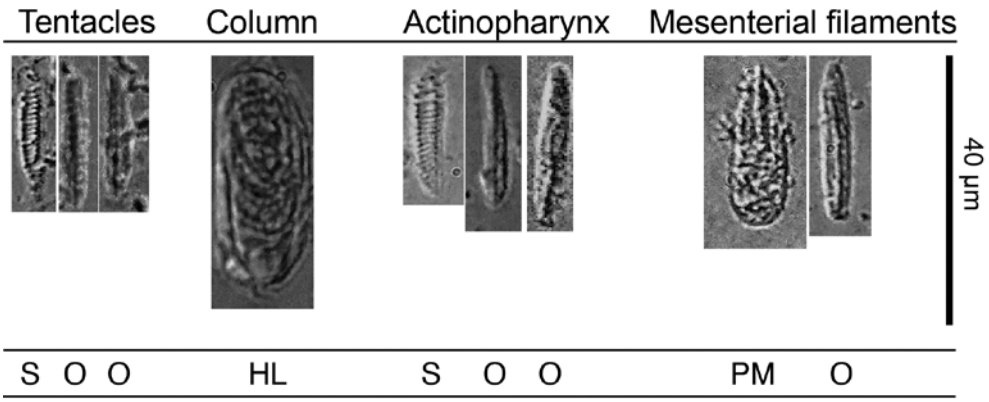

FIGURE 22 Diversity of cnidae found in *Umimayanthus raksasa* sp. nov. across tissues in specimen RMNH.COEL.46521. (S) spriocysts, (O) basitrichs and microbasic b-mastigophores, (HL) holotrich large and (PM) microbasic p-mastigophores

TABLE 7 Results for the cnidocyte analyses for *Umimayanthus raksasa* sp. nov., holotype specimen RMNH.COEL.46520

Tissue	Category	Length (max–min, average)	Width (max–min, average)	*n*	Frequency
Tentacles	Spirocysts	23.0–12.0, 18.1	4.0–1.0, 2.5	31	Common
	Bastrichs and microbasic b-mastigophores	23.0–16.0, 20.3	4.0–1.0, 2.5	25	Common
Column	Holotrichs (L)	37.0–25.0, 30.0	13.0–10.0, 11.0	5	Rare
Pharynx	Spirocysts	24.0–13.0, 18.5	4.0–1.0, 2.7	41	Common
	Bastrichs and microbasic b-mastigophores	28.0–17.0, 22.1	4.0–2.0, 2.9	47	Common
Mesenterial Filaments	Bastrichs and microbasic b-mastigophores	25.0–22.0, 23.8	5.0–2.0, 3.3	10	Occasional
	Microbasic p-mastigophores	23.0–19.0, 20.5	6.0–4.0, 4.8	4	Rare

observed in specimens RMNH.COEL.46520 and RMNH.COEL.4652 where the polyps are fully extended.

The large size of the polyps of *U. raksasa* sp. nov. clearly set it apart from the other species in the genus *Umimayanthus* (fig. 20A–D). *U. aruensis* as described in Pax (1911) is the only species that slightly resembles *U. raksasa* sp. nov. Nonetheless, the maximum height of polyps of *U. raksasa* sp. nov. was found to be 15.7 mm in preserved specimens, approximately four times the height of polyps reported in *U. aruensis*. As well, colonies of *U. raksasa* sp. nov. primarily extended along the edges of host sponges, while *U. aruensis* colonies extended indiscriminately across the whole surface of sponges in a reticulate pattern.

Key to the valid species of *Umimayanthus*

This key is provided to aid field workers in identification of formally described *Umimayanthus* species, and is thus largely based on gross morphological attributes along with associated organisms and occasionally geography. More detailed identification can be made using supplementary table 1. This key should not be used as a basis to erect new species.

1. Associated with *Ellisella* sp. octocoral – *U. kanabou* Fujii et al., 2021.
– Not associated with octocorals, but sponges 2
2. Associated with Caribbean sponges ..... *U. parasiticus* (Duchassaing & Michelotti, 1860)
– Associated with Indo-Pacific sponges 3
3. Associated with encrusting, cushion-like, or massive sponges 4
– Associated with erect or flabellate sponges 6
4. Polyps often organized in clusters of more than one ..... *U. nakama* Montenegro, Sinniger & Reimer, 2015
– Polyps not organized in clusters 5
5. Associated with massive sponges, polyps often solitary ..... *U. miyabi* Montenegro, Sinniger & Reimer, 2015
– Association with encrusting or cushion-shape sponges, colonies often spread across neighboring sponges ..... *U. chanpuru* Montenegro, Sinniger & Reimer, 2015
6. Up to 24 tentacles per polyp 7
– More than 24 tentacles per polyp 9
7. Colonies formed by chains of polyps extending in a reticulated pattern, on Raspailiidae sponges; in association with *Trikentrion flabelliforme* sponges ..... *U.* cf. *aruensis*
– Colonies not formed by reticulated chains of polyps 8
8. Solitary polyps, with 10 to 12 capitulary ridges visible; associated with Biemnidae; in association with *Sigmaxinella soelae* sponges .... *U. lynherensis* sp. nov.
– Polyps arranged in branching chains not interconnected. No capitulary ridges visible; associated with Microcionidae or Raspailiidae; in association with *Trikentrion flabelliforme* and *Clathria* (*Thalysias*) *cactiformis* sponges ..... *U. discolor* sp. nov.
9. Associated with sponges in Bubaridae, colony often growing in the edges of the host sponge, polyp heights up to 16 mm, brown or white;

in association with sponges in genus *Phakelia* ..... *U. raksasa* sp. nov.

– Associated with sponges in Raspailiidae; yellow, white, cream or orange in color. 10

10. Orange polyps, extending linearly, and with a poorly developed coenenchyma; in association with sponges in genus *Endectyon* .... *U. jebarra* sp. nov.

– Polyps of color other than orange 11

11. Yellowish polyps, solitary and coenenchyma absent .... *U. mirnangga* sp. nov.

– White/cream polyps, extending in linear chains, and coenenchyma clearly visible; in association with *Endectyon* (Endectyon) *fruticosum* and *E.* (Endectyon) *thurstoni* sponges ..... *U. wunanggu* sp. nov.

Discussion

Importance of museum collections

In this survey we examined 31 voucher specimens of sponges with associated zoantharians, and three type specimens of sponge-associated zoantharians, gathering data on morphological and molecular traits that could lead to their identification. Surprisingly, our results led to the discovery of six species new to science in the genus *Umimayanthus*, highlighting the importance of proper maintenance and curation of biological collections.

Museum collections have played a crucial role on the study of the ecology, taxonomy and systematics of sponge-associated zoantharians in families Epizoanthidae and Parazoanthidae. For instance, Swain & Wulff (2007), after a meticulous examination of the Porifera collection in the United States National Museum of Natural History in Washington, DC, USA (NMNH), published the first comprehensive analyses of host specificity in sponge-Zoantharia associations for the Caribbean region. The results of Swain & Wulff (2007) played a crucial role in the study of Montenegro et al. (2020) for the identification of extensive legacy material from the RMNH and ZMA collections of NBC in the Netherlands, and specimens recently collected in the Dutch Caribbean. The study published by Montenegro et al. (2020) remains to date the most comprehensive revision of the diversity of zoantharians in the Caribbean region and includes the original description of *Parazoanthus atlanticus* and the first record for four potentially undescribed species for the region. The work of Swain & Wulff (2007) also set the basis for later reexamination of *P. tunicans* (Duerden, 1900) by Sinniger et al. (2010), who transferred *P. tunicans* into the newly created genus *Hydrozoanthus*. Similarly, Kise et al. (2022) reexamined voucher specimens from the coelenterate collection in NHMUK and the Porifera collections of NBC, and revealed the existence of two new genera and three new species within the family Parazoanthidae.

It is important to note that the oldest specimen analysed by Kise et al. (2022) was collected in 1963 during the "Equalant II Expedition" to the Gulf of Guinea, while some of the specimens from the Dutch Caribbean analysed by Montenegro et al. (2020) were collected in Curaçao by C.J. van der Horst in 1920 (Pax, 1924), and the oldest specimens analysed in the current study can be traced back to 1908 (table 2).

Therefore, biological collections not only play a crucial role as reference materials for the identification of species, but also as time capsules for future generations of scientists to access information in light of modern technological developments such as molecular data, thus collecting data in ways beyond the imagination of scientists at the original time of collection, preservation and curation of specimens. Furthermore, the representation of species in old collections also offers the opportunity to return to the same localities where they were originally found and examine whether they still occur there or may have disappeared (Hoeksema & Koh, 2009; van der Meij et al., 2009, 2010). This information is vital to document possible local species extinctions.

Host specificity in the genus Umimayanthus

The specificity of host-zoantharian associations in *Umimayanthus* has not been thoroughly studied, primarily because of the taxonomic uncertainty of the groups involved in the symbioses. This study provided a rare situation where taxonomists with specialties in both taxa worked in collaboration to provide a more complete picture of associations (see also Swain & Wulff, 2007).

Earlier work on host-zoantharian associations concluded that it is relatively common for a single zoantharian species to associate with multiple host species, but it is more unusual to find one host associated with more than one zoantharian species (Swain & Wulff, 2007). It is worth noting that multiple exceptions are known for host sponges in the genera *Agelas* Duchassaing & Michelotti, 1864, *Cribrochalina* Schmidt, 1870, *Xestospongia* de Laubenfels, 1932, *Svenzea* Alvarez, van Soest & Rützler, 2002 and *Hymeniacidon* Bowerbank, 1858 (Swain & Wulff, 2007; Montenegro et al., 2020). However, in general terms, this pattern first observed by Swain & Wulff (2007) appears to be valid for host-*Umimayanthus* associations (table 2). For instance, *U. wunanggu* sp. nov. was found in association with two different sponge species in the genus *Endectyon*; *U. mirnangga* sp. nov. was in association with two species in two genera, as was *U. discolor* sp. nov.; and *U. raksasa* sp. nov. is likely associated with more than one species in the genus *Phakellia*. Remarkably, Caribbean *U. parasiticus* has been reported in association with 23 species of sponges across 10 different genera of host sponges (Swain & Wulff, 2007; Montenegro et al., 2020). Other species such as *U. chanpuru*, *U. miyabi* and *U. nakama* are likely associated with multiple genera of encrusting and calcareous sponges, but no detailed taxonomic data are yet available on the identity of their host sponges (Montenegro, pers. observ.).

The only confirmed exceptions to this generalized pattern are *U.* cf. *aruensis*, which appears to have a specialized association with *Trikentrion flabelliforme*, and *U. kanabou* consistently found in association with a gorgonian in the genus *Ellisella*, although the identity of the species remains unknown (Fujii et al., 2021). Other species such as *U. jebarra* sp. nov. and *U. lynherensis* sp. nov. are only known from a single record, and thus is not possible to draw conclusions on the specificity of the associations for these species.

On the other hand, the host sponges in this study appear to be quite restricted to

the specific *Umimayanthus* species, with most of them associated with a single zoantharian species. Two exceptions were found: *Trikentrion flabelliforme*, which had associations with two phylogenetically distinct species, *U.* cf. *aruensis* and *U. discolor* sp. nov.; and *Endectyon* (*Endectyon*) *fruticosum*, which was associated with *U. wunanggu* sp. nov. and *U. mirnangga.* sp. nov. Given that the latter two sibling species are closely phylogenetically related, we speculate that some level of overlap in host preference is to be expected (Brändle et al., 2000; Blomberg & Garland, 2002).

Based on the results of our phylogenetic analyses, it is clear that these species represent a large radiation of sponge-associated *Umimayanthus*, with species and clades having generally different niches, based on host species and depth. For instance, Clade I was found inhabiting depths of 12–39 m, Clade II between 41–59 m, and Clade III overlapping all other depth ranges with records from depths of 4–100 m. However, a closer look revealed stratification by depth within Clade III, with *U. raksasa* sp. nov. and *U. lytherensis* sp. nov. restricted to deeper waters while *U. discolor* sp. nov. inhabits shallow waters.

Many studies have shown the Central Indo-Pacific (the Coral Triangle) to be the center of marine biodiversity for a variety of marine taxa such as algae, larger benthic forams, crustaceans, fishes, molluscs, and scleractinian corals (Hoeksema, 2007; Förderer et al., 2018); but whether the region also harbors high diversities of many less studied taxa, including zoantharians, still needs to be examined (Reimer et al., 2014). The current study, focused on species associated with only four families of sponges, indicates that zoantharians may also follow the Coral Triangle centre of biodiversity, and further studies are needed to better confirm this.

Systematics and phylogeny within genus Umimayanthus

Fujii et al. (2021) recently described *U. kanabou* from Amamioshima Island in southern Japan, and established three subgenera within *Umimayanthus* based on the results of their phylogenetic analyses. However, as revealed by our study, the evolutionary independence of these "subgeneric" lineages is brought into question. Our results cannot establish with certainty the phylogenetic position of *U. parasiticus*, *U. chanpuru*, and *U. kanabou*, with a lack of support in both ML and BPP phylogenetic analyses. This result renders the phylogenetic distinction between the subgenera *Gorgoniazoanthus* and *Umimayanthus* to possibly be invalid. The remaining subgenus proposed by Fujii et al. (2021) was *Paraumimayanthus* and included the species *U. miyabi* and *U. nakama*. This lineage remains well-supported in our analyses, but its position within the genus *Umimayanthus* is uncertain.

In Fujii et al. (2021) the primary characters used to tell apart subgenera were insertions and deletions across the ITS-rDNA and 16S-rDNA regions, but alignments were extensively masked using GBlock (Castresana, 2000) previous to the phylogenetic reconstructions; the masking resulted in the exclusion of 61.7% of the positions, 556 bp out of 901 bp, from the ITS-rDNA region (Fujii et al., 2021). This calls the diagnostic genetic characters used to differentiate the subgenera into

question. Furthermore, the best-fitting model seems to have been only evaluated for the ITS region, and extrapolated to the 16S-rDNA and COI regions. Therefore, in light of the phylogenetic results presented here (fig. 2), the issues mentioned above in Fujii et al. (2021), and the fact that the diversity within the genus *Umimayanthus* remains clearly underestimated as demonstrated by our results, in this study we refrain from using subgeneric categories within *Umimayanthus*. Furthermore, we recommend a comprehensive census of the diversity within *Umimayanthus* to achieve a better understanding of the relationships among all *Umimayanthus* species; at this point a reassessment of subgeneric or possibly generic divisions can be conducted.

Conclusions

Currently, the genus *Umimayanthus* includes three well supported subclades and four well supported monophylies formed by single species. The single species monophylies are *U. chanpuru*, *U. parasiticus*, *U. kanabou*, and *U.* cf. *aruensis* (fig. 2), while the lineages forming well supported subclades are: (A) *U. miyabi* and *U. nakama* (Montenegro et al., 2015; Fujii et al., 2021), (B) *U. wunanggu* sp. nov., *U. mirnangga* sp. nov., and *U. jebarra* sp. nov. (Clade II in fig. 2), and (C) *U. discolor* sp. nov., *U. lynherensis* sp. nov., and *U. raksasa* sp. nov. (Clade III in fig. 2). Additionally, the genus also includes two potentially undescribed species *Umimayanthus* sp. Madagascar in Sinniger & Häussermann (2009), and *Umimayanthus* sp. MISE JDR170619-20-94 (Reimer et al., 2018; Montenegro et al., 2020).

This study highlights the need for further examining in detail the Porifera collections at museums around the world to better expose the undescribed diversity of sponge-associated zoantharians, which effectively remain hidden in plain sight on their host species. It would also be advantageous to conduct genome-wide analyses to further clarify the phylogenetic position of *Umimayanthus* species, and identify potential hotspots of genetic variation that may have fueled the diversification of this genus in the central Indo-Pacific region as uncovered in this study. Genome-wide comparative analyses may also offer clues on the genetic regions linked to the evolution of symbiotic associations, capitalizing on the fact that the genus *Umimayanthus* is an obligate symbiont with the rare evolutionary capacity of switching across phylogenetically unrelated host species, as demonstrated by the association of *U. kanabou* with gorgonians (Fujii et al., 2021).

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Supplementary material

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