Journal of the Marine Biological Association of the United Kingdom

cambridge.org/mbi

Molecular genetic biodiversity assessment of the Wallis Island sponge fauna in the Tropical Pacific

Adrian Galitz[1], Merrick Ekins[2,3,4], Maggie M. Reddy[5,6], Eric Folcher[7], Mahé Dumas[7,8], John Butscher[9], Olivier P. Thomas[6], Oliver Voigt[1], Gert Wörheide[1,10,11], Sylvain Petek[12] and Dirk Erpenbeck[1,10]

[1]Department of Earth- and Environmental Sciences, Palaeontology & Geobiology, Ludwig-Maximilians-Universität München, 80333 Munich, Germany; [2]Queensland Museum, South Brisbane, PO Box 3300, Brisbane, QLD 4101, Australia; [3]School of Biological Sciences, University of Queensland, St Lucia, QLD, 4072 Australia; [4]Griffith Institute for Drug Discovery, Griffith University, Brisbane 4111, QLD, Australia; [5]Department of Biological Sciences, University of Cape Town, Private Bag X3, Rondebosch 7701, South Africa; [6]School of Biological and Chemical Sciences, Ryan Institute, University of Galway, H91TK33 Galway, Ireland; [7]IRD, SEOH, BPA5, F-98848 Nouméa, New Caledonia; [8]IRD, Université de la Réunion, CNRS, Ifremer, Université de Nouvelle-Calédonie, ENTROPIE, F-98848 Nouméa, New Caledonia; [9]IRD, Sorbonne Universités, CNRS, MNHN, LOCEAN, F-98848 Nouméa, New Caledonia; [10]GeoBio-Center, Ludwig-Maximilians-Universität München, 80333 Munich, Germany; [11]SNSB-Bavarian State Collection of Palaeontology and Geology, 80333 Munich, Germany and [12]IRD, Univ Brest, CNRS, Ifremer, LEMAR, IUEM, F-29280 Plouzane, France

Abstract

Polynesia is a hotspot for marine biodiversity in the South Pacific Ocean, yet the distribution of many invertebrate taxa in this region is still often poorly assessed. Information on the diversity and phylogeography of sponges in particular remains limited in spite of their importance for coral reef ecosystems. Recent expeditions to the island group of Wallis and Futuna enabled the first larger-scale assessment of the Wallis Island sponge fauna, resulting in the molecular identification of 82 unique Molecular Operational Taxonomic Units (MOTUs) from 339 sponge samples based on 28S C-region rDNA and CO1 mtDNA data. Faunal comparisons with both adjacent archipelagos and more distant Indo-Pacific regions were predominantly based on the MOTUs obtained from Wallis Island ecoregions, and suggest high levels of endemism of sponges in Wallis and Futuna, corroborating previous data on the biodiversity of sponges and other marine phyla in the South Pacific. The results of this molecular taxonomic survey of the Wallis and Futuna sponge fauna aim to lay solid foundations for a sustainable 'Blue Economy' in Wallis and Futuna for the conservation of their local coral reefs.

Introduction

The French overseas territory of Wallis and Futuna is a volcanic island group located in the South Pacific between Fiji, Samoa and Tokelau, comprising the Wallis Islands and the Hoorn Islands (Futuna and Alofi) 260 km further southwest (Chase, 1971) (Figure 1). The wide lagoons around the main island of Wallis ('Uvea) and its 22 smaller surrounding islets are confined by a large barrier reef and smaller fringing reefs (see e.g., Stearns, 1945). Their coral reef structure differs from Futuna and Alofi, where the absence of such protective offshore barriers causes lower coral coverage and reef health due to their higher exposure to both human and natural stress factors compared to Wallis (Chancerelle, 2008).

The tropical South Pacific is divided into two large biogeographic marine realms, the Central Indo-Pacific realm and the Eastern Indo-Pacific realm, which are further subdivided into marine provinces and marine ecoregions (sensu Spalding *et al.*, 2007). The islands of Wallis and Futuna are located in the Eastern Indo-Pacific realm (Central Polynesia marine province, Samoa Islands marine ecoregion) in close proximity to the border of the Central Indo-Pacific realm. This geographical location makes them pivotal for understanding the biogeographic connectivity of both realms and their role as a 'melting pot' for marine biodiversity, influenced by the faunal influx of multiple ecoregions (Galitz *et al.*, 2023). With the rapid loss of species and ecological resources in the ongoing biodiversity crisis of both terrestrial and marine biota, it is urgent to comprehensively assess the state of current reef biodiversity and monitor changes, in order to identify key species for the 'Blue Economy' (i.e., economic growth based on sustainable use of oceanic resources) and at the same time apply appropriate conservation measures for the most endangered ones (Singh, 2002; Elahi *et al.*, 2015). Compared to the neighbouring regions in the Central Indo-Pacific and adjacent marine provinces, knowledge on the reef biodiversity of Wallis and Futuna is limited to only a few taxonomic groups, like macrophytes (Payri *et al.*, 2002), corals (Cairns, 1999; Payri *et al.*, 2002), fishes (Wantiez and Chauvet, 2003; Williams *et al.*, 2006), crustaceans (Buckeridge, 1994), brachiopods (Bitner, 2008), and a small range of other invertebrates (Bouchet *et al.*, 2008).

Research Article

Cite this article: Galitz A *et al.* (2024). Molecular genetic biodiversity assessment of the Wallis Island sponge fauna in the Tropical Pacific. *Journal of the Marine Biological Association of the United Kingdom* **104**, e56, 1–11. https://doi.org/10.1017/S0025315424000432

Received: 14 November 2023
Revised: 4 March 2024
Accepted: 10 April 2024

Keywords:
Central Polynesia; Eastern Indo-Pacific; molecular taxonomy; Porifera

Corresponding authors:
Dirk Erpenbeck;
Email: erpenbeck@lmu.de;
Sylvain Petek;
sylvain.petek@ird.fr

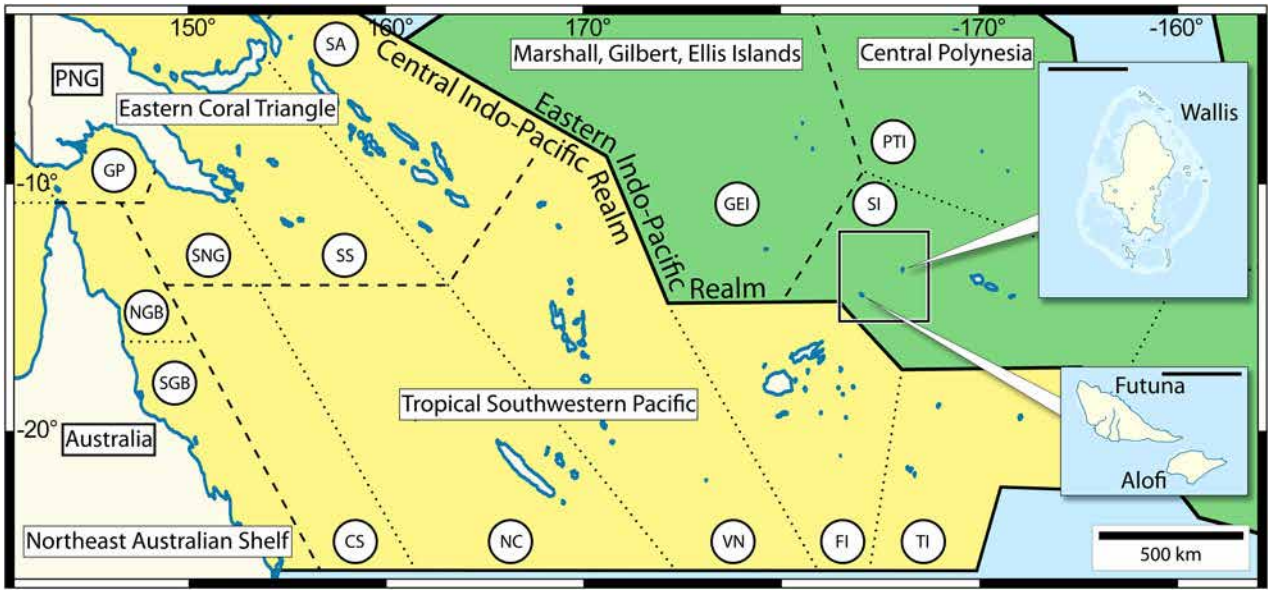

Figure 1. Location of Wallis and Futuna in proximity to the border of the Eastern Indo-Pacific (green highlight) and Central Indo-Pacific (yellow highlight) realms. Marine realms separated by solid lines, provinces by dashed lines, ecoregions by dotted lines (simplified, *sensu* Spalding *et al.*, 2007). Marine province names in boxes; abbreviated ecoregion names in circles: GP, Gulf of Papua; NGB, Torres Strait Northern Great Barrier Reef; SGB, Central and Southern Great Barrier Reef; SNG, Southeast Papua New Guinea; SS, Solomon Sea; SA, Solomon Archipelago; CS, Coral Sea; NC, New Caledonia; VN, Vanuatu; FI, Fiji Islands; TI, Tonga Islands; GEI, Gilbert/Ellis Islands; SI, Samoa Islands; PTI, Phoenix/Tokelau/Northern Cook Islands; Inset scale bars equal 10 km. Wallis and Futuna inset location maps by Eric Gaba for Wikimedia Commons.

Data on the biodiversity of marine sponges (Phylum Porifera) of Wallis and Futuna are particularly scarce, with only a handful of taxa reported from natural product studies for the region (Demospongiae) (Böhm *et al.*, 2003; Miguel-Gordo *et al.*, 2019, 2020, 2022), as well as several taxonomic reports on deep sea sponges (Hexactinellida) (Tabachnick and Reiswig, 2000; Tabachnick *et al.*, 2011). This scarcity of regional taxonomic knowledge on sponges stands in contrast with their importance in the marine ecosystem in terms of nutrient circulation, reef consolidation, and provision of micro- and macro habitats (see e.g., Bell, 2008; Rix *et al.*, 2018; Pawlik and McMurray, 2020). Sponges are also considered to be key organisms for the discovery of novel marine bioactive compounds for pharmaceutical development and application, with increasing reports from Wallis and Futuna (Miguel-Gordo *et al.*, 2019, 2020, 2022). Unravelling sponge taxonomic diversity has also repeatedly shown to further assessments of their biochemical potential (see Galitz *et al.*, 2021).

In this study we assess the biodiversity of the yet undescribed Wallisian sponge fauna by conducting a molecular taxonomic survey on a collection of sponges acquired during an IRD (Institut de Recherche pour le Développement) expedition in 2018 that aimed to fill knowledge gaps on sponge bio- (and chemo)diversity in this area. We then also compare the sponge fauna of Wallis Island to neighbouring Futuna and further adjacent marine regions, to gain a better understanding of their ecological similarities and differences.

Material and methods

Sample collection

339 Sponge samples (70% EtOH fixation) from Wallis Island in the marine province of *Central Polynesia* were collected during the WALLIS 2018 expedition (Petek *et al.*, 2018a, 2018b) with the aim to investigate the chemo- and biodiversity of this island and its surrounding reefs and lagoons (see Figure 2 for sampling sites). Sections of the specimens were used for morphological identifications (see Supplementary Methods S1), with subsamples for molecular analyses. Specimens were collected by SCUBA in depths from zero to 51 metres. For specimen details see Table S1 in supplementary material.

Application of molecular methods for species identification and biodiversity assessment

After an initial morphological classification (See Supplementary Methods S1), molecular taxonomic methods were employed for identification, as molecular genetic approaches have been shown to facilitate rapid and less ambiguous biodiversity estimation (see Galitz *et al.*, 2021). We have sequenced the standard barcoding fragment of the mitochondrial cytochrome oxidase subunit 1 gene ('CO1') (for Demospongiae and Homoscleromorpha), in combination with the C-region of the nuclear ribosomal long subunit ('28S') (for all sponge classes) as successfully applied in other sponge biodiversity studies of the Indo-Pacific (e.g., Erpenbeck *et al.*, 2016, 2020). Based on these markers the specimen set was divided into molecular operational taxonomic units (abbreviated 'MOTU' in the following) as units for faunal comparison.

DNA extraction, amplification, and sequencing

DNA of the sponge material was extracted using the CTAB (Cetyltrimethylammonium bromide) extraction method (Porebski *et al.*, 1997), except the phenol-octanol and RNase steps were skipped. Each PCR reaction (12.5 µl) comprised of 2.5 µl 5x green GoTaq ® PCR Buffer (Promega Corp, Madison, WI), 1.5 µl 25 mM $MgCl_2$ (Promega Corp, Madison, WI), 0.5 µl 10 mM dNTPs, 0.5 µl of the respective primer (5 µM) (Table 1), 1.15 µl BSA (100 µg/ml), 4.75 µl water, 0.1 µl GoTaq® DNA polymerase (5u/µl, Promega Corp, Madison, WI), and 1 µl DNA template.

DNA amplification of the respective fragments was conducted according to defined temperature profiles: Initial denaturation for 3 min at 95°C, 35 cycles of denaturation at 95°C for 30 s, annealing at 51°C (28S) or 40°C (CO1) for 30 s and extension at 72°C for 1 min, with a final extension step at 72°C for 5 min. The

https://doi.org/10.1017/S0025315424000432 Published online by Cambridge University Press

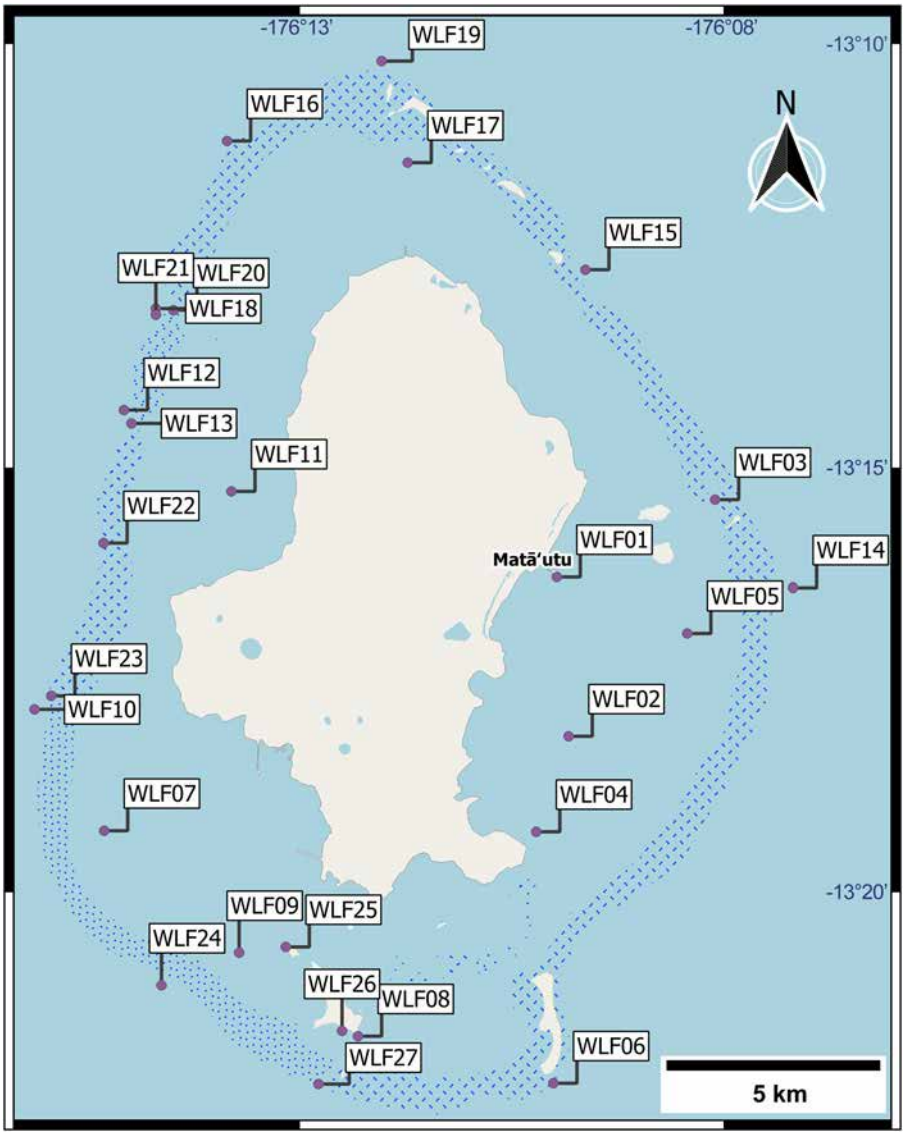

Figure 2. Sampling sites (WLF##) of the WALLIS 2018 expedition, in SCUBA-accessible depth ranges to up to 51 m. Reef locations are shaded in darker blue. © OpenStreetMap contributors.

successful amplification of PCR products was verified on 1% TAE agarose gels with added peqGREEN (peqlab) fluorescent dye, with apparent multi-bands and primer-dimers being purified with a modified Freeze-Squeeze Gel extraction protocol by Tautz and Renz (1983). Sanger sequencing was performed with a BigDye® terminator v3.1 (Applied Biosystems®) at the Sequencing Service of the Department Biology, LMU – Genomics Service Unit (Martinsried, Munich) on an ABI 3730 capillary sequencing machine. Initial sequence processing (base-calling and trimming) was conducted in CodonCode Aligner v9.0.1 (www.codoncode.com), with assembly, further processing, and analysis tasks carried out in Geneious Prime 2019 (v2019.2.5). Every assembly has been manually inspected for intragenomic polymorphisms (IGPs) and suspected positions (double peaks) corrected with the respective IUPAC code. GenBank BLAST (Altschul *et al.*, 1990) was used to check for possible contaminations and verify sponge sequences. Finalized sequences have been deposited in the European Nucleotide Archive (ENA) database under the accession number ranges OX421511 – OX421811 and OX422227 – OX422451 and in the Sponge Barcoding Database (www.spongebarcoding.org, Wörheide and Erpenbeck, 2007) under accession numbers SBD # 2566 – 2878. See Supplementary Table S1 for all details.

Table 1. List of primers used in this study

Name	Nucleotide sequence	Marker	Reference
dgLCO1490 (fwd)	5′ GGT CAA CAA ATC ATA AAG AYA TYG G 3′	CO1	Meyer and Paulay (2005)
dgHCO2198 (rev)	5′ TAA ACT TCA GGG TGA CCA AAR AAY CA 3′	CO1	Meyer and Paulay (2005)
28S-C2-fwd	5′ GAA AAG AAC TTT GRA RAG AGA GT 3′	28S	Chombard *et al.* (1998)
28S-D2-rev	5′ TCC GTG TTT CAA GAC GGG 3′	28S	Chombard *et al.* (1998)

OTU detection and statistical biodiversity analyses

For the faunal comparison 28S sequences longer than 350 bp and CO1 sequences longer than 500 bp were aligned with ClustalW (Thompson *et al.*, 1994) incorporated in the msa package for R v.4.1.1 (Bodenhofer *et al.*, 2015; R Core Team, 2023) with subsequent MOTU clustering using the UPGMA algorithm (Kreft and Jetz, 2010; following Cowman *et al.*, 2017) of DECIPHER 2.0 (Wright, 2016). Further biodiversity analyses were performed in R using the packages VEGAN (v4.2.4) and picante (v1.8.2) (Dixon, 2003; Kembel *et al.*, 2010).

https://doi.org/10.1017/S0025315424000432 Published online by Cambridge University Press

We applied a MOTU delineation for Demospongiae that has successfully been applied in earlier molecular biodiversity assessments on demosponges in the Indo-Pacific (Erpenbeck *et al.*, 2016, 2020; Galitz *et al.*, 2023) as following: For 28S, a MOTU delineating threshold of 0.3% has been set for every sequence of a minimal sequence length of 350 bp following Galitz *et al.* (2023), which was found to consider the genetic differences detected in several case studies between selected sympatric shallow water demosponge species (e.g., Erpenbeck *et al.*, 2017). For CO1, no base pair differences over a sequence length of 500 bp were allowed within a MOTU (following the approach in Erpenbeck *et al.*, 2016, 2020), due to the slow evolutionary rates of mitochondrial genes in sponges and the resulting conservative nature of the CO1 fragment (Shearer *et al.*, 2002). With no established delineation strategies for Calcarea and Homoscleromorpha MOTUs to date, sequences of these classes were excluded from the statistical computations. Their MOTUs were assigned based on the resulting phylogenetic trees (Supplementary Figures S2 to S12).

For the assessment and extrapolation of species diversity and sampling coverage of the Wallis Island sponge fauna rarefaction curves were computed and visualized using the iNEXT online tool (Chao *et al.*, 2016). The Wallis data was complemented with a total of 52 28S and 16 CO1 (Total unique sequences: 53) demosponge sequences generated by one of the authors (MMR) from specimens collected around Futuna Islands during the 2016 *Tara Pacific* expedition (Planes *et al.*, 2019). The full details on the sponge chemo- and biodiversity of Futuna Islands will be published at a later stage.

Likewise, sequences of other, adjacent Pacific regions published on NCBI Genbank, have been used for comparative molecular taxonomic analyses. For these, sequence alignments were conducted with the MAFFT v7.450 (Katoh and Standley, 2013) plugin for Geneious Prime® (v2019.2.5). Maximum-likelihood reconstructions for each fragment were conducted in RAxML v8.2.11 (Stamatakis, 2014) under the model best suited for the data as suggested by ModelTest-NG v0.1.7 (Darriba *et al.*, 2020) (GTRGAMMAI model, 100 rapid bootstraps) for Maximum Likelihood analysis. For further validation of the MOTU classifications, additional available sequences of type material (28S and/or CO1), representing a majority of the sponge orders present in this study, were also included (Figure 3; Supplementary Figures S2 to S12).

Results

Sequence yield and taxonomy

We obtained sequences (CO1, or 28S, or both) from a total of 339 Wallis Island sponge specimens. The high quality yield from the entire collection comprised 322 28S sequences (i.e., from 95% of the specimens) and 236 CO1 sequences (i.e., from 69.6% of the specimens). We managed to obtain both markers from 227 specimens (66.7%).

After initial size filtration we retained 302 samples from Wallis Islands (89.1% of the initial specimens), which shared 51 MOTUs with at least one other specimen (16.9% of the size-filtered samples, 49 in 28S and CO1, 12 only in 28S, 2 only in CO1), while 34 specimens were singleton MOTUs (10.6%, 8 in 28S and CO1, 21 only in 28S, 5 only in CO1) (See Supplementary Tables S1 and S3).

The available Futuna data comprised 52 28S sequences and 16 CO1 sequences, pooled into 41 MOTUs, of which 7 (17.1%) were shared and 34 (82.9%) were singleton MOTUs. After additional quality control of both Wallis and Futuna data, and the removal of incorrect molecular data and sequences with insufficient length or quality, the final datasets for Wallis and Futuna consisted of 302 sequences and 475 molecular characters (i.e., bases and gaps) in 28S (Wallis only: 250 sequences and 459 characters), and 243 sequences and 694 characters in CO1 (Wallis only: 227 sequences and 683 characters). The identified MOTUs correspond to 74 morphologically identified species (see Supplementary Table 1). Additionally included type material sequences, where available, provided reference points for the classification (Supplementary Figures S2 to S12).

Demospongiae from the order Dictyoceratida made up the largest proportion of the Wallisian specimens and MOTUs (22 MOTUs/26.8%), followed by Haplosclerida by a considerable margin (11/13.4%) and Verongiida (10/12.2%). Poecilosclerida and Bubarida made up less than 10% each, while tetracinellid, dendroceratid, suberitid, axinellid, agelasid, scopalinid, and tethyid sponges are represented with fewer than 5% of MOTUs from each of these demosponge orders (Figure 4). For several species the presence in Wallis and Futuna constitutes a range extension and fills gaps in their distribution between the Central and Eastern Indo-Pacific marine realms (e.g., *Echinodictyum asperum* Ridley and Dendy, 1886, and *Dactylospongia metachromia* de Laubenfels, 1954; for a comprehensive list of documented distributions see Supplementary Table S1).

Sponges from Class Calcarea comprise 9 MOTUs (11%), with eight in Subclass Calcinea and one in Subclass Calcaronea. Morphologically, some of the MOTUs could be identified as *Leucetta chagosensis* Dendy, 1913 (28S MOTU #375), *Pericharax orientalis* Van Soest and De Voogd, (2015) (28S MOTU #377), *Leucetta* aff. *microraphis* Haeckel, 1872 (28S MOTU #376), all quite conspicuous species. Additionally, others were identified belonging to the genera *Ascandra* Haeckel, 1872 and *Neoernsta* Deshmukh, 2023, while their species identity remained uncertain. In these cases, BLAST confirmed that the closest hits in GenBank belong to these morphologically recognized taxa. In the case of one unidentified calcinean (28S MOTU #371) and one calcaronean specimen, the genus identity remains uncertain, although for the calcaronean sponge, a close relationship to a sequence of the polyphyletic genus *Grantessa* Lendenfeld, 1885 is apparent from its DNA sequence (see Supplementary Table S2).

Among the 111 MOTUs (28S: 110, CO1: 64) spanning both Wallis as well as Futuna, only 8 MOTUs (7.6%) are shared between the two islands, comprising 4 MOTUs of Dictyoceratida and 2 MOTUs each of Verongiida and Agelasida.

Statistical biodiversity estimation of the collected Wallis demosponge specimens indicates that sampling under the applied strategy is yet incomplete, however with the species-individual curve (Figure 5A) beginning to approach a stationary phase, further emphasized by the estimated sampling coverage also being close to 90% (Figure 5B).

Discussion

Sampling strategy and effort

Prior to this study the sponge fauna of Wallis and Futuna was largely undescribed, except for two littoral (*Vaceletia* sp., *Narrabeena nigra* Kim and Sim, 2010) and three deep sea species (*Euryplegma auriculare*, *Aspidoscopulia bisymmetrica* Tabachnick, Menshenina, Pisera and Ehrlich, 2011, *A. tetrasymmetrica* Tabachnick, Menshenina, Pisera and Ehrlich, 2011) reports (Tabachnick and Reiswig, 2000; Böhm *et al.*, 2003; Tabachnick *et al.*, 2011; Miguel-Gordo *et al.*, 2019, 2020, 2022). The recent expeditions to Wallis (and Futuna) have, as the rarefaction analyses suggest, substantially aided in filling knowledge gaps on sponge biodiversity in the region (see e.g., Van Soest *et al.*,

https://doi.org/10.1017/S0025315424000432 Published online by Cambridge University Press

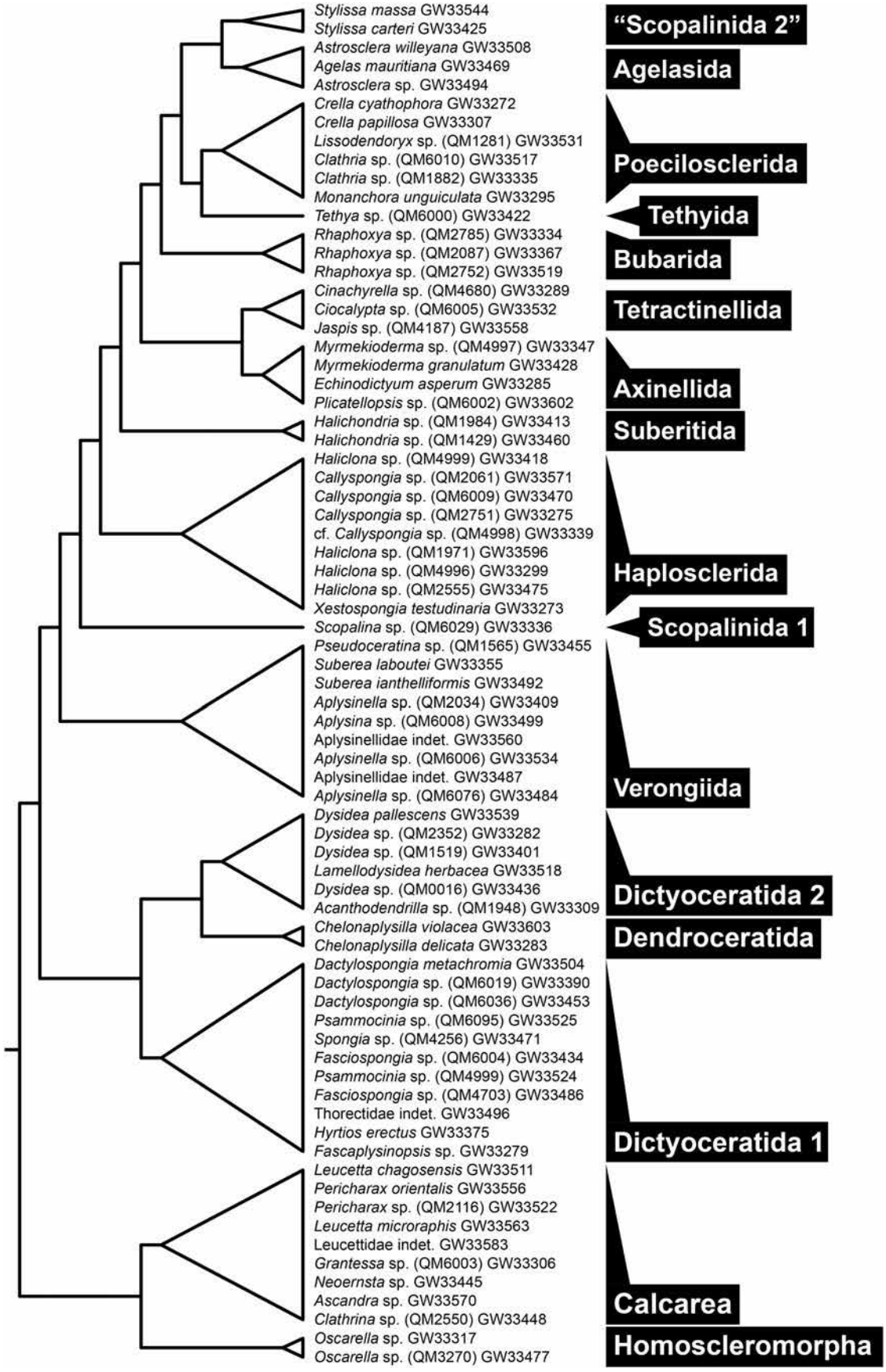

Figure 3. Simplified cladogram of the 28S Maximum Likelihood phylogenetic tree (Supplementary Figure S2) with representative taxa. Taxon names include reference to SNSB-BSPG collection numbers (GWxxxxx). Branch lengths not representative.

2012) (Figure 3). Sampling with SCUBA covered a wide variety of Wallis reef areas (Figure 2) and (SCUBA-accessible-) depth ranges (see Supplementary Table S1). For Futuna the samples were collected by SCUBA close to the shore at a maximum depth of 20 m. Naturally, the depth constraint of this sampling strategy restricted collection effort to shallow-water sampling sites.

https://doi.org/10.1017/S0025315424000432 Published online by Cambridge University Press

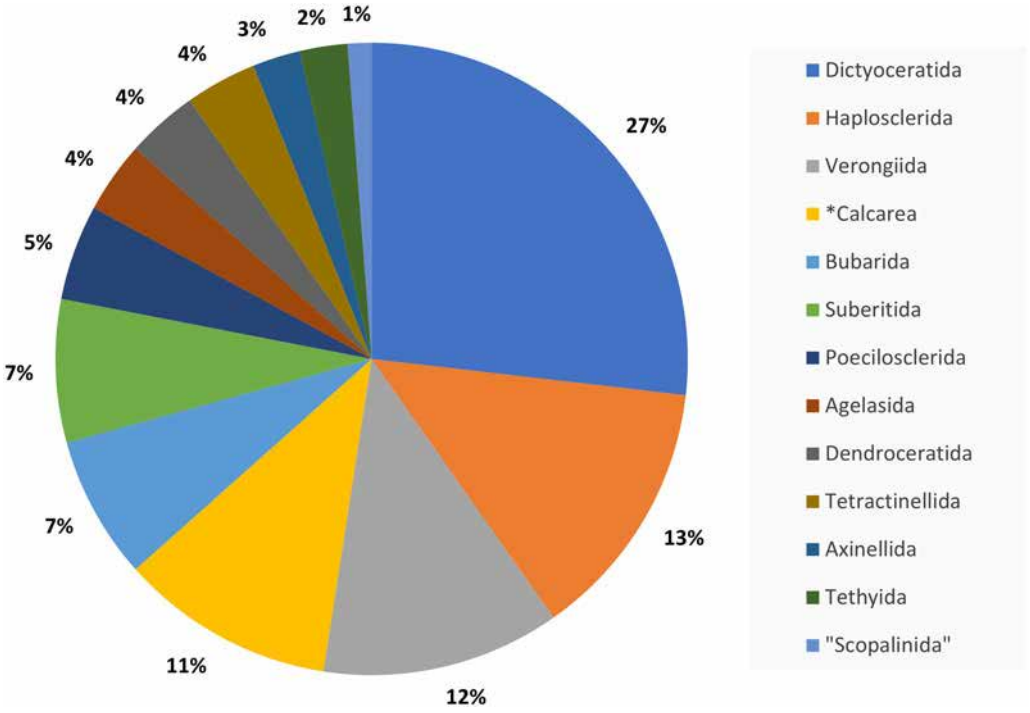

Figure 4. Relative taxonomic distribution (approximated) of combined 28S and CO1 MOTUs per Demospongiae order or other sponge class (denoted with an asterisk). For absolute numbers per marker and detailed relative distributions see Supplementary Table S2.

Additionally, the focus on macroscopic, epibenthic sponges ignored the biodiversity hidden within the reef matrix, i.e., the endobenthos. This cryptic sponge biodiversity remains widely unexplored here as in almost all reef systems around the world (Richter *et al.*, 2001; Vicente *et al.*, 2022; Timmers *et al.*, 2022). In this respect, sampling still was not statistically random, and remaining differences in the habitat types may influence the results. The restriction on pure absence / presence data, however, aims to minimize the collection bias. Nonetheless, the sampling carried out in the course of this expedition allows for a first large-scale assessment of the Wallis sponge fauna, while additional studies and collection campaigns will be needed to comprehend the complete sponge biodiversity of this locality.

Composition of the Wallis sponge fauna

Our current analysis increased the number of sponge MOTUs reported from Wallis by 82, as none of the previously reported species were detected in this study (see previous paragraph). Our finding of Dictyoceratida (25 MOTUs) and Haplosclerida (12 MOTUs) as demosponge orders of highest taxonomic diversity under the current sampling scheme parallels findings from similar (sub)tropical coral reef biodiversity monitorings such as the Red Sea or the Gulf of Oman (Erpenbeck *et al.*, 2016, 2020), and suggests that this may be a common pattern in the Indo-Pacific (see e.g., Wilkinson, 1988; Duckworth *et al.*, 2008; Wulff, 2012). Likewise, Núñez Pons *et al.* (2017) reported Haplosclerida as the most common order in their barcoding study of Hawaiian sponges, although followed by Poecilosclerida.

Presence of widespread Indo-Pacific demosponge species in Wallis and Futuna

Molecular tools have repeatedly revised many assumed cosmopolitan sponge taxa as endemic (Wörheide *et al.*, 2008; Pöppe *et al.*, 2010; Xavier *et al.*, 2010; Reveillaud *et al.*, 2011; Setiawan *et al.*, 2016; Erpenbeck *et al.*, 2017). This is consistent with the hypothesis of high levels of endemism in some marine invertebrates (Palumbi *et al.*, 1997; Klautau *et al.*, 1999; Solé-Cava and Boury-Esnault, 1999; Bierne *et al.*, 2003; Plotkin and Boury-Esnault, 2004), for sponges this is most likely due to the short lifespan of their larvae, limiting their theoretical dispersal

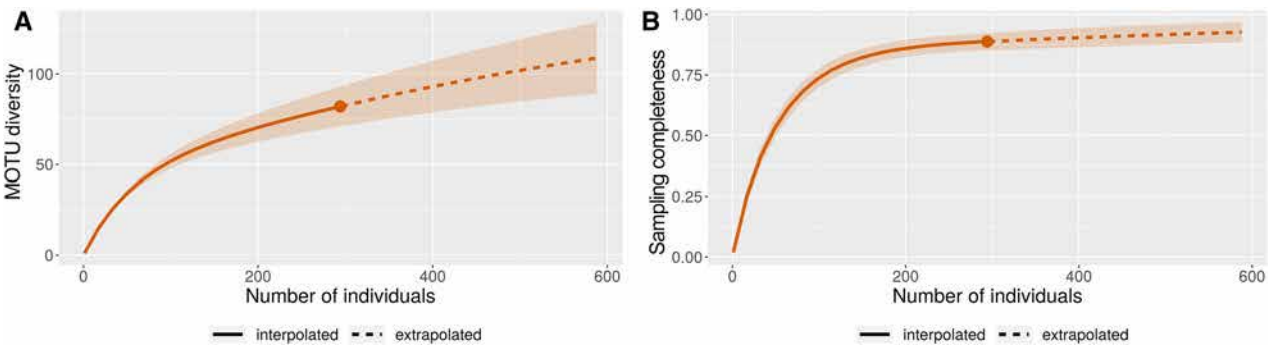

Figure 5. (A) Sampling size-based biodiversity estimation and extrapolation based on 28S data of Demospongiae; (B) Curve of estimated sampling completeness (sample coverage).

https://doi.org/10.1017/S0025315424000432 Published online by Cambridge University Press

potential (Maldonado, 2006; but see also Carballo *et al.*, 2013; Turner, 2020 for widespread sponge species).

Nevertheless, several species still display a wide distribution across the Indo-Pacific as evident by shared 28S MOTUs detected over large spatial distances, including several realms. Among those species is *S. carteri*, as reported from the Western Indian Ocean to Melanesia (de Voogd *et al.*, 2023). Its populations share the same 28S genotype (and mitochondrial intergenic hairpin regions) distinct from its sympatric sister species *Stylissa massa* Carter, 1887 across the entire range from the Red Sea to Fiji (Erpenbeck *et al.*, 2017). Our data add further confirmation of the presence of *S. carteri* in Polynesia, solidifying its known distribution in the Eastern Indo-Pacific realm (Miguel-Gordo *et al.*, 2020). However, recent biodiversity campaigns did not report on the presence of this species in French Polynesia (see Hall *et al.*, 2013; Petek *et al.*, 2017), suggesting that a biogeographic separation exists between different marine provinces within the Eastern Indo-Pacific realm.

In contrast, several other taxa identified from Wallis Island (Samoa Islands ecoregion) are also present in the French Polynesian ecoregions, as reported from Petek *et al.* (2017) and Galitz *et al.* (2023). These common taxa comprise a *Suberea* sp. (morphotype QM2121 in Hall *et al.*, 2013), an *Aplysilla* sp. (QM2034), a *Cinachyrella* sp. (QM4680), and a *Haliclona* sp. (QM2555), and likewise *Craniella abracadabra* de Laubenfels, 1954 and *Chelonaplysilla delicata* Pulitzer-Finali and Pronzato, 1999 as species determined to species level.

Furthermore, *Echinodictyum asperum* was described from the Society Islands (Ridley and Dendy, 1887) and reported from Tuamotu and Gambier (ecoregion Tuamotus) (Petek *et al.*, 2017). Its Wallis MOTU is shared with specimens of the Hawaiian (> 4000 km distance) cryptofauna (Hawaii ecoregion; Genbank MW016122, Vicente *et al.*, 2022) as well. Further extension of this species to the Eastern Indian Ocean including the Andaman Islands (Andaman and Nicobar Islands ecoregion, Andaman province) as reported by Burton and Rao (1932), is yet not supported by molecular data.

We can report on a further widespread distribution of (cf.) *Callyspongia* sp. (QM4998), which differs from specimens collected in the Persian (Arabian) Gulf (>15,000 km) only by one transversion (e.g., Genbank LR596455, Erpenbeck *et al.*, 2020), and likewise from a *Callyspongia* sp. collected from the Hawaiian cryptofauna (e.g., Genbank MW016058, Vicente *et al.*, 2022), consequently spreading over the entire Indo-Pacific and making it one of the most widely dispersed sponge species according to molecular data. Similarly, wide distributions are reported for *Neopetrosia chaliniformis* Thiele, 1899 (East African Coral Coast ecoregion, Western Indo-Pacific realm to Samoa Islands ecoregion, Eastern Indo-Pacific realm) and a yet not further named *Hyrtios* cf. *erectus*, a cryptic sister to *Hyrtios erectus* Keller, 1889 (Northern and Central Red Sea and Southern Red Sea ecoregions, Western Indo-Pacific realm *sensu* Erpenbeck *et al.*, 2017 to Samoa Islands and Marshall Islands ecoregions, Eastern Indo-Pacific realm), which now also is reported from Wallis (de Voogd *et al.*, 2023). While cosmopolitan distribution has been rejected for many sponge species (see earlier section), endemism should not be viewed as the general rule of thumb for all sponges (e.g., Carballo *et al.*, 2013; Turner, 2020).

Dactylospongia metachromia has been reported from the Solomon to Society Islands (de Voogd *et al.*, 2023). Specimens of Tuamotu (Tuamotus ecoregion, French Polynesia) have been subject to bioactive compound studies, as their quinone sesquiterpenes display a large array of biological properties (e.g., Bonneau *et al.*, 2017; Boufridi *et al.*, 2017). Further investigation of our discovered Wallis sponge populations, ca. 3000 km to the west of Tuamotu, will help to assess patterns of spatial variability in metabolite composition in sponges.

Wallis sponge fauna in comparison to adjacent islands

Most island systems in the Central and Eastern Indo-Pacific realms display both high biodiversity and high rates of endemism among sponge species, with comparatively few taxa being shared within and between ecoregions (Lévi, 1998; Hooper *et al.*, 2002; Feussner *et al.*, 2012; Van Soest *et al.*, 2012; Hall *et al.*, 2013). This also applies to the islands of Wallis and Futuna (Samoa Islands ecoregion) which, despite their comparatively short distance (260 km), display a distinct sponge fauna, with less than 8% of MOTUs being shared among the reefs of these two islands. The faunal differences observed may be accountable to a number of reasons: (a) there is large dissimilarity in reef structure and exposition between both islands, with a prominent barrier reef and small islets in the lagoon around Wallis acting as a natural protection for the lagoon, while the sole reef around Futuna lacks such a barrier and appears to be more prone to potential anthropogenic activities (e.g., agriculture, marine traffic) and elemental impacts (e.g., storms and other natural phenomena) (Chancerelle, 2008), (b) likewise the complex and fluctuating ocean surface currents may affect species dispersal between Wallis, Futuna, and the adjacent islands, as large scale marine current systems like the *Western Pacific Warm Pool*, the *South Pacific Convergence Zone*, and the *South Pacific Gyre* have a large influence on the islands in the Central Polynesia province, as do seasonal and climatic variations due to the El Niño-Southern Oscillation (ENSO) (Alory and Delcroix, 1999; Wörheide *et al.*, 2008; Bell *et al.*, 2017).

We compared the Wallis and Futuna sponge fauna with taxonomic reports and (NCBI Genbank-) published molecular data from the adjoining island groups of Samoa (400 km distance to Wallis) and Tuvalu (730 km) both within the same marine province ('Central Polynesia' in the Eastern Indo-Pacific realm), and furthermore Fiji (550 km) and Tonga (400 km) in the adjacent marine province 'Tropical Southwest Pacific' of the Central Indo-Pacific realm (Figure 1).

Samoa shares the same marine ecoregion 'Samoa Islands' (sensu Spalding *et al.*, 2007) with Wallis and Futuna. Shared MOTUs are *Neofibularia hartmani* Hooper and Lévi, 1993 (Thacker *et al.*, 2013) and *Hyrtios* cf. *erectus* (but see Erpenbeck *et al.*, 2017 regarding the species complex in the Pacific). Furthermore, *S. carteri* (Rohde *et al.*, 2012) and *Leucetta chagosensis* (Wörheide *et al.*, 2008) have been reported from both regions. However, reports on sponges from Samoa are comparatively scarce making further comparisons (e.g., sponge order frequency) impossible.

Tuvalu, despite being one of the closest island groups to Wallis and Futuna, does not share the same marine province 'Central Polynesia' with Wallis (and Futuna) and Samoa, but is located in the 'Marshall, Gilbert, and Ellis Islands' marine province (Gilbert/Ellis Island ecoregion). In comparison to Samoa, information on the sponge fauna from the literature is comprehensive, but dating back to the 19th century (Whitelegge, 1897; Kirkpatrick, 1900), their corroboration to extant coral reefs remains to be assessed. From these publications we identify *Astrosclera willeyana* Lister, 1900 (see Kirkpatrick, 1900) and *E. asperum* (see Whitelegge, 1897) as shared with Wallis and Futuna. Based on the available publications, Dictyoceratida constitutes the dominant sponge order in Tuvalu, followed by the Orders Axinellida and Clionaida. The abundance of Haplosclerida is low in comparison to other faunas, while Verongiida is yet unreported (Whitelegge, 1897; Kirkpatrick, 1900).

Fiji (Fiji Islands ecoregion) is approximately as distant to Wallis and Futuna as Samoa, but is, like Tonga (see below), classified into a different biogeographic realm (Central Indo-Pacific

https://doi.org/10.1017/S0025315424000432 Published online by Cambridge University Press

realm). We find three shared molecular MOTUs from Fiji comprising the biemnid sponge *Neofibularia hartmani*, the haplosclerid *Neopetrosia chaliniformis* and an *Agelas* species, which is also the only Fijian species shared with both, Wallis *and* Futuna in our data. The *N. chaliniformis* MOTU is, however, not exclusive to Fiji and has also been reported from Vanuatu (Vanuatu ecoregion). Furthermore, *S. carteri* (as *Stylotella aurantium*) and a *Hyrtios* cf. *erectus* are reported (Feussner *et al.*, 2012; but see Erpenbeck *et al.*, 2017 for a discussion on the species complexes of both), as well as the calcareous sponge *Leucetta chagosensis* (Wörheide *et al.*, 2002). Consolidated reports from the literature suggest that Dictyoceratida, Haplosclerida, and Verongiida are among the most frequently encountered orders in the Fijian archipelago (Bowerbank, 1874; Tendal, 1969; Feussner *et al.*, 2012).

For Tonga (Tonga Islands ecoregion) we found the Wallis and Futuna *Astrosclera willeyana* MOTU shared with records from Thacker *et al.* (2013) and Jiang *et al.* (2021), likewise MOTUs of *H. erectus* as identified in the course of natural product studies (Crews *et al.*, 1985; Crews and Bescansa, 1986). Compared to other island groups investigated in this study, the numerous biochemical publications on Tongan sponge secondary metabolites also allow for a better estimation of order frequency, with Dictyoceratida comprising the most common sponge order, followed by Poecilosclerida and Verongiida, as well as Haplosclerida and Homoscleromorpha (see review of Taufa *et al.*, 2021) although a bias towards particularly bioactive taxa can be expected.

The compiled information from both molecular data and literature sources coincides well with prior assessments of highly specialized and endemic sponge faunas of the Central and Eastern Indo-Pacific realms (e.g., Hooper *et al.*, 2002; Van Soest *et al.*, 2012). However, the faunal connectivity between Wallis and Futuna and their surrounding islands does not perfectly match the biogeographic delineation of Spalding *et al.* (2007), at least on a small scale. The current data showed no sharp faunal differentiation between Fiji and Tonga of the Tropical Southwestern Pacific marine province (Central Indo-Pacific realm), Wallis and Futuna, and Samoa in the Central Polynesia marine province (Eastern Indo-Pacific realm), and Tuvalu in the Marshall, Gilbert, and Ellis Islands marine province (Eastern Indo-Pacific realm). On the contrary, there is more evidence of sponge species shared between Wallis and Futuna and Fiji (cross-realm) than to the adjacent islands within their own marine province Central Polynesia. As such, the ecoregion classification by Spalding *et al.* (2007) appears suitable for most marine animal taxa, and especially on higher levels (provinces, realms), but has to be viewed more critically and on a case-by-case basis on smaller scales and in specific organismal groups like sponges and based on the currently available data. However, since a significant proportion of the available information on sponges in the Central and Eastern Indo-Pacific originates from biochemical publications, a data bias towards bioactive taxa seems likely.

Calcareous sponges of Wallis and Futuna

Although Calcarea have been studied in the Central and Eastern Indo-Pacific realms (e.g., Wörheide and Hooper, 1999; Borojevic and Klautau, 2000), their biodiversity is probably still vastly underestimated in many regions, especially in the French Polynesian archipelagos as described by Klautau *et al.* (2020). According to our MOTU definition, none of the nine new sequence types of calcareous sponges from Wallis matched previously published calcareous sponge sequences from French Polynesia (see Supplementary Table S1).

However, morphologically some specimens were identified as the wide-spread species *Pericharax orientalis* and *Leucetta chagosensis*, and sponges similar to *Leucetta microraphis* (*Leucetta* aff. *microraphis*) with a documented wide distribution in the Indo-Pacific. In *Pericharax orientalis*, the observed differences of up to 3 bp rather represent local intraspecific variation occurring over large distances between the population of Wallis and distant regions. *Leucetta chagosensis* (Wörheide *et al.*, 2002, 2008; Pasnin *et al.*, 2020) and *Leucetta* aff. *microraphis* (Van Soest and De Voogd, 2018; Klautau *et al.*, 2020) are believed to represent a complex of closely related species with considerable genetic variation, but species boundaries are not yet defined.

The remaining specimens of the subclass Calcinea could not be morphologically identified to species level (*Ascandra*, *Neoernsta*, *Clathrina*) and the distribution range of most of the known species in these genera is not very well known. At least some of these may represent species new to science, but further morphological observations will be required to evaluate their species identity.

In Calcaronea, revision of the taxonomy is required, and even many genera appear not to be monophyletic (Voigt *et al.*, 2012; Alvizu *et al.*, 2018). 28S MOTU #378 showing the closest molecular genetic similarity to *Grantessa* sp. (Family Heteropiidae) is morphologically supported by its visual appearance and the presence of pseudosagittal triradiates and oxea tufts (Borojevic *et al.*, 2002). However, both genus and family are considered to be polyphyletic, and the respective branch in the maximum-likelihood trees lacks sufficient bootstrap support (see Supplementary Figures S2 and S9). A more detailed morphological analysis would be required to evaluate the species identity of this MOTU.

Conclusion

The results of this study represent a first larger-scale assessment of the Wallis sponge fauna, constituting an important step in advancing the sponge biodiversity research of the Indo-Pacific Ocean. Despite high levels of endemism between the two islands and the surrounding archipelagos, and the implication of limited dispersal and colonization due to long distances and complex ocean current systems, Wallis and Futuna are still an important junction of faunal exchange in the region. While the number of shared MOTUs per region is limited, many sponge taxa from all over the Indo-Pacific are present in Wallis and Futuna, making it a 'melting pot' of sponge biodiversity. Ultimately, our data contribute to a molecular taxonomic and biochemical inventory of the Wallis Island sponge fauna, providing a basis for a sustainable local 'Blue Economy' (Ebarvia, 2016; Smith-Godfrey, 2016; van de Water *et al.*, 2021).

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315424000432

Acknowledgements. We would like to thank Gabriele Büttner and Simone Schätzle (LMU) for their supporting lab work for this study. We thank his majesty Lavelua Takumasiva Aisake, King of Wallis, and the territorial authorities for allowing us to collect in their country, Atoloto Malau and Florian Le Bail from the Wallis and Futuna Environment service, for their help and assistance regarding the Wallis 2018 oceanographic cruise. We acknowledge the crew of the R/V ALIS and IRD's diving team (SEOH IRD Noumea, New Caledonia) for their essential contribution to the field trip. Finally, we sincerely thank Cécile Debitus who initiated the project in Wallis. Support and permission to undertake the study on Futuna samples were provided by Atoloto Malau (Service de l'Environnement, Wallis and Futuna) to the Tara Pacific Foundation and NUI Galway. We would like to express our gratitude to the administrative and customary authorities of the Territoire des iles Wallis et Futuna for their support in the sample collection. Special thanks to the Tara Ocean Foundation, the R/V Tara crew and the *Tara* Pacific Expedition Participants (https://doi.org/10.5281/zenodo.3777760).

Author contributions. AG, SP, and DE conceived and designed research. JB, MD, ME, EF, SP, and OPT conducted initial sample collection and identification. ME and OV conducted morphological identification. DE, AG, MMR, and GW performed molecular data generation and analysis, DE, AG, and GW processed and evaluated the generated data. AG wrote the initial manuscript. All authors read, contributed to, and approved the manuscript.

Financial support. The Wallis 2018 oceanographic cruise was funded by the French Oceanographic Fleet, IRD, MNHN, Labex Mer and the Wallis and Futuna Environment Service. This research was funded by IRD and IUEM (WASP project). AG acknowledges financial support from the LMU via the LMU mentoring programme. We are keen to thank the commitment of the following institutions for their financial and scientific support that made the unique Tara Pacific Expedition possible: CNRS, PSL, CSM, EPHE, Genoscope, CEA, Inserm, Université Côte d'Azur, ANR, agnès b., UNESCO-IOC, the Veolia Foundation, the Prince Albert II de Monaco Foundation, Région Bretagne, Billerudkorsnas, AmerisourceBergen Company, Lorient Agglomération, Oceans by Disney, L'Oréal, Biotherm, France Collectivités, Fonds Français pour l'Environnement Mondial (FFEM), Etienne Bourgois, and the Tara Ocean Foundation teams. Tara Pacific would not exist without the continuous support of the participating institutes. The authors also particularly thank Serge Planes, Denis Allemand, and the *Tara* Pacific consortium.

Competing interest. None.

Ethical standards. No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with an unregulated invertebrate species. All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable. The study is compliant with CBD and Nagoya protocols.

Data availability. The datasets generated during and/or analysed during the current study are available in the European Nucleotide Archive (ENA) under the accession number ranges OX421511–OX421811 and OX422227–OX422451, with additional specimen information available in the Sponge Barcoding Database (SBD) under the accession numbers SBD#2566 – 2878.

References

Alory G and Delcroix T (1999) Climatic variability in the vicinity of Wallis, Futuna, and Samoa islands (13°–15° S, 180°–170° W). *Oceanologica Acta* **22**, 249–263.

Altschul SF, Gish W, Miller W, Myers EW and Lipman DJ (1990) Basic local alignment search tool. *Journal of Molecular Biology* **215**, 403–410.

Alvizu A, Eilertsen MH, Xavier JR and Rapp HT (2018) Increased taxon sampling provides new insights into the phylogeny and evolution of the subclass Calcaronea (Porifera, Calcarea). *Organisms, Diversity & Evolution* **18**, 279–290.

Bell JJ (2008) The functional roles of marine sponges. *Estuarine, Coastal and Shelf Science* **79**, 341–353.

Bell JJ, Shaffer M, Bennett H, McGrath E, Mortimer C, Rovellini A, Marlow J, Biggerstaff A and Carballo JL (2017) Impacts of short-term large-scale climatic variation on sponge assemblages. In Carballo JL and Bell JJ (eds), *Climate Change, Ocean Acidification and Sponges: Impacts Across Multiple Levels of Organization*. Cham: Springer International Publishing, pp. 143–177.

Bierne N, Bonhomme F and David N (2003) Habitat preference and the marine-speciation paradox. *Proceedings of the Royal Society of London, Biological Sciences* **270**, 1399–1406.

Bitner MA (2008) New data on the recent brachiopods from the Fiji and Wallis and Futuna islands, South-West Pacific. *Zoosystema* **30**, 419–461.

Bodenhofer U, Bonatesta E, Horejš-Kainrath C and Hochreiter S (2015) msa: an R package for multiple sequence alignment. *Bioinformatics (Oxford, England)* **31**, 3997–3999.

Böhm F, Gussone N, Eisenhauer A, Heuser A, Haase-Schramm A, Vacelet J, Reitner J and Dullo WC (2003) Calcium isotopic composition of marine biogenic carbonates: Influences of mineralogy and biology. In Geophysical Research Abstracts, Vol. 5.

Bonneau N, Chen G, Lachkar D, Boufridi A, Gallard J-F, Retailleau P, Petek S, Debitus C, Evanno L, Beniddir MA and Poupon E (2017) An unprecedented blue chromophore found in nature using a 'chemistry first' and molecular networking approach: discovery of dactylocyanines A-H. *Chemistry – A European Journal* **23**, 14454–14461.

Borojevic R, Boury-Esnault N, Manuel M and Vacelet J (2002) Order Leucosolenida Hartman, 1958. In Hooper John NA, Van Soest Rob WM and Willenz P (eds), *Systema Porifera: A Guide to the Classification of Sponges*. Boston, MA: Springer US, pp. 1157–1184.

Borojevic R and Klautau M (2000) Calcareous sponges from New Caledonia. *Zoosystema* **22**, 187–201.

Bouchet P, Héros V, Lozouet P and Maestrati P (2008) A quarter-century of deep-sea malacological exploration in the South and West Pacific: where do we stand? How far to go. In Héros V, Cowie RH and Bouchet P (eds), *Tropical Deep-Sea Benthos*, vol. **25**. Paris: Mémoires du Muséum national d'Histoire naturelle, pp. 9–40.

Boufridi A, Lachkar D, Erpenbeck D and Beniddir MA (2017) Ilimaquinone and 5-epi-ilimaquinone: beyond a simple diastereomeric ratio, biosynthetic considerations from NMR-based analysis. *Australian Journal of Chemistry* **70**, 743–750.

Bowerbank JS (1874) Contributions to a general history of the spongiadae. Part VI. *Proceedings of the Zoological Society of London* **42**, 298–305.

Buckeridge JS (1994) Cirripedia thoracica: verrucomorpha of New Caledonia, Indonesia, Wallis and Futuna Islands. In Crosnier A (ed.), *Résultats des Campagnes MUSORSTOM 12*, vol. **161**. Paris: Editions du Muséum, pp. 87–125.

Burton M and Rao HS (1932) Report on the shallow-water marine sponges in the collection of the Indian museum. Part I. *Records of the Zoological Survey of India* **34**, 299–356.

Cairns SD (1999) Cnidaria anthozoa: deep-water azooxanthellate Scleractinia from Vanuatu, and Wallis and Futuna Islands. In: Crosnier, A. (Ed.) Résultats Des Campagnes MUSORSTOM 20. *Mémoires Du Muséum National d'Histoire Naturelle. Série A, Zoologie* **20**, 31–167.

Carballo JL, Aguilar-Camacho JM, Knapp IS and Bell JJ (2013) Wide distributional range of marine sponges along the Pacific Ocean. *Marine Biology Research* **9**, 768–775.

Carter HJ (1887) Report on the marine sponges, chiefly from King Island in the mergui archipelago, collected for the trustees of the Indian Museum, Calcutta, by Dr. John Anderson, F.R.S., Superintendent of the Museum. *The Journal of the Linnean Society* **21**, 61–84.

Chancerelle Y (2008) Coral reefs of Wallis and futuna: biological monitoring, health and future. *La Revue d'Écologie (La Terre et La Vie)* **63**, 133–143.

Chao A, Ma KH and Hsieh TC (2016) User's guide for iNEXT online: software for interpolation and extrapolation of species diversity. *CoDesign* **30043**, 1–14.

Chase CG (1971) Tectonic history of the Fiji plateau. *GSA Bulletin* **82**, 3087–3110.

Chombard C, Boury-Esnault N and Tillier S (1998) Reassessment of homology of morphological characters in tetractinellid sponges based on molecular data. *Systematic Biology* **47**, 351–366.

Cowman PF, Parravicini V, Kulbicki M and Floeter SR (2017) The biogeography of tropical reef fishes: endemism and provinciality through time. *Biological Reviews of the Cambridge Philosophical Society* **92**, 2112–2130.

Crews P and Bescansa P (1986) Sesterterpenes from a common marine sponge, *Hyrtios erecta*. *Journal of Natural Products* **49**, 1041–1052.

Crews P, Bescansa P and Bakus GJ (1985) A non-peroxide norsesterterpene from a marine sponge *Hyrtios erecta*. *Experientia* **41**, 690–691.

Darriba D, Posada D, Kozlov AM, Stamatakis A, Morel B and Flouri T (2020) ModelTest-NG: a new and scalable tool for the selection of DNA and protein evolutionary models. *Molecular Biology and Evolution* **37**, 291–294.

De Laubenfels MW (1954) *The Sponges of the West-Central Pacific*, vol. **7**. Oregon: Oregon State College Corvallis, pp. 11–12.

Dendy A (1913) The Percy Sladen trust expedition to the Indian ocean in 1905 (V). report on the calcareous sponges collected by H.M.S. 'Sealark' in the Indian Ocean. *Transactions of the Linnean Society of London 2nd Series Zoology* **16**, 1–29.

Deshmukh UB (2023) Neoernsta nom. nov. (Calcarea, Porifera), a new genus name to replace Ernsta Klautau, Azevedo & Cóndor-Luján, 2021. *Zootaxa* **5330**, 597–599.

de Voogd NJ, Alvarez B, Boury-Esnault N, Carballo JL, Cárdenas P, Díaz M-C, Dohrmann M, Downey R, Goodwin C, Hajdu E, Hooper JNA, Kelly M, Klautau M, Lim SC, Manconi R, Morrow C, Pinheiro U, Pisera AB, Ríos P, Rützler K, Schönberg C, Vacelet J, van Soest RWM and Xavier J (2023) World Porifera Database. Accessed at http://www.marinespecies.org/porifera on 2023-11-10. VLIZ.

Dixon P (2003) VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science: Official Organ of the International Association for Vegetation Science* **14**, 927–930.

https://doi.org/10.1017/S0025315424000432 Published online by Cambridge University Press

Duckworth AR, Wolff C, Evans-Illidge E, Whalan S and Lui S (2008) Spatial variability in community structure of Dictyoceratida sponges across Torres Strait, Australia. *Continental Shelf Research* **28**, 2168–2173.

Ebarvia MCM (2016) Economic assessment of oceans for sustainable blue economy development. *Journal of Ocean and Coastal Economics* **2**, 7.

Elahi R, O'Connor MI, Byrnes JEK, Dunic J, Eriksson BK, Hensel MJS and Kearns PJ (2015) Recent trends in local-scale marine biodiversity reflect community structure and human impacts. *Current Biology: CB* **25**, 1938–1943.

Erpenbeck D, Aryasari R, Benning S, Debitus C, Kaltenbacher E, Al-Aidaroos AM, Schupp P, Hall K, Hooper JNA, Voigt O, de Voogd NJ and Wörheide G (2017) Diversity of two widespread Indo-Pacific demosponge species revisited. *Marine Biodiversity: A Journal of the Senckenberg Research Institute / Senckenberg Forschungsinstitut Und Naturmudeum* **47**, 1035–1043.

Erpenbeck D, Gholami A, Hesni MA, Ranjbar MS, Galitz A, Eickhoff B, Namuth L, Schumacher T, Esmaeili HR, Wörheide G and Teimori A (2020) Molecular biodiversity of Iranian shallow water sponges. *Systematics and Biodiversity* **18**, 192–202.

Erpenbeck D, Voigt O, Al-Aidaroos AM, Berumen ML, Büttner G, Catania D, Guirguis AN, Paulay G, Schätzle S and Wörheide G (2016) Molecular biodiversity of Red Sea demosponges. *Marine Pollution Bulletin* **105**, 507–514.

Feussner K-D, Ragini K, Kumar R, Soapi KM, Aalbersberg WG, Harper MK, Carte B and Ireland CM (2012) Investigations of the marine flora and fauna of the Fiji Islands. *Natural Product Reports* **29**, 1424–1462.

Galitz A, Ekins M, Folcher E, Büttner G, Hall K, Hooper JNA, Reddy MM, Schätzle S, Thomas OP, Wörheide G, Petek S, Debitus C and Erpenbeck D (2023) Poriferans rift apart: molecular demosponge biodiversity in central and French Polynesia and comparison with adjacent marine provinces of the Central Indo-Pacific. *Biodiversity and Conservation* **32**, 2469–2494.

Galitz A, Nakao Y, Schupp PJ, Wörheide G and Erpenbeck D (2021) A soft spot for chemistry-current taxonomic and evolutionary implications of sponge secondary metabolite distribution. *Marine Drugs* **19**, 448.

Haeckel E (1872) *Die Kalkschwämme: Eine Monographie in Zwei Bänden Text und Einem Atlas mit 60 Tafeln Abbildungen*. Berlin: Georg Reimer.

Hall KA, Sutcliffe PR, Hooper JNA, Alencar A, Vacelet J, Pisera A, Petek S, Folcher E, Butscher J, Orempuller J, Maihota N and Debitus C (2013) Affinities of sponges (Porifera) of the Marquesas and Society Islands, French Polynesia. *Pacific Science* **67**, 493–511.

Hooper JNA, Kennedy JA and Quinn RJ (2002) Biodiversity 'hotspots', patterns of richness and endemism, and taxonomic affinities of tropical Australian sponges (Porifera). *Biodiversity and Conservation* **11**, 851–885.

Hooper JNA and Lévi C (1993) Poecilosclerida (Porifera : Demospongiae) from the New Caledonia lagoon. *Invertebrate Systematics* **7**, 1221–1302.

Jiang W, Wang D, Wilson BAP, Kang U, Bokesch HR, Smith EA, Wamiru A, Goncharova EI, Voeller D, Lipkowitz S, O'Keefe BR and Gustafson KR (2021) Agelasine diterpenoids and Cbl-b inhibitory ageliferins from the coralline demosponge *Astrosclera willeyana*. *Marine Drugs* **19**, 361.

Katoh K and Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**, 772–780.

Keller C (1889) Die Spongienfauna des Rothen Meeres. *Zeitschrift Fur Wissenschartliche Zoologie* **48**, 311.

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP and Webb CO (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics (Oxford, England)* **26**, 1463–1464.

Kim H-R and Sim C-J (2010) A new species of the genus *Narrabeena* (Demospongiae: Dictyoceratida: Thorectidae) from Korea. *Animal Systematics, Evolution and Diversity* **26**, 83–86.

Kirkpatrick R (1900) XLIII. –description of sponges from Funafuti. *Annals and Magazine of Natural History* **6**, 345–362.

Klautau M, Lopes MV and Debitus C (2020) Calcareous sponges from the French Polynesia (Porifera: Calcarea). *Zootaxa* **4748**, 261–295.

Klautau M, Russo CAM, Lazoski C, Boury-Esnault N, Thorpe JP and Sole-Cava AM (1999) Does cosmopolitanism result from overconservative systematics? A case study using the marine sponge *Chondrilla nucula*. *Evolution; International Journal of Organic Evolution* **53**, 1414–1422.

Kreft H and Jetz W (2010) A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography* **37**, 2029–2053.

Lendenfeld R von (1885) A monograph of the Australian Sponges (continued). Part III. Preliminary description and classification of the Australian Calcispongiae. *Proceedings of the Linnean Society of New South Wales* **9**, 1083–1150, pls 59-67.

Lévi C (1998) *Sponges of the New Caledonian Lagoon*. Paris, France: IRD Editions.

Lister JJ (1900) Astrosclera willeyana, the type of a new family of sponges. *Willey's Zoological Results* **4**, 459–483.

Maldonado M (2006) The ecology of the sponge larva. *Canadian Journal of Zoology* **84**, 175–194.

Meyer CP and Paulay G (2005) DNA barcoding: error rates based on comprehensive sampling. *PLoS Biology* **3**, e422.

Miguel-Gordo M, Gegunde S, Calabro K, Jennings LK, Alfonso A, Genta-Jouve G, Vacelet J, Botana LM and Thomas OP (2019) Bromotryptamine and bromotyramine derivatives from the tropical Southwestern Pacific sponge *Narrabeena nigra*. *Marine Drugs* **17**, 319.

Miguel-Gordo M, Gegunde S, Jennings LK, Genta-Jouve G, Calabro K, Alfonso A, Botana LM and Thomas OP (2020) Futunamine, a pyrrole–imidazole alkaloid from the sponge stylissa aff. carteri collected off the Futuna Islands. *Journal of Natural Products* **83**, 2299–2304.

Miguel-Gordo M, Reddy MM, Sánchez P, Buckley JJ, Mackenzie TA, Jennings LK, Reyes F, Calabro K and Thomas OP (2022) Antifungal mono- and dimeric nitrogenous bisabolene derivatives from a sponge in the order Bubarida from Futuna Islands. *Organic & Biomolecular Chemistry* **20**, 1031–1040.

Núñez Pons L, Calcinai B and Gates RD (2017) Who's there? – first morphological and DNA barcoding catalogue of the shallow Hawai'ian sponge fauna. *PloS One* **12**, e0189357.

Palumbi SR, Grabowsky G, Duda Jr TF, Geyer L and Tachino N (1997) Speciation and population genetic structure in tropical Pacific sea urchins. *Evolution; International Journal of Organic Evolution* **51**, 1506–1517.

Pasnin O, Voigt O and Wörheide G, Murillo Rincón AP and von der Heyden S (2020) Indo-Pacific phylogeography of the lemon sponge *Leucetta chagosensis*. *Diversity* **12**, 466.

Pawlik JR and McMurray SE (2020) The emerging ecological and biogeochemical importance of sponges on coral reefs. *Annual Review of Marine Science* **12**, 315–337.

Payri CE, Pichon M, Benzoni F, N'Yeurt ADR, Verbruggen H and Andréfouët S (2002) Contribution à l'étude de la biodiversité dans les récifs coralliens de Wallis: scléractiniaires et macrophytes. *Rapport Atelier Marin Wallis, IRD Noumea*.

Petek S, Debitus C, Alencar A, Bourgeois B, Butscher J, Ekins M, Fleurisson D, Folcher E, Hall KA, Hertrich L, Hooper JNA, Lerouvreur F, Levy P, Maihota N, Orempuller J, Pisera A, Renaud A, Sutcliffe PR and Vacelet J (2017) *Sponges of Polynesia*. (S. Petek & C. Debitus, Eds.). Papeete (PYF): IRD, 829 p. https://doi.org/10.23708/fdi:010070137, online: https://sponges-polynesia.ird.fr/

Petek S, Folcher E, Ekins M, Oliverio M, Dumas M and Butscher J (2018a) Campagne Wallis 2018 du NO Alis: inventaire des spongiaires, des mollusques et des gorgones de l'île de Wallis (18 juillet-03 août 2018): rapport de mission. IRD. Retrieved from https://www.documentation.ird.fr/hor/fdi:010075822

Petek S, Folcher E, Ekins M, Oliverio M, Dumas M and Butscher J (2018b) *WALLIS 2018 Cruise, R/V Alis, (Wallis is.)*. Paris, France: Sismer. https://doi.org/10.17600/18000524

Planes S, Allemand D, Agostini S, Banaigs B, Boissin E, Boss E, Bourdin G, Bowler C, Douville E, Flores JM, Forcioli D, Furla P, Galand PE, Ghiglione J-F, Gilson E, Lombard F, Moulin C, Pesant S, Poulain J, Reynaud S, Romac S, Sullivan MB, Sunagawa S, Thomas OP, Troublé R, de Vargas C, Vega Thurber R, Voolstra CR, Wincker P and Zoccola D and Tara Pacific Consortium (2019) The Tara Pacific expedition - A pan-ecosystemic approach of the '-omics' complexity of coral reef holobionts across the Pacific Ocean. *PLoS Biology* **17**, e3000483.

Plotkin A and Boury-Esnault N (2004) Alleged cosmopolitanism in sponges: the example of a common Arctic polymastia (Porifera, Demospongiae, Hadromerida). *ZOOSYSTEMA-PARIS* **26**, 13–20.

Pöppe J, Sutcliffe P, Hooper JNA, Wörheide G and Erpenbeck D (2010) COI Barcoding reveals new clades and radiation patterns of Indo-Pacific sponges of the family irciniidae (Demospongiae: Dictyoceratida). *PloS One* **5**, e9950.

Porebski S, Bailey LG and Baum B (1997) Modification of a CTAB DNA extraction protocol for plants containing high polysaccharide and polyphenol components. *Plant Molecular Biology Reporter / ISPMB* **15**, 8–15.

Pulitzer-Finali G and Pronzato R (1999) Horny sponges from the north-eastern coast of Papua New Guinea, Bismark Sea. *Journal of the Marine Biological Association of the United Kingdom. Marine Biological Association of the United Kingdom* **79**, 593–607.

R Core Team (2023) *R: A Language and Environment for Statistical Computing (Version 4.1.1)*. Vienna, Austria: R Foundation for Statistical Computing.

Reveillaud J, van Soest RWM, Derycke S, Picton B, Rigaux A and Vanreusel A (2011) Phylogenetic relationships among NE Atlantic *Plocamionida* Topsent (1927) (Porifera, Poecilosclerida): under-estimated diversity in reef ecosystems. *PloS One* **6**, e16533.

Richter C, Wunsch M, Rasheed M, Kötter I and Badran MI (2001) Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. *Nature* **413**, 726–730.

Ridley SO and Dendy A (1886) Preliminary report on the Monaxonida collected by H.M.S. 'Challenger'. *Annals and Magazine of Natural History* **18**, 325–351.

Ridley SO and Dendy A (1887) Report on the Monaxonida collected by H.M.S. 'Challenger' during the years 1873–1876. Report on the scientific results voyage HMS 'Challenger', 1873–76. *Zoology* **20**, 1–275.

Rix L, de Goeij JM, van Oevelen D, Struck U, Al-Horani FA, Wild C and Naumann MS (2018) Reef sponges facilitate the transfer of coral-derived organic matter to their associated fauna via the sponge loop. *Marine Ecology Progress Series* **589**, 85–96.

Rohde S, Gochfeld DJ, Ankisetty S, Avula B, Schupp PJ and Slattery M (2012) Spatial variability in secondary metabolites of the indo-pacific sponge *Stylissa massa*. *Journal of Chemical Ecology* **38**, 463–475.

Setiawan E, De Voogd NJ, Swierts T, Hooper JNA, Wörheide G and Erpenbeck D (2016) MtDNA diversity of the Indonesian giant barrel sponge *Xestospongia testudinaria* (Porifera: Haplosclerida) – implications from partial cytochrome oxidase 1 sequences. *Journal of the Marine Biological Association of the United Kingdom. Marine Biological Association of the United Kingdom* **96**, 323–332.

Shearer TL, Van Oppen MJH, Romano SL and Wörheide G (2002) Slow mitochondrial DNA sequence evolution in the Anthozoa (Cnidaria). *Molecular Ecology* **11**, 2475–2487.

Singh JS (2002) The biodiversity crisis: a multifaceted review. *Current Science* **82**, 638–647.

Smith-Godfrey S (2016) Defining the blue economy. *Maritime Affairs: Journal of the National Maritime Foundation of India* **12**, 58–64.

Solé-Cava AM and Boury-Esnault N (1999) Patterns of intra and interspecific genetic divergence in marine sponges. In Hooper J. N. A. (ed.) Memoirs of the Queensland Museum, Proceedings of the 5th International Sponge Symposium, Brisbane, June-July 1998, Vol. 44, pp. 591–602.

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, McManus E, Molnar J, Recchia CA and Robertson J (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Bioscience* **57**, 573–583.

Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics (Oxford, England)* **30**, 1312–1313.

Stearns HT (1945) Geology of the Wallis Islands. *GSA Bulletin* **56**, 849–860.

Tabachnick KR, Menshenina LL, Pisera A and Ehrlich H (2011) Revision of *Aspidoscopulia* Reiswig, 2002 (Porifera: Hexactinellida: Farreidae) with description of two new species. *Zootaxa* **2883**, 1–22.

Tabachnick KR and Reiswig HM (2000) Porifera hexactinellida: on *Euryplegma auriculare* schulze, 1886, and formation of a new order. *Mémoires Du Muséum National d'Histoire Naturelle (A, Zoologie)* **184**, 39–52.

Taufa T, Subramani R, Northcote PT and Keyzers RA (2021) Natural products from Tongan marine organisms. *Molecules* **26**, 4534.

Tautz D and Renz M (1983) An optimized freeze-squeeze method for the recovery of DNA fragments from agarose gels. *Analytical Biochemistry* **132**, 14–19.

Tendal OS (1969) Demospongiae from the Fiji islands. *Videnskabelige Meddelelser Fra Dansk Naturhistorisk Forening I Kjøbenhavn* **132**, 31–44.

Thacker RW, Hill AL, Hill MS, Redmond NE, Collins AG, Morrow C, Spicer L, Carmack CA, Zappe ME, Pohlmann D, Hall C, Diaz MC and Bangalore PV (2013) Nearly complete 28S rRNA gene sequences confirm new hypotheses of sponge evolution. *Integrative and Comparative Biology* **53**, 373–387.

Thiele J (1899) Studien über pazifische Spongien. II. Über einige Spongien von Celebes. Zoologica. *Original-Abhandlungen aus dem Gesamtgebiete der Zoologie. Stuttgart*.

Thompson JD, Higgins DG and Gibson TJ (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research* **22**, 4673–4680.

Timmers MA, Vicente J, Webb M, Jury CP and Toonen RJ (2022) Sponging up diversity: evaluating metabarcoding performance for a taxonomically challenging phylum within a complex cryptobenthic community. *Environmental DNA* **4**, 239–253.

Turner T (2020) The marine sponge *Hymeniacidon perlevis* is a globally-distributed exotic species. *Aquatic Invasions / European Research Network on Aquatic Invasive Species* **15**, 542–561.

van de Water JA, Tignat-Perrier R, Allemand D and Ferrier-Pagès C (2021) Coral holobionts and biotechnology: from blue economy to coral reef conservation. *Current Opinion in Biotechnology* **74**, 110–121.

Van Soest RWM, Boury-Esnault N, Vacelet J, Dohrmann M, Erpenbeck D, De Voogd NJ, Santodomingo N, Vanhoorne B, Kelly M and Hooper JNA (2012) Global diversity of sponges (Porifera). *PloS One* **7**, e35105.

Van Soest RWM and De Voogd NJ (2015) Calcareous sponges of Indonesia. *Zootaxa* **3951**, 1–105.

Van Soest RWM and De Voogd NJ (2018) Calcareous sponges of the Western Indian Ocean and Red Sea. *Zootaxa* **4426**, 1–160.

Vicente J, Webb MK, Paulay G, Rakchai W, Timmers MA, Jury CP, Bahr K and Toonen RJ (2022) Unveiling hidden sponge biodiversity within the Hawaiian reef cryptofauna. *Coral Reefs* **41**, 727–742.

Voigt O, Wülfing E and Wörheide G (2012) Molecular phylogenetic evaluation of classification and scenarios of character evolution in calcareous sponges (Porifera, Class Calcarea). *PloS One* **7**, e33417.

Wantiez L and Chauvet C (2003) First data on community structure and trophic networks of Uvea coral reef fish assemblages (Wallis and Futuna, South Pacific Ocean). *Cybium* **27**, 83–100.

Whitelegge T (1897) The sponges of Funafuti. *Memoirs of the Australian Museum* **3**, 323–332.

Wilkinson CR (1988) Foliose dictyoceratida of the Australian great barrier reef. *Marine Ecology* **9**, 321–327.

Williams JT, Wantiez L, Chauvet C, Galzin R, Harmelin-Vivien M, Jobet E, Juncker M, Mou-Tham G, Planes S and Sasal P (2006) Checklist of the shorefishes of Wallis Islands (Wallis and Futuna French Territories, South-Central Pacific). *Cybium* **30**, 247–260.

Wörheide G, Epp LS and Macis L (2008) Deep genetic divergences among Indo-Pacific populations of the coral reef sponge *Leucetta chagosensis* (Leucettidae): founder effects, vicariance, or both? *BMC Evolutionary Biology* **8**, 24.

Wörheide G and Erpenbeck D (2007) DNA taxonomy of sponges – progress and perspectives. *Journal of the Marine Biological Association of the United Kingdom. Marine Biological Association of the United Kingdom* **87**, 1629–1633.

Wörheide G and Hooper JNA (1999) Calcarea from the Great Barrier Reef. 1: cryptic calcinea from Heron Island and Wistari Reef (Capricorn-Bunker Group). *Memoirs of the Queensland Museum* **43**, 859–891.

Wörheide G, Hooper JNA and Degnan BM (2002) Phylogeography of western Pacific *Leucetta* '*chagosensis*' (Porifera: Calcarea) from ribosomal DNA sequences: implications for population history and conservation of the Great Barrier Reef World Heritage Area (Australia). *Molecular Ecology* **11**, 1753–1768.

Wright E (2016) Using DECIPHER v2.0 to analyze big biological sequence data in R. *The R Journal* **8**, 352.

Wulff J (2012) Ecological interactions and the distribution, abundance, and diversity of sponges. *Advances in Marine Biology* **61**, 273–344.

Xavier JR, Rachello- Dolmen PG, Parra-Velandia FJ, Schönberg CHL, Breeuwer JA and van Soest RWM (2010) Molecular evidence of cryptic speciation in the 'cosmopolitan' excavating sponge *Cliona celata* (Porifera, Clionaidae). *Molecular Phylogenetics and Evolution* **56**, 13–20.

https://doi.org/10.1017/S0025315424000432 Published online by Cambridge University Press