

Research Article

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

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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).

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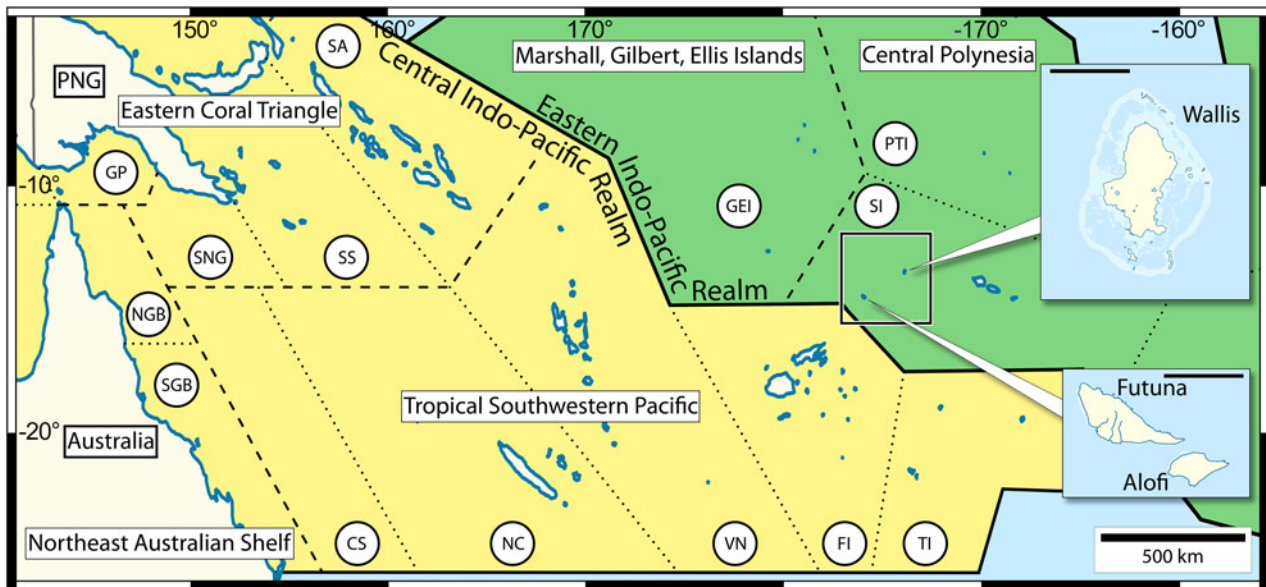


Figure 1. Location of Wallis and Futuna in proximity to the border of the Eastern Indo-Pacific (green highlight) and Central Indo-Pacific (yellow highlight) realms. Marine realms separated by solid lines, provinces by dashed lines, ecoregions by dotted lines (simplified, *sensu* Spalding *et al.*, 2007). 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 Reisinger, 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 MgCl₂ (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

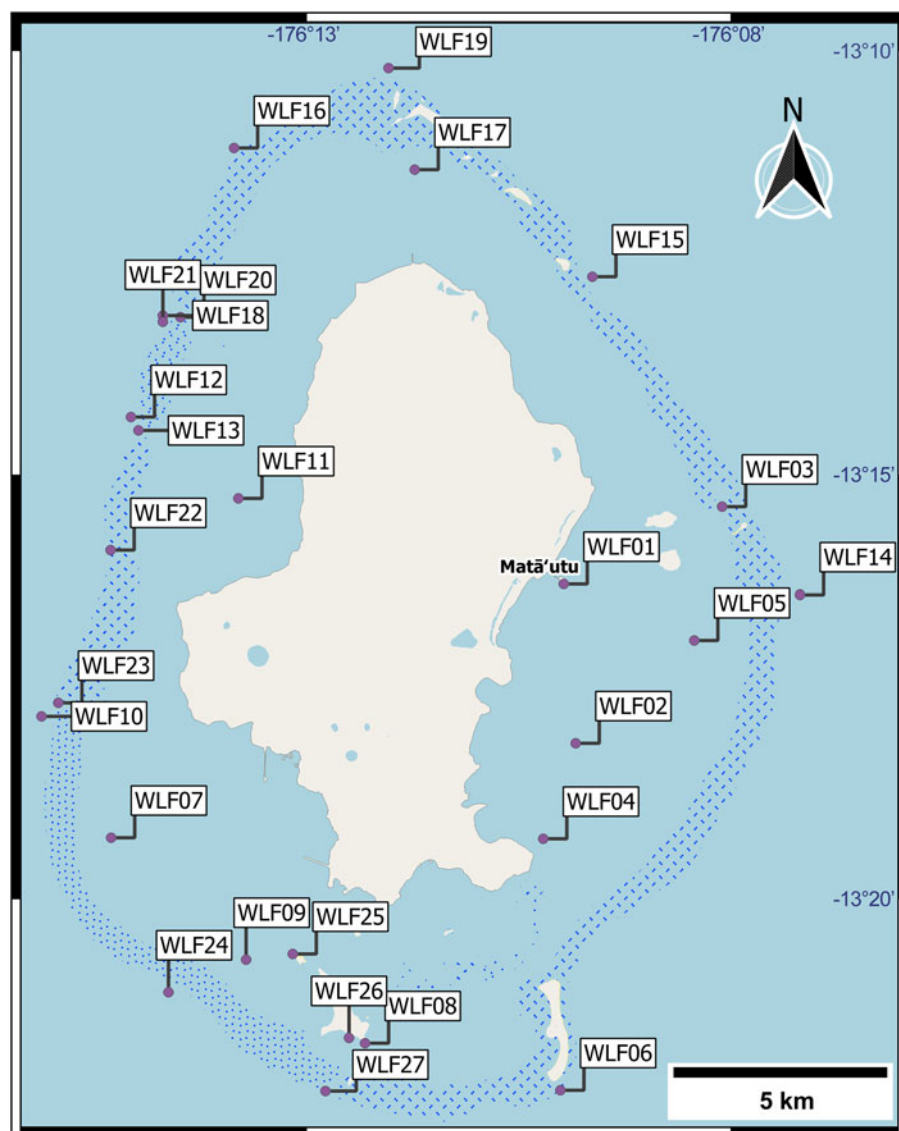


Figure 2. Sampling sites (WLF#) of the WALLIS 2018 expedition, in SCUBA-accessible depth ranges to up to 51 m. Reef locations are shaded in darker blue. © OpenStreetMap contributors.

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 <i>et al.</i> (1998)
28S-D2-rev	5' TCC GTG TTT CAA GAC GGG 3'	28S	Chombard <i>et al.</i> (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).

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 (Kato 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 Reisinger, 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.*,

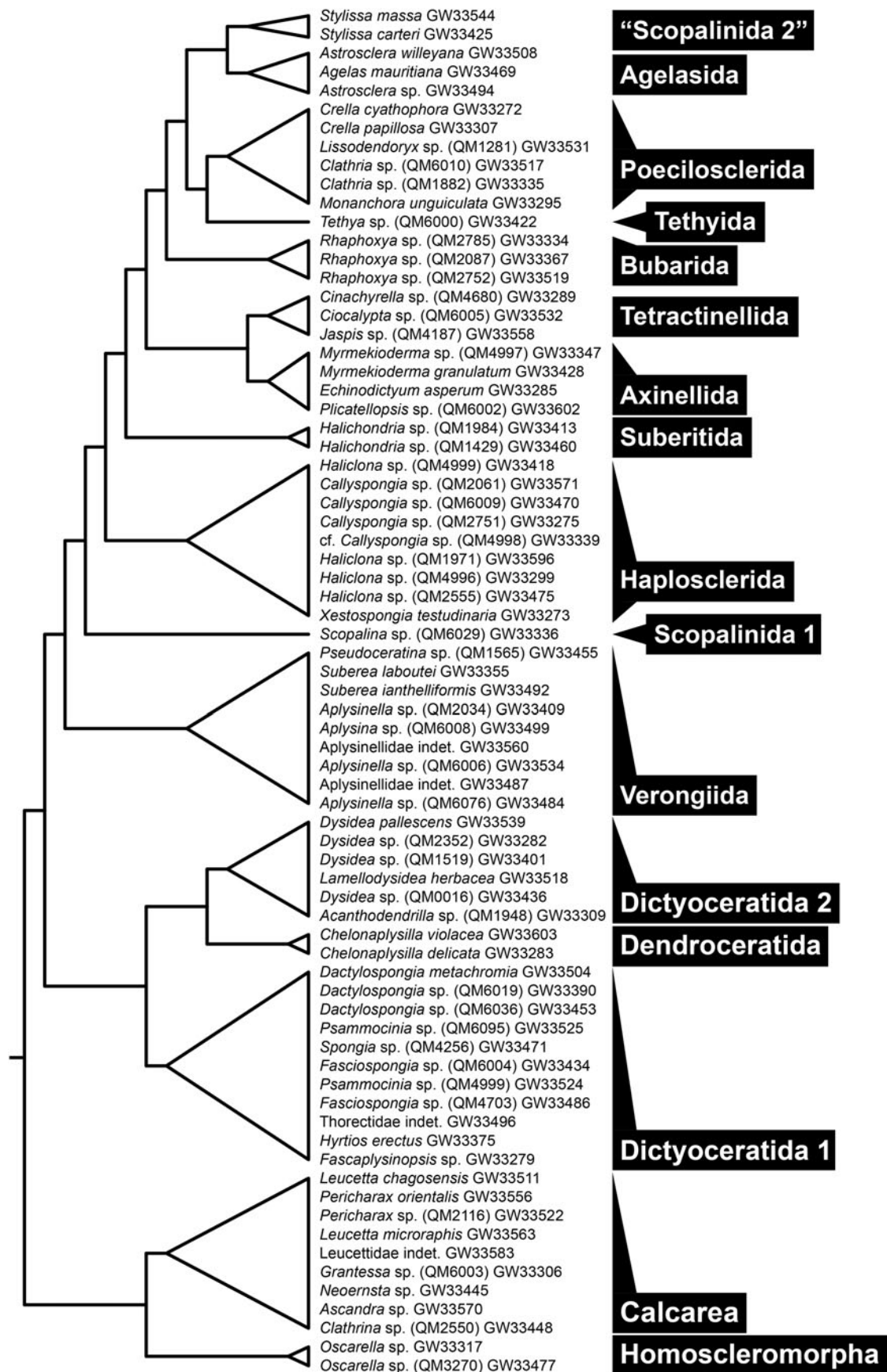


Figure 3. Simplified cladogram of the 28S Maximum Likelihood phylogenetic tree (Supplementary Figure S2) with representative taxa. Taxon names include reference to SNSB-BSPG collection numbers (GWxxxxx). Branch lengths not representative.

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.

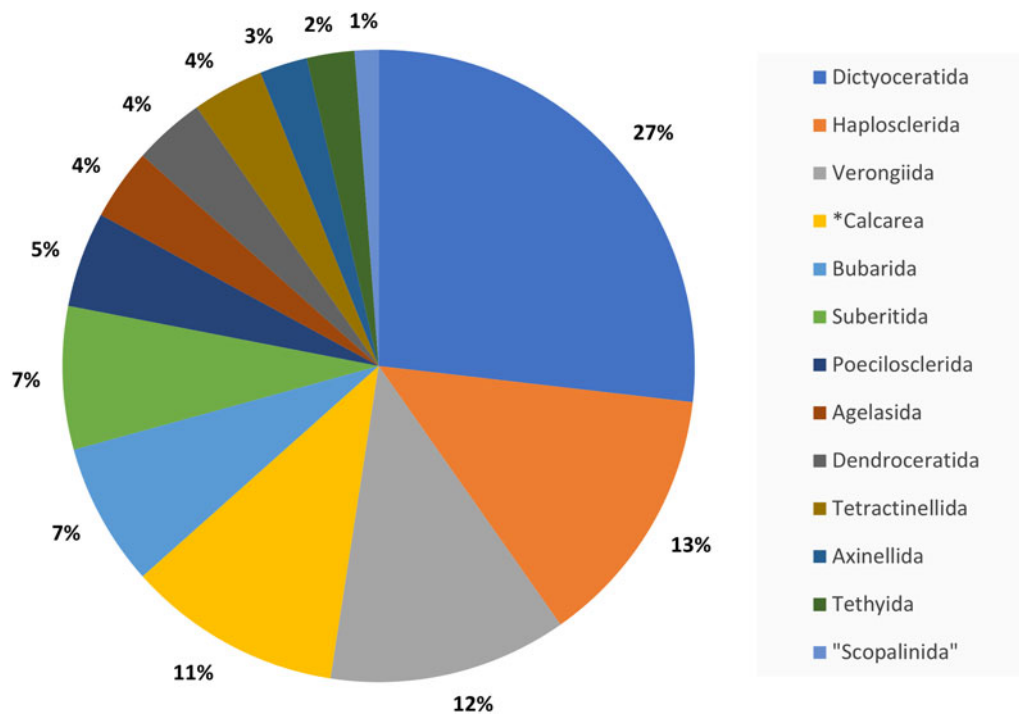


Figure 4. Relative taxonomic distribution (approximated) of combined 28S and CO1 MOTUs per Demospongiae order or other sponge class (denoted with an asterisk). For absolute numbers per marker and detailed relative distributions see Supplementary Table S2.

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

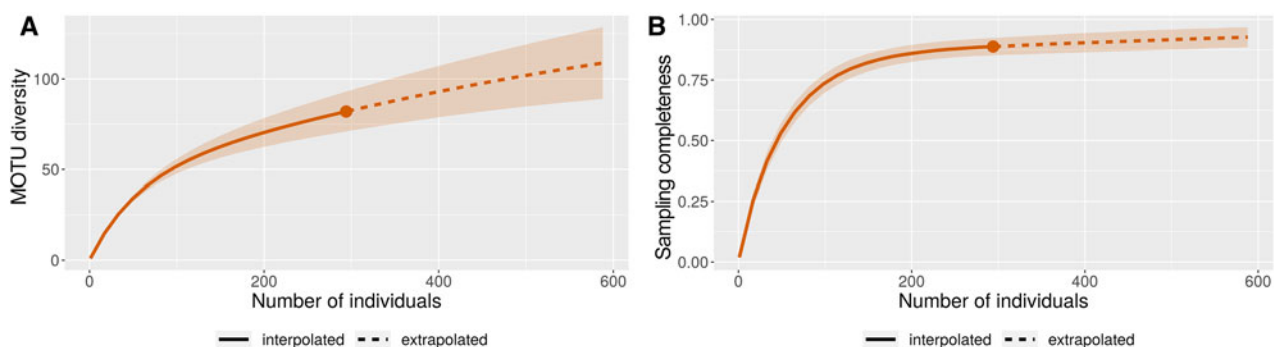


Figure 5. (A) Sampling size-based biodiversity estimation and extrapolation based on 28S data of Demospongiae; (B) Curve of estimated sampling completeness (sample coverage).

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 Polynesia 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

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>

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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 OX42227–OX422451, with additional specimen information available in the Sponge Barcoding Database (SBD) under the accession numbers SBD#2566 – 2878.

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