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A genomic approach to *Porites* (Anthozoa: Scleractinia) megadiversity from the Indo-Pacific

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A B S T R A C T

Porites corals are vital components of tropical reef ecosystems worldwide, serving as ecosystem engineers and hubs of biodiversity in shallow water coral reefs. Despite their ecological significance and the widespread use of *Porites* spp. as models for research, the richness and evolutionary relationships of species within the genus remain elusive. In this study, we analyzed genomic data from 330 colonies of *Porites* from 17 localities across the Indo-Pacific region based on the reduced representation genomic approach ezRAD. We retrieved 25,163 SNPs and provided a phylogenomic hypothesis for 29 nominal species and 10 unknown morphologies, recovering 15 deeply rooted molecular clades. Among these, 12 clades included samples corresponding to single distinct morphospecies. One did not match any nominal species. The remaining two clades comprised species complexes, which included various massive and encrusting morphologies commonly used in experimental biology. Within these complexes, we observed additional geographic or morphological structure, indicating complex evolutionary dynamics, possibly reflecting distinct species, isolated populations or hybridization. Additionally, a series of divergent samples underscored the importance of more sampling to define species boundaries and refine phylogenomic relationships. We also integrated our findings with previous phylogenetic datasets and their respective sampling localities, challenging traditional notions about *Porites* species geographic distributions. Overall, our findings indicate a need to revise past synonymies and to formally establish new species. A precise understanding of *Porites* species and their diversity and distributions is necessary for effective reef conservation and management.

1. Introduction

Tropical coral reefs are undergoing rapid worldwide decline due to a combination of local and global threats, such as increasing sea water temperature and deoxygenation (Hughes et al., 2018, 2020; Smale et al., 2019; Pezner et al., 2023). Among the primary architects of these ecosystems are calcifying organisms belonging to the order Scleractinia (Cnidaria, Anthozoa). Despite their crucial ecological role, our understanding of species boundaries and distribution ranges within scleractinian corals remains limited, impeding the formulation of effective conservation and management strategies (Fisher et al., 2011).

The scleractinian family Poritidae Gray, 1840 is a common element and significant contributor to the architecture of coral reefs globally (Bellwood and Hughes, 2001). In particular, the genus *Porites* Link, 1807

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stands out for its pivotal role in supporting shallow coral reef ecosystems and their structural and topographic complexity (Bellwood et al., 2004). *Porites* species are also renowned for their longevity and resilience to stressors (*e.g.*, Marshall and Baird 2000; Kawakubo et al., 2017; Shinzato et al., 2021). The importance of *Porites* is well indicated by the numerous studies using the genus as a model to investigate the impacts of environmental changes, pollutant exposure and coral health (*e.g.*, Inoue and Tanimizu, 2008), as well as to reconstruct historical environmental conditions (*e.g.*, DeCarlo et al., 2017) and coral stress responses (*e.g.*, Fitt et al., 2009).

Despite their ecological significance, identification of *Porites* species has predominantly relied on outdated taxonomy, primarily assessing colony growth forms and macromorphological skeletal characters, alongside untested assumptions about species distributions (Veron, 2000). Throughout the taxonomic history of the genus, many have contended that *Porites* species exhibit a continuum of morphological traits, questioning the notion of discrete morphological units and traditional species biogeography (Bernard, 1905; Zlatarski, 1990). This challenge in *Porites* results from extensive phenotypic plasticity, morphological variability, homoplasy, and convergent evolution of morphological traits (Muko et al., 2000; Smith et al., 2007; Padilla-Gamiño et al., 2012), making species identification based solely on morphology inherently complex (Veron, 2000; Forsman et al., 2009, 2015; Tisthammer and Richmond, 2018).

The emergence of molecular phylogenetics has revolutionized our understanding of coral evolutionary history, biodiversity, and biogeography (Fukami et al., 2004, 2008; Huang et al., 2011; Kitahara et al., 2016; Cowman et al., 2020; Grinblat et al., 2021; Quek and Huang, 2022; Gijsbers et al., 2023; Oury et al., 2023; Feldman et al., 2021; Quek et al., 2023). A growing body of literature has identified a genetic break between Indian and Pacific coral populations previously treated as single widespread species (Arrigoni et al., 2016, 2018; Kitano et al., 2014; Richards et al., 2016; Gélin et al., 2017, 2018; Bongaerts et al., 2021). In *Porites*, phylogenetic analyses revealed the presence of unknown genetic diversity as well as unresolved complexes of species (Forsman and Birkeland, 2009; Forsman et al., 2009, 2017; 2020; Benzoni and Stefani, 2012; Prada et al., 2014; Hellberg et al., 2016; Dimond et a., 2017; Terraneo et al., 2019a, 2021; Combosch et al., 2024). Forsman et al. (2017) failed to distinguish two sympatric species of *Porites* with contrasting morphologies in Hawaii based on genome-wide data. Similarly, based on ezRAD data, an unresolved species complex including several massive morphospecies was highlighted by Terraneo et al. (2021) in the seas surrounding the Arabian Peninsula. To date, no systematic work encompassing a widespread sampling including both the Indian and Pacific Ocean has been carried out for the genus. In an era of ongoing biodiversity loss, conservation strategies are in urgent need of accurate coral species identities (Huang, 2012; Bridge et al., 2020). Without precise species delimitation, conservation efforts may fail to address the specific ecological needs of distinct species (Bongaerts et al., 2021; Johnston et al., 2022). This can lead to inadequate protection and management, particularly in vulnerable ecosystems like coral reefs where species loss can have cascading effects on biodiversity and ecosystem function (Pratchett et al., 2011). Particularly, species with limited distributions, such as endemic species, often play crucial roles in their ecosystems and have specialized requirements, making them vulnerable to environmental stressors like ocean warming and habitat degradation (Grupstra et al., 2024). Furthermore, identifying species boundaries is essential towards tailored approaches for restoration (Riginos et al., 2024). Preserving corals' genetic diversity is key to ensure long-term reef resilience. However, the actual diversity, taxonomy, and systematics of *Porites* remain matters of debate, impeding a proper understanding of their biodiversity, ecology, and evolutionary history, and posing fundamental problems for downstream research and ultimately conservation (Forsman et al., 2009, 2017, 2020; Terraneo et al., 2019a, 2021; Combosch et al., 2024).

In this study, we aimed to elucidate the evolutionary relationships among 39 morphospecies of *Porites* collected from 17 localities spanning the Indian and Pacific Oceans. We based our morphological identification on original descriptions and type material. We reconstructed 254 ezRAD libraries and combined these with 76 libraries previously published by Terraneo et al., (2021) to provide a well-supported phylogenetic hypothesis of the genus based on 25,163 genome-wide SNPs. We additionally evaluated our results incorporating previous mitochondrial phylogenetic datasets (Forsman et al., 2009; Combosch et al., 2024) and geographic distribution data and discussed the taxonomic and ecological implications of our findings.

2. Materials and Methods

2.1. Collection and identification

This works includes a total of 254 newly collected *Porites* colonies and 76 colonies from Terraneo et al. (2021) sampled from 17 localities throughout the Indo-Pacific Ocean (11 new, 6 from Terraneo et al. 2021) (Table S1, Fig. 1). Each colony was imaged underwater and a portion of the colony was collected with hammer and chisel. Tissue from each colony was preserved in either 99 % ethanol or CHAOS solution (not an acronym; 4 M guanidine thiocyanate, 0.1 % N-lauroyl sarcosine sodium, 10 mM Tris pH 8, 0.1 M 2-mercaptoethanol) and the remaining portion of the sample was bleached with sodium hypochlorite for 24 h and air-dried. Specimens are deposited at Museum of Tropical Queensland (MTQ, Australia), University of Milano-Bicocca (UNIMIB, Italy), King Abdullah University of Science and Technology (KAUST, Saudi Arabia), Institute de Recherche pour le Développement (IRD, New Caledonia), Lee Kong Chian Natural History Museum (Zoological Reference Collection, ZRC; Singapore), Sultan Qaboos University (Oman), and Qatar University (Qatar) under unique voucher numbers (Table S1). Dried skeletons were imaged with a Canon G15 camera.

Specimens were morphologically identified following comparisons with the original descriptions and, when available, the type material (holotypes or type series) of the nominal species. Table S2 summarizes the most updated reconstruction of *Porites* nomenclature and outlines the type material and original descriptions that we were able to retrieve. Names from Bernard (1905) were not included due to being not compliant to the ICZN code (WoRMS, Hoeksema and Cairns, 2024). Specimens collected from the type locality with skeletons that closely resembled the original type were given the nominal species name. Specimens that resembled the type of a nominal species but were not sampled from the type locality were given the qualifier 'cf.'. Specimens that had morphological affinities to a nominal species but could not be reliably identified using the information available were given the qualifier 'aff.' (see also Cowman et al., 2020) (Table S1). This uncertainty in species identification in *Porites* reflects the limited utility of some original descriptions or uncertainty surrounding the type material (see Combosch et al. 2024).

2.2. DNA extraction and ezRAD libraries preparation

Total DNA was extracted using DNeasy® Blood & Tissue Kit (Qiagen, Hilden, Germany) for samples stored in ethanol or using a phenol–chloroform-based method for samples stored in CHAOS solution. Extracted DNA was quantified with the Qubit dsDNA High Sensitivity Assay kit (Thermo Fisher Scientific, Waltham, MA, USA) using Qubit® fluorometer (Thermo Fisher Scientific). Protocols by Toonen et al. (2013) and Knapp et al. (2016) were followed for DNA digestion and ezRAD library preparation. After DNA quantification, each sample was digested using frequent cutter restriction enzymes *MboI* and *Sau3AI* (New England BioLabs, Ipswich, MA, USA) to cleave sequences at GATC cut sites. Library preparation was performed using the TruSeq® Nano DNA Library Prep Kit (Illumina, San Diego, CA, USA), following the manufacturer's protocol. Libraries were size-selected at 350 bp following the manufacturer's protocol and Knapp et al. (2016), and

Fig. 1. Geographic distribution of sampling localities (numbers from 1 to 17; Table S1) of *Porites* specimens collected for phylogenetic reconstruction. Colours indicate broad bioregions. Numbers from 1 to 6 correspond to sampling localities from Terraneo et al. (2021).

ligated to dual index Illumina adapters unique combinations. Finally, ezRAD libraries were normalized at 10 nM following the manufacturer's protocol, pooled (N = ~64), and their size and concentration were checked using 2100 Bioanalyzer (Agilent, Santa Clara, CA, USA) and QuantStudio 3 real-time PCR system (Thermo Fisher Scientific), respectively. Each library pool was run in a single 150 bp paired-end lane on Illumina HiSeq 4000 System at KAUST Bioscience Core Lab (Thuwal, Saudi Arabia). The raw sequences are available at the Sequence Read Archive (SRA) under the BioProject number PRJNA1121665.

2.3. ezRAD data processing

Together with newly generated data from 254 samples, we included ezRAD data from 76 samples from Terraneo et al. (2021) (project number PRJNA7141989). The total Illumina raw data consisted of 1,792,281,465–150 bp reads. Samples were demultiplexed using their unique barcode and adapter sequences under the Illumina pipeline bcl2fastq/2.17.1.14 (with no mismatches allowed for the barcode), effectively removing reads that lacked identifiable barcode pairs. Slightly over 5 million reads per individual (N = 330) were trimmed using Trimmomatic v.0.36 (Bolger et al., 2014) using the ILLUMINACLIP:adapters.fa:2:30:10 LEADING:3 TRAILING:3 SLIDINGWINDOW:4:20 MINLEN:36 parameters. Trimmed reads were aligned to the transcriptome of *P. lobata* obtained from Forsman et al. (2017) using Bowtie 2 v.2.3.4 (Langmead and Salzberg, 2012) to create bins including only reads belonging to the coral host. These initial trimming and alignment steps were performed to reduce noise from reads belonging to other organisms for downstream analyses. The processed reads were further used to perform reference-based variant calling via the dDocent v.2.25 pipeline (Puritz et al., 2014) under the default parameters using the *P. lobata* transcriptome.

The resulting *vcf* file included a total of 1,820,817 variants and was further filtered using VCFtools v.0.1.16 (Danecek et al., 2011) by removing indel sites and by retaining only SNPs with minimum quality = 30, minimum mean depth = 6, minimum bp distance between consecutive SNPs = 5, and minor allele frequency (MAF) = 0.05. Three filtered datasets, hereafter named as 6 − sm25, 6 − sm12.5, and 6 − sm5, were generated to allow a maximum missing data of 25 %, 12.5 %, and 5 %, respectively. Moreover, we tested the effect of increasing the minimum mean depth = 12, with 25 % missing data, and created an additional filtered dataset, 12 − sm25. The script *vcf2phylip.py* (Ortiz, 2019) was used to convert the *vcf* datasets to the required file formats for further phylogenetic analyses. The 6 − sm25 matrix contained 25,163 SNPs, the 6 − sm12.5 matrix was composed of 18,782 SNPs, while the 6 − sm5 included 7,431 SNPs. Finally, the 12 − sm25 dataset included 8,030 SNPs. Additionally, for each of the two retrieved molecular clades that hosted the highest diversity of morphospecies and the highest number of analysed samples (clade V with 100 samples and clade XV with 97 samples), we produced with VCFtools v.0.1.16 (Danecek et al., 2011) two separate matrices to evaluate the intra-clade structuring, testing the potential effect of MAF on phylogenetic inference: no indels, minimum quality = 30, minimum mean depth = 6, minimum bp distance between consecutive SNPs = 5, maximum missing data 25 %, and minor allele frequency (MAF) = 0.02 or 0.05. The matrices included 38,732 SNPs (clade V) and 32,485 SNPs (clade XV) with MAF = 0.02, and 23,585 SNPs (clade V) and 18,320 SNPs (clade XV) with MAF = 0.05.

Each of the resulting SNPs datasets was analysed in IQ-TREE v2.0.5 (Minh et al., 2020), for maximum likelihood (ML) phylogenetic inference including + ASC parameter to account for SNP-based ascertainment bias (Lewis, 2001). The best-fit models according to BIC scores were assessed using the ModelFinder (Kalyaanamoorthy et al., 2017) in IQ-TREE v2.0.5 and were determined to be the following: 6 − sm25: GTR + F + ASC + R7, 6 − sm12.5: GTR + F + ASC + R7, 6-sm5: SYM + ASC + R6, 12 − sm25: TVM + F + ASC + R7, clade V − 0.02: GTR + F + ASC + R4, clade V − 0.05: GTR + F + ASC + R4, clade XV − 0.02: GTR + F + ASC + R4, clade XV − 0.05: GTR + F + ASC + R4. Branch supports were assessed using 1,000 ultrafast bootstrap iterations.

To compare our data with the largest and most recent published phylogenetic reconstructions of *Porites* from Forsman et al. (2009) and Combosch et al. (2024), from our ezRAD libraries we retrieved the four

mitochondrial (mt) regions used in Combosch et al. (2024), namely MT09, MT12, MT16, and MT20 (for details on mt genes associated with these four loci, see Combosch et al., 2024). We selected a total of 71 samples that represented all 39 morphospecies collected in our study, with the exception of *Porites hadramauti*, *Porites mayeri*, *Porites* sp. 4, and *Porites* sp. 5 for which we failed to retrieve the targeted mt loci. We used SPAdes v.3.15.5 (Prjibelski et al. 2020) to perform *de novo* assembly of *fastq* trimmed paired-end reads with –careful option to minimize the number of mismatches and short indels in the final contigs. The retrieved contigs from each sample were probed using BLASTn for the four mt regions of interest (reference sequences: MT09 – OR509223.1, MT12 – OR509160.1, MT16 – OR509110.1, MT20 – OR509054.1) to extract the selected loci. To the four obtained datasets we added data from 67 samples from Combosch et al. (2024) and data from 11 *Porites* mt genomes downloaded from NCBI. The same regions were extracted from the available mitochondrial genome of *Goniopora columna* (NC0156439) and used as outgroup. Each single-locus dataset was aligned using MAFFT v.7.450 (Katoh and Standley, 2013) using the E-INS-I option under default parameters and, subsequently, GBlocks v.0.91b (Castresana, 2000) was used to remove nucleotide positions of ambiguous homology. The four regions were finally concatenated in a single dataset using Geneious® v.10.1.3 (Biomatters Ltd., Auckland, New Zealand). RAxML-HPC2 v.8.0 (Stamatakis, 2014) was used to reconstruct phylogeny. We applied the GTR + G substitution model and the branch support was assessed by 500 bootstrap replicates. ML analysis was run on the CIPRES Science Gateway (Miller et al., 2010).

For the molecular lineages obtained in this study (see Fig. 2), numbers are consistent with Terraneo et al. (2019a, 2019b, 2021). Comparison with clade numbers *sensu* Forsman et al. (2009) and Combosch et al. (2024) are discussed in the results and discussion section.

3. Results and discussion

3.1. Morphological identification of Porites

The 330 *Porites* specimens were assigned to 39 morphospecies (Table S1). Of these, 29 were good matches for the type material or original description of existing nominal species, 25 of which are considered valid, one is a junior synonym and three are *taxa inquirenda* (species of doubtful identity requiring further investigation; WoRMS, Hoeksema and Cairns, 2024) (Tables S1, S3, Figs. S1, S2a). For 14 of these 29 nominal species, we collected material from the type locality (Table S3), while the remaining 15 closely resembled the morphology of the type material (for which the "cf." qualifier was given). We also encountered three morphospecies which resembled the type material of nominal species already included in the dataset, but with less certainty (for which the "aff." qualifier was used and they were not counted as separate morphospecies). The remaining 10 morphospecies did not match any of the type material or original descriptions that we could access and are hereafter reported as *Porites* sp. 1 to *P.* sp. 10 (Table S1, Figs. S1, S2). Given the 200 nominal species of *Porites* from many different localities (Table S2 – 208 nominal species, of which 8 were misspelled), some of the 10 unidentified morphospecies found might correspond to existing names in *Porites* nomenclature for which previous synonymies might need to be re-assessed, while the restricted geographic distribution of others, *i.e.*, *P.* sp. 5 from Lord Howe Island

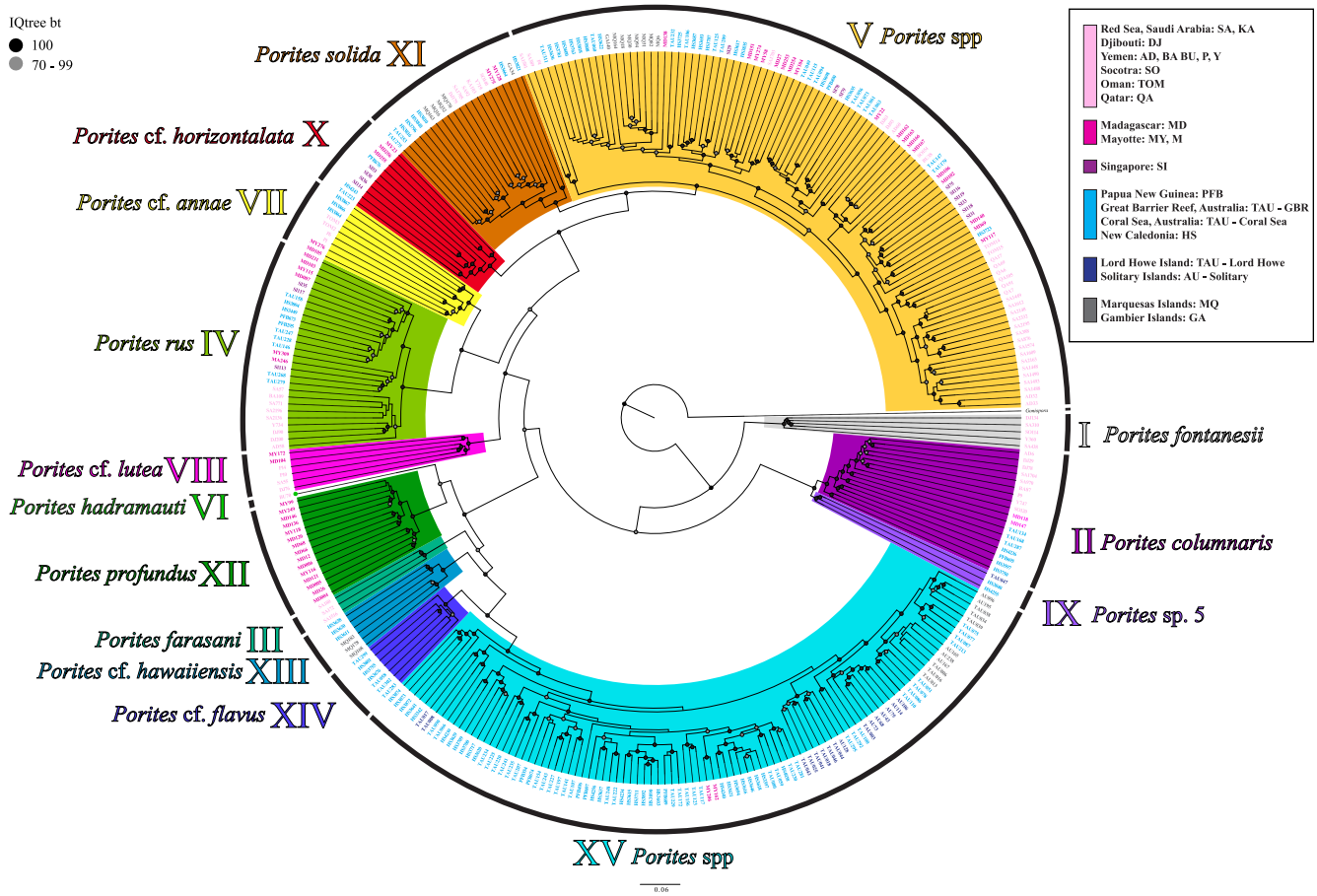

Fig. 2. IQ-TREE phylogenetic tree of 330 *Porites* samples based on the 6 – sm25 dataset, allowing for 25% maximum missing data, and consisted of 25,163 SNPs. Circles at nodes indicate ML bootstrap supports at 100% (black) or between 70–99% (grey). Major clades are distinguished by colour. *Goniopora* sp. was used as outgroup. Coloured labels at tips correspond to broad sampling region as per legend.

and New Caledonia, likely indicates they are new to science. A taxonomic revision of the genus is beyond the scope of this research and will require more sampling over a greater geographical range.

3.2. Phylogenomic analyses

The phylogenomic trees based on the three retrieved SNPs datasets (6 − sm25, 6 − sm12.5, 6 − sm5, 12 − sm25) were well supported and generally concordant resolving the same major 15 molecular clades (clades I to XV) and phylogenomic relationships with moderate to high bootstrap values (Figs. 2, S3, S4, S5). The 12 − sm25 tree retrieves different relationship for clades II and IX, and for clades III, VI, and XII. Moreover, with respect to clades II and IX, the position of two samples was not consistent with the other reconstructions (Figs. 2, S3, S4, S5).

3.2.1. Resolved clades

A total of 13 clades were comprised of a single morphospecies (12 corresponding to nominal species and one unknown morphology). The monophyly of 12 of these was highly supported in all topologies: clade I = *Porites fontanesii*; clade II = *Porites columnaris*; clade III = *Porites farasani*; clade IV = *Porites rus*; clade VII = *Porites* cf. *annae*; clade VIII = *Porites* cf. *lutea*; clade IX = *Porites* sp. 5; clade X = *Porites* cf. *horizontalata*; clade XI = *Porites solida*; clade XII = *Porites profundus*; clade XIII = *Porites* cf. *hawaiiensis*; clade XIV = *Porites* cf. *flavus*. The monophyly of clade VI = *Porites hadramauti* could not be confirmed from this dataset as it comprised only one individual, yet unpublished data (Terraneo et al. *in prep*) including more representatives of this species further support this as a monophyletic lineage.

Clades I to VIII were recovered from the Arabian Peninsula in Terraneo et al. (2021). Nevertheless, the integration of newly-collected samples from additional Indo-Pacific localities and the combination of our molecular data with other phylogenetic datasets (Forsman et al., 2009, 2017; Combosch et al., 2024) helped to clarify the identification of samples in clade VII and clade VIII as discussed below. Moreover, the geographical distribution of clade II, clade IV, clade VII, and clade VIII is also re-evaluated in light of the present widespread sampling.

3.2.2. Species complexes: Clade V and clade XV

Of the remaining 26 morphospecies, 15 were clustered in clade V and 11 in clade XV. In particular clade V included 15 morphospecies + *Porites* aff. *lutea* (Figs. 2 and 3, S3, S4, S5). In particular, specimens identified as *Porites alveolata, Porites arenacea, Porites* cf. *arnaudi, Porites australiensis, Porites conglomerata*, *Porites* cf. *cylindrica, Porites harrisoni, Porites* cf. *lobata, Porites* aff. *lutea, Porites mayeri*, *Porites nodifera, Porites*

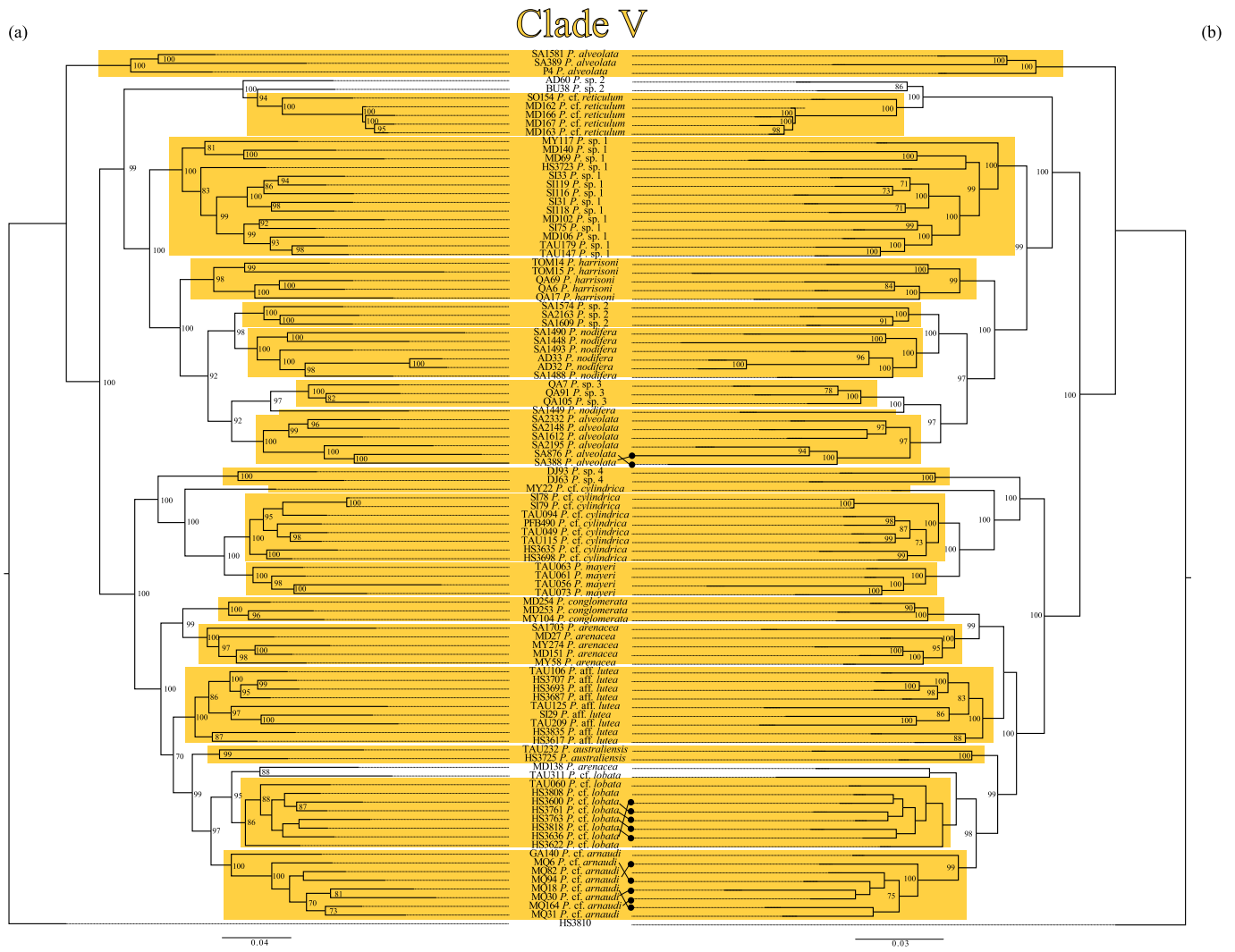

Fig. 3. IQ-TREE phylogenetic trees of 100 *Porites* samples nested in species complex clade V (see Fig. 2). (a) 23,585 SNPs (maximum missing data = 25 %, minor allele frequency = 0.05), (b) 38,732 SNPs (maximum missing data = 25 %, minor allele frequency = 0.02). Sample HS3810 from clade XI was used as outgroup. Numbers at nodes are ML bootstrap supports (≥ 70 %). Highlights in the tree correspond to concordant morpho-molecular subclusters. Samples were not highlighted when their phylogenetic position remained uncertain.

cf. *reticulum*, clustered within clade V, together with *Porites* sp. 1 to *Porites* sp. 4 (Figs. 3, S2a). These were recovered in 18 subclades, each corresponding broadly to one of the 15 morphospecies, with the exception of *P. alveolata* which was recovered in two distinct subclades that were not sister groups (Figs. 3, S2a), and *P.* cf *cylindrica* which also was recovered in two non-sister subclades. Additionally, *P.* sp. 2, *P. nodifera*, and *P. arenacea*, were not resolved as monophyletic since single samples (AD60, BU38, SA1449, and MD138) clustered in different lineages.

Clade XV included 11 morphospecies + *Porites* aff. *heronensis, Porites* aff. *tuberculosus,* and *Porites* aff. *lichen* (Figs. 2 and 4, S3, S4, S5). In particular, it clustered *Porites* cf. *lichen, Porites* cf. *reticulosa, Porites* cf. *tuberculosus, Porites* cf. *silimaniana, Porites* cf. *heronensis, Porites vaughani,* together with *P.* aff. *lichen*, *P.* aff. *tuberculosus, P.* aff. *heronensis*, and *Porites* sp. 6 to *Porites* sp. 10 (Figs. 4, S2b). Within clade XV, we recovered 20 subclades. Of these, eight were comprised of a single morphospecies, *i.e.*, *P.* cf. *reticulosa, P.* cf. *tuberculosus*, *P. vaughani*, *P.* sp. 6, *P.* sp. 7, *P.* sp. 8, *P.* sp. 9, and *P.* sp. 10. The remaining subclades were *P.* cf. *lichen* (one subclade), *P.* aff. *lichen* (two subclades) and *P. heronensis* (one subclade), *P.* cf. *heronensis* (one subclade), *P.* aff. *tuberculosus* (one subclade), *P.* cf. *silimaniana* (two subclades) and *P.* aff. *heronensis* (two subclades) (Figs. 4, S2b). Similar to the situation in clade V, a few samples in clade XV (PFB496, TAU003, TAU100, TAU292, and TAU295) did not cluster with samples having similar or identical morphologies, underscoring the importance of widespread sampling.

The subclusters recovered were consistent between MAF values, confirming the reliability of the analyses in reconstructing the phylogenetic relationships within these clades (Figs. 2–4). The presence of very similar morphologies among the subclades recovered in clade V and clade XV underscores the complex evolutionary scenario occurring within these lineages, for which an integration of geographic distribution data will be discussed in the next paragraph and stressed the difficulties to correctly identify specimens of *Porites* within these two major clades. The presence of singleton divergent samples might indicate that

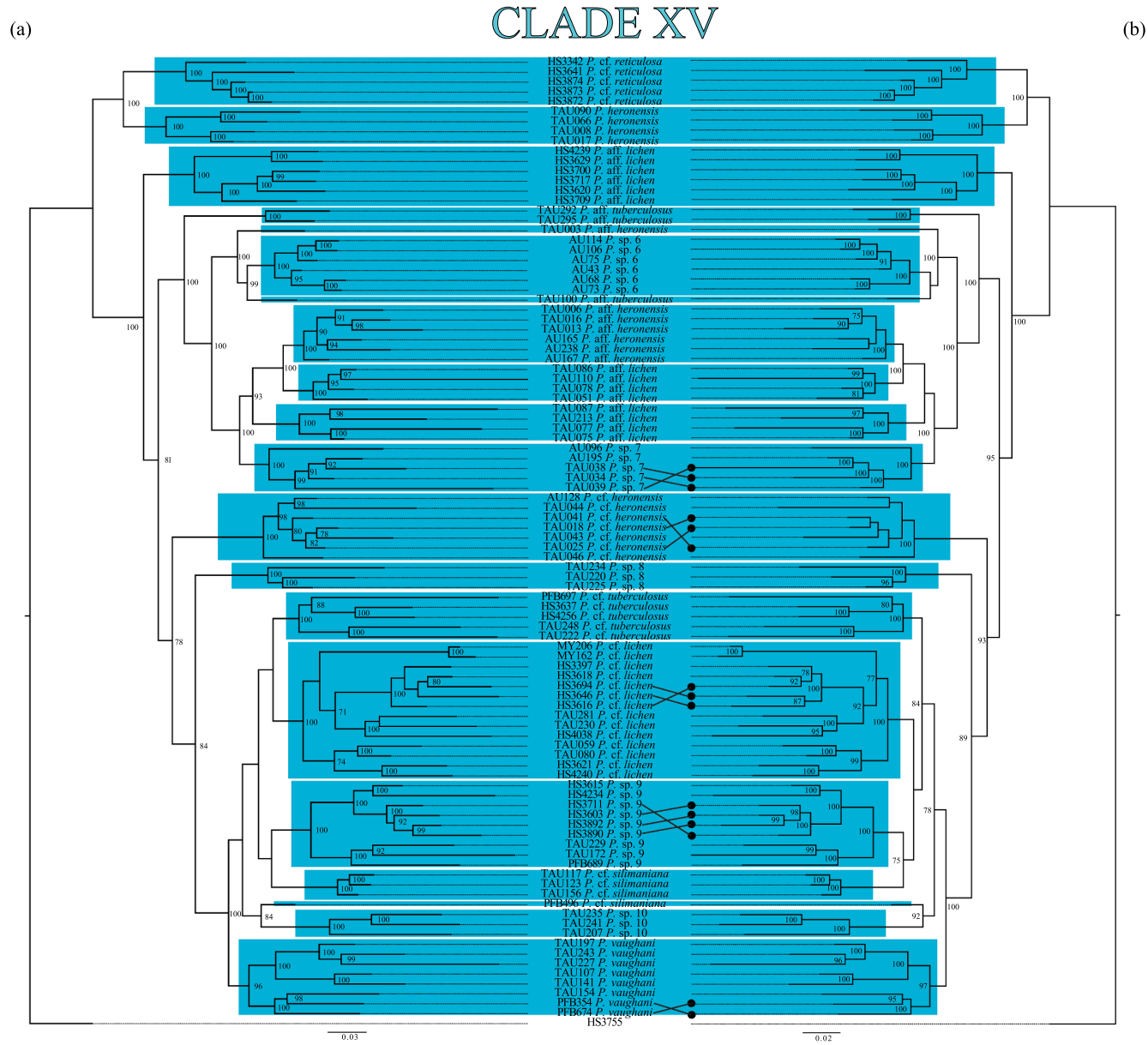

Fig. 4. IQ-TREE phylogenetic trees of 97 *Porites* samples nested in species complex clade XV (see Fig. 2). (a) 18,320 SNPs (maximum missing data = 25 %, minor allele frequency = 0.05), (b) 32,485 SNPs (maximum missing data = 25 %, minor allele frequency = 0.02). Sample HS3755 from clade XIV was used as outgroup. Numbers at nodes are ML bootstrap supports (≥ 70 %). Highlights in the tree correspond to concordant morpho-molecular subclusters.

the overall picture regarding *Porites* diversity is yet to be complete and further widespread geographical sampling is needed.

The recovery of these two species complexes is not surprising. Indeed, clade V was retrieved by Forsman et al. (2009, 2017, 2020) – clade I, Terraneo et al. (2019a, 2019b, 2021) – clade V, and Combosch et al. (2024) – clades 6, 7, 8, 9 10, 12. Clade V includes a number of massive morphologies that are notoriously hard to discriminate. Clade XV includes some putatively widespread morphologies in the Pacific Ocean, *e.g.*, *P. lichen* and *P. heronensis*. Given their large geographic range size, high levels of morphological, geographical, or genomic variation are to be expected. The use of genome-wide data helped retrieve phylogenetic structure within these species complexes. Together with geographic distribution data and information regarding species type locality, the analyses helped identify corresponding morphospecies for most subclusters in clades V and XV. Nevertheless, most of these could not be resolved, and morpho-molecular boundaries among these subclades remain uncertain. Indeed, convergence events among close related entities can be challenging to resolve, as a result of a combination of the following aspects: a) high morphological variability of one or few separate evolving entities that led to a high number of nominal species and thus confused taxonomy; b) incomplete lineage sorting (Mendes and Hahn, 2016) and species of recent origin; c) hybridization and introgression. A possible scenario is that these species groups, *i.e.*, clades V and XV, consist of genetically determined morphs within a single species, but this is unlikely because they include species with different ecology and biology, as for example in the most obvious case of the branching *P.* cf. *cylindrica* together with several massive morphospecies in clade V. In some cases, the presence of different morphs can be considered a precursor to speciation, where phenotypic morphs evolve into distinct species (West-Eberhard, 1986; Potkamp and Fransen, 2019), or where polymorphism expands the niche that a species can exploit, potentially leading to speciation (Galeotti and Rubolini, 2004). An alternative hypothesis is that incomplete lineage sorting and weak genetic drift has resulted in a misleading phylogenetic reconstruction (de Queiroz, 1998, 2007). Under this scenario, the polyphyly of species found in these groups can be explained by rapid diversification or recent speciation of the clustered lineages (Funk and Omland, 2003). Finally, rapid species radiations or very recent speciation events produce co-occurring closely related species that are not yet completely reproductively isolated, providing an opportunity for introgression. In this case, phylogenetic signals may be hidden by gene transfer among divergent lineages undergoing hybridization and introgression (Frade et al., 2010; Combosch and Vollmer, 2015; Richards and Hobbs, 2015; Forsman et al., 2017; Mao et al., 2018; Mao, 2020). Overall, it is important to underline that all these pathways are not mutually exclusive, and indeed the current complex scenario might be best explained by a combination of the above-mentioned possibilities. Unresolved groups of species in corals are common, yet our understanding of these remains incomplete (Frade et al., 2010; Arrigoni et al., 2016; Cunha et al., 2019).

3.3. Comparison and integration of previous studies on Porites

The concatenated mitochondrial dataset comprising MT09, MT12, MT16, and MT20 regions (see Combosch et al., 2024), consisted of 150 terminals (of which 71 were extracted from our ezRAD data, while the remainder were downloaded from NCBI including *G. columna* – NC0156439 as outgrup) for a final length of 3,349 bp. Of these, 2,965 positions were conserved, 119 sites were parsimony informative, while 265 were singleton. The sequences clustered into 15 distinct molecular clades, of which 12 matched our genomic dataset (clade I, clade II, clade III, clade IV, clade V, clade VII, clade VIII, clade X, clade XII, clade XIII, clade XIV, and clade XV), while three comprised only sequences from NCBI: clades 4, 11, and 13 *sensu* Combosch et al. (2024), and X and XI *sensu* Forsman et al. (2009) (Fig. S6). From our ezRAD data, we could not retrieve the mitochondrial regions from samples in clade VI (*P. hadramauti*) and clade IX (*P.* sp. 5), which positions could thus not be matched with Forsman et al. (2009) and Combosch et al. (2024). Finally, samples belonging to clade X and XI from our SNPs data were nested within clade V based on the mitochondrial phylogenetic analysis.

Out of the 15 clades in the mitochondrial tree, a total of five matched those from Forsman et al. (2009), out of the 12 clades that were identified by Forsman et al. (2009): clade IV corresponds to clade II *sensu* Forsman et al. (2009), clade V corresponds to clade I *sensu* Forsman et al. (2009), clade VII corresponds to clade II *sensu* Forsman et al. (2009), and clade VIII corresponds to clade V *sensu* Forsman et al. (2009) (Fig. S6, Table S4). Seven out of 15 clades also matched clades identified by Combosch et al. (2024) (on a total of 11 identified clades by Combosch et al. (2024)): clade II corresponds to clade 12 *sensu* Combosch et al. (2024), clade IV corresponds to clade 2 *sensu* Combosch et al. (2024), clade V corresponds to clades 6 to 10 *sensu* Combosch et al. (2024), clade VII corresponds to clade 1 *sensu* Combosch et al. (2024), clade VIII corresponds to clade 3 *sensu* Combosch et al. (2024), clade X corresponds to clade 15 *sensu* Combosch et al. (2024), and clade XV corresponds to clade 5 *sensu* Combosch et al. (2024) (Fig. S6, Table S4). The position of clade I was also consistent with phylogenetic reconstruction by Combosch et al. (2024), but no clade number was assigned by the latter.

Integrating morphospecies identifications from the present work with the ones provided by Forsman et al. (2009) and Combosch et al. (2024), we can conclude that of the shared clades, four are monophyletic, comprising each a single morphospecies: clade II included only representatives of *P. columnaris*; Clade IV included only *P. rus* (Terraneo et al., 2019a, 2021 already discussed the taxonomic position of *P. monticulosa* which should be regarded as a junior synonym of *P. rus*); Clade VIII included only samples of *P.* cf. *lutea.* Terraneo et al. (2021) identified samples within this clade as *P. somaliensis*, since samples were only retrieved from the Arabian Peninsula, the type locality of *P. somaliensis*, and given the strong morphological similarity between the two species. Indeed, both species have a massive growth form, with small and shallow corallites, 5–6 distinctive pali, and a small or absent columella. Nevertheless, as stated in the original description of *P. somaliensis*, these features do vary from the top to the side of the colonies. Further complicating a proper species identification, the holotype of *P. lutea* is a small colony likely not fully representative of the species. With the inclusion of material from other localities in the Indo-Pacific into this clade, we decided to avoid complicating the taxonomic situation, and herby follow identification from Forsman et al. (2009) and Combosch et al. (2020) and identify samples in this clade as *P.* cf. *lutea*. It must be noted that a topotype of *P. lutea* from Tonga was not included in any of these works, thus uncertainty remains. Forsman et al. (2009) included in this clade also *P.* cf. *lobata*, but at this stage we cannot comment on the position of these samples. Clade X is represented only by *P.* cf. *horizontalata*.

Incorporating data from Forsman et al. (2009) and Combosch et al. (2024), clade VII included the morphospecies *P.* cf. *annae*, *P.* cf. *deformis*, and *P. evermanni*. In our dataset, we sampled both *P.* cf. *annae* like and *P.* cf. *deformis* like colonies. *P. annae* was originally described from the GBR, and it is odd we have no samples of *P. annae* from the GBR despite our extensive sampling in that area. The original description of the species is based on four specimens, with remarkable colony and corallite level differences. At the same time, *P. deformis* was described based on samples from the Philippines, so we are also uncertain about this identification given the lack of a topotype. From a morphological perspective, the two species share similarities with colony growth form characterized by short branches, yet differ at the corallite level (with deeper corallites in *P. annae* vs superficial in *P. deformis*). However, the lateral, and basal corallites in *P. annae* can also be superficial on occasion. We provisionally identify our samples as *P.* cf. *annae* but further work is needed to confirm this identification. We are also unable to comment on *P. evermanni*, since we did not include any samples of this species whose type locality is Hawaii. Clade XV represented a species

complex. Previous literature – clade XIII *sensu* Forsman et al. (2009) and clade 5 *sensu* Combosch et al. (2024) included likely only one morphology, *i.e.*, *P. lichen*, in this clade because of limited sampling, but our genomic data corroborates the species complex scenario. Finally, clade V also remained a complex of multiple species, with at least two of the three distinct lineages in Singapore recovered here as *P.* sp. 1 and *P.* aff. *lutea* (Afiq-Rosli et al., 2021).

3.4. Geographical distributions

Molecular analyses have fundamentally altered our understanding of scleractinian biogeography. Indeed, in many taxa that were traditionally considered widespread, breaks between Indian and Pacific populations are now evident (Kitahara et al., 2016). The integration of our genomic results with Forsman et al. (2009) and Combosch et al. (2024) shows that eight clades of *Porites* (clade II, clade IV, clade V, clade VII, clade VIII, clade X, clade XI, and clade XV) are widespread in the Indo-Pacific and seven clades are restricted to either the Indian or Pacific Ocean (Fig. S7, Table S3, S4). In contrast, specimens from clade I = III, and = VI were found only in the seas around the Arabian Peninsula, clade XII is restricted to the south-western Indian Ocean, clade IX, XIII, and XIV are restricted to the Pacific Ocean. Within some of the widely distributed clades (clade II, clade VII, and clade X) there is strong geographic structure, with a distinction between the Arabian plus Indian Ocean lineages, *versus* the Pacific Ocean lineages (Figs. 2, S7, Table S4). Conversely, within clade IV and V, the partitioning between Arabian and Indian *versus* Pacific populations is unclear, corroborating the complex evolutionary patterns previously discussed. In clade IV, one cluster of samples from the Arabian Peninsula was sister to two additional Indo-Pacific groups. Notably within these Indo-Pacific subclusters, further geographic structure between Indian and Pacific populations was recovered, suggesting that the clade includes more lineages undergoing speciation or that have since gone extinct. The same results were encountered in clade V where, seven subclusters were restricted to the seas around the Arabian Peninsula (two subclusters of *P. alveolata*, *P. harrisoni*, *P.* sp. 2, *P. nodifera*, *P.* sp. 3, and *P.* sp. 4), two subclusters included Arabian Peninsula and south-western Indian Ocean samples (*P.* cf. *reticulum* and *P. arenacea*), and one included only south-western Indian Ocean samples (*P. conglomerata*). One subcluster was widespread in the Indo-Pacific, *P.* sp. 1. Finally, six subclusters were only Pacific (*P.* cf. *cylindrica*, *P. australiensis*, *P.* cf. *lobata*, *P.* aff. *lutea, P.* cf. *arnaudi*, and *P. mayeri*). Clade XV was mainly found in the Pacific Ocean, with the exception of two samples from the south-western Indian Ocean that we identified as *P.* cf. *lichen*. Yet, within this clade, we retrieved smaller subclusters corresponding to distinct morphospecies and presenting specific restricted geographical distribution at different localities of the Pacific Ocean. In particular, we retrieved five subclusters that occurred in multiple localities in the Pacific, while nine groups had restricted distributions in only one locality. The former group of subclusters included: *P. heronensis* from the Great Barrier Reef and Lord Howe Island, *P.* cf. *tuberculosus* from Papua New Guinea, the Great Barrier Reef, and New Caledonia, *P.* cf. *lichen* from the Great Barrier Reef and New Caledonia (+ Mayotte in the Indian Ocean). Finally, *P.* sp. 9 from Papua New Guinea, the Great Barrier Reef, and New Caledonia, and *P. vaughani* from Papua New Guinea and the Great Barrier Reef. The clades with restricted distributions included: *P.* cf. *reticulosa* and *P.* aff. *lichen* from New Caledonia, two distinct subclusters of *P.* cf. *heronensis* from Lord Howe Island, as well as an additional unidentified subcluster of *P.* sp. 7 from Lord Howe Island. Three subclusters were restricted to the Great Barrier Reef: *P.* sp. 8, *P.* sp. 10, and *P.* cf. *silimaniana*. Finally, one morphospecies, *P.* sp. 6, was encountered only in the Solitary Islands. Considering their peculiar and restricted distributions, all these subclades, or at least those retrieved from peripheral regions such as New Caledonia, Lord Howe Island, and the Solitary Islands, likely encompass diverging lineages. In fact, vicariance at sea can arise when population connectivity gets severed due to long oceanic distances (Cowman and Bellwood, 2013a, 2013b) and rare dispersal events can lead to founder-speciation events. This would indeed also explain their retained skeletal morphologies with respect to counterparts from the Great Barrier Reef as in the case of *P. heronensis*, which might represent source populations.

Finally, this work corroborates findings by Terraneo et al. (2019a, 2021) on *P. fontanesii* (clade I), *P. farasani* (clade III), and *P. hadramauti* (clade VI) being Arabian endemic lineages. Additionally, *P. profundus* (clade XII) was restricted to Mayotte and Madagascar, however, additional sampling in the Indian Ocean will be necessary to confirm if this species is indeed endemic to these localities.

3.5. Overall considerations

Integrating morphology, phylogenomics, and species distribution, this study provides the most comprehensive reconstruction of *Porites* diversity from the Indo-Pacific to date. We increased the geographic representation of the genus in genomic studies beyond the tropical Pacific (*e.g.*, Forsman et al., 2009, 2017; Tisthammer et al., 2018, 2020, 2021; Combosch et al., 2024) and the Arabian Peninsula (Terraneo et al., 2021). From the current 68 valid species of *Porites*, 59 have been described from localities in the Indo-Pacific, while 9 in the Atlantic (Table S2). In our dataset, we recovered 25 currently valid nominal species of *Porites* (Table S3), 12 of which were clustered in distinct and deeply divergent clades, while 13 in species complexes. Moreover, thanks to the review of the genus nomenclature (Table S2), we identified four additional nominal species which have either been previously synonymized (*P. conglomerata*) or are currently considered *taxa inquirenda* (Table S2, S3) for which further analyses will be necessary to confirm their taxonomic status. Further, we identified 10 morphospecies (*P.* sp. 1 to *P.* sp. 10) which could not be matched with any species in *Porites* nomenclature. Of these, *P.* sp. 5 is morpho-molecularly resolved within clade IX, and its limited geographic range confined to Australia and New Caledonia, supports the designation of a new species (Fig. 2, S7). The other nine unidentified morphologies were nested within species complex V and XV (Figs. 3, 4). While the status of *P.* sp. 1 to. sp. 4 remains uncertain within clade V, *P.* sp. 6, *P.* sp. 7, *P.* sp. 8, *P.* sp. 9, and *P.* sp. 10 morphology (Fig. S2b) and geographic distribution (Fig. 2), coupled with their molecular signature within clade XV (Figs. 2, 4), also indicates possible new species.

Our dataset builds upon previous works, and confirms boundaries and geographic distribution for clade I, III, and VI around the Arabian Peninsula. We expand the known distribution for clade II, IV, VII, VIII, and XI to the Indo-Pacific, and clade XIII to an additional locality of the Pacific Ocean. Moreover, we retrieved for the first time four additional highly supported morpho-molecular clades: clade X from the Indo-Pacific, clade XII from the Indian Ocean, and clades IX and XIV from the Pacific Ocean. The genetic structure retrieved within clade II, VII, VIII, X, and XIII seems consistent with geographic clustering, while clades IV and XI require further population genomic studies including samples from further localities to assess if they represent different populations or multiple species. Indeed, adaptation is fundamentally driven by variation within populations, yet in corals, the boundaries between population-level and species-level variation are often difficult to delineate. The species complex in clade XV has been retrieved for the first time in the current study, while the existence of the species complex in clade V is not new (*e.g.*, Forsman et al., 2009; Terraneo et al., 2021; Combosch et al., 2024). The genome-wide SNP tree (Figs. 2, 3) revealed stronger patterns of clustering by morphospecies which was not achievable from multilocus reconstructions, as further demonstrated by our mitochondrial concatenated dataset (Fig. S6). Particularly, in relation to mitochondrial data, Forsman et al. (2020), highlight the presence in this species complex of morphospecies with identical mitochondrial genomes, which might indicate recent divergence, supporting the use of genome-wide datasets to provide a better understanding of evolutionary dynamics in these complexes of species.

4. Conclusions

The present study on *Porites* offers insights into their taxonomy, phylogenetic relationships, and geographical distributions across the Indo-Pacific region. We first provided a nomenclature review for *Porites* to aid species identification, providing information on type localities, and museum type material, which we hope aid future research. Indeed, the challenge of associating 10 morphospecies (designated as *P.* sp. 1 to *P.* sp. 10) with existing type material highlights the pressing need for further taxonomic investigation. Incorporating topotypes into future studies is crucial for a thorough comprehension of the diversity within one of the most species-rich genera in the Scleractinia order. Overall, our work is the first genomic study on *Porites* encompassing a widespread Indo-Pacific sampling. We identified 15 major molecular clades of which 12 included samples ascribed to single morphospecies that resulted as monophyletic, while the status of clade VI could not be further verified using this dataset. The remaining two clades showed complex evolutionary patterns, with 15 morphospecies in clade V clustering in at least 18 subclusters presenting peculiar geographic distributions, and 11 morphospecies in clade XV clustered within at least 20 subclusters.

The integration of our newly-generated genomic data with previous mitochondrial phylogenetic data and information about geographical distributions allowed us to identify eight widespread clades of *Porites* across the Indo-Pacific. Among these clades, five showed a clear genetic distinction between Indian and Pacific populations for which further studies may elucidate whether these populations can be interpreted as distinct species. Additionally, geographic subclustering in the species complexes underscored complex evolutionary dynamics, likely encompassing recent or ongoing speciation, introgression processes, and/or population structuring. Further research and extensive geographical samplings are needed to unravel the potential contribution of these evolutionary dynamics in the unresolved species complexes and will enhance our understanding of *Porites* coral evolution and biogeography. Moreover, detailed morphological analyses of corallite level structures (*e.g.*, Forsman et al., 2015) and information regarding reproductive strategies will be necessary to further clarify species boundaries in the genus. Ultimately, different genomic approaches such as the target enrichment of ultra- conserved elements and exon loci might be better suited to achieve this aim. When compared to RADseq, such approaches can provide high coverage of the targeted regions with fewer missing data, which is crucial for constructing robust phylogenies. In fact, hybrid capture approaches span both deep evolutionary timescales and shallow taxonomic relationships, which make this technique powerful for resolving species boundaries in both recently and deeply divergent lineages (Quattrini et al., 2018; Cowman et al., 2020; Glon et al., 2021). Ultimately, this interdisciplinary approach contributes to a more comprehensive understanding of *Porites* diversity, an essential step for effective conservation and management efforts in shallow water coral reef ecosystems.

CRediT authorship contribution statement

Tullia I. Terraneo: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Francesca Benzoni:** Writing – review & editing, Supervision, Resources, Funding acquisition, Data curation, Conceptualization. **Roberto Arrigoni:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Michael L. Berumen:** Writing – review & editing, Supervision, Resources, Conceptualization. **Kiruthiga G. Mariappan:** Writing – review & editing, Formal analysis. **Chakkiath P. Antony:** Writing – review & editing. **Hugo B. Harrison:** Writing – review & editing, Resources, Funding acquisition. **Claude Payri:** Writing – review & editing, Resources, Funding acquisition. **Danwei Huang:** Writing – review & editing, Resources, Funding acquisition. **Andrew H. Baird:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2024.108238.

Data availability

Data will be made available on request.

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