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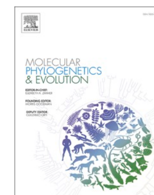
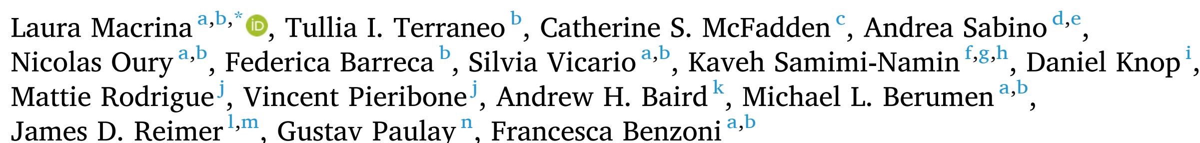


Beyond *Tubipora musica*: Phylogenomics unveils the overlooked diversity and endemism of the hermatypic octocoral genus *Tubipora*



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A B S T R A C T

Although scleractinians are typically considered the main reef-building corals, a few octocoral taxa also contribute to coral reef framework formation. The genus *Tubipora* deposits hard calcareous skeletons organised in tubes connected by horizontal stolonic platforms constituted of fused sclerites. The genus is broadly distributed across the tropical Indo-Pacific, but its diversity and evolutionary history remain poorly understood. Most recent treatments have recognized only the type species *Tubipora musica*, albeit historically ten species have been named. Here, using an integrative approach combining morphological and phylogenomic (based on Ultra-Conserved Elements and exon loci) analyses of 136 *Tubipora* colonies collected across six marine provinces in the Indo-Pacific, we delimited 15 morphologically distinct and genetically strongly supported lineages. All lineages retrieved in our results exhibited restricted geographic distributions, limited to single areas, highlighting potential regional endemism. Endemic diversification is suggested by sister species restricted to the Red Sea, Madagascar, and Eastern Australia, as well as regional diversification in Arabia, the Western Indian Ocean, and the Western Pacific. Our results reveal deep diversification within the Western Pacific and are consistent with colonization of the Western Indian Ocean by a single clade that subsequently diversified there. Accordingly, these findings underscore the need for broader sampling across the Indo-Pacific to assess *Tubipora* diversity and diversification and highlight the power of genomics in clarifying species boundaries and evolutionary relationships, providing a foundation towards the taxonomic revision of *Tubipora*. Accurate species definition is essential for biodiversity assessment and conservation planning, particularly for reef-building taxa that may include geographically restricted lineages vulnerable to environmental change, ultimately enhancing our ability to monitor and mitigate such impacts on these organisms.

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1. Introduction

Hermatypic scleractinian corals are the main builders of shallow-water tropical coral reefs; however, some hydrocorals and octocorals also contribute to reef building, contributing to the formation and complexity of reef habitats (Edmunds et al., 2016; Jeng et al., 2011; Shoham et al., 2019; Schuhmacher, 1997). Among octocorals the blue coral *Heliopora* de Blainville, 1830 and the organ-pipe coral *Tubipora* Linnaeus, 1758 form massive hard calcareous skeletons (Hickson, 1883; Hill, 1960; Fabricius and Alderslade, 2001), have established a symbiotic relationship with lineages of zooxanthellae in the family Symbiodiniaceae Fensome, Taylor, Norris, Sarjeant, Wharton & Williams, 1993 (Goulet et al., 2008a, 2008b; Guzman et al., 2018), and provide habitat for several associated invertebrates (Kim, 2004), thus fulfilling similar ecological roles to scleractinians. They are, in fact considered reef-building corals (Fabricius and Alderslade, 2001; Guzman et al., 2018) and are often included in treatments of reef corals (*e.g.*, Veron, 2000). Despite their ecological significance, while recent studies have addressed species diversity within *Heliopora* (Richards et al., 2018; Taninaka et al., 2021; Casilagan et al., 2025), our understanding of the

Table 1
Summary of the nominal species included in the genus *Tubipora*, reporting the information available on the morphology of their skeletons, tubes, polyps and tentacles, based on their original descriptions and subsequent redescriptions (Linnaeus, 1758; Pallas, 1766; Quoy and Gaimard, 1833; Ehrenberg, 1834; Dana, 1846; Carter, 1880; May 1898; Yabe and Sugiyama, 1937).

Nominal species	Type locality	Skeleton	Tubes	Polyps	Tentacles
Tubipora musica Linnaeus, 1758	Indian Ocean and Red Sea	Arranged in parallel, combined: separated by smooth, flat partitions	Subcylindrical tubes, smooth, hollow all the way to the base	Not described	Not described
Tubipora purpurea Pallas, 1766	Mare Americanum & Orientale	Deep red, composed of distinct, parallel, jointed tubes that are connected through transverse septa	The tubes are as thick as the upper part of a rush stem, slightly thicker than a thread. The segments are straight, cylindrical, measuring from about 2 mm to in some cases even half an inch or more in length, especially when the tubes are thicker	Inside, the tissue runs continuously through all segments, linear in shape, and at the top of each segment, it is star-shaped with calcified radial projections and attached to the inner side of the tube	Not described
Tubipora rubeola Quoy & Gaimard, 1833	Papua New Guinea	Bright lacquer red. Septa often 1 to 3 in. apart	Cylindrical tubes, long, loose, red, with separate partitions	Slightly reddish polyps	Pointed tentacles, fringed at the edges. Pinnules in 2 series
Tubipora chamissonis Ehrenberg, 1834	Radack Chain, Marshall Island	Bright red. 10–15 tubes in the space of one inch. Septa quite numerous	Tubes of the corallum about 1.6 mm broad. Rather closely crowded. Larger than in *T. musica*	Not described	Pinnules of the tentacles arranged in two series
Tubipora hemprichi Ehrenberg, 1834	Red Sea	Dark red. 9–12 tubes in the space of one inch. Septa remote (3 to 5 lines)	Tubes of the corallum about 1.7 mm, spaced out	Not described	Tentacles bluish or greenish, in a simple series
Tubipora fimbriata Dana, 1846	Fiji	Tubes of the corallum a very little larger than in *T. musica*, and not so regular	Tubes of the corallum scarcely 1.5 mm thick, very much crowded and irregular, septa quite numerous	Disk of the polyps brownish-red, mouth yellow. The yellow ring around the mouth has eight small squares on its outer margin, one towards each tentacle, and the brownish-red portion is octagonal, with the sides of the octagon a little concave	Tentacles pale yellow, loosely fringed, pinnules violet, in 2 or 3 series. The pinnules are irregularly divaricated
Tubipora syringa Dana, 1846	Fiji	As in *T. fimbriata*	Tubes of the corallum as in *T. fimbriata*	Polyps pale violet	Pinnules in contact and arranged neatly in an even plane. Owing to the even arrangement of the pinnules, the tentacles appear at first to be destitute of the usual fringe. The margin, when examined with a high power, shows a series of punctures, one of which is at the extremity of each pinnule
Tubipora reptans Carter, 1880	Gulf of Mannar, Indian Ocean	Colour crimson, translucent. Surface uniformly rough and foraminated, from the holes being sunk in the substance of the coral and the intervals in relief	Stolons about 0.5 mm broad and 0.2 mm high, including the walls above and below. Vertical thickness of the cavity about 0.06 mm. Stolon compressed vertically: wall in structure the same as that of the calycle; cavity compressed in like manner, reduced to a minimum, like that in the horizontal plate of *T. musica*	Short, erect, cylindrical calycles situated at unequal distances from each other. Almost colourless, especially towards the centre	Composed towards the extremities of small, cylindrical, curved and colourless spicules, larger, longer, and tuberculated towards the base, where they begin to assume a pink colour, finally becoming red
Tubipora rubeola var. *sansibarica* May, 1898	Zanzibar, Tanzania	As in *T. rubeola*	Tubes about 2 cm in width	Reddish	Bearing small, scleroproteinaceous lamellae. Toothed edges
Tubipora musica forma *sulcata* Yabe & Sugiyama, 1937	NW Pacific (Taiwan, Yap, Marshalls)	As in *T. musica*	Octagonal. Corallites 1–1.8 mm broad, much crowded, 5 or 6 in 10 mm. Walls 0.2 mm or slightly less thick. Continuous and parallel platforms, 4–6 mm distant	Not described	Not described

diversity, species boundaries, and distribution of *Tubipora* remains limited (McFadden et al., 2022).

The genus *Tubipora* (order Malacalcyonacea McFadden, van Ofwegen and Quattrini, 2022, family Tubiporidae Ehrenberg, 1828) is widespread in shallow-water coral reefs from the Red Sea and Indian Ocean to the Western Pacific (Fabricius and Alderslade, 2001). Commonly known as the organ pipe coral, it owes its name to its unique skeleton of hard calcareous tubes connected by horizontal stolonic platforms at various levels (Hickson, 1883). Each tube is made of fused sclerites and hosts a single polyp which can retract within it (Hickson, 1883; Spiro, 1971). Polyps vary in colour, from creamy white to green, brown or grey, and bear eight tentacles that can be smooth with fused pinnules, present pseudopinnules, or have true pinnules which give them a feathery appearance (see Bayer et al. (1983) and Alderslade and McFadden (2007) for illustrations of pinnule morphologies). Due to its unique skeletal morphology, the taxonomy of the genus has been historically oversimplified, leading to the identification and reporting of only *Tubipora musica* Linnaeus, 1758 in most literature, despite evidence of morphological, ecological, and genetic variability (Veron, 2000; Ammar, 2005; Haverkort-Yeh et al., 2013; Richards et al., 2013; Agustiadi and Luthfi, 2017; Koido, 2022).

Ten species-level names are available in *Tubipora*: *Tubipora chamissonis* Ehrenberg, 1834, *Tubipora fimbriata* Dana, 1846, *Tubipora hemprichi* Ehrenberg, 1834, *T. musica*, *T. musica* forma *sulcata* Yabe & Sugiyama, 1937, *Tubipora purpurea* Pallas, 1766, *Tubipora reptans* Carter, 1880, *Tubipora rubeola* Quoy & Gaimard, 1833, *Tubipora rubeola* var. *sansibarica* May, 1898, and *Tubipora syringa* Dana, 1846 (Table 1). However, the original descriptions of several were based on dry skeletons, and some were based on poorly preserved material haphazardly collected, and/or do not include detailed reference to polyp and sclerite morphologies (Fabricius and Alderslade, 2001), recognised as diagnostic features to identify octocoral species (Bayer et al., 1983). As a result, the only information available for most of these species is limited to the type localities, skeletal measurements (*e.g.*, tube density and diameter), and inaccurate indications of polyp features, with few descriptions referring to tentacle and sclerite morphologies (Table 1).

After re-examination of the material, Vaughan (1918) and Yabe and Sugiyama (1937) recognised only *T. musica* and *T. purpurea* as valid species. Nevertheless, most subsequent authors have only recognised *T. musica* (*e.g.*, Hickson, 1924; Williams, 1992; Benayahu, 2002). Given that the type material for several species is considered lost, it becomes even more challenging to assess the identity of species within the genus.

Diverse morphologies have been documented for *Tubipora* (Veron, 2000; Fabricius and Alderslade 2001; Perez et al., 2016). Yet, the diversity and systematics of the genus have been sparsely studied to date (Hickson, 1883; Nicholson, 1884; Yabe and Sugiyama, 1937; Spiro, 1971; Ammar, 2005; Richards et al., 2013; Luthfi et al., 2019) and no integrated studies combining genetic or genomic with other lines of evidence have thoroughly investigated species boundaries in the genus. In the Red Sea, *Tubipora* has been reported to occur from shallow reef flats at less than 1 m depth down to 45 m depth (Haverkort-Yeh et al., 2013; Bruckner and Dempsey, 2015; Benayahu et al., 2019; Macrina et al., 2025). Although three polyp morphotypes have been observed in the Red Sea, the only molecular study was not able to distinguish species with four barcode markers (Haverkort-Yeh et al., 2013). This is not surprising, as single loci are limited in their efficacy to distinguish congeneric octocorals (McFadden et al., 2011; Quattrini et al., 2019). Accordingly, the unavailability of a thorough systematic work for the genus, coupled with a lack of comprehensive biogeographic assessments, has left unanswered key questions regarding the diversity of the genus (McFadden et al., 2022).

The development of High-Throughput Sequencing has allowed sequencing of multiple regions of the genome and has greatly improved our understanding of anthozoan evolutionary history, species boundaries, and biogeographic patterns (Quattrini et al., 2018; Arrigoni et al., 2020; Cowman et al., 2020; Quattrini et al., 2020; Erickson et al., 2021; Terraneo et al., 2021; McFadden et al., 2022; Bridge et al., 2023; Quek et al., 2023; Terraneo et al., 2025). Target enrichment or hybrid capture of Ultra-Conserved Elements and exons (hereby collectively referred to as UCEs) has been particularly useful for shedding light on the diversity of many coral taxa, for which convergent evolution of morphological traits and plasticity were obscuring patterns of evolution (*e.g.*, for the scleractinian *Acropora* Oken, 1815; Bridge et al., 2023). Studies on octocorals have leveraged these approaches to refine species boundaries (addressing for instance the genera *Alcyonium* Linnaeus, 1758 (Erickson et al., 2021) and *Chrysogorgia* Duchassaing & Michelotti, 1864 (Untiedt et al., 2021)), revise the systematics of the class (McFadden et al., 2022), and enhance our understanding of species diversity and distribution (McFadden et al., 2025).

In this study, we aimed to explore the diversity, species boundaries, and evolutionary history of *Tubipora* by using an integrative phylogenomic and morphological approach. By sampling across six Indo-Pacific marine provinces (Spalding et al., 2007), we reassessed patterns of lineage distribution of *Tubipora*, presenting a preliminary but foundational framework for its future taxonomic revision.

2. Materials and methods

2.1. Sampling

A total of 136 *Tubipora* colonies were sampled during SCUBA diving at 48 sites across six Indo-Pacific marine provinces (see Spalding et al., 2007 for marine province boundaries), from 1 to 30 m depth (Fig. 1, Table S1). Live colonies were imaged *in situ* with a Nikon Coolpix W300 Waterproof camera or with an Olympus Tough TG-6 Waterproof camera in a PT-059 Underwater Housing. A typically 5 × 5 cm fragment was collected with hammer and chisel for each colony. Samples were assigned voucher numbers and processed as soon as possible after sampling. A tissue subsample was preserved in 99% ethanol for subsequent DNA extraction and molecular analyses, while the remaining skeleton was air-dried out of direct sunlight or bleached with sodium hypochlorite for 24 h.

2.2. Morphological analyses

Morphospecies were delineated based on the morphology of extended polyps and of the dry skeleton. Classical morphological features of the polyps used in octocoral systematics, such as the shape of the tentacles, the number of pinnule rows, and the spacing between adjacent pinnules (Gohar, 1940; Reinicke, 1997; Halàsz et al., 2014; Halàsz et al., 2015), were scored from *in situ* pictures. Only polyps with fully extended tentacles visible in the image were considered. Relative measurements of pinnule width and spacing were made using the software ImageJ v2.0.0 (Schneider et al., 2012).

Dry colonies were imaged using a Nikon D7500 camera equipped with a Nikkor 18–55 mm lens, and macro-morphological characters were examined at KAUST. Dry skeletons and ethanol-preserved samples were inspected using a Motic SMZ-171 stereomicroscope (Motic, Hong Kong) and imaged with a Leica M205 A stereomicroscope equipped with a Leica DMC 5004 camera (Leica Microsystems, Wetzlar, Germany) to examine skeletal features. Dry skeletons and ethanol-preserved specimens are deposited at King Abdullah University of Science and Technology (KAUST) (Thuwal, Saudi Arabia), Queensland Museum Tropics (QMT) (Townsville, Australia), University of Milano-Bicocca (UNIMIB) (Milan, Italy), University of the Ryukyus (Okinawa, Japan), and Florida Museum of Natural History, University of Florida (UF) (Gainesville, FL, USA) (Table S1). Images of dry skeletons were used to measure the diameter of 10 tubes per colony using the software ImageJ v2.0.0 (Schneider et al., 2012).

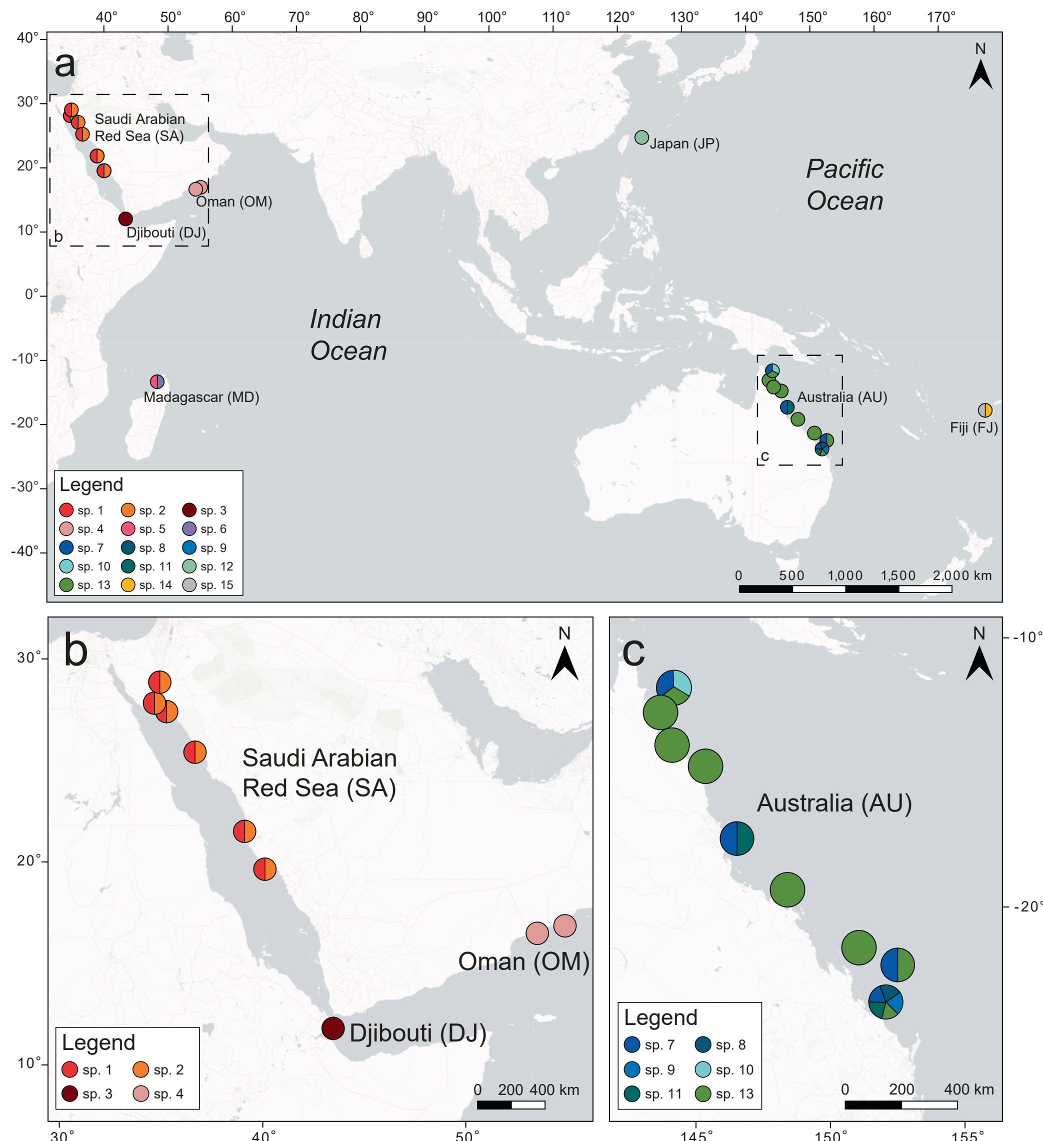


Fig. 1. Maps showing a) sampling localities (coloured circles) across the Indo-Pacific of *Tubipora* specimens examined in this study and focal areas showing; b) the sampling sites (coloured circles) around the Arabian Peninsula (SA, DJ, OM); and c) the sampling sites (coloured circles) in Australia along the Great Barrier Reef (AU). Circles are colour-coded to show the occurrence of different *Tubipora* morphospecies, corresponding to the colours of the rectangles in Fig. 2 and to the colours of the triangles and sample codes in Fig. 3. Collection information and sampling coordinates for each specimen analysed in this study are available in Table S1.

2.3. DNA extraction and quantification, libraries preparation, target enrichment, and sequencing

DNA was extracted from 136 ethanol-preserved specimens. One to two polyps were sub-sampled from each sample for genomic DNA extraction using a DNeasy® Blood and Tissue kit (Qiagen Inc., Hilden, Germany), following the manufacturer's protocol. Quality and quantity of the extracted DNA were checked using a NanoDrop® 2000c spectrophotometer (Thermo Fisher Scientific, Wilmington, USA) and a Qubit 4 Fluorometer (Thermo Fisher Scientific, Wilmington, USA), following the manufacturer's protocol. Raw genomic DNA is stored at KAUST (Thuwal, Saudi Arabia). Quantified raw DNA was sent for sequencing to Arbor Biosciences (Ann Arbor, MI, USA) and the platform iGenSeq (ICM, Paris, France), where libraries were prepared and target-enriched (Quattrini et al., 2018). The octocoral-v2 bait set outlined in Erickson et al. (2021) was used to target-enrich UCEs and exon regions of the genome. Libraries were then sequenced in PE150 on an Illumina NovaSeq platform (San Diego, CA, USA), following the protocols outlined in Quattrini et al. (2018).

2.4. UCEs data processing

Previously published raw UCE reads from a *Tubipora* specimen (N = 1; SRR6178958), publicly available on the NCBI Sequence Read Archive database (https://www.ncbi.nlm.nih.gov/sra), were included in the dataset prior to beginning data processing and bioinformatic analyses. Published and newly generated raw UCE reads were checked for quality using FastQC v0.12.0 (Andrews, 2010) and multiQC v1.19 (Ewels et al., 2016) and then trimmed with cutadapt v4.6 (Martin, 2011). Clean reads were then assembled using SPAdes v3.1 (Bankevich et al., 2012) and subsequently processed through the PHYLUCE pipeline v1.7.2 (Faircloth, 2016). To match the contigs to the octocoral baits (Erickson et al., 2021) and identify targeted loci, the command *phyluce_assembly_match_contigs_to_probes* was used to identify loci with a 70% identity and a 70%

coverage. The command *phyluce_assembly_get_match_counts* was used to extract loci, which were then aligned using MAFFT v7.130 (Katoh and Standley, 2013). Alignments were edge-trimmed using the command *phyluce_align_seqcap_align*. Internal trimming was also conducted with Gblocks v0.91b (Castresana, 2000; Talavera and Castresana, 2007) using the command *phyluce_align_get_gblocks_trimmed_alignments_from_untrimmed*. Finally, the commands *phyluce_align_get_only_loci_with_min_taxa* and *phyluce_align_concatenate_alignments* were used to generate aligned data matrices and concatenate the alignments, respectively. Alignment matrices were created and analysed for both 75% and 50% sample occupancy for each locus.

2.5. Phylogenomic analyses

Phylogenomic analyses were performed by running Maximum Likelihood (ML) analyses with IQ-Tree v2.1.2 (Minh et al., 2020) on both the 75% and 50% data matrices. Model selection and partitioning were performed using ModelFinder (Kalyaanamoorthy et al., 2017), with the best-fitting substitution models chosen according to Bayesian Information Criterion (BIC) scores using the settings −m TESTMERGE −merge-model GTR −merge-rate G −rcluster 10. Branch support was assessed using the UltraFast Bootstrap approximation (UFBoot; Hoang et al., 2018) with 1,000 bootstrap replicates. UFBoot is a rapid resampling-based method designed to provide accurate and computationally efficient estimates of branch support in large phylogenomic datasets, while reducing biases associated with standard non-parametric bootstrap approaches (Hoang et al., 2018). UFBoot values ≥ 95% were interpreted as strong clade support, whereas values between 90% and 95% were considered as moderate support.

To further evaluate the robustness of inferred relationships and quantify topological discordance among loci, gene Concordance Factors (gCF) and site Concordance Factors (sCF) were calculated (Minh et al., 2020). Specifically, gCF measure the proportion of gene trees that are decisive for, and support, a given branch, whereas sCF quantify the proportion of parsimony-informative alignment sites supporting the corresponding quartet topology (Minh et al., 2020). In addition, branch-level support was evaluated using the approximate Likelihood Ratio Test (aLRT; Anisimova et al., 2011). Together, these complementary metrics provide insight into both statistical support and underlying gene- and site-level concordance across the phylogenomic dataset.

The resulting phylogenomic trees were rooted on *Stragulum bicolor* van Ofwegen & Haddad, 2011, which is the closest taxon to the genus *Tubipora* for which UCE data are available to date (SRR20862043; McFadden et al., 2022). Raw sequence data are deposited in the NCBI Sequence Read Archive database (BioProject ID PRJNA1243197).

2.6. SNP-based analyses

Single-Nucleotide Polymorphisms (SNPs) were called from the UCE dataset following the modified pipeline from Oury et al. (2026). For both the whole dataset and three subsets (lineage L1, lineage L2, and lineage L4), locus reference sequences were constructed *de novo* from the UCE contigs obtained with *phyluce_assembly_get_fastas_from_match_counts* using the Contig Assembly Program (CAP3) v1.0 (Huang and Madan, 1999). Trimmed reads were mapped to the reference using BWA v0.7.17 (https://github.com/lh3/bwa; Li and Durbin, 2009). The resulting alignments were then sorted with SAMtools v1.16.1 (https://github.com/samtools/samtools; Li et al., 2009), and duplicate-marked and locally realigned using Picard v2.20.7 (https://broadinstitute.github.io/picard/) following Van der Auwera et al. (2013). Further, SNP calling was carried out with BCFtools v1.9 (https://samtools.github.io/bcftools/) across all specimens, and filtering was done through VCFtools (see https://github.com/vcftools/vcftools; Danecek et al., 2011), applying minimum base quality (BQ) and mapping quality (MQ) thresholds of 20 and 30, respectively. Only SNPs with a minimum quality score (QUAL) of 20 and genotypes with a minimum read depth (DP) ≥ 12 and non-significant strand bias (SP ≤ 13) were retained. Finally, a single bi-allelic SNP per locus was randomly selected, retaining only loci with less than 20% missing data and a minor allele frequency (MAF) ≥ 0.05.

Assignment analyses were conducted using sNMF (Frichot et al., 2014) as implemented in the R package *LEA* (Frichot and François, 2015). Five independent runs were performed for each value of k (ranging from 2 to 20), with a maximum of 500 iterations to reach convergence, and results were visualised using CLUMPAK (Kopelman et al., 2015). In addition, a discriminant analysis of principal components (DAPC; Jombart et al., 2010) was carried out using the R package *adegenet* (Jombart, 2008). All analyses were run in RStudio v4.2.0 (R Core Team, 2022), first on the entire dataset, and subsequently repeated for three subsets (lineage L1, lineage L2, and lineage L4) according to primary species hypotheses (PSHs) based on morphological and phylogenomic analyses.

3. Results

3.1. Morphological differentiation

Based on morphological analyses of *in situ* polyps (Fig. 2), and dry skeletal measurements (Table 2), the 136 *Tubipora* colonies included in our dataset were assigned to 15 morphospecies and will be hereafter referred to as *Tubipora* sp. 1 to *Tubipora* sp. 15. Two morphotypes were collected in the Saudi Arabian Red Sea (SA, sp. 1 and sp. 2), one was sampled in Djibouti (DJ, sp. 3), one in Oman (OM, sp. 4), two in Madagascar (MD, sp. 5 and sp. 6), six along the Great Barrier Reef (GBR) in Australia (AU, spp. 7–11 and sp. 13), one in Japan (JP, sp. 12), and two in Fiji (FJ, sp. 14 and sp. 15).

Morphological differentiation among species was evident both in the polyps and the skeletons of specimens studied. Specimens exhibited different shades of red in their skeletons, varying from dark red (in sp. 1, sp. 6, sp. 12, sp. 15), to bright red (in spp. 2–3, sp. 5, spp. 7–11, and spp. 13–14), to pale pink and white (in sp. 4) (Fig. S4). The mean diameter of the tubes (±SD) ranged from 1.28 mm ± 0.16 (sp. 1) to 2.84 mm ± 0.4 (sp. 12). Species with longer tentacles, such as sp. 2, spp. 4–6, or sp. 12, showed larger tube diameters. The number of pinnule rows was typically 1, however sp. 5 exhibited 2 rows, and sp. 3, sp. 7, sp. 8, and sp. 13 showed variability with both 1 and 2 rows exhibited among specimens. The number of pinnules varied among species, with some having fewer than 15 pinnules (*e.g.*, sp. 3 and sp. 10), while others had over 25 pinnules (*e.g.*, sp. 5 and sp. 12). Finally, the spacing of pinnules also showed considerable differences, ranging from smaller (spp. 3–5, spp. 7–9, and sp. 12) to larger (sp. 2, sp. 6, and spp. 10–11), while in some colonies in sp. 1 and sp. 13, pinnules were fused (Table 2).

3.2. Ultra-Conserved Elements dataset

Following Illumina sequencing, the total number of reads obtained per sample varied from 152,804 to 8,013,532 (N = 980,716,652 for the total dataset) (Table S2). A mean of 3,579,053 ± 1,748,494 SD trimmed reads per sample was retained after quality and adapter filtering (Table S2). Trimmed reads were assembled into 49,395 ± 74,994 SD contigs per sample (range: 4,955–312,720), with a mean length of 289.52 ± 106.65 SD bp, using SPAdes (Table S2). An average of 1,549.82 ± 129.56 SD unique loci per sample (range: 384–1,710) were retrieved from the assembled contigs (Table S2), of which 328 ± 157.13 SD UCE loci per sample (range 16–1,450) were removed for matching multiple contigs (Table S2), and an average of 60 ± 31.55 SD contigs per sample (range 10–168) were removed for matching multiple UCE loci (Table S2). Extracted loci were aligned from 75% and 50% sample occupancy matrices. The final combined concatenated alignments included 2,507 loci, of which 1,273 were retained in the 75% matrix and 1,785 were kept in the 50% matrix (Fig. S5). The alignments had an average of 78.98 ± 36.29 SD (range: 13 to 249) parsimony informative

Fig. 2. *In vivo* polyp morphology of the 15 morphospecies of *Tubipora* examined in this study. Rectangle colours match those of the lineages in Fig. 3. Polyp morphology *in situ* for each colony in this study is shown in Figs. S1-S3.

Table 2
Summary of the main morphological characters of 15 *Tubipora* morphotypes (sp. 1 to 15). Sampling location (AU, Australia; DJ, Djibouti; FJ, Fiji; JP, Japan; MD, Madagascar; OM, Oman; SA, Saudi Arabian Red Sea), skeleton colour (see also Fig. S4), mean diameter of tubes (mm) ± SD, number of rows of pinnules (1 or 2), number of pinnules per row (< 15; 15–25; > 25), spacing between the pinnules (fused: no space; small: gap between pinnules < pinnule width; large: gap between pinnules > pinnule width), and number of specimens examined.

Species	Location	Skeleton colour	Mean diameter of tubes (mm) ± SD	Number of rows of pinnules	Number of pinnules	Spacing between pinnules	Number of specimens
sp. 1	SA	Dark red	1.28 ± 0.16	1	15–25	small or fused	22
sp. 2	SA	Bright red	1.70 ± 0.31	1	> 15	large	40
sp. 3	DJ	Bright red	1.35 ± 0.22	1 or 2	< 15	small	5
sp. 4	OM	Pale pink	1.80 ± 0.01	1	15–25	small	7
sp. 5	MD	Bright red	1.88 ± 0.27	2	> 25	small	11
sp. 6	MD	Dark red	2.09 ± 0.24	1	< 15	large	3
sp. 7	AU	Bright red	1.63 ± 0.16	1 or 2	15–25	small	9
sp. 8	AU	Bright red	1.90 ± 0.13	1 or 2	15–25	small	1
sp. 9	AU	Bright red	2.05 ± 0.34	1	15–25	small	1
sp. 10	AU	Bright red	1.68 ± 0.03	1	< 15	large	2
sp. 11	AU	Bright red	1.45 ± 0.18	1	< 15	large	7
sp. 12	JP	Dark red	2.84 ± 0.40	1	> 25	small	3
sp. 13	AU	Bright red	1.77 ± 0.16	1 or 2	> 15	small or fused	21
sp. 14	FJ	Bright red	1.65 ± 0.28	1	> 25	fused	1
sp. 15	FJ	Dark red	1.88 ± 0.44	1	> 25	fused	3

sites in the 75% matrix and an average of 76.45 ± 37.79 SD (range: 1 to 249) in the 50% matrix.

3.3. Phylogenomic results

The best fit substitution model selected through ModelFinder was GTR + F + I + G4 for both the 75% and the 50% matrices. Both matrices produced robust phylogenetic reconstructions, and given the congruent topologies obtained, we hereafter discuss only results for the 75% matrix (Fig. 3). The phylogenomic reconstructions obtained with the 50% matrix are reported in Fig. S5. The ML reconstructions resolved six major lineages (L1-L6, Fig. 3) and 15 strongly supported PSHs (Fig. 3), congruent with the 15 *Tubipora* morphotypes, and hereby referred to as sp. 1 to sp. 15 (Fig. 2). The analyses recovered six clades from the Arabian Peninsula and Indian Ocean: two from the Saudi Arabian Red Sea (sp. 1 and sp. 2), one from Djibouti (sp. 3) and Oman (sp. 4), and two from Madagascar (sp. 5 and sp. 6). Nine *Tubipora* lineages were recovered from the Pacific, six from Australia (spp. 7–11, and sp. 13), one from Japan (sp. 12), and two from Fiji (sp. 14 and sp. 15). The lineage grouping specimens from the Saudi Arabian Red Sea and Djibouti (spp. 1–3; L1) was sister to the one grouping Oman and Madagascar samples (spp. 4–6; L2). Together, these form a lineage sister to an Australian lineage (sp. 7; L3), followed by several other Australian lineages (sp. 8–11; L4) each showing remarkable differences in their *in vivo* polyp morphologies (Fig. 2; Table 2). *Tubipora* sp. 12 (Japan; L5) was recovered as sister to a grouping of all the aforementioned lineages (spp. 1–11). Finally, a lineage grouping specimens from Australia (sp. 13) and Fiji (spp. 14–15) was recovered as sister to all the other species (spp. 1–12; L6; Fig. 3).

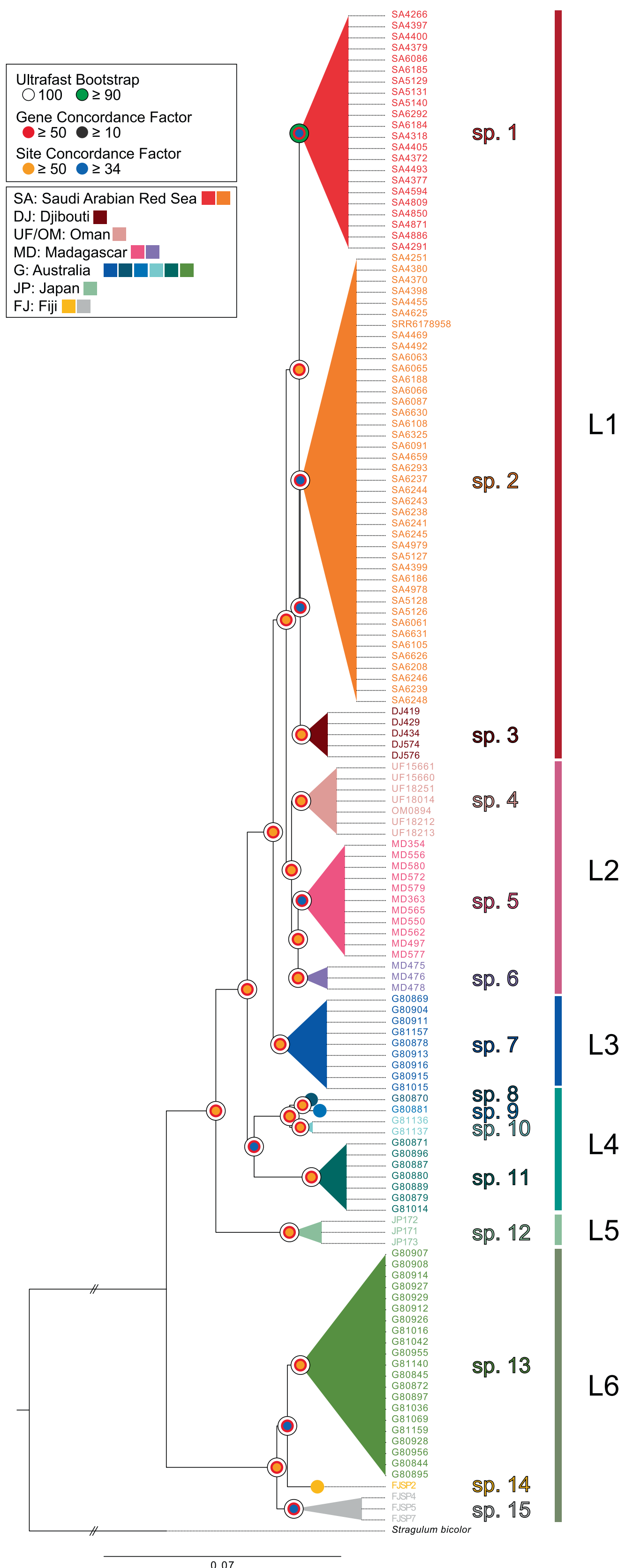
3.4. SNP-based analyses

Considering the entire dataset, mapping of the trimmed reads on the 2,542 *de novo* constructed locus reference sequences (mean sequence length = 773.92 ± 6.62 SE bp) resulted in an average of 54.23 ± 1.66% SE reads successfully mapped (Table S3). Subsequent SNP calling and filtering led to a dataset of 123 specimens with 1,483 SNPs, a mean SNP coverage of 59.88× ± 4.27 SE, and an average 6.91 ± 0.89% SE missing data per individual (13 specimens were removed from the final dataset due to low quality). Assignment tests with sNMF at K = 6 retrieved the six major lineages found with the phylogenomic reconstructions (L1-L6; Fig. 3; Fig. 4a). Increasing K up to 20 resulted in the separation of some, but not all, of the PSHs (Fig. S6), probably due to unequal sampling sizes. Thus, at K = 11, six PSHs (sp. 1, sp. 4, sp. 7, sp. 11, sp. 12, and sp. 13) were separated, while spp. 2–3, spp. 5–6, spp. 8–10, and spp. 14–15 were grouped in four other clusters, respectively (the 11th cluster was representing < 30% admixture in three individuals from three different PSHs). From K = 12, most of the additional clusters started to introduce more admixture within individuals rather than actual splits, however, sp. 14 and sp. 15 separated. At K = 20, spp. 2–3, spp. 5–6, and spp. 8–10 were still not separated, therefore the corresponding major lineages were rerun separately to refine structuring patterns. DAPC also retrieved the six major lineages, with substantial separation within L6 according to PSHs (*i.e.*, spp. 13–14; Fig. 4c). However, specimens from PSHs within L1 (spp. 1–3), L2 (spp. 4–6), and L4 (spp. 9–11) were mixed. Thus, the dataset was split into subsets to further test PSHs within these three lineages.

For the L1 dataset (comprising 68 individuals), mapping of the trimmed reads on the 2,236 *de novo* constructed locus reference sequences (mean sequence length = 1,337.29 ± 11.54 SE bp) resulted in an average of 80.49 ± 1.55% SE reads successfully mapped (Table S3). Subsequent SNP calling and filtering led to a dataset of 63 specimens with 1392 SNPs, a mean SNP coverage of 80.18× ± 3.99 SE, and an average 6.63 ± 1.21% SE missing data per individual (5 specimens were removed from the final dataset due to low quality). Assignment tests with sNMF and DAPC at K = 3 were concordant in distinguishing three genetic clusters, confirming the presence of two PSHs in the Red Sea (sp. 1 and sp. 2) and one in Djibouti (sp. 3) (Fig. 4d). Within sp. 2, individuals showed signs of geographic structure along a north–south Red Sea gradient; however, no evidence of admixture with sp. 3 was detected when increasing the number of clusters to K = 4.

For the L2 dataset (comprising 21 individuals), mapping of the trimmed reads on the 2,184 *de novo* constructed locus reference sequences (mean sequence length = 1,111.79 ± 17.89 SE bp) resulted in an average of 38.18 ± 5.7% SE reads successfully mapped (Table S3). Subsequent SNP calling and filtering led to a dataset of 20 specimens with 1,190 SNPs, a mean SNP coverage of 36.53× ± 2.17 SE, and an average 3.42 ± 0.87% SE missing data per individual (1 specimen was removed from the final dataset due to low quality). Results of the sNMF and DAPC analyses at K = 3 both distinguished three genetic clusters, confirming the presence of one PSH in Oman (sp. 4) and two in Madagascar (sp. 5 and sp. 6) (Fig. 4e). No evidence of further structure was found when increasing the number of clusters to K = 4.

For the L4 dataset (comprising 10 individuals), mapping of the trimmed reads on the 2,004 *de novo* constructed locus reference sequences (mean sequence length = 706.70 ± 3.70 SE bp) resulted in an average of 80.62 ± 1.7% SE reads successfully mapped (Table S3). Subsequent SNP calling and filtering led to a dataset of 9 specimens with



(caption on next column)

Fig. 3. Maximum-Likelihood phylogenomic tree of 136 *Tubipora* specimens inferred in IQ-Tree v2.1.2 from a concatenated alignment of 1,273 UCE and exon loci (75% taxon-occupancy matrix). Node support was assessed using 1,000 UltraFast Bootstrap (UFBoot) replicates, complemented by gene Concordance Factors (gCF) and site Concordance Factors (sCF). UFBoot values represent branch support based on resampled alignments, whereas gCF and sCF quantify the proportion of individual gene trees and informative sites, respectively, that are concordant with each branch. Colours of the triangles and sample codes correspond to those of the geographic localities in Fig. 1 and those of the rectangles in Fig. 2. The annotation L1-L6 next to the species numbering denotes the six major lineages retrieved.

1,373 SNPs, a mean SNP coverage of 64.94× ± 4.93 SE, and an average 6.79 ± 2.19% SE missing data per individual (2 specimens were removed from the final dataset due to low quality). Both sNMF and DAPC for K = 4 only managed to distinguish three genetic clusters for the four PSHs in L4 (Fig. 4f). Specifically, one cluster grouped together the two specimens belonging to sp. 8 and sp. 9, while the other two clusters corresponded to sp. 10 and sp. 11, respectively (Fig. 4f). No deeper structure was found for K = 5 either, which only introduced more admixture (Fig. S7).

4. Discussion

In this work, we combined morphology and target enrichment of UCEs and exon loci to reconstruct the diversity and evolutionary relationships among potential species of the octocoral genus *Tubipora*. Our findings revealed 15 distinct morphotypes that corresponded to 15 genetic lineages of *Tubipora* among samples from the Red Sea to the Western Pacific. Each species-level lineage was recovered from a single sampled location in our dataset, suggesting potential regional endemism within the genus. This work represents the first attempt to rigorously evaluate the diversity and evolutionary history of this important reef-building genus, integrating morphological, genomic, and biogeographic data.

4.1. Diversity of the genus Tubipora

The phylogenomic hypotheses inferred through UCE data revealed 15 highly supported clades, each corresponding to a single morphotype (sp. 1 – sp. 15) differing in the morphology of polyps and tentacles, diameter of tubes, and skeletal colouration (Fig. 2; Table 2). The highly supported and congruent topologies of the phylogenies built with different occupancy matrices (Fig. 3, Fig. S5) highlight their robustness compared with reconstructions based on barcode markers. These results were also supported by those of the SNP-based analyses for 13 out of the 15 species-level lineages hypothesised through the combination of morphology and phylogenomics (Figs. 2-4). While sNMF and DAPC analyses did not distinguish sp. 8 and sp. 9 in L4, strong morphological evidence and phylogenomic results supported their separation (Figs. 2-4). Their genetic clustering in sNMF and DAPC may be due to the low sampling size in our dataset, because each of these PSHs is only represented by a single specimen (Fig. 4f). Accordingly, based on two lines of evidence (morphology and phylogenomics, Figs. 2-3), the two PSHs (sp. 8 and sp. 9) are considered distinct in our study, but further sampling and analyses are needed to fully confirm their genetic separation (Fig. 4f).

Previous molecular studies including *Tubipora* specimens from the Red Sea (Haverkort-Yeh et al., 2013; Macrina et al., 2025) were unable to differentiate species due to the low resolution provided by the traditional barcode markers of mitochondrial MutS homolog (*mtMutS*), Cytochrome *C* Oxidase subunit one (*COI*), nuclear Internal Transcribed Spacer (*ITS*), and ATP Synthetase Subunit α (*ATPSα*). Our results revealed deep lineage separation, providing a clear integrative framework for species delimitation in the genus. The robust differentiation of molecular lineages that correspond to morphotypes in *Tubipora* confirms

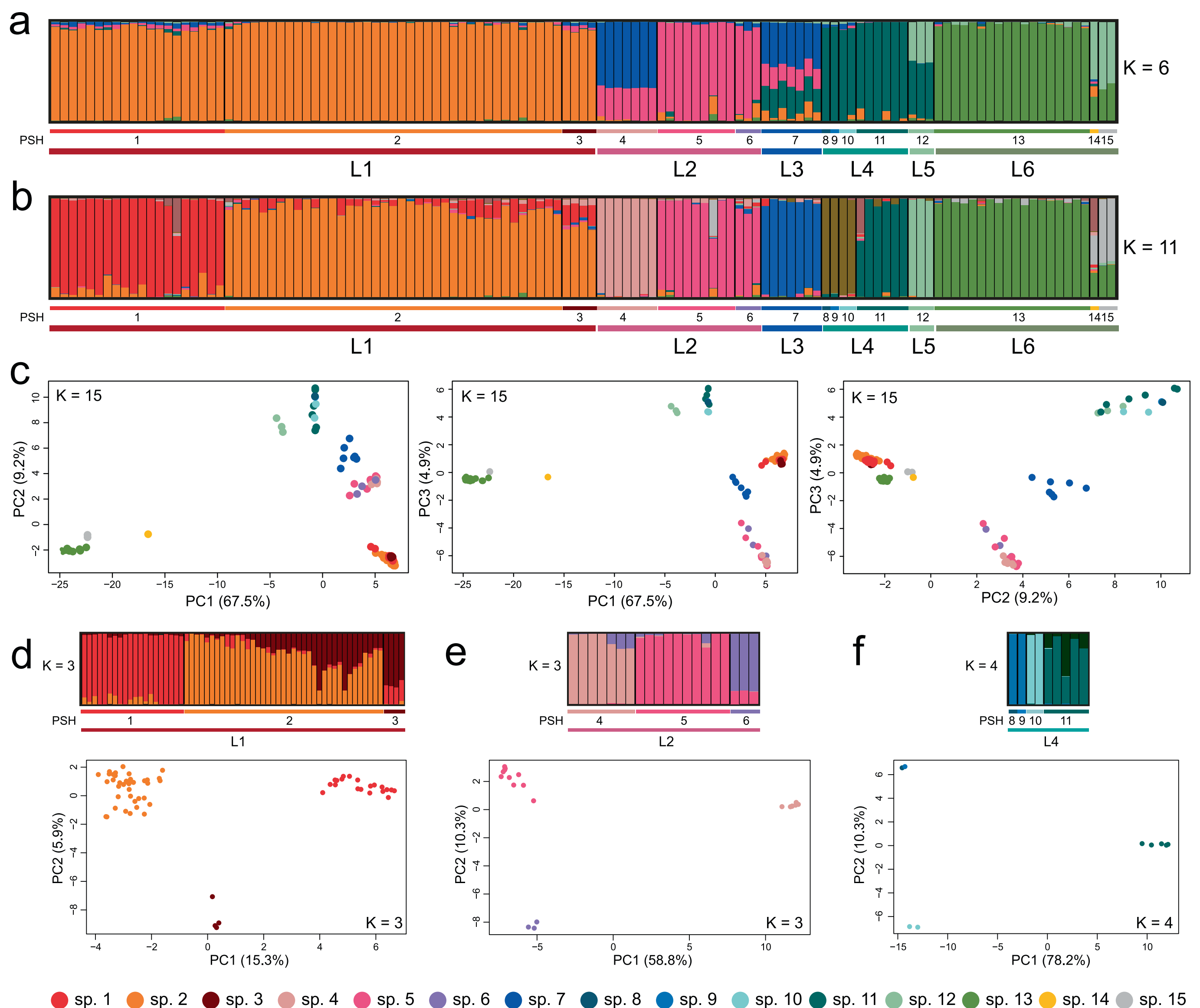


Fig. 4. Assignment tests using sNMF and Discriminant Analyses of Principal Components (DAPC). a) Ancestral lineage proportions for the entire dataset inferred with sNMF for K = 6. Vertical bars show the contribution of the predicted ancestral lineages to each sample. Sample order follows that of the phylogenomic tree in Fig. 3; b) Same as (a) for K = 15; c) Results of DAPC for K = 15 for the entire dataset; d) Results of sNMF and DAPC at K = 3 for the L1 subset; e) Results of sNMF and DAPC at K = 3 for the L2 subset; f) Results of sNMF and DAPC at K = 4 for the L4 subset.

the power of phylogenomics in disentangling species boundaries for octocorals, aligning with the findings of previous studies (*e.g.*, Quattrini et al., 2019; Erickson et al., 2021; McFadden et al., 2022). The alignment of morphological and phylogenomic species is noteworthy, and contrasts with the high degree of morphological homoplasy reported in some other coral groups (*e.g.*, Arrigoni et al., 2014; McFadden et al., 2017). This may indicate rapid morphological differentiation within *Tubipora*, or reflect the utility of specific polyp traits (Gómez-Gras et al., 2025) as reliable characters to distinguish species.

Integrative approaches combining phylogenomic and morphological data have also begun to yield resolution in other taxonomically challenging reef-building coral groups, such as *Acropora* (*e.g.*, Cowman et al., 2020; Bridge et al., 2023; Rassmussen et al., 2025) and *Pocillopora* Lamarck, 1816 (*e.g.*, Gélin et al., 2017; Oury et al., 2023), where multi-locus and genomic datasets have uncovered cryptic diversity missed through Sanger sequencing, and helped explain challenging morphological variation.

4.2. Distribution and endemism

The highly restricted species distributions found in our dataset need to be corroborated by further sampling and a full re-assessment of the genus, to draw definitive conclusions regarding species ranges and endemism. However, the restricted patterns of species distribution in *Tubipora* suggested by our analyses may reflect limited larval dispersal capacity (Paulay and Meyer, 2006), together with ecological and geological limitations to dispersal (Wafar et al., 2011). Although sampling is limited to seven areas, several of these are in close proximity (Red Sea, Djibouti, Oman; E Australia, Fiji), yet not a single species was sampled in more than one area. This pattern is consistent with high regional endemism, as reported in some other octocoral taxa by McFadden et al. (2025). Research on scleractinian corals and zooxanthellate soft corals has shown the correlation of species distribution with geographical clusters in the Indo-Pacific (Keith et al., 2013; McFadden et al., 2025) and supports multiple centres of diversification in the Indian and Pacific Oceans (Obura, 2015; McFadden et al., 2025).

The genus *Tubipora* also shows diversification on remarkably fine

spatial scales based on our sampling and findings (Hoareau et al., 2013). Two sympatric species in the Red Sea, two in Madagascar, and four in Australia suggest endemic diversification, via sympatric, ecological, or fine-scale allopatric speciation. The six species from the Western Indian Ocean are also part of a single radiation. These results indicate that the Western Indian Ocean and the Western Pacific may represent important centres of diversity for *Tubipora* in the present dataset.

Phylogenetic relationships among *Tubipora* species are consistent with a Western Pacific origin followed by westward dispersal. The deepest nodes occur within the Western Pacific, while Western Indian Ocean species from Madagascar, Oman, Djibouti, and the Red Sea form a derived, relatively younger, endemic clade. The diversification of Indo-Pacific reef fauna varies across taxa, with some groups radiating in the western end of the region first, colonizing the Pacific later in their history, as reefs and diversity shifted from the Western Tethys in the Paleogene to the Western Pacific in the Neogene (Renema et al., 2008). In such groups, deep diversity and divergence is common in the Western Indian Ocean (McFadden et al., 2025). In contrast, younger clades are more likely to originate and diversify in the more diverse Western Pacific. *Tubipora* appears to be a relatively young genus, with all but one of the 14 fossil occurrences dating from the late Pliocene to the Holocene (PBDB, 2025), with the single, oldest record from the late Miocene (Umbgrove, 1945).

Our findings confirm the presence of two sympatric species of *Tubipora* in the Red Sea, refining previous taxonomic assessments including the genus *Tubipora* in the area (Haverkort-Yeh et al., 2013). This aligns with previous studies (DiBattista et al., 2016; Terraneo et al., 2021; 2025; McFadden et al., 2025), which found multiple invertebrate and vertebrate taxa to have centres of endemism in the basin. High level of endemism observed around the Arabian Peninsula, and especially in the Red Sea, is linked to the isolation of reefs in the region, together with the highly variable and extreme environmental conditions around the Peninsula, and complex geological and paleoclimatic history of the region (Bosworth et al., 2005, Sheppard et al., 1992; DiBattista et al., 2016; Berumen et al., 2019). The phylogenetic relationships indicate recent connectivity between the Red Sea and Djibouti, and in turn with Oman and the Southwestern Indian Ocean (Madagascar). Regional ocean currents may therefore have shaped lineage divergence, especially considering the restricted water exchange between the Red Sea and the Indian Ocean due to lowered sea levels during the Pleistocene glacial cycles (Mitchell et al., 2015), the presence of cold-water upwelling along the southern Arabian coast (Watanabe et al., 2017), and coral reef dynamics in the area (Oury et al., 2025; Teillet et al., 2025).

Our findings demonstrate fine-scale geographic differentiation in *Tubipora*, as in numerous other taxa (*e.g.*, Keshavmurthy et al., 2013; McFadden et al., 2019; Bridge et al., 2023; Rassmussen et al., 2025), and indicate that broad geographic sampling will be essential to fully characterize the genus and its distribution. Despite extensive fieldwork across multiple biodiversity surveys, we did not detect *Tubipora* in Réunion Island (L. Macrina, personal observation), the Republic of the Maldives (Ari Atoll, F. Benzoni, personal observation), French Polynesia (N. Oury, G. Paulay, personal observation), Niue, Cook Islands, Line Islands, and Hawaiian Islands (G. Paulay, personal observation). Nevertheless, we cannot exclude its presence in unsampled localities. Our observations across Natural History Museum collections (*e.g.*, the Natural History Museum (NHM), London, UK; the Naturalis Biodiversity Center, formerly Rijksmuseum van Natuurlijke Historie (RMNH), Leiden, The Netherlands; and the Smithsonian National Museum of Natural History (USNM), Washington DC, USA) confirm the broader distribution of *Tubipora* throughout the Central Indian Ocean, the Coral Triangle, Coral Sea, and Western Pacific Ocean (L. Macrina, personal observation) – regions that we were unable to survey directly. These areas may harbour additional diversity and offer valuable material for expanding the genomic assessments of the genus. Museum specimens represent a valuable resource to assess the diversity and distribution in areas that may be difficult to reach or sample due to current regulations (Connelly et al., 2024).

4.3. Beyond Tubipora musica

Most recent and many historical studies have recognized only one species of *Tubipora, viz. T. musica*, presumed to be widely distributed across the Indo-Pacific (Veron, 2000; Fabricius and Alderslade, 2001; Haverkort-Yeh et al., 2013; Richards et al., 2013; Agustiadi and Luthfi, 2017; Koido, 2022). Our results challenge this assumption, with evidence from skeletal and polyp morphologies coupled with genomic results confirming that the genus encompasses a far greater diversity than previously recognized. Based on the information reported in the original descriptions of *Tubipora* nominal species as well as on their type localities (Table 1), only three of the recovered lineages likely correspond to previously described species based on shared morphological characters and geographic provenance. *Tubipora* sp. 2 closely aligns with the original description of *T. hemprichi*, based on type locality and bluish or greenish tentacles in a simple series, and tubes measuring about 1.7 mm, as indicated by Ehrenberg (1834) (Table 1; Fig. 2). *Tubipora* sp. 14 and sp. 15 exhibit morphologies and geographical occurrences consistent with those of *T. fimbriata* and *T. syringa* (Dana, 1846), respectively. *Tubipora* sp. 14 matches the description of *T. fimbriata* in having yellow tentacles and a brownish to red line with octagonal markings around the oral disk, while *Tubipora* sp. 15 seems to match closely the known polyp morphology of *T. syringa* in having fused pinnules that give its tentacles a smooth appearance (Table 1; Fig. 2). However, the remaining 12 species identified in this study cannot be assigned with confidence to any of the known nominal species, as they differ in tube diameter, pinnule number and arrangement, and geographic distribution, and may represent undescribed *Tubipora* species. The morphology of several nominal species, including the type species of the genus *T. musica*, is too poorly known, and/or has too broad or vague type locality to allow clear attribution to species among the material studied (Table 1).

While a taxonomic and systematic revision of *Tubipora* is beyond the scope of this study at this stage, the findings reported here provide a solid framework for such work. Importantly, to fully delimit species morphologically, further microscopic analyses would be needed, both on freshly collected samples and on type specimens, including detailed Scanning Electron Microscopy of the sclerites and their analysis. The 15 species-level lineages delimited here further need to be confirmed by more extensive sampling, and to be aligned with the ten available nomina, for a formal revision of the genus. This will require additional samples to complement our dataset (especially to clarify the distinction between PSH 8 and 9), comparison of our specimens with available types (which we unfortunately could not source for this study), resampling of species at other type localities (*e.g.*, Gulf of Mannar, Micronesia, Papua New Guinea), designation of neotypes, and description of new species (Bridge et al., 2023). Accordingly, the 15 PSHs presented here should be regarded as a first assessment and hypothesis of the diversity of the genus *Tubipora* across the Indo-Pacific and will need to be further verified before attempting a formal taxonomic revision.

4.4. Life-history and ecological considerations

In marine benthic invertebrates, dispersal mechanisms and capacity are influenced by larval type, dispersal duration, reproductive timing, and seasonality, all of which can play a major role in determining population connectivity and selection, and the spatial scale at which genetic divergence occurs (Cowen et al., 2015). Although the patterns of fine-scale genetic structuring and geographically restricted lineages observed in our dataset seem to be consistent with diversification influenced by limited dispersal, information on the reproductive mode, larval type, and pelagic larval duration remains unavailable for *Tubipora* and closely related octocoral taxa. Therefore, while dispersal-related processes are plausible drivers of the observed patterns, rigorous work integrating reproductive biology, larval ecology, and oceanographic data (D'Aloia et al., 2015) is required to rigorously test these hypotheses and match reproductive traits with speciation.

Importantly, as a hermatypic octocoral, *Tubipora* contributes to the formation of tropical shallow-water benthic habitats in the Indo-Pacific (Fabricius and Alderslade, 2001). The potential existence of multiple geographically restricted lineages within the genus and limited larval dispersal underscore the importance of also considering how these species interact with their environment and their potential vulnerabilities to environmental stressors (Manes et al., 2021). For instance, understanding how these species interact with both ecto- and endosymbiotic taxa is essential for assessing their resilience to climate change and their capacity for adaptation (Goulet et al., 2008b; Sgrò et al., 2010; Hendry et al., 2011; Hoey et al., 2016; Coffroth et al., 2023). Because *Tubipora* is a zooxanthellate octocoral genus, further research is especially needed to characterise the diversity, distribution, and interactions of these species with their symbionts and photosymbionts (Symbiodiniaceae). Studies of other tropical octocoral (van Oppen et al., 2005; Goulet et al., 2008a) and scleractinian genera (LaJeunesse et al., 2004; Terraneo et al., 2019) have revealed species-specificity and biogeographic structuring of symbioses in different lineages. Different Symbiodiniaceae lineages may occur in different *Tubipora* species and if so, may shape their distribution and confer varying levels of thermotolerance (Naugle et al., 2024): symbiont specificity may have significant implications for the persistence of the endemic hosts under climate change scenarios (Goulet et al., 2008b).

4.5. Implications for conservation and management

As reef-building corals are facing increasing decline due to climate change, ocean acidification, habitat degradation, and increasing sea water temperature (Hughes et al., 2017; 2018), concerns about the potential extinction of many species have intensified in recent years (Carpenter et al., 2008). Understanding the actual diversity and distribution of reef organisms is of fundamental importance for developing effective conservation and management strategies (Raven and Wackernagel, 2020). This necessitates comprehensive evaluation of species boundaries to accurately assess biodiversity and ensure effective protective measures (Ward et al., 2022). From a conservation perspective, the improved taxonomic resolution of *Tubipora* has direct implications for monitoring and management efforts. Recognizing *Tubipora* as a diverse genus rather than a monotypic taxon will help refine species distribution models, reassess extinction risks, and inform policies aimed at protecting and conserving these reef-building corals locally. For instance, *T. musica* is the only species within the genus included in the IUCN Red List of Threatened species, and it is listed as Least Concern as it is considered to have a broad geographic range, despite reports of a currently declining population trend (Shlesinger and Johnson, 2024). Considering that endemic species may fulfil particular roles and require specific conditions to survive in their environments (Grupstra et al., 2024), a full reassessment of the threat status and extinction risk for *Tubipora* spp. would be especially important. Since *Tubipora* is also considered a charismatic taxon among ornamental coral reef wildlife, stricter assessments and more tailored regulations of aquarium trade for all species should be reinforced across countries, to limit the further harvesting of endemic species and the introduction of non-native species into new environments (Dee et al., 2014; Hoeksema, 2026).

Coral-associated symbiotic invertebrates and microorganisms rely on specific coral hosts for habitat and resources (Stella et al., 2011). The decline or extinction of reef-building corals will lead to the loss of highly specialised dependent species (Macrina et al., 2024), further exacerbating biodiversity decline and ecosystem instability (Hughes et al., 2002; Vanwonterghem and Webster, 2020). Given these challenges, coral reef restoration efforts incorporating *Tubipora* species may also be considered, as initiatives that focus on transplanting or mariculturing *Tubipora* could enhance reef resilience and promote habitat recovery. However, given the geographically restricted distribution documented in this study, such interventions must be guided by ecological and genetic research to prevent unintended consequences.

5. Conclusions

This study provides the first phylogenomic assessment of the octocoral genus *Tubipora*, revealing high species diversity across six of the 15 marine provinces where the genus is currently known to occur. Regional endemism is high, with each species restricted to a single province. Our findings challenge historical taxonomic assumptions on this group and highlight the need for a systematic revision of the genus through an integrated morphological, genomic, and biogeographic approach. The results presented here emphasize the utility of UCEs in resolving species boundaries, clarifying evolutionary processes, and ultimately informing the planning of conservation strategies and priorities for this reef-building octocoral genus. Future research on the genus should focus on expanding sampling efforts, integrating symbiont and reproductive data, and evaluating the potential resilience of *Tubipora* species in the face of environmental change.

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CRediT authorship contribution statement

Laura Macrina: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Tullia I. Terraneo:** Conceptualization, Validation, Investigation, Writing – review & editing, Supervision. **Catherine S. McFadden:** Writing – review & editing, Validation, Supervision, Data curation, Conceptualization. **Andrea Sabino:** Investigation, Formal analysis, Data curation. **Nicolas Oury:** Writing – review & editing, Validation, Supervision, Software, Data curation. **Federica Barreca:** Data curation. **Silvia Vicario:** Data curation. **Kaveh Samimi-Namin:** Writing – review & editing, Data curation. **Daniel Knop:** Data curation. **Mattie Rodrigue:** Resources. **Vincent Pieribone:** Resources, Funding acquisition. **Andrew H. Baird:** Writing – review & editing, Resources, Funding acquisition. **Michael L. Berumen:** Resources, Funding acquisition. **James D. Reimer:** Resources, Funding acquisition. **Gustav Paulay:** Writing – review & editing, Resources, Funding acquisition. **Francesca Benzoni:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization.

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 data

Supplementary material to this article can be found online at https://doi.org/10.1016/j.ympev.2026.108622.

Data availability

The data generated during and/or analysed during the current study are available from the GenBank SRA and included in the manuscript and its supplementary information

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